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

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...
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 Fröselv 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., *Balauastini* Moënne-Locc. & Reumaux, *Camphorati* Liimat., Niskanen & Ammirati, *Fulvescentes* Melot, *Illumini* Liimat., Niskanen & Kytöv., *Obtusi* Melot, *Renidentes* Moënne-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* Moënne-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. confirma tus* 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, Moënne-Loccoz, Murril, Nespiak, Orton, Pearson, Peck, Ramm, Reumaux, Sasia, Seidl, Smith, Schwöbel, Soop, Srůček, Velenovsky, 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 synonyms.

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 1x 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 GTR+GAMMA 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.

C. diasimospermus CFP657 Sweden
C. udolivascens var. lilacinostipitatus 2001-112 TYPE France
C. conocyboïdes 99102504 TYPE France
C. altipes 01-10-134 TYPE France
C. distinctus 2004-165 TYPE France
C. pillati 655887 TYPE Czech
C. pelargoniobtusus RH70579 TYPE France
C. rusticellus 13512 TYPE Switzerland
C. rusticellus 6029429 Finland
C. fragrantissimus 10MWB111913 TYPE USA, WA
C. fragrantissimus QG159881 Canada, BC
C. subparvannulatus 1728 TYPE France
C. subparvannulatus UDB002161 Sweden
C. plicatus 91-08-51 TYPE France
C. vulpicolor 83/355 TYPE USA, MT
C. glandicolor var. exilis 13282 TYPE Switz.
C. subdepressus 4705 TYPE France
C. difficillum 97.12.28.08 TYPE France
C. goniosporus 2001-138 TYPE France
C. ammophilus 109694 TYPE UK
C. desertorum 154750 TYPE France
C. micmus 2003-57 TYPE France
C. frisiansus 97112425 TYPE France
C. pertris 13308 TYPE Switzerland
C. impolitus 10366 TYPE USA, MI
C. violiiamelatus CFP1304 Sweden
C. aff. cucumisporus IK01-046 Sweden
C. umbrinolutescens 2858 TYPE France
C. umbrinolutescens JQ347072 China
C. pelargoniostriatus 07-08-42 TYPE France
C. pelargoniostriatus TN09-080 USA, WA
C. sp. GQ159914 Canada, BC
C. fagetorum GQ159777 Canada, BC
C. fagetorum MM1948-0743 TYPE Austria
C. fagetorum TN07-179 Canada, ON
C. violaceopapillatus 06-10-196 TYPE France
C. violaceopapillatus IK11-020 Norway
C. subcarcharias 03-11-74 TYPE France
C. geraniolens 95-09-88 TYPE France
C. fufuraceus 1240 TYPE France
C. fuscoruber 909 TYPE France
C. gurdus 2006-170 TYPE France
C. flabellus CFP672 TYPE Sweden
C. flabellus f. iners 00-09-81 TYPE France
C. pseudodepressus 2009-73 TYPE France
C. fufuraceus AY669678
C. flexipes var. flabellus CFP690 Sweden
C. lindstromii CFP626 TYPE Sweden
C. flabellus f. biolens 01-09-121 TYPE France
C. lindstromii FJ039709 Canada, BC
C. pseudoflabellus 96-08-16 TYPE France
C. pseudoflabellus 6001842 Finland
C. paleifer 655884/a TYPE Czech
C. flexipes CFP802 TYPE Sweden
C. paleifer 655884/b TYPE Czech
C. flexipes KC842395 Norway

sect. Flexipedes
Fig. 1 (continued)
Fig. 1 (continued)
Fig. 1 (continued)
Fig. 1 (continued)

sect. Verni

sect. Nucilocores

sect. Caliginosis

sect. Megaspori

sect. Atroalbi
Fig. 1 (continued)
| Species                  | Type Location          | Synonyms |
|-------------------------|------------------------|----------|
| C. subumidicola         | TYPE France            |          |
| C. pseudoprivignus      | RH2883 TYPE France     |          |
| C. triformis f. strenuus| TYPE France            |          |
| C. turgidoides          | 431 TYPE France        |          |
| C. bucknallii          | RH71385 TYPE France    |          |
| C. renidentoides        | 71560 TYPE France      |          |
| C. hydrotelamonioides   | RH3372 TYPE France     |          |
| C. castanearum          | 71309 TYPE France      |          |
| C. subcompar           | 96933 TYPE Hungary     |          |
| C. subsedens           | RH324 TYPE France      |          |
| C. compressus           | 10338 TYPE USA, TN     |          |
| C. kauffmanianus        | TN09-085 USA, WA       |          |
| C. biformis             | CFP665 Sweden          |          |
| C. biformis             | CFP614 Sweden          |          |
| C. kauffmanianus        | 10369 TYPE USA, MI     |          |
| C. kauffmanianus        | AY669688               |          |
| C. melitosarx           | F12652 TYPE Sweden     |          |
| C. circumins            | RH908 TYPE France      |          |
| C. millaresensis        | KU953933 TYPE Spain    |          |
| C. submilvinus          | 000861 TYPE France     |          |
| C. substriatus s. lato  | GQ159851 Canada, BC    |          |
| C. substriatus s. lato  | TN07-362 USA, WA       |          |
| C. violaceostriatus     | 1130 TYPE France       |          |
| C. propinquus           | 5404 TYPE France       |          |
| C. quarciticus          | CFP765 TYPE Sweden     |          |
| C. substriatus          | TN07-426 USA, WA       |          |
| C. substriatus          | 10427 TYPE USA          |          |
| C. pseudobiformis       | 00-09-67 TYPE France   |          |
| C. pseudophlegma        | RH70487 TYPE France    |          |
| C. mixtus var. foetulentus| 0093368 TYPE France    |          |
| C. fusciolakenscens     | PC977 TYPE France      |          |
| C. mystagogi            | 98102404 TYPE France   |          |
| C. mixtus              | 925 TYPE France        |          |
| C. fusciolakenscens     | G977 TYPE France       |          |
| C. albiovioleatus       | CFP432 TYPE Sweden     |          |
| C. grisioviolaceus      | 17228 TYPE USA, WA     |          |
| C. albiovioleatus       | AF325597               |          |
| C. obliquus             | TN14-137 USA, FL       |          |
| C. obliquus             | TYPE USA, NY           |          |
| C. geophilus var. subauroreus| 4532 TYPE France     |          |
| C. acutispissipes       | 2002-21 France         |          |
| C. acutispissipes       | 1610 TYPE France       |          |
| C. acutispissipes       | AY669657               |          |
| C. paralbicyaneus       | UDB011349 Estonia      |          |
| C. paralbicyaneus       | TN10-136 Canada, QC    |          |
| C. caesioarmeniaceus    | KP137498 TYPE Canada, NL|       |
| C. caesioarmeniaceus    | KP137501 Finland       |          |
| C. ornithopus           | RH2397 TYPE France     |          |
| C. turgidus             | AY669889               |          |
| C. isabellae            | 70728 TYPE France      |          |
| C. coteclarus           | 412 TYPE France        |          |
| C. productus            | RH81-175 TYPE France   |          |
| C. subadelphus          | RH80848 TYPE France    |          |
| C. turgidus             | AY669663               |          |
| C. albollascens         | CFP846 TYPE Belgium    |          |
| sect. Firmiores         | syn. sect. Armeniaci   |          |
| syn. sect. Biveli       | syn. sect. Hydrotelamonia|        |
| syn. sect. Sericeocybe  | syn. sect. Sericeocybe |          |

Fig. 1 (continued)
Fig. 1 (continued)
Fig. 1 (continued)
Fig. 1 (continued)
### Table 1: Distribution of Cladosporium spp.

