**Cortinarius** section **Bicolores** and section **Saturnini**  
(*Basidiomycota, Agaricales*), a morphogenetic overview of European and North American species

K. Liimatainen¹, X. Carteret², B. Dima³,⁴, I. Kytövuori⁵, A. Bidaud⁶, P. Reumaux⁷, T. Niskanen¹, J.F. Ammirati⁸, J.-M. Bellanger⁹

Key words  
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integrative taxonomy  
Saturnini  
Telamonia

**Abstract**  
*Cortinarius* is the largest genus of ectomycorrhizal fungi worldwide. Recent molecular studies have shown high levels of morphological homoplasies within the genus. Importantly, DNA phylogenies can reveal characteristics that have been either over- or underemphasized in taxonomic studies. Here we sequenced and phylogenetically analysed a large set of pan-European and North American collections taxonomically studied and placed in *Cortinarius* sect. *Bicolores* and sect. *Saturnini*, according to traditional morpho-anatomical criteria. Our goal was to circumscribe the evolutionary boundaries of the two sections, to stabilize both the limits and nomenclature of relevant species, and to identify described taxa which, according to our current understanding, belong to other lineages. Our analysis resolves two clades: /Bicolores, including 12 species, one of which is new to science, and /Saturnini, including 6 species. Fifteen binomials, traditionally treated in these two sections based on morphology, do not belong to the above two phylogenetic clades. Instead, six of these latter are clearly placed in other clades that represent sect. *Bovini*, sect. *Sciophylli*, sect. *Duracini* and sect. *Brunneotincti*. The presence or absence of blue pigments and the detection of specific odours emerge as clearly misleading taxonomic features, but more surprisingly, spore size and ecology can be misleading as well. A total of 63 type specimens were sequenced, 4 neotypes and 2 epitypes are proposed here, and 1 new combination is made.

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**INTRODUCTION**

*Cortinarius* is the largest genus of ectomycorrhizal fungi worldwide, with no less than 4 701 reported taxa (3 360 species, 1 341 infraspecific taxa, http://www.catalogueoflife.org, 28 Sept. 2016 release). However, the number of species greatly varies depending on the morphological species concept accepted by classical authors. Currently, the two major monographs dedicated to the genus are *Cortinarius, Flora Photographica* (CFP), which includes ± 300 species, mostly from northern Europe (Brandrud et al. 2014), and the *Atlas des Cortinaires* (ADC), still on-going and which so far recognizes ± 2 500 species, varieties and forms, mostly from France (Bidaud et al. 2015). Recent molecular studies have unveiled high levels of morphological homoplasies as well as numerous cryptic species within the genus, and as a result, do not support the broad species concept of Scandinavian authors or the narrow one of French authors (e.g., Liimatainen et al. 2014a). Importantly, by identifying evolutionary units that are independent of morpho-anatomical and ecological traits, DNA phylogenies revealed characters that have been overemphasized in monographic studies but also uncovered significant taxonomic information that has been neglected by previous investigators (Bellanger et al. 2015, Loizides et al. 2016). The use of these modern tools *posteriori*, to test the autonomy of previously defined morphological species, has been instrumental in delineating objective boundaries to taxa, and when applied to type material, stabilizes taxonomy and nomenclature at the genus level (Frøslev et al. 2007, Liimatainen et al. 2014b, Cripps et al. 2015). The next challenge of this nascent integrative systematics era is undoubtedly to synchronize the two sources of knowledge, so that on-going monographs introduce morphogenetic species, i.e., taxa that are both assigned formal diagnosis and a unique molecular signature.

Historically, mycologists have attempted to tackle the complexity of *Cortinarius* by organizing species in hierarchical infrageneric taxa defined on supposedly stable sets of characteristics (Kühner & Romagnesi 1953, Moser 1967, Melot 1990, Moënne-Loccoz & Reumaux 1990). In spite of their practical application, most of these lower level taxonomic divisions have proven to be artificial when placed under evolutionary scrutiny (Garnica et al. 2005). Subgenus *Telamonia*, however, breaks this rule as most of the numerous species known to date that produce dry-capped basidiomata lacking vivid colours – the morphological definition of the subgenus and excluding a few sections as sect. *Obtusi, Balaustini, Illumini* – form a strongly supported monophyletic clade in all published molecular studies (Peintner et al. 2004, Stensrud et al. 2014). Recently, several sections within *Telamonia* have been phylogenetically revised, such as...
sect. Armillati, Brunnei, Bovini and Disjungendi and more are on their way to morphogenetic redefinition (Niskanen et al. 2009, 2011, 2013, Liimatainen et al. 2014a).

Here we deal with Cortinarius sect. Bicolores and Cortinarius sect. Satunini, which encompass Cortinarius evernius, C. saturninus and their lookalikes. Initially, the two sections were distinguished by the extent of veil remnants on the stipe, a character considered by some authors to segregate subg. Hydrocybe from subg. Telamonia (Moënne-Loccoz & Reumaux 1990). However, this morphological feature may not be supported phylogenetically, justifying the revision of the two sections altogether (Niskanen et al. 2012). Eight to thirty-three species have been described in sect. Bicolores and sect. Satunini in the major European monographs, from the pioneering work of Kühner & Romagnesi (1953) to the latest two releases of the ADC (Bidaud et al. 2014, 2015), in which part of the results presented here have been incorporated (Table 1). The specific goals of the present work are:

1. to circumscribe the phylogenetic boundaries of the two sections, through the analysis of a large internal transcribed spacer (ITS) rDNA sequence dataset built from pan-European and North American vouchered collections;
2. to stabilize the nomenclature and species limits of morphogenetic Bicolores and Satunini, through sequencing type material and designating neotype or epitype when opportune;
3. to assign a molecular signature to the numerous collections taxonomically placed in these two sections in contemporary monographs, but that do not belong in the two clades.

**Table 1** Cortinarius species classified in sections Bicolores and Satunini by the main European authors.

| This study | Bidaud et al. (1992, 2014, 2015) | Brandrud et al. (1990, 1994, 1998), Niskanen et al. (2012) | Moser (1967) | Kühner & Romagnesi (1953) |
|------------|-------------------------------|----------------------------------------------------------|--------------|--------------------------|
| Sect. Bicolores | Sect. Bicolores | Sect. Bicolores | Key 3.11.7.6.11 | Sect. Bicolores |
| C. cagei | C. minicolor, C. peridolens ad. int. | C. cagei | C. bicolor? | C. bicolor? |
| *C. dolabrioides* sp. nov. | C. imbutoiodes | | | |
| C. dolabatus | C. imbutoiodes | | | |
| C. evernius | C. evernius, C. parvulor ad. int. | C. evernius | C. evernius, C. scutulatus | C. evernius |
| C. glaphurus | C. tubulosus, C. paranomalus (Sat.) | | | |
| C. hircinomus | C. livor | | C. livor? | |
| C. plumulosus | C. fundatus | | C. bicolor? | C. bicolor? |
| C. reflectus | C. reflectus, C. testaceoviolaceus | | C. bicolor? | C. bicolor? |
| C. sp1 | | | | |
| C. sp2 | | | | |
| C. tortuosus | C. tortuosus | C. plumbosus | C. tortuosus, C. plumbosus | |
| C. turgidipes | | | | |
| C. cinnamoviolaceus | C. cinnamoviolaceus, C. parevernius, C. basicyneus | C. imbutus | C. cinnamoviolaceus, C. parevernius | |
| C. disjungendum | C. cyanosterix | | | |
| C. mattae | C. mattae | C. mattae | C. subviolascens | |
| C. parevernioides | C. parevernioides | | | |
| C. salicinus | C. salicinus, C. deceptivoideae | | | |
| | C. quadrilocularis | | | |
| Sect. Satunini | Sect. Satunini | Sect. Firmiores + sect. Telamonia | Key 3.11.7.6.11 | Sect. Bicolores |
| C. confirmatus | C. confirmatus | | | |
| C. cyprinus | C. cyprinus | | | |
| C. imbutus | C. imbutus | | | |
| C. lucorum | C. lucorum | | C. lucorum, C. umidicola | |
| C. saturninus | C. saturninus | C. saturninus, C. subtorvus | C. saturninoides, C. deceptivus, C. subtorvus | |
| C. stuntzii | | | | |
| *C. cyriacoides* | C. cyriacoides | | C. cypriacus | C. cypriacus |
| C. furiosus | C. furiosus | | | |
| C. nefastus | C. nefastus | | | |
| C. serratissimus* | C. serratissimus | | | |
| C. scaphyllioides | C. scaphyllioides | | C. serratissimus | C. saturninus |
| C. subbulliardoides* | C. illepidus | | | |
| C. subfirma | C. subfirma | | | |
| C. suboxytoneus | C. suboxytoneus, C. fuscocinctus | | | |
| | | | | |

**Bold** names indicate sequenced species. Dotted lines separate morphogenetic species included in /Bicolores and /Saturnini (upper parts) from those (morphological species, lower parts) phylogenetically unrelated to the two clades. (Sat.), Satunini. Asterisk indicates unpublished data of nomenclatural significance.
MATERIAL AND METHODS

DNA extraction, amplification and sequencing

The material analysed in the present work was made available to us by the public herbaria of the University of Helsinki (H, Finland), the Museum National d’Histoire Naturelle de Paris (PC, France), the Swedish Museum of Natural History (S, Sweden), the Conservatoire et Jardin botaniques de la Ville de Genève (K & G, Switzerland), the Universität Innsbruck (IB, Austria), the University of Michigan (MICH, USA), and the University of Washington (WTU, USA), as well as by European field mycologists (Table 2). Scandinavian, North American, and part of the French material was extracted, amplified, and sequenced following Liimatainen et al. (2014b). DNA extraction and PCR amplification of most of the French and south European material was conducted with the REDEextract-N-Amp™ Plant PCR Kit (Sigma-Aldrich, St. Louis, MO, USA), following the manufacturer’s instructions. The internal transcribed spacer 5.8S rDNA (ITS) was amplified from each collection, following the manufacturer’s instructions. The internal transcribed spacer 5.8S rDNA (ITS) was amplified from each collection, as described in Richard et al. (2015). When no band was detected by agarose-gel electrophoresis analysis, one microliter of the PCR product was used as template in a second PCR using the ITS1F/ITS4 primer pair (White et al. 1990). The remaining, most problematic extracts, were submitted to separate ITS1F/ITS2 and ITS3/ITS4 PCRs (White et al. 1990). Amplicons were purified and sequenced by Eurofins Genomics, Ebersberg, Germany. Raw sequence data were edited and assembled with Codon Code Aligner 4.1.1 (CodonCode Corp., Centerville, MA, USA) and deposited in GenBank under the accession numbers indicated in Table 2.

Datasets

Out of the 348 sequences analysed in the present study, 290 (83 %) have been newly generated from vouchered material collected and taxonomically studied by expert field mycologists, biased towards French authors. In an effort to stabilize nomenclature, 63 sequences were obtained from type collections, which, together with 26 additional publically available sequences, represent more than a quarter of type material (89 out of 348) within the whole dataset. Also, to further contribute to fix the usage of some well-known binomials, especially when reference material was not available or not amenable to successful sequencing, we included in the dataset 24 Species Hypothesis representative sequences (‘SH repseq’) from the UNITE database (Köjalg et al. 2013). These phylogenetic species can be labelled or not and their name may be misapplied, but because they are built from sequences of wide origins, their occurrence in a clade often extends our knowledge of the biogeographical distribution and sometimes the ecology, of the corresponding species. Dataset 1 (analysed in Fig. 1) includes 343 Telamonia sequences that belong in the /Bicolores and /Saturnini clades as well as collections phylogenetically or morphologically related to species traditionally treated in the two sections, as well as 5 sequences from sect. Anomali and subg. Plegmacium as outgroup. We intended to define phylogenetic boundaries and robustness of the two sections and to reveal phylogenetically positions of species that were formerly classified in the morphological sections /Bicolores and /Saturnini, but are not part of the phylogenetic clades /Bicolores or /Saturnini. Datasets 2 and 3 (analysed in Fig. 2 and 3, respectively) focus on the species content of the revised sections and include, respectively, 124 and 131 sequences.

Phylogenetic analyses

Phylogenetic analyses were all performed online at phylogeny.lirmm.fr (Dereeper et al. 2008) and on the CIPRES Science Gateway (www.phylo.org/index.php/). Multiple sequence alignment was carried out with MUSCLE 3.7 (Edgar 2004) using full processing mode and 16 iterations. When required, alignments were edited with Gblocks 0.91b, set to lowest stringency and the selection of conserved blocks (Castresana 2000, Talavera & Castresana 2007). Maximum likelihood (ML) phylogenetic analyses were performed with PhyML 3.0 (Guindon et al. 2010), using the GTR + I + Γ model of evolution. Branch support was assessed using the non-parametric, Shimodaira-Hasegawa, version of the approximate likelihood-ratio test (SH-aLRT), implemented in the latest release of PhyML and which ensures high accuracy when SH-aLRT > 0.8 (Anisimova et al. 2011, Bellanger et al. 2015). Bayesian inference of phylogeny was performed using MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003). Two runs of four Monte Carlo Markov Chains each were performed for 1 000 000 generations, with stationarity convergence estimated by the Potential Scale Reduction Factor = 1 (Gelman & Rubin 1992). Trees and parameters were sampled every 1 000 generations (1 000 trees). The initial burn-in was set to 25 % (250 trees). A 50 % majority-rule consensus phylogram was computed from the remaining trees with Bayesian posterior probabilities (BPP) reported as percentages on supported branches of the phylograms. Trees were visualized using FigTree 1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/) and edited with Inkscape 0.91 (https://inkscape.org/fr/).

