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RESEARCH ARTICLE

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

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Key words

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Abstract *Cortinarius* is the largest genus of ectomycorrhizal fungi worldwide. Recent molecular studies have shown high levels of morphological homoplasy 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 homoplasy 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 *a 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

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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. *Saturnini*, 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. *Saturnini* 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 *Saturnini*, 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 *Saturnini* 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*
Cortinarius cagei	***C. minicolor***, ***C. periodolens ad. int.***	***C. cagei***	*C. bicolor*?	*C. bicolor*?
***C. dolabratoides* sp. nov.**				
C. dolabratus	***C. imbutoides***			
C. evernius	***C. evernius***, ***C. parvulior ad. int.***	***C. evernius***	*C. evernius*, *C. scutulatus*	*C. evernius*
C. glaphurus	***C. tubulosus***, ***C. paranomalus* (Sat.)**			
C. hircinosmus	***C. livor***		*C. livor*?	
C. plumulosus	***C. fundatus***		*C. bicolor*?	*C. bicolor*?
C. refectus	***C. refectus***, ***C. testaceoviolaceus***		*C. bicolor*?	*C. bicolor*?
***C.* sp1**				
***C.* sp2**				
C. tortuosus	***C. tortuosus***	***C. tortuosus***	*C. plumbosus*	*C. tortuosus*, *C. plumbosus*
C. turgidipes				
C. cinnamoviolaceus	***C. cinnamoviolaceus***, ***C. parevernius***, ***C. basicyaneus***	***C. imbutus***	***C. cinnamoviolaceus***, ***C. parevernius***	***C. parevernius***
C. disjungendus	***C. cyanosterix***			
C. mattiae	***C. mattiae***	***C. mattiae***	*C. subviolascens*	
C. parevernioides	***C. parevernioides***			
C. salicinus	***C. salicinus***, *C. deceptivoides* *C. quadricolor*			
Sect. *Saturnini*	Sect. *Saturnini*	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. vilior*	*C. imbutus*
C. lucorum	***C. lucorum***	***C. lucorum***	*C. lucorum*, ***C. umidicola***	
C. saturninus	***C. saturninus***	***C. saturninus***, ***C. subtorvus***	***C. saturninus***, ***C. deceptivus***, ***C. subtorvus***	
C. stuntzii				
C. cypriacoides	***C. cypriacoides***		*C. cypriacus*	*C. cypriacus*
C. furiosus	***C. furiosus***			
C. nefastus	***C. nefastus***			
C. serratissimus*	***C. saturninoides***		*C. serratissimus*	*C. saturninus*
C. sciophylloides	***C. sciophylloides***			
C. subbulliardioides*	***C. illepidus***			
C. subfirmus	***C. subfirmus***			
C. suboxytoneus	***C. suboxytoneus***, *C. fuscocinctus*			
			C. sciophyllus	*C. sciophyllus*
			C. castaneus	*C. castaneus*
			C. calopus	
			C. torvus	
			C. impennis	
				C. myrtillinus

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.), Saturnini. 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 Muséum 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 (GK & 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 REDExtract-N-Amp$^{\text{tm}}$ Plant PCR Kit (Sigma-Aldrich, St. Louis, MO, USA), following the manufacturer's instructions. The internal transcribed spacers and 5.8S rDNA (ITS) was amplified from each collection, with the ITS-1F / ITS-4b primer pair (Gardes & Bruns 1993) 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 (Kõljalg 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 subclade 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. *Phlegmacium* 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 in 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 Bidaud 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. refectus*), we stabilized 9 names and identified 8 synonymous binomials at the species rank. In addition, we describe *C. dolabratoides* 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. evernius*, *C. plumulosus*, *C. refectus* and *C. tortuosus* as genuine members of the revised sect. *Bicolores*, but it also reveals that *C. dolabratus*, *C. glaphurus*, *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 D_{intra} max = 3 nucleotide (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-

(text continues on p. 185)

Table 2 Specimens included in phylogenetic analyses.

Species C. = *Cortinarius*	Voucher/SH	Voucher/SH annotation	Leg.	Collection date	Country	Taxonomy	Herbarium	Accession*
/Bicolores								
C. cagei	CFP 1260	cagei (neotype)	T.E. Brandrud, H. Lindström, H. Marklund, S. Muskos	1994	Sweden	CFP: D48 (1998)	S	**KX964295**
	AB 04-09-266	minicolor	A. Bidaud	2004	France	AC 22: f1419 (2014)	ADC private	**KX964296**
	AB 92-10-256	minicolor	A. Bidaud & R. Fillion	1992	France	AC 22: f1419 (2014)	ADC private	**KX964297**
	PML 738	minicolor	R. Fillion	1987	France	AC 22: f1419 (2014)	ADC private	**KX964298**
	XC 2014-02	periodolens ad int.	A. Ferville	1993	France	AC 22: f1417 (2014)	ADC private	**KX964299**
	PML 3588	basicyaneus	A. Ferville	1993	France	this study	ADC private	**KX964300**
	PML 1057	basicyaneus	R. Fillion	1988	France	this study	ADC private	**KX964301**
	SH188634.07FU (2 sequences)	cagei	na	na	Germany/Italy	na	na	AY669676
C. dolabratoides sp. nov.	H:6033567	sp. (holotype)	I. Kytövuori	2008	Finland	this study	H	**KX964302**
	AB 07-08-48	marcellae cf.	A. Bidaud & R. Fillion	2007	France	this study	ADC private	**KX964303**
	H:6033615	sp.	I. Kytövuori	2004	Finland	this study	H	**KX964304**
	H:6033575	sp.	I. Kytövuori	2008	Finland	this study	H	**KX964305**
	H:6033570	sp.	I. Kytövuori	2008	Finland	this study	H	**KX964306**
	IK 04-051	‘smell-of-viola’	I. Kytövuori	2004	Finland	this study	H	**KX964307**
	IK 01-062	‘smell-of-viola’	I. Kytövuori	2001	Finland	this study	H	**KX964308**
C. dolabratus	CFP 990	dolabratus (epitype)	T.E. Brandrud, H. Lindström, H. Marklund, S. Muskos	1990	Sweden	CFP: D52 (1998)	S	**KX964309**
	AB 04-09-186	imbutoides (holotype)	A. Bidaud	2004	France	AC 22: f1409 (2014)	PC	**KX964310**
	RH 80814	phaeoruber (holotype)	G. Chevassut	1980	France	DM 12(47): 52 (1982)	PC	**KX964311**
	AB 13-10-120	saturninus cf.	A. Bidaud	2013	France	this study	ADC private	**KX964312**
	AB 04-09-169	armillariellus cf.	A. Bidaud	2004	France	this study	ADC private	**KX964313**
	AB 01-09-41	privignus sensu Quélet cf.	A. Bidaud	2001	France	this study	ADC private	**KX964314**
	AB 98-09-94	saturninus cf.	A. Faurite	1998	Canada	this study	ADC private	**KX964315**
	AB 89-11-309	orastriatus	A. Bidaud	1989	France	this study	ADC private	**KX964316**
	H:6033519	dolabratus	I. Kytövuori	2001	Finland	this study	H	**KX964317**
	IK 02-033	dolabratus	I. Kytövuori	2002	Finland	this study	H	**KX964318**
	IK 95-1576	dolabratus	I. Kytövuori	1995	Finland	this study	H	**KX964319**
	IK 95-347	dolabratus	I. Kytövuori	1995	Finland	this study	H	**KX964320**
	KS CO1576	imbutoides	K. Soop	2005	Sweden	this study	K. Soop private	**KX964321**
	KS CO1290	imbutoides	K. Soop	2001	Sweden	this study	K. Soop private	**KX964322**
	TN 12-200	dolabratus	T. Niskanen	2012	USA	this study	H	**KX964323**
	TN 11-246	dolabratus	T. Niskanen	2011	USA	this study	H	**KX964324**
	TN 09-196	dolabratus	T. Niskanen	2009	USA	this study	H	**KX964325**
	TN 09-139	dolabratus	T. Niskanen	2009	USA	this study	H	**KX964326**
	TN 03-1713	dolabratus	T. Niskanen	2003	Slovakia	this study	H	**KX964327**
	TN 02-1095	dolabratus	T. Niskanen	2002	Finland	this study	H	**KX964328**
	TN 02-959	dolabratus	T. Niskanen	2002	Finland	this study	H	**KX964329**
	XC 2013-103	privignus sensu Quélet	P. Reumaux	1998	France	this study	ADC private	**KX964330**
	SH188528.07FU (10 sequences)	dolabratus	na	na	NA/FS/Slovakia	na	na	UDB018659
C. evernius	CFP 792	evernius (neotype)	T.E. Brandrud, H. Lindström, H. Marklund, S. Muskos	1988	Sweden	CFP: A11 (1990)	S	**KX964331**
	AB 00-09-83	evernius f. pseudoscutulatus (holotype)	A. Bidaud	2000	France	AC 22: f1407 (2014)	PC	**KX964332**
	PML 1727	evernius f. fragrans (holotype)	D. Mazuir	1990	France	AC 22: f1406 (2014)	PC	**KX964333**
	AB 96-09-47	parvulior ad int.	M. Martin	1996	France	AC 22: f1418 (2014)	ADC private	**KX964334**
	AB 91-08-42	evernius f. pseudoscutulatus	A. Bidaud & C. Blanc	1991	France	AC 22: f1407 (2014)	ADC private	**KX964335**
	PML 622	evernius f. fragrans	P. Moënne-Loccoz	1987	France	AC 22: f1406 (2014)	ADC private	**KX964336**
	AB 09-07-44	evernius var. insignis	A. Bidaud & A. Faurite	2009	France	AC 22: f1405 (2014)	ADC private	**KX964337**
	PML 3469	evernius var. evernius	A. Bidaud	1993	France	AC 22: f1404 (2014)	ADC private	**KX964338**

