Persoonia 46, 2021: 188 – 215
www.ingentaconnect.com/content/nhn/pimj

RESEARCH ARTICLE

ISSN (Online) 1878-9080
https://doi.org/10.3767/persoonia.2021.46.07

Cortinarius subgenus *Leprocybe* in Europe: expanded Sanger and Next Generation Sequencing unveil unexpected diversity in the Mediterranean

A. Bidaud[1], M. Loizides[2], F. Armada[3], J. de Dios Reyes[4], X. Carteret[5], G. Corriol[6],
G. Consiglio[7], P. Reumaux[8], J.-M. Bellanger[9,*]

Key words

Cedrus brevifolia
endemism
phylogeny
taxonomy
Veneti

Abstract Molecular phylogenies in the past decade have demonstrated that the described diversity of *Cortinarius* is still underestimated, especially outside continental and boreal ecoregions where the genus has been historically investigated. We tackled this issue by revisiting the so far unresolved subgenus *Leprocybe*, and focused on the largely unexplored Mediterranean hotspot of biodiversity. The sequencing and phylogenetic analysis of 161 vouchered collections from Austria, Cyprus, France, Germany, Italy and Spain, including 16 types, allowed for the delineation of 11 species in this lineage, three of them recognised as new to science and formally introduced as *C. jimenezianus*, *C. selinolens* and *C. viridans* spp. nov., respectively. Interestingly, the newly described species exhibit a strict Mediterranean distribution, and one of them is putatively endemic to the island of Cyprus, highlighting the remarkable potential of this neglected ecoregion to uncover further undescribed diversity of *Cortinarius* in the future. The present work also unveils 23 synonymies in this subgenus, as well as previously undetected crypticism within *C. venetus*. Next Generation Sequencing carried out on three old and contaminated holotypes, successfully decrypts their phylogenetic identity, including that of *C. leproleptopus*, finally settling the long-standing controversy over the taxonomic status of this species. A brief overview of each species in the subgenus is lastly provided and a key is proposed to facilitate the identification of presently known European taxa of *Leprocybe* in the field.

Citation: Bidaud A, Loizides M, Armada F, et al. 2021. Cortinarius subgenus Leprocybe in Europe: expanded Sanger and Next Generation Sequencing unveil unexpected diversity in the Mediterranean. Persoonia 46: 188 – 215. https://doi.org/10.3767/persoonia.2021.46.07.
Effectively published online: 27 May 2021 [Received: 6 May 2020; Accepted: 1 December 2020].

INTRODUCTION

Cortinarius is the largest genus of macrofungi in the order Agaricales, widely distributed in the Holarctic and Austral realms (Tedersoo & Nara 2010, Garnica et al. 2016, Soop et al. 2019a). Over 4 500 species names of *Cortinarius* have been published to date, mostly from Europe and North America (http://www.catalogueoflife.org, http://www.mycobank.org, accessed 31 Oct. 2019). However, many of these appear to be synonyms, while the phylogenetic and taxonomic relationships within many groups are still poorly understood, and the number of taxa in the genus is expected to significantly increase in the coming years (Garnica et al. 2016, Soop et al. 2019a). As ectomycorrhizal (EcM) symbionts, *Cortinarius* species are integral components of woodland ecosystems, enhancing plant productivity and facilitating the cycling of vital nutrients such as nitrates and phosphates (Smith & Read 2010, Bödeker et al. 2014, Martin et al. 2016, Pellitier & Zak 2017). Most frequently reported tree-hosts are members of the *Fagaceae*, *Pinaceae* and *Salicaceae*, but several *Cortinarius* taxa are also associated with sclerophyllous shrubs of the *Cistaceae* family, most notably *Cistus* (Henry & Contu 1986, Comandini et al. 2006, Vila & Llimona 2006, Loizides 2016) and *Helianthemum* (Cheype 2014, Liimatainen & Ainsworth 2018).

In spite of some noteworthy systematic advances in recent years, our knowledge of species diversity in *Cortinarius* remains incomplete and many sections that have been historically defined based on morphological or biochemical taxonomic criteria, have yet to be phylogenetically revised (Niskanen et al. 2012, Soop et al. 2019a). European monographic treatments of the genus have traditionally focussed on continental and northern European ecoregions, and species from southern European/Mediterranean regions have been for the most part poorly represented. Nevertheless, a number of studies and some notable pioneers from France, Italy and Spain (e.g., Chevassut & Henry 1975, Chevassut & Trescol 1986, Ortega & Mahiques 1995, Consiglio & Moënne-Loccoz 2004), have significantly contributed to documenting the diversity of Mediterranean cortinarii in regional bulletins. Among several novelties introduced from the Mediterranean, many were later included in two major monographs, the *Atlas des Cortinaires* (*ADC*), published as 24 '*Pars*' between 1990 and 2017 (e.g., Moënne-Loccoz & Reumaux 1990, Bidaud et al. 2017) and *Il Genere Cortinarius in Italia* published as 6 '*parte*' between 2003 and 2012 (e.g., Consiglio et al. 2003, Consiglio 2012).

