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Phylogenetic relationships in Cortinarius with focus on North European species

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Cortinarius is an ectomycorrhizal Agaricales genus with high diversity of which rDNA sequences of 86 species together with four outgroup taxa were investigated phylogenetically by aid of Maximum Likelihood and Bayesian analyses. The *Cortinarius* data set represents 81 taxa from the Northern Hemisphere showing the main variation spectrum among the species. In addition, five species from the Southern Hemisphere are included. The phylogenetic tree of *Cortinarius* gives statistical support to twelve monophyletic groups in the upper level. They are discussed in context of morphology, chemistry (secondary compounds), and ecology. The phylogenetic tree lacks, however, satisfactory support for its backbone. Several species could not be included in any group, especially those forming the basal framework of the tree. Of special interest is a "superclade" comprising eight of our monophyletic clades and two singletons. Here we find the majority of species with soluble pigments of octaketide origin, all species with compounds of nonaketide origin, the majority of species with hygrophaneous pileus, few species with viscid pileus, and no species with bulbous stipe base. Moreover, all species except one have duplex pileus cuticle. The morphological traits are not indicative for any clade, although some are more frequent in some clades than others. During the evolution they have been gained and lost several times. The chemical characteristics are – to a certain degree – more indicative for the clades. The evolution and ecological role of these compounds are discussed. Concerning the North European species, there are ecological differences between the clades, especially between clades specializing to rich or calcareous forests and clades specializing to poor forests or arctic-alpine environments.

Key words: *Cortinarius*, phylogeny, morphology, secondary compounds, ecology

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Introduction

Cortinarius (Pers.) Gray is a genus of Agaricales (Basidiomycota) characterised by a fugacious veil enveloping the basidiocarp, and a cortina at first covering the lamellae, but later vanishing in expanding basidiocarps. The basidiocarp size, shape, and colour vary considerably among species. The lamellae are emarginate to adnate, variously coloured, soon becoming brownish from mature, brown-pigmented basidiospores. The basidiospores are usually verrucose, highly variable

in size, and the colour may vary from pale ochre fulvous to rusty brown.

Diversity within the *Cortinarius* is high; over 2000 species are referred to the genus (Brandrud et al. 1990-2013). *Cortinarius* spp. are important ectomycorrhiza formers (Kårén et al. 1996) in temperate deciduous and boreal coniferous forests and arctic and alpine tundra (Ammirati & Smith 1978, Moser 1983, Gulden & Torkelsen 1996, Brandrud et al. 1990-2013) but do occur in tropical areas (Peintner et al. 2003) or Mediterranean evergreen thickets (Suáres-Santiago et al. 2009). The genus is also common and widespread in the Southern hemisphere (Moser & Horak 1975, Keller et al. 1988, Chambers et al. 1999, Garnica et al. 2003a, Soop 2013, Stefani et al. 2014). The genus *Cortinarius* is inferred to be originally associated with angiosperms with a probable origin in late Cretaceous (Ryberg & Matheny 2011).

Secondary compunds in the genus are frequent in many species, often characterising whole groups. *Cortinarius orellanus* Fr. and *C. rubellus* Cooke contain the highly nephrotoxic bipyridine orellanine (Schumacher & Høiland 1983, Danel et al. 2001). Interesting alkaloids or (R)-β-dopa derivatives are found in *C. infractus* (Pers.) Fr., *C. subtortus* (Pers.) Fr., and *C. violaceus* (L.) Gray (von Nussbaum et al. 1998, Spiteller et al. 2000, Brondz et al. 2007, Brondz & Høiland 2008, Teichert et al. 2008). All species of the infrageneric group *Dermocybe* (Fr.) Trog and some species belonging to the groups *Telamonia* (Fr.) Trog. and *Phlegmacium* (Fr.) Trog (the latter in the traditional circumscription (Brandrud et al. 1990-2013)) contain vividly coloured anthraquinones or preanthraquinones belonging to the octaketides (Gill & Steglich 1987). *Cortinarius venetus* (Fr.) Fr., *C. cotoneus* Fr., and *C. colymbadinus* Fr. contain yellow-green fluorescent xanthones and anthraquinones belonging to the nonaketides or octaketides (Gill & Steglich 1987).

Traditionally *Cortinarius* has been divided into several infrageneric groups according to various authors (see Garnica et al. (2005) for a nice overview). The traditional subgenera included in this paper follow the treatment by Moser (1983) and Moser & Horak (1975): *Cortinarius*, *Dermocybe* (by us at subgenus level), *Leprocybe* M.M. Moser., *Myxacium* (Fr.) Trog, *Phlegmacium*, *Sericeocybe* P.D. Orton, and *Telamonia.* The aforementioned traditional classifications are only partly supported by molecular phylogenetic studies (Høiland & Holst-Jensen 2000, Peintner et al. 2003, Peintner et al. 2004, Garnica et al. 2005, Harrower et al. 2011, Ryberg & Matheny 2011). *Cortinarius violaceus*, the type species of the genus (Clements & Shear 1931), belongs to subgenus *Cortinarius* in the traditional classification. This subgenus has only ten global species (Peintner et al. 2004) and is characterised by basidiocarps with dry, squamulose pileus surface, lamellae with cheilo- and pleurocystidia, and spores with a distinct suprahilar smooth spot, a plage. The peculiar violet iron complex is unique for *C. violaceus* (von Nussbaum et al. 1998, Spiteller et al. 2000).

The monophyly of *Telamonia* is supported by several authors (Liu et al. 1995, Chambers et al. 1999, Høiland & Holst-Jensen 2000, Peintner et al. 2003, Peintner et al. 2004, Garnica et al. 2005, Harrower et al. 2011), only *Acetosi*, *Camphorati*, *Fulvescentes*, *Illumini*, *Laeti*, *Obtusi*, and *Renidentes* are not included based on molecular studies (Niskanen 2008). The name *Telamonia* is vindicated since the clade includes the type species, *C. torvus* (Fr.) Fr. (Singer & Smith 1946), of this subgenus (Garnica et al. 2005). The traditional subgenus *Sericeocybe* (Orton 1958) is, however, engulfed in clade *Telamonia* (Peintner et al. 2004, Garnica et al. 2005), since it contains the type species of the former: *C. alboviolaceus* (Pers.) Fr. (Singer 1986). A sister relationship between *C. brunneus* (Pers.) Fr. and *C. gentilis* (Fr.) Fr. has previously been documented (Høiland & Holst-Jensen 2000, Niskanen et al. 2009), as well as between *C. alboviolaceus* and *C. armeniacus* (Schaeff.: Fr.) Fr. (Peintner et al. 2001).

Dermocybe s. str., (Høiland 1984), including the type, *C. cinnamomeus* (L.) Fr. (Singer 1986), is well supported (Liu et al. 1995, 1997; Chambers et al. 1999; Høiland & Holst-Jensen 2000; Peintner et al. 2004; Garnica et al. 2005; Harrower et al. 2011). Common for all species are pigments of octaketide origin (Høiland 1984, Gill & Steglich 1987). Two monophyletic lineages are identified in European and North American material, one *Dermocybe* line and one *Sanguinei* line, where *C. malicorius* Fr. occupies a basal position (Niskanen et al. 2012, 2013b). However, the Southern Hemispere species previously put in *Dermocybe* (Moser & Horak 1975) form clades outside this group: *Splendidi* (with *C. splendidus* (E. Horak) K. Griffiths and *C. kula* Grgurinovic) forms an own clade; *Icteri-*

nula (with *C. icterinus* (E. Horak) E. Horak and *C. amoenus* (M.M. Moser & E. Horak) G. Garnier) form a third entity; and *Pauperae* (with *C. luteostriatulus* (M.M. Moser & E. Horak) E. Valenz. & G. Moreno, *C. obscuroolivaceus* (M.M. Moser) Kuhn.-Fink. & Peintner, and *C. flavifucatus* (E. Horak & M.M. Moser) E. Valenz & G. Moreno), a fourth group (Garnica et al. 2003a, 2005; Peintner et al. 2004; Stefani et al. 2014).