	PML 212	evernius var. evernius	P. Moënne-Loccoz	1982	France	AC 22: f1404 (2014)	ADC private	**KX964339**
	AB 04-09-212	evernius	A. Bidaud	2004	France	this study	ADC private	**KX964340**
	IK 00-038	evernius	I. Kytövuori	2000	Finland	this study	H	**KX964341**
	IK 97-123	evernius	I. Kytövuori	1997	Finland	this study	H	**KX964342**
	PML 376	evernius	P. Moënne-Loccoz	1986	France	this study	ADC private	**KX964343**
	PML 230	evernius	P. Moënne-Loccoz	1984	France	this study	ADC private	**KX964344**
	TN 10-074	evernius	T. Niskanen	2010	Canada	this study	H	**KX964345**
	TN 10-055	evernius	T. Niskanen	2010	Canada	this study	H	**KX964346**
	TN 10-054	evernius	T. Niskanen	2010	Canada	this study	H	**KX964347**
	TN 07-328	evernius	T. Niskanen	2007	Canada	this study	H	**KX964348**
	TN 07-312	evernius	T. Niskanen	2007	Canada	this study	H	**KX964349**
	TN 07-223	evernius	T. Niskanen	2007	Canada	this study	H	**KX964350**
	TN 05-238	evernius	T. Niskanen	2005	Norway	this study	H	**KX964351**
	SH188514.07FU (11 sequences)	evernius	na	na	Canada/FS/Germany	na	na	AY669686
C. glaphurus	RH 71421	glaphurus (holotype)	G. Chevassut	1978	France	DM 12(47): 78 (1982)	PC	**KX964352**
	AB 03-11-87	tubulosus (holotype)	A. Bidaud & A. Faurite	2003	France	AC 22: f1414 (2014)	PC	**KX964353**
	AB 92-10-350	cedriosmus (holotype)	A. Bidaud	1992	France	AC 19: f1144 (2010)	PC	**KX964354**
	XC 2009-41	violaeolens (holotype)	A. & R. Bardet	1996	France	AC 19: f1112 (2010)	PC	**KX964355**
	GK1142	paranomalus (holotype)	G. Redeuilh	1987	France	K&R: 305 (1953, invalid), AC 4: f163 (1992)	GK	**KX964356**
	AB 08-11-445	tubulosus	M. Martin	2008	France	AC 22: f1414 (2014)	ADC private	**KX964357**
	AB 92-10-332	turibulosus	R. Fillion	1992	France	AC 19: f1108 (2010)	ADC private	**KX964358**
	AB 91-11-360	turibulosus	A. Bidaud	1991	France	AC 19: f1108 (2010)	ADC private	**KX964359**
	PML 2390	turibulosus	P. Moënne-Loccoz	1991	France	AC 19: f1108 (2010)	ADC private	**KX964360**
	PML 1067	turibulosus	P. Moënne-Loccoz	1988	France	AC 19: f1108 (2010)	ADC private	**KX964361**
	AB 14-11-138	minicolor cf.	P.-Y. Courio	2014	France	this study	ADC private	**KX964362**
	AB 03-10-56	sciophyllus cf.	A. Bidaud	2003	France	this study	ADC private	**KX964363**
	AB 99-11-345	livor cf.	M. Martin	1999	France	this study	ADC private	**KX964364**
	TN 12-221	sp.	T. Niskanen	2012	USA	this study	H	**KX964365**
	XC 2011-212	laetior cf.	X. Carteret	2011	France	this study	ADC private	**KX964366**
	XC 2009-64	paranomalus cf.	X. Carteret	2009	France	this study	ADC private	**KX964367**
	SH094444.07FU (3 sequences)	turibulosus	na	na	NA/France	na	na	GQ159774
	SH094485.07FU (2 sequences)	sp.	na	na	Poland	na	na	HQ115588
C. hircinosmus	PML 334	hircinosmus (holotype)	P. Moënne-Loccoz	1986	France	AC 12: f575 (2002)	PC	**KX964368**
	AB 02-09-32	livor	A. Bidaud	2002	France	AC 23: f1459 (2015)	ADC private	**KX964369**
	F44390	sp.	K. Soop	na	Sweden	FN: 849 (2012)	S	**KX964370**
	H:6033565	hircinosmus	I. Kytövuori	2009	Finland	FN: 849 (2012)	H	**KX964371**
	AB 97-10-341	scriptor	G. Chamonaz	1997	France	AC 19: f1109 (2010)	ADC private	**KX964372**
	AB 04-10-357	imbutus cf.	A. Bidaud	2004	France	this study	ADC private	**KX964373**
C. plumulosus	RH 3417	plumulosus (holotype)	R. Henry	1972	France	SMF 93(3): 359 (1977)	PC	**KX964374**
	AB 10-09-183	fundatus	A. Bidaud & R. Fillion	2010	France	AC 22: f1411 (2014)	ADC private	**KX964375**
	AB 98-09-119	fundatus	E. & A. Bidaud, A. Faurite	1998	Canada	AC 22: f1411 (2014)	ADC private	**KX964376**
	PML 657	fundatus	P. Moënne-Loccoz	1987	France	AC 22: f1411 (2014)	ADC private	**KX964377**
	PML 3308	perscutulatus	A. Bidaud	1992	France	this study	ADC private	**KX964378**
	IK 98-1612	sp.	I. Kytövuori	1998	Finland	this study	H	**KX964379**
	TN 04-730	sp.	T. Niskanen	2004	Finland	this study	H	**KX964380**
C. refectus	AB 96-09-73	refectus (epitype)	A. Bidaud	1996	Germany	AC 22: f1410 (2014)	PC	**KX964385**
	AB 05-09-138	refectus	A. Bidaud	2005	France	AC 22: f1410 (2014)	ADC private	**KX964382**
	AB 04-10-321	refectus	A. Bidaud	2004	France	AC 22: f1410 (2014)	ADC private	**KX964383**
	AB 99-09-121	refectus	A. Bidaud	1999	France	AC 22: f1410 (2014)	ADC private	**KX964384**
	PML 2159	refectus	A. Bidaud	1990	France	AC 22: f1410 (2014)	ADC private	**KX964386**
	PML 769	refectus	P. Moënne-Loccoz	1987	France	AC 22: f1410 (2014)	ADC private	**KX964387**
	PML 17	refectus	P. Moënne-Loccoz	1985	France	AC 22: f1410 (2014)	ADC private	**KX964388**
	AB 92-10-293	testaceoviolaceus	A. Bidaud	1992	France	AC 22: f1402 (2014)	ADC private	**KX964389**
	AB 94-10-268	scriptor	A. Bidaud	1994	France	AC 19: f1109 (2010)	ADC private	**KX964390**
	IK 96-1031	refectus	I. Kytövuori	1996	Germany	this study	H	**KX964381**

Table 2 (cont.)

Species *C.* = *Cortinarius*	Voucher/SH	Voucher/SH annotation	Leg.	Collection date	Country	Taxonomy	Herbarium	Accession*
C. tortuosus	IB 79/533	tortuosus (neotype)	D. Lamoure	1979	Sweden	Opera Botanica 100: 182 (1989)	IB	**KX964391**
	XC 2008-43	flabelloides (holotype)	M. Pèlerin	2008	France	AC 19: f1136 (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: f1413 (2014)	ADC private	**KX964394**
	AB 96-08-19	tortuosus	A. Bidaud	1996	France	AC 22: f1413 (2014)	ADC private	**KX964395**
	AB 95-09-34	tortuosus	C. Blanc	1995	France	AC 22: f1413 (2014)	ADC private	**KX964396**
	PML 3551	tortuosus	A. Bidaud & R. Fillion	1993	France	AC 22: f1413 (2014)	ADC private	**KX964397**
	PML 1225	tortuosus	P. Moënne-Loccoz	1989	France	AC 22: f1413 (2014)	ADC private	**KX964398**
	PML 1214	tortuosus	P. Moënne-Loccoz	1989	France	AC 22: f1413 (2014)	ADC private	**KX964399**
	PML 386	tortuosus	P. Moënne-Loccoz	1986	France	AC 22: f1413 (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**
	TN 10-087	tortuosus	T. Niskanen	2010	Canada	this study	H	**KX964405**
	TN 09-046	tortuosus	T. Niskanen	2009	USA	this study	H	**KX964406**
	TN 07-307	tortuosus	T. Niskanen	2007	Canada	this study	H	**KX964407**
	TN 05-006	tortuosus	T. Niskanen	2005	Finland	this study	H	**KX964408**
	SH094369.07FU (7 sequences)	tortuosus	na	na	USA/U/Japan	na	na	AY669669
C. turgidipes	AB 93-10-425	turgidipes (holotype)	A. & E. Bidaud	1993	France	AC 17(1): f885 (2008)	PC	**KX964409**
C. sp1	TN 12-217	sp.	T. Niskanen	2012	USA	na	H	**KX964410**
	UBCOGTR194	sp. (ectomycorrhiza)	na	na	Canada	na	na	EU597034
C. sp2	TN 05-033	sp.	T. Niskanen	2005	Finland	na	H	**KX964411**
OTHER (MORPHOLOGICAL) *BICOLORES*								
C. cinnamoviolaceus	IB 48/590	cinnamoviolaceus (holotype)	M. Moser	1948	Austria	Nova Hedwigia XIV(2-4): 514 (1967)	IB	**KX964412**
	RH 70942	basicyaneus (holotype)	M. Trimbach	1976	France	FAMM 25: 38 (2004)	PC	**KX964413**
	RH 4000	cylindratus (holotype)	R. Henry	1972	France	SMF 99(1): 91 (1983)	PC	**KX964414**
	RH 526	subparevernius (holotype)	R. Henry	1956	France	SMF 85(4): 442 (1969)	PC	**KX964415**
	RH 1240	contractus (holotype)	R. Henry	1960	France	SMF 85(4): 387 (1969)	PC	**KX964416**
	RH 3258a78	parevernius (holotype)	R. Henry	1955	France	K&R: 303 (1953, invalid)	PC	**KX964417**
	AB 02-10-71	dolabratus	A. & M. Burat	2002	France	AC 17(1): f817 (2008)	ADC private	**KX964418**
	CFP 574	imbutus	T.E. Brandrud, H. Lindström, H. Marklund, S. Muskos	1987	Sweden	CFP: D60 (1998)	S	**KX964419**
	AB 12-11-240	imbutus	A. Bidaud	2012	France	this study	ADC private	**KX964420**
	TN 05-198	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	na	na	Sweden/Italy	na	na	UDB001160
C. cyanosterix (= *C. disjungendus*)	RH 338	cyanosterix (holotype)	R. Henry	1952	France	SMF 71(3): 259, 261 (1956)	PC	**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: f1415 (2014)	ADC private	**KX964425**
	AB 99-09-77	subviolascens	A. Bidaud	1999	France	AC 12: f565 (2002)	ADC private	**KX964426**
	PML 650	subviolascens	P. Moënne-Loccoz	1987	France	AC 12: f565 (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/poecilopus aff.	A. Bidaud, F. Armada & R. Fillion	2006	France	this study	ADC private	**KX964429**
	H:6029375	mattiae	T. Niskanen	2004	Finland	this study	H	**KX964430**