Morpho-anatomic analyses

Microscopic characteristics were observed from dried material mounted in Melzer’s reagent. The pileipellis structure was studied from both freehand radial and scalp sections from the pileus centre. The measurements of the elements of pileipellis were made from scalps. Basidiospores were measured from the veil or top of the stipe. Sporograms depicted in Fig. 4 have been mounted following the method of the ADC, described in Bidau et al. 1994. Briefly, spores have been observed and measured at the 1 000× magnification and 8 of them drawn and aligned by increasing length order (0.5 µm step).

RESULTS

Our analysis resolved two strongly supported clades, referred to as /Bicolores (BPP = 99 %, SH-aLRT = 0.92) and /Saturnini (BPP = 100 %, SH-aLRT = 0.88) in the present work, and that include most representative European species described in sect. Bicolores and sect. Saturnini, respectively (Fig. 1, Table 2).

In its current sampling, /Bicolores includes 12 species, each represented by 1 to 23 sequences (Fig. 2, Table 2). Sequencing existing type material and designating 1 neotype (C. cagei) and 2 epitypes (C. dolabratus and C. reflectus), we stabilized 9 names and identified 8 synonymous binomials at the species rank. In addition, we describe C. dolabratoideus as a new species akin to C. dolabratus and so far found in Finland and France. We postponed naming the North American C. sp1 and the Finnish C. sp2, awaiting further sampling to formally describe them. Overall, our work confirms C. cagei, C. everniius, C. plumulosus, C. reflectus and C. tortuosus as genuine members of the revised sect. Bicolores, but it also reveals that C. dolabratus, C. glaphonus, C. hircinosmus and C. turgidipes, previously reported in other sections of Telamonia, actually belong in the section as well.

Intraspecific ITS variability in /Bicolores was generally low, with a maximum number of changes Dmax = 3 nucleotides (nts) in the case of C. dolabratus, representing 0.5 % of sequence divergence. Most species in the clade do not vary at all or only by one substitution and one or two indels in spite of transcon-
Table 2  Specimens included in phylogenetic analyses.

| Voucher | SH | Annotation | Leg. | Collection | Country | Taxonomy | Herbarium Accession |
|---------|----|------------|------|------------|---------|----------|---------------------|
| C. cagei | CFP 1260 | | | | | | |
| | | | | | | | |
| C. dolabratus | CFP 990 | | | | | | |
| | | | | | | | |
| C. evernius | CFP 792 | | | | | | |
| | | | | | | | |
| Specimen          | Collection Date | Location         | GenBank Accession | Notes                      |
|-------------------|-----------------|------------------|------------------|---------------------------|
| PML 212 evernius  | 1982            | France           | KX964340         | ADC private               |
| PML 213 evernius  | 1990            | Finland          | KX964319         | ADC private               |
| PML 214 evernius  | 1991            | Canada           | KX964320         | ADC private               |
| PML 215 evernius  | 1992            | Norway           | KX964321         | ADC private               |
| PML 216 evernius  | 1993            | Norway           | KX964322         | ADC private               |
| PML 217 evernius  | 1994            | Switzerland      | KX964323         | ADC private               |
| PML 218 evernius  | 1995            | Germany          | KX964324         | ADC private               |
| PML 219 evernius  | 1996            | France           | KX964325         | ADC private               |
| PML 220 evernius  | 1997            | France           | KX964326         | ADC private               |
| PML 221 evernius  | 1998            | Finland          | KX964327         | ADC private               |
| PML 222 evernius  | 1999            | Norway           | KX964328         | ADC private               |
| PML 223 evernius  | 2000            | Norway           | KX964329         | ADC private               |
| PML 224 evernius  | 2001            | Norway           | KX964330         | ADC private               |
| PML 225 evernius  | 2002            | Norway           | KX964331         | ADC private               |
| PML 226 evernius  | 2003            | Norway           | KX964332         | ADC private               |
| PML 227 evernius  | 2004            | Norway           | KX964333         | ADC private               |
| PML 228 evernius  | 2005            | Norway           | KX964334         | ADC private               |
| PML 229 evernius  | 2006            | Norway           | KX964335         | ADC private               |
| PML 230 evernius  | 2007            | Norway           | KX964336         | ADC private               |
| PML 231 evernius  | 2008            | Norway           | KX964337         | ADC private               |
| PML 232 evernius  | 2009            | Norway           | KX964338         | ADC private               |
| PML 233 evernius  | 2010            | Norway           | KX964339         | ADC private               |
| PML 234 evernius  | 2011            | Norway           | KX964340         | ADC private               |
| PML 235 evernius  | 2012            | Norway           | KX964341         | ADC private               |
| PML 236 evernius  | 2013            | Norway           | KX964342         | ADC private               |
| PML 237 evernius  | 2014            | Norway           | KX964343         | ADC private               |
| PML 238 evernius  | 2015            | Norway           | KX964344         | ADC private               |
| PML 239 evernius  | 2016            | Norway           | KX964345         | ADC private               |
| PML 240 evernius  | 2017            | Norway           | KX964346         | ADC private               |
| PML 241 evernius  | 2018            | Norway           | KX964347         | ADC private               |
| PML 242 evernius  | 2019            | Norway           | KX964348         | ADC private               |
| PML 243 evernius  | 2020            | Norway           | KX964349         | ADC private               |
| PML 244 evernius  | 2021            | Norway           | KX964350         | ADC private               |

**Note:** The above table lists specimens associated with species of *Cortinarius* section *Bicolores* and *Saturnini*. Each entry includes the specimen number, collection date, location, GenBank accession number, and notes regarding the study.
| Speciation | Voucher/SH | Voucher/SH annotation | Leg. | Collection date | Country | Taxonomy | Herbarium | Accession* |
|------------|------------|-----------------------|------|----------------|---------|----------|-----------|-----------|
| C. tortuosus | IB 79/533 | tortuosus (neotype) | D. Lamothe | 1979 | Sweden | Opera Botanica 100: 182 (1989) | IB | KX964391 |
| | XC 2008-43 | flabelloloides (holotype) | M. Părăianu | 2008 | France | AC 19: 11138 (2010) | PC | KX964392 |
| | PAK 354 | laetior (holotype) | P.A. Karsten | 1879 | Finland | BFNF 32: 387 (1879) | H | KX964393 |
| | AB 01-09-19 | tortuosus | A. Bidaud | 2001 | France | AC 22:11413 (2014) | ADC private | KX964394 |
| | AB 96-08-19 | tortuosus | A. Bidaud | 1996 | France | AC 22:11413 (2014) | ADC private | KX964395 |
| | AB 95-09-34 | tortuosus | C. Blanc | 1995 | France | AC 22:11413 (2014) | ADC private | KX964396 |
| | PML 3551 | tortuosus | A. Bidaud & R. Fillion | 1993 | France | AC 22:11413 (2014) | ADC private | KX964397 |
| | PML 1225 | tortuosus | P. Moënne-Loccoz | 1989 | France | AC 22:11413 (2014) | ADC private | KX964398 |
| | PML 1214 | tortuosus | P. Moënne-Loccoz | 1989 | France | AC 22:11413 (2014) | ADC private | KX964399 |
| | PML 386 | tortuosus | P. Moënne-Loccoz | 1986 | France | AC 22:11413 (2014) | ADC private | KX964400 |
| | CFP 493 | tortuosus | T.E. Brandrud, H. Lindström, H. Marklund, S. Muskos | 1986 | Norway | CFP: A06 (1990) | S | KX964401 |
| | AB 02-09-41 | saturninus cf. | A. Bidaud | 2002 | France | this study | ADC private | KX964402 |
| | AB 96-10-124 | saturninus cf. | C. Blanc | 1996 | France | this study | ADC private | KX964403 |
| | IK 99-709 | tortuosus | I. Kytövuori | 1999 | Finland | this study | H | KX964404 |
| | AB 12-11-240 | dolabratus | A. & E. Bidaud | 1993 | France | AC 17(1): 885 (2008) | PC | KX964409 |
| | UBCOGR194 | sp. | T. Niskanen | 2012 | USA | this study | H | KX964410 |
| | TN 05-033 | sp. | T. Niskanen | 2005 | Finland | this study | H | KX964411 |
| | SH094369.07FU (7 sequences) | tortuosus | A. & E. Bidaud | 1993 | France | AC 17(1): 885 (2008) | PC | KX964409 |
| | C. n trumpetus | TN 12-217 | sp. | T. Niskanen | 2012 | USA | this study | H | KX964410 |
| | C. sp1 | TN 05-051 | sp. (ectomycorrhiza) | T. Niskanen | 2005 | Finland | this study | H | KX964411 |
| | C. sp2 | TN 05-006 | sp. | T. Niskanen | 2005 | Finland | this study | H | KX964411 |
| | SH188640.07FU (2 sequences) | imbutus | T.E. Brandrud, H. Lindström, H. Marklund, S. Muskos | 1986 | Sweden | CFP: D60 (1998) | S | KX964419 |
| | AB 12-11-240 | imbutus | A. Bidaud | 2012 | France | this study | ADC private | KX964420 |
| | TN 05-051 | imbutus sensu Funga Nordica | T. Niskanen | 2005 | Finland | this study | H | KX964421 |
| | TN 05-051 | imbutus sensu Funga Nordica | T. Niskanen | 2005 | Finland | this study | H | KX964422 |
| | SH188640.07FU (2 sequences) | imbutus | T. Niskanen | 2005 | Finland | this study | H | KX964422 |
| | C. cyanosterix | RH 338 | cyanoesterix (holotype) | R. Henry | 1952 | France | this study | H | KX964423 |
| C. mattiae | KS CO1936 | mattiae (isotype) | K. Soop | 2009 | Sweden | JEC 13(12): 3 (2010) | S | KX964424 |
| | AB 13-08-35 | mattiae | A. Bidaud, F. Armada & R. Fillion | 2013 | France | AC 22: 11415 (2014) | ADC private | KX964425 |
| | AB 99-09-77 | subviolascens | A. Bidaud | 1999 | France | AC 12: 11955 (2002) | ADC private | KX964426 |
| | PML 650 | subviolascens | P. Moënne-Loccoz | 1987 | France | AC 12: 11955 (2002) | ADC private | KX964427 |
| | CFP 1204 | mattiae | T.E. Brandrud, H. Lindström, H. Marklund, S. Muskos | 1993 | Sweden | CFP: D30 (1998) | S | KX964428 |
| | AB 06-09-153 | licinipes/poeclibus aff. | A. Bidaud, F. Armada & R. Fillion | 2006 | France | this study | ADC private | KX964429 |
| | H:029375 | mattiae | T. Niskanen | 2004 | Finland | this study | H | KX964430 |
Cortinarius

IK 01-039  mattiae I. Kytövuori 2007 Finland this study H
KX964431

IK 98-1127 mattiae I. Kytövuori 1998 Finland this study H
KX964433

PML 3989 umbinocornatus forma A. Bidau 1993 France this study ADC private
KX964434

PML 2298 oxycorns A. Bidau 1991 France this study ADC private
KX964435

SH094374.07FU (1 sequence) sp. na Canada na this study H
KX964436

C. parevernioides

AB 02-09-50 parevernioides (holotype) C. Gérard 2002 France AC 22: f1408 (2014) PC
KX964437

SH188502.07FU (15 sequences) malachius na na AC 22: f1416 (2014) PC
KX964438

/section Bicolores

C. confirmatus

RH 3195 confirmatus (holotype) R. Henry 1970 France SMF 99(1): 67 (1983) PC
KX964439

JVG 990125-31 assiduus var. plesiocistus (isotype) X. Llimona & J. Vila 1999 Spain Mycotaxon 101: 140 (2007) J. Vila private AM713178

PML 3989 umbrinoconnatus forma A. Bidaud 1993 France this study ADC private
KX964440

PML 2298 oxytoneus A. Bidaud 1991 France this study ADC private
KX964441

SH009438.07FU (1 sequence) sp. na Canada na this study H
KX964442

C. confirmatus

IK 97-1162 imbutus (neotype) I. Kytövuori 1997 Finland this study H
KX964443

PML 4557 laccatus (holotype) P. Reumaux 1978 France SMF 98(4): 348 (1982) PC
KX964444

RH 3123 betulaeomoses (holotype) R. Henry 1976 France SMF 93(3): 347 (1977) PC
KX964445

/section Saturnini

C. confirmatus

RH 84/159 bulbosovolvatus (isotype) M. Contu & L. Curreli 1984 Italy DM 26 (61): 32 (1985) PC
KX964446

XC 2013-03 salicinus (holotype) C. Hugouvieux 2005 France AC 23: f1441 (2015) PC
KX964447

C. cyprinus

AB 11-11-324 confirmatus 'asp. paracohabitans' F. Armada, A. Bidaud & J. Pardo 2011 France AC 23: f1437 (2015) ADC private
KX964448

PML 81 cyprinus P. Moënne-Loccoz 1981 France AC 23: f1443 (2015) ADC private
KX964449

AB 11-11-251 cyprinus A. Bidaud 2011 France AC 23: f1443 (2015) ADC private
KX964450

AB 11-10-192 cyprinus A. Bidaud 2011 France AC 23: f1443 (2015) ADC private
KX964451

AB 06-09-144 cyprinus A. & E. Bidaud 2012 France AC 23: f1443 (2015) ADC private
KX964452

PAM 344 cyprinus P. Moliné-Loozo 1986 France AC 23: f1443 (2015) ADC private
KX964453

PML 425 myrtillinus P. Moënne-Loccoz 1986 France AC 23: f1443 (2015) ADC private
KX964454

XC 2007-95 mutabilis cf. X. Carteret 2007 France AC 23: f1443 (2015) ADC private
KX964455

TEB 348-10 saturninus aff. T.E. Brandrud na Norway na this study ADC private
KX964456

C. imbutus

IK 97-1162 imbutus (neotype) I. Kytövuori 1997 Finland this study H
KX964457

PML 4557 laccatus (holotype) P. Reumaux 1978 France SMF 98(4): 348 (1982) PC
KX964458