| Species                | GenBank Accession | Location          |
|------------------------|-------------------|-------------------|
| C. raphanoides         | MM1974-0434       | Sweden            |
| C. raphanoides TN09-197| USA, WA           |
| C. raphanoides CFP956  | Sweden            |
| C. panellus            | KC842407 Norway   |
| C. phaeoannulatus      | F129865 Type Sweden|
| C. pholideus           | CFP602 TYPE Sweden|
| C. pholideus KC842406  | Norway            |
| C. subpholideus        | RH70649 TYPE France|
| C. subpenicillatus     | XC2005-18 TYPE France|
| C. orbiculonarius      | RH70617 TYPE France|
| C. theubarbainus       | 1862 TYPE France  |
| C. fuliginosus         | 109660 TYPE UK    |
| C. depexus var. luminosus| 98101804 TYPE France|
| C. olivaceostipitatus  | 98102507 TYPE France|
| C. valgas              | MM1970-0190 TYPE Sweden|
| C. valgas              | CFP652 Sweden     |
| C. privignipallens    | TN09-195 USA, WA  |
| C. privignipallens    | TN07-360 USA, WA  |
| C. privignipallens    | F148849 Type Sweden|
| C. alboamibitus        | NR131825 TYPE USA, WA |
| C. alboamibitus        | FJ17499 Canada, BC|
| C. luteo-ornatus       | NR119930 TYPE Austria|
| C. luteo-ornatus       | 12.09.01 Canada, BC|
| C. rossiciorenchica    | MF379633 TYPE Russia|
| C. suboenchis          | NR119929 TYPE Finland|
| C. suboenchis          | TN09-038 USA, WA  |
| C. paragaudis          | NR131814 TYPE Norway|
| C. paragaudis          | JFA11514 USA, WA  |
| C. pinigaudis          | HQ845162 TYPE Finland|
| C. pinigaudis          | HQ845168 Finland  |
| C. amillatus           | KC842408 Norway   |
| C. amillatus           | TN11-207 USA, AK  |
| C. roseoamillatus      | HQ845117 TYPE Finland|
| C. roseoamillatus      | HQ845118 Sweden   |
| C. alboglobosus        | NR131841 TYPE Finland|
| C. alboglobosus        | AY669661          |
| C. alboglobosus        | KM273100 USA, WA  |
| C. pseudoruspicus      | 5329 TYPE France  |
| C. niveoglobosus       | CFP6831 TYPE Sweden|
| C. bovinus             | AY669691          |
| C. bovarius            | NR131830 TYPE USA, AK |
| C. bovarius            | KC905159 Canada, AB|
| C. oulankaensis        | JX407292 TYPE Finland|
| C. oulankaensis        | FJ039672 Canada, BC|
| C. bovinus             | NR131821 TYPE Finland|
| C. bovinus             | JX407269 Sweden   |
| C. bovinaster          | JX407264 TYPE Finland|
| C. bovinaster          | JX407268 Sweden   |
| C. fuscoamibaster      | JX407310 France   |
| C. fuscoamibaster      | JX407316 TYPE Norway|
| C. fuscovarius         | NR131824 TYPE Finland|
| C. fuscovarius         | TN11-172 USA, AK  |
| C. sp.                 | FJ039671 Canada, BC|
| C. bubulus             | DQ1339983 TYPE Austria|
| C. terribilis          | 5268 TYPE France  |
| C. terribilis s. lato  | 4061 France       |
| C. pseudobulbosus      | XC2010-101 TYPE France|

### Diagram 1: Phylogenetic Relationships

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
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. paralbocyaneus* Eyssart. Based on the current data *C. alboviolaceus* s. auctores has the widest distribution of the three species and is also the

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

| Current name | Younger synonyms |
|--------------|------------------|
| *C. aavae* Liimat. & Niskanen 2012 | *C. geophilus* var. *subauroreus* Bidaud, Moënne-Locc. & Reumaux 2002 |
| *C. acutispissipes* Rob. Henry 1981 | |
| *C. adustorimosus* Rob. Henry 1988 | |
| *C. ahsii* McKnight 1975 | |
| *C. alboadustus* Bidaud 2012 | |
| *C. alboambitus* Niskanen, Liimat. & Ammirati 2013 | |
| *C. alboglobosus* Kytöv., Liimat., Niskanen & Ammirati 2014 | |
| *C. albolens* Bidaud, Carteret & Reumaux 2012 | |
| *C. albosericeus* Ammirati, Beug, Liimat., Niskanen & O. Ceska 2016 | |
| *C. alboviaceus* (Pers.) Fr. 1838 | |
| *C. aleuriodor* Rob. Henry 1981 | *C. perrenii* Rob. Henry & Ramm 1989; *C. umbrinoconnatus* var. *brunnescentipes* Bidaud, Moënne-Locc., Reumaux & Rob. Henry 2000 |
| *C. americanus* A.H. Sm. 1934 | |
| *C. ammoniloides* Bohus 1979 | |
| *C. andreae* H. Lindstr. 1999 s. lato | |
| *C. angelesianus* A.H. Sm. 1944 | *C. sporagnitus* Bidaud 2010 |
| *C. angustisporus* Kytöv., Niskanen & Liimat. 2014 | |
| *C. anisatus* H. Lindstr., Kytöv. & Niskanen 2005 | |
| *C. anisochrous* Kytöv., Liimat., Niskanen & H. Lindstr. 2013 | |
| *C. anthracinicolor* Reumaux 2001 | |
| *C. anthracinus* (Fr.) Sacc. 1887 s. Funga Nordica | |
| *C. aptecohaerens* Rob. Henry 1983 | |
| *C. argyroneotus* Bidaud 2008 | |
| *C. armeniacus* (Schaeff.) Fr. 1838 | |
| *C. armillatus* (Fr.) Fr. 1838 | |
| *C. atrocaeruleus* M.M. Moser 1967 | |
| *C. auroripes* Carteret & Reumaux 2001 | |
| *C. biastifolius* Ammirati, Beug, Niskanen, Liimat. & Bojantchev 2016 | |
| *C. biolaeflavus* Niskanen, Liimat., Mahiques, Ballarà & Kytöv. 2011 | |
| *C. bialevoestittus* M.M. Moser 1968 | |
| *C. bibulus* Quël. 1881 | |
| *C. biformis* Fr. 1838 | |
| *C. bistroides* Kauffman 1921 | |
| *C. biveloides* Rob. Henry 1948 | |
| *C. bivelosimilis* Kytöv., Niskanen & Liimat. 2017 | |
| *C. bivelus* (Fr.) Fr. 1838 | |

Note: Some synonyms are not listed for each species, indicating that they are not considered relevant or authoritative for the current study.
Table 1 (continued)