	H:6000560	mattiae	I. Kytövuori	2007	Finland	this study	H	**KX964431**
	IK 01-039	mattiae	I. Kytövuori	2001	Sweden	this study	H	**KX964432**
	IK 98-1127	mattiae	I. Kytövuori	1998	Finland	this study	H	**KX964433**
	PML 3989	umbrinoconnatus forma	A. Bidaud	1993	France	this study	ADC private	**KX964434**
	PML 2298	oxytoneus	A. Bidaud	1991	France	this study	ADC private	**KX964435**
	SH009438.07FU (1 sequence)	sp.	na	na	Canada	na	na	FJ039684
C. parevernioides	AB 02-09-50	parevernioides (holotype)	C. Gérard	2002	France	AC 22: f1408 (2014)	PC	**KX964436**
	SH188502.07FU (15 sequences)	malachius	na	na	NA/U	na	na	KF617653
C. salicinus	XC 2014-03	salicinus (holotype)	C. Hugouvieux	2005	France	AC 22: f1416 (2014)	PC	**KX964437**
/Saturnini								
C. confirmatus	RH 3195	confirmatus (holotype)	R. Henry	1970	France	SMF 99(1): 67 (1983)	PC	**KX964438**
	JVG 990125-31	assiduus var. plesiocistus (isotype)	X. Llimona & J. Vila	1999	Spain	Mycotaxon 101: 140 (2007)	J. Vila private	AM713178
	MES 3541	assiduus (holotype)	R. Mahiques	1999	Spain	FMDS 162: 42 (2001)	MES	**KX964439**
	RH 84/159	bulbosovolvatus (isotype)	M. Contu & L. Curreli	1984	Italy	DM 26 (61): 32 (1985)	PC	**KX964440**
	XC 2013-160	confirmatus ‘asp. subcylindratus’	na	2013	France	AC 23: f1441 (2015)	PC	**KX964441**
	AB 13-10-97	confirmatus ‘asp. kuehneri’	A. Bidaud	2013	France	AC 23: f1440 (2015)	ADC private	**KX964442**
	XC 2011-199	confirmatus ‘asp. spurcatocephalus’	X. Carteret	2011	France	AC 23: f1439 (2015)	ADC private	**KX964443**
	XC 95-10-04-06	confirmatus ‘asp. spurcatocephalus’	X. Carteret	1995	France	AC 23: f1439 (2015)	ADC private	**KX964444**
	AB 09-11-452	confirmatus ‘asp. rubricosissimus’	A. Bidaud	2009	France	AC 23: f1438 (2015)	ADC private	**KX964445**
	AB 00-10-193	confirmatus ‘asp. rubricosissimus’	A. Bidaud	2000	France	AC 23: f1438 (2015)	ADC private	**KX964446**
	AB 11-11-324	confirmatus ‘asp. paracohabitans’	F. Armada, A. Bidaud & J. Pardo	2011	France	AC 23: f1437 (2015)	ADC private	**KX964447**
	PML 4722	confirmatus ‘asp. imbutus’	P. Reumaux	1990	France	AC 23: f1436 (2015)	ADC private	**KX964448**
	XC 2012-171	confirmatus ‘asp. imbutus’	A. Lantz	2012	France	AC 23: f1436 (2015)	ADC private	**KX964449**
	AB 09-11-514	confirmatus ‘asp. assiduus’	A. Bidaud	2009	France	AC 23: f1435 (2015)	ADC private	**KX964450**
	AB 05-11-423	confirmatus ‘asp. assiduus’	A. & E. Bidaud	2005	France	AC 23: f1435 (2015)	ADC private	**KX964451**
	AB 02-11-201	confirmatus ‘asp. assiduus’	F. Lopez	2002	France	AC 23: f1435 (2015)	ADC private	**KX964452**
	XC 2013-156	confirmatus ‘asp. assiduus’	F. Valade	2013	France	AC 23: f1435 (2015)	ADC private	**KX964453**
	AB 03-11-78	confirmatus ‘asp. confirmatus’	A. Faurite	2003	France	AC 23: f1434 (2015)	ADC private	**KX964454**
	AB 92-11-422	cistoadelphus ad int.	A. Bidaud	1992	France	FAMM 6: 41 (1994)	ADC private	**KX964455**
	AB 09-11-450	cohabitans cf.	A. Bidaud	2009	France	this study	ADC private	**KX964456**
	FR2016052	assiduus	J.-M. Ourcival	2016	France	this study	CEFE private	**KX964457**
	FR2012405	assiduus	P.-A. Moreau	2012	France	this study	CEFE private	**KX964458**
	FR2012089	assiduus	F. Richard	2011	France	this study	CEFE private	**KX964459**
	FR2012076	assiduus	E. Taschen	2011	France	this study	CEFE private	**KX964460**
	XC 2006-204	bresadolae cf.	na	2006	France	this study	ADC private	**KX964461**
	XC 2005-249	saturninus cf.	X. Carteret	2005	France	this study	ADC private	**KX964462**
	SH094374.07FU (6 sequences)	sp.	na	na	U/Iran	na	na	HQ204652
C. cyprinus	XC 2012-26	cyprinus (holotype)	G. Redeuilh	1993	France	AC 23: f1443 (2015)	PC	**KX964463**
	AB 11-11-251	cyprinus	A. Bidaud	2011	France	AC 23: f1443 (2015)	ADC private	**KX964464**
	AB 11-10-192	cyprinus	A. Bidaud	2011	France	AC 23: f1443 (2015)	ADC private	**KX964465**
	AB 06-09-144	cyprinus	A. Bidaud	2006	France	AC 23: f1443 (2015)	ADC private	**KX964466**
	PML 344	cyprinus	P. Moënne-Loccoz	1986	France	AC 23: f1443 (2015)	ADC private	**KX964467**
	PML 81	cyprinus	P. Moënne-Loccoz	1981	France	AC 23: f1443 (2015)	ADC private	**KX964468**
	XC 2013-15	cyprinus	P. Reumaux	2013	France	AC 23: f1443 (2015)	ADC private	**KX964469**
	XC 2007-103	cyprinus	X. Carteret	2007	France	AC 23: f1443 (2015)	ADC private	**KX964470**
	AB 04-09-167	sciophyllus cf.	A. Bidaud	2004	France	this study	ADC private	**KX964471**
	JMB 2014111802	circumvelatus cf.	P.-A. Moreau	2014	France	this study	CEFE private	**KX964472**
	PAM 13092901	circumvelatus	P.-A. Moreau	2013	France	this study	CEFE private	**KX964473**
	PML 425	myrtillinus	P. Moënne-Loccoz	1986	France	this study	ADC private	**KX964474**
	XC 2007-95	mutabilis cf.	na	2007	France	this study	ADC private	**KX964475**
	TEB 348-10	saturninus aff.	T.E. Brandrud	na	Norway	this study	na	**KX964476**
	TAAM 128765	sp.	A. Kollom	2008	Estonia	na	na	UDB016164
C. imbutus	IK 97-1162	imbutus (neotype)	I. Kytövuori	1997	Finland	this study	H	**KX964498**
	PML 4557	laccatus (holotype)	P. Reumaux	1978	France	SMF 98(4): 348 (1982)	PC	**KX964478**
	RH 3123	betulaecomes (holotype)	R. Henry	1976	France	SMF 93(3): 347 (1977)	PC	**KX964479**

Table 2 (cont.)

Species *C.* = *Cortinarius*	Voucher/SH	Voucher/SH annotation	Leg.	Collection date	Country	Taxonomy	Herbarium	Accession*
	XC 2013-13	imbutus 'asp. laetior'	P. Reumaux	1998	France	AC 23: f1447 (2015)	ADC private	**KX964480**
	XC 2014-77	imbutus 'asp. saturnalis'	P. Reumaux	1978	France	AC 23: f1446 (2015)	ADC private	**KX964481**
	XC 2014-61	imbutus 'asp. saturnalis'	P. Reumaux	1986	France	AC 23: f1446 (2015)	ADC private	**KX964482**
	XC 2007-104	imbutus 'asp. vilior'	X. Carteret	2007	France	AC 23: f1445 (2015)	ADC private	**KX964483**
	AB 10-10-237	imbutus 'asp. imbutus'	A. Bidaud	2010	France	AC 23: f1444 (2015)	ADC private	**KX964484**
	AB 09-11-471	imbutus 'asp. imbutus'	A. Bidaud & R. Fillion	2009	France	AC 23: f1444 (2015)	ADC private	**KX964485**
	AB 04-09-228	imbutus 'asp. imbutus'	A. Bidaud & A. Faurite	2004	France	AC 23: f1444 (2015)	ADC private	**KX964486**
	AB 98-10-358	imbutus 'asp. imbutus'	A. Bidaud	1998	France	AC 23: f1444 (2015)	ADC private	**KX964487**
	PML 375	imbutus 'asp. imbutus'	P. Reumaux	1986	France	AC 23: f1444 (2015)	ADC private	**KX964488**
	XC 2002-122	imbutus 'asp. imbutus'	X. Carteret	2002	France	AC 23: f1444 (2015)	ADC private	**KX964489**
	XC 2002-108	imbutus 'asp. imbutus'	X. Carteret	2002	France	AC 23: f1444 (2015)	ADC private	**KX964490**
	XC 2002-107	imbutus 'asp. imbutus'	X. Carteret	2002	France	AC 23: f1444 (2015)	ADC private	**KX964491**
	XC 2002-106	imbutus 'asp. imbutus'	X. Carteret	2002	France	AC 23: f1444 (2015)	ADC private	**KX964492**
	AB 08-10-307	cohabitans	J. Garin	2008	France	this study	ADC private	**KX964493**
	AB 02-10-106	cohabitans	M. Renard	2002	France	this study	ADC private	**KX964494**
	AB 02-09-58	cohabitans	A. Bidaud	2002	France	this study	ADC private	**KX964495**
	AB 00-09-127	cohabitans cf.	A. Bidaud	2000	France	this study	ADC private	**KX964496**
	IK 98-2242	sp.	I. Kytövuori	1998	Sweden	this study	H	**KX964497**
	IK 94-1236	sp.	I. Kytövuori	1994	Finland	this study	H	**KX964477**
	JMB 2008092703	salicis cf.	J.-M. Bellanger	2008	France	this study	CEFE private	**KX964499**
	RH 71030	betulaecomes	R. Henry	1976	France	this study (Rob. Henry, ined.)	PC	**KX964500**
	TN 11-257	sp.	T. Niskanen	2011	USA	this study	H	**KX964501**
	TN 11-252	sp.	T. Niskanen	2011	USA	this study	H	**KX964502**
	TN 11-151	sp.	T. Niskanen	2011	USA	this study	H	**KX964503**
	TN 11-150	sp.	T. Niskanen	2011	USA	this study	H	**KX964504**
	TN 05-167	sp.	T. Niskanen	2005	Finland	this study	H	**KX964505**
	XC 2012-96	laetior forma	X. Carteret	2012	France	this study	ADC private	**KX964506**
	XC 2002-109	renidentoides cf.	X. Carteret	2002	France	this study	ADC private	**KX964507**
	SH188563.07FU (6 sequences)	saturninus	na	na	Canada/Estonia/China	na	na	UDB018346
C. lucorum	CFP 490	lucorum (neotype)	T.E. Brandrud, H. Lindström, H. Marklund, S. Muskos	1986	Norway	CFP: C10 (1994)	S	**KX964585**
	RH 71502	incarnatolilascens (holotype)	R. Henry	1979	France	AC 23: f1431 (2015), SMF 97(3): 170 (1981)	PC	**KX964508**
	PML 4142	montis-dei (holotype)	P. Reumaux	1980	France	AC 23: f1430 (2015), SMF 96(3): 357 (1980)	PC	**KX964509**
	PML 34	circumvelatus (holotype)	P. Reumaux	1976	France	AC 23: f1429 (2015), SMF 96(3): 355 (1980)	PC	**KX964510**
	10433	umidicola (syntype)	C.H. Kauffman	1903	USA	Bull. Torrey Bot. Club 32(6): 322 (1905)	MICH	**KX964511**
	PML 4143	lucorum 'asp. montis-dei'	P. Reumaux	1980	France	AC 23: f1430 (2015)	ADC private	**KX964512**
	PAM 14090808	lucorum 'asp. circumvelatus'	P.-A. Moreau	2014	France	AC 23: f1429 (2015)	ADC private	**KX964513**
	IK 89-748	lucorum	I. Kytövuori	1989	Finland	this study	H	**KX964514**
	KS CO513	diabolicus	K. Soop	na	Sweden	this study	na	**KX964515**
	TN 10-002	lucorum	T. Niskanen	2010	Canada	this study	H	**KX964516**
	TN 03-1169	lucorum	T. Niskanen	2003	Sweden	this study	H	**KX964517**
	SH188495.07FU (21 sequences)	lucorum	na	na	NA/FS	na	na	UDB019872
C. saturninus	CFP 514	saturninus (neotype)	T.E. Brandrud, H. Lindström, H. Marklund, S. Muskos	1986	Sweden	CFP: C09 (1994)	S	**KX964584**
	PML 4578	urbicus var. sporanotandus (holotype)	A. Bidaud	1996	France	AC 23: f1455 (2015), AC 12: f560 (2002)	PC	**KX964518**

