Taming the beast: a revised classification of *Cortinariaceae* based on genomic data

Kare Liimatainen¹ · Jan T. Kim² · Lisa Pokorny¹,³ · Paul M. Kirk⁴ · Bryn Dentinger⁵ · Tuula Niskanen¹,⁶

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Abstract

Family *Cortinariaceae* currently includes only one genus, *Cortinarius*, which is the largest *Agaricales* genus, with thousands of species worldwide. The species are important ectomycorrhizal fungi and form associations with many vascular plant genera from tropicals to arctic regions. Genus *Cortinarius* contains a lot of morphological variation, and its complexity has led many taxonomists to specialize in particular infrageneric groups. The previous attempts to divide *Cortinarius* have been shown to be unnatural and the phylogenetic studies done to date have not been able to resolve the higher-level classification of the group above section level. Genomic approaches have revolutionized our view on fungal relationships and provide a way to tackle difficult groups. We used both targeted capture sequencing and shallow whole genome sequencing to produce data and to perform phylogenomic analyses of 75 single-copy genes from 19 species. In addition, a wider 5-locus analysis of 245 species, from the Northern and Southern Hemispheres, was also done. Based on our results, a classification of the family *Cortinariaceae* into ten genera—*Cortinarius*, *Phlegmacium*, *Thaxterogaster*, *Calonarius*, *Aureonarius*, *Cystinarius*, *Volvanarius*, *Hygronarius*, *Mystinarius*, and *Austrocortinarius*—is proposed. Seven genera, 10 subgenera, and four sections are described as new to science and five subgenera are introduced as new combinations in a new rank. In addition, 41 section names and 514 species names are combined in new genera and four lecto- and epitypes designated. The position of *Stephanopus* in suborder *Agaricineae* remains to be studied. Targeted capture sequencing is used for the first time in fungal taxonomy in Basidiomycetes. It provides a cost-efficient way to produce -omics data in species-rich groups. The -omics data was produced from fungarium specimens up to 21 years old, demonstrating the value of museum specimens in the study of the fungal tree of life. This study is the first family revision in Agaricales based on genomics data and hopefully many others will soon follow.

Keywords Agaricales · Fungariomics · Fungi · HybPiper · Museomics · Targeted capture sequencing · Whole genome sequencing

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¹ Jodrell Laboratory, Royal Botanic Gardens, Kew, Surrey TW9 3AB, UK
² Department of Computer Science, School of Physics, Engineering and Computer Science, University of Hertfordshire, Hatfield, Hertfordshire AL10 9AB, UK
³ Present Address: Institut Botànic de Barcelona (IBB, CSIC-Ajuntament de Barcelona), 08038 Barcelona, Catalonia, Spain
⁴ Biodiversity Informatics and Spatial Analysis, Jodrell Laboratory, Royal Botanic Gardens, Kew, Surrey TW9 3AB, UK
⁵ Natural History Museum of Utah and School of Biological Sciences, University of Utah, Salt Lake City, UT, USA
⁶ Botanical Museum, University of Helsinki, P.O. Box 7, 00014 Helsinki, Finland
Introduction

Genomic-level data have revolutionized our views on fungal relationships and helped us create better phylogenies for previously unresolved lineages (e.g., Chang et al. 2021; Li et al. 2021). These data have been used to tackle macroevolutionary events, e.g., mushroom morphological evolution (Varga et al. 2019, Sánchez-García et al. 2020) or the evolution of symbiotic traits (Miyachi et al. 2020). High-throughput sequencing (HTS) techniques have also allowed genomic data to be generated from fungarium specimens (Dentinger et al. 2016).

Fungal genomes are small, ranging from 7.67 to 720.2 Mbp/1C (Kullman et al. 2005), with an average size of ~63 Mbp/1C in Ascomycota (Hill et al. 2021) and ~50 Mbp/1C in Basidiomycota (Mohanta and Bae 2015; Li et al. 2018), compared to those of plants and animals, e.g., ranging 64 Mbp/1C to 140 Gbp/1C in angiosperms (Pellicer et al. 2018) and 1.6 to 6.3 Gbp/1C in mammals (Kapusta et al. 2017). Therefore, in phylogenomics studies of fungi, in depth or shallow whole genome sequencing (WGS) have been an affordable option to generate HTS data, with the vast majority of the fungal genomic studies to date having relied on this approach. However, for species-rich groups where hundreds to thousands of samples might be included, targeted capture sequencing provides a more cost-effective alternative (Hale et al. 2020). Enrichment methods have been widely used to study the systematics of plants and animals (e.g., Johnson et al. 2019; Faircloth 2017) and they have recently been applied in fungal systematics to study lichen-forming Ascomycota families Lobariaceae (Widhem et al. 2019) and Parmeliaceae (Grewe et al. 2020), as well as the Peltigeralean backbone (Widhem et al. 2021).

The family Cortinariaceae belongs to suborder Agariceae, which contains mainly the brown and dark-spored Agaricales with thick-walled and pigmented basidiospores (Matheny et al. 2015; Dentinger et al. 2016). According to the most recent phylogenetic studies, the family Cortinariaceae only includes one genus, Cortinarius (Pers.) Gray. Several genera formerly placed in the Cortinariaceae, e.g., Phaeocollybia R. Heim, Hebeloma (Fr.) P. Kumm., and Galerina Earle, have been moved to other families in the Agariceae (Matheny et al. 2015). On the other hand, many taxa previously treated as separate genera are currently included into Cortinarius: Bulbopodium Earle, Cuphocybe R. Heim, Dermocybe (Fr.) Wünsche, Inoloma (Fr.) Wünsche, Myxacium (Fr.) P. Kumm., Phlegmacium (Fr.) Wünsche, Rapaceae E. Horak, Rozites P. Karst., and Telamonia (Fr.) Wünsche, as well as sequestrate genera Gigasperma E. Horak, Hymenogaster Vittad. p.p., Protoglossum Mass. Quadrirspora Bougher & Castellano, and Thaxterogaster Singer (Peintner et al. 2001, 2002, 2004; Garnica et al. 2005; Soop et al. 2019; Nouhra et al. 2021). Other than Cortinarius, the only genus currently placed in the family Cortinariaceae is the South American Stephanoascus M.M. Moser & E. Horak, a small genus with five described species associated with Nothofagaceae, but it is lacking any sequence data and thus its position in the suborder Agaricinae remains unresolved.

As currently delimited, Cortinarius is by far the largest genus of Agaricales, and its representatives are found from the tropics to arctic habitats in the Northern and Southern Hemispheres. To date, over 5000 taxa, including subspecies and varieties, have been recorded in Index Fungorum (2021). ITS sequence data exist for close to 3000 species (UNITE 2021, using an SH threshold of 1.5%), including both described and undescribed taxa. However, sequence data from many regions of the world are still lacking and, thus, many more species are in urgent need of sequencing and/or description.

Cortinariaceae species are important ectomycorrhizal fungi and form associations with many vascular plants, including mainly woody species (trees and some shrubs) in the gymnosperms (Pinaeaceae) and the rosids angiosperms—orders Fabales (Fabaceae), Fagales (Betulaceae, Fagaceae, Nothofagaceae), and Rosales (Rhamnaceae, Rosaceae), in the so-called nitrogen fixing clade; core Malvales (Malvaceae, plus the Cistaceae, Diterocarpaceae, and Sarco- laenaceae clade); and, even, orders Malpighiales (Phyllanthaceae, Salicaceae) and Myrtales (Myrtaceae)—as well as some herbaceous angiosperms, both in the monocots (Cyperaceae and Orchidaceae) and in the Caryophyllids eudicots (Polygonaceae) (Moser and Horak 1975; Harrington and Mitchell 2002; Froslie et al. 2005; Garnica et al. 2005; Jacquemyn et al. 2010; Tedersoo et al. 2011; Harrower et al. 2015a; Thoen et al. 2019). The species of Cortinariaceae provide access to nitrogen for vascular plants in nutrient poor habitats, and their role in carbon cycling has been studied for northern European (Bödeker et al. 2014; Lindahl et al. 2021) and North American (Fernandez et al. 2020) boreal forests.

The first study based on molecular data (Høiland and Holst-Jensen 2000) indicated that many of the traditional infragenetic groupings of Cortinarius were unnatural (e.g., Moser 1983; Brandrud et al. 1989; Bidaud et al. 1994). During the following 20 years many studies were conducted to gain a better understanding of their natural relationships. Most of these datasets were based only on sequences from the ITS and LSU regions (Høiland and Holst-Jensen 2000; Peintner et al. 2004; Garnica et al. 2005; Harrower et al. 2011; Lii- matainen et al. 2014, 2020a; Steinsrud et al. 2014), and only two extensive studies of the genus also included data from RPB1 and/or RPB2 regions (Garnica et al. 2016; Soop et al. 2019). So far, the only study to include more than a handful
of DNA markers (ITS, nLSU, GPD, MCM7, RPB1, RPB2, and TEF1) was conducted by Stefani et al. (2014) for the delimitation of Australian dermocyboid Cortinarius species. Despite these efforts, no genus-wide, revised subgeneric classification of Cortinarius has been presented because it has not been possible to resolve the backbone of the phylogeny. Existing sequence data have, however, allowed the revision of various sections within Cortinarius, with studies by Soop et al. (2019), Liimatainen et al. (2020a), Ammirati et al. (2021), and Niskanen and Liimatainen (2021) presenting the most updated morpho-genetic, section-level classification of Cortinarius, including a total of 172 sections.

The aim of this study was to conduct the first phylogenomic study of family Cortinariaceae to resolve higher-level relationships and allow for a revised genus-level classification of the group.

Materials and methods

Molecular sampling

Sampling was designed to cover as many of the major lineages of Cortinariaceae as possible, based on the latest phylogenetic trees published for the family (Garnica et al. 2016; Soop et al. 2019). Vouchers of 19 dried fungarium specimens sampled for genomics work are deposited in the collections of the Royal Botanic Gardens, Kew, United Kingdom (K) and/or (H) University of Helsinki, Finland.

DNA extraction and genomic library preparation

DNA was extracted from 2 to 4 mg of dried grounded lamella with the DNeasy Plant Mini kit (Qiagen, Germantown, USA). Extracted DNA was quantified using a Quantus™ fluorometer and the Quantifluor dsDNA system kit (Promega Corporation, Madison, WI, USA). To get an estimation of the average fragment size, samples were assessed on a 2100 Bioanalyzer (Agilent Technologies, Santa Clara, CA, USA), using the appropriate DNA chips and reagents, or a 4200 TapeStation System (Agilent Technologies), using the corresponding Genomic DNA ScreenTapes and reagents. The DNA was then fragmented using an M220 Focused-ultrasonicator™ (Covaris, Woburn, MA, USA) with varied shearing times (30–45 s) depending on the DNA fragment size profile. The average fragment size in the specimens that were used for WGS ranged from 680 to 745 bp, and from 660 to 880 bp for the specimens used for the targeted capture sequencing.

Dual-indexed libraries for WGS were prepared using a TruSeq® Nano DNA LT (Illumina Inc.) sample kit following the manufacturer’s protocols. Dual-indexed libraries for the targeted capture sequencing were prepared using the NEBNext® UltraTM II Library Prep kit and the NEBNext® Multiplex Oligos for Illumina® (Dual Index Primer Set 1), according to the manufacturer’s protocols (New England BioLabs, Ipswich, MA, USA), although at half the recommended volumes. The resulting genomic libraries were quantified and qualified as above (i.e. Quantus and Bioanalyzer/TapeStation).

WGS, genome assembly, and extraction of single-copy orthologs

For WGS, five to six libraries were pooled following Dentinger et al. (2016). The sequencing was performed on an Illumina MiSeq with v3 (2 x 300 bp paired-end reads) chemistry (Illumina, San Diego, CA, USA) at Jodrell Laboratory, Royal Botanic Gardens, Kew.

Demultiplexed reads were quality-checked with FastQC (Andrews 2010) before trimming with Trimmomatic v0.39 (Bolger et al. 2014) with settings: LEADING:3 TRAILING:3 SLIDINGWINDOW:4:15 MINLEN:36. The genomes were then assembled using ABySS (Simpson et al. 2009) with a k-mer size ranging 51–96 bp, depending on the quality of the sequence data.

Next, the 208 single-copy genes identified by Dentinger et al. (2016) were extracted from the nine assembled genomes using exonerate v2.2.0 (Slater and Birney 2005) with Cortinarius glaucopus (Miyauchi et al. 2020) amino acid (AA) sequences (for the 208 single-copy genes) as queries in searches against our nine assemblies. The top-scoring hit was retained in each case. Additionally, we included the AA sequences of the five single-copy loci currently used in phylogenetic studies of family Cortinariaceae, which were not part of the 208-gene queries in the exonorate search: RPB1 (RNA polymerase II largest subunit B220; also RPO21; C. odorifer GenBank no. DQ083857), RPB2 (RNA polymerase II second largest subunit B150; also RPO22; Coprinopsis cinerea, GenBank no. XM_001829088), MCM7 (component of the Mmc2-7 hexameric helicase complex; also CDC47; C. basirubescens Genbank no. JN985546), GPD (glyceraldehyde-3-phosphate dehydrogenase (GAPDH), isozyme 3; also TDH3; C. austrosanguineus JX675721), and TEF1 (Translational elongation factor EF-1 alpha; also eEF1A; C. sodagnitus GenBank no. DQ061275) to also retrieve sequences of those regions from the genome assemblies. These regions were compared against the assemblies to verify that they were truly single-copy ones in our species.

Enrichment panel probe design

Our goal was to design a 20,000-probe custom myBaits® enrichment panel for target capture of phylogenetically-informative, single-copy nuclear orthologs. Four out of
nine Cortinarius species (C. victoriaensis, C. neofurvolae-sus, C. scaurus, and C. typicus), for which most single-copy orthologs recovered by exonorate and representing different lineages across Cortinariaceae, were selected for probe design. The size of the dataset exceeded the limits of the 20,000 probe enrichment panel and we therefore discarded 20 target genes with the most missing data from all four species. The final dataset included 188 targets, from those identified by Dentinger et al. (2016), with the addition of the currently used loci (RPB1, RPB2, MCM7, GPD, and TEF1), resulting in a total of 193 targets. For the probe design, nucleotide sequences containing both intron and exon regions were used. Based on the visual inspection of the alignments of each target, the intron regions were generally short (< 50 bp) and largely conserved within the family making it possible to include them in the enrichment panel. The design and production of the probes was done by Arbor Biosciences (Ann Arbor, Michigan, USA) based on the sequence data provided. The probes were 120 nucleotides long and designed with ~ 2 × tiling density.

Hybridisation and targeted capture sequencing

Dual-indexed genomic libraries were pooled and hybridised with our custom myBaits® enrichment panel, following v3.0 manufacturer’s protocols, with the exception of pooling four or nine libraries per hybridisation reaction and each reaction having a total of ¼ of the recommended volume. Hybridisations were performed at 65 °C for 20 h in Vapo Protect Mastercycler 6325 thermocycler (Eppendorf, Arlington, UK). Captured targets were amplified with a KAPA HiFi 2 × Hot-Start ReadyMix PCR kit (Roche, Basel, Switzerland) for 10 cycles, and the PCR products were cleaned using Agencourt AMPure XP magnetic beads. Final products were quantified and qualified as above. Thirteen enriched libraries were further pooled for sequencing on an Illumina MiSeq platform (Illumina, San Diego, CA, USA) using v2 Nano chemistry (2 × 250 bp paired-end reads) at the Jodrell Laboratory, Royal Botanic Gardens, Kew.

Target retrieval and sequence assembly

Demultiplexed reads were quality-checked as above before trimming with Trimmomatic v0.39 (Bolger et al. 2014) with settings: LEADING:20 TRAILING:20 SLIDING-WINDOW:4:20 MINLEN:36. The HybPiper v1.3.1 (Johnson et al. 2019) pipeline was used for downstream analyses. First, quality-filtered, trimmed reads were mapped to amino acid (AA) sequences corresponding to our target loci using BLASTx (Altschul et al. 1990). Second, paired, mapped reads were assembled into contigs using SPAdes v3.13.1 (Bankevich et al. 2012), using default settings with the exception of minimum coverage, which was set to 4x. Third, the intronate.py script was used to generate supercontigs (scaffolded merged SPAdes contigs containing both complete exon and intron sequences) and retrieve_sequences.py was used to retrieve the final supercontig sequences (of the target loci from each of our specimens) to build the data matrices required for subsequent phylogenetic analyses. Finally, summary statistics (e.g., percent of reads mapped to target) were generated using SAMtools (Li et al. 2009) and the hybpiper_stats.py script.

Data mining and data matrix generation

Two different data matrices were assembled for downstream phylogenetic analyses. The first consisted of the single-copy orthologs from both the shallow WGS and the targeted capture sequencing data, for a total of 19 species. Of the original 193 single-copy orthologs targeted, 75 of them (including RPB1, RPB2, MCM7, GPD, and TEF1), present at least in > 50% of the species sampled and with > 500 bp of average length recovered, were selected for further analysis. For Cortinarius crassus, the data matrices originating from WGS versus targeted capture sequencing were kept separate to allow direct comparison of these two approaches.

For the second data matrix, we mined NCBI GenBank for RPB1 sequences from Cortinariaceae species, which we combined with 17 newly generated RPB1 sequenced from the WGS and targeted capture sequencing data. When available, we also mined RPB2 (from 18 genomes), MCM7 (9), GPD (12), and TEF1 (10) for these same samples. The final data matrix included 245 species.

Multiple sequence alignment and phylogenetic analyses

For both data matrices, all loci were individually aligned using MAFFT v7 with iterative refinement (i.e., E-INS-i algorithm; Katoh and Standley 2013) and, then, manually adjusted in SeaView (Galtier et al. 1996) following the guidelines summarized in Morrison (2006). The individual alignments were then concatenated in Mesquite v3.2 (Maddison and Maddison 2017). Phylogenetic trees were generated from the two concatenated data matrices, with model parameter estimation partitioned by loci, using RAxML v8.2.12 with 1000 traditional bootstrap (BS) replicates under the GTR + Γ model (Stamatakis 2014), as advised by Young & Gillung (2020). For the first data matrix, Crepidotus sp. (Dentinger et al. 2016) and Hebeloma cylindrosporum (Kohler et al. 2015) were used as outgroups. For the second data matrix, the backbone topology inferred from the first data matrix was used as a topological constraint.
Data availability

The nine new Cortinariaceae genomes sequenced for the present study are deposited in the European Nucleotide Archive (Study ID PRJEB49625) and the raw reads resulting from the targeted capture sequencing in the NCBI GenBank Sequence Read Archive, SRA (BioProject PRJNA791499). The DNA sequences used to design the enrichment panel probes are available on Dryad (https://doi.org/10.5061/dryad.0p2ngf238).

Molecular results

WGS and targeted capture sequencing performance

Summary statistics for the WGS, targeted capture sequencing, and locus mining used in the phylogenomic analysis are presented in Tables 1 and 2. There was substantial variation in the quality of the assemblies from WGS data and, thus, in the recovery rate of the targeted single-copy orthologs. Anywhere from 33 to 100% of the 75 target markers chosen for the final phylogenomics analysis were recovered and the recovery rate was >70% for only four out of nine specimens. The recovery rate for the targeted capture sequencing was far better: it was >85% (of the 75 loci) for nine out of eleven specimens and substantially less (35% and 45%) in only two specimens. Reads mapped to the initial 193 targets ranged from 10,101 to 93,312. On average, over 23,000 reads were needed to reach >85% coverage for the 75 loci, and over 33,000 reads were needed to reach >95% coverage. Pooling nine specimens in one baiting reaction generally produced good results: in 8 out of 9 specimens >88% of the 75 target loci were recovered, only in one specimen the recovery rate was low, <35%.

Phylogenomic inference and systematic rearrangements

The phylogeny inferred from 75 single-copy nuclear orthologs for 20 accessions is shown in Fig. 1. The results of the wider 5-locus analysis, containing 245 species, are presented in Fig. 2. Nodal support BS values below 85% are considered weak, between 85 and 95% moderate, between 95 and 99% BS strong, and lastly, 100% denotes full support. Based on the results, the division of the family Cortinariaceae into ten putative genera is proposed and these names are used hereon.

In the phylogenomics tree (Fig. 1), Thaxterogaster (BS 68%) is sister to a clade encompassing all other genera (BS 79%), both weakly supported. This latter clade is further divided into a strongly supported Cortinarius (BS 95%) and a weakly supported clade containing the remaining genera (BS 82%). The strongly supported (BS 95%) crown of this latter clade is composed of fully supported Aureonarius (BS 100%), Phlegmacium (BS 100%), as well as Calonarius, here represented by just one species. Austrocorrotinarius, also represented by one accession, and fully supported Cystinarius (BS 100%) are in a grade leading to the aforementioned crown clade. From the sampled genera represented by more than one species, only one, Thaxterogaster, received a suboptimal BS value (<95%).

The results of the phylogenetic analysis, based on the five most-used single-copy marker genes in Cortinarius from 245 taxa, are presented in Fig. 2. All genera represented by more than one accession in this analysis received moderate to full support: Aureonarius (BS 100%), Austrocorrotinarius (BS 100%), Calonarius (BS 100%), Cystinarius (BS 99%), Hygronarius (BS 92%), Phlegmacium (BS 88%), Thaxterogaster (BS 99%), Volvanarius (BS 100%). The only exception was genus Cortinarius s. str. that received lower support (BS 70%). The diversity, distribution, and selected morphological characters for the proposed genera are summarized in Table 3.

The infrageneric relationships were variably resolved in different genera (Fig. 2). In genus Calonarius, three weakly to moderately supported subgenera were recognized: C. subgen. Calonarius (BS 63%), C. subgen. Calochroi (BS 87%), and C. subgen. Fulvi (BS 75%). Genus Aureonarius was divided into two strongly to fully supported subgenera: A. subgen. Aureonarius (BS 100%) and A. subgen. Callistei (BS 98%). In genus Phlegmacium, four moderately to strongly supported subgenera were recognized: P. subgen. Phlegmacium (BS 91%), P. subgen. Carbonella (BS 98%), P. subgen. Bulbodium (BS 96%), and C. subgen. Cyanicum (represented by just one species in our analysis). The genus Cystinarius has two subgenera: C. subgen. Crassi (BS 100%) and C. subgen. Cystinarius (represented by one species in the analysis). The infrageneric relationships in the genus Cortinarius remained mostly unresolved but the following lineages with more than one species in our analysis received moderate to full support: C. subgen. Dermocybe (BS 93%), C. subgen. Leprocye (BS 93%), C. subgen. Iodolentes (BS 100%), C. subgen. Telamonia (BS 100%), C. subgen. Myxacium (BS 97%), and C. subgen. Cortinarius (BS 100%). In the genus Thaxterogaster many relationships remained unresolved, although the following subgenera received weak to full support: T. subgen. Multi-formes (BS 83%), T. subgen. Aureonarius (BS 96%), T. subgen. Thaxterogaster (BS 99%), T. subgen. Scauri (BS 92%), and T. subgen. Riederorum (BS 100%).

Taxonomy

New and emended generic descriptions are presented below, as well as descriptions of new subgenera and short notes on the previously existing subgenera. The diversity, distribution
Table 1 *Cortinariaceae* specimens used for WGS and summary statistics for the genome assembly and recovery rate of the single-copy nuclear orthologs curated by Dentinger et al. (2016)

| Genus name | Species name | Voucher number (fungarium) | Collection year | Yield of DNA from extr. (ng/µl) | 260/280 (1.7–1.9) | 260/230 (2.0–2.2) | Pool of five or six | Number of reads | Assembly size | Number of contigs | Max contig length (bp) | N50 | Number (percent) of single-copy orthologs, out of the 75 used |
|------------|--------------|----------------------------|------------------|-------------------------------|------------------|------------------|-------------------|----------------|--------------|----------------------|------------------------|-----|--------------------------------------------------------|
| *Cortinarius* | *C. bovarius* | TN11-191 (K(M), H) | 2011 | 17 | 1.92 | 1.49 | 5 | 4,545,983 | 3.59E + 07 | 386,493 | 48,684 | 1935 | 44 | 59% |
| *Cortinarius* | *C. alces* | TN11-065 (K(M), H) | 2011 | 29 | 1.96 | 1.68 | 5 | 5,256,187 | 3.72E + 07 | 558,926 | 53,036 | 2176 | 54 | 72% |
| *Cortinarius* | *C. glandicolor* | TN15-018 (K(M)) | 2015 | 104 | 1.69 | 0.88 | 6 | 3,479,379 | 3.27E + 07 | 748,987 | 47,177 | 1519 | 30 | 40% |
| *Cortinarius* | *C. neofurfurolaeus* | TN11-113 (K(M), H) | 2011 | 21 | 1.95 | 1.74 | 5 | 5,015,654 | 3.70E + 07 | 374,514 | 59,009 | 3335 | 64 | 85% |
| *Aureonarius* | *A. tofaceus* | TN10-061 (K(M), H) | 2010 | 96 | 1.93 | 2.42 | 5 | 5,867,977 | 2.41E + 07 | 2,450,611 | 14,723 | 1550 | 31 | 41% |
| *Austrocortinarius* | *A. victorinaevis* | K(M)162,337 | 1995 | 123 | 1.77 | 1.34 | 6 | 3,542,880 | 4.32E + 07 | 113,713 | 94,283 | 5713 | 74 | 99% |
| *Calonarius* | *C. typicus* | TN14-281 (K(M), H) | 2014 | 6.7 | 2 | 1.1 | 6 | 3,746,677 | 3.74E + 07 | 178,051 | 160,564 | 5178 | 75 | 100% |
| *Cystinarius* | *C. crassus* | TN07-305 (K(M), H) | 2007 | 29 | 1.89 | 1.67 | 5 | 5,018,344 | 2.31E + 07 | 403,693 | 22,643 | 1593 | 25 | 33% |
| *Thaxterogaster* | *T. scaurus* | TN15-013 (K(M)) | 2015 | 81 | 1.81 | 1.3 | 6 | 3,508,661 | 2.72E + 07 | 1,012,788 | 25,636 | 2090 | 33 | 44% |

The four species used to design the baits for the *Cortinariaceae* enrichment panel are in bold.
| Genus name | Species name       | Voucher number (fungarium) | Collection year | Yield of DNA from extr. (ng/µl) | 260/280 (1.7–1.9) | 260/230 (2.0–2.2) | MiSeq Nano output file size (Mb) | Reads mapped to target | Capture pool No. (%) of single-copy orthologs, out of the 75 used | No. (%) of single copy orthologs recovered, out of 193 total |
|------------|--------------------|---------------------------|-----------------|-------------------------------|------------------|------------------|---------------------------------|------------------------|---------------------------------------------------------------|---------------------------------------------------------------|
| **Cortinarius** | *C. ominosus* | TN06-077 (K(M), H) | 2006            | 11                            | 1.88             | 2.24             | 14.1               | 36,403                              | 4                                    | 75 (100%)                                                   | 188 (97%)                                                   |
| **Cortinarius** | *C. rubellus*    | TN15-009 (K(M))         | 2015            | 44                            | 1.74             | 0.94             | 6.2                | 12,003                              | 4                                    | 30 (40%)                                                   | 49 (25%)                                                   |
| **Cortinarius** | *C. cremeoglobo-| TN15-028 (K(M))         | 2015            | 11                            | 1.75             | 1.56             | 12.3               | 27,626                              | 9                                    | 70 (93%)                                                   | 167 (87%)                                                   |
| **Cortinarius** | *C. subtortus*  | MT16-001 (K(M))         | 2016            | 11                            | 1.75             | 1.44             | 13.2               | 33,168                              | 9                                    | 71 (95%)                                                   | 177 (92%)                                                   |
| **Aureonarius** | *A. callisteus* | TN07-395 (K(M), H)     | 2007            | 55                            | 1.84             | 1.81             | 6.6                | 10,101                              | 9                                    | 26 (35%)                                                   | 52 (27%)                                                   |
| **Aureonarius** | *A. limonius*   | TN07-282 (K(M), H)     | 2007            | 44                            | 1.92             | 2.17             | 15.2               | 32,781                              | 9                                    | 74 (99%)                                                   | 184 (95%)                                                   |
| **Cystinarius** | *C. crassus*    | TN07-305 (K(M), H)     | 2007            | 25                            | 1.81             | 1.5              | 15.3               | 40,731                              | 9                                    | 74 (99%)                                                   | 177 (92%)                                                   |
| **Phlegmacium** | *P. glaucopus*  | TN12-286 (K(M), H)     | 2012            | 19                            | 1.8              | 1.55             | 23.4               | 72,481                              | 9                                    | 75 (100%)                                                   | 193 (100%)                                                  |
| **Phlegmacium** | *P. volvatum*   | TN12-267 (K(M), H)     | 2012            | 24                            | 1.93             | 1.83             | 10.8               | 23,690                              | 9                                    | 67 (89%)                                                   | 149 (77%)                                                   |
| **Thaxterogaster** | *T. malachioides* | TN07-313 (K(M), H)  | 2007            | 17                            | 1.87             | 0.98             | 18.9               | 51,199                              | 9                                    | 74 (99%)                                                   | 185 (96%)                                                   |
| **Thaxterogaster** | *T. variegatus* | TN07-252 (K(M), H)     | 2007            | 20                            | 1.85             | 2.03             | 31.5               | 93,312                              | 9                                    | 75 (100%)                                                   | 193 (100%)                                                  |
and selected morphological characteristics of the proposed genera are summarized in Table 3.

**Cortinariaceae** R. Heim ex Pouzar, Česká Mykol. 37(3): 174 (1983) **em. Niskanen & Liimat.**

Nom. cons. (Art. 14)

Current name of the type species: **Cortinarius violaceus** (L.) Gray, Nat. Arr. Brit. Pl. (London) 1: 628 (1821). Sanctioned in Fr., Syst. mycol. 1: 217 (1821). Basionym of the type species: **Agaricus violaceus** L., Sp. pl. 2: 1173 (1753). Lectotype: Bulliard, Herbier de la France: pl. 598 Fig. 2A, 1793 (lectotypus hic designatus, IF551873, as *Agaricus araneosus*).

Epitype: Sweden, Ångermanland, Hännösand, Geresta, 25 Aug 1993, coll. H. Lindström et al. CFP 1197 (S, epitypus hic designatus IF551874), GenBank No. OL958654 (ITS).

**Synonyms:** **Gigaspermacae** Jülich, Bibliothca Mycol. 85: 367 (1982) [1981]. Nom. illegit., Art. 53.1. Type genus: **Gigasperma** E. Horak, N.Z. Jl Bot. 9(3): 491 (1971). Current name of the type species: **Thaxterogaster crypticus** (E. Horak) Niskanen & Liimat., comb. nov. IF551875. Basionym of the type species: **Gigasperma cryptica** E. Horak, N.Z. Jl Bot. 9(3): 491 (1971). Holotype: 27002 (PDD).

Currently included genera: **Cortinarius**, **Aureonarius**, **Austrocortinarius**, **Calonarius**, **Cystinarius**, **Hygronarius**, **Mystinarius**, **Phlegmacium**, **Thaxterogaster**, and **Volvanarius**.