---

[1] 2436, route de Brailles, F-38510 Vézeronce-Curtin, France.
[2] P.O. Box 58499, Limassol 3734, Cyprus.
[3] 203, montée St Mamert le haut, 38138 Les Côtes d'Arey, France.
[4] Pº Virgen de Linarejos 6, 23700 Linares, Spain.
[5] 68, rue Alexis Maneyrol, F-92370 Chaville, France.
[6] Conservatoire botanique national des Pyrénées et de Midi-Pyrénées et Herbier BBF, Vallon de Salut, BP 315 F-65203 Bagnères-de-Bigorre Cedex, France.
[7] Associazione Micologica Bresadola, Trento, Italy.
[8] 84, avenue de Wagram, F-75017 Paris, France.
[9] CEFE, CNRS, Univ. Montpellier, EPHE, IRD, INSERM, 1919, route de Mende, F-34293 Montpellier Cedex 5, France;
corresponding author e-mail: jean-michel.bellanger@cefe.cnrs.fr.

Table 1 *Cortinarius* species classified in subg. *Leprocybe* (= sect. *Veneti*) by the main European authors.

This study	Niskanen & Kytövuori (2012)*	Bidaud et al. (2005)	Consiglio et al. (2003, 2004, 2006)	Moser (1969)
Cortinarius cotoneus	***C. cotoneus***	***C. conopus,*** *C. cotoneus*, ***C. cotoneus* var. *mellinoides, C. perannulatus, C. psittacinus* p.p., *C. subnotatus***	*C. cotoneus* p.p. ?	***C. cotoneus, C. subannulatus***
C. jimenezianus sp. nov.	absent	absent	absent	absent
C. leproleptopus	absent	***C. leproleptopus***, *C. leptopus*, ***C. melleifolius* var. *basiluteus* p.p., *C. psittacinus* p.p.**	***C. leproleptopus***	***C. mellinus* p.p.**, *C. psittacinus* p.p. ?
C. melanotus	*C. melanotus*	***C. colymbadinus, C. melanotus, C. submelanotus, C. zonatus***	*C. melanotus*	*C. melanotus*
C. pescolanensis	absent	***C. argyrocognitus, C. junquilleovestitus, C. mellinus, C. psittacinus* p.p.**	absent	*C. mellinus* p.p.
C. phrygianus	***C. phrygianus***	***C. phrygianus* (sect. *Pholidei*)**	absent	*C. phrygianus*
C. selinolens sp. nov.	absent	absent	absent	absent
C. squamivenetus	absent	absent	absent	absent
C. subcotoneus	absent	***C. borealis, C. melleifolius var. basiluteus*** p.p., ***C. subcotoneus, C. xantholamellatus***	*C. cotoneus* p.p. ?	*C. sublanatus* ss Fries ?
C. venetus	***C. venetus***	***C.* cf. *nothoraphanoides*, *C. pseudovenetus*, *C. venetus*, *C. venetus* var. *viridis***	*C. venetus*	***C. nothoraphanoides, C. venetus***
C. viridans sp. nov.	absent	absent	absent	absent

* includes Brandrud et al. 1990, 1991, 1994 and 1998. **Bold** names indicate sequenced species, p.p. = pro parte.

Still, perhaps with the exception of some impressive fleshy species belonging to subg. *Phlegmacium*, the Mediterranean basin has not been as thoroughly investigated as other parts of the continent, despite the fact that this region is a well-known hotspot of biodiversity (Médail & Quézel 1997, Myers et al. 2000, Médail & Myers 2004).

More recently, a number of studies employed molecular tools to unveil overlooked diversity in Mediterranean cortinarii and test the phylogenetic autonomy of previously published species described on the basis of morphology (Ortega et al. 2008, Suárez-Santiago et al. 2009, Clericuzio et al. 2017, Bellanger et al. 2018, Mahiques et al. 2018, Soop et al. 2019b). In the present paper, we investigate subg. *Leprocybe* (= sect. *Veneti*), which includes species akin to *C. cotoneus* and *C. venetus*. Basidiomata in this group display dry and tomentose pilei cuticles with green-olivaceous to yellow-rusty tinges, subglobose to broadly ellipsoid warty spores, and unique UV-fluorescent pigments known as 'leprocybins' (Moser 1969, Brandrud et al. 1990, 1992, 1994, 1998, 2014, Consiglio et al. 2003, 2004, Bidaud et al. 2005, Niskanen & Kytövuori 2012). Currently, approx. 30 published names from Europe, North America and Costa Rica fit this circumscription and are thus included in this subgenus (Table 1, 2). Because some defining features are shared by *C. callisteus*, *C. limonius*, *C. orellanus* and other related taxa, a subg. *Leprocybe* in a broad sense was initially proposed by Moser (1969). However, phylogenetic studies have since indicated that such 'leprocyboid' fungi do not constitute a monophyletic arrangement and, taking into consideration the novelties from the southern hemisphere, this group is in need of an in-depth taxonomic revision (Peintner et al. 2004, Ammirati et al. 2012, Stensrud et al. 2014, Niskanen et al. 2016, Soop et al. 2019a).