	PML 2215	marginatosplendens (isotype)	P. Reumaux	1978	France	AC 23: f1453 (2015), SMF 96(3): 356 (1980)	G	**KX964519**
	XC 2007-14	fulvorimosus (holotype)	A. & R. Bardet	1992	France	AC 23: f1452 (2015), AC 17: f869 (2008)	PC	**KX964520**
	RH 3758	denseconnatus (holotype)	na	1973	France	SMF 99(1): 65 (1983)	PC	**KX964521**
	RH 81181	gramineus (holotype)	R. Henry	1981	France	SMF 99(1): 64 (1983)	PC	**KX964522**
	RH 71682	rastetteri (holotype)	V. Rastetter	1980	France	SMF 97(3): 177 (1981)	PC	**KX964523**
	PR 258	dissidens (holotype)	P. Reumaux	1978	France	SMF 96(3): 370 (1980)	PC	**KX964524**
	RH 2623	salicis (holotype)	R. Henry	1968	France	SMF 93(3): 364 (1977)	PC	**KX964525**
	RH 476	umbrinoconnatus (holotype)	R. Henry	1955	France	SMF 73(1): 53 (1957)	PC	**KX964526**
	AB 02-10-179	saturninus 'asp. urbicoides'	A. Faurite	2002	France	AC 23: f1457 (2015)	ADC private	**KX964527**
	AB 95-11-144	saturninus 'asp. urbicoides'	R. Fillion	1995	France	AC 23: f1457 (2015)	ADC private	**KX964528**
	XC 2001-107	saturninus 'asp. urbicoides'	X. Carteret & P. Reumaux	2001	France	AC 23: f1457 (2015)	ADC private	**KX964529**
	AB 14-11-160 (= AB 14-11-161)	saturninus 'asp. salicis'	A. Bidaud, J. Cavet, R. Fillion & G. Raffini	2014	France	AC 23: f1454 (2015)	ADC private	**KX964530**
	XC 2014-109	saturninus 'asp. salicis'	X. Carteret	2014	France	AC 23: f1454 (2015)	ADC private	**KX964531**
	XC 2011-205	saturninus 'asp. salicis'	X. Carteret	2011	France	AC 23: f1454 (2015)	ADC private	**KX964532**
	XC 2008-55	saturninus 'asp. salicis'	X. Carteret	2008	France	AC 23: f1454 (2015)	ADC private	**KX964533**
	XC 2007-108	saturninus 'asp. salicis'	X. Carteret	2007	France	AC 23: f1454 (2015)	ADC private	**KX964534**
	AB 14-09-47	saturninus 'asp. dionisiae'	E. Bidaud	2014	France	AC 23: f1451 (2015)	ADC private	**KX964535**
	AB 04-10-344	saturninus 'asp. deceptivus'	A. Bidaud	2004	France	AC 23: f1450 (2015)	ADC private	**KX964536**
	AB 98-10-381	saturninus 'asp. deceptivus'	Dr. Misermont	1998	France	AC 23: f1450 (2015)	ADC private	**KX964537**
	XC 2014-63	saturninus 'asp. cohabitans'	M. Pèlerin	1996	France	AC 23: f1449 (2015)	ADC private	**KX964538**
	XC 2014-116	saturninus 'asp. saturninus'	na	2014	France	AC 23: f1448 (2015)	ADC private	**KX964539**
	XC 2014-114	saturninus 'asp. saturninus'	L. Tarahu	2014	France	AC 23: f1448 (2015)	ADC private	**KX964540**
	XC 2007-97	saturninus 'asp. saturninus'	na	2007	France	AC 23: f1448 (2015)	ADC private	**KX964541**
	AB 97-09-187, PML 5347	urbicus	E. & A. Bidaud	1997	France	AC 12: f560 (2002)	ADC private	**KX964542**
	PML 3967	salicis var. salicis	M. Citérin	1994	France	AC 12: f559 (2002)	ADC private	**KX964543**
	CFP 408	subtorvus	T.E. Brandrud, H. Lindström, H. Marklund, S. Muskos	1986	Sweden	CFP: A04 (1990)	S	**KX964544**
	AB 05-10-273	deceptivus sensu Moser	R. Fillion	2005	France	this study	ADC private	**KX964545**
	H:6029320	saturninus	I. Kytövuori	1998	Finland	this study	H	**KX964546**
	IK 94-631	saturninus	I. Kytövuori	1994	Finland	this study	H	**KX964547**
	JMB 2009101002	cohabitans	J.-M. Bellanger	2009	France	this study	CEFE private	**KX964548**
	KH14	subtorvus	na	2011	Norway (Svalbard)	na	na	GU234058
	O50591	subtorvus	na	2011	Norway (Svalbard)	na	na	GU234013
	PML 75	urbicus	P. Moënne-Loccoz	1984	France	this study	ADC private	**KX964549**
	TN 09-208	saturninus	T. Niskanen	2009	USA	this study	H	**KX964550**
	XC 2016-12	euprivignus aff.	P. Reumaux	1977	France	this study	ADC private	**KX964551**
	XC 2008-61	salicis	X. Carteret	2008	France	this study	ADC private	**KX964552**
	XC 2007-90	mutabilis cf.	X. Carteret	2007	France	this study	ADC private	**KX964553**
	XC 2006-194	salicis	X. Carteret	2006	France	this study	ADC private	**KX964554**
	XC 2002-167	holophaeus sensu Henry	M. Pèlerin	2002	France	this study	ADC private	**KX964555**
	XC 2001-104	mutabilis	X. Carteret	2001	France	this study	ADC private	**KX964556**
	XC 96-10-26-09	subprivignus	X. Carteret	1996	France	this study	ADC private	**KX964557**
	SH094324.07FU (13 sequences)	saturninus	na	na	USA/U	na	na	UDB017613
C. stuntzii	Rehner 394	stuntzii (holotype)	S.A. Rehner	1981	USA	Mycologia 80(6): 903 (1988)	WTU	**KX964558**
Other (morphological) *Saturnini*								
C. cypriacoides	PML 1269	cypriacoides 'asp. cypriacoides' (holotype)	R. Fillion	1989	France	AC 23: f1423 (2015), AC 2: f81 (1990)	PC	**KX964559**
	PML 3984	cypriacoides 'asp. cypriacoides'	C. Guyot	1989	France	AC 23: f1423 (2015)	ADC private	**KX964560**
	PML 3979	cypriacoides 'asp. lucorum'	A. Bidaud	1992	France	AC 23: f1424 (2015), AC 9: f419 (1999)	ADC private	**KX964561**
C. furiosus	XC 2014-64c	furiosus (holotype)	D. Brion	2012	France	AC 23: f1458 (2015)	PC	**KX964562**
	LM5411	sp. (Quercus ectomycorrhiza)	na	na	Austria	na	na	KM576363

Table 2 (cont.)

Species *C.* = *Cortinarius*	Voucher/SH	Voucher/SH annotation	Leg.	Collection date	Country	Taxonomy	Herbarium	Accession*
C. illepidus sensu *ADC* (= *C. subbulliardioides*)	AB 11-11-331	illepidus	A. Bidaud & C. Gérard	2011	France	AC 23: f1422 (2015)	ADC private	**KX964563**
	AB 11-11-330	illepidus	A. Bidaud & C. Gérard	2011	France	AC 23: f1422 (2015)	ADC private	**KX964564**
C. nefastus	XC 2014-60	nefastus (holotype)	D. Brion	2012	France	AC 23: f1426 (2015)	PC	**KX964565**
C. ortovernus	JB 604808	ortovernus (holotype)	J. Ballará	2008	Spain	JEC 12(11): 56 (2009)	J. Ballara private	**KX964566**
C. oxytoneus	RH 931	oxytoneus (holotype)	R. Henry	1957	France	SMF 97(3): 277 (1981)	PC	**KX964567**
C. saturninoides sensu *ADC* (= *C. serratissimus*)	AB 12-10-93	saturninoides	A. Bidaud & M. Renard	2012	France	AC 23: f1421 (2015)	ADC private	**KX964568**
	AB 00-10-148	saturninoides	A. Bidaud	2000	France	AC 23: f1421 (2015)	ADC private	**KX964569**
	RH 3451	oxytoneus	R. Henry	1972	France	SMF 97(3): 277 (1981)	ADC private	**KX964570**
	XC 2014-119	saturninoides	R. Chalange	2014	France	AC 23: f1421 (2015)	ADC private	**KX964571**
	XC 2014-64b	saturninoides	D. Brion	2012	France	AC 23: f1421 (2015)	ADC private	**KX964572**
	XC 2013-144	saturninoides	F. Valade	2013	France	AC 23: f1421 (2015)	ADC private	**KX964573**
	XC 2010-56	saturninoides	X. Carteret	2010	France	AC 23: f1421 (2015)	ADC private	**KX964574**
	XC 2010-29	saturninoides	X. Carteret	2010	France	AC 23: f1421 (2015)	ADC private	**KX964575**
	SH188624.07FU (3 sequences)	lucorum	na	na	USA/Estonia/Italy	na	na	UDB016052
C. sciophylloides	AB 99-10-254	sciophylloides (holotype)	A. Bidaud	1999	France	AC 23: f1425 (2015)	PC	**KX964576**
	AB 91-10-291	sciophylloides	J. Garin	1991	France	AC 23: f1425 (2015)	ADC private	**KX964577**
	PML 5446	sciophylloides	J. Cavet	1999	France	AC 23: f1425 (2015)	ADC private	**KX964578**
	PML 2381	raphanodiabolicus	P. Reumaux	1991	France	na	ADC private	**KX964579**
	SH188568.07FU (6 sequences)	valgus	na	na	Canada/U	na	na	UDB002444
C. subfirmus	AB 08-10-363	subfirmus (holotype)	A. Bidaud & G. Raffini	2008	France	AC 23: f1433 (2015)	PC	**KX964580**
C. suboxytoneus	AB 01-09-56	suboxytoneus (holotype)	A. Bidaud	2001	France	AC 23: f1442 (2015)	PC	**KX964581**
	MFT60	sp. (Fagus ectomycorrhiza)	na	na	Germany	na	na	FJ403502
OTHER *TELAMONIA*								
C. alboviolaceus s.lat.	SH188487.07FU (26 sequences)	alboviolaceus	na	na	NA/U	na	na	AF325596
C. anisatus	CFP 1200	anisatus (holotype)	T.E. Brandrud, H. Lindström, H. Marklund, S. Muskos	1993	Sweden	CFP: E25 (2014)	S	DQ117931
C. anisochrous	IK 01-030	anisochrous (holotype)	T. Niskanen & I. Kytövuori	2001	Estonia	Mycologia 105(4): 988 (2013)	H, S, NY	JX407297
C. athabascus	DBB27618, UC1860905	athabascus (holotype)	D. Bojantchev	2011	USA	Mycotaxon 123: 382 (2013)	UC	JN133295
C. biformis	SH188479.07FU (41 sequences)	biformis	na	na	NA/U	na	na	UDB002252
C. bovinus	IK 04-038	bovinus (neotype)	I. Kytövuori	2004	Finland	Mycologia 105(4): 981 (2013)	H, S, NY	JX407276
C. brunneifolius	TN 06-146	brunneifolius (holotype)	T. Niskanen	2006	Finland	Mycol. Progress 7(4): 241 (2008)	H	EU259284
C. caesioarmeniacus	H:7000901	caesioarmeniacus (holotype)	K. Liimatainen & T. Niskanen	2007	Canada	IF 198: 1 (2014)	H	KP137498
C. claroplaniusculus	RH 2334	claroplaniusculus (holotype)	R. Henry	1967	France	SMF 99(1): 65 (1983)	PC	KP013184
C. decipiens	PML 366	decipiens f. decipiens (neotype)	P. Moënne-Loccoz	1986	France	AC 11(1): f507 (2001), AC 2: f52 (1990)	G	FN428988
C. disjungendus	PAK 4370	disjungendus (lectotype)	P.A. Karsten	< 1893	Finland	ASFFF 9(1): 6 (1893)	H	KP013190
C. duracinus	PML 349	duracinus (neotype)	P. Moënne-Loccoz	1986	France	AC 2: f76 (1990)	G	**KX964582**
C. duracinus s.lat.	SH188648.07FU (2 sequences)	sp.	na	na	Denmark/Germany	na	na	AJ889943
C. duracinus s.lat.	SH094372.07FU (6 sequences)	rigens	na	na	NA/Italy	na	na	JF907880
C. fuscescens	H:6001898	fuscescens (holotype)	K. Liimatainen & T. Niskanen	2008	Finland	IF 201: 2 (2014)	H	KP165546
C. fuscobovinaster	IK 09-537	fuscobovinaster (holotype)	I. Kytövuori	2009	Norway	Mycologia 105(4): 990 (2013)	H, S, NY	JX407316
C. gallurae	CONS 00076	gallurae (holotype)	D. & M. Antonini, G. Consiglio	2002	Italy	Il genereCortinarius in Italia 3: C101 (2005)	CONS	FN428979
C. murinascens	IK 08-958	murinascens (holotype)	I. Kytövuori	2008	Finland	IF 201: 3 (2014)	H	KP165570
C. neofurvolaesus	CFP 1438	neofurvolaesus (holotype)	T.E. Brandrud, H. Lindström, H. Marklund, S. Muskos	1999	Sweden	CFP: E24 (2014)	S	DQ139999

