



Mission impossible completed: unlocking the nomenclature of the largest and most complicated subgenus of *Cortinarius*, *Telamonia*

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Abstract

So far approximately 144,000 species of fungi have been named but sequences of the majority of them do not exist in the public databases. Therefore, the quality and coverage of public barcode databases is a bottleneck that hinders the study of fungi. *Cortinarius* is the largest genus of Agaricales with thousands of species world-wide. The most diverse subgenus in *Cortinarius* is *Telamonia* and its species have been considered one of the most taxonomically challenging in the Agaricales. Its high diversity combined with convergent, similar appearing taxa have earned it a reputation of being an impossible group to study. In this study a total of 746 specimens, including 482 type specimens representing 184 species were sequenced. Also, a significant number of old types were successfully sequenced, 105 type specimens were over 50 years old and 18 type specimens over 100 years old. Altogether, 20 epi- or neotypes are proposed for recently commonly used older names. Our study doubles the number of reliable DNA-barcodes of species of *C.* subgenus *Telamonia* in the public sequence databases. This is also the first extensive phylogenetic study of the subgenus. A majority of the sections and species are shown in a phylogenetic context for the first time. Our study shows that nomenclatural problems, even in difficult groups like *C.* subgenus *Telamonia*, can be solved and consequently identification of species based on ITS barcodes becomes an easy task even for non-experts of the genus.

Keywords ITS · Type study · Barcode · Neotype · Phylogeny · Section

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Introduction

So far approximately 144,000 species of fungi have been named (Willis 2018) but sequences of the majority of them do not exist in the GenBank or UNITE. Moreover, only a small percentage of the names in the GenBank, about 4800

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species, are based on sequences from type materials or other reliable sources (Schoch et al. 2014).

Currently species identification of fungi in academic studies is almost solely based on nrDNA ITS barcodes (Lindahl et al. 2013). Thus, those collections with taxonomically correct names that are not in any public sequence repositories are basically omitted in academic research. Therefore, the quality and coverage of public barcode databases is a bottleneck that hinders the study of fungi (Schoch et al. 2014). Depositing the ITS sequences in public repositories like GenBank does not automatically make them useful for identification. Two excellent platforms for delivering sequence-based identification information for the end-users include RefSeq under GenBank (Schoch et al. 2014) and UNITE (Köljalg et al. 2013). However, in both cases an extra step by an expert, in addition to the normal sequence submission, is required, but unfortunately often is left undone, making part of the already existing information unusable.

Cortinarius (Pers.) Gray is the largest genus of Agaricales with thousands of species world-wide (Kirk et al. 2008). They are important ectomycorrhizal fungi and often discovered in ecological studies. Only three large studies of type specimens based on ITS sequence data in *Cortinarius* have been made so far. Two of them are from *C.* subgen. *Phlegmacium* (Fr.) Trog; Liimatainen et al. (2014) includes over 230 sequences of type specimens representing over 150 species and Frøslev et al. (2007) has over 50 sequences of 79 species. The third one is from *C.* subgen. *Telamonia* (Fr.) Trog and includes over 60 sequences of 33 species (Liimatainen et al. 2017).

The most species-rich subgenus in *Cortinarius* is *Telamonia*. Members of this subgenus mainly occur in the Northern Hemisphere (Garnica et al. 2005, Soop et al. 2019) and are especially dominant in coniferous forests. Six relatively large phylogenetic studies of *Cortinarius* have been published so far (Garnica et al. 2005, 2016; Harrower et al. 2011; Peintner et al. 2004; Soop et al. 2019; Stensrud et al. 2014). The number of species of *Telamonia* included in these studies varies from 8 to 70, and the phylogenies have been mainly based on the analysis of ITS and LSU regions, with some also including sequences of *rpb1* or *rpb2* regions. These studies have shown that the majority of the traditionally morphologically delimited species of *Telamonia* (Bidaud et al. 2017; Brandrud et al. 2012; Moser 1983; Niskanen et al. 2012) form a monophyletic group. However, sections or subgenera that have been shown not to belong to *Telamonia* include *Anomali* Konrad & Maubl., *Balaustini* Moëne-Locc. & Reumaux, *Camphorati* Liimat., Niskanen & Ammirati, *Fulvescentes* Melot, *Illumini* Liimat., Niskanen & Kytöv., *Obtusi* Melot, *Reidentes* Moëne-Locc. & Reumaux, and *Rigentes* Melot. Morphological characters that define the species of *Telamonia* are basidiomata with dry pileus and dry stipe and mainly brownish colours, with the exception of some whitish, bluish-purple or orange-red species. No larger phylogenetic

analysis on the infrasubgeneric relationships have been done so far, but studies on specific sections including sequences from type specimens have been published: *Armillati* M.M. Moser (Niskanen et al. 2011), *Bovini* M.M. Moser (Niskanen et al. 2013), *Brunnei* Melot (Niskanen et al. 2009), *Colymbadini* Melot/*Cinnabarini* Melot/*Uracei* Melot (Ammirati et al. 2017; Dima et al. 2014), *Disjungendi* Kytöv., Liimat., Niskanen & Ammirati (Liimatainen et al. 2015), *Hydrocybe* (Fr. ex Rabenh.) Gillot & Lucand (Suárez-Santiago et al. 2009) and *Saturnini* Moëne-Locc. & Reumaux/*Bicolores* (M.M. Moser) Melot (Liimatainen et al. 2017).

The nuclear ribosomal internal transcribed spacer (ITS), which has been proposed as the universal barcode marker for fungi (Schoch et al. 2012), is also the main locus used in the species level taxonomy of *Cortinarius*. The threshold value for barcoding *Cortinarius* species has been proposed to be 99% (Garnica et al. 2016). However, there already is evidence that a few morphologically distinct *Telamonia* species only have 1 base difference (99.8% similarity) in the ITS region, e.g. *C. laniger* Fr./*C. solis-occaus* Melot (Niskanen et al. 2012) and *C. paragaudis* Fr./*C. pinigaudis* Niskanen, Kytöv. & Liimat. (Niskanen et al. 2011) and in the case of *C. confirmatus* Rob. Henry the intraspecific variation is > 1%, although the species has a wide morphological and ecological range and based on ITS sequences there are 3 supported subclades which might be separate taxa (Liimatainen et al. 2017).

In this study our aim was to provide a revision of *Cortinarius*, subgen. *Telamonia* as well as an extensive ITS database for the identification of the species. Almost all type specimens of the species described in the subgenus were studied and an epi- or neotype is proposed for all recent frequently used older names when possible. In addition, a phylogenetic tree is produced as a framework for the infrasubgeneric classification of the species; including many that are included in a phylogenetic analysis for the first time.

Materials and methods

Taxon sampling

The type specimens of *Telamonia* species published over many years by Ammirati, D. Antonini, M. Antonini, Bergeron, Bidaud, Bohus, Bouteville, Bresadola, Carteret, Chevassut, Consiglio, Daniele, Eyssartier, A. Favre, J. Favre, Fellner, Ferville, Fillion, Henry, Hesler, Høiland, Hongo, Karsten, Kauffman, Kühner, Landa, Lindström, Matheny, McKnight, Moser, Moëne-Loccoz, Murril, Nespiak, Orton, Pearson, Peck, Ramm, Reumaux, Sasia, Seidl, Smith, Schwöbel, Soop, Svrček, Velenovský, and Vialard were sampled as well as all the *Telamonia* collections published and illustrated in Brandrud et al. (1989, 1992, 1994, 1998). A total of 482 types are included here. An additional

183 previously published sequences of *Telamonia* types were added to our dataset for the best overview of current available data.

We aimed to have at least two sequences per species in our study. Therefore, some additional sequences, either our own unpublished ones or from databases GenBank and UNITE, were included. Information on the sequences of type specimens is available in Supplementary Table 1 and information on other sequences included in the phylogenetic analysis is available in Supplementary Table 2. Fungarium acronyms follow Index Herbariorum (Thiers 2013).

Species concept

Based on criteria mentioned in the introduction we have used 1 % (5 differences) as a cut-off value for species. When type sequences differ in at least 5 sites from one another we have treated them as different species. We are not claiming that all the variation below 1 % is automatically intraspecific. Separating species below the 1% cut-off value, however, does require careful study. Therefore, we have added ‘aff.’ prefix to the Latin name in cases where there are 3 to 4 differences to another type sequences. With 2 differences we have used the *s. lato* notation in the Fig. 1 and Supplementary Tables 1 and 2. Using this approach indicates places where determining taxonomic synonyms might be problematic and require further study. Also, when macroscopic, microscopic and/or ecology data differ considerably although the ITS sequences are the same, we have not placed the taxa in synonymy. Furthermore, in cases where a species complex has previously been shown to include several species supported by morphology and small, but constant barcode gaps, we have avoided making synonymys.

One cannot emphasize enough that using a small cut-off value requires good quality sequences. In this study all the specimens have been sequenced from both directions and the chromatograms of the sequences were checked and edited manually before any preliminary analyses. When small, less than ten base or indel changes and/or odd differences are found between sister species or within species those differences have been confirmed by combining the relevant chromatograms and checking manually the base sites that differ. Also, base or length polymorphisms sites are not counted as a difference and an indel is counted as one difference despite its length.

Molecular analyses

DNA was extracted from a few milligrams of dried material (a piece of lamella) with the NucleoSpin Plant kit (Macherey-Nagel, Düren, Germany). The same protocol was used for all materials. Primers ITS 1F and ITS 4 (Gardes and Bruns 1993; White et al. 1990) were used to amplify ITS regions. The same primer pairs were used in direct sequencing. For problematic material the primer combinations ITS

1F/ITS 2 and ITS 3/ITS 4 were also used. PCR amplifications were performed in a 25 µl reaction mix with about 70 ng extracted DNA, 1 U Phusion High-Fidelity DNA polymerase and 1× HF buffer (ThermoFisher), 200 mM of each dNTP and 0.5 µM of each primer. The PCR were run on a MBS 0.2 G Thermal Cycler (Thermo Hybaid) with the following settings: denaturation for 30 s at 98 °C, followed by 35 cycles of denaturation for 10 s at 98 °C, annealing for 30 s at 50 °C, and extension for 30 s at 72 °C. The PCR products were purified using an ExoSAP-IT purification kit (Amersham Biosciences). Sequencing was performed on both strands using a BigDye Terminator v1.1 Sequencing kit (Applied Biosystems). Reactions were performed in 10 µl with 1 µl of PCR product, 1.3 mM of primer (ITS 1F or ITS 4), 1 µl 5X sequencing buffer, and 1 µl of Terminator Ready Reaction Mix. Reactions were run for 1 min at 96 °C, followed by 30 cycles of 30 s at 96 °C, 15 s at 50 °C, and 4 min at 60 °C. Unincorporated dye terminators and primers were removed by Sephadex G-50 DNA Grade Fine (Amersham Biosciences) purification system, and the reactions were analysed by ABI 3730 DNA Analyzer (Applied Biosystems) automatic sequencer. Sequences were assembled and edited with Sequencher 4.1 (Gene Codes, Ann Arbor, Michigan, USA). A total of 755 new ITS sequences were produced for this study. Collections and GenBank sequences used for the phylogenetic analysis are given in Supplementary Tables 1 and 2.

The short ITS sequences of type specimens were excluded from the phylogenetic analysis. To improve the resolution of phylogenetic analyses we included 146 published LSU sequences from GenBank to our dataset. The chosen LSU sequences are from different parts of *Telamonia* and they were mostly obtained from Garnica et al. (2005), Harrower et al. (2011), and Stensrud et al. (2014). Sequences from section *Dermocybe* Pers. were selected as an outgroup based on Stensrud et al. (2014). A total of 919 ITS and 146 LSU sequences were aligned separately for both regions using MAFFT 7 (Katoh and Standley 2013) with the G-ING-i algorithm (Katoh et al. 2005). The alignments were then manually improved in SeaView (Galtier et al. 1996). The phylogenetically informative indels in the ITS region were coded as characters following the simple indel coding algorithm (Simmons and Ochoterena 2000) with FastGap 1.2 (Borchsenius 2009). The binary and aligned nucleotide data were concatenated in Mesquite 3.2 (Maddison and Maddison 2017). The alignment is 2008 nucleotides long (including gaps) and is available at TreeBASE under S26824 (<http://www.treebase.org/treebase-web/home.html>). A phylogenetic tree was generated from the concatenated dataset using maximum likelihood (ML) analyses with 1000 bootstrap replicates under the GTRGAMMA model for nucleotide partitions (ITS + LSU) and the default setting for binary (indel) data in RAXML 8 (Stamatakis 2014).

Fig. 1 A phylogram resulting from the RAxML analysis of the concatenated dataset including 919 aligned ITS and 146 LSU sequences and the binary data resulting from the coding of the phylogenetically informative insertions/deletions in the ITS alignment. Bootstrap values greater than 50% are indicated above branches. The current names of species are in boldface

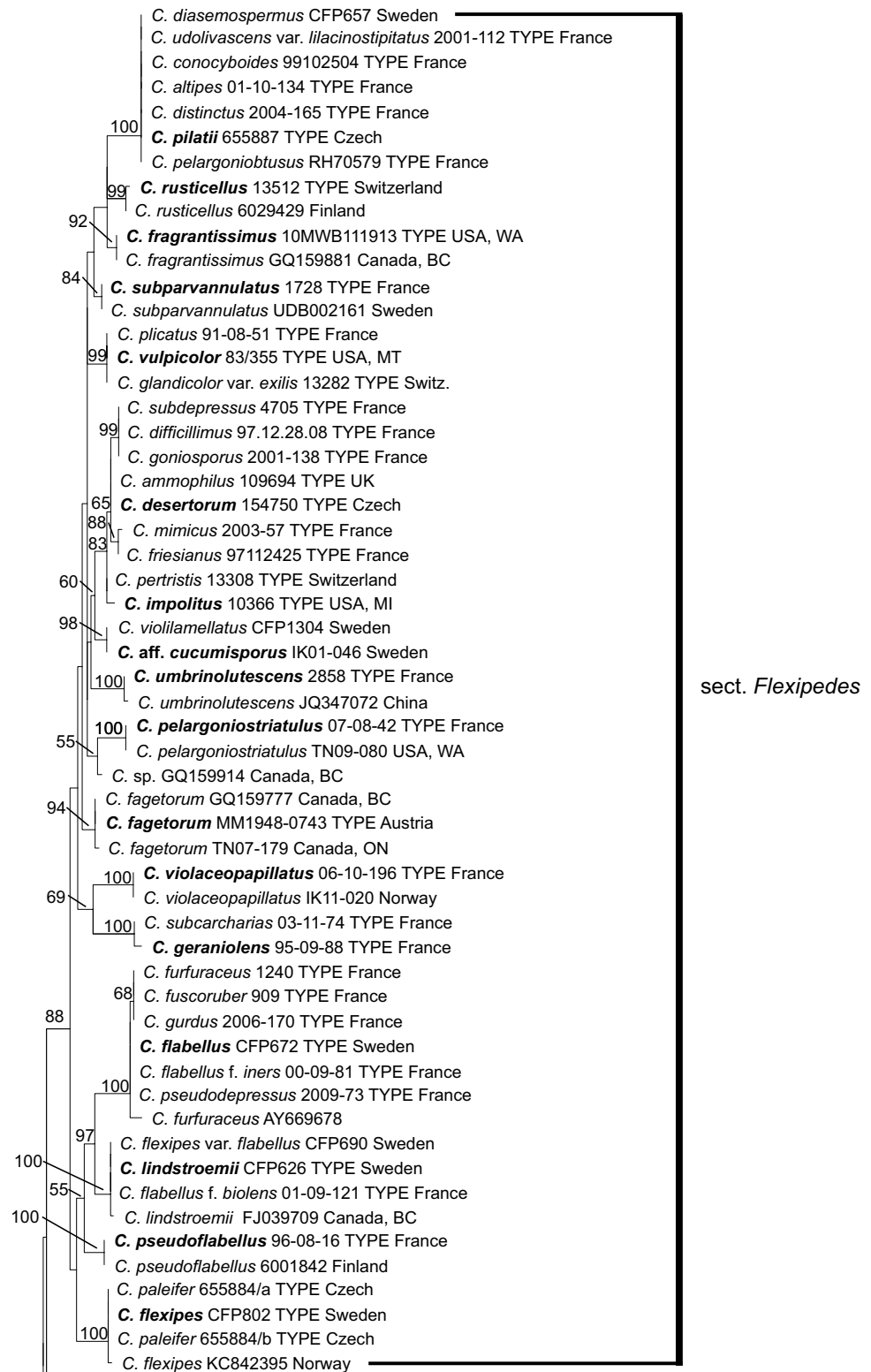


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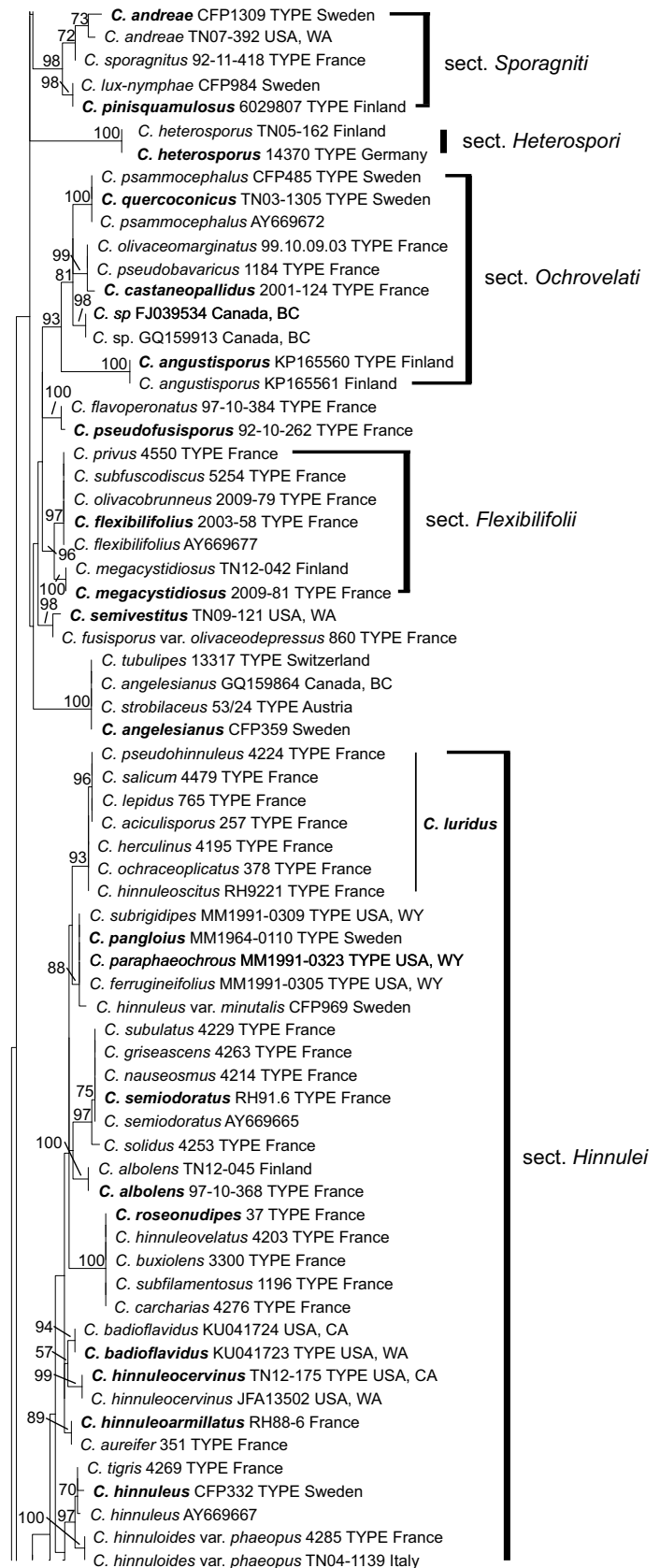