The thin fleshed hygrophaneous, *Telamonia*-like *C. obtusus* (Fr.) Fr. and *C. acutus* (Pers.) Fr. have repeatedly been demonstrated as a clade, *Obtusi*, outside *Telamonia* (Høiland & Holst-Jensen 2000, Peintner et al. 2003, 2004; Garnica et al. 2005; Harrower et al. 2011; Niskanen 2008).

Clade *Leprocybe* comprises species with strongly fluorescent nonaketide xanthones (Gill & Steglich 1987). This clade represents the remains of subgenus *Leprocybe* (Peintner et al. 2004, Harrower et al. 2011), since it contains *C. cotoneus*, the type species (Singer 1986).

Clade *Orellani* comprises the toxigenic *C. orellanus* and *C. rubellus*. Biosynthesis of the bipyridines orellanine and orelline (Schumacher & Høiland 1983, Gill & Steglich 1987) is a monophyletic trait. *Orellani* was originally described as a section of subgenus *Leprocybe* (Moser 1969), but later elevated to a subgenus of its own (Gasparini 2004).

The subgenus *Myxacium*, as traditionally treated, has been divided into four sections: *Myxacium*, *Defibulati*, *Delibuti*, and *Vibratiles/Ochroleuci* (Høiland & Holst-Jensen 2000, (Seidl 2000, Peintner et al. 2004, Garnica et al. 2005, Harrower et al. 2011). Section *Myxacium* comprises the core of this subgenus, including the type species, *C. collinitus* (Pers.) Fr. (Singer 1986), with *Defibulati* as sister clade. The two other sections are not related to these clades, and subgenus *Myxacium* with its original inventory is polyphyletic.

Subgenus *Phlegmacium* in its traditional sense appears para- or polyphyletic in molecular phylogenies (Høiland & Holst-Jensen 2000; Garnica et al. 2003b, 2005, 2009); Peintner et al. 2004). *Calochroi* forms a distinct and strongly supported clade and comprises species with stout basidiocarps, simple cutis, and emarginated bulb at stipe base (Garnica et al. 2003b, 2005; Peintner et al. 2004; Frøslev et al. 2005, 2007); (Harrower et al. 2011). *Scauri/Purpurascentes* includes species with violet-red reaction in KI_3 (Høiland & Holst-Jensen 2000; Garnica et al. 2003b, 2005; Harrower et al. 2011). The aforementioned studies also reveal several smaller, isolated clades. The remaining part of the traditional subgenus *Phlegmacium* constitutes a weakly supported group, comprising several evolutionary lineages (Garnica et al. 2005), e.g. *Caerulescentes*, *Phlegmacioides*, *Percomes*, *Phlegmacium*, containing the type species *C. saginus* (Fr.) Fr. (Singer 1986), and *Praestantes*.

The genus *Rozites* P. Karst. is characterised by having membranaceous partial veil forming a persistent ring and a membranaceous universal veil. It has previously been shown that *Rozites* should be included within *Cortinarius* (Høiland & Holst-Jensen 2000, Peintner et al. 2002, Garnica et al. 2005, Harrower et al. 2011). It has been demonstrated that *Rozites* is polyphyletic, suggesting that a membranaceous veil has evolved in multiple independent events in *Cortinarius* (Peintner et al. 2002). Some fungi with sequestrate (gastroid or partially closed) basidiocarps, have a polyphyletic origin within genus *Cortinarius* (Peintner et al. 2001, Danks et al. 2010).

The aim of this study was to (1) evaluate the evolutionary relationship in a molecular data set of *Cortinarius*, including representative species for the different subgenera and sections, performing phylogenetic analyses of the ribosomal gene locus, containing the 18S, 5.8S, and 28S rDNA genes and the internal transcribed spacer regions (ITS1 and ITS2), and (2) trace infrageneric evolution of macro- and micromorphological, chemical, and ecological characteristics in light of the inferred molecular phylogeny, with focus on the North European species.

Material and methods

Fungal material

The *Cortinarius* samples (Table 1) were collected in Norway between 1985 and 2008. The sampling is covering the main variation within North European species and is ranging from arctic tundra to broadleaved temperate forests. To give the correct name for clades, the type species for the traditional subgenera and (some) sections are included in the sampling (Clements & Shear 1931, Singer & Smith 1946; Moser & Horak 1975, Høiland 1984, Singer 1986). In addition, some sequences (Table 1) were acquired from the NCBInr nucleotide database (http://www.ncbi.nlm.nih.gov/, as of 12.2012) to broaden our species sample to include some species outside North Europe. Suitable out-

group species (Table 1) (*Agrocybe praecox* (Pers.) Fayod, *Galerina stordalii* A.H. Sm., *Hebeloma alpinum* (J. Favre) Bruchet, and *Phaeogalera stagnina* (Fr.) Pegler & T.W.K. Young) were established based on previous molecular phylogenies of dark spored agarics including *Cortinarius* (Gulden et al. 2005). The nomenclature follows Index Fungorum (http://www.indexfungorum.org/Names/Names.asp, as of 12.2013). Dried, field-collected specimens are deposited in the fungal herbarium of the Natural History Museum, University of Oslo (O).

DNA extraction and PCR

DNA was obtained from dried specimens. Various protocols for DNA extraction were used: the 2% CTAB miniprep method (Murray & Thompson 1980), the microwave miniprep procedure (Goodwin & Lee 1993) and the Dynabeads R DNA DirectTM System 1 extraction kit (Rudi et al. 1997). Primer pairs used in the PCR reactions included PNS1/NS41 for the partial nr18S region, ITS5/ITS4 for the complete ITS1-5.8S-ITS2 region, and LR0R/LR5 for the partial nr28S region (White et al. 1990). Template was amplified with PuReTaq Ready-To-Go PCR Beads (GE-Healthcare). PCRs were run with the following cycling conditions: 1 x (3 min/ 94 °C), 40 x (30 s/ 94 °C, 30 s/ 50-52 °C, 1 min/ 72 °C), 1 x (10 min/ 72 °C).

PCR products were purified using ExoSAP-IT (Amersham Biosciences), prior to sequencing. Sequences were generated with an ABI 3730 high-throughput capillary electrophoresis sequencers using the PCR primers as sequencing primers.