Several *Leprocybe* have been reported from Mediterranean ecosystems, either as range-restricted specialists (e.g., *C. leproleptopus*, *C. subcotoneus*, *C. xantholamellatus*), or as biogeographically widespread species also present in other ecoregions (e.g., *C. cepistipes*, *C. cotoneus*, *C. melanotus*) (Favre & Moreau 2001, Bidaud et al. 2005). Extensive taxon sampling and phylogenetic assessment of concerned collections are nonetheless lacking, therefore the full range of intraspecific ecological plasticity, as well as diagnostic criteria between taxa, remain ambiguous. Being the first *Leprocybe* to be described from thermophilous Mediterranean *Quercus* woodlands, *Cortinarius leproleptopus* is one such case. This species has long been known as 'the Mediterranean *Leprocybe*' and was believed to be confined to Mediterranean and sub-Mediterranean ecoregions, occurring in exclusive association with evergreen oaks (Chevassut & Henry 1988, Consiglio et al. 2004, Bidaud et al. 2005). As a result, when slightly deviant collections outside the Mediterranean region were found, the new taxon *C. cepistipes* was controversially introduced to accommodate them (Favre & Moreau 2001), sparking a heated debate (Bidaud et al. 2005, Favre & Moreau 2006).

Resolving this taxonomic controversy through an in-depth phylogenetic analysis of a wide sampling of all concerned species, has been the starting point of the present study. Beyond this primary objective, we further aimed at phylogenetically revising the group by

1 obtaining informative sequences from as many European holotypes assigned to subg. *Leprocybe* as possible;
2 defining evolutionary limits and phylogenetic relationships among identified lineages;
3 clarifying the status of a number of Mediterranean collections not comfortably fitting the concepts of currently described taxa in the subgenus;

4. identifying reliable diagnostic traits to enable the recognition of phylogenetically confirmed species by morphological criteria; and
5. updating the ecology and biogeography for all concerned taxa.

Because type collections for a number of critical taxa in the subgenus are few decades old and not well preserved for DNA analyses, with some of them contaminated by parasitic moulds, we further sought to evaluate whether Next Generation Sequencing (NGS), including metabarcoding/Illumina methodology, could provide an alternative to conventional Sanger sequencing in resolving old holotypes. This promising approach has been successfully applied to yield DNA barcodes from century-old type specimens of insects (Prosser et al. 2015), and its application was more recently validated in Ascomycota (Forin et al. 2018). However, the latter study did not include type material so, prior to the present work, no study has been published using NGS to barcode nomenclaturally-linked material in higher fungi.

MATERIALS AND METHODS

Taxon sampling

For the purpose of this study, we assembled and sequenced a dataset of 161 vouchered specimens from Austria, Cyprus, France, Germany, Italy, Spain and Tunisia, including 16 *Typus* samples and 37 collections previously published in the *Atlas des Cortinaires* (Bidaud et al. 2005). Together with 56 sequences selected from GenBank and UNITE, our dataset encompasses 217 ITS sequences overall, including 11 sequences selected as outgroup. Information on these collections and the GenBank accessions of their sequences are provided in Table 2. Herbaria abbreviations follow Index Herbariorum [constantly updated] (http://sweetgum.nybg.org/science/ih/).

Morphological studies

Freshly collected basidiomata were photographed *in situ* and the habitat, altitude, soil characteristics and nearby trees and shrubs were documented. Detailed observations on the size, colour and odour were made on fresh material and at least one basidioma from each collection was longitudinally sectioned to observe context colour. Basidioma slenderness was assessed, using the ratio S = , adapted from Kuyper (1986). When S < 4, we deduced that the habitus of the mushroom was often qualified as stout. Additional macromorphological characters were observed on both fresh and dehydrated material. Potassium hydroxide (KOH), silver nitrate ($AgNO_3$), gaïacol (Gaiac), phenolaniline, Tl4 and metol, were applied to test possible colour changes on the pileus, context and stipe. Colours are coded according to Séguy (1936, 'Ség.') and Cailleux (1981, 'Caill.'). Micro-anatomical features were studied in water (fresh material) or in KOH 5 % (exsiccatae), at ×400 and ×1000 magnifications, under a trinocular Leitz Ortholux II, an Infinity plan achromatic trinocular, and an Olympus CH-2 research, microscopes. Spore measurements were obtained from naturally discharged spores on a glass slide, or spores deposited on the cortina or the apex of the stipe (fresh material). When fresh material was not available, spores were studied and measured from dried lamellae (exsiccata), always mounted in water. A minimum of 30 mature spores were measured from each basidioma and the median spore quotient (Qm) was calculated. For each new species, a sporogram was produced, following methods and art style applied in the *Atlas des Cortinaires* (Bidaud et al. 2005). To better observe and image detailed epispore ornamentation, spores from the novel taxa proposed in this work were coated with gold in a sputter coater (Quorum Q150R S Plus) and subsequently examined under a Hitachi S-3000-N scanning electron microscope (SEM), with photographs taken at 15 kV (Y. Ruiz, Real Jardin Botánico, Madrid, Spain).