**Description:** Basidiomata small- to large-sized, agaricoid or sequestrate, development type stipitocarpic or pileocarpic. Pileus at first conical to low convex to plane, with or without an umbo; surface smooth, innately fibrillose, tomentose or ± scaly; ± brown, ± yellow/ochraceous, white, ± grey, more or less purple or blackish brown to black, more rarely orange, red, or green/olivaceous; dry, viscid or glutinous, hygrophanous, with hygrophanous spots or streaks or non-hygrophanous. Lamellae crowded to distant; adnate, adnexed or emarginate; when young greyish white, pale grey, pale to dark brown, or with a purplish tint or purple, more rarely yellow, green/olivaceous, orange or red. Stipe cylindrical, clavate, bulbous or rooting; usually silky-fibrillose, white, pale to dark brown, with purplish tints or purple or ± yellow/ochraceous, more rarely green/olivaceous, orange, red or blackish; dry to glutinous. Universal veil white, yellow/ochraceous, purple, grey/brown, pink/red, or green/olivaceous, in some species changing colour with age or on exposure; sparse to abundant, in pileocarpic species found from the margin of the bulb, in species of the genus **Volvanarius** often forming a volva at the base of the stipe. In stipitocarpic species forming incomplete and/or complete girdles on the stipe, or a sock-like sheet on the lower part of the stipe, more rarely forming a ring at the upper part of the stipe; dry or viscid. Odour in many species indistinct, when present in most species then best observed in
lamellae and then raphanoid, fruity, earthy, cellar-like, cedar tree-like, perfume-like, yeast-like, farinaceous, grassy, rubbery, pelargonium-like, curry-like, anise or unpleasant. The honey-like odour, typical to part of the species of *Cortinarius* subgen. *Myxacium*, *Thaxterogaster* subgen. *Multiformes* and *T*. subgen. *Scauri*, is best observed in the context of the stipe. In part of the species of *C*. subgenus *Iodolentes* the base of the stipe has an odour of iodorm that is best observed when the basidiomata are slightly dried and in *Aureonarius* subgen. *Callistei* the odour of the surface of the pileus in some species is like a recently extinguished candle (ozone) or apple-like. KOH/NaOH reaction useful in identification of the species of *Calonarius* and *Phlegmacium*. Basidiospores 4.5–20 × 3–10 μm, in vast majority of the species ± amygdaloïd, ± ellipsoid, ± citriform or ± subglobose, less commonly obovoidly ellipsoid, fusoid, lacrymoid, or boletoid, finely to strongly verrucose, somewhat to strongly dextrinoid in Melzer’s reagent, some species non-dextrinoid. Cystidia present in genus *Cystinarius*, *Cortinarius* subgen. *Cortinarius*, *C*. sect. *Camphorati*, *C*. sect. *Subtorti*, and some species of *C*. subgen. *Iodolentes*, *C*. sect. *Bicolores* and genus *Volvanarius*. Pileipellis in vast majority of the taxa ± duplex with a more or less developed hypoderm, simplex in *Calonarius*, *Austrocortinarius*, *Phlegmacium* subgen. *Cyanicium*, *Cortinarius* subgen. *Cortinarius* and *C*. sect. *Subtorti* and in part of the species of *Phlegmacium* subgen. *Phlegmacium*, *Cortinarius* sect. *Delibuti*. In genus *Cystinarius* somewhat duplex-like, the hypoderm is poorly developed but the hyphae beneath the epicutis are hypoderm-like (elements that are short and wide).

Ecology and Distribution: With a world-wide distribution; species occur both in Northern and Southern Hemisphere from tropical to arctic-alpine habitats. The species of *Cortinariaceae* are ectomycorrhizal and form associations with the trees and shrubs from *Fagales*, *Salicaceae*, *Cistaceae*, *Dipterocarpaceae*, *Myrtaceae*, *Fabaceae* (e.g., *Dicymbe*), *Rhamnaceae*, *Rosaceae*, and *Pinaceae*, as well as with some herbaceous angiosperms in the *Cyperaceae*, *Orchidaceae*, and *Polygonaceae*.

Notes: Typical for the species of the family *Cortinariaceae* are ornamented basidiospores that are cinnamon brown in deposit. Most species also have a cobweb-like inner veil covering the young lamellae and the remnants of it can often still been found at the upper part of the stipe in older basidiomata. Characteristic is also the silky-fibrillose stipe, at least easily observed at the top of the stipe. Majority of the species lack cheilo- and/or pleurocystidia which are only found in genus *Cystinarius* and some lineages of genera.
Cortinarius and Volvanarius. The structure of the pileipellis in the majority of genera and subgenera is duplex with a more or less developed hypoderm.

Variation in size and coloration of basidiomata is large. One of the smallest species, Cortinarius bibulus, has a pileus of 0.3–1.5 cm in diam. and a stipe 1.5–5 × 0.1–0.3 cm, and one of the largest, Phlegmacium praestans, has a pileus up to 20 cm in diam. and a stipe up to 20 × 3 cm. A wide variety of colored pigments can be found from the basidiomata although brownish, ochreous/yellow, greyish, whitish, and purplish colours are most common.

**Table 3**

| Genus       | Generic synonyms | Estimated no. of species | Subgen./section no. | Distribution | Cystidia Stipitocarpic | Pileipellis | Sequestrate | Appearance of the agaricoid basidiomata | Rozitoid/cuphocyboid | Myxacioid | Phlegmac Telamonioid Cortinarioid |
|-------------|------------------|--------------------------|--------------------|--------------|------------------------|------------|-------------|----------------------------------------|-----------------------|-----------|-------------------------------|
| Cortinarius |                  | > 2000                   | 3                  | N + S        | (X)                    | S/(P)      | X X (X)     | Sequestrate sp                        | Cystidia Simplex/Duplex | X         | Duplex                        |
| Phlegmacium |                  | > 200                    | 3                  | N + S        | N + S                  | S/P        | X X X       | Sequestrate sp                        | Cystidia Simplex/Duplex | X         | Duplex                        |
| Thaxterogaster |              | > 2000                   | 3                  | N + S        | N + S                  | S/P        | X X X       | Sequestrate sp                        | Cystidia Simplex/Duplex | X         | Duplex                        |
| Calonarius  |                  |                          |                    | N + S        | N + S                  | S/P        | X X X       | Sequestrate sp                        | Cystidia Simplex/Duplex | X         | Duplex                        |
| Aureonarius |                  |                          |                    | N + S        | N + S                  | S/P        | X X X       | Sequestrate sp                        | Cystidia Simplex/Duplex | X         | Duplex                        |
| Volvanarius |                  |                          |                    | N + S        | N + S                  | S/P        | X X X       | Sequestrate sp                        | Cystidia Simplex/Duplex | X         | Duplex                        |
| Hygroatractus |               |                          |                    | N + S        | N + S                  | S/P        | X X X       | Sequestrate sp                        | Cystidia Simplex/Duplex | X         | Duplex                        |
| Mystinarius |                  |                          |                    | N + S        | N + S                  | S/P        | X X X       | Sequestrate sp                        | Cystidia Simplex/Duplex | X         | Duplex                        |
| Myxophilus |                  |                          |                    | N + S        | N + S                  | S/P        | X X X       | Sequestrate sp                        | Cystidia Simplex/Duplex | X         | Duplex                        |
| Myxacidum |                  |                          |                    | N + S        | N + S                  | S/P        | X X X       | Sequestrate sp                        | Cystidia Simplex/Duplex | X         | Duplex                        |

*Note: Telamonia includes 80 section.*

**Cortinarius (Pers.)** Gray, Nat. Arr. Brit. Pl. (London) 1: 627 (1821) _em. Niskanen & Liimat._

Nom. cons. (Art. 14)

_Basionym:_ Agaricus sect. Cortinaria Pers., Syn. method. fung. (Göttingen) 2: 276 (1801).

_Current name of the type species:_ Cortinarius violaceus (L.) Gray, Nat. Arr. Brit. Pl. (London) 1: 628 (1821). _Basionym of the type species:_ Agaricus violaceus L., Sp. pl. 2: 1173 (1753).

_Synonyms:_ Cuphocybe R. Heim, Revue Mycol., Paris 16: 8 (1951). _Current name of the type species:_ Cortinarius elaiochrous E. Horak, M.M. Moser, Peintner & Vilgalys, Mycotaxon 83: 449 (2002). _Basionym of the type species:_ Cuphocybe olivacea R. Heim, Revue Mycol., Paris 16: 8 (1951).

_Dermocybe_ (Fr.) Wünsche, Die Pilze: 87, 125 (1877). _Basionym:_ Agaricus trib. Dermocybe Fr., Syst. mycol. (Lundae) 1: 10, 227 [‘217’] (1821). _Current name of the type species:_ Cortinarius cinnamomeus (L.) Gray [as ‘Cortinaria’], Nat. Arr. Brit. Pl. (London) 1: 630 (1821). _Basionym of the type species:_ Agaricus cinnamomeus L. 1753.

_Hydrocybe_ (Fr. ex Rabenh.) Wünsche, Die Pilze: 87, 119 (1877). _Basionym:_ Agaricus trib. Hydrocybe Fr., Syst. mycol. (Lundae) 1: 10, 227 [‘217’] (1821). _Current name of the type species:_ Cortinarius duracinus Fr., Epicr. syst. mycol. (Upsaliae): 304 (1838) [1836–1838].

_Inoloma_ (Fr.) Wünsche, Die Pilze: 87, 126 (1877). _Basionym:_ Agaricus trib. Inoloma Fr., Syst. mycol. (Lundae) 1: 10, 227 [‘217’] (1821). _Current name of the type species:_ Cortinarius violaceus (L.) Gray, Nat. Arr. Brit. Pl. (London) 1: 628 (1821). _Basionym of the type species:_ Agaricus violaceus L., Sp. pl. 2: 1173 (1753).

_Myxacium_ (Fr.) P. Kumm., Führ. Pilzk. (Zerbst): 22 (1871). _Basionym:_ Agaricus trib. Myxacium Fr., Syst. mycol. (Lundae) 1: 247 (1821). _Current name of the type species:_ Cortinarius collinitus (Sowerby) Gray [as ‘Cortinaria collinita’], Nat. Arr. Brit. Pl. (London) 1: 628 (1821). _Basionym of the type species:_ Agaricus violaceus L., Sp. pl. 2: 1173 (1753).

_Myxyphilus_ Locq., Fl. Mycol., 3. Cortinariales-A.: 146 (1979) [1977]. _Basionym and current name of the type...
species: Cortinarius mucifluus Fr., Epicr. syst. mycol. (Upsaliae): 274 (1838) [1836–1838].

Protoglossum Masssee, Grevillea 19(no. 92): 97 (1891). Current name of the type species: Cortinarius atatus (Roadway) Gasparini, Mycosphere 5(4): 542 (2014). Basionym of the type species: Protoglossum luteum Masssee, Grevillea 19(no. 92): 97 (1891).

Quadrispora Bouagher & Castellano, Mycologia 85(2): 285 (1993). Current name of the type species: Cortinarius oblongisporus (G.W. Beaton, Pegler & T.W.K. Young) Gasparini, IOSR Journal of Pharmacy 6(4): 3 (2014). Basionym of the type species: Hymenogaster oblongisporus G.W. Beaton, Pegler & T.W.K. Young, Kew Bull. 40(1): 188 (1985).

Rozites P. Karst., Bidr. Känn. Finl. Nat. Folk 32: XX (1879). Current name of the type species: Cortinarius caperatus (Pers.) Fr., Epicr. syst. mycol. (Upsaliae): 256 (1838) [1836–1838]. Basionym of the type species: Rozites caperatus (Pers.) P. Karst., Bidr. Känn. Finl. Nat. Folk 32: 290 (1879).

Sericeocybe Rob. Henry, Bull. trimest. Soc. mycol. Fr. 109(1): 19 (1993). Current name of the type species: Cortinarius caninus (Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 285 (1838) [1836–1838]. Basionym of the type species: Agaricus anomalus var. caninus Fr. 1821.

Telmamonia (Fr.) Wünsche, Die Pilze: 87, 122 (1877). Basionym: Agaricus trib. Telamonia Fr., Syst. mycol. (Lundae) 1: 10, 210 (1821). Current name of the type species: Cortinarius torvus (Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 293 (1838) [1836–1838]. Basionym of the type species: Agaricus torvus Fr., Observ. mycol. (Havniae) 2: 80 (1818).

Currently included subgenera: Cortinarius, Camphorati, Dermocybe, Illumini, Infracti, Iodolentes, Leprocybe, Myxacium, Orellani, Paramyxacium, and Telamonia (Fig. 3).

Description: Basidiomata small- to large-sized, agaricoid in some species, with a more or less developed hypoderm. The basidiomata are characterized by mainly stipitocarpic development and a pileipellis duplex, hypoderm usually more developed, lacking from subgenus Telamonia. KOH reaction in most species negative in pileus, context and/or stipital veil, in some groups red, yellow to orange-yellow, brown or black. Basidiospores 4.5–20 × 3–10 μm, in vast majority of the species ± amygdaloid, ± ellipsoid or ± subglobose, less commonly ovoidally ellipsoid, fusoid, lacrymoid, citriform or boletoid, finely to strongly verrucose. Cystidia absent in vast majority of the species, cheilo- and/or pleurocystidia present in some groups. Pileipellis ± duplex, hypoderm usually more or less developed, lacking from C. subgen. Cortinarius.

Ecology and Distribution: In the Northern and Southern Hemisphere with a wide range of hosts.

Notes: The species of this globally distributed, exceptionally species-rich genus of Cortinariaceae are characterized by mainly stipitocarpic development and a pileipellis duplex with a more or less developed hypoderm. The basidiomata range from very small to large, from dry to glutinous, and are of varied colours although brown colours are the most common. Secondary metabolites containing nitrogen are currently only known from this genus of the family and are present in the subgenera Cortinarius, Infracti, Orellani, and section Subtortii (Stensrud et al. 2014).

Morphologically similar species, previously included in this entity but phylogenetically distinct from the genus Cortinarius, are found in the genera Aureonarius, Cystinarius, Hygronarius, Thaxterogaster sect. Vibratiles and Phlegmacium subgen. Carbonella.

Cortinarius subgen. Cortinarius

Synonym: Inoloma (Fr.) Wünsche, Die Pilze: 87, 126 (1877). Basionym: Agaricus trib. Inoloma Fr., Syst. mycol. (Lundae) 1: 216 (1821).

Currently included sections: Cortinarius.

Notes: The species of this small bihemispheric subgenus have a unique combination of characters and are easy to identify at the subgeneric level. The basidiomata are medium to rather large-sized, deep violet to almost blackish...
Fig. 3 Photos of the representatives of genus *Cortinarius*. A. C. subgen. *Cortinarius*, *C. harcynicus* TN 04-525 (H), B. C. subgen. *Der- mocybe*, *C. neosanguineus* TN 09-130 (H), C. subgen. *Orellani*, *C. rubellus* TN 05-024 (H), D. C. subgen. *Iodolentes*, *C. mammillatus* TN 06-249, E. C. subgen. *Telamonia*, *C. badiolaevis* TN 04-960 (H), F. C. sect. *Subtorii*, *C. subtortus* TN 05-021 (H), G. C. subgen. *Myxaci- cium*, *C. seidliae* TN09-063 (H), and H. C. subgen. *Paramyxacium*, *C. caperatus* TN 06-149 (H). Photos K. Liimatainen
violet, stipitocarpic, agaricoid (ctinarioid) with a dry pileus and a dry stipe. The pileus is tomentose to scaly and non-hygrophanous, and the KOH reaction on any surface of the basidiomata is red. Pleurocystidia and cheilocystidia are present and the pileipellis lacks a well-developed hypoderm. For a recent morpho-genetic revision see Harrower et al. (2015a, b).

**Cortinarius subgen. Camphorati Liimat., Niskanen & Ammirati, Index Fungorum 256: 2 (2015)**

*Current name of the type species: Cortinarius camphoratus* (Fr.) Fr., Epicr. syst. mycol. (Upsalieae): 280 (1838) [1836–1838]. Basionym of the type species: *Agaricus camphoratus* Fr., Syst. mycol. (Lundae) 1: 218 (1821). Neotype: S F-44851, in Niskanen, Index Fungorum 221: 1 (2015).

*Possible synonym: Sericeocybe* Rob. Henry, Bull. trimest. Soc. mycol. Fr. 109(1): 19 (1993). *Current name of the type species: Cortinarius caninus* (Fr.) Fr., Epicr. syst. mycol. (Upsalieae): 285 (1838) [1836–1838]. Basionym of the type species: *Agaricus anomalous* var. *caninus* Fr. 1821.

*Current included sections: Camphorati.*

*Notes:* The core group of this subgenus, the small bihemispheric *C. sect. Camphorati,* is easy to delimit based on morphology: The basidiomata are medium to large-sized, blue/purple, white to pale yellowish brown, stipitocarpic, agaricoid (telamonioid) with a dry pileus and dry stipe. The odour in many species is strong and unpleasant. Cheilocystidia are present and the pileipellis is somewhat duplex, but the hypoderm is not that well-developed. In the phylogenetic analysis of Soop et al. (2019) this group was placed within a larger entity including sections Anomali, Spilomei, Bolares, Delibati and Suborti but without support. Further studies will be needed to define the limits of the subgenus.

**Cortinarius subgen. Dermocybe (Fr.) Trog, Mitt. naturf. Ges. Bern 15–23: 43 (1844)**

*Basionym:* Agaricus trib. Dermocybe Fr., Syst. mycol. (Lundae) 1: 10, 227 ['217'] (1821).

*Current name of the type species: Cortinarius cinnamomeus* (S. F.) S. F-41138, in Lii. Niskanen, Index Fungorum 101: 3 (1838) [1836–1838] (Lundae) 1: 218 (1821). Neotype: S F-44877, in Niskanen et al., Index Fungorum 256: 1 (2015).

*Current included sections: Illumini.*

*Notes:* This is a small bihemispheric subgenus that includes agaricoid (telamonioid), stipitocarpic, medium-sized species with a vivid red-brown to brown, dry, hygrophanous pileus, dry stipe, subglobose basidiospores and a pileipellis duplex.

**Cortinarius subgen. Infracti Niskanen & Liimat., subgen. nov.**

IndexFungorum IF551876

*Current name and basionym of the type species: Cortinarius infractus* (Pers.) Fr., Epicr. syst. mycol. (Upsalieae): 261 (1838) [1836–1838]. Neotype: S F-41138, in Liimatainen et al., Persoonia 33: 120, (2014).

*Etymology:* Named after the type species of the subgenus.

*Current included sections: Infracti.*

*Description:* Basidiomata medium-sized to large-sized, agaricoid (phlegmacioid), development type stipitocarpic. Pileus 3–10 cm, at first hemispherical, then low convex to almost plane, sometimes with a very low and broad umbo, innately fibrillose; olivaceous grey, olivaceous brown or umber brown, some species becoming yellow/ochraceous brown with age; viscid or glutinous; not hygrophanous. Lamellae crowded, adnate, adnexed to emarginate, dark olivaceous brown to dark olivaceous grey at least when young, sometimes with a purplish tint. Stipe 3–9 cm long, 0.8–1.5 cm wide at the apex, up to 2.5 cm at base, cylindrical to clavate; whitish grey to olivaceous grey, sometimes with a purplish tint at the apex, dry. Universal veil yellow to yellow brown, in some species white when young, rather sparse, fibrillose. Context in pileus and stipe whitish grey to olivaceous grey, sometimes purple at the apex of the stipe, marbled hygrophanous. Odour in lamellae indistinct. Taste bitter. NaOH reaction yellow to orange–yellow (Soop et al. 2018). Basidiospores 7–9.5 × 5–7 μm, subglobose to broadly ellipsoid, moderately verrucose. Lamellar trama preparation with abundant small red granules in Melzer’s. Cystidia absent. Pileipellis duplex, hypoderm present but poorly developed.

*Ecology and Distribution:* In the Northern Hemisphere with Fagaceae and Pinaceae.

*Notes:* A small subgenus of about 10 to 15 agaricoid (phlegmacioid) species occurring in the Northern Hemisphere. The species of this subgenus can be distinguished by the combination of bitter taste, olivaceous tints, viscid
to glutinous, innately fibrillose pileus, clavate to sometimes almost cylindrical stipe and subglobose to broadly ellipsoid spores. The development type is stipitocarpic.

*Cortinarius* subgenus *Iodolentes* Niskanen & Liimat., subgen. nov.

*Index Fungorum* IF552140

*Current name and basionym of the type species:* *Cortinarius aurae* Niskanen & Liimat., in Hyde et al., *Fungal Diversity* 100: 247 (2020). *Holotype:* K(M) 200315.

*Etymology:* The name refers to the iodoform-like odour that many of the species of this subgenus have.

*Currently included sections:* Acetosi, Fragrantiores and Obtusi.

*Description:* Basidiomata small- to medium-sized, agaricoid (telamonioid) or sequestrate, development type stipitocarpic. Pileus 1–7 cm, at first conical to hemispherical, then low conical to low convex to plane, with an acute or broader umbo, pileus margin in many smaller species more or less pellucid-striate, surface often somewhat rimy; yellow brown, red brown to dark brown; dry; hygrophanous. Lamellae medium spaced to distant, adnate, adnexed or emarginate, yellow brown to strong brown, often with a white edge. Stipe 2.5–11 cm long, 0.15–1.4 cm wide at the apex, cylindrical or rooting; at first white fibrillose, later very pale brown to yellow brown. Universal veil white, sparse, or forming complete and/or incomplete girdles on stipe. Context in pileus ± brown, usually somewhat paler in stipe. The context of the stipe is often more or less pellucid-striate, surface often somewhat rimy; yellow brown, red brown to dark brown; dry; hygrophanous. Lamellae medium spaced to distant, adnate, adnexed or emarginate, yellow brown to strong brown, often with a white edge. Stipe 2.5–11 cm long, 0.15–1.4 cm wide at the apex, cylindrical or rooting; at first white fibrillose, later very pale brown to yellow brown. Universal veil white, sparse, or forming complete and/or incomplete girdles on stipe. Context in pileus ± brown, usually somewhat paler in stipe. Odour in lamellae indistinct or in some species raphanoid or celllar-like, at the base of stipe indistinct, raphanoid or iodoform-like, the latter best observed when slightly dried. Basidiospores 6.5–10.5 × 4.5–6.5 μm, ovoid, amygdaloid to ellipsoid, in *C. fragrantior* ovoid-subglobose, finely to strongly verrucose. Cheilocystidia present in part of the species, clavate to balloon-shaped. Pileipellis duplex, hypoderm developed.

*Ecology and Distribution:* In Northern and Southern Hemisphere with a wide range of hosts plants.

*Notes:* *Cortinarius* subgenus *Iodolentes* includes small- to medium-sized talamontiodi species with dry, ± brown pileus and dry, initially white stipe. The context of the stipe is often somewhat paler than in the pileus and does not become darker towards the base of the stipe. Many species have an iodoform-like odour at the base of the stipe and clavate to balloon-shaped cheilocystidia.

The species of this subgenus were traditionally included in the *C.* subgenus. Telamonia due to their dry pileus and dry stipe, but the first molecular studies showed that they should be recognized as a separate taxon (Høiland and Holst-Jensen 2000; Peintner et al 2004; Garnica et al. 2005), which is also supported by our phylogenetic analysis. *Iodolentes* belongs to a well-supported branch (BS 94%) in genus *Cortinarius* that also includes subgenera * Dermocybe*, *Leprocye*, *Illumini* and *Orellani*. Since the species of *Iodolentes* morphologically differ from the species of other related subgenera we here describe the subgenus as new.

*Cortinarius* subgen. *Leprocye* M.M. Moser, Z. Pilz. 35(3 + 4): 232 (1969) em. Niskanen & Liimat

*Current name and basionym of the type species:* *Cortinarius cotoneus* Fr., Epicr. syst. mycol. (Upsaliæ): 289 (1838) [1836–1838]. *Neotype:* S F-44846, in Ammirati et al., Persoonia 46: 221 (2021).

*Currently included sections:* *Leprocye*, Fuscotomentosi, Melanoti, Persplendidi, Squamiveneti, Veneti, and Veronicae.

*Notes:* The species of this subgenus occur in both the Northern and Southern Hemispheres. The basidiomata are small- to medium-sized (occasionally large-sized), agaricoid (leprocyboid/dermocyboid) or sequestrate, and with a dry pileus and dry stipe and with yellow, red, or greenish-olive colours. At least some parts of the basidiomata are fluorescent. For a recent morpho-genetic revision of Northern Hemispheric *Leprocye* see Ammirati et al. (2021) and Bidaud et al. (2021).

*Cortinarius* subgen. *Myxacium* (Fr.) Trog, Mitt. naturf. Ges. Bern 15–23: 42 (1844)

*Basionym:* Agaricus trib. *Myxacium* Fr., Syst. mycol. (Lundae) 1: 247 (1821)

*Current name of the type species:* *Cortinarius collinitus* (Sowerby) Gray [as 'Cortinaria collinita'], Nat. Arr. Brit. Pl. (London) 1: 628 (1821). *Basionym of the type species:* *Agaricus collinitus* Sowerby, Col. fig. Engl. Fung. Mushr. (London) 1(no. 2): tab. 9 (1796). *Lectotype:* Sowerby, Col. Fig. Engl. Fungi 1: pl. 9. 1795, in Gómez & Cadiñanos-Aguirre, J des JEC 2: 135, (2018).

*Synonyms:* *Myxacium* (Fr.) P. Kumm., Führ. Pilzk. (Zerbst): 22 (1871). *Basionym:* Agaricus trib. *Myxacium* Fr., Syst. mycol. (Lundae) 1: 247 (1821).

*Myxopholis* Locq., Fl. Mycol., 3. Cortinariales-A.: 146 (1979) [1977]. *Basionym and current name of the type species:* *Cortinarius mucifluus* Fr., Epicr. syst. mycol. (Upsaliæ): 274 (1838) [1836–1838].

*Quadrispora* Bougher & Castellano, Mycologia 85(2): 285 (1993). *Current name of the type species:* *Cortinarius oblongisporus* (G.W. Beaton, Pegler & T.W.K. Young) Gasparini, IOSR Journal of Pharmacy 6(4): 3 (2014). *Basionym of the type species:* *Hymenogaster oblongisporus* G.W. Beaton, Pegler & T.W.K. Young, Kew Bull. 40(1): 188 (1985).

*Currently included sections:* *Myxacium*, *Cuphomorphi*, *Defibulati*, *Marmorati*, *Mycytophyllum*, and *Quadrispora*.

*Notes:* This is a bihemispherical subgenus with about 50 species. The basidiomata are medium-sized to small, agaricoid (cibpccboid, myxacioid) or sequestrate with a viscid to glutinous pileus and glutinous to dry stipe with
white, brown and/or purplish colours. Cylindrical stipes and relatively large (up to 20 μm long), mainly amygdaloid to citriform basidiospores are also typical. For a recent morpho-genetic revision of the subgenus see Soop et al. (2021).

The type species of the subgenus, *C. collinitus*, is described from Britain. Recently, a lectotype for the species was designated by Gómez and Cadafanos-Aguirre (2018). They also challenged the current interpretation of the name and concluded the species to be more *C. trivialis*-like. We agree with this conclusion and materials from Britain will need to be sequenced for selection of a suitable epitype. However, since both the current species called as *C. collinitus* as well as *C. trivialis*-like fungi belong to this subgenus, we conclude that the subgeneric name *Myxacium* can be confidently used for this clade although the fixing of the name *C. collinitus* still requires a selection of an epitype.

*Cortinarius subgen. Orellani* (M.M. Moser) Gasparini, Australas. Mycol. 23(2): 69 (2004)

**Basionym:** *Cortinarius sect. Orellani* M.M. Moser, Z. Pilzk. 35(3 + 4): 224 (1969)

*Current name and basionym of the type species:* *Cortinarius orellanus* Fr., Epicr. syst. mycol. (Upsaliae): 288 (1838) [1836–1838]. **Lectotype:** Junghuhn, Observationes Mycologicae in species fungorum tam novas tam male cognitas, Linnaea V, t. 6, f. 9. 1830 (lectotypus hic designatus, IF552141). **Epitype:** Norway, Ågerd; Tvedestrand, Eidebo, in forest with *Tilia, Quercus* and *Corylus*, 21 Sep 2014, coll. I-L. Fonneland & D. Pettersen (O F-251482, epitypus hic designatus IF552142), UNITE No. UDB036242 (ITS).

*Currently included sections: Orellani.*

**Notes:** This small bihemispherical subgenus is characterized by the lethal nephrotoxin bipyridine orellanine that has caused severe poisonings and deaths in humans (Schumacher & Høiland 1983; Danel et al. 2001) and is not found in any other lineage in *Cortinariaceae*. The basidiomata of the species of *C. subgen. Orellani* are medium-sized, stipitocarpic, agaricoid (cortinarioid) with yellow, orange-brown to somewhat clavate stipe is also typical. The pileipellis is and saturated reddish-brown colours, and with a dry pileus carpic, agaricoid (cortinarioid) with yellow, orange-brown to medium-sized (to large), stipitocarpic, agaricoid (telamonioid) with a dry pileus and stipe. The basidiomata are relatively large (up to 20 μm long), mainly amygdaloid to citriform basidiospores are also typical.

*Cortinarius subgen. Paramyxacium* M.M. Moser & E. Horak, Beih. Nova Hedwigia 52: V, 263 (1975) **em. Niskanen & Liimat.**

*Current name of the type species: Cortinarius paradoxus* M.M. Moser & E. Horak, Beih. Nova Hedwigia 52: 264 (1975). **Holotype:** IB 19650506.

**Synonyms:** *Cuphyocybe* R. Heim, Revue Mycol., Paris 16: 8 (1951). *Rozites* P. Karst., Bidr. Känn. Finl. Nat. Folk 32: XX (1879). *Current name of the type species: Cortinarius caperatus* (Pers.) Fr., Epicr. syst. mycol. (Upsaliae): 256 (1838) [1836–1838]. **Basionym of the type species: Rozites caperati** (Pers.) P. Karst., Bidr. Känn. Finl. Nat. Folk 32: 290 (1879).

*Currently included sections: Cuphyocybe, Paramyxacium, Rozites, Subcastanelli and cladel/Achroi.*

**Notes:** The centre of the diversity of this subgenus is in the Southern Hemisphere with only a few species occurring in the Northern Hemisphere. This subgenus contains agaricoid (rozitoid, cuphocyboid) and sequestrate species and the development type of agaricoid species is stipitocarpic. Typical for the agaricoid species of this subgenus is the membraneous veil that in most species forms a distinct ring or collar on the stipe, or in a few species, thick girdles or scales on the stipe. The pileus is viscid/glutinous to dry, and many species also have squamules or scales on the pileus, or the pileus is innately fibrillose, radially wrinkled and/or rimy. The basidiomata are usually medium- to large-sized. The basidiospores are medium to large-sized (8–16 × 5.5–9.5 μm), usually ovoid, amygdaloid or citriform, more rarely ellipsoid to very short and broadly ellipsoid.

*Cortinarius subgen. Telamonia* (Fr.) Trog., Mitt. naturf. Ges. Bern 15–23: 43 (1844) **em. Niskanen & Liimat.**

*Current name of the type species: Cortinarius torvus* (Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 293 (1838) [1836–1838]. **Basionym of the type species: Agaricus torvus* Fr., Observ. mycol. (Havniae) 2: 80 (1818). **Lectotype:** Bulliard, Herb. Fr. (Paris) 2: Tab. 96, pl. 600, 1782 [1781–82], in Liimatainen et al., Fungal Diversity 104: 323 (2020). **Epitype:** S F-248482, in Liimatainen et al., Fungal Diversity 104: 323 (2020).

**Synonym:** *Hydrocybe* (Fr. ex Rabenh.) Wünsche, Die Pilze: 87, 119 (1877). **Basionym:** *Cortinarius a Hydrocybe* Fr. ex Rabenh., Deutschl. Krypt.-Fl. (Leipzig) 1: 488 (1844). **Type species Cortinarius duracensis* Fr., Epicr. syst. mycol. (Upsaliae): 304 (1838) [1836–1838].

**Telamonia** (Fr.) Wünsche, Die Pilze: 87, 122 (1877). **Basionym:** *Agaricus trib. Telamonia Fr.*, Syst. mycol. (Lundae) 1: 10, 210 (1821).

*Currently included sections: 80 sections, see Liimatainen et al. (2020a).*

**Notes:** This predominantly Northern Hemispheric lineage is the most species-rich subgenus in *Cortinariaceae* including hundreds of species. The basidiomata are small-to medium-sized (to large), stipitocarpic, agaricoid (telamonioid) with a dry pileus and stipe. The basidiomata are...
predominantly with brown, grey, white, and/or purplish colours. The pileipellis is duplex, with a more or less developed hypoderm. For a recent morpho-genetic revision of the subgenus see Liimatainen et al. (2020a).

**Aureonarius Niskanen & Liimat.** gen. nov.

IndexFungorum IF552143

Current name of the type species: *Aureonarius kroegeri* (Niskanen, Liimat., E. Harrower, Berbee, Garnica & Ammirati) Niskanen & Liimat. comb. nov. IF552144. Basionym of the type species: *Cortinarius kroegeri* Niskanen, Liimat., E. Harrower, Berbee, Garnica & Ammirati, Index Fungorum 294: 1 (2016). Holotype: UBC F15952.

Etymology: Derived from the Latin word aureus meaning golden, since species of this genus have yellow colours in their basidiomata, and the generic name *Cortinarius*.

Currently included subgenera: *Aureonarius* and *Calinotei* (Fig. 4).