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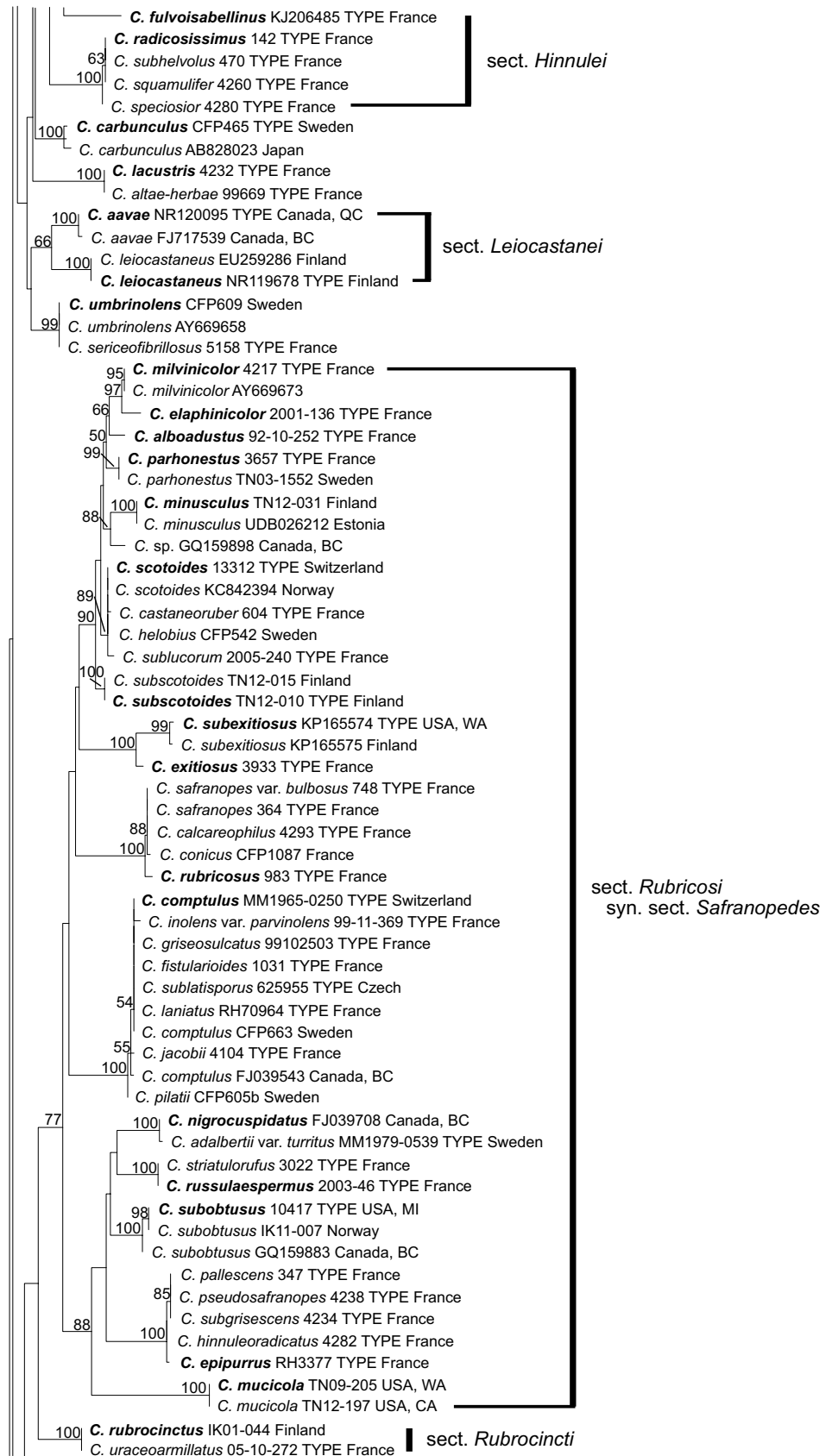


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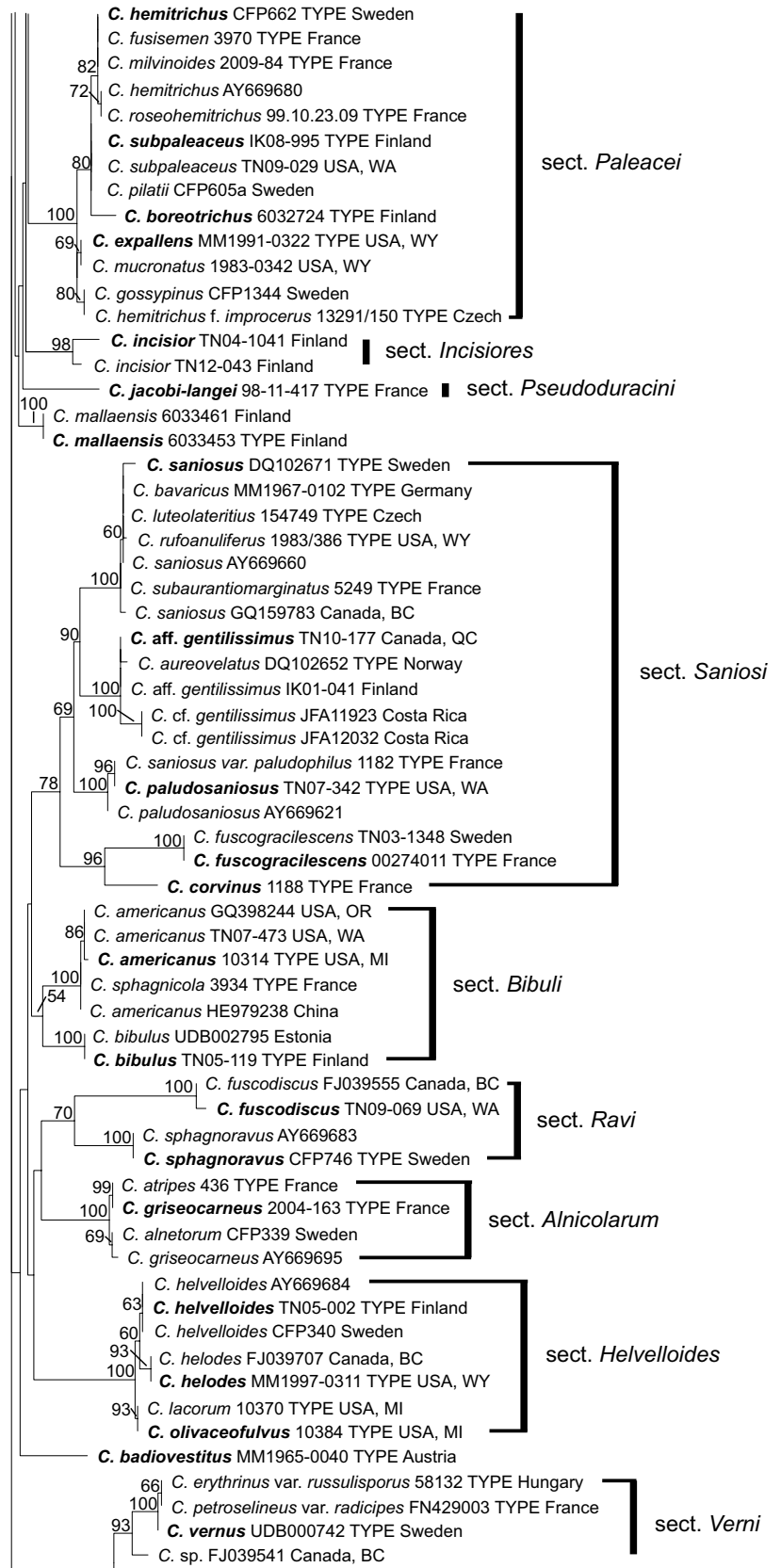


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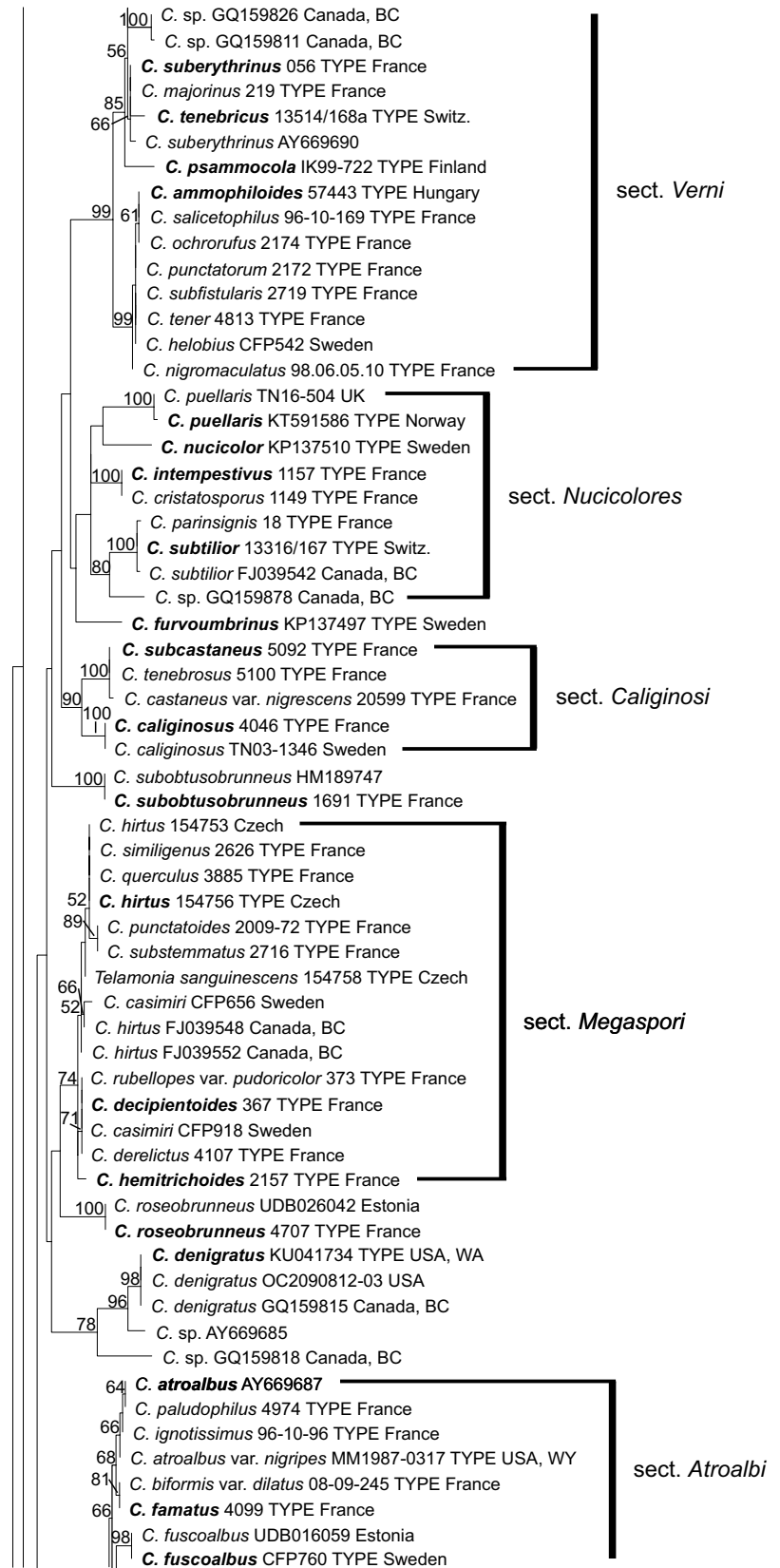


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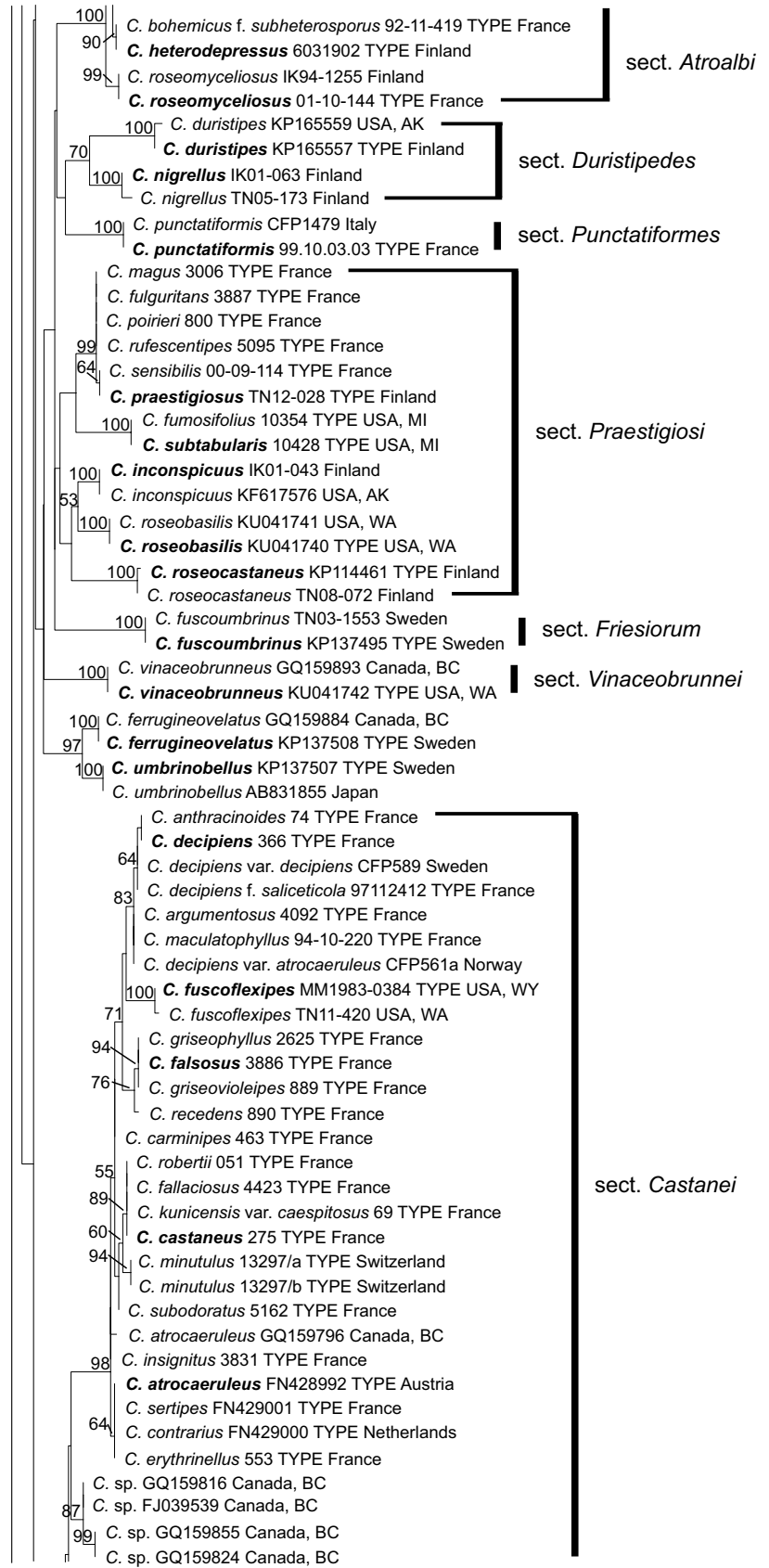


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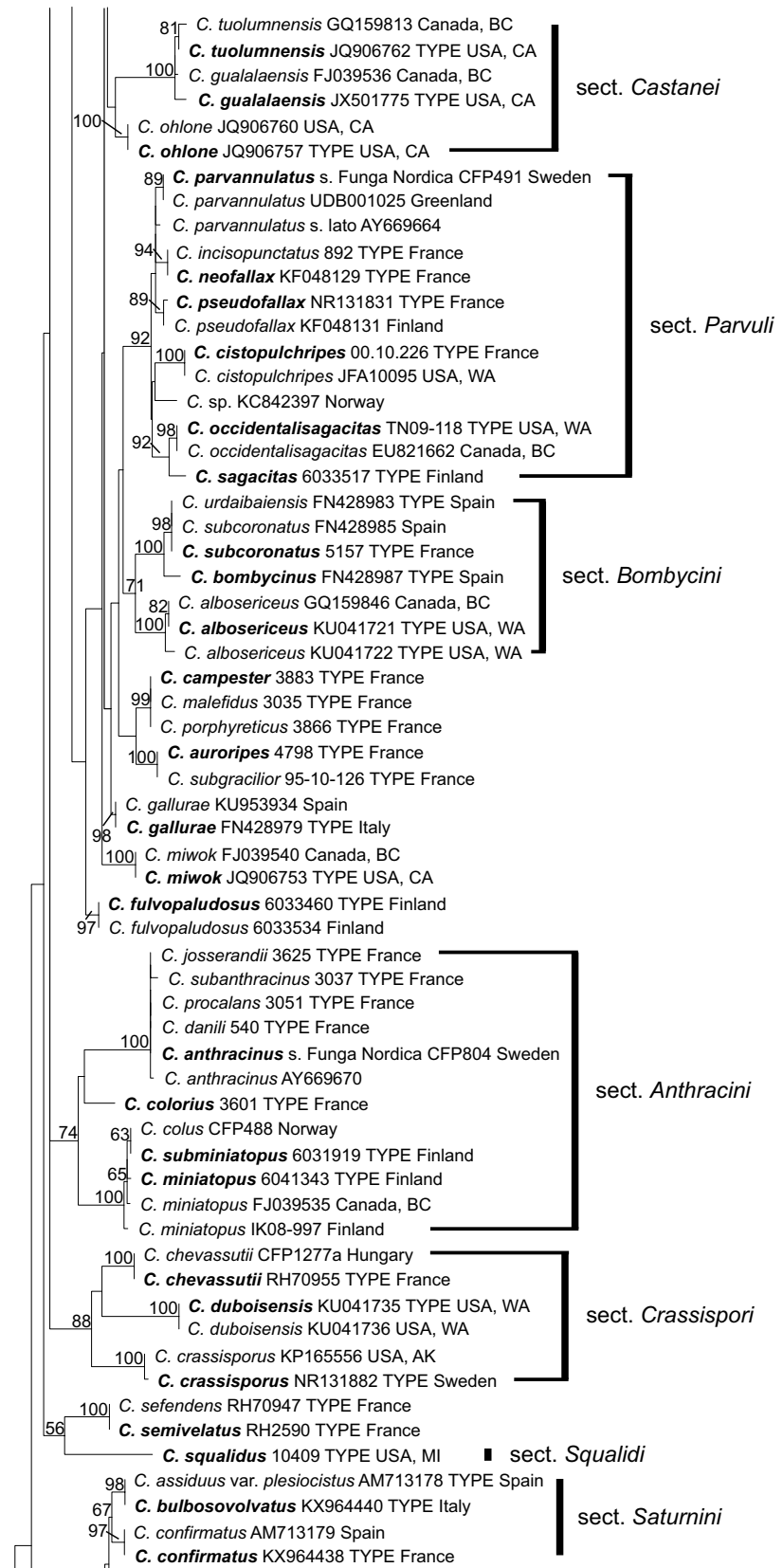


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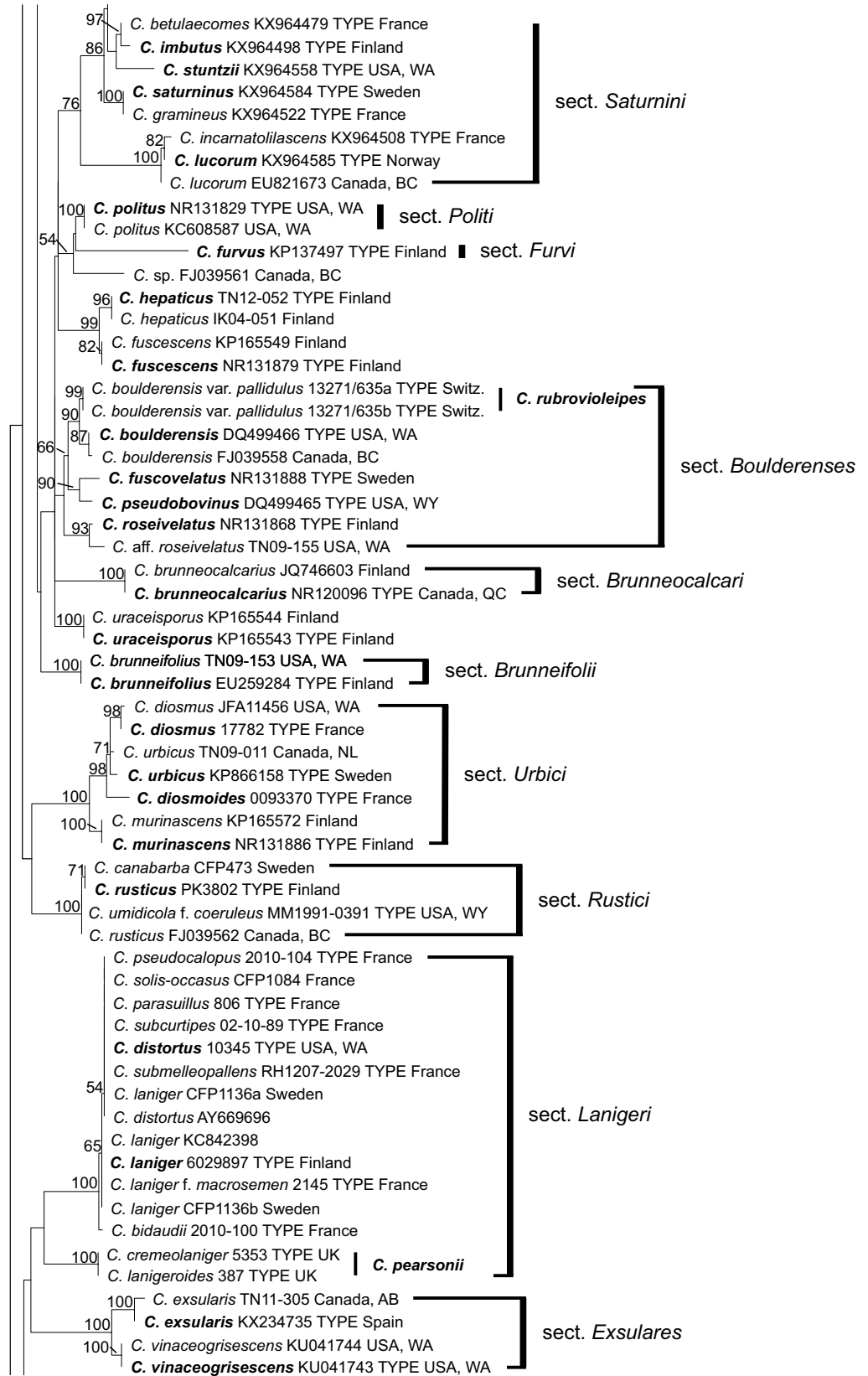