DNA extraction, amplification and Sanger sequencing

DNA extraction and PCR amplification were conducted with the REDExtract-N-Amp^{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 primers ITS-1F, ITS-4b, ITS-4, ITS-2 and ITS-3 (White et al. 1990, Gardes & Bruns 1993), as described in Liimatainen et al. (2017). Amplicons were purified and sequenced by Eurofins Genomics, Ebersberg, Germany. Raw sequence data were edited and assembled with Codon Code Aligner v. 4.1.1 (CodonCode Corp., Centerville, MA, USA) and deposited in GenBank under the accession numbers indicated in Table 2.

Phylogenetic analyses

Phylogenetic analyses were all performed online at www.phylogeny.fr (Dereeper et al. 2008) and on the CIPRES Science Gateway (www.phylo.org/index.php/). Multiple sequence alignment was carried out with MUSCLE v. 3.7 (Edgar 2004). Maximum likelihood (ML) phylogenetic analyses were performed with PhyML v. 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 (BI) of phylogeny was performed using MrBayes v. 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). Tree and parameters were sampled every 1 000 generations (1 000 trees). The initial burn-in was set to 25 % (250 trees). Branch support was assessed by Bayesian posterior probabilities (BPP). Trees were built using FigTree v. 1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/) and edited with Inkscape v. 0.91 (https://inkscape.org/fr/).

Illumina sequencing and dataset analysis

Amplicon libraries from R. Henry 3412 (holotype of *Cortinarius pseudovenetus*), R. Henry 84.109 (holotype of *Cortinarius leproleptopus*) and PML 5410 (holotype of *Cortinarius xantholamellatus*) were prepared in two steps. A first PCR reaction was conducted as described in Liimatainen et al. (2017) but with the Phusion^{tm} polymerase, on one microliter of extract prepared with solutions E and D of the REDExtract-N-Amp^{tm} Plant PCR Kit (Sigma-Aldrich, St. Louis, MO, USA), with primers ITS3 and ITS4 (White et al. 1990) modified by the addition in 5' of the following linkers: TCGTCGGCAGCGTCAGATGTGTATAAGAGACAG and GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAG, respectively. A second PCR reaction (10 cycles), priming on these linkers, introduced Illumina adapters and sample-specific short indices. Libraries were then sequenced on a MiSeq analyser, at the GenSeq platform of the Labex CeMEB (Montpellier). Because the expected size of the target amplicon is ~400 nucleotides, a 2 × 250 nt paired-end strategy has been adopted to ensure a sufficient overlap (~100 nt) of most forward and reverse reads. More than 12 000 reads were generated for each sample, from both amplicon ends. After an automated quality-filtering step performed by the Illumina software, forward and reverse reads were imported in CodonCode Aligner v. 4.1.1 for further processing. Firstly, reads shorter than 150 nt were discarded. Secondly, full-length sequences were assembled

Table 2 Material included in the phylogenetic analysis.

