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A phylogenetic approach to a global supraspecific taxonomy of *Cortinarius* (*Agaricales*) with an emphasis on the southern mycota

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Maximum Likelihood
phylogeny
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Abstract A section-based taxonomy of *Cortinarius*, covering large parts of the temperate North and South Hemispheres, is presented. Thirty-seven previously described sections are reviewed, while another forty-two sections are proposed as new or as new combinations. Twenty additional clades are recovered but not formally described. Furthermore, six new or combined species names are introduced, and one species is neotypified. The structure is supported by morphological characters and molecular evidence, based on two (nrITS and nrLSU) and four (nrITS, nrLSU, *rpb1* and *rpb2*) loci datasets and analysed by Maximum Likelihood methods (PhyML, RAxML). Altogether 789 *Cortinarius* samples were included in the study.

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INTRODUCTION

It is self-evident that large fungal genera are in a special need for structuring into lower-rank taxa in order to assist the mycologist in navigating the genus and to provide an overview of its taxonomy. *Cortinarius* is the most diverse and species-rich genus of macrofungi (cf. Niskanen et al. 2016). Historically, several systems of subgenera, sections, and other infrageneric taxa were erected in *Cortinarius*, based on the macromorphology of geographically limited samplings. These taxa were in many cases emended, combined, or divided as micromorphological, chemical, and later molecular data became available from a widening geographical span. In his ground-breaking work, Moser in Singer (1986) listed all then known sections and other supraspecific taxa of the genus, a base that was later used to expand the taxonomy in different directions (e.g., Bidaud et al. 1994, Brandrud et al. 1994: 31). We expect this process to continue, especially when considering that many geographical areas (e.g., Africa) remain poorly sampled, and will no doubt prove to contain additional *Cortinarius* taxa.

Many studies during the past twenty years have explored different aspects of the phylogeny of *Cortinarius.* Most of the species are described from Europe (c. 1900 out of a total 2700 worldwide), followed by North America, which means that the Northern Hemisphere tends to dominate in extant works (cf. Peintner et al. 2004). But in their barcoding study, Garnica et al. (2016) addressed the genus on a global scale and revealed a cladal structure of c. 900 species based on the internal transcribed spacer regions (nrITS) of the nuclear ribosomal DNA. Garnica et al. (2016: Fig. S2) also produced a phylogram of a limited sampling based on five loci, annotated with support figures. This showed that the genus contains two major lineages that appear to be endemic to the Northern Hemisphere, namely sect. *Calochroi* and subg. *Telamonia* s.str., thus corroborating previous works on these particular groups (Høiland & Holst-Jensen 2000, Frøslev et al. 2006b, Niskanen 2008, Ortega et al. 2008, Garnica et al. 2009, 2011, Niskanen et al. 2012, cf. Soop & Gasparini 2011). In addition, several other works provide the outline of a phylogeny-based infrageneric taxonomy for selected groups within the genus, based on northern taxa (Brandrud et al. 2013, 2014, Liimatainen et al. 2014, Saar et al. 2014).

On the other hand, it is evident from the cited works, as well as from other studies (Peintner et al. 2004, Garnica et al. 2005, Stensrud et al. 2014, Soop 2016, Soop et al. 2018), that the genus contains many lineages that are shared between the Northern and Southern Hemispheres, as well as others that appear to be endemic to either. They are often also widely distributed within their hemispheres; for example, a substantial number of clades are shared between North America and Europe (Garnica et al. 2011, Harrower et al. 2011, Niskanen et al. 2012, Ammirati et al. 2013, Liimatainen et al. 2015). One notes, however, that so far little has been done on the *Cortinarius* taxonomy in north-eastern Asia and in Africa, leaving an important gap in our knowledge of the genus (cf. Horak 1983).

A common result from many of the cited phylogenetic studies, is that most traditional subgenera (such as *Phlegmacium* and *Telamonia*) turn out to be polyphyletic, while many smaller, lower-rank taxa look promising for structuring the genus from well-supported monophyletic clades. The phylogenetic delineation of well-supported subgenera within *Cortinarius* remains to be achieved through the sequencing of additional genes, or more promisingly, using a phylogenomics approach. In the interim, sections suggest themselves as suitable, monophyletic building-blocks, that may be used later to construct higher taxa. Consequently, in this study we aimed at the following:

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- Combine morphological markers with suitable genetic markers to map the sections of the genus, based on as large a sample set as possible.
- Use existing sections or other suitable taxa as far as possible, sometimes in the form of new combinations. When not possible, describe new sections.
- Provide, for each proposed section, a list of species, either species sampled in the study, or putative species that we assume to be members.
- Map out the geographical distribution of *Cortinarius* sections, with particular attention to the Southern Hemisphere, an area that has so far been sparingly studied (Horak 1983).

With this approach to a supraspecific taxonomy, based on a large number of globally sampled species, we hope to provide a useful framework for expanding the taxonomy of the genus, into higher ranks (e.g., subgenera) or lower ranks (e.g., subsections), as further supported clades become apparent. Thus, in a future effort the sections may be combined or divided, or they may form the basis for new combinations.

MATERIALS AND METHODS

Geographical scope

As mentioned in the Introduction, due to scarcity of material, African and Northeast-Asian species are grossly underrepresented. The following principal areas have been sampled: Europe, North/Central/South America, Australia, and New Zealand.

Taxonomic scope

All the samples are specimens of *Cortinarius* s.lat., including the genera *Cuphocybe*, *Protoglossum*, *Quadrispora*, *Rapacea*, *Rozites*, *Thaxterogaster*, and *Hymenogaster* p.p., these being synonyms of *Cortinarius* (Peintner et al. 2001, 2002, Gasparini 2013, 2016). We also include the genus *Gigasperma*. Two important boreal groups, *Calochroi* and *Telamonia* s.str., are represented only by a few token species, due to several recent and ongoing studies cited in the Introduction, which explore the infrageneric ranks involved.

Molecular sampling

Sequences from 634 collections were chosen from GenBank (http://www.ncbi.nlm.nih.gov/) or UNITE (http://unite.ut.ee/), and another 346 sequences were newly generated in this study (Table 1). For a detailed description of the methods used for DNA extraction and PCRs see Soop et al. (2016) and Papp & Dima (2018). Where possible, type collections were included in the dataset; 140 samples represent holo-, neo-, epi- or paratypes. All samples were sequenced in the nrITS (ITS1+5.8S+ITS2) region, and in addition most were sequenced in one or more of the nrLSU, *rpb1*, and *rpb2* regions. Seventy collections are represented only by ITS; in these cases the taxon was considered important to confirm a position in the phylogeny. When many sequences of a species were available and their similarity in a separate alignment (not shown) was > 99 %, only one or two samples were chosen. Three species in genera *Conocybe*, *Descolea*, and *Flammula* were chosen as outgroup. See Table 1 for GenBank and fungarium voucher numbers, sections, and provenance.

Phylogenetic reconstruction

The sequences were pre-checked and edited in MEGA 5.2 (Tamura et al. 2011). Multiple sequence alignments were performed separately on the individual gene regions using the online version of MAFFT v. 7 (Katoh & Standley 2013). We generated two datasets: a 2-loci (ITS+LSU) and a 4-loci (ITS+LSU+*rpb1*-*rpb2*) alignment. For the 2-loci dataset ITS and LSU sequences from 730 specimens were aligned separately using the E-INS-i algorithm (Katoh & Standley 2013), following Garnica et al. (2016). The alignments were manually corrected, trimmed and concatenated in SeaView 4 (Gouy et al. 2010). Preliminary analysis was run in PhyML 3.1 (Guindon & Gascuel 2003) using the following settings: GTR+I+G model of evolution, gamma distribution of 10 rate categories, and tree topology search as SPR.

Thereafter FastGap 1.2 (Borchsenius 2009) was used to code the phylogenetically informative insertion/deletion positions (indel) in both the ITS and LSU alignments following the simple indel coding algorithm (Simmons et al. 2001). After concatenating the nucleotide and binary data in SeaView 4, the partitioned alignment was submitted to maximum likelihood analysis using RAxML (Stamatakis 2014) as implemented in raxmlGUI 1.5.2 (Silvestro & Michalak 2012). The GTRGAMMA substitution model for the nucleotide partitions (ITS1+5.8S+ITS2+LSU) and the default setting for binary (indel) data was chosen. Rapid bootstrap analysis with 1 000 replicates was applied for testing branch support.

Based on the results of the 2-loci analyses, we selected representative sequences of species in each putative section to assemble a 4-loci dataset composed of 460 ITS, 417 LSU, 161 *rpb1*, and 87 *rpb2* sequences. For the ITS and *rpb1* loci we used the E-INS-i (Katoh & Standley 2013), for the LSU locus the G-INS-i (Katoh et al. 2005), and for the *rpb2* locus the FFT-NS-i algorithms (Katoh et al. 2002), all under default settings. Referring to the 2-loci dataset (above), we used the same programs for manual inspection of the separate alignments as well as for concatenating the individual alignments and binary data. Six nucleotide (ITS1+5.8S+ITS2+LSU+*rpb1*+*rpb2*) and one binary (indel) partitions were defined in our supermatrix which was then submitted to raxmlGUI (Silvestro & Michalak 2012) with the same options as above. Alignments are available in TreeBase (S22220), newly generated sequences are deposited in GenBank (Table 1). The trees were in all cases edited and visualized in MEGA 7 (Tamura et al. 2013).

Section descriptions

Major morphological characters have been chosen for each new section. Lamellar colour always pertains to immature specimens. Odour, taste, and marginal lamellar elements are mentioned only when significant. The alkaline reaction was made with a 30 % NaOH (or KOH) solution. Unless otherwise specified, stipes are dry, and the hyphae are provided with clamp connections.

RESULTS

The final concatenated 2-loci data matrix comprises 730 sequences and 2 412 sites plus 1 324 binary characters, whereas the 4-loci data matrix comprises 460 sequences and 4 669 sites plus 1 118 binary characters. In total these datasets represent 601 *Cortinarius* species.

The resulting 4-loci and 2-loci phylograms (Fig. 1, 2) reveal a number of distinct clades, many of which exhibit a moderate (60–70 %; cf. Frøslev et al. 2005, Jeewon & Hyde 2016) to robust (80–100 %) bootstrap support values. The PhyML tree is not shown in this study, but its support values for sections and clades are mapped to the 2-loci phylogram (Fig. 2). Not unexpectedly we thereby recover a number of traditionally recognised and named sections and other supraspecific taxa. Other sections, preponderantly those with a bihemispherical or southern distribution, are described here as new. Some of

Table 1 Sequences newly generated and first published in this study.

		GenBank accession no.					
Species	Herbarium ID	ITS	LSU	*rpb1*	*rpb2*	Section/Clade	Country
C. achrous cf.	PDD107722/CO2192	KT875175	in ITS			/Achroi	New Zealand
C. aegrotus (type)	PDD27270		GU233389				New Zealand
C. aerugineoconicus (type)	PDD27258		GU233408			/Entheosi	New Zealand
C. alboaggregatus	JAC12509/PDD96523	MH101554	MH108393	MH141038		*Alboaggregati*	New Zealand
C. alboamarescens	TEB334-14/DB5405	MK358079				*Vibratiles*	Norway
C. alboroseus	PDD105432/JAC13150		MH108404				New Zealand
C. alienatus	PDD27180		GU233384				New Zealand
	PDD96972/JAC12868	MH101562	MH108401				New Zealand
C. amblyonis cf.	PDD94049/CO1801	MH101544	MH108383			*Obtusi*	New Zealand
C. anisodorus	PDD88506	KT334133	KT334145				New Zealand
C. ardesiacus cf.	PDD72855	MH101533	MH108374			/Ardesiaci	New Zealand
C. areni-silvae	MIKH-T508	MK358080	MK358059	MK340950		*Phlegmacioides*	Russia
C. areolatoimbricatus	PSC1552	MK358081		MK340951	MK340969		Australia
C. armiae	PDD105600/JAC13347	MH101568	MH108406			*Limonii*	New Zealand
C. atrolazulinus	PDD97542/CO1917	KJ635241	in ITS				New Zealand
C. australiensis	PERTH 6434991	MG553064		MK340952	MK340970	/Australienses	Australia
C. australiensis cf.	JAC12796	MK358082	MK358060	MK340953	MK340971	/Australienses	New Zealand
C. australis	PDD107712/CO2182	KT875192	in ITS			*Purpurascentes*	New Zealand
	PDD80010/JAC8617	MH101535	MH108375			*Purpurascentes*	New Zealand
C. austrovaginatus	PDD80251/JAC8985	MH101537	MH108377			*Austrovaginati*	New Zealand
	PDD94052/CO1808	MK358083				*Austrovaginati*	New Zealand
C. badiohepaticus ined.	PDD72785	MH101530	MH108364			*Lustrabiles*	New Zealand
C. *balteatibulbosus*	SSt16-073	MK358084	MK358061	MK340954		*Phlegmacioides*	Germany
C. barbatus	TEB582b-15	MK358085				*Vibratiles*	Norway
C. basifibrillosus ined.	PDD72794	MH101531	MH108368			*Obtusi*	New Zealand
C. bellus	PDD103880/CO1238		KF727319				New Zealand
C. brunneotinctus	DB6257	MK358086	MK358062	MK340955			Hungary
C. brunneus	DB2548		MK358063			*Telamonia*	Hungary
C. caesiostramineus	DB6237			MK340956		*Caerulescentes*	Norway
C. calaisopus	PDD103678/CO2106		KF727338			*Delibuti*	New Zealand
C. calaisopus II	PDD80264/JAC8990	MH101538				*Delibuti*	New Zealand
C. camptoros	GS16-5	MK358087		MK340957		/Camptori	Germany
C. carbonellus (type)	PDD70502/CO1045		GU233391	MH141041	MH141021	*Carbonelli*	New Zealand
C. cardinalis (type)	PDD27174		GU233415				New Zealand
C. carneipallidus	PDD103682/CO2110		KF727337			*Cortinarius*	New Zealand
C. cartilagineus	PDD105768/JAC13517		MH108409			/Cartilaginei	New Zealand
C. caryotis (type)	PDD71004/CO1043		GU233407	MH141039		*Limonii*	New Zealand
C. caryotoides	PDD105781/JAC13530	MH101572	MH108410			*Limonii*	New Zealand
C. castaneiceps (type)	PDD27269	GU233332					New Zealand
C. castaneiceps cf.	PDD106108/JAC13905	MH101580	MH108418			*Malvacaei*	New Zealand
C. castaneodiscus	PDD72712	MH101525	MH108347			*Ignelli*	New Zealand
C. castaneodiscus II	PDD107509/CO1236	MG019348	MG019374			*Ignelli*	New Zealand
C. castoreus	JAC12825/PDD96929	MH101557	MH108396	MH141045		*Rapacea*	New Zealand
C. chlorophyllus (type)	PDD103681/CO2109		KF727327			*Scauri*	New Zealand
C. chrysma (type)	PDD68469/CO788		GU233393			*Chrysmata*	New Zealand
	F44428/CO1234	MK358088	MK358064	MK340958		*Chrysmata*	New Zealand
C. chrysoconius cf.	PDD105532/JAC13280	MH101567	MH108405			/Chrysoconii	New Zealand
C. collybianus (type)	PDD70509/CO1074		GU233417		MH141024	*Callistei*	New Zealand
C. collybianus cf.	PDD72676	MH101523				*Callistei*	New Zealand
C. conei	PDD83709/JAC9578	MH101539				*Austrovaginati*	New Zealand
C. cramesinus (type)	PDD27173		GU233420				New Zealand
C. cremeolina (type)	PDD70506/CO1058		JX000380			*Cremeolinae*	New Zealand
C. cremeolina cf.	PDD105601/JAC13348	MH101569	MH108407			*Cremeolinae*	New Zealand
C. cremeolina var. *subpicoides*	PDD105782/JAC13531		MH108411			*Cremeolinae*	New Zealand
	PDD107719/CO2189	KT875196	in ITS			*Cremeolinae*	New Zealand
C. cruentoides (type)	PDD101864/CO2038			MH141051	MH141014	*Cruentoides*	New Zealand
C. crypticus (type)	PDD27002	JQ063072				*Gigasperma*	New Zealand
	PDD100127	JQ063070	JQ063071			*Gigasperma*	New Zealand
C. cucumeris	PDD96335/JAC12095		MH108392			*Cycnei*	New Zealand
C. cuphomorphus (type)	PDD103680/CO2108		KF727317			*Cuphomorphi*	New Zealand
C. cupreonatus (type)	PDD70503/CO1048		JX000379				New Zealand
	JAC13774/PDD105979	MH101577	MH108415	MH141040	MH141020		New Zealand
C. cycneus	PDD103783	MH101565	MH108403			*Cycnei*	New Zealand
C. cypripedi (type)	PDD107723/CO2193			MH141050		*Illumini*	New Zealand
C. daulnoyae	SSt15-097	MK358089	MK358065	MK340959		*Phlegmacioides*	Germany
C. diaphorus ined.	PDD107503/CO1447	MG019351	MG019370				New Zealand
C. dulciolens	FUNNZ2013-26	MK358090	MK358066			*Dulciolentes*	New Zealand
C. dulciorum (type)	PDD78797/CO1460		JX000395			*Cremeolinae*	New Zealand
C. durifoliorum	PDD107700/CO2170			MH141033	MH141028	*Anomali*	New Zealand
C. dysodes (type)	PDD70499/CO1038		GU233394			*Camphorati*	New Zealand
C. dysodes cf.	PDD96310/JAC12070	MH101551	MH108390			*Camphorati*	New Zealand
C. elaiops (type)	PDD88271/CO1649		JX000400			*Pauperae*	New Zealand
C. emollitoides	DB1576	MK358091				*Vibratiles*	Hungary
C. eunomalus	PDD107706/CO2176			MH141035	MH141029		New Zealand
C. eutactus (type)	PDD78807/CO1483		JX000397			*Crassi*	New Zealand
C. exlugubris (type)	PDD67181/CO818		GU233409				New Zealand
C. fasciatus cf.	TEB517-15/DB5839	MK358092	MK358067	MK340960		*Laeti*	Norway
C. faucium ined.	PDD94046/CO1795	KP343698	KP343699			/Rufoaurantii	New Zealand
C. georgiolens	GS03-1	MK358093	MK358068	MK340961		*Caerulescentes*	Germany

Table 1 (cont.)