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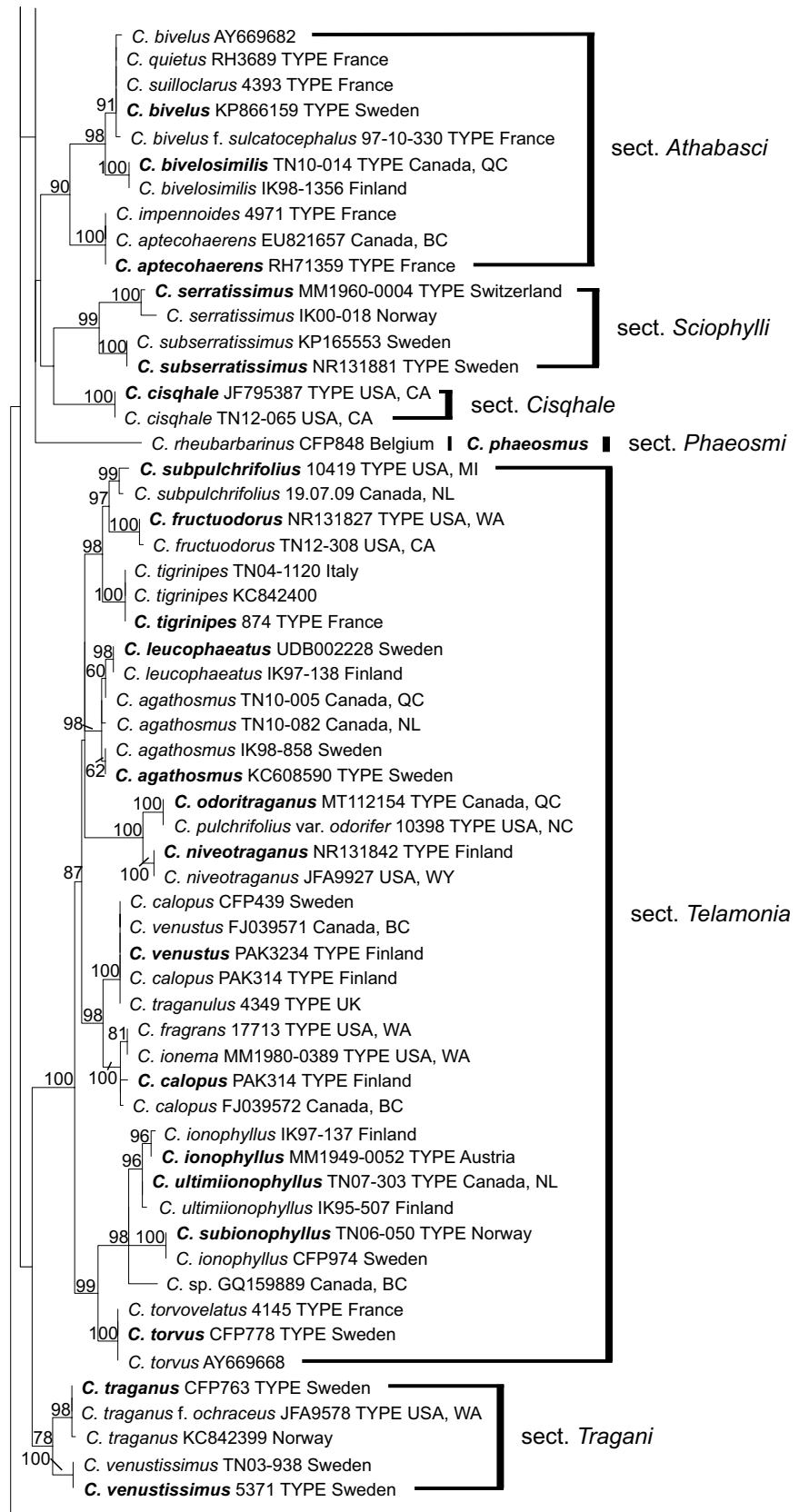


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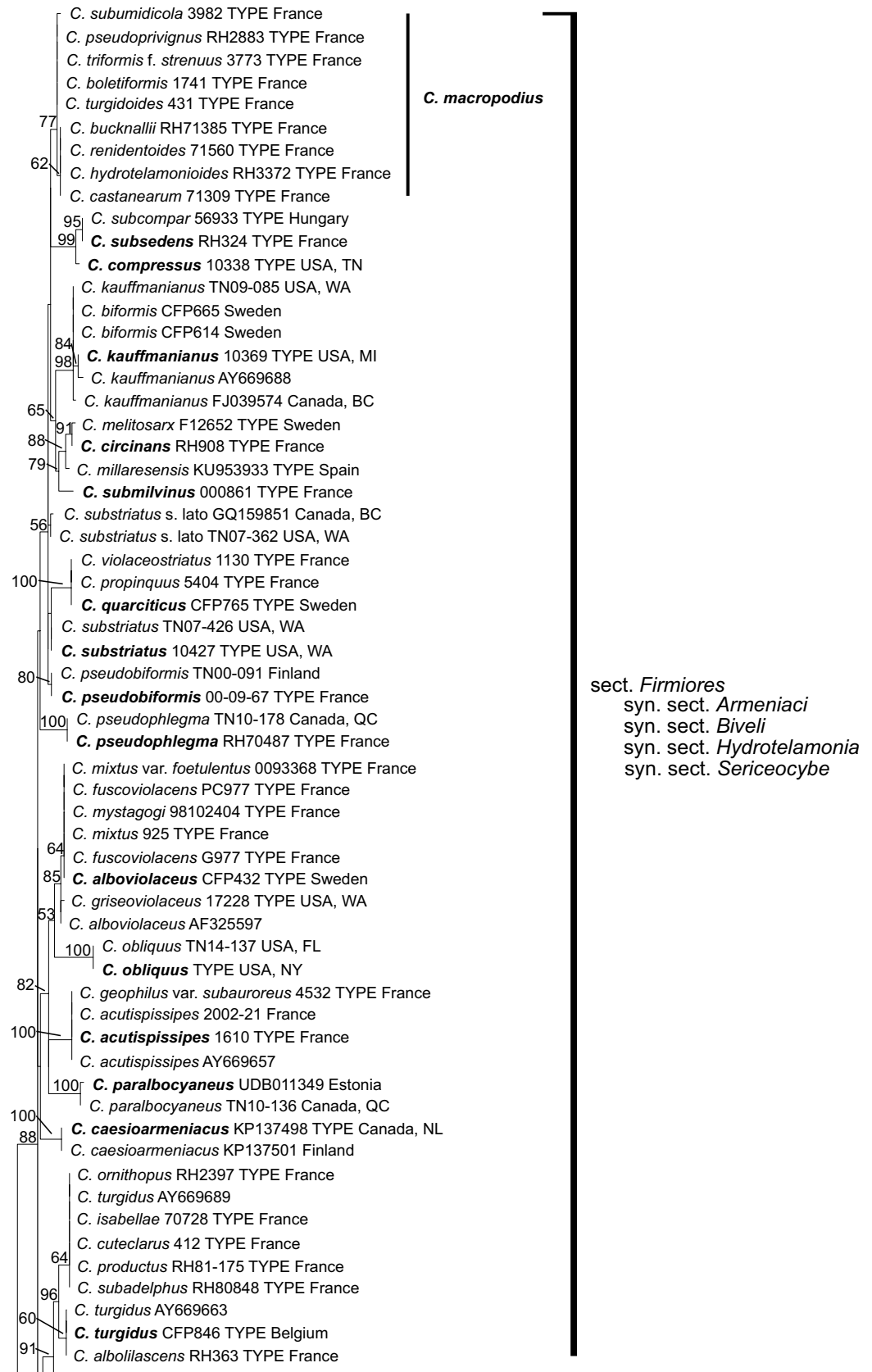


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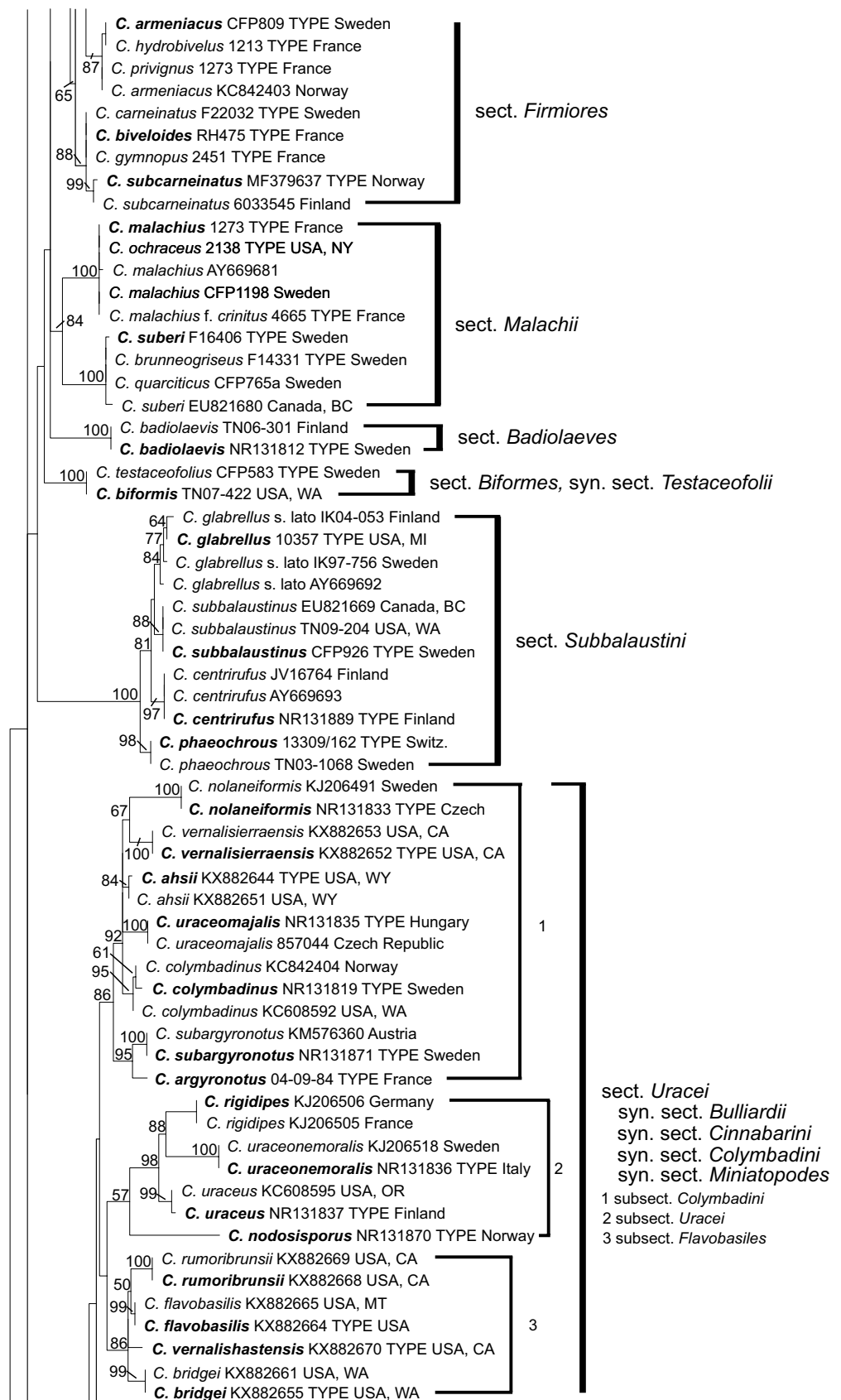


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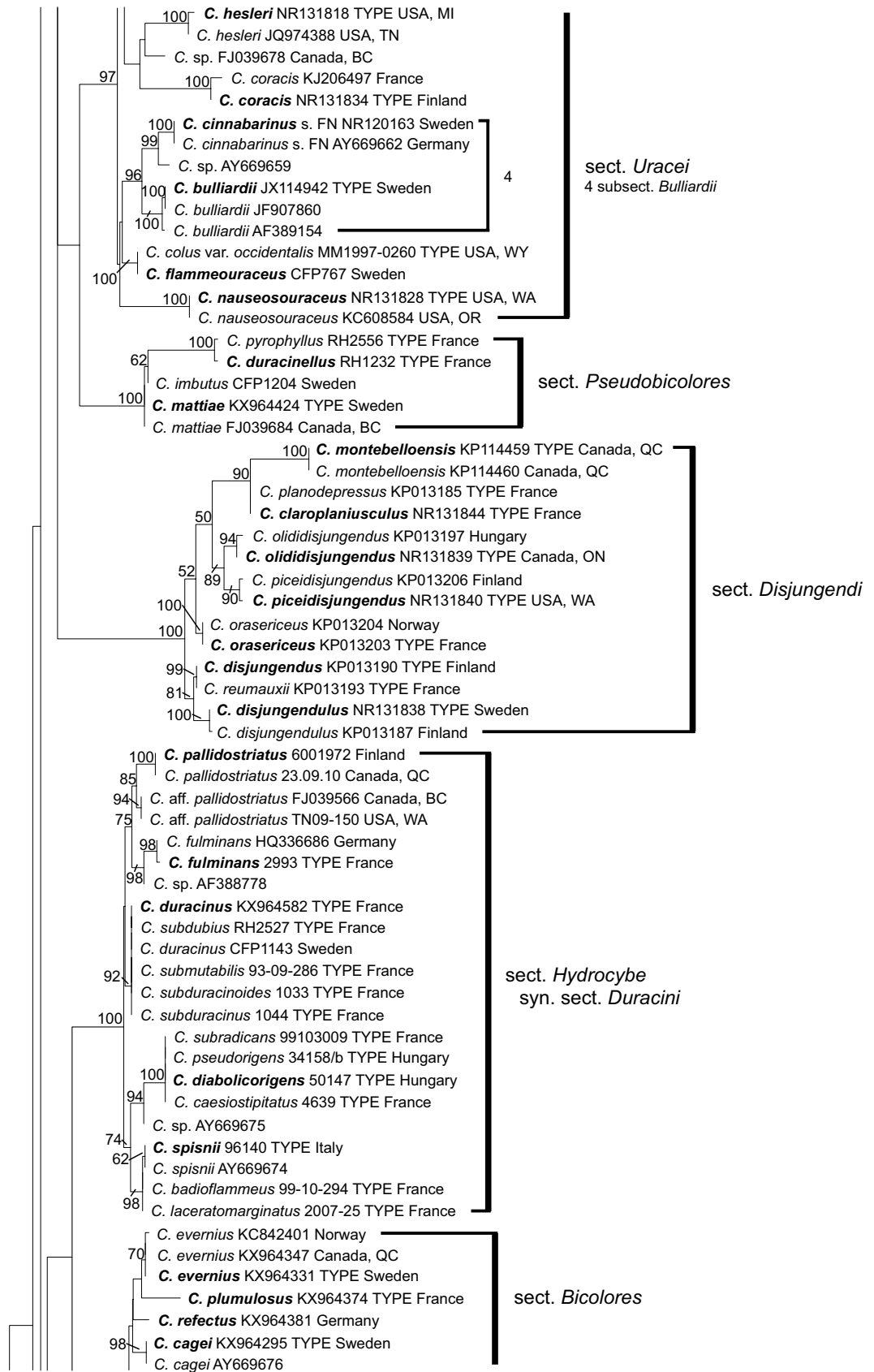


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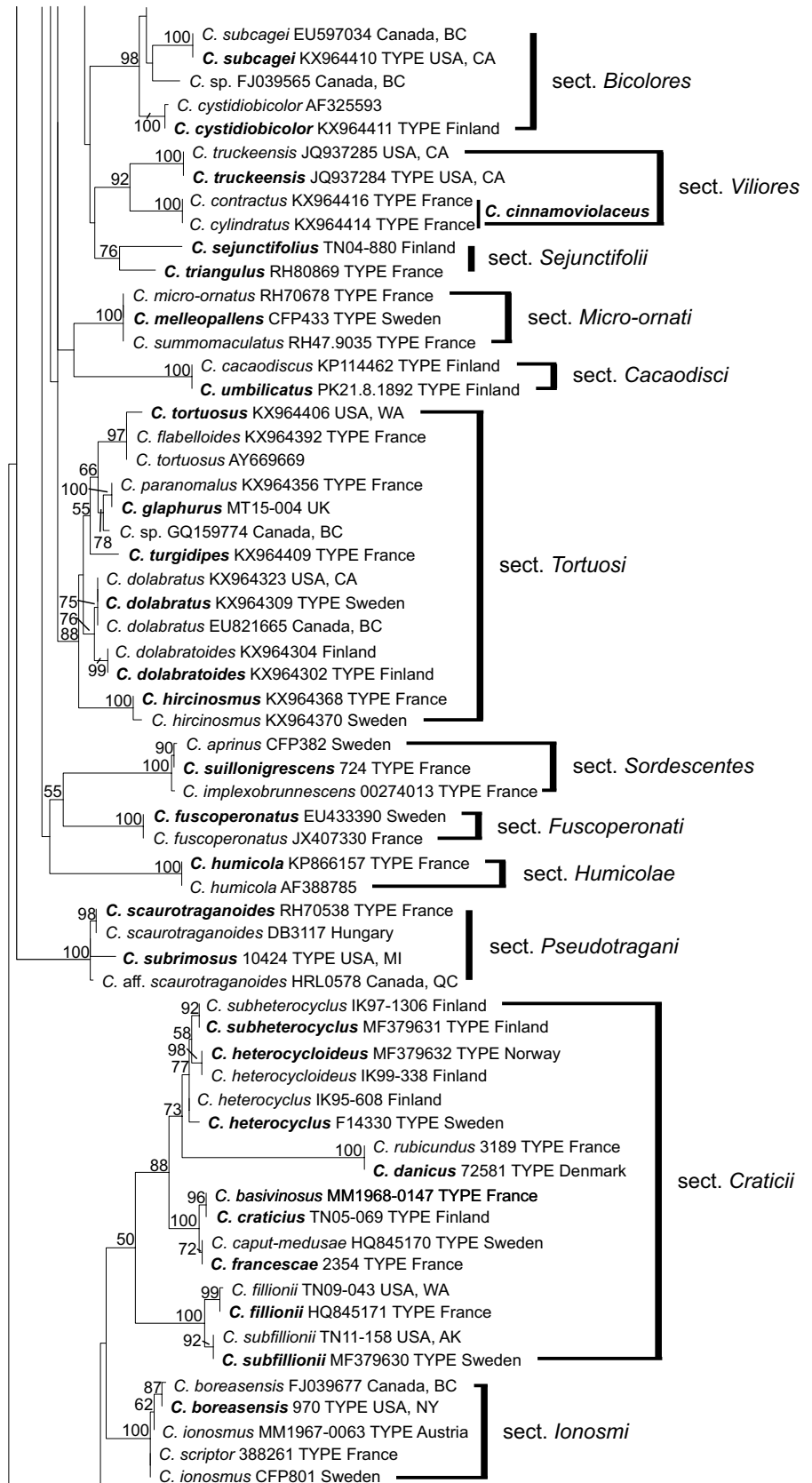


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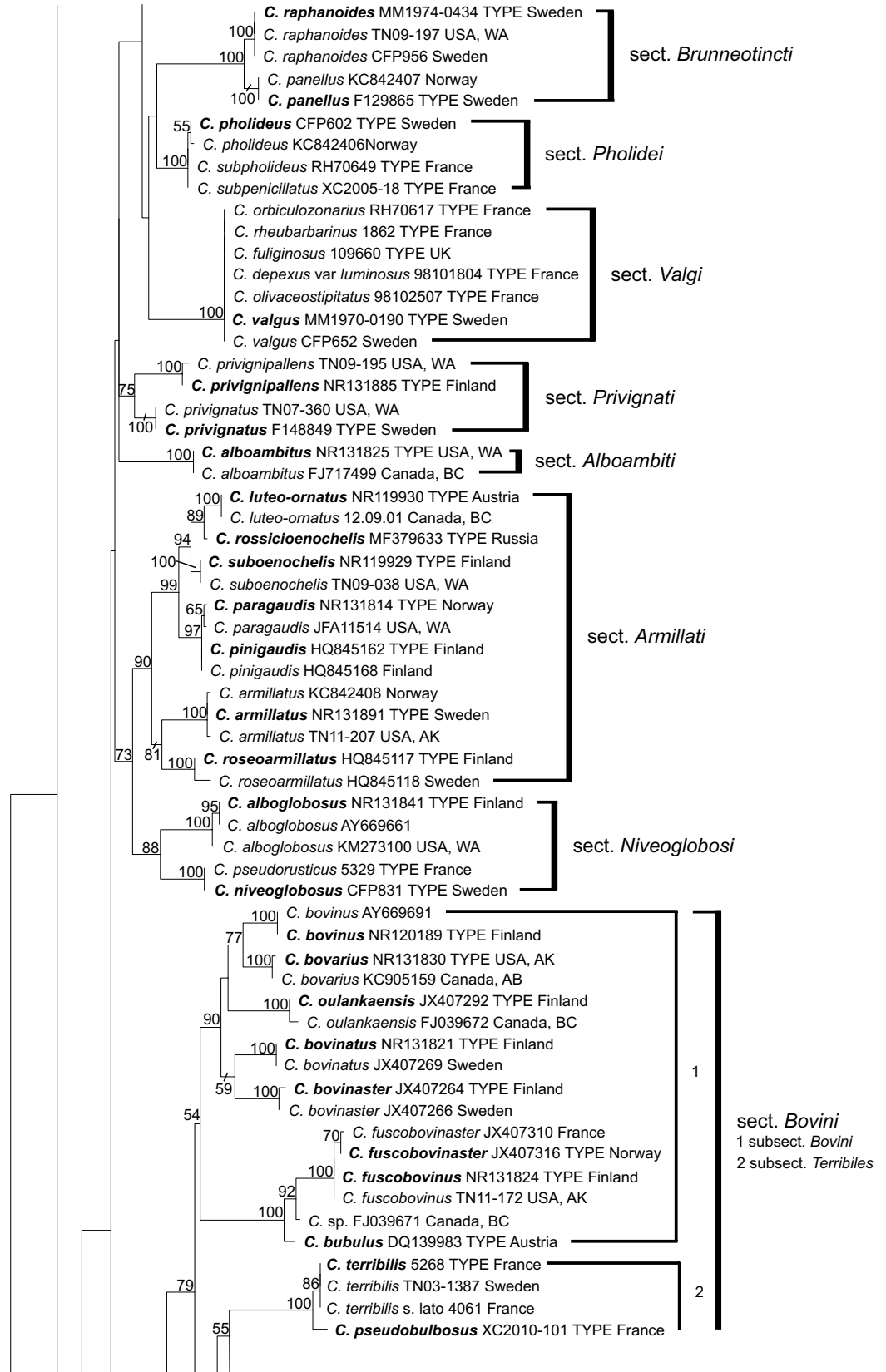