C. niveotraganus	SH188538.07FU (8 sequences)	niveotraganus	na	na	FS	na	na	KM273103
C. olididisjungendus	TN 07-191, H:7000854	olididisjungendus (holotype)	na	2007	Canada	IF 186: 2 (2014)	H	KM273091
C. orasericeus	RH 70239	orasericeus (holotype)	R. Henry	1975	France	SMF 99(1): 69 (1983)	PC	KP013203
C. quarciticus	CFP 765	quarciticus (holotype)	T.E. Brandrud, H. Lindström, H. Marklund, S. Muskos	1988	Sweden	CFP: C59 (1994)	S	UDB000748
C. sordidemaculatus	RH 1122	sordidemaculatus (holotype)	R. Henry	< 1981	France	SMF 97(3): 196 (1981)	PC	DQ139984
C. sp.	IB 86/172	bovinus cf.	M. Moser	1986	Austria	na	IB	DQ139983
C. sp.	TF-01-034	aprinus	T. Frøslev	na	Denmark	na	C	AJ889942
C. subserratissimus	IK 11-017	subserratissimus (holotype)	I. Kytövuori	2011	Sweden	IF 201: 4 (2014)	H	KP165552
C. subturibulosus	SH188545.07FU (7 sequences)	subturibulosus	na	na	France/Spain/Portugal	na	na	FJ928484
C. tacitus	AB 05-09-72	tacitus (holotype)	A. Bidaud	2005	France	AC 22: f1400 (2014)	PC	**KX964583**
C. torvus	SH009362.07FU (10 sequences)	torvus	na	na	NA/FS/Germany	na	na	UDB001345
C. urbicus	SH188612.07FU (3 sequences)	urbicus	na	na	Canada/FS	na	na	UDB000743
OUTGROUP								
C. anomalovelatus	JFA13109	anomalovelatus (holotype)	J.F. Ammirati	2007	USA	IF 93: 1 (2014)	WTU	FJ717605
C. lepidopus sensu auct.	SH196665.07FU (12 sequences)	anomalus	na	na	U	na	na	UDB002227
C. caesiocinctus	Sa57-13	caesiocinctus (holotype)	R. Kühner	1957	France	DM 20(77): 92 (1989)	G	DQ663239
C. flavipallens	IK 08-1729, H:6032393	flavipallens (holotype)	I. Kytövuori	2008	Finland	Persoonia 33 : 125 (2014)	H	KF732554
C. sannio	MM 97/352, IB:1997/0352	sannio (holotype)	M. Moser	1997	USA	Mycotaxon 72 : 315 (1999)	IB	KF732420

CFP, Cortinarius, Flora Photographica; AC, Atlas des Cortinaires; FN, Funga Nordica; DM, Documents Mycologiques; SMF, Bulletin de la Société Mycologique de France; FMDS, Bulletin de la Fédération Mycologique Dauphiné-Savoie; JEC, Journal des Journées Européennes du Cortinaire; K&R, Flore analytique des Champignons supérieurs (Küehner & Romagnesi); IF, Index Fungorum; ASFFF, Acta Societatis pro Fauna et Flora Fennica; BFNF, Bidrag till kännedom av Finlands Natur och Folk; NA, North America (USA, Canada); FS, Fennoscandia (Denmark, Sweden, Norway, Finland, Estonia, Lithuania, Latvia); U, Europe.

* Sequences generated for the present work are highlighted in **bold**.

tinental biogeographical distribution in some cases (Table 3). Minimal interspecific phylogenetic distances D_{inter} 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_{intra} 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. evernius*, *C. plumulosus*, *C. refectus*, *C.* sp1 and *C.* sp2, and another one including *C. dolabratoides*, *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 not 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_{intra} 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_{inter} min = 16 substitutions plus 3 indels to *C. confirmatus*, representing 3.1 % of sequence divergence). Although not significantly lower than in /Bicolores, these distances exceed D_{intra} 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* (incl. *C. parevernius*, *C. subparevernius*, *C. basicyaneus* and *C. imbutus* sensu *CFP*), *C. mattiae*, *C. parevernioides*, *C. salicinus* and *C. disjungendus*. 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. cypriacoides*, *C. subfirmus* and *C. illepidus* in sect. *Bovini*, *C. saturninoides* in sect. *Sciophylli*, *C. oxytoneus* in sect. *Duracini* and *C. sciophylloides* in sect. *Brunneotincti* (Fig. 1, Table 1).

(text continues on p. 190)

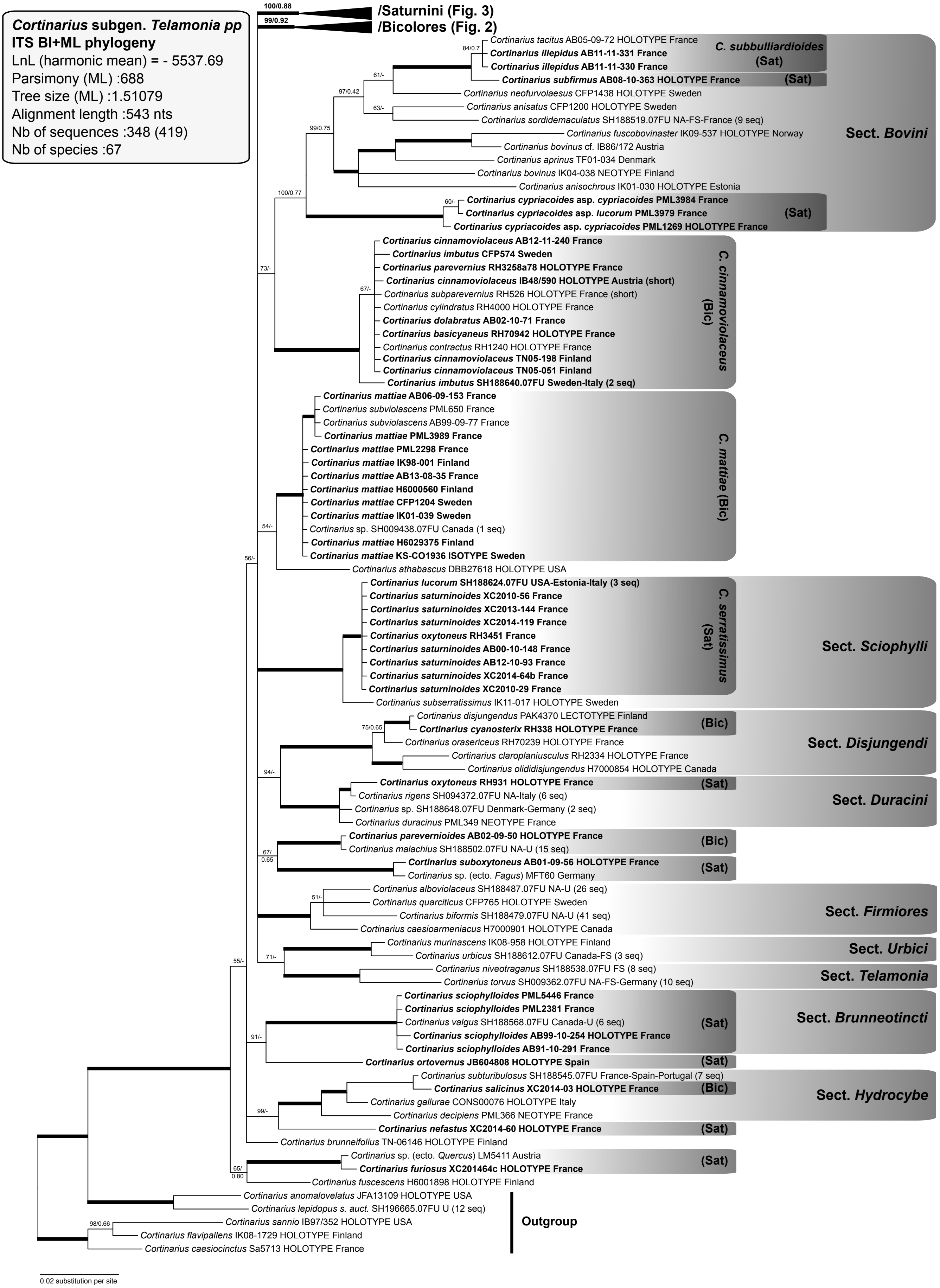

Fig. 1 Sections *Bicolores* and *Saturnini* within subg. *Telamonia*. — Bayesian 50 % majority-rule consensus tree inferred from the analysis of 348 ITS sequences (419 represented, due to Species Hypotheses, see Material and Methods) spanning subg. *Telamonia* plus 5 outgroup sequences, with collapse 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).