Description: Basidiomata small- to medium-sized (rather large-sized), agaricoid, development type stipitocarpic. Pileus 1–11 cm, at first hemispherical or conical, then low convex or low conical to almost plane, some species with an umbo; smooth, finely scaly, innately fibrillose or almost tomentose yellow; orange, orange-red, orange-brown, brownish red, yellow–brown, red-brown, red-brown, umber or blackish brown; dry or viscid, hygrophanous or not. Lamellae rather crowded, medium spaced to distant, adnate, adnexed to emarginate, white, ± yellow, bright orange, yellow–brown or ± red. Stipe 2–11 cm long, 0.2–1.8 cm wide at the apex, up to 2.5 cm wide at the base, clavate, cylindrical or tapering downwards, yellowish white, yellow, yellow–brownish to orange-brown, in some species becoming more brownish when pressed with the thumb or with age, dry to somewhat viscid. Universal veil yellow, ochraceous, yellow–brown, orange–red, orange-brown, brownish red, red-brown to umber, in stipe yellow, yellow–brown, orange, orange-red, orange-brown, or brown–red, sparse or more abundant and then forming complete and incomplete girdles on the stipe. Context in pileus yellow, ochraceous, yellow–brown, orange–brown, or brown–red, sparse or more abundant and then forming complete and incomplete girdles on the stipe. Context in pileus, or context. This taxon is well supported in our phylogenetic analyses, and we here describe it as a new genus.

**Aureonarius subgenus Aureonarius**

IndexFungorum IF552145

Etymology: Derived from the Latin word aureus meaning golden, since species of this genus have yellow colours in their basidiomata, and the generic name *Cortinarius*.

Currently included sections: *Aureonarius* (= *Cortinarius* sect. *Limonii* Nezdojm).

Description: Basidiomata small- to medium-sized, agaricoid (cortinarioid/leprocyboid), development type stipitocarpic. Pileus 1–8 cm, at first hemispherical or conical, then low convex or low conical to almost plane, often with an umbo, yellow, orange, orange-red, orange-brown, brownish red, yellow–brown, red-brown, umber, or blackish brown, dry or viscid, hygrophanous or not. Lamellae rather crowded, medium spaced to somewhat distant, adnate, adnexed to emarginate, ± yellow, bright orange, pale yellow–brown or ± red. Stipe 2–11 cm long, 0.2–1.8 cm wide at the apex, cylindrical to fusoid, often tapering downwards, yellowish white, yellow, yellow–brown to orange-brown, dry to somewhat viscid. Universal veil yellow, ochraceous, yellow–brown, orange–brown, or brown–red, sparse or more abundant and then forming complete and incomplete girdles on the stipe. Context in pileus yellow–brown, orange–brown, red-brown to umber, in stipe yellow, yellow–brown, orange or red–orange. Odour in lamellae or pileus surface indistinct. KOH reaction red to dark red in stipitate veil, pileus and/or context, or negative. UV fluorescence weak or absent (Soop et al. 2018). Basidiospores 5–10.5 × 4.5–7 μm, subglobose, broadly ellipsoid, ellipsoid or amygdaloid, finely, moderately to coarsely verrucose. Chrysobasidia present in two species, *A. rubrocastaneus* and *A. rubrimarginatus*. Cystidia absent. Pileipellis duplex, hypoderm developed, some species with a thin gelatinous layer at the top of the epicutis.

Ecology and Distribution: The centre of the diversity of this lineage is in New Zealand where the species occur in *Myrtaceae* and *Nothofagaceae* forests. The three species known from the Northern Hemisphere, associated with *Fagaceae* and *Pinaceae*, are clustered in one monophyletic lineage within one of the New Zealand lineages.

Notes: The species of this small, bihemispheric subgenus have small- to medium-sized, stipitocarpic, agaricoid
(cortinaroid/leprocyboid) basidiomata with yellow, orange-red and reddish-brown colours. The pileus is dry to viscid, and the stipe is cylindrical to fusoid and dry. The lamellae are ± yellow, bright orange, pale yellow–brown or ± red and the basidiospores are subglobose, broadly ellipsoid, ellipsoid or amygdaloid. A distinct odour in the lamellae or at the pileus surface is lacking. The species of the sister subgenus *Callistei* differ from the species of subgenus *Aureonarius* by having white, pale yellow or greyish ochraceous lamellae at least when young and somewhat yellow UV fluorescence. In addition, some species of the subgenus *Callistei* have a clavate stipe and a distinct smell at the pileus surface, context or lamellae, and none of the species have amygdaloid or ellipsoid spores.

**Aureonarius subgenus Callistei (Liim., Niskanen & Ammirati) Niskanen & Liimat.,* comb. nov.

*Index Fungorum* IF552146

**Basionym:** *Cortinarius* subgen. *Callistei* Liim., Niskanen & Ammirati, in Niskanen, Liimatainen, Kyttövuori & Ammirati, *Index Fungorum* 256: 2 (2015).

**Current name of the type species:** *Aureonarius callisteus (Fr.) Niskanen & Liimat.***

*Basionym of the type species: Agaricus callistes Fr.,* Observ. mycol. (Havnae) 2:51. 1818. *Neotype:* S CFP1219, in Brandrud et al., *Cortinarius flora photographica* 5: pl. E30, (2012).

**Currently included sections:** *Callistei* and *Collybiani.*

**Description:** Basidiomata small- to medium-sized, agaricoid (cortinaroid/leprocyboid), development type stipitocarpic. Pileus 2–11 cm, at first hemispherical to somewhat conical, then low convex to almost plane, some species with an umbo, smooth, finely scaly, innately fibrillose or almost tomentose, yellow, yellow-orange, yellow–brown, orange-brown, brownish red to mahogany-red, dry, hygrophanous or not. Lamellae medium spaced to distant, adnate to emarginate, at first almost white, pale yellow or yellowish brown, later brownish yellow to brown. Stipe 3.5–11 cm long, 0.5–1.5 cm wide at the apex, up to 2.5 cm wide at the base, clavate, cylindrical to somewhat tapering; yellowish white, pale yellow, yellow–brown, becoming more brownish when pressed with the thumb and with age. Universal vein yellow, yellow–brown, orange-red or purple-brown, forming complete and/or incomplete zones on the stipe, or sparse. Context in pileus white to pale yellow, in stipe pale yellow, yellow–brown to orange-brown, in many species becoming darker with age. Odour of pileus surface or context like a recently extinguished candle (ozone), apple-like or indistinct, odour in lamellae indistinct, raphanoid, cellular-like or raw potato-like. KOH reaction in pileus and/or stipitcal vein brownish red to red. UV fluorescence somewhat yellow. Basidiospores 6.5–9×5.5–7 μm, subglobose, ovoid to broadly ellipsoid, finely to moderately verrucose. Cystidia absent. Pileipellis duplex, hypoderm at least somewhat developed.

**Ecology and Distribution:** In the Northern and Southern Hemispheres in coniferous and deciduous forests.

**Notes:** The species of this small, bihemispheric subgenus have small- to medium-sized, stipitocarpic, agaricoid (cortinaroid/leprocyboid) basidiomata with yellow, orange and brownish-red colours. The pileus is dry, and the stipe is clavate or cylindrical and dry. The lamellae are at first almost white, pale yellow or yellowish brown and the basidiospores are subglobose, ovoid to broadly ellipsoid. Many species have a distinct odour either at the pileus surface or in the lamellae. The species of the sister subgenus *Aureonarius* have ± yellow, bright orange, pale yellow–brown or ± red lamellae and an indistinct odour in the lamellae or at the pileus surface. In addition, there is no UV fluorescence in the basidiomata of the species of subgenus *Aureonarius.*

**Aureonarius section Callistei Niskanen & Liimat., sect. nov.

*Index Fungorum* IF552148

**Current name of the type species:** *Aureonarius callisteus (Fr.) Niskanen & Liimat.***

**Etymology:** Named after *A. callisteus,* a species belonging to this section.

**Currently included species:** *C. neocallisteus,* *C. callisteus,* *C. infucatus,* *C. tofaceus.*

**Description:** Basidiomata medium-sized (to large-sized), agaricoid (cortinaroid/leprocyboid), development type stipitocarpic. Pileus 3–11 cm, at first hemispherical, then low convex to almost plane, smooth to finely scaly to almost tomentose, yellow, yellow-orange, yellow–brown to orange-brown, dry, somewhat to not hygrophanous. Lamellae medium spaced to distant, adnate to emarginate, at first almost white, pale yellow or yellowish brown, later brownish yellow to brown. Stipe 3.5–11 cm long, 0.6–1.5 cm wide at the apex, up to 2.5 cm wide at the base, clavate or cylindrical; pale yellow, yellow brown, becoming more brownish when pressed with the thumb and with age. Universal veil yellow to yellow–brown, forming complete and/or incomplete zones on the stipe, sometimes sparse. Context in pileus white to pale yellow, in stipe yellow–brown to orange-brown, becoming darker with age. Odour of pileus surface like a recently extinguished candle (ozone), apple-like or indistinct, odour in lamellae raphanoid, cellular-like or raw potato-like. KOH reaction in pileus and/or stipitcal vein brownish red to red. UV fluorescence somewhat yellow. Basidiospores 6.5–9×5.5–7 μm, subglobose to ovoid, moderately verrucose. Cystidia absent. Pileipellis duplex, hypoderm somewhat developed.

**Ecology and Distribution:** In the Northern Hemispheric lineages in *A. subgenus Callistei.* The representatives of the sister lineage, *A. sect. Collybiani* from the Southern Hemispheric *Nothofagaceae*
Aureonarius section Collybiana Niskanen & Liimat., sect. nov.

IndexFungorum IF552149

Current name of the type species: Aureonarius collybiana (Soop) Niskanen & Liimat., comb. nov. IF552150. Basionym of the type species: Cortinarius collybiana Soop, Bull. Soc. mycol. Fr. 117(2): 121 (2001). Holotype: PDD 70509.

Etymology: Named after the type species of the section.

Currently included species: C. collybiana, C. eucalybianus, C. rubroactylus.

Description: Basidiomata small- to medium-sized, agaricoid (cortinarioid/leprocyboid), development type stipitocarpic. Pileus 2–8.5 cm, at first hemispherical to somewhat conical, then convex to plano-convex, often with an umbo, smooth to finely innately fibrillose, orange-red, apricot-brown, brownish red to mahogany red, dry, hygrophanous or not. Lamellae medium spaced to distant, adnate to emarginate, at first white, pale yellow or greyish ochraceous later more brownish. Stipe 4–9 cm long, 0.5–1.2 cm wide at the apex, somewhat clavate, cylindrical to somewhat tapering, yellowish white, pale yellow, yellow or brown-yellow, becoming more brownish at the base with age. Universal veil orange-red, orange-brown, or purple-brown, sparse. Context white or pale yellow. Odour in context like wax-candles. KOH reaction dark red on pileipellis and stipital veil or trivial. Not UV fluorescent. Basidiospores 5.5–8.5 × 5–6 μm, subglobose to broadly ellipsoid, finely to moderately verrucose. Cystidia absent. Pileipellis duplex, hypoderm not developed.

Ecology and Distribution: In the Southern Hemisphere in Nothofagaceae forests.

Notes: A Southern Hemispheric lineage in A. subgenus Callistei. The representatives of the sister lineage, A. sect. Callistei from the Northern Hemisphere, often have a somewhat paler, less reddish pileus and a yellow to yellow-brown universal veil. The group received full support in the phylogenetic analysis of Soop et al. (2018, 2019).

Austrocortinarius Niskanen & Liimat., gen. nov.

IndexFungorum IF552197

Current name of the type species: Austrocortinarius victoriaensis (Liimat.) Niskanen, comb. nov. IF552198 Basionym of the type species: Cortinarius victoriaensis Liimat., Index Fungorum 506: 2 (2021); Holotype: K(M) 162337

Etymology: A genus of family Cortinariaceae that is currently only known from the Southern Hemisphere.

Currently included subgenera: The genus includes only a few species and no infrageneric classification is proposed at present.

Description: Basidiomata (medium- to) large-sized, agaricoid (phlegmacioid), development type stipitocarpic. Pileus 6–15 cm, at first hemispherical, then convex to plano-convex, margin often with hanging remnants of veil, white to brownish white. Lamellae crowded, adnate to emarginate, at first almost white to very pale brown, later pale brown to brown. Stipe 7–15 cm long, 1.2–3 cm wide at the apex, rooting, white. Universal veil white, peronate, often forming a distinct ring at the upper part of the stipe. Context white. Odour not recorded. KOH reaction not recorded. Basidiospores 10–12 × 5–6.5 μm, amygdaloid to citriform, finely verrucose. Cystidia absent. Pileipellis simplex, hypoderm not developed.

Ecology and Distribution: In the Southern Hemisphere in Australia and New Zealand. In Myrtaceae forests.

Notes: Austrocortinarius is a small, Southern Hemispheric genus currently only known from Australia and New Zealand. The representatives of the genus are easy to recognize by the combination of pileipellis simplex, large, ± white basidiomata and a peronate universal veil often forming a distinct ring at the upper part of the rooting stipe. In addition, the basidiomata are agaricoid (phlegmacioid), stipitocarpic and the spores are rather large and amygdaloid. The sequence data deposited in the public repositories, as well as morphology, indicates that C. australiensis would also belong to this genus but the type specimen of the species has not been studied to confirm the placement. The species of genus Austrocortinarius are most reminiscent of those in P. subgenus Phlegmacium, sect. Arguti and clades Obsoleti and Caligati but those lineages of Phlegmacium are only known from the Northern Hemisphere. Rooting, phlegmacioid species are also found from genus Thaxterogaster, but none of those species has the same, unique combination of characters than the representatives of the genus Austrocortinarius. Based on the morphological and molecular data we here consider this distinct lineage as its own genus.

Calonarius Niskanen & Liimat., gen. nov.

IndexFungorum IF552199

Current name of the type species: Calonarius typicus (Liimat.) Niskanen, comb. nov. IF552200. Basionym of the type species: Cortinarius typicus Liimat., in Niskanen & Liimatainen, Index Fungorum 487: 2 (2021). Holotype: H 7068019.

Etymology: Derived from the section name Calochroi and the generic name Cortinarius.

Currently included subgenera: Calonarius, Calochroi and Fulvi (Fig. 4).

Description: Basidiomata medium- to large-sized, usually agaricoid (phlegmacioid) but a few species sequestrate,
development type pileocarpic. Pileus 3–15 cm, at first hemi-spherical, then convex to plano-convex, surface in part of the species with small appressed scales or patches of veil and/or innately fibrillose, often colourful with white, yellow, orange, green, olivaceous, brown, blackish and/or purple colours, glutinous. Lamellae crowded, adnate to adnexed to emarginate, white, pale grey, yellow, greenish, olivaceous, pale brown or purple. Stipe 3–12 cm long, 0.7–3 cm wide at the apex, with more or less, usually distinctly, marginated bulb at the base (up to 4.5 cm wide), bulb in some species flattened; white, pale grey, yellow, olivaceous green or purple. Universal veil white, ochraceous yellow, olivaceous green or yellow, orange, brown, brown-olive or purple, found at the bulb margin. Context white, greyish white, yellow or greenish yellow, in some species with a purplish, greenish or olivaceous tint. Odour in lamellae indistinct, earth-like, malty or yeast-like, curry-like, sweet, in one species of anise. KOH reaction pink, red, yellowish or orange-earth-like, malty or yeast-like, curry-like, sweet, in one species with patches or scales of veil or spots, with grey, greenish, olivaceous, yellow, orange-brown, copper brown, red brown, umbre brown and purplish colours, rarely cream-coloured, glutinous. Lamellae crowded, adnate to adnexed to emarginate, greyish white, pale ochraceous grey, pale yellow, greenish grey, greyish green, yellowish green or olivaceous, rarely with a purplish tint at the stipe. Amygdaloid to citriform, coarsely verrucose. Basidiospores 10–16 × 6–9.5 μm, amygdaloid to citriform, distinctly and coarsely verrucose. Cystidia absent. Pileipellis simplex with a well-developed gelatinous layer, hypoderm not developed.

Ecology and Distribution: In the Northern Hemisphere. Forming ectomycorrhizal associations mainly with the trees of Fagaceae (Castanea, Castanopsis, Chrysolepis, Fagus, Notholithocarpus, Quercus) and Pinaceae (Abies, Larix, Picea, Pinus, Pseudotsuga, Tsuga), some species also with Betulaceae (Alnus, Corylus, Carpinus), Cistaceae (Cistus, Helianthemum) and Malvaceae (Tilia) (Garnica et al. 2011). Most species are rare and have narrow ecological preferences (Frøslev et al. 2007), and the majority are calcicolous or calciphilous.

Notes: This species-rich genus is currently only known from the Northern Hemisphere. The species are predominantly calcicolous or calciphilous, many are rare and have narrow ecological preferences and are thus included in national red lists in several countries and/or used as indicator species. One species, C. meinhardii, is also included in the global red list of fungi. Typical for the members of this genus are medium- to large-sized, pileocarpic, agaricoid (phlegmacioid) or sometimes sequestrate, often brightly coloured basidiomata with a more or less, usually distinctly margined bulb at the base of the stipe. Amygdaloid to citriform coarsely verrucose basidiospores and simplex pileipellis are also typical. Some species have a positive KOH-reaction (± red, yellowish or orange-brown, olivaceous green, black). The species are most reminiscent of those in the genera Phlegmacium and Thaxterogaster, but the combination of simplex pileipellis, margined bulb and amygdaloid to citriform, coarsely verrucose basidiospores distinguish the members of Calonarius from the other phlegmacioid species. This group has been recognized as a separate, well-supported lineage since early molecular studies (Peintner et al. 2004; Garnica et al. 2005) and is also supported by morphological characteristics, and here we propose a name for it in generic level. For the most recent morpho-genetic study of the group see Frøslev et al. (2007) and Garnica et al. (2009).

Calonarius subgenus Calonarius
Indexfungorum IF552151

Etymology: Derived from the section name Calochroi and the generic name Cortinarius.

Currently included sections: Calonarius, Humolentes, and Rufoolivacei.

Description: Basidiomata medium- to large-sized, usually agaricoid (phlegmacioid) but at least one species sequestrate, development type pileocarpic. Pileus 4–14 cm, at first hemispherical, then convex to plano-convex, surface in some species with patches or scales of veil or spots, with grey, greenish, olivaceous, yellow, orange-brown, copper brown, red brown, umbre brown and purplish colours, rarely cream-coloured, glutinous. Lamellae crowded, adnate to adnexed to emarginate, greyish white, pale ochraceous grey, pale yellow, greenish grey, greyish green, yellowish green or olivaceous, rarely with a purplish tint. Stipe 4–12 cm long, 0.8–2.5 cm wide at the apex, with a marginated or more rarely rounded bulb at the base (up to 4.5 cm wide), bulb in a few species flattened; white, in some species purplish, greyish green or yellowish green or with a purple, yellow or olivaceous tint. Universal veil white, yellow, greyish or yellowish green, brown, brown-olive, purple or purplish red, in some species somewhat glutinous, found at the bulb margin. Context white to grey, rarely greenish yellow, in some species with a purplish, greenish or olivaceous tint at the stipe. Odour in lamellae indistinct, earth-like, malty or yeast-like, curry-like, sweet, in two species of anise. KOH reaction negative or in some species yellow–brown, orange-brown, olivaceous green, brown–red or purplish, rarely blood-red. Basidiospores 10–16 × 6–9.5 μm, amygdaloid to citriform, distinctly and coarsely verrucose. Cystidia absent. Pileipellis simplex with a well-developed gelatinous layer, hypoderm not developed.

Ecology and Distribution: In the Northern Hemisphere. Forming ectomycorrhizal associations mainly with the species of Fagaceae, Pinaceae, Betulaceae, and Malvaceae. Most species are rare and have narrow ecological preferences, and the majority are calcicolous or calciphilous.

Notes: The species of this subgenus mainly have lamellae without purple tones and the context is white to grey, rarely greenish-yellow, and in some species with a purplish, greenish or olivaceous tint at the stipe. The KOH-reaction, if present, is not red for most species. The basidiomata are medium- to large-sized, pileocarpic, agaricoid (phlegmacioid) and the pileipellis is simplex.
**Calonarius section Humolentes Niskanen & Liimat., sect. nov.**

IndexFungorum IF552330

Current name of the type species: *Calonarius humolens* (Brandrud) Niskanen & Liimat., comb. nov. IF552331. Basionym of the type species: *Cortinarius humolens* Brandrud, in Brandrud, Lindström, Marklund, Melot & Muskos, Cortinarius, Flora Photographica (Matfors) 4: 20. 1998. Holotype: O CFP1281.

Etymology: Named after the type species of the section.

Currently included species: C. anaunianus, C. cario- lacoce, C. elorus, C. elotoides, C. glaucelotus, C. hildegardiae, C. humolens, C. lavandulochlorus, C. mariekristtane, C. osloensis, C. praeterrissus, C. pseudoglaucopus, C. rapaceoides, C. saporatus, and C. xanthodryophilus.

Description: Basidiomata medium- to large-sized, agaricoid (phlegmacioid), development type pileocarpic. Pileus 4–14 cm, at first hemispherical, then convex to plano-convex, in some species with small drop-like spots or appressed scales, or more rarely innately fibrillose; with ochraceous/yellow, grey, greenish/olivaceous, and/or or ochraceous brown colours, rarely orange/reddish brown, glutinous. Lamellae crowded (to medium spaced), adnate to adnexed to emarginate, at first pale ochraceous grey, more or less yellow, olivaceous or with a yellow, olivaceous or greenish tint, later more ochraceous brown. Stipe 3–8 cm long, 0.8–2.5 cm wide at the apex, with a margined or rounded bulb at the base (up to 4.5 cm wide), bulb in some species flattened; white, pale yellow, or with a yellow, olivaceous or purple tint. Universal veil white, yellow, greyish or yellowish green, purple or brown, in some species somewhat glutinous, found at the bulb margin, in some species volva-like when young. Context white, greyish or yellowish green, purple or brown, in some species somewhat glutinous, found at the bulb margin, in some species volva-like when young. Basidiospores 9–14 × 5–8 µm, amygdaloid to citri- form, distinctly and coarsely verrucose. Cystidia absent. Pileipellis simplex with a well-developed gelatinous layer, hypoderm not developed.

Ecology and Distribution: In the Northern Hemisphere. In deciduous and coniferous forests on calcareous or base-rich ground. Forming ectomycorrhizal associations mainly with the species of *Fagaceae, Pinaceae, Betulaceae* and *Tilia.*

Notes: The species of this section are found from the Norther Hemisphere and grow on calcareous or base-rich ground with deciduous or coniferous trees. Basidiomata have ochraceous/yellow, grey, greenish/olivaceous and ochraceous brown colours and most species have an earth-like or raphanoid odour in flesh/lamellae. In addition, the species lack KOH reaction and they do not have purplish colours in lamellae. The basidiomata are medium- to large-sized, pileocarpic, agaricoid (phlegmacioid) and the pileipel- lis is simplex.

The clade name/Humolentes was first introduced for this group by Brandrud et al. (2019) and includes clades/Pseu- doglaucopodes and Caroviolacei recognized by Garnica et al. (2009). For the most recent phylogenetic study of the group see Brandrud et al. (2019) and Fellin et al. (2021).

**Calonarius subgenus Calochroi Niskanen & Liimat., sub- gen. nov.**

IndexFungorum IF552332

Current name of the type species: *Calonarius flavipallens* (Kytöv., Liimat. & Niskanen) Niskanen & Liimat., comb. nov. IF552333. Basionym of the type species: *Cortinarius flavipallens* Kytöv., Liimat. & Niskanen, in Liimatainen, Niskanen, Dima, Kytövöuri, Ammirati & Frøslev, Persoonia 33: 125 (2014). Holotype: H 6032745.

Etymology: Named after *C. calochrous,* a species belonging to this subgenus.

Currently included sections: *Calochroi,* Nymphicocolores, Platypodes, and Sodagniti.

Description: Basidiomata medium- to large-sized, usually agaricoid (phlegmacioid) but at least one species seques- trate development type pileocarpic. Pileus 3–10 cm, at first hemispherical, then convex to plano-convex, surface in most species with small appressed scales or patches of veil, ochra- ceous white, yellow, ochraceous to brown, in some species with bluish, purplish, greenish or olivaceous tints, in some species completely purple, glutinous. Lamellae crowded, adnate to adnexed to emarginate, greyish white with a purplish tint to pale greyish purple to distinctly purple, in a few species yellow to brown. Stipe 3–12 cm long, 0.7–2.5 cm wide at the apex, with a distinctly margined bulb at the base (up to 4 cm wide), bulb in some species flattened, greyish white, in many species with a purplish tint at the top of the stipe, in some species completely purple at least when young. Universal veil whitish to ochraceous yellow, in some species purple or olivaceous, found at the bulb margin. Context whitish to greyish white, in part of the species pale purpl to purple at least at the top of the stipe. Odour in many species in lamellae somewhat earth-like in older basidi- omata. KOH reaction in many species pink, reddish brown or blood red in some parts of the basidiomata, indistinct in part of the species. Basidiospores 8.5–13 × 5.5–8.5 µm, amygdaloid to citriiform, distinctly and coarsely verrucose. Cystidia absent. Pileipellis simplex with a well-developed gelatinous layer, hypoderm not developed.

Ecology and Distribution: In the Northern Hemisphere. Forming ectomycorrhizal associations mainly with the species of *Fagaceae, Pinaceae, Betulaceae,* and *Cistaceae* and
Calonarius. Most species are rare and have narrow ecological preferences, and the majority are calcicolous or calciphilous.

Notes: This is the most species-rich lineage within the genus Calonarius. Most species are characterized by a combination of lamellae with a purplish tint or completely purplish and lack of anthraquinonoid pigments (Frøslev et al. 2007). The basidiomata are medium- to large-sized, pileocarpic, agaricoid (phlegmacioid) and the pileipellis is simplex. The clade Calochroi was also recovered as a well-supported lineage in previous studies by Frøslev et al. (2007) and Garnica et al. (2009).

Calonarius section Nymphicolores Niskanen & Liimat., sect. nov.

IndexFungorum IF552334

Current name of the type species: Calonarius molochinus (Bidaud & Ramm) Niskanen & Liimat., comb. nov. IF552335. Basionym of the type species: Cortinarius molochinus Bidaud & Ramm, in Bidaud, Moënne-Loccoz, Reumaux, Carteret & Eyssartier, Atlas des Cortinaires (Mezieu) 11: 613. 2001. Holotype: PC 3676.

Etymology: Named after C. nymphicolor, a species belonging to the section.

Currently included species: C. nymphicolor and C. molochinus.

Description: Basidiomata medium- to large-sized, agaricoid (phlegmacioid), development type pileocarpic. Pileus 3.5–10 cm, at first hemispherical, then convex to plano-convex, with small patches of whitish veil at centre, entirely pinkish purple or at least margin purple when young, centre cream, pale ochraceous yellow to ± brownish; glutinous. Lamellae crowded, adnate to adnexed to emarginate, greyish to purple. Stipe 3–7.5 cm long, 0.7–2 cm wide at the apex, with a flattened bulb; white, with a purplish tint at the apex. Universal veil white or yellow, becoming yellow to ochraceous brown with age. Context white. Odour indistinct or ± earthy. KOH reaction pink on pileus and bulbipellis, somewhat rose or negative in context. Basidiospores 8.5–11 × 5–6.5 μm, amygdaloid to ellipsoid, coarsely verrucose. Cystidia absent. Pileipellis simplex with a well-developed gelatinous layer, hypoderm not developed.

Ecology and Distribution: In the Northern Hemisphere. In deciduous forests on calcareous ground. Forming ectomycorrhizal associations mainly with the species of Fagaceae.

Notes: The species of the section are found from the Northern Hemisphere deciduous forests on calcareous ground. Typical are purplish colours in pileus and stipe and often also in lamellae as well as initially white or yellow universal veil. The KOH reaction is pink on pileus and bulbipellis and the spores are amygdaloid to ellipsoid, coarsely verrucose. The basidiomata are medium- to large-sized, pileocarpic, agaricoid (phlegmacioid) and the pileipellis is simplex. The clade received full support in our phylogenetic analysis.

Calonarius subgenus Fulvi Niskanen & Liimat., subgen. nov.

IndexFungorum IF552337

Current name of the type species: Calonarius eleganctio-occidentalis (Garnica & Ammirati) Niskanen & Liimat., comb. nov. IF552338. Basionym of the type species: Cortinarius eleganctio-occidentalis Garnica & Ammirati, in Garnica, Spahn, Oertel, Ammirati & Oberwinkler, BMC Evol. Biol. 11(213): 13 + Additional file 3: 23 (2011). Holotype: WTU, Ammirati 13226.

Etymology: This subgenus includes part of the species previously included in section Fulvi.

Currently included sections: Fulvi, Atrovirentes, Aureopulverulenti, Dibaphi, and Splendentes.

Description: Basidiomata medium- to large-sized, agaricoid (phlegmacioid), development type pileocarpic. Pileus 3–15 cm, at first hemispherical, then convex to plano-convex, surface in many species with small appressed scales and/or innately fibrillose, ± yellow, olivaceous green, greyish green, yellow brown, orange-brown, rose brown to red brown, in some species with purplish tints, in one species completely purplish, center saffron orange, brown, chestnut brown, purplish brown to blackish; glutinous. Lamellae crowded, adnate to adnexed to emarginate, greyish white, grey, yellow, greenish yellow, olivaceous yellow, ochraceous yellow to olivaceous green, in some species with a purplish tint. Stipe 4–12 cm long, 1–3 cm wide at the apex, with more or less, usually distinctly margined bulb at the base (up to 4.5 cm wide), bulb in some species flattened; white, pale yellow, yellow, greenish yellow to olivaceous green, in some species with a purplish tint or completely purplish. Universal veil ± yellow, orange or purple, found at the bulb margin. Context yellow, greenish yellow, pale yellow or white, in some species with a purplish tint. Odour in lamellae indistinct or malt-like. KOH reaction pink, vinaceous, blood-red, olivaceous green, olivaceous brown, red brown or black. Basidiospores 9–15 × 5.5–9 μm, amygdaloid to citriform, distinctly and coarsely verrucose. Cystidia absent. Pileipellis simplex with a well-developed gelatinous layer, hypoderm not developed.

Ecology and Distribution: In the Northern Hemisphere. Forming ectomycorrhizal associations mainly with the species of Fagaceae, Pinaceae, Betulaceae, and Malvaceae. Most species are rare and have narrow ecological preferences, and the majority are calcicolous or calciphilous.

Notes: Most species of this subgenus are characterized by yellow colours in the lamellae and/or stipe. If the lamellae are purple, then the pileus is not yellow. Part of the species have anthraquinonoid pigments (Frøslev et al. 2007). The basidiomata are medium- to large-sized, pileocarpic,
agaricoid (phlegmacioid) and the pileipellis is simplex. The group also received good support (BS 96%) in the analysis by Garnica et al. (2009).

**Cystinarius Niskanen & Liimat., gen. nov.**

IndexFungorum IF552491

*Current name of the type species: Cystinarius rubiginosus* (Ammirati, Bojantchev, Niskanen & Liimat.) Liimat. & Niskanen, *comb. nov*. IF552943. *Basionym of the type species: Cortinarius rubiginosus* Ammirati, Bojantchev, Niskanen & Liimat., *Index Fungorum* 506: 1 (2021). *Holotype*: H 7072000.

*Etymology*: Derived from the word *cystidia*, a property of this genus, and the generic name *Cortinarius*.

*Currently included subgenera: Cystinarius and Crassi* (Fig. 4).

*Description*: Basidiomata medium- to large-sized, agaricoid (phlegmacioid/cortinarioid), development type stipitocarpic. Pileus 1.5–11 cm, at first hemispherical, then convex to plano-convex, surface fibrillose, orange yellow, yellow brown, greyish brown, red brown to blackish brown, in some species with spots, dry or viscid. Lamellae crowded to medium spaced, adnate to adnexed to emarginate, white to greyish yellow. Stipe 3–11 cm long, 0.7–2.5 cm wide at the apex, cylindrical, clavate to fusiform, white, pale grey to greyish yellow, in some species staining yellow or pinkish, dry to somewhat viscid. Universal veil white, pale grey to ochraceous yellow, in some species darker in the pileus, staining more or less yellow when exposed. Odour in lamellae indistinct. KOH reaction negative. Basidiospores 6–9 × 3.5–5 μm, ellipsoid to amygdaloid to subfusoid, very finely and indistinctly verrucose. Lamellae with cylindrical, clavate or capitate cheilo- and pleurocystidia. Pileipellis somewhat duplex-like, the hypoderm is poorly developed but the hyphae beneath the epitcups are hypoderm-like (elements that are short and wide).

*Ecology and Distribution*: In the Northern and Southern Hemisphere with coniferous and deciduous trees.

*Notes*: This small bihemispheric subgenus includes medium- to large-sized, stipitocarpic, agaricoid (cortinarioid) species whose context stains more or less yellow when exposed. Small basidiospores and the presence of cheilo- and pleurocystidia is also typical. The pileus is dry to viscid and the stipe is dry and the pileipellis is somewhat duplex with a poorly developed hypoderm. The species of the sister group, *C. subgen. Crassi*, lack bright yellow colours in their basidiomata.