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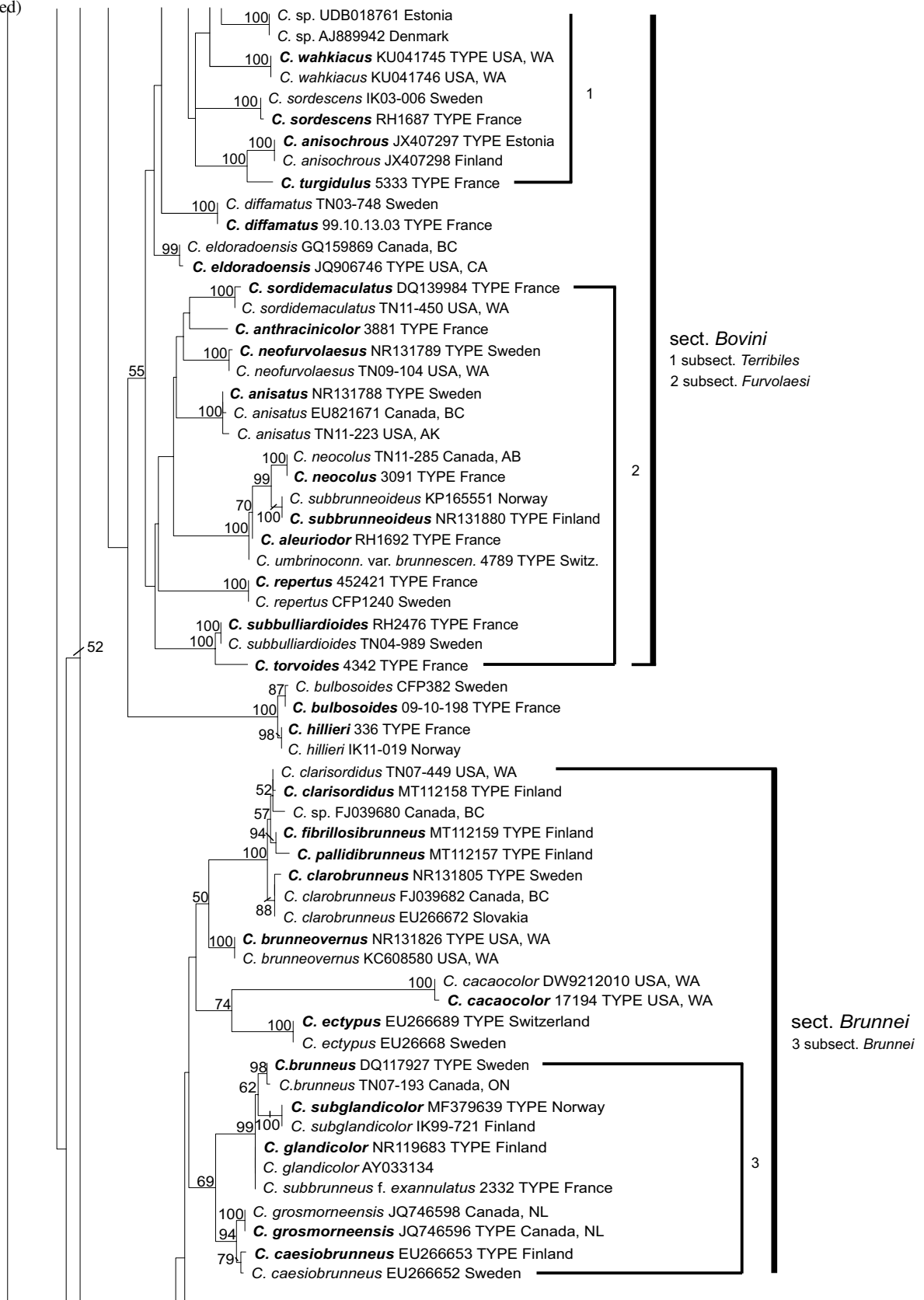
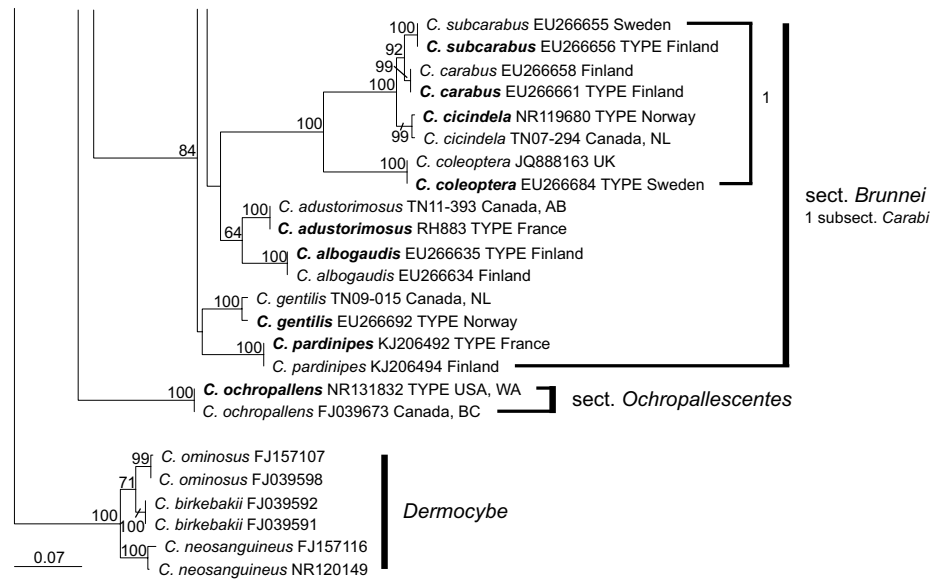


Fig. 1 (continued)



Molecular results

The phylogenetic tree resulting from the analysis, ITS and LSU regions including binary data from gap coding of the ITS region, is shown in FIG. 1 and a schematic drawing of the relationships of the sections based on the phylogenetic analysis in Fig. 2. Altogether, we recognize 80 sections which all form monophyletic groups in our analysis and examples of the sections are shown in Supplementary Figs. 1–11. We almost entirely used section names with clear identity, i.e., the concept of the type species of a section was well known.

A total of 482 types representing 184 species were successfully sequenced. Of these, about half of the species had one or more synonyms. A significant number of old types were successfully sequenced, 105 types over 50 years old and 18 types over 100 years. All the major *Cortinarius* taxonomists have described new species that already had an older name, but the portion of younger taxonomic synonyms in terms of the total number of described species (synonym rate) varies among the different authors. Here are synonym rates for authors who have described most of the *Telamonia* species, based only on morphological characters: Peck 17%, Kauffman 7%, Smith 40%, Moser 47%, Henry 55%, and French Atlas team 72%. Current names of *Cortinarius* species used in this study with their synonyms are listed in Table 1. All the names of the types are listed in alphabetical order in Supplementary Table 1, followed by the current name.

Sometimes it was only possible to amplify part of the ITS region, in most cases it was then the ITS1 region that was successful. Often in *Cortinarius* the ITS1 region alone is

enough for a proper identification, but especially in the case of small *Telamonia* species several sister species can have an identical or almost identical ITS1 region. Therefore, all of the unclear cases are marked in Supplementary Tables 1 and 2 with a prefix ‘cf.’ in the Latin name under the current name.

Taxonomy

Neo- and epitypifications

All older names without a type specimen that are included in the *Cortinarius* subgen. *Telamonia* key in *Funga Nordica* (Niskanen et al. 2012) and not yet typified are typified here with the exceptions of *C. paleaceus* Fr. and *C. miniatopus* J.E. Lange (not included in Niskanen et al. 2012) and *C. psammocephalus* (Bull.) Fr. (*nomen dubium*, no type proposed). In addition, for *C. colus* Fr. an epitype that differs from the current use of the name is proposed, and in the case of *C. alboviolaceus* (Pers.) Fr., *C. flabellus* (Fr.) Fr. and *C. hinnuleus* Fr. the best fitting candidate from two or more available ones in a species group was selected. For *C. anthracinus* Fr. and *C. cinnabarinus* Fr. neotypes have been chosen by Høiland (1983) but were not sequenced in this study. Altogether, neotypes for 11 species originally described by Fries, Liljeblad and Persoon are proposed as well as epitypes for 9 species described by Fries, Lange, Persoon, Quélet and Schaeffer. Citations of descriptions and illustrations of the species are provided. Notes under the name have only been added if our typification does not fit with the protologue and/or differs from the current use of the name in Niskanen et al. (2012). Synonyms are based on

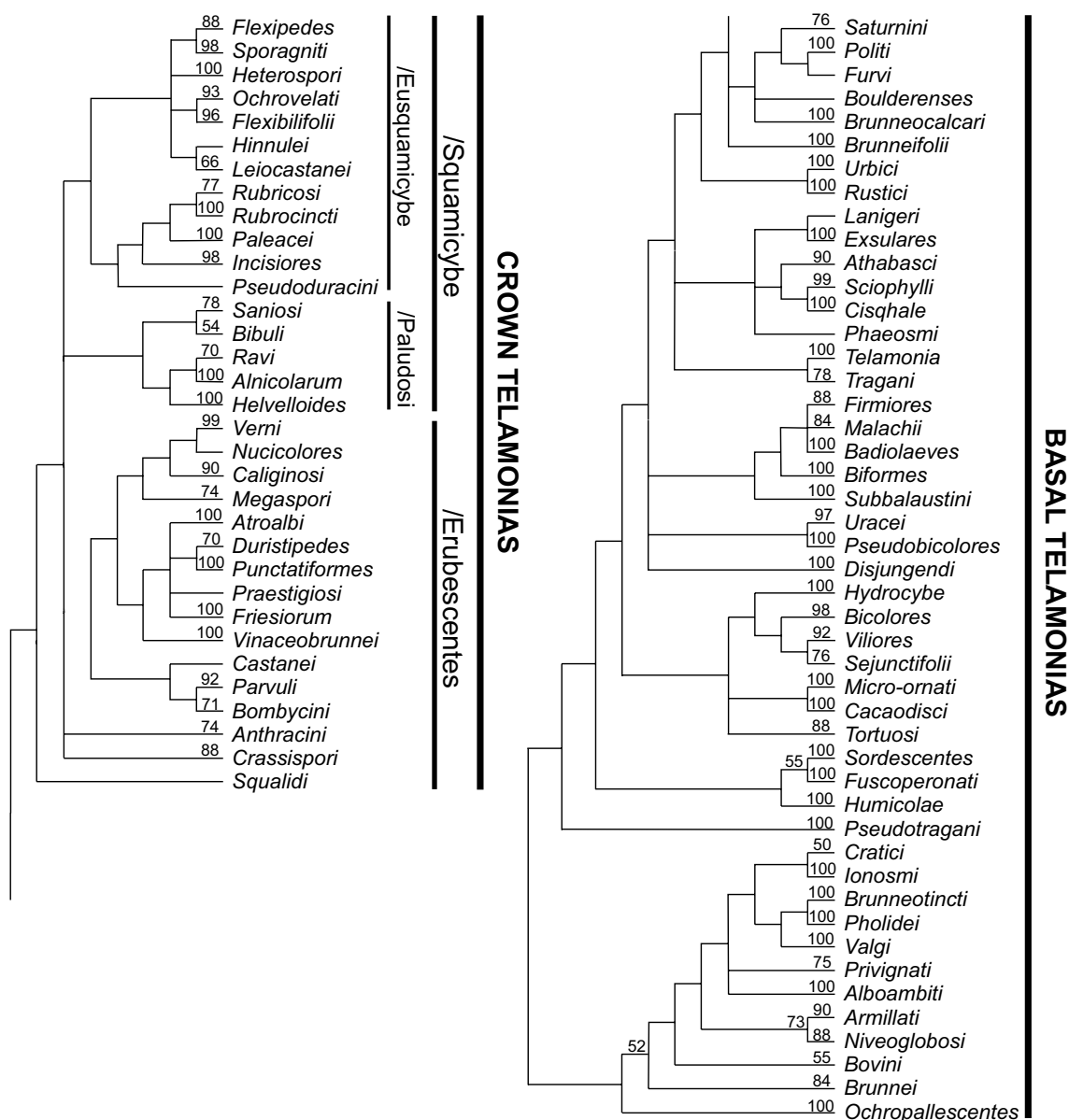


Fig. 2 A schematic drawing of the relationships of the 80 sections of *Cortinarius* subgen. *Telamonia* accepted in this study. The drawing is based on our phylogenetic analysis with bootstrap values greater than 50% gained in the analysis indicated above branches

DNA studies of the type specimens and the information on the types is presented in Table 1.

Cortinarius alboviolaceus (Pers.) Fr., Epicr. syst. mycol. (Upsaliae): 280 (1838) [1836–1838]

Basionym: *Agaricus alboviolaceus* Pers., Syn. meth. fung. (Göttingen) 2: 286 (1801): sanctioned in Fr., Syst. mycol. 1: 218 (1821).

Type: Sweden, Härjedalen, Storsjö sn, Flatruet, in subalpine zone with *Betula pubescens*, 16 Aug 1986, coll. H.

Lindström et al. CFP 432, F41130 (*S. neotypus hic designatus*, IF 557454), GenBank No. MT934857 (ITS).

Illustration. Brandrud et al. (1989: pl. A59).

Descriptions of the species. Brandrud et al. (1989: pl. A59), Niskanen et al. (2012).

Notes—Currently, we know three species in Europe that fit into Fries' description of *C. alboviolaceus*: *C. acutispisipes* Rob. Henry, *C. alboviolaceus* s. Brandrud et al. (1989) & Niskanen et al. (2012), and *C. paralbocyanus* Eysart. Based on the current data *C. alboviolaceus* s. *auctores* has the widest distribution of the three species and is also the

Table 1 Current names of the *Cortinarius* species accepted in this study with their synonyms

Current name	Younger synonyms
<i>C. aavae</i> Liimat. & Niskanen 2012	
<i>C. acutispissipes</i> Rob. Henry 1981	<i>C. geophilus</i> var. <i>subauroreus</i> Bidaud, Moëgne-Locc. & Reumaux 2002
<i>C. adustorimosus</i> Rob. Henry 1988	
<i>C. ahsii</i> McKnight 1975	
<i>C. alboadustus</i> Bidaud 2012	
<i>C. alboambitus</i> Niskanen, Liimat. & Ammirati 2013	
<i>C. albogaudis</i> Kytöv., Niskanen & Liimat. 2009	
<i>C. alboglobosus</i> Kytöv., Liimat., Niskanen & Ammirati 2014	
<i>C. albolens</i> Bidaud, Carteret & Reumaux 2012	
<i>C. albosericus</i> Ammirati, Beug, Liimat., Niskanen & O. Ceska 2016	
<i>C. alboviolaceus</i> (Pers.) Fr. 1838	<i>C. fuscoviolascens</i> Reumaux 1990; <i>C. mixtus</i> Reumaux 2002; <i>C. mixtus</i> var. <i>foetulentus</i> Carteret, Moëgne-Locc. & Reumaux 2002; <i>C. mystagogi</i> Carteret & Reumaux 2002; <i>C. radicatoviolaceus</i> Rob. Henry 1981; <i>C. griseoviolaceus</i> A.H. Sm. 1944
<i>C. aleuriodor</i> Rob. Henry 1981	<i>C. perrinii</i> Rob. Henry & Ramm 1989; <i>C. umbrinoconnatus</i> var. <i>brunnescens</i> Bidaud, Moëgne-Locc., Reumaux & Rob. Henry 2000
<i>C. americanus</i> A.H. Sm. 1934	<i>C. sphagnicola</i> Carteret & Reumaux 2004
<i>C. ammophiloides</i> Bohus 1979	<i>C. ochrorufus</i> Moëgne-Locc. & Fillion 2001; <i>C. punctatorum</i> Moëgne-Locc. & Fillion 2012; <i>C. salicetophilus</i> Bidaud & Fillion 2012; <i>C. subfistularis</i> Fillion 2012; <i>C. tener</i> Carteret 2001; <i>C. nigromaculatus</i> Carteret 2012
<i>C. andreae</i> H. Lindstr. 1999 s. lato	<i>C. sporagnitus</i> Bidaud 2010
<i>C. angelesianus</i> A.H. Sm. 1944	<i>C. angelesianus</i> var. <i>elakatopus</i> M.M. Moser 2001; <i>C. strobilaceus</i> M.M. Moser 1967; <i>C. tubulipes</i> J. Favre 1960
<i>C. angustisporus</i> Kytöv., Niskanen & Liimat. 2014	
<i>C. anisatus</i> H. Lindstr., Kytöv. & Niskanen 2005	
<i>C. anisochrous</i> Kytöv., Liimat., Niskanen & H. Lindstr. 2013	
<i>C. anthracinicolor</i> Reumaux 2001	
<i>C. anthracinus</i> (Fr.) Sacc. 1887 s. Funga Nordica	<i>C. danili</i> Rob. Henry 1943; <i>C. ignifluus</i> Bidaud 1994; <i>C. josserandii</i> Bidaud 1994; <i>C. procalans</i> Moëgne-Locc. & Reumaux 1994; <i>C. subanthracinus</i> Rob. Henry 1944;
<i>C. aptecoherens</i> Rob. Henry 1983	<i>C. impennoides</i> Bidaud, Moëgne-Locc. & Reumaux 2000
<i>C. argyronotus</i> Bidaud 2008	
<i>C. armeniacus</i> (Schaeff.) Fr. 1838	<i>C. hydrobivelus</i> Rob. Henry & Reumaux 2010; <i>C. privignorum</i> Rob. Henry 1985; <i>C. privignus</i> (Fr.) Fr. 1838
<i>C. armillatus</i> (Fr.) Fr. 1838	
<i>C. atroalbus</i> M.M. Moser 1993	<i>C. atroalbus</i> var. <i>nigripes</i> M.M. Moser 1993; <i>C. ignotissimus</i> Bidaud 2012; <i>C. paludophilus</i> Carteret & Reumaux 2001
<i>C. atrocaeruleus</i> M.M. Moser 1967	<i>C. carminipes</i> Moëgne-Locc. & Reumaux 1988; <i>C. erythrinellus</i> Reumaux 1988; <i>C. insignitus</i> Reumaux 2004
<i>C. auroripes</i> Carteret & Reumaux 2001	<i>C. subgracilior</i> Bidaud & Carteret 2008
<i>C. badioflavus</i> Ammirati, Beug, Niskanen, Liimat. & Bojantchev 2016	
<i>C. badiolaevis</i> Niskanen, Liimat., Mahiques, Ballarà & Kytöv. 2011	
<i>C. badiovestitus</i> M.M. Moser 1968	
<i>C. bibulus</i> Quéf. 1881	
<i>C. biformis</i> Fr. 1838	<i>C. testaceofolius</i> H. Lindstr. & Soop 1995
<i>C. bistreoides</i> Kauffman 1921	
<i>C. biveloides</i> Rob. Henry 1948	<i>C. carneinatus</i> Soop 2002; <i>C. gymnopus</i> Rob. Henry 1983
<i>C. bivelosimilis</i> Kytöv., Niskanen & Liimat. 2017	
<i>C. bivelus</i> (Fr.) Fr. 1838	<i>C. amphibalaustius</i> Rob. Henry 1983; <i>C. bivelus</i> f. <i>sulcatocephalus</i> Bidaud 2010; <i>C. insolitus</i> Rob. Henry 1981; <i>C. quietus</i> Rob. Henry 1977; <i>C. suilloclarus</i> Reumaux 2002

Table 1 (continued)