		GenBank accession no.					
Species	Herbarium ID	ITS	LSU	*rpb1*	*rpb2*	Section/Clade	Country
C. icterinoides	CO1690	MK358094		MK340962		*Chrysmata*	New Zealand
C. ignellus (type)	PDD73154/CO1245		JX000390			*Ignelli*	New Zealand
	PDD103698/CO2123		KF727313			*Ignelli*	New Zealand
C. incensus (type)	PDD73147/CO1225	MK358095	JX000387			*Incensi*	New Zealand
C. indolicus	PDD103881/CO1246		KF727334				New Zealand
C. indotatus	PDD107733/CO2203	KT875182	in ITS			*Pauperae*	New Zealand
C. ionomataius (type)	PDD78765/CO1406		JX000393				New Zealand
	PDD80011/JAC8615	MH101536	MH108376				New Zealand
C. ixomolynus	PDD107720/CO2190	KT875207	in ITS				New Zealand
C. kaimanawa (type)	PDD73133/CO1259		JX000383			*Purpurascentes*	New Zealand
	PDD101841/CO2014	KJ635213	in ITS			*Purpurascentes*	New Zealand
C. laetiluteinus ined.	PDD101852/CO2025	KJ635215	in ITS			*Laeti*	New Zealand
C. lamproxanthus (type)	PDD78780/CO1429		JX000394				New Zealand
C. laquellus	PDD72766	MH101527	MH108355			*Laquelli*	New Zealand
C. leptospermorum (type)	PDD27183		GU233395			*Pauperae*	New Zealand
C. lubricanescens	PDD75709		GU233402			*Cycnei*	New Zealand
	PDD95404/JAC10948	MH101546	MH108385			*Cycnei*	New Zealand
C. luteinus (type)	PDD73137/CO1257		JX000386			*Luteini*	New Zealand
C. mariae	PDD72487	MH101518	MH108318	MH141044		*Rapacea*	New Zealand
C. marmoratus	PDD71007/CO1014	GU233381	GU233381			*Marmorati*	New Zealand
C. medioscaurus (type)	PDD103691/CO2121		KF727332			*Austrovaginati*	New Zealand
C. meleagris	PDD72781		HM060323			*Rozites*	New Zealand
	PDD96207/JAC11811	MH101549	MH108388			*Rozites*	New Zealand
C. melimyxa	PDD94024/CO1768		GU233405				New Zealand
C. melleomitis	PDD107704/CO2174	KT875184	in ITS	MH141043	MH141026	*Vibratiles*	New Zealand
C. memoria-annae	JAC8614	MK358096	MK358069				New Zealand
C. minorisporus ined.	PDD95306/JAC10838	KT334129	KT334142				New Zealand
C. minoscaurus (type)	PDD71005/CO1013		GU233377				New Zealand
	PDD87013/JAC9904	MH101540	MH108379				New Zealand
C. miwok	CO610	MK358097				*Telamonia*	USA
C. mycenarum (type)	PDD107715/CO2185			MH141048	MH141013		New Zealand
C. myrticaryotis ined.	PDD103635/CO815	KF727388	KF727339			*Limonii*	New Zealand
C. naphthalinus (type)	PDD70505/CO1054		GU233401				New Zealand
C. napivelatus	PDD72728		MH108348			*Subcastanelli*	New Zealand
C. neocallisteus	CO2145	MK358098				*Callistei*	Sweden
C. olidoamarus	DB6012	MK358099		MK340963	MK340972	*Glaucopodes*	Hungary
C. olivaceoniger	PDD96938/JAC12834	MH101558	MH108397	MH141049	MH141012	*Walkeri*	New Zealand
C. olivaceopictus cf.	JAC12554/PDD96679	MH101556	MH108395	MH141047	MH141011	*Pauperae*	New Zealand
C. olorinatus	PDD72753		HM060331				New Zealand
C. ophryx (type)	PDD78769/CO1411	KJ547667				*Persplendidi*	New Zealand
C. ophryx cf.	PDD103688/CO2117	MK358100				*Persplendidi*	New Zealand
C. orixanthus (type)	PDD88253/CO1614		JX000398			/Orixanthi	New Zealand
C. papaver (type)	PDD71003/CO1066		GU233399				New Zealand
C. paraonui (type)	PDD77471/CO1316		JX000392				New Zealand
C. paraxanthus (type)	PDD78802/CO1472		JX000396			*Paraxanthi*	New Zealand
C. peraureus (type)	PDD67177/CO785		JX000378				New Zealand
	PDD103638/CO1047	KF727391	KF727321				New Zealand
C. peraurilis	PDD103660/CO2087	MH101564		MK340964			New Zealand
C. perelegans (type)	PDD70500/CO1040		GU233398				New Zealand
C. periclymenus (type)	PDD71008/CO1060		GU233379				New Zealand
C. persplendidus (type)	PDD27168		GU233387			*Persplendidi*	New Zealand
	PDD96608/JAC12491	MH101555	MH108394	MH141052	MH141017	*Persplendidi*	New Zealand
C. phaeomyxa	PDD107511/CO1025		MG019367			*Cuphocybe*	New Zealand
C. pholiotellus	PDD96959/JAC12855	MH101560	MH108399	MH141042	MH141016		New Zealand
	PDD96960/JAC12856	MH101561	MH108400				New Zealand
C. picoides	PDD103886/CO1643		KF727302			*Turmales*	New Zealand
	PDD94019	GU233371	GU233424	MH141037	MH141022	*Turmales*	New Zealand
C. pisciodorus	JAC13813/PDD106018		MH108417	MH141031		*Dulciolentes*	New Zealand
C. poliotrichus ined.	PDD103684/CO2112	KF727390	KF727333			*Austrocyanites*	New Zealand
C. porphyroideus	CO1663	MK358102					New Zealand
C. porphyrophaeus (type)	PDD27263	GU233331	GU233416				New Zealand
C. promethenus (type)	PDD94059/CO1815			MK340965			New Zealand
C. pseliocaulis	PDD105646/JAC13394	MH101570	MH108408				New Zealand
C. pseudoarcuatorum	TEB584-16	MK358103		MK340966			Russia
C. pyrrhomarmarus ined.	PDD78789/CO1449	MK358104				*Austroduracini*	New Zealand
C. rattinoides (type)	PDD88283/CO1673		JX000406			*Anomali*	New Zealand
C. rattinus (type)	PDD71009/CO1061		GU233419			*Carbonelli*	New Zealand
C. reverendissimus	TEB630-16	MK358105	MK358071	MK340967		/Varii	Russia
C. rhipiduranus (type)	PDD88269/CO1645		JX000399			*Purpurascentes*	New Zealand
	PDD103673/CO2101		KF727323			*Purpurascentes*	New Zealand
C. rotundisporus	PDD96298/JAC12057	MH101550	MH108389			*Delibuti*	New Zealand
C. rotundisporus cf.	PDD72733	MH101526	MH108349			*Delibuti*	New Zealand
C. rubripurpuratus	PDD103883/CO1453		KF727306				New Zealand
C. rubrodactylus	PDD105784/JAC13533	MH101574	MH108412			*Callistei*	New Zealand
C. saturniorum (type)	PDD67176/CO783		GU233388				New Zealand
	JAC13780/PDD105985	MH101578	MH108416	MH141034	MH141019		New Zealand
C. sciurellus (type)	PDD103641/CO1679		KF727303		MH141015	*Pauperae*	New Zealand
C. sclerophyllorum cf.	PDD72685/ZT9610	MH101524	MH108339			*Bolares*	New Zealand
C. singularis cf.	PDD103675/CO2103	KF727376	KF727326			*Scauri*	New Zealand

Table 1 (cont.)

		GenBank accession no.					
Species	Herbarium ID	ITS	LSU	*rpb1*	*rpb2*	Section/Clade	Country
C. singularis II cf.	PDD72665	MH101521	MH108335			*Scauri*	New Zealand
C. sp.	PDD96951/JAC12847	MH101559	MH108398			*Verniciori*	New Zealand
C. sp.	PDD97072/JAC12973	MH101563	MH108402			*Pauperae*	New Zealand
C. sp.	Buyck 08-153	MK358106	MK358072			*Cortinarius*	Madagascar
C. sp.	Buyck 08-252	MK358107	MK358073			*Persplendidi*	Madagascar
C. sp. I	PDD72770	MH101528	MH108357			*Laeti*	New Zealand
C. sp. I	PDD107520/CO1319	MK358108				/Minilaci	New Zealand
C. sp. I	PDD87652/JAC10807	MH101542	MH108381			*Obtusi*	New Zealand
C. sp. II	PDD72798/ZT9699	MH101532	MH108370			/Minilaci	New Zealand
C. sp. II	PDD72773	MH101529	MH108359			*Obtusi*	New Zealand
C. sp. III	PDD87651/JAC10806	MH101541	MH108380			*Laeti*	New Zealand
C. sp. III	JAC12593	MK358109	MK358074			*Obtusi*	New Zealand
C. sp. IV	PDD87682/JAC10674	MH101543	MH108382			*Laeti*	New Zealand
C. sp. IV	JAC13734	MK358110				*Obtusi*	New Zealand
C. sp. V	PDD72670	MH101522				*Laeti*	New Zealand
C. sp. V	PDD95246/JAC10673	MH101545	MH108384	MH141046	MH141010	*Obtusi*	New Zealand
C. squameopercomis ined.	TEB397-16	MK358111	MK358075			*Percomes*	Norway
C. subcastanellus	PDD95557/JAC11107		MH108386			*Subcastanelli*	New Zealand
	FUNNZ2013 1219	MK358112	MK358076			*Subcastanelli*	New Zealand
C. subgemmeus	PDD72620	MH101520	MH108325			*Rubicunduli*	New Zealand
	PDD78793/CO1455	MH101534				*Rubicunduli*	New Zealand
C. suborixanthus ined.	PDD101824/CO1994	KJ635208	in ITS			/Orixanthi	New Zealand
C. suecicolor (type)	PDD74698/CO1185		JX000391			*Anomali*	New Zealand
C. suecicolor cf.	PDD105967/JAC13762	MH101576	MH108414	MH141032	MH141027	*Anomali*	New Zealand
C. taylorianus cf.	PDD107692/CO2162	MH101581	MH108419			*Archeriani*	New Zealand
C. tessiae	PDD107517/CO1450	MG019356	MG019365			*Delibuti*	New Zealand
C. turcopes cf.	PDD97513/CO1885	KJ635235	in ITS			/Turcopedes	New Zealand
C. ursus (type)	PDD70510/CO1075		JX000381				New Zealand
C. variosimilis	TEB642-16	MK358113	MK358077	MK340968		/Varii	Russia
C. velicopia cf.	CO611	MK358114				*Subolivascentes*	USA
C. vernicifer (type)	PDD88273/CO1654		JX000401				New Zealand
C. verniciorum	JAC13232	MK358115	MK358078			*Verniciori*	New Zealand
C. viscilaetus	JAC13736/PDD105941	MH101575	MH108413	MH141053	MH141023	*Limonii*	New Zealand
	PDD107734/CO2204	KT875206	in ITS			*Limonii*	New Zealand
	PDD71010/CO812		GU233378			*Limonii*	New Zealand
C. viscoviridis	PDD101840/CO2013	JQ282171	JQ282174				New Zealand
C. vitreofulvus (type)	PDD97545/CO1920			MH141036	MH141018	*Marmorati*	New Zealand
C. vitreofulvus cf.	PDD107727/CO2197	KT875200	in ITS			*Marmorati*	New Zealand
C. waiporianus	PDD107705/CO2175	KT875191	in ITS			*Laeti*	New Zealand
	PDD95907/JAC11512	MH101548	MH108387		MH141009	*Laeti*	New Zealand
C. wallacei	JAC12076/PDD96316	MH101552	MH108391	MH141030	MH141025	*Subcastanelli*	New Zealand
C. xenosma (type)	PDD73149/CO1182		JX000389				New Zealand

these new taxa were anticipated in earlier works on the global phylogeny of the genus (Peintner et al. 2004, Garnica et al. 2005), and were sometimes given clade names that inform our section names. We identify 37 previously described sections, while 42 sections are here either described as new or based on taxa previously at a different rank. Monotypic sections (with the exception of *Gigasperma*) are not considered, even if typified by an included species. In addition, due to ongoing research into the taxonomy of several *Cortinarius* groups (including cases of insufficiently known taxa), 20 putative new sections are here discussed merely as named clades.

Morphological similarities among the species of a section are often obvious, even though clear synapomorphies are fairly rare. Especially in lineages with austral members, several phenotypic forms are sometimes present, while possessing other shared attributes that can be used to characterise the section. For example, a section may contain taxa with both agaricoid and sequestrate habits, but which all present a yellowish coloration and a viscid universal veil that may be regarded as sectional traits.

There are many singleton species in our phylograms, which our analysis could not associate with other taxa with any confidence (Fig. 1). Others appear to form loose but consistent associations with low bootstrap values; these are listed as Unsupported Groups in the context of a related section.

TAXONOMY

The sections are presented in a number of main groupings, largely based on the principal lineages recovered in the phylogeny of Fig. S2 in Garnica et al. (2016). The groupings also roughly correspond to subgenera of a traditional taxonomy (e.g., that of Brandrud et al. 1989, 1992, 1994, 1998, 2012) and are ordered accordingly. The following main groupings are used:

1. The type section (*Cortinarius*)
2. Dermocyboid sections
3. Leprocyboid sections
4. Phlegmacioid sections
    - 4.1. Euphlegmacia
    - 4.2. *Calochroi* s.lat.
    - 4.3. Pseudophlegmacia
5. Anomaloid sections
6. *Gigasperma*
7. Myxacioid sections
8. Telamonioid sections
    - 8.1. Subgenus *Telamonia* s.str.
    - 8.2. Other telamonioid sections

For each section, the type is specified and the section or clade members are listed (epithets only, the name *Cortinarius* being subsumed). Our dataset comprises about 20 undescribed species whose formal protologues will be presented in future publications. Another 64 undescribed species are designated as ‘cf.’ or ‘*C.* sp.’.

Fig. 1 Maximum likelihood (RAxML) phylogenetic tree of a selection of the *Cortinarius* samples included in this study, depicting the supraspecific structure of the genus. The dataset of 460 samples consists of nrITS, nrLSU, *rpb1*, and *rpb2* sequences with binary data from gap coding of ITS and LSU. Seven partitions are used: ITS1: 1–554, 5.8S: 555–705, ITS2: 706–1244, LSU: 1245–2355, *rpb1*: 2356–3901, *rpb2*: 3902–4670, BIN: 4671–6030. Vouchers and abbreviated geographical provenances are included in the labels. Assigned section or clade names are shown with gross morphological traits (i.e., belonging to the main categories of this study) indicated by colours (dark violet = sect. *Cortinarius*; red = dermocyboid sections; greenish yellow = leprocyboid sections; dark blue = Euphlegmacia + *Calochroi*; light blue = Pseudophelgmacia; pink = anomaloid groups; black = sect. *Gigasperma*; green = myxacioid sections; brown = telamonioid sections). RAxML bootstrap support values are shown only above 50 %.


C. limonius JFA12559 Eur
C. limonius KH8 Eur
C. aurantiobrunneus JFA11937 CAm
C. caryotis PDD71004 CO1043 Typus NZ
C. armiae PDD105600 JAC13347 NZ
C. rubrimarginatus PDD107502 CO1467 Typus NZ
C. viscilaetus JAC13736 PDD105941 NZ
sect. Limonii
C. controversus A20523A0R Aus
C. infucatus TUB011827 Eur
C. callisteus T45 Eur
C. neocallisteus F18486 Typus NAm
C. eucollybianus PDD107518 CO1230 NZ
C. collybianus PDD70509 CO1074 Typus NZ
C. rubrodactylus PDD105784 JAC13533 NZ
C. austrolimonius var. ochrovelatus TUB011468 SAm
sect. Callistei
C. australiensis PERTH6434991 Aus
C. cf. australiensis JAC12796 NZ
/Australienses
C. subgemmeus PDD78793 CO1455 NZ
C. rubicundulus TUB011829 Eur
sect. Rubicunduli
C. crassus TUB020415 + TUB019696 Eur
C. eutactus PDD78807 CO1483 Typus NZ
sect. Crassi
C. arcifolius TUB020414 Eur
C. subhygrophanus TUB020412 Eur
/Arcifolii
C. aurora JFA12724 NAm
C. prasinus TSJ2002-034 Eur
C. ochraceopallescens TUB012774 Eur
C. magnivelatus OSC81327 NAm
C. metarius TSJ2000-069 Eur
C. fulvocitrinus TUB012713 Eur
C. violaceipes TSJ2002-015 + TUB011439 Eur
sect. Calochroi s.l.
C. lustrabilis TUB011835 Eur
C. badiohepaticus ined. PDD72785 NZ
/Lustrabiles
C. rattinus PDD71009 CO1061 Typus NZ
C. carbonellus PDD70502 CO1045 Typus NZ
sect. Carbonelli
C. cupreonatus JAC13774 PDD105979 NZ
C. exlugubris PDD67181 CO818 Typus NZ
C. aleuriosmus TUB011840 Eur
C. amoenolens TUB011459 Eur
sect. Amoenolentes
C. gracilior TUB011857 Eur
C. subdecolorans TUB019755 Eur
C. olivaceodionysae TUB011856 Eur
C. dionysae TSJ2000-102 Eur
/Dionysae
C. luteoimmarginatus TUB019767 Eur
C. camptoros GS16-5 Eur
C. viridocoeruleus TF2000-056 Eur
/Camptori
C. eucaeruleus TUB011878 Eur
C. eucaeruleus TF2002-007 Eur
C. coerulescentium TF2002-002 Eur
C. perpallens JV991105 Eur
C. terpsichores IB93/619 Eur
/Eucaerulei
C. xanthoochraceus TF1999-084 Eur
C. subrugulosus CO901 Eur
C. mediterraneensis IB19800618 Typus Eur
C. aureocistophilus SCMB5145 Typus Eur
C. fulminoides TUB019817 Eur
sect. Aureocistophili
C. brunnescens AHS68806 Typus NAm
C. subcaeruleus AHS68260 Typus NAm
sect. Subhymenogaster
C. caesiostramineus TUB011845 + DB6237 Eur
C. georgiolens GS03-1 Eur
C. caesiocanescens TUB011847 Eur
C. foetens TUB019736 Eur
C. subalbescens TUB020394 Eur
C. caerulescens TUB012146 Eur
sect. Caerulescentes
C. olidoamarus DB6012 + DB4307 Eur
C. olidovolvatus TUB019720 Eur
C. magicus TSJ1999-050 Eur
C. glaucopus SMIA20 NAm
C. subrubrovelatus TUB011414 Eur
sect. Glaucopodes
C. glaucocephalus UBC-F19524 NAm
C. subsolitarius MICH10426 Typus NAm
/Glaucocephali
C. luhmannii TUB019808 + TF2001-120 Eur
C. moenne-loccozii TUB019711 Eur
C. barrentium TUB019743 Eur
C. subolivascens JFA12891 NAm
/Subolivascentes
C. ponderosus BW 2004-10241 NAm
C. prasinocyaneus TSJ2003-033 Eur
C. bulbolatens TUB019806 Eur
C. caesiocortinatus TUB011400 Eur
sect. Caesiocortinati
C. vernicifer PDD88273 CO1654 Typus NZ
C. memoria-annae PDD107638 CO1482 NZ
C. rufoaurantius TUB011291 SAm
C. faucium ined. PDD94046 CO1795 NZ
/Rufoaurantii
C. violaceorubens TUB011885 Eur
C. cyanites AT2004089 Eur
sect. Cyanites
C. areolatoimbricatus PSC1552 Aus
C. argutus T44 Eur
C. paracephalixus Reinders-87 Eur
C. subfraudulosus CO607 Eur
C. herculeus TUB019805 Eur
C. fraudulosoides TUB011870 Eur
sect. Arguti
C. squameoradicans TUB019726 Eur
C. maculosus JV991102 5 Eur
C. caligatus TEB153-84 Eur
/Caligati
C. pseudovulpinus TUB011874 Eur
C. vulpinus TUB011406 Eur
C. oertelii ined. TUB011409 Eur
C. obsoletus TUB019791 Eur
/Obsoleti
C. variosimilis TEB642-16 Eur
C. cf. variosimilis EH33 NAm
C. varius TUB019715 Eur
C. decolorans TUB011392 Eur
C. reverendissimus TEB630-16 Eur
/Varii
C. pini MES4265 Eur
C. blattoi IB19970296 (C. pseudovariegatus Typus) NAm
C. cumatilis TUB011417 Eur
C. praestans TUB011448 Eur
C. claricolor TUB011852 Eur
sect. Claricolores
C. spadicellus O-F-65723 Eur
C. variecolor TUB011416 Eur
C. patibilis O-F-125906 Eur
C. coalescens F319 Eur
C. balteatoalbus CO854 Eur
C. areni-silvae MIKH-T508
C. daulnoyae SSt15-097 Eur
C. durus F17037 NAm
C. lavendulensis PERTH05506735 Aus
C. balteatus F18476 NAm
C. balteatocumatilis TUB019792 Eur
C. balteatibulbosus SSt16-073 Eur
C. violaceomaculatus TUB019724 Eur
sect. Phlegmacioides
C. saginus TUB011419 Eur
C. norrlandicus CFP562 F14270 Typus Eur
C. populinus O-F-58647 Eur
sect. Phlegmacium
C. pseudoarcuatorum TEB584-16 Eur
C. inexspectatus CFP540 F14264 Typus Eur
C. serarius O-F-65724 Eur
C. cliduchus OS578 Eur
C. viscidoamarus GDA53706 Eur
C. rhizophorus TUB019783 Eur
/Rhizophori
C. coelopus HO990504A3 Aus
C. artosus PDD77486 CO1348 Typus NZ
C. papulosus TUB011867 Eur
sect. Elastici
C. xanthosuavis TUB019746 Eur
C. superbus F14965 NAm
C. russeoides TUB011412 Eur
C. percomis TSJ2002-096 Eur
C. nanceiensis TUB011389 Eur
C. aurilicis TSJ1998-101 + TUB019807 Eur
sect. Percomes
C. aerugineoconicus PDD27258 Typus NZ
C. entheosus PDD103639 CO1210 Typus NZ
sect. Entheosi
C. anomalochrascens TUB019769 Eur
C. fulvoochrascens TUB019735 Eur
C. malachioides CO1708 Eur
sect. Riederi
C. turmalis TUB011393 Eur
C. picoides PDD103886 CO1643 + PDD94019 Aus
sect. Turmales
C. variegatus TUB 019764 Eur
C. turcopes PDD94058 CO1814 NZ
C. cf. turcopes PDD97513 CO1885 NZ
/Turcopedes
C. cremeolina PDD70506 CO1058 Typus NZ
C. cf. austrorapaceus TUB011485 SAm
C. cremeolina var. subpicoides PDD107719 CO2189 NZ
C. iringa PDD73135 CO1255 Typus NZ
C. cremeorufus PDD94056 CO1812 Typus NZ
C. dulciorum PDD78797 CO1460 Typus NZ
sect. Cremeolinae
C. myxenosma PDD88282 CO1672 Typus NZ
C. rufoallutus CO747 Eur
C. talus TUB011877 Eur
C. talimultiformis TUB011841 0 Eur
C. multiformis IB19940224 NAm
sect. Multiformes
C. cf. castaneiceps JAC13905 NZ
C. malvaceus TUB011836 SAm
sect. Malvacei
C. periclymenus PDD71008 CO1060 Typus NZ
C. olorinatus PDD72753 NZ
C. microspermus IB19850073 Eur
C. pluviorum PK5640 NAm
C. melleomitis PDD107704 CO2174 NZ
C. croceocoeruleus TUB011833 Eur
C. psilomorphus PDD103885 CO1492 Typus NZ
C. vibratilis M4 Eur
sect. Vibratiles
C. pseudotriumphans TUB011873 SAm
C. alboaggregatus JAC12509 PDD96523 NZ
C. alboaggregatus PDD77472 CO1318 NZ
sect. Alboaggregati
C. comparioides JFA11998 NAm
C. ovreboi JFA13000 CAm
C. lustratus TUB012148 Eur
C. comarostaphylidis JFA12930 CAm
C. leucophanes F67711 CO1518 Eur
sect. Lustrati
C. laquellus PDD72766 NZ
C. urbiculus PDD88259 CO1627 Typus NZ
sect. Laquelli
C. myxoclaricolor TUB011481 SAm
C. austrocyanites PDD70498 CO1034 Typus NZ
C. poliotrichus PDD103684 CO2112 NZ
sect. Austrocyanites
C. crypticus PDD100127 NZ
Gigasperma
C. pinophilus SLB2004-103119 NAm
C. mariae PDD72487 NZ
C. castoreus JAC12825 PDD96929 NZ
sect. Rapacea
C. effundens TUB011854 Eur
C. cretax PDD73148 CO1180 Typus NZ
C. cervinus TUB011472 SAm
C. austroturmalis TUB011469 SAm
C. caelicolor TUB011470 SAm
sect. Cretaces
C. fiordlandensis PDD94013 CO1755 Typus NZ
C. ixomolynus PDD107720 CO2190 NZ
C. dulcamarus PDD97534 CO1909 Typus NZ
C. verniciorum JAC13232 NZ
sect. Verniciori
C. peristeris PDD88270 CO1647 Typus NZ
C. rhodophyllus TUB020416 SAm
C. austrovaginatus PDD94052 CO1808 Aus
C. medioscaurus PDD73138 CO1174 NZ
C. conei PDD83709 JAC9578 NZ
sect. Austrovaginati
C. herpeticus TUB019814 Eur
C. violaceonitens F18482 NAm
C. scaurus TUB011387 Eur
C. singularis PDD78767 CO1409 Typus NZ
C. chlorophyllus PDD103681 CO2109 Typus NZ
sect. Scauri
C. persicanus HO510371 NZ
C. australis HO522426 Typus Aus
C. submagellanicus HO-A20518A1 Aus
C. chalybaeus PDD77482 CO1342 NZ
C. kaimanawa PDD73133 CO1259 Typus NZ
C. rhipiduranus PDD88269 CO1645 Typus NZ
C. purpurascens TUB011401 Eur
C. porphyropus KH9 Eur
sect. Purpurascentes
C. chlorophanus TUB020419 + TUB019700 SAm
C. thaumastus PDD78804 CO1474 Typus NZ
C. vaginatus TUB020418 + TUB019699 SAm
sect. Coleopodes
C. flammuloides TUB011475 SAm
C. incensus PDD73147 CO1225 Typus NZ
sect. Incensi
C. austroduracinus TUB011522 SAm
C. viscincisus PDD97544 CO1919 Typus NZ
C. viridibasalis TUB011490 SAm
sect. Austroduracini
C. parahumilis TUB011293 SAm
C. renidens TUB011516 Eur
sect. Renidentes
Cortinarius
Conocybe lactea CUW-PBM2706
Descolea recedens TENN063870 PBM3211
Flammula alnicola CUW-PBM2608
0.03

Fig. 1 (cont.)