RH 3123 betulaeomoses (holotype) R. Henry 1976 France SMF 93(3): 347 (1977) PC
KX964459

/section Satyrium

C. confirmitus

RH 3195 confirmatus (holotype) R. Henry 1970 France SMF 99(1): 67 (1983) PC
KX964460

JVG 990125-31 assiduus var. plesiocistus (isotype) X. Llimona & J. Vila 1999 Spain Mycotaxon 101: 140 (2007) J. Vila private AM713178

PML 3989 umbrinoconnatus forma A. Bidaud 1993 France this study ADC private
KX964461

PML 2298 oxytoneus A. Bidaud 1991 France this study ADC private
KX964462

SH009438.07FU (1 sequence) sp. na Canada na this study H
KX964463

C. cyprinus

XC 2013-03 salicinus (holotype) C. Hugouvieux 2005 France AC 23: f1441 (2015) PC
KX964464

C. imbutus

IK 97-1162 imbutus (neotype) I. Kytövuori 1997 Finland this study H
KX964465

PML 4557 laccatus (holotype) P. Reumaux 1978 France SMF 98(4): 348 (1982) PC
KX964466

RH 3123 betulaeomoses (holotype) R. Henry 1976 France SMF 93(3): 347 (1977) PC
KX964467

C. parevernioides

AB 02-09-50 parevernioides (holotype) C. Gérard 2002 France AC 22: f1408 (2014) PC
KX964468

SH188502.07FU (15 sequences) malachius na na AC 22: f1416 (2014) PC
KX964469

/section Bicolores

C. confirmatus

RH 84/159 bulbosovolvatus (isotype) M. Contu & L. Curreli 1984 Italy DM 26 (61): 32 (1985) PC
KX964470

XC 2013-03 salicinus (holotype) C. Hugouvieux 2005 France AC 23: f1441 (2015) PC
KX964471

C. cyprinus

AB 11-11-324 confirmatus 'asp. paracohabitans' F. Armada, A. Bidaud & J. Pardo 2011 France AC 23: f1437 (2015) ADC private
KX964472

PML 81 cyprinus P. Moënne-Loccoz 1981 France AC 23: f1443 (2015) ADC private
KX964473

AB 11-11-251 cyprinus A. Bidaud 2011 France AC 23: f1443 (2015) ADC private
KX964474

AB 11-10-192 cyprinus A. Bidaud 2011 France AC 23: f1443 (2015) ADC private
KX964475

AB 06-09-144 cyprinus A. & E. Bidaud 2012 France AC 23: f1443 (2015) ADC private
KX964476

PAM 344 cyprinus P. Moliné-Loozo 1986 France AC 23: f1443 (2015) ADC private
KX964477

PML 425 myrtillinus P. Moënne-Loccoz 1986 France AC 23: f1443 (2015) ADC private
KX964478

XC 2007-95 mutabilis cf. X. Carteret 2007 France AC 23: f1443 (2015) ADC private
KX964479

TEB 348-10 saturninus aff. T.E. Brandrud na Norway na this study ADC private
KX964480

C. imbutus

IK 97-1162 imbutus (neotype) I. Kytövuori 1997 Finland this study H
KX964481

PML 4557 laccatus (holotype) P. Reumaux 1978 France SMF 98(4): 348 (1982) PC
KX964482

RH 3123 betulaeomoses (holotype) R. Henry 1976 France SMF 93(3): 347 (1977) PC
KX964483
Table 2 (cont.)

| Species       | Voucher/SH annotation | Leg. | Collection Country | Taxonomy | Herbarium | Accession* |
|---------------|-----------------------|------|--------------------|----------|-----------|------------|
| C. laetior forma | X. Carteret 2012 France | this study | ADC private | H | KX964506 |
| C. renidentoides cf. | X. Carteret 2002 France | this study | ADC private | H | KX964507 |

SH188563.07FU (6 sequences) saturninus na na NA/FS na na UDB018346

C. lucorum (neotype) T.E. Brandrud, H. Lindström, 1986 Norway CFP: C10 (1994) S

SH188495.07FU (21 sequences) lucorum na na NA/FS na na UDB019872
| Specimen ID | Description | Location | Accession Number | Other Information |
|-------------|-------------|----------|-----------------|------------------|
| AB 02-10-179 | saturninus 'asp. urbicoides' | France | AC 23: f1457 (2015) | ADC private |
| AB 95-11-144 | saturninus 'asp. urbicoides' | France | AC 23: f1457 (2015) | ADC private |
| AB 14-11-160 | saturninus 'asp. salicis' | France | AC 23: f1454 (2015) | ADC private |
| AB 14-09-47 | saturninus 'asp. dionisiae' | France | AC 23: f1451 (2015) | ADC private |
| AB 98-10-381 | saturninus 'asp. deceptivus' | France | AC 23: f1450 (2015) | ADC private |
| XC 2001-107 | saturninus 'asp. salicis' | France | AC 23: f1454 (2015) | ADC private |
| XC 2014-116 | saturninus 'asp. saturninus' | France | AC 23: f1448 (2015) | ADC private |
| XC 2007-97 | saturninus 'asp. saturninus' | France | AC 23: f1448 (2015) | ADC private |
| AB 14-09-47 | saturninus 'asp. deceptivus' | France | AC 23: f1450 (2015) | ADC private |
| AB 98-10-381 | saturninus 'asp. deceptivus' | France | AC 23: f1450 (2015) | ADC private |
| XC 2014-63 | saturninus 'asp. salicis' | France | AC 23: f1454 (2015) | ADC private |
| XC 2007-90 | mutabilis cf | France | AC 23: f1448 (2015) | ADC private |
| XC 2008-61 | salicis | France | AC 23: f1448 (2015) | ADC private |
| XC 2007-97 | saturninus 'asp. saturninus' | France | AC 23: f1448 (2015) | ADC private |
| XC 2007-90 | mutabilis cf | France | AC 23: f1448 (2015) | ADC private |
| XC 2006-194 | salicis | France | AC 23: f1448 (2015) | ADC private |
| XC 2002-167 | holophaeus sensu Henry | France | AC 23: f1448 (2015) | ADC private |
| XC 96-10-26-09 | subprivignus | France | AC 23: f1448 (2015) | ADC private |
| SH094324.07FU | saturninus | USA | H | UDB017613 |
| PML 75 | urbicus P. Moënne-Loccoz | France | AC 12: f560 (2002) | ADC private |
| CN 092646 | cypriacoides | Sweden | CFP: A04 (1990) | S |
| H 073930 | cypriacoides | Sweden | CFP: A04 (1990) | S |
| X 79-93-27 | holophagus sensu Henry | France | AC 12: f560 (2002) | ADC private |
| CX 2014-62 | euprivignus aff | France | AC 12: f560 (2002) | ADC private |
| XC 2011-92 | mutabilis | France | AC 12: f560 (2002) | ADC private |
| XC 2008-61 | salicis | France | AC 12: f560 (2002) | ADC private |
| XC 2007-97 | saturninus 'asp. saturninus' | France | AC 12: f560 (2002) | ADC private |
| XC 2014-62 | euprivignus aff | France | AC 12: f560 (2002) | ADC private |
| XC 2008-61 | salicis | France | AC 12: f560 (2002) | ADC private |
| XC 2007-90 | mutabilis | France | AC 12: f560 (2002) | ADC private |
| XC 2006-194 | salicis | France | AC 12: f560 (2002) | ADC private |
| XC 2002-167 | holophaeus sensu Henry | France | AC 12: f560 (2002) | ADC private |
| XC 96-10-26-09 | subprivignus | France | AC 12: f560 (2002) | ADC private |

**Cortinarius section Bicolores and section Saturnini**
Table 2 (cont.)

| Species | Voucher/SH | Voucher/SH annotation | Leg. | Collection date | Country | Taxonomy | Herbarium | Accession* |
|---------|------------|-----------------------|------|----------------|---------|----------|-----------|------------|
| C. tepidus sensu ADC | AB 11-11-331 | illepidus | A. Bidaud & C. Gérard | 2011 | France | AC 23: f1422 (2015) | ADC private | KX964563 |
| (= C. subtiliadioides) | | | | | | | | |
| C. nefastus | AB 11-11-330 | illepidus | A. Bidaud & C. Gérard | 2011 | France | AC 23: f1422 (2015) | ADC private | KX964564 |
| C. oxytoneus | RH 931 | oxytoneus | A. Bidaud & C. Gérard | 1957 | France | SMF 97(3): 277 (1981) | PC | KX964567 |
| C. Saturninoides sensu | AB 00-10-148 | illepidus | A. Bidaud & C. Gérard | 2011 | France | AC 23: f1422 (2015) | ADC private | KX964568 |
| (= C. serratifolius) | | | | | | | | |
| C. subfirmus | AB 08-10-363 | subfirmus | A. Bidaud & G. Raffini | 2008 | France | AC 23: f1442 (2015) | PC | KX964571 |
| C. suboxytoneus | AB 01-09-56 | suboxytoneus | A. Bidaud | 2001 | France | AC 23: f1442 (2015) | PC | KX964572 |
| C. alboviolaceus | AB 99-10-254 | sciophylloides | A. Bidaud | 1999 | France | AC 23: f1425 (2015) | PC | KX964573 |
| C. anisatus | AB 91-10-291 | sciophylloides | J. Garin | 1991 | France | AC 23: f1425 (2015) | ADC private | KX964574 |
| C. anisochrous | PML 5446 | sciophylloides | J. Cavet | 1999 | France | AC 23: f1425 (2015) | ADC private | KX964575 |
| C. athabascanus | DBB27618, UC1860905 | athabascanus | D. Bojantchev | 2011 | USA | Mycotaxon 123: 382 (2013) | UC | JN133295 |
| C. biformis | PML 2381 | raphanoidiobolius | P. Reumaux | 1991 | France | AC 23: f1433 (2015) | ADC private | KX964576 |
| C. brunneifolius | TN 06-146 | brunneifolius | T. Niskanen | 2006 | Finland | Mycol. Progress 7(4): 241 (2008) | H | EU259284 |
| C. caesioarmeniacus | H:7000901 | caesioarmeniacus | K. Liimatainen & T. Niskanen | 2007 | Canada | IF 198: 1 (2014) | H | KP137498 |
| C. claroplaniusculus | RH 2334 | claroplaniusculus | R. Henry | 1967 | France | SMF 99(1): 65 (1983) | PC | KP013184 |
| C. decipiens | PML 366 | decipiens f. decipiens | P. Molinée-Loozoo | 1986 | France | AC 11(1): 507 (2001), 507 (2001) | G | FN428988 |
| C. disjungendus | PAK 4370 | disjungendus (lectotype) | P. A. Karsten | c 1893 | Finland | AC 2: f78 (1990) | G | KX964582 |
| C. duracinus | PML 349 | duracinus (neotype) | P. Molinée-Loozoo | 1986 | France | AC 23: f78 (1990) | G | KX964582 |
| C. duracinus s.l. | SH188487.07FU (26 sequences) | alboviolaceus | T.E. Brandrud, H. Lindström, H. Marklund, S. Muskos | 2014 | Sweden | CFP: E25 (2014) | S | DQ117931 |
| C. fuscobovinaster | IK 04-038 | bovinus | I. Kytövuori | 2004 | Finland | Mycol. Progress 7(4) | H | EU259284 |
| C. galeina | CONS 00076 | galeina | D. & M. Antonini, G. Consiglio | 2002 | Italy | Il genere Cortinarius in Italia 3: C101 (2005) | CONS | FN428979 |
| C. murina | IK 08-958 | murina | I. Kytövuori | 2008 | Finland | IF 198: 1 (2014) | H | KP137498 |
| C. neofurvolaesus | CFP 1438 | neofurvolaesus | T.E. Brandrud, H. Lindström, H. Marklund, S. Muskos | 1999 | Sweden | CFP: E24 (2014) | S | DQ139999 |
Minimal interspecific phylogenetic distances \( D_{\text{min}} \) range from 3 to 9 substitutions plus 2–4 indels, representing 0.5–2 % of sequence divergence. Those are, with one exception, longer than \( D_{\text{max}} \) for a given pair of sister species clades (Table 3). The topology of /Bicolores strongly supports two distinct lineages within the section, one including C. cagei, C. everniius, C. plumulosus, C. reflectus, C. sp1 and C. sp2, and another one including C. dolabratoideas, C. dolabratus, C. glaphurus, C. hircinosmus, C. tortuosus and C. turgidipes (Fig. 2).

As sampled here, /Saturnini includes 6 species in Europe and North America, each represented by 1 to 44 sequences (Fig. 3, Table 2). Sequencing existing type material revealed a much higher rate of synonymy when compared to species in /Bicolores, with 17 binomials identified as later names for C. confirmatus, C. imbutus, C. lucorum or C. saturninus. A comparatively wider species concept has emerged in this section, as illustrated by the case of C. saturninus, which merged less than 9 holotypes previously reported to belong in unrelated sections. The considerable rise in species polymorphism resulting from such finding has been dealt with at the infraspecific taxonomic level in the last release of the ADC (Bidaud et al. 2015). In order to stabilize the nomenclature and fix the concept of species widely accepted as genuine members of the Saturnini section – or interpreted by some authors in sect. Bicolores, we designated neotypes for C. saturninus, C. imbutus and C. lucorum (see Taxonomy). Our work also positioned C. stuntzii and a morphogenetic, widened concept of C. confirmatus in the revised section, and it unravelled C. cyprinus as an overlooked species in sect. Saturnini (Fig. 3, Table 2, 3).

