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## ***Cortinarius* subgenus *Phlegmacium* section *Multiformes* in Europe**

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### **SUMMARY**

The taxonomy and phylogeny of sect. *Multiformes* (*Cortinarius*, subgen. *Phlegmacium*) are presented. The present circumscription of the section is supported by molecular data and morphological features. The taxonomy is complex and many taxa are quite new and little known. Two new species are described. Altogether ten European species are recognized: *C. multiformis*, *C. talimultiformis*, *C. frondosomultiformis* sp. nov., *C. rufoallutus*, *C. talus*, *C. melleicarneus*, *C. caesiolamellatus*, *C. caesiophylloides*, *C. pallidirimosus* and *C. armenicorius* sp. nov.

The ten recognized species are (i) more or less well-supported phylogenetically, but (ii) with a fairly low morphological differentiation. The species differs by >1% in ITS DNA from sister taxa, and each species pair show a morphological differentiation, though in most cases with overlapping characters. For instance, most species have overlapping variation in size and shape of the spores, and less than half of the species have formerly been recognized in morphological studies.

### **ZUSAMMENFASSUNG**

Es wird die Taxonomie und Phylogenie der Sekt. *Multiformes* (*Cortinarius*, Untergattung *Phlegmacium*) vorgestellt. Die gegenwärtige Abgrenzung der Sektion wird durch molekulare Daten und morphologische Eigenschaften gestützt. Die Taxonomie ist kompliziert, und viele Arten sind ganz neu und wenig bekannt. Zusammen 10 europäische Arten sind anerkannt: *C. multiformis*, *C. talimultiformis*, *C. frondosomultiformis* sp. nov., *C. rufoallutus*, *C. talus*, *C. melleocarneus*, *C. caesiolamellatus*, *C. caesiophylloides*, *C. pallidirimosus* und *C. armenicorius* sp. nov.

Diese 10 Arten sind (i) phylogenetisch mehr oder wenig gut gesichert, allerdings (ii) morphologisch ziemlich wenig differenziert. Die Arten unterscheiden sich in >1% ihrer ITS-DNA von den Schwester-Arten, und jedes Arten-Paar zeigt zwar eine morphologische Differenzierung, die sich aber meist überlappt. So sind die Sporenmaße und die Sporenform der meisten Arten recht

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ähnlich, und weniger als die Hälfte der hier vorgestellten Arten wurden früher in morphologischen Studien unterschieden.

#### RÉSUMÉ

On présente la taxinomie et la phylogénie de la section *Multiformes* (*Cortinarius*, sous-genre *Phlegmacium*). La délimitation actuelle de la section est étayée par des données moléculaires et des caractères morphologiques. La taxinomie est compliquée et beaucoup d'espèces sont tout à fait nouvelles et peu connues. On reconnaît en tout 10 espèces européennes : *C. multiformis*, *C. talimultiformis*, *C. frondosomultiformis* sp. nov., *C. rufoallutus*, *C. talus*, *C. melleocarneus*, *C. caesiolamellatus*, *C. caesiophylloides*, *C. pallidirimosus* et *C. armenicorius* sp. nov.

Ces 10 espèces sont (i) plus ou moins bien identifiées au plan phylogénétique, toutefois (ii) assez peu différenciées morphologiquement. Les espèces diffèrent des espèces soeurs à raison de >1% quant à leur ITS d'ADN, et chaque paire d'espèces présente certes une différenciation morphologique, mais avec des chevauchements. C'est ainsi que les dimensions et la forme des spores de la plupart des espèces sont très semblables, et moins de la moitié des espèces présentées ici étaient autrefois distinguées dans les études morphologiques.

#### RIASSUNTO

Viene presentata la tassonomia e la filogenetica della sezione *Multiformes* (*Cortinarius*, sottogenere *Phlegmacium*). L'attuale distinzione della sezione si basa su dati molecolari e caratteri morfologici. La tassonomia è complicata e molte specie sono completamente nuove e poco note. Complessivamente sono riconosciute 10 specie europee: *C. multiformis*, *C. talimultiformis*, *C. frondosomultiformis* sp. nov., *C. rufoallutus*, *C. talus*, *C. melleocarneus*, *C. caesiolamellatus*, *C. caesiophylloides*, *C. pallidirimosus* and *C. armenicorius* sp. nov.

Queste 10 specie sono supportate più o meno bene da un punto di vista filogenetico (i), ma (ii) differenziate abbastanza poco da un punto di vista morfologico.

In >1% del loro ITS-DNA, le specie si distinguono dai taxa sorella ed ogni copia di specie permette una differenziazione morfologica, però con frequenti sovrapposizioni. Pertanto, dimensioni e forma delle spore sono molto simili tra di loro, e meno della metà delle specie qui presentate venivano in passato distinte attraverso studi morfologici.

#### RESUMEN

Presentamos la taxonomía y la filogenia de la secc. *Multiformes* (*Cortinarius*, subgén. *Phlegmacium*). La presente circunscripción de la sección está basada en los resultados moleculares y en las características morfológicas. La taxonomía es compleja por lo que muchos taxones son totalmente nuevos y poco conocidos. Se describen dos nuevas especies. En total se reconocen diez especies europeas: *C. multiformis*, *C. talimultiformis*, *C. frondosomultiformis* sp. nov., *C. rufoallutus*, *C. talus*, *C. melleicarneus*, *C. caesiolamellatus*, *C. caesiophylloides*, *C. pallidirimosus* and *C. armenicorius* sp. nov.

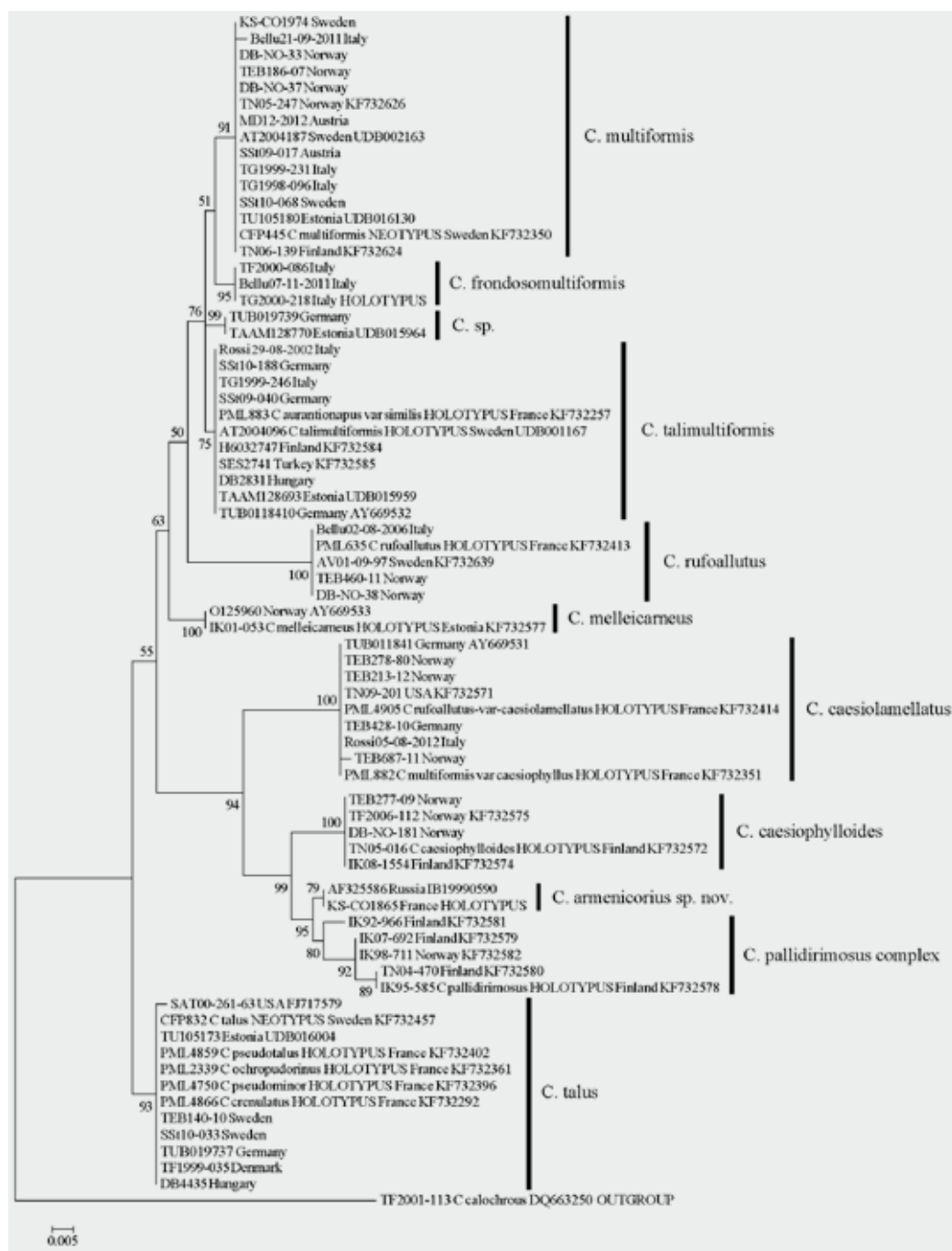
Las diez especies reconocidas lo son (i) con más o menos buen soporte filogenético, pero (ii) con una diferenciación morfológica bastante baja. Las especies difieren por >1% en ITS DNA de los taxones más cercanos, y cada par de especies muestra una diferenciación morfológica, aunque en muchos casos haya una superposición de caracteres. Por ejemplo: muchas especies muestran una variación en la superposición del tamaño y la forma de las esporas, y sin embargo menos de la mitad de las especies han sido diferenciadas anteriormente mediante estudios morfológicos.

**Table 1.** Collections used for phylogenetic analysis. Species are presented in alphabetical order.

| Species                                                  | Collector* | Locality                                                               | Herbarium                        | GenBank     |
|----------------------------------------------------------|------------|------------------------------------------------------------------------|----------------------------------|-------------|
| <i>C. armenicorius</i><br>sp. nov.                       | KS         | France, Jura, Prénovel                                                 | KS-CO1865<br>(Holotypus)         | KM504515    |
| <i>C. armenicorius</i>                                   | UP         | Russia, Sakha, Khangalassky Ulus                                       | IB19990590                       | AF325586    |
| <i>C. caesiolamellatus</i>                               | UL         | Germany, Thüringen, Thölendorf                                         | TUB011841                        | AY669531    |
| <i>C. caesiolamellatus</i>                               | SSt, TEB   | Baden-Württemberg, Schwaben,<br>Ehingen a.d. Donau, Kohlhaus           | TEB428-10                        | unpublished |
| <i>C. caesiolamellatus</i>                               | TEB        | Norway, Oslo, Grorud,<br>Steinbruvannet                                | TEB687-11                        | unpublished |
| <i>C. caesiolamellatus</i>                               | TEB        | Norway, Oslo, Vestfold, Tønsberg                                       | TEB278-80                        | unpublished |
| <i>C. caesiolamellatus</i>                               | TEB        | Norway, Sogn & Fjordane, Lærdal                                        | TEB213-12                        | unpublished |
| <i>C. caesiolamellatus</i>                               | CR         | Italy, Malga di Nemes                                                  | Rossi05-08-012                   | unpublished |
| <i>C. caesiolamellatus</i>                               | JFA, TN    | USA, Washington, Olympic pen-<br>insula                                | TN09-201                         | KF732571    |
| <i>C. rufoallutus</i> var. <i>cae-<br/>siolamellatus</i> | AB         | France, Ain, col des Bérentin                                          | PML4905 (Holotypus)              | KF732414    |
| <i>C. multiformis</i> var. <i>cae-<br/>siophyllus</i>    | PML        | France, Savoie, Arith                                                  | PML882 (Holotypus)               | KF732351    |
| <i>C. caesiophylloides</i>                               | TEB        | Norway, Nord-Trøndelag, Stjørdal,<br>Beistadvollen                     | TEB277-09                        | unpublished |
| <i>C. caesiophylloides</i>                               | TF         | Norway, Oppland, Lunner                                                | TF2006-112                       | KF732575    |
| <i>C. caesiophylloides</i>                               | TEB        | Norway, Buskerud, Ringerike,<br>Eggemoen northeast                     | DB-NO-181<br>TEB720-13           | unpublished |
| <i>C. caesiophylloides</i>                               | KL, TN     | Finland, ES, Joutsa, Koivuranta                                        | TN05-016 (Holotypus)             | KF732572    |
| <i>C. caesiophylloides</i>                               | IK         | Finland, Kn, Paltamo                                                   | IK08-1554                        | KF732574    |
| <i>C. frondosomultiformis</i><br>sp. nov.                | GT         | Italy, South Tyrol, Kaltern east,<br>Montigglerwald near Eppan         | TG2000-218<br>(Holotypus)        | KM504516    |
| <i>C. frondosomultiformis</i>                            | TF, TSJ    | Italy, South Tyrol, Kaltern west,<br>Matschatsch (route to Mendelpass) | TF2000-086                       | unpublished |
| <i>C. frondosomultiformis</i>                            | AC         | Italy, South Tyrol, Kaltern west,<br>Matschatsch (route to Mendelpass) | Bellu07-11-2011 (BOZ<br>2011/71) | unpublished |
| <i>C. melleicarneus</i>                                  | IK         | Estonia, Hiiumaa, Sarve, Soonlepa                                      | IK01-053 (Holotypus)             | KF732577    |
| <i>C. melleicarneus</i>                                  | ILF        | Norway, Aust Agder, Grimstad                                           | O125960                          | AY669533    |
| <i>C. multiformis</i>                                    | KS         | Sweden, Dalarna, Revnes                                                | KS-CO1974                        | unpublished |
| <i>C. multiformis</i>                                    | FB         | Italy, South Tyrol, Sarntal,<br>Reinswald                              | Bellu21-09-2011                  | unpublished |
| <i>C. multiformis</i>                                    | TEB, BD    | Norway, Oppland, Øystre Slidre,<br>Reieåsen                            | DB-NO-33<br>TEB410-13            | unpublished |
| <i>C. multiformis</i>                                    | TEB        | Norway, Oppland, Vestre Slidre,<br>Mosåni                              | TEB186-07                        | unpublished |
| <i>C. multiformis</i>                                    | TEB, BD    | Norway, Oppland, Øystre Slidre,<br>Volbu fjorden                       | DB-NO-37<br>TEB413-13            | unpublished |
| <i>C. multiformis</i>                                    | TN et al.  | Norway, Hordaland, Voss                                                | TN05-247                         | KF732626    |
| <i>C. multiformis</i>                                    | MD         | Austria, Zillertal                                                     | MD12-2012                        | unpublished |
| <i>C. multiformis</i>                                    | AT         | Sweden, Jämtland, Ragunda,<br>Bispgården                               | AT2004187                        | UDB002163   |
| <i>C. multiformis</i>                                    | SSt        | Austria, Gepatsch-Stausee                                              | SSt09-017                        | unpublished |
| <i>C. multiformis</i>                                    | GT         | Italy, Corti, Grünbachalm                                              | TG1999-231                       | unpublished |
| <i>C. multiformis</i>                                    | GT         | Italy, Pochi di Salorno, Val Fredda                                    | TG1998-096                       | unpublished |
| <i>C. multiformis</i>                                    | SSt        | Sweden, Borgsjö/Jämtgaveln                                             | SSt10-068                        | unpublished |
| <i>C. multiformis</i>                                    | AK         | Estonia, Võru, Rõuge, Saarlase                                         | TU105180                         | UDB016130   |
| <i>C. multiformis</i>                                    | TEB et al. | Sweden, Ångermanland,<br>Häggdånger, Sjö                               | CFP445 (Neotypus)                | KF732350    |