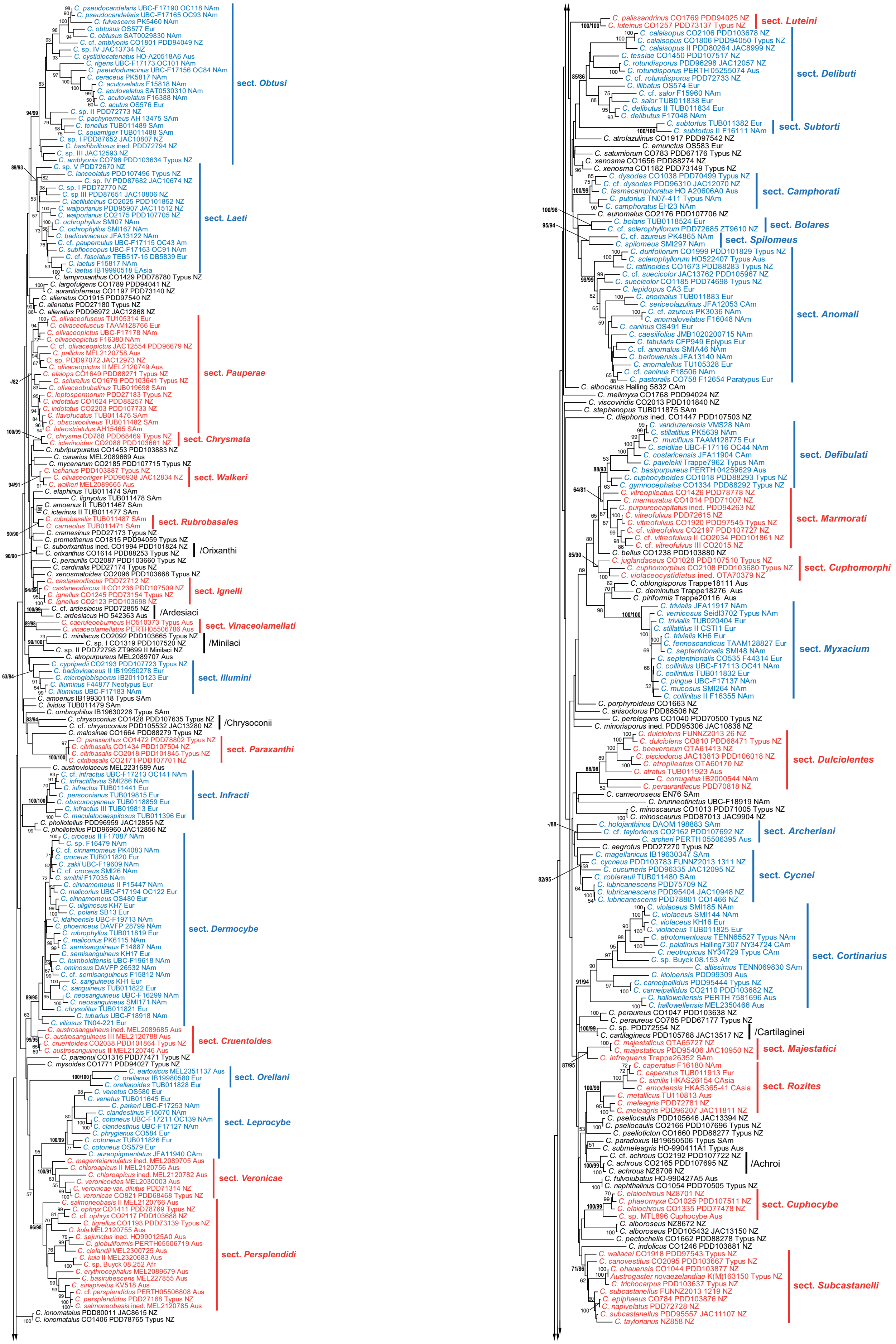

Fig. 2 Maximum likelihood (RAxML) phylogenetic tree based on 730 *Cortinarius* samples and nrITS and nrLSU ribosomal genes with binary data from gap coding (BIN). Five partitions are used: ITS1: 1–610, 5.8S: 611–762, ITS2: 763–1334, LSU: 1335–2412, BIN: 2413–3736. Vouchers and abbreviated geographical provenances are included in the labels. Extant sections are marked blue, while new sections proposed in this study are marked red. Bootstrap support values are shown only above 50 %. RAxML support values, followed by the corresponding PhyML values, are shown in **bold** for sections and clades.

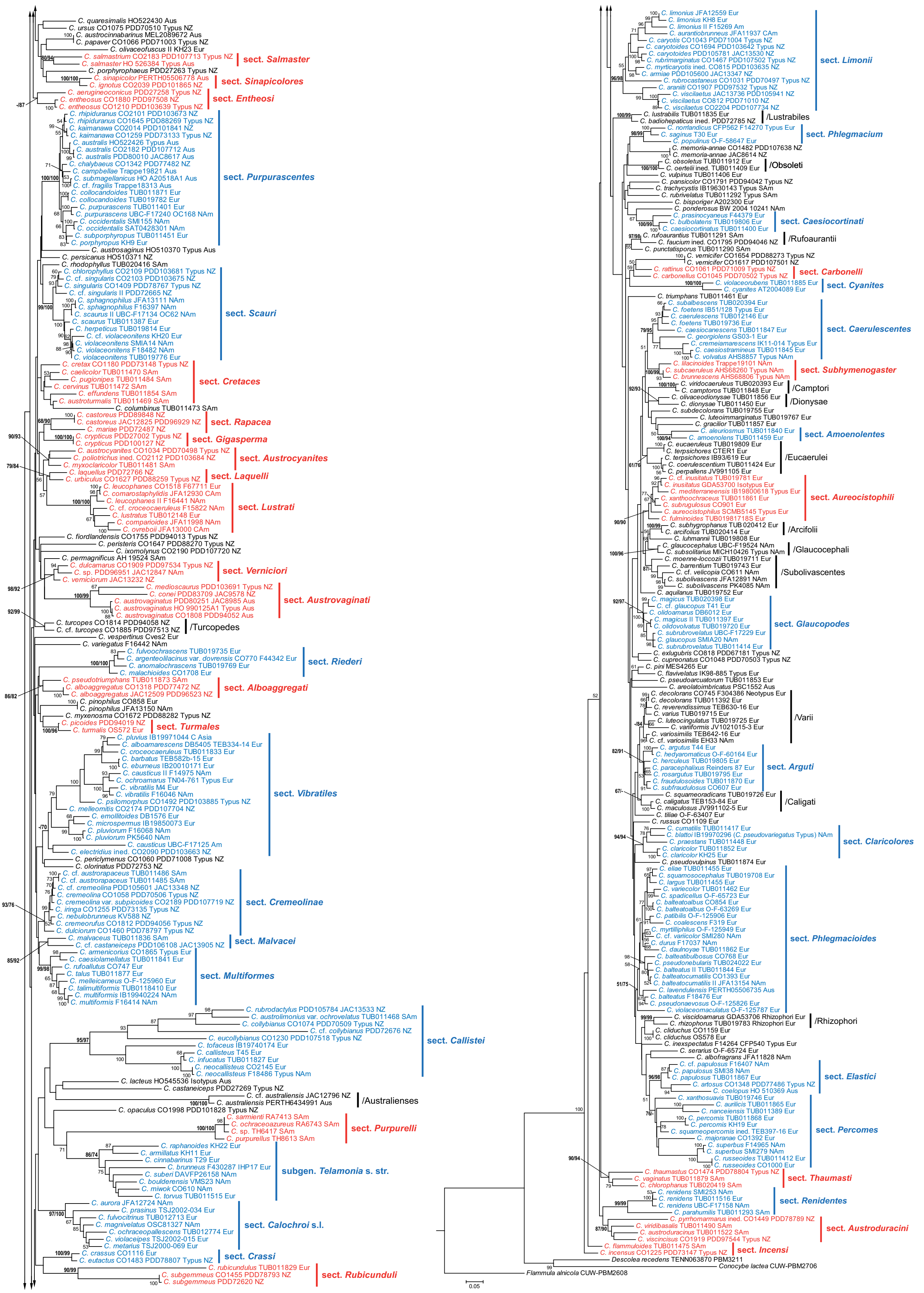
C. quaresimalis HO522430 Aus
C. ursus CO1075 PDD70510 Typus NZ
C. austrocinnabarinus MEL2089672 Aus
C. papaver CO1066 PDD71003 Typus NZ
C. olivaceofuscus II KH23 Eur
C. salmastrium CO2183 PDD107713 Typus NZ
C. salmaster HO 526384 Typus Aus
sect. Salmaster
C. porphyrophaeus PDD27263 Typus NZ
C. sinapicolor PERTH05506778 Aus
C. ignotus CO2039 PDD101865 NZ
sect. Sinapicolores
C. aerugineoconicus PDD27258 Typus NZ
C. entheosus CO1880 PDD97508 NZ
C. entheosus CO1210 PDD103639 Typus NZ
sect. Entheosi
C. rhipiduranus CO2101 PDD103673 NZ
C. rhipiduranus CO1645 PDD88269 Typus NZ
C. kaimanawa CO2014 PDD101841 NZ
C. kaimanawa CO1259 PDD73133 Typus NZ
C. australis HO522426 Typus Aus
C. australis CO2182 PDD107712 Aus
C. australis PDD80010 JAC8617 Aus
C. chalybaeus CO1342 PDD77482 NZ
C. campbellae Trappe19821 Aus
C. submagellanicus HO A20518A1 Aus
C. cf. fragilis Trappe18313 Aus
C. collocandoides TUB011871 Eur
C. collocandoides TUB019782 Eur
C. purpurascens TUB011401 Eur
C. purpurascens UBC-F17240 OC168 NAm
C. occidentalis SMI155 NAm
C. occidentalis SAT0428301 NAm
C. subporphyropus TUB011451 Eur
C. porphyropus KH9 Eur
sect. Purpurascentes
C. austrosaginus HO510370 Typus Aus
C. persicanus HO510371 NZ
C. rhodophyllus TUB020416 SAm
C. chlorophyllus CO2109 PDD103681 Typus NZ
C. cf. singularis CO2103 PDD103675 NZ
C. singularis CO1409 PDD78767 Typus NZ
C. cf. singularis II PDD72665 NZ
C. sphagnophilus JFA13111 NAm
C. sphagnophilus F16397 NAm
C. scaurus II UBC-F17134 OC62 NAm
C. scaurus TUB011387 Eur
C. herpeticus TUB019814 Eur
C. cf. violaceonitens KH20 Eur
C. violaceonitens SMIA14 NAm
C. violaceonitens F18482 NAm
C. violaceonitens TUB019776 Eur
sect. Scauri
C. cretax CO1180 PDD73148 Typus NZ
C. caelicolor TUB011470 SAm
C. pugionipes TUB011484 SAm
C. cervinus TUB011472 SAm
C. effundens TUB011854 SAm
C. austroturmalis TUB011469 SAm
sect. Cretaces
C. columbinus TUB011473 SAm
C. castoreus PDD89848 NZ
C. castoreus JAC12825 PDD96929 NZ
C. mariae PDD72487 NZ
sect. Rapacea
C. crypticus PDD27002 Typus NZ
C. crypticus PDD100127 NZ
sect. Gigasperma
C. austrocyanites CO1034 PDD70498 Typus NZ
C. poliotrichus ined. CO2112 PDD103684 NZ
C. myxoclaricolor TUB011481 SAm
sect. Austrocyanites
C. laquellus PDD72766 NZ
C. urbiculus CO1627 PDD88259 Typus NZ
sect. Laquelli
C. leucophanes CO1518 F67711 Eur
C. comarostaphylidis JFA12930 CAm
C. leucophanes II F16441 NAm
C. cf. croceocaeruleus F15822 NAm
C. lustratus TUB012148 Eur
C. comparioides JFA11998 NAm
C. ovreboii JFA13000 CAm
sect. Lustrati
C. fiordlandensis CO1755 PDD94013 Typus NZ
C. peristeris CO1647 PDD88270 Typus NZ
C. ixomolynus CO2190 PDD107720 NZ
C. permagnificus AH 19524 SAm
C. dulcamarus CO1909 PDD97534 Typus NZ
C. sp. PDD96951 JAC12847 NAm
C. verniciorum JAC13232 NZ
sect. Verniciori
C. medioscaurus PDD103691 Typus NZ
C. conei PDD83709 JAC9578 NZ
C. austrovaginatus PDD80251 JAC8985 Aus
C. austrovaginatus HO 990125A1 Typus Aus
C. austrovaginatus CO1808 PDD94052 Aus
sect. Austrovaginati
C. turcopes CO1814 PDD94058 NZ
C. cf. turcopes CO1885 PDD97513 NZ
/Turcopedes
C. vespertinus Cves2 Eur
C. variegatus F16442 NAm
C. fulvoochrascens TUB019735 Eur
C. argenteolilacinus var. dovrensis CO770 F44342 Eur
C. anomalochrascens TUB019769 Eur
C. malachioides CO1708 Eur
sect. Riederi
C. pseudotriumphans TUB011873 SAm
C. alboaggregatus CO1318 PDD77472 NZ
C. alboaggregatus JAC12509 PDD96523 NZ
sect. Alboaggregati
C. pinophilus CO858 Eur
C. pinophilus JFA13150 NAm
C. myxenosma CO1672 PDD88282 Typus NZ
C. picoides PDD94019 NZ
C. turmalis OS572 Eur
sect. Turmales
C. pluvius IB19971044 C Asia
C. alboamarescens DB5405 TEB334-14 Eur
C. croceocaeruleus TUB011833 Eur
C. barbatus TEB582b-15 Eur
C. eburneus IB20010171 Eur
C. causticus II F14975 NAm
C. ochroamarus TN04-761 Typus Eur
C. vibratilis M4 Eur
C. vibratilis F16046 NAm
C. psilomorphus CO1492 PDD103885 Typus NZ
C. melleomitis CO2174 PDD107704 NZ
C. emollitoides DB1576 Eur
C. microspermus IB19850073 Eur
C. pluviorum F16068 NAm
C. pluviorum PK5640 NAm
C. causticus UBC-F17125 Am
C. electridius ined. CO2090 PDD103663 NZ
sect. Vibratiles
C. periclymenus CO1060 PDD71008 Typus NZ
C. olorinatus PDD72753 NZ
C. cf. austrorapaceus TUB011486 SAm
C. cf. austrorapaceus TUB011485 SAm
C. cf. cremeolina PDD105601 JAC13348 NZ
C. cremeolina CO1058 PDD70506 Typus NZ
C. cremeolina var. subpicoides CO2189 PDD107719 NZ
C. iringa CO1255 PDD73135 Typus NZ
C. nebulobrunneus KV588 NZ
C. cremeorufus CO1812 PDD94056 Typus NZ
C. dulciorum CO1460 PDD78797 Typus NZ
sect. Cremeolinae
C. malvaceus TUB011836 SAm
C. cf. castaneiceps PDD106108 JAC13905 NZ
sect. Malvacei
C. armenicorius CO1865 Typus Eur
C. caesiolamellatus TUB011841 Eur
C. rufoallutus CO747 Eur
C. talus TUB011877 Eur
C. melleicarneus O-F-125960 Eur
C. talimultiformis TUB011841O Eur
C. multiformis IB19940224 NAm
C. multiformis F16414 NAm
sect. Multiformes
C. rubrodactylus PDD105784 JAC13533 NZ
C. austrolimonius var. ochrovelatus TUB011468 SAm
C. collybianus CO1074 PDD70509 Typus NZ
C. cf. collybianus PDD72676 NZ
C. eucollybianus CO1230 PDD107518 Typus NZ
C. tofaceus IB19740174 Eur
C. callisteus T45 Eur
C. infucatus TUB011827 Eur
C. neocallisteus CO2145 Eur
C. neocallisteus F18486 Typus NAm
sect. Callistei
C. lacteus HO545536 Isotypus Aus
C. castaneiceps PDD27269 Typus NZ
C. cf. australiensis JAC12796 NZ
C. australiensis PERTH6434991 Aus
/Australienses
C. opaculus CO1998 PDD101828 Typus NZ
C. sarmienti RA7413 SAm
C. ochraceoazureus RA6743 SAm
C. sp. TH6417 SAm
C. purpurellus TH8613 SAm
sect. Purpurelli
C. raphanoides KH22 Eur
C. armillatus KH11 Eur
C. cinnabarinus T29 Eur
C. brunneus F430287 IHP17 Eur
C. suberi DAVFP26158 NAm
C. boulderensis VMS23 NAm
C. miwok CO610 NAm
C. torvus TUB011515 Eur
subgen. Telamonia s. str.
C. aurora JFA12724 NAm
C. prasinus TSJ2002-034 Eur
C. fulvocitrinus TUB012713 Eur
C. magnivelatus OSC81327 NAm
C. ochraceopallescens TUB012774 Eur
C. violaceipes TSJ2002-015 Eur
C. metarius TSJ2000-069 Eur
sect. Calochroi s.l.
C. crassus CO1116 Eur
C. eutactus CO1483 PDD78807 Typus NZ
sect. Crassi
C. rubicundulus TUB011829 Eur
C. subgemmeus CO1455 PDD78793 NZ
C. subgemmeus PDD72620 NZ
sect. Rubicunduli
C. limonius JFA12559 Eur
C. limonius KH8 Eur
C. limonius II F15269 Am
C. aurantiobrunneus JFA11937 CAm
C. caryotis CO1043 PDD71004 Typus NZ
C. caryotoides CO1694 PDD103642 Typus NZ
C. caryotoides PDD105781 JAC13530 NZ
C. rubrimarginatus CO1467 PDD107502 Typus NZ
C. myrticaryotis ined. CO815 PDD103635 NZ
C. armiae PDD105600 JAC13347 NZ
C. rubrocastaneus CO1031 PDD70497 Typus NZ
C. araniiti CO1907 PDD97532 Typus NZ
C. viscilaetus JAC13736 PDD105941 NZ
C. viscilaetus CO812 PDD71010 NZ
C. viscilaetus CO2204 PDD107734 NZ
sect. Limonii
C. lustrabilis TUB011835 Eur
C. badiohepaticus ined. PDD72785 NZ
/Lustrabiles
C. norrlandicus CFP562 F14270 Typus Eur
C. saginus T30 Eur
C. populinus O-F-58647 Eur
sect. Phlegmacium
C. memoria-annae CO1482 PDD107638 NZ
C. memoria-annae JAC8614 NZ
C. obsoletus TUB011912 Eur
C. oertelii ined. TUB011409 Eur
/Obsoleti
C. vulpinus TUB011406 Eur
C. pansicolor CO1791 PDD94042 Typus NZ
C. trachycystis IB19630143 Typus SAm
C. rubrivelatus TUB011292 Typus SAm
C. bisporiger A202300 Eur
C. ponderosus BW 2004 10241 NAm
C. prasinocyaneus F44379 Eur
C. bulbolatens TUB019806 Eur
C. caesiocortinatus TUB011400 Eur
sect. Caesiocortinati
C. rufoaurantius TUB011291 SAm
C. faucium ined. CO1795 PDD94046 NZ
/Rufoaurantii
C. punctatisporus TUB011290 SAm
C. vernicifer CO1654 PDD88273 Typus NZ
C. vernicifer CO1617 PDD107501 NZ
C. rattinus CO1061 PDD71009 Typus NZ
C. carbonellus CO1045 PDD70502 Typus NZ
sect. Carbonelli
C. violaceorubens TUB011885 Eur
C. cyanites AT2004089 Eur
sect. Cyanites
C. triumphans TUB011461 Eur
C. subalbescens TUB020394 Eur
C. foetens IB51/128 Typus Eur
C. caerulescens TUB012146 Eur
C. foetens TUB019736 Eur
C. caesiocanescens TUB011847 Eur
C. georgiolens GS03-1 Eur
C. cremeiamarescens IK11-014 Typus Eur
C. caesiostramineus TUB011845 Eur
C. volvatus AHS8857 Typus NAm
sect. Caerulescentes
C. lilacinoides Trappe19101 NAm
C. subcaeruleus AHS68260 Typus NAm
C. brunnescens AHS68806 Typus NAm
sect. Subhymenogaster
C. viridocaeruleus TUB020393 Eur
C. camptoros TUB011848 Eur
/Camptori
C. olivaceodionysae TUB011856 Eur
C. dionysae TUB011450 Eur
/Dionysae
C. subdecolorans TUB019755 Eur
C. luteoimmarginatus TUB019767 Eur
C. gracilior TUB011857 Eur
C. aleuriosmus TUB011840 Eur
C. amoenolens TUB011459 Eur
sect. Amoenolentes
C. eucaeruleus TUB019809 Eur
C. terpsichores CTER1 Eur
C. terpsichores IB93/619 Eur
C. coerulescentium TUB011424 Eur
C. perpallens JV991105 Eur
/Eucaerulei
C. cf. inusitatus TUB019781 Eur
C. inusitatus GDA53700 Isotypus Eur
C. mediterraneensis IB19800618 Typus Eur
C. xanthochraceus TUB011861 Eur
C. subrugulosus CO901 Eur
C. aureocistophilus SCMB5145 Typus Eur
C. fulminoides TUB019817 18S Eur
sect. Aureocistophili
C. subhygrophanus TUB 020412 Eur
C. arcifolius TUB020414 Eur
/Arcifolii
C. luhmannii TUB019808 Eur
C. glaucocephalus UBC-F19524 NAm
C. subsolitarius MICH10426 Typus NAm
/Glaucocephali
C. moenne-loccozii TUB019711 Eur
C. barrentium TUB019743 Eur
C. cf. velicopia CO611 NAm
C. subolivascens JFA12891 NAm
C. subolivascens PK4085 NAm
/Subolivascentes
C. aquilanus TUB019752 Eur
C. magicus TUB020398 Eur
C. cf. glaucopus T41 Eur
C. olidoamarus DB6012 Eur
C. magicus II TUB011397 Eur
C. olidovolvatus TUB019720 Eur
C. subrubrovelatus UBC-F17229 Eur
C. glaucopus SMIA20 NAm
C. subrubrovelatus TUB011414 Eur
sect. Glaucopodes
C. exlugubris CO818 PDD67181 Typus NZ
C. cupreonatus CO1048 PDD70503 Typus NZ
C. pini MES4265 Eur
C. flavivelatus IK98-885 Typus Eur
C. pseudoarcuatorum TUB011853 Eur
C. areolatoimbricatus PSC1552 Aus
C. decolorans CO745 F304386 Neotypus Eur
C. decolorans TUB011392 Eur
C. reverendissimus TEB630-16 Eur
C. varius TUB019715 Eur
C. luteocingulatus TUB019725 Eur
C. variiformis JV1021015-3 Eur
C. variosimilis TEB642-16 Eur
C. cf. variosimilis EH33 NAm
/Varii
C. argutus T44 Eur
C. hedyaromaticus O-F-60164 Eur
C. herculeus TUB019805 Eur
C. paracephalixus Reinders 87 Eur
C. rosargutus TUB019795 Eur
C. fraudulosoides TUB011870 Eur
C. subfraudulosus CO607 Eur
sect. Arguti
C. squameoradicans TUB019726 Eur
C. caligatus TEB153-84 Eur
C. maculosus JV991102-5 Eur
/Caligati
C. tiliae O-F-63407 Eur
C. russus CO1109 Eur
C. cumatilis TUB011417 Eur
C. blattoi IB19970296 (C. pseudovariegatus Typus) NAm
C. praestans TUB011448 Eur
C. claricolor TUB011852 Eur
C. claricolor KH25 Eur
sect. Claricolores
C. pseudovulpinus TUB011874 Eur
C. eliae TUB011455 Eur
C. squamosocephalus TUB019708 Eur
C. largus TUB011455 Eur
C. variecolor TUB011462 Eur
C. spadicellus O-F-65723 Eur
C. balteatoalbus CO854 Eur
C. balteatoalbus O-F-63269 Eur
C. patibilis O-F-125906 Eur
C. coalescens F319 Eur
C. myrtilliphilus O-F-125949 Eur
C. cf. variicolor SMI280 NAm
C. durus F17037 NAm
C. daulnoyae TUB011862 Eur
C. balteatibulbosus CO768 Eur
C. pseudonebularis TUB024022 Eur
C. balteatus II TUB011844 Eur
C. balteatocumatilis CO1393 Eur
C. balteatocumatilis II JFA13154 NAm
C. lavendulensis PERTH05506735 Aus
C. balteatus F18476 Eur
C. pseudonaevosus O-F-125826 Eur
C. violaceomaculatus O-F-125787 Eur
sect. Phlegmacioides
C. viscidoamarus GDA53706 Rhizophori Eur
C. rhizophorus TUB019783 Rhizophori Eur
/Rhizophori
C. cliduchus CO1159 Eur
C. cliduchus OS578 Eur
C. inexspectatus F14264 CFP540 Typus Eur
C. serarius O-F-65724 Eur
C. albofragrans JFA11828 NAm
C. cf. papulosus F16407 NAm
C. papulosus SMI38 NAm
C. papulosus TUB011867 Eur
C. artosus CO1348 PDD77486 Typus NZ
C. coelopus HO 510369 Aus
sect. Elastici
C. xanthosuavis TUB019746 Eur
C. aurilicis TUB011865 Eur
C. nanceiensis TUB011389 Eur
C. percomis TUB011868 Eur
C. percomis KH19 Eur
C. squameopercomis ined. TEB397-16 Eur
C. majoranae CO1392 Eur
C. superbus F14965 NAm
C. superbus SMI279 NAm
C. russeoides TUB011412 Eur
C. russeoides CO1000 Eur
sect. Percomes
C. thaumastus CO1474 PDD78804 Typus NZ
C. vaginatus TUB011879 SAm
C. chlorophanus TUB020419 SAm
sect. Thaumasti
C. renidens SMI253 NAm
C. renidens TUB011516 Eur
C. renidens UBC-F17158 NAm
C. parahumilis TUB011293 SAm
sect. Renidentes
C. pyrrhomarmarus ined. CO1449 PDD78789 NZ
C. viridibasalis TUB011490 SAm
C. austroduracinus TUB011522 SAm
C. viscincisus CO1919 PDD97544 Typus NZ
sect. Austroduracini
C. flammuloides TUB011475 SAm
C. incensus CO1225 PDD73147 Typus NZ
sect. Incensi
Descolea recedens TENN063870 PBM3211
Conocybe lactea CUW-PBM2706
Flammula alnicola CUW-PBM2608
0.05