Current name	Younger synonyms
<i>C. bombycinus</i> Mahiques & Burguete 2001	
<i>C. bonamei</i> Rob. Henry 1970	
<i>C. boreasensis</i> A.H. Sm. 1944	<i>C. ionosmus</i> M.M. Moser, Nespiak & Schwöbel 1969; <i>C. scriptor</i> Kühner 1989
<i>C. boreotrichus</i> Kytöv., Niskanen & Liimat. 2017	
<i>C. boulderensis</i> A.H. Sm. 1944	
<i>C. bovarius</i> Liimat. & Niskanen 2013	
<i>C. bovinaster</i> Niskanen, Kytöv. & Liimat. 2013	
<i>C. bovinatus</i> Kytöv., Liimat., Niskanen & H. Lindstr. 2013	
<i>C. bovinus</i> Fr. 1838	
<i>C. bridgei</i> Ammirati, Niskanen, Liimat., Bojantchev, & Fang 2017	
<i>C. brunneifolius</i> Kytöv., Niskanen & Liimat. 2008	
<i>C. brunneocalcarius</i> Niskanen, Liimat. & Kytöv. 2012	
<i>C. brunneoclarus</i> Niskanen, Kytöv. & Liimat. 2020	
<i>C. brunneovernus</i> Niskanen, Liimat. & Ammirati 2013	
<i>C. brunneus</i> (Pers.) Fr. 1838	<i>C. brunneus</i> var. <i>incommixtus</i> Bidaud 2009
<i>C. bubulus</i> Liimat., Kytöv. & Niskanen 2020	
<i>C. bulbosolvatus</i> Rob. Henry & Contu 1985	
<i>C. bulliardii</i> (Pers.) Fr. 1838	<i>C. colus</i> Fr. 1838; <i>C. georgianae</i> Moënné-Locc. 1994
<i>C. cacaocolor</i> A.H. Sm. 1944	
<i>C. caesioarmeniacus</i> Kytöv., Niskanen & Liimat. 2014	
<i>C. caesiobrunneus</i> Kytöv., Niskanen & Liimat. 2009	
<i>C. cagei</i> Melot 1990	
<i>C. californicus</i> A.H. Sm. 1939	
<i>C. caliginosus</i> Bidaud, Moënné-Locc. & Reumaux 2000	
<i>C. calopus</i> P. Karst. 1881	<i>C. fragrans</i> A.H. Sm. 1944; <i>C. ionema</i> M.M. Moser & Ammirati 1996
<i>C. campester</i> Reumaux 2001	<i>C. malefidus</i> Moënné-Locc. 2001; <i>C. porphyreticus</i> Moënné-Locc. 2001
<i>C. canaliculatus</i> Bidaud & Carteret 2008	
<i>C. carabus</i> Kytöv., Niskanen & Liimat. 2009	
<i>C. carbunculus</i> H. Lindstr. & H. Markl. 2010	
<i>C. castaneopallidus</i> Carteret 2004	<i>C. franceschini</i> Consiglio, D. Antonini & M. Antonini 2006; <i>C. olivaceomarginatus</i> Carteret 2012; <i>C. pseudobavaricus</i> Bidaud & Reumaux 2012
<i>C. castaneus</i> (Bull.) Fr. 1838	<i>C. fallaciosus</i> Bidaud 2001; <i>C. kunicensis</i> var. <i>caespitosus</i> Moënné-Locc. 2001; <i>C. robertii</i> Moënné-Locc. & Reumaux 1988; <i>C. subodoratus</i> Bidaud 2001
<i>C. centrirufus</i> Kytöv., Niskanen & Liimat. 2014	
<i>C. chevassutii</i> Rob. Henry 1982	<i>C. subsordescens</i> Rob. Henry 1985
<i>C. cicindela</i> Kytöv., Niskanen & Liimat. 2009	
<i>C. cinereobrunneolus</i> Chevassut & Rob. Henry 1982	
<i>C. cinnamoviolaceus</i> M.M. Moser 1968	
<i>C. circinans</i> Rob. Henry 1985	<i>C. melitosarx</i> Soop 1999
<i>C. cisqhale</i> Bojantchev 2013	
<i>C. cistopulchripes</i> Bidaud 2004	
<i>C. clarobrunneus</i> (H. Lindstr. & Melot) Niskanen, Kytöv. & Liimat. 2009	
<i>C. claroplaniusculus</i> Rob. Henry 1983	
<i>C. clarosordidus</i> Niskanen, Kytöv. & Liimat. 2020	
<i>C. coccineus</i> Reumaux 1994	
<i>C. coleoptera</i> H. Lindstr. & Soop 1999	
<i>C. colorius</i> (Bidaud) Niskanen, Dima & Liimat. 2020	

Table 1 (continued)

Current name	Younger synonyms
<i>C. colymbadinus</i> Fr. 1838	
<i>C. compressus</i> A.H. Sm. 1944	
<i>C. comptulus</i> M.M. Moser 1968	<i>C. fistularioides</i> Reumaux, Bidaud & Fillion 2001; <i>C. griseosulcatus</i> Carteret 2004; <i>C. hemitrichus</i> var. <i>americanus</i> A.H. Sm. 1944; <i>C. inolens</i> var. <i>parvinolens</i> Bidaud & Carteret 2010; <i>C. jacobii</i> Bidaud, Moënné-Locc. & Reumaux 2001; <i>C. laniatus</i> Rob. Henry 1983; <i>C. sublatisporus</i> Svrček 1968
<i>C. confirmatus</i> Rob. Henry 1983	
<i>C. coracis</i> Kytöv., Niskanen, Liimat. & Dima 2014	
<i>C. corvinus</i> Reumaux 2012	
<i>C. crassisporus</i> Kytöv., Niskanen & Liimat. 2014	
<i>C. craticius</i> Fr. 1838	<i>C. basivinosus</i> M.M. Moser 1996
<i>C. cucumisporus</i> M.M. Moser 1967	
<i>C. cystidiobicolor</i> Liimat. & Niskanen 2017	
<i>C. danicus</i> Høil. 1983	<i>C. rubicundus</i> Bidaud, Moënné-Locc. & Reumaux 1994
<i>C. deceptivissimus</i> Reumaux 1984	<i>C. damascenoides</i> Bidaud 2008
<i>C. decipiens</i> (Pers.) Fr. 1838	<i>C. anthracinoides</i> Rob. Henry 2001; <i>C. argumentosus</i> Moënné-Locc. & Reumaux 2000; <i>C. decipiens</i> f. <i>saliceticola</i> Reumaux & Carteret 2001; <i>C. maculatophyllus</i> Bidaud 2012; <i>C. washingtonensis</i> A.H. Sm. 1939
<i>C. decipientoides</i> Moënné-Locc. & Reumaux 1988	<i>C. alutaceogrisescens</i> Bidaud 1997; <i>C. derelictus</i> Reumaux 2001; <i>C. rubellopes</i> var. <i>puddricolor</i> Bidaud, Moënné-Locc. & Reumaux 2001
<i>C. denigratus</i> Ammirati, Beug, Niskanen, Liimat. & O. Ceska 2016	
<i>C. desertorum</i> (Velen.) G. Garnier 1991	<i>C. ammophilus</i> A. Pearson 1946; <i>C. diasemospermus</i> var. <i>leptospermus</i> H. Lindstr. 1998; <i>C. difficillimus</i> Carteret 2012; <i>C. goniosporus</i> Carteret 2004; <i>C. pertristis</i> J. Favre 1955; <i>C. subdepressus</i> Carteret 2012; <i>C. subrigidus</i> Bidaud, Carteret & Reumaux 2010; <i>C. friesianus</i> Carteret & Reumaux 2001
<i>C. diabolicorigens</i> Bohus 1976	<i>C. caesiostipitatus</i> Reumaux 2008; <i>C. pseudorigens</i> Bohus 1976; <i>C. subradicans</i> Carteret & Reumaux 2008
<i>C. diffamatus</i> Carteret 2012	
<i>C. diffractosuavis</i> Chevassut & Rob. Henry 1978	
<i>C. diosmoides</i> Rob. Henry 1989	<i>C. diosmoides</i> Rob. Henry 1989
<i>C. diosmus</i> Kühner 1955	
<i>C. disjungendulus</i> Kytöv., Liimat. & Niskanen 2014	
<i>C. disjungendus</i> P. Karst. 1893	<i>C. reumauxii</i> Rob. Henry 1996
<i>C. distortus</i> Kauffman 1932	<i>C. parasuillus</i> Reumaux 2010; <i>C. pseudocalopus</i> Reumaux 2010; <i>C. subcurtipes</i> Bidaud 2010; <i>C. submelleopallens</i> Rob. Henry 1981
<i>C. dolabratooides</i> Kytöv., Carteret, Bidaud, Liimat., Niskanen, Bel-langer, Dima, Reumaux & Ammirati 2017	
<i>C. dolabratus</i> Fr. 1838	
<i>C. duboisensis</i> Ammirati, Beug, Niskanen & Liimat. 2016	
<i>C. dumetorum</i> J. Favre 1960	
<i>C. duracinellus</i> Rob. Henry 1970	<i>C. pyrophyllus</i> Rob. Henry 1970
<i>C. duracinus</i> Fr. 1838	<i>C. subdubius</i> Rob. Henry 1970; <i>C. subduracinoides</i> Moënné-Locc. & Reumaux 2008; <i>C. subduracinus</i> Bidaud & Moënné-Locc. 2008; <i>C. submutabilis</i> Bidaud & Carteret 2008
<i>C. duristipes</i> Kytöv., Niskanen & Liimat. 2014	
<i>C. ectypus</i> J. Favre 1960	
<i>C. elaphinicolor</i> Carteret 2004	
<i>C. eldoradoensis</i> Bojantchev 2013	

Table 1 (continued)

Current name	Younger synonyms
<i>C. epipurrus</i> Chevassut & Rob. Henry 1978	<i>C. hinnuleoradicatus</i> Bidaud, Moëgne-Locc. & Reumaux 1997; <i>C. pallescens</i> Moëgne-Locc. & Reumaux 1997; <i>C. pseudosafranopes</i> Moëgne-Locc. & Reumaux 1997; <i>C. subgriseescens</i> Bidaud, Moëgne-Locc. & Reumaux 1997
<i>C. evernius</i> (Fr.) Fr. 1838	
<i>C. exitiosus</i> Bidaud, Moëgne-Locc. & Reumaux 2001	
<i>C. expallens</i> M.M. Moser 1993	<i>C. mucronatus</i> M.M. Moser & McKnight 1987, nom. illegit.; <i>C. hemitrichus</i> f. <i>improcerus</i> J. Favre 1955; <i>C. gossypinus</i> H. Lindstr. 2010
<i>C. exsularis</i> Garrido-Ben., Ballarà & Mahiques 2016	
<i>C. fagetorum</i> M.M. Moser 1967	<i>C. fagetorum</i> M.M. Moser 1967
<i>C. falsosus</i> Moëgne-Locc. & Reumaux 2001	<i>C. griseophyllus</i> Reumaux 2001; <i>C. griseovioleipes</i> Moëgne-Locc. & Reumaux 2001; <i>C. recedens</i> Bidaud, Moëgne-Locc. & Reumaux 2001
<i>C. famatus</i> Moëgne-Locc. & Reumaux 2001	<i>C. biformis</i> var. <i>dilatatus</i> Bidaud, Carteret & Reumaux 2012
<i>C. ferrugineovelatus</i> Kytöv. Liimat. & Niskanen 2014	
<i>C. fibrillosobrunneus</i> Kytöv., Niskanen & Liimat. 2020	
<i>C. fillionii</i> Bidaud, Moëgne-Locc. & Reumaux 1995	
<i>C. flabellus</i> (Fr.) Fr. 1838	<i>C. flabelliformis</i> Bidaud 2010; <i>C. flabellus</i> f. <i>iners</i> Bidaud 2010; <i>C. furfuraceus</i> Bidaud 1997; <i>C. fuscoruber</i> Reumaux 2001; <i>C. gurdus</i> Carteret 2012; <i>C. pseudodepressus</i> Carteret & Reumaux 2010
<i>C. flammeouraceus</i> Niskanen, Kytöv., Liimat., Dima & Ammirati 2020	<i>C. colus</i> var. <i>occidentalis</i> M.M. Moser 2002
<i>C. flavobasilis</i> Peintner, Kuhnert-Finkernagel, Cripps & Ammirati 2017	
<i>C. flexibilifolius</i> Carteret 2004	<i>C. olivaceobrunneus</i> Reumaux 2012; <i>C. privus</i> Reumaux 2004; <i>C. subfuscodiscus</i> Reumaux 2004
<i>C. flexipes</i> (Pers.) Fr. 1838	<i>C. paleifer</i> Svrček 1968
<i>C. fragrantissimus</i> Ammirati, Beug, Liimat., Niskanen & O. Ceska 2016	
<i>C. francescae</i> Reumaux 1992	<i>C. caput-medusae</i> H. Lindstr. 1998
<i>C. fructuodorus</i> Niskanen, Liimat. & Ammirati 2013	
<i>C. fulminans</i> Moëgne-Locc. & Reumaux 2008	
<i>C. fulvoisabellinus</i> Rob. Henry 1941	
<i>C. fulvopaludosus</i> Kytöv., Niskanen & Liimat. 2017	
<i>C. furfurellus</i> Peck 1880	
<i>C. furvoumbrinus</i> Liimat., Niskanen & Kytöv. 2014	
<i>C. furvus</i> Liimat., Niskanen & Kytöv. 2014	
<i>C. fuscescens</i> Kytöv., Niskanen & Liimat. 2014	
<i>C. fuscoalbus</i> Kytöv., Niskanen & Liimat. 2017	
<i>C. fuscobovinaster</i> Kytöv., Liimat., Niskanen & H. Lindstr. 2013	
<i>C. fuscobovinus</i> Kytöv., Niskanen & Liimat. 2013	
<i>C. fuscodiscus</i> A.H. Sm. 1944	
<i>C. fuscoflexipes</i> M.M. Moser & McKnight 1987	
<i>C. fuscogracilescens</i> A. Favre 2009	
<i>C. fuscoperonatus</i> Kühner 1953	
<i>C. fuscoumbrinus</i> Liimat., Niskanen & Kytöv. 2014	
<i>C. fuscovelatus</i> Kytöv., Niskanen & Liimat. 2014	
<i>C. gallurae</i> D. Antonini, M. Antonini & Consiglio 2005	
<i>C. gentilis</i> (Fr.) Fr. 1838	
<i>C. gentilissimus</i> A.H. Sm. 1939	
<i>C. geraniolens</i> Bidaud 2010 s. lato	<i>C. subcarcharias</i> Bidaud 2010
<i>C. glabrellus</i> Kauffman 1907	<i>C. leiopus</i> Rob. Henry 1981
<i>C. glandicolor</i> (Fr.) Fr. 1838	<i>C. subbrunneus</i> f. <i>exannulatus</i> Moëgne-Locc. 2009
<i>C. glaphurus</i> Chevassut & Rob. Henry 1982	<i>C. paranomalus</i> Rob. Henry 1992

Table 1 (continued)

Current name	Younger synonyms
<i>C. griseocarneus</i> Carteret 2010	<i>C. atripes</i> Reumaux 2012
<i>C. grosborneënsis</i> Liimat. & Niskanen 2012	
<i>C. gualalaensis</i> Bojantchev 2013	
<i>C. helodes</i> M.M. Moser, Matheny & Daniele 2001	
<i>C. helvelloides</i> (Bull.) Fr. 1838	
<i>C. hemitrichoides</i> Bidaud & Moëgne-Loec. 2010	
<i>C. hemitrichus</i> (Pers.) Fr. 1838	<i>C. fusisemen</i> Reumaux 2000; <i>C. milvinoides</i> Carteret & Reumaux 2010; <i>C. paleaceus</i> Fr. 1838; <i>C. roseohemitrichus</i> Carteret & Reumaux 2010
<i>C. heparinus</i> Kytöv., Niskanen & Liimat. 2020	
<i>C. hesleri</i> Ammirati, Niskanen, Liimat. & Matheny 2013	
<i>C. heterocycloideus</i> Kytöv., Niskanen & Liimat. 2017	
<i>C. heterocyclus</i> Soop 1990	
<i>C. heterodepressus</i> Kytöv., Niskanen & Liimat. 2017	<i>C. bohemicus</i> f. <i>subheterosporus</i> Bidaud 2010
<i>C. heterosporus</i> Bres. 1889	
<i>C. hillieri</i> Rob. Henry 1938	
<i>C. hinnuleoarmillatus</i> Reumaux 1989	<i>C. aureifer</i> Reumaux 1989
<i>C. hinnuleocervinus</i> Niskanen, Liimat. & Ammirati 2017	<i>C. distans</i> var. <i>olympianus</i> A.H. Sm. 1944
<i>C. hinnuleus</i> Fr. 1838	<i>C. tigris</i> Bidaud 1997
<i>C. hircinosmus</i> Moëgne-Loec. 2002	
<i>C. hirtus</i> (Velen.) G. Garnier 1991	<i>C. querculus</i> Moëgne-Loec. & Reumaux 2001; <i>C. punctatoides</i> Reumaux 2012; <i>Telamonia sanguinescens</i> Velen. 1939; <i>C. similigenus</i> Moëgne-Loec. & Reumaux 2001; <i>C. subargyropus</i> Bidaud, Moëgne-Loec. & Reumaux 2001; <i>C. substemmatus</i> Moëgne-Loec. & Reumaux 2001
<i>C. humicola</i> (Quél.) Maire 1911	
<i>C. hydrotelamonioides</i> Rob. Henry 1970	<i>C. boletiformis</i> Bidaud & Reumaux 2010; <i>C. bucknallii</i> Reumaux 2010; <i>C. castanearum</i> Rob. Henry 1981; <i>C. macropodius</i> Rob. Henry 1961 Nom. inval.; <i>C. pseudoprivignus</i> Rob. Henry 1985; <i>C. renidentoides</i> Rob. Henry 1981; <i>C. subumidicola</i> Bidaud, Moëgne-Loec. & Reumaux 2000; <i>C. triformis</i> f. <i>strenuus</i> Rob. Henry 1981; <i>C. turgidoideus</i> Rob. Henry 1981
<i>C. imbutus</i> Fr. 1838	
<i>C. impolitus</i> Kauffman 1918	<i>C. subacutus</i> A.H. Sm. 1944
<i>C. incisor</i> Bidaud, Moëgne-Loec. & Reumaux 1997	<i>C. perzonatus</i> Reumaux 2004; <i>C. spurcatus</i> Moëgne-Loec. & Reumaux 2001
<i>C. inconspicuus</i> J. Favre 1955	<i>C. erubescens</i> M.M. Moser 1968
<i>C. iners</i> (Bidaud) Liimat., Dima & Niskanen 2020	
<i>C. intempestivus</i> Moëgne-Loec. & Reumaux 2001	<i>C. cristatosporus</i> Reumaux 2004
<i>C. ionophyllus</i> M.M. Moser 1968	
<i>C. jacobi-langei</i> Bidaud 2008	
<i>C. kauffmanianus</i> A.H. Sm. 1933	
<i>C. lacustris</i> Moëgne-Loec. & Reumaux 1997	<i>C. altae-herbae</i> Moëgne-Loec. & Reumaux 1999
<i>C. laniger</i> Fr. 1838	<i>C. laniger</i> f. <i>macrosemen</i> Bidaud, Carteret & Reumaux 2010
<i>C. leiocastaneus</i> Niskanen, Liimat. & Soop 2008	
<i>C. leucophaeatus</i> Rob. Henry 1985	
<i>C. lindstroemii</i> Niskanen, Kytöv. & Liimat. 2020	<i>C. flabellus</i> f. <i>biolens</i> Bidaud 2010
<i>C. lucorum</i> (Fr.) Berger 1846	

Table 1 (continued)

Current name	Younger synonyms
<i>C. luridis</i> Rob. Henry 1969	<i>C. aciculispurus</i> Moëgne-Loec. 1997; <i>C. armillifer</i> Moëgne-Loec. & Reumaux 1997; <i>C. aspilus</i> Moëgne-Loec. 1997; <i>C. collybioides</i> Reumaux 1997; <i>C. conicoides</i> Bidaud 1997; <i>C. herculinus</i> Reumaux 1997; <i>C. hinnuleoscitus</i> Ramm & Rob. Henry 1995; <i>C. hinnuleus</i> f. <i>parincisus</i> Bidaud, Moëgne-Loec. & Reumaux 1997; <i>C. lepidus</i> Moëgne-Loec. 1997; <i>C. ochraceoplicatus</i> Reumaux 1997; <i>C. pseudohinnuleus</i> Bidaud, Moëgne-Loec. & Reumaux 1997; <i>C. salicum</i> Reumaux 1997
<i>C. luteo-ornatus</i> (M.M. Moser) Bidaud, Moëgne-Loec. & Reumaux 1995	
<i>C. malachus</i> (Fr.) Fr. 1838	<i>C. cinereoviolascens</i> Moëgne-Loec. & Reumaux 1988; <i>C. malachus</i> f. <i>chologogus</i> Bidaud, Moëgne-Loec. & Reumaux 2002; <i>C. malachus</i> f. <i>crinitus</i> Bidaud & Reumaux 2002; <i>C. ochraceus</i> Peck 1872
<i>C. mallaensis</i> Kytöv., Niskanen & Liimat. 2020	
<i>C. mattiae</i> Soop 2010	
<i>C. megacystidiosus</i> Reumaux 2012	
<i>C. melleopallens</i> (Fr.) Britzelm. 1892	<i>C. micro-ornatus</i> Chevassut & Rob. Henry 1978; <i>C. summomaculatus</i> Rob. Henry 1995
<i>C. milvinicolor</i> Moëgne-Loec. & Reumaux 1997	
<i>C. miniatopus</i> J.E. Lange 1940	
<i>C. minusculus</i> Liimat. & Niskanen 2019	
<i>C. miwok</i> Bojantchev 2013	
<i>C. montebelloensis</i> Niskanen & Liimat. 2014	
<i>C. mucicola</i> A.H. Sm. 1944	
<i>C. murinascens</i> Kytöv., Niskanen & Liimat. 2014	
<i>C. nauseosouraceus</i> Niskanen, Liimat. & Ammirati 2013	
<i>C. neocolus</i> Reumaux & Sasia 2011	
<i>C. neofallax</i> Carteret & Reumaux 2004	<i>C. incisopunctatus</i> Reumaux 2012
<i>C. neofurvolaeus</i> Kytöv., Niskanen, Liimat. & H. Lindstr. 2005	
<i>C. nigrellus</i> Peck 1873	
<i>C. nigrocupidatus</i> Kauffman 1921	<i>C. adalbertii</i> var. <i>turritus</i> M.M. Moser 1980; <i>C. inolens</i> (H. Lindstr.) Bidaud 2010; <i>C. striaepilus</i> J. Favre 1948 <i>C. pseudorusticus</i> Bidaud 2002
<i>C. niveoglobosus</i> H. Lindstr. 1992	
<i>C. niveotraganus</i> Kytöv., Niskanen & Liimat. 2014	
<i>C. nodosisporus</i> Kytöv., Niskanen & Liimat. 2014	
<i>C. nolaneiformis</i> (Velen.) Dima, Niskanen & Liimat. 2014	
<i>C. nucicolor</i> Liimat., Niskanen & Kytöv. 2014	
<i>C. obliquus</i> Peck 1902	
<i>C. ochropallens</i> Liimat., Niskanen & Ammirati 2013	
<i>C. ohlone</i> Bojantchev 2013	
<i>C. olididisjungendus</i> Liimat., Niskanen, Dima & Kytöv. 2014	
<i>C. olivaceofulvus</i> Kauffman & A.H. Sm. 1933	<i>C. lacorum</i> A.H. Sm. 1934
<i>C. orasericeus</i> Rob. Henry 1983	
<i>C. oulankaënsis</i> Kytöv., Niskanen, Liimat. & H. Lindstr. 2013	
<i>C. pallidostriatus</i> Rob. Henry 1968	
<i>C. paludosaniosus</i> Liimat., Niskanen, Dima & Ammirati 2017	<i>C. saniosus</i> var. <i>paludophilus</i> Carteret & Reumaux 2012
<i>C. panellus</i> Soop 2009	
<i>C. pangloius</i> M.M. Moser 1969	<i>C. ferrugineifolius</i> M.M. Moser 1993; <i>C. paraphaeochrous</i> M.M. Moser 1993; <i>C. subrigidipes</i> M.M. Moser 1993
<i>C. paragaudis</i> Fr. 1838	
<i>C. paralbocyaneus</i> Eyssart. 2002	
<i>C. pardinipes</i> Romagn. 1977	