**Cystinarius subgen. Crassi Niskanen & Liimat., subgen. nov.**

IndexFungorum IF552339

*Currently included sections: Cystinarius.*

*Description*: Basidiomata medium- to large-sized, agaricoid (cortinarioid), development type stipitocarpic. Pileus 1.5–8 cm, at first hemispherical, then convex to plano-convex, surface fibrillose, orange yellow, yellow brown, greyish brown, red brown to blackish brown, in some species with spots, dry or viscid. Lamellae crowded to medium spaced, adnate to adnexed to emarginate, white to greyish yellow. Stipe 3–8 cm long, 0.7–2 cm wide at the apex, cylindrical to clavate, white, pale grey to greyish yellow, staining yellow or pinkish, dry to somewhat viscid. Universal veil white, pale grey to ochraceous yellow, in some species darkening, often sparse, forming thin bands on the stipe. Context in the whole basidiomata white to yellowish brown, in some species darker in the pileus, staining more or less yellow when exposed. Odour in lamellae indistinct. KOH reaction negative. Basidiospores 6–9 × 3.5–μm, ellipsoid to amygdaloid to subfusoid, very finely and indistinctly verrucose. Lamellae with cylindrical, clavate or capitate cheilo- and pleurocystidia. Pileipellis somewhat duplex-like, the hypoderm is poorly developed but the hyphae beneath the epitcups are hypoderm-like (elements that are short and wide).

*Ecology and Distribution*: In the Northern and Southern Hemisphere with coniferous and deciduous trees.

*Notes*: This small bihemispheric genus is easy to recognize by the unique combination of small basidiospores (6–9 × 3.5–5 μm) and presence of cheilo- and pleurocystidia. The basidiomata are medium- to large-sized, stipitocarpic and agaricoid (phlegmacioid/cortinarioid). The pileipellis is somewhat duplex. The species form a well-supported lineage (BS 99%) distinct from the other genera of *Cortinariaceae*, a relationship already recovered by the phylogenetic analysis of Stensrud et al. (2014) and Soop et al. (2019), and we here describe the genus as new.
Fig. 4 Photos of the representatives of Cortinariaceae. A Calonarius subgen. Calochroi, C. metarius TN 06-268 (H), B C. subgen. Calonarius, C. odorifer TN 05-138 (H), C C. subgen. Fulvi, C. sp. TN 11-128 (H), D Aureonarius limonius, TN 07-282 (H), E Cystinarius rubiginosus TN 12-223 (H), F Hygronarius renidens TN 05-197 (H), G Mystinarius lustrabilis TN 05-218 (H), H. Volvanarius olivaceovaginatus K235015. Photos A–F K. Liimatainen, H R. Healy
1–2.5 cm wide at the apex, fusiform, cylindrical to clavate, white, in one species becoming brownish red from the apex, dry. Universal veil white, ochraceous to red brown, sparse. Context in stipe white, in pileus very pale brown to brown. Odour in lamellae indistinct. KOH reaction negative. Basidiospores 6–10 × 4.5–6 μm, when young. Universal veil white to yellow–brown, sparse.

Ecology and Distribution: In the Northern and Southern Hemisphere with deciduous and coniferous trees.

Notes: The members of this small bihemispheric subgenus have medium- to large-sized, stipitocarpic, agaricoid (phlegmacioid) basidiomata with dry to somewhat viscid, ± brown pileus and a white, dry stipe. Small, narrow basidiospores and the presence of cheilo- and pleurocystidia is also typical. The pileipellis is somewhat duplex with a poorly developed hypoderm. The species of the sister subgenus Cystinarius differ by having bright colours at least in some parts of their basidiomata and a context that stains more or less yellow when exposed.

Hygronarius Niskanen & Liimat., gen. nov.

IndexFungorum IF552519

Current name of the type species: Hygronarius renidens (Fr.) Niskanen & Liimat., comb. nov. IF552520. Basionym of the type species: Cortinarius renidens Fr., Epicr. syst. mycol. (Upsaliae): 308 (1838) [1836–1838]. Lectotype: Batsch, Elench. Fung., tab. 6: 23. 1783 (lectotypus hic designatus, IF552494). Epitypus: Finland, Varsinais-Suomi; Lohja, herb-rich spruce forest, on calcareous ground, 20 Aug 2000, coll. I. Kytövuori 00–021, H 6107047 (epitypus hic designatus IF552495), GenBank No. OL958653 (ITS).

Etymology: Derived from the word hygrophanous, since this species has a hygrophanous pileus, and the generic name Cortinarius.

Notes: Typical for this small bihemispheric subgenus have a hygrophanous pileus, and the generic name Cortinarius. Current included subgenera: Hygronarius and Viscinisci (Fig. 4).

Description: Basidiomata small- to medium-sized, agaricoid (telamonoid), development type stipitocarpic. Pileus 1–6 cm, at first somewhat hemispherical or conical, then convex to plano-convex, with or without an umbo, yellow–brown to red-brown, dry to viscid, hygrophanous. Lamellae medium spaced to almost crowded, adnate to emarginate, pale brown to rusty brown. Stipe 2.5–9 cm long, 0.3–0.8 cm wide at the apex, cylindrical to somewhat clavate; greyish white, pale brown, brownish yellow to brown, in some species covered by silky-white fibrils when young. Universal veil white to yellow–brown, sparse to distinct. Context ± brown. Odour in lamellae indistinct or slightly raphanoid. Basidiospores 6–10 × 4.5–6 μm, subglobose, broadly ellipsoid to ellipsoid, finely to coarsely verrucose. Cystidia absent. Pileipellis duplex, hypoderm developed.

Hygronarius subgen. Hygronarius

IndexFungorum IF552521

Currently included sections: Hygronarius (= C. sect. Renidentes Moënne-Locc. & Reumaux).

Description: Basidiomata small- to medium-sized, agaricoid (telamonoid), development type stipitocarpic. Pileus 1.5–6 cm, at first somewhat hemispherical, then convex to plano-convex, sometimes with an umbo, red-brown, dry to viscid, hygrophanous. Lamellae medium spaced to almost crowded, adnate to emarginate, pale brown to rusty brown. Stipe 2.5–7 cm long, 0.3–0.6 cm wide at the apex, cylindrical (to somewhat clavate); greyish white, pale brown to brownish yellow, in some species covered by silky-white fibrils when young. Universal veil absent or very sparse. Context ± brown. Odour in lamellae indistinct or slightly raphanoid. Basidiospores 6–7 × 4.5–6 μm, subglobose to broadly ellipsoid, finely verrucose. Cystidia absent. Pileipellis duplex, hypoderm developed.

Ecology and Distribution: In the Northern and Southern Hemisphere with deciduous and coniferous trees.

Notes: Typical for this small bihemispheric subgenus have a hygrophanous pileus, and the generic name Cortinarius. Currently included subgenera: Hygronarius and Viscinisci (Fig. 4).

Description: Basidiomata small- to medium-sized, stipitocarpic, agaricoid (telamonoid) basidiomata with red-brown colours, absent or sparse universal veil and subglobose to broadly ellipsoid basidiospores. They can most easily be distinguished from the species of H. subgen. Viscinisci by the size of the basidiospores: the basidiospores of Viscinisci species are larger, 7–10 × 4.5–6 μm.

Hygronarius subgen. Viscinisci Niskanen & Liimat., subgen. nov.

IndexFungorum IF552522

Current name of the type species: Hygronarius viscincisus (Soop) Niskanen & Liimat., comb. nov. IF552523 Basionym of the type species: Cortinarius viscincisus Soop, Australas. Mycol. 31: 6 (2013). Holotype: PDD 97544.
Fig. 5 Photos of the representatives of genera *Phlegmacium* and *Thaxterogaster*. A *Phlegmacium* subgen. *Phlegmacium*, *P. saginum* TN 05-232 (H), B *P. subgen. Phlegmacium*, *P. largum* TN 08-060 (H), C *P. subgen. Bulbopodium*, *P. olivaceodionysae* TN 06-311 (H), D *P. subgen. Cyanicium*, *P. violaceorubens* TN 07-062 (H), E *T. sect. Lustrati*, *T. leucophanes* TN 05-161 (H), F *T. subgen. Variegiati*, *T. variegatus* TN 05-182 (H), G *T. sect. Vibratiles*, *T. sp* TN 05-210 (H), H *T. subgen. Scauri*, *T. subpurpurascens* TN 08-059 (H). Photos K. Liimatainen
**Etymology:** Named after the type species of this genus.

**Currently included sections:** Austroduracini, Viscincisi.

**Description:** Basidiomata small- to medium-sized, agaricoid (telamonioid), development type stipitocarpic. Pileus 1–6 cm, at first somewhat hemispherical or conical, then convex to plano-convex, with or without an umbo, yellow–brown to red-brown, dry to viscid, hygrophanous. Lamellae medium spaced to almost crowded, adnate to emarginate, pale brown to rusty brown. Stipe 2.5–9 cm long, 0.3–0.8 cm wide at the apex, cylindrical to somewhat clavate; greyish white, pale brown, brownish yellow to brown, in some species covered by silky-white fibrils when young. Universal veil white to yellow–brown, sparse to distinct. Context ± brown. Odour in lamellae indistinct or sweetish. Taste in pileus context somewhat bitter. Basidiospores 7–10 × 4.5–6 μm, elipsoid, moderately to coarsely verrucose. Cystidia absent.

**Notes:** The species of this small, bihemispheric genus have medium-sized, stipitocarpic, agaricoid (myxacioid/phlegmacioid) basidiomata with a yellow to reddish brown, somewhat viscid to almost dry pileus and a white to yellow, dry stipe. The basidiospores are medium-sized and the pileipellis is duplex. The species of this genus resemble morphologically most of those in *Thaxterogaster* subgenus *Multiformes*, *T.* sect. *Pinophil* or *T.* sect. *Vibratiles*. However, they are not closely related to *Thaxterogaster* or other genera of *Cortinariaceae* and we here propose a new genus, *Mystinarius*, for them.

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**Phlegmacium** (Fr.) Wünsche, *Die Pilze*: 87, 128 (1877) em. Niskanen & Liimat.

*Basionym:* *Agaricus* trib. *Phlegmacium* Fr., *Syst.* mycol. (Lundae) 1: 10, 227 ['217'] (1821).

**Sanctioning citation:** Fr., *Syst.* mycol. 1: 10 (1821).

**Current name of the type species:** *Phlegmacium saginus* (Fr.) Niskanen & Liimat., *comb. nov.* IF552795. *Basionym of the type species:* *Agaricus saginus* Fr., *Syst.* mycol. (Lundae) 1: 226 (1821). *Neotype:* IB 19770098, in Melot, Docum. Mycol. XVI (63–64): 130, (1986).

**Synonyms:** *Bulbopodium* Earle, *Bull.* New York Bot. Gard. 5: 441 (1909). *Current name of the type species:* *Phlegmacium caerulescens* (Schaeff.) Wünsche, *Die Pilze*: 131 (1877). *Basionym of the type species:* *Agaricus caerulescens* Schaeff., *Fung.* bavar. palat. nasc. (Ratisbonae) 4: 17 (1774).

*Cyanicium* Locq., *Fl.* Mycol., 3. Cortinariales-A.: 146 (1979) [1977]. *Current name of the type species:* *Phlegmacium cyanites* (Fr.) M.M. Moser, *DieGatt.* Phlegm.: 337 (1960). *Basionym of the type species:* *Cortinarius cyanites* Fr., *Epicr.* syst. mycol. (Upsaliae): 279 (1838) [1836–1838].

*Meliderma* Velen., *České Houby* 2: 399 (1920). *Current name of the type species:* *Phlegmacium mussivum* (Fr.) Niskanen & Liimat., *comb. nov.* IF552796. *Basionym of the type species:* *Agaricus mussivus* Fr., *Epicr.* syst. mycol. (Upsaliae): 178 (1838) [1836–1838].

**Notes:** The species of this small, bihemispheric genus have medium-sized, stipitocarpic, agaricoid (myxacioid/phlegmacioid) basidiomata with a yellow to reddish brown, somewhat viscid to almost dry pileus and a white to yellow, dry stipe. The basidiospores are medium-sized and the pileipellis is duplex. The species of this genus resemble morphologically most of those in *Thaxterogaster* subgenus *Multiformes*, *T.* sect. *Pinophil* or *T.* sect. *Vibratiles*. However, they are not closely related to *Thaxterogaster* or other genera of *Cortinariaceae* and we here propose a new genus, *Mystinarius*, for them.

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**Ecology and Distribution:** In Northern and Southern Hemisphere in coniferous and *Nothofagaceae* forests.

**Notes:** The species of this small, bihemispheric genus have medium-sized, stipitocarpic, agaricoid (myxacioid/phlegmacioid) basidiomata with a yellow to reddish brown, somewhat viscid to almost dry pileus and a white to yellow, dry stipe. The basidiospores are medium-sized and the pileipellis is duplex. The species of this genus resemble morphologically most of those in *Thaxterogaster* subgenus *Multiformes*, *T.* sect. *Pinophil* or *T.* sect. *Vibratiles*. However, they are not closely related to *Thaxterogaster* or other genera of *Cortinariaceae* and we here propose a new genus, *Mystinarius*, for them.
species medium spaced, emarginate. at first pale greyish white to purple, later pale brown to purplish brown, darker in the species of subgenus Carbonella. Stipe 3–13 (–20) cm long, (0.4–)0.8–2 (–3) cm wide at the apex, up to 5 cm at base, clavate to bulbous with a rounded or a marginate bulb, or cylindrical to rooting, in the vast majority of the species more or less white, sometimes with purplish tints, in some species grey, dry. Universal veil white, grey, yellow, greenish yellow, more or less brown or purple, sparse to abundant, forming incomplete and complete girdles on the stipe. Context in many species in pileus and stipe white, sometimes with purplish colours, in some species grey, yellow-greenish, olive-grey, pale greyish purple to vinaceous brown, in the species of subgenus Cyanicium becoming vinaceous red on exposure. Odour in lamellae indistinct or in some species raphanoid, earthy, grassy, sweetish, fruity or on exposure. KOH reaction in pileus context negative, yellow, orange, reddish lilac, olivaceous or pale brown. Basidiospores 7–12.5 (–17) × 4–8.5 (–10) μm, amygdaloid, ellipsoid or citriform, in some species subglobose, finely to strongly verrucose. Pileipellis duplex, simplex in P. subgen. Cyanicium and some lineages of P. subgen. Phlegmacium, epicutis in many species ± gelatinous.

Ecology and Distribution: In the Northern Hemisphere with the species of Fagales, Pinaceae and Tilia. In the Southern Hemisphere at least in Nothofagaceae forests. The centre of the diversity is in the Northern Hemisphere: two of the four subgenera, Bulbopodium and Cyanicium, are only known from the Northern Hemisphere and the vast majority of the species of the P. subgenus Bulbopodium are also boreal.

Notes: This genus includes many of the species traditionally placed in the Cortinarius subgenus Phlegmacium. Typical for the species are a dry stipe and viscid to glutinous pileus, or if dry, then the KOH reaction in the context of the pileus is usually yellow. Most species have a pileipellis duplex with a more or less developed hypoderm but the species of the subgenus Cyanicium and some lineages of P. subgen. Phlegmacium have a simplex pileipellis. The species of the genus Calonarius that were previously included in this group can be distinguished from the species of the genus Phlegmacium by the combination of pileocarpic basidiomata, a marginated bulb and simplex pileipellis. For the phlegmacioid species in the genus Thaxterogaster, a distinguishing combination of characters that would work for all groups is harder to give, but as a rule the phlegmacioid species encountered in the Southern Hemisphere mainly belong to the genus Thaxterogaster and the lineages in the Northern Hemisphere that can be confused with the species of the genus Phlegmacium are subgenera Multiformes, Riederorum, Scauri and Variegati and sections Pinophilus and Vesperitini. Some phlegmacioid lineages also exist in the genus Cortinarius, namely Infracti and Subtorti, but they have stipitocarpic basidiomata and round spores. The species of the small Southern Hemispheric genus Volvanarius have a phlegmacioid appearance as well, but they are small in size and the majority of the species have a volva. Some species of the genus Cystinarius may also be confused with the species of the genus Phlegmacium, but Cystinarius species have distinct cheilo- and pleurocystidia and a dry pileus. Lastly, the basidiomata of the genus Austrocorinarius resemble those in P. subgenus Phlegmacium, sect. Arguta and clades/Obsoleti and Caligati but those lineages of Phlegmacium are only known from the Northern Hemisphere whereas the genus Austrocorinarius occurs in the South Pacific.

Phlegmacium subgen. Phlegmacium

Currently included sections: Phlegmacium, Arguta, Claricoloria, Elastica, Obsoletia, Phlegmacioida, Perconia, Rhizophora, Seraria, and Varia as well as clade/Caligata.

Notes: The centre of the diversity of this species-rich lineage is in the Northern Hemisphere but some members of the group are also encountered in the Southern Hemisphere. Basidiomata are medium- to large-sized, predominantly stipitocarpic, agaricoid (phlegmacioid). The stipe is dry, and the pileus is viscid to glutinous, or if dry then the KOH reaction in the context of the pileus is usually yellow. The pileipellis is either duplex or simplex. The members of the other species-rich subgenus, Bulbopodium, have mainly pileocarpic basidiomata.

Phlegmacium subgen. Bulbopodium (Earle) Niskanen & Liimat., comb. & stat. nov.

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Basionym: Bulbopodium Earle, Bull. New York Bot. Gard. 5: 441 (1909).

Current name of the type species: Phlegmacium caeruleus (Schaeff.) Wünsche, Die Pilze: 131 (1877). Basionym of the type species: Agaricus caeruleus Schaeff., Fung. bavar. palat. nasc. (Ratisbonae) 4: 17 (1774). Lectotype: Schaeffer, Fung. Bav. 1: Tab. 34, figs I, II, III, 1762, in Brandrud et al., Cortinarius Flora Photographica II, pl. B11 (1992). Epitype: S F-44815, in Liimatainen et al., Persoonia 33:118 (2014).

Currently included sections: Amoenolentia, Arcifolia, Aureocistophila, Bulbopodium (= Caeruleentes s.s. Soop et al. 2019), Caerulea (= Eucaerulei s.s. Soop et al. 2019), Caerulescentia (= Camptori s.s. Soop et al. 2019), Dionysae, Glaucocophala, Glaucopodes, Subhymenogaster, and Taura.

Notes: Representatives of this species-rich subgenus are thus far only known from the Northern Hemisphere. Basidiomata are medium- to large-sized, predominantly pileocarpic, agaricoid (phlegmacioid) or rarely sequestrate. The pileus is viscid to glutinous, and the stipe is dry. The
members of the other species-rich subgenus, Phlegmacium, have mainly stipitocarpic basidiomata and some species also have a yellow to pale brown KOH reaction in the pileus context.

**Phlegmacium subgen. Carbonella (Soop) Niskanen & Liimat., comb. & stat. nov.**

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*Basionym*: Cortinarius sect. Carbonelli Soop, in Soop, Dima, Cooper, Park & Oertel, Persoonia 42: 286 (2019).

*Current name of the type species*: Phlegmacium carbonellum (Soop) Niskanen & Liimat., *comb. nov*. IF552947.

*Basionym of the type species*: Cortinarius carbonellus Soop, Bull. Soc. mycol. Fr. 117(2): 120 (2001). *Holotype*: PDD 70502.

*Current included sections*: Carbonella.

*Notes*: The species of this subgenus occur in the Nothofagaceae forests of New Zealand. The species are characterized by small-sized, agaricoid (telamonioid), stipitocarpic basidiomata with dark grey-brown to bluish-grey, or purple-brown to umbraculiform, development type of the basiodiomata stipitocarpic) but phylogenetically the subgenus is most closely related to the other species-rich subgenus, Phlegmacium, characterized by small-sized, agaricoid (telamonioid), stipitocarpic with greyish-blue, greyish-brown to darker purplish-brown colors. The pileus is at first viscid but soon dry. A context that becomes vinaceous-red on exposure and lamellar trama hyphae with abundant small to large to worm-like blood red guttules in Melzer’s reagent is typical. The KOH reaction is negative in the context and the pileipellis structure is simplex.

**Thaxterogaster Singer.** Mycologia 43(2): 216 (1951) *em. Niskanen & Liimat.*

*Current name and basionym of the type species*: Thaxterogaster magnellanicus Singer [as ‘maggellanicum’], Mycologia 43(2):219. 1951. *Neotype*: Argentina, Tierra del Fuego, Ushuaia, los Humedales, under Nothofagaceae, 16 Feb 2015. L. Domínguez LSD2380b, CORDC00006504, GenBank no. MN855076 (ITS), in Nouhra et al., Mycologia 113: 1040 (2021).

*Synonyms*: Gigasperma E. Horak, N.Z. Jl Bot. 9(3): 491 (1971). *Current name of the type species*: Thaxterogaster crypticus (E. Horak) Niskanen & Liimat.

**Hygramaricium Locq., Fl. Mycol., 3. Cortinari-ales-A.: 146 (1979) [1977]. *Current name of the type species*: Thaxterogaster causticus (Fr.) Niskanen & Liimat., *comb. nov*. IF552948. *Basionym of the type species*: Cortinarius causticus Fr., Epicr. syst. mycol. (Upsaliæ): 270 (1838) [1836–1838]. *Neotype*: 6031321 (H), in Niskanen et al., Index Fungorum 477: 3 (2021).

**Rapacea E. Horak, Kew Bull. 54(3): 789 (1999). *Current name of the type species*: Thaxterogaster mariae (E. Horak) Niskanen & Liimat., *comb. nov*. IF552949. *Basionym of the type species*: Rapacea mariae E. Horak, Kew Bull. 54(3): 789 (1999). *Holotype*: PDD 69747.

*Current included subgenera*: Thaxterogaster, Cretaces, Multiformes, Riederorum, Scauri, and VariegtariFig. 5.

*Description*: Basidiomata small- to large-sized, agaricoid (phlegmacioid, myxacioid) or sequestrate, development type stipitocarpic to pileocarpic. Pileus 1–12 cm, at first hemispherical, then convex to plano-convex; surface smooth, innately fibrillose or somewhat scaly; ± white, ± yellow, pale to dark brown with greyish, ochraceous or reddish tints, umber to blackish, ± purple or with a purplish tint, some species with olivaceous colours; dry, viscid or glutinous, with hygrophanous spots or streaks or non-hygrophanous. Lamellae crowded to medium spaced, adnate, adnexed or emarginate; when young white, pale grey, pale brown, green, ± purple or with a purplish tint. Stipe 4–13 cm long, 0.3–2.5 cm wide at the apex, up to 5 cm at the base; cylindrical, clavate, rooting or bulbous, bulb rounded to ± marginate; white, pale brown, ± purple, some species with greenish colours, in species of sect. Purpurascens usually turning deeper purple when bruised, dry. Universal veil white, purplish white, purple, in some species turning pink; sparse to more abundant, in pileocarpic species at the bulb margin and pileus margin, in stipitocarpic species forming a
thin sock-like sheath or incomplete and complete girdles on the stipe, usually dry but in some species viscid. Context in pileus white, pale brown, purple or dark blue/blackish green, in stipe white, ± yellow, pale brown, ± purple or with purplish or green/olivaceous colours. Odour in lamellae indistinct, in the context of the stipe indistinct, honey-like or sweet, garlic-like in *T. cripticus*. KOH reaction negative or red in pileus, context and/or stipital veil. Basidiospores 6–18 × 3.5–9 μm, subglobose, amygdaloid, fusoid to ellipsoid, finely to strongly verrucose (subglobose, smooth and very large in *T. cripticus* 25–35 μm in diam.). Cystidia absent. Pileipellis duplex, hypoderm present.

**Ecology and Distribution:** In the Northern Hemisphere with species of *Fagaceae, Betulaceae, Tilia* and *Pinaceae*. In the Southern Hemisphere in *Nothofagaceae* forests.

**Notes:** The species of this bihemispherical genus have traditionally been classified in phlegmacioid and myxacioid taxa in genus *Cortinarius* or in sequestrate general taxa. The size of the basidiomata ranges from small to large and vary in coloration from white, ochraceous, greenish, brown to purple. Typical for all agaricoid species, however, is a pileipellis duplex and a negative or, more rarely, red (in pileus, context and/or stipital veil) KOH reaction. Several lineages of this genus have a honey-like or sweet smell in the context, not typical in other genera of the family *Cortinariaceae* and otherwise known only in *Cortinarius* subgenus *Myxacium*. The development type of basidiomata ranges from stipitocarpic to pileocarpic.

**Thaxterogaster subgen. Thaxterogaster**

**Currently included sections:** *Alboaggregati, Thaxterogaster.*

**Description:** Basidiomata medium- to large-sized, agaricoid (phlegmacioid) or sequestrate, development type stipitocarpic. Pileus 3.5–7.5(–12) cm, at first hemispherical, then convex to plano-convex, with an umbo, finely fibrillose, white, yellow–brown or with purplish tint, dry to viscid. Lamellae crowded, adnate to adnexed to emarginate, white to greyish white. Stipe 4–10 cm long, 1–2 cm wide at the apex, cylindrical to rooting; white. Universal veil white, rather abundant in agaricoid species, peronate, wide at the apex, cylindrical to rooting; white. Universal veil white to greyish white. Stipe 4–10 cm long, 1–2 cm wide at the apex, up to 3.5 cm at the base, clavate to bulbous, bulb rounded to slightly marginate, rarely almost cylindrical, at first white, later pale brown, in some species with a bluish tint at the apex, dry. Universal

**Thaxterogaster subgen. Cretaces (Soop & Dima) Niskanen & Liimat.,** comb. et stat. nov.

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**Basionym:** *Cortinarius* sect. *Cretaces* Soop & Dima, in Soop, Dima, Cooper, Park & Oertel, Persoonia 42:279. 2019. **Current name of the type species:** *Thaxterogaster cretax* (Soop) Niskanen & Liimat., comb. nov. IF552951. **Basionym of the type species:** *Cortinarius cretax* Soop, Bull. Soc. Mycol. Fr. 118(3):185. 2003. (2002). **Holotype:** PDD 73148.

**Currently included sections:** *Cretaces.*

Notes: The representatives of this small subgenus are only encountered in the Southern Hemisphere. The basidiomata are medium- to large-sized, stipitocarpic, agaricoid (phlegmacioid) with a viscid pileus and a dry stipe. The colour of the pileus ranges from white to yellow–brown, lamellae are white to pale grey and crowded, the stipe is usually rooting and the universal veil is sparse. The odour in the lamellae is indistinct or marzipan-like. Basidiospores are fusoid-amygdaloid, 6–10 × 3–5.5 μm and weakly verrucose. The species are most reminiscent of those in *T.* subgen. *Thaxterogaster* but the agaricoid species in subgenus *Thaxterogaster* have larger basidiospores and more abundant universal veil.

**Thaxterogaster subgen. Multiformes Niskanen & Liimat.,** subgen. nov.

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**Current name of the type species:** *Thaxterogaster caesiophylloides* (Kytöv., Liimat., Niskanen, Brandrud & Frøslev) Niskanen & Liimat., comb. nov. IF552953. **Basionym of the type species:** *Cortinarius caesiophylloides* Kytöv., Liimat., Niskanen, Brandrud & Frøslev, in Liimatainen, Niskanen, Dima, Kytövuori, Ammirati & Frøslev, Persoonia 33: 130. 2014. **Holotype:** H 6029792.

**Etymology:** Named after *C. multiformis*, a species belonging to this subgenus.

**Currently included sections:** *Multiformes.*

**Description:** Basidiomata medium- to large-sized, agaricoid (phlegmacioid), development type pileocarpic. Pileus 4–12 cm, at first hemispherical, then convex to plano-convex, in some species innately fibrillose, white, cream-coloured, pale yellow, ochraceous yellow, orange-yellow, grey-brown or red brown, rarely bluish brown, viscid to glutinous, with hygrophanous spots or streaks. Lamellae crowded to almost crowded, emarginate, at first greyish white, later very pale greyish brown, in some species with a bluish tint. Stipe 4–13 cm long, 0.7–2 cm wide at the apex, up to 3.5 cm at the base, clavate to bulbous, bulb rounded to slightly marginate, rarely almost cylindrical, at first white, later pale brown, in some species with a bluish tint at the apex, dry. Universal
Thaxterogaster subgen. Malvacei Moser, but the group did not receive strong support. The phylogenetic analysis of Soop et al. (2019) indicated that morphologically similar species of T. sect. Cremeolini could also belong to this subgenus as well as species of sect. Malvacei Moser, but the group did not receive strong support.

**Ecology and Distribution:** In the Northern Hemisphere with coniferous (Pinaceae) and deciduous trees (Fagaceae, Betulaceae).

**Notes:** The species of this Northern Hemispheric subgenus are medium- to large-sized and phlegmacioid with a viscid to glutinous pileus and a dry stipe. They are characterised by having a pileocarpic development type of the basidiomata, pileipellis duplex, greyish-white lamellae when young and a honey-like smell in the context. In addition, the colour of the pileus ranges from cream-coloured to yellow- ochraceous to red-brown and the stipe is white. Some species have bluish tints in their basidiomata. The phylogenetic analysis of Soop et al. (2019) indicated that morphologically similar species of T. sect. Cremeolini could also belong to this subgenus as well as species of sect. Malvacei Moser, but the group did not receive strong support.

**Thaxterogaster subgen. Scauri** Niskanen & Liimat., subgen. nov.

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**Current name of the type species:** Thaxterogaster malachioides (P.D. Orton) Niskanen & Liimat., comb. nov. IF553568. Basionym of the type species: Cortinarius malachioides P.D. Orton, Naturalist, Leeds (Suppl.): 148. 1958. Holotype: K(M) 94426.

**Etymology:** Named after C. riederi, a species belonging to this subgenus.

**Currently included sections:** Riederorum.

**Description:** Basidiomata medium- to large-sized, agaricoid (phlegmacioid), development type pileocarpic. Pileus 2.5–12 cm, at first hemispherical, then convex to plano-convex, innately fibrillose; cream-coloured, greyish white, pale grey, yellow ochraceous, ochraceous brown, fulvous brown or grey-brown, sometimes with an olivaceous tint; viscid to glutinous, in some species with hygrophanous spots or streaks. Lamellae crowded, emarginate, at first violet-blue, later greyish brown. Stipe 5–12 cm long, 0.7–2.5 cm wide at the apex, up to 5 cm at the base; clavate to bulbous, bulb rounded to ± marginate; at first white with a bluish tint to completely bluish violet, later greyish white to pale ochraceous brown, becoming ± brown if damaged, bruised or with age, dry. Universal veil bluish white, very sparse, remnants, if visible, near the bulb margin and on the pileus margin. Context in pileus and bulb bluish white to white, in stipe bluish white to bluish violet, violet colour fading with age. Odour in lamellae indistinct. KOH reaction negative. Basidiospores 10–14.5 × 6–9 μm, ellipsoid to amygdaloid, moderately to strongly verrucose. Cystidia absent. Pileipellis duplex, epicutis with a glutinous layer on the top, hypoderm present, well to somewhat developed.

**Ecology and Distribution:** In the Northern Hemisphere with coniferous (Pinaceae) and deciduous trees (Fagaceae, Betulaceae).

**Notes:** The species of this small Northern Hemispheric subgenus are characterized by having medium- to large-sized, agaricoid (phlegmacioid), pileocarpic basidiomata with a viscid to glutinous, innately fibrillose pileus, dry stipe and bluish-violet colours in the lamellae and stipe. Typical are also large (> 10 μm long) ellipsoid to amygdaloid basidiospores, a negative KOH-reaction and pileipellis duplex. For a recent morpho-genetic revision of the group see Brandrud et al. (2018).

**Thaxterogaster subgen. Scauri Niskanen & Liimat., subgen. nov.**

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**Current name of the type species:** Thaxterogaster herpeticus (Fr.) Niskanen & Liimat., comb. nov. IF553570. Basionym of the type species: Cortinarius herpeticus Fr., Epicr. syst. mycol. (Upsaliae): 268. 1838 (1836–1838). Neotype: S F-44759, in Liimatainen et al., Persoonia 33:119 (2014).