Fig. 2 (cont.)

In the species list the second column gives the known geographical provenance (see the abbreviations below). The third column specifies the source of genetic information, unless the species is sampled in both 2-loci and 4-loci trees (the normal case). Species that were only sampled in the 2-loci tree are marked 2L, and those that were sampled with at least one *rpb* sequence in the 4-loci tree are marked R. Species that were not sampled in our analysis, but were shown to belong to the same clade in Garnica et al. 2016 (based on ITS) are marked G2016. A few unpublished results from the ITS sequencing project of the DNA group of the European Cortinarius Association (Journées européennes du Cortinaire, JEC) were included and are marked JEC. Putative taxa that were not sampled in either study are listed in parentheses; these are taxa that have been described as being (likely) members of the section.

If at least two species were included in a section or clade, the ML bootstrap support (in %) is given. This refers to the 4-loci tree, unless specified otherwise. If the type of a new section is represented in GenBank (GB), this is also noted.

Notes on terminology

Refer to Fig. 3 and 4 for illustrations of some of these terms:

By *agaricoid* is meant the predominant habit of a *Cortinarius* basidiome with a pileus, stipe and distinct lamellae. The opposite term *sequestrate*, refers to a habit where the lamellae are replaced by a gleba, the pileus being more or less closed, and the stipe sometimes rudimentary.

Fig. 3 Phenotypic forms and habits of *Cortinarius* I. a. Agaricoid habit (*C. violaceus*); b. myxacioid habit (*C. collinitus*); c. dermocyboid habit (*C. fervidus*); d. leprocyboid habit (*C. phrygianus*); e. sequestrate habit 1 (*C. beeverorum*); f. sequestrate habit 2 (*C. epiphaeus*). — Photos K. Soop.

Refer to the introductory text of headings 2, 3, 4.1, 5, 7, 8.1 for subgeneric adjectives (*dermocyboid*, *telamonioid*, etc.). By *rozitoid* is meant possessing a membranous partial veil (homologous with the cortina), like in the former genus *Rozites*. *Cuphocyboid* means lacking a cortina, like in the former genus *Cuphocybe*.

Pileocarpic and *stipitocarpic* refer to the development of a *Cortinarius* basidiome (Locquin 1953). The former implies an early expansion of the pileus, leaving an often marginate bulb on the stipe. In the latter case, the stipe develops earlier, leaving the stipe less bulbous, often clavate or cylindrical.

By *boreal* and *austral* we mean occurring in the Northern and Southern Hemisphere, respectively; *bihemispherical* implies

Fig. 4 Phenotypic forms and habits of *Cortinarius* II. a. Phlegmacioid habit, stipitocarpic 1 (*C. varius*); b. phlegmacioid habit, stipitocarpic 2 (*C. papulosus*); c. phlegmacioid habit, pileocarpic (*C. chlorophyllus*); d. telamonioid habit (*C. waiporianus*); e. cuphocyboid habit (*C. phaeomyxa*); f. rozitoid habit (*C. wallacei*). — Photos K. Soop.

both. These terms do not imply an ecological or climatological aspect.

The following geographical abbreviations are used: Eur (Europe), NAm/SAm/CAm (North/South/Central America), Aus (Australia), NZ (New Zealand).

1. Section *Cortinarius* (99 %)

Typus. C. violaceus (L.: Fr.) Gray.

altissimus	Guyana	
atrotomentosus	NAm	R
carneipallidus	NZ	R
hallowellensis	Aus	R
kioloensis	Aus, NZ	R
neotropicus	CAm	2L
palatinus	CAm	R
violaceus	Eur, NAm	R
(*atroviolaceus*	NZ, SE Asia)	
(*hercynicus*	Eur)	
(*jenolanensis*	Aus)	
(*paraviolaceus*	SE Asia)	
(*subcalyptrosporus*	NZ)	

Notes — The type section of the genus *Cortinarius* is widely distributed globally. The species are characterised by a dark blue to violet coloration overall, due to the (R)-β-dopa pigment, a dry velvety-granulose pileus, and lageniform cheilocystidia. See Harrower et al. (2015b).

The morphologically similar singletons *C. atrolazulinus* (New Zealand) and *C. austroviolaceus* (Australia) are placed in remote positions in our phylogeny, indicating that section characters are convergent. In addition, Moser (1986) described four southern species in the section (of which three from Malaysia, Borneo), but sequences of their holotypes have so far not been available.

2. Dermocyboid sections

This heading regroups taxa that correspond approximately to the *Dermocybe* lineage in Fig. S2 of Garnica et al. (2016). Basidiomata are usually small and slender, characterised by often brightly red/yellow/olive colours, due to anthraquinonic pigments, which also cause a positive (usually red) alkaline reaction in the tissues.

Section *Dermocybe* (Fr.) Gillot & Lucand (100 %)

Typus. C. cinnamomeus (L.: Fr.) Gray.

aurantiobasis	NAm	G2016
bataillei	Eur	R
cascadensis	NAm	G2016
chrysolitus	NAm, Eur	R
cinnamomeoluteus	Eur, NAm	G2016
cinnamomeus	Eur, NAm	R
cinnamomeus II		2L
cistoadelphus	Eur	R
croceoconus	Eur, NAm	R
croceus	Eur, NAm	R
croceus II		2L
fervidus	Eur	G2016
harrisonii	NAm	G2016
humboldtensis	NAm	2L
huronensis	NAm	G2016
idahoënsis	NAm	
malicorius	Eur, NAm	R
marylandensis	NAm	G2016
neosanguineus	NAm	R
ominosus	Eur, NAm	
phoeniceus	Eur, NAm	
polaris	Eur	2L
puniceus	Eur	G2016
rubrophyllus	Eur	R
rubrosanguineus	Eur	R
sanguineus	Eur, NAm	R
semisanguineus	Eur, NAm	
sierraensis	NAm	G2016
smithii	NAm	2L
sommerfeltii	Eur	R
tillamookensis	NAm	G2016
tubarius	Eur, NAm	2L
uliginosus	Eur, NAm	R
vitiosus	Eur	R
zakii	NAm	
cf. *cinnamomeus*	NAm	2L
cf. *croceus*	NAm	2L
cf. *semisanguineus*	NAm	2L
(*cruentiphyllus*	NAm, Eur)	

Notes — This large section is strictly boreal and consists of small to medium-sized fungi with a dry, felty/squamulose and non-hygrophanous pileus. The pigments are based on the octaketide pathway (Stensrud et al. 2014).

Cortinarius **sect.** ***Pauperae*** (M.M. Moser & E. Horak) Soop, *comb. nov.* (59 %, 82 % in PhyML tree)

Basionym. Dermocybe sect. *Pauperae* M.M. Moser & E. Horak, Beih. Nova Hedwigia 52: 500. 1975.
Typus. D. luteostriatula M.M. Moser & E. Horak.
MycoBank MB822986.

elaiops	NZ	
indotatus	NZ	R
leptospermorum	NZ	
luteostriatulus (*flavofucatus*, *obscurooliveus*)	SAm	
olivaceobubalinus	SAm	R
olivaceobubalinus II	SAm	G2016
olivaceofuscus	Eur	2L
olivaceopictus	NAm	2L
olivaceopictus II	Aus	R
sciurellus	NZ	R
cf. *olivaceopictus*	NZ	R
C. sp.	NZ	2L
C. sp. II	Aus	2L
(*austronanceiensis*	SAm)	
(*cartagoënsis*	CAm)	
(*egmontianus*	NZ)	
(*nothovenetus*	SAm)	
(*olivaceoluteus*	NAm)	

Notes — *Pauperae* contains dermocyboid species, typical for the Southern Hemisphere, of which only two are boreal. They present a yellow, olive, or citrinous coloration, with pigments of the skyrine and hypericine type (Stensrud et al. 2014). Unlike sect. *Dermocybe*, some members possess a glabrous or hygrophanous pileus. Three taxa (see *C. luteostriatulus*) are assumed conspecific with a 99.6 % similarity in the ITS-LSU region. The taxon *C.* sp. II was labelled '*pallidus*' (Stefani et al. 2013), which would be a nom. illeg. (*Cortinarius pallidus* Peck 1889).

Cortinarius **sect.** ***Cruentoides*** Soop, *sect. nov.* (100 %)

Typus. C. cruentoides Soop, GB (ITS, LSU).
MycoBank MB822924.

austrosanguineus ined.	Aus	R
austrosanguineus II	Aus	R
austrosanguineus III	Aus	R
cruentoides	NZ	R

Basidiomata small, dry, reminiscent of the boreal subsect. *Sanguinei*. Pileus 10–30 mm diam, deep red, minutely granulose-fibrillose. Lamellae red. Stipe cylindrical, reddish. Veil dark red to purple red, rather copious. Context white to pinkish. Alkaline reaction blood red. Spores ellipsoid to subglobose, 6–8 × 4–5 µm, fairly coarsely verrucose. In *Myrtaceae* forests, New Zealand, Australia.

Notes — The section is sister to sect. *Dermocybe*, and might alternatively be considered part of the latter, which then becomes bihemispherical.

Cortinarius sect. ***Walkeri*** Soop, sect. nov. (99 %)

Typus. C. walkeri Cooke & Massee.
MycoBank MB822925.

lachanus	NZ	
olivaceoniger	NZ	
walkeri (*austrovenetus*)	Aus	R

Basidiomata small to medium-sized, dry to glutinous, yellowish to greenish. Pileus 10–60 mm diam, greenish, often with yellow or blue tints, minutely silky. Stipe cylindrical, pale green, flavescent or blushing. Lamellae citrinous, often blushing. Veil greenish, sparse. Context pale green to pale yellowish. Alkaline reaction blood red. Spores ellipsoid to amygdaloid, 8–10 × 4.5–6 µm, weakly verrucose. In *Nothofagaceae* and *Myrtaceae* forests, New Zealand, Australia.

Notes — The Patagonian sister taxon *C. elaphinus* deviates morphologically, and was described in subg. *Telamonia*. On the other hand, the morphologically similar *C. alienatus* from New Zealand appears as a singleton in our phylogeny.

Cortinarius sect. ***Chrysmata*** Soop, *sect. nov.* (100 %)

Typus. C. chrysma Soop, GB (ITS, LSU).
MycoBank MB822926.

chrysma	NZ	R
icterinoides	NZ	R

Basidiomata small, pileus dry, brilliantly yellow. Pileus 15–50 mm diam, yellow, finely fibrillose. Lamellae yellow. Stipe cylindrical to clavate, pale yellow. Veil dark yellow, sparse. Context yellow. Alkaline reaction blood red to vinaceous. Spores ellipsoid, 7–10 × 4.5–5.5 µm, weakly to moderately verrucose. In *Nothofagaceae* forests, New Zealand.

Cortinarius sect. ***Rubrobasales*** Soop & Dima, *sect. nov.* (93 %)

Typus. C. rubrobasalis M.M. Moser & E. Horak.
MycoBank MB822927.

carneolus	SAm	
rubrobasalis	SAm	
teraturgus	SAm	G2016

Basidiomata telamonioid, small to medium sized, dry, red-brown. Pileus 30–70 mm diam, red-brown to date brown, minutely fibrillose. Lamellae pale brown to rusty yellow-brown. Stipe ± cylindrical, red-brown to pale reddish or yellowish. Veil incarnate to cinnabar red. Context white to red-brown. Alkaline reaction brownish to black. Spores ellipsoid, 8–10.5 × 4.5–6 µm, weakly verrucose. In *Nothofagaceae* forests, Patagonia.

Cortinarius sect. ***Ignelli*** Soop, *sect. nov.* (96 %)

Typus. C. ignellus Soop, GB (ITS, LSU).
MycoBank MB822928.

castaneodiscus	NZ	
castaneodiscus II	NZ	
ignellus	NZ	

Basidiomata small, dry to viscid, yellow and reddish. Pileus 15–50 mm diam, yellow to orange-brown with a darker disc. Lamellae yellow-brown to olive yellow or orange. Stipe cylindrical, yellow with reddish veil remnants. Veil yellow to brick red. Context pale yellow to orange. Alkaline reaction red. Spores ovoid to subamygdaloid, 7–9.5 × 5–7 µm, moderately verrucose. In *Nothofagaceae* forests, New Zealand.

Clade /*Orixanthi* (91 %)

orixanthus	NZ	R
suborixanthus ined.	NZ	

Notes — Basidiomata are medium-sized, viscid, coloration yellow to yellow-brown. In *Nothofagaceae* forests.

Unsupported group *Icterinula*

alienatus	NZ	
amoenus II	SAm	2L
cardinalis	NZ	
cramesinus	NZ	
icterinus II	SAm	
mycenarum	NZ	R
papaver (*austrocinnabarinus*)	NZ, Aus	R
peraurilis	NZ	R
promethenus	NZ	R
rubripurpuratus	NZ	2L
xenosmatoides	NZ	
cf. *cramesinus*	Aus	2L
(*acutipapillatus* [*mastoideus*]	Aus)	
(*laetelamellatus*	Aus)	
(*vinicolor*	NZ)	

Notes — The group has low support and is intermixed with several of the smaller sections treated above, and all the species in the list are singletons in the present study. Basidiomata are often brightly yellow and red, but *C. xenosmatoides* deviates by its drab telamonioid habit and lack of alkaline reaction. The Australian *C. austrocinnabarinus* is shown by our analysis to be a late synonym of *C. papaver* from New Zealand.

The type of *Dermocybe* sect. *Icterinula*, *D. amoena*, has been sequenced, but is poorly supported as a member of the group in our analysis. ITS sequences of the types of *C. amoenus* and *C. icterinus* are 99.8 % similar. Moreover, under a different interpretation, Garnica et al. (2003) place these two species in a separate clade, which was also recovered in our analysis (marked 'II' in the list). Due to these partial contradictions, *Icterinula* cannot be used as a section name in the present study.

3. Leprocyboid sections

In 1969 Moser described subg. *Leprocybe*, whose taxa are mainly characterised by yellow/brownish/greenish basidiomata whose context fluoresces in UV light. Many of the taxa have been shown to contain anthraquinonic pigments of the nonaketide pathway (Stensrud et al. 2014). Earlier studies (Peintner et al. 2004, Garnica et al. 2005, 2016) have shown that the subgenus is polyphyletic, while some of its sections are here recovered as clades. The South Pacific taxon *C. canarius* is basal to the leprocyboid clades, despite its original placement in the genus *Dermocybe* (cf. Stefani et al. 2013). Under the present heading we consider taxa that are approximately consistent with the concept of *Leprocybe* s. Moser. Only a few were sampled in Fig. S2 of Garnica et al. (2016).