| Species                                    | Collector* | Locality                                       | Herbarium              | GenBank     |
|--------------------------------------------|------------|------------------------------------------------|------------------------|-------------|
| <i>C. multiformis</i>                      | TN et al.  | Finland, PK, Kitee                             | TN06-139               | KF732624    |
| <i>C. pallidirimosus</i>                   | IK         | Finland, InL, Utsjoki, Kevo                    | IK95-585 (Holotypus)   | KF732578    |
| <i>C. pallidirimosus</i>                   | IK         | Finland, PeP, Tervola                          | IK07-692 (H6000925)    | KF732579    |
| <i>C. pallidirimosus</i>                   | TN, KL     | Finland, PeP, Rovaniemi                        | TN04-470               | KF732580    |
| <i>C. pallidirimosus</i>                   | IK         | Finland, SoL, Sodankylä                        | IK92-966               | KF732581    |
| <i>C. pallidirimosus</i>                   | IK         | Norway, Troms, Storfjord                       | IK98-711               | KF732582    |
| <i>C. rufoallutus</i>                      | CR         | Italy, South Tyrol, Anterselva                 | Rossi02-08-2006        | unpublished |
| <i>C. rufoallutus</i>                      | TEB, BD    | Norway, Oppland, Øystre Slidre, Volbufjorden   | DB-NO-38<br>TEB 415-13 | unpublished |
| <i>C. rufoallutus</i>                      | TEB        | Norway, Oppland, Øystre Slidre                 | TEB460-11              | unpublished |
| <i>C. rufoallutus</i>                      | PML, JM    | France, Haute-Savoie, Plateau de Glières       | PML635 (Holotypus)     | KF732413    |
| <i>C. rufoallutus</i>                      |            | Sweden, Jämtland, Borgsjö                      | AV01-09-97             | KF732639    |
| <i>C. sp.</i>                              | AK         | Estonia, Hiiu, Pühalepa, Salinõmme             | TAAM128770             | UDB015964   |
| <i>C. sp.</i>                              |            | Germany                                        | TUB019739              | unpublished |
| <i>C. talimultiformis</i>                  | CR         | Italy, Tovare Male'                            | Rossi29-08-2002        | unpublished |
| <i>C. talimultiformis</i>                  | SSt        | Germany, Baden-Württemberg, Ehingen a.d. Donau | SSt10-188              | unpublished |
| <i>C. talimultiformis</i>                  | GT         | Italy, Brunico/Amaten                          | TG1999-246             | unpublished |
| <i>C. talimultiformis</i>                  | SSt        | Germany, Niedersachsen, Ahlsburg/Dörigsen      | SSt09-040              | unpublished |
| <i>C. aurantonapus</i> var. <i>similis</i> | PML        | France, Haute-Savoie, Avernioz                 | PML883 (Holotypus)     | KF732257    |
| <i>C. talimultiformis</i>                  | AT         | Sweden, Uppsala, Hässelby Park                 | AT2004096 (Holotypus)  | UDB001167   |
| <i>C. talimultiformis</i>                  | IK         | Finland, PH, Virrat                            | H6032747               | KF732584    |
| <i>C. talimultiformis</i>                  |            | Turkey, Trabzon, Macka                         | SES2741                | KF732585    |
| <i>C. talimultiformis</i>                  | LA, BD     | Hungary, Vas, Felsőszölnök                     | DB2831                 | unpublished |
| <i>C. talimultiformis</i>                  | KP         | Estonia, Tartu, Nõo, Vellavere                 | TAAM128693             | UDB015959   |
| <i>C. talimultiformis</i>                  | GS         | Germany, Baden-Württemberg, Titisee-Neustadt   | TUB0118410             | AY669532    |
| <i>C. talus</i>                            |            | USA                                            | SAT00-261              | FJ717579    |
| <i>C. talus</i>                            | TEB et al. | Sweden, Jämtland, Ragunda                      | CFP832 (Neotypus)      | KF732457    |
| <i>C. talus</i>                            | AK         | Estonia, Tartu, Vara, Alajõe                   | TU105173               | UDB016004   |
| <i>C. pseudotalus</i>                      | JCM        | France                                         | PML4859 (Holotypus)    | KF732402    |
| <i>C. ochropudorinus</i>                   | AB         | France, Ain, Meyriat                           | PML2339 (Holotypus)    | KF732361    |
| <i>C. pseudominor</i>                      | PR         | France, Ardennes, Bois des Alleux              | PML4750 (Holotypus)    | KF732396    |
| <i>C. crenulatus</i>                       | FL         | France, Allier, Forêt de Tronçais              | PML4866 (Holotypus)    | KF732292    |
| <i>C. talus</i>                            | TEB, SSt   | Sweden, Borgsjö                                | TEB140-10              | unpublished |
| <i>C. talus</i>                            | SSt, TEB   | Sweden, Borgsjö                                | SSt10-033              | unpublished |
| <i>C. talus</i>                            |            | Germany                                        | TUB019737              | unpublished |
| <i>C. talus</i>                            | TF         | Denmark, Sealand                               | TF1999-035             | unpublished |
| <i>C. talus</i>                            | KT         | Hungary, Vas, Farkasfa                         | DB4435                 | unpublished |
| <i>C. calochrous</i> (outgroup)            | TF         | Sweden, Skåne                                  | TF2001-113             | DQ663250    |

\* Abbreviation of names: AB = André Bidaud, AC = A. Cester, AK = Anu Kollom, AT = Andy Taylor, BD, DB = Bálint Dima, CR = Claudio Rossi, FB = Francesco Bellù, FL = F. Lopez, GS = Günter Saar, GSS = Geert Schmidt-Stohn, GT = Gianni Turrini, ILF = I-L. Fonneland, IK = Ilkka Kytövuori, JCM = J.-C. Malaval, JFA = Joseph F. Ammirati, JM = Jacques Melot, KL = Kare Liimatainen, KP = Kai Piirsoo, KT = Katalin Takács, LA = László Albert, MD = Martin Dondl, PML = Pierre Moëgne-Loccoz, PR = Patrick Reumaux, TEB = Tor Erik Brandrud, TF = Tobias G. Frøslev, TM = Thomas Münzmay, TN = Tuula Niskanen, TSJ = Thomas Stjernegaard Jeppesen, UL = Udo Luhmann, UP = Ursula Peintner.



Phylogram: Bálint Dima

**Fig. 1** – Maximum likelihood ITS phylogram of *Cortinarius* sect. *Multiformes* in Europe calculated with RAxML. Bootstrap values are given above branches. The bar indicates the number of expected substitutions per position. For each collection, herbarium number, locality (country), and GenBank/UNITE accession numbers if existed are provided.

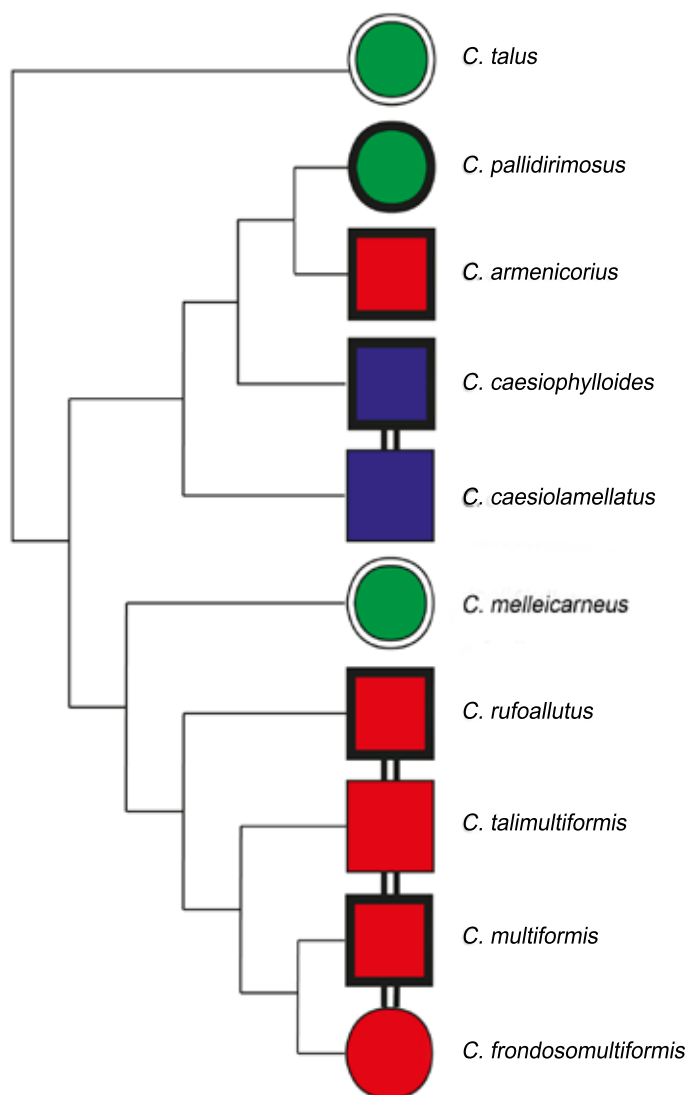


Illustration: Marie K. Brandrud

**Fig. 2** – Schematic illustration of the morphological, ecological and phylogenetic affinity among the sect. *Multiformes* species. Circles: deciduous forest species. Squares: coniferous forest species. thick line: preferentially northern (middle- northern boreal) species. Thin line: more southern species (mainly S. Scandinavia-C Europe). Green: species with pale yellowish (whitish to honey brown) pileus. Red: species with vivid ochraceous brown to red brown pileus. Blue: species with violaceous blue tinges on young lamellae and stipe. Double line between taxa = sister species with a high morphological similarity (overlap in character variation).

## Introduction

The section *Multiformes* (Rob. Henry) Moënne-Loec. & Reumaux (*Cortinarius*, subgen. *Phlegmacium*) is here treated in a strict sense, including species with (i) a more or less abruptly bulbous stipe, (ii) context with a honey-like smell, (iii) a duplex pileipellis structure and (iv) sub-amygdaloid-ellipsoid, pale, rather densely verrucose spores. This group, in contrast to the resembling sect. *Claricolores* treated in BRANDRUD et al. (2013), consists of a number of little known, critical species, and its taxonomy has not been well-established. According to morphological taxonomy, only two or three species have frequently been distinguished up to now; the ochraceous (orange-)brown *C. multiformis* (sometimes also *C. allutus* or *C. rufoallutus*) in coniferous forests and the paler *C. talus* (= *C. ochropallidus*, *C. multiformis* s. Moser) in deciduous forests (cfr. e.g. BRANDRUD et al. 1990–2014, JEPPESEN et al. 2012, KRIEGLSTEINER & GMINDER 2010, SOOP 2011). MOSER (1961) distinguished three species in coniferous forests referable to the present *C. multiformis* (*C. allutus*, *C. hundellii* and *C. subhygrophanicus*) and three in deciduous forests referable to *C. talus* as applied here (*C. multiformis*, *C. ochropallidus* and *C. talus*).

However, recent and ongoing molecular studies performed by the present authors in the JEC DNA group, by the Tübingen group (GARNICA et al. 2014 in prep.) and by the Helsinki group (LIIMATAINEN et al. 2014) have shown that the taxonomy of sect. *Multiformes* is much more complex than formerly thought. With this new, phylogenetic knowledge, it has become impossible to maintain the old, wide species concept based on discontinuous morphological variation.

The sect. *Multiformes* has often been treated in a wider concept, including most phlegmacioid species with whitish-greyish lamellae and context. For instance, species with a more cylindric-clavate stipe, a duplex pileipellis and amygdaloid-ellipsoid spores, covering the *C. claricolor*-*C. cumatilis*-*C. praestans* group (sect. *Claricolores*) as well as the *C. turmalis*-*C. variegatus* group has been included here (see e.g. BRANDRUD et al. 1990–2014). However, GARNICA et al. (2005, 2014 in prep.) have shown that sect. *Claricolores* («clade *Praestantes*») and the *C. turmalis*-*C. variegatus* group are phylogenetically rather dissimilar from sect. *Multiformes*, especially the former, which appears to be more closely related to sect. *Phlegmacioides* and to sect./clade *Vulpini* (cfr. also BRANDRUD et al. 2013). Phylogenetically, sect. *Multiformes* s. str. as applied here appears to be a well supported clade (see GARNICA et al. 2005; sub nom. clade *Alluti*).

Species such as *C. saporatus* and *C. corrosus* with (i) whitish-greyish lamellae and context, (ii) a strongly marginate bulbous stipe, (iii) a simplex, thick pileipellis and (iv) and strongly-coarsely ornamented citriform-amygdaloid spores have also often been included in (sub)sect. *Multiformes* (see e.g. MOSER 1961, BIDAUD et al. 2006), but these are clearly both micromorphologically and phylogenetically quite dissimilar from the «true» *Multiformes* species, and belong to the well-circumscribed sect. *Calochroi* (cfr. e.g. FRØSLEV et al. 2007, GARNICA et al. 2005).

## Material and Methods

The presented species have been studied from various parts of Europe, including documentations with photographs and descriptions of macro- and micromorphology. The study of macro- and micromorphology follows BRANDRUD (1996). For spore measurements, unripe or aberrant spores are avoided, and only spore deposits (including spores on the stipe/Cortina) are measured. Spore size variation as shown in spore-scattergrams is based on mean values per basidiome. One or two basidiomes are measured per collection. For method of spore photos with stacking techniques, see SCHMIDT-STOHN (2011). A selected set of samples were also used for phylogenetic studies, combined with already available sequences from the online DNA-sequence depositories GenBank (<http://www.ncbi.nlm.nih.gov/gen-bank/>) and UNITE (<http://unite.ut.ee/>).

Laboratory work was organized/performed by some member of the JEC DNA group (Geert Schmidt-Stohn, Tobias G. Frøslev, Tor Erik Brandrud, Bálint Dima) in the following universi-

ties: Greifswald and Senckenberg (Germany), Copenhagen (Denmark), Oslo (Norway) and in the Eötvös Loránd University, Budapest (Hungary). Main responsible for the laboratory work at the University of Greifswald was Martin Unterseher, and at the research centre Senckenberg (Frankfurt a. M.) Ali Tahir and Marco Thines.

For the DNA extraction and PCR reactions mainly the Phire® Plant Direct PCR Kit (Finnzymes, Finland) was used, but also other DNA extraction kits were applied (see FRØSLEV et al. 2005, 2007, cfr. also SCHMIDT-STOHN & OERTEL 2009).

The ITS region of the nrDNA was amplified with the primer pairs ITS1/ITS4, ITS1F/ITS4 or ITS1F/ITS4B. Majority of PCR products were sequenced by LGC Genomics (Berlin, Germany) with the same primers used in PCR reactions. The electropherograms were checked, assembled and edited with the CodonCodeAligner 4.1. (CodonCode Corporation, Centerville, MA, U.S.A.).

Sequences produced by the JEC-DNA Group are unpublished; the data are available from the second author. Alignment was performed by webPRANK (LÖYTENOJA & GOLDMAN 2010, <http://www.ebi.ac.uk/goldman-srv/webPRANK/>). Maximum Likelihood analysis was carried out with RAXML BlackBox (STAMATAKIS et al. 2008, <http://embnet.vital-it.ch/raxml-bb/>). *Cortinarius calochrous* (DQ663250, FRØSLEV et al. 2007) was chosen as outgroup.

Altogether 72 sequences (+ outgroup) were included in our RAXML analysis of which 34 were generated in this study (Fig. 1). Many of our sequenced collections were, however, excluded from the analysis due to their insufficient length or quality. Nevertheless, these sequences could be used for identification using BLAST algorithm of GenBank and/or UNITE databases.

All collections examined morphologically by us are listed under each species description. The sequenced collections (own and public databases) are marked (DNA), and those included in the phylogenetic analysis are marked with an additional asterisk (DNA\*).

## Section *Multiformes* – 10 species recognized in Europe

As presented and discussed below, the phylogenetic data provides support for a considerably number of new, formerly little known taxa in sect. *Multiformes*. Four of these species are described as new in LIIMATAINEN et al. (2014), and two in the present study. In some cases, close taxa are more or less geographically differentiated. For instance in the *C. multiformis* complex, the more Northern European, oligotrophic-acidophilous *C. multiformis* s. str. (= *C. lundelli* (M. M. Moser) M. M. Moser) can be distinguished from the apparently more Central-Southern European *C. talimultiformis* (= *C. aurantionapus* var. *similis* Moëgne-Locc.), while showing overlapping morphological features. The blue gilled species show a similar differentiation; *C. caesiophylloides* appears to be a predominantly Northern European, middle boreal-northern boreal taxon, whereas the closely related *C. caesiolamellatus* seems to be predominantly South Scandinavian-Central(-South) European, southern boreal-montane.