GenBankSpecies	Voucher Id	Leg	Collection date	Putative host tree	Country	Locality	GenBank ITS*
Cortinarius atkinseae	TENN071879 (holotype)	R.M. Atkins & P.B. Matheny	18/09/2017	*Fagus*, *Quercus*, *Carya*	USA	Tennessee	MG663233
Cortinarius aureopigmentatus	JFA 11940	R. Halling & J.F. Ammirati	07/06/1996	*Quercus*	Costa Rica	San José	EF420140
Cortinarius clandestinus	JMB165	J.M. Birkebak	01/05/2004	*Pseudotsuga*, *Tsuga*	USA	Washington	FJ717551
Cortinarius cotoneus	PML 5260 (holotype of *C. cotoneus* var. *mellinoides*)	G. Redeuilh	07/10/1994	*Broadleaved trees*	France	Yvelines	**MW010117**
	PML 5429 (holotype of *C. perannulatus*)	J. Cavet	14/08/1994	*Fagus*, *Abies*	France	Isère	**MW010116**
	HMAS260331	NA	NA	NA	China	NA	KX513578
	HMAS254210	NA	NA	NA	China	NA	KX513580
	QL060 (ecto.)	NA	NA	*Quercus*	China	NA	HM105543
	ZWL560 (ecto.)	NA	NA	*Quercus*	China	Shaanxi	KX444284
	TU105155	A. Kollom	24/08/2011	*Quercus*	Estonia	Harju	UDB015877
	AB 04-10-338 (as *C. subnotatus*)	G. Raffini	05/10/2004	*Fagus*	France	Ain	**MW010155**
	AB 06-09-61	A. Bidaud	01/09/2006	*Fagus*, *Carpinus*	France	Ain	**MW010160**
	AB 06-09-69	A. Bidaud	03/09/2006	*Picea*	France	Ain	**MW010161**
	AB 09-09-277	A. Bidaud & R. Fillion	29/09/2009	*Fagus*, *Quercus*	France	Ain	**MW010173**
	AB 11-08-49	A. Bidaud	07/08/2011	*Carpinus*, *Quercus*	France	Ain	**MW010175**
	AB 11-09-83	A. Bidaud	21/09/2011	*Carpinus*, *Quercus*	France	Ain	**MW010176**
	AB 11-10-206	A. Bidaud & R. Fillion	17/10/2011	*Fagus*, *Quercus*	France	Ain	**MW010177**
	AB 12-10-96	A. Bidaud	02/10/2012	*Carpinus*	France	Ain	**MW010179**
	AB 09-10-336	A. Bidaud	25/10/2009	*Carpinus*, *Quercus*	France	Côte-d'or	**MW010174**
	PML 5427 (as *C. conopus*)	A. Faurite-Gendron	06/10/1994	*Fagus*, *Abies*	France	Drôme	**MW010136**
	AB 06-10-223	A. Bidaud	10/10/2006	*Fagus*	France	Drôme	**MW010162**
	PML 5430 (as *C. subnotatus*)	A. Bidaud	21/10/1998	*Fagus*, *Pinus*	France	Hautes-Alpes	**MW010138**
	AB 04-09-81 (as *C. psittacinus*)	A. Bidaud & R. Fillion	05/09/2004	Broadleaved trees	France	Haute-Savoie	**MW010153**
	PML 5417 (as *C. conopus*)	A. Bidaud	13/10/1999	*Fagus*, *Abies*	France	Isère	**MW010132**
	AB 05-09-66	A. Bidaud	02/09/2005	*Fagus*, *Abies*	France	Isère	**MW010157**
	AB 05-10-241	A. Bidaud	04/10/2005	*Fagus*, *Abies*	France	Isère	**MW010159**
	JMB2013092505	J.-M. Bellanger	25/09/2013	*Abies*, *Fagus*	France	Isère	**MW010108**
	GS2	G. Saar	30/08/2004	*Picea*, *Abies*, *Pinus*	Germany	Baden-Würtemberg	**MW010093**
	GS3	G. Saar	17/09/2008	*Picea*, *Abies*, *Pinus*, *Fagus*	Germany	Baden-Würtemberg	**MW010094**
	GH20131018a	G. Hensel	18/10/2013	*Carpinus*	Germany	Saxony-Anhalt	**MW010083**
	GH20110930	G. Hensel	30/09/2011	*Corylus*	Germany	Saxony-Anhalt	**MW010086**
	GH20050820	G. Hensel	20/08/2005	*Quercus*, *Carpinus*	Germany	Saxony-Anhalt	**MW010087**
	MH4836-2	M. Huth	29/10/2009	*Quercus*, *Carpinus*	Germany	Saxony-Anhalt	**MW010091**
	GH20140811	G. Hensel	11/08/2014	*Carpinus*	Germany	Saxony-Anhalt	**MW010113**
	GH20140914	G. Hensel	14/09/2014	*Corylus*	Germany	Saxony-Anhalt	**MW010114**
	SSt01-100	G. Schmidt-Stohn	09/10/2001	*Fagus*	Germany	Schleswig-Holstein	**MW010080**
	Ir22 (ecto.)	NA	NA	Fagales	Iran	NA	FR852015
	ecto.	NA	NA	*Fagaceae*	Iran	Nowshahr	UDB005580
	IB19860257	M. Moser	20/09/1986	*Tilia*	Italy	Trento	UDB001029
	OS579	NA	NA	NA	Norway	Oslo	KC842423
Cortinarius flavifolius	TENN071880	A.M. Overholt	11/09/2017	*Pinus*, *Fagus*, *Quercus*, *Carya*	USA	Tennessee	MG663246
Cortinarius fuscoflavidus	ecto.	NA	NA	NA	Canada	British Columbia	UDB032444
	OSC 80195	NA	NA	NA	USA	Oregon	EU669233
	115-1 (ecto.)	NA	NA	*Pseudotsuga*	USA	Oregon	DQ365640
Cortinarius hugheseae	TENN:TLB11 (as *C. cotoneus*)	T.L. Bailey & P.B. Matheny	12/10/2015	*Pinus*, *Fagus*	USA	Tennessee	MF686506
Cortinarius jimenezianus	JA-CUSSTA 9402 (holotype)	F. Armada & J.D. Reyes	17/12/2018	*Cistus ladanifer*, *Q. ilex*	Spain	Jaén	**MW010204**
	JDRG26120401	J.D. Reyes	26/12/2004	*Cistus ladanifer*, *Pinus*	Spain	Jaén	**MW010205**
	AMI3777	A. Mateos Izquierdo	09/12/2014	*Cistus ladanifer*	Spain	Jaén	**MW010050**
	JDRG17121801/FA4792	F. Armada & J.D. Reyes	17/12/2018	*Cistus ladanifer*, *Q. ilex*	Spain	Jaén	**MW010195**