Phylogenetic inference

The three rDNA genes (18S, 5.8S, and 28S) and the internal transcribed spacer regions (ITS1 and ITS2) were collectively aligned using MAFFTv6 Q-INS-I model (Hofacker et al. 2002, Kiryu et al. 2007, Katoh & Toh 2008), considering secondary RNA structure (default parameters used) as a criterion for the alignment. The alignment was checked manually using MacClade v4.07 (Maddison & Maddison 1992), before being inferred with Gblocks v0.91b (Castresana 2000), under the least stringent parameters, to exclude poorly aligned positions and divergent regions from subsequent phylogenetic inferences. The inference of a concatenated rDNA alignment gave a 68% increase in informative nucleotide characters (825 to 491) compared to that of inferring just the 5.8S and the ITS regions. Ambiguous species were subsequently excluded from downstream analysis upon evaluation of the alignment and preliminary ML (RAxML) topologies. The dataset was analysed with MODLETEST (Posada & Crandall 1998) to establish the optimal model of nucleotide evolution; for all alignments the General Time Reversible (GTR) model was preferred for both the Akaike and Bayesian information Criterion (AiC and BiC). Maximum Likelihood (ML) analyses were performed with RAxML-VI-HPCv7.2.6, GTRCAT model with 25 rate categories (Stamatakis 2006). The most likely topology was established from 100 separate searches, and bootstrap analyses were performed with 500 pseudoreplicates. Bayesian analyses were carried out with MrBayes MPI version 3.1.2 (Huelsenbeck et al. 2001, Ronquist & Huelsenbeck 2003). Trees were generated from two independent runs with one heated and one cold chain in the Markov Chain Monte Carlo (MCMC) with 40,000,000 generations, sampling every 1000. Analyses ran until the average standard deviation of split frequencies was <0.01. Burn-in trees were set based on the assessment of likelihood plots and convergence diagnostics implemented in MrBayes. The Potential Scale Reduction Factor (PSRF) values for all inferences were ~1.0, indicating a good posterior probability distribution sample. The majority rule tree and posterior probabilities for each inference was constructed from a consensus of the sampled post burn-in trees. Species with an uncertain phylogenetic affinity (rogue taxa), were established using the RogueNaRok-algorithm (Aberer et al. 2013), with the following parameters; a majority-rule consensus threshold, support optimization and a Max dropset size of 5. Topological congruence between the inferred phylogenies was calculated using the l_{cong} index: http://max2.ese.u-psud.fr/bases/upresa/pages/devienne/index.html (de Vienne et al. 2007). All model estimation and phylogenetic analyses, unless otherwise stated, were done on the freely available Bioportal (Kumar et al. 2009) at the University of Oslo (http://www.bioportal.uio.no/, as of 12.2013).

Morphological, chemical, and ecological data

Morphological and ecological features were acquired from literature (Moser 1983, Moser & Horak 1975, Ammirati & Smith 1978, Brandrud et al. 1990-2013, Høiland & Holst-Jensen 2000, Niskanen et al. 2008) and our own observations. Information about chemistry was taken from reviews or discrete works dealing with *Cortinarius* chemistry (Høiland 1984, Gill & Steglich 1987, Keller et al. 1988, von Nussbaum et al. 1998, Spiteller et al. 2000, Brondz et al. 2007, Brondz & Høiland 2008, Teichert et al. 2008).

Results

Sequence amplification and assembly

205 DNA sequences from 69 *Cortinarius* species and four outgroup species were successfully amplified for the whole rDNA gene locus, except for *C. gentilis*, which failed for 28S, and *C. torvus*, which failed for 18S. The sequences are deposited in Genbank under the accession

Table 1. DNA sequences used in this study: [a]Species names follow Index Fungorum (www.indexfungorum.org/Names/Names.asp, as of 12.2013). [b]Accession numbers in EMBL/GenBank/DDBJ (www.ncbi.nlm.nih.gov). m.d. = missing data. Asterisks * indicate sequences generated in this study. The capital letter after the species name author indicates the subgenus/genus in traditional systematics (Moser & Horak 1975); (Moser 1983). *Dermocybe* D, *Leprocybe* L, *Myxacium* M, *Phlegmacium* P, *Rozites* R, *Sericeocybe* S, and *Telamonia* T. Hashtags # denote type species for subgenus/genus.