On re-examination of the morphology of phylogenetic units, it appears that some degree of morphological differentiation can be found between all taxa, but some taxa will be difficult to unambiguously identify in the field or under the microscope. In fact, it is not possible to fully understand the taxonomy of sect. *Multiformes* without the aid of molecular characters and phylogeny. This is partly due to (i) the low degree of morphological differentiation, with sister species showing overlap in morphological characters, but also due to (ii) the rarity of some of the taxa. For instance, *C. melleicarneus* is hitherto found twice, once in Estonia (2001) and once in southernmost Norway (1994), and *C. armenicorius* is also found only twice; once in Russia (1999) and once in French Jura (2008). *Cortinarius frondosomultiformis* is only found in two sites in N Italy (2000, 2011). It will probably take more than a lifetime to get good data on the morphological variation and ecogeographical range of such rarities, and sequence data are thus essential.

This taxonomy of *Multiformes* is comparable to that of some critical groups of subgenus *Telamonia*, where many taxa are well-supported phylogenetically, but with comparatively little

morphological differentiation (e.g. sect. *Brunnei*, NISKANEN et al. 2009, sect. *Bovini* NISKANEN et al. 2013). These seem to represent young groups in active speciation, and introducing molecular methods has resulted in (more than) a doubling of the number of species. In other groups of subgenus *Phlegmacium*, such as sect. *Claricolores* (BRANDRUD et al. 2013), sect. *Phlegmacium* (cfr. BRANDRUD 1996 versus GARNICA et al. 2005) and some fulvoid groups (e.g. the *Rufoolivacei*) of sect. *Calochroi* (BRANDRUD et al. in prep.) the new, molecular data has hardly changed the wide, well-established morphology-based species concepts formerly applied.

Since the new combined phylogenetic and morphological species concept support the inclusion of a number of morphologically relatively weakly differentiated species that sometimes might even be difficult to distinguish morphologically, this might be taken as an argument for a general, narrow morphological species concept. However, the phylogenetic results do not support the former «splitting taxonomy» which has been performed mainly in France. For instance, BIDAUD et al. (2006) included at least 16 species in sect. *Multiformes* s. str., but these apparently do not cover more than 4 of the species accepted here. So 75% of the species names applied at present in sect. *Multiformes* s. str. in France are synonyms or probable synonyms. For instance, at least 9 of the species distinguished in BIDAUD et al. (2006), appears to be within the rather wide morphological variation of *C. talus*.

### Morphology and delimitation towards related groups

The species of sect. *Multiformes* are characterized macromorphologically by a more or less abruptly bulbous stipe with only little universal veil remnants at the bulb margin. Veil remnants are sparse also on the pileus, but some thin, silvery white veil hyphae might give the surface a frosty or marbled-innately fibrillose pattern on young basidiomes. Cortina remnants are also thin, often rendering the stipe surface smooth and glossy, initially being whitish(-bluish) and often becoming shiny brass brown with age. The pileus is often bicoloured, that is, darker hygrophanous (water-soaked) in outer part, at least with age and when growing in humid habitats, or the surface may be pseudohygrophanous, that is with a dense pattern of darker spots at centre and hygrophanous streaks or veins towards margin. Some species become radially rugulose-sulcate (wrinkled) with age due to the cap cuticle structure.

Micromorphologically, the following features are characteristic; (i) a duplex (two-layered) pileipellis structure including a subcellular hypoderm with tightly cemented elements provided with golden yellow, parietal, amber-like pigment (usually without spirally-zebra-striped encrustations), and (ii) the rather pale, amygdaloid-ellipsoid spores with somewhat rounded warts.

The spore ornamentation usually consists of irregular, low, rounded and often confluent warts, which might appear rather diffuse in the microscope (Figure 3, 12). The spore morphology is rather uniform in the section, however with some small differences in size and shape that can be used to more or less distinguish closely related taxa. One «series» of species with rather strictly(-acutely) amygdaloid spores can be distinguished from species with more broadly ellipsoid spores (Figure 3, 12). The former group has slightly narrower spores, with average Q-values ranging from 1.68–1.81, whereas the ones with more broadly ellipsoid spores possess mean Q values of 1.60–1.71. Normally, the strictly amygdaloid spores are paler, with dense ornamentation, whereas the more ellipsoid spores are darker (more thick-walled) with more coarse, confluent ornamentation (Figure 1). For instance, the close species pair *C. multiformis* versus *C. talimultiformis* can be distinguished on more broadly ellipsoid, coarsely verrucose spores versus strictly amygdaloid more densely verrucose and pale spores, respectively. The same applies for *C. caesiolamellatus* versus *C. caesiophylloides*. However, it should be noted that the spore morphology variation might overlap, for instance, species with mainly ellipsoid spores might sometimes have dominating amygdaloid spores. Mature spores shed to the stipe or in spore deposits should always be compared for these patterns.

According to material seen so far, *C. frondosomultiformis* have smaller spores than the others ( $7\text{--}8.5 \times 4.5\text{--}5 \mu\text{m}$  versus «standard» *Multiformes* spores  $8\text{--}9.5 \times 5\text{--}5.5 \mu\text{m}$ ), and also *C. melleicarneus* has slightly smaller spores than the average *Multiformes* species ( $8\text{--}8.5 \times 4.5\text{--}5 \mu\text{m}$ ) (Figure 3, 12). On the other hand, *C. armenicorius*, *C. pallidirimosus* and *C. talimultiformis* possess slightly larger spores than average.

Macrochemical reactions vary considerably within the species (dependent on age, weather conditions, etc.) and are regarded as of limited taxonomic value, so is not included here. Chemically, the section *Multiformes* taxa are characterized by a strong, bluish fluorescent substance (possibly a sterol). This can be observed on dried specimens under UV light, and is pronounced when tissue is extracted and run by chromatographical methods (BRANDRUD 1980).

The sect. *Multiformes* species share a number of the above mentioned features with the members of some other, morphologically resembling taxa, such as sect. *Claricolores* and the *C. turmalis*-*C. variegatus* group. Section *Claricolores*, however, does not belong to the same major clade as sect. *Multiformes*, and the species of the former are distinguished by their thick, almost membranous veil, rendering the stem more or less volvate or repeatedly girdled, and the cap often with whitish patches when young. Furthermore, the species never possess an abruptly bulbous stipe, they never smell of honey, and their spores are acutely amygdaloid with little/no ornamentation or much larger (BRANDRUD et al. 2013). The *C. turmalis*-*C. variegatus* group belongs to the same major clade as the *Multiformes* group, but is not in a sister relationship, and differs by small, smooth, very pale brown spores, persistently rather pale lamellae and veil/basal mycelium which turns pink on exposure to air (cfr. BRANDRUD et al. 1990–2014).

## Molecular phylogeny

A number of taxa appear to be well supported phylogenetically as shown by a study of the barcoding marker ITS, with (i) a clear barcoding gap (discontinuous sequence variation) between sister taxa, including (ii) an average ITS sequence difference between sister species of  $>1\%$  ( $<99\%$  similarity: 6–8–15 nucleotide differences; see Figure 1). The *C. pallidirimosus* complex differs from this pattern; possessing a rather large internal ITS variation of six nucleotide differences (Figure 1). At least most of this variation is apparently not reflected in corresponding morphological-ecological variation, and seems to represent infraspecific variation. These variants, however, needs further study. As stated above, a number of sister species are morphologically very similar, especially the taxa around *C. multiformis*. One of the genotypes/OTU's around *C. multiformis* («*C. sp.*») with 5–6 ITS differences from *C. multiformis* is not treated here due to lack of morphological data. The phylogenetic, morphological and ecogeographical affinities of the ten European *Multiformes* species recognized here are summarized in Figure 2.

The circumpolar species *C. multiformis* and *C. talus* show 1–2 ITS sequence difference between European populations and North American populations (data not shown). The many European specimens of *C. talus* studied show genetically uniformity, even though the taxon is rather variable as to spore-morphology and eco-geography (see under *C. talus*).

The extensive ITS-barcoding analyses performed lately by us and others (see e.g. GARNICA et al. 2003, 2005, 2014 in prep., LIIMATAINEN et al. 2014) give a clear support for the delimitation of the clade/section *Multiformes* (= clade *Alluti*) as applied here, but show conflicting and not well-supported results for infrageneric affinity and phylogeny. However, yet unpublished data using other gene markers (GARNICA et al. 2014 in prep., HØILAND et al. 2014 in prep.) indicate that sect./clade *Multiformes* is most closely related to the sect./clade *Scauri* and *Purpurascetes*, as well as to some smaller clades containing the European taxa *C. lustratus*, *C. pinophilus*, *C. turmalis*, and *C. variegatus*. See separate paper on sect. *Purpurascetes* in present volume of *Journ. J.E.C.* The phylogeny of these phlegmacioid groups should be regarded as not yet fully resolved.

## Taxonomy

### Key to the European species of sect. *Multiformes*

Note: The differentiation in macrocharacters is little or little known between a number of closely related species. Therefore, microcharacters (spore characters) are emphasized in the key. The often occurring honey-smell is most pronounced in bulb context.

- 1 In deciduous forests. Pileus when young pale ochraceous yellow (-honey brown) to almost whitish (if more ochre brown, then spores small,  $MV < 8.5\ \mu m$ ) ..... **2**
- 1\* In coniferous (mainly *Picea*) forests. Pileus when young darker ochraceous brown-fulvous to vividly apricot-red brown ..... **5**
- 2 Pileus initially silvery-frosty at centre, distinctly innately fibrillose towards margin; almost whitish, later (pale) ochraceous yellow; sometimes more ochre brown. Robust species with a distinct marginate bulb. Smell strong of honey. Spores variable,  $(7-)-7.5-9.5 \times 4.5-5.5\ \mu m$ ; northern, subalpine *Betula pubescens* populations have small spores (normally  $< 8.5\ \mu m$  long). Widespread, mainly under *Betula*, *Fagus*, *Quercus*, *Carpinus*, *Corylus* ..... ***C. talus***
- 2\* Pileus not so frosty-innately fibrillose (if innately fibrillose, then northern, with slender stipe, and with larger spores) ..... **3**
- 3 Spores relatively large,  $9-10(-10.5) \times 5-6\ \mu m$ , amygdaloid; in northern Fennoscandian (boreal/subalpine) mixed *Betula pubescens* forests. Pileus initially (very) pale and somewhat innately fibrillose. Basidiomes slender, bulb indistinct; smell of honey .. ***C. pallidirimosus***
- 3\* Spores small,  $7-8.5 \times 4-5\ \mu m$ ; in thermophilous *Quercus-Corylus-Fagus* forests; pileus weakly innately fibrillose or not; basidiomes robust, with a distinctly marginate bulb ..... **4**
- 4 Spores narrowly amygdaloid,  $(7.5-)-8-8.5(-9) \times (4-)-4.5-5\ \mu m$ ; pileus pale honey brown to more grey brown or flesh-coloured; no smell of honey noted. In *Quercus-Corylus* forests on calcareous, sandy soil. Very rare (S Norway, Estonia) ..... ***C. melleicarneus***
- 4\* Spores ellipsoid-subamygdaloid,  $7-8.5(-9) \times 4-5(-5.5)\ \mu m$ , with often somewhat coarser, confluent warts; pileus ochraceous yellow to pale ochraceous brown, smell of honey. In rich *Quercus-Carpinus-Fagus(-Abies)* forests. Very rare (N Italy) ..... ***C. frondosomultiformis***
- 5 Lamellae and stipe (apex) with bluish tinges when young; strong smell of honey ..... **6**
- 5\* Without any bluish tinges; honey smell almost absent to (rarely) strong ..... **7**
- 6 Spores usually ellipsoid and rather strongly and coarsely verrucose,  $8-9(-9.5) \times 5-6\ \mu m$ . Pileus vividly, warm ochraceous brown to red brown, often bicoloured with a dark, hygrophanous outer zone. Mainly in S Scandinavia and C Europe ..... ***C. caesiolamellatus***
- 6\* Spores distinctly (acutely) amygdaloid, weakly and densely verrucose,  $8.5-9.5(-10) \times (4.5-)-5-6\ \mu m$ . Pileus less vividly coloured (more fulvous-grey brown), rarely bicoloured. Northern Europe (Fennoscandia) ..... ***C. caesiophylloides***
- 7 Spores strictly amygdaloid, densely verrucose,  $(8.5-)-9-10 \times (4.5-)-5-6\ \mu m$ . Usually robust, with distinctly marginate bulb. Pileus often silvery-fibrillose from thin veil remnants. Honey smell weak or absent. Associated with *Picea* and *Abies*, mainly in S Fennoscandia and C Europe ..... ***C. talimultiformis***
- 7\* Spores (broadly) ellipsoid-subamygdaloid, with somewhat coarser (confluent-rounded), diffuse ornaments. Robust or not ..... **8**

- 8 Pileus strongly apricot-redbrown, with distinct pattern of dark, hygrophanous spots. Spores ellipsoid-subamygdaloid,  $8\text{--}9.5 \times (4.5\text{--})5\text{--}5.5 \mu\text{m}$ , weakly verrucose to almost smooth. Subcutis (hypoderm) with some distinctly zebra-striped encrusted hyphae. Honey smell weak or absent ..... ***C. rufoallutus***
- 8\* Pileus ochraceous brown-fulvous brown, usually without a pattern of hygrophanous spots. Subcutis (almost) without zebra-striped encrusted hyphae ..... **9**
- 9 Spores  $8\text{--}9.5 \times (4.5\text{--})5\text{--}5.5(6) \mu\text{m}$ , ellipsoid-subamygdaloid; basidiomes often slender and with an indistinct bulb, almost without veil remnants; honey smell weak or absent. Mainly in Northern Europe. Widespread. Associated with *Picea* ..... ***C. multiformis***
- 9\* Spores  $9\text{--}10 \times 5.5\text{--}6.5 \mu\text{m}$ , (broadly) ellipsoid; basidiomes robust, with distinct, white veil remnants at bulb (and pileus) margin; with a distinct honey smell. Recorded from *Picea* and *Larix-Betula* forests. Very rare (E Siberia, E France) ..... ***C. armenicorius***

### The *C. multiformis*–*C. rufoallutus* subclade

#### ***Cortinarius multiformis* Fr.**

**Figs. 3, 4, 5**

*Epicr. Syst. Mycol.*: 263 (1838).

**Type:** Sweden, Cortin. *Fl. Photogr.*, CFP 445, herb. S; neotype designated in LIIMATAINEN et al. (2014).

**Syn.:** *C. lundellii* (M. M. Moser) M. M. Moser, *Kleine Kryptogamenflora* Bd IIb/2: 286 (1967)

*Phlegmacium lundellii* M. M. Moser, *Die Gattung Phlegmacium*: 349 (1961)

*C. subhygrophanicus* (M. M. Moser) M. M. Moser, *Kleine Kryptogamenflora* Bd IIb/2: 286 (1967)

*Phlegmacium subhygrophanicus* M. M. Moser, *Die Gattung Phlegmacium*: 349 (1961)

?*C. coniferarum* (M. M. Moser) Moënné-Locc. & Reumaux, *Atlas des Cortinaires* III: Fiche 114 (1991)

*Phlegmacium multifforme* (Fr.) Wünsche var. *coniferarum* M. M. Moser, *Die Gattung Phlegmacium*, p. 349 (1961)

?*C. herbarum* Rob. Henry, *Bull. Soc. Mycol. Fr.* 67(3): 270–271 (1951)

?*C. pseudorugulosus* Rob. Henry ex Bidaud & Reumaux, *Atlas des Cortinaires* XVI: 1096 (2006).

**Misapplied name:** *C. allutus* Fr. s. auct.

**Icones:** BRANDRUD et al. (1990–2014): A 85 (CFP 445; neotype), BIDAUD et al. (2006): Pl. 579 (sub nom. *C. lundellii*), MOSER (1961): Pl. IV (sub nom. *C. lundellii*, *C. subhygrophanicus*), Pl. I (sub nom. *C. allutus*). KRIEGLSTEINER & GMINDER (2010): p. 141 (sub nom. *C. multiformis* var. *coniferarum*).