| Current name                  | Younger synonyms                                                                 |
|-------------------------------|----------------------------------------------------------------------------------|
| C. bombycinus Mahiques & Burguete 2001 |                                                                                 |
| C. bonamei Rob. Henry 1970    |                                                                                 |
| C. boreasensis A.H. Sm. 1944  |                                                                                 |
| C. boreotrichus Kytöv., Niskanen & Liimat. 2017 |                                                                                 |
| C. bouldereusis A.H. Sm. 1944 |                                                                                 |
| C. bovarius Liimat. & Niskanen 2013 |                                                                                 |
| C. bovinaster Niskanen, Kytöv. & Liimat. 2013 |                                                                                 |
| C. bovinus Fr. 1838            |                                                                                 |
| C. bridgei Ammirati, Niskanen, Liimat., Bojantchev, & Fang 2017 |                                                                                 |
| C. brunneifolius Kytöv., Niskanen & Liimat. 2008 |                                                                                 |
| C. brunneocalcarius Niskanen, Liimat. & Kytöv. 2012 |                                                                                 |
| C. brunneoclarius Niskanen, Kytöv. & Liimat. 2020 |                                                                                 |
| C. brunnoversus Niskanen, Liimat. & Ammirati 2013 |                                                                                 |
| C. brunneus (Pers.) Fr. 1838   | C. bruneus var. incommixtus Bidaud 2009                                                                                 |
| C. bubulus Liimat., Kytöv. & Niskanen 2020 |                                                                                 |
| C. bulbosolventus Rob. Henry & Contu 1985 |                                                                                 |
| C. bulliardii (Pers.) Fr. 1838 | C. colus Fr. 1838; C. georgianae Moënne-Locc. 1994                                                                                 |
| C. cacaoicolor A.H. Sm. 1944   |                                                                                 |
| C. caesioarmeniacus Kytöv., Niskanen & Liimat. 2014 |                                                                                 |
| C. caesiobrunneus Kytöv., Niskanen & Liimat. 2009 |                                                                                 |
| C. cagei Melot 1990           |                                                                                 |
| C. californicus A.H. Sm. 1939  |                                                                                 |
| C. caliginosus Bidaud, Moënne-Locc. & Reumaux 2000 |                                                                                 |
| C. calopus P. Karst. 1881     | C. fragrans A.H. Sm. 1944; C. ionema M.M. Moser & Ammirati 1996                                                                                 |
| C. campester Reumaux 2001    | C. malefidus Moënne-Locc. 2001; C. porphyreus Moënne-Locc. 2001                                                                                 |
| C. canaliculatus Bidaud & Carteret 2008 |                                                                                 |
| C. carabus Kytöv., Niskanen & Liimat. 2009 |                                                                                 |
| C. carbunculus H. Lindstr. & H. Markl. 2010 |                                                                                 |
| C. castaneopallidus Carteret 2004 |                                                                                 |
| C. castaneus (Bull.) Fr. 1838  | C. franceschinii Consiglio, D. Antonini & M. Antonini 2006; C. olivaceocernatinus Carteret 2012; C. pseudobavaricus Bidaud & Reumaux 2012 |                                                                                 |
| C. centrirufus Kytöv., Niskanen & Liimat. 2014 |                                                                                 |
| C. chevassutii Rob. Henry 1982 | C. fallaciosus Bidaud 2001; C. kunicenii var. caespitosus Moënne-Locc. 2001; C. robertii Moënne-Locc. & Reumaux 1988; C. subsordatus Bidaud 2001 |
| C. cecindela Kytöv., Niskanen & Liimat. 2009 |                                                                                 |
| C. cinereobrunneus Chevassut & Rob. Henry 1982 |                                                                                 |
| C. cinnamoviolaceus M.M. Moser 1968 |                                                                                 |
| C. circinans Rob. Henry 1985  | C. subsordsens Rob. Henry 1985                                                                                 |
| C. cissipalae Bojantchev 2013 |                                                                                 |
| C. cistophulcripes Bidaud 2004 |                                                                                 |
| C. cloroarbrinus (H. Lindstr. & Melot) Niskanen, Kytöv. & Liimat. 2009 |                                                                                 |
| C. cloroanlariasus Rob. Henry 1983 |                                                                                 |
| C. clorosordidae Niskanen, Kytöv. & Liimat. 2020 |                                                                                 |
| C. coccus Reumaux 1994        |                                                                                 |
| C. coleoptera H. Lindstr. & Soop 1999 |                                                                                 |
| C. colorius (Bidaud) Niskanen, Dima & Liimat. 2020 |                                                                                 |
| Current name         | Younger synonyms                                                                 |
|----------------------|----------------------------------------------------------------------------------|
| C. colymbadinus Fr. 1838 |                                                                                |
| C. compressus A.H. Sm. 1944 |                                                                                |
| C. comptulus M.M. Moser 1968 |                                                                                |
| C. confirmatus Rob. Henry 1983 |                                                                                |
| C. coracis Kytöv., Niskanen, Liimat. & Dima 2014 |                                |
| C. corvinus Reumaux 2012 |                                                                                |
| C. crassisorus Kytöv., Niskanen & Liimat. 2014 |                                   |
| C. craticius Fr. 1838 |                                                                                |
| C. cucumisporus M.M. Moser 1967 |                                                             |
| C. cystidiobicolor Liimat. & Niskanen 2017 |                                    |
| C. danicus Høil. 1983 |                                                                                |
| C. deceptivissimus Reumaux 1984 |                                            |
| C. decipiens (Pers.) Fr. 1838 |                                                                                |
| C. decipientoides Moënne-Locc. & Reumaux 1988 |                                 |
| C. denigratus Ammirati, Beug, Niskanen, Liimat. & O. Ceska 2016 |                             |
| C. desertorum (Velen.) G. Garnier 1991 |                                               |
| C. diabolicorigens Bohus 1976 |                                                                                 |
| C. diagnostatus Carteret 2012 |                                                                                |
| C. diagnostatus Chevassut & Rob. Henry 1978 |                                               |
| C. diosmooides Rob. Henry 1989 |                                                                                 |
| C. diosmus Kühner 1955 |                                                                                |
| C. disjungendulus Kytöv., Liimat. & Niskanen 2014 |                             |
| C. disjungendus P. Karst. 1893 |                                                                               |
| C. distortus Kauffman 1932 |                                                                                |
| C. dolabratooides Kytöv., Carteret, Bidaud, Liimat., Niskanen, Bel-langer, Dima, Reumaux & Ammirati 2017 | |
| C. dolabratus Fr. 1838 |                                                                                |
| C. daboisensis Ammirati, Beug, Niskanen & Liimat. 2016 |                             |
| C. dumetorum J. Favre 1960 |                                                                                 |
| C. duracellus Rob. Henry 1970 |                                                                                |
| C. duracinus Fr. 1838 |                                                                                |
| C. duristipes Kytöv., Niskanen & Liimat. 2014 |                                |
| C. ectypus J. Favre 1960 |                                                                                |
| C. elaphinicolor Carteret 2004 |                                                                                 |
| C. eldoradoensis Bojantchev 2013 |                                                                                  |
Table 1 (continued)