Species[a]	Geographic origin	GenBank acc. no. 18S region[b]	GenBank acc. no. ITS1-5.8S-ITS2 region[b]	GenBank acc. no. 28S region[b]
Agrocybe praecox (Pers.) Fayod Outgroup	Norway: Hordaland	KC171232*	KC842389*	KC842460*
Galerina stordali A.H. Sm. Outgroup	Norway: Hordaland	KC171235*	KC842392*	KC842463*
Hebeloma alpinum (J. Favre) Bruchet Outgroup	Norway: Hordaland	KC171234*	KC842391*	KC842462*
Phaeogalera stagnina (Fr.) Pegler & T.W.K. Young Outgroup	Norway: Hordaland	KC171233*	KC842390*	KC842461*
Cortinarius acutus (Pers.) Fr. T	Norway: Oslo	KC171262*	KC842420*	KC842490*
Cortinarius albonigrellus J. Favre T	Norway: Oppland	KC171239*	KC842396*	KC842467*
Cortinarius alboviolaceus (Pers.) Fr. S#	Norway: Rogaland	KC171244*	KC842402*	KC842473*
Cortinarius amoenus (M.M. Moser & E. Horak) G. Garnier D	Chile: Valdivia	m.d.	AF539721	AF539721
Cortinarius anomalus (Fr.) Fr. S	Norway: Sogn og Fjordane	KC171267*	KC842425*	KC842495*
Cortinarius anserinus (Velen.) Rob. Henry P	Germany: Tondorf	m.d.	AY174805	AY174805
Cortinarius armeniacus (Schaeff.: Fr.) Fr. T	Norway: Oslo	KC171245*	KC842403*	KC842474*
Cortinarius armillatus (Fr.) Fr. T	Norway: Rogaland	KC171250*	KC842408*	KC842479*
Cortinarius austroduracinus M.M. Moser T	Chile	m.d.	AY669653	AY669653
Cortinarius balteatocumatilis Rob. Henry ex P.D. Orton P	France: Piroulette	m.d.	AY174801	AY174801
Cortinarius balteatus (Fr.) Fr. P	Germany	m.d.	AY669526	AY669526
Cortinarius bolaris (Pers.) Fr. L	Norway: Telemark	KC171268*	KC842426*	KC842496*
Cortinarius brunneus (Pers.) Fr. T	Norway: Oslo	KC171252*	KC842410*	KC842480*
Cortinarius caerulescens (Schaeff.) Fr. P	Canada: British Columbia	m.d.	HQ604682	HQ604682
Cortinarius callisteus (Fr.) Fr. L	Norway: Telemark	KC171277*	KC842435*	KC842505*
Cortinarius caninus (Fr.) Fr. S	Norway	KC171266*	KC842424*	KC842494*
Cortinarius caperatus (Pers.) Fr. R#	Norway: Oslo	KC171285*	KC842443*	KC842513*
Cortinarius cinnabarinus Fr. D	Norway: Vestfold	KC171247*	KC842405*	KC842476*
Cortinarius cinnamomeus (L.) Fr. D#	Norway: Oslo	KC171255*	KC842413*	KC842483*
Cortinarius claricolor (Fr.) Fr. P	Norway: Aust-Agder	KC171292*	KC842450*	KC842520*
Cortinarius collinitus (Pers.) Fr. M#	Norway: Nord-Trøndelag	KC171276*	KC842434*	KC842504*
Cortinarius colymbadinus Fr. L	Norway: Buskerud	KC171246*	KC842404*	KC842475*
Cortinarius cotoneus Fr. L#	Norway: Oslo	KC171265*	KC842423*	KC842493*
Cortinarius crassus Fr. P	Norway: Aust-Agder	KC171279*	KC842437*	KC842507*
Cortinarius croceus (Schaeff.) Gray D	Norway: Oslo	KC171256*	KC842414*	KC842484*
Cortinarius cumatilis Fr. P	Norway: Oslo	KC171291*	KC842449*	KC842519*
Cortinarius delibutus Fr. M	Norway: Oslo	KC171283*	KC842441*	KC842511*
Cortinarius evernius (Fr.) Fr. T	Norway: Oslo	KC171243*	KC842401*	KC842472*
Cortinarius flexipes (Fr.) Fr. T	Norway: Oslo	KC171238*	KC842395*	KC842466*
Cortinarius fraudulosus Britzelm. P	Norway: Østfold	KC171288*	KC842446*	KC842516*
Cortinarius gentilis (Fr.) Fr. L	Norway: Nord-Trøndelag	KC171251*	KC842409*	m.d.
Cortinarius glaucopus (Schaeff.) Fr. P	Norway: Oslo	KC171287*	KC842445*	KC842515*
Cortinarius icterinus (E. Horak) E. Horak D	Chile: Valdivia	m.d.	AF539720	AF539720
Cortinarius idahoensis Ammirati & A.H. Sm. D	Canada: British Columbia	m.d.	FJ039596	FJ039596
Cortinarius infractus (Pers.) Fr. P	Norway: Oslo	KC171269*	KC842427*	KC842497*
Cortinarius laniger Fr. T	Norway: Telemark	KC171241*	KC842398*	KC842469*
Cortinarius limonius (Fr.) Fr. L	Norway: Rogaland	KC171298*	KC842456*	KC842526*
Cortinarius luteostriatulus (M.M. Moser & E. Horak) E. Valenz. & G. Moreno D	Chile: Osborno	m.d.	AF539707	AF539707
Cortinarius malicorius Fr. D	Austria	m.d.	AY669583	AY669583
Cortinarius multiformis (Fr.) Fr. P	Norway: Hordaland	KC171300*	KC842458*	KC842528*
Cortinarius napus Fr. P	Norway: Oppland	KC171270*	KC842428*	KC842498*
Cortinarius obscurooliveus (M.M. Moser) Kuhn.-Fink. & Peintner D	Chile: Temuco	m.d.	AF539708	AF539708
Cortinarius obtusus (Fr.) Fr. T	Norway: Oslo	KC171263*	KC842421*	KC842491*
Cortinarius olearioides Rob. Henry P	Norway: Oslo	KC171271*	KC842429*	KC842499*
Cortinarius olidus J.E. Lange P	Norway: Oslo	KC171293*	KC842451*	KC842521*
Cortinarius olivaceofuscus Kühner D	Norway: Sogn og Fjordane	KC171259*	KC842417*	KC842487*
Cortinarius orellanus Fr. L	Norway: Aust-Agder	KC171261*	KC842419*	KC842489*
Cortinarius parvannulatus Kühner T	Norway: Oppland	KC171236*	KC842393*	KC842464*
Cortinarius percomis Fr. P	Norway: Rogaland	KC171294*	KC842452*	KC842522*
Cortinarius phaeopygmaeus J. Favre T	Norway: Oppland	KC171240*	KC842397*	KC842468*
Cortinarius phoeniceus (Vent.) Maire var. occidentalis A.H. Sm. D	Canada: British Columbia	m.d.	FJ039592	FJ039592
Cortinarius pholideus (Lilj.) Fr. S	Norway: Oslo	KC171248*	KC842406*	KC842477*
Cortinarius piceae Frøslev, T.S. Jeppesen & Brandrud P	Norway: Oppland	KC171272*	KC842430*	KC842500*
Cortinarius polaris Høil. D	Norway: Svalbard	KC171253*	KC842411*	KC842481*
Cortinarius porphyropus (Alb. & Schwein.) Fr. P	Norway: Rogaland	KC171295*	KC842453*	KC842523*
Cortinarius pseudoglaucopus (Jul. Schäff. ex M.M. Moser) Quadr. P	Germany	m.d.	AY669573	AY669573
Cortinarius raphanoides (Pers.) Fr. L	Norway: Buskerud	KC171249*	KC842407*	KC842478*
Cortinarius renidens Fr. T	Norway: Oslo	KC171301*	KC842459*	KC842529*
Cortinarius rubellus Cooke L	Norway: Oslo	KC171260*	KC842418*	KC842488*
Cortinarius rubicundulus (Rea) A. Pearson L	Norway: Oslo	KC171278*	KC842436*	KC842506*
Cortinarius saginus (Fr.) Fr. P#	Norway: Telemark	KC171290*	KC842448*	KC842518*
Cortinarius salor Fr. M	Norway: Aust-Agder	KC171280*	KC842438*	KC842508*
Cortinarius sanguineus (Wulfen) Fr. D	Norway: Oslo	KC171258*	KC842416*	KC842486*
Cortinarius scaurus (Fr.) Fr. P	Norway: Rogaland	KC171296*	KC842454*	KC842524*
Cortinarius scotoides J. Favre T	Norway: Oppland	KC171237*	KC842394*	KC842465*
Cortinarius semisanguineus (Fr.) Gillet D	Norway: Buskerud	KC171257*	KC842415*	KC842485*
Cortinarius stillatitius Fr. M	Norway: Oppland	KC171274*	KC842432*	KC842502*
Cortinarius subbalaustinus Rob. Henry T	Sweden	m.d.	AF195592	AF195592
Cortinarius subtortus (Pers.) Fr. P	Norway: Oslo	KC171281*	KC842439*	KC842509*
Cortinarius sulphurinus Quél. P	Norway: Akershus	KC171273*	KC842431*	KC842501*
Cortinarius terpsichores Melot P	Norway: Oslo	KC171286*	KC842444*	KC842514*
Cortinarius tiliae Brandrud P	Norway: Oslo	m.d.	AY669556	AY669556
Cortinarius torvus (Fr.) Fr. T#	Norway: Telemark	m.d.	KC842400*	KC842471*
Cortinarius traganus (Fr.) Fr. S	Norway: Oslo	KC171242*	KC842399*	KC842470*
Cortinarius triumphans Fr. P	Germany: Ramersbach	m.d.	AY174799	AY174799
Cortinarius trivialis J.E. Lange M	Norway: Oppland	KC171275*	KC842433*	KC842503*
Cortinarius turmalis Fr. P	Norway: Oslo	KC171297*	KC842455*	KC842525*
Cortinarius uliginosus Berk. D	Norway: Oslo	KC171254*	KC842412*	KC842482*
Cortinarius vacciniophilus Brandrud P	Norway: Oppland	m.d.	AY669518	AY669518
Cortinarius variicolor (Pers.) Fr. P	Norway: Akershus	KC171289*	KC842447*	KC842517*
Cortinarius varius (Shaeff.) Fr. P	Germany: Oberjoch	m.d.	AY174792	AY174792
Cortinarius venetus (Fr.) Fr. L	Norway: Oslo	KC171264*	KC842422*	KC842492*
Cortinarius vespertinus (Fr.) Fr. P	Norway: Aust-Agder	KC171299*	KC842457*	KC842527*
Cortinarius vibratilis (Fr.) Fr. M	Norway: Rogaland	KC171282*	KC842440*	KC842510*
Cortinarius violaceus (L.) Gray C#	Norway: Rogaland	KC171284*	KC842442*	KC842512*
Cortinarius viridocoeruleus Chevassut & Rob. Henry P	Germany: Eschweiler	m.d.	AY174788	AY174788

numbers KC171232-KC171301 and KC842389-KC842529 (Table 1). In addition, sequences from 17 species were retrieved from the NCBInr nucleotide database (Table 1).

Alignments generated in this study have been made freely available through the authors ResearchGate pages (http://www.researchgate.net/).

Phylogenetic inference

The following species were pruned upon evaluation of the RogueNaRok-algorithm (Aberer et al. 2013): *Cortinarius rubicundulus* (Rea) A. Pearson, *C. saginus*, *C. salor* Fr., and *C. callisteus* (Fr.) Fr. However, pruning gave no additional support (data not shown). The inferred *Cortinarius* phylogenies (pruned or non-pruned analysed with ML or MrBayes, respectively) demonstrated good topological congruence with an l_{cong} P-value <0.05. Removal of long-branching species, likewise, had minimal topological impact (data not shown). For this reasoning, the full dataset was preferred for visualization of the results. For interpretation of the phylogenetic inferences (Fig. 1), statistical support is defined as: full 1.00 posterior probability (PP)/100 bootstrap support (BS), high >90 BS, moderate >65 BS, and low >50 BS, highlighted with red lines in Fig. 1. Additionally, PP support over 0.95 in cases where BS ≤ 50 is highlighted with blue lines in Fig. 1.