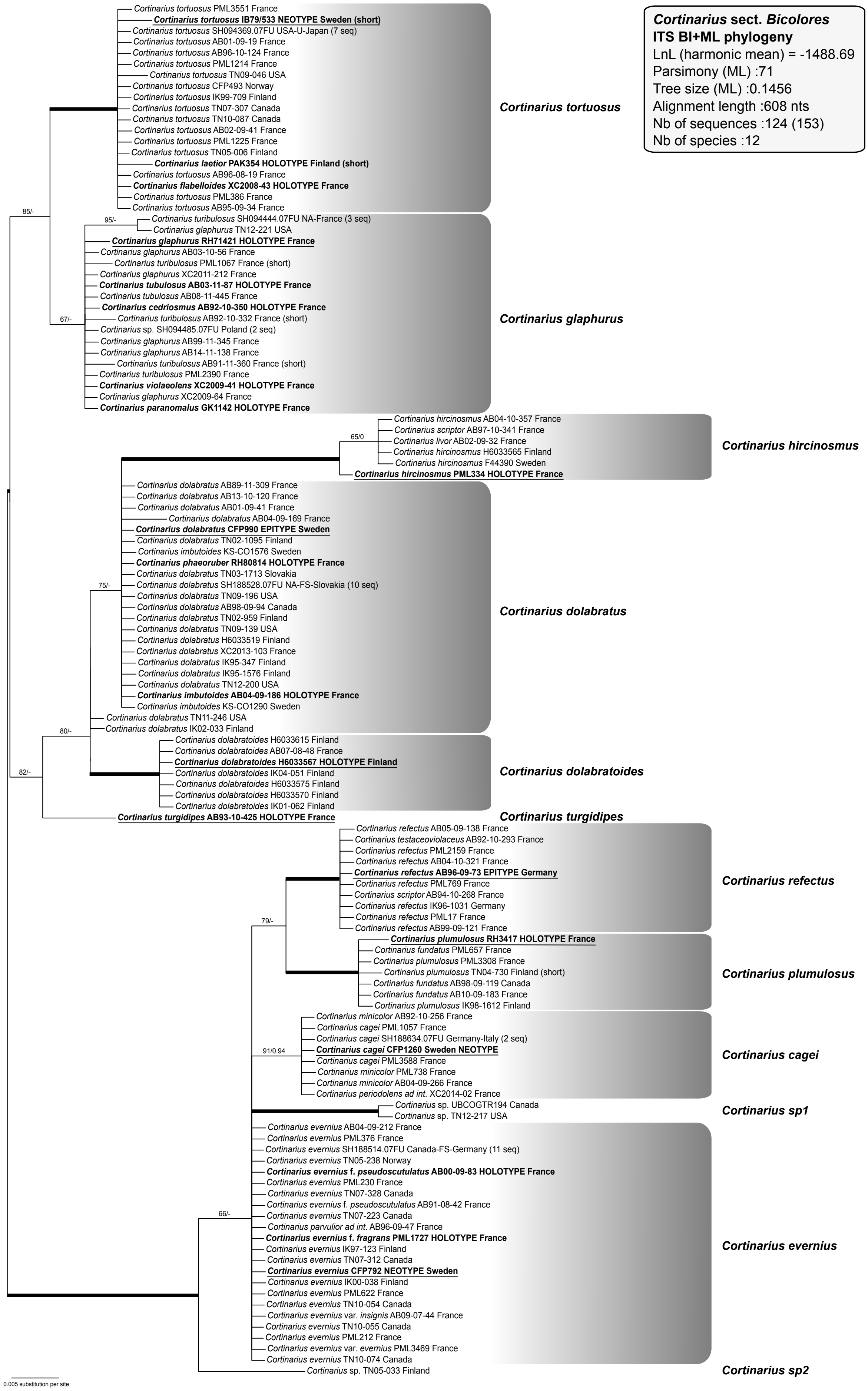

Fig. 2 The morphogenetic *Bicolores* section. — Bayesian 50 % majority-rule consensus tree inferred from the analysis of the ITS sequence of 124 (153 represented, due to Species Hypotheses, see Material and Methods) *Telamonia* sequences nested in /Bicolores. Branches with strong statistical support (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 **bold**, those having nomenclatural priority are further underlined.

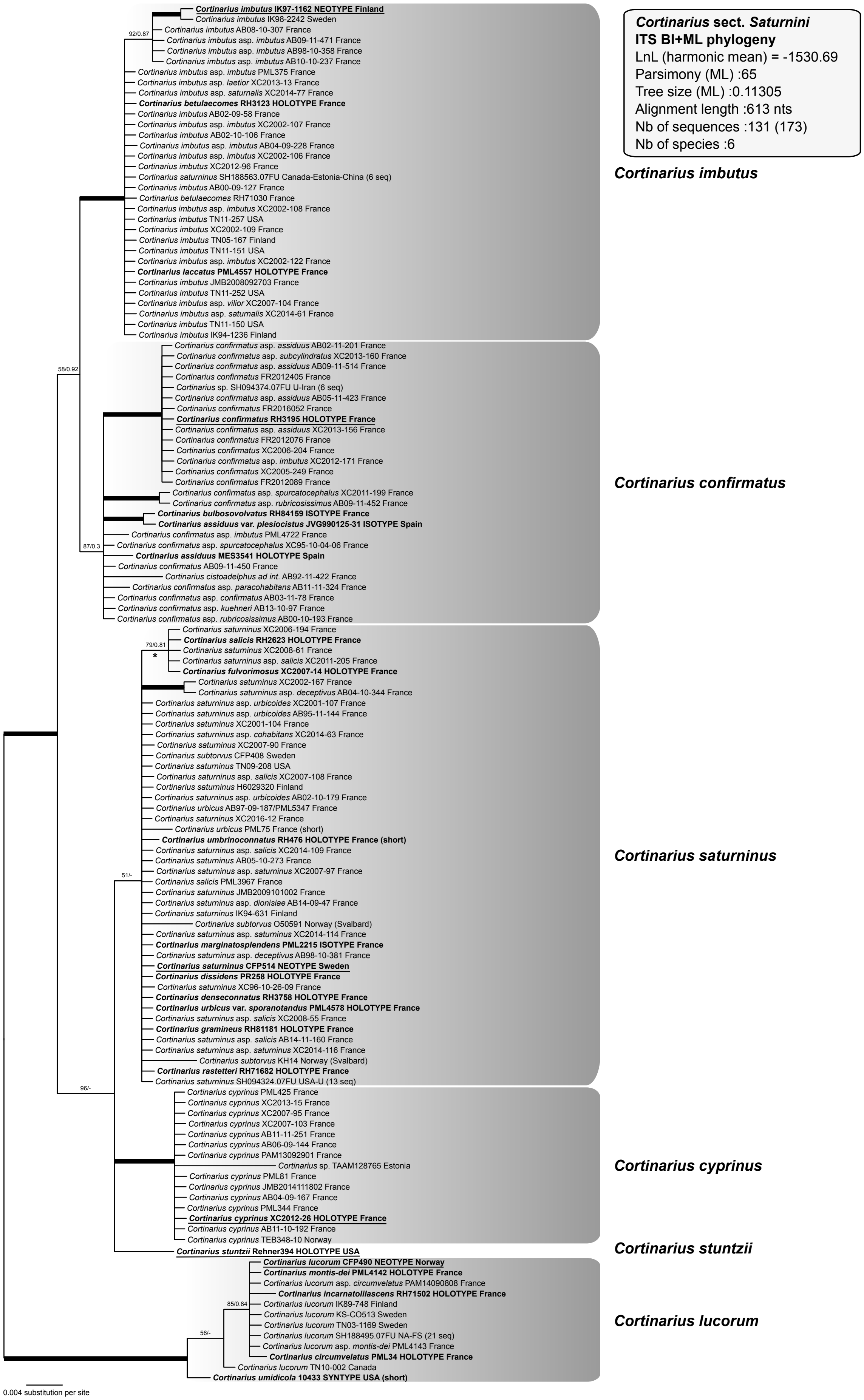

Fig. 3 The morphogenetic *Saturnini* section. — Bayesian 50 % majority-rule consensus tree inferred from the analysis of the ITS sequence of 131 (173 represented, due to Species Hypotheses, see Material and Methods) *Telamonia* sequences nested in /Saturnini. Branches with strong statistical support (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 2011-205 (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[a]	Odour(s)[b]	L min	Av L	L max	I min	Av I	I max	Av Q	Reported host[c,d]	D_{intra} max / difference rate (incl. indels)[a]	D_{inter} min / difference rate (incl. indels)[c]
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
Sect. *Bicolores*												
C. cagei	+	**0**, **r**, e, I	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. dolabratoides 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. dolabratoides) / 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*, *Picea*, *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 nts / 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. turgidipes	(–)	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	0 nt / 0 %	**8 nts + 4 indels (to *C. evernius*) / 2 %**
C. sp2	na	na	na	na	na	na	na	na	na	na	na	**8 nts + 4 indels (to C. evernius) / 2 %**
Sect. *Saturnini*												
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*, *Picea*	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 % (7 nts + 3 indels / 1.6 %)	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.

[a] Brackets mark uncertainty because of single collections (column 'Blue hues') or lack of available trace files for public sequences (column 'D_{intra} max').

[b] 0 = odourless; b = burnt keratin; ca = camphorated; ce = cedar wood; co = coconut; e = earth-like; g = grass-like; i = iodine; p = plum; r = radish. Upper/lower case relates to odour intensity. **Bold** indicates the most frequent odour.

[c] **Bold** indicates proven interaction (ectomycorrhizal sequences, column 'Reported host') or species with D_{inter} min > D_{intra} max (column D_{inter} min).

[d] 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. dolabratoides* 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. *Saturnini* 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 basicyaneus* Rob. Henry & Trescol ex Bidaud & Eyssart., Bull. Semestriel Féd. Assoc. Mycol. Méditerranéennes 25: 38. 2004.
= *Cortinarius contractus* Rob. Henry, Doc. Mycol. 16, 61: 27. 1985.
= *Cortinarius cylindratus* 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. Anal. Champ. Sup.: 303. 1953, nom. inval. (no diagnosis, no type designated)].

Type. Austria, Tirol, near Hötting, in mixed forest, 18 Sept. 1948, *M. Moser*, IB *48/590*, holotype. MycoBank MBT#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 *Duracini*. In addition, the /C. cinnamoviolaceus clade here delineated sheds new lights on the intricate links between these two sections and sect. *Saturnini* (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 *Duracini* concepts – *C. subparevernius*, *C. cylindratus* and *C. contractus*;
iii. a species defined by its author as intermediate between these two sections – *C. basicyaneus;*
iv. a *Duracini* concept hiding a phylogenetic *Bicolores* – *C. dolabratus*; and
v. a *Saturnini* 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 *Duracini* 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, fruiting 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 '1988', sensu Bidaud et al. (2014).
[= *Cortinarius periodolens* Carteret & Reumaux *ad int.*, Atlas des Cortinaires XXII: f. 1417. 2014, nom. inval. (no diagnosis, no type designated)].

Type. Sweden, Gotland, Lummelunda, Prästänget, under broadleaf trees, 1 Oct. 1994, *T.E. Brandrud*, *H. Lindström*, *H. Marklund*, *S. Muskos* CFP1260, S, neotype designated here. MycoBank MBT#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

iii. there is so far no convincing candidate for the second *C. bicolor*, even though *C. plumulosus* has been postulated to represent that one by the authors of the *ADC* (cf. notes under *C. plumulosus*), we fix here the species in its primary concept through designating the sequenced CFP1260 collection of plate D48 to neotypify *C. cagei*.

In these new morphogenetic boundaries, *C. cagei* is described in the *ADC* under *C. minicolor*, an obvious lookalike that, however, fruits under coniferous trees. Unfortunately, the holotype of *C. minicolor* could not be located in PC, preventing phylogenetic placement of the species within /Bicolores. *Cortinarius cagei* also includes *C. periodolens*, a *Bicolores* species described *ad interim* in the *ADC*, as a *C. obtusus* with violaceous stipe and strong iodine smell. Phylogenetically, *C. cagei* is well resolved due to the absence of any intraspecific sequence polymorphism and of a minimal distance to its sister species *C. evernius* of 3 substitutions plus 3 indels (Table 3). In the field, confusions are possible with *C. refectus* and *C. plumulosus* but spore shape ratios and host trees of the three species should prevent misidentification (Table 3).

Cortinarius dolabratoides 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, Koillismaa, Taivalkoski, Loukusa, the nature reserve of Loukusanharju, dry *Pinus* forest on the esker, with some *Picea* and *Betula*, some *Picea*-dominated depressions, 30 Aug. 2008, *I. Kytövuori* 08-465, H:6033567 (holotype H; isotype K). ITS sequence deposited in GenBank under KX964302.

Pileus 2–7 cm, conical when young, later expanding to plain with a distinct button-like umbo, clay brown to purplish brown, hygrophanous. *Lamellae* moderately distant, strongly emarginate, at first bluish then brown. *Stipe* 5–12 cm cylindrical to weakly clavate, sometimes slightly routing, white, with pale lavender blue top. *Veil* white, as a thin coating or obscure bands or patches on the stipe. *Context* whitish to purplish in the pileus, watery whitish bluish in the stipe. *Exsiccated* pileus dark blackish greyish brown, stipe much paler. *Smell* weakly grass-like or stronger, of cedar wood. *Macrochemistry* (on the context of the French collection only): Gaïac: ++; phénolaniline: +++; FMP: +++; AgNO3: 0. *Spores* 7–*8.3*–9.5 × 3.5–*4.6*–5.0 µm, Q = 1.68–*1.82*–1.96, (250 spores, 7 specimens), narrowly fusoid (to almost cylindrical), with a low suprahilar depression, often somewhat elongated at apex, fairly finely, densely verrucose, often prominently more strongly at the very apex, somewhat dark-coloured, faintly dextrinoid. *Lamellar trama hyphae* pale olive brownish, smooth to very finely densely scabrous. *Basidia* distinctly darker, olive brown (in MLZ). In damp to dryish boreal or alpine *Picea abies* forests, sometimes in dry *Pinus sylvestris*-dominated forests mixed by *Picea abies*.