| Current name | Younger synonyms |
|--------------|------------------|
| *C. epipurrus* Chevassut & Rob. Henry 1978 | *C. himuleoradicatus* Bidaud, Moënne-Locc. & Reumaux 1997; *C. pallescens* Moënne-Locc. & Reumaux 1997; *C. pseudosafranipes* Moënne-Locc. & Reumaux 1997; *C. subgrisescens* Bidaud, Moënne-Locc. & Reumaux 1997 |
| *C. evernius* (Fr.) Fr. 1838 | *C. mucronatus* M.M. Moser & McKnight 1987, nom. illegit.; *C. hemitrichus f. improcerus* J. Favre 1955; *C. gossypinus* H. Lindstr. 2010 |
| *C. exitiosus* Bidaud, Moënne-Locc. & Reumaux 2001 | |
| *C. expallens* M.M. Moser 1993 | |
| *C. exsularis* Garrido-Ben., Ballarà & Mahiques 2016 | |
| *C. fagetorum* M.M. Moser 1967 | |
| *C. falsosus* Moënne-Locc. & Reumaux 2001 | |
| *C. famatus* Moënne-Locc. & Reumaux 2001 | |
| *C. ferrugineovelatus* Kytöv., Liimat. & Niskanen 2014 | |
| *C. fibrillosobrunneus* Kytöv., Niskanen & Liimat. 2020 | |
| *C. fillionii* Bidaud, Moënne-Locc. & Reumaux 1995 | |
| *C. flavobasilis* Peintner, Kuhnert-Finkernagel, Cripps & Ammirati 2017 | |
| *C. flexibilifolius* Carteret 2004 | |
| *C. flexipes* (Pers.) Fr. 1838 | |
| *C. fragrantissimus* Ammirati, Beug, Liimat., Niskanen & O. Ceska 2016 | |
| *C. francescae* Reumaux 1992 | |
| *C. fructuodorus* Niskanen, Liimat. & Ammirati 2013 | |
| *C. fulvus* Liimat., Niskanen & Kytöv. 2014 | |
| *C. furvus* Liimat., Niskanen & Kytöv. 2014 | |
| *C. fuscoruber* Reumaux 2001; *C. gurdus* Carteret 2012; *C. pseudepipurrus* Bidaud, Moënne-Locc. & Reumaux 2001 | |
| *C. gallurae* D. Antonini, M. Antonini & Consiglio 2005 | |
| *C. gentilis* (Fr.) Fr. 1838 | |
| *C. gentilissimus* A.H. Sm. 1939 | |
| *C. geraniolens* Bidaud 2010 s. lato | |
| *C. glabrellus* Kühner 1953 | |
| *C. glandicolor* (Fr.) Fr. 1838 | |
| *C. glaphurus* Chevassut & Rob. Henry 1982 | |
| *C. glaphurus* Chevassut & Rob. Henry 1982 | |
| *C. glaphurus* Chevassut & Rob. Henry 1982 | |
| *C. glaphurus* Chevassut & Rob. Henry 1982 | |
| *C. glaphurus* Chevassut & Rob. Henry 1982 | |
| *C. glaphurus* Chevassut & Rob. Henry 1982 | |
| *C. glaphurus* Chevassut & Rob. Henry 1982 | |
| *C. glaphurus* Chevassut & Rob. Henry 1982 | |
| Current name | Younger synonyms |
|-------------|------------------|
| *C. griseocarneus* Carteret 2010 | *C. atripes* Reumaux 2012 |
| *C. grumariensis* Liimat. & Niskanen 2012 | |
| *C. guadalfeis* Bojantchev 2013 | |
| *C. helodes* M.M. Moser, Matheny & Daniele 2001 | |
| *C. helvilloides* (Bull.) Fr. 1838 | |
| *C. hemitrichoides* Bidaud & Moënne-Locc. 2010 | |
| *C. hemitrichus* (Pers.) Fr. 1838 | *C. fusiemen* Reumaux 2000; *C. milvinoides* Carteret & Reumaux 2010; *C. paleaceus* Fr. 1838; *C. roseohemitrichus* Carteret & Reumaux 2010 |
| *C. heparinus* Kytöv., Niskanen & Liimat. 2020 | |
| *C. hesleri* Ammirati, Niskanen, Liimat. & Matheny 2013 | |
| *C. heterocycloideus* Kytöv., Niskanen & Liimat. 2017 | |
| *C. heterocyclus* Soop 1990 | |
| *C. heterodepressus* Kytöv., Niskanen & Liimat. 2017 | *C. bohemicus* f. *subheterosporus* Bidaud 2010 |
| *C. heterosporus* Bres. 1889 | |
| *C. hiliieri* Rob. Henry 1938 | *C. daurefer* Reumaux 1989 |
| *C. hinnuleocarnillatus* Reumaux 1889 | *C. distans* var. *olympianus* A.H. Sm. 1944 |
| *C. hinnuleocervinus* Niskanen, Liimat. & Ammirati 2017 | *C. tigris* Bidaud 1997 |
| *C. hinnuleus* Fr. 1838 | |
| *C. hinnuleus* var. *olympianus* A. H. Sm. 1944 | |
| *C. hinnuleus* var. *tigris* Bidaud 1997 | |
| *C. hircinosmus* Moënne-Locc. 2002 | |
| *C. hircinosmus* Moënne-Locc. & Reumaux 2001; *C. punctatoides* Reumaux 2001; *Telamonia sanguinescens* Velen. 1939; *C. similigenus* Moënne-Locc. & Reumaux 2001; *C. subargyropus* Bidaud, Moënne-Locc. & Reumaux 2001; *C. substemmatus* Moënne-Locc. & Reumaux 2001 | |
| *C. humicola* (Quél.) Maire 1911 | *C. querculus* Moënne-Locc. & Reumaux 2001; *C. punctatoides* Reumaux 2001; *Telamonia sanguinescens* Velen. 1939; *C. similigenus* Moënne-Locc. & Reumaux 2001; *C. subargyropus* Bidaud, Moënne-Locc. & Reumaux 2001; *C. substemmatus* Moënne-Locc. & Reumaux 2001 |
| *C. hydrotelamonioides* Rob. Henry 1970 | |
| *C. hydrotelamonioides* Rob. Henry 1970 | *C. boletiformis* Bidaud & Reumaux 2010; *C. bucknallii* Reumaux 2010; *C. castanearum* Rob. Henry 1981; *C. macropodus* Rob. Henry 1961 Nom. inval.; *C. pseudoprivignus* Rob. Henry 1985; *C. renidentoides* Rob. Henry 1981; *C. subamidicola* Bidaud, Moënne-Locc. & Reumaux 2000; *C. triformis* f. *strenus* Rob. Henry 1981; *C. turgidoides* Rob. Henry 1981 |
| *C. imbutus* Fr. 1838 | |
| *C. impolitus* Kauffman 1918 | |
| *C. incisior* Bidaud, Moënne-Locc. & Reumaux 1997 | |
| *C. inconspicuus* J. Favre 1955 | |
| *C. inconspicuus* J. Favre 1955 | |
| *C. iners* (Bidaud) Liimat., Dima & Niskanen 2020 | |
| *C. interstinctus* Moënne-Locc. & Reumaux 2001 | |
| *C. ionophyllus* M.M. Moser 1968 | |
| *C. jacobii-langei* Bidaud 2008 | |
| *C. kauffmanianus* A.H. Sm. 1933 | |
| *C. lacustris* Moënne-Locc. & Reumaux 1997 | |
| *C. laniger* Fr. 1838 | |
| *C. laniger* Fr. 1838 | |
| *C. leiocestaneus* Niskanen, Liimat. & Soop 2008 | |
| *C. leucopaethus* Rob. Henry 1985 | |
| *C. lindstroemii* Niskanen, Kytöv. & Liimat. 2020 | |
| *C. lucorum* (Fr.) Berger 1846 | |