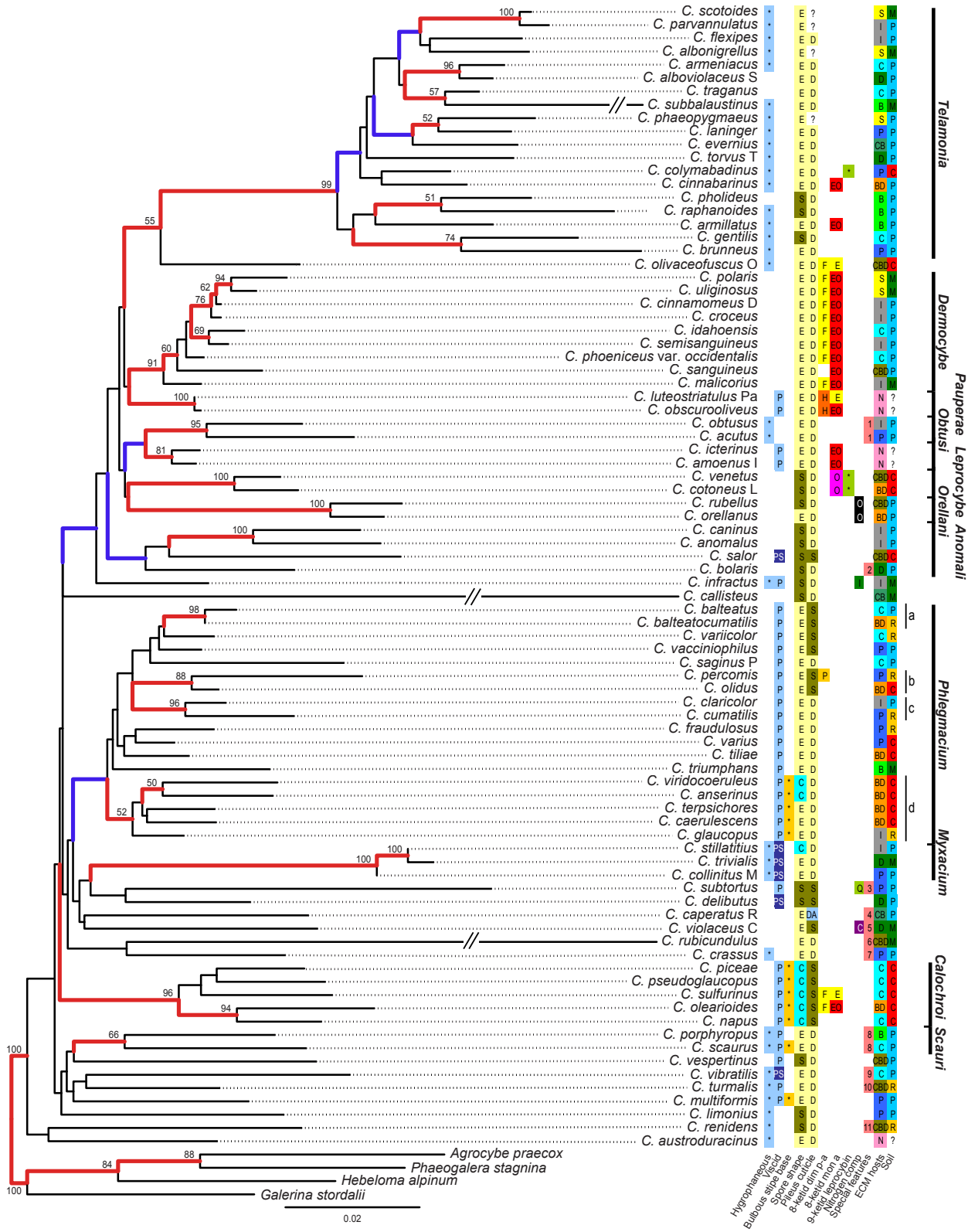
The first and most basal clade to diverge from the main branch constituted *C. austroduracinus* M.M. Moser and *C. renidens* Fr. However, the basal position and the monophyly of these species were unsupported. The next grouping to diverge, again unsupported, was a lineage encompassing the terminal *Scauri* clade, recovered with moderate support (1.00/66). The following divergence was the *Calochroi* clade: The split was unsupported, however the grouping of the *Calochroi* clade was highly supported (1.00/96), as was the sister relationship between *C. olearioides* Rob. Henry and *C. napus* Fr. (1.00/94). The subsequent unsupported divergence was a large grouping harbouring the *Phlegmacium* and *Myxacium* lineages. The branching pattern between species was uncertain with lack of support for relationships apart from; the fully supported monophyly of the *Myxacium* clade, the low supported clade formed by *C. glaucopus* (Schaeff.) Fr., *C. caerulescens* (Schaeff.) Fr., *C. terpsichores* Melot, *C. anserinus* (Velen.) Rob. Henry, and *C. viridocoeruleus* Chevassut & Rob. Henry (0.98/52), and the moderate to highly supported sister relationships recovered between *C. cumatilis* Fr. and *C. claricolor* (Fr.) Fr. (1.00/96), *C. olidus* J.E. Lange and *C. percomis* Fr. (1.00/88), and *C. balteatocumatilis* Rob. Henry ex P.D. Orton and *C. balteatus* (Fr.) Fr. (1.00/98). The next species to split from the main branch was *C. callisteus*, subsequently followed by *C. infractus*, with both lacking support. The ensuing branch to split formed the unsupported *Anomali* clade. Only the

Figure 1. The rDNA phylogeny of *Cortinarius*.

ML tree for 86 Cortinarius species and four outgroup species (2373 rDNA characters). Red lines full (=100) to low BS (>50); blue lines PP ≥0.95 for BS ≤50. Main clades are named after subgenera or sections, sub-clades are named with letters.

Letter(s) following a species names indicates type species for genus *Rozites* R, subgenera *Dermocybe* D, *Leprocybe* L, *Myxacium* M, *Phlegmacium* P, *Sericeocybe* S, and *Telamonia* T, and sections *Icterinula* I, *Olivaceofusci* O, and *Pauperae* Pa.

Morphological, chemical, and ecological traits (blank = actual characteristic is lacking). Viscid: P = pileus, PS = pileus and stipe; spore shape: E = ellipsoid- amygdaloid, S = subglobose, C = citriniform; cuticle: S = simple, D = duplex, DA = duplex and amyloid, ? = no data; octaketide dimeric pre-anthraquinones: F = flavomannins, P = phlegmacins, H = hypericin and skyrin; octaketide monomeric anthraquinones: E = only endocrocin, EO = endocrocin and other anthraquinones, O = only other anthraquinones; nitrogen compounds: O = orellanine, C = 1:2 iron (III) (R)-β-dopa complex, I = infractopicrin, Q = (iso)-quinoline alkaloids; mycorrhizal partner(s): B = *Betula*, C = conifers, CB = conifers and *Betula*, CBD = conifers and broad leaved deciduous trees, D = deciduous trees, BD = broad leaved deciduous trees, I = indifferent, P = *Picea*, N = *Nothofagus*, S = *Salix*; soil: P = poor, M = medium, R = rich, C = calcareous, ? = no data; special characteristics: 1 = balloon shaped cells on lamella, 2 = flesh yellowing, 3 = cystidia with epiparietal pigment, 4 = ring, ectomycorrhizae with amyloid mantle, 5 = cystidia with bluish pigment, spores with plage, 6 = flesh yellowing, clavate cheilocystidia, spores indistinctly verrucose, 7 = cylindrical cystidia, 8 = flesh purple in KI_3, 9 = crystallopicrin, 10 = basal mycelium staining rose, spores smooth, 11 = veil and cortina absent.