Section *Leprocybe* (M.M. Moser) Melot (100 %)

Typus. C. cotoneus Fr.

aureopigmentatus	CAm	2L
clandestinus	NAm	2L

cotoneus	Eur, NAm	R
flavifolius	NAm	G2016
parkeri	NAm	
phrygianus	Eur	
venetus	Eur	
(*cepistipes*	Eur)	
(*melanotus*	Eur)	
(*psittacinus*	Eur)	

Notes — The boreal section is characterised by predominantly yellow and greenish olive basidiomata with a strong fluorescence, due to xanthone pigments. Section *Persplendidi* often forms a sister clade. See also Ammirati et al. (2007).

Cortinarius sect. ***Persplendidi*** Soop & Dima, *sect. nov.* (90 %)

Typus. *C. persplendidus* Gasparini, GB (ITS, LSU).
MycoBank MB822929.
Non subsect. *Splendidi* Bidaud, Moënne-Locc. & Reumaux.

basirubescens (*fuscoumbonatus*)	Aus	R
clelandii	Aus	R
erythrocephalus	Aus	R
globuliformis	Aus	R
kula	Aus	R
kula II	Aus	R
melleilpileus ined.	Aus	Stefani et al. (2013)
ophryx	NZ	
persplendidus	NZ	R
salmoneobasis ined.	Aus	R
salmoneobasis II	Aus	R
sejunctus ined.	Aus	
sinapivelus	Aus	2L
tigrellus	NZ	2L
cf. *persplendidus* II	Aus	R
cf. *ophryx*	NZ	2L

Basidiomata agaricoid or sequestrate, dry, small to medium-sized, typically presenting a dark, tomentose pileus, a clavate stipe, and a yellow and strongly fluorescent context, recalling taxa in sect. *Leprocybe.* A few species dermocyboid (e.g., the blood-red *C. kula*). Anthraquinonic pigments based on the non-aketide pathway (Gill 1995). Pileus 10–60 mm diam, yellow, dark red-brown, dark orange-brown to umber or blackish, fibrillose/tomentose to granulose. Lamellae yellow, orange, or red. Stipe cylindrical to clavate or rudimentary, citrinous to saffron yellow or red. Veil red-brown to dark yellow, darkening, sparse to fairly copious. Context red to yellow. Alkaline reaction red to blackish brown, ± trivial in some species. Spores ovoid to subglobose, 8–11 × 5.5–8 µm, coarsely verrucose. In *Nothofagaceae* and *Myrtaceae* forest, New Zealand, Australia.

Notes — The section appears to be endemic for the South Pacific, but has so far not been recorded in Patagonia. The clade was named *Splendidi* in Garnica et al. (2005) and Stefani et al. (2013); however, to avoid connotation with *Cortinarius splendidus* Peck 1873, or with *C. splendidus* (E. Horak) K. Griffiths 1985, nom. illeg., we propose a new name here.

One of the members, *C.* cf. *persplendidus* II, has traditionally been named *Dermocybe splendida* in Australia, but forms a sister clade to the latter. *Dermocybe splendida* was described from New Zealand and later recombined as *Cortinarius persplendidus* (Gasparini 2006).

Cortinarius sect. ***Veronicae*** Soop, *sect. nov.* (99 %)

Typus. *C. veronicae* Soop, GB (ITS).
MycoBank MB822930.

chloroapicus ined.	Aus	
chloroapicus II	Aus	
magenteiannulatus ined.	Aus	R
veronicae	NZ	R
veronicoides	Aus	R
(*vinosipes*	Aus)	

Basidiomata dermocyboid, dry, with cinnabar red to scarlet coloration, recalling the boreal *C. cinnabarinus*, fluorescence yellow. Pileus 20–50 mm diam, cinnabar red, tomentose to finely fibrillose. Lamellae red-orange to brick. Stipe cylindrical, pink to yellowish pink. Veil cinnabar-red or pink, fairly sparse to copious. Context pale yellow. Alkaline reaction blood red on pileus, bluish lilac on stipital veil. Spores subglobose, 5.5–7 × 4.5–5.5 µm, moderately verrucose. In *Nothofagaceae* forest, New Zealand, Australia.

Notes — The section is sister to sect. *Leprocybe* and might be considered part of the latter despite morphological differences (cf. Stefani et al. 2013).

Section *Limonii* Kühner & Romagn. ex Nezdojm. (99 %)

Typus. *C. limonius* (Fr.: Fr.) Fr.

araniiti	NZ	2L
armiae	NZ	
aurantiobrunneus	CAm	
caryotis	NZ	R
caryotoides	NZ	2L
kroegeri	NAm	Liimatainen (2016)
limonius	Eur, NAm	
limonius II	Eur, NAm	2L
myrticaryotis ined.	NZ	2L
rubrimarginatus	NZ	
rubrocastaneus	NZ	2L
viscilaetus	NZ	R

Notes — This section, and the morphologically similar sect. *Callistei*, are recovered as well separated but closely related clades in our analyses. The taxa of both sections are characterised by vividly yellow and orange pigments, often with a positive alkaline reaction, but fluorescence is weak. *Limonii* has its core population in New Zealand with at least eight species, and no member has so far been reported from Australia. Two of them, *Cortinarius rubrocastaneus* and *C. rubrimarginatus*, possess remarkable chrysobasidia, a rare feature in *Cortinarius*. See further Soop et al. (2018).

Cortinarius sect. ***Callistei*** (Liimat., Niskanen & Ammirati) Soop, B. Oertel & Dima, *stat. nov.* (100 %)

Basionym. *Cortinarius* subg. *Callistei* Liimat., Niskanen & Ammirati, Index Fungorum 256: 2. 2015. IF551473.
Typus. *C. callisteus* (Fr.: Fr.) Fr., neotypus GB (ITS).
MycoBank MB823024.

austrolimonius var. *ochrovelatus*	SAm	R
callisteus	Eur, NAm	
collybianus	NZ	R
controversus	Aus	R
eucollybianus	NZ	
infucatus	Eur, NAm	R
neocallisteus	NAm, Eur	
rubrodactylus	NZ	
tophaceus	Eur, NAm	2L
cf. *collybianus*	NZ	2L

Notes — *Cortinarius austrolimonius* was described in the South American subg. *Cystogenes*, characterised by the presence of remarkable cheilocystidia. But the type (*C. formosus*) of the subgenus has not been sequenced, and remaining species in the subgenus do not exhibit this character state. Garnica et al. (2003) grouped *C. austrolimonius* var. *ochrovelatus* with *C. pugionipes* and *C. cervinus*, also from South America, but this affinity is not recovered in our analysis. See further Niskanen et al. (2016).

Section ***Orellani*** M.M. Moser (100 %)

Typus. *C. orellanus* Fr.

eartoxicus	Aus	2L
orellanoides	Eur, NAm	R
orellanus	Eur, NAm	R
(*catarracticus*	Aus)	
(*fluorescens*	SAm)	

Notes — This bihemispherical section was placed by Moser (1969) in subg. *Leprocybe*, and later promoted to subgeneric rank by Gasparini (2004). It is characterised by yellow and orange pigments and is unique in *Cortinarius* by containing appreciable quantities of the lethal toxin orellanine.

Cortinarius sect. ***Sinapicolores*** (Gasparini) Soop, *stat. nov.* (100 %)

Basionym. *Cortinarius* subser. *Sinapicolores* Gasparini, New Zealand J. Bot. 45: 228. 2007.
Typus. *C. sinapicolor* Cleland.
MycoBank MB822989.

sinapicolor	Aus
ignotus	NZ
(*wirrabara*	Aus)

Notes — This small southern clade consists of medium-sized, glutinous cortinars of a golden-yellow colour that react strongly with alkaline solutions. The type of the section is also part of sect. *Pyromyxa* M.M. Moser, a name we cannot use, since no sequence of its type, *C. pyromyxa*, is available.

Cortinarius sect. ***Rubicunduli*** Soop, B. Oertel & Dima, *sect. nov.* (100 %)

C. stirps *rubicundulus* M.M. Moser in Singer (1986).
Typus. *C. rubicundulus* (Rea) A. Pearson.
MycoBank MB822931

paurigarhwalensis ined.	C Asia	Fungal Diversity Notes (in prep.)
rubicundulus	Eur	R
subgemmeus	NZ	

Basidiomata agaricoid, medium-sized, dry to viscid, coloration yellowish with a tendency to darken on bruising, fluorescence weak. Pileus 15–70 mm diam, pale yellow to yellow-brown with orange-red to dark brown spots and zones, matt, mottled with reddish to pale ochraceous fibrils, blushing to dark orange. Lamellae greyish yellow to pale tan. Stipe cylindrical to clavate, white to greyish yellow, blushing or flavescent. Veil, pale grey to pale ochraceous, blushing and darkening to red or orange, rather copious to sparse. Context pale yellow to tan, ± flavescent when cut and bruised. Alkaline reaction insignificant. Spores ellipsoid to subfusoid, 6–9 × 3.8–5 µm, weakly verrucose. Cheilo- and pleurocystidia prominent, cylindrical or capitate. In *Picea*, *Nothofagaceae*, and *Quercus leucotrichophora* forests, Europe, New Zealand, Asia, respectively.

Notes — These species are recovered on very long branches in a basal position of the phylogeny. The section is a strongly supported sister to *Crassi*, indicating an affinity consistent with some shared morphological characters, such as the cheilocystidia and a soft context.

Cortinarius sect. ***Incensi*** Soop, *sect. nov.* (79 %)

Typus. *C. incensus* Soop, GB (ITS, LSU).
MycoBank MB822932.

flammuloides	SAm
incensus	NZ

Basidiomata agaricoid, medium-sized, yellowish. Pileus 15–80 mm diam, slightly viscid, saturated to pale yellowish, disk often more orange with brownish stains or squamules. Lamellae whitish to grey-yellow. Stipe cylindrical, often slightly bulbous/clavate, pale yellow to orange, staining brownish. Veil yellow to orange-brown, fairly copious. Context white, often flushing yellow with age or on manipulation. Odour ± spicy. Alkaline reaction yellow to red-brown or red, fluorescence greenish yellow. Spores ellipsoid to subcitriform, 9–12 × 5–6.5 µm, moderately verrucose. In *Nothofagaceae* forest, South Pacific.

Notes — Moser in Singer (1986) assigned the Patagonian member to stirps *Flammuloides* in subg. *Phlegmacium*.

4. Phlegmacioid sections

4.1. Euphlegmacia

Under this provisional name we regroup most of the taxa that were included in Phlegmacioid lineages I and II in Garnica et al. (2016: Fig. S2). They are traditionally and morphologically assigned to subg. *Phlegmacium*, characterised by a viscid pileus, a dry stipe, relatively crowded lamellae, and a more or less robust habit, even though a fair number of exceptions do occur. The *Calochroi* complex is discussed in the next subchapter.

Section ***Phlegmacium*** (Fr.) Gillot & Lucand (99 %)

Typus. *C. saginus* (Fr.: Fr.) Fr.

norrlandicus	Eur	
populinus	Eur	
saginus	Eur	R

Notes — The section is boreal and includes the type of the traditional subg. *Phlegmacium*. Basidiomata are stipitocarpic and present a yellow to brownish veil. But *C. triumphans*, often assigned here, occupies an isolated position.

Section ***Scauri*** (Fr.) Henn. (100 %)

Typus. *C. scaurus* (Fr.: Fr.) Fr., neotypus GB (ITS).

chlorophyllus	NZ	
fuligineofolius	NAm	G2016
herpeticus	Eur	2L
montanus	NAm	2L
scaurus	Eur, NAm	R
scaurus II	Eur	2L
singularis	NZ	R
sphagnophilus	Eur, NAm	2L
violaceonitens	Eur	
virentophyllus	NAm	G2016
cf. *singularis*	NZ	2L
cf. *singularis* II	NZ	2L
cf. *violaceonitens*	Eur	2L

Notes — This section is bihemispherical and sister to sect. *Purpurascentes*. The morphological and chemical plasticity within the section is remarkably low. The species are characterised by a pileocarpic development, a viscid pileus, often with an olive or greenish tint, and a positive iodine-based reaction (Garnica et al. 2005).

Section ***Purpurascentes*** M.M. Moser (100 %)

Typus. *C. purpurascens* Fr., neotypus GB (ITS).

argyrionus	Aus	G2016
australis	Aus, NZ	
caesibulga	Aus	G2016

campbellae	Aus	2L
chalybaeus	NZ	R
cinereoroseolus	Aus	G2016
collocandoides	Eur	2L
kaimanawa	NZ	R
occidentalis (*mutabilis*)	NAm, Eur	2L
porphyropus	NAm, Eur	
purpurascens	NAm, Eur	R
rhipiduranus	NZ	
submagellanicus	Aus	
subporphyropus (*mendax*)	Eur	2L
subpurpurascens	NAm, Eur	G2016
cf. *fragilis*	Aus	2L

Notes — This section is bihemispherical. Like in *Scauri* (above) the basidiomata present a positive iodine-based reaction, though most deviate by a stipitocarpic habit, and four of the Australian species are sequestrate. In addition, parts of the basidiomata typically darken with a violet tinge on bruising (Saar et al. 2014). *Cortinarius* cf. *fragilis* appears to be a sequestrate form of a morphospecies that includes the agaricoid *C. submagellanicus*. The morphologically deviating South Pacific singleton *C. persicanus* is a sister.

Section *Multiformes* (Rob. Henry) Moënne-Locc. & Reumaux (100 %)

Typus. *C. multiformis* Fr., neotypus GB (ITS).

armenicorius	Eur, Asia	2L
caesiolamellatus	NAm, Eur	2L
caesiophylloides	Eur, NAm	G2016
frondosomultiformis	Eur	JEC
melleicarneus	Eur	2L
multiformis	NAm, Eur	
pallidirimosus	NAm, Eur	G2016
rufoallutus	Eur	
talimultiformis	Eur	
talus	Eur, NAm	R

Notes — The section appears to be endemic to the Northern Hemisphere. See further Liimatainen et al. (2014) and Brandrud et al. (2014).

Section *Cremeolinae* Soop (93 %)

Typus. *C. cremeolina* Soop, GB (ITS, LSU).

cremeolina	NZ	
cremeolina var. *subpicoides*	NZ	
cremeorufus	NZ	
dulciorum	NZ	
iringa	NZ	
nebulobrunneus	Aus	2L
cf. *austrorapaceus*	SAm	
cf. *cremeolina*	NZ	2L
cf. *cremeolina* II	NZ	2L

Notes — This is an austral section morphologically similar to the sister sect. *Multiformes*. The Australian taxon, however, is sequestrate. See further Soop (2016).

Section *Claricolores* Moënne-Locc. & Reumaux (95 %)

Typus. *C. claricolor* Fr., neotypus GB (ITS).

blattoi (*pseudovariegatus*)	Eur, NAm	2L
claricolor	NAm, Eur	R
cumatilis	Eur	R
praestans	Eur	
rex-claricolorum	Eur	G2016

Notes — See further Brandrud et al. (2013).

Clade /*Rhizophori* (100 %)

rhizophorus	Eur	R
viscidoamarus	Eur	

Notes — Taxa in this boreal clade possess a slightly bulbous stipe and yellowish tints.

Section *Elastici* (Fr.) Henn. (100 %)

Typus. *C. papulosus* Fr., neotypus GB (ITS).

artosus	NZ	
castaneicolor	NAm	G2016
coelopus	Aus	
luteobrunnescens	Eur, NAm	G2016
ochraceobrunneus	Eur	G2016
papulosus	Eur, NAm	R
cf. *papulosus*	Eur, NAm	2L

Notes — Taxa in this bihemispherical section possess clavate stipes and often have a characteristic grassy odour. The section is strongly supported as sister to the following one, but is kept segregated from it due to morphological differences.

Section *Percomes* (Moënne-Locc. & Reumaux) Melot (77 %)

Typus. *C. percomis* Fr., neotypus GB (ITS).

aurilicis	Eur	R
cephalixoides	NAm	G2016
citrinifolius	NAm	G2016
nanceiensis	Eur	R
pallidopercomis ined.	Eur	G2016
percomis	Eur	R
russeoides	Eur	2L
squameopercomis ined.	Eur	2L
stjernegaardii	Eur	G2016
superbus	NAm	
xanthosuavis	Eur	
(*mussivus*	Eur)	

Notes — This boreal section consists of yellowish taxa, often with a citrinous or olive tint, and mostly a stipitocarpic habit. Many have characteristic odours.

Section *Caesiocortinati* Frøslev & T.S. Jeppesen (100 %)

Paronym. *C.* subsect. *Caesiocortinati* Brandrud & Melot.
Typus. *C. caesiocortinatus* Jul. Schäff.

bulbolatens (*turbinatorum*)	Eur	
caesiocortinatus	Eur	R
prasinocyaneus	Eur	R
cf. *caesiocortinatus*	Asia	JEC

Notes — Basidiomata are large with an irregularly bulbous stipe. The spores are subglobose and strongly verrucose. The North American *C. ponderosus* is closely related to the section, but not morphologically similar.

Section *Phlegmacioides* (Fr.: Fr.) Brandrud, H. Lindstr. & Melot (80 %)

Typus. *C. variecolor* (Pers.: Fr.) Fr., neotypus GB (ITS).

areni-silvae	Eur	R
balteatialutaceus	Eur	G2016
balteatibulbosus	Eur	R
balteatoalbus	Eur	
balteatocumatilis	NAm, Eur	R
balteatocumatilis II	NAm	G2016
balteatus	NAm, Eur	
balteatus II	NAm	2L
brunneiaurantiaus	Eur	G2016

brunneolividus	Eur	G2016
caesiocolor	Eur	G2016
coalescens	Eur	2L
daulnoyae (*chromataphilus*)	Eur	R
durus	Eur	
eliae (*lividoviolaceus*)	Eur	2L
largus	Eur	2L
lavendulensis	Aus	
myrtilliphilus	Eur	2L
patibilis	Eur	
pseudodaulnoyae (*squamosocephalus*)	Eur	2L
pseudonaevosus (*vacciniophilus*)	Eur	2L
pseudonebularis	Eur	2L
sobrius	Eur	G2016
spadicellus	Eur	
variecolor	NAm, Eur	R
violaceomaculatus	Eur	R
cf. *variecolor*	NAm	2L

Notes — Apart from one Australian species, the section is boreal. It consists of stipitocarpic taxa of *Phlegmacium* habit, though the pileus is sometimes almost dry. The core of the section consists of subsect. *Variecolores* and *Balteati* (Brandrud 1998).

Clade /*Varii* (86 %)

decolorans	Eur	
luteocingulatus	Eur	2L
reverendissimus	Eur	R
variiformis	Eur	2L
variosimilis	NAm, Eur	R
varius	Eur	
cf. *variosimilis*	NAm	

Notes — Basidiomata are stipitocarpic with an ochraceous pileus, violaceous lamellae, and a white to yellow veil. In coniferous and broad-leaf forests.

Cortinarius decolorans (Pers.) Fr.

Neotypus. Sweden, Gotland, Tjaukle Änge, with *Picea*, *K. Soop* CO745, herb. S F304386, GenBank KJ421062 (ITS+LSU), hic designatus.
MycoBank MBT378826.

Notes — This species was labelled '*C. varius* II' in Garnica et al. (2016). Basidiomata resemble *C. varius*, but (almost) lack violet hues. They match Fries' taxon well (Fries 1821, 1851); we hence propose to neotypify his epithet for the present taxon, even though the name has not often been used in modern literature.

Clade /*Obsoleti* (100 %)

obsoletus	Eur	R
oertelii ined.	Eur	R

Notes — Basidiomata are stipitocarpic with an ochraceous pileus, violaceous lamellae, and a white veil. In broad-leaf forests.

Section *Amoenolentes* Brandrud & Melot (99 %)

Typus. C. amoenolens Rob. Henry.

aleuriosmus	Eur	R
amoenolens (*anserinus* s. auct.)	Eur	
griseocoeruleus	Eur	G2016

Notes — A boreal section of pileocarpic and odorous fungi with violaceous lamellae. Clade /*Dionysae* may be considered part of the section, despite deviating in several characters. See further Fernández-Brime et al. (2014) and Liimatainen et al. (2014).

Clade /*Dionysae* (96 %)

boreidionysae	Eur	JEC
dionysae	NAm, Eur	R
dionysae II	Eur	G2016
mahiquesii	Eur	G2016
olivaceodionysae	Eur	
palazonianus	Eur	G2016

Notes — Taxa are pileocarpic with a greyish or olivaceous pileus, violaceous lamellae, and often a farinaceous odour.

Clade /*Camptori* (100 %)

calyptrodermus	NAm	G2016
camptoros	Eur	
velicopia	NAm	JEC
viridicoeruleus (*lepistoides*)	Eur	R

Notes — Basidiomata are pileocarpic, medium-sized, with a typically viscid and hygrophanous cutis. In broad-leaf forests.

Cortinarius sect. *Turmales* Soop, B. Oertel & Dima, *sect. nov.* (100 %)

Typus. C. turmalis Fr., neotypus GB (ITS).
MycoBank MB822933.

picoides	NZ	R
turmalis (*corrugis*)	Eur, NAm	R

Basidiomata stipitocarpic, medium-sized, often caespitose. Pileus 30–100 mm diam, yellow-brown to dark brown, viscid, finely fibrillose. Lamellae greyish white, crowded. Stipe cylindrical to tapering and radicant, white, silky fibrillose, often staining brownish or violaceous. Veil white, rather sparse. Alkaline reaction insignificant. Spores fusoid to amygdaloid, 6.5–9 × 3.3–4.5 µm, weakly verrucose. In *Picea* and *Nothofagaceae* forests, Europe, North America, South Pacific.