**Etymology:** Named after C. scaurus, a species belonging to this subgenus.

**Currently included sections:** Scauri and Purpurascientes.

**Description:** Basidiomata medium- to large-sized, agaricoid (phlegmacioid), in T. sect. Purpurascientes some species sequestrate, development type pileocarpic (Scauri) or somewhat stipitocarpic to stipitocarpic (Purpurascientes). Pileus 1–10 cm, at first hemispherical, then convex to plano-convex; surface innately fibrillose or not; greyish white, pale (greyish) ochraceous, pale ochraceous brown, olivaceous brown, red brown, dark brown, blackish brown, purplish grey or pale purple; viscid to glutinous, many species with hygrophanous spots or veins. Lamellae crowded to medium spaced, emarginate, greyish brown, green to olivaceous, soon brown, in part of the species with a purplish tint, completely purple or bluish grey. Stipe 3–12 cm long, 0.3–2 cm wide at the apex, up to 3.5 cm at the base; cylindrical, clavate or more or less bulbous, bulb usually ± marginate; at first pale greyish purple/blue, pale purple to purplish green, later yellowish grey, yellow–brown or purple, in species of sect. Purpurascientes usually turning deeper purple when bruised, dry. Universal veil green, purple, ochraceous yellow or white, sparse to more abundant, in pileocarpic species at the bulb and pileus margin, in stipitocarpic species forming a sock/like sheet or incomplete and/or complete girdles on the stipe. Context in pileus white, brownish white,
pale brown, purple or dark blue/blackish green, in stipe pale purple, greenish purple, pale olivaceous to yellow-green. Odour in the context of the stipe honey-like or sweet in many species. KOH reaction negative, in a few species blood red on pileus and/or stipital veil (Soop 2017). Basidiospores 7–12×4.5–7 μm, broadly ellipsoid, ellipsoid to amygdaloid, moderately to coarsely verrucose. Cystidia absent. Pileipellis duplex, epicutis with a glutinous layer on the top, hypoderm present.

**Ecology and Distribution:** In the Northern Hemisphere with coniferous (*Pinaceae*) and deciduous trees (*Fagaceae*, *Betulaceae*, *Tilia*), and in the Southern Hemisphere in *Nothofagaceae* forests.

**Notes:** Typical for the species of this bihemispheric subgenus are medium- to large-sized, agaricoid (phlegmacioid) basidiomata with purplish and/or greenish tints/colours and a pileipellis duplex. The pileus is viscid to glutinous, and the stipe is dry, and many species have a honey-like or sweet smell in the context. The iodine (lugol) reaction is positive in the context and lamellae (Garnica et al. 2005; Soop et al. 2019). The development type of the basidiomata is pileocarpic or stipitocarpic, or for at least 14 Australian species sequestrate.

**Thaxterogaster subgen. Variegati Niskanen & Liimat.,** subgen. nov.

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*Current name of the type species:* *Thaxterogaster variegatus* (Bres.) Niskanen & Liimat., *comb. nov.* IF553573. *Basionym of the type species:* *Cortinarius variegatus* Bres., *Fung. trident.* 1(4–5):56. 1884. *Lectotype:* Bresadola, *Fung. trident.* 1(4–5): tab. LXII, 1884. *Epi-type:* Finland, Kuusamo; Oulanka botanical station, dry pine heath forest (*Pinus sylvestris*) on sandy soil, 20 Sept. 2005, coll. K. Liimatainen & T. Niskanen, 05–182, H 6031519 (epitypus hic designatus IF553602), GenBank No. OL985940 (ITS).

*Currently included sections:* Variegati.

*Description:* Basidiomata medium- to large-sized, agaricoid (phlegmacioid), development type ± stipitocarpic. Pileus 3.5–10 cm, at first hemispherical then plano-convex; surface rimin at least when young: red-brown, darker from the centre; viscid to glutinous, with some hygrophanous spots. Lamellae crowded, adnate to emarginate, greyish white to pale grey. Stipe 5–15 cm long, 1–1.5 cm wide at the apex, up to 2 cm at the base; cylindrical, clavate to bulbous, bulb margiinate or not; silky-fibrillose, white, dry. Universal veil at first white, later pink to purplish pink, forming a thin sheet or some girdles on the 1/3 lowest part of the stipe. Context white. Odour in lamellae indistinct. KOH reaction negative. Basidiospores 6–8×3–4 μm, amygdaloid-fusoid, smooth to finely verrucose. Cystidia absent. Pileipellis duplex, hypoderm present.

*Ecology and Distribution:* In the Northern Hemisphere with coniferous (*Pinaceae*) and more rarely with deciduous trees (*Fagaceae*).

**Notes:** The most characteristic features of this monotypic boreal subgenus are the initially white universal veil that becomes pinkish with age and small, almost smooth amygdaloid-fusoid spores. In addition, the basidiomata are medium- to large-sized, the development type is ± stipitocarpic and the pileipellis has a well-developed hypoderm. The pileus is red-brown, and the stipe is white. Our phylogenetic analysis also suggests that *T*. sect. *Turmales* could be included in this subgenus, but the relationship is not well-supported. Section *Turmales* includes morphologically similar species with small (<9 μm long), amygdaloid-fusoid, finely verrucose spores, and in at least one species of the section, *C. turialis*, the mycelium becomes rose-coloured after exposure to air.

**Volvanarius Niskanen & Liimat.,** gen. nov.

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*Current name of the type species:* *Volvanarius chlorosplendidus* (Furci, Niskanen, San-Fabian, Liimat. & Salgado Salomón) Niskanen & Liimat., *comb nov.* IF553604. *Basionym of the type species:* *Cortinarius chlorosplendidus* Furci, Niskanen, San-Fabian, Liimat. & Salgado Salomón, in Liimatainen, Niskanen, San-Fabian, Mujic, Peintner, Dresch, Furci, Nouhra, Matheny & Smith, Mycologia 112(2): 335. 2020. *Holotype:* K(M) 235086.

*Etymology:* Derived from the word volva, that many species of this genus have, and the generic name *Cortinarius*.

*Currently included subgenera:* Thaumasti, Volvanarius (Fig. 4).

*Description:* Basidiomata small- to rather small-sized, agaricoid (phlegmacioid) or rarely sequestrate, development type pileocarpic. Pileus 1.5–6 cm, at first hemispherical, then low convex to almost plane, yellow, ochraceous, ochraceous brown, orange-brown, olive brown to greenish, dry or viscid. Lamellae medium crowded to almost crowded, adnate, at first very pale brownish grey, later pale greyish brown. Stipe 3–8.5 cm long, 0.4–1.2 cm wide at the apex, cylindrical, with a bulbous base (up to 2.5 cm), with silky fibrillose surface, white, pale yellow, or pale greenish. Universal veil white or ochraceous, in some species with orange spots, often forming a volva at the base of the stipe. Context in most species white with ochraceous, greenish or brownish tints, in some species context in pileus brown. Odour in lamellae indistinct. Chemical reactions: context of the bulb turns red with ammonia (Moser and Horak 1975; Soop et al. 2019). Basidiospores 7–11.5×4–6.5 μm, citriform to amygdaloid, rarely ellipsoid, finely to strongly verrucose. Cystidia (cheilocystidia) balloon-shaped, present in some species. Pileipellis duplex, hypoderm developed.
Notes: This small genus is only known from the Southern Hemispheric Nothofagaceae forests. Members of this group can easily be identified in the field by the small and Phlegmacium-like basidiomata with a bulbous stipe, and the universal veil that in most species forms a distinct volva at the base of the stipe. Typical are also citriform to amygdaloid, rarely ellipsoid basidiospores and pileipellis duplex. A few species have balloon-shaped cheilocystidia. For a recent morphogenetic revision of C. sect. Thaumastii see Liimatainen et al. (2020b).

Discussion

Which criteria make a good genus?

The primary criterion for recognizing a taxonomic rank such as genus is a natural, monophyletic group of species that is supported, for a given phylogenetic analysis. However, the rank and what other criteria should be used to delimit it are more or less subjective. Ultimately, the aim is to find a community consensus for practical solution to describing diversity. At least in species-rich fungal groups, monophyletic clades with good support often exist at different nested levels for a given phylogeny and there are, therefore, multiple ways in which generic limits could be drawn.

A genus is usually also defined by its morphological, chemical, or ecological characteristics that distinguish it from its relatives. Our proposed classification is largely in-line with circumscription of other genera in the same order based on a combination of phylogenetic, morphological, chemical, and ecological traits. Although a universal set of objective criteria is not realistic for classifying all life with its multitudes of variation, the objective of achieving both coherence and practicality in recognizing evolutionary uniqueness of the generic rank within a higher taxon could be applied at approximately the same level of inclusiveness. This ideal exists not only because a basic assumption is that a certain taxonomic rank reflects a level of cohesion around a similar set of traits and phylogenetic patterns, but also because in practice it makes comparisons between different genera across different groups of organisms (e.g., in ecological, evolutionary, and conservation studies) more meaningful.

One additional aspect to take into consideration when delimiting genera is the amount of diversity to be included. Within reason, monotypic genera should be avoided, since the general aim of classification above the species level is to group closely related units together towards increasingly larger units, so that each taxonomic level, with cumulative inclusiveness, would deliver information that is something more than the previous unit. In practise, however, monotypic entities are hard to completely avoid since some clades are just less diverse than others. On the opposite end, if made possible by the other criteria above, we also try to avoid overly diverse entities in which we run out of infrageneric taxonomic ranks, i.e., subgenera and sections, to classify the distinct monophyletic groups identified within the genus. When delimiting genera, we aim to find a balance between the number of genera and the amount of diversity they include.

The trend in fungal taxonomy, after the introduction of molecular tools, has in many cases been towards smaller and natural genera (e.g., Buyck et al. 2008, Sánchez-García et al. 2014, Matheny et al. 2020). The work is still ongoing and it would be important that all genera would go through the same re-evaluation so that, in the end, we would be applying a similar set of criteria for recognizing genera across higher fungal taxa. This process has and will, without a doubt, lead to nomenclatural changes, but the end result should be improvement—a natural, more meaningful, and stable classification that will provide a good framework for understanding and classifying fungal diversity in an evolutionary context.

Generic delimitation within Cortinariaceae

Current delimitation of the genus Cortinarius and associated problems

The size of genus Cortinarius with thousands of species and tremendous morphological variation among them have contributed to a poor understanding of their true diversity and evolutionary relationships. Even at local scales, Cortinarius has often been too diverse to manage accurately as a whole and taxonomists have tended to specialize on certain groups. For example, in Funga Nordica (Niskanen et al. 2008) Cortinarius is the only genus in which different authors have written different subkeys of the genus.

The idea of splitting the genus Cortinarius into several genera is not a new one. Based on morphological data, different genera—i.e., Dermocybe, Phlegmacium, and Rozites—have been recognized in the past (e.g., Moser 1960; Moser and Horak 1975). The main issue with all previous classifications, however, has been that they were either unnatural or keeping them would have led to the splitting of the genus into far too many, upractical entities. Alternative solutions on how to divide the genus into natural units have not been possible until now, because the phylogenetic studies done so far have not been able to resolve the deeper nodes of the phylogeny, beyond the section level (e.g., Peintner et al. 2004; Garnica et al. 2005; Soop et al. 2019).

If we look at how the current situation lines with other families in the suborder Agaricineae, the ectomycorrhizal...
family Inocybaceae provides a good point of reference for a comparison. It is a species-rich family, around 2600 species are recognized based on ITS sequence data using an SH threshold of 1.5% in UNITE (2021). Before its most recent molecular revisions (Matheny and Bougher 2006; Alvarado et al. 2010; Matheny et al. 2020), it used to be a monotypic family including one genus, Inocybe. Now, the family is delimited into seven genera based on morpho-genetic data.

If the current system to delimit genus Cortinarius is neither practical nor does it align well with comparable genera in the suborder, the reasonable conclusion would be to split the genus. It is hard to see a reason, other than keeping nomenclatoric stability, to maintain Cortinarius as a single genus.

**New classification proposed and justification for the new generic delimitations**

Here we propose the classification of family Cortinariaceae into ten genera—Aureonarius, Astrocortinarius, Calonarius, Cortinarius, Cystinarius, Hygromnus, Mystinarius, Phlegmacium, Thaxterogaster, and Volvanarius—based on the phylogenetic analysis of 75 single-copy nuclear orthologs from 19 species, complemented with a wider 5-locus analysis of 245 recognized species. There are names already in existence for the three largest genera, as well as three to eleven generic level synonyms. Where several names of a genus are possible, the most ancient synonym must be chosen (Art. 11.4, 52.1), which explains why a name like Thaxterogaster now applies to a large taxon with only some gastroid members. Seven genera are described as new to science. The position of Stephanopus within suborder Agaricineae, for which no sequence data exist, remains to be studied. The genera have been delimited (i) to be the largest monophyletic units with statistical support, (ii) to be supported by morphological traits, (iii) to facilitate classification of Cortinariaceae diversity into infrageneric ranks, (iv) to avoid oversplitting, and (v) to be in line with other genera of gilled macrofungi.

To strike a balance between the number of genera and the amount of morphological and species diversity they include, a few exceptions to the principles above have been made. For example, we propose that the small telamonioid subgenus Carbonella should be included in an otherwise rather uniform genus Phlegmacium, because treating Carbonella as a separate genus would have required the division of the genus Phlegmacium into four separate genera. Also, the genus Cortinarius s. str. has been kept as one unit, rather than further split it into several smaller genera, even though morphologically it still is quite a variable genus (and six out of eleven entities currently recognized as subgenera already have a generic level name), because many relationships still remain unresolved and many species are not currently included in any well-supported group.

Based just on monophyly, the phylogeny would have allowed us to propose also other solutions for the generic classification within family Cortinariaceae. We could have delimited just two genera, Thaxterogaster and Cortinarius, but that would not have led to any major taxonomic improvements that accurately capture the morphological variation contained within a single genus. Also, having five genera—Thaxterogaster, Hygromnus, Astrocortinarius, Cortinarius, and Phlegmacium—could have been an option. However, in this scenario, the species-rich genera Phlegmacium and Calocroci, as well as the smaller Aureonarius, Cystinarius, and Mystinarius (all entities with morphological characteristics that make them easily distinguishable from one another) would have been grouped together.

All genera recognized have a combination of morphological traits that distinguish them from their closely related taxa. The smaller genera are more uniform morphologically and thus more easily defined and recognized. Additionally, one of the four species-rich genera, Calonarius, is also morphologically very uniform. However, the three largest genera contain clades that differ morphologically from the others within that genus. This broadens the infrageneric variation and affects the diagnostic value of the generic descriptions, although the vast majority of the species in those genera can still be distinguished based on morphology from members of other genera.

An estimation of the species diversity in the ten putative genera of Cortinariaceae is given in Table 3. Genus Cortinarius s. str. still remains the largest genus in the family, with ≥ 2000 species estimated worldwide, classified into eleven subgenera and more than a hundred sections. In the Northern Hemisphere, the next most species-rich genera are Phlegmacium (four subgenera, 15 sections) and Calonarius (three subgenera), while in the Southern Hemisphere (where Calonarius does not occur and where the diversity of Phlegmacium is low) the second largest genus is Thaxterogaster (six subgenera, 18 sections). All these three genera are estimated to have more than or ~ 200 species. The remaining six genera are smaller, containing ≤ 25 species.

Thus, how does the suggested delimitation of genera compare to other groups of gilled fungi? When comparing our proposal to the new Inocybaceae classification the new proposal and its justification are very similar. In both cases, after careful examination of global morpho-genetic data, the previously monotypic family has been divided into several genera to better recognize and communicate the amount of morphological, ecological, and biological diversity observed within each of them. We propose four larger and six smaller genera, whereas the current framework for Inocybaceae includes four larger (> 50 species) and three smaller genera of which one is monotypic. In both cases the genus on
which the family name is based remains the largest one with hundreds of species. The refined classification will be more practical to use for comparative studies and is more appropriate for conservation studies and for identification of diversity hotspots than the previous, more inclusive one (Matheny et al. 2020).

When comparing the sizes of the four most species-rich genera—Cortinarius, Phlegmacium, Thaxterogaster, and Calonarius—to other genera of gilled fungi, the new classification still retains the size signature of the old classification, only now with more segregated units that are better refined. Because comparison at a global scale is challenging since, for many genera, data are still lacking and/or can be strongly biased, and because local keys or checklists from the most intensively studied areas of the world can provide a better basis for a more accurate comparison, we here use species numbers from Funga Nordica (Niskanen et al. 2008) to give an idea of the sizes of the new genera. Based on the proposed classification, Cortinarius would still be at least the second largest genus (206 species) after Entoloma (232 species) in Northern Europe and, most likely even remain the largest when all species from the region are recorded. The size of Calonarius (~80 species) would be equal with Psathyrella, while the size of Phlegmacium (~60 species) with Tricholoma and the size of Thaxterogaster (~30 species) with Amanita although for the latter the comparison does not strictly apply, since Thaxterogaster has its centre of the diversity in the Southern Hemisphere and, globally, the size of this genus is equal to that of Phlegmacium.

To maintain nomenclatural stability as much as possible, we have kept the currently accepted sectional framework that has been created based on molecular data. In addition, the new generic names have been designed to have the same ending -narius as in Cortinarius, to keep the species epithets as they currently are, whenever possible.

In ecological and conservation studies, the go-to operational taxonomic unit is the species rank. Under current usage, the next rank used is the genus level, since no information on infrageneric ranks are associated with a name in fungal DNA barcoding databases. Therefore, the new classification proposed here will benefit ecological and other research by providing more biologically relevant categories. For example, the recognition of genus Calonarius, with many rare representatives that have narrow ecological preferences, will help highlight its uniqueness. Moreover, this classification will also advance communication of conservation priorities, as many of the species in Calonarius are included on national red lists across Europe (e.g. Stoltze and Pihl 1998; SLU Artdatabanken 2020) with C. meinhartii also making it into the global red list (Brandrud 2019). Having Calonarius as a separate genus will help draw focus into this group and provide a tool to better recognize it by ecologists and conservation biologists.

**Previous phylogenetic studies in Cortinariaceae**

Genera recognized in this study have also been recovered in the two previous multi-gene studies of Cortinariaceae that included data from the RPB1 region, in addition to the traditionally used ITS and LSU regions (Garnica et al. 2016; Soop et al 2019). Garnica et al. (2016) recognized the following clades: Phlegmacioid clade 1 (=Phlegmacium), Phlegmacioid clade 2 (=Thaxterogaster), Phlegmacioid clade 3 (=Calonarius), Renidentes (=Hygronarius), and Coleopodes (=Volvanarius). Also, Aureonarius, Cortinarius, Cystinarius, and Mystinarius were included in their analysis and formed their own respective clades, although they were not named in the tree. The only genus not represented in this earlier study is Austrocortinarius, but it was included in the phylogeny of Soop et al. (2019), which also recovered the same clades inferred by Garnica et al. (2016). Although many lineages in Garnica et al. (2016) received good support, they were unsupported in the analysis of Soop et al. (2019) and, therefore, were not recognized as formally named taxa.

The phylogenies based on ITS and LSU alone can recover the proposed genera to some extent, but these two gene regions do not suffice to resolve all of the infrafamilial relationships correctly. Particularly, they fail in recovering the monophyly of genera Cortinarius s. str. and Aureonarius (Garnica et al. 2005; Stensrud et al. 2014). Rather, the ITS and LSU regions are most suitable for shallow level classification, i.e., species and sections. To get a better idea on the higher level classification of Cortinariaceae, at least RPB1 would be needed, in addition to ITS and LSU. For optimal resolution, genome-wide data should be used.

**How does the new proposed classification differ from the existing one?**

Moving from one to ten genera is a big change, but our proposal is not a large leap in circumscribing the known diversity. First, most of the diversity belongs to four large genera, Cortinarius (species-rich in the Northern and Southern Hemispheres), Phlegmacium (species-rich in the Northern Hemisphere, but far fewer species in the Southern Hemisphere), Thaxterogaster (species-rich in the Southern Hemisphere, but far fewer species in the Northern Hemisphere) and Calonarius (restricted to the Northern Hemisphere). Secondly, most of the species-level diversity remains within genus Cortinarius s. str., which includes most of the species with telamonioid, cortinarioid (including dermocyboid and leprocyboid) or myxacioid habits, and all species with
rozetoid or cuphyceoid habits (Table 3). Third, except for *Aureonarius* and *Hygronarius*, the small genera *Austrocortinarius*, *Cystinarius*, *Mystinarius*, and *Volvanarius* have long been enigmatic and difficult to confidently place within the previous classifications based on morphological traits only.

The main difference to the previous classification is the transfer of most phlegmacioid species to three separate genera: *Phlegmacium*, *Calonarius*, and *Thaxterogaster*. Of these, *Calonarius* is the easiest one to distinguish based solely on morphology. It has been recognized as a separate lineage from very early phylogenetic studies onwards (Peintner et al. 2004; Gärntner et al. 2005) and several molecular studies have focused on it (e.g., Frøslev et al. 2007; Gärntner et al. 2009, 2011). In the Northern Hemisphere, genus *Phlegmacium* contains most of the species traditionally included in *C. subgenus Phlegmacium*, except for sections *Multiformes*, *Scauri/Purpurascentes*, *Riederorum*, *Lustrati*, *Pinophili*, *Turmales*, and *C. variegatus* which instead belong to genus *Thaxterogaster*. In the Southern Hemisphere *Nothofagaceae* forests, however, the default genus for phlegmacioid species is *Phlegmacium*. So far, no *Calonarius* species have been found in the Southern Hemisphere and far fewer species of *Phlegmacium* occur in the Southern than in the Northern Hemisphere. The peculiar species of Southern Hemisphere *C. sect. Thaumasti*, which look like miniature, volvate *Phlegmacium*, are treated in their own genus, *Volvanarius*; whereas the two distinctive, big, white species that occur in Australia and New Zealand are placed in genus *Austrocortinarius*. In addition, sections *Crassi* and *Rubicunduli*, traditionally classified with either phlegmacioid or cortinarioid species, are retained in their own genus, *Cystinarius*. Consequently, few stipitocarpic lineages with a phlegmacioid appearance—sections *Subtorri*, *Infracti*, *Dulciolentes*, *Cuphocybe*, and *Vinaceolamellati*—are kept in genus *Calonarius*.

The myxacioid species mostly remain in genus *Cortinarius* and only sections *Vibratiles* and *Austrocyanites* are moved into *Thaxterogaster*, while *C. lustrabilis* and *C. badiohepaticus* are placed in the genus *Mystinarius*. Also, cortinarioid species mainly remain in genus *Cortinarius* and the only changes are the placement of sections *Callistei* and *Limonii* in their own genus *Aureonarius*, and the placement of section *Rubicunduli* in genus *Cystinarius*. In addition, most telamonioid species belong to genus *Cortinarius* and only some tens of species are placed in other lineages: genus *Hygronarius* and *P. subgenus Carbonella*. All rozetoid and cuphyceoid species belong to genus *Cortinarius*.

Sequestrate species have already been shown to belong to different lineages of *Cortinariaceae* (Peintner et al. 2001; Nouhra et al. 2021). Although most of them belong to either *Cortinarius* or *Thaxterogaster*, they are found in all four of the largest *Cortinariaceae* genera (*Cortinarius*, *Phlegmacium*, *Calonarius*, and *Thaxterogaster*), as well as in the small genus *Volvanarius*.

### Infrageneric classification

Our main goal for this study, was to produce a revised generic framework for family *Cortinariaceae* based on a robust phylogeny derived from genomic data. Furthermore, a base for subgeneric classification is also proposed by recognizing clades with strong to full support, while indicating the possible limits of the already existing subgenera. In some genera, i.e., *Aureonarius* and *Phlegmacium*, for which single-copy gene data from a wide range of species already exist, all species were placed in moderately to fully supported groups (Fig. 2). Elsewhere, e.g., the two species-rich genera *Cortinarius* and *Thaxterogaster*, further multi-gene studies will be needed to clarify the infrageneric relationships and, at present, only the morphologically and genetically most distinct groups are here recognized. A total of 30 subgenera are recognized of which 10 are here described as new to science.

For the most species-rich genus, *Cortinarius*, 11 subgenera and 130 sections are currently recognized, although most of these sections (80) belong to the most species-rich subgenus of *Cortinariaceae*, *C. subgen. Telamonia*. Morphological variation in the genus is broad but correlates rather well with the phylogeny. The vast majority of cortinarioid (dermocyboid, leprocyboid) and telamonioid species are placed in the strongly supported (BS 97%) crown group of *Cortinarius*. The group includes the cortinarioid subgenera *Dermocybe*, *Lepocybe*, and *Orellani*, and the telamonioid subgenera *Iodolentes*, *Illumini*, and *Telamonia*, plus several sections and species whose relationships were not well-resolved (Fig. 2). The small phlegmacioid subgenus *Infracti* and the New Zealand endemic *C. pholiottellus* form a fully supported (BS 100%) sister group to the crown group. Leading to this crown clade, we find a grade comprised mainly myxacioid, rozetoid, cuphyceoid, and sequestrate species, together with *C. sect. Anomali*, which was previously placed in *C. subgen. Telamonia*. Tentative limits of the previously described subgenera are marked in the tree (Fig. 2). Subgenus *Cortinarius*, which includes the type species of the genus *C. violaceus*, is tentatively placed in an unsupported clade sister to all other *Cortinarius* species. It is a morphologically unique group characterized by dark purple to blackish-purple species with dry velvety-squamulose pileus and cheilocystidia (Harrower et al. 2015a, b).

In the genus *Phlegmacium*, four subgenera and 22 sections are recognized. The subgenera are all moderately to fully supported in the phylogenetic analysis and are also supported by morphological traits. The two large groups, *P. subgen. Phlegmacium* and *P. subgen. Bulbopodium*, are
characterized by different basidiomata development types: the basidiomata of Phlegmacium are stipitocarpic and those of Bulbopodium pileocarpic. The small subgenus Cyanicium includes species with bluish to violet (brownish)grey basidiomata and reddening context. They are phlegmacioid in appearance but have previously also been placed in Telamonia and Sericeocybe (Soop et al. 2019). Also, Carbonella is placed with moderate support in genus Phlegmacium in our analysis. It differs from all other lineages of Phlegmacium by having telamonioid basidiomata and is thus recognized here as its own subgenus.

Thaxterogaster includes phlegmacioid, myxacioid and a few telamonioid species. At present, five new subgenera, in addition to the autonym, are proposed to describe the morphologically most distinct units and to serve as anchors for further studies. Twenty-eight sections are recognized. More sampling of species from the Southern Hemisphere is needed to better understand the infrageneric relationships and evolution of the genus.

In Calonarius, three subgenera and 11 sections are recognized. In the smaller genera Aureonarius, Cystinarius, and Hygrenarius, two subgenera are recognized for each genus, and this division is also supported by morphological traits. In Austrocortinarius, Mystinarius, and Volvanarius, which only contain a few species, no further infrageneric classification is proposed.

Fungariomics

Two approaches were used to create genomic data for our phylogenomic study: shallow WGS and targeted capture sequencing. For the shallow WGS, the goal was to produce sufficient sequence data representative of the whole genome to assemble into contiguous sequences and then fish our targets from the resulting assemblies. For the targeted capture sequencing, the baits are first designed for the chosen targets, then genomic libraries of chosen samples are enriched, via in solution hybridization with our baits, so that only the targets will be sequenced. We wanted to compare the performance of these two methods in fungi, for which the genome size is relatively small and thus producing low cost WGS data is possible.

Results obtained from targeted capture sequencing were remarkably better than those achieved via shallow WGS. With targeted capture sequencing, over 85% of the 75 targets used for the phylogenomics analysis were recovered, for nine out of 11 specimens. Whereas with WGS, the same percentage was only achieved for three out of nine specimens. The same specimen of Cystinarius crassus was processed with both methods and 33% of the targets were recovered with WGS, compared to 99% with targeted capture sequencing. The advantage of the targeted capture sequencing approach is that only the targeted regions of the systematic group studied are sequenced whereas in WGS the whole genome is sequenced, including possible contaminants present in the basidiomata collected from the wild or gained during the preservation process (Dentinger et al. 2016). Thus, prior knowledge of the genome size of the studied species might help optimize the number of specimens to be pooled for WGS; although, even then, some of the capacity might be lost to sequencing accompanying organisms. Somewhat better results could potentially have also been achieved by improved assembly quality through assembly refinement and it could also be possible that differences in the preservation state and molecular processing of sampled Cortinariaceae species might as well have had some impact in the results (Brewer et al. 2019; Forrest et al. 2019). However, a thorough comparison and evaluation of the effects of these different factors to the success rate is beyond the scope of this study and overall, they would not entirely explain the differences observed in performance.

The age of the fungarium specimens sampled ranged from one to 21 year for the WGS and from four to 13 year for the targeted capture sequencing. Targeted capture sequencing studies in plants have used herbarium specimens ~50–200 years old (Brewer et al. 2019; Shee et al. 2020), and even thousands of years old aDNA in archaeogenomic studies (Kistler et al. 2020). Therefore, targeted capture sequencing is also a very promising approach for fungariomics and provides a way to unlock the full potential of specimens stored in fungaria worldwide for phylogenetic analysis. In our study we generated genomic libraries with medium sized inserts, which we chose to sequence in a MiSeq using the Nano chemistry (250 × 250 bp), due to the small number of specimens processed in total. However, especially for the older specimens, where the DNA is likely to be more degraded, the Illumina platforms (i.e., HiSeq, NextSeq, NovaSeq), taking shorter sized fragments as template, would be more suitable.

Our results join the existing evidence (Dodsworth et al. 2019) showing that targeted capture sequencing provides a cost-efficient approach (Hale et al. 2020) to produce data for phylogenomic analyses for species-rich groups, like Cortinariaceae, in which one can use the same set of baits for a large range of species (e.g., see Liu et al. 2019, mosses; Johnson et al. 2019, angiosperms; or Widhelm et al. 2021, peltigeralean lichens). The initial bait design and capture reactions add costs compared to the WGS and therefore the latter approach can be more appropriate for smaller taxonomic groups, unless an enrichment panel is already available. It is difficult to provide a precise threshold on the number of species for which targeted capture sequencing becomes cheaper than WGS in fungi, since costs of genomic data are in constant flux and costs also depend
on the genome size and intended sequencing coverage, as well as the number of baits to be included in the enrichment panel. Nonetheless, to give some idea of the difference in volume between these two methods, for Cortinariaceae we estimated that about ~200 specimens could be pooled into a single Illumina MiSeq 2×300 bp paired end run, when using targeted capture sequencing, compared to five to six specimens in total for the WGS approach. On the other hand, in some cases it might be justified to choose the WGS approach for other reasons, e.g., its potential added value of providing data on other genomic features or other loci, not included for a given enrichment panel, for analyses at different taxonomic levels.

Conclusions

This study is the first family revision in Agaricales based on genomic data and hopefully many others will soon follow. We have come a long way from the time of Fries when all gilled fungi were in one genus, Agaricus (Fries 1821). Since then, mycologists have, in most cases, created smaller and smaller genera due to the increased understanding of the diversity and enhanced ability to collect data of the organisms for taxonomic studies. The same phenomenon has happened in plants and animals. The genus Cortinarius has been an especially difficult group for taxonomists, because it includes an enormous amount of morphological and species diversity. While there have been previous efforts to divide the genus into more manageable, practical, and natural units, none have achieved a natural classification for the whole group. Our proposed classification for Cortinariaceae is more equilevant to contemporary concepts in other genera of gilled fungi and we hope that our framework will be more user-friendly, facilitating the identification, conservation and ecological studies on these fascinating organisms.

Additional new combinations of the species and sections belonging to the different genera of family Cortinariaceae

Aureonarius

Aureonarius armiae (Soop) Niskanen & Liimat., comb. nov.

IF553605

Basionym: Cortinarius armiae Soop, Bresadoliana 1(2): 19. 2013.

Aureonarius aurantiobrunneus (Ammirati, Halling & Garnica) Niskanen & Liimat., comb. nov.

IF553606

Basionym: Cortinarius aurantiobrunneus Ammirati, Halling & Garnica, in Ammirati, Garnica, Halling, Mata, Mueller & Carranza, Can. J. Bot. 85(9): 801. 2007.

Aureonarius austrolimonius (M.M. Moser & E. Horak) Liimat. & Niskanen, comb. nov.

IF553607

Basionym: Cortinarius austrolimonius M.M. Moser & E. Horak, Beih. Nova Hedwigia 52: 454. 1975.

Aureonarius callisteus (Fr.) Niskanen & Liimat., comb. nov.

IF553608

Basionym: Agaricus callisteus Fr., Observ. mycol. (Havniae) 2: 51. 1818.

Aureonarius caryotis (Soop) Niskanen & Liimat., comb. nov.

IF553621

Basionym: Cortinarius caryotis Soop, Bull. Soc. mycol. Fr. 117(2): 97. 2001.

Aureonarius caryotoides (Soop) Niskanen & Liimat., comb. nov.

IF553622

Basionym: Cortinarius caryotoides Soop, in Soop, Wallace & Dima, N.Z. Jl Bot. 56(2): 166. 2018.

Aureonarius controversus (Gasparini) Niskanen & Liimat., comb. nov.