Table 2 (cont.)

GenBankSpecies	Voucher Id	Leg	Collection date	Putative host tree	Country	Locality	GenBank ITS*
Cortinarius leproleptopus	R. Henry 84.109 (holotype)	probably G. Chevassut	probably 1984	probably *Quercus*	France	probably Hérault	**MW010056**
	MCVE763/E.C. 94190 (epitype)	G. Consiglio & B. Bigazzi	09/10/1994	*Castanea*, *Q. pubescens*, *Fagus*, *Pinus*	Italy	Reggio Emilia	**MW010049**
	G00126720/AF-99-10-17CC (holotype of *C. cepistipes*)	A. Favre	17/10/1999	*Q. robur*	France	Haute-Savoie	**MW010197**
	AB 99-10-257 (paratype of *C. cepistipes*)	A. Bidaud	16/10/1999	*Quercus*	France	Ain	**MW010147**
	PAM00103106 (paratype of *C. cepistipes*)	J.-C. Hermite	31/10/2000	*Quercus*	France	Bouches-du-Rhône	**MW010052**
	PAM99101703 (paratype of *C. cepistipes*)	J.-C. Deïana, R. Fillion, P.-A. Moreau	17/10/1999	*Q. robur*, *Carpinus*	France	Haute-Savoie	**MW010187**
	PAM99111001 (paratype of *C. cepistipes*)	P.-A. Moreau	10/11/1999	*Q. ilex*, *Q. pubescens*	France	Var	**MW010188**
	ML21211CL	M. Loizides	01/12/2012	*Q. alnifolia*, *Pinus*, *Arbutus*	Cyprus	Mavro Dasos	**MW010208**
	AB 08-09-199	A. Bidaud	20/09/2008	*Quercus*, *Carpinus*	France	Ain	**MW010164**
	AB 03-11-81 (as *C. melleifolius* var. *basiluteus*)	A. Bidaud	05/11/2003	*Q. ilex*	France	Ardèche	**MW010151**
	AB 18-11-159	A. Bidaud	15/11/2018	*Q. ilex*	France	Ardèche	**MW010194**
	FR2312003	P.-A. Moreau	NA	NA	France	Bouches-du-Rhône	**MW010065**
	AB 08-09-215	A. Bidaud & F. Armada	22/09/2008	*Fagus*	France	Drôme	**MW010165**
	AB 08-10-320	A. Bidaud	17/10/2008	*Q. ilex*	France	Drôme	**MW010166**
	AB 08-10-395	A. Bidaud	31/10/2008	*Q. ilex*	France	Gard	**MW010171**
	PML 2949 (as *C. psittacinus*)	A. Bidaud & R. Fillion	30/09/1992	Broadleaved trees	France	Haute-Savoie	**MW010128**
	PML 5420	P. Bertéa	31/10/1999	*Quercus*	France	Hérault	**MW010133**
	JMB2010110201	J.-M. Bellanger	02/11/2010	*Q. ilex*	France	Hérault	**MW010207**
	OTU27 (ecto.)	E. Taschen & F. Richard	02/2011	*Q. ilex*	France	Pyrénées-Orientales	KM247711
	GE01-049	NA	13/10/2001	NA	France	Val-de-Marne	**MW010150**
	PAM99111002	P.-A. Moreau	10/11/1999	*Q. ilex*, *Q. pubescens*	France	Var	**MW010196**
	PML 5421	A. Bidaud & M. Heullant	02/11/1993	*Quercus*	France	Vaucluse	**MW010134**