Intraspecific phylogenetic distances were considerably larger in /Saturnini when compared to /Bicolores, with a \( D_{\text{max}} \) up to 6 substitutions plus 1 indel, representing 1.2 % of sequence divergence, only considering sequences with trace files (Table 3). The interspecific genetic distance within the clade is of 3 substitutions plus up to 5 indels, representing 0.5–1.3 % of sequence divergence, except for C. lucorum, which is more distantly related to the other species (\( D_{\text{min}} \) max values only for C. cyprinus and C. lucorum (Table 3). The topology of the phylogenetic tree depicted in Fig. 3 indicates that C. lucorum represents an early-diverging lineage in the section and it supports C. saturninus, C. cyprinus and C. stuntzii as part of a distinct lineage within /Saturnini.

The wide survey of subg. Telamonia depicted in Fig. 1 also allows phylogenetic positioning of morphological Bicolores and Saturnini, i.e., of those species that have been included in the two sections based on purely morpho-anatomical criteria, but which evolutionary history is unrelated to that of Bicolores and Saturnini. Eight binomials usually treated in Bicolores could be assigned to five morphogenetic species (Fig. 1, Table 1): C. cinnamoviolaceus (incd. C. parevernius, C. subparevernius, C. basicyaneus and C. imbutus sensu CFP), C. mattiae, C. parevernioides, C. salicinus and C. disjungendi. Similarly, ten species formerly treated in Saturnini based on morphology, turned out to be phylogenetically distant from /Saturnini. Six of them could further be assigned to other known sections: C. cypricioides, C. subfirmus and C. ilipennis in sect. Bovini, C. saturninoides in sect. Sciophylli, C. oxyteneus in sect. Dura-cini and C. sciophylloides in sect. Brunneotincti (Fig. 1, Table 1).

(text continues on p. 190)
Fig. 1 Sections Bicolores and Saturnini within subg. Telamonia. — Bayesian 50 % majority-rule consensus tree inferred from the analysis of 348 ITS sequences (419 represented, due to Species Hypotheses, see Material and Methods) spanning subg. Telamonia plus 5 outgroup sequences, with collapse of the /Bicolores and /Saturnini clades that are developed in Fig. 2 and 3, respectively. Branches with strong statistical support (BPP ≥ 95 % and SH-aLRT > 0.8) are highlighted as thick lines, others display support values as % BPP/SH-aLRT. Species excluded from these two clades but morphologically included in sect. Bicolores and sect. Saturnini and for which molecular data are available, are indicated by (Bic) and (Sat), respectively. Sequences of collections taxonomically described in these two sections are highlighted in bold. Section assignment follows Niskanen et al. (2012).
**Telamonia**

Presented, due to Species Hypotheses, see Material and Methods.

**Fig. 2**

The morphogenetic Bicolores section. — Bayesian 50 % majority-rule consensus tree inferred from the analysis of the ITS sequence of 124 (153 represented, due to Species Hypotheses, see Material and Methods) Telamonia sequences nested in Bicolores. Branches with strong statistical support (BPP > 95% and SH-aLRT > 0.8) are highlighted as thick lines, others display support values as % BPP/SH-aLRT. Sequences from ‘type’ material are highlighted in those having nomenclatural priority are further underlined.

**Cortinarius**

- **obscure**: AB04-10-321 NEOTYPE Sweden
- **milky**: AB97-10-341 France
- **livor**: AB02-09-32 France
- **hircinosmus**: AB94-09-31 Sweden
- **scriptor**: AB97-10-341 France
- **bicolorus**: PML2534 HOLOTYPE France
- **refectus**: AB04-10-321 France
- **plumulosus**: TN04-730 Finland (short)
- **fundatus**: CFP1260 Sweden NEOTYPE
- **minicolor**: AB04-09-266 France
The morphogenetic Saturnini section.— Bayesian 50 % majority-rule consensus tree inferred from the analysis of the ITS sequence of 131 (173 represented, due to Species Hypotheses, see Material and Methods) Telamonia sequences nested in Saturnini. Branches with strong statistical support (BPP ≥ 95 % and SH-aLRT > 0.8) are highlighted as thick lines, others display support values as % BPP/SH-aLRT. Sequences from ‘type’ material are highlighted in bold, those having nomenclatural priority are further underlined. The asterisk points to a subclade that segregates a 1 nt intra-individual polymorphism, as XC 2011-199 (within the subclade) was fruiting from the same mycelium as XC 2007-108 and XC 2014-109 (outside the subclade).
### Table 3 Morphogenetic features of *C. cinnamoviolaceus* and species in sect. *Bicolores* and sect. *Saturnini*.

| Species                  | Blue hues | Odour(s) | L min | Av L | L max | I min | Av I | I max | Av Q | Reported host | D_{max} / difference rate (incl. indels) | D_{min} / difference rate (incl. indels) |
|--------------------------|-----------|----------|-------|------|-------|-------|------|-------|------|---------------|----------------------------------------|----------------------------------------|
| *Cortinarius cinnamoviolaceus* + or – | R, r, i    | 8.25     | 9.65  | 11.07| 4.66  | 5.21  | 6.00 | 1.86  |      | *Picea, Abies, Pinus, Tilia, Quercus, Betula, Populus* | na                                     | na                                     |
| *C. cagei* + or –         | 0, r, e, l | 7.80     | 9.04  | 10.50| 5.10  | 5.54  | 6.18 | 1.64  |      | Deciduous trees | 0 nt / 0 %                            | 3 nts + 3 indels (to *C. evernius*) / 1 % |
| *C. dolabratus* sp. nov. + or – | CE, g     | 7.50     | 8.30  | 9.50 | 3.50  | 4.60  | 5.00 | 1.82  |      | *Picea, Pinus* | 0 nt / 0 %                            | 3 nts (to *C. dolabratus*) / 0.5 %        |
| *C. dolabratus* + or –    | ce, co     | 7.42     | 8.62  | 9.86 | 4.41  | 4.90  | 5.51 | 1.76  |      | *Pinus, Picea, Betula, Fagus, Quercus* | 3 nts / 0.5 %                          | 3 nts (to *C. dolabratus*) / 0.5 %        |
| *C. evernius* +           | 0, ce, r, R| 8.75     | 10.34 | 11.85| 5.35  | 6.01  | 6.77 | 1.72  |      | *Picea, Abies* | 1 nt / 0.2 % (1 nt + 1 indel / 0.3 %) | 3 nts + 3 indels (to *C. cagei*) / 1 %     |
| *C. glaphurus* + or –     | ce, r, CE, V| 8.03    | 9.32  | 10.60| 4.82  | 5.23  | 5.78 | 1.78  |      | *Pinus, Quercus, Fagus, Abies, Ricea, Populus, Betula* | 2 nts + 4 indels / 1 %                    | 4 nts + 2 indels (to *C. tortuosus*) / 1 % |
| *C. hircinosmus* + or –   | 0, r, B    | 8.00     | 9.04  | 10.00| 4.70  | 4.98  | 5.40 | 1.82  |      | *Picea* | 2 nt / 0.3 %                          | 9 nts + 2 indels (to *C. dolabratus*) / 1.8 % |
| *C. plumulosus* + or –    | ca, r, i   | 8.75     | 9.78  | 11.08| 4.80  | 5.53  | 6.10 | 1.77  |      | *Picea, Abies* | 1 nt + 4 indels / 0.8 %                 | 7 nts + 3 indels (to *C. evernius*) / 1.6 %     |
| *C. refectus* +           | g, r       | 8.06     | 9.50  | 10.94| 5.58  | 6.30  | 6.92 | 1.51  |      | *Abies, Picea, Fagus, Quercus* | 0 nt + 1 indel / 0.2 %                    | 4 nts + 3 indels (to *C. evernius*) / 1.2 %     |
| *C. tortuosus* +          | ce, 0, E   | 8.00     | 9.30  | 10.61| 4.83  | 5.44  | 6.00 | 1.71  |      | *Tsuga, Abies, Picea, Pinus* | 1 nt + 1 indel / 0.3 %                    | 4 nts + 2 indels (to *C. glaphurus*) / 1 %     |
| *C. surgidipes* (~)       | 0          | 7.50     | 8.50  | 9.50 | 5.00  | 5.30  | 6.00 | 1.60  |      | *Picea* | na                                           | 3 nts + 4 indels (to *C. dolabratus*) / 1.2 %     |
| *C. sp1*                  | na         | na      | na    | na   | na   | na   | na   | na   |      | na                                           | 8 nts + 4 indels (to *C. evernius*) / 2 %     |
| *C. sp2*                  | na         | na      | na    | na   | na   | na   | na   | na   |      | na                                           | 8 nts + 4 indels (to *C. evernius*) / 2 %     |
| *C. confirmatus* + or –   | 0, ca, r, g| 6.91     | 8.26  | 9.79 | 4.27  | 4.79  | 5.61 | 1.73  |      | *Quercus, Cistus, Pinus, Betula, Populus, Pluosa* | 6 nts + 1 indel / 1.2 %                    | 3 nts (to *C. imbutus*) / 0.5 %            |
| *C. cyprinus* +           | ca, p      | 6.90     | 8.40  | 9.90 | 4.18  | 4.77  | 5.45 | 1.76  |      | Deciduous trees | 0 nt / 0 % (5 nts / 0.8 %)                | 3 nts + 2 indels (to *C. saturninus*) / 0.8 %     |
| *C. imbutus* + or –       | 0, g, ca   | 7.27     | 8.68  | 10.21| 4.09  | 4.62  | 5.41 | 1.88  |      | *Betula, Salix, Alnus, Fagus, Populus, Carpinus, Picea* | 3 nts + 1 indel (0.7 %)                    | 3 nts (to *C. confirmatus*) / 0.5 %         |
| *C. lucorum* +            | r, ca, 0   | 8.07     | 9.56  | 11.07| 5.36  | 5.86  | 6.71 | 1.63  |      | *Populus, Betula, Carpinus, Quercus, Picea, Tsuga* | 2 nts + 1 indel (0.5 %)                    | 16 nts + 3 indels (to *C. confirmatus*) / 3.1 %  |
| *C. saturninus* + or –    | 0, ca, g   | 7.10     | 8.38  | 9.59 | 4.38  | 4.78  | 5.39 | 1.76  |      | *Salix, Betula, Corylus, Tilia, Fagus, Quercus, Populus, Carpinus, Picea, Abies* | 4 nts + 1 indel / 0.8 %                    | 3 nts + 2 indels (to *C. cyprinus*) / 0.8 %      |
| *C. stuntzii* (+)         | 0          | 9.60     | 11.50 | 14.40| 5.90  | 6.70  | 8.50 | 1.72  |      | *Salix* | na                                           | 3 nts + 5 indels (to *C. saturninus*) / 1.3 %     |

**nt = nucleotide change; indel = insertion or deletion; na = not applicable (single sequence) or not available.**

* Bold indicates the most frequent odour.

**Bold** indicates proven interaction (ectomycorrhizal sequences, column 'Reported host') or species with *D_{max}* (column).

* Names are in the order of citation frequency.

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**nt** = nucleotide change; **indel** = insertion or deletion; na = not applicable (single sequence) or not available.

* Bold indicates the most frequent odour.

**Bold** indicates proven interaction (ectomycorrhizal sequences, column 'Reported host') or species with *D_{max}* (column).

* Names are in the order of citation frequency.
TAXONOMY

Each morphogenetic (i.e., defined by both morpho-anatomic features and unique molecular signature) species that belongs in the two revised sections is here introduced. To keep the present survey reasonably short, taxonomic descriptions are restricted to the new C. dolabratus species, and major changes relative to the current use of the other names are highlighted in the notes. Because of its intricate taxonomic relationships with C. imbutus and C. dolabratus, we also provide below a taxonomic update of C. cinnamoviolaceus, even though the species is not part of sect. Bicolores nor sect. Saturninia dealt with here. A key to species treated in the present work is proposed at the end of the article.

Cortinarius cinnamoviolaceus

M.M. Moser, Nova Hedwigia 14: 514. 1967 — MycoBank MB#329008

= Cortinarius basicyanus Rob. Henry & Trescot ex Bidaud & Eyssart., Bull. Semestriel Féd. Assoc. Mycol. Méditerranéennes 25: 38. 2004.
= Cortinarius contractus Rob. Henry, Doc. Mycol. 16: 61. 1985.
= Cortinarius cinna-moviolaceus Rob. Henry, Bull. Soc. Mycol. France 99: 91. 1983.
= Cortinarius subparevernius Rob. Henry, Bull. Soc. Mycol. France 85: 442. 1970.
[= Cortinarius parevernius Rob. Henry, Fl. Amph. Champ. Sup.: 303. 1953, nom. inval. (no diagnosis, no type designated)].

Type. AUTRUA, Tirol, near Höting, in mixed forest, 18 Sept. 1948, M. Moser, IB 48/590, holotype. MycoBank MB#372783. ITS (partial) sequence deposited in GenBank under KX964412.

Misapplied names
— Cortinarius dolabratus Fr., Epicr. Syst. Mycol.: 311. 1838, sensu Bidaud et al. (2008).
— Cortinarius imbutus Fr., Epicr. Syst. Mycol.: 306. 1838, sensu Brandrud et al. (1998).
— Cortinarius evernius Fr., Epicr. Syst. Mycol.: 294. 1838, sensu auct.

Illustrations — Bidaud et al. 2008: pl. 639 (as C. dolabratus); Brandrud et al. 1998: pl. D60 (as C. imbutus).

Taxonomic descriptions — Bidaud et al. 2008: f. 817 (as C. dolabratus); Brandrud et al. 1998: pl. D60 (as C. imbutus).

Notes — This is C. evernius sensu Konrad & Maublanc (1930) and sensu Henry (1937), with smaller spores and raphanoid smell. Our phylogenetic analysis reveals a much wider range of chromatic variability for this species, making it compatible with both sect. Bicolores and Duracinia. In addition, the /C. cinnamoviolaceus clade here delineated sheds new lights on the intricate links between these two sections and sect. Saturninia (Fig. 1). Indeed, as redefined here, the species falls outside the three sections but it merges:

i. typical Bicolores concepts – C. parevernius and C. cinnamoviolaceus;
ii. typical Duracinia concepts – C. subparevernius, C. cylindrus and C. contractus;
iii. a species defined by its author as intermediate between these two sections – C. basicyanus;
iv. a Duracinia concept hiding a phylogenetic Bicolores – C. dolabratus; and
v. a Saturninia binomial interpreted by contemporary Nordic authors as a Bicolores species – C. imbutus.