**Pileus:** (3–)4–8 cm, (hemi-)spherical, then plano-convex, viscid, often radially rugulose with age; often with a dense pattern of hygrophanous spots (centre) or streaks/veins (near margin) (pseudohygrophanous structure), with age sometimes entire marginal zone hygrophanous, centre sometimes silvery-micaceous from thin veil remnants when young; rather uniformly (dark) ochraceous yellow, fulvous to almost red brown, often becoming pale ochraceous yellow with age.

**Lamellae:** crowded, 4–8 mm broad, initially greyish white.

**Stipe:** 5–12(–14)  $\times$  0.8–1.5 cm, usually slender, with a faintly to rather distinctly marginate-bulbous base (@2.5 cm), often becoming quite non-marginate (almost cylindric) with age; glossy, white, turning distinctly brass-brown with age. Universal veil near the bulb very sparse, whitish at bulb margin.

**Context:** white, somewhat (ochre)greyish hygrophanous-spotted (marbled) towards surface of stipe (apex). Smell none or faint of honey, at least in bulb when bruised.

**Macrochemical reactions:** negative or indistinct.

**Spores:**  $8\text{--}9.5 \times (4.5\text{--})5\text{--}5.5(-6) \mu\text{m}$  ( $MV = 8.8 \times 5.3 \mu\text{m}$ ),  $Q = 1.67$ , ellipsoid to subamygdaloid, pale, weakly to distinctly and rather densely to diffusely verrucose, warts irregular to slightly confluent, rounded, sometimes warts very flat and hardly visible in the outline of the spores.

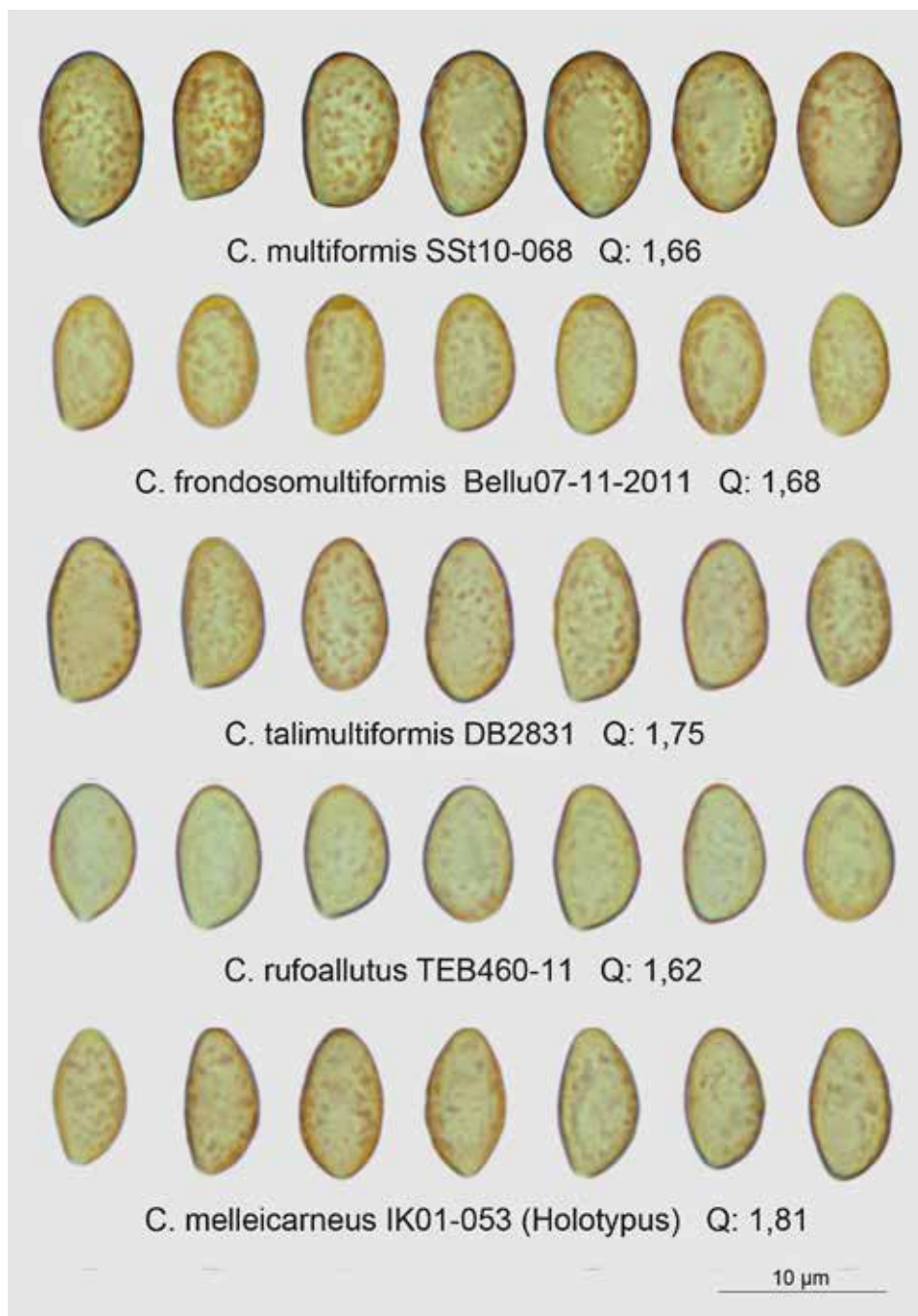


Photo: Geert Schmidt-Stohn

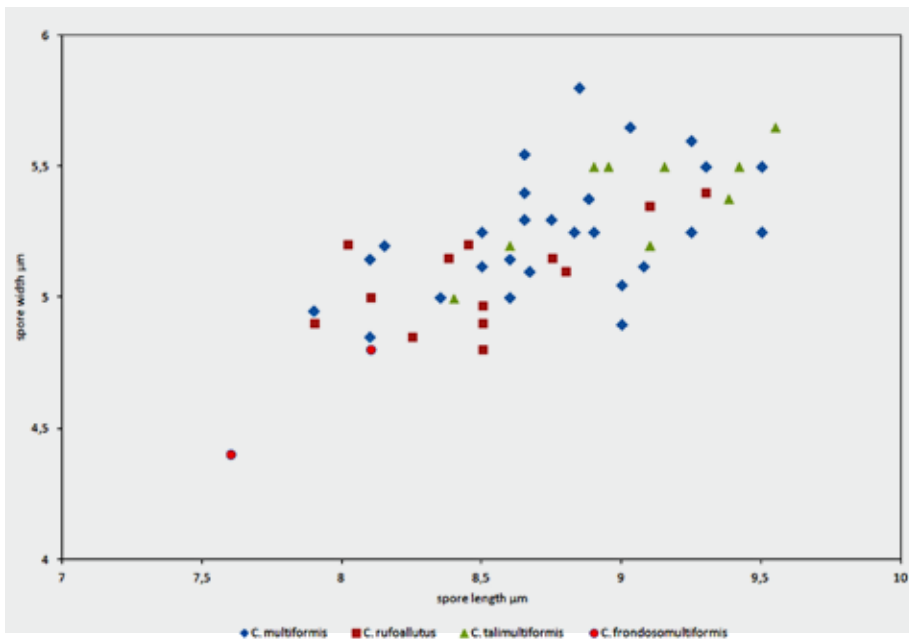
**Fig. 3** – Spore morphology of species in the *C. multiformis* subclade.

Spores 2000 : 1.



Photo: Geert Schmidt-Stohn

**Fig. 4** – *Cortinarius multiformis* (Sweden, SSt10-068; +DNA)



Scatter diagram: Geert Schmidt-Stohn

**Fig. 5** – Variation in spore size amongst species in the *C. multiformis* subclade. Each symbol = MV of spores measured per basidiome.

**Pileipellis:** duplex, at surface of thin, erect-entangled gelatinous,  $\pm$ hyaline hyphae. Subcutis/hypodermium subcellular, hyphae tightly cemented, with yellow brown parietal-encrusting pigment, forming an amber-like embedment. Thick, brown walls especially pronounced in corners between the cells; forming irregular-triangular «lenses», to more diffuse, brown pigments lumps. More narrow, longer transition hyphae between subcutis with and epicutis with yellow walls, and sometimes with zebra-striped encrustation.

**DNA (ITS) sequence:** Fifteen of the European ITS sequences available, including the neotype, are identical. However, 1 collection shows a minor difference without support. Two North American (Canadian) collections of *C. multiformis* differ by 1 nucleotide from the European ones (data not shown).

**Habitat:** Boreal (-boreonemoral) and (more rarely) montane-subalpine coniferous forests. Associated with *Picea abies*, mainly in oligotrophic-acid, mossy sites, often in large numbers in young plantations.

**Distribution:** Frequent and widely distributed in the Nordic boreal spruce forest region (JEPPESEN et al. 2012), including Estonia. Apparently more rare in the montane-subalpine regions of C Europe, but distribution poorly known due to confusion with *C. talimultiformis*. So far material of *C. multiformis* s. str. outside Northern Europe documented with ITS sequences only from the Prealps (N Italy, Austria) and one collection from Spain (see below). Probably also recorded from France; the plates of *C. lundellii* and *C. herbarum*, possibly also *C. pseudorugulosus* in BIDAUD et al. (2006) apparently depict our species (material not investigated).

**Collections examined:** NORWAY. Oppland: Øystre Slidre, Reieåsen, TEB 410-13, DB-NO-33 (herb. O) (DNA\*). Øystre Slidre, Volbufjorden, TEB 413-13, DB-NO-37 (herb. O) (DNA\*). Vestre Slidre, Mosåni, TEB 186-07 (herb. O) (DNA\*). Gjøvik, Biri, K. H. Brandrud & TEB 102-85 (herb. O). Lunner, S. Oppdalen, TEB 205-77, 277-78 (herb. O). Jevnaker, Sinner seter, E. Bendiksen & TEB 40-81 (herb. O). Hordaland, Voss, T. Niskanen et al., TN05-247 (herb. H) GenBank No. KF732626 (DNA\*). SWEDEN. Ångermanland: Häggdånger, Cortinarius, Flora Photographica, CFP 445 (neotype, herb. S) (DNA\*), CFP 88 (to herb. S). Halland: Mästocka, 9. July 1998, T. Münzmay H.15.98 (herb. TUB 4848) (DNA). Dalarna: Mora, T. Münzmay 11 Sept. 2007 (herb. TUB 9481) (DNA). Revnes, K. Soop 18. Sept. 2010, KS-CO1974 (herb. S F189954) (DNA\*). Jämtland: Ragunda, TEB 15-93 (herb. O). Ragunda, Bispgården, A. Taylor, AT2004187 (herb. UPS), UNITE No. UDB002163 (DNA\*). Offerdal, TEB 25-82, 26-82 (herb. O). Medelpad: Borgsjö, CFP 16 (to herb. S), K. Leonardsson & TEB 47-82 (herb. O). Borgsjö, Jämtgaveln, G. Schmidt-Stohn, SSt10-068 (DNA\*). Svartede W of Sundsvall, TEB 66-82 (herb. O). Norrbotten: Gällivare, K. Høiland & TEB 131-81 (herb. O). ITALY. South Tyrol: Sarntal, Reinswald, F. Bellù 21. Sept. 2011, Bellu21-09-2011 (herb. BOZ) (DNA\*). Corti, Grünbachalm, G. Turrini, TG1999-231 (herb. BOZ) (DNA\*). Valdaora di mezzo/Mitterberg, G. Turrini, TG2001-098 (herb. Turrini) (DNA). Pochi di Salorno, Val Fredda, G. Turrini, TG1998-096 (herb. Trento) (DNA\*). AUSTRIA. Gepatsch Stausee, SSt 09-017, G. Schmidt-Stohn (herb. TUB) (DNA\*), Zillertal, M. Dondl, MD12-2012 (DNA\*). SPAIN. J. Ballarà, JB 6591-09 (DNA).

**Comments:** *Cortinarius multiformis* is characterized by its vivid and uniformly yellow brown pileus colour, resembling that of ripe *Rubus chamaemorus* berries. Furthermore the stipe is initially shiny white, slender and usually with only a poorly developed marginate bulb, often sitting in deep moss. The description and plate of *C. lundellii* in MOSER (1961) well illustrates this often slender habit (see also Figure 4). Until recently, *C. multiformis* has usually been treated collectively, including *C. talimultiformis*, and possibly also *C. armenicorius*, *C. frondosomultiformis* and *C. rufoallutus*. These have overlapping morphological variation, but are quite well distinguished phylogenetically. *Cortinarius talimultiformis* is normally more robust, with a more distinctly and persistently marginate bulb, and on average possess a more vividly orange/red brown pileus and more whitish veil remnants on the pileus. *Cortinarius armenicorius* is paler, with more veil rem-

nants, and a distinct honey-like smell. The often co-occurring *Cortinarius rufoallutus* is more red brown, has a coarser, more pronounced hygrophanous spotted pileus surface, and early becomes brown spotted at stipe surface and in context. Pale forms of *C. multiformis* can sometimes be difficult to separate from the deciduous forest species *C. talus* and *C. frondosomultiformis* but these have a silky-micaceous-innately fibrillose structure of young pilei, and have a stronger smell of honey. *Cortinarius talus* has distinctly paler colours than *C. multiformis* when young and fresh, but *C. frondosomultiformis* and *C. multiformis* apparently might have overlapping colours, but is distinguished on the habitat (*Quercus/Fagus* versus *Picea* association).

The European material available shows a minor variation in ITS sequence. *Cortinarius frondosomultiformis* comes out as sister species in the phylogram, with 9–10 differences in ITS from *C. multiformis* (Figure 1). Another very close genotype («*C. sp.*» in Figure 1) is distinguished from *C. multiformis* by 5–6 nucleotide differences. Due to limited knowledge, this is preliminary regarded as cryptic species, without a formal, taxonomic recognition.

***Cortinarius frondosomultiformis*** Bellù, Brandrud & Dima sp. nov.

**Figs. 3, 5-8**

**MycoBank** No. MB809862

**Etymology:** from latin *frondosis* and *multiformis*, meaning „a *C. multiformis* in frondose forests”

**Typus:** Italy, South Tyrol, Kaltern east, leg. G. Turrini, TG 2000-218 (herb. BOZ, holotype)

**GenBank** No. KM504516.

**Pileus:** 5–7 cm, (hemi-)spherical, then plano-convex, viscid, initially slightly marbled-pseudohygrophanous of a dense pattern of small, darker spots, sometimes larger hygrophanous spots/streaks near margin, margin often undulate and with a narrow, hygrophanous zone with age; sometimes slightly innately fibrillose towards margin when young; ochraceous yellow(-brown), somewhat paler towards margin and with age. Universal veil remnants sparse, but when young often with thin, silvery-micaceous-frosty remnants, especially at centre.

**Lamellae:** crowded, with entire to later often sinuate-dentate margin, initially greyish white.

**Stipe:** 4–7(–9) × 1–1.5(–2) cm, robust to sometimes slender, with an usually distinctly marginate, rather broad bulb (≈3 cm), silky-fibrillose to glossy, initially pure white, turning slightly brass-brown with age, especially when bruised. Universal veil at the bulb very sparse, white.

**Context:** white, somewhat (ochre)greyish hygrophanous-spotted (marbled) towards surface of stipe (apex). Smell distinct of honey in bulb context.

**Spores:** 7–8.5(–9) × 4–5(–5.5) µm (MV = 7.9 × 4.6 µm), Q = 1.71, ellipsoid to subamygdaloid, pale, distinctly and rather densely to more coarsely, diffusely verrucose, warts rounded and often confluent.

**Pileipellis:** duplex, cutis of gelatinous, loosely erect-entangled, hyaline hyphae at surface, subcutis/hypodermium subcellular, hyphae tightly cemented, with yellow brown to golden yellow parietal-encrusting pigment, forming an amber-like embedment. Very thick walls in corners between the cells forming brown, irregular-triangular “lenses” to more diffuse pigment lumps.

**DNA (ITS) sequence:** All 3 ITS sequences generated in this study are identical.

**Habitat:** Nemoral-colline to montane, thermophilous deciduous forests. Apparently associated mainly with *Quercus* spp., probably also with *Fagus sylvatica*, *Carpinus betulus*, *Castanea sativa* and possibly *Abies alba*, in richer, but not typically calcareous sites.