C. flabellus f. *biolens* Bidaud 2010
Table 1 (continued)

| Current name                          | Younger synonyms                                                                 |
|---------------------------------------|-------------------------------------------------------------------------------|
| *C. luridis* Rob. Henry 1969          | *C. aciculisorus* Moënne-Locc. 1997; *C. armillifer* Moënne-Locc. & Reumaux 1997; *C. aspilus* Moënne-Locc. 1997; *C. collybioides* Reumaux 1997; *C. conoideus* Bidaud 1997; *C. herculinus* Reumaux 1997; *C. hinnuleociris* Ramm & Rob. Henry 1995; *C. hinnuleus f. parincisus* Bidaud, Moënne-Locc. & Reumaux 1997; *C. lepidus* Moënne-Locc. 1997; *C. ochraceocephalus* Reumaux 1997; *C. pseudohinnuleus* Bidaud, Moënne-Locc. & Reumaux 1997; *C. salicum* Reumaux 1997 |
| *C. luteo-ornatus* (M.M. Moser) Bidaud, Moënne-Locc. & Reumaux 1995 |                                                                                   |
| *C. malachius* (Fr.) Fr. 1838         | *C. cinereoviolascens* Moënne-Locc. & Reumaux 1988; *C. malachius f. chologogus* Bidaud, Moënne-Locc. & Reumaux 2002; *C. malachius f. crinitus* Bidaud & Reumaux 2002; *C. ochraceus* Peck 1872 |
| *C. mallaensis* Kytöv., Niskanen & Liimat. 2020 |                                                                                   |
| *C. mattiae* Soop 2010                |                                                                                   |
| *C. megacystidiosus* Reumaux 2012     |                                                                                   |
| *C. melleopallens* (Fr.) Britzelm. 1892 |                                                                                   |
| *C. milvinicolor* Moënne-Locc. & Reumaux 1997 |                                                                                   |
| *C. miniatus* J.E. Lange 1940         |                                                                                   |
| *C. minusculus* Liimat. & Niskanen 2019 |                                                                                   |
| *C. miwok* Bojantchev 2013            |                                                                                   |
| *C. montebelloensis* Niskanen & Liimat. 2014 |                                                                                   |
| *C. mucicola* A.H. Sm. 1944           |                                                                                   |
| *C. murinascens* Kytöv., Niskanen & Liimat. 2014 |                                                                                   |
| *C. nauseosouraceus* Reumaux, Liimat. & Ammirati 2013 |                                                                                   |
| *C. neoculus* Reumaux & Sasia 2011    |                                                                                   |
| *C. neofallax* Carteret & Reumaux 2004 |                                                                                   |
| *C. neofurvalaesa* Kytöv., Niskanen, Liimat. & H. Lindstr. 2005 |                                                                                   |
| *C. nigrellus* Peck 1873              |                                                                                   |
| *C. nigrospidatus* Kauffman 1921      |                                                                                   |
| *C. nigrinervis* Kauffman 1921        |                                                                                   |
| *C. niveoglobothus* H. Lindstr. 1992   |                                                                                   |
| *C. niveotraganus* Kytöv., Niskanen & Liimat. 2014 |                                                                                   |
| *C. nodosisorus* Kytöv., Niskanen & Liimat. 2014 |                                                                                   |
| *C. nolaneiformis* (Velen.) Dima, Niskanen & Liimat. 2014 |                                                                                   |
| *C. nucicola* Liimat., Niskanen & Kytöv. 2014 |                                                                                   |
| *C. obliquus* Peck 1902               |                                                                                   |
| *C. ochropallens* Liimat., Niskanen & Ammirati 2013 |                                                                                   |
| *C. ohlone* Bojantchev 2013           |                                                                                   |
| *C. olididiumgundens* Liimat., Niskanen, Dima & Kytöv. 2014 |                                                                                   |
| *C. olivaceofulvus* Kauffman & A.H. Sm. 1933 |                                                                                   |
| *C. orasericeus* Rob. Henry 1983      |                                                                                   |
| *C. oulankaënsis* Kytöv., Niskanen, Liimat. & H. Lindstr. 2013 |                                                                                   |
| *C. palidostriatus* Rob. Henry 1968   |                                                                                   |
| *C. paludosaniosus* Liimat., Niskanen, Dima & Ammirati 2017 |                                                                                   |
| *C. panellus* Soop 2009               |                                                                                   |
| *C. pangloius* M.M. Moser 1969        |                                                                                   |
| *C. paragaudis* Fr. 1838              |                                                                                   |
| *C. paralbocyaneus* Eyssart. 2002     |                                                                                   |
| *C. pardinipes* Romagn. 1977          |                                                                                   |
### Table 1 (continued)

| Current name | Younger synonyms |
|--------------|------------------|
| *C. parhonestus* Reumaux 2012 | *C. cremeolaniger* P.D. Orton 1983; *C. lanigeroides* P.D. Orton 1983 |
| *C. pearsonii* P.D. Orton 1958 | *C. pholideoides* Bidaud & Reumaux 2005; *C. subpenicillatus* Carteret & Reumaux 2005; *C. subpholideus* Rob. Henry 1992 |
| *C. cremeolaniger* P.D. Orton 1983; *C. lanigeroides* P.D. Orton 1983 | *C. altipes* Bidaud 2010; *C. conocyboideus* Carteret 2004; *C. distinctus* Carteret 2012; *C. pelargoniohystatus* Rob. Henry 1985; *C. pseudorigidus* Bidaud, Carteret & Reumaux 2012; *C. udolivascens* var. *lilacinostipitatus* Carteret 2004 |
| *C. pelargoniostriatulus* Bidaud & Fillion 2010 | *C. fulguritans* Reumaux 2000; *C. magus* Moënne-Locc. 2001; *C. poirieri* Reumaux 1988; *C. rufescintipes* Bidaud 2001; *C. sensibilis* Bidaud 2010 |
| *C. phaeochrous* J. Favre 1955 | *C. privignatus* Soop 2010 |
| *C. phaeosmus* Rob. Henry 1981 | *C. privignipallens* Kytöv., Niskanen & Liimat. 2014 |
| *C. pilatei* Svřeček 1968 | *C. psammocola* Kytöv., Niskanen & Liimat. 2020 |
| *C. pinigaudis* Niskanen, Kytöv. & Liimat. 2011 | *C. plumulosus* Rob. Henry 1977 |
| *C. pinosquamulosus* Kytöv., Niskanen & Liimat. 2020 | *C. politus* Niskanen, Liimat. & Ammirati 2013 |
| *C. politus* Niskanen, Liimat. & Ammirati 2013 | *C. praepallens* Peck 1887 |
| *C. praestigiosus* (Fr.) M.M. Moser 1965 | *C. praestigiosus* (Fr.) M.M. Moser 1965 |
| *C. privignatus* Soop 2010 | *C. raphanoides* (Pers.) Fr. 1838 |
| *C. privignipallens* Kytöv., Niskanen & Liimat. 2014 | *C. repertus* A. Favre & Vialard 2004 |
| *C. psammocola* Kytöv., Niskanen & Liimat. 2017 | *C. rigidipes* M.M. Moser 1967 |
| *C. pseudobiformis* Bidaud & Carteret 2012 | *C. roseivelatus* Kytöv., Liimat. & Niskanen 2014 |
| *C. pseudobivirus* M.M. Moser & Ammirati 1995 | *C. roseoarmillatus* Niskanen, Kytöv. & Liimat. 2011 |
| *C. pseudobulbus* Carteret & Reumaux 2010 | *C. roseosarmillatus* Niskanen, Kytöv. & Liimat. 2014 |
| *C. pseudofallax* Carteret 2004 | *C. roseofusisporus* Bidaud 2010 |
| *C. pseudofilabella* Bidaud 2010 | *C. pseudophleboginata* Bidaud 2010 |
| *C. pseudophlebiopsis* Bidaud 2010 | *C. pseudophlegma* Rob. Henry 1981 |
| *C. pseudophlegma* Rob. Henry 1981 | *C. puellaris* Brandrud, Bendiksen & Dima 2015 |
| *C. puellaris* Brandrud, Bendiksen & Dima 2015 | *C. quercocomicus* Liimat., Kytöv. & Niskanen 2017 |
| *C. punctatiformis* Carteret 2012 | *C. radicosissimus* Moënne-Locc. & Reumaux 1997 |
| *C. quarciticus* H. Lindstr. 1994 | *C. squamulifer* Bidaud & Reumaux 2012 |
| *C. quercocomicus* Liimat., Kytöv. & Niskanen 2017 | *C. speciosior* Bidaud, Moënne-Locc. & Reumaux 1997; *C. squamulifer* Bidaud & Reumaux 1997; *C. subhelvolus* Moënne-Locc. & Reumaux 1997 |
| *C. radicosissimus* Moënne-Locc. & Reumaux 1997 | *C. raphanoides* (Pers.) Fr. 1838 |
| *C. raphanoides* (Pers.) Fr. 1838 | *C. repertus* A. Favre & Vialard 2004 |
| *C. repertus* A. Favre & Vialard 2004 | *C. rigidipes* M.M. Moser 1967 |
| *C. rigidipes* M.M. Moser 1967 | *C. roseivelatus* Kytöv., Liimat. & Niskanen 2014 |
| *C. roseivelatus* Kytöv., Liimat. & Niskanen 2014 | *C. roseoarmillatus* Niskanen, Kytöv. & Liimat. 2011 |
| *C. roseoarmillatus* Niskanen, Kytöv. & Liimat. 2011 | *C. roseosarmillatus* Niskanen, Kytöv. & Liimat. 2014 |
| *C. roseosarmillatus* Niskanen, Kytöv. & Liimat. 2014 | *C. roseofilunus* Carteret 2000 |
| *C. roseofilunus* Carteret 2000 | *C. roseofusisporus* Bidaud 2009 |
| *C. roseomyceliosus* Bidaud 2009 | *C. roseomyceliosus* Bidaud 2009 |
| *C. roseomyceliosus* Bidaud 2009 | *C. roseonudipes* Rob. Henry & Moënne-Locc. 1997 |
| *C. roseonudipes* Rob. Henry & Moënne-Locc. 1997 | *C. bisoliensis* Bidaud 1997; *C. carcharias* Bidaud 1997; *C. hinnuleovelatus* Reumaux 1997; *C. subfilamentosus* Reumaux 1997 |
| *C. roseonudipes* Rob. Henry & Moënne-Locc. 1997 | *C. rosicinocochelis* Kytöv. & Niskanen 2017 |
| *C. rosicinocochelis* Kytöv. & Niskanen 2017 | *C. rubipes* Kauffman 1909 |
| *C. rubipes* Kauffman 1909 |
Table 1 (continued)