C. scotoides
C. parvannulatus
C. flexipes
C. albonigrellus
C. armeniacus
C. alboviolaceus S
C. traganus
C. subbalaustinus
C. phaeopygmaeus
C. laninger
C. evernius
C. torvus T
C. colymabadinus
C. cinnabarinus
C. pholideus
C. raphanoides
C. armillatus
C. gentilis
C. brunneus
C. olivaceofuscus O
C. polaris
C. uliginosus
C. cinnamomeus D
C. croceus
C. idahoensis
C. semisanguineus
C. phoeniceus var. occidentalis
C. sanguineus
C. malicorius
C. luteostriatulus Pa
C. obscurooliveus
C. obtusus
C. acutus
C. icterinus
C. amoenus I
C. venetus
C. cotoneus L
C. rubellus
C. orellanus
C. caninus
C. anomalus
C. salor
C. bolaris
C. infractus
C. callisteus
C. balteatus
C. balteatocumatilis
C. variicolor
C. vaccinophilus
C. saginus P
C. percomis
C. olidus
C. claricolor
C. cumatilis
C. fraudulosus
C. varius
C. triumphans
C. viridocoeruleus
C. anserinus
C. terpsichores
C. caerulescens
C. glaucopus
C. stillatitius
C. trivialis
C. collinitus M
C. subtortus
C. delibutus
C. caperatus R
C. violaceus C
C. rubicundulus
C. crassus
C. piceae
C. pseudoglaucopus
C. sulfurinus
C. olearioides
C. napus
C. porphyropus
C. scaurus
C. vespertinus
C. vibratilis
C. turmalis
C. multiformis
C. limonius
C. renidens
C. austroduracinus
Agrocybe praecox
Phaeogalera stagnina
Hebeloma alpinum
Galerina stordalii
0.02
Telamonia
Dermocybe
Icterinula
Pauperae
Leprocybe
Anomali
Obtusi
Orellani
Phlegmacium
Myxacium
Calochroi
Scauri
a
b
c
d
Hygrophaneus
Viscid
Bulbous stipe base
Spore shape
Pileus cuticle
8-ketid dim p-a
8-ketid mon a
9-ketid leprocybin
Nitrogen comp
Special features
ECM hosts
Soil

sister relationship of *C. anomalus* (Fr.) Fr. and *C. caninus* (Fr.) Fr. was confirmed with full support. The next grouping to diverge, again with lacking support, constituted four supported sister relationships; the fully supported *Orellani* clade, the fully supported *Leprocybe* clade, the moderately supported *Icterinula* clade (1.00/81), and the highly supported *Obtusi* clade (1.00/95). The subsequent unsupported divergence constituted a grouping where the fully supported *Pauperae* clade split first, recovering the highly supported *Dermocybe* clade (1.00/91). The ensuing divergence of *C. olivaceofuscus* Kühner from the main branch was inferred with low support (0.99/55). The subsequent split was highly supported (1.00/99), constituting the *Telamonia* clade. The branching pattern in the clade, however, was unclear with few sister relationships being recovered with support; *C. gentilis* with *C. brunneus* (1.00/74), *C. pholideus* (Lilj.) Fr. with *C. raphanoides* (Pers.) Fr. (0.99/51), C. *phaeopygmaeus* J. Favre with *C. laniger* Fr. (0.99/52), *C. traganus* (Fr.) Fr. with *C. subbalaustinus* Rob. Henry (0.99/57), *C. armeniacus* with *C. alboviolaceus* (1.00/96), and finally the fully supported *C. scotoides* J. Favre with *C. parvannulatus* Kühner.

Discussion

Phylogeny

Although the branching pattern between clades might be questionable due to uncertain phylogenetic signal, twelve infrageneric groups received satisfactory support (Fig. 1). These are: *Telamonia*, *Dermocybe*, *Pauperae*, *Obtusi*, *Icterininula*, *Leprocybe*, *Orellani*, *Anomali*, *Phlegmacium*, *Myxacium*, *Calochroi*, and *Scauri*. As mentioned in the introduction chapter most of these groups have recurrently been identified by several authors, e.g. (Høiland & Holst-Jensen 2000; Garnica et al. 2003a, 2003b, 2005; Peintner et al. 2004; Niskanen 2008; Harrower et al. 2011). Our results confirm their findings, and except for *Anomali* and *Phlegmacium*, the phylogeny will not be discussed further.

Our analyses show that *C. olivaceofuscus* is recovered, with low BS, as a sister group to *Telamonia*, and we may discuss whether it should be included in *Telamonia* or not. Previously it has been included in *Dermocybe* section *Olivaceofusci* (Høiland 1984). With *Telamonia* it shares a hygrophaneous pileus, with *Dermocybe* the octaketide anthraquinones typical for this group (Høiland 1984, Gill & Steglich 1987). Based on morphology and pigment chemistry *C. olivaceofuscus* has only one known relative, *Dermocybe leptospermarum* E. Horak (not yet combined in *Cortinarius*) from New Zealand (Høiland 1984, Gill & Steglich 1987, Horak 1988, Keller et al. 1988). It is tempting to consider this small, strictly bi-Hemispheric group as an evolutionary link between *Dermocybe* and *Telamonia*, representing the ancestral state of the latter. The sequence of *C. olivaceofuscus* included in the *Dermocybe* clade by Garnica et al. (2005) is not matching this species, but is similar to *C. cinnamomeus* (BLASTn hit with 99 % identity and/or coverage, as of 09.2014).

The Bayesian inference supports a relationship between clade *Obtusi* and *Icterinula* (0.95/46), but no recognised morphological or chemical features combine these two clades. The same relationship was also shown by a previous analysis (Peintner et al. 2004).

Clade *Anomali* in its most narrow sense comprises *C. anomalus* and *C. caninus*, characterised by subglobose spores and dry basidiocarps often with glimmery pileus. *Anomali* was originally recognised as a section of subgenus *Telamonia* or alternatively subgenus *Sericeocybe* (Moser 1983, Niskanen et al. 2008). The European *C. spilomeus* (Fr.) Fr. and the South Hemispheric *C. tristis* E. Horak and *C. sclerophyllarum* Gasparini are added to this lineage (Garnica et al. 2005). According to the Bayesian tree, the clade can be broadened to include *C. salor* and *C. bolaris* (Pers.) Fr. (0.99/32). *Cortinarius salor* shows morphological similarity to *C. delibutus* Fr. by its slimy stipe and pileus, with which some earlier phylogenetic analyses indicate a possible relationship (Peintner et al. 2004, Harrower et al. 2011, Ryberg & Matheny 2011). Our result does not support this relationship. The inclusion of *C. bolaris* in clade *Anomali* seems, however, more justified based on morphological features (Garnica et al. 2005, Niskanen et al. 2008). A chemically unknown compound staining the flesh yellow, is characteristic for this species (Høiland 1980).

Cortinarius infractus is tentatively placed as a sister group to the assemblage spanning from clade *Telamonia* to *Anomali*. It has a *Phlegmacium*-like basidiocarp with a viscid pileus, subglo-

bose spores, and contains indole alkaloids (Brondz et al. 2007, Brondz & Høiland 2008), probably unique for *Cortinarius*.

It is worth noting that the Bayesian phylogeny gives support to a "superclade" (0.98/16) spanning from clade *Telamonia* to clade *Anomali*, including *C. infractus*. In this superclade we find the majority of species with soluble pigments of octaketide origin, all species with compounds of nonaketide origin, the majority of species with hygrophaneous pileus, few species with viscid pileus, and no species with bulbous stipe base. Moreover, all species (except *C. salor*) have duplex pileus cuticle.

Interestingly, it is demonstrated that the ectomycorrhizal structure of species in clade *Dermocybe*, *Obtusi*, and *Leprocybe* possesses emanating hyphae closed by a clamp, a feature not seen in the other clades (although only a limited number of species were investigated) (Agerer 2006). This may confirm the relationship between these clades. Species from the other clades have emanating hyphae with open anastomoses, except for *C. caperatus* (Pers.) Fr. in which they are smooth with clamps (Agerer 2006).