**Distribution:** Hitherto known only from a few collections from N Italy (South Tyrol; three collections, two sites). The absence from Western Europe and temperate parts of Northern Europe is remarkable: many specimens from this group have been ITS investigated from these regions, with no match on this one so far.



Photo: Gianni Turrini

**Fig. 6 – *Cortinarius frondosomultiformis* Holotype (N Italy, TG2000-218; +DNA)**



Photo: Gianni Turrini

**Fig. 7 – *Cortinarius frondosomultiformis* Holotype (N Italy, TG2000-218; +DNA)**



Photo: Tobias G. Frøslev

**Fig. 8** –*Cortinarius frondosomultiformis* (N Italy, TF 2000-086; +DNA)  
(The mossy background is not from the collecting site.)

**Collections examined:** ITALY. South Tyrol, Kaltern east, Montigglerwald near Eppan (ca. 450–470 m a.s.l.), leg. G. Turrini 22. Oct. 2000, TG 2000-218 (herb. BOZ, holotype) (DNA\*); Kaltern west, Matschatsch (route to Mendelpass), 882 m a.s.l., T. Frøslev & T. S. Jeppesen, TF 2000-086 (herb. C) (DNA\*); Matschatsch, leg. A. Cester, det. F. Bellù (as *C. talus*) 07.11.2011 (herb. BOZ 2011/71) (DNA\*).

**Comments:** *Cortinarius frondosomultiformis* is characterized by its (i) small spores, (ii) moderately pale ochraceous yellow pileus, (iii) frosty-micaceous appearance of pileus centre, (iv) robust specimens with a rather distinctly marginate bulb and (v) a distinct honey-like smell. It is furthermore the only species in sect. *Multiformes* which seems restricted to thermophilous deciduous forests (with *Quercus-Carpinus-Fagus*), possibly including *Abies alba* forests, which often can harbour frondose forest species. All three collections examined have smaller spores than related taxa, and if constant, this is an important differential character. The species is macroscopically intermediate between *C. multiformis*/*C. talimultiformis* on the one hand and *C. talus* on the other; the pileus is darker than that of *C. talus* and paler than that of *C. multiformis* and *C. talimultiformis*. The frosty-micaceous-marbled surface structure is more pronounced than in *C. multiformis* and *C. talimultiformis* but less than in *C. talus*. However, the pileus colour (and the parietal pigment of subcutis) when young comes closer to *C. multiformis* than *C. talus*, whereas the distinct smell (honey) and the habitat (*Quercus-Fagus* forests) comes closer to *C. talus*. Phylogenetically, *C. frondosomultiformis* is most similar to *C. multiformis*, with 9–10 nucleotide differences.

***Cortinarius talimultiformis*** Kytöv., Liimat., Niskanen, A.F.S. Taylor & Sesli

**Figs. 3, 5, 9**

*Persoonia*: 33 (2014).

**Type:** Sweden, A. Taylor, AT2004096, herb. UPS, holotype; S, isotype

**Syn.:** *Cortinarius aurantionapus* Bidaud & Reumaux var. *similis* Moëgne-Locc., *Atlas des Cortinaires* XVI: 1096 (2006).

**Misapplied name:** *C. multiformis* Fr. s. auct.

**Icons:** BIDAUD et al. (2006): Pl. 596 (holotype), 597 (both sub nom. *C. aurantionapus* var. *similis*).

**Pileus:** 4–10 cm, (hemi-)spherical, then plano-convex, viscid; uniformly fulvous brown to more orange brown, and slightly more red brown at centre. Universal veil sparse, but when young often whitish fibrillose towards margin, and sometimes also silvery-micaceous at centre.

**Lamellae:** crowded, initially greyish white.



Photo: Bálint Dima

**Fig. 9** –*Cortinarius talimultiformis* (Hungary, DB2831; +DNA)

**Stipe:** 4–6(–10) × 1–2 cm, usually robust, with a more or less distinctly marginate bulb (®3.5 cm), glossy-silky, white, turning slightly brass brown with age. Universal veil at the bulb sparse, sometimes more distinct, white.

**Context:** white, somewhat (ochre)greyish hygrophanous-spotted (marbled) towards surface of stipe (apex), sometimes brownish spotted in the bulb. Smell indistinct or faint of honey in the bulb when cut.

**Spores:** (8.5–)9–10 × (4.5–)5–6 µm (MV = 9.1 × 5.4 µm), Q = 1.68, (sub)amygdaloid, sometimes acutely amygdaloid, sometimes with a slight suprahilar depression, distinctly and rather densely verrucose, warts rounded and sometimes confluent.

**Pileipellis:** duplex, cutis of gelatinous, loosely erect-entangled, hyaline hyphae at surface. Subcutis/hypodermium subcellular, hyphae tightly cemented, with strong yellow brown parietal-

encrusting pigment, forming an amber-like embedment, often with thick, brown irregular-triangular «lenses» between the cells, grading into more diffuse, brown pigment-lumps.

**DNA (ITS) sequence:** All 11 ITS sequences included in our analysis (5 generated in this study) are identical. Although with a somewhat lower bootstrap value in our RAxML analysis (Figure 1), it is still well-separated phylogenetically from the other species in sect. *Multiformes*. The study of LIIMATAINEN et al. (2014) also clearly supports the separation of this species.

**Habitat:** Montane-subalpine and (more rarely) boreal (-boreonemoral) and nemoral coniferous forests. Associated with *Picea* and *Abies*, in oligotrophic to richer/calcareous sites, including young plantations. Very rarely also in mixed broad-leaf forests (with *Picea/Abies*?).

**Distribution:** Widely distributed and probably not infrequent in Central Europe, including The Black Forest region, The Prealps, the Jura and W Hungary (cfr. BIDAUD et al. 2006, as *C. aurantionapus* var. *similis*). Recorded in S Europe southeast to Turkey (LIIMATAINEN et al. 2014). Apparently rarer in N Europe (collections confirmed by ITS sequences only one from Norway, one from Sweden but several from Finland; LIIMATAINEN et al. 2014). Frequency and distribution uncertain due to confusion with the closely related *C. multiformis* s. str. and *C. rufoallutus*.

**Collections examined:** GERMANY. Baden-Württemberg: Titisee-Neustadt, 9. Sept. 2002, G. Saar (herb. TUB 011864, GenBank No. AY669532 as «*C. allutus*») (DNA\*); Schwaben, Ehingen a.d. Donau, 28. Sept. 2010, G. Schmidt-Stohn, SSt 10-188 (herb. TUB) (DNA\*). Niedersachsen: Ahlsburg, Dörrigsen, G. Schmidt-Stohn, SSt 09-040 (herb. TUB) (DNA\*). Bavaria: Bad Hindelang, Oberjoch, 25. Sept. 2007, G. Saar, SG 01722 (herb. TUB 019722) (DNA); Oberjoch, 2. Oct. 2002, G. Saar, SG 0677 (herb. TUB) (DNA). ITALY. Trentino: Tovarè Malè, val di Sole, 29. Aug. 2002, C. Rossi, det. F. Bellù (as *C. allutus*) (herb. Rossi29-08-2002; photo no. 5897) (DNA\*). South Tyrol: Pochi di Salorno, Val Fredda, 19. July 1998, G. Turrini, TG 1998-096 (herb. Turrini, as *C. allutus*; photo no. 754) (DNA). Brunico, Amaten, Montassilone, Taurerntal, 10. Aug. 1999, G. Turrini, TG 1999-246 (herb. Turrini, as *C. multiformis*; photo no. 1556) (DNA\*). HUNGARY. Vas, Felsőszölnök, L. Albert, B. Dima, DB2831 (herb. BP) (DNA\*). SWEDEN. Uppland: Hässelby near Uppsala, Andy Taylor, AT2004036 (herb. UPS, holotype; S isotype) (DNA\*). FINLAND. Kainuu: Puolanka, T. Niskanen & K. Liimatainen, TN01-057 (herb. H) (DNA). Pohjois-Häme, Virrat, Killinkoski, 30. Aug. 1966, H6032747 (herb. H), GenBank No. KF732584 (DNA\*).

**Comments:** *Cortinarius talimultiformis* is characterized by its comparatively large, rather strictly amygdaloid spores and vivid and uniformly fulvous-orange brown pileus with fine whitish-silvery fibrillose veil remnants when young. Furthermore, the stipe is initially shiny white, short and robust and usually with a distinctly marginate bulb. Until recently, *C. multiformis* has usually been treated collectively, including *C. talimultiformis* and *C. multiformis* s. str., which now are documented to be well distinguished phylogenetically. However, these are difficult and sometimes probably impossible to distinguish morphologically. The somewhat larger and strictly amygdaloid spores of *C. talimultiformis* (versus more subamygdaloid-ellipsoid in *C. multiformis*) might be the best differential character, but size and probably also shape of the spores can be overlapping. Also the robust habit, including a rather wide, more or less distinctly marginate bulb and the initially white veil remnants on pileus of *C. talimultiformis* will often be distinguishing towards *C. multiformis*. Most of these macro-features are well demonstrated in the plates 596, 597 and front cover in Atlas des Cortinaires XVI (BIDAUD et al. 2006; as *C. aurantionapus* var. *similis*) and in our photo of sequenced material (Figure 9). *Cortinarius talimultiformis* occur sometimes in *Picea* plantations in nemoral regions (cfr. Figure 9), and might in such areas possibly occur also in deciduous tree-dominated forests, and our species can then be difficult to distinguish from *C. frondosomultiformis*. The latter, however has paler, not so vivid orange-brown pileus colours, and smaller spores.

*Cortinarius talimultiformis* can also be difficult to distinguish from *C. rufoallutus*, but the latter has smaller spores, a hygrophanous-spotted pileus, with zebra-striped encrusted pigment in pileipellis and pigment that often also goes into the pileus trama, and the latter also becomes more strongly brass brown spotted on stipe and in the context.

*Cortinarius talimultiformis* is most closely related to *C. multiformis*, distinguished by 6 nucleotide differences in the ITS regions.

***Cortinarius rufoallutus*** Rob. Henry ex Bidaud & Reumaux

**Figs. 3, 5, 10, 11**

*Atlas des Cortinaires* XVII: 1095 (2006).

**Type:** France, leg. P. Moëgne-Loccoz & J. Melot, PML 635, herb. PC, holotype.

**Syn.:** *C. rufoallutus* Rob. Henry nom. inval., *Bull Soc. Mycol. Fr.* 74(3): 329–331 (1958)

*C. allutus* var. *rufescens* Rob. Henry nom. inval., *Bull Soc. Mycol. Fr.* 55(1): 66–68 (1939).

**Misapplied name:** *C. aurantiacus* M. M. Moser s. auct.

**Icons:** BIDAUD et al. (2006): Pl. 580 (holotype), Soop (2011): Fig. 22.

**Pileus:** 5–8(–10) cm, (hemi-)spherical, then plano-convex, viscid-glutinous; usually with distinct, dense, dark hygrophanous spots and sometimes more elongated streaks near margin, centre sometimes silvery-micaceous from thin veil remnants when young; rather uniformly dark and vividly fulvous brown, apricot to almost red brown.

**Lamellae:** crowded, 4–8 mm broad, initially greyish white.

**Stipe:** 5–7(–9) × 1–2 cm, with a usually distinct marginate-bulbous base (@3.5 cm); rather robust/thick-fleshed (stipe length/width ratio 3.5–5.5 cm); fibrillose, whitish, but soon turning turning strongly, spot-wise brass brown, especially when bruised, entire stipe (dark) brown with age. Universal veil near the bulb very sparse, initially whitish at bulb margin.

**Context:** whitish, with with a distinct thin, brown zone beneath pileipellis and in stipe cortex, also somewhat ochraceous grey hygrophanous-spotted (marbled) towards surface of stipe (apex). Smell none or faint of honey in bulb when bruised.



Photo: Karl Soop

**Fig. 10 – *Cortinarius rufoallutus*** (Sweden, KS CO246; +DNA)



Photo: Tor Erik Brandrud

**Fig. 11 – *Cortinarius rufoallutus*** (Norway, TEB 460-11; +DNA)

**Spores:**  $8-9.5 \times (4.5-5)5-5.5 \mu\text{m}$  ( $MV = 8.5 \times 5.1 \mu\text{m}$ ),  $Q = 1.68$ , ellipsoid to subamygdaloid, pale, weakly to distinctly and rather densely to diffusely verrucose, warts irregular to slightly confluent, rounded.

**Pileipellis:** duplex, at surface of thin, erect-entangled gelatinous,  $\pm$ hyaline hyphae. Subcutis/hypodermium subcellular, hyphae tightly cemented, with strong, yellow brown parietal-encrusting pigment, forming an amber-like embedment. Very thick walls in corners appear like brown irregular-triangular «lenses», or as more diffuse, oleiferous, brown pigments lumps. Some more narrow, long hyphae (4-8  $\mu\text{m}$  wide) also with distinct, zebra-striped, encrusted pigment (especially at surface; transition to epicutis).

**DNA (ITS) sequence:** All European ITS sequences available (5), including the holotype, are identical.

**Habitat:** Boreal (-boreonemoral) and montane-subalpine coniferous forests. Associated with *Picea abies*, mainly in oligotrophic-acid, mossy sites, sometimes in young plantations.

**Distribution:** Rare but widespread in the Nordic boreal spruce forest region (pers. obs., cfr. Soop 2011). Apparently very rare in the montane-subalpine regions of C Europe but sequenced material is documented from France (holotype) and from Italy. Distribution poorly known due to confusion with *C. multiformis* and *C. talimultiformis*.

**Collections examined:** NORWAY. Oppland: Øystre Slidre, Volbufjorden, TEB 415-13, DB-NO-38 (herb. O) (DNA\*). Øystre Slidre, Heggen church, TEB 460-11 (herb. O) (DNA\*). Øyer, Skardsmoen, M. K. Brandrud & TEB 217-11 (herb. O). Lunner, S. Oppdalen, TEB 1-89 (herb. O). Gran, Øytjernet, E. Bendiksen & TEB 74-80 (herb. O), Buhammeren, TEB 115-79 (herb. O). Gjøvik, Glæstadj., K. H. Brandrud & TEB 107-85 (herb. O). Akershus: Nannestad, Hornsjøen, TEB 211-78 (herb. O). Nordmorkorset, K. H. Brandrud & TEB 8-86 (herb. O). Oslo: Grorud, TEB 688-11 (herb. O).

SWEDEN. Dalarna, K. Soop KS-CO246 (herb. S) (DNA), KS-CO747 (herb. S) (DNA). ITALY. South Tyrol: Anterselva, leg. C. Rossi 02. Aug. 2006 (herb. Rossi02-08-2006, as *C. multiformis*) (DNA\*).

**Comments:** *Cortinarius rufoallutus* is macroscopically fairly characteristic with its robust basidiomes, warm, vivid fulvous-orange brown-red brown pileus, usually with distinct, small hygrophanous spots, and a stipe that turns vividly brass brown. A vivid ochre brown line beneath pileipellis is also characteristic. The species often co-occur with *C. multiformis*, but is much rarer. The mentioned features normally distinguish it from *C. multiformis* when specimens are young and fresh, but sometimes their colours might overlap. However, the shape of stipe hardly overlap; being more slender in *C. multiformis*, with a length/width ratio of 5.0–9.5, versus 3.5–5.5 in *C. rufoallutus*. Furthermore, *C. rufoallutus* can be separated also microscopically by presence of distinct zebra-striped encrusted hyphae in the transition between epicutis and subcutis. This feature also distinguishes it from *C. talimultiformis*, which also might be vividly apricot-red-brown, but rarely with a hygrophanous-dotted structure. The latter also often have more veil remnants on pileus. Phylogenetically, *C. rufoallutus* comes closest to *C. talimultiformis* and *C. multiformis*, but is well-distinguished from these by 18–20 nucleotide differences.