When displaying blue tinges, C. cinnamoviolaceus may be confused with C. evernius but the spores of the latter are larger, gills lack reddish hues and the smell is weak or indistinct. Cortinarius mattiae may fruit in the same places and is similar in appearance but the pileus is less dark coloured, not glabrous and almost not hygrophanous, while lamellae display even deeper red tinges. When blue pigments are absent, C. cinnamoviolaceus looks like a Duracinia with reddish lamellae and is nearly identical to C. dolabratus, from which it can fortunately be distinguished by larger spores (9.7 × 5.2 µm vs 8.6 × 4.9 µm, respectively) and stronger smell (Table 3).

Cortinarius sect. Bicolores

(M.M. Moser) Melot, Doc. Mycol. 20, 77: 97. 1989, emend.

Type. Cortinarius cagei Melot, Doc. Mycol. 20, 80: 58. 1990.

Notes — As phylogenetically revised here, Cortinarius sect. Bicolores has been redefined to a rather severe extent, with well-known representative species excluded from the revised section and half of its new content previously described outside Bicolores. The original diagnosis of the section should be emended as follow: young basidiomata usually (but not always) with violet tinges outside and/or in the context. Pileus strongly hygrophanous, yellowish brown, chocolate brown to reddish brown. Stipe cylindrical, often attenuate to rooting, usually with remnants of the white universal veil. Smell indistinct, weakly raphanoid, of cedar-wood, rarely of geosmin (earth-like, dusty). Spores amygdaloid to ellipsoid, sometimes fusiform, (6.5–7–12(13) × (4–)4.3–7(–7.2) µm (on average: 9.3 × 5.4 µm), verrucose. Widely distributed in the Northern Hemisphere, flowering solitary or gregarious, rarely cespitose, mostly under coniferous trees.

In its current sampling, it includes 12 species, 10 of which have been or can be assigned a Latin binomial.

Cortinarius cagei

Melot, Doc. Mycol. 20, 80: 58. 1990 — MycoBank MB#129526

= Cortinarius bicolor Cooke, Grevillea XVI: 45. 1873, nom. illeg.
= Cortinarius minicolor Rob. Henry, Bull. Soc. Mycol. France 104, 4: 300. 1989 ’1958’, sensu Bidaud et al. (2014).
[= Cortinarius periodolens Carteret & Réumaux ad int., Atlas des Cortinaires XXII: f. 1417. 2014, nom. inval. (no diagnosis, no type designated)].

Type. SWEDEN, Gotland, Luminelanda, Præstänget, under broadleaf trees, 1 Oct. 1994, T.E. Brandrud, H. Lindström, H. Marklund, S. Muskos CFP1260, S. neotype designated there. MycoBank MB#373139. ITS sequence deposited in GenBank under KX964295.

Illustrations — Bidaud et al. 2014: pl. 959 (as C. minicolor and C. periodolens); Brandrud et al. 1998: pl. D48.

Taxonomic descriptions — Bidaud et al. 2014: f. 1419 (as C. minicolor) but also f. 1417 (as C. periodolens); Niskanen et al. 2012: 864; Brandrud et al. 1998: pl. D48.

Notes — Historically, C. cagei was introduced to fix the nomenclatural issue associated with C. bicolor Cooke, an illegitimate name because of an earlier use of the name for another, unrelated taxon. However, by omitting to designate a holotype or other voucher specimen for his new name, Melot did not clarify the taxonomic ambiguity of C. bicolor. Indeed, C. bicolor was initially described as a species with medium-sized spores (10 × 5–6 µm) fruiting under deciduous trees. However, five years later, it was attributed much larger spores (12–14 × 6–7 µm), and also a broader ecology – mixed woods. It is likely that Cooke actually lumped together two phylogenetically distinct, but morphologically very similar species, in his latest diagnosis, making C. bicolor a nomen dubium. As such, the name may just be discarded but the authors of the CFP proposed an interpretation of C. cagei that fits very well the initial concept of C. bicolor. Because:

i. the CFP plate D48 is well-known and widely recognized as a good illustration of C. cagei;
ii. our work considerably extends our morphogenetic, biogeographical and ecological knowledge of this species; and
Cortinarius dolabratoïdes

Kytöv., Carteret, Bidaud, Liimat., Niskanen, Bellanger, Dima, Reumaux & Ammirati, sp. nov. — MycoBank MB#818596; Fig. 4

Etymology. The name refers to the close phylogenetic and morphological affinities with C. dolabratus.

Type. FINLAND, Varsinais-Suomi, Kisko, Kaukuri, mesic Picea forest, 16 Aug. 2000. T. Niskanen & I. Kytövuori, H:6033518; Etelä-Häme, Juupajoki, Hyytiala, mesic Picea forest, 18 Aug. 2004. I. Kytövuori H:6033615; Virrat, Monkosylä, Korpilärvä E, mesic Picea forest, 15 Oct. 2001. I. Kytövuori 01-062*, H; Pohjola-Häme, Laukaa, Äijälä, Heinäaho, mesic Picea forest, 10 Sept. 2004. I. Kytövuori 04-051*, H; Kainuu, Paltamo, Kontiomäki, Tololanmäki W, Kylmänpuro, W sloping, mesic Picea forest with some Pinus, Betula, Populus tremula and Salix, 14 Sept. 2008. I. Kytövuori 08-1771*, H:6033570; Koliissimaa, Taivalkoski, Metsäkylä SW, Katajavaara, N sloping, old, mesic Picea forest with damp depressions, some Pinus, Betula and Populus tremula, 2 Sept. 2008. I. Kytövuori 08-788*, H:6033575. — FRANCE, Haute-Savoie, Tanninges, cespite under Picea abies on a decalcified substrate, elev. 1500 m, 17 Aug. 2007. A. Bidaud & R. Fillion AB 07-08-48*, personal herbarium of A. Bidaud.

Notes — Morphologically, C. dolabratoïdes is reminiscent of its sister phylogenetic species C. dolabratus. Fortunately, the two species can be distinguished microscopically, C. dolabratoïdes delivering the narrowest spores in the section (width = 3.5–4.6–5.0 μm, Av Q = 1.82, Table 3). By comparison, the spores of C. dolabratus are distinctly wider (width = 4.4–4.9–5.5 μm, Av Q = 1.76, Table 3) and strongly verrucose throughout (Fig. 4b–c). Finnish collections consistently smelled of cedar wood, but this criterion, as a diagnostic feature, may be used with caution since the French material displayed only a weak grass-like odour. At the molecular level, C. dolabratoïdes differs from C. dolabratus by 3 substitutions only, but is not polymorphic at the ITS locus across its pan-European distribution range, making it well resolved within sect. Bicolores (Fig. 2, Table 3).
Cortinarius dolabratus Fr., Epicr. Syst. Mycol.: 311. 1838 — MycoBank MB#216747; Fig. 5a

= Cortinarius imbutoides Bidaud & Carteret, Atlas des Cortinaires XXII: 1887. 2014.
= Cortinarius phaeoruber Chevassut & Rob. Henry, Doc. Mycol. 12, 47: 52. 1982.

Types. Plate ined. 181 directed/approved by Fries, S, neotype (iconotype) designated here (Fig. 5a), MycoBank MBT#373156. Sweden, Jämtland, Östansjö, Häsjö, under coniferous trees, 2 Sept. 1990, T.E. Brandrud, H. Lindström, H. Marklund, S. Muskos CFP990, S, epitype designated here, MycoBank MBT#373157. ITS sequence deposited in GenBank under KX986309.

Illustrations — Bidaud et al. 2014: pl. 951 (as C. imbutoides); Brandrud et al. 1998: pl. D52.

Taxonomic descriptions — Bidaud et al. 2014: f. 1409 (as C. imbutoides); Niskanen et al. 2012: 863; Brandrud et al. 1998: pl. D52.

Notes — The original description of C. dolabratus is apparently not a critical one and a plate later approved by Fries further defined the species as a Duracini with reddish gills. Consistently, the authors of the CFP and of the ADC delivered very similar interpretations of C. dolabratus, both in good accordance with the protologue and compatible with the unpublished plate. However, sequencing the French and Scandinavian materials of this species, unexpectedly, revealed that they are actually phylogenetically distinct and unrelated to sect. Duracini (Fig. 1, 2). Homoplasy is reinforced by our finding that both species encompass collections with or without blue pigments (Table 3). The CFP version of C. dolabratus is part of /Bicolores and is phylogenetically conspecific with C. imbutoides, a species with obvious blue hues described as a typical Bicolores in the ADC. Conversely, the version of C. dolabratus published in the ADC falls, together with three other Duracini binomials, in the clade of C. cinnamoviolaceus, of which it represents a collection lacking blue colour (cf. above). The name is stabilized here in its strict – and original – Nordic sense, through its neotypification with the unpublished plate 181 and by epitypifying it with the widely known and sequenced collection CFP990, illustrated on plate D52 of the Scandinavian monograph. The intraspecific polymorphism of C. dolabratus is the highest in the section

Fig. 5 Type material designated here. — a. Plate ined. 181 directed/approved by Fries, S, neotype (iconotype) of C. dolabratus; b. Atl. Tab. 377, f. 202 (1890), lectotype (iconotype) of C. refectus; c. A. Bidaud 96-09-73, epitype of C. refectus; d. I. Kytövuori 97-1162, neotype of C. imbutus.
Cortinarius evernius (Fr.) Fr., Epicr. Syst. Mycol.: 294. 1838 — MycoBank MB#233378

In Europe, the species is well resolved (Table 3). In the proto-

Cortinarius cinnamovioluteus has so far been only found in

Notes — As redefined here, the concept of C. glaphurus

shoule be substantially widen so as to include those of C. cedriosmus, C. paranomalus and C. violaeolens, as well as C. tubulosus sensu Bidaud et al. (2010). The protol-

ogy should then be edited as follows: pileus diameter up to 55

mm, pileus dark chocolate-brown to reddish brown, not glabrous and hygrophanous. Stipe not always straight rather isodiametric

but often (always?) hollow, with or without blue pigments and with variable amounts of veil remnants that may form a mem-

branous ring. Often cespitose. Odour weakly raphanoid or of

cedar wood or viola. Associated with coniferous trees as well

as broad-leaved trees (Pinus, Quercus and Fagus confirmed as

hosts by ectomycorrhizal sequences). Phylogenetically, the spec-

ies is a bit polymorphic but is still well separated from its sister

species C. tortuosus (Table 3). When collected under Picea abies

on calcareous soils and weakly smelling of cedar wood, C. glaphurus may be difficult to distinguish from C. hircinosmus, but the latter produces slightly smaller spores (Table 3). When collected in hygrophilic and acidic soils under coniferous trees, the species may be confused with C. tortuosus, but the latter displays obvious blue tinges on the stipe, blood-red hues in the gills, and is never cespitose.

Cortinarius hircinosmus Moënne-Loccoz, Atlas des Cortinaires XII: 692. 2002 — MycoBank MB#489854

— Cortinarius livor Fr., Epicr. Syst. Mycol.: 306. 1838, sensu Bidaud et al. (2015).
— Cortinarius scriptor Kühner, Doc. Mycol. 20, 77: 92. 1989, sensu Bidaud et al. (2010) p.p.

Illustrations — Bidaud et al. 2015: pl. 991 (as C. livor); 2002: pl. 389.

Taxonomic descriptions — Bidaud et al. 2015: f. 1459 (as C. livor); 2002: f. 575; Niskanen et al. 2012: 850.

Notes — This species has been initially described in subsect. Hirici because of the strong smell of C. hircinosmus and C. cam-

phoratus of the holotype specimens. However, five additional collections from France and Scandinavia, lacking such odour,

were later identified in the same clade. As revised here and at least in France, C. hircinosmus fruits under Picea abies on
calcareous soils and includes the French concept of C. livor and pro parte, that of C. scriptor. The original binomial is obvi-

ously unfortunate for an odorless or weakly smelling species, so, provided additional collections confirm the strong smell of some populations, infraspecific taxa may be introduced to more adequately reflect the organoleptic diversity of the species. Phylogenetically, the species is well resolved (Table 3). In the field, C. hircinosmus may be confused with C. glaphurus (as redefined here), but the latter displays a much broader ecological niche, typically smells of cedar wood and has slightly larger spores (9.3 × 5.2 µm vs 9 × 5 µm, on average).

Illustrations — Bidaud et al. 2014: pl. 957 (as C. tubulosus); 2010: pl. 795 (as C. tubulosus), pl. 796 (as C. violaeolens) and pl. 807 (as C. cedriosmus); 1992: pl. 83 (as C. paranomalus).

Taxonomic descriptions — Bidaud et al. 2014: f. 1414 (as C. tubulosus) and 2010: f. 1108 (as C. tubulosus); Kühner & Romagnesi 1953: 305 (as C. paranomalus); Chevassut & Henry 1982: 78.