| Current name | Younger synonyms |
|--------------|------------------|
| C. rubricosus (Fr.) Fr. 1838 | C. calcareophilus Bidaud 1997; C. crassogriseascens A. Favre 2009; C. phaeomaculatus Rob. Henry 1989; C. safranopes Rob. Henry 1938; C. safranopes var. bulbosus Rob. Henry 1997; C. safranopes var. laevipes Reumaux 1997 |
| C. rubrocinctus Reumaux 1995 | C. uraceoarmillatus Bidaud 2012 |
| C. rubroviolaeipes Bendiksen & K. Bendiksen 1991 | C. boleterius var. pallidulus J. Favre 1960 |
| C. rumoridrumsii Bojantchev, Ammirati, Niskanen, & Liimat. 2017 | C. striatulorufus Moënne-Locc. 2004 |
| C. russulaespermus Carteret 2004 | C. canarbarba M.M. Moser 1966; C. umidicola f. coeruleus M.M. Moser & Ammirati 1995 |
| C. rusticellus J. Favre 1955 | C. bavaricus M.M. Moser 1983; C. luteolateritius (Velen.) G. Garnier 1991; C. rufomalifera M.M. Moser & McKnight 1987; C. subaurantiomarginatus Bidaud & Ferville 2012 |
| C. rusticus P. Karst. 1882 | C. castaneoruber Bidaud & Reumaux 2012; C. sublactorum Carteret 2012 |
| C. sagacitas Kyttö., Niskanen & Liimat. 2020 | C. raphanicus Bidaud & Moëne-Locc. 2008 |
| C. sagacito-occidentalis Liimat., Niskanen, Kyttö, & Ammirati 2020 | C. griseascens Bidaud, Moëne-Locc. & Reumaux 1997; C. immaculatus Bidaud 1997; C. nauseosmus Bidaud, Moëne-Locc. & Reumaux 1997; C. subulatus Bidaud, Moëne-Locc. & Reumaux 1997; C. solidus Bidaud, Moëne-Locc. & Reumaux 1997 |
| C. saniosus (Fr.) Fr. 1838 | C. sefendons Rob. Henry 1983 |
| C. saturninus (Fr.) Fr. 1838 | C. fasspiorus var. olivaceodepressus Reumaux 2010 |
| C. scocoides J. Favre 1955 | C. terribilis Reumaux 2002 |
| C. sejunctifolius Rob. Henry 1995 | C. sordescens var. vestitissimus Eyssart. 2002; C. streunipes var. subacuminatus Reumaux 2002 |
| C. semiodoratus Rob. Henry 1944 | C. sordidemaculatus Bidaud 1998; C. laceratomarginatus Carteret & Reumaux 2008 |
| C. semivelatus Rob. Henry 1970 | C. sordescens var. nigrescens Reumaux 1989; C. tenebrosus Reumaux 2001 |
| C. semivestitus M.M. Moser 1968 | C. urdaibaiensis Fernández Sas. 2003 |
| C. serratissimus M.M. Moser 1968 | C. brunneogriseus Soop 1993 |
| C. sociatus Rob. Henry 1983 | C. squalidus A.H. Sm. 1942 |
| C. sordescens Rob. Henry 1944 | C. stipitatum Rehner & Ammirati 1989 |
| C. sordidemaculatus Rob. Henry 1981 | C. sargyronotus Niskanen, Liimat. & Kyttö, 2014 |
| C. sphagnoravus Liimat., Kyttö., Niskanen & Ammirati 2017 | C. subbalaustinus Rob. Henry 1991 |
| C. spisnii Consiglio, D. Antonini & M. Antonini 2004 | C. subbalaustinus Rob. Henry 1991 |
| C. squalidus A.H. Sm. 1942 | C. subcarabus Liimat., Kyttö, & Niskanen 2014 |
| C. stipitatum Rehner & Ammirati 1989 | C. subbalaustinus Rob. Henry 2000 |
| C. subglandicolor Niskanen, Liimat. & Kyttö, 2017 | C. subbalaustinus Rob. Henry 2000 |
| C. suillibus A.H. Sm. 1942 | C. subglandicolor Niskanen, Liimat. & Kyttö, 2017 |
| C. squalidus A.H. Sm. 1942 | C. subbalaustinus Rob. Henry 2000 |
| Current name                                      | Younger synonyms                      |
|-------------------------------------------------|---------------------------------------|
| *C. subheterocyclus* Liimat., Niskanen & Kytöv. 2017 |                                       |
| *C. subionophyllus* Niskanen, Liimat. & Kytöv. 2017 |                                       |
| *C. subgilvus* Bidaud 2010                       |                                       |
| *C. subminiatopus* Kytöv., Niskanen & Liimat. 2017 | *C. miniatopus* var. konradii M.M. Moser 1965 |
| *C. subobtusobrunneus* Bidaud 2004               |                                       |
| *C. subobtusus* Kauffman & A.H. Sm. 1933         |                                       |
| *C. suboenochelis* Kytöv., Liimat. & Niskanen 2011 |                                       |
| *C. subpalaeaceus* Kytöv., Niskanen & Liimat. 2017 |                                       |
| *C. subparvannulatus* Moënne-Locc. & Fillion 2010 |                                       |
| *C. subpulchrifolius* Kauffman 1918              |                                       |
| *C. subrigens* Kauffman 1918                     |                                       |
| *C. subrimosus* A.H. Sm. & Hesler 1944           |                                       |
| *C. subsclerotides* Niskanen & Liimat. 2019      |                                       |
| *C. subsedens* Rob. Henry 1956                   | *C. subcompar* Bohus 1979              |
| *C. subserratissimus* Kytöv., Liimat. & Niskanen 2014 |                                   |
| *C. substratiatus* Kauffman 1932                 |                                       |
| *C. subtabularis* Kauffman 1918                  | *C. fumosifolius* A.H. Sm. 1942       |
| *C. subtilior* J. Favre 1955                     | *C. parinsignis* Moënne-Locc. & Carteret 2001; *C. percaucus* J. Favre 1955 |
| *C. suillonigrescens* Reumaux 2002               | *C. impexobrunnescens* A. Favre 2009  |
| *C. tatrensis* R. Fellner & Landa 1993           |                                       |
| *C. tenebricus* J. Favre 1955                    |                                       |
| *C. tigrinipes* Bergeron 1997                    |                                       |
| *C. tortuosus* (Fr.) Fr. 1838                    |                                       |
| *C. torvoides* Rob. Henry 2000                   |                                       |
| *C. torvus* (Fr.) Fr. 1838                       | *C. bidiscendus* Rob. Henry 1985; *C. subamethysteus* Rob. Henry 2000; *C. testaceofibrillosus* Carteret & Reumaux 2000; *C. torvovellatus* Reumaux 2000 |
| *C. tragano-odorus* Niskanen, Liimat. & Ammirati 2020 |                                   |
| *C. traganus* (Fr.) Fr. 1838                     | *C. pulchrifolius* var. odorifer Hesler 1944 |
| *C. triangulus* Rob. Henry 1983                  | *C. pyriodorus* Kauffman 1932; *C. traganus* f. ochraceus M.M. Moser, Ammirati & M.T. Seidl 1995 |
| *C. truckeensis* Bojantchev 2013                 |                                       |
| *C. tuolumnensis* Bojantchev 2013                |                                       |
| *C. turgidipes* Bidaud & Carteret 2008           |                                       |
| *C. turgidulus* Bidaud 2002                      |                                       |
| *C. turgidus* Fr. 1838                           | *C. albolilascens* Rob. Henry 1988; *C. cutoclarius* Bidaud, Moënne-Locc. & Reumaux 2008; *C. isabellae* Rob. Henry 1981; *C. ornithopus* Rob. Henry 1970; *C. productus* Chevassut & Rob. Henry 1988; *C. subadelphus* Rob. Henry 1981 |
| *C. ultimionophyllus* Kytöv., Niskanen & Liimat. 2017 |                                       |
| *C. umbilicatus* P. Karst. 1893                  | *C. cacaodiscus* Liimat., Niskanen & Kytöv. 2014 |
| *C. umbrinobellus* Liimat., Niskanen & Kytöv. 2014 |                                       |
| *C. umbrinolens* P.D. Orton 1980                 | *C. sericeofibrillosus* Bidaud & Boutev. 2001 |
| *C. umbrinolutescens* Reumaux 2004               |                                       |
| *C. uraceisporus* Niskanen, Kytöv. & Liimat. 2014 |                                       |
| *C. uraceomajalis* Dima, Liimat., Niskanen & Bojantchev 2014 |                                   |
| *C. uraceonemoralis* Niskanen, Liimat., Dima, Kytöv., Bojantchev & H. Lindstr. 2014 |                                   |
| *C. uraceus* Fr. 1838                            | *Hydrocybe praecox* Velen. 1939        |
| *C. urbiculus* (Fr.) Fr. 1838                     | *C. alsomatii* Rob. Henry 1992         |
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 bulliardii (Pers.) Fr. [as ‘bulliardi’], Epicr. syst. mycol. (Upsaliae): 282 (1838) [1836–1838]
Basionym: Agaricus bulliardii Pers. [as ‘bulliardi’], 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: 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 calcareus soil (Corylus, Quercus, Tilia), 15 Sep 1886, coll. H. Lindström et al. CFP 499, F41127 (S, epitypus hic designatus, IF 557460), GenBank No. MT934978 (ITS).
Illustration. Brandrud et al. (1989: pl. A37).
Descriptions of the species. Brandrud et al. (1989: pl. A37), Niskanen et al. (2012).