After introduced by HENRY (1939) as *C. allutus* var. *rufescens* nom. inval., this species has been little known and described. The senior author has since 1978 recognized this one and collected it as *C. multiformis* var. *rufescens*, but has doubted specific rank, due to more or less continuous morphological variation with *C. multiformis* s. str. However, most of the taxa treated as varieties by Scandinavian authors in the 1980–1990ies (cfr. BRANDRUD et al. 1990–2014) have later showed to be well-supported species phylogenetically. Nevertheless, the taxon was treated as a separate species in early versions of «*Cortinarius* in Sweden» by K. Soop under the name *C. aurantiacus*, later changed to *C. rufoallutus* (SOOP 2011). The plate illustrates well the brown-spotted basidiomes of our species. The name *C. rufoallutus*, introduced by HENRY (1958), was validated by BIDAUD et al. (2006) and the type material and plate correspond well morphologically and phylogenetically with our concept.

### ***Cortinarius melleicarneus* Kytöv., Liimat., Niskanen & Brandrud**

**Fig. 3**

*Persoonia*: 33 (2014).

**Type:** Estonia. Hiiumaa: Sarve, Soonlepa, 16 Sep 2001, I. Kytövuori 01-053, herb. H, holotype

**Icon:** LIIMATAINEN et al., *Persoonia* 33 (2014) (holotype).

**Pileus:** 4–10 cm broad, hemispherical to convex, with rather persistently incurved margins, then expanded sometimes somewhat silvery-silky from fine veil remnants, cream-coloured, pale yellow brown, honey brown to more grey brown or flesh-coloured, with hygrophanous streaks or patches/zone towards margin. Hygrophanous zone somewhat darker grey brown, almost with an olivaceous brown tinge.

**Lamellae:** crowded, first pale greyish white, later pale greyish brown.

**Stipe:** short/robust; 5–7(–9) cm long, 1.2–2 cm thick at apex, 2–3 cm wide at base, clavate or with a somewhat marginate bulb, white. Universal veil: very sparse at bulb margin, white.

**Context:** in pileus pale yellow brown, marbled hygrophanous flesh-coloured, in stipe white. Smell: not recorded.

**Spores:** (7.5–)8–8.5(–9) × (4–)4.5–5 µm, MV = 8.3 × 4.6 µm, Q = 1.81, narrowly (sub)amygdaloid, sometimes with a faint suprahilar depression, medium (to fairly strongly), densely to fairly coarsely verrucose, warts rounded and more or less confluent.

**Pileipellis:** duplex, at surface of thin, erect-entangled gelatinous, ±hyaline hyphae. Subcutis/hypoderm subcellular, hyphae tightly cemented, with pale yellowish parietal, amber-like pigment, a few (more narrow) hyphae with zebra-striped encrusted pigment occur intermixed.

**DNA/ITS sequence:** Sequences from the two, known collections are identical (cfr. LIIMATAINEN et al. 2014).

**Ecology:** With thermophilous deciduous trees (*Corylus*, *Quercus*) on calcareous ground, including near-shore sandy shell-beds (remnants of sandy soil on both collections).

**Distribution:** Known from the boreonemoral zone of S Scandinavia-Balticum (Estonia and Norway).

**Collection examined:** ESTONIA. Hiiumaa: Sarve, 16. Sept. 2001, I. Kytövuori, IK01-053 (herb. H, holotype), GenBank No. KF732577 (DNA\*). NORWAY. Aust-Agder, Grimstad, Fevik, 21. Sept. 1994, I-L. Fonneland, det. T. E. Brandrud 86-94, O 125960 (herb. O; sub nom. *C. areni-silvae*), GenBank No. AY669533 (DNA\*).

**Comments:** *Cortinarius melleicarneus* is characterized by robust, short-stiped basidiomes, honey-brown pileus with initially pale centre, and slightly smaller and narrower spores than related taxa. It is further characterized by habitat in broad-leaf forests on calcareous ground. *Cortinarius talus* resembles in pale pileus colours and habitat, but this usually has an innately fibrillose pileus structure, and rarely possess short-stemmed, compact basidiomes. No honey-smell was noted in the two collections, and the lack of this smell might be a diagnostic character towards the usually strongly honey-smelling *C. talus*. In dry conditions, this might resemble the more fibrillose *C. areni-silvae* (Brandrud) Brandrud which also occur in sandy soils, and the Norwegian collection was originally determined as *C. areni-silvae* (based on dry material and collectors notes). ITS sequences of the two *C. melleicarneus* collections are identical. It differs by 11 nucleotides from *C. talimultiformis*, 14 from *C. talus*, and 15 from *C. multiformis*.

### The *C. talus* subclade

#### *Cortinarius talus* Fr.

Figs. 12, 13-15

*Epicr. Syst. Mycol.*: 263 (1838).

**Type:** Sweden, Cortin. *Fl. Photogr.* CFP 832, herb. S; neotype designated in LIIMATAINEN et al. (2014).

**Syn.:** *C. ochropallidus* Rob. Henry, *Bull. Soc. Mycol. Fr.* 52(2): 153 (1936)

*C. melliolens* Jul. Schäffer ex P. D. Orton, *Trans. Brit. Mycol. Soc.* 43(2): 2010 (1960)

*C. ochropudorinus* Rob. Henry ex Bidaud & Reumaux, *Atlas des Cortinaires XVI*: 1097 (2006)

*C. crenulatus* Rob. Henry ex Bidaud & Reumaux, *Atlas des Cortinaires XVI*: 1097 (2006)

*C. pseudotalus* Rob. Henry ex Bidaud & Reumaux, *Atlas des Cortinaires XVI*: 1098 (2006)

*C. aurantonapus* Bidaud & Reumaux, *Atlas des Cortinaires XVI*: 1096 (2006)

*C. pudorinus* Reumaux, *Atlas des Cortinaires XVI*: 1098 (2006)

*C. pseudominor* Rob. Henry ex Reumaux, *Atlas des Cortinaires XVI*: 1098 (2006).

**Misapplied name:** *C. multiformis* Fr. sensu Moser.

**Icons:** BRANDRUD et al. (1990–2014): B 47 (CFP 835; neotype). BIDAUD et al. (2006): Pl. 601–601 (sub nom. *C. ochropudorinus*) 603, 604, 605, 608 (sub nom. *C. pseudotalus*, *C. gregis*), 609 (sub nom. *C. minor*, *C. pseudominor*), 610 (sub nom. *C. leptcephalus*), 611 (sub nom. *C. minor*), 612 (sub nom. *C. ochropallidus*).

**Pileus:** 3–9 cm broad, hemispherical to plano-convex, viscid, centre often silvery-«frosty» when young due to a thin cover of veil remnants, towards margin initially often very finely innately fibrillose-marbled or with hygrophanous spots or streaks; ochraceous yellow, sometimes almost whitish when young, sometimes almost ochraceous brown when young (if the whitish superficial hyphae are washed away).

**Lamellae:** crowded, pale greyish white when young.

**Stipe:** 4–8(–10) x 0.8–1.5 cm, with a (slightly) marginate bulb (→ 2.5 cm), glossy, whitish, then brass-brown spotted. *Universal veil*: white, sparse.

**Context:** whitish. Smell: distinctly to strongly of honey when cut.

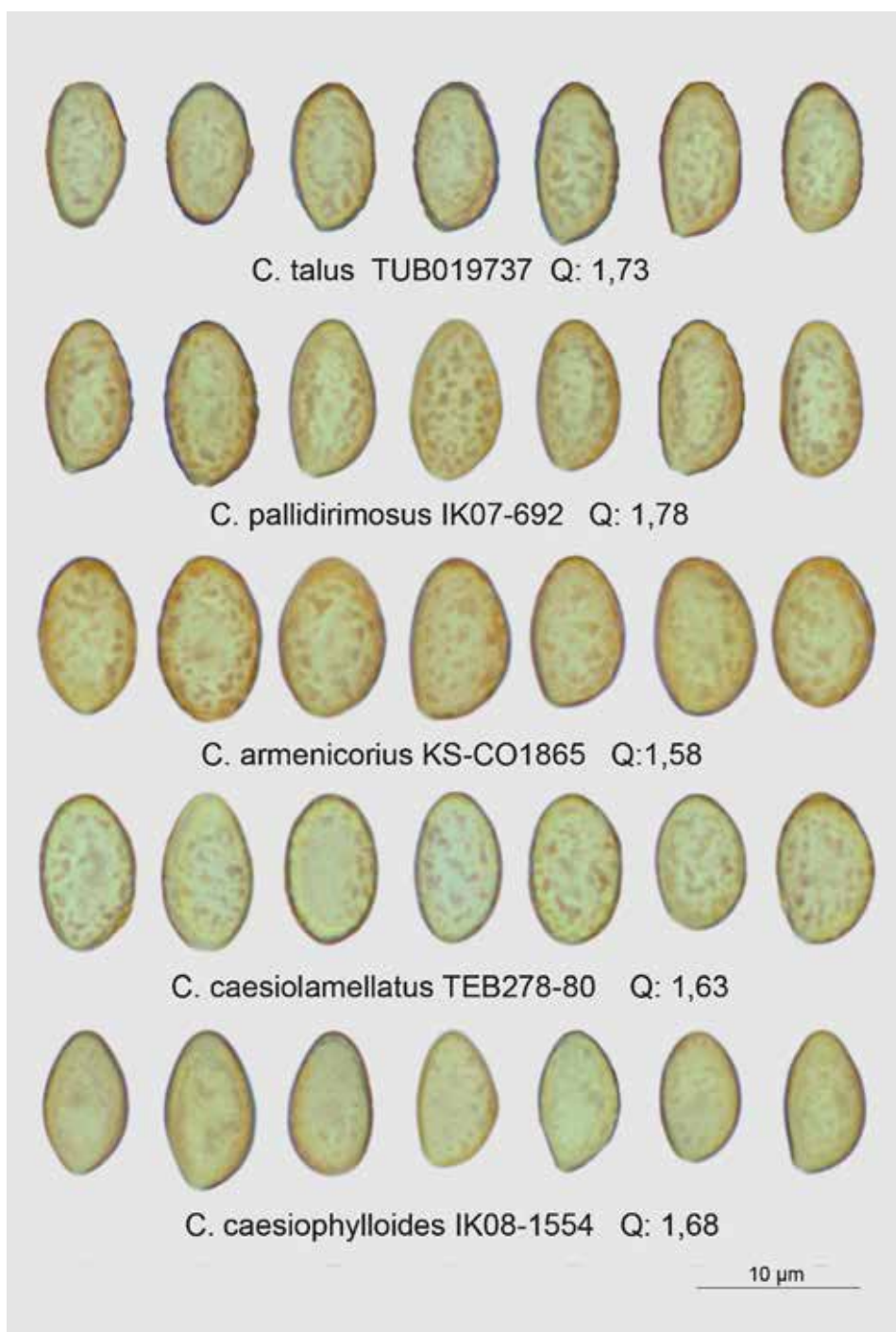


Photo: Geert Schmidt-Stohn

**Fig. 12** – Spore morphology of species in the *C. talus* and *C. pallidirimosus*-*C. caesiolamellatus* subclades. Spores 2250:1.

**Spores:** (7–)7.5–9.5 × 4.5–5.5 µm, (MV = 8.25 × 4.95 µm, Q = 1.68), amygdaloid to ellipsoid, sometimes broadly amygdaloid-ellipsoid, pale, weakly to moderately and rather densely verrucose, warts rounded and often somewhat confluent-diffuse.

**Pileipellis:** duplex, at surface of thin, erect-entangled gelatinous, ±hyaline hyphae. Subcutis/hypoderm subcellular, hyphae tightly cemented, with (very) pale yellowish parietal, amber-like pigment.

**DNA/ITS sequence:** all 11 available sequences from N and S Europe are identical, while one North American collection differs by 2 nucleotides in the ITS regions (Figure 1).

**Habitat:** in nemoral to montane/subalpine deciduous forests, sometimes also low alpine-subarctic heaths. In northern and subalpine regions of Scandinavia mainly associated with *Betula pubescens*, sometimes with *Betula nana*; elsewhere associated with *Fagus*, *Quercus*, *Carpinus*, *Corylus* and *Betula pendula*, in rich to oligotrophic forests (very rarely in calcareous sites together with calciphilous *Phlegmacium* species).

**Distribution:** Occasional to rather frequent and widespread in Europe; from northern Scandinavia to the Mediterranean Sea. Also known from Greenland (KNUDSEN & BORGES 1987; with *Betula pubescens*) and from W North America (sequenced material, cfr. Figure 1). Probably with a wide, circumpolar distribution.



Photo: Tor Erik Brandrud

**Fig. 13** – *Cortinarius talus* (Norway; from northern *Betula pubescens* forest; TEB 184-78)

**Collections examined:** NORWAY. Oppland: Vågå, Gjende, TEB 184-78, 105-80 (herb. O). Hedmark: Åmot, Osdammen, R. Halvorsen & E. Bendiksen 528-80 (herb. O). Buskerud: Hol, Vikastølen, TEB 174-79 (herb. O). Vestfold: Tønsberg, Slagentangen, TEB 86-82 (herb. O). Østfold: Råde, Kajalunden, Ø. Weholt & TEB 610-80 (herb. O). Hvaler, Vesterøya, TEB 440-81 (herb. O). SWEDEN. Jämtland: Ragunda, Cortinarius Flora Photographica, CFP 832 (TEB 21-93) (neotype, herb. S) (DNA\*). Undersåker, Välliste, TEB 85-83 (herb. O). Medelpad: Borgsjö, SSt

10-033 (DNA\*), TEB 139-10 (DNA\*), TEB 140-10 (SSt 10-038) (DNA\*). Dalarna: Gesunda, near Mora, 11. Sept. 2007, G. Saar, T. E. Brandrud (herb. TUB) (DNA). Ångermanland: CFP 81, CFP 322 (to herb. S). Norrbotten: Gällivare, K. Høiland & TEB 159-81 (herb. O). Kiruna, K. Høiland & TEB 191-81 (herb. O). Småland: Femsjö, M. Moser & TEB 140-79 (herb. O). Scania: Degerberga, TEB 99-88 (herb. O). Ivö, TEB 312-87 (herb. O). DENMARK. Sealand: TF 1999-035 (herb. C) (DNA\*). GERMANY. Baden-Württemberg: Tübingen, 16. Oct. 2001, G. Saar, SG 0613 (herb. TUB 19713) (DNA). Saarland: Schmelz, 30. Sept. 2001, T. Münzmay, TM H.32.01 (herb. TUB 011877) (DNA). Thüringen: Schellroda, 12. Oct. 2009, leg. Felix Hampe FHC010 (DNA). AUSTRIA. Burgenland: St. Margarethen, 2. Oct. 2003, G. Saar (herb. TUB 19737) (DNA). FRANCE. Rhone-Alps: Ain, Ordonnaz, TEB 51-91 (herb. O).