Notes — As redefined here, the concept of C. glaphurus

should be substantially widen so as to include those of C. cedriosmus, C. paranomalus, C. tubulosus and C. violaeolens, as well as C. tubulosus sensu Bidaud et al. (2010). The proto-

logue should then be edited as follows: pileus diameter up to 55

mm, pileus dark chocolate-brown to reddish brown, not glabrous and hygrophanous. Stipe not always straight rather isodiametric

but often (always?) hollow, with or without blue pigments and with variable amounts of veil remnants that may form a mem-

branous ring. Often cespitose. Odour weakly raphanoid or of
cedar wood or viola. Associated with coniferous trees as well

as broad-leaved trees (Pinus, Quercus and Fagus confirmed as

hosts by ectomycorrhizal sequences). Phylogenetically, the spec-

ies is a bit polymorphic but is still well separated from its sister

species C. tortuosus (Table 3). When collected under Picea abies

on calcareous soils and weakly smelling of cedar wood, C. glaphurus may be difficult to distinguish from C. hircinosmus, but the latter produces slightly smaller spores (Table 3). When collected in hygrophilic and acidic soils under coniferous trees, the species may be confused with C. tortuosus, but the latter displays obvious blue tinges on the stipe, blood-red hues in the gills, and is never cespitose.

Cortinarius hircinosmus Moënne-Loccoz, Atlas des Cortinaires XII: 692. 2002 — MycoBank MB#489854

— Cortinarius livor Fr., Epicr. Syst. Mycol.: 306. 1838, sensu Bidaud et al. (2015).
— Cortinarius scriptor Kühner, Doc. Mycol. 20, 77: 92. 1989, sensu Bidaud et al. (2010) p.p.

Illustrations — Bidaud et al. 2015: pl. 991 (as C. livor); 2002: pl. 389.

Taxonomic descriptions — Bidaud et al. 2015: f. 1459 (as C. livor); 2002: f. 575; Niskanen et al. 2012: 850.

Notes — This species has been initially described in subsect. Hirici because of the strong smell of C. hircinosmus and C. cam-

phoratus of the holotype specimens. However, five additional collections from France and Scandinavia, lacking such odour,

were later identified in the same clade. As revised here and at least in France, C. hircinosmus fruits under Picea abies on
calcareous soils and includes the French concept of C. livor and pro parte, that of C. scriptor. The original binomial is obvi-

ously unfortunate for an odorless or weakly smelling species, so, provided additional collections confirm the strong smell of some populations, infraspecific taxa may be introduced to more adequately reflect the organoleptic diversity of the species. Phylogenetically, the species is well resolved (Table 3). In the field, C. hircinosmus may be confused with C. glaphurus (as redefined here), but the latter displays a much broader ecological niche, typically smells of cedar wood and has slightly larger spores (9.3 × 5.2 µm vs 9 × 5 µm, on average).

Illustrations — Bidaud et al. 2014: pl. 957 (as C. tubulosus); 2010: pl. 795 (as C. tubulosus), pl. 796 (as C. violaeolens) and pl. 807 (as C. cedriosmus); 1992: pl. 83 (as C. paranomalus).

Taxonomic descriptions — Bidaud et al. 2014: f. 1414 (as C. tubulosus) and 2010: f. 1108 (as C. tubulosus); Kühner & Romagnesi 1953: 305 (as C. paranomalus); Chevassut & Henry 1982: 78.
**Cortinarius plumulosus** Rob. Henry, Bull. Soc. Mycol. France 93, 3: 362. 1977 — MycoBank MB#132090

— *Cortinarius fundatus* Britzelm., Ber. Naturhist. Vereins Augsburg 28: 127. 1885, sensu Bidaud et al. (2014).

**Type. FRANCE**, Voges, Hennezel, in *Abies* forests, gregarious, 1972, *R. Henry* 3417, PC, holotype, MycoBank MB#155523. ITS sequence deposited in GenBank under KX964374.

Illustrations — Bidaud et al. 2014: pl. 954 (as *C. fundatus*).

Taxonomic descriptions — Bidaud et al. 2014: f. 1411 (as *C. fundatus*); Henry 1977: 359.

Notes — This conifer-associated species has been treated in the ADC as *C. fundatus*, and suspected by French authors, on the basis of frequent macrospores up to 12 µm long observed in some collections, to represent the second *C. bicolor* of Cooke — the one with large spores and possible fruiting under coniferous trees (cf. notes under *C. cagei*). Phylogenetically, *C. plumulosus* is well separated from its closest neighbour *C. eternius* (7 substitutions plus 3 indels, Table 3). Morphologically, *C. plumulosus* is typically covered by small flakes that are not found on that of its two lookalikes.

**Cortinarius refectus** Britzelm., Ber. Naturhist. Vereins Augsburg 28: 127. 1885 — MycoBank MB#506269; Fig. 5b–c

— *Cortinarius refectus* Britzelm., Ber. Naturhist. Vereins Augsburg 28: 127. 1885.

— *Cortinarius scriptor* Kühner, Doc. Mycol. 20, 77: 92. 1989, sensu Bidaud et al. (2010) p.p.

Misapplied name — *Cortinarius testaceoviolaceus* Rob. Henry, Bull. Soc. Mycol. France 73, 1: 51. 1957; sensu Bidaud et al. (2014).

**Type. ATL. TAB.**, f. 202 (1890), lectotype (iconotype) designated here (Fig. 5b), MycoBank MB#373159. GERMANY, Lombach, in *Picea* et *Abies* forest, on calcareous soil, elev. 600 m, 24 Sept. 1996, *A. Bidaud* 96-09-73, epitype designated here (Fig. 5c), MycoBank MB#373159. ITS sequence deposited in GenBank under KX964385.

Illustrations — This study: Fig. 5c; Bidaud et al. 2014, pl. 952, 953 but also pl. 945 (as *C. testaceoviolaceus*).

Taxonomic descriptions — Bidaud et al. 2014: f. 1410 but also 2010: f. 1109 (as *C. scriptor*).

Notes — No original material was kept by Britzelmayr to assign *C. refectus* a molecular signature. The diagnosis is not very elaborate but the atypical reported ovoid spores (8–9 × 5–6 µm, *Av Q = 1.5*) prompted the authors of the ADC to resurrect this old binomial as their best candidate to the original — i.e., the one with short spores (cf. notes under *C. cagei*) — *C. bicolor*. Although the latter hypothesis cannot be supported here for ecological reasons, the French interpretation of *C. refectus* does not contradict the protologue and it is compatible with the original plate — although spore drawings on that plate do not really support the protologue. We thus stabilize here the name by lectotypifying it with plate n° 202, and epitypifying it with the sequenced AB 96-09-73 collection from Germany. As delineated here, *C. refectus* includes the ADC interpretations of *C. scriptor* (p.p.) and *C. testaceoviolaceus*. The latter name is, however, misapplied because the holotype of *C. testaceoviolaceus* falls outside *Telamonia* (in subg. *Myxacium*, data not shown). Phylogenetically, *C. refectus* is well resolved but in the field, it could easily be confused with *C. plumulosus* and *C. cagei* until spores examination and host trees are carefully considered (Table 3).

**Cortinarius tortuosus** (Fr.) Fr., Epicr. Syst. Mycol.: 305. 1838 — MycoBank MB#165676

*Basionym.* — *Agaricus tortuosus* Fr., Syst. Mycol. 1: 235. 1821.

— *Hydrocybe tortuosa* (Fr.) Wünsche, Die Pilze. A Anleitung zur Kenntniss derselben: 121. 1877.

— *Cortinarius flabelloides* Carteret, Atlas des Cortinaires XIX: 1510. 2010.

— *Cortinarius laetor* P. Karst., Bidrag Kändom Finlands Natur Folk 32: 387. 1879.

**Type. SWEDEN**, Smoland, Femjö, Södra Färgen, Gatebäck, among *Sphagnum* in spruce forest, 11 Sept. 1979, *D. Lamoure*, IB 79/533, neotype designated in Opera Botanica 100: 182. 1989, MycoBank MB#372784. ITS sequence deposited in GenBank under KX964391.

Illustrations — Bidaud et al. 2014: pl. 955–956 but also 2010: pl. 804 (as *C. flabelloides*); Brandrud et al. 1990: pl. A06.

Taxonomic descriptions — Bidaud et al. 2014: f. 1413 but also 2010: f. 1136 (as *C. flabelloides*); Niskanen et al. 2012: 863; Brandrud et al. 1990: pl. A06.

Notes — This Friesian name has been interpreted in rather similar ways by past and modern mycologists — with the notable exception of J. Favre, who referred to this species as *C. plumulosus* — so that *C. tortuosus* taxonomy is not a problematic issue. The species can be diagnosed by its narrow ecological niche (hygrophilous and acidic soils, with conifer trees) and the special purple-red tinges of the gills that tend to darken upon bruising. The odour is usually reported as null or weak of cedar wood but the conspecificity with *C. flabelloides*, revealed in this work, indicates that basidiomata can also smell of geosmin (i.e., of earth or dust, as *C. variicolor* for instance). Phylogenetically, the species is remarkably stable at the ITS locus and is well separated from its sister species *C. glaphurus* (Table 3).

**Cortinarius turgidipes** Rob. Henry ex Rob. Henry, Atlas des Cortinaires XVII, 1: 1179. 2008 — MycoBank MB#533088

**Type. FRANCE**, Creuse, Lavaud, under *Pilea*, on granitic soil, subspecies, 19 Oct. 1993, *A. & E. Bidaud*, AB 93-10-425, PC, holotype, MycoBank MB#372796. ITS sequence deposited in GenBank under KX964409.

Illustration — Bidaud et al. 2008, pl. 672.

Taxonomic description — Bidaud et al. 2008: f. 885.

Notes — More collections of this species, originally described in sect. *Damasceni* by its authors, are required to better assess its morphogenetic variability as well as to define its ecological niche. In its current sampling — limited to the holotype, *C. turgidipes* is closest to *C. dolabratus*, from which it differs by 3 substitutions and 4 indels at the ITS locus (Table 3).

**Cortinarius sect. Saturnini** Rob. Henry ex Möenne-Locc. & Reumaux, Atlas des Cortinaires I: 21 (1990), emend.

**Type. Cortinarius saturninus** (Fr.) Fr., Epicr. Syst. Mycol.: 306. 1838.

— *Cortinarius subsect. Saturnini* Bidaud, Möenne-Locc. & Reumaux, Doc. Mycol. 24, 95: 41. 1994.

— *Cortinarius sect. Firmiores* (Fr.) Henn., in Engler & Prantl, Naturl. Pflanzenf. 1, 181: 246. 1900, p.p.

Notes — As revised here, sect. *Saturnini* is widely distributed in the Northern Hemisphere and includes 6 species. They are medium-sized, rarely stout *Telamonia* species, pale ochraceous, brown to reddish brown, lilac-violet, hygrophanous, with or without blue tinges in young lamellae and the upper part of the stipe, with various amounts of veil remnants on the stipe and on the pileus margin where it often forms a continuous covering or discontinuous patches. Smell indistinct or weak. Spores broadly or narrowly ellipsoid, (6–)6.5–11(–14.4) × (3–)4–7(–8.5) µm (on average: 8.6 × 4.9 µm), verrucose. Gregarious to densely
cespite, rarely solitary, typically fruiting under hygrophilous deciduous trees (*Salix, Populus, Betula*) but also under *Quercus* and *Cistus* in the Mediterranean area, rarely under coniferous trees.

**Cortinarius saturninus** (Fr.) Fr., Epicr. Syst. Mycol.: 306. 1838 — MycoBank MB#177635

Basionym. = *Agaricus saturninus* Fr., Syst. Mycol. 1: 219. 1821.
- *Cortinarius vulgaris* Lamoure & Reumaux, Atlas des Cortinaires XVII: 1178. 2008.
- *Cortinarius cohabitanus* var. *ubricoides* Bidaud & Fillion, Bull. Soc. Mycol. France 119, 1–2: 70. 2004.
- *Cortinarius urbicus* var. *sporanotandus* Bidaud & Fillion, Atlas des Cortinaires XII: 695. 2002.
- *Cortinarius deneveronnatus* Rob. Henry, Bull. Soc. Mycol. France 99, 1: 65. 1983.
- *Cortinarius graminineus* Rob. Henry, Bull. Soc. Mycol. France 99, 1: 64. 1983.
- *Cortinarius rastelli* Rob. Henry, Bull. Soc. Mycol. France 97, 3: 177. 1981.
- *Cortinarius dissidens* Reumaux, Bull. Soc. Mycol. France 96, 3: 356. 1980.
- *Cortinarius marginatospodendens* Reumaux, Bull. Soc. Mycol. France 98, 3: 356. 1980.
- *Cortinarius salicis* Rob. Henry, Bull. Soc. Mycol. France 93, 3: 364. 1977.
- *Cortinarius umbrinonconnatus* Rob. Henry, Bull. Soc. Mycol. France 73, 1: 53. 1957.

[= *Cortinarius dionisiae* Bidaud ad int., Atlas des Cortinaires XXIII: f. 1451. 2015, nom. inval. (no diagnosis, no type designated)].
- *Cortinarius subtorvus* Lamoure, Schweiz. Z. Pilzk. 47, 9: 169. 1969, sensu auct.
- *Cortinarius bresadolei* Schluter, Hedwigia 24, 4: 138. 1885, sensu Lamoure (1978).
- *Cortinarius cohabitanus* P. Karst., Bidrag Kannedoms Natur Folk 32: 388. 1879, sensu auct.
- *Cortinarius urbicus* (Fr.) Fr., Epicr. Syst. Mycol.: 293. 1838, sensu Bidaud et al. (2002) p.p.

**Type.** SWEDEN. Västergötland, Eggby, Drottningkullen, deciduous forest on calcareous ground (*Coryllus, Tilia, Quercus*), 17 Sept. 1986, T.E. Brandrud, H. Lindsström, H. Marklund, S. Muskos CFPS154, S, neotype designated here, MBT#373160. ITS sequence deposited in GenBank under KX964584.

Illustrations — Bidaud et al. 2015: pl. 983–989; Brandrud et al. 1994: pl. C09, but also 1990: pl. A04 (as *C. subtorvus*).

Taxonomic descriptions — Bidaud et al. 2015: f. 1448–1457; Niskanen et al. 2012: 847–848; Brandrud et al. 1994: pl. C09, but also 1990: pl. A04 (as *C. subtorvus*).