Cortinarius sect. *Aureocistophili* Fern.-Brime ex Soop, B. Oertel & Dima, *sect. nov.* (87 %)

Typus. C. aureocistophilus Vila, Contu & Llimona, GB (ITS, LSU).
MycoBank MB822934.

aureocistophilus	Eur	
fulminoides	Eur	
inusitatus	Eur	2L
kytoevuorii	Eur	G2016
mediterranensis	Eur	
subrugulosus	Eur	
xanthoochraceus	Eur	R
cf. *inusitatus*	Eur	G2016

Basidiomata pileocarpic or stipitocarpic, medium-sized to large, evoking species of both sect. *Multiformes* and sect. *Glaucopodes*. Pileus 30–120 mm diam, viscid, yellow to orange or ochraceous, rarely violaceous when young, finely to coarsely white fibrillose, often with veil remnants near margin. Lamellae greyish white, rarely with a pink tinge. Stipe cylindrical with a rounded or marginate bulb, white, often flushing yellow with age. Veil white to yellowish, rarely with a blue tinge, sparse to rather copious. Context white, often flushing yellow with age or manipulation. Alkaline reaction reddish to brownish, or insignificant. Spores ellipsoid to amygdaloid, 7.5–11 × 4.5–6 µm, moderately verrucose. Mainly in *Picea*, *Abies* and *Quercus* forests, Europe.

Notes — See further Fernández-Brime et al. (2014).

Section *Riederi* (Brandrud & Melot) Brandrud, Dima, Niskanen & Liimat. (100 %)

Typus. C. riederi (Weinm.) Fr., neotypus Melot (1986) (ITS in Brandrud et al. 2018).

anomaloochrascens	Eur	R
argenteolilacinus	Eur	G2016
var. *dovrensis*	Eur	2L
burlinghamiae	NAm	JEC
fulvoochrascens	NAm, Eur	R
glaucocyanopus	Eur	JEC
malachioides	Eur	
pallidoriederi	Eur	JEC
parksianus	NAm	JEC
riederi (*pseudoarquatus*)	NAm, Eur	G2016

Notes — A boreal section of robust taxa evoking members of sect. *Glaucopodes*. See Brandrud et al. (2018).

Section *Glaucopodes* (Konrad & Maubl.) Moënne-Locc. & Reumaux (99 %)

Typus. C. glaucopus Fr., neotypus GB (ITS).

alticaudus	Eur, NAm	G2016
cistoglaucopus	Eur	G2016
glaucopus	NAm, Eur	
glaucopus II	Eur	G2016
glaucopus III	Eur	G2016
magicus	Eur	R
magicus II	Eur	2L
olidoamarus (*misermontii*, *van-campiae*)	Eur	R
olidovolvatus	Eur	
pansa	Eur	G2016
perstrenuus (*subaccedens*)	Eur	G2016
subfoetens	NAm	G2016
subrubrovelatus	Eur	R
tirolianus	Eur	G2016
cf. *glaucopus*	Eur	2L

Notes — A boreal section of pileocarpic fungi, often with violet lamellae and a fibrillose cutis.

Clade /*Arcifolii* (94 %)

arcifolius	Eur	R
subhygrophanus	Eur	R
cf. *arcifolius*	Eur	JEC

Notes — Basidiomata are pileocarpic, medium-sized, with a pale to dark ochraceous coloration, often with an olivaceous tint, veil yellowish. In *Fagaceae* forests.

Clade /*Glaucocephali* (99 %)

glaucocephalus	NAm
subsolitarius	NAm

Notes — Basidiomata are pileocarpic, medium-sized, dark greenish, lamellae blue. In coniferous forests.

Section *Arguti* (Brandrud & Melot) Liimat., Ammirati, Niskanen, Dima & C. Cripps (82 %)

Typus. C. argutus Fr.

argutus	NAm, Eur	
fraudulosus	NAm, Eur	JEC
fraudulosoides	Eur, NAm	
hedyaromaticus	NAm, Eur	2L
herculeus	Eur	R
paracephalixus	Eur	
patrickensis	NAm, Eur	G2016
rioussetiae	Eur	G2016
rosargutus	Eur	2L
subfraudulosus	Eur	

Notes — A boreal section of stipitocarpic fungi, whose stipe often tapers towards the base coupled with a caespitose growth. Colours are mostly pale, the lamellae conspicuously crowded, and the pileus is only slightly viscid or even dry. The European *Cortinarius pseudovulpinus* is morphologically similar but not closely related.

Clade /*Caligati* (67 %)

caligatus	Eur	
maculosus	Eur	
squameoradicans	Eur	R

Notes — Closely related to the morphologically similar sect. *Arguti*. Basidiomata are stipitocarpic, with the stipe tapering towards the base and a copious veil. Growth caespitose, in *Fagaceae* forests.

Section *Caerulescentes* Rob. Henry ex Moënne-Locc. & Reumaux (90 %)

Typus. C. caerulescens (Schaeff.: Fr.) Fr., neotypus GB (ITS).

albescens	NAm, Eur	G2016
caerulescens	NAm, Eur	
caesiocanescens	Eur	R
caesiostramineus	Eur	R
cremeiamarescens	NAm, Eur	2L
foetens (*aurantiobasalis*)	Eur	
georgiolens	Eur	R
subalbescens	Eur	R
volvatus	NAm, Eur	2L

Notes — A boreal section of pileocarpic fungi, most of which display violaceous colours.

Clade /*Eucaerulei* (96 %)

aurescens	NAm	JEC
caerulescentium	Eur	R
eucaeruleus	Eur	R
perpallens	Eur	
terpsichores	NAm, Eur	

Notes — Basidiomata are medium-sized, pileocarpic with violaceous hues, resembling species in the sister sect. *Caerulescentes*. In broad-leaf forests.

Clade /*Subolivascentes* (89 %)

atrochalybaeus	NAm, Eur	G2016
barrentium (*tauri*)	NAm, Eur	R
moënne-loccozii	Eur	
subolivascens	NAm	
cf. *atrochalybaeus*	NAm	JEC
cf. *velicopia*	NAm	2L

Notes — Basidiomata medium-sized, pileocarpic, coloration brown to violaceous. In coniferous and broad-leaf forests.

Cortinarius sect. ***Vinaceolamellati*** Soop & Gasparini, *sect. nov.* (86 %)

Typus. C. vinaceolamellatus Cleland.
MycoBank MB822935.

caeruleoëburneus	Aus
vinaceolamellatus	Aus

Basidiomata medium-sized, stipitocarpic. Pileus 30–60 mm diam, viscid, pale violaceous, brunnescent, finely fibrillose. Lamellae lilac-violet. Stipe clavate, white to pale violet. Veil white to pale violet, sparse to rather copious. Context white to pale brownish, marbled violet. Alkaline reaction insignificant. Spores ellipsoid to ovoid, 7.5–10.5 × 4.5–6.5 µm, moderately verrucose. Cheilocystidia prominent in one species. In *Myrtaceae* forests, Australia.

Cortinarius sect. ***Alboaggregati*** Soop, *sect. nov.* (100 %)

Typus. C. alboaggregatus Soop, GB (ITS).
MycoBank MB822936.

alboaggregatus	NZ	R
pseudotriumphans	SAm	R

Basidiomata medium-sized to large, stipitocarpic. Pileus 35–75 mm diam, viscid, white to yellow-brown, somewhat brunnescent on disk, finely fibrillose, margin involute. Lamellae white, crowded. Stipe tapering downwards or fusoid, rooted, white with rather thick, white girdles, often peronate. Veil white, copious. Context white. Alkaline reaction orange-brown or insignificant. Spores fusoid-amygdaloid, 10.5–13.5 × 5.5–7.5 µm, moderately verrucose. In *Nothofagaceae* forests, New Zealand and South America.

Cortinarius sect. ***Cretaces*** Soop & Dima, *sect. nov.* (57 %, 90 % in PhyML tree)

Typus. C. cretax Soop, GB (ITS).
MycoBank MB822937.

austroturmalis	SAm	
caelicolor	SAm	
cervinus	SAm	
cretax	NZ	
effundens	SAm	
lacteus	Aus	2L
pugionipes	SAm	2L
(*xiphidipus*	SAm)	

Basidiomata medium-sized to large, stipitocarpic, often caespitose. Pileus 25–120 mm diam, viscid, white to yellow-brown, occasionally flavescent or brunnescent on disk, glabrous to finely fibrillose. Lamellae white to pale grey-brown, crowded. Stipe tapering downwards, rooted, white, ± glabrous. Veil white, sparse. Context white. Odour weak or like bitter almonds. Alkaline reaction insignificant. Spores fusoid-amygdaloid, 6–10 × 3–5.5 µm, weakly verrucose. In *Nothofagaceae* forests, South Pacific.

Notes — This predominantly Patagonian section is part of stirps *Xiphidipus* (see Moser & Horak 1975), but as no sequence of the paronymous species *C. xiphidipus* is available, we cannot use the name as the base of a new combination. The fungi resemble those of sections *Arguti* and *Alboaggregati*, which are genetically remote.

Clade */Turcopedes* (99 %)

turcopes	NZ
cf. *turcopes*	NZ

Notes — A small austral clade of stipitocarpic fungi with a blue to blue-green coloration. In *Nothofagaceae* forests.

4.2. *Calochroi* s.lat.

This large monophyletic group of over 80 species appears to be endemic for the Northern Hemisphere. Basidiomata generally present a pileocarpic habit with a wide stipital bulb. Many of the species are rare and most grow exclusively on calcareous soil. Their hosts belong to a range of broad-leaf and coniferous genera, but *Quercus* is a dominant partner, especially in the southern parts of the region.

The phylogeny reveals a number of closely related clades, many of which are recovered as traditional sections. These are not further discussed in this study, having been extensively documented in several dedicated efforts (Frøslev et al. 2006a, b, Ortega et al. 2008, Garnica et al. 2009, 2011). They are represented in Garnica et al. (2016: Fig. S2) by Phlegmacioid clade III.

4.3 Pseudophlegmacia

Under this provisional name we consider taxa that in various respects (habit, viscidity, hygrophanity, etc.) deviate from typical *Phlegmacium*, and/or have sometimes been assigned to other genera or subgenera. Only a few were sampled in Fig. S2 of Garnica et al. (2016).

Cortinarius sect. ***Lustrati*** Ammirati ex Soop, B. Oertel & Dima, *sect. nov*. (100 %)

Typus. C. lustratus Fr.
MycoBank MB822938

comparioides	CAm	2L
leucophanes (*comarostaphylides*)	Eur, NAm, CAm	
leucophanes II	NAm	2L
lustratus	Eur	R
oregonensis	CAm	G2016
ovreboii	CAm	

Basidiomata medium-sized to small, stipitocarpic, pale. Pileus 25–70 mm diam, viscid, ivory to creamy-yellow or pale violet, disk yellowish, glabrous to silky. Lamellae greyish, sometimes with a rosy or violet tinge, crowded. Stipe clavate to cylindrical with a small bulb, silky white, often ± violaceous at apex. Veil white to pale violet, sparse to fairly copious. Context white, occasionally marbled violet. Odour none or farinaceous, sometimes fruity. Alkaline reaction insignificant. Spores 5.5–8 × 3.5–4.5 µm, ellipsoid, weakly verrucose. In *Pinus*, *Fagaceae*, and *Comarostaphylis* forests, Europe, North/Central America.

Notes — The boreal section forms a well-supported clade with two sister sections in the South Pacific, *Laquelli* and *Austrocyanites*. See further Ammirati et al. (2007).

Cortinarius sect. **Laquelli** Soop, *sect. nov.* (80 %)

Typus. C. laquellus Soop, GB (ITS).
MycoBank MB822939.

laquellus	NZ
urbiculus	NZ

Basidiomata small, stipitocarpic, coloration pale, recalling those of sect. *Lustrati*. Pileus 7–35 mm diam, dry to viscid, matt with a white, velvety or pruinose coating, finely fibrillose. Lamellae pale violet to greyish violet, medium crowded. Stipe cylindrical to clavate, silvery white with a faint violaceous tint. Veil white, fairly copious. Context white, young marbled violet or entirely bright violet-lilac, odour faint, ± like wax candles, taste ± bitter. Alkaline reaction insignificant. Spores ellipsoid to subamygdaloid, 6.5–8.5 × 3.8–5 µm, weakly to moderately verrucose. In *Nothofagaceae* forests, New Zealand.

Cortinarius sect. ***Thaumasti*** Soop, *sect. nov.* (93 %)

Typus. C. thaumastus Soop, GB (ITS, LSU).
MycoBank MB822965.

chlorophanus	SAm	R
thaumastus	NZ	
vaginatus	SAm	R
(*coleopus*	SAm)	

Basidiomata small, with a peronate or volvate stipe. Pileus 15–50 mm diam, dry to slightly viscid, hygrophanous, olive-green, yellow, or apricot-brown to red-orange, finely granulose to fibrillose, with white to ochraceous tufts. Lamellae pale greyish to ochraceous, fairly crowded. Stipe with a ± marginate bulb, white to pale yellow, orange, or olivaceous. Veil white to ochraceous, fairly copious, on stipe fibrillose to peronate with thick tufts near base, sometimes forming a membranous volva or collar. Context greyish ochraceous to olivaceous. Alkaline reaction orange to red-brown in context, red to red-brown on cutis. Spores citriform to amygdaloid, 8–11 × 3.5–5 µm, up to 7 µm wide in one species, weakly verrucose. In *Nothofagaceae* forests, New Zealand and Patagonia.

Notes — Several taxa in this austral section are members of *Cortinarius* subsect. *Coleopodes* (see Moser & Horak 1975). However, since no sequence of the type *C. coleopus* is available, we cannot use *Coleopodes* as a basionym.

Clade /*Rufoaurantii* (79 %)

faucium ined.	NZ
rufoaurantius	SAm

Notes — A small austral clade of phlegmacioid/telamonioid taxa. Basidiomata are small to medium-sized, stipitocarpic; the coloration is yellow-brown to orange-brown. In *Nothofagaceae* forests.

Cortinarius rufoaurantius Soop, *nom. nov.*

Basionym: *Cortinarius aurantiorufus* Garnica, in Garnica et al., Mycologia 94 (1):136. 2002, nom. illeg.
MycoBank MB823022.

Notes — The name *C. aurantiorufus* Bidaud is in use (Bidaud et al. 2001).

Cortinarius sect. *Dulciolentes* Soop, *sect. nov.* (95 %)

Typus. Cuphocybe melliolens Soop, GB (ITS).
MycoBank MB822940.

atratus (*P. luteum*)	Aus, NZ	R
atropileatus	NZ	2L
beeverorum	NZ	
corrugatus	CAm	
dulciolens (*Cu. melliolens*)	NZ	
peraurantiacus	NZ	
pisciodorus	NZ	

Basidiomata medium-sized to large, cuphocyboid or sequestrate. Pileus 25–100 mm diam, viscid to glutinous, pale greyish brown to ochraceous, dark orange, or copper red, coarsely fibrillose to granulose, margin sometimes striate or sulcate. Lamellae/gleba pale cinnamon to argillaceous, sometimes with a violet tinge, crowded. Stipe cylindrical to clavate or rudimentary, often with a small rounded bulb, fibrillose, white, later darkening with red-brown tufts and squamules. Veil pale ochraceous, darkening to red-brown, fairly copious. Context white, slightly canescent or flavescent, sometimes marbled violet. Odour often aromatic or melleous. Alkaline reaction insignificant. Spores ellipsoid to subglobose, 9.5–17 × 7–11 µm, coarsely verrucose. In *Fagaceae*, *Nothofagaceae*, and *Myrtaceae* forests, South Pacific and Central America.

Notes — The bihemispherical section consists of taxa of varying morphology with the type originally described in the genus *Cuphocybe* and four members sequestrate (formerly in genera *Thaxterogaster* and *Protoglossum*).

Cortinarius sect. *Cuphocybe* (R. Heim) Soop, *comb.* & *stat. nov.* (100 %)

Basionym. Cuphocybe R. Heim, Rev. Mycol. 16: 8. 1951.
Typus. Cuphocybe olivacea R. Heim.
MycoBank MB822941.

elaiochrous (*Cu. olivacea*)	NZ	R
phaeomyxa	NZ	
C. sp.	Aus	2L

Notes — The former genus *Cuphocybe* is characterised by phlegmacioid taxa with a lacking cortina, which causes the veil to distribute as scales, tufts, and girdles along the full length of the stipe. Basidiomata are medium-sized to large, glutinous, coloration olive-brown to chocolate brown. Spores ellipsoid, large, 11–16 × 7–9 µm, moderately verrucose. In *Nothofagaceae* forests, South Pacific.

Cortinarius sect. *Rapacea* (E. Horak) Soop, *comb.* & *stat. nov.* (97 %)

Basionym. Rapacea E. Horak, Kew Bulletin 54: 789. 1999.
Paronym. C. series *Rapacea* Gasparini.
Typus. R. mariae E. Horak.
MycoBank MB822987.

castoreus	NZ	R
mariae	NZ, Aus, N Guinea	R

Notes — Basidiomata are medium-sized to large, robust, dry, sericeocyboid, with large spores (–18 µm). The section type, originally published in the genus *Rapacea* (named after *C. rapaceus* of similar colours), is unique in *Cortinarius* from its almost smooth spores, leaving an olive-yellow deposit. The boreal *C. pinophilus* appears as a sister with high support, but is morphologically not similar.

Section *Crassi* Melot (100 %)

Typus. C. crassus Fr., neotypus GB (ITS).

crassus	Eur, NAm	R
eutactus	NZ	

Notes — Taxa in this small bihemispherical section evoke *Phlegmacium*, but were traditionally difficult to place in the taxonomy of the genus. Basidiomata are robust with a clavate stipe, dry, coloured pale to dark brown, with narrow, weakly verrucose spores and prominent cheilocystidia (cf. sect. *Rubicunduli*).

Cortinarius sect. *Majestatici* Soop, *sect. nov.* (89 %)

Typus. Descolea majestatica E. Horak, GB (ITS, LSU).
MycoBank MB822942.

infrequens	SAm	
majestaticus	NZ	R

Basidiomata rozitoid or sequestrate, medium-sized, viscid, cutis structure partly cellular. Pileus 30–60 mm diam, glutinous, dark yellow-brown, young with an olivaceous tinge, later darkening to umber, glabrous, margin striate to sulcate. Lamellae/gleba cinnamon, medium crowded. Stipe cylindrical or rudimentary, yellow-brown to pale yellowish grey, with thick yellow-brown fibrils and girdles, collar grey-brown, membranous. Veil yellow-brown, sparse to fairly copious. Context dirty white to yellowish white with an olivaceous tinge. Alkaline reaction red on cutis. Hypodermal cells in pileipellis with vesiculose ends. Spores amygdaloid, 12–14 × 7–8.5 µm, coarsely verrucose. In *Notho fagaceae* forests, South Pacific.

Notes — The type of this small austral section was originally described in the genus *Descolea*, but shares major characters with sect. *Subcastanelli* (Anderson & Orlovich 2016). The South American taxon is sequestrate.

Cortinarius sect. ***Rozites*** (P. Karst.) Soop, B. Oertel & Dima, *comb.* & *stat. nov.* (100 %)

Basionym. Rozites P. Karst., Bidrag Kannedom Finlands Natur Folk 32: 290. 1879.
Typus. C. caperatus Fr.
MycoBank MB822988.

caperatus	Eur, NAm	R
emodensis	C Asia	2L
fuegianus	SAm	G2016
meleagris	NZ	
metallicus	Aus	2L
similis	N Guinea	
(*colombianus*	CAm)	

Notes — Taxa published in the former genus *Rozites* are distributed over several clades, of which the above forms the bihemispherical type section. Basidiomata are characterised by a membranous inner veil, homologous with the cortina, amyloidal tissues, and strongly dextrinoid spores. One may also note that *Rozites* sect. *Rozites* (autonym) was described by Moser & Horak (1975).

Clade /*Achroi* (100 % in 2-loci tree)

achrous	NZ	
cf. *achrous*	NZ	2L
(*elacatipus*	NZ)	
(*rugosiceps*	NZ)	

Notes — Basidiomata are medium-sized to large, rozitoid, glutinous, hygrophanous, with a pale coloration and large spores. In *Nothofagaceae* forests.

Cortinarius sect. ***Subcastanelli*** Soop, *sect. nov.* (77 %)

Typus. *Rozites castanellus* E. Horak & G.M. Taylor.
MycoBank MB822943.

canovestitus	NZ	
epiphaeus	NZ	
ohauensis	NZ	
subcastanellus (*R. castanellus*)	NZ	
taylorianus	NZ	
trichocarpus	NZ	
wallacei	NZ	R

Basidiomata medium-sized to large of various habits: rozitoid, cuphocyboid, myxacioid, or sequestrate. Pileus 25–90 mm diam, dry to glutinous, red-brown to dark yellow-brown or tan, rarely with a violet tinge, coarsely fibrillose, sometimes with thick, greyish white to reddish tufts, margin striate to rimose when old. Lamellae/gleba cinnamon to yellow-brown or brownish pink, rarely violaceous, crowded to rather distant. Stipe cylindrical to clavate, often with a small rounded bulb, violaceous to white, pale grey, or pale yellow, with thick grey to brownish pink girdles, often with a striate, membranous collar. Veil greyish white to greyish yellow or reddish brown, rather sparse to copious. Context grey to pale grey-brown, ± marbled darker grey, yellow, or violet. Alkaline reaction reddish on cutis or insignificant. Spores ellipsoid to subamygdaloid, 8–14 × 5–8.5 µm, moderately to weakly verrucose. In *Nothofagaceae* forests, New Zealand.

Notes — This section is so far known only from New Zealand. Some of our *C. epiphaeus* samples were labelled *C. napivelatus*, a morphologically almost identical sequestrate fungus. Since the holotype of neither has been sequenced, it is too early to judge on their conspecificity, and we here use the dominant (and prioritary) epithet.