Cortinarius bipulus Quél., Compt. Rend. Assoc. Franç. Avancem. Sci. 9: 666 (1881) [1880]
Types: Quél., Compt. Rend. Assoc. Franç. Avancem. Sci. 9: 666, Pl. VIII, fig. 7, 1881 (lectotypus hic designatus, IF 557457). Finland, Kainuu, Puolanka, Pihlahavaara 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, isoneotypos), 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 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 calcareus soil (Corylus, Quercus, Tilia), 15 Sep 1986, coll. H. Lindström et al. CFP 499, F41127 (S, epitypus hic designatus, IF 557460), GenBank No. MT934978 (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 calcareus soil (Corylus, Quercus, Tilia), 15 Sep 1986, coll. H. Lindström et al. CFP 499, F41127 (S, epitypus hic designatus, IF 557460), 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. (Upsalae): 282 (1838) [1836–1838]

Type: Finland, Satakunta, Ikaalinen, Seitseminen National Park, Multiharju strict protections area, old, mesic spruce forest (*Picea abies*) with some *Picea abies* spruce forest (*Pinus sylvestris*), 15 Sep 1983, coll. H. Lindström et al. CFP 672, F44866 (S, neotypus hic designatus, IF 557465), GenBank No. MT935017 (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 diosmus* Kühner, Bull. mens. Soc. linn. Soc. Bot. Lyon 24: 39 (1955)

Type: France, Haute-Savoie, Environ 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. (Upsalae): 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. (Upsalae): 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. (1998: pl. B31).

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

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

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

Type: Finland, Uusimaa, Espoo, Hindsby-Svartbôle, 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. MT935032 (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. (Upsalinae): 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 557469), GenBank No. MT935113 (ITS).

Illustration: Brandrud et al. (1989: pl. A13).

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

**Cortinarius hinnuleus** Fr., Epicr. syst. mycol. (Upsalinae): 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 (H, isoneotypus 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 obvoidly 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. (Upsalinae): 292 (1838) [1836–1838]

Type: Finland, Joutsa, Koivuranta, W of Rakkolanselkä, birch forest with some *Betula*, 30 Aug 2005, coll. K. Kytöv., IS019, 13 Sep 1997, coll. I. Kytövuori 97-1369, H6041343 (S, miniatopus). Sweden, Härjedalen, Storsjö sn, Flatruet, in subalpine 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 melleopallens** 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, Näljänkää, Lohivaara, W of Kiviario, 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. Kytöv. 97-1369, H6041343 (S, 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, Qv.= 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. (Upsalinae): 302 (1838) [1836–1838]

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

Type: Sweden, Skåne, Maglehem sn, "Piraten rasten", in birch forest, 21 Sep 1987, coll. H. Lindström et al. CFP 662,
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 umbo, 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. quercococos Limat., Kytöv. & Niskanen that usually have a much narrower, acutely umbo, scaly 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 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 umbo, 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. quercococos Limat., Kytöv. & Niskanen that usually have a much narrower, acutely umbo, scaly 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. 1-V, 1774 (lectotypus hic designatus, IF 557480), as Agaricus amethystinus). Sweden,
Angermanland, 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., Epicer. syst. mycol. (Upsal.: 278 (1838) [1836–1838]

Types: Battarra, Fungorum agri Arimenis 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

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 reliably 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. macrophalus* 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 redescribed 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 dubiurn. 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 rising 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 ≥ 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 alfa diversity are the nomenclatural problems, i.e. what is the correct name for the species or is
it an undescribed one? The species of \textit{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 \textit{Telamonia}, can be solved and identification based on ITS barcodes becomes an easy task even for non-experts.

\textbf{Infrasubgeneric classification}

\textbf{Relationships of the sections within \textit{Cortinarius} subgen. \textit{Telamonia}}

The relationships of the sections within \textit{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 \textit{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 \textit{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: \textit{Hinnulei} Melot, \textit{Rubricosi} Moënne-Locc. & Reumaux \textit{Leiocastanei} Niskanen, \textit{Kytöv.} & \textit{Liimat.}, and the monotypic sections \textit{Pseudoduracini} \textit{Liimat.}, \textit{Niskanen} & \textit{Kytöv.}, \textit{Friesiorum} \textit{Liimat.}, \textit{Kytöv.} & \textit{Niskanen}, and \textit{Vinaceobrunnei} Ammirati, \textit{Niskanen} & \textit{Liimat.}. The most basal part of this clade also includes sections \textit{Anthracini} Melot, \textit{Crassispori} \textit{Kytöv.}, \textit{Niskanen} & \textit{Liimat.} and \textit{Squalidi} \textit{Liimat.}, \textit{Ammirati} & \textit{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, \textit{Incrustati} Melot and \textit{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 /\textit{Squamicybe} (\textit{Incrustati} s. Brandrud et al.) and /\textit{Erubcsentes} (\textit{Hydrocybe} s. Brandrud et al.). The new names are introduced because the type species of sect. \textit{Hydrocybe}, \textit{Cortinarius duracinus}, does not belong to “Crown Telamonias” but to “Basal Telamonias” and the type species of sect. \textit{Incrustati}, \textit{C. luxnymphae}, was not available for study and thus the identity of the species remains unclear.