Distribution — Fairly poorly known, but considered occasional.

Other specimens examined (sequenced collections marked with an asterisk, see Table 2 for GenBank accession numbers). Finland, Varsinais-Suomi, Kisko, Kaukuri, mesic *Picea* forest, 16 Aug. 2000, *T. Niskanen* & *I. Kytövuori*, H:*6033518*; Etelä-Häme, Juupajoki, Hyytiälä, mesic *Picea* forest, 18 Aug. 2004, *I. Kytövuori* H:*6033615**; Virrat, Monoskylä, Korpijärvi E, mesic *Picea* forest, 15 Oct. 2001, *I. Kytövuori* 01-062*, H; Pohjois-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*; Koillismaa, 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, cespitose 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. dolabratoides* is reminiscent of its sister phylogenetic species *C. dolabratus*. Fortunately, the two species can be distinguished microscopically, *C. dolabratoides* 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. dolabratoides* 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).

Fig. 4 *Cortinarius dolabratoides* sp. nov. — a. In situ photograph of the French collection *A. Bidaud* 07-08-48; b. sporogram of the holotype collection H:6033567; c. sporogram of the *C. dolabratus* collection *T. Niskanen* 02-959 (for comparison purposes). — Scale bars: a = 5 cm; b–c = 10 µm.

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, Håsjö, 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 KX964309.

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*.

(3 substitutions, Table 3) but it should be considered with respect to its wide biogeographical distribution and thorough sampling (23 sequences analysed, Fig. 2). Its sister species, *C. dolabratoides*, is distant by 3 substitutions (Table 3). *Cortinarius dolabratus* and *C. cinnamoviolaceus* share similar ecological niches and can both produce basidiomata with or without blue hues. Fortunately, the distinction of the species is usually fairly easy – the latter has a strong smell of radish, its spores are, on average, larger than those of *C. dolabratus*, and it is often also more robust than *C. dolabratus* (Table 3). *Cortinarius cinnamoviolaceus* has so far been only found in Europe whereas *C. dolabratus* displays a wide distribution extending to western North America.

Cortinarius evernius (Fr.) Fr., Epicr. Syst. Mycol.: 294. 1838 — MycoBank MB#233378

Basionym. ≡ *Agaricus evernius* Fr., Observ. Mycol. 2: 79. 1818: sanctioned in Fr., Syst. Mycol. 1: 212. 1821.

≡ *Hydrocybe evernia* (Fr.) M.M. Moser, Kleine Kryptogamenflora von Mitteleuropa II: 161. 1953.

≡ *Telamonia evernia* (Fr.) Ricken, Die Blätterpilze. 1915.

= *Cortinarius evernius* f. *fragrans* M.M. Moser ex Bidaud & Carteret, Atlas des Cortinaires XXII: 1887. 2014.

= *Cortinarius evernius* f. *pseudoscutulatus* Rob. Henry ex Bidaud & Reumaux, Atlas des Cortinaires XXII: 1887. 2014.

[= *Cortinarius evernius* var. *insignis* Fr., Atlas des Cortinaires XXII: f. 1405. 2014, nom. inval. (no diagnosis, no type designated)].

[= *Cortinarius parvulior* Bidaud *ad int.*, Atlas des Cortinaires XXII: f. 1418. 2014, nom. inval. (no diagnosis, no type designated)].

Type. Sweden, Ångermanland, Specksta, Härnösand, under coniferous trees, 22 Sept. 1988, *T.E. Brandrud*, *H. Lindström*, *H. Marklund*, *S. Muskos* CFP792, S, neotype designated in Cortinarius Flora Photographica I (French version), pl. A11 (1990), MycoBank MBT#372785. ITS sequence deposited in GenBank under KX964331.

Illustrations — Bidaud et al. 2014: pl. 946–949 but also pl. 959 (as *C. parvulior*); Brandrud et al. 1990: pl. A11.

Taxonomic descriptions — Bidaud et al. 2014: f. 1404–1407 but also f. 1418 (as *C. parvulior*); Niskanen et al. 2012: 863; Brandrud et al. 1990: pl. A11.

Notes — All contemporary authors seem to interpret this widespread Friesian species the same way and, not considering infraspecific taxa and species described *ad interim*, no later synonym of *C. evernius* has been introduced – however, older authors like Konrad and Henry misapplied the name to *C. cinnamoviolaceus* (see above). Phylogenetically, the species displays very low intraspecific polymorphism despite its wide biogeographical distribution (1 substitution plus one length polymorphism out of 22 available sequences) and is separated from its sister species *C. cagei* by 3 substitutions plus 3 length polymorphisms (Table 3). In Europe, the species may be confused only with *C. cinnamoviolaceus*, but the latter strongly smells of radish, has smaller spores and displays a much broader ecological range.

Cortinarius glaphurus Chevassut & Rob. Henry, Doc. Mycol. 12, 47: 78. 1982 — MycoBank MB#109708

= *Cortinarius tubulosus* Bidaud, Atlas des Cortinaires XXII: 1888. 2014.

= *Cortinarius cedriosmus* Bidaud, Atlas des Cortinaires XIX: 1510. 2010.

= *Cortinarius violaeolens* Carteret & Reumaux, Atlas des Cortinaires XIX: 1509. 2010.

= *Cortinarius paranomalus* Rob. Henry, Atlas des Cortinaires IV: 105. 1992.

– *Cortinarius turibulosus* (Jul. Schäff. & E. Horak) Bon & G. Garnier, Doc. Mycol. 21, 83: 10. 1991, sensu auct.

Type. France, Hérault, La Salvetat-sur-Agout, Lac de la Raviège, under *Picea*, cespitous, 29 Oct. 1978, *R. Henry* 71421, PC, holotype, MycoBank MBT#70172. ITS sequence deposited in GenBank under KX964352.

Illustrations — Bidaud et al. 2014: pl. 957 (as *C. tubulosus*); 2010: pl. 795 (as *C. turibulosus*), 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. turibulosus*); 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. turibulosus* sensu Bidaud et al. (2010). The protologue 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 nor isodiametric but often (always?) hollow, with or without blue pigments and with variable amounts of veil remnants that may form a membranous 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 species 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-Locc., 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.

Type. France, Haute-Savoie, Les Puisots, in *Picea* forest, elev. 700 m, 15 Sept. 1986, *P. Moënne-Loccoz* 334, PC, holotype, MycoBank MBT#101337. ITS sequence deposited in GenBank under KX964368.

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. *Hircini* because of the strong smell of *C. hircinus* and *C. camphoratus* 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 obviously unfortunate for an odourless 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).

Cortinarius plumulosus Rob. Henry, Bull. Soc. Mycol. France 93, 3: 362. 1977 — MycoBank MB#312090

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

Type. France, Vosges, Hennezel, in *Abies* forests, gregarious, 1972, *R. Henry* 3417, PC, holotype, MycoBank MBT#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. evernius* (7 substitutions plus 3 indels, Table 3). Morphologically, the species resembles *C. refectus* and *C. cagei* but the former produces ovoid spores (Av Q = 1.5), the latter fruits under deciduous trees and the cap of *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#560269; Fig. 5b–c

≡ *Cortinarius reflectus* 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. 377, f. 202 (1890), lectotype (iconotype) designated here (Fig. 5b), MycoBank MBT#373158. Germany, Lombach, in *Picea* and *Abies* forest, on calcareous soil, elev. 600 m, 24 Sept. 1996, *A. Bidaud* 96-09-73, epitype designated here (Fig. 5c), MycoBank MBT#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. Eine Anleitung zur Kenntniss derselben: 121. 1877.

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

= *Cortinarius laetior* P. Karst., Bidrag Kannedom Finlands Natur Folk 32: 387. 1879.

Type. Sweden, Smoland, Femsjö, 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 MBT#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. plumbosus* – 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. variecolor* 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 *Picea*, on granitic soil, subcespitose, 19 Oct. 1993, *A.* & *E. Bidaud*, AB 93-10-425, PC, holotype, MycoBank MBT#372786. 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, Moënne-Locc. & Reumaux, Doc. Mycol. 24, 95: 41. 1994.

≡ *Cortinarius* sect. *Firmiores* (Fr.) Henn., in Engler & Prantl, Naturl. Pfanzenf. I, 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 cespitose, 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 fulvorimosus* Carteret & Reumaux, Atlas des Cortinaires XVII, 1: 1178. 2008.

= *Cortinarius cohabitans* var. *urbicoides* Bidaud & Fillion, Bull. Soc. Mycol. France 119, 1–2: 70. 2004.

= *Cortinarius urbicus* var. *sporanotandus* Bidaud & Fillion, Atlas des Cortinaires XII: 695. 2002.

= *Cortinarius denseconnatus* Rob. Henry, Bull. Soc. Mycol. France 99, 1: 65. 1983.

= *Cortinarius gramineus* Rob. Henry, Bull. Soc. Mycol. France 99, 1: 64. 1983.

= *Cortinarius rastetteri* Rob. Henry, Bull. Soc. Mycol. France 97, 3: 177. 1981.

= *Cortinarius dissidens* Reumaux, Bull. Soc. Mycol. France 96, 3: 356. 1980.

= *Cortinarius marginatosplendens* Reumaux, Bull. Soc. Mycol. France 96, 3: 356. 1980.

= *Cortinarius salicis* Rob. Henry, Bull. Soc. Mycol. France 93, 3: 364. 1977.

= *Cortinarius umbrinoconnatus* 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 bresadolae* Schulzer, Hedwigia 24, 4: 138. 1885, sensu Lamoure (1978).

– *Cortinarius cohabitans* P. Karst., Bidrag Kannedom Finlands 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 (*Corylus*, *Tilia*, *Quercus*), 17 Sept. 1986, *T.E. Brandrud*, *H. Lindström*, *H. Marklund*, *S. Muskos* CFP514, 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 CFP514 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. cohabitans*, 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_{intra} 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_{intra} 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 04-10-344 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 cespitose 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' *salicis*, 'aspect' *urbicoides* 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#818598 (var. *confirmatus*); MycoBank MB#818597 (var. *plesiocistus*)

= *Cortinarius assiduus* var. *plesiocistus* A. Ortega et al., Mycotaxon 101: 140. 2007.

= *Cortinarius assiduus* Mahiques, A. Ortega & Bidaud, Bull. Féd. Mycol. Dauphiné-Savoie 162: 42. 2001.

= *Cortinarius bulbosovolvatus* 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 spurcatocephalus* Carteret *ad int.*, Atlas des Cortinaires XXIII: f. 1439. 2015, nom. inval. (no diagnosis, no type designated)].

[= *Cortinarius paracohabitans* Bidaud *ad int.*, Atlas des Cortinaires XXIII: f. 1437. 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 cistoadelphus* Bidaud *ad int.*, Bull. Féd. Assoc. Mycol. Méditerranéennes 6: 41 (1994), nom. inval. (no diagnosis, no type designated)].