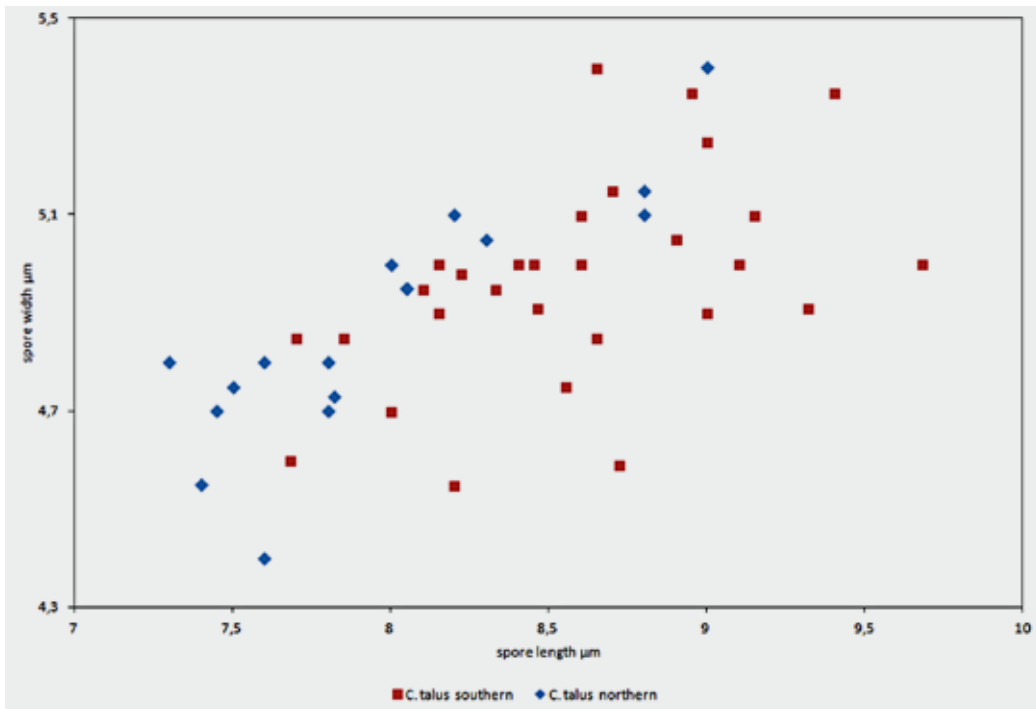


Photo: Geert Schmidt-Stohn

**Fig. 14** – *Cortinarius talus* (Sweden; from northern *Betula pubescens* forest; SSt10-033; specimens with dark pileus, illustrating the large, infraspecific variation; +DNA)

**Comments:** *Cortinarius talus* is characterized by the pale, marbled-silvery-frosty-innately fibrillose pileus, usually strongly honey-like smell and a stipe with rather distinct marginate bulb. The marbled-frosty appearance of pileus centre when young resembles that of *Cortinarius (Rozites) caperatus*, the innately fibrillose structure towards margin reminds of e.g. *C. riederi*. The species is distinguished from *C. multiformis* by the paler, innately fibrillose pileus, the stronger honey smell and the habitat in deciduous forest. *Cortinarius frondosomultiformis*, also occurring in (thermophilous) deciduous forests might be more difficult to distinguish; it often possess a marbled-frosty pileus centre, but rarely an innately fibrillose margin. Furthermore, the colour beneath the pale, «frosty» surface hyphae is initially darker yellow brown in *C. frondosomultiformis* than in *C. talus*. *Cortinarius talus* is further distinguished from the northern *C. pallidirimosus* by the more robust basidiomes with a more marginate bulb. The *C. talus* populations of northern *Betula*

*pubescens* forests have also distinctly smaller and more broadly ellipsoid spores ( $7\text{--}9 \times 4.5\text{--}5.5\ \mu\text{m}$ ) than those of *C. pallidirimosus* ( $9\text{--}10 \times 5.5\text{--}6\ \mu\text{m}$ ) (see below).



Scatter diagram: Geert Schmidt-Stohn

**Fig. 15** – Variation in spore size of *C. talus*. Each symbol = MV of spore measures per basidiome.

Northern = middle/northern boreal (subalpine) *Betula pubescens* populations.

Southern = more southern *Fagus-Quercus-Carpinus-Corylus-Betula pendula* populations.

The spore size and shape of *C. talus* shows a larger variation than normally seen in sect. *Multiformes*. Whereas species such as *C. multiformis* and *C. rufoallutus* has spores with mean values ranging from approx.  $8\text{--}9.5 \times 4.75\text{--}5.75\ \mu\text{m}$ , the *C. talus* mean values ranges from  $7.25\text{--}9.7 \times 4.4\text{--}5.4\ \mu\text{m}$  (Figure 15). The populations of northern Fennoscandia, from northern/middle boreal *Betula pubescens* forests (or mixed birch-spruce forests) normally possess small and rather broad spores, with average values ranging from  $7.25\text{--}8.75 \times 4.5\text{--}5.25\ \mu\text{m}$  (MV =  $7.9 \times 4.9\ \mu\text{m}$ ,  $Q = 1.63$ ), whereas the populations of southern boreal-boreonemoral-nemoral-montane *Betula pendula-Fagus-Quercus-Carpinus* forests normally have larger and more narrow spores with average values of  $8\text{--}9.5 \times 4.5\text{--}5.25\ \mu\text{m}$  (MV =  $8.6 \times 5.0\ \mu\text{m}$ ,  $Q = 1.73$ ). These populations have identical ITS sequences, but this ecogeographically correlated spore variation might yet reflect some population genetic differentiation, and these variants should be investigated by population genetic methods (e.g. using RAD sequencing, DAVEY & BLAXTER 2010). Furthermore, this spore size differentiation should be better documented by more samples and more measurements. For instance, it seems that some southern *Fagus-Quercus* associated *C. talus* populations included in BIDAUD et al. (2006) possess small and wide spores, especially the *C. ochropudorinus* and *C. pseudominor* variants (with spores  $6.5\text{--}8 \times (4\text{--})4.5\text{--}5\ \mu\text{m}$ ). Conclusively, for the time being, we have decided not give these spore variants any taxonomic rank.

*Cortinarius talus* can be rather variable also in macrocharacters such as size and in pileus col-

our; for instance in dry weather the whitish, superficial (veil) hyphae may be more pronounced than when exposed to moist weather (compare Figure 13 versus 14). These features certainly reflect only a habitat-based, phenotypic variation, and are not correlated with genetics or geographical patterns. Based on this variation, *C. talus* has been splitted in many species, but according to the morphological variation seen, as well as phylogenetic studies of a number of type specimens (see LIIMATAINEN et al. 2014), we conclude that e.g. at least 9 of the species presented in BIDAUD et al. (2006) are within the variation spectrum of our polymorphous *C. talus*. The following new taxa introduced in BIDAUD et al. (2006) are furthermore identical in ITS sequences with *C. talus*, and is here regarded as synonyms: *C. aurantionapus*, *C. ochropudorinus*, *C. crenulatus*, *C. pudorinus*, *C. pseudotalus* and *C. pseudominor* (cfr. Figure 1).

### The *C. pallidirimosus*–*C. caesiolamellatus* subclade

***Cortinarius pallidirimosus*** Kytöv., Liimat. & Niskanen

Fig. 12

*Persoonia*: 33 (2014).

**Type**: Finland, I. Kytövuori 95-585, H6035694 (herb. H, holotype; NY, isotype).

**Icon**: LIIMATAINEN et al., *Persoonia* 33 (2014) (holotype).

**Pileus**: 3–9 cm broad, hemispherical to plano-convex, viscid, very finely innately fibrillose-marbled or with hygrophanous streaks; whitish to cream-coloured, centre ochraceous yellow, becoming more ochraceous brown with age.

**Lamellae**: crowded, pale greyish white when young, later pale brown.

**Stipe**: 6–10(–13) × 0.7–1.5 cm, with a clavate to faintly marginate bulb (→ 2.5 cm), whitish, then very pale brownish. Universal veil: white, sparse. Context: white. Smell: of honey when cut.

**Spores**: 9–10(–10.5) × 5–6 µm, (MV = 9.6 × 5.6 µm, Q = 1.72), (sub)amygdaloid, rarely more ellipsoid, medium strongly and rather densely verrucose, warts rounded and sometimes coalescent.

**Pileipellis**: Epicutis with a gelatinous layer of 1.5–3 µm wide, smooth, colourless hyphae. Hypoderm well-developed, subcellular, with very pale yellowish parietal, amber-like pigment, or almost colourless.

**DNA/ITS sequence**: The *C. pallidirimosus* complex shows a comparative large sequence variation. Two sequences, both from Finland (including type material) are identical. Two sequences are slightly deviating (3 nucleotide differences from the type), whereas one sequence is more different (6 nucleotide differences (cfr. Figure 1).

**Habitat**: Middle to northern boreal, in rich to oligotrophic mixed forests with *Betula pubescens* and *Picea abies* or *Pinus sylvestris*. Probably associated with *Betula*.

**Distribution**: So far known from a number of localities in C/N Finland, a couple in C/N Sweden and one station from N Norway (LIIMATAINEN et al. 2014).

**Collections examined**: FINLAND. Kainuu: Puolanka, Väyrylä, Körölä, 15. Sept. 1997, I. Kytövuori, IK97-1523, H6035715 (herb. H) (DNA); Perä-Pohjanmaa: Tervola, Louepalo, 23. Aug. 2007, I. Kytövuori, IK07-692, H6000925 (herb. H) (DNA\*). Inari Lappi: Utsjoki, Kevo, Tsieskula, I. Kytövuori, IK95-540, (herb. H) (DNA).

**Comments**: The species is not seen fresh by the authors, and the description of macrocharacters is based on LIIMATAINEN et al. (2014). *Cortinarius pallidirimosus* is characterized by the (very) pale, innately fibrillose pileus, an almost non-marginate bulb and comparatively large spores. The slender habit and pale pileus makes it look somewhat like a *C. pinophilus*, which, however, almost lacks a gelatinous pileus surface, turns yellowish and is not genetically related. With its pale,

marbled-innately fibrillose pileus, distinct honey-smell and habitat in (mixed) *Betula pubescens* forests, the species resembles *C. talus*. The latter, however is distinguished on (i) the more robust basidiomes with a more marginate bulb, a finer and often more distinct innately fibrillose-marbled structure of of pileus surface, and smaller spores. The *C. talus* populations found in northern Fennoscandian birch-spruce forests where *C. pallidirimosus* occur, have distinctly smaller and more ellipsoid spores ( $7\text{--}9 \times 4.5\text{--}5.5 \mu\text{m}$ ) than those of *C. pallidirimosus* ( $9\text{--}10 \times 5\text{--}6 \mu\text{m}$ ). When mean values per collection is considered, there is hardly any overlap in spore size variation between *C. pallidirimosus* and the northern *Betula C. talus* populations.

Phylogenetically, *C. armenicorius* is the closest sister species to *C. pallidirimosus*. It has 8 nucleotide differences in the ITS regions from the type of *C. pallidirimosus*, but due to some internal, genetic variation in the latter, the barcoding gap between these two are not large. *Cortinarius armenicorius* differs from the latter in a more vividly ochre yellow (-apricot) pileus colour, a more robust habit and a distinctly marginate bulb with rather thick veil remnants. *Cortinarius pallidirimosus* is also rather closely related to *C. caesiophylloides* (distinguished by 17 nucleotide differences), but this is easily recognized on bluish tinges on the lamellae and at stipe apex.

*Cortinarius pallidirimosus* shows a comparatively large ITS sequence variation; two collections have 3 ITS sequence differences, and one collection shows 6 sequence differences (Figure 1). The former appears to be (micro)morphologically and ecologically quite similar to the type of *C. pallidirimosus*, and this ITS variation is thus so far regarded as infraspecific. The latter might represent a separate taxon, but is not treated further due to limited knowledge on morphology.

*Cortinarius pallidirimosus* is apparently a northern species in Europe, so far found only in N/C Finland, N Sweden and N Norway. According to LIIMATAINEN et al. (2014), it is associated with *Betula* (*B. pubescens*). However, all finds referred by these authors are from mixed forests including conifers, and an association with conifers cannot be ruled out. It seems anyhow that *Betula* is the primary associate. Some finds are e.g. from dry, mixed birch-pine forests, and *Pinus* is a very rare associate among the *Multiformes*, and it seems most likely that the species here is associated with *Betula*.

***Cortinarius armenicorius* Soop & Brandrud, sp. nov.**

**Figs. 12, 16**

**Mycobank** No. MB809871

**Etymology:** from Latin *armeniacum* and *corium*, «apricot peel», due to the appearance and colour of the pileus.

**Typus:** France, Jura, Prénovel, in *Picea* forest, 6 Oct. 2008, leg. K. Soop, KS-CO1865 (herb. S (F251131), holotype).

**GenBank** No. KM504515.

**Pileus:** 2.5–4.5 cm, (hemi-)spherical, then plano-convex, viscid, not hygrophanous, glabrous; rather uniformly warmly apricot yellow to ochraceous yellow, becoming somewhat paler ochraceous yellow with age. Universal veil remnants rather prominent, leaving white, fibrillose patches towards margin.

**Lamellae:** L = 60–70, rather crowded, 3–5 mm broad, initially greyish white, soon pale brown.

**Stipe:** 3–4.5 × 0.8–1 cm, rather robust, with a rather distinctly (to faintly) marginate bulb (®2 cm), dry; white without any shade of blue, remaining whitish with only weak brownish spots where bruised. Universal veil white, forming a sheath around the bulb, fairly copious; cortina white.

**Context:** white, somewhat (ochre)greyish hygrophanous-spotted (marbled) towards surface of stipe (apex). Smell strong of honey, especially when cut.

**Spores:**  $9\text{--}10 \times 5.5\text{--}6.5 \mu\text{m}$ ,  $MV = 9.5 \times 6.1 \mu\text{m}$ ,  $Q = 1.58$ , (broadly) ellipsoid to subamygdaloid, medium strongly to rather strongly and rather coarsely verrucose, warts rounded and confluent.

**Pileipellis:** duplex, cutis thin, surface hyphae gelatinous, loosely erect-entangled, hyaline. Subcutis/hypodermium hyphae tightly cemented, with rather strong, yellow brown parietal-encrusting pigment, forming an amber-like embedment. Very thick walls between the cells in corners form distinct, irregular-triangular, brown pigment «lenses», grading into more diffuse, intracellular pigment lumps. Long and narrow transition hyphae between subcutis and epicutis with yellow walls (no zebra-striped encrustation observed).



Photo: Karl Soop

**Fig. 16 – *Cortinarius armenicorius*** Holotype (E France, KS CO1865; +DNA)

**DNA (ITS) sequence:** The two ITS sequences available have one nucleotide difference.

**Habitat and distribution:** So far known from France (Jura) and Russia (Sakha republic, Siberia). In Siberia reported from *Larix gmelinii* forest with *Betula platyphylla*, in the Frence Jura from *Picea abies* forest.

**Collections examined:** FRANCE: Jura, Prénovel, in *Picea* forest, 6. Oct. 2008, K. Soop, KS-CO1865 (F251131) (herb. S, holotype) (DNA\*). RUSSIA: Sakha republic, Khangalassky Ulus, Myachei-Sise Mountains, *Larix gmelinii* forest with *Betula platyphylla*, 8. Aug. 1999, U. Peintner IB19990590 (herb. IB), GenBank No. AF325586, UNITE No. UDB001073 (DNA\*).

**Comments:** *Cortinarius armenicorius* is characterized by its comparatively large, more or less ellipsoid spores, vivid ochre yellow-apricot yellow pileus colours, the comparatively thick veil remnants at bulb and pileus margin, and the distinct/strong honey smell. Phylogenetically, this taxon comes closest to *C. pallidirimosus*. The two collections of *C. armenicorius* possess only 8

nucleotide differences in ITS regions from the holotype of *C. pallidirimosus*, however, morphologically, these sister taxa are easily distinguished, *C. pallidirimosus* being more slender-clavate, and with a much paler, innately fibrillose pileus without white veil patches at margin. According to available material, *C. armenicorius* is morphologically much more similar to *C. talimultiformis* and *C. multiformis*, but seems to be (i) smaller, (ii) less (pseudo)hygrophanous, (iv) having a thicker veil, and (v) a stronger honey odour than those taxa. Furthermore, the spores of *C. armenicorius* are larger and more strongly ornamented than those of *C. multiformis*, and are more (broadly) ellipsoid than those of *C. talimultiformis*.

With one collection from the very little surveyed Eastern Siberia, one might expect this to be a primarily northeastern Eurasian species. However, the find from French Jura shows that this is distributed not only in the northern boreal taiga belt, but also in the coniferous forest belt of the Jura-Prealps. The collection from the French Jura indicates that this is a coniferous forest species with an association with *Picea abies*. The collection from the larch-dominated taiga forest of E Siberia indicate an association with *Larix gmelinii*. As association with *Larix* spp. is hitherto not documented for *Multiformes* species. However, also the East Asian *Betula platyphylla* was present at the Siberian site, and an association with northern-eastern *Betula* species cannot be ruled out. The sister taxon *C. pallidirimosus* is apparently mainly associated with northern *Betula*.

***Cortinarius caesiolamellatus*** (Bidaud) Kytöv., Liimat., Niskanen, Brandrud, Frøslev & A.F. Taylor

**Figs. 12, 17, 18**

**Type:** France., P. Moëgne-Loccoz 3. Oct. 1993, PML4905, herb. PC, holotype.

**Syn.:** *Cortinarius rufoallutus* var. *caesiolamellatus* Bidaud, Atlas des Cortinaires XVI: 1095 (2006).

*Cortinarius multiformis* var. *caesiophyllus* Moëgne-Locc., Atlas des Cortinaires XVI: 1095 (2006). Type: France, P. Moëgne-Loccoz 3. June 1988, PML882, herb. PC, holotype.