The previous members of the \textit{C. sect. Incrustati} are all placed in/\textit{Squamicybe} (Fig. 2) in two monophyletic groups/\textit{Eusquamicybe} and/\textit{Paludosi} but the group also includes sections of species with medium- to large-sized basidiomata. Many species of this group have a ±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 \textit{C. sect. Rubrocincti} that resembles more the species in/\textit{Erubescentes}). Typical examples of this group are \textit{C. flexipes} (\textit{C. sect. Flexipes}), \textit{C. hemitrichus} (\textit{C. sect. Paleacei}) and \textit{C. saniosus} (Fr.) Fr. (\textit{C. sect. Saniosi Moënne-Locc. & Reumaux}) and from the larger species \textit{C. hinnuleus} (\textit{C. sect. Hinnulei}) and \textit{C. rubricosus} (Fr.) Fr. (syn. \textit{C. safranopes} Rob. Henry, \textit{C. sect. Rubricosi}). Species associated with \textit{Alnus}, i.e. \textit{C. bibulus} (\textit{C. sect. Bibuli}), \textit{C. griseocarneus} Carteret (\textit{C. alnetorum} (Velen.) M.M. Moser sensu Brandrud et al. 1989, \textit{C. sect. Alnicolarum}) and \textit{C. helvelloides} (\textit{C. sect. Helvelloides}), also belong to this larger group. Together with \textit{C. sect. Saniosi} they form a monophyletic group/\textit{Paludosi}, although without support, indicating that within \textit{C. subgen. Telamonia} the ability to form mycorrhizae with \textit{Alnus} may only have evolved once.

A majority of the species classified earlier in \textit{C. sect. Hydrocybe} are placed in another, monophyletic, group /\textit{Erubcescentes} (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 ± reddish with time. The universal veil varies from indistinct to forming distinct girdles on the stipe. Typical examples of this group are \textit{C. fuscoalbus} \textit{Kytöv.}, \textit{Niskanen} & \textit{Liimat.}, \textit{C. sect. Atroalbi} \textit{Niskanen}, \textit{Kytöv.} & \textit{Liimat.}, \textit{C. decipiens} (Pers.) Fr. (\textit{C. sect. Castanei} Moënne-Locc. & Reumaux), \textit{C. praestigosus} (\textit{C. sect. Praestigiosi} \textit{Kytöv.}, \textit{Niskanen} & \textit{Liimat.}) and \textit{C. vernus} H. Lindstr. & \textit{Melot} (\textit{C. sect. Verni} \textit{Kytöv.}, \textit{Niskanen} & \textit{Liimat.}).

\textbf{Sections}

The aim of this study was not to solve the infrasubgeneric classification of \textit{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. Cacaocephalinae 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. uraceofolius 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. Brumneotincti M.M. Moser, sect. Cinnabarini Melot, and sect. Purvuli 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 Moënne-Locc. & 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. Miniaptopodes Moënne-Locc. & 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. Brumneocalcarii Niskanen, Liimat. & Kytöv. to middle-sized groups i.e. C. sect. Armillati and C. sect. Diisjugendi 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. Firmiorees (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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References

Ammirati JF, Hughes KW, Limmatainen K, Niskanen T, Matheny PB (2013) Cortinarius hesleri from eastern North America and related species from Europe and western North America. Botany 91(2):91–98

Ammirati JF, Niskanen T, Limmatainen K, Dimitar B, Peintner U, Kühner-Finkernagel R, Cripps C (2017) Spring and early summer species of Cortinarius, subgenus Telamonia, section Colymbadini and /Flavobasilis, in the mountains of western North America. Mycologia 109(3):443–458

Bidaud A, Bellanger J-M, Carteret X, Reumaux P, Moëne-Loccoz P (2017) Atlas des Cortinaires. Pars XXIV, Editions Fédération mycologique Dauphiné-Savoie, Lomazzo, France

Bidaud A, Carteret X, Eyssartier G, Moëne-Loccoz P, Reumaux P (2004) Atlas des Cortinaires. Pars XVII, Éditions Fédération mycologique Dauphiné-Savoie, Lomazzo, France

Bidaud A, Moëne-Loccoz P, Reumaux P (1994) Atlas des Cortinaires. Pars VI, Éditions Fédération mycologique Dauphiné-Savoie, France

Bidaud A, Moëne-Loccoz P, Reumaux P, Carteret X, Eyssartier G (2008) Atlas des Cortinaires. Pars XVII, Éditions Fédération mycologique Dauphiné-Savoie, Lomazzo, France

Borchsenius F (2009) FastGap 1.2. Department of Biosciences, Aarhus University, Denmark. Published online at http://www.aubot.dk/FastGap_home.htm

Brandrud TE, Lindström H, Marklund H, Melot J, Muskos S (1989) Cortinarius Flora Photographica. Vol. I (Swedish version). Cortinarius HB, Matfors, Sweden

Brandrud TE, Lindström H, Marklund H, Melot J, Muskos S (1992) Cortinarius Flora Photographica. Vol. II (Swedish version).— Cortinarius HB, Matfors, Sweden

Brandrud TE, Lindström H, Marklund H, Melot J, Muskos S (1994) Cortinarius Flora Photographica. Vol. III (Swedish version).— Cortinarius HB, Matfors, Sweden

Brandrud TE, Lindström H, Marklund H, Melot J, Muskos S (1998) Cortinarius Flora Photographica. Vol. IV (Swedish version).— Cortinarius HB, Matfors, Sweden

Brandrud TE, Lindström H, Marklund H, Melot J, Muskos S (2012) Cortinarius Flora Photographica. Vol. V (Swedish version).— Cortinarius HB, Matfors, Sweden

Bulliard P (1793) Herbier de la France 13. Paris, France

Burnham SH (1919) Charles Horton Peck. Mycologia 11(1):33–39. https://doi.org/10.1080/00275514.1919.12016772

Dima B, Limmatainen K, Niskanen T, Kytövuori I, Bojantchev D (2014) Two new species of Cortinarius, subgenus Telamonia, sections Colymbadini and Uracel, from Europe. Mycol Progress 13:867–879. https://doi.org/10.1017/s11557-014-0970-6

Favre J (1955) Les champignons supérieurs de la zone alpine du Parc National suisse. Ergebn. wiss. Unters. schweiz. NatnParks 13:867–879. https://doi.org/10.1007/s11557-014-0970-6

Fries EM (1818) Observationes Mycologicae 2. Bonn, Germany

Fries EM (1836–1838) Epicrisis systematis mycologici seu synopsis Hymenomycetum. Uppsala, Sweden.
Stamatakis A (2014) RAxML. Version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30:1312–1313
Stensrud Ø, Orr RJS, Reier-Røberg K, Schumacher T, Høiland K (2014) Phylogenetic relationships in Cortinarius with focus on North European species. Karstenia 54:57–71
Suárez-Santiago VN, Ortega A, Peintner U, López-Flores I (2009) Study on Cortinarius subgenus Telamonia section Hydrocybe in Europe, with especial emphasis on Mediterranean taxa. Mycol Res 113:1070–1090
Thiers B (2013) Index Herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden’s Virtual Herbarium. http://sweetgum.nybg.org/ih/
Velenovský J (1939) Novitates Mycologicae. Prague, Czech
White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Michael AJ, Gelfand DH, Sninsky JJ, White TJ (eds) PCR protocols: a guide to the methods and applications. Academic Press, New York, pp 315–322
Willis KJ (ed) (2018) State of the world’s fungi 2018. Report. Royal Botanic Gardens, United Kingdom.