Cortinarius trichocarpus could be considered an agaricoid form of a morphospecies that includes the sequestrate *C. ohauensis*. Moreover, *C. ohauensis* is a late synonym of *Austrogaster novaezelandiae*, not yet combined into *Cortinarius*.

Cortinarius sect. ***Subhymenogaster*** Soop, B. Oertel & Dima, *sect. nov.* (100 %)

Typus. Hymenogaster sublilacinus A.H. Sm., GB (ITS).
MycoBank MB822944.

brunnescens	NAm	
lilacinoides	NAm	2L
subcaeruleus	NAm	
(*Hymenogaster subolivaceus*	NAm)	

Basidiomata sequestrate, globose to ovate or lobed. Peridium 10–55 mm diam, thin, dry, silky, whitish to lilac, flushing brown, purple, or bluish on manipulation. Gleba loculate, cinnamon to rusty brown. Columella white, tenous, dendrous to percurrent, or absent. Odour aromatic. Spores ellipsoid, 9–13 × 6.5–8 µm, weakly to moderately verrucose. In coniferous forests, North America.

Notes — The section is sister to sect. *Caerulescentes*. It has also been informally described as the genus *Cortinogaster* ined. See Smith (1966).

Cortinarius lilacinoides Soop, B. Oertel & Dima, *nom. nov.*

Basionym. Hymenogaster sublilacinus A.H. Sm., Mycologia 58(1): 108. 1966.
MycoBank MB823023.

Notes — The name *C. sublilacinus* is in use (Murrill 1944).

Cortinarius brunnescens (A.H. Sm.) Soop, B. Oertel & Dima, *comb. nov.*

Basionym: *Hymenogaster brunnescens* A.H. Sm., Mycologia 58(1): 111. 1966.
MycoBank MB822991.

Cortinarius subcaeruleus (A.H. Sm.) Soop, B. Oertel & Dima, *comb. nov.*

Basionym. *Hymenogaster subcaeruleus* A.H. Sm., Mycologia 58(1): 106. 1966.
MycoBank MB822992.

Section *Cyanites* Nespiak (100 %)

Typus. C. cyanites Fr., neotypus GB (ITS).

boreicyanites	Eur	G2016
cyanites	Eur	
spurcus	Eur	G2016
violaceorubens	Eur	R

Notes — A boreal section of similar species, characterised by dry and robust basidiomata, mainly of a greyish blue coloration and reddening context. The type has variously been placed in subg. *Phlegmacium*, *Sericeocybe*, and *Telamonia*.

Cortinarius sect. ***Austrocyanites*** Soop, *sect. nov.* (97 %)

Typus. C. austrocyanites Soop, GB (ITS, LSU).
MycoBank MB822945.

austrocyanites	NZ, Aus
myxoclaricolor	SAm
poliotrichus ined.	NZ

Basidiomata medium-sized to large, stipitocarpic, phlegmacioid or myxacioid. Pileus 25–100 mm diam, dry to viscid, grey-brown to yellow-brown or olive grey, coarsely grey fibrillose to squamulose. Lamellae greyish blue to argillaceous, crowded. Stipe dry to viscid, clavate with a rounded or marginate bulb, white to bluish. Veil pale grey to pale yellow or white with a

± violet tinge, rather sparse to copious. Context white, often marbled greyish blue to turquoise. Alkaline reaction red-brown to black on cutis, reddish lilac on lamellae. Spores ellipsoid to amygdaloid, 8–12 × 5–7 µm, moderately to rather weakly verrucose. In *Nothofagaceae* forests, South Pacific.

Cortinarius sect. ***Austrovaginati*** Soop, *sect. nov.* (100 %)

Typus. *C. austrovaginatus* Gasparini, GB (ITS, LSU).
MycoBank MB822946.

austrovaginatus	Aus, NZ	
conei	NZ	
medioscaurus	NZ	R

Basidiomata medium-sized, pileocarpic or sequestrate. Pileus 25–60 mm diam, viscid, yellow-brown to vinaceous brown or violaceous, disk ± red-brown, fibrillose, margin with white to yellow-brown tufts. Lamellae greyish violet to vinaceous, fairly crowded, sometimes sinuate or poorly developed. Stipe with a marginate bulb, sometimes volvate, silvery violet to lilac, coated white to yellowish on bulb. Veil white to greyish yellow, fairly copious. Context white to pale violet, taste sometimes bitter. Alkaline reaction reddish or insignificant. Spores ellipsoid to amygdaloid or citriform, 9–13 × 5.5–8 µm, coarsely verrucose. In *Myrtaceae* and *Nothofagaceae* forests, New Zealand, Australia.

Notes — The type species shows a tendency for sequestrate development, while *C. conei* is strictly sequestrate.

Cortinarius sect. ***Verniciori*** Soop, *sect. nov.* (99 %)

Typus. *C. verniciorum* Soop, GB (ITS).
MycoBank MB822947.

dulcamarus	NZ	
verniciorum	NZ	
C. sp.	NZ	2L

Basidiomata medium-sized to small, stipitocarpic, phlegmacioid or telamonioid. Pileus 15–50 mm diam, viscid, apricot to yellow-brown with a ± orange disk, glabrous to finely fibrillose. Lamellae white to pale grey-brown, medium crowded. Stipe cylindrical to ± clavate, whitish to pale grey-brown, flavescent. Veil white, sparse. Context pale yellow, marbled yellow-brown. Odour melleous or insignificant, taste acerbic to bitter. Alkaline reaction red to red-brown. Spores fusoid to subamygdaloid, 5.5–8 × 3–4 µm, weakly verrucose. In *Nothofagaceae* forests, New Zealand.

Section *Infracti* (Kühner & Romagn.) Moënne-Locc. & Reumaux (100 %)

Typus. *C. infractus* (Fr.: Fr.) Fr., neotypus GB (ITS).

anfractoides	Eur	JEC
ayanamii	Eur	JEC
infractiflavus	Eur, NAm	2L
infractiflavus II	Eur, India	JEC
infractus	Eur, NAm	
infractus II	Eur	JEC
infractus III	Eur, NAm	2L
maculatocaespitosus	Eur	R
obscurocyaneus	Eur	
persoonianus	Eur	
cf. *infractus*	NAm	2L

Notes — A boreal section of phlegmacioid, stipitocarpic taxa, whose basidiomata present dark colours with a more or less pronounced olive component, growing with a wide range of coniferous and frondose hosts. It is further characterised by the presence of the alkaloid infractopicrin (Stensrud et al. 2014). The New Zealand species *C. pholiotellus* is closely related, but is not included due to morphological differences.

Section *Subtorti* Brandrud & Melot (100 % in 2-loci tree)

Typus. *C. subtortus* Fr., neotypus GB (ITS).

subtortus	Eur, NAm	R
subtortus II	NAm	2L
(*amurceus*	Eur)	

Notes — A small boreal, phlegmacioid or myxacioid section, characterised by olivaceous-yellow tints and the presence of the alkaloid quinoline (Stensrud et al. 2014). It often appears as a sister to sect. *Delibuti*.

Cortinarius sect. ***Purpurelli*** Soop, *sect. nov.* (100 %)

Typus. *Rozites violacea* E. Horak, Beih. Nova Hedwigia 52: 516. 1975.
MycoBank MB822950.

ochraceoazureus	SAm	
purpurellus (*R. violacea*)	SAm	
sarmienti (*togularis*)	SAm	2L
C. sp.	SAm	2L

Basidiomata stipitocarpic, rozitoid, or sequestrate. Pileus 30–80 mm diam, viscid, violet to greyish purple or yellow-brown, margin sometimes with violaceous tufts. Lamellae white to pale brown or rusty yellow, rather distant, sometimes sinuous/wrinkled and bifurcate. Stipe cylindrical to clavate, violet to whitish, brunnescent, silky, girdled or collared. Veil white to violet, brunnescent, fairly copious. Context white to pale yellowish, brunnescent. Odour rarely strong, sweetish. Alkaline reaction insignificant. Spores ovoid to amygdaloid, 8–11 × 5.5–8 µm, weakly verrucose. In *Nothofagaceae* forests, South America.

Notes — Several members were described in the former genera *Thaxterogaster* and *Rozites* (Horak & Moser 1965).

Cortinarius sect. ***Entheosi*** Soop, *sect. nov.* (87 % in PhyML tree)

Typus. *C. entheosus* Soop, GB (ITS, LSU).
MycoBank MB824054.

aerugineoconicus	NZ
entheosus	NZ

Basidiomata medium-sized, stipitocarpic, phlegmacioid or myxacioid, with a vivid coloration. Pileus 25–60 mm, viscid, tan to yellowish with a brownish orange disk, or greenish blue, glabrous to finely fibrillose. Lamellae blue to violet, crowded. Stipe cylindrical to ± fusoid, dry or viscid, white to pale blue, fibrillose. Veil white to pale violet, fairly copious. Context grey buff to yellowish, marbled violet. Alkaline reaction blue or insignificant. Spores ellipsoid to amygdaloid, 7.5–10 × 4.5–6 µm, moderately to coarsely verrucose. In *Nothofagaceae* forests, New Zealand.

Cortinarius sect. ***Salmaster*** Soop, *sect. nov.* (81 %)

Typus. *C. salmaster* Gasparini.
MycoBank MB822951.

salmaster	Aus
salmastrium	NZ

Basidiomata medium-sized to small, stipitocarpic, phlegmacioid or telamonioid, greenish. Pileus 20–35 mm diam, viscid, dark olive brown to greyish green, glabrous to finely fibrillose. Lamellae grey to pale grey-brown, medium crowded. Stipe cylindrical, often rooted, silky white or pale green-grey to pale green-blue. Veil yellowish white to brownish, sparse. Context white to green-grey or lilac. Alkaline reaction insignificant. Spores ellipsoid, 7–8 × 4–5.2 µm, moderately verrucose. In *Myrtaceae* forests, South Pacific.

Section *Malvacei* M.M. Moser (87 %)

Typus. *C. malvaceus* E. Horak.

malvaceus	SAm	R
cf. *castaneiceps*	NZ	
(*austroalbidus*	SAm)	

Notes — Basidiomata are medium-sized to small, stipitocarpic, phlegmacioid or myxacioid, with a pale lilac coloration. In *Nothofagaceae* forests.

Clade /*Ardesiaci* (100 %)

ardesiacus	Aus
cf. *ardesiacus*	NZ

Notes — Basidiomata are medium-sized, stipitocarpic, phlegmacioid, coloration grey-brown to brown. In *Myrtaceae* forests.

Clade /*Cartilaginei* (100 %)

cartilagineus	NZ
C. sp.	NZ

Notes — Basidiomata are sequestrate or cuphocyboid, coloration ochraceous. In *Nothofagaceae* forests.

Clade /*Australienses* (100 %)

australiensis	Aus	R
cf. *australiensis*	NZ R	

Notes — Basidiomata are large, whitish, viscid, with a peronate veil. Spores 9–12 × 5.5–6.5 µm, amygdaloid. The taxa have also been attributed to the genus *Rozites*. In *Myrtaceae* forests.

5. Anomaloid sections

Three sections are bihemispherical and the basidiomata are characterised by a yellowish or reddish veil, a relatively slender habit, and rounded spores. The sections are represented by two lineages in Fig. S2 of Garnica et al. (2016).

Section *Anomali* Konrad & Maubl. (100 %)

Typus. *C. anomalus* (Fr.: Fr.) Fr., neotypus GB (ITS).

albocyaneus	Eur	G2016
anomalellus	Eur	2L
anomalovelatus	NAm	
anomalus (*azureus*)	Eur, NAm	R
azureovelatus	Eur	Dima et al. (in prep.)
barlowensis	NAm	
caesiifolius	NAm	2L
caninus	Eur, NAm	
durifoliorum	NZ	R
lebretonii	Eur	Dima et al. (in prep.)
lepidopus	Eur	2L
pastoralis (*anomalus* subsp. *campestris*)	Eur	2L
rattinoides	NZ	
sclerophyllorum	Aus	
sericeolazulinus	NAm	
suecicolor	NZ	R
tabularis	Eur	2L
tristis	SAm	G2016
xanthocephalus	Eur	G2016
cf. *anomalus*	NAm	2L
cf. *azureus*	NAm	2L
cf. *caninus*	NAm	2L
cf. *durifoliorum*	NZ	2L
cf. *suecicolor*	NZ	

Notes — This section has sometimes been presumed close to the morphologically similar sect. *Delibuti* (below), a relation that is not borne out by our analysis. The New Zealand species *C. eunomalus* appears as basal to this and the following two sections. See further Dima et al. (2016).

Section *Bolares* Kühner & Romagn. (100 %)

Typus. *C. bolaris* (Fr.: Fr.) Fr., neotypus GB (ITS).

bolaris	Eur, NAm, CAm	R
cf. *sclerophyllorum*	NZ	

Notes — The section is bihemispherical and consists of anomaloid fungi with a brightly red veil.

Section *Spilomei* (Bidaud, Moënne-Locc. & Reumaux) Cons., D. Antonini & M. Antonini (96 %)

Typus. *C. spilomeus* (Fr.: Fr.) Fr., neotypus GB (ITS).

ferrusinus	Eur	Ballarà et al. (2017)
spilomeus	Eur	
cf. *azureus*	NAm	
(*depauperatus*	Eur)	

Notes — The section is boreal and consists of anomaloid fungi with a reddish veil.

Section *Delibuti* (Fr.) Sacc. (96 %)

Typus. *C. delibutus* Fr.

calaisopus	NZ, Aus	
calaisopus II	NZ	2L
delibutus	Eur, NAm	2L
delibutus II	Eur, NAm	R
illibatus	Eur	2L
illitus	SAm	G2016
rotundisporus	Aus, NZ	
salor	Eur, NAm	R
tessiae	NZ	
cf. *rotundisporus*	NZ	G2016
cf. *salor*	NAm	2L
(*betulinus*	Eur)	
(*largodelibutus*	Eur)	
(*transiens*	Eur)	

Notes — The species are recognised by the same characters as in sect. *Anomali*, exhibiting in addition a viscid to glutinous veil. Basidiomata are coloured yellow, blue, or green, where the green pigment appears to occur mainly in the South Pacific. Unexpectedly, the European taxon *C. emunctus* is a singleton outside the section.

6. *Cortinarius* sect. *Gigasperma* (E. Horak) Soop & B. Oertel, *comb.* & *stat. nov.*

Basionym. *Gigasperma* E. Horak, New Zealand J. Bot. 9: 491. 1970.
Typus. *G. crypticum* E. Horak, GB (ITS).
MycoBank MB822990.

crypticus	NZ

Cortinarius crypticus (E. Horak) Soop & B. Oertel, *comb. nov.*

Basionym. *Gigasperma crypticum* E. Horak, New Zealand J. Bot. 9: 491. 1970.
MycoBank MB822995.

Notes — A small sequestrate fungus with very large, thick-walled, smooth spores. Two other species have been described in *Gigasperma*, none of which, however, is part of *Cortinarius* (Index Fungorum).

7. Myxacioid sections

The subsequent four sections, along with *Cortinarius bellus* (New Zealand), form a robust clade, which contains the type section of subg. *Myxacium*. They are represented by the main *Myxacium* lineage in Fig. S2 of Garnica et al. (2016). Also the sequestrate *C. porphyroideus* from New Zealand may possibly be included.

Section ***Myxacium*** (Fr.) Gillot & Lucand (100 %)

Typus. *C. collinitus* (Pers.: Fr.) Fr.

alpinus	Eur, NAm	G2016
collinitus	Eur, NAm	R
collinitus II	Eur, NAm	2L
fennoscandicus	Eur	2L
mucosus	Eur, NAm	
pingue	NAm	
septentrionalis	Eur, NAm	2L
stillatitius II	Eur	2L
trivialis	Eur, NAm	
vernicosus	NAm	2L
(*grallipes*	Eur)	

Notes — A boreal section of glutinous taxa, presenting white, brown, and violet colours. *Cortinarius pingue* is sequestrate.

Section ***Defibulati*** M.M. Moser (75 %)

Typus. *C. elatior* Fr.

basipurpureus	Aus	
brunneoalbus	NAm	Ariyawansa et al. (2015)
costaricensis	CAm	2L
cuphocyboides	NZ	
gymnocephalus	NZ	
mucifluus	Eur	2L
pavelekii	NAm	2L
phlegmophorus	India	G2016
seidliae	NAm	
stillatitius	Eur, NAm	R
subviolaceus (*P. violaceum*)	Aus	G2016
vanduzerensis	NAm	
(*elatior*	Eur)	
(*pumilus*	Eur)	

Notes — A widely distributed section of taxa, morphologically similar to sect. *Myxacium* and *Cuphocybe*. Two species are sequestrate. All taxa are characterised by hyphae without clamp connections.

Cortinarius sect. ***Marmorati*** Soop, *sect. nov.* (62 %)

Typus. *C. marmoratus* E. Horak, GB (ITS).
MycoBank MB822952.

marmoratus (*anauensis*)	NZ	
purpureocapitatus ined.	NZ	2L
vitreofulvus	NZ	R
vitreopileatus	NZ	
cf. *vitreofulvus*	NZ	
cf. *vitreofulvus* II	NZ	
(*viscostriatus*	NZ)	

Basidiomata medium-sized, myxacioid or sequestrate. Pileus, 25–60 mm diam, glutinous, white to yellow-brown, purple-brown, chocolate-brown, or lilac, disk often paler grey to ochraceous, glabrous. Lamellae white, greyish or deeply violet, medium crowded. Stipe cylindrical to slightly clavate, sometimes with a small rounded bulb, viscid, white to violaceous-grey. Veil pale violaceous, ± brunnescent, sparse. Context grey-white, sometimes marbled violet. Alkaline reaction insignificant or ± red-brown on cutis. Spores amygdaloid, 11–15 × 6.5–8 µm, moderately to strongly verrucose. Clamp connections present. In *Nothofagaceae* forests, New Zealand.

Notes — The section is so far endemic to New Zealand, but has some morphological similarity with sect. *Myxacium*.

Cortinarius sect. ***Cuphomorphi*** Soop, *sect. nov.* (97 %)

Typus. *C. cuphomorphus* Soop, GB (ITS, LSU).
MycoBank MB822953.

cuphomorphus	NZ	
juglandaceus	NZ	
violaceocystidiatus ined.	NZ	2L

Basidiomata medium-sized to small, cuphocyboid, myxacioid, or sequestrate. Pileus 15–55 mm diam, viscid, pale grey-brown to dark brown or violet, ± provided with fibrils and squamules when young, glabrous when older. Lamellae grey-blue, medium crowded to rather distant. Stipe cylindrical, sometimes with a small rounded bulb, dry to viscid, white to grey-brown, young with a violet tinge, sometimes with grey or yellowish squamules over the whole length. Veil pale yellow to ochraceous, fairly copious. Context white to pale violet, marbled grey-blue, odour sweetish, sometimes strong. Alkaline reaction insignificant. Spores amygdaloid, 10–12.5 × 6–8 µm, rather strongly verrucose. Clamp connections sparse or absent. In *Nothofagaceae* forests, New Zealand.

Section ***Cycnei*** Soop (87 %)

Typus. *C. cycneus* E. Horak.

capitellinus	SAm	Salgado Salomón et al. (2018)
cucumeris	NZ	
cycneus	NZ	
lubricanescens	NZ	R
magellanicus	SAm	
roblerauli	SAm	2L
(cf. *magellanicus*	N Caledonia)	

Notes — A section of myxacioid taxa, confined to the Southern Hemisphere (Soop 2016). *Cortinarius magellanicus* has been reported several times from New Zealand, but our analyses show that it is a violet form of *C. lubricanescens*. See further Salgado Salomón et al. (2018).

Section ***Vibratiles*** Melot (91 %)

Typus. *C. vibratilis* (Fr.: Fr.) Fr.

alboamarescens	Eur	2L
barbatus	Eur	
causticus	Eur, NAm	2L
causticus II	NAm	2L
croceocoeruleus	Eur	
electridius ined.	NZ	2L
emollitoides	Eur	2L
melleomitis	SAm, NZ	R
microspermus	Eur	
ochroamarus	Eur	2L
pluviorum	Eur	
pluvius	Eur	
psilomorphus	NZ	
vibratilis	Eur, NAm	
(*decumbens*	Eur)	
(*emollitus*	Eur)	
(*galeobdolon*	Eur)	
(*gemmeus*	NZ)	
(*ochroleucus*	Eur)	

Notes — This section is bihemispherical, consisting of glutinous fungi of a relatively modest size. Many of the taxa are further distinguished by a bitter context. We have only examined *C. melleomitis* samples from New Zealand, whereas the type is described from Patagonia.

Section ***Archeriani*** M.M. Moser & E. Horak (88 % in PhyML tree)

Typus. *C. archeri* Berk.

archeri	Aus	
holojanthinus	SAm	2L
cf. *taylorianus*	NZ	2L

Notes — A small South Pacific section of glutinous agaricoid or sequestrate fungi with violaceus and whitish colours.

Clade ***/Lustrabiles*** (100 %)

badiohepaticus ined.	NZ	
lustrabilis	Eur	R

Notes — A small bihemispherical clade of rare taxa that resemble those in sect. *Vibratiles*. Basidiomata are medium-sized to small, myxacioid, coloration red-brown to yellow-brown. In *Fagaceae* and *Nothofagaceae* forests.

8. Telamonioid sections

8.1. Subgenus *Telamonia* s.str.

This large monophyletic entity was recovered as the main *Telamonia* lineage in Fig. S2 of Garnica et al. (2016). It contains the vast majority of species described in the subgenus, and appears to be endemic for the Northern Hemisphere. Basidiomata are dry and generally present a stipitocarpic habit with a hygrophanous context. Colours are usually drab brownish or greyish, occasionally with a violet component. Many of the species are of a modest size. Recently many new species were described from the northern coniferous taiga belt, making this the most diversified region for *Telamonia* known to date.