IF553623

Basionym: Cortinarius controversus Gasparini, in Gasparini & Soop, Australas. Mycol. 27(3): 190. 2008.
Aureonarius eucollybianus (Soop) Niskanen & Liimat., *comb. nov.*

IF553624

Basionym: *Cortinarius eucollybianus* Soop, in Soop, Wallace & Dima, N.Z. Jl Bot. 56(2): 171. 2018.

*Aureonarius infucatus* (Fr.) Niskanen & Liimat., *comb. nov.*

IF553625

Basionym: *Cortinarius infucatus* Fr., Öfvers. K. Svensk. Vetensk.-Akad. Förhandl. 18(1): 26. 1861.

*Aureonarius limonius* (Fr.) Niskanen & Liimat., *comb. nov.*

IF553626

Basionym: *Agaricus limonius* Fr., Observ. mycol. (Havniae) 2: 56. 1818.

*Aureonarius neocallisteus* (Kranab., Ammirati, Liimat. & Niskanen) Niskanen & Liimat., *comb. nov.*

IF553640

Basionym: *Cortinarius neocallisteus* Kranab., Ammirati, Liimat. & Niskanen, in Niskanen, Liimatainen, Kytövuori, Lindström, Dentinger & Ammirati, Mycologia 108(5): 1024. 2016.

*Aureonarius rubrimarginatus* (Soop) Niskanen & Liimat., *comb. nov.*

IF553641

Basionym: *Cortinarius rubrimarginatus* Soop, in Soop, Wallace & Dima, N.Z. Jl Bot. 56(2): 169. 2018.

*Aureonarius tofaceus* (Fr.) Niskanen & Liimat., *comb. nov.*

IF553645

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

*Aureonarius viscilaetus* (Soop) Niskanen & Liimat., *comb. nov.*

IF553777

Austrocortinarius

*Austrocortinarius australiensis* (Cleland & Cheel) Liimat. & Niskanen, *comb. nov.*

IF553778

Basionym: *Rozites australiensis* Cleland & Cheel, Trans. & Proc. Roy. Soc. S. Australia 42: 90. 1918.

Calonarius

*Calonarius sect. Atrovirentes* (Bidaud, Moënne-Locc. & Reumaux) Niskanen & Liimat., *comb. & stat. nov.*

IF553779

Basionym: *Cortinarius ser. Atrovirens* Bidaud, Moënne-Locc. & Reumaux, in Bidaud, Carteret, Eyssartier, Moënne-Loccoz & Reumaux, Atlas des Cortinaires (Meyzieu) 14: 958. 2004.

*Calonarius sect. Aureopulverulenti* (Brandrud & Melot) Niskanen & Liimat., *comb. & stat. nov.*

IF553780

Basionym: *Cortinarius subsect. Aureopulverulenti* Brandrud & Melot, Nordic Jl Bot. 10(5): 535. 1990.

*Calonarius sect. Dibaphi* (Brandrud & Melot) Niskanen & Liimat., *comb. & stat. nov.*

IF553781
Basionym: *Cortinarius* subsect. *Dibaphi* Brandrud & Melot, Nordic Jl Bot. 10(5): 537. 1990.

*Calonarius* sect. *Flavovirentes* (Bidaud, Moënne-Locc. & Reumaux) Niskanen & Liimat., *comb. & stat. nov.*

IF553782

Basionym: *Cortinarius* ser. *Flavovirens* Bidaud, Moënne-Locc. & Reumaux, in Bidaud, Carteret, Eyssartier, Moënne-Loccoz & Reumaux, Atlas des Cortinaires (Meyzieu) 14: 958. 2004.

*Calonarius* sect. *Osmophori* (Bidaud & Reumaux) Niskanen & Liimat., *comb. & stat. nov.*

IF553783

Basionym: *Cortinarius* stirps *Osmophorus* Bidaud & Reumaux, in Bidaud, Moënne-Loccoz, Reumaux, Carteret & Eyssartier, Atlas des Cortinaires (Meyzieu) 16: 1097. 2006.

*Calonarius* sect. *Platypodes* (Bidaud, Moënne-Locc. & Reumaux) Niskanen & Liimat., *comb. & stat. nov.*

IF553784

Basionym: *Cortinarius* ser. *Platypodes* Bidaud, Moënne-Locc. & Reumaux, in Bidaud, Moënne-Loccoz, Reumaux, Carteret & Eyssartier, Atlas des Cortinaires (Meyzieu) 11: 611. 2001.

*Calonarius* sect. *Rufoolivacei* (Brandrud & Melot) Niskanen & Liimat., *comb. & stat. nov.*

IF553785

Basionym: *Cortinarius* subsect. *Rufoolivacei* Brandrud & Melot, Nordic Jl Bot. 10(5): 538. 1990.

*Calonarius* sect. *Sodagniti* (Bidaud, Moënne-Locc. & Reumaux) Niskanen & Liimat., *comb. & stat. nov.*

IF553786

Basionym: *Cortinarius* ser. *Sodagniti* Bidaud, Moënne-Locc. & Reumaux, Docums Mycol. 24(no. 95): 43. 1994.

*Calonarius* sect. *Splendentes* (Kühner & Romagn. ex Brandrud & Melot) Niskanen & Liimat., *comb. & stat. nov.*

IF553787

Basionym: *Cortinarius* subsect. *Splendentes* Kühner & Romagn. ex Brandrud & Melot, Nordic J. Bot. 10(5): 538. 1990.

*Calonarius* adonis (Bojantchev & Ammirati) Niskanen & Liimat., *comb. nov.*

IF553788

Basionym: *Cortinarius* adonis Bojantchev & Ammirati, in Bojantchev, Index Fungorum 247: 1. 2015.

*Calonarius* albertii (Dima, Frøslev & T.S. Jeppesen) Niskanen & Liimat., *comb. nov.*

IF553789

Basionym: *Cortinarius* albertii Dima, Frøslev & T.S. Jeppesen, in Frøslev, Jeppesen & Læssøe, Mycol. Res. 110(9): 1050. 2006.

*Calonarius* albidolilacinus (Ammirati, Bojantchev, Beug, Liimat., Niskanen & Garnica) Niskanen & Liimat., *comb. nov.*

IF553790

Basionym: *Cortinarius* albidolilacinus Ammirati, Bojantchev, Beug, Liimat., Niskanen & Garnica, in Liimatainen, Index Fungorum 241: 1. 2015.

*Calonarius* alcalinophilus (Rob. Henry) Niskanen & Liimat., *comb. nov.*

IF553791

Basionym: *Cortinarius* alcalinophilus Rob. Henry, Bull. trimest. Soc. mycol. Fr. 67(3): 301. 1952. (1951).

*Calonarius* alnobetulae (Kühner) Niskanen & Liimat., *comb. nov.*

IF553792

Basionym: *Cortinarius* alnobetulae Kühner, Docums Mycol. 20(77): 92. 1989.

*Calonarius* amabilis (Bojantchev, Ammirati & Pastorino) Niskanen & Liimat., *comb. nov.*

IF553793
Basionym: *Cortinarius amabilis* Bojantchev, Ammirati & Pastorino, in Bojantchev, Index Fungorum 247: 1. 2015.

*Calonarius amnicola* (A.H. Sm.) Niskanen & Liimat., *comb. nov.*

IF553794

Basionym: *Cortinarius amnicola* A.H. Sm., Bull. Torrey bot. Club 69(1): 48. 1942.

*Calonarius anaunianus* (Fellin & R.J. Ferrari) Niskanen & Liimat., *comb. nov.*

IF553795

Basionym: *Cortinarius anaunianus* Fellin & R.J. Ferrari, in Fellin, Ercole, Ferrari & Vizzini, Phytotaxa 520(3): 230. 2021.

*Calonarius anetholens* (Ammirati, Garnica, Bojantchev, Beug, Liimat. & Niskanen) Niskanen & Liimat., *comb. nov.*

IF553800

Basionym: *Cortinarius anetholens* Ammirati, Garnica, Bojantchev, Beug, Liimat. & Niskanen, in Liimatainen, Index Fungorum 241: 1. 2015.

*Calonarius arcuatorum* (Rob. Henry) Niskanen & Liimat., *comb. nov.*

IF553801

Basionym: *Cortinarius arcuatorum* Rob. Henry, Bull. trimest. Soc. mycol. Fr. 55(1): 80. 1939.

*Calonarius arenicola* (A.H. Sm.) Niskanen & Liimat., *comb. nov.*

IF553802

Basionym: *Cortinarius arenicola* A.H. Sm., Bull. Torrey bot. Club 69(1): 49. 1942.

*Calonarius atrovirens* (Kalchbr.) Niskanen & Liimat., *comb. nov.*

IF553803

Basionym: *Cortinarius atrovirens* Kalchbr., Icon. Sel. Hymenomyc. Hung. (Budapest) 2: tab. 19. 1874.

*Calonarius aureocalceolatus* (M.M. Moser & Peintner) Niskanen & Liimat., *comb. nov.*

IF553804

Basionym: *Cortinarius aureocalceolatus* M.M. Moser & Peintner, *Journal des JEC, Journées Européennes du Cortinaire* 5(no. 4): 30. 2002.

*Calonarius aureofulvus* (M.M. Moser) Niskanen & Liimat., *comb. nov.*

IF553851

Basionym: *Cortinarius aureofulvus* M.M. Moser, *Sydowia* 6(1–4): 154. 1952.

*Calonarius aureopulverulentus* (M.M. Moser) Niskanen & Liimat., *comb. nov.*

IF553852

Basionym: *Cortinarius aureopulverulentus* M.M. Moser, *Sydowia* 6(1–4): 152. 1952.

*Calonarius aurora* (M.M. Moser & Ammirati) Niskanen & Liimat., *comb. nov.*

IF553853

Basionym: *Cortinarius aurora* M.M. Moser & Ammirati, in Moser, McKnight & Ammirati, *Mycotaxon* 55: 305. 1995.

*Calonarius barbaricus* (Brandrud) Niskanen & Liimat., *comb. & stat. nov.*

IF553854

Basionym: *Cortinarius callochrous var. barbaricus* Brandrud, *Cortinarius, Flora Photographica* (Matfors) 3: 27. 1994.

*Calonarius barbarorum* (Bidaud, Moënne-Locc. & Reumaux) Niskanen & Liimat., *comb. nov.*

IF553855

Basionym: *Cortinarius barbarorum* Bidaud, Moënne-Locc. & Reumaux, in Bidaud, Moënne-Loccoz, Reumaux, Carteret & Eyssartier, *Atlas des Cortinaires* (Meyzieu) 11: 612. 2001.

*Calonarius bigelowii* (Thiers & A.H. Sm.) Niskanen & Liimat., *comb. nov.*
Calonarius cacodes (M.M. Moser & Ammirati) Niskanen & Liimat., *comb. nov.*

Calonarius caesiocinctus (Kühner) Niskanen & Liimat., *comb. nov.*

Calonarius cacodes M.M. Moser & Ammirati, Mycotaxon 74(1): 6. 2000.

Calonarius caesiocinctus (Rob. Henry ex Bidaud & Reumaux) Niskanen & Liimat., *comb. nov.*

Calonarius callochrous (Pers.) Niskanen & Liimat., *comb. nov.*

Calonarius callochrous Kühner, Docums Mycol. 20(77): 92. 1989.

Calonarius caesiocinctus Rob. Henry ex Bidaud & Reumaux, in Bidaud, Carteret, Eyssartier, Moënne-Loccoz & Reumaux, Atlas des Cortinaires (Meyzieu) 14: 960. 2004.

Calonarius callochrous (Pers.) Niskanen & Liimat., *comb. nov.*

Calonarius callochrous (Pers.) Syn. meth. fung. (Göttingen) 2: 282. 1801.

Calonarius callochrous (M.M. Moser & Ammirati) Niskanen & Liimat., *comb. nov.*

Calonarius callochrous Frøslev & T.S. Jeppesen, in Frøslev, Jeppesen & Læssøe, Mycol. Res. 110(9): 1051. 2006.

Calonarius cisticola (Frøslev & T.S. Jeppesen) Niskanen & Liimat., *comb. nov.*

Calonarius cisticola Frøslev & T.S. Jeppesen, in Frøslev, Jeppesen & Læssøe, Mycol. Res. 110(9): 1051. 2006.

Calonarius cisticola (A.H. Sm.) Niskanen & Liimat., *comb. nov.*

Calonarius cisticola A.H. Sm., Bull. Torrey bot. Club 69(1): 54. 1942.

Calonarius citrinipes (J.E. Lange ex P.D. Orton) Niskanen & Liimat., *comb. nov.*

Calonarius citrinipes A.H. Sm., Bull. Torrey bot. Club 69(1): 54. 1942.

Calonarius citrinipes (J.E. Lange ex P.D. Orton) Niskanen & Liimat., *comb. nov.*

Calonarius citrinipes J.E. Lange ex P.D. Orton, Bull. trimest. Soc. mycol. Fr. 55(2): 176. 1960.
Calonarius claroflavus (Rob. Henry) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius claroflavus* Rob. Henry, Bull. trimest. Soc. mycol. Fr. 67(3): 297. 1952. (1951).

Calonarius cobaltinus (Kytöv., Liimat. & Niskanen) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius cobaltinus* Kytöv., Liimat. & Niskanen, in Liimatainen, Index Fungorum 22: 1. 2013.

Calonarius coniferarum (M.M. Moser) Niskanen & Liimat., *comb. & stat. nov.*

Basionym: *Phlegmacium multiforme* var. *coniferarum* M.M. Moser, Gatt. Phlegm.: 349. 1960.

Calonarius corrosus (Fr.) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius corrosus* Fr., Epicr. syst. mycol. (Upsaliae): 266. 1838. [1836–1838].

Calonarius cupreorufus (Brandrud) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius cupreorufus* Brandrud, in Brandrud, Lindström, Marklund, Melot & Muskos, Cortinarius, Flora Photographica (Matfors) 3: 27. 1994.

Calonarius dalecarlicus (Brandrud) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius dalecarlicus* Brandrud, in Brandrud, Lindström, Marklund, Melot & Muskos, Cortinarius, Flora Photographica vol. 2 (Sweden): 33. 1992.

Calonarius dibaphus (Fr.) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius dibaphus* Fr., Epicr. syst. mycol. (Upsaliae): 266. 1838. [1836–1838].

Calonarius elegantiomontanus (Garnica & Ammirati) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius elegantiomontanus* Garnica & Ammirati, in Garnica, Spahn, Oertel, Ammirati & Oberwinkler, BMC Evol. Biol. 11(213 [reprint]): 13 + Additional file 3: 20. 2011.

Calonarius elegantiomontanus (Garnica & Ammirati) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius elegantiomontanus* Garnica & Ammirati, in Garnica, Spahn, Oertel, Ammirati & Oberwinkler, BMC Evol. Biol. 11(213 [reprint]): 13 + Additional file 3: 20. 2011.

Calonarius elegantior (Fr.) Niskanen & Liimat., *comb. & stat. nov.*

Basionym: *Agaricus multiformis* β *elegantior* Fr., Observ. mycol. (Havniae) 2: 64. 1818.

Calonarius elegantissimus (Rob. Henry) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius elegantissimus* Rob. Henry, Docums Mycol. 20(77): 69. 1989.

Calonarius elotoides (M.M. Moser & McKnight) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius elotoides* M.M. Moser & McKnight, in Moser, McKnight & Ammirati, Mycotaxon 55: 311. 1995.

Calonarius elotus (Fr.) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius elotus* Fr., Epicr. syst. mycol. (Upsaliae): 264. 1838. (1836–1838).

Calonarius evosmus (Joachim ex Bidaud & Reumaux) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius evosmus* Joachim ex Bidaud & Reumaux, in Bidaud, Moënne-Loccoz, Reumaux, Carteret & Eyssartier, Atlas des Cortinaires (Meyzieu) 16: 1097. 2006.
Calonarius flavaurora (M.M. Moser & McKnight) Niskanen & Liimat., *comb. nov.*

Calonarius flavoaurantians (Boccardo, Cleric. & Vizzini) Niskanen & Liimat., *comb. nov.*

Calonarius flavobulbus (Ammirati & M.M. Moser) Niskanen & Liimat., *comb. nov.*

Calonarius flavovirens (Rob. Henry) Niskanen & Liimat., *comb. nov.*

Calonarius frondosophilus (Bidaud) Niskanen & Liimat., *comb. nov.*

Calonarius fulvocitrinus (Brandrud) Niskanen & Liimat., *comb. nov.*

Calonarius fulvoincarnatus (Joachim ex Bidaud, Moënne-Loccc. & Reumaux) Niskanen & Liimat., *comb. nov.*

Calonarius glaucescens (Jul. Schäff.) Niskanen & Liimat., *comb. nov.*

Calonarius glaucoelotus (Brandrud, Dima, Krisai, Ballarà & Peintner) Niskanen & Liimat., *comb. nov.*

Calonarius haasii (M.M. Moser) Niskanen & Liimat., *comb. & stat. nov.*

Calonarius hildegardiae (Schmidt-Stohn, Brandrud & Dima) Niskanen & Liimat., *comb. nov.*

Calonarius fulvoarcuatorum (Garnica & Ammirati) Niskanen & Liimat., *comb. nov.*

Calonarius fulvoarcuatorum (Garnica & Ammirati) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius flavaurora* M.M. Moser & McKnight, in Moser, McKnight & Ammirati, Mycotaxon 55: 321. 1995.

Basionym: *Cortinarius flavoaurantians* Boccardo, Cleric. & Vizzini, in Vizzini, Clericuzio, Boccardo & Ercole, Mycologia 104(6): 1504. 2012.

Basionym: *Cortinarius flavobulbus* Ammirati & M.M. Moser, in Moser & Ammirati, Sydowia 49(1): 34. 1997.

Basionym: *Cortinarius flavovirens* Rob. Henry, Bull. trimest. Soc. mycol. Fr. 55(2): 182. 1939.

Basionym: *Cortinarius frondosophilus* Bidaud, in Bidaud, Moënne-Locoz, Reumaux, Carteret & Eyssartier, Atlas des Cortinaires (Meyzieu) 11: 613. 2001.

Basionym: *Cortinarius fulvoarcuatorum* Garnica & Ammirati, in Garnica, Spahn, Oertel, Ammirati & Oberwinkler, BMC Evol. Biol. 11(213 [reprint]): 13 + Additional file 3: 5. 2011.
Calonarius insignibilbus (Bidaud & Moënne-Locc.) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius insignibilbus* Bidaud & Moënne-Locc., in Bidaud, Moënne-Loccoz, Reumaux, Carteret & Eyssartier, Atlas des Cortinaires (Meyzieu) 11: 613. 2001.

IF554430

Calonarius intricatus (Bojantchev, Ammirati & N. Siegel) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius intricatus* Bojantchev, Ammirati & N. Siegel, in Bojantchev, Index Fungorum 247: 1. 2015.

IF554431

Calonarius ionochlorus (Maire) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius ionochlorus* Maire, Publ. Inst. Bot. Barcelona 3(no. 4): 113. 1937.

IF554432

Calonarius jardinensis (Garnica, Ammirati & Halling) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius jardinensis* Garnica, Ammirati & Halling, in Garnica, Spahn, Oertel, Ammirati & Oberwinkler, BMC Evol. Biol. 11(213 [reprint]): 13 + Additional file 3: 7. 2011.

Calonarius juxtadibaphus (Rob. Henry) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius juxtadibaphus* Rob. Henry, Bull. trimest. Soc. mycol. Fr. 99(1): 11. 1983.

IF554434

Calonarius kristinae (Brandrud) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius kristinae* Brandrud, in Frøslev, Brandrud & Dima, Mycol. Progr. 16(2): 151. 2017.

Calonarius laberiae (Münzmay, B. Oertel & Saar) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius laberiae* Münzmay, B. Oertel & Saar, Journal des JEC, Journées Européennes du Cortinaire 12(11): 36. 2009.

Calonarius langeorum (Frøslev & T.S. Jeppesen) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius langeorum* Frøslev & T.S. Jeppesen, in Frøslev, Jeppesen & Læsøe, Mycol. Res. 110(9): 1052. 2006.

Calonarius lavandulochlorus (Eyssart.) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius lavandulochlorus* Eyssart., Journal des JEC, Journées Européennes du Cortinaire 14(no. 13): 53. 2011.

Calonarius lentus (Boccardo, Cleric., Dovana & Vizzini) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius lentus* Boccardo, Cleric., Dovana & Vizzini, in Dovana, Boccardo, Clericuzio & Vizzini, Phytotaxa 447(1): 35. 2020.

Calonarius lilacinovelatus (Reumaux & Ramm) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius lilacinovelatus* Reumaux & Ramm, in Bidaud, Moëne-Loccoz, Reumaux, Carteret & Eyssartier, Atlas des Cortinaires (Meyzieu) 11: 613. 2001.

Calonarius lilaciotinctus (Garnica & Ammirati) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius lilaciotinctus* Garnica & Ammirati, in Garnica, Spahn, Oertel, Ammirati & Oberwinkler, BMC Evol. Biol. 11(213 [reprint]): 13 + Additional file 3: 10. 2011.

Springer
Calonarius luteicolor (Ammirati, Bojantchev, Niskanen & Liimat.) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius luteicolor* Ammirati, Bojantchev, Niskanen & Liimat., in Liimatainen, Niskanen, Dima, Kytövuori, Ammirati & Frøslev, Persoonia 33: 126. 2014.

Calonarius luteolus (M.M. Moser) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius luteolus* M.M. Moser, in Moser & Horak, Beih. Nova Hedwigia 52: 322. 1975.

Calonarius mariekristinae (Brandrud & Dima) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius mariekristinae* Brandrud & Dima, in Brandrud, Schmidt-Stohn & Dima, Sydowia 71: 122. 2019.

Calonarius meinhardii (Bon) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius meinhardii* Bon, Docums Mycol. 16(63–64): 66. 1986.

Calonarius metarius (Kauffman) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius metarius* Kauffman, Pap. Mich. Acad. Sci. 1: 137. 1921.

Calonarius mikedavisii (Bojantchev) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius mikedavisii* Bojantchev, Mycotaxon 118: 267. 2011. (2012).

Calonarius moseri (E. Horak) Niskanen & Liimat., *comb. nov.*

Basionym: *Phlegmacium moseri* E. Horak, Schweiz. Z. Pilzk. 40: 93. 1962.

Calonarius murellensis (Cors. Gut., Ballarà, Cadiñanos, Palazón & Mahiques) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius murellensis* Cors. Gut., Ballarà, Cadiñanos, Palazón & Mahiques, Butll. Soc. Micol. Valenciana 10: 160. 2005.

Calonarius natalis (D. Antonini & M. Antonini) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius natalis* D. Antonini & M. Antonini, Fungi Non Delineati, Raro vel Haud Perspecte et Explorate Descripti aut Definite Picti 22: 19. 2002.

Calonarius nymphicolor (Reumaux) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius nymphicolor* Reumaux, in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires, Pars V (Annecy): 151. 1993.

Calonarius ochraceopallescens (Moënne-Locc., Reumaux) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius ochraceopallescens* Moënne-Locc. & Reumaux, in Bidaud, Moënne-Loccoz, Reumaux, Carteret & Eyssartier, Atlas des Cortinaires (Meyzieu) 11: 613. 2001.

Calonarius odoratus (Joguet ex M.M. Moser) Niskanen & Liimat., *comb. nov.*

Basionym: *Phlegmacium odoratum* Joguet ex M.M. Moser, Gatt. Phlegm.: 360. 1960.
Calonarius odorifer (Britzelm.) Niskanen & Liimat., *comb. nov.*

Basionym: Cortinarius odorifer Britzelm., *Ber. naturhist. Augsburg* 28: 123. 1885.

Calonarius olearioides (Rob. Henry) Niskanen & Liimat., *comb. nov.*

Basionym: Cortinarius olearioides Rob. Henry, *Docums Mycol.* 17(no. 68): 36. 1987.

Calonarius oliveopetasatus (M.M. Moser) Niskanen & Liimat., *comb. nov.*

Basionym: Cortinarius oliveopetasatus M.M. Moser, in Moser & Ammirati, *Mycotaxon* 74(1): 29. 2000.

Calonarius olympianus (A.H. Sm.) Niskanen & Liimat., *comb. nov.*

Basionym: Cortinarius olympianus A.H. Sm., *Contr. Univ. Mich. Herb.* 2: 13. 1939.

Calonarius osloensis (Brandrud, T.S. Jeppesen & Frøslev) Niskanen & Liimat., *comb. nov.*

Basionym: Cortinarius osloensis Brandrud, T.S. Jeppesen & Frøslev, in Frøslev, Brandrud & Jeppesen, *Mycotaxon* 97: 369. 2006.

Calonarius osmophorus (P.D. Orton) Niskanen & Liimat., *comb. nov.*

Basionym: Agaricus prasinus Schaeff., *Fung. bavar. palat. nasc.* (Ratisbonae) 4: 51. 1774.

Calonarius prasinus (Schaeff.) Niskanen & Liimat., *comb. nov.*

Basionym: Agaricus prasinus Schaeff., *Fung. bavar. palat. nasc.* (Ratisbonae) 4: 51. 1774.

Calonarius pseudocisticola (Boccardo, Dovana, Dima, L. Albert, Borovička, Mikšík, Saar & Vizzini) Niskanen & Liimat., *comb. nov.*

Basionym: Cortinarius pseudocisticola Boccardo, Dovana, Dima, L. Albert, Borovička, Mikšík, Saar & Vizzini, in Dovana, Boccardo, Borovička, Vizzini, Saar, Albert, Mikšík, Clericuzio & Dima, *Phytotaxa* 518(1): 17. 2021.
Calonarius pseudocupreorufus (Niskanen, Liimat. & Ammirati) Niskanen & Liimat., *comb. nov.*

Calonarius pseudoglaucopus (Jul. Schäff. ex M.M. Moser) Niskanen & Liimat., *comb. nov.*

Calonarius pseudoparvus (Bidaud) Niskanen & Liimat., *comb. nov.*

Calonarius quercus-ilicis (Chevassut & Rob. Henry) Niskanen & Liimat., *comb. & stat. nov.*

Calonarius rapaceoides (Bidaud, G. Riousset & Riousset) Niskanen & Liimat., *comb. nov.*

Calonarius saxamontanus (Fogel) Niskanen & Liimat., *comb. nov.*

Calonarius rufo-olivaceus (Pers.) Niskanen & Liimat., *comb. nov.*

Calonarius sancti-felicis (Frøslev & T.S. Jeppesen) Niskanen & Liimat., *comb. nov.*

Calonarius sannio (M.M. Moser) Niskanen & Liimat., *comb. nov.*

Calonarius saporatus (Britzelm.) Niskanen & Liimat., *comb. nov.*

Calonarius saxamontanus (Fogel) Niskanen & Liimat., *comb. nov.*

Calonarius sodagnitus (Rob. Henry) Niskanen & Liimat., *comb. nov.*
Basionym: *Cortinarius sodagnitus* Rob. Henry, Bull. trimest. Soc. mycol. Fr. 51(1): 44. 1935.

*Calonarius spectabilis* (M.M. Moser) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius spectabilis* M.M. Moser, *Sydowia* 6(1–4): 152. 1952.

*Calonarius speculum* (Moënne-Locc.) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius speculum* Moënne-Locc., in Bidaud, Moënne- loccoz, Reumaux, Carteret & Eyssartier, Atlas des Cortinaires (Meyzieu) 11: 614. 2001.

*Calonarius splendens* (Rob. Henry) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius splendens* Rob. Henry, Bull. Soc. mycol. Fr. 36(2): 85. 1920.

*Calonarius subpurpureophyllus* (A.H. Sm.) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius subpurpureophyllus* A.H. Sm., Contr. Univ. Mich. Herb. 2: 17. 1939.

*Calonarius subsulfurinus* (Ammirati, Dima, Liimat., Niskanen & Garnica) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius subsulfurinus* Ammirati, Dima, Liimat., Niskanen & Garnica, Index Fungorum 252: 1. 2015.

*Calonarius sulfurinus* (Quél.) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius sulfurinus* Quél., C. r. Assoc. Franç. Avancem. Sci. 12: 501. 1884.

*Calonarius verrucisporus* (Thiers & A.H. Sm.) Niskanen & Liimat., *comb. nov.*
Basionym: *Cortinarius verrucisporus* Thiers & A.H. Sm., Mycologia 61: 533. 1969.

*Calonarius vesterholtii* (Frøslev & T.S. Jeppesen) Niskanen & Liimat., *comb. nov.*

IF558858

Basionym: *Cortinarius vesterholtii* Frøslev & T.S. Jeppesen, in Frøslev, Jeppesen & Læssøe, Mycol. Res. 110(9): 1055. 2006.

*Calonarius violaceipes* (Bidaud & Consiglio) Niskanen & Liimat., *comb. nov.*

IF558859

Basionym: *Cortinarius violaceipes* Bidaud & Consiglio, in Bidaud, Moënne-Loccot, Reumaux, Carteret & Eyssartier, Atlas des Cortinaires (Meyzieu) 11: 615. 2001.

*Calonarius viridirubescens* (M.M. Moser & Ammirati) Niskanen & Liimat., *comb. nov.*

IF558860

Basionym: *Cortinarius viridirubescens* M.M. Moser & Ammirati, Sydowia 49(1): 44. 1997.

*Calonarius xanthochlorus* (Rob. Henry) Niskanen & Liimat., *comb. nov.*

IF558861

Basionym: *Cortinarius xanthochlorus* Rob. Henry, Bull. trimest. Soc. mycol. Fr. 82: 117. 1966.

*Calonarius xanthodryophilus* (Bojantchev & R.M. Davis) Niskanen & Liimat., *comb. nov.*

IF558862

Basionym: *Cortinarius xanthodryophilus* Bojantchev & R.M. Davis, Mycotaxon 116: 321. 2011.

*Calonarius xanthophyllus* (Cooke) Niskanen & Liimat., *comb. & stat. nov.*

IF558863

Basionym: *Cortinarius dibaphus* var. *xanthophyllus* Cooke, Ill. Brit. Fung. (London) 5: pl.713 (753) 1886.

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*Basionym: Cortinarius verrucisporus* Thiers & A.H. Sm., Mycologia 61: 533. 1969.

*Cystinarius*

*Cystinarius crassus* (Fr.) Niskanen & Liimat., *comb. nov.*

IF558864

Basionym: *Cortinarius crassus* Fr., Epicr. syst. mycol. (Upsaliae): 257. 1838. [1836–1838].

*Cystinarius paurigarhwalensis* (Semwal, Dima & Soop) Niskanen & Liimat., *comb. nov.*

IF558865

Basionym: *Cortinarius paurigarhwalensis* Semwal, Dima & Soop, in Yuan et al., Fungal Diversity: https://doi.org/10.1007/s13225-020-00461-7, [108]. 2020.

*Cystinarius rubicundulus* (Rea) Niskanen & Liimat., *comb. nov.*

IF558866

Basionym: *Agaricus rubicundulus* Rea, Grevillea 22(no. 102): 40 1893.

*Cystinarius subgemmeus* (Soop) Niskanen & Liimat., *comb. nov.*

IF558867

Basionym: *Cortinarius subgemmeus* Soop, Bull. Soc. mycol. Fr. 118(3): 182. 2003. [2002].

*Hygronarius*

*Hygronarius sect. Austroduracini* (Soop & Dima) Niskanen & Liimat., *comb. nov.*

IF553403

Basionym: *Cortinarius sect. Austroduracini* Soop & Dima, in Soop, Dima, Cooper, Park & Oertel, Persoonia 42: 285. 2019.

*Hygronarius austroduracinus* (M.M. Moser) Liimat. & Niskanen, *comb. nov.*

IF558868

Basionym: *Cortinarius austroduracinus* M.M. Moser, in Moser & Horak, Beih. Nova Hedwigia 52: 400. 1975.
**Hygronarius parahumilis** (Garnica) Liimat. & Niskanen, *comb. nov.*

IF558869

Basionym: *Cortinarius parahumilis* Garnica, Mycologia 94(1): 142. 2002.

**Hygronarius viridibasalis** (M.M. Moser) Liimat. & Niskanen, *comb. nov.*

IF558870

Basionym: *Cortinarius viridibasalis* M.M. Moser, in Moser & Horak, Beih. Nova Hedwigia 52: 321. 1975.

**Phlegmacium**

*Phlegmacium* sect. *Amoenolentia* (Brandrud & Melot) Niskanen & Liimat., *comb. nov.*

IF558871

Basionym: *Cortinarius* sect. *Amoenolentes* Brandrud & Melot, Nord. J. Bot. 10: 535 (1990).