**Icons:** BIDAUD et al. (2006): pl. 581 (sub nom. *C. rufoallutus* v. *caesiolamellatus*), 587 (sub nom. *C. multiformis* var. *caesiophyllus*). SOOP (2011): fig. 21 (sub nom. *C. multiformis* var. *cyanoallutus* ined.). ?KRIEGLSTEINER & GMINDER (2010): p. 81 (sub nom. *C. allutus*).

**Pileus:** 4–8 cm, (hemi)spherical, then plano-convex, sometimes radially rugulose towards margin, viscid, red brown to bluish ochraceous brown, becoming paler ochraceous brown with age; often bicoloured, outer part hygrophanous and darker (grey) brown.

**Lamellae:** crowded, edge even to crenulated; 4–7 mm broad, initially pale grey with a bluish tinge, later pale brown.

**Stipe:** 4.5–8 (–11) × 1–1.7 cm, with a more or less distinct marginate bulb (→3.5 cm), fibrillose (not glossy like *C. multiformis*), whitish, but usually with a bluish tint at apex when (very) young, often becoming pale brown with age. Universal veil: white, sparse, sometimes viscid (at bulb margin).

**Context:** in the pileus whitish, brownish below the cuticle, in the stipe apex with a bluish tint when (very) young. Smell: distinct of honey when cut, especially in the bulb.

**Spores:** 8–9(–9.5) × 5–6 µm, MV = 8.6 × 5.3, Q = 1.64, ellipsoid(–ovoid) to more (sub)amygdaloid, sometimes broadly ellipsoid, medium strongly (to strongly) verrucose, warts small/dense to rather coarse and rounded, often somewhat confluent.

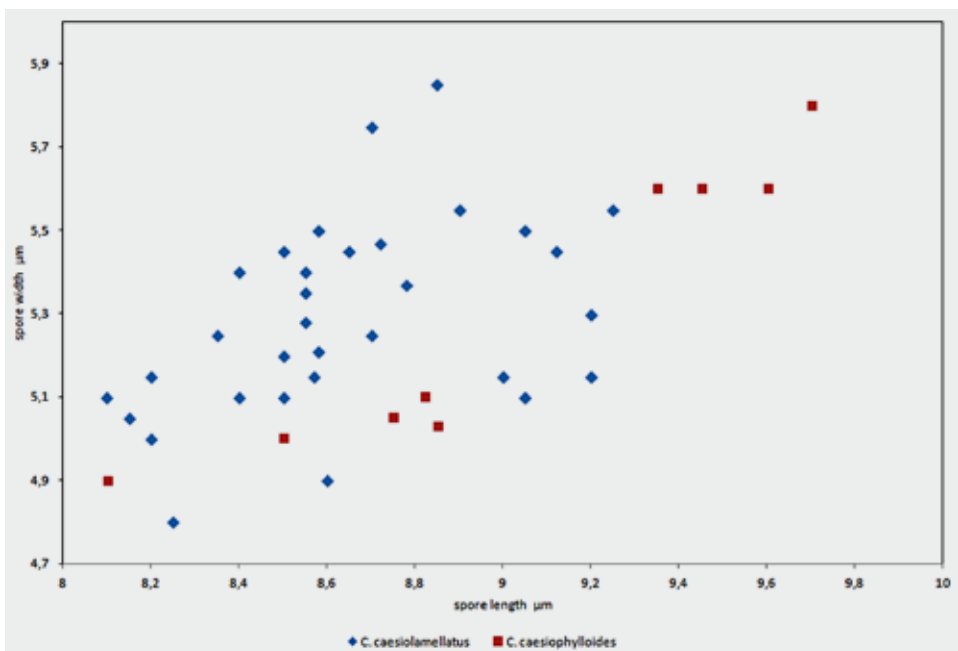
**Pileipellis:** duplex, cutis thin, at surface of 2–3 µm wide, gelatinous, erect-entangled, hyaline hyphae. Subcutis/hypoderm tightly cemented, subcellular, with yellow brown-golden yellow parietal pigment, forming an amber-like embedment, some small brown, oleiferous spots present, and a few, more narrow zebra-striped, encrusted hyphae.

**DNA/ITS sequence:** Eight of the 9 analysed sequences (including 5 generated here) are identical, only 1 differs by 1 nucleotide from the others.



Photo: Tor Erik Brandrud

**Fig. 17** – *Cortinarius caesiolamellatus* (Germany, TEB 428-10; +DNA)



Scatter diagram: Geert Schmidt-Stohn

**Fig. 18** – Variation in spore size of *C. caesiolamellatus* and *C. caesiophylloides*.  
Each symbol = MV of spores measured per basidiome.

**Ecology:** In boreal-boreonemoral, montane and subalpine coniferous forests, often on rich, sometimes calcareous ground. In Europe apparently mainly/only under *Picea*, but in U.S.A. also found under *Pinus*.

**Distribution:** Known mainly from C Europe and from S Fennoscandia, with a few outposts in SW Europe and N Fennoscandia. Widespread, but more precise distribution is uncertain due to confusion with *C. caesiophylloides* and *C. multiformis*. Also recorded from Washington, U.S.A.

**Collections examined:** GERMANY. Baden-Württemberg, Schwaben, Ehingen a.d. Donau, Kohlhaus, 28. Sept. 2010, G. Schmidt-Stohn, T. E. Brandrud, TEB 428-10 (herb. O) (DNA\*); Kohlhaus, 28. Sept. 2010, G. Turrini (herb. Turrini) (DNA); Bockinhofer Holz, leg. K. Soop, KS-CO1938, (herb. S) (DNA). Bavaria: Bad Hindelang, Oberjoch, 4. Oct. 2003, S. Garnica SG 0828 (herb. TUB) (DNA). Saarland: Schmelz, Hüttersdorf, 31. Oct. 2004, K. Montag (herb. TUB) (DNA). Thüringen: Thölendorf, 11.10.98, U. Luhmann UL 98/122 (herb. TUB 011841), GenBank No. AY669531 (as "*C. allutus*") (DNA\*). FRANCE. Hérault: Bedarieux, TEB 223-83, 242-83 (herb. O). ITALY. Trento, Santa Colomba, TEB 315-82 (herb. O). NORWAY. Oslo: Grorud, Steinbruvannet, 4 Sept. 2011, TEB 687-11 (herb. O) (DNA\*). Vestfold, Tønsberg, TEB 278-80 (DNA\*). Sogn & Fjordane: Lærdal, TEB 213-12 (herb. O) (DNA\*). Oppland: Gran, Buhammeren, TEB 116-79 (herb. O). Lunner, Rustad, TEB 478-80 (herb. O). Lunner, S. Oppdalen, E. Bendiksen 10. Sept. 1978, TEB 72-88 (herb. O). Buskerud, Notodden, TEB 129-11 (herb. O). Hedmark: Ringsaker, Brumunddal, TEB 171-80 (herb. O). FINLAND. Uusimaa, Espoo, Kunnarla, I. Kytövuori, IK94-852 (herb. H) (DNA). Perä-Pohjanmaa, Tervola, Peura, XXI Nordic Myc. Congr., 5. Sept. 2013, H. Lindström, E. Bendiksen, det. I. Kytövuori (herb. O; H). U.S.A. Washington, Olympic peninsula, Ocean Shore Park, 11. Nov. 2009, J. Ammirati & T. Niskanen, TN09-201 (herb. H), GenBank No. KF732571 (DNA\*).

**Comments:** *Cortinarius caesiolamellatus* and *C. caesiophylloides* are easily distinguished from related taxa in *Multiformes* by their initially bluish tinged lamellae and stipe apex. Based on material seen so far and available descriptions, these two blue-gilled taxa appear to be difficult to distinguish macromorphologically, but *C. caesiolamellatus* seems to have warmer, more redbrownish pileus colours, a more pronounced bicoloured pileus with a dark, hygrophanous outer part, and furthermore they differ in spore characters: *C. caesiolamellatus* has more ellipsoid, wider and more strongly verrucose spores. Finally, there seems to be a geographical differentiation in Europe; *C. caesiolamellatus* apparently being mainly a C. European taxon including southern parts of N Europe, whereas *C. caesiophylloides* is hitherto found only in Northern Europe. However, these taxa seem to be overlapping in morphological variation, and probably cannot always be identified on morphological features. When all evidence is taken together (phylogenetically distinct, with <99% similarity + some morphological differentiation), it seems nevertheless reasonable to treat these as two species. More studies may reveal that these are possible to distinguish and recognize by macro/micromorphological characters.

If the bluish tints have faded, *C. caesiolamellatus* can also be mixed with the conifer associated *C. rufoallutus*, *C. multiformis* and *C. talimultiformis*. The latter three, however, have less strongly ornamented spores and possess yellow brown, oleiferous pigment lumps and (*C. rufoallutus*) zebra-striped encrusted pigment in the hypodermium.

*Cortinarius caesiolamellatus* is phylogenetically close to *C. caesiophylloides*, *C. pallidimosus* and *C. armenicorius*, forming one of the two major subclades of sect. *Multiformes*. The species was described in BIDAUD et al. (2006) both as *C. rufoallutus* var. *caesiolamellatus* and *C. multiformis* var. *caesiophyllus*, and their types conform 100% phylogenetically with our species (Figure 1, cfr. LIIMATAINEN et al. 2014). Bluish variants probably referable to this taxon are otherwise mentioned by SCHÄFFER (1949, sub nom. *C. melliolens* var. *violascens* ad. int.) and by KRIEGLSTEINER & GMINDER (2010, sub nom. *C. allutus* p.p.).

*Cortinarius multiformis* variants with bluish lamellae and a distinct honey smell were distinguished

by the senior author as a separate taxon already in the late 1970ies, with the working name *C. cyanoallutus* (= *C. caesiolamellatus*). However, due to limited material and the complex variation in the *C. multiformis* complex, with only little micromorphological differences, this was never validly published (but introduced in SOOP 2011 as *C. multiformis* var. *cyanoallutus* ined.). Bluish carpophores were not mentioned by MOSER (1961), but he found that mycelium cultures of *C. allutus* could develop bluish colours. When later discussing the matter with M. Moser, he was of the opinion that presence/absence of bluish pigments were not taxonomic relevant in the *C. multiformis*-*C. allutus* group. Then much later, bluish variants was first formally published as *C. rufoallutus* var. *caesiolamellatus* (= *C. multiformis* var. *caesiophyllus*) by BIDAUD et al. (2006), both covering the present *C. caesiolamellatus*.

***Cortinarius caesiophylloides*** Kytöv., Liimat., Niskanen, Brandrud & Frøslev **Figs. 12, 18-20**

*Persoonia* 33 (2014).

**Type:** Finland. T. Niskanen 05-016, H6029792 (H, holotype).

**Icon:** LIIMATAINEN et al., *Persoonia* 33 (2014).

**Pileus:** 4–8 cm broad, (hemi)spherical to plano-convex, viscid, centre with a dense pattern of small, darker, hygrophanous spots (pseudohygrophanous), towards margin with more elongated hygrophanous streaks/veins, or hygrophanous (water soaked) in outer zone; ochraceous brown to more clay brown, possibly also more fulvous brown, hygrophanous part somewhat darker umber to less vivid (grey) brown, becoming pale ochraceous brown-ochraceous yellow with age, even whitish ochre at centre.

**Lamellae:** L = 60–80, crowded, edge even to crenulated; 4–7 mm broad; initially pale grey with a bluish tinge, later pale brown.

**Stipe:** 5–11 cm long, 1–1.5 cm, with a more or less distinct marginate bulb (→3.5 cm), fibrillose (not glossy like *C. multiformis*); whitish but usually, with a bluish tint at apex when (very) young, often becoming pale brown with age. *Universal veil:* white, sparse, sometimes viscid (at bulb margin).

**Context:** white, brownish below the cuticle; slightly bluish at the apex of the stipe when (very) young. *Smell:* distinct of honey when cut, especially in the bulb.

**Spores:** 8.5–9.5(–10) × (4.5–)5–6 μm, (MV = 9.0 × 5.3 μm) Q = 1.70, (sub)amygdaloid, sometimes acutely amygdaloid, pale, weakly (to moderately) verrucose, warts dense, and often rounded-confluent.

**Pileipellis:** duplex, epicutis with a gelatinous layer with sparse, erect-entangled, 2–3 μm wide, smooth, hyaline hyphae. Hypoderm present, of fairly thin-walled elements, with pale yellowish brown amber-like parietal pigment, some hyphae with yellow brown zebra-striped encrustations present, large yellow brown pigment lumps absent.

**DNA (ITS) sequence:** All 6 ITS sequences available (including 3 analysed in the present study) are identical.

**Habitat:** Boreal coniferous forests, associated mainly or only with *Picea abies* (one Finnish collection from dry *Pinus* forest apparently without *Picea*; LIIMATAINEN et al. 2014). Mainly in richer low-herb types, sometimes on calcareous ground, once found in a rich sandy pine-spruce forest (TEB 720-13/DB-NO-181).

**Distribution:** So far known only from Fennoscandia, with a core area probably in some north-eastern regions (such as Trøndelag, Jämtland and N/C Finland); rare (known from seven localities).

**Collections examined:** NORWAY. Nord-Trøndelag: Stjørdal, Beistadvollen, 13 Aug 2009, TEB 277-09 (herb. O) (DNA\*). Buskerud: Ringerike, Eggemoen northeast, TEB 720-13, DB-NO-181 (herb. O) (DNA\*). Oppland: Lunner, TF 2006-112 (herb. C), GenBank No. KF732575 (DNA\*). SWEDEN. Jämtland, Bräcke, Bodsjö, Sidsjö, I. Kytövuori 97-697 (herb. H) (DNA).

FINLAND. Kainuu: Paltamo, Oikarilankylä, Kivesvaara, I. Kytövuori, IK08-1554, H6032621 (herb. H), GenBank No. KF732574 (DNA\*).



Photo: Tor Erik Brandrud

**Fig. 19** – *Cortinarius caesiophylloides* Norway, TEB 277-09; +DNA)



Photo: Tor Erik Brandrud

**Fig. 20** – *Cortinarius caesiophylloides* Norway, TEB 277-09; +DNA)

**Comments:** *Cortinarius caesiophylloides* is characterized by bluish tinges on the lamellae and stipe apex when (very) young, and a distinct honey smell in (bulb) context. However, these features the species share with *C. caesiolamellatus*, and these taxa may not always be possible to distinguish morphologically. The spore shape and ornamentation stand out as the best differential character(s): *C. caesiophylloides* has more strictly amygdaloid, somewhat narrower spores with usually dense and pale ornaments, whereas the spores of *C. caesiolamellatus* usually are more (broadly) ellipsoid, and with stronger and coarser/more confluent warts. Furthermore, the latter has a more vivid/warmer red brownish pileus colour, and a dark, hygrophanous outer zone. Phylogenetically, these are well-supported units, distinguished by 25 nucleotide differences in ITS regions. *Cortinarius caesiophylloides* is in fact phylogenetically closer to *C. pallidirimosus* (17 nucleotide differences) than to *C. caesiolamellatus* (Fig. 1, 2).

These two taxa are also differentiated geographically; *C. caesiophylloides* appears to be a more northern species, hitherto only found in the boreal zone of Fennoscandia, and mainly in the northeastern taiga regions, whereas *C. caesiolamellatus* is more southern, with most finds from S Fennoscandia and montane C and S Europe. Their habitat preferences seem alike; they both occur mainly in richer *Picea* forests. With (i) distinct phylogenetical differentiation (<99% similarity), (ii) a geographical differentiation, and (iii) some morphological differentiation especially the spore shape, these qualify to the rank of species. Few collections have been studied fresh of these, and more material could throw light on some more possible macromorphological differences.

The presence of two bluish European Multiformes taxa did not become apparent before extensive ITS sequencing of the group was performed, and this was published as *C. caesiophylloides* this year by LIIMATAINEN et al. (2014). Without the aid of molecular methods, this rare *C. caesiolamellatus* look-a-like would probably not have been discovered. The bluish tinges on *C. caesiolamellatus* and *C. caesiophylloides* soon fade with exposure and age. When bluish tints are absent they can be mixed with *C. multiformis* and *C. talimultiformis* (see comments under *C. caesiolamellatus*).

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