Notes — All contemporary and past authors agree on the fact that *C. saturninus* is a collective species, that Fries himself contributed to confuse through multiple diagnoses across his successive monographs, which, in addition, do not fit the plates he later directed. The French mycologist Robert Henry devoted decades of his life trying to sort out this complex, adding to the literature many new names and interpretations (for review, see Bidaud et al. 2015). The simplest way to clarify this issue would undoubtedly be to consider *C. saturninus* as a *nomen dubium* and readily discard it. However, the wide use of the name that pertained throughout modern literature and the general consensus about the species illustrated on the plate C09 of the CFP, prompted us to fix *C. saturninus* in its current, Nordic concept, through the neotypification of the name with the CFPS154 collection. Our phylogenetic analysis reveals a tremendously polymorphic species, with no less than 9 holotypes previously thought to be unrelated to sect. *Saturnini*, falling as later synonyms of *C. saturninus*. *Cortinarius subtorvus* and *C. cohabitanus*, usually considered as akin to *C. saturninus*, are most likely two additional synonyms, although their respective type material could not be sequenced to ascertain conspecificity. This work also establishes that *C. oxytoneus*, considered by Henry as the most typical form of *C. saturninus*, is evolutionarily unrelated to sect. *Saturnini* (sect. *Duracini*; Fig. 1). As revised here, *C. saturninus* displays highly apparent ITS sequence polymorphism ($D_{\text{max}}$ = 7 substitutions + 3 indels; Table 3) but the latter is essentially driven by two Norwegian (Svalbard) sequences for which no trace file is available. In addition, the one substitution segregating a subclade within the lineage (see * in Fig. 3) could demonstrably be attributed to intra-individual polymorphism. Thus, the unbiased $D_{\text{max}}$ in *C. saturninus* is actually of 4 nt changes, a value that stems from three French collections (PML 75 in one hand and AB 04-10-334 and XC 2002-167 in the other) which may deserve taxonomic autonomy — at the infraspecific rank — when more thoroughly sampled (Table 3, Fig. 3). Although its suspected association with *Salix* is here demonstrated by the presence in the clade of several ectomycorrhizal sequences isolated from willow roots (within SH094324.07FU, Table 2, Fig. 3), *C. saturninus* may also be associated with other deciduous, but also coniferous trees. Morphologically, the species displays unprecedented levels of variability that represent a serious issue for field diagnosis. Practically, one should consider *C. saturninus* as a possible hit — and check the numerous aspects of this species in the last release of the ADC for instance (Bidaud et al. 2015) — whenever collecting a cespite or gregarious medium-size *Telamonia*: i) under *Salix* spp. or other hygrophilous deciduous trees (and *Dryas octopetala* in the alpine zone), with or without blue hues at the stipe apex and with veil remnants ranging from none to white patches or covering at the cap margin, to copious and web-like covering the whole young fruit body; or ii) under coniferous trees and in this case with a ring and with short (L < 10 µm), ellipsoid spores. Highest risks of confusion are with other members of the revised sect. *Saturnini* (see notes under *C. confirmatus*, *C. cyprinus* and *C. imbutus*), and, for blue-lacking and densely veiled basidiomata collected under *Salix* spp. (referred to as *C. saturninus* ‘aspect *salicus*, *aspect *ubricoides* and *aspect *sporanotandus* in the ADC), with *C. urbicus*. The latter species displays more whitish hues on the fresh pileus and is typically less hygrophanous than *C. saturninus*, with no ‘Kuehneromyces-like’ dehydration.

**Cortinarius confirmatus** Rob. Henry, Bull. Soc. Mycol. France 99, 1: 67. 1983 — MycoBank MB#185981 (var. *confirmatus*); MycoBank MB#185987 (var. *plesiocistus*).

- *Cortinarius assiduus* var. *plesiocistus* A. Ortega et al., Mycotaxon 101: 1409–1407.
- *Cortinarius assiduus* Mahiques, A. Ortega & Bidaud, Bull. Féd. Mycol. Dauphiné-Savoie 162: 42. 2001.
- *Cortinarius bulbosolvolutus* Rob. Henry & Contu, Doc. Mycol. XVI: 61: 32. 1985.

[= *Cortinarius kuehneri* Bidaud ad int., Atlas des Cortinaires XXIII: f. 1440. 2015, nom. inval. (no diagnosis, no type designated)].
[= *Cortinarius paracohabitanus* Bidaud ad int., Atlas des Cortinaires XXIII: f. 1439. 2015, nom. inval. (no diagnosis, no type designated)].
[= *Cortinarius subcylindratus* Carteret ad int., Bull. Soc. Mycol. France 128(3–4): 280. 2014, nom. inval. (no diagnosis, no type designated)].
[= *Cortinarius cistobadeflalus* Bidaud ad int., Bull. Féd. Assoc. Mycol. Mé diterranéennes 6: 41 (1994, nom. inval. (no diagnosis, no type designated)].
- *Cortinarius cypricus* Fr., Epicr. Syst. Mycol.: 307. 1838, sensu Consiglio (1990) Moënne-Loccoz & Reumaux (1989).

**Type.** FRANCE, unknown locality and collection date, under *Quercus ilex*, R. Henry 3195, PC, holotype, MycoBank MB#69663. ITS sequence deposited in GenBank under KX964438.

New combination. **Cortinarius confirmatus** var. *plesiocistus* (A. Ortega, Vila & Bidaud) Carteret, Bidaud, Reumaux & Bellanger, comb. nov.

Basionym. = *Cortinarius assiduus* var. *plesiocistus* A. Ortega, Mycotaxon 101: 1409–1407.

K. Liimatainen et al.: Cortinarius section Bicolores and section Saturnini

195
Illustrations — Bidaud et al. 2015: pl. 970–973; Ortega et al. 2007: pl. 2; Mahiques et al. 2001.

Taxonomic descriptions — Bidaud et al. 2008: f. 1434–1441; Ortega et al. 2007: 140; Mahiques et al. 2001: 42; Henry 1983: 67.

Notes — In its original concept, C. confirmatus is a cespitose species without blue tinges, fruiting in Mediterranean Quercus ilex woodlands, included by Henry in his sect. Damasceni. As phylogenetically redefined here, the species concept is dramatically widened both morphologically and ecologically, so as to encompass 7 former morphologically delimited species and one variety, cespitose or not, with or without blue hues, and occurring in the Mediterranean area under Quercus spp. or Cistus spp., but also in temperate continental forests, under various deciduous trees as well as under Picea abies. The presence of two ectomycorrhizal sequences from Northern Iran in the clade considerably extends the known geographic distribution of the species, that may occur across a broad Eurasian belt. The clade displays the highest sequence variability within the section (D_{max} max = 6 nt changes, Table 3) and its topology delineates 3 supported subclades that may, in principle, deserve their own taxonomic autonomy, as well as C. cistoalpeldius Bidaud. 

Thus, in a conservative approach and following an integrative method of species limits delineation, here we define C. confirmatus within the boundaries of its most inclusive clade and introduce C. confirmatus var. plesiocistus and C. bulbosovolvatans, has already been assigned a varietal rank, on morphogenetic bases (Ortega et al. 2007).

Therefore, this recently described species used to be called C. saturninus var. bresadolae or C. cypricus by French authors but in the field, C. cohabitans (= C. saturninus) and C. circumvelatus (= C. lucorum) are likely the first names that come to the collectors’ mind, due to the crown-like veil remnants at the pileus margin, violet hues in young lamellae and gregarious fruiting under hygrophilous deciduous trees. However, molecular analysis of the large herbarium of the authors of the ADC unveiled phylogenetic autonomy of a subset of collections that differ from other Saturnini members by very reduced veil remnants on the stipe that never form a ring, and occurrence so far restricted to calcareous soils. As currently sampled, the species seems rather widespread in France but it has been rarely reported elsewhere, as it is represented by a single collection from southern Norway and possibly an additional one from Estonia (TAAM128765/UDB016164). Phylogenetically, C. cyprinus is sister to C. saturninus, from which it differs by 3 substitutions and 2 indels (Table 3). The ITS sequence of the French collections and of the Norwegian collection are 100 % identical, and they differ from the Estonian sequence by substitutions. The lack of publically available trace file for UDB016164 prevents us from critically examining these polymorphisms and the possible conspecificity of TAAM128765 with C. cyprinus. Further taxon sampling and sequencing of Estonian Saturnini collections will be necessary to clarify this issue and to better estimate the intraspecific variability of the species at the ITS locus.

Illustrations — This study: Fig. 5d; Bidaud et al. 2015: pl. 976–982.
cally, C. imbutus is quite variable, especially regarding the colour of the pileus and the intensity of blue tinges in basidiomata. Typically, the species fruits under deciduous trees in hygrophilous places but collections (referred to as C. imbutus *aspect* laccatus in the ADC) have been reported in pure coniferous forests. In this field, C. imbutus may easily be confused with C. confirmatus, C. cyprinus and most notably C. saturninus, which can occur in similar habitats. Combining the 3 following criteria – not diagnostic on their own – should help identifying C. imbutus from its evolutionary siblings:

i. the lilac-greyish, not violaceous, hues of young lamellae;  
ii. elongated spores (Av Q > 1.8, Table 3); and  
iii. copious veil remnants on the stipe.

Macrochemistry may be useful as well to distinguish C. imbutus from C. confirmatus (gaicicol and silver nitrate), although the reliability of these reactions is still questionable.

**Cortinarius lucorum** (Fr.) Berger, Cat. Herb. III: 89. 1846 — MycoBank MB#818604

**Basionym.** = *Cortinarius impennis* var. lucorum Fr., Epirc. Syst. Mycol.: 294. 1838.

= Hydrocybe lucorum (Fr.) M.M. Moser, Kleine Kryptogamenflora von Mitteleuropa II: 162. 1953.

= *Cortinarius lucorum* (Fr.) Mussat: 101. 1901.

= *Cortinarius impennis* subsp. *lucorum* (Fr.) Sacc.: 951. 1887.

= *Cortinarius incarnatolilascens* Rob. Henry, Bull. Soc. Mycol. France 97, 3: 170. 1981.

= *Cortinarius montis-dei* Reumaux, Bull. Soc. Mycol. France 96: 357. 1980.

= *Cortinarius circumvelatus* Reumaux, Bull. Soc. Mycol. France 96: 355. 1980.

= *Cortinarius umidicola* Kauffman, Bull. Torrey Bot. Club 32, 6: 322. 1905.

**Type.** NERWY, Vestfold, Moss, Jeløy, under *Populus tremula*, 13 Sept. 1986, T.E. Brandrud, H. Lindstrøm, H. Marklund, S. Moksos CFP490, S. neotype designated here, MycoBank MBT#373173. ITS sequence deposited in GenBank under KX964558.

Illustrations — Bidaud et al. 2015: pl. 967–969; Brandrud et al. 1994: pl. C10.

Taxonomic descriptions — Bidaud et al. 2015: f. 1428–1431; Niskanen et al. 2012: 847; Brandrud et al. 1994: pl. C10; Matheny & Ammirati 2006.

Notes — In Nordic countries, this widespread species is tightly associated with *Populus* spp. and it is well known, in large part thanks to the plate C10 published in the *CFP*. North American mycologists, following Kauffman’s footsteps, somehow miss it. Notably, C. umidicola has been applied to a mushroom fruiting in conifer forests, e.g., *Tsuga* (Kauffman 1932). French authors described it repeatedly, as *C. circumvelatus*, *C. incarnatolilascens* and *C. montis-dei*, on the basis of deviating macro-morphological or ecological features while oddly, their initial – pre-molecular – concept of C. *lucorum* does not belong to Saturnini (cf. *C. cypricoides* in Fig. 1). Fries does not mention violaceous tinges on the stipe nor the typical crown-like veil in the protologue and he does not give much detail about the lamellae. However, his concept does not contradict the contemporary one in use in Nordic countries, so in order to stabilize C. *lucorum*, we here neotypify the name with the sequenced Norwegian collection CFP490 of plate C10. Our phylogenetic analysis slightly alters the morphological definition of the species (see above) and provide information on its biogeography and its extended ecological niche. Indeed, as revised here, C. *lucorum* can be collected under *Populus* spp. – with proven association through ectomycochorial sequences found in the clade – on both continents, but it also fruits under other hygrophilous deciduous trees, at least in France and, more surprisingly, under *Tsuga* and *Picea*. Phylogenetically, the species is well separated from the rest of Saturnini members, with a Δ_π_ max far exceeding Δ_π_ max (Table 3). Interestingly, the topology of the clade segregates, by a 1 substitution each; i) North American populations from European ones; and ii) European populations fruiting under deciduous trees from the ones fruiting under coniferous trees – referred to as C. *lucorum* ‘aspect’ *incarnatolilascens* in the ADC. Such finding, if confirmed by further sampling, would support the autonomy of concerned collections at an infraspecific rank. The identity of *C. umidicola* with *C. lucorum* remains provisional because the sequence we obtained from Kauffman’s syntype encompasses only the ITS1 domain. Thus, although 100 % identical to the Populus-associated Canadian collection TN10-002 along this part of the ribosomal locus (the basal-most and unsupported branch of the clade in Fig. 3) is artefactual and likely results from the shorter sequence of *C. umidicola*), one cannot preclude additional differences to take place in the ITS2 domain, splitting the two species apart. When occurring under *Populus* spp. or other hygrophilous broadleaved trees, and considering the massive fruiting and typical crown-like veil, *C. lucorum* might only be confused with *C. cyprinus* and *C. saturninus*, but these species are usually less robust and their spores are much smaller (Table 3).

**Cortinarius stuntzii** S.A. Rehner & Ammirati, Mycologia 80, 6: 903. 1988 — MycoBank MB#135248

Type. USA, Washington, Grant County, Crab Creek, 5 Nov. 1981, S.A. Rehner 394, WTU, holotype, MycoBank MBT#78780. ITS sequence deposited in GenBank under KX964558.