	JMB2011112628	J.-M. Bellanger	26/11/2011	*Q. pubescens*, *Q. ilex*, *Pinus*	France	Vaucluse	**MW010068**
	JMB2011112629	J.-M. Bellanger	26/11/2011	*Q. pubescens*, *Q. ilex*, *Pinus*	France	Vaucluse	**MW010067**
	GS9	G. Saar	01/10/2012	*Fagus*	Germany	Baden-Würtemberg	**MW010100**
	SSt12-039	G. Saar	27/09/2012	*Fagus*	Germany	Bavaria	**MW010077**
	GH20140907	G. Hensel	07/09/2014	*Corylus*	Germany	Bavaria	**MW010112**
	GS1	G. Saar	27/09/2012	*Fagus*	Germany	Bavaria	**MW010092**
	GS4	G. Saar	26/09/2012	*Fagus*, *Carpinus*, *Quercus*	Germany	Bavaria	**MW010095**
	GS8	G. Saar	08/10/1998	*Fagus*	Germany	Bavaria	**MW010099**
	FR2014330	M. Huth	29/10/2009	*Quercus*, *Carpinus*	Germany	Saxony-Anhalt	**MW010053**
	FR2014332	M. Huth	14/10/2009	*Quercus*	Germany	Saxony-Anhalt	**MW010074**
	MH4835-4	M. Huth	12/10/2013	*Quercus*, *Carpinus*	Germany	Saxony-Anhalt	**MW010076**
	SSt13-173	G. Schmidt-Stohn	11/10/2013	*Carpinus*	Germany	Saxony-Anhalt	**MW010079**
	GH20091024	G. Hensel	24/10/2009	*Betula*, *Carpinus*	Germany	Saxony-Anhalt	**MW010085**
	GH20131018b	G. Hensel	18/10/2013	*Quercus*	Germany	Saxony-Anhalt	**MW010089**
	GH20140911b	G. Hensel	11/09/2014	*Carpinus*, *Quercus*	Germany	Saxony-Anhalt	**MW010115**
	ST40	S. Toninelli	11/10/2014	*Q. cerris*	Italy	Grosseto	**MW010181**
	IB19960212 (as *C. mellinus*)	M. Moser	06/10/1986	*Q. cerris*	Italy	Parma	UDB001105
	MES4373	R. Mahiques Santandreu	02/11/2007	*Q. ilex*	Spain	Alicante	**MW010048**
Cortinarius melanotus	PML 5454 (holotype of *C. submelanotus*)	B. Rainon	11/11/2000	Broadleaved trees	France	Rhône	**MW010120**
	XC2005-20 (holotype of *C. zonatus*)	P. Reumaux	24/10/2004	*Quercus*	France	Ardennes	**MW010121**
	PML 5461	A. Bidaud	27/10/1990	*Fagus*, *Carpinus*, *Castanea*, *Abies*	France	Ain	**MW010142**
	PML 5455 (as *C. perannulatus*)	A. Bidaud	01/11/1997	*Abies*, *Castanea*	France	Ain	**MW010141**
	AB 04-09-70	A. Faurite-Gendron	02/09/2004	*Abies*	France	Ain	**MW010152**
	AB 05-09-83	T. Trémont	04/09/2005	*Abies*	France	Ain	**MW010158**
	GC08101103	G. Corriol	11/10/2008	*Abies*	France	Aude	**MW010190**
	FR2019579	J.-M. Bellanger	10/11/2019	*Fagus*, *Quercus*, *Castanea*	France	Aveyron	**MW010200**
	FR2012264	NA	02/11/2012	NA	France	Gard	**MW010070**