*Phlegmacium* sect. *Arcifolia* (Bidaud & Reumaux) Niskanen & Liimat., *comb. & stat. nov.*

IF558872

Basionym: *Cortinarius* subsect. *Arcifolii* Bidaud & Reumaux, in Bidaud, Moënne-Loccoz, Reumaux, Carteret & Eyssartier, Atlas des Cortinaires (Meyzieu) 17(2): 1235. 2008.

*Phlegmacium* sect. *Arguta* (Brandrud & Melot) Niskanen & Liimat., *comb. & stat. nov.*

IF558873

Basionym: *Cortinarius* subsect. *Arguti* Brandrud & Melot in Nord. J. Bot. 10: 535. 1990.

*Phlegmacium* sect. *Aureocistophila* (Fernàndez-Brime ex Soop, B. Oertel & Dima) Niskanen & Liimat., *comb. nov.*

IF558874

Basionym: *Cortinarius* sect. *Aureocistophili* Soop, B. Oertel & Dima, in Soop, Dima, Cooper, Park & Oertel, Persoonia 42: 277. 2019.

**Phlegmacium** sect. *Caerulescensia* (Rob. Henry ex Moënne-Locc. & Reum) Niskanen & Liimat., *comb. nov.*

IF558875

Basionym: *Cortinarius* sect. *Caerulescentes* Rob. Henry ex Moënne-Locc. & Reum, in Atlas des Cortinaires, Pars I (Annecy): 16. 1990.

**Phlegmacium** sect. *Caesiocortinata* (Frøslev & T.S. Jeppesen) Niskanen & Liimat., *comb. nov.*

IF558876

Basionym: *Cortinarius* sect. *Caesiocortinati* Frøslev & T.S. Jeppesen, in Frøslev, Matheny & Hibbett, Mol. Phylogen. Evol. 37(2): 616. 2005.

**Phlegmacium** sect. *Carbonella* (Soop) Niskanen & Liimat., *comb. nov.*

IF558877

Basionym: *Cortinarius* sect. *Carbonelli* Soop, in Soop, Dima, Cooper, Park & Oertel, Persoonia 42: 286. 2019.

**Phlegmacium** sect. *Claricoloria* (Kühner & Romagn. ex Moënne-Locc. & Reumaux) Niskanen & Liimat., *comb. nov.*

IF558878

Basionym: *Cortinarius* sect. *Claricolores* Kühner & Romagn. ex Moënne-Locc. & Reumaux, Atlas des Cortinaires, Pars 1 (Annecy): 17. 1990.

**Phlegmacium** sect. *Elastica* (Fr.) Niskanen & Liimat., *comb. & stat. nov.*

IF558879

Basionym: *Cortinarius* †††† *Elastici* Fr., Epicr. syst. mycol. (Upsaliae): 269. 1838 (1836–1838).

**Phlegmacium** sect. *Glaucopodes* (Kühner & Romagn. ex Moënne-Locc. & Reumaux) Niskanen & Liimat., *comb. nov.*

IF558880

Basionym: *Cortinarius* sect. *Glaucopodes* Kühner & Romagn. ex Moënne-Locc. & Reumaux, Atlas des Cortinaires, Pars 1 (Annecy): 16. 1990.
Phlegmacium sect. *Percomes* (M. M. Moser ex Moënne-Locc. & Reumaux) Niskanen & Liimat., *comb. & stat. nov.*

IF558881

Basionym: *Cortinarius* subsect. *Percomes* M. M. Moser ex Moënne-Locc. & Reumaux, Atlas des Cortinaires, Pars 1 (Annecy): 17. 1990.

Phlegmacium sect. *Phlegmacioda* (Fr.) Niskanen & Liimat., *comb. & stat. nov.*

IF558882

Basionym: *Agaricus†† Phlegmacioidea* Fr., Syst. mycol. (Lundae) 1: 222. 1821.

Phlegmacium sect. *Seraria* (Brandrud) Niskanen & Liimat., *comb. & stat. nov.*

IF558884

Basionym: *Cortinarius* subsect. *Serarii* Brandrud, Edinb. J. Bot. 54(1): 115. 1997.

Phlegmacium sect. *Subhymenogaster* (Soop, B. Oertel & Dima) Niskanen & Liimat., *comb. nov.*

IF558885

Basionym: *Cortinarius* sect. *Subhymenogaster* Soop, B. Oertel & Dima, in Soop, Dima, Cooper, Park & Oertel, Persoonia 42: 281. 2019.

Phlegmacium sect. *Varia* (Soop, Brandrud, Saar & Dima) Niskanen & Liimat., *comb. & stat. nov.*

IF558886

Basionym: *Cortinarius* subsect. *Varii* Soop, Brandrud, Saar & Dima, in Schmidt-Stohn, Saar, Soop, Brandrud & Dima, Journal des J.E.C 22: 37. 2020.

Phlegmacium *acidophilum* (Brandrud) Niskanen & Liimat., *comb. nov.*

IF558887

Basionym: *Cortinarius acidophilus* Brandrud, Edinb. J. Bot. 54(1): 114. 1997.

Phlegmacium *acystidiosum* (Thiers) Niskanen & Liimat., *comb. nov.*

IF558888

Basionym: *Cortinarius acystidiosus* Thiers, Mycologia 51(4): 530. 1960.

Phlegmacium *alboescens* (A.H. Sm.) Niskanen & Liimat., *comb. nov.*

IF558889

Basionym: *Cortinarius alboescens* A.H. Sm., Lloydia 7(3): 180. 1944.

Phlegmacium *albofragrans* (Ammirati & M.M. Moser) Niskanen & Liimat., *comb. nov.*

IF558890

Basionym: *Cortinarius albofragrans* Ammirati & M.M. Moser, in Moser & Ammirati, Sydowia 49(1): 27. 1997.

Phlegmacium *alticaudum* (Reumaux) Niskanen & Liimat., *comb. nov.*

IF558891

Basionym: *Cortinarius alticaudus* Reumaux, in Bidaud, Moënne-Lococo, Reumaux, Carteret & Eyssartier, Atlas des Cortinaires (Meyzieu) 17(2): 1236. 2008.

Phlegmacium *americanomussivum* (Liimat. & Niskanen) Niskanen & Liimat., *comb. nov.*

IF558892

Basionym: *Cortinarius americanomussivus* Liimat. & Niskanen, in Niskanen & Liimatainen, Index Fungorum 487: 6. 2021.

Phlegmacium *amoenolens* (Rob. Henry ex P.D. Orton) Niskanen & Liimat., *comb. nov.*

IF558893

Basionym: *Cortinarius amoenolens* Rob. Henry ex P.D. Orton, Trans. Br. mycol. Soc. 43(2): 206. 1960.

Phlegmacium *aquilanum* (T.S. Jeppesen & Frøslev) Niskanen & Liimat., *comb. nov.*

IF558894
Basionym: *Cortinarius aquilanus* T.S. Jeppesen & Frøslev, Mycotaxon 106: 470. 2009. (2008).

Phlegmacium areni-silvae (Brandrud) Niskanen & Liimat., *comb. & stat. nov.*

IF558895

Basionym: *Cortinarius balteatoalbus* var. *areni-silvis* Brandrud, Edinb. J. Bot. 54(1): 114. 1997.

Phlegmacium areolatoimbricatum (Cleland) Niskanen & Liimat., *comb. nov.*

IF558896

Basionym: *Cortinarius areolatoimbricatus* Cleland, Trans. & Proc. Roy. Soc. S. Australia 57: 191. 1933.

Phlegmacium argutum (Fr.) Niskanen & Liimat., *comb. nov.*

IF558897

Basionym: *Cortinarius argutus* Fr., Epicr. syst. mycol. (Upsaliae): 278. 1838. (1836–1838).

Phlegmacium aurantiobasalis (Bidaud) Niskanen & Liimat., *comb. nov.*

IF558899

Basionym: *Cortinarius aurantiobasalis* Bidaud, in Bidaud, Moëène-Loccoz, Reumaux, Carteret & Eyssartier, Atlas des Cortinaires (Meyzieu) 16: 1100. 2006.

Phlegmacium aureocistophilum (Vila, Contu & Liimatona) Niskanen & Liimat., *comb. nov.*

IF558900

Basionym: *Cortinarius aureoicistophilus* Vila, Contu & Liimatona, Revta Catal. Micol. 28: 173. 2006.

Phlegmacium aurescens (Ammirati, Bojantchev, Garnica, Beug, Liimat. & Niskanen) Niskanen & Liimat., *comb. nov.*

IF558901

Basionym: *Cortinarius aurescens* Ammirati, Bojantchev, Garnica, Beug, Liimat. & Niskanen, in Liimatainen, Index Fungorum 241: 1. 2015.

Phlegmacium aurilicis (Chevassut & Trescol) Niskanen & Liimat., *comb. nov.*

IF558902

Basionym: *Cortinarius aurilicis* Chevassut & Trescol, Docums Mycol. 16(63–64): 71. 1986.

Phlegmacium balteatialutaceum (Kytöv., Liimat. & Niskanen) Niskanen & Liimat., *comb. nov.*

IF558904

Basionym: *Cortinarius balteatialutaceus* Kytöv., Liimat. & Niskanen, in Liimatainen, Niskanen, Dima, Kytövuori, Ammirati & Frøslev, Persoonia 33: 134. 2014.

Phlegmacium balteatibulbosum (Kytöv., Niskanen, Liimat., Bojantchev & A.F.S. Taylor) Niskanen & Liimat., *comb. nov.*

IF558905

Basionym: *Cortinarius balteatibulbosus* Kytöv., Niskanen, Liimat., Bojantchev & A.F.S. Taylor, in Liimatainen, Niskanen, Dima, Kytövuori, Ammirati & Frøslev, Persoonia 33: 134. 2014.

Phlegmacium balteaticlavatum (Kytöv., Liimat. & Niskanen) Niskanen & Liimat., *comb. nov.*
Basionym: *Cortinarius balteaticlavatus* Kytöv., Liimat. & Niskanen, in Liimatainen, Niskanen, Dima, Kytövuori, Ammirati & Frøslev, Persoonia 33: 135. 2014.

*Phlegmacium balteaticlumatile* (Rob. Henry ex P.D. Orton) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius balteatocumatilis* Rob. Henry ex P.D. Orton, Trans. Br. mycol. Soc. 43(2): 207. 1960.

*Phlegmacium balteatatum* (Fr.) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius balteatus* Fr., Epicr. syst. mycol. (Upsaliae): 257. 1838. (1836–1838).

*Phlegmacium beugii* (Ammirati, Bojantchev, Liimat., Niskanen & Garnica) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius beugii* Ammirati, Bojantchev, Liimat., Niskanen & Garnica, in Liimatainen, Index Fungorum 241: 2. 2015.

*Phlegmacium bisporiger* (Contu) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius bisporiger* Contu, Cryptog. Mycol. 13(2): 100. 1992.

*Phlegmacium blattoi* (R. Mazza) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius blattoi* R. Mazza, Boll. Circolo Micologico 'Giovanni Carini' 23: 15. 1992.

*Phlegmacium boreicyanites* (Kytöv., Liimat., Niskanen & A.F.S. Taylor) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius boreicyanites* Kytöv., Liimat., Niskanen & A.F.S. Taylor, in Liimatainen, Niskanen, Dima, Kytövuori, Ammirati & Frøslev, Persoonia 33: 127. 2014.

*Phlegmacium borgsjoeense* (Brandrud) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius borgsjoeensis* Brandrud, in Brandrud, Lindström, Marklund, Melot & Muskos, Cortinarius, Flora Photographica vol. 2 (Sweden): 33. 1992.

*Phlegmacium brunneiaurantium* (Kytöv., Liimat. & Niskanen) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius brunneiaurantium* Kytöv., Liimat. & Niskanen, in Liimatainen, Index Fungorum 241: 2. 2015.

*Phlegmacium brunneocoerulescens* (Rob. Henry) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius brunneocoerulescens* Rob. Henry, Bull. trimest. Soc. mycol. Fr. 73(1): 25. 1957.

*Phlegmacium brunneolividum* (Bidaud) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius brunneolividus* Bidaud, in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 8: 290. 1996.

*Phlegmacium brunneoviolaceum* (Bidaud) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius brunneoviolaceus* Bidaud, in Bidaud, Moëmine-Loccoz, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 8: 291. 1996.

*Phlegmacium brunnescens* (A.H. Sm.) Niskanen & Liimat., *comb. nov.*

Basionym: *Hymenogaster brunnescens* A.H. Sm., Mycolog. 58(1): 111. 1966.
Phlegmacium bulbolatens (Chevassut & Rob. Henry) Niskanen & Liimat., comb. nov.

Basionym: Cortinarius bulbolatens Chevassut & Rob. Henry, Docums Mycol. 16(63–64): 83. 1986.

Phlegmacium caesiocolor (Kytöv., Liimat. & Niskanen) Niskanen & Liimat., comb. nov.

Basionym: Cortinarius caesiocolor Kytöv., Liimat. & Niskanen, in Liimatainen, Niskanen, Dima, Kytövuori, Ammirati & Frøslev, Persoonia 33: 136. 2014.

Phlegmacium caesiocortinatum (Jul. Schäff.) Niskanen & Liimat., comb. nov.

Phlegmacium caligatum (Malençon) Niskanen & Liimat., comb. nov.

Basionym: Cortinarius caligatus Malençon, in Malençon & Bertault, Champignon Supérieurs du Maroc 1: 482. 1970.

Phlegmacium callimorphum (Bojantchev & R.M. Davis) Niskanen & Liimat., comb. nov.

Basionym: Cortinarius callimorphus Malençon, in Malençon & Bertault, Champignon Supérieurs du Maroc 1: 482. 1970.

Phlegmacium calyptratum (A.H. Sm.) Niskanen & Liimat., comb. nov.

Basionym: Cortinarius calyptratus A.H. Sm., Lloydia 7(3): 165. 1944.

Phlegmacium calyptrodermum (A.H. Sm.) Niskanen & Liimat., comb. nov.

Basionym: Cortinarius calyptrodermus A.H. Sm., Bull. Torrey bot. Club 69(1): 51. 1942.

Phlegmacium camptoros (Brandrud & Melot) Niskanen & Liimat., comb. nov.

Basionym: Cortinarius camptoros Brandrud & Melot, Bull. trimest. Soc. mycol. Fr. 99(2): 219. 1983.

Phlegmacium castaneicolor (A.H. Sm.) Niskanen & Liimat., comb. nov.

Basionym: Cortinarius castaneicolor A.H. Sm., Lloydia 7(3): 165. 1944.

Phlegmacium cephalixoides (M.M. Moser & Thiers) Niskanen & Liimat., comb. nov.

Basionym: Cortinarius cephalixoides M.M. Moser & Thiers, in Moser, McKnight & Ammirati, Mycotaxon 55: 309. 1995.

Phlegmacium cephalixolargum (Rob. Henry) Niskanen & Liimat., comb. nov.

Basionym: Cortinarius cephalixolargus Rob. Henry, Bull. trimest. Soc. mycol. Fr. 93(3): 323. 1977.

Phlegmacium chromataphilum (Rob. Henry) Niskanen & Liimat., comb. nov.

Basionym: Cortinarius chromataphilus Rob. Henry, Bull. trimest. Soc. mycol. Fr. 105(1): 97. 1989.

Phlegmacium cinctipes (Bidaud, Eyssart. & Hermitte) Niskanen & Liimat., comb. nov.

Basionym: Cortinarius cinctipes Bidaud, Eyssart. & Hermitte, in Bidaud & Eyssartier, Bulletin Semestriel de la Fédération des Associations Mycologiques Méditerranéennes 25: 32. 2004.
Phlegmacium cistoglaucopus (A. Ortega, Vila, J.C. Campos & Fern.-Brime) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius cistoglaucopus* A. Ortega, Vila, J.C. Campos & Fern.-Brime, Mycologia 106(3): 499. 2014.

Phlegmacium citrinifolium (A.H. Sm.) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius citrinifolius* A.H. Sm., Contr. Univ. Mich. Herb. 2: 9. 1939.

Phlegmacium citriolens (Ammirati & M.M. Moser) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius citriolens* Ammirati & M.M. Moser, in Moser & Ammirati, Mycotaxon 72: 296. 1999.

Phlegmacium clarobaltoides (Rob. Henry) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius clarobaltoides* Rob. Henry, Bull. trimest. Soc. mycol. Fr. 67(3): 282. 1952. (1951).

Phlegmacium clarum (Reumaux) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius clarus* Reumaux, in Bidaud, Moënne-Locc., Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 7: 228. 1995.

Phlegmacium coalescens (Kärcher & Seibt) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius coalescens* Kärcher & Seibt, Z. Mykol. 54(1): 78. 1988.

Phlegmacium coelopus (Gasparini) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius coelopus* Gasparini, N.Z. Jl Bot. 45(1): 177. 2007.

Phlegmacium coerulescentium (Rob. Henry) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius coerulescentium* Rob. Henry, Bull. trimest. Soc. mycol. Fr. 105(1): 97. 1989.

Phlegmacium congeminum (Moënne-Locc. & Reumaux) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius congeminus* Moënne-Locc. & Reumaux, in Bidaud, Moënne-Locc. & Reumaux, Atlas des Cortinaires (Meyzieu) 7: 228. 1995.

Phlegmacium cremeiamarescens (Kytöv., Liimat. & Niskanen) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius cremeiamarescens* Kytöv., Liimat. & Niskanen, in Liimatainen, Niskanen, Dima, Kytövuori, Ammirati & Frøslev, Persoonia 33: 122. 2014.

Phlegmacium cruentipellis (Kytöv., Liimat., Niskanen & Dima) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius cruentipellis* Kytöv., Liimat., Niskanen & Dima) Niskanen & Liimat., *comb. nov.*
Basionym: *Cortinarius cruentipellis* Kytöv., Liimat., Niskanen & Dima, in Liimatainen, Niskanen, Dima, Kytövuori, Ammirati & Frøslev, Persoonia 33: 128. 2014.

*Phlegmacium cupreonatum* (Soop) Niskanen & Liimat., *comb. nov.*

IF558946

Basionym: *Cortinarius cupreonatus* Soop, Bull. Soc. mycol. Fr. 117(2): 99. 2001.

*Phlegmacium cupreoviolaceum* (Bidaud & Reumaux) Niskanen & Liimat., *comb. nov.*

IF558947

Basionym: *Cortinarius cupreoviolaceus* Bidaud & Reumaux, in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 8: 292. 1996.

Phlegmacium delaportei (Rob. Henry) Niskanen & Liimat., *comb. nov.*

IF558949

Basionym: *Cortinarius delaportei* Rob. Henry, Docums Mycol. 19(no. 73): 70. 1988.

*Phlegmacium durus* (P.D. Orton) Niskanen & Liimat., *comb. nov.*

IF558950

Basionym: *Cortinarius durus* P.D. Orton, Trans. Br. mycol. Soc. 43(2): 209. 1960.

*Phlegmacium eliae* (Bidaud, Moënne-Locc. & Reumaux) Niskanen & Liimat., *comb. nov.*

IF558951

Basionym: *Cortinarius eliae* Bidaud, Moënne-Locc. & Reumaux, in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 8: 292. 1996.

*Phlegmacium eucerauleum* (Rob. Henry) Niskanen & Liimat., *comb. nov.*

IF558952

Basionym: *Cortinarius eucerauleus* Rob. Henry, Docums Mycol. 20(no. 77): 69. 1989.

*Phlegmacium exlugubre* (Soop) Niskanen & Liimat., *comb. nov.*

IF558953

Basionym: *Cortinarius exlugubre* Soop, Bull. Soc. mycol. Fr. 117(2): 98. 2001.

*Phlegmacium flavivescentipes* (Reumaux) Niskanen & Liimat., *comb. nov.*

IF558954

Basionym: *Cortinarius flavivescentipes* Reumaux, in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 8: 292. 1996.

*Phlegmacium flavivelatum* (Kytöv., Liimat. & Niskanen) Niskanen & Liimat., *comb. nov.*

IF558955

Basionym: *Cortinarius flavivelatus* Kytöv., Liimat. & Niskanen, in Liimatainen, Niskanen, Dima, Kytövuori, Ammirati & Frøslev, Persoonia 33: 123. 2014.

*Phlegmacium fraudulosoides* (Liimat. & Niskanen) Niskanen & Liimat., *comb. nov.*

IF558956

Basionym: *Cortinarius fraudulosoides* Liimat. & Niskanen, in Niskanen, Index Fungorum 186: 1. 2014.

*Phlegmacium fraudulosum* (Britzelm.) Niskanen & Liimat., *comb. nov.*
Basionym: *Cortinarius fraudulosus* Britzelm., Ber. naturhist. Augsburg 28: 122. 1885.

*B. gentianeum* (Bidaud) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius gentianeus* Bidaud, in Bidaud, Moënné-Loccoz, Reumaux & Henry, *Atlas des Cortinaires*, Pars V (Annecy): 150. 1993.

*B. georgiolens* (Rob. Henry) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius georgiolens* Rob. Henry, *Bull. trimest. Soc. mycol*. Fr. 102(1): 76. 1986.

*B. glaucopoides* (Kauffman) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius glaucopoides* Kauffman, *Pap. Mich. Acad. Sci.* 1: 133. 1921.

*B. griseocoeruleum* (Ammirati & M.M. Moser) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius griseocoeruleus* Ammirati & M.M. Moser, in Moser & Ammirati, *Sydowia* 49(1): 33. 1997.

*B. hedyaromaticum* (C.L. Cripps & O.K. Mill.) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius hedyaromaticus* C.L. Cripps & O.K. Mill., *Mycotaxon* 50: 316. 1994.

*B. herculeum* (Malençon) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius herculeus* Malençon, C. r. Seanc. mens. Soc. Sci. nat. phys. Maroc 23: 159. 1958.

*B. hysginicolor* (Bidaud) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius hysginicolor* Bidaud, in Bidaud, Moënné-Loccoz, Reumaux & Henry, *Atlas des Cortinaires* (Meyzieu) 7: 229. 1995.

*B. inexspectatum* (Brandrud) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius inexspectatus* Brandrud, *Docums Mycol.* 20(no. 77): 110. 1989.

*B. inusitatum* (A. Ortega, Bidaud, Suár.-Sant. & Vila) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius inusitatus* A. Ortega, Bidaud, Suár.-Sant. & Vila, *Fungal Diversity* 36: 91. 2009.

*B. josephii* (Reumaux) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius josephii* Reumaux, in Bidaud, Moënné-Loccoz, Reumaux, Carteret & Eyssartier, *Atlas des Cortinaires* (Meyzieu) 16: 1099. 2006.

*B. kuehneri* (M.M. Moser) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius kuehneri* M.M. Moser, *Bull. mens. Soc. linn. Lyon* 43(Num. spéc.): 288. 1974.

*B. kytoevuorii* (Niskanen & Liimat.) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius kytoevuorii* Niskanen & Liimat., in Liimatainen, Niskanen, Dima, Kytövuori, Ammirati & Frøslev, *Persoonia* 33: 124. 2014.

*B. langei* (Rob. Henry) Niskanen & Liimat., *comb. nov.*
Phlegmacium latoclaricolor (Rob. Henry) Niskanen & Liimat., comb. nov.

Phlegmacium lavendulense (Cleland) Niskanen & Liimat., comb. nov.

Phlegmacium leonicolor (Reumaux) Niskanen & Liimat., comb. nov.

Phlegmacium lepistoides (T.S. Jeppesen & Frøslev) Niskanen & Liimat., comb. nov.

Phlegmacium lilacinoides (Soop, B. Oertel & Dima) Niskanen & Liimat., comb. nov.

Phlegmacium luhmannii (Münzmay, Saar & B. Oertel) Niskanen & Liimat., comb. nov.
Basionym: *Cortinarius luteovaginans* Bidaud & Faurite-Gendron, in Bidaud, Moëne-Loccoz, Reumaux, Carteret & Eyssartier, Atlas des Cortinaires (Meyzieu) 16: 1100. 2006.

*Phlegmacium maculipes* (Peck) Niskanen & Liimat., *comb. nov.*

IF558983

Basionym: *Cortinarius maculipes* Peck, Ann. Rep. Reg. N.Y. St. Mus. 54: 150. 1902. (1901).

*Phlegmacium maculosum* (Pers.) Niskanen & Liimat., *comb. nov.*

IF558984

Basionym: *Agaricus maculosus* Pers., Syn. meth. fung. (Göttingen) 2: 288. 1801.

*Phlegmacium mahiquesii* (Vila, A. Ortega & Suá.-Sant.) Niskanen & Liimat., *comb. nov.*

IF558985

Basionym: *Cortinarius mahiquesii* Vila, A. Ortega & Suá.-Sant., Persoonia 21: 154. 2008.

*Phlegmacium majoranae* (Frøslev & T.S. Jeppesen) Niskanen & Liimat., *comb. nov.*

IF558986

Basionym: *Cortinarius majoranae* Frøslev & T.S. Jeppesen, Mycotaxon 106: 472. 2009. (2008).

*Phlegmacium mediterraneense* (A. Ortega & Vila) Niskanen & Liimat., *comb. nov.*

IF558987

Basionym: *Cortinarius mediterraneensis* A. Ortega & Vila, Mycologia 106(3): 494. 2014.

*Phlegmacium memoria-annae* (Gasparini) Niskanen & Liimat., *comb. nov.*

IF558988

Basionym: *Cortinarius memoria-annae* Gasparini, N.Z. Jl Bot. 45(1): 195. 2007.

*Phlegmacium miserontii* (Chevassut & Rob. Henry) Niskanen & Liimat., *comb. nov.*

IF558989

Basionym: *Cortinarius miserontii* Chevassut & Rob. Henry, Docums Mycol. 16(nos 63–64): 93. 1986.

*Phlegmacium moenne-loccozi* (Bidaud) Niskanen & Liimat., *comb. nov.*

IF558990

Basionym: *Cortinarius moenne-loccozi* Bidaud, in Bidaud, Moëne-Loccoz, Reumaux & Henry, Atlas des Cortinaires, Pars V (Annecy): 151. 1993.

*Phlegmacium muricinicolor* (Moënne-Loccc.) Niskanen & Liimat., *comb. nov.*

IF558991

Basionym: *Cortinarius muricinicolor* Moënne-Loccc., in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 8: 295. 1996.

*Phlegmacium myrtilliphilum* (Kytöv., Liimat., Niskanen & Brandrud) Niskanen & Liimat., *comb. nov.*

IF558992

Basionym: *Cortinarius myrtilliphilus* Kytöv., Liimat., Niskanen & Brandrud, in Liimatainen, Niskanen, Dima, Kytövuori, Ammirati & Frøslev, Persoonia 33: 136. 2014.

*Phlegmacium neotriumphans* (Bidaud, Moënne-Loccc. & Reumaux) Niskanen & Liimat., *comb. nov.*

IF558993

Basionym: *Cortinarius neotriumphans* Bidaud, Moënne-Loccc. & Reumaux, in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 10: 372. 2000.

*Phlegmacium norrlandicum* (Brandrud) Niskanen & Liimat., *comb. nov.*

IF558994

Basionym: *Cortinarius norrlandicus* Brandrud, Docums Mycol. 20(77): 110. 1989.
Phlegmacium ochraceobrunneum (Rob. Henry ex Bidaud, Moënne-Loc. & Reumaux) Niskanen & Liimat., *comb. nov.*

IF558995

Basionym: *Cortinarius ochraceobrunneus* Rob. Henry ex Bidaud, Moënne-Loc. & Reumaux, in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 10: 372. 2000.

Phlegmacium ochribubalinum (Kytöv., Liimat. & Niskanen) Niskanen & Liimat., *comb. nov.*

IF558996

Basionym: *Cortinarius ochribubalinus* Kytöv., Liimat. & Niskanen, in Liimatainen, Niskanen, Dima, Kytövuori, Ammirati & Frøslev, Persoonia 33: 124. 2014.

Phlegmacium ochroclarum (Rob. Henry) Niskanen & Liimat., *comb. nov.*

IF558997

Basionym: *Cortinarius ochroclarus* Rob. Henry, in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 8: 295. 1996.

Phlegmacium olidoamarum (A. Favre) Niskanen & Liimat., *comb. nov.*

IF558998

Basionym: *Cortinarius olidoamarus* A. Favre, in Favre, Moënne-Loccoz & Trescol, Bull. trimest. Féd. Mycol. Dauphiné-Savoie 25(no. 100): 6. 1986.

Phlegmacium olidoamethysteum (Rob. Henry & Ramm) Niskanen & Liimat., *comb. nov.*

IF558999

Basionym: *Cortinarius olidoamethysteus* Rob. Henry & Ramm, Bull. trimest. Féd. Mycol. Dauphiné-Savoie 29(no. 115): 11. 1989.

Phlegmacium olidovolvatum (Bon & Trescol) Niskanen & Liimat., *comb. nov.*

IF559000

Basionym: *Cortinarius olidovolvatus* Bon & Trescol, Docums Mycol. 19(no. 73): 36. 1988.

© Springer
Basionym: *Cortinarius pansicolor* Soop, Bresadolina 1(2): 23. 2013.

*Phlegmacium papulosum* (Fr.) Niskanen & Liimat., *comb. nov.*

IF559008

Basionym: *Cortinarius papulosus* Fr., Epicr. syst. mycol. (Upsaliae): 271. 1838. (1836–1838).

*Phlegmacium paracephalixum* (Bohus) Niskanen & Liimat., *comb. nov.*

IF559009

Basionym: *Cortinarius paracephalixus* Bohus, Annls hist.-nat. Mus. natn. hung. 68: 51. 1978.

*Phlegmacium pardinum* (Reumaux) Niskanen & Liimat., *comb. nov.*

IF559010

Basionym: *Cortinarius pardinus* Reumaux, in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 7: 230. 1995.

*Phlegmacium patrickense* (M.M. Moser) Niskanen & Liimat., *comb. & stat. nov.*

IF559011

Basionym: *Cortinarius fraudulosus var. patrickensis* M.M. Moser, in Moser & Ammirati, Mycotaxon 74(1): 10. 2000.

*Phlegmacium patibile* (Brandrud & Melot) Niskanen & Liimat., *comb. nov.*

IF559012

Basionym: *Cortinarius patibilis* Brandrud & Melot, Bull. trimest. Soc. mycol. Fr. 99(2): 228. 1983.

*Phlegmacium percome* (Fr.) Niskanen & Liimat., *comb. nov.*

IF559013

Basionym: *Cortinarius percomis* Fr., Epicr. syst. mycol. (Upsaliae): 260. 1838. (1836–1838).

*Phlegmacium perstrenuus* (Chevassut & Rob. Henry) Niskanen & Liimat., *comb. nov.*

IF559014

Basionym: *Cortinarius perstrenuus* Chevassut & Rob. Henry, Docums Mycol. 8(no. 32): 20. 1978.

*Phlegmacium pini* (Brandrud) Niskanen & Liimat., *comb. nov.*

IF559015

Basionym: *Cortinarius pini* Brandrud, Edinb. J. Bot. 53(3): 360. 1996.

*Phlegmacium piriodolens* (Moënne-Locc.) Niskanen & Liimat., *comb. nov.*

IF559016

Basionym: *Cortinarius piriodolens* Moënne-Locc., in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 8: 296. 1996.

*Phlegmacium ponderosum* (A.H. Sm.) Niskanen & Liimat., *comb. nov.*

IF559017

Basionym: *Cortinarius ponderosus* A.H. Sm., Contr. Univ. Mich. Herb. 2: 6. 1939.

*Phlegmacium populinum* (Brandrud) Niskanen & Liimat., *comb. nov.*

IF559018

Basionym: *Cortinarius populinus* Brandrud, in Brandrud, Lindström, Marklund, Melot & Muskos, Cortinarius, Flora Photographica vol. 2 [Swedish version by Brandrud] (Sweden): 33. 1992.

*Phlegmacium prasinocyaneum* (Rob. Henry) Niskanen & Liimat., *comb. nov.*

IF559019

Basionym: *Cortinarius prasinocyaneus* Rob. Henry, Bull. trimest. Soc. mycol. Fr. 55(1): 91. 1939.

*Phlegmacium psalliotoides* (Chevassut & Rob. Henry) Niskanen & Liimat., *comb. nov.*

IF559020
**Basionym:** *Cortinarius psalliotoides* Chevassut & Rob. Henry, Docums Mycol. 8(no. 32): 19. 1978.

**Phlegmacium pseudocephalixum** (Bidaud & Moënne-Locc.) Niskanen & Liimat., *comb. nov.*

IF559022

**Basionym:** *Cortinarius pseudocephalixus* Bidaud & Moënne-Locc., in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 10: 372. 2000.

**Phlegmacium pseudocyanopus** (Rob. Henry) Niskanen & Liimat., *comb. nov.*

IF559023

**Basionym:** *Cortinarius pseudocyanopus* Rob. Henry, in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 8: 296. 1996.