Clade *Phlegmacium* is not supported by ML, however, the Bayesian inference provides support (0.97/28) for this large group spanning from the couple *C. balteatus* and *C. balteatocumatilis* to *C. glaucopus*. This clade may represent the retained part of subgenus *Phlegmacium* since *Cortinarius saginus*, the type species (Singer 1986), is a member of the group. Common for all these species is a viscid pileus, a dry stipe, and stout basidiocarps. Inside this clade ML gives support to some subordinate monophyletic groups marked a, b, c, and d in Fig. 1.

Cortinarius balteatus and *C. balteatocumatilis* (sub-clade a) are sister species with high BS support. Although not supported by ML or Mr. Bayes, both analyses are congruent in inferring a monophyletic relationship with *C. variicolor* (Pers.) Fr. and *C. vacciniophilus* Brandrud. This broadened concept of sub-clade a represents clade *Phlegmacioides* (Garnica et al. 2005).

Cortinarius percomis and *C. olidus* are monophyletic with moderate BS support (sub-clade b). This clade also includes species as *C. nanceiensis* Maire, *C. mussivus* (Fr.) Melot, and *C. papulosus* Fr. represening *Percomes* (Garnica et al. 2005). *Cortinarius percomis*, *C. nanceiensis*, and *C. mussivus* contain special octaketide pigments not found outside this group (Gill & Steglich 1987).

Cortinarius claricolor and *C. cumatilis* (subclade c) are sister species with high BS support, representing *Praestantes* (Garnica et al. 2005).

The group spanning from the couple *C. viridocoeruleus* and *C. anserinus* to *C. glaucopus* forms a monophyletic clade with low BS support (sub-clade d). A monophyletic relationship between these species in this, still unnamed, clade has also previously been demonstrated (Garnica et al. 2003b).

A number of species in our dataset are found in unsupported groups. *Cortinarius violaceus* contains a violet iron complex, unique for this species (von Nussbaum et al. 1998, Spiteller et al. 2000). *Cortinarius caperatus* has, in addition to the membranous ring, an amyloid reaction in the cutis hyphae and the ectomycorrhizal mantle together with smooth emanating hyphae with clamps (Agerer 2006). Despite forming an unsupported monophyly, the very dissimilar morphological and chemical characteristics indicate that *C. violaceus* and *C. caperatus* are not closely related, thus this can be considered a topological artefact. The couple *C. subtortus* and *C. delibutus* constitute another unconfirmed monophyletic group. Common for both species is a slimy pileus and subglobose spores. *Cortinarius subtortus* has in addition prominent pleuro- and cheilocystidia and content of (iso)-quinoline alkaloids (Teichert et al. 2008). *Cortinarius delibutus* has additionally a slimy stipe. *Cortinarius rubicundulus* and *C. crassus* Fr. is by ML, but not by Mr. Bayes, put in an unsupported group. They share some morphological similarities such as stout basidiocarps and cystidia, but the spore ornamentation is different; indistinctly verrucose in *C. rubicundulus*, distinctly verrucose in *C. crassus*. Moreover *C. rubicundulus* contains a chemically unknown compound staining the flesh yellow, reminiscent to *C. bolaris* (Høiland 1980). *Cortinarius callisteus* is by ML put in an isolated, single position and by Mr. Bayes in an unsupported group together with *C. rubicundulus*. Unique for *C. callisteus* (and its close relative *C. citrinofulvescens* M.M. Moser) is a strong and peculiar smell of ozone (Niskanen et al. 2008). Both *C. callisteus* and *C. rubicundulus* have exceptionally long evolutionary branch lengths, as also shown by other authors (Peintner et al. 2004, Garnica et al. 2005, Harrower et al. 2011, Ryberg & Matheny 2011).

The species in clade *Scauri*, together with *C.*

vespertinus (Fr.) Fr., *C. vibratilis* (Fr.) Fr., *C. turmalis* Fr., *C. multiformis* (Fr.) Fr., and *C. limonius* (Fr.) Fr., occupy basal positions in the phylogenetic tree. Few characteristics combine these species, but many of them have unique features not seen in the other species of the dataset (Fig. 1). For instance, the viscid pileus cuticle of *C. vibratilis* contains the intensely acrid triterpenoid crystallopicrin (Steglich et al. 1990). The most basal position is taken by the unsupported couple *C. renidens* (characterised by lacking veil and cortina) and the South American *Nothofagus* associated species *C. austroduracinus*. This monophyletic relationship is also indicated earlier (Garnica et al. 2005).

Morphological characteristics

A hygrophaneous pileus is dominating among the species in clade *Telamonia* together with its sister *C. olivaceofuscus*. It is also met with in clades *Obtusi* and *Myxacium*, although weak in the last clade. It is worth noting that hygrophanity is also regular among the more basal species spanning from the couple *C. austroduracinus* and *C. renidens* to clade *Scauri*. Therefore we consider that hygrophanity is an ancestral character state in genus *Cortinarius*, which has been retained in some phylogenetic groups and reduced in other groups. The clades *Dermocybe*, *Phlegmacium*, and *Calochroi* are the most prominent examples of non-hygrophaneous groups.

Conversely, a slimy pileus or a slimy pileus and stipe seem derived. This morphological feature seems to have developed independently on multiple occasions in our phylogeny and represents a key characteristic for clades *Pauperae*, *Icterinula*, *Phlegmacium*, *Calochroi*, and *Scauri*. The combination slimy pileus and stipe has developed four times in our phylogeny and is a key characteristic for clade *Myxacium*. It is tempting to believe that the slimy layers have developed to protect the basidiocarps against fungivorous insects and/or temporarily dry weather conditions.

A bulbous stipe base is also considered derived and has probably been evolved due to a pileocarp (subterranean) development as an adaptation to dry soils. It is found in all species in clade *Calochroi* and sub-clade d of clade *Phlegmacium*. In our phylogeny this characteristic has evolved on four separate occasions.

The ellipsoid to amygdaloid spores may represent the ancestral spore outline in genus *Cortinarius* since this outline is dominating in the lower branches of the tree (Fig. 1). Subglobose spores have evolved several times and do not seem to infer a good phylogenetic signal, except in clade *Leprocybe* and clade *Anomali* (in its widest sense). Citriniform spores are distinctive for clade *Calochroi*, but are also encountered in clade *Phlegmacium* (subclade d) and clade *Myxacium*. It could be speculated whether the relatively voluminous citriniform spores represent an adaptation to dry environments (Kauserud et al. 2011, Høiland 2012).

A duplex pileus cuticle may also represent an ancestral character state from which a simple cutis has evolved six independent times in our phylogeny. The simple cutis is distinctive for clade *Calochroi* and also for sub-clades a and b of clade *Phlegmacium*. *Cortinarius caperatus* is outstanding by its amyloid duplex cutis (Agerer 2006).

Secondary chemistry

The most conspicuous secondary compounds in genus *Cortinarius* are the anthraquinones of the octaketide biosynthetic pathway (Gill & Steglich 1987). They are distinctive for clades *Dermocybe*, *Pauperae*, *Icterinula*, and *Leprocybe*, but are also encountered in C. *olivaceofuscus*, and sporadically in clade *Telamonia*, *Phlegmacium* (sub-clade b), and *Calochroi*. Typical for clade *Dermocybe* (except *C. sanguineus* (Wulfen) Fr.), *C. olivaceofuscus*, and some species in clade *Calochroi* is content of dimeric pre-anthraquinones of flavomannin type. The dimeric pre-anthraquinones hypericin and skyrin are regularly found in clade *Pauperae*. In sub-clade b of clade *Phlegmacium*, dimeric pre-anthraquinones of phlegmacin type are found in *C. percomis* in our phylogeny, but they are also found in the related C. *nanceiensis* and *C. mussivus* (Gill & Steglich 1987, Garnica et al. 2005). Various monomeric anthraquinones, such as endocrocin, dermolutein, and dermorubin, are found in all species of clade *Dermocybe*, *Pauperae*, *Icterinula*, and *Leprocybe*, and in *C. olivaceofuscus* (only endocrocin), and the two species of clade *Calochroi* that also contain flavomannin pre-anthraquinones. The momomeric anthraquinones emodin, dermoglaucin, and dermocybin are only found in clade *Dermocybe*. In clade *Icterinu-*

la and *Leprocybe*, together with *C. cinnabarinus* Fr. and *C. armillatus* (Fr.) Fr. in clade *Telamonia*, only monomeric anthraquinones are found, no dimeric pre-anthraquinones.