Table 1 (continued)

Current name	Younger synonyms
<i>C. parhonestus</i> Reumaux 2012	
<i>C. pearsonii</i> P.D. Orton 1958	<i>C. cremeolaniger</i> P.D. Orton 1983; <i>C. lanigeroides</i> P.D. Orton 1983
<i>C. pelargoniostriatulus</i> Bidaud & Fillion 2010	
<i>C. phaeochrous</i> J. Favre 1955	
<i>C. phaeosmus</i> Rob. Henry 1981	
<i>C. pholideus</i> (Lilj.) Fr. 1838	<i>C. pholideoides</i> Bidaud & Reumaux 2005; <i>C. subpenicillatus</i> Carteret & Reumaux 2005; <i>C. subpholideus</i> Rob. Henry 1992
<i>C. piceidisjungendus</i> Kytöv., Liimat., Niskanen & Ammirati 2014	
<i>C. pilatii</i> Svrček 1968	<i>C. altipes</i> Bidaud 2010; <i>C. conocyboides</i> Carteret 2004; <i>C. distinctus</i> Carteret 2012; <i>C. pelargoniobtusus</i> Rob. Henry 1985; <i>C. pseudo-rigidus</i> Bidaud, Carteret & Reumaux 2012; <i>C. udolivascens</i> var. <i>lilacinostipitatus</i> Carteret 2004
<i>C. pinigaudis</i> Niskanen, Kytöv. & Liimat. 2011	
<i>C. pinosquamulosus</i> Kytöv., Niskanen & Liimat. 2020	
<i>C. plumulosus</i> Rob. Henry 1977	
<i>C. politus</i> Niskanen, Liimat. & Ammirati 2013	
<i>C. praepallens</i> Peck 1887	
<i>C. praestigiosus</i> (Fr.) M.M. Moser 1965	<i>C. fulguritans</i> Reumaux 2000; <i>C. magus</i> Moënné-Locc. 2001; <i>C. poirieri</i> Reumaux 1988; <i>C. rufescentipes</i> Bidaud 2001; <i>C. sensibilis</i> Bidaud 2010
<i>C. privignatus</i> Soop 2010	
<i>C. privignipallens</i> Kytöv., Niskanen & Liimat. 2014	
<i>C. psammocola</i> Kytöv., Niskanen & Liimat. 2017	
<i>C. pseudobiformis</i> Bidaud & Carteret 2012	
<i>C. pseudobovinus</i> M.M. Moser & Ammirati 1995	
<i>C. pseudobulbosus</i> Carteret & Reumaux 2010	
<i>C. pseudofallax</i> Carteret 2004	
<i>C. pseudoftabellus</i> Bidaud 2010	
<i>C. pseudofusisporus</i> Bidaud 2010	<i>C. flavoperonatus</i> Bidaud & Reumaux 2012
<i>C. pseudophlegma</i> Rob. Henry 1981	
<i>C. puellaris</i> Brandrud, Bendiksen & Dima 2015	
<i>C. punctatiformis</i> Carteret 2012	
<i>C. quarcticus</i> H. Lindstr. 1994	<i>C. propinquus</i> Eyssart. & Bidaud 2002; <i>C. violaceostriatus</i> Moënné-Locc. & Reumaux 2002
<i>C. quercoconicus</i> Liimat., Kytöv. & Niskanen 2017	
<i>C. radicosissimus</i> Moënné-Locc. 1997	<i>C. speciosior</i> Bidaud, Moënné-Locc. & Reumaux 1997; <i>C. squamulifer</i> Bidaud & Reumaux 1997; <i>C. subhelvolus</i> Moënné-Locc. & Reumaux 1997
<i>C. raphanoides</i> (Pers.) Fr. 1838	
<i>C. repertus</i> A. Favre & Vialard 2004	
<i>C. rigidipes</i> M.M. Moser 1967	
<i>C. roseivelatus</i> Kytöv., Liimat. & Niskanen 2014	
<i>C. roseoarmillatus</i> Niskanen, Kytöv. & Liimat. 2011	
<i>C. roseobasilis</i> Ammirati, Beug, Liimat., Niskanen & O. Ceska 2016	
<i>C. roseobrunneus</i> Carteret 2000	
<i>C. roseocastaneus</i> Niskanen, Liimat. & Kytöv. 2014	
<i>C. roseomyceliosus</i> Bidaud 2009	
<i>C. roseonudipes</i> Rob. Henry & Moënné-Locc. 1997	<i>C. buxiolens</i> Bidaud 1997; <i>C. carcharias</i> Bidaud 1997; <i>C. hinnuleovelatus</i> Reumaux 1997; <i>C. subfilamentosus</i> Reumaux 1997
<i>C. rossicioenochelis</i> Liimat., Kytöv. & Niskanen 2017	
<i>C. rubipes</i> Kauffman 1909	

Table 1 (continued)

Current name	Younger synonyms
<i>C. rubricosus</i> (Fr.) Fr. 1838	<i>C. calcareophilus</i> Bidaud 1997; <i>C. crassogriseascens</i> A. Favre 2009; <i>C. phaeomaculatus</i> Rob. Henry 1989; <i>C. safranopes</i> Rob. Henry 1938; <i>C. safranopes</i> var. <i>bulbosus</i> Rob. Henry 1997; <i>C. safranopes</i> var. <i>laevipes</i> Reumaux 1997
<i>C. rubrocinctus</i> Reumaux 1995	<i>C. uraceoarmillatus</i> Bidaud 2012
<i>C. rubrovioleipes</i> Bendiksen & K. Bendiksen 1991	<i>C. boulderensis</i> var. <i>pallidulus</i> J. Favre 1960
<i>C. rumoribrunsii</i> Bojantchev, Ammirati, Niskanen, & Liimat. 2017	
<i>C. russulaespermus</i> Carteret 2004	<i>C. striatulorufus</i> Moënné-Locc. 2004
<i>C. rusticellus</i> J. Favre 1955	
<i>C. rusticus</i> P. Karst. 1882	<i>C. canabarba</i> M.M. Moser 1966; <i>C. umidicola</i> f. <i>coeruleus</i> M.M. Moser & Ammirati 1995
<i>C. sagacitas</i> Kytöv., Niskanen & Liimat. 2020	
<i>C. sagacito-occidentalis</i> Liimat., Niskanen, Kytöv. & Ammirati 2020	
<i>C. saniosus</i> (Fr.) Fr. 1838	<i>C. bavaricus</i> M.M. Moser 1983; <i>C. luteolateritius</i> (Velen.) G. Garnier 1991; <i>C. rufoanuliferus</i> M.M. Moser & McKnight 1987; <i>C. subaurantiomarginatus</i> Bidaud & Ferville 2012
<i>C. saturninus</i> (Fr.) Fr. 1838	
<i>C. scaurotraganoides</i> Rob. Henry 1986	
<i>C. scotoides</i> J. Favre 1955	<i>C. castaneoruber</i> Bidaud & Reumaux 2012; <i>C. sublucorum</i> Carteret 2012
<i>C. sejunctifolius</i> Rob. Henry 1995	<i>C. raphanicus</i> Bidaud & Moënné-Locc. 2008
<i>C. semiodoratus</i> Rob. Henry 1993	<i>C. griseascens</i> Bidaud, Moënné-Locc. & Reumaux 1997; <i>C. immaculatus</i> Bidaud 1997; <i>C. nauseosmus</i> Bidaud, Moënné-Locc. & Reumaux 1997; <i>C. subulatus</i> Bidaud, Moënné-Locc. & Reumaux 1997; <i>C. solidus</i> Bidaud, Moënné-Locc. & Reumaux 1997
<i>C. semivelatus</i> Rob. Henry 1970	<i>C. sefendens</i> Rob. Henry 1983
<i>C. semivestitus</i> M.M. Moser 1968	<i>C. fusisporus</i> var. <i>olivaceodepressus</i> Reumaux 2010
<i>C. serratissimus</i> M.M. Moser 1968	
<i>C. sociatus</i> Rob. Henry 1983	<i>C. terribilis</i> Reumaux 2002
<i>C. sordescens</i> Rob. Henry 1944	<i>C. sordescens</i> var. <i>vestitissimus</i> Eyssart. 2002; <i>C. strenuipes</i> var. <i>subacuminatus</i> Reumaux 2002
<i>C. sordidemaculatus</i> Rob. Henry 1981	
<i>C. sphagnoravus</i> Liimat., Kytöv., Niskanen & Ammirati 2017	
<i>C. spisnii</i> Consiglio, D. Antonini & M. Antonini 2004	<i>C. badioflammeus</i> Bidaud 2008; <i>C. laceratomarginatus</i> Carteret & Reumaux 2008
<i>C. squalidus</i> A.H. Sm. 1942	
<i>C. stipitemirus</i> Rob. Henry 1995	
<i>C. stuntzii</i> S.A. Rehner & Ammirati 1989	
<i>C. subargyronotus</i> Niskanen, Liimat. & Kytöv. 2014	
<i>C. subbalaustinus</i> Rob. Henry 1991	
<i>C. subbrunneoideus</i> Kytöv., Liimat. & Niskanen 2014	
<i>C. subbulliardoides</i> Rob. Henry 1970	
<i>C. subcagei</i> Niskanen & Liimat. 2017	
<i>C. subcarabus</i> Liimat., Kytöv. & Niskanen 2017	
<i>C. subcarneinatus</i> Niskanen, Kytöv. & Liimat. 2017	
<i>C. subcastaneus</i> Bidaud & Reumaux 2000	<i>C. castaneus</i> var. <i>nigrescens</i> Reumaux 1989; <i>C. tenebrosus</i> Reumaux 2001
<i>C. subcoronatus</i> Bidaud 2001	<i>C. urdaibaiensis</i> Fernández Sas. 2003
<i>C. suberi</i> Soop 1990	<i>C. brunneogriseus</i> Soop 1993
<i>C. subexitiosus</i> Liimat., Niskanen, Kytöv. & Ammirati 2014	
<i>C. subfillionii</i> Kytöv., Niskanen & Liimat. 2017	
<i>C. subglandicolor</i> Niskanen, Liimat. & Kytöv. 2017	

Table 1 (continued)

Current name	Younger synonyms
<i>C. subheterocyclus</i> Liimat., Niskanen & Kytöv. 2017	
<i>C. subionophyllus</i> Niskanen, Liimat. & Kytöv. 2017	
<i>C. submilvinus</i> Bidaud 2010	
<i>C. subminiatopus</i> Kytöv., Niskanen & Liimat. 2017	<i>C. miniatopus</i> var. <i>konradii</i> M.M. Moser 1965
<i>C. subobtusobrunneus</i> Bidaud 2004	
<i>C. subobtusus</i> Kauffman & A.H. Sm. 1933	
<i>C. suboenocheilis</i> Kytöv., Liimat. & Niskanen 2011	
<i>C. subpaleaceus</i> Kytöv., Niskanen & Liimat. 2017	
<i>C. subparvannulatus</i> Moëgne-Loec. & Fillion 2010	
<i>C. subpulchrifolius</i> Kauffman 1918	
<i>C. subrigens</i> Kauffman 1918	
<i>C. subrimosus</i> A.H. Sm. & Hesler 1944	
<i>C. subscotoides</i> Niskanen & Liimat. 2019	
<i>C. subsedens</i> Rob. Henry 1956	<i>C. subcompar</i> Bohus 1979
<i>C. subserraticus</i> Kytöv., Liimat. & Niskanen 2014	
<i>C. substriatus</i> Kauffman 1932	
<i>C. subtabularis</i> Kauffman 1918	<i>C. fumosifolius</i> A.H. Sm. 1942
<i>C. subtilior</i> J. Favre 1955	<i>C. parinsignis</i> Moëgne-Loec. & Carteret 2001; <i>C. percavus</i> J. Favre 1955
<i>C. suillonigrescens</i> Reumaux 2002	<i>C. implexobrunnescens</i> A. Favre 2009
<i>C. tatrensis</i> R. Fellner & Landa 1993	
<i>C. tenebricus</i> J. Favre 1955	
<i>C. tigrinipes</i> Bergeron 1997	
<i>C. tortuosus</i> (Fr.) Fr. 1838	
<i>C. torvoides</i> Rob. Henry 2000	
<i>C. torvus</i> (Fr.) Fr. 1838	<i>C. bidiscendus</i> Rob. Henry 1985; <i>C. subamethysteus</i> Rob. Henry 2000; <i>C. testaceofractus</i> Carteret & Reumaux 2000; <i>C. torvovellatus</i> Reumaux 2000
<i>C. tragano-odorus</i> Niskanen, Liimat. & Ammirati 2020	<i>C. pulchrifolius</i> var. <i>odorifer</i> Hesler 1944
<i>C. traganus</i> (Fr.) Fr. 1838	<i>C. pyriodorus</i> Kauffman 1932; <i>C. traganus</i> f. <i>ochraceus</i> M.M. Moser, Ammirati & M.T. Seidl 1995
<i>C. triangulus</i> Rob. Henry 1983	
<i>C. truckeensis</i> Bojantchev 2013	
<i>C. tuolumnensis</i> Bojantchev 2013	
<i>C. turgidipes</i> Bidaud & Carteret 2008	
<i>C. turgidulus</i> Bidaud 2002	
<i>C. turgidus</i> Fr. 1838	<i>C. albolilascens</i> Rob. Henry 1988; <i>C. cuteclarus</i> Bidaud, Moëgne-Loec. & Reumaux 2008; <i>C. isabellae</i> Rob. Henry 1981; <i>C. ornithopus</i> Rob. Henry 1970; <i>C. productus</i> Chevassut & Rob. Henry 1988; <i>C. subadelphus</i> Rob. Henry 1981
<i>C. ultimionophyllus</i> Kytöv., Niskanen & Liimat. 2017	
<i>C. umbilicatus</i> P. Karst. 1893	<i>C. cacaodiscus</i> Liimat., Niskanen & Kytöv. 2014
<i>C. unbrinobellus</i> Liimat., Niskanen & Kytöv. 2014	
<i>C. unbrinolens</i> P.D. Orton 1980	<i>C. sericeofibrillosus</i> Bidaud & Boutev. 2001
<i>C. unbrinolutescens</i> Reumaux 2004	
<i>C. uraceisporus</i> Niskanen, Kytöv. & Liimat. 2014	
<i>C. uraceomajalis</i> Dima, Liimat., Niskanen & Bojantchev 2014	
<i>C. uraceonemoralis</i> Niskanen, Liimat., Dima, Kytöv., Bojantchev & H. Lindstr. 2014	
<i>C. uraceus</i> Fr. 1838	<i>Hydrocybe praecox</i> Velen. 1939
<i>C. urbicus</i> (Fr.) Fr. 1838	<i>C. alsomatii</i> Rob. Henry 1992

Table 1 (continued)

Current name	Younger synonyms
<i>C. wahkiacus</i> Ammirati, Beug, Liimat. & Niskanen 2016	
<i>C. valgus</i> Fr. 1838	<i>C. depexus</i> var. <i>luminosus</i> Carteret 2005; <i>C. fuliginosus</i> P.D. Orton 1964; <i>C. olivaceostipitatus</i> Carteret 2012; <i>C. orbiculozonarius</i> Rob. Henry 1983; <i>C. rheubarbarinus</i> Rob. Henry 1956
<i>C. venustissimus</i> Bidaud 2002	
<i>C. venustus</i> P. Karst. 1881	<i>C. traganulus</i> P.D. Orton 1983
<i>C. vernalishastensis</i> Bojantchev, Ammirati, Niskanen, & Liimat. 2017	
<i>C. vernalisierraensis</i> Bojantchev, Ammirati, Niskanen, & Liimat. 2017	
<i>C. vernus</i> H. Lindstr. & Melot 1994	<i>C. erythrinus</i> var. <i>russulisporus</i> Bohus 1979
<i>C. vinaceobrunneus</i> Ammirati, Beug, Liimat., Niskanen & O. Ceska 2016	
<i>C. vinaceogrisescens</i> Ammirati, Beug, Liimat. & Niskanen 2016	
<i>C. violaceopapillatus</i> Bidaud 2010	
<i>C. vulpicolor</i> M.M. Moser & McKnight 1987	<i>C. glandicolor</i> var. <i>exilis</i> J. Favre 1955; <i>C. plicatus</i> Bidaud 2010

most common one at least in the Nordic countries. Therefore, we choose to follow the current Nordic concept of the species and propose the collection H. Lindström et al. CFP 432 as the neotype of the species.

Cortinarius armeniacus (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 304 (1838) [1836–1838]

Basionym: *Agaricus armeniacus* Schaeff., Fung. bavar. palat. nasc. (Ratisbonae) 4: 35 (1774): sanctioned in Fr., Syst. mycol. 1: 234 (1821).

= *Cortinarius privignus* (Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 304 (1838) [1836–1838]

Types: Schaeff., Fung. bavar. palat. nasc. (Ratisbonae) 1–2: Tab LXXXI, 1774 (*lectotypus hic designatus*, IF 557455) as *Agaricus armeniacus*). Sweden, Ångermanland; Häggdånger sn, Torrom, in spruce forest with blueberry, 26 Sep 1988, coll. H. Lindström et al. CFP 809, F37506 (S, *epitypus hic designatus*, IF 557456), GenBank No. DQ117925 (ITS).

Illustration. Brandrud et al. (1989: pl. A46).

Descriptions of the species. Brandrud et al. (1989: pl. A46), Niskanen et al. (2012).

Cortinarius bibulus Quélet, Compt. Rend. Assoc. Franç. Avancem. Sci. 9: 666 (1881) [1880]

Types: Quélet, Compt. Rend. Assoc. Franç. Avancem. Sci. 9: 666, Pl. VIII, fig. 7, 1881 (*lectotypus hic designatus*, IF 557457). Finland, Kainuu, Puolanka, Pihlajavaara S., old, mossy, mesic grass-herb spruce forest (*Picea abies*) with some *Betula*, *Pinus sylvestris* and *Populus tremula*, 240–270 m, 15 Sept 2005, coll. K. Liimatainen & T. Niskanen 05-119, H6031525 (H, *epitypus hic designatus*, IF 557458, K, *isoneotypus*), GenBank No. MT934904 (ITS).

Illustration: Brandrud et al. (1992: pl. B25).

Descriptions of the species: Brandrud et al. (1992: pl. B25), Niskanen et al. (2012) as *C. lilacinopusillus* P.D. Orton.

Cortinarius bulliardii (Pers.) Fr. [as ‘bulliardii’], Epicr. syst. mycol. (Upsaliae): 282 (1838) [1836–1838]

Basionym: *Agaricus bulliardii* Pers. [as ‘bulliardii’], Observ. mycol. (Lipsiae) 2: 43 (1800) [1799]: sanctioned in Fr., Syst. mycol. 1: 221 (1821).

= *Cortinarius colus* Fr., Epicr. syst. mycol. (Upsaliae): 308 (1838) [1836–1838]

Types: Bulliard, Herbar de la France: pl. 431 Fig. 3, 1780 (*lectotypus hic designatus*, IF 557459, as *Agaricus araneosus*). Sweden, Västergötland, Österplana sn, Österplana hed, deciduous forest on calcareous soil (*Corylus*, *Quercus*, *Tilia*), 15 Sep 1986, coll. H. Lindström et al. CFP 499, F41127 (S, *epitypus hic designatus*, IF 557460), GenBank No. JX114942 (ITS).

Illustration. Brandrud et al. (1989: pl. A37).