– *Cortinarius cypriacus* Fr., Epicr. Syst. Mycol.: 307. 1838, sensu Consiglio (1999) non Moënne-Loccoz & Reumaux (1989).

Type. FRANCE, unknown locality and collection date, under *Quercus ilex*, *R. Henry* 3195, PC, holotype, MycoBank MBT#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, Vila & Bidaud in Ortega et al., Mycotaxon 101: 140. 2007. ITS sequence deposited in GenBank under AM713178.

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, caespitose 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 Eurasiatic belt. The clade displays the highest sequence variability within the section (D_{intra} 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. cistoadelphus* Bidaud *ad int.* (Fig. 3). The infraspecific rank should be favoured for such distal lineages because:

i. electing these subclades at the species level would leave 8 basal sequences unresolved, in paraphyletic relationships with the 3 recognized species;
ii. two of the resulting species would be totally cryptic, as none of the morphological, ecological or geographical features identified in the inclusive clade segregate into the two relevant subclades; and
iii. the third subclade, which overlaps with the cisticolous *C. assiduus* var. *plesiocistus* and *C. bulbosovolvatus*, has already been assigned a varietal rank, on morphogenetic bases (Ortega et al. 2007).

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* (A. Ortega, Vila & Bidaud) *comb. nov.* to accommodate the cisticolous populations. Future studies may unveil cryptic criteria to diagnose the two other subclades. When collected under meridional oaks or *Cistus* spp., *C. confirmatus* cannot be misidentified as one of the other *Saturnini* members, as none of the latter have so far been reported in the Mediterranean area. However, in more continental locations, especially in mixed deciduous forests, the species may co-occur with *C. saturninus*, *C. imbutus* and *C. cyprinus* and the risk of confusing these taxa is high. In this biome, *C. confirmatus* differs from its morphogenetic lookalikes by one of the following combinations of features:

i. absence of veil remnants on the stipe ***and*** not fruiting densely cespitose; or
ii. abundant veil remnants on the stipe ***and*** densely cespitose under *Populus alba* ('aspect' *paracohabitans*); or
iii. reddish hues on the cap ***and*** densely cespitose under *Betula pendula* ('aspect' *rubricosissimus*).

Cortinarius cyprinus Bidaud, Carteret & Reumaux, Atlas des Cortinaires XXIII: 1981. 2015 — MycoBank MB#815172

[= *Cortinarius saturninus* var. *bresadolae* M.M. Moser, Kleine Kryptogamenflora von Mitteleuropa II: 162. 1953, nom inval. (ined.)].

– *Cortinarius cypriacus* Fr., Epicr. Syst. Mycol.: 307. 1838, sensu Moënne-Loccoz & Reumaux (1989), non Consiglio (1999).

Type. France, Yvelines, Gambais, under deciduous trees, on calcareous soil, 3 Oct. 1993, *G. Redeuilh*, XC 2012-26, PC, holotype, MycoBank MBT#373189. ITS sequence deposited in GenBank under KX964463.

Illustration — Bidaud et al. 2015: pl. 973–976.

Taxonomic description — Bidaud et al. 2015, f. 1443.

Notes — This recently described species used to be called *C. saturninus* var. *bresadolae* or *C. cypriacus* 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.

Cortinarius imbutus Fr., Epicr. Syst. Mycol.: 306. 1838 — MycoBank MB#233557; Fig. 5d

= *Cortinarius laccatus* Reumaux, Bull. Soc. Mycol. France 98, 4: 348. 1982.

= *Cortinarius betulaecomes* Rob. Henry, Bull. Soc. Mycol. France 93, 3: 347. 1977.

[= *Cortinarius saturnalis* Reumaux *ad int.*, Atlas des Cortinaires XXIII: f. 1446. 2015, nom. inval. (no diagnosis, no type designated)].

Type. Finland, Perä-Pohjanmaa, Tornio, Arpela, Runteli, rich grass-herb spruce forest with deciduous bushes and some pines, slightly paludified depressions, calcareous ground, 10 Sept. 1997, *I. Kytövuori* 97-1162, H, neotype designated here, MycoBank MBT#373161 (Fig. 5d). ITS sequence deposited in GenBank under KX964498.

Illustrations — This study: Fig. 5d; Bidaud et al. 2015: pl. 976–982.

Taxonomic descriptions — Bidaud et al. 2015: f. 1445–1447.

Notes — The two major contemporary interpretations of *C. imbutus* are in marked contrast, as the *CFP* authors consider the species in sect. *Bicolores*, while those of the *ADC* place it in sect. *Saturnini*. The Friesian diagnosis of *C. imbutus* is, as often with old names, not precise enough to support a single, unequivocal interpretation. However, Fries described his species between *C. saturninus* and *C. cypriacus*, indicating that the original concept would be naturally placed in sect. *Saturnini*. Our work reveals that the French version of *C. imbutus* is one of the morphogenetic *Saturnini*, widely distributed across the northern hemisphere, whereas the *CFP* one corresponds to a blue-pigmented collection of *C. cinnamoviolaceus* (and is then conspecific with the French *C. dolabratus*, see notes under this species). We thus here stabilize the name in the revised sect. *Saturnini*, by neotypifying it with the sequenced IK97-1162 collection from Finland. Phylogenetically, *C. imbutus* is rather polymorphic at the ITS locus (D_{intra} max = 3 substitutions + 1 indel) and simultaneously very close from its closest species *C. confirmatus* (D_{inter} min = 3 nt changes, Table 3). Morphologically, *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 the 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* (gaïacol 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., Epicr. 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. Norway, Vestfold, Moss, Jelöy, under *Populus tremula*, 13 Sept. 1986, *T.E. Brandrud*, *H. Lindström*, *H. Marklund*, *S. Muskos* CFP490, S, neotype designated here, MycoBank MBT#373173. ITS sequence deposited in GenBank under KX964585.

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, sometimes name this species *C. umidicola*, even though the latter binomial has been originally 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 macromorphological or ecological features while oddly, their initial – pre-molecular – concept of *C. lucorum* does not belong to /Saturnini (cf. *C. cypriacoides* 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 ectomycorrhizal 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 D_{inter} min far exceeding D_{intra} 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. *Telamonia*, or even in subg. *Sericeocybe* – due to its low hygrophaneity – 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* . . . . *C. saturninus*
1\. Mediterranean thermophilic area, under *Quercus ilex* or *Cistus* spp. . . . . *C. confirmatus*
1\. Continental zone 2

2\. Coniferous trees 3
2\. Deciduous trees 20

3\. Acidic soils, in or near peatlands, *Picea* or *Abies* 4
3\. Dry to mesic acidic woodlands 6
3\. Basic to neutral, often calcareous woodlands 13

4\. Average spore length > 10 µm, blue tinges obvious, usually odourless . . . . *C. evernius*
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 . . . . *C. refectus*

7. Spores narrowly fusoid (Av Q > 1.8) and finely verrucose . . . . *C. dolabratoides*
7. Spores elongated (1.7 < Av Q < 1.8) and strongly verrucose . . . . *C. dolabratus*
7. Spores ellipsoid (Av Q = 1.6) and strongly verrucose . . . . *C. saturninus*

8. *Tsuga*, *Pseudotsuga* (North America) . . . . . . *C. lucorum*
8. *Picea*, *Abies*, *Pinus* (Europe) 9

9. Spores ovoid to ellipsoid (Av Q < 1.7) 10
9. More elongated spores (Av Q > 1.7) 11

10. Average spore size < 9 × 5.5 µm, smooth pileus . . . . *C. turgidipes*
10. Average spore size > 9 × 5.5 µm, fibrillose pileus . . . . *C. lucorum*

11. Average spore size < 9 × 5 µm . . . . *C. saturninus*
11. Average spore size > 9 × 5 µm 12

12. Average spore width < 5.5 µm, smooth pileus . . . . *C. glaphurus*
12. Average spore width ≥ 5.5 µm, pileus covered with flakes . . . . *C. plumulosus*

13. Cespitose 14
13. Not cespitose 16

14. Strong veil remnants on the stipe 15
14. Naked silky stipe . . . . *C. glaphurus*

15. Average spore length < 8 µm . . . . *C. saturninus*
15. Average spore length > 8 µm . . . . *C. confirmatus*

16. Average spore length < 9 µm . . . . *C. imbutus*
16. Average spore length ≥ 9 µm 17

17. Average spore width > 6 µm . . . . *C. refectus*
17. Average spore width < 6 µm 18

18. Average spore length > 9.5 µm, pileus covered with flakes . . . . *C. plumulosus*
18. Average spore length < 9.5 µm, smooth pileus 19

19. Smell of cedar wood . . . . *C. glaphurus*
19. Smell weak or different . . . . *C. hircinosmus*

20. Average spore width > 6 µm 21
20. 5 µm < average spore width < 6 µm 22
20. Average spore width ≤ 5 µm 24

21. Average spore length > 10.5 µm, *Salix*, USA . *C. stuntzii*
21. Average spore length < 10.5 µm, *Fagaceae*, Europe . . . . *C. refectus*

22. Spores elongated (1.7 < Av Q < 1.8), smell of cedar wood or Viola . . . . *C. glaphurus*
22. Spores ovoid to ellipsoid (Av Q ≤ 1.7), smell null or different 23

23. Stout basidiomata, average spore size > 9.5 × 5.7 µm, hygrophilous . . . . *C. lucorum*
23. Small to medium-size basidiomata, average spore size ≤ 9.5 × 5.7 µm . . . . *C. cagei*

24. Smell of cedar wood . . . . *C. dolabratus*
24. Smell null or different 25

25. Spores ovoid (Av Q ≤ 1.6) 26
25. Spores ellipsoid (1.6 < Av Q < 1.7), orange hues on the pileus . . . . *C. imbutus*
25. Spores elongated to subcyndrical (1.7 ≤ Av Q ≤ 1.9) . 27

26. Naked silky stipe . . . . *C. confirmatus*
26. Persistent veil remnants on the stipe . . . . *C. saturninus*

27. Densely cespitose 28
27. Gregarious or loosely cespitose 29

28. *Populus alba* . . . . *C. confirmatus*
28. Other deciduous trees, mostly *Salix* spp. . . *C. saturninus*

29. Persistent veil remnants on the stipe . . . . *C. imbutus*
29. Naked silky stipe 30

30. Average spore length < 8.3 µm . . . . *C. imbutus*
30. 8.3 µm < average spore length < 8.6 µm 31
30. Average spore length > 8.6 µm . . . . *C. confirmatus*

31. AgNO3: – . . . . *C. confirmatus*
31. AgNO3: + ... *C. cyprinus*

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 homoplasic 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 *Sciophylli*.

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. assiduus*, *C. denseconnatus*, *C. gramineus*, *C. imbutoides*, *C. phaeoruber*, *C. rastetteri*, *C. umbrinoconnatus*, and *C. cedriosmus*, *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. circumvelatus*, *C. fulvorimosus*, *C. parvulior* or *C. salicis* 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. saturninus* collections, and *C. deceptivus*, *C. incarnatolilascens*, *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 homoplasia. 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. *Sciophylli* (*C. saturninoides*), defined to accommodate very similar blue taxa, but more hygrophanous than genuine *Saturnini*, and revised sect. *Bovini* (*C. cypriacoides*, *C. illepidus* and *C. subfirmus*), 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. fulvorimosus*, 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. parevernius*, and *C. imbutus* sensu CFP), in traditional *Duracini* (*C. contractus*, *C. cylindratus*, *C. subparevernius* and *C. dolabratus* sensu *ADC*), or somewhere in between the two sections (*C. basicyaneus*). 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 epitypified in the revised sect. *Bicolores* despite the fact that all authors have initially 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*, *Clitocybe*, *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 delinate 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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