The anthraquinones may act as deterrents to insects and other animals feeding on basidiocarps since it has been demonstrated that anthraquinones in plants (many of them similar to those in fungi, e.g. emodin) have defensive effects upon insects or birds (Trial & Dimond 1979, Michael et al. 1997). Focusing on clade *Dermocybe* it is therefore interesting that the basal lines, spanning from *C. malicorius* to the couple *C. semisanguineus* (Fr.) Gillet and *C. idahoensis* Ammirati & A.H. Sm., have a broad range of anthraquinones, including emodin, dermoglaucin, and dermocybin. The aforementioned species are found in lowland boreal forests (Høiland 1984) rich in fungivorous insects, and they are lacking in arctic-alpine environments. Presumably, these anthraquinones may have been reduced in the derived lineage leading to the group spanning from *C. croceus* (Schaeff.) Gray to the couple *C. uliginosus* Berk. and *C. polaris* Høil. This group only contains endocrocin, dermolutein, and dermorubin, which are universal for all members of *Dermocybe*, and penetrate the cooler, boreal to arctic-alpine environments with less fungivorous insects. For instance, the fungivorous Mycetophilidae, fungus gnats, are particularly species rich in lowland boreal North European forests, but with only few species in alpine environments (Søli & Kjærandsen 2008).

Compounds of nonaketide biosynthetic origin, i.e. the strongly fluorescent xanthones leprocybin and leprocyboside, and the monomeric anthraquinone leprolutein, are distinctive for clade *Leprocybe* (Gill & Steglich 1987). However, these compounds (except leprolutein) are also found in one species, *C. colymbadinus*, in clade *Telamonia*. Like anthraquinones, the xanthones may act as feeding deterrents against insects, as demonstrated for plants (Larson et al. 2010).

An interesting question is whether the possession of the recorded octaketide and nonaketide compounds represents a derived or ancestral character state. Since the actual substances are not seen in the most basal lines in our phylogeny, we may hypothesise that the octaketide pigments were evolved after the split leading to species spanning from clade *Telamonia* to clade *Calochroi*, although the phylogenetic support for this split is limited. The nonaketide compounds may have been evolved later, perhaps after the split leading to species spanning from clade *Telamonia* to clade *Orellani*. Later, the biosyntheses of octaketides or nonaketides may have switched off in many evolutionary lineages, and sometimes replaced by biosyntheses of other compounds, such as substances with nitrogen. A hypothesis has been put forward that the possession of pigments in large quantities in species of *Calochroi* is an ancestral state for this clade, giving rise to species with less or no pigments (Frøslev et al. 2007).

Clade *Telamonia* is, with few exceptions, remarkably "empty" concerning pigments with octaketide or nonaketide pathways. However, our phylogeny indicates that it probably has originated from fungi possessing such pathways, shown by its sister species, *C. olivaceofuscus*, and the few *Telamonia* species containing octaketide or nonaketide substances.

Secondary metabolites containing nitrogen are represented in clade *Orellani*, with the bipyridines orellanine and orelline (Schumacher & Høiland 1983, Gill & Steglich 1987), in the single lines leading to *C. infractus*, with the indole alkaloids pre-infractin (β-carboline-1-propionic acid) and infractopicrin (Brondz et al. 2007, Brondz & Høiland 2008), in *C. subtortus* with (iso)-quinoline alkaloids (Teichert et al. 2008), and in *C. violaceus* with an 1:2 iron (III) (R)-β-dopa complex (von Nussbaum et al. 1998, Spiteller et al. 2000). The metabolites infer good phylogenetic signals for the clades and species at hand, but their diverse chemical nature and erratic occurrence indicate that they have evolved several independent times via different biosynthetic pathways; probably as a response to environmental conditions. The bitter taste due to the alkaloids in *C. infractus* and *C. subtortus* may protect the basidiocarps from being eaten, since animals usually avoid this (Steglich et al. 1990, Spiteller 2008). The same applies to the non-nitrogen compound crystallopicrin in *C. vibratilis*. Orellanine in *C. rubellus* and *C. orellanus* may have evolved as a response of enhanced soil acidity and liberation of aluminum ions in soil water since it is a good aluminum ion chelator (Høiland 1994).

Ecology

The majority of species in clade *Telamonia* and *Dermocybe* prefer poor, acidic coniferous or *Betula* forests or they are indifferent of forest type. The same applies to the few investigated species of clade *Obtusi*, *Anomali*, *Myxacium*, and *Scauri*. Several species of *Telamonia* and a few of *Dermocybe*, *Obtusi*, *Anomali*, and *Myxacium* have emerged from boreal forests into arctic-alpine environments where they established mycorrhiza with *Salix*, *Betula nana*, *Dryas*, or *Bistorta vivipara* (Høiland 1984, Gulden & Torkelsen 1996, Peintner 2008, Bjorbækmo et al. 2010, Geml et al. 2012). Clade *Telamonia* is remarkably species rich in boreal coniferous forests (Brandrud et al. 1990-2013; Kytövuori et al. 2005; Lindström et al. 2008; Niskanen 2008; Niskanen et al. 2008, 2009, 2011, 2013a), and we expect these forests to represent vigorous evolutionary arenas for clade *Telamonia*.

Contrary, clade *Leprocybe* and *Calochroi*, and sub-clade b and d of *Phlegmacium* prefer richer forest types, often on calcareous soils (Brandrud et al. 1990-2013, Niskanen et al. 2008). The many species in clade *Calochroi* are exclusively Northern Hemispheric (Garnica et al. 2009), usually preferring calcareous, dry soils in well-established low boreal coniferous or temperate broadleaved (Fagaceae) forests (Frøslev et al. 2007). These forest types may represent vigorous evolutionary arenas for clade *Calochroi*. Species in clade *Calochroi* and sub-clade d of *Phlegmacium* are rare and have narrow ecological preferences, and many are included in national red lists in Europe (Brandrud et al. 1990-2013, Frøslev et al. 2007). *Calochroi* may have relatively ancient evolutionary history with a tentative stem about 30 million years (Ryberg & Matheny 2011).

Clade *Pauperae* and clade *Icterinula* are exclusively Southern Hemispheric with preference for mycorrhiza with *Nothofagus* (Moser & Horak 1975, Keller et al. 1988).

The two species in clade *Orellani* have different ecology. *Cortinarius orellanus* is found in warm and dry Mediterranean to temperate broadleaved (Fagaceae) forests, while *C. rubellus* prefers cool and moist boreal coniferous forests, seldom under Fagaceae (Høiland 1980, Brandrud et al. 1990-2013, Niskanen et al. 2008). However, a common trait is that both are specialised to acidic soils (Brandrud et al. 1990-2013, Høiland 1994). Very few orellanine containing *Cortinarius* species are known on global scale, but they occur in both hemispheres (Moser & Horak 1975, Gasparini 2004). The split between *C. orellanus* and *C. rubellus* is set about 10 million years and the tentative stem for the *Orellani* group about 20 million years (Ryberg & Matheny 2011). *Orellani* may represent an isolated evolutionary lineage of which only a few species have survived up to now (Gasparini 2004).

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