Descriptions of the species. Brandrud et al. (1989: pl. A37), Niskanen et al. (2012).

Cortinarius colus Fr., Epicr. syst. mycol. (Upsaliae): 308 (1838) [1836–1838]

= *Cortinarius bulliardii* (Pers.) Fr., Epicr. syst. mycol. (Upsaliae): 282 (1838) [1836–1838]

Types: Paulet, Traité des Champignons: t. 99 spec. solita majus 1793–1835 (*lectotypus hic designatus*, IF 557461, as *Hypophyllum colus*). Sweden, Västergötland, Österplana sn, Österplana hed, deciduous forest on calcareous soil (*Corylus*, *Quercus*, *Tilia*), 15 Sep 1986, coll. H. Lindström et al. CFP 499, F41127 (S, *epitypus hic designatus*, IF 557462), GenBank No. MT934978 (ITS).

Illustration. Brandrud et al. (1989: pl. A37) as *C. bulliardii*.

Descriptions of the species. Brandrud et al. (1989: pl. A37), Niskanen et al. (2012) as *C. bulliardii*.

Notes—The protologue by Fries (1838) has a reference to Paulet's illustration of *Hypophyllum colus* that is designated as the lectotype of the species. It shows a fungus most similar to *C. bulliardii* although the lamellae are pale and decurrent. Fries (1838) describes the species with a pileus about 2.5–5 cm wide, a stipe about 3 mm wide and growing in *Pinus* forests near Uppsala. The width of the stipe is too narrow for *C. bulliardii*, the species has not been found from Uppsala and is normally associated with *Quercus*, *Fagus* and *Corylus*. Due to these contradictions, Brandrud et al. (1989, 1992) decided to apply the name to another species that occurs in pine forests which has a narrow stipe and a red orange veil, a character emphasized by Fries (1838). However, in this case the species chosen by Brandrud et al. (1989) does not fit with the type illustration or Fries's measurements of the pileus since *C. colus sensu* Brandrud et al. (1989) is a very small and slender species (pileus 0.5–3 cm wide). Our conclusion is that a species that would completely fit to Fries's description and the holotype does not exist. However, since the name has been widely used in the Nordic countries after its publication in Brandrud et al. (1989) it is better to stabilize the name rather than treat it as *nomen dubium*. Here, we choose to follow the type of the species and suggest an epitype for the species that will make *C. bulliardii* and *C. colus* synonyms.

Cortinarius craticius Fr., Epicr. syst. mycol. (Upsaliae): 282 (1838) [1836–1838]

Type: Finland, Satakunta, Ikaalinen, Seitsemien National Park, Multiharju strict protections area, old, mesic spruce forest (*Picea abies*) with some *Pinus sylvestris*, *Betula* and *Populus tremula*, 8 Sep 2005, coll. K. Liimatainen & T. Niskanen 05-069, H6029911 (H, *neotypus hic designatus*, IF 557463; K, *isoneotypus*), GenBank No. MT934988 (ITS).

Illustration. Stockholm's herbarium, S0279; <http://herbarium.nrm.se/specimens/S0279>

Description of the species. Niskanen et al. (2012).

Cortinarius diosmus Kühner, Bull. mens. Soc. linn. Soc. Bot. Lyon 24: 39 (1955)

Type: France, Haute-Savoie, Environs de Samoëns; forêt de Bostan, sentier montant au chalet de Bostan, 6 Sep 1948, coll. R. Kühner 00110647 (G, *lectotypus hic designatus*, IF 557464), GenBank No. MT935017 (ITS).

Descriptions of the species. Niskanen et al. (2012) as *C. argillaceosericeus* ined.

Notes—Kühner (1955) made two collections of *C. diosmus* that are considered syntypes: 00110646 and 00110647 (G). The syntypes represent two different species that have

the following younger names: *C. diosmoides* Rob. Henry and *C. argillaceosericeus* ined. Niskanen et al. (2012). Both species fit the original concept of *C. diosmus*, but we choose the specimen 110647 as the lectotype of *C. diosmus* (syn. *C. argillaceosericeus* ined.) since that represents the more common and more widespread species based on our current data.

Cortinarius flabellus (Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 300 (1838) [1836–1838]

Basionym: *Agaricus flabellus* Fr., Syst. mycol. (Lundae) 1: 231 (1821); sanctioned in Fr., Syst. mycol. 1: 231 (1821).

Type: Sweden, Uppland, Lena sn, S of Salsta slott, in rich coniferous forest on calcareous ground, 23 Sep 1987, coll. H. Lindström et al. CFP 672, F44866 (S, *neotypus hic designatus*, IF 557465), GenBank No. MT935053 (ITS).

Illustration. Brandrud et al. (1998: pl. D35).

Descriptions of the species. Brandrud et al. (1998: pl. D35).

Notes—In Brandrud et al. (1998) three collections of *C. flexipes* var. *flabellus* (Fr.) H. Lindstr. & Melot are presented. They represent two species D35 and D45/D34. The basidiomata in plate D35 fit best to Fries' description of *Agaricus flabellus* that has a dark olive to blackish brown pileus whereas the other species, represented by plates D45 and D34 sometimes has a red brown pileus. Therefore, we propose coll. H. Lindström et al. CFP 672 as the neotype of this species. The name of the other species is *C. lindstroemii* Niskanen, Kytöv. & Liimat.

Cortinarius gentilis (Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 297 (1838) [1836–1838]

Basionym: *Agaricus gentilis* Fr., Syst. mycol. (Lundae) 1: 212 (1821); sanctioned in Fr., Syst. mycol. 1: 212 (1821).

Type: Norway, Oppland, Dokka kn, Vest-Torpa, in spruce forest with blueberry (*Picea*, *Salix*), 15 Sep 1983, coll. H. Lindström et al. CFP 178, F256849 (S, *neotypus hic designatus*, IF 557466), GenBank No. EU266692 (ITS).

Illustration. Brandrud et al. (1992: pl. B31).

Descriptions of the species. Brandrud et al. (1992: pl. B31), Niskanen et al. (2012).

Cortinarius helvelloides (Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 297 (1838) [1836–1838]

Basionym: *Agaricus gentilis e helvelloides* Fr., Syst. mycol. (Lundae) 1:213 (1821).

Type: Finland, Uusimaa, Espoo, Hindsby-Svartböle, under *Alnus incana* and *Alnus glutinosa*, among grasses, 17 Aug 2005, coll. anonymous, T. Niskanen 05-002, H6031432 (H, *neotypus hic designatus*, IF 557467; K, *isoneotypus*), GenBank No. MT935110 (ITS).

Illustration. Brandrud et al. (1989: pl. A17).

Descriptions of the species. Brandrud et al. (1989: pl. A17), Niskanen et al. (2012).

Cortinarius hemitrichus (Pers.) Fr., *Epicr. syst. mycol. (Upsaliae)*: 302 (1838) [1836–1838]

Basionym: *Agaricus hemitrichus* Pers., *Syn. meth. fung. (Göttingen)* 2: 296 (1801): sanctioned in Fr., *Syst. mycol.* 1: 230 (1821).

Type: Sweden, Skåne, Maglehem sn, "Piraten rasten", in birch forest, 21 Sep 1987, coll. H. Lindström et al. CFP 662, F44875 (S, *neotypus hic designatus*, IF 557468), GenBank No. MT935113 (ITS).

Illustration. Brandrud et al. (1989: pl. A31).

Descriptions of the species. Brandrud et al. (1989: pl. A31), Niskanen et al. (2012).

Cortinarius hinnuleus Fr., *Epicr. syst. mycol. (Upsaliae)*: 296 (1838) [1836–1838]

Types: Sowerby, Col. Fig. Engl. Fungi Mushr.1: tab. 173, 1805 (*lectotypus hic designatus*, IF 557469). Sweden, Medelpad, Torp sn, Hussborg, in cultivated grassland under *Betula*, 28 Sep 1985, coll. H. Lindström et al. CFP 332, F37503 (S, *epitypus hic designatus*, IF 557470), GenBank No. DQ117926 (ITS).

Illustration. Brandrud et al. (1989: pl. A19).

Descriptions of the species. Brandrud et al. (1989: pl. A19).

Notes—The name *C. hinnuleus* has been collectively used for several deciduous forest species that have a yellowish brown to reddish brown pileus, distant lamellae with an earthy odour, white universal veil and strongly verrucose, subglobose to obovoidly subglobose spores. They collectively more or less fit to the Fries's protologue (Fries 1838) that describes a species with fulvous cinnamon pileus, distant lamellae and a white veil ring on the stipe that grows early in the season in deciduous forests. The species in the photograph of Brandrud et al. (1989), plate A19, fits Fries's protologue as well as Sowerby's colour plate and therefore we propose it as an epitype of the species.

Cortinarius laniger Fr., *Epicr. syst. mycol. (Upsaliae)*: 292 (1838) [1836–1838]

Type: Finland, Joutsa, Koivuranta, W of Rakkolanselkä, fairly young, mesic to damp, spruce-dominated (*Picea abies*) forest with some *Betula* and *Pinus*, 30 Aug 2005, coll. K. Liimatainen, S. Miettinen & T. Niskanen 05-019, 6029897 (H, *neotypus hic designates*, IF 557471; K, *isoneotypus*), GenBank No. MT935187 (ITS).

Illustrations: Brandrud et al. (1994: pl. C53, mixed collection), Fries (1867–1884: pl. 156)

Descriptions of the species: Brandrud et al. (1994: pl. C53, mixed collection), Niskanen et al. (2012).

Notes — The plate C53 of *C. laniger* in Brandrud et al. (1994) is a mixed collection also including *C. distortus* Kauffman and therefore another specimen is proposed as a neotype here.

Cortinarius melleopallens (Fr.) Britzelm., *Bot. Zbl.* 51(2-3): 38 (1892)

Basionym: *Cortinarius triformis* var. *melleopallens* Fr., *Epicr. syst. mycol. (Upsaliae)*: 299 (1838) [1836–1838].

Type: Sweden, Härjedalen, Storsjö sn, Flatruet, in sub-alpine zone with *Betula*, *Pinus*, *Picea*, 16 Aug 1986, coll. H. Lindström et al. CFP 433, F44880 (S, *neotypus hic designatus*, IF 557472), GenBank No. MT935221 (ITS).

Illustration: Brandrud et al. (1992: pl. B12)

Descriptions of the species: Brandrud et al. (1992), Niskanen et al. (2012).

Notes—Fries' protologue does not perfectly fit to any currently known *Cortinarius* species. Since there is no clear solution, we decide to follow the Nordic concept of this name (Brandrud et al. 1992, Niskanen et al. 2012). For more nomenclatural discussion of this name and the reasoning for the current interpretation see the booklet of Brandrud et al. (1992).

Cortinarius miniatopus J.E. Lange, *Fl. Agaric. Danic.* 5 (Taxon. Consp.): III (1940)

Types: Lange, *Fl. Agaric. Danic.* 5(Taxon. Consp.): III, Plate 103 Fig. B, 1940 (*lectotypus hic designatus*, IF 557473). Finland, Kainuu, Suomussalmi, Näljänkä, Lohivaara, W of Kiviaro, SW side of the forest road, NE sloping spruce forest with fairly rich grass-herb depressions, *Pinus*, *Betula*, *Populus tremula* and *Salix* spp., 230 m, 13 Sep 1997, coll. I. Kytövuori 97-1369, H6041343 (H, *epitypus hic designatus*, IF 557474), GenBank No. MT935228 (ITS).

Notes—This species has recently been called *C. colus* (see also *C. colus* above) in the Nordic literature and listed as a synonym of *C. miniatopus* in Brandrud et al. (1989). However, the concept included two species, one with large spores currently named *C. subminiatopus* Kytöv., Niskanen & Liimat., (photograph Brandrud et al. (1989; A55)) and a sister species with smaller spores (7.0–9.0 x 4.5–5.5 µm, av.= 7.5–8.2 x 5.0–5.2 µm, Q=1.45–1.70, Qav.= 1.52–1.62). The macroscopic description of *C. miniatopus* by Lange (1940) fits both species well but the spore size given is 6.5–7 x 4.3–4.5 µm. Although the spore size in the protologue is even smaller than that of the small-spored species we conclude that the small-spored species fits best to the original description and here propose collection H6041343 as the epitype of the species.

Cortinarius paleaceus Fr., *Epicr. syst. mycol. (Upsaliae)*: 302 (1838) [1836–1838]

current name *Cortinarius hemitrichus* (Pers.) Fr., *Epicr. syst. mycol. (Upsaliae)*: 302 (1838) [1836–1838]

Type: Sweden, Skåne, Maglehem sn, "Piraten rasten", in birch forest, 21 Sep 1987, coll. H. Lindström et al. CFP 662,

F44875 (*S. neotypus hic designatus*, IF 557475), GenBank No. MT935265 (ITS).

Illustrations: Brandrud et al. (1989: pl. A31), Fries (1867–1884: pl. 160)

Descriptions of the species: Brandrud et al. (1989: pl. A31) as *C. hemitrichus*, Niskanen et al. (2012) as *C. hemitrichus*.

Notes—The name *C. paleaceus* has often been applied to *C. flexipes* (Pers.) Fr. coll. However, no odour, which is very typical of species of *C.* sect. *Flexipedes* Kytöv., Niskanen & Liimat., is mentioned in Fries's protologue (Fries 1838) and the lamellae are described as whitish when young. In addition, a plate from Fries (1867–1884) illustrates a species with pale lamellae and context of the stipe, a species that looks like *C. hemitrichus*, and not like *C. flexipes* and relatives that have darker lamellae and stipe context. Based on this we conclude that our current interpretation of *C. hemitrichus* best represents also this species and a neotype making these two names synonyms is suggested. Both names, *C. paleaceus* and *C. hemitrichus*, were described by Fries (1838) in the Epicrisis. Here we choose to continue the use of the name *C. hemitrichus* as the current name of the species to avoid a name change and confusion.

Cortinarius pholideus (Lilj.) Fr., Epicr. syst. mycol. (Upsaliae): 282 (1838) [1836–1838]

Basionym: *Agaricus pholideus* Lilj., Utkast. Sv. Fl., Edn 3: 645 (1816).

Type: Sweden, Ångermanland, Säbrå sn, Näs, in dry coniferous forest with blueberry and lichen (*Betula*, *Picea*), 29 Aug 1987, coll. H. Lindström et al. CFP 602, F248484 (*S. neotypus hic designatus*, IF 557476), GenBank No. MT935303 (ITS).

Illustration: Brandrud et al. (1992: pl. B37).

Descriptions of the species: Brandrud et al. (1992: pl. B37), Niskanen et al. (2012).

Cortinarius praestigiosus (Fr.) M.M. Moser, Schweiz. Z. Pilzk. 43(8): 131 (1965)

Basionym: *Cortinarius paragaudis* var. *praestigiosus* Fr., Hymenomyc. eur. (Upsaliae): 379 (1874)

Type: Finland, Uusimaa, Vantaa, Tammisto, Tammisto Nature Reserve Area, herb-rich mesic to dryish mixed forest (*Quercus*, *Corylus*, *Betula*, *Pinus sylvestris* and *Populus tremula*), 17 Sept 2012, coll. K. Liimatainen & T. Niskanen 12-028, H6083157 (*H. neotypus hic designatus*, IF 557477; *K. isoneotypus*), GenBank No. MT935314 (ITS).

Illustration: Brandrud et al. (2012: pl. E04).

Descriptions of the species: Brandrud et al. (2012: pl. E04), Niskanen et al. (2012).

Cortinarius psammocephalus (Bull.) Fr., Epicr. syst. mycol.: 301 (1838) *nomen dubium*

Basionym: *Agaricus psammocephalus* Bull., Herb. Fr. (Paris) 13: 12, tab. 531, fig. 2 (1793).

Notes—This species was described by Bulliard (1793) and the only original material is the painted figure that has been chosen as a lectotype of the species in Brandrud et al. (1998). The plate illustrates a rather slender, brown species with a wide, convex to low convex, sometimes low umbonate, scaly pileus, and a scaly stipe, the lamellae are brown. However, it is not obvious that *Agaricus psammocephalus* would be a *Cortinarius*. The illustrated basidiomata are also reminiscent of species in the genus *Inocybe* and the clustered growing habit reminds one of a saprotrophic fungus. The epithet *psammocephalus* was combined in the genus *Cortinarius* by Fries (1838), who interpreted it as a species growing in coniferous forests. Because Bulliard worked in the Paris region, already Brandrud et al. (1998) concluded, that Fries's species most likely is different from Bulliard's species that supposedly was growing in a deciduous forest. Currently, the name is applied to a species pair *C. castaneopallidus* Carteret/*C. quercoconicus* Liimat., Kytöv. & Niskanen that usually have a much narrower, acutely umbonate pileus (Bidaud et al. 2004, plate 481; Brandrud et al. 1998, plate D57).

Taking into consideration that i) the basidiomata illustrated in the Bulliard's plate do not fit the species for which the name has currently been used, ii) the plate may represent a species from another genus, and iii) we have not found another candidate for the name from the genus *Cortinarius*, we refrain to use the name for a species in genus *Cortinarius* and treat it as a *nomen dubium*.

Cortinarius torvus (Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 293 (1838) [1836–1838]

Basionym: *Agaricus torvus* Fr., Observ. mycol. (Havniae) 2: 80 (1818): sanctioned in Fr., Syst. mycol. 1: 211 (1821).

Types: Bulliard, Herb. Fr. (Paris) 2: Tab. 96, pl. 600, 1782 [1781–82] (*lectotypus hic designatus*, IF 557478, as *Agaricus araneosus*). Sweden, Skåne, Degeberga sn, Forsakar, in beech forest on calcareous ground, 17 Sep 1988, coll. H. Lindström et al. CFP 778, F248482 (*S. epitypus hic designatus*, IF 557479), GenBank No. MT935556 (ITS).

Illustration: Brandrud et al. (1992: pl. B13).

Descriptions of the species: Brandrud et al. (1992: pl. B13), Niskanen et al. (2012).

Cortinarius traganus (Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 281 (1838) [1836–1838]

Basionym: *Agaricus traganus* Fr., Observ. mycol. (Havniae) 2: 82 (1818): sanctioned in Fr., Syst. mycol. 1: 217 (1821).

Types: Schaeff., Fung. bavar. palat. nasc. (Ratisbonae) 1–2: Tab 56, Fig. I–V, 1774 (*lectotypus hic designatus*, IF 557480), as *Agaricus amethystinus*). Sweden,

Ångermanland, Härnösand, Härnön at Myran, in dry sandy pine forest, 13 Sep 1988, H. Lindström et al. CFP763, F248486 (*S. epitypus hic designatus*, IF 557481), GenBank No. MT935361 (ITS).

Illustration. Brandrud et al. (1994: pl. C04).

Descriptions of the species. Brandrud et al. (1994: pl. C04), Niskanen et al. (2012).

Notes—The protologue by Fries (1818) is very short but mentions the main characteristics of the species currently considered as *C. traganus* (Brandrud et al. 1994; Niskanen et al. 2012): Basidiomata with a smell. Pileus pale lilac, stipe whitish purplish and bulbous, context yellow. Fries (1818) also refers to an illustration of Schaeffer (1774) that then becomes the type of the species. A majority of the figures in the illustration represent our interpretation of *C. traganus* (Fig. I–V), but Fig. VII clearly shows a typical characteristic of *C. cyanites* Fr.: the context of the stipe and pileipellis have become vinaceous red on exposure. In Fig. IX the spores are round which does not fit either of the above species, a potential species could be found from *C. sect. Anomali* where species with round spores and bluish colours occur. It seems that the type of *C. traganus* is a mixed illustration, but since the majority of the figures and the protologue fit the current concept of *C. traganus*, we here choose an epitype to support this interpretation.

Cortinarius turgidus Fr., Epicr. syst. mycol. (Upsaliae): 278 (1838) [1836–1838]

Types: Battarra, Fungorum agri Arimensis historia: tab. 9 fig. C, 1755 (*lectotypus hic designatus*, IF 557482; as *Monomyces ventricosus*). Sweden, Bohuslän, Sotenäs, Tossene, E of Bovallstrand, Hogsäms bokskog, *Fagus* forest with some *Betula* and *Populus*, seashells on ground, 29 Sep 2004, coll. K. Liimatainen & T. Niskanen 04-1020, H7017832 (H, *epitypus hic designatus*, F 557483; K, *isoepitypus*), GenBank No. MT935565 (ITS).

Illustration: Brandrud et al. (1992: pl. B58).

Descriptions of the species: Brandrud et al. (1992: pl. B58), Niskanen et al. (2012).

New combinations

Cortinarius colorius (Bidaud) Niskanen, Dima & Liimat. *comb. nov.*

IF 557484

Basionym: *Cortinarius ignifluus* var. *colorius* Bidaud, in Bidaud et al., Atlas des Cortinaires (Meyzieu) 6: 190 (1994)

Cortinarius iners (Bidaud) Liimat., Dima & Niskanen *comb. nov.*

IF 557485

Basionym: *Cortinarius duracinus* f. *iners* Bidaud, in Bidaud et al., Atlas des Cortinaires (Meyzieu) 17(1): 1176 (2008)

Discussion

Studies of type specimens

There are two ways for naming a barcode in a sequence database: either sequence a named voucher specimen based on a morphological identification or sequence a type specimen. Paradoxically, the first approach is currently the most widely used although the core reason for using the DNA-based identification is the unreliability of the morphological identification. The gold standard should be sequencing the type specimens to achieve an unambiguous, good quality identification database, but this unfortunately has thus far been generally neglected.