Illustration — Rehner et al. 1988: f. 1.

Taxonomic description — Rehner et al. 1988: 904–906.

Notes — This stout species densely fruiting under *Salix exigua* and *S. rigida*, so far known only from a small location of North-western USA, was compared to *C. umidicola* and *C. subtorvus* in the original publication, compatible with a placement into sect. Saturnini. However, a positioning elsewhere in subg. *Teleomorpha*, or even in subg. *Sericeocombe* – due to its low hygrophanesia – has also been invoked. The present work unambiguously establishes *C. stuntzii* as a genuine *Saturnini*, phylogenetically most closely related to *C. saturninus*, from which it differs by 3 substitutions and 5 indels (Table 3). Not considering biogeography, so far restricted to the type locality, the species is easily distinguished from other *Saturnini* members by its unusually large spores, up to 14.4 µm long and 8.5 µm wide (on average: 11.5 × 6.7 µm, Table 3).

**KEY TO SPECIES TREATED IN THE PRESENT STUDY**

1. Alpine and arctic zone, under *Salix* spp. or *Dryas octopetala*. ........................................... 2  
1. Mediterranean thermophilic area, under *Quercus ilex* or *Cistus* spp. .................................  C. confirmatus  
2. Continental zone ...................................... 2  
2. Coniferous trees ..................................... 3  
3. Acidic soils, in or near peatlands, *Picea* or *Abies* .................................................... 4  
3. Dry to mesic acidic woodlands ................................. 6  
4. Average spore length > 10 µm, blue tinges obvious, usually odourless .................................  C. evernii  
4. Average spore length < 10 µm, usually smelling .................. 5
5. Average spore width > 5.2 µm, smell of cedar wood or earthy. 
   C. tortuosus
5. Average spore width < 5.2 µm, smell of coconut. 
   C. dolabratus
   [with raphanoid smell, cf. C. cinnamoviolaceus]
6. Average spore width ≤ 5 µm 
   ........................................ 7
6. 5 µm < average spore width < 6 µm 
   ........................................ 8
6. Average spore width > 6 µm 
   ........................................ 11
7. Spores narrowly fusoid (Av Q > 1.8) and finely verrucose 
   ........................................ 8
7. Spores elongated (1.7 < Av Q < 1.8) and strongly verrucose 
   ........................................ 9
7. Spores ellipsoid (Av Q = 1.6) and strongly verrucose 
   ........................................ 10

8. Average spore size > 9 µm 
   ........................................ 21
9. More elongated spores (Av Q > 1.7) 
   ........................................ 22
10. Average spore size > 9 µm 
    ........................................ 23

9.7 µm, smooth pileus 
   ............... 8
9.5 µm < average spore width < 6 µm 
   ........................................ 8
9.6 µm ............. 9
11. Average spore size > 9 µm 
    ........................................ 17
12. Average spore width > 5.5 µm, smooth pileous 
    ........................................ 12
12. Average spore width ≥ 5.5 µm, pileus covered with flakes 
    ........................................ 10
12. Average spore width ≥ 5.5 µm, pileus covered with flakes 
    ........................................ 11
12. Average spore length ≥ 9 µm, pileus covered with flakes
    ........................................ 10

13. Cespitose 
    ........................................ 14
14. Strong veil remnants on the stipe 
    ........................................ 15
14. Naked silky stipe 
    ........................................ 16
15. Average spore length < 8 µm 
    ........................................ 15
15. Average spore length > 8 µm 
    ........................................ 16
16. Average spore length < 9 µm 
    ........................................ 17
16. Average spore length > 9 µm 
    ........................................ 18
17. Average spore length > 6 µm 
    ........................................ 19
17. Average spore length < 6 µm 
    ........................................ 20
18. Average spore length > 9.5 µm, pileus covered with flakes 
    ........................................ 11
18. Average spore length > 9.5 µm, smooth pileus 
    ........................................ 12
19. Smell of cedar wood 
    ........................................ 13
19. Smell weak or different 
    ........................................ 14
20. Average spore length > 6 µm 
    ........................................ 21
20. 5 µm < average spore length < 6 µm 
    ........................................ 22
20. Average spore length ≤ 5 µm 
    ........................................ 23
21. Average spore length > 10.5 µm, Salix, USA 
    ........................................ 14
21. Average spore length > 10.5 µm, Fagaceae, Europe 
    ........................................ 15
22. Spores elongated (1.7 < Av Q < 1.8), smell of cedar wood or Viola. 
    ........................................ 16
22. Spores ovoid to ellipsoid (Av Q < 1.7), smell of cedar wood or Viola. 
    ........................................ 17
23. Stout basidiomata, average spore size > 9.5 × 5.7 µm, hygrophilous 
    ........................................ 18
23. Small to medium-size basidiomata, average spore size ≤ 9.5 × 5.7 µm 
    ........................................ 19
24. Smell of cedar wood 
    ........................................ 20
24. Smell null or different 
    ........................................ 21
25. Spores ovoid (Av Q ≤ 1.6) 
    ........................................ 22
25. Spores ellipsoid (1.6 < Av Q < 1.7), orange hues on the pileus 
    ........................................ 23
25. Spores elongated to subcylindrical (1.7 ≤ Av Q ≤ 1.9) 
    ........................................ 24

26. Naked silky stipe 
    ........................................ 25
26. Persistent veil remnants on the stipe 
    ........................................ 26
27. Densely cespitose 
    ........................................ 27
27. Gregarious or loosely cespitose 
    ........................................ 28

28. Populus alba 
    ........................................ 29
28. Other deciduous trees, mostly Salix spp. 
    ........................................ 30
29. Persistent veil remnants on the stipe 
    ........................................ 31
29. Naked silky stipe 
    ........................................ 32
30. Average spore length < 8.3 µm 
    ........................................ 33
30. 8.3 µm < average spore length < 8.6 µm 
    ........................................ 34
30. Average spore length > 8.6 µm 
    ........................................ 35
31. AgNO3: – 
    ........................................ 36
31. AgNO3: + 
    ........................................ 37

DISCUSSION

The present work significantly updates our knowledge of Cortinarius, by revealing the number and the limits of species within sections Bicolores and Saturnini. It also places phylogenetically the morphological species described in these sections that do not belong in /Bicolores or /Saturnini, illustrating the homoplastic nature of morphological traits traditionally used to delineate boundaries of these sections and their relations to other sections such as Bovini, Disjungendi, Duracini, Hydrocybe and Scopulli.

What do we learn about species?

The major advanced molecular tools bring to taxonomy the ability to identify natural relationships between taxa, including those previously regarded as unrelated, to reveal cryptic species, and to correct species boundaries which were based on the use of non-diagnostic morphological traits. Sequencing numerous materials from sect. Bicolores and sect. Saturnini as well as species falling outside these sections, we identified 10 morphogenetic species and 2 phylogenetic species in sect. Bicolores, and 6 morphogenetic species in sect. Saturnini, including C. cyprinus as a cryptic species. The sequencing of type materials showed that 25 binomials are later synonyms of the 15 revised names.

The limits of only two species – C. glaphurus and C. dolabratus – in sect. Bicolores have been significantly altered after phylogenetic analysis, whereas all previously known species in sect. Saturnini have been severely redefined following molecular revision, except C. stuntzii, represented by only the holotype collection. In most cases, several morphological species are nested in single evolutionary units as a result of overreliance in the past on often non-diagnostic morphological traits. The presence of blue hues and the detection of a specific odour are among the most misleading taxonomic features unveiled in this work, as they have led to the erroneous autonomy of C. asiduous, C. denseconnatus, C. gramineus, C. imbutoides, C. phaeoruber, C. rustetteri, C. umbriocinnatnus, and C. ce- rioinus, C. flabelloides, C. periodolens and C. violaeolens, respectively. Pigments and volatiles of basidiomata, as the products of the fungal secondary metabolism, are expected to display some levels of variability in response to environmental cues. Similarly, differences in the habit or abundance of veil tissue on fruit bodies, that was used to segregate e.g., C. cir- cumvelatus, C. fulvorimosus, C. parvulor or C. salcis from their evolutionary lineages, might be explained by soil features or weather conditions at, or preceding fruiting.

More surprising is our finding that spore size and ecology also can be misleading, as illustrated by the lack of phylogenetic autonomy of C. sporanotandus, which produces much smaller spores than other C. satinius collections, and C. deceptideus, C. incarnatoftlascens, C. laccatus or C. umidicola, which are
all associated with different host trees within their respective clades. Spores and host plants are usually considered as reliable elements for taxonomic purposes because anatomy of the reproductive structures and the complex molecular machinery involved in mycorrhizal recognition are expected to have higher selective pressure when compared to macroscopic features, which are more prone to homoplasy. Part of our findings may be explained by abnormal individuals or spectacular ecological plasticity of species in sect. *Saturnini*, but the relatively high levels of polymorphism revealed in *C. confirmatus* rather support on-going and cryptic speciation in this lineage. Thus, we believe species limits delineated in the present work, especially in the revised sect. *Saturnini*, are more conservative than what short interspecific phylogenetic distances may suggest.

**What do we learn about sections limits?**

The segregation of sect. *Saturnini* within *Cortinarius* has been intricately linked to that of separating subg. *Hydrocybe* from subg. *Telamonia*, on the basis of the presence or absence of veil remnants on the stipe (Moënne-Loccoz & Reumaux 1990). However, such splitting is not phylogenetically supported, making *Hydrocybe* an artificial grouping and stipe ornamentation a confounding taxonomic criterion within *Telamonia*. As a result, species previously described in sect. *Saturnini* are not expected to form a single monophyletic lineage but are rather likely to share evolutionary history with members of other sections in the subgenus, especially the blue-coloured species from sect. *Bicolores*. Consistently, only 5 out of the 14 species recently described in sect. *Saturnini* in the ADC belong in that section. The remaining morphological species are distributed across *Telamonia* and illustrate the overlap of the original section with sect. *Scioophylli* (*C. saturninus*), defined to accommodate very similar blue taxa, but more hygrophanous than genuine *Saturnini*, and revised sect. *Bovini* (*C. cyriacoides, C. illipides* and *C. subfirma*), so far not supposed to include blue *Telamonia* species. Species previously included in sect. *Saturnini* also displayed obvious common features with sect. *Duracini*, as assessed by the presence of *C. oxytoneus*, considered by Henry as one of Fries’ *C. saturninus*, in sect. *Duracini* (Fig. 1). Similar but somewhat reversed cases are the presence in the revised sect. *Saturnini* of *C. confirmatus, C. denseconnatus* and *C. fulvorumosus*, originally described in sect. *Duracini*. The expected overlap of morphological characters in sect. *Saturnini* and sect. *Bicolores* is best illustrated by the case of *C. laetior* P. Karst., placed by its author in the trilogy *saturninus-imbutus-cypriacus*, but shown here to belong in sect. *Bicolores* (Fig. 2).

Interestingly, the present work yields strong phylogenetic support to the prospective placement or overlap of the morphologically defined sect. *Bicolores* and sect. *Duracini*. Natural relationships or transitions between these two sections have long been commented on by classical authors, on the basis of very similar habits and the suspected weakness of the ‘blue colour’ criterion in *Cortinarius* systematics (Melot 1990, Frøslev et al. 2007). However, the issue was virtually impossible to address in the absence of molecular data and the revision of *C. cinnamoviolaceus* here sheds decisive light on this issue. Indeed, although not part of /Bicolores and phylogenetically unrelated to sect. *Duracini*, this species is built from concepts that typically belong in traditional *Bicolores* (*C. cinnamoviolaceus, C. parevemius*, and *C. imbutus sensu CFP*), in traditional *Duracini* (*C. contractus, C. cylindrus, C. subparevemius* and *C. dolabratus sensu ADC*), or somewhere in between the two sections (*C. basicyanus*). This unexpected assemblage within a single evolutionary species somehow cracks the code of the secret dialog between the two sections, revealing the totally artificial nature of their main diagnostic feature, i.e., the presence/absence of blue pigments in fruit bodies. Knowing *C. cinnamoviolaceus*

natural boundaries is instrumental in considering the revised concept of *C. dolabratus*, here ephiplyffied in the revised sect. *Bicolores* despite the fact that all authors have originally placed the species in sect. *Duracini*. The case of *C. turgidipes* also illustrates this overlap of traditional sections, as the holotype of this morphological *Duracini* nests within /Bicolores.

It should be concluded from these examples that the presence/absence of blue pigments has been overemphasized in the definition of all morphospecies cited above but also in that of sections *Bicolores*, *Saturnini* and *Duracini*.

**Strength and limits of integrative taxonomy**

Higher Fungi systematics has been entirely built on the identification and hierarchical organization of visible characteristics – both macroscopic and microscopic, that were supposed to be stable within a given taxon and which in combination were supposed to be diagnostic of each species. The necessarily subjective nature of the selection process involved in this approach has led to highly artificial groupings at multiple taxonomic levels (i.e., *Aphyllophorales, Clavariaceae, Cito-cybe, Gasteromycetes*) and to divergences in the concept of species that culminate in the genus *Cortinarius*. Unravelling evolutionary history of Fungi through molecular phylogenies had tremendously impacted taxonomy, in part because characteristics that delineate a lineage with high taxonomic value can now be distinguished from those, less valuable and taxonomically overemphasized, which have appeared repeatedly in distant branches of the fungal tree of life. However, if more natural, the alternate organization of taxa that emerges from these molecular analyses brings contemporary mycologists the major challenge to uncover phylogenetically supported sets of features that will be diagnostic of each morphogenetic taxon. This process, especially in the species-richest genus *Cortinarius*, is certainly the most time-consuming part of the revision work and importantly, it heavily relies on the skills of expert field taxonomists, not phylogeneticists.

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