The phylogeny reveals a number of clades, many of which are recovered as traditional sections. These are not further discussed in this study, having been extensively documented in several dedicated efforts (e.g., Kytövuori et al. 2005, Niskanen 2008, Niskanen et al. 2009, 2011, 2012, 2013), some of which are currently being pursued.

8.2. Other telamonioid sections

This is a polyphyletic assembly of sections, some bihemispherical. A number of the northern taxa have traditionally been included in subg. *Telamonia* (s.lat.), and their basidiomata look like what is known as ‘typical *Telamonia*’. One of these lineages (*Obtusi*) was recovered in Fig. S2 of Garnica et al. (2016). Southern taxa, on the other hand, often exhibit several deviating characters, such as bright colours and a positive alkaline reaction.

Section ***Renidentes*** Rob. Henry ex Moënne-Locc. & Reumaux (92 %)

Typus. *C. renidens* Fr.

parahumilis	SAm	
renidens	Eur, NAm	R

Notes — The section is bihemispherical. *Cortinarius renidens* appears to be unique in the genus by lacking both universal veil and cortina. Garnica et al. (2005) and Stensrud et al. (2014), report a strong support for including sect. *Austroduracini* (below), but we prefer to keep them as separate entities since their affinity is inconsistent in our study.

Cortinarius sect. ***Austroduracini*** Soop & Dima, *sect. nov.* (87–90 % in 2-loci tree)

Typus. *C. austroduracinus* M.M. Moser.
MycoBank MB822958.

austroduracinus	SAm	R
pyrrhomarmarus ined.	NZ	2L
viridibasalis	SAm	
viscincisus	NZ	

Basidiomata small, telamonioid, yellow-brown to red-brown. Pileus 10–40 mm diam, viscid, yellow-brown to dark red-brown, finely fibrillose. Lamellae greyish or pale cinnamon to dark yellow-brown, medium crowded. Stipe cylindrical, pale brown to greyish yellow with white to dark yellow-brown thin bands or girdles. Veil white to dark yellow-brown, sparse to copious. Context pale brown to yellowish, often marbled brownish. Alkaline reaction insignificant. Spores ellipsoid, 7–9.5 × 4.5–6, moderately to fairly coarsely verrucose. In *Nothofagaceae* forests, South America, New Zealand.

Cortinarius sect. ***Camphorati*** (Liimat., Niskanen & Ammirati) Soop, B. Oertel & Dima, *stat. nov.* (100 %)

Basionym. *Cortinarius* subg. *Camphorati* Liimat., Niskanen & Ammirati, Index Fungorum 256: 2. 2015. IF551459.

Synonym. *Cortinarius* sect. *Camphorati* Liimat. & Niskanen, in Niskanen (2008: 19), nom. inval.

Typus. *C. camphoratus* Fr.
MycoBank MB824052.

camphoratus	Eur, NAm	
dysodes	NZ	
putorius	NAm	2L
tasmacamphoratus	Aus	
cf. *dysodes*	NZ	2L
(*austrotorvus*	Aus)	

Notes — This taxon is bihemispherical. Basidiomata are dry with grey-brown and violet colours, but are mainly characterised by a strong, obnoxious odour reminding of acetylene, which appears to be synapomorphic. See further Niskanen (2008) and Niskanen et al. (2015).

Section ***Obtusi*** Melot (81 %)

Typus. *C. obtusus* (Fr.: Fr.) Fr.

acutovelatus	Eur	2L
acutus	Eur, NAm	
amblyonis	NZ	
basifibrillosus ined.	NZ	
ceraceus	Eur, NAm	2L
conopileus	India	G2016
cystidiocatenatus	Aus	
leucocephalus	NZ	G2016
obtusus	Eur, NAm	
pachynemeus	SAm	
pseudocandelaris	Eur	2L
pseudoduracinus	Eur	2L
rigens	Eur	2L
squamiger	SAm	2L
tenellus	SAm	2L
walpolensis	Aus	G2016
cf. *amblyonis*	NZ	R
cf. *levisporus*	Aus	G2016
C. sp. I	NZ	2L
C. sp. II	NZ	2L
C. sp. III	NZ	2L

C. sp. IV	NZ	2L
C. sp. V	NZ	R
(*albovariegatus*	Eur)	
(*fibrillosus*	Aus)	
(*trossingenensis*	Eur)	

Notes — A bihemispherical section of small brownish fungi, characterised by the frequent presence of vesiculose cheilocystidia. Two of the austral species are sequestrate.

Section *Laeti* Melot (97 %)

Typus. *C. laetus* M.M. Moser.

badiovinaceus	Eur, NAm	
bulliardioides	Eur	G2016
floccopus	Eur	G2016
laetiluteinus ined.	NZ	
laetus (*detonsus*?)	Eur, NAm	
lanceolatus	NZ	2L
ochrophyllus	Eur	
subfloccopus	Eur, NAm	2L
veregregius	Eur	G2016
waiporianus	NZ	
C. sp. I	NZ	2L
C. sp. III	NZ	2L
C. sp. IV	NZ	2L
C. sp. V	NZ	R
cf. *fasciatus*	Eur	R
cf. *pauperculus*	Eur	2L
(*bayeri*	Eur)	
(*fulvescens*	Eur, NAm)	
(*fulvescentoides*	Eur, NAm)	
(*nymphatus*	Eur, NAm)	
(*pseudobulliardioides*	Eur, NAm)	
(*tenuifulvescens*	Eur, NAm)	

Notes — A bihemispherical section of medium-sized to small fungi that often present a yellowish or reddish veil. It appears as a sister to sect. *Obtusi*. See also Garrido-Benavent et al. (2014), Niskanen (2008), Hyde et al. (2016).

Cortinarius sect. ***Illumini*** (Liimat., Niskanen & Kytöv.) Soop, B. Oertel & Dima, *stat. nov.* (80 %)

Basionym. *Cortinarius* subg. *Illumini* Liimat., Niskanen & Kytöv., Index Fungorum 256: 2. 2015. IF551474.

Synonym. *Cortinarius* sect. *Illumini* Liimat., Niskanen & Kytöv. in Niskanen (2008: 19), nom. inval.

Typus. *C. illuminus* Fr., neotypus GB (ITS, LSU).
MycoBank MB824053.

badiovinaceus II	Eur	
balaustinus	Eur	G2016
cypripedii	NZ	R
illuminus	Eur, NAm	
microglobisporus	Eur	

Notes — A bihemispherical taxon of medium-sized fungi displaying a vividly red-brown pileus and rounded spores. See further Niskanen (2008) and Niskanen et al. (2015).

Cortinarius sect. ***Carbonelli*** Soop, *sect. nov.* (80 %)

Typus. *C. carbonellus* Soop, GB (ITS, LSU).
MycoBank MB822959.

carbonellus	NZ	R
rattinus	NZ	

Basidiomata small, telamonioid, grey-brown to dark brown. Pileus 10–45 mm diam, dry, dark grey-brown to bluish grey, or purple-brown, later umber, finely fibrillose. Lamellae purple-brown to violet, greyish blue, or dark grey soon ± black, fairly crowded. Stipe cylindrical to clavate, silvery grey to yellowish grey with a violet tinge. Veil violet to red-brown, sparse. Context greyish to vinaceous brown, marbled violet. Alkaline reaction orange to reddish lilac in context, cherry red on lamellae. Spores ellipsoid to ± amygdaloid, 7–10 × 4–5.5 µm, moderately to rather weakly verrucose. In *Nothofagaceae* forest, New Zealand.

Unsupported group *Pseudoxenosmatae*

This austral group is formed by sect. *Carbonelli* and the following taxa:

areolatoimbricatus	Aus	R
cupreonatus	NZ	R
exlugubris	NZ	
punctatisporus	SAm	2L
vernicifer	NZ	

Notes — The group mainly contains of dry, often robust, sericeocyboid fungi. It receives low support, except in the PhyML tree (89 %). It contains several members of sect. *Xenosmatae* (see Soop 2002). The latter is not recovered in our study, which reveals its type *C. xenosma* as a singleton.

Cortinarius sect. ***Paraxanthi*** Soop, *sect. nov.* (100 %)

Typus. *C. paraxanthus* Soop, GB (ITS, LSU).
MycoBank MB822960.

citribasalis	NZ
paraxanthus	NZ

Basidiomata small, telamonioid, yellow-brown to olivaceous. Pileus 15–45 mm diam, dry, olive-brown to orange-brown or mahogany brown, often with an umber disk, finely fibrillose, margin yellow, often with an olive shade. Lamellae yellow-brown to orange, rather distant. Stipe cylindrical, lemon-yellow to yellow-green, base with white or yellow rhizomorphs. Veil greenish yellow, blushing red-brown, sparse. Context brown-yellow or orange to grey-brown, sometimes with an olive tinge. Alkaline reaction reddish or insignificant. Spores ellipsoid to amygdaloid, 7–9.5 × 4–6 µm, moderately to weakly verrucose. In *Nothofagaceae* forest, New Zealand.

Cortinarius sect. **Luteini** Soop, *sect. nov.* (100 %)

Typus. *C. luteinus* Soop. GB (ITS, LSU).
MycoBank MB822961.

luteinus	NZ
palissandrinus	NZ

Basidiomata small, telamonioid, yellow to red-brown. Pileus 10–30 mm diam, dry, dark yellow to brownish orange or mahogany red, later with a yellow-orange disk, finely fibrillose. Lamellae dark yellow to orange, brick red, or orange-red, distant. Stipe cylindrical, yellow to greyish yellow or pale brownish orange, sometimes ± citrinous, with thin, yellowish fibrils. Veil yellow, later darkening with a reddish tone, sparse. Context greyish yellow, marbled darker yellow. Odour raphanoid. Alkaline reaction weak or red on cutis and lamellae. Spores obtusely ellipsoid, 6.5–8.5 × 4.5–6 µm, moderately verrucose, marginal elements vesiculose, 20–35 × 9–12 µm. In *Nothofagaceae* forest, New Zealand.

Clade /*Minilaci* (99 %)

minilacus	NZ	
C. sp. I	NZ	
C. sp. II	NZ	2L

Notes — This austral clade consists of telamonioid fungi with yellow-brown lamellae and subglobose spores. In *Myrtaceae* and *Nothofagaceae* forest.

Clade /*Chrysoconii* (96 %)

chrysoconius	NZ
cf. *chrysoconius*	NZ

Notes — Basidiomata are small, telamonioid, coloration yellow with a squamulose pileus. In *Nothofagaceae* forests.

DISCUSSION

Higher ranks

In the present study we are not formally introducing taxonomic structures of higher rank than section. Robust phylogenetic support for higher ranks, such as subgenera, would presumably require a dataset built on more loci than the current nrITS, nrLSU, *rpb1*, and *rpb2* (cf. Frøslev et al. 2005). It may nevertheless be appropriate, as part of a discussion, to review a few major tentative lineages suggested by our phylograms, albeit with modest support in some cases. The history of a couple of lineages is reviewed in more detail.

- *Anomali* — This lineage would include sect. *Anomali*, *Bolares*, *Camphorati*, and *Spilomei*.
- *Calochroi* — This taxon would form an own lineage with clade /*Arcifolii*.
- *Cortinarius* — The type section of the genus would form its own lineage.
- *Crassi* — This lineage would include sect. *Crassi* and *Rubicunduli*.
- *Delibuti* — This lineage would include sect. *Delibuti* and *Subtorti*.
- *Dermocybe* — This lineage would include sect. *Dermocybe*, *Cruentoides*, and *Pauperae*.
- *Icterinula* — This lineage would include sect. *Walkeri*, *Chrysmata*, *Rubrobasales*, *Ignelli*, and clade /*Orixanthi*, as well as the singleton species in the unsupported group *Icterinula*.
- *Leprocybe* — This lineage would include sect. *Leprocybe*, *Persplendidi*, and *Veronicae*. It is sister to the *Dermocybe* lineage.
- *Limonii* and *Callistei* — The two sections form their own lineages in our phylogeny. The first name was introduced by Kühner & Romagnesi (1953) for a group based on the European *Cortinarius limonius*. Moser (1969) promoted *Limonii* to a section, expanded it with a number of boreal taxa, and attributed it to his new subg. *Leprocybe*. But he wisely refrained to include the morphologically similar *C. callisteus*, which had originally been present. Orlovich & Oliver (2002) found that *C. rubrocastaneus*, a species from New Zealand, is also part of the section. Our analysis now shows that at least eight recently discovered species belong to the section, making New Zealand the most diversified area for sect. *Limonii* known today (Soop et al. 2018). *Cortinarius callisteus*, on the other hand, is part of the bihemispherical sect. *Callistei*, a separate lineage, consistent with the concept of subg. *Callistei* (Niskanen et al. 2016).
- *Multiformes* — This lineage would include sect. *Cremeolinae*, *Malvacei*, *Multiformes*, and *Vibratiles*.
- *Myxacium* — This lineage would include sect. *Cuphomorphi*, *Defibulati*, *Marmorati*, and *Myxacium*, as well as a number of sequestrate species from the South Pacific.
- *Phlegmacium* I — This lineage would include sect. *Arguti*, *Claricolores*, *Elastici*, *Percomes*, *Phlegmacioides*, *Phlegmacium*, clades /*Caligati*, /*Obsoleti*, /*Rhizophori*, /*Varii*, and a number of singleton species. Virtually all species in this lineage have a stipitocarpic development.
- *Phlegmacium* II — This lineage would include sect. *Amoenolentes*, *Aureocistophili*, *Caerulescentes*, *Glaucopodes*, *Subhymenogaster*, clades /*Camptori*, /*Dionysae*, /*Eucaerulei*, /*Glaucocephali*, /*Subolivascentes*, and a number of singleton species. Virtually all species in this lineage have a pileocarpic development.
- *Rozites* — This lineage would include sect. *Cuphocybe*, *Majestatici*, *Rozites*, *Subcastanelli*, clade /*Achroi*, and several rozitoid species from the South Pacific.
- *Scauri* — This lineage would include sect. *Purpurascentes* and *Scauri*, as well as one singleton species from the South Pacific.
- *Telamonia* — This lineage would include *Telamonia* s.str., and possibly sect. *Purpurelli*, which is consistently basal to the former but morphologically different. The subgenus goes back to Fries and circumscribes today, in its traditional sense, at least 900 taxa. These are morphologically fairly homogeneous, presenting a dry, more or less hygrophanous pileus and generally drab brown, grey, or violet colours. Høiland & Holst-Jensen (2000) and Peintner et al. (2004) showed that a large core portion of the subgenus was monophyletic, leaving the common telamonioid sect. *Obtusi* in a separate lineage. The core portion, here termed *Telamonia* s.str., seemed to be confined to the Northern Hemisphere, as later confirmed by Garnica et al. (2005, 2016). These and our own studies show that not only *Obtusi* but several other telamonioid taxa (*Camphorati*, *Illumini*, *Laeti*, *Renidentes*) are positioned outside *Telamonia* s.str. and are in fact bihemispherical (cf. Niskanen 2008). Originally, also a number of austral species were classified as *Telamonia* (Moser & Horak 1975, Grgurinovich 1997, Soop 1998, 2001, 2005, Gasparini & Soop 2008), in many cases despite traits not usually associated with what may be called a 'typical *Telamonia*'. Our analysis shows that some of these species form endemic sections (e.g., *Austroduracini*) in the South Pacific, genetically well separated from the northern core clade, and no published southern species has so far been shown to belong to *Telamonia* s.str.
- *Telamonioidae* — This lineage would include part of the remains of *Telamonia* s.lat.: sect. *Obtusi*, *Laeti*, and *Illumini* (but neither *Camphorati* nor *Renidentes*), as well as the clade /*Minilaci*. It is sister to the *Dermocybe*-*Icterinula*-*Leprocybe* complex, an interesting topology that was also implicitly shown by the 5-loci phylogram of Garnica et al. (2016).

Traditional vs phylogenetic sections

In several cases traditional sections were shown by our study to be polyphyletic, while often retaining a monophyletic core of species around the type. In other cases the sections were broken up into disparate lineages. For example, the boreal sect. *Claricolores* was earlier defined by the fusoid spore shape and caespitose growth, and then contained notably *Cortinarius claricolor*, *C. variegatus*, and *C. turmalis* (cf. Brandrud et al. 1989, 1992, 1994, 1998, 2012). Our analysis recovered *C. variegatus* as a singleton, while *C. turmalis* unexpectedly forms a well-supported clade with the austral *C. picoides*. The new sect. *Turmales* in fact retains the two mentioned character states, while the emended sect. *Claricolores* (Brandrud et al. 2013) shows characters like a sulcate pileus margin, and includes species such as *C. praestans*.

The relatively recent discovery of many new species from the Southern Hemisphere has resolved a number of singletons into small clades, some of which are here described as new bihemispherical sections, like *Turmales* mentioned above. Another example of this pattern is the boreal *Cortinarius crassus*, traditionally considered an odd entity, difficult to place in the taxonomy, and long the only member of its sect. *Crassi*. But as in the case of *Turmales*, the discovery of the austral *C. eutactus* has revealed *Crassi* as bihemispherical. The two species share the habit and the presence of remarkable cheilocystidia. The pattern is replicated by the boreal *C. rubicundulus* having now found a southern 'partner' in *C. subgemmeus*, with which it shares the characters of cheilocystidia and a flavescent context.

In larger clades the core of species sometimes lies in one of the hemispheres. *Cortinarius* sect. *Pauperae*, for example, consists almost exclusively of austral species, *C. olivaceofuscus* in Europe (cf. Høiland 1983) being one of the notable exceptions. Conversely, sect. *Phlegmacioides*, with more than 20 boreal species, contains the single Australian species *C. lavendulensis.* Other sections, such as *Purpurascentes* and *Anomali* exhibit a fairly even distribution between the hemispheres. An extreme case is sect. *Defibulati*, which is found in Europe, North and Central America, the South Pacific, and India. Among the telamonioid sections *Anomali* and *Obtusi* constitute other widely distributed taxa.

A number of lineages appear to occur exclusively in either hemisphere (Soop & Gasparini 2011). In our analysis a conspicuous number of phlegmacioid clades are confined to the North. In the Introduction, we mentioned *Calochroi* s.lat., but also *Multiformes*, *Claricolores*, *Riederi*, *Glaucopodes*, *Arguti*, and *Caerulescentes*, just to name a few, belong to this category. In the South the endemic sect. *Cremeolinae* is closely related to the boreal *Multiformes*, to which there is also a strong morphological resemblance. Other section pairs exhibiting a similar biogeographical pattern are *Leprocybe-Persplendidi* and *Myxacium-Marmorati*.

Biogeographical section concept

Even though a number of sections are bihemispherical, our study corroborates the fact that no *Cortinarius* species is known to occur naturally in both hemispheres (pers. obs., and cf. Harrower et al. 2015a: 705). This could be explained by the strict ectomycorrhizal host specificity within the genus (Wang & Qiu 2006, and cf. also Brandrud 1996 and Kytövuori et al. 2005). Few, if any, of the putative host genera are naturally present in the temperate regions of both hemispheres (the exceptions may be *Quercus* and *Alnus* in South America). A strict analysis of this biogeographical relationship would involve the history of plant evolution, which is beyond the scope of the present study. Such a study was presented by Wilson et al. (2017) on the subject of the genus *Laccaria*. But whereas Wilson et al. (2017) report a distinct north-south split into two major clades for *Laccaria*, our topology shows a mosaic of smaller, intermixed, boreal and austral clades for *Cortinarius*, similar to the clade structure of Garnica et al. (2016).

Looking closer at this structure, one notes that a number of potential section clades can be neatly split into two subclades, one endemic for each hemisphere. This topology often exhibits two important patterns: (a) one can significantly boost the bootstrap support by excluding one of the subclades from the section; and (b) the austral subclade tends to be 'basal' in the sense that its branch is shorter than the boreal one. The interesting pattern (b) and its hypothetical connection with the evolution of the genus would be a subject for future research.

With reference to (a), one is faced with the choice of conceiving the clade as one bihemispherical section with lower support, or as two well-supported, geographically separated sections. Where the two subclades are morphologically similar we have sometimes opted for the first choice. For example, we chose to retain a bihemispherical sect. *Illumini* (with a lower support) due to phenotypical similarity across the clade. A contrary example is the pair *Leprocybe*-*Veronicae*, kept separate due to morphological differences despite a robust joint support. On the other hand, sect. *Anomali*, *Cortinarius*, and *Delibuti* are examples of bihemispherical, morphologically homogeneous sections with a robust support.

Merits of going beyond ITS/LSU

Comparing the 4-loci tree (Fig. 1) with the 2-loci tree (Fig. 2) one finds that they recover largely the same sections, while the bootstrap support is in many cases higher in the former. The 4-loci tree even reveals several smaller sections that were not present with two loci. It appears, in fact, that the mere addition of an *rpb* sequence to one sample often has a definitely positive effect on clade support (cf. Frøslev et al. 2005). Moreover, this 'grafting' of *rpb* sequences sometimes produces an extended effect, which is in retrospect perhaps not so surprising, in that it stabilises not only the 'grafted' clade but also neighbouring clades, even if the latter do not include the extra loci.

The use of gap coding (Nagy et al. 2012) has also proved beneficial in the present study in order to confirm many sections and increase their support.

Extent of sampling

As indicated by the number of putative section members listed (in parentheses) under Taxonomy, many species remain to be sequenced in the appropriate loci. In some cases it is especially important to provide the data to confirm (or refute) a proposed section.

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