**Phlegmacium pseudodaulnoyae** (Rob. Henry & Ramm) Niskanen & Liimat., *comb. nov.*

IF559024

**Basionym:** *Cortinarius pseudodaulnoyae* Rob. Henry & Ramm, Docums Mycol. 21(83): 54. 1991.

**Phlegmacium pseudolargus** (Rob. Henry) Niskanen & Liimat., *comb. nov.*

IF559025

**Basionym:** *Cortinarius pseudolargus* Rob. Henry, in Chevassut & Henry, Docums Mycol. 17(no. 68): 27. 1987.

**Phlegmacium pseudonebulare** (Moënne-Locc.) Niskanen & Liimat., *comb. nov.*

IF559026

**Basionym:** *Cortinarius pseudonebularis* Moënne-Locc., in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 8: 296. 1996.

**Phlegmacium pseudopimum** (Rob. Henry) Niskanen & Liimat., *comb. nov.*

IF559027

**Basionym:** *Cortinarius pseudopimus* Rob. Henry, in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 10: 373. 2000.

**Phlegmacium pseudopansa** (Bidaud) Niskanen & Liimat., *comb. nov.*

IF559028

**Basionym:** *Cortinarius pseudopansa* Bidaud, in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 10: 373. 2000.

**Phlegmacium pseudoturmalis** (Rob. Henry) Niskanen & Liimat., *comb. nov.*

IF559029

**Basionym:** *Cortinarius pseudoturmalis* Bidaud & Moënne-Locc., in Bidaud, Moënne-Loccoz, Reumaux & Carteret, Atlas des Cortinaires (Meyzieu) 19: 1503. 2010.

**Phlegmacium pseudovariegatum** (M.M. Moser) Niskanen & Liimat., *comb. nov.*

IF559030

**Basionym:** *Cortinarius pseudovariegatus* M.M. Moser, in Moser & Ammirati, Mycotaxon 72: 302. 1999.

**Phlegmacium pseudovarium** (Moënne-Locc. & Reumaux) Niskanen & Liimat., *comb. nov.*

IF559031

**Basionym:** *Cortinarius pseudovarium* Moënne-Locc. & Reumaux, in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 10: 373. 2000.

**Phlegmacium pseudovulpinum** (Rob. Henry & Ramm) Niskanen & Liimat., *comb. nov.*

IF559032

**Basionym:** *Cortinarius pseudovulpinus* Rob. Henry & Ramm, Bull. trimest. Féd. Mycol. Dauphiné-Savoie 29(no. 115): 9. 1989.

**Phlegmacium punctatisporum** (Garnica) Niskanen & Liimat., *comb. nov.*

IF559033
Basionym: *Cortinarius punctatisporus* Garnica, *Mycologia* 94(1): 138. 2002.

*Phlegmacium rattinum* (Soop) Niskanen & Liimat., *comb. nov.*

IF559034

Basionym: *Cortinarius rattinus* Soop, *Bull. Soc. mycol. Fr.* 117(2): 124. 2001.

*Phlegmacium reverendissimum* (Bidaud, Moënne-Locc. & Reumaux) Niskanen & Liimat., *comb. nov.*

IF559035

Basionym: *Cortinarius reverendissimus* Bidaud, Moënne-Locc. & Reumaux, in Bidaud, Moënne-Loccoz, Reumaux & Henry, *Atlas des Cortinaires* (Meyzieu) 10: 373. 2000.

*Phlegmacium rex-claricolorum* (Bidaud, Carteret & Reumaux) Niskanen & Liimat., *comb. nov.*

IF559036

Basionym: *Cortinarius rex-claricolorum* Bidaud, Carteret & Reumaux, in Bidaud, Moënne-Loccoz, Reumaux & Carteret, *Atlas des Cortinaires* (Meyzieu) 19: 1504. 2010.

*Phlegmacium rhizophorum* (Bidaud & Consiglio) Niskanen & Liimat., *comb. nov.*

IF559037

Basionym: *Cortinarius rhizophorus* Bidaud & Consiglio, *Il Genere Cortinarius in Italia* 6: F161. 2012.

*Phlegmacium rioussetiae* (Chevassut & Rob. Henry) Niskanen & Liimat., *comb. nov.*

IF559038

Basionym: *Cortinarius rioussetiae* Chevassut & Rob. Henry, *Docums Mycol.* 16(no. 63–64): 103. 1986.

*Phlegmacium rosargutum* (Chevassut & Rob. Henry) Niskanen & Liimat., *comb. nov.*

IF559039

Basionym: *Cortinarius rosargutus* Chevassut & Rob. Henry, *Docums Mycol.* 8(no. 32): 37. 1978.

Basionym: *Cortinarius rubrivelatus* Garnica, *Mycologia* 94(1): 140. 2002.

*Phlegmacium rufior* (Reumaux) Niskanen & Liimat., *comb. nov.*

IF559041

Basionym: *Cortinarius rufior* Reumaux, in Bidaud, Moënne-Loccoz, Reumaux & Henry, *Atlas des Cortinaires* (Meyzieu) 10: 374. 2000.

*Phlegmacium rufaaurantium* (Soop) Niskanen & Liimat., *comb. nov.*

IF559042

Basionym: *Cortinarius rufaaurantium* Soop, in Soop, Dima, Cooper, Park & Oertel, *Persoonia* 42: 280. 2019.

*Phlegmacium rufolatum* (Moënne-Locc.) Niskanen & Liimat., *comb. nov.*

IF559043

Basionym: *Cortinarius rufolatus* Moënne-Locc., in Bidaud, Moënne-Loccoz, Reumaux & Henry, *Atlas des Cortinaires* (Meyzieu) 8: 297. 1996.

*Phlegmacium russeum* (Fr.) Niskanen & Liimat., *comb. nov.*

IF559044

Basionym: *Cortinarius russeum* Fr., *Epicr. syst. mycol.* (Upsalae): 261. 1838. (1836–1838).

*Phlegmacium saginoides* (Bidaud & Reumaux) Niskanen & Liimat., *comb. nov.*

IF559045

Basionym: *Cortinarius saginoides* Bidaud & Reumaux, in Bidaud, Moënne-Loccoz, Reumaux & Henry, *Atlas des Cortinaires* (Meyzieu) 10: 374. 2000.

*Phlegmacium scaurocaninum* (Chevassut & Rob. Henry) Niskanen & Liimat., *comb. nov.*
Phlegmacium serariicolor (Rob. Henry) Niskanen & Liimat., *comb. nov.*

IF559047

Basionym: *Cortinarius serariicolor* Rob. Henry, Bull. trimest. Soc. mycol. Fr. 82: 137. 1966.

Phlegmacium serarium (Fr.) Niskanen & Liimat., *comb. nov.*

IF559048

Basionym: *Cortinarius serarius* Fr., Epicr. syst. mycol. (Upsaliae): 269. 1838. (1836–1838).

IF559049

Basionym: *Cortinarius sobrius* P. Karst., Hedwigia 29: 177. 1890.

Phlegmacium spurcum (Weinm.) Niskanen & Liimat., *comb. & stat. nov.*

IF559050

Basionym: *Agaricus violaceocinereus* var. *spurcus* Weinm., Hym. à Gast. Imp. Ross. Obs. (Petropoli): 165. 1836.

Phlegmacium squameoradicans (Bellivier ex Cheype) Niskanen & Liimat., *comb. nov.*

IF559051

Basionym: *Cortinarius squameoradicans* Bellivier ex Cheype, Docums Mycol. 27(no. 106): 18. 1997.

Phlegmacium squamosocephalum (Bidaud, Moënne-Locc. & Reumaux) Niskanen & Liimat., *comb. nov.*

IF559052

Basionym: *Cortinarius squamosocephalus* Bidaud, Moënne-Locc. & Reumaux, Bull. trimest. Soc. mycol. Fr. 115(4): 417. 1999.

Phlegmacium stjernegaardii (Brandrud & Frøslev) Niskanen & Liimat., *comb. nov.*

IF559053

Basionym: *Cortinarius stjernegaardii* Brandrud & Frøslev, in Frøslev, Brandrud & Dima, Mycol. Progr. 16(2): 148. 2017.

Phlegmacium subaccedens (Rob. Henry) Niskanen & Liimat., *comb. nov.*

IF559054

Basionym: *Cortinarius subaccedens* Rob. Henry, Bull. trimest. Soc. mycol. Fr. 105(1): 98. 1989.

Phlegmacium subalbescens (Reumaux) Niskanen & Liimat., *comb. nov.*

IF559055

Basionym: *Cortinarius subalbescens* Reumaux, in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires, Pars V (Annecy): 152. 1993.

Phlegmacium subamaricatum (Bidaud) Niskanen & Liimat., *comb. nov.*

IF559056

Basionym: *Cortinarius subamaricatus* Bidaud, in Bidaud, Moënne-Loccoz, Reumaux, Carteret & Eyssartier, Atlas des Cortinaires (Meyzieu) 17(2): 1238. 2008.

Phlegmacium subbalteatum (Kühner) Niskanen & Liimat., *comb. nov.*

IF559057

Basionym: *Cortinarius subbalteatus* Kühner, Bull. mens. Soc. linn. Soc. Bot. Lyon 24(2): 40. 1955.

Phlegmacium subcaeruleum (A.H. Sm.) Niskanen & Liimat., *comb. nov.*

IF559058

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

Phlegmacium subcyanites (Bidaud) Niskanen & Liimat., *comb. nov.*
Basionym: *Cortinarius subcyanites* Bidaud, in Bidaud, Moënne-Loccoz, Carteret, Reumaux & Eyssartier, Atlas des Cortinaires (Meyzieu) 15: 1032. 2005.

*Phlegmacium subdecolorans* (M. Langl. & Reumaux) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius subdecolorans* M. Langl. & Reumaux, in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 10: 374. 2000.

*Phlegmacium subdecoloratum* (Reumaux) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius subdecoloratus* Reumaux, in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 10: 374. 2000.

*Phlegmacium subfoetens* (M.M. Moser & McKnight) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius subfoetens* M.M. Moser & McKnight, in Moser, McKnight & Ammirati, Mycotaxon 55: 310. 1995.

*Phlegmacium subfoetidum* (A.H. Sm.) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius subfoetidus* A.H. Sm., Lloydia 7(3): 183. 1944.

*Phlegmacium subfuligineum* (Bidaud) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius subfuligineus* Bidaud, in Bidaud, Moënne-Loccoz, Reumaux, Carteret & Eyssartier, Atlas des Cortinaires (Meyzieu) 17(2): 1238. 2008.

*Phlegmacium subhygrophanum* (Bidaud) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius subhygrophanus* Bidaud, in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires, Pars V (Annecy): 152. 1993.

*Phlegmacium sublilacinum* (A.H. Sm.) Niskanen & Liimat., *comb. nov.*

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

*Phlegmacium subolivascens* (A.H. Sm.) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius subolivascens* A.H. Sm., Lloydia 7(3): 183. 1944.

*Phlegmacium subsolitarium* (A.H. Sm.) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius glaucopus* var. *subrubrovelatus* Bidaud, in Bidaud, Moënne-Loccoz, Reumaux, Carteret & Eyssartier, Atlas des Cortinaires (Meyzieu) 17(2): 1237. 2008.

*Phlegmacium subrubrovelatum* (Bidaud) Niskanen & Liimat., *comb. & stat. nov.*

Basionym: *Cortinarius subrugulosus* Bidaud & Armada, in Bidaud, Moënne-Loccoz, Reumaux, Carteret & Eyssartier, Atlas des Cortinaires (Meyzieu) 16: 1096. 2006.

*Phlegmacium subrubugulosum* (Bidaud & Armada) Niskanen & Liimat., *comb. nov.*
Basionym: *Cortinarius subsolitarius* A.H. Sm., Bull. Torrey bot. Club 69(1): 57. 1942.

*Phlegmacium subvariiforme* (Bidaud) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius subvariiformis* Bidaud, in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 10: 374. 2000.

*Phlegmacium superbum* (A.H. Sm.) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius superbus* A.H. Sm., Lloydia 7(3): 195. 1944.

*Phlegmacium tauri* (Mahiques & Reumaux) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius tauri* Mahiques & Reumaux, Bull. Mycol. Bot. Dauphiné-Savoie 49(no. 193): 5. 2009.

*Phlegmacium terpsichores* (Melot) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius terpsichores* Melot, Docums Mycol. 20(no. 77): 96. 1989.

*Phlegmacium tiliae* (Brandrud) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius tiliae* Brandrud, Edinb. J. Bot. 53(3): 358. 1996.

*Phlegmacium tirolianum* (Bidaud, Moënne-Loccoz & Reumaux) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius tirolianum* Bidaud, Moënne-Loccoz, & Reumaux, in Bidaud, Moënne-Loccoz, Carteret, Reumaux & Eyssartier, Atlas des Cortinaires (Meyzieu) 15: 1033. 2005.

*Phlegmacium tomentosum* (Rob. Henry) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius tomentosus* Rob. Henry, Docums Mycol. 16(no. 61): 24. 1985.

*Phlegmacium trachycystis* (M.M. Moser) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius trachycystis* M.M. Moser, in Moser & Horak, Beih. Nova Hedwigia 52: 469. 1975.

*Phlegmacium triumphale* (Bidaud, Moënne-Loccoz & Reumaux) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius triumphalis* Bidaud, Moënne-Loccoz, & Reumaux, in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 9: 374. 1999.

*Phlegmacium triumphans* (Fr.) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius triumphans* Fr., Epicr. syst. mycol. (Upsaliae): 256. 1838. (1836–1838).

*Phlegmacium turbinate* (Cors. Gut. & Vila) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius turbinate* Cors. Gut. & Vila, Revta Catal. Micol. 23: 14. 2001.

*Phlegmacium wiebeae* (Thiers & A.H. Sm.) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius wiebeae* Thiers & A.H. Sm., Mycologia 61: 529. 1969.
Phlegmacium vacciniophilum (Brandrud) Niskanen & Liimat., comb. nov.

IF559084

Basionym: Cortinarius vacciniophilus Brandrud, Edinb. J. Bot. 54(1): 114. 1997.

Phlegmacium van-campiae (Consiglio) Niskanen & Liimat., comb. nov.

IF559085

Basionym: Cortinarius van-campiae Consiglio, Micologia 2000 (Trento): 115. 2000.

Phlegmacium variiforme (Malençon) Niskanen & Liimat., comb. nov.

IF559086

Basionym: Cortinarius variiformis Malençon, in Malençon & Bertault, Champignon Supérieurs du Maroc 1: 526. 1970.

Phlegmacium variosimile (M.M. Moser & Ammirati) Niskanen & Liimat., comb. nov.

IF559087

Basionym: Cortinarius variosimilis M.M. Moser & Ammirati, Mycotaxon 72: 306. 1999.

Phlegmacium velicopium (Kauffman) Niskanen & Liimat., comb. nov.

IF559088

Basionym: Cortinarius velicopius Kauffman, Publications Mich. geol. biol. Surv., Biol. Ser. 5 26: 339. 1918.

Phlegmacium veneris (Bidaud, Moënne-Locc. & Reumaux) Niskanen & Liimat., comb. nov.

IF559089

Basionym: Cortinarius veneris Bidaud, Moënne-Locc. & Reumaux, in Bidaud, Moënne-Loccoz, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 8: 298. 1996.

Phlegmacium vernicifer (Soop) Niskanen & Liimat., comb. nov.

IF559090

Basionym: Cortinarius vernicifer Soop, in Gasparini & Soop, Australas. Mycol. 27(3): 199. 2008.

Phlegmacium violaceomaculatum (Brandrud) Niskanen & Liimat., comb. nov.

IF559091

Basionym: Cortinarius violaceomaculatus Brandrud, Edinb. J. Bot. 54(1): 115. 1997.

Phlegmacium violaceorubens (Moënne-Locc. & Reumaux) Niskanen & Liimat., comb. nov.

IF559092

Basionym: Cortinarius violaceorubens Moënne-Locc. & Reumaux, Atlas des Cortinaires, Pars II (Annecy): 27. 1990.

Phlegmacium viridocoeruleum (Chevassut & Rob. Henry) Niskanen & Liimat., comb. nov.

IF559093

Basionym: Cortinarius viridocoeruleus Chevassut & Rob. Henry, Docums Mycol. 5(no. 20): 24. 1975.

Phlegmacium vixolivascens (Rob. Henry) Niskanen & Liimat., comb. nov.

IF559094

Basionym: Cortinarius vixolivascens Rob. Henry, Bull. trimest. Soc. mycol. Fr. 108(4): 203. 1992.

Phlegmacium vulpinum (Velen.) Niskanen & Liimat., comb. nov.

IF559095

Basionym: Inoloma vulpinum Velen., České Houby 3: 428. 1921.

Phlegmacium xantho-ochraceum (P.D. Orton) Niskanen & Liimat., comb. nov.

IF559096

Basionym: Cortinarius xantho-ochraceus P.D. Orton, Trans. Br. mycol. Soc. 43(2): 216. 1960.

Phlegmacium xanthosuave (Bon & Trescol) Niskanen & Liimat., comb. nov.
Thaxterogaster

**Thaxterogaster sect. Alboaggregati** (Soop) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius* sect. *Alboaggregati* Soop, in Soop, Dima, Cooper, Park & Oertel, Persoonia 42: 279. 2019.

**Thaxterogaster sect. Austrocyanites** (Soop) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius* sect. *Austrocyanites* Soop, in Soop, Dima, Cooper, Park & Oertel, Persoonia 42: 279. 2019.

**Thaxterogaster sect. Austrovaginati** (Soop) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius* sect. *Austrovaginati* Soop, in Soop, Dima, Cooper, Park & Oertel, Persoonia 42: 281. 2019.

**Thaxterogaster sect. Caustici** (Niskanen & Liimat.) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius* sect. *Caustici* Niskanen & Liimat., Index Fungorum 477: 1. 2021.

**Thaxterogaster sect. Cremeolinae** (Soop) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius* sect. *Cremesinae* Soop, in Soop, Dima, Cooper, Park & Oertel, Persoonia 42: 276. 2019.

**Thaxterogaster sect. Cretaces** (Soop & Dima) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius* sect. *Cretaces* Soop & Dima, in Soop, Dima, Cooper, Park & Oertel, Persoonia 42: 279. 2019.

**Thaxterogaster sect. Gigasperma** (E. Horak) Niskanen & Liimat., *comb. & stat. nov.*

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

**Thaxterogaster sect. Laquelli** (Soop) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius* sect. *Laquelli* Soop, in Soop, Dima, Cooper, Park & Oertel, Persoonia 42: 279. 2019.

**Thaxterogaster sect. Lustrati** (Ammirati ex Soop, B. Oertel & Dima) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius* sect. *Lustrati* Ammirati ex Soop, B. Oertel & Dima, in Soop, Dima, Cooper, Park & Oertel, Persoonia 42: 279. 2019.

**Thaxterogaster sect. Malvacei** (M.M. Moser) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius* sect. *Malvacei* M.M. Moser, Beih. Nova Hedwigia: 240. 1975.

**Thaxterogaster sect. Olorinati** (Soop & Dima) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius* sect. *Olorinati* Soop & Dima, in Soop, Dima, Cooper, Park & Oertel, Persoonia 42: 276. 2019.

**Thaxterogaster sect. Pinophili** (Niskanen & Liimat.) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius* sect. *Pinophili* Niskanen & Liimat., Index Fungorum 477: 2. 2021.
**Thaxterogaster sect. Purpurascentes** (Kühner & Romagn. ex Brandrud & Melot) Niskanen & Liimat., *comb. & stat. nov.*

**Thaxterogaster sect. Rapacea** (E. Horak) Niskanen & Liimat., *comb. & stat. nov.*

**Thaxterogaster sect. Turmales** (Soop, B. Oertel & Dima) Niskanen & Liimat., *comb. nov.*

**Thaxterogaster sect. Verniciori** (Soop) Niskanen & Liimat., *comb. nov.*

**Thaxterogaster sect. Vibratiles** (Melot) Niskanen & Liimat., *comb. nov.*

**Thaxterogaster aggregatus** (Kauffman) Niskanen & Liimat., *comb. nov.*

**Thaxterogaster alboaggregatus** (Soop) Niskanen & Liimat., *comb. nov.*

**Thaxterogaster alboamarescens** (Kytöv., Niskanen & Liimat.) Niskanen & Liimat., *comb. nov.*

**Thaxterogaster anomalochrascens** (Chevassut & Rob. Henry) Niskanen & Liimat., *comb. nov.*

**Thaxterogaster argenteolilacinus** (M.M. Moser) Niskanen & Liimat., *comb. nov.*

**Thaxterogaster argyrionus** (Danks, T. Lebel & Vernes) Niskanen & Liimat., *comb. nov.*

**Thaxterogaster armenicorius** (Soop & Brandrud) Niskanen & Liimat., *comb. nov.*

**Thaxterogaster aurantionapus** (Bidaud & Reumaux) Niskanen & Liimat., *comb. nov.*

**Thaxterogaster alboamarescens** Kytöv., Niskanen & Liimat., in Ariyawansa et al., Fungal Diversity: [https://doi.org/10.1007/s13225-015-0346-5](https://doi.org/10.1007/s13225-015-0346-5), [192] 2015.

**Thaxterogaster anomalochrascens** Chevassut & Rob. Henry, Docums Mycol. 16(63–64): 84. 1986.

**Thaxterogaster argenteolilacinus** M.M. Moser Niskanen & Liimat., *comb. nov.*

**Thaxterogaster argyrionus** Danks, T. Lebel & Vernes, Persoonia 24: 113. 2010.

**Thaxterogaster armenicorius** Soop & Brandrud, Journal des JEC, Journées Européennes du Cortinaire 16: 191. 2014.

**Thaxterogaster aurantionapus** Bidaud & Reumaux Niskanen & Liimat., *comb. nov.*

**Thaxterogaster alboaggregatus** Soop, N.Z. Jl Bot. 43(2): 555. 2005.

**Thaxterogaster alboamarescens** Kytöv., Niskanen & Liimat., in Ariyawansa et al., Fungal Diversity: [https://doi.org/10.1007/s13225-015-0346-5](https://doi.org/10.1007/s13225-015-0346-5), [192] 2015.

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**Thaxterogaster argyrionus** Danks, T. Lebel & Vernes, Persoonia 24: 113. 2010.

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**Thaxterogaster aurantionapus** Bidaud & Reumaux Niskanen & Liimat., *comb. nov.*

**Thaxterogaster alboaggregatus** Soop, N.Z. Jl Bot. 43(2): 555. 2005.

**Thaxterogaster alboamarescens** Kytöv., Niskanen & Liimat., in Ariyawansa et al., Fungal Diversity: [https://doi.org/10.1007/s13225-015-0346-5](https://doi.org/10.1007/s13225-015-0346-5), [192] 2015.
Thaxterogaster australis (Gasparini) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius australis* Gasparini, N.Z. Jl Bot. 45(1): 205. 2007.

Thaxterogaster astrocyanites (Soop) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius astrocyanites* Soop, Bull. Soc. mycol. Fr. 117(2): 108. 2001.

Thaxterogaster austrosaginus (Gasparini) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius austrosaginus* Gasparini, N.Z. Jl Bot. 45(1): 174. 2007.

Thaxterogaster austroturmalis (M.M. Moser & E. Horak) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius austroturmalis* M.M. Moser & E. Horak, Beih. Nova Hedwigia 52: 151. 1975.

Thaxterogaster austrovaginatus (Gasparini) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius austrovaginatus* Gasparini, N.Z. Jl Bot. 45(1): 189. 2007.

Thaxterogaster barbatus (Batsch) Niskanen & Liimat., *comb. nov.*

Basionym: *Agaricus barbatus* Batsch, Elench. fung. (Halle):39, t. 3: 11. 1783.

Thaxterogaster burlinghamiae (Bojantchev) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius burlinghamiae* Bojantchev, in Brandrud, Schmidt-Stohn, Liimatainen, Niskanen, Froslev, Soop, Bojantchev, Kytövuori, Jeppesen, Bellù, Saar, Oertel, Ali, Thines & Dima, Mycol. Progr. 17(12): 1350. 2018.

Thaxterogaster caesibulga (Vernes, Danks & T. Lebel) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius caesibulga* Vernes, Danks & T. Lebel, in Danks, Lebel & Vernes, Persoonia 24: 116. 2010.

Thaxterogaster caesiolamellatus (Bidaud) Niskanen & Liimat., *comb. & stat. nov.*

Basionym: *Cortinarius rufoallatus* var. *caesiolamellatus* Bidaud, in Bidaud, Moënne-Loccoz, Reumaux, Carteret & Eyssartier, Atlas des Cortinaires (Meyzieu) 16: 1095. 2006.

Thaxterogaster caledoniensis (P.D. Orton) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius caledoniensis* P.D. Orton, Notes R. bot. Gdn Edinb. 26: 44. 1964.

Thaxterogaster castoreus (Soop) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius castoreus* Soop, N.Z. Jl Bot. 43(2): 552. 2005.

Thaxterogaster cervinus (M.M. Moser & E. Horak) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius cervinus* M.M. Moser & E. Horak, Beih. Nova Hedwigia 52: 148. 1975.

Thaxterogaster chalybeus (Soop) Niskanen & Liimat., *comb. nov.*

Basionym: *Cortinarius chalybeus* Soop, Bull. Soc. mycol. Fr. 118(3): 187. 2002.
Thaxterogaster chlorophyllus (Soop) Niskanen & Liimat., 
comb. nov.

IF559135

Basionym: Cortinarius chlorophyllus Soop, N.Z. Jl Bot. 52: 337. 2014.

Thaxterogaster cinereoroseolus (Danks, T. Lebel & Vernes) Niskanen & Liimat., comb. nov.

IF559136

Basionym: Cortinarius cinereoroseolus Danks, T. Lebel & Vernes, Persoonia 24: 118. 2010.

Thaxterogaster collocandoides (Reumaux) Niskanen & Liimat., comb. nov.

IF559137

Basionym: Cortinarius collocandoides Reumaux, in Bidaud, Moënne-Loccoz, Reumaux & Carteret, Atlas des Cortinaires (Meyzieu) 18(1–2): 1377. 2009.

Thaxterogaster columbinus (M.M. Moser & E. Horak) Niskanen & Liimat., comb. nov.

IF559138

Basionym: Cortinarius columbinus M.M. Moser & E. Horak, Beih. Nova Hedwigia 52: 250. 1975.

Thaxterogaster comarostaphylidis (Ammirati, Halling & Garnica) Niskanen & Liimat., comb. nov.

IF559139

Basionym: Cortinarius comarostaphylidis Ammirati, Halling & Garnica, in Ammirati, Garnica, Halling, Mata, Mueller & Carranza, Can. J. Bot. 85(9): 803. 2007.

Thaxterogaster comparoides (Ammirati, Halling & Garnica) Niskanen & Liimat., comb. nov.

IF559140

Basionym: Cortinarius comparoides Ammirati, Halling & Garnica, in Ammirati, Garnica, Halling, Mata, Mueller & Carranza, Can. J. Bot. 85(9): 804. 2007.

Thaxterogaster corrugis (A.H. Sm.) Niskanen & Liimat., comb. nov.

IF559141

Basionym: Cortinarius corrugis A.H. Sm., Lloydia 7(3): 189. 1944.

Thaxterogaster cremeolina (Soop) Niskanen & Liimat., comb. nov.

IF559142

Basionym: Cortinarius cremeolina Soop, Bull. Soc. mycol. Fr. 117(2): 103. 2001.

Thaxterogaster cremeorufus (Soop) Niskanen & Liimat., comb. nov.

IF559143

Basionym: Cortinarius cremeorufus Soop, N.Z. Jl Bot. 54(3): 347. 2016.

Thaxterogaster crenulatus (Rob. Henry ex Bidaud & Reumaux) Niskanen & Liimat., comb. nov.

IF559144

Basionym: Cortinarius crenulatus Rob. Henry ex Bidaud & Reumaux, in Bidaud, Moënne-Loccoz, Reumaux, Carteret & Eyssartier, Atlas des Cortinaires (Meyzieu) 16: 1097. 2006.

Thaxterogaster croceocoeruleus (Pers.) Niskanen & Liimat., comb. nov.

IF559145

Basionym: Agaricus croceocoeruleus Pers., Icon. Desc. Fung. Min. Cognit. (Leipzig) 1: 2. 1798.

Thaxterogaster dulcamarus (Soop) Niskanen & Liimat., comb. nov.

IF559146

Basionym: Cortinarius dulcamarus Soop, N.Z. Jl Bot. 54(3): 355. 2016.

Thaxterogaster dulciorum (Soop) Niskanen & Liimat., comb. nov.

IF559147

Basionym: Cortinarius dulciorum Soop, in Gasparini & Soop, Australas. Mycol. 27(3): 197. 2008.
Thaxterogaster eburneus (Velen.) Niskanen & Liimat., *comb. nov.*

*Thaxterogaster eburneus* (Velen.) Niskanen & Liimat., *comb. nov.*

**Basionym:** Phlegmacium eburneum Velen., České Houby 2: 422. 1920.

**Thaxterogaster effundens** (M.M. Moser, E. Horak & Singer) Niskanen & Liimat., *comb. nov.*

*Thaxterogaster effundens* (M.M. Moser, E. Horak & Singer) Niskanen & Liimat., *comb. nov.*

**Basionym:** Cortinarius effundens M.M. Moser, E. Horak & Singer, in Moser & Horak, Beih. Nova Hedwigia 52: 144. 1975.

**Thaxterogaster emollitoides** (Bidaud, Moënne-Locc. & Reumaux) Niskanen & Liimat., *comb. nov.*

*Thaxterogaster emollitoides* (Bidaud, Moënne-Locc. & Reumaux) Niskanen & Liimat., *comb. nov.*

**Basionym:** Cortinarius emollitoides Bidaud, Moënne-Locc. & Reumaux, in Bidaud, Moënne-Locc, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 10: 491. 2000.

**Thaxterogaster eumarginatus** (Rob. Henry ex Bidaud, Carteret & Reumaux) Niskanen & Liimat., *comb. nov.*

*Thaxterogaster eumarginatus* (Rob. Henry ex Bidaud, Carteret & Reumaux) Niskanen & Liimat., *comb. nov.*

**Basionym:** Cortinarius eumarginatus Rob. Henry ex Bidaud, Carteret & Reumaux, in Bidaud, Moënne-Locoz, Reumaux & Carteret, Atlas des Cortinaires (Meyzieu) 18(1–2): 1378. 2009.

**Thaxterogaster fiordlandensis** (Soop) Niskanen & Liimat., *comb. nov.*

*Thaxterogaster fiordlandensis* (Soop) Niskanen & Liimat., *comb. nov.*

**Basionym:** Cortinarius fiordlandensis Bidaud, Moënne-Locoz & Reumaux, in Bidaud, Moënne-Locoz, Reumaux & Henry, Atlas des Cortinaires (Meyzieu) 10: 491. 2000.

**Thaxterogaster fuligineofolius** (M.M. Moser) Niskanen & Liimat., *comb. & stat. nov.*

*Thaxterogaster fuligineofolius* (M.M. Moser) Niskanen & Liimat., *comb. & stat. nov.*

**Basionym:** Cortinarius montanus var. fuligineofolius M.M. Moser, Fungi Non Delineati, Raro vel Haud Perspecte et Explorate Descripti aut Definite Picti 15: 25. 2001.

**Thaxterogaster fulvo-ochrascens** (Rob. Henry) Niskanen & Liimat., *comb. nov.*

*Thaxterogaster fulvo-ochrascens* (Rob. Henry) Niskanen & Liimat., *comb. nov.*

**Basionym:** Cortinarius fulvo-ochrascens Rob. Henry, Bull. trimest. Soc. mycol. Fr. 59: 55. 1943.

**Thaxterogaster galeobdolon** (Rob. Henry) Niskanen & Liimat., *comb. nov.*

*Thaxterogaster galeobdolon* (Rob. Henry) Niskanen & Liimat., *comb. nov.*

**Basionym:** Cortinarius galeobdolon Melot, Acta Botanica Islandica 12: 91. 1995.

**Thaxterogaster genuinus** (Bidaud & Carteret) Niskanen & Liimat., *comb. nov.*

*Thaxterogaster genuinus* (Bidaud & Carteret) Niskanen & Liimat., *comb. nov.*

**Basionym:** Cortinarius genuinus Bidaud & Carteret, in Bidaud, Moënne-Locoz, Reumaux & Carteret, Atlas des Cortinaires (Meyzieu) 18(1–2): 1378. 2009.

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