To improve the sequence-based identification of the important ectomycorrhizal genus *Cortinarius* and create a solid base for future taxonomic work 482 type specimens were sequenced. This is more than twice as many as the largest type study of *Cortinarius* so far (Liimatainen et al. 2014). We were able to successfully sequence many old type specimens; 105 types which were over 50 years old and 18 over 100 years old. This shows that most available *Cortinarius* type specimens can likely be sequenced regardless of the age of the specimen. The dataset, including the already published type sequences in this group, contains a total of 363 species. About half of these species' names, altogether 184, are published now for the first time in GenBank, thus doubling the reliability of barcoded species of *Cortinarius*, subgen. *Telamonia* in the public sequence databases. Also 33% of the species represented here have been described over the last decade using DNA sequences alongside morphology and ecological data. Adding DNA tools for fungal taxonomy has accelerated the process of discovering and describing fungus diversity.

Synonyms

Our dataset shows that many species have been described several times. Of the 363 species recognized in this study 31% have a synonym, the synonym rate is even higher with species described using only morphological characters (46%). The two main reasons for synonyms are that the interpretation of the existing names has been challenging and there have been problems based on the morphological species concept. The high number of species, convergent evolution and the small number of useful morphological characters for classification have not made the task any easier. Also, the lack of uniform and stable

infrageneric classification has made it more difficult to find potential, already existing descriptions of the species and thus many species have been subsequently named as new again. In the future, the problem of synonyms will be much reduced when sequences from type specimens are available and the description of new species without ITS barcodes are strongly discouraged.

One example of the difficulty of interpret existing names is *C. impolitus* Kauffman. It was the species described the most times by multiple authors over decades, e.g. by Kauffman (1918) and Smith (1944) from North America and by Velenovský (1939), Pearson (1946), Favre (1955) and Lindström (Brandrud et al. 1998) from Europe (Table 1 and Figure 1). The species is small and brown which partly explains the problem but it also has two good characters, odour of *Pelargonium* in the lamellae and narrow basidiospores, but despite these characteristics it has been very challenging to recognize it from the works of different mycologists based on morphology only.

Examples of the second problem, the challenges of using the morphological species concept, are *C. macropodius* Rob. Henry and *C. luridus* Rob. Henry that overall had the highest number of synonyms, 13 and 9 respectively. In this case, all synonyms come from the French authors and are due to a too narrow species concept. Some of the synonyms are also placed in different infrageneric groups in their classification system. This error rate and unnatural classification make it very difficult to use the earlier parts of the Atlas des Cortinaires series for identification of *Cortinarius*. However, the individual descriptions of the species are usually of good quality and 61 species names that have been described by the team are the oldest names for the species: representing about 15 % of all the currently known species of *C.* subgenus *Telamonia*. In recent years they have also included molecular data into their work which has greatly improved the outcome (e.g. Bidaud et al. 2017).

When looking at the rate at which the different authors described synonyms it is self-evident that it was easier to describe new species earlier when more species were undescribed. For example, the error rate of Kauffman is only 7% whereas Smith's error is double that, most likely because he was partly describing the species from the same area where Peck and Kauffman had previously worked. Half of the Smith's synonyms are Kauffman's species. The error rate of Moser and Henry are rather similar, which is a bit surprising since they mainly worked in different habitats and with a different species concept.

Interpretation and typification of the early names without type materials

Many early names without type specimens have been re-described by later authors. From all the old names used in this study only 10 of them are without synonyms: *C. armillatus* (Fr.) Fr., *C. bibulus*, *C. bovinus* Fr., *C. cinnabarinus* Fr., *C. colymbadinus* Fr., *C. dolabratus* Fr., *C. evernius* (Fr.) Fr., *C. gentilis*, *C. glandicolor* (Fr.) Fr., and *C. helvelloides*. About half of them are rather characteristic and easy to interpret so taxonomists after Fries understood his concept and therefore did not describe those species again, i.e. *C. armillatus* and *C. evernius*. On the other hand, some of these species are really difficult to interpret and might not have been described again just because of the restricted distribution, infrequent occurrence or just a matter of chance, i.e. *C. bovinus* and *C. dolabratus*.

Interpreting the early names, like those of Fries and Persoon, when often no physical specimen is left to study and the descriptions themselves are short, vague and without microscopical characters, is extremely difficult. In many cases their species concept most likely included several species and was too generalized. They surely did their best but the state of knowledge in those times was far from what we know now. For example, *C. paragaudis* and *C. praestigiosus*, two species which based on current, widely accepted concept are far from each other both phylogenetically and morphologically, were included as varieties of one species in Fries' concept (Fries 1874). In *Cortinarius* sect. *Bovini* only one species was described by Fries although the section includes at least seven species in Sweden (Niskanen et al. 2013). Of course, Fries might not have found all those species in the areas he collected or did not have time to work with them, but it is still rather certain that many Fries' names included several species. Thus, due to the broad species concept there often is not any correct one candidate for epi- or neotypification. And even if there has been a clear concept behind the early species descriptions, it is often very difficult to interpret based on short and vague descriptions.

The interpretation of a name based only on morphology is a demanding, often impossible, task. In this study ca. 80% of the species described by Fries have been described again. The poor record can not be explained by a few poor studies or unprofessional authors—all major *Telamonia* authors have misinterpreted Fries' names or simply overlooked them. Studying the type specimens of Karsten's species gave a similar result. Karsten's descriptions are somewhat better than Fries' since they also include microscopical characteristics, but the critical difference is that Karsten's specimens are available and can be sequenced, thus we really can confirm the true identity of his species. The result was that all the seven *Telamonia* species described by Karsten, which we studied, have been re-described later by other authors

confirming the conclusion from Fries' materials. No current data supports the claim that the early names could be interpreted correctly and consistently by anyone.

Because of the problems mentioned above the interpretation of early names in general is not a very meaningful thing to do and often the outcome is highly questionable. The majority of early names should probably be treated as *nomen dubium*. Therefore, we only typified those early names that have been widely used, e.g. appear on many national check lists or are commonly used in books like *Funga Nordica* (Niskanen et al. 2012). In these cases, the typification is a quicker and a more efficient way to stabilize nomenclature than trying to convince users to stop using the name. Also, it is important to point out that when typifying early names, we do not claim that the outcome would be correct, i.e. would represent the original concept of the author. We simply try to find the species that would best fit to the original description and in the case of several equally suitable candidates choose the most practical solution, i.e. the one that causes fewest changes in the current use of the name, the species itself would be the most common and wide spread of the candidate species and/or the easiest to recognize.

Another problem with the old names is the references to the illustrations. At those early times authors did not know that the references would later turn out to be the most important part of the descriptions—based on the current International Code of Nomenclature for algae, fungi, and plants (<https://www.iapt-taxon.org/nomen/main.php>), they are considered as 'original material' of the species. At the time there was not a huge amount of published illustrations to choose from. It seems that in some cases Fries referred to an illustration that did not fit perfectly to his concept of the species but was the closest one with some similarity. This is e.g. obvious with *C. colus* and *C. turgidus*.

Nomenclatural coverage of the dataset and conclusions

In this study we tried to sequence all species level type specimens belonging to *Cortinarius* subgen. *Telamonia* that have not been previously studied. Our aim also was to stabilize all commonly used early names for which a type specimen does not exist. Obviously, all names in *Telamonia* are not in this dataset. Some type specimens could not be sequenced, especially Hongo's and Murrill's types failed almost without exception. Also, Henry's material was difficult to sequence and in addition, many of his type specimens were not found, the names are nomenclaturally invalid, or had other problems. Most of the Peck's material could not be acquired from NYS during the time of the molecular study of this paper. Some of Favre's type specimens were too small to sample or have already been sequenced but not published by other authors. Melot's type specimens are in his personal

collection and despite several attempts to acquire them on loan, they were not available for molecular study. Unless this situation changes the identity of the names remains unclear and it would be better not to use them to avoid confusion arising from the different interpretations of the names. There are a few authors whose materials we have not studied, e.g. Bon and Lamoure, but the number of *Telamonia* species they described is relatively small, only some tens of species.

After this study there will only be a few dozen valid names that have not yet been studied with molecular methods and where the type specimens are good quality for sequencing and available for study. Most likely many of them have an earlier name which already have been studied. There are a few exceptions, however, for example if one is working with the sub-alpine *Telamonia* species the names described by Favre (e.g. 1955) and Lamoure (1977, 1978) are relevant, for Eastern North America species described by C. H. Peck's should be checked (Burnham 1919; Gilbertson 1962), and for European Mediterranean areas the works of local authors would be appropriate to study (e.g. Mahiques and Ortega 2002). Otherwise, if a new sequence does not have $\geq 99\%$ similarity to any published type sequence it can be rather certain that it derived from an undescribed species, given that the quality of the sequence is good.

Overall, our data set contains about 300 species from Europe and 150 species from North America and many of which they have in common. There may only be a few hundred more *Telamonia* species to be found from Europe, but certainly in North America the quest has just begun. The situation in Africa, Asia and Central and South America is practically unknown, but it would not be an exaggeration to predict that the world-wide diversity of *Cortinarius* subgen. *Telamonia* would be a four-digit number. Thus far, members of the subgenus have not been found in the *Nothofagus* forests of New Zealand (Soop et al. 2019) and from *Nothofagus* forests of South America only one species is confirmed (Garnica et al. 2005).

As species are discovered and named the easier the identification based on ITS will become. Unfortunately, the same does not apply to morphological identification. All the current keys we use would require extensive rewriting and even though there often are morphological and/or ecological differences between the species, identifying many of the species of *Telamonia* using keys without deeper experience and knowledge of the group will be challenging if not impossible. Having local keys (i.e. Scandinavian boreal *Telamonias* or *Telamonias* of the Pacific North West) and in certain cases only trying to identify sections or species complexes rather than species would be the most realistic approach when using morphological identification.

Many times, the biggest obstacle for efficient identification and naming of alpha diversity are the nomenclatural problems, i.e. what is the correct name for the species or is

it an undescribed one? The species of *C.* subgenus *Telamonia* have been considered one of the most challenging cases in the Agaricales at the species level. Its high diversity combined with convergent, similar appearing taxa have earned it a reputation of being an impossible group to study, one better left in the forest. Our study shows that nomenclatorial problems, even in difficult groups like *Telamonia*, can be solved and identification based on ITS barcodes becomes an easy task even for non-experts.

Infrasubgeneric classification

Relationships of the sections within *Cortinarius* subgen. *Telamonia*

The relationships of the sections within *Telamonia* remain unclear in our phylogenetic analysis. The grouping of the sections in the tree, however, does not seem random and makes sense when compared to the morphological characteristics. Therefore, the main findings that we feel would be of importance are summarized below and could be used as starting hypotheses for future studies.

Based on our phylogenetic analysis *C.* subgen. *Telamonia* is roughly divided into two main entities (Fig. 2): (i) The basal groups of the tree (“Basal Telamonias”) that only contain species with medium- to large-sized basidiomata (the apex of the stipe is > 4 mm wide) with the exception of a few species in *C.* sect. *Brunnei*. (ii) The monophyletic upper part of the tree (“Crown Telamonias”) that mainly contains species with small basidiomata (the apex of the stipe is < 4 mm wide), and the following sections including species with mainly small- to medium-, less commonly large-sized basidiomata: *Hinnulei* Melot, *Rubricosi* Moënné-Loec. & Reumaux *Leiocastanei* Niskanen, Kytöv. & Liimat., and the monotypic sections *Pseudoduracini* Liimat., Niskanen & Kytöv., *Friesiorum* Liimat., Kytöv. & Niskanen, and *Vinaceobrunnei* Ammirati, Niskanen & Liimat.. The most basal part of this clade also includes sections *Anthracini* Melot, *Crassispori* Kytöv., Niskanen & Liimat. and *Squalidi* Liimat., Ammirati & Niskanen.

Within the “Crown Telamonias” some further grouping can be observed. Brandrud et al. (1989) initially classified the species with small basidiomata into two sections, *Incrustati* Melot and *Hydrocybe* (Fr. ex Rabenh.) P. Karst. Although not forming well supported clades, these two earlier groups seem to correlate with the phylogeny to some extent. In the Fig. 2 the groups are named as /Squamicybe (*Incrustati* s. Brandrud et al.) and /Erubescetes (*Hydrocybe* s. Brandrud et al.). The new names are introduced because the type species of sect. *Hydrocybe*, *Cortinarius duracinus*,

does not belong to “Crown Telamonias” but to “Basal Telamonias” and the type species of sect. *Incrustati*, *C. luxnymphae*, was not available for study and thus the identity of the species remains unclear.

The previous members of the *C.* sect. *Incrustati* are all placed in/Squamicybe (Fig. 2) in two monophyletic groups/Eusquamicybe and/Paludosi but the group also includes sections of species with medium- to large-sized basidiomata. Many species of this group have a \pm scaly pileus, a universal veil that forms distinct girdles on the stipe and a stipe/context of the stipe that becomes darker towards the base, especially with age. No part of the basidiomata turns reddish (except in *C.* sect. *Rubrocincti* that resembles more the species in /Erubescetes). Typical examples of this group are *C. flexipes* (*C.* sect. *Flexipedes*), *C. hemitrichus* (*C.* sect. *Paleacei*) and *C. saniosus* (Fr.) Fr. (*C.* sect. *Saniosi* Moënné-Loec. & Reumaux) and from the larger species *C. hinnuleus* (*C.* sect. *Hinnulei*) and *C. rubricosus* (Fr.) Fr. (syn. *C. safranopes* Rob. Henry, *C.* sect. *Rubricosi*). Species associated with *Alnus*, i.e. *C. bibulus* (*C.* sect. *Bibuli*), *C. griseocarneus* Carteret (*C. alnetorum* (Velen.) M.M. Moser sensu Brandrud et al. 1989, *C.* sect. *Alnicolarum*) and *C. helvelloides* (*C.* sect. *Helvelloides*), also belong to this larger group. Together with *C.* sect. *Saniosi* they form a monophyletic group /Paludosi, although without support, indicating that within *C.* subgen. *Telamonia* the ability to form mycorrhizae with *Alnus* may only have evolved once.

A majority of the species classified earlier in *C.* sect. *Hydrocybe* are placed in another, monophyletic, group /Erubescetes (Fig 2). They all have small basidiomata and a smooth pileus and in most species the stipe/context of the stipe does not become darker towards the base. In addition, in quite a few species either the base of the stipe, universal veil and/or basal mycelium turns \pm reddish with time. The universal veil varies from indistinct to forming distinct girdles on the stipe. Typical examples of this group are *C. fuscoalbus* Kytöv., Niskanen & Liimat. (*C.* sect. *Atroalbi* Niskanen, Kytöv. & Liimat.), *C. decipiens* (Pers.) Fr. (*C.* sect. *Castanei* Moënné-Loec. & Reumaux), *C. praestigiosus* (*C.* sect. *Praestigiosi* Kytöv., Niskanen & Liimat.) and *C. vernus* H. Lindstr. & Melot (*C.* sect. *Verni* Kytöv., Niskanen & Liimat.).

Sections

The aim of this study was not to solve the infrasubgeneric classification of *C.* subgen. *Telamonia* but to show the preliminary placement of the studied species and existing sections (Figs. 1 and 2). Examples of the species belonging to the sections are shown in Supplementary Fig. 1–11. We included representative photographs for all but the following

three sections: *C. sect. Cacaodisci* Kytöv., Niskanen & Liimat., *C. sect. Pseudoduracini*, and *C. sect. Squalidi*. In this study, 80 previously described sections and 9 subsections are used, and additional 11 section names are considered synonyms. A small number of species are not currently placed in any of the sections. The “Basal *Telamonias*” with medium- to large-sized basidiomata have been easier to study and are thus better known and only four species, *C. hepaticus* Kytöv., Niskanen & Liimat., *C. hillieri* Rob. Henry, *C. uraceisporus* Niskanen, Kytöv. & Liimat. and one *C. sp.*, remain outside the currently accepted sections. In the “Crown *Telamonias*”, that have been more overlooked mainly due to their small size, 18 species included in our phylogenetic analysis remain unclassified. Some of them, like *C. denigratus* Ammirati, Beug, Niskanen, Liimat. & O. Ceska and the related *C. spp* from North America that form a monophyletic group and differ > 4% (> 20 indels and substitutions) from other species of *Cortinarius* subgen. *Telamonia*, might be considered as a new section in the future. Some may be grouped with existing sections with further analysis using additional DNA regions, i.e. *C. ferrugineovelatus* Kytöv. Liimat. & Niskanen and *C. umbrinobellus* Liimat., Niskanen & Kytöv. that share morphological characteristics with the species in *C. sect. Praestigiosi* but were currently placed in a basal position of the branch containing that section.

We wanted the section names to be as unambiguous as the species names as far as possible and therefore we only accepted section names that can be interpreted without a doubt, i.e. the type specimen of the type species of a section is sequenced. Exceptions were made with four names: sect. *Anthracini* Melot, sect. *Brunneotincti* M.M. Moser, sect. *Cinnabarini* Melot, and sect. *Parvuli* Melot. For these sections we have not been able to study the type specimen of the type species for several reasons or the sequencing failed but we believe that the concept of the type species is rather uniform and clear (e.g. Niskanen et al. 2012). Therefore, it seems acceptable to use these common section names. We are aware that this kind of approach is risky as the case of sect. *Testaceofolii* Liimat., Niskanen & Kytöv. shows. At the time, it was clear that *C. biformis* Fr. sensu *Funga Nordica* (e.g. Niskanen et al. 2012) was a different species than *C. testaceofolius* H. Lindstr. & Soop. However, later it turned out that the neotype Moser had selected for *C. biformis* was in fact an older synonym for *C. testaceofolius*, an outcome that no one had previously thought possible. Therefore, sect. *Biformes* Moëne-Loec. & Reumaux and sect. *Testaceofolii* are now synonyms.

If the species concept is often difficult to apply, then classification above species becomes even more subjective. In general, we should try to avoid having too many monotypic entities since they are less meaningful in classification.

However, the risk with bigger entities is having units which would have very little, if any, exclusive morphological characters that would define those groups, since one of the main reasons of having a higher-level classification is to recognize groups with unique character states. For example, *C. armillatus*, *C. sect. Armillati*, *C. subgen. Telamonia*, genus *Cortinarius* represent four levels of classification in which the species *C. armillatus* belongs to all four groups that have their own, unique defining characters that other groups in higher or lower levels do not have.

In this study, one example of the difficulties of delimiting a section is *C. sect. Uracei*. With a wider concept it includes several previously recognized sections, *C. sect. Cinnabarini*, *C. sect. Colymbadini*, and *C. sect. Miniatopodes* Moëne-Loec. & Reumaux, that all form a monophyletic clade with good support value and morphological differences from *C. sect. Uracei* s. str. Therefore, keeping all above-mentioned sections separate would be an arguable choice, but then there would be at least more than four monotypic sections inside the clade *Uracei* that would need a new name. In this case we have currently delimited *C. sect. Uracei* in a broad sense because the group is also supported by morphological characters. The other existing sections are treated at the subsection level.

We have tried to delimit the sections to be the widest monophyletic group with a reasonable support value and with at least some shared morphological character states. This approach and level of grouping mainly corresponds to the concepts previously used to delimit the sections in the genus *Cortinarius* in the era of molecular data (e.g. Ammirati et al. 2013, 2017; Dima et al. 2014; Liimatainen et al. 2015, 2017, 2020; Niskanen et al. 2009, 2011, 2013; San Fabian et al. 2018; Soop et al. 2019).

The sections identified here vary from monotypic entities i.e. *C. sect. Brunneocalcarii* Niskanen, Liimat. & Kytöv. to middle-sized groups i.e. *C. sect. Armillati* and *C. sect. Disjungendi* to very diverse groups i.e. *C. sect. Bovini* and *C. sect. Uracei*. The imbalance is unlikely to be solved due to the speciation history of different groups, likely some of them have diversified more than the others which has led to the current species-poor and species-rich groups. Also, this dataset only contains a fraction of the true diversity of *C. subgen. Telamonia* worldwide and therefore the number and the species diversity of sections will change when more data are available. Most of the monotypic sections will most likely turn out to be multi-species sections as shown e.g. by Soop et al. (2019).

This is the first extensive phylogenetic study of *C. subgen. Telamonia*. The great majority of sections and species are shown in a phylogenetic context for the first time. Also, many sections previously included in phylogenetic studies

now contain more species and therefore seem to have better support values. For example, Harrower et al. (2011) used the same two DNA regions, ITS and LSU, in their study and got less than BS 50% support for *C. sect. Firmiores* (Fr.) Hennings when including three species in their analysis. In our study that contains 20 species the support value for the same section was BS 88%. For *C. sect. Armillati* the corresponding values were BS 54% (2 species) and 90% (7 species).

Conclusions

Fig. 1 shows our current view of the number of the sections in *Cortinarius* subgen. *Telamonia* and which species we include in them. The earlier delimitations based on morphology have been partly incorrect and included only a part, often a small fraction, of the species (Bidaud et al. 2017; Brandrud et al. 2012; Niskanen et al. 2012). The classification presented here is a major step forward and can be used as a basis for a more thorough revision of morphological characteristics of the groups in the future.

Now that the nomenclatorial history of the last 100 years has been sorted out for many taxa, everyone can benefit from the outcome and continue to improve the understanding of this diverse group of species. Fortunately, all current *Cortinarius* taxonomists produce an ITS barcode of the type specimen of new species and upload and annotate the new sequence in GenBank. We hope that mycologists working on *Cortinarius* and other genera will build on the findings reported here.

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