Table 2 (cont.)

GenBankSpecies	Voucher Id	Leg	Collection date	Putative host tree	Country	Locality	GenBank ITS*
Cortinarius melanotus (cont.)	PAM19110411	N. Suberbielle & P.-A. Moreau	06/11/2019	*Q. suber*, *Pinus*, *Arbutus*	France	Haute-Corse	**MW010201**
	PML 5462 (as *C. submelanotus*)	P. Chapon	16/10/1997	*Abies*	France	Haute-Loire	**MW010143**
	GC13092202	G. Corriol	22/09/2013	*Fagus*, *Abies*	France	Hautes-Pyrénées	**MW010191**
	GC18102206	G. Corriol	22/10/2018	*Abies*	France	Hautes-Pyrénées	**MW010193**
	AB 06-10-254	A. Bidaud & A. Faurite-Gendron	13/10/2006	*Fagus*, *Picea*, *Pinus*	France	Isère	**MW010163**
	PML 5428 (as *C. colymbadinus*)	G. Delavenat	24/09/1999	*Abies*	France	Jura	**MW010137**
	PML 2344	P. Moënne-Loccoz	10/10/1991	*Fagus*, *Abies*	France	Savoie	**MW010125**
	GS10	G. Saar	29/09/2012	*Abies*	Germany	Baden-Würtemberg	**MW010101**
	GS12	G. Saar	01/11/2012	*Fagus*, *Quercus*	Germany	Baden-Würtemberg	**MW010103**
	GS14	G. Saar	08/10/2004	*Abies*, *Picea*, *Pinus*	Germany	Baden-Würtemberg	**MW010105**
	GS11	G. Saar	13/10/2013	*Fagus*, *Quercus*	Germany	Bavaria	**MW010102**
	GS5	G. Saar	07/10/1998	*Carpinus*, *Quercus*	Germany	North Rhine-Westphalia	**MW010096**
	MH4735-4	M. Huth	08/09/2006	*Quercus*	Germany	Saxony-Anhalt	**MW010073**
	FR2014334	M. Huth	29/10/2009	*Fagus*	Germany	Saxony-Anhalt	**MW010075**
	SSt10-253	G. Schmidt-Stohn	04/10/2010	*Quercus*, *Carpinus*	Germany	Saxony-Anhalt	**MW010078**
	JM281014	J. Mora Gómez	28/10/2014	*Pinus*, *Cistus*	Spain	Guadalajara	**MW010063**
	JA-CUSSTA 2774	L. Romero de la Osa	30/11/2002	*Q. suber*, *Castanea*, *Cistus*	Spain	Huelva	**MW010058**
Cortinarius parkeri	WTU:ADP000502-1 (holotype)	D. Parker	22/04/2013	Conifers	USA	Washington	JN976987
Cortinarius pescolanensis	MCVE29054 (holotype)	B. Picillo & M. Marchionni	14/10/2012	*Abies*, *Fagus*	Italy	Molise	NR_153070
	BP13/291 (isotype)	B. Picillo & M. Marchionni	14/10/2012	*Abies*, *Fagus*	Italy	Molise	KX010945
	PML 5448 (as *C. argyrocognitus ad int*)	A. Faurite-Gendron	06/10/1994	*Abies*, *Fagus*	France	Drôme	**MW010139**
	PML 5426 (as *C. junquilleovestitus ad int*)	T. Tremont	05/09/1999	*Abies*, *Picea*	France	Jura	**MW010135**
	PML 3262 (as *C. psittacinus*)	J. Garin	09/10/1992	*Abies*, *Fagus*, *Pinus*	France	Drôme	**MW010129**
	PML 5449 (as *C. mellinus*)	A. Bidaud	01/10/1995	*Abies*, *Fagus*	France	Isère	**MW010140**
	JMB2013092404	J.-M. Bellanger	24/09/2013	*Abies*, *Fagus*	France	Isère	**MW010107**
	JMB2013092503	J.-M. Bellanger	25/09/2013	*Abies*, *Fagus*	France	Isère	**MW010109**
	PAM02082506	P.-A. Moreau	25/08/2002	*Abies*, *Fagus*	France	Savoie	**MW010186**
	JB-8114/13	J. Ballarà	21/09/2013	*Abies*, *Fagus*, *Pinus*	Spain	Lérida	KY657256
Cortinarius phrygianus	TU105353	T. Ploompuu	27/09/2012	*Picea*, *Pinus*	Estonia	Lääne	UDB018645
	PML 5451/AB 97-10-332	G. Chamonaz	16/10/1997	*Picea*, *Pinus*	France	Ain	**MW010146**
	KS-CO584	K. Soop	10/09/1992	*Pinus*	Sweden	Dalarna	KJ421031
	AT2002139	A.F.S. Taylor	17/08/2002	*Picea*	Sweden	Västerbotten	UDB000688
Cortinarius selinolens	MPU1116858 (holotype)	A. Bidaud	31/10/2008	*Q. ilex*	France	Gard	**MW010172**
	AB 11-11-377/JMB2011112503	A. Bidaud & J.-M. Bellanger	25/11/2011	*Q. ilex*	France	Hérault	**MW010071**
	JDRG02121005	J.D. Reyes	02/12/2010	*Q. ilex*	Spain	Jaén	**MW010059**
	FR2013185	F. Richard	01/11/2010	*Arbutus*	Tunisia	Jendouba	**MW010072**
Cortinarius squamivenetus	H:TN 07-119 (holotype)	T. Niskanen, I. Kytövuori & K. Liimatainen	01/09/2007	*Picea*, *Pinus*, *Populus*	Finland	Koillismaa	KP114458
Cortinarius subcotoneus	PML 2143 (holotype)	A. Bidaud	09/11/1990	*Q. pubescens*	France	Drôme	**MW010122**
	PML 5412 (holotype of *C. borealis*)	C. Guyot	23/09/1993	*Q. pubescens*, *Carpinus*	France	Isère	**MW010119**
	PML 5410 (holotype of *C. xantholamellatus*)	C. Guyot	03/11/1990	*Q. pubescens*	France	Drôme	**MW010054**
	JLC001029-8 (as *C. melleifolius* var. *basiluteus*)	J.-L. Cheype	29/10/2000	*Q. ilex*, *Q. pubescens*	France	Alpes de Haute-Provence	**MW010149**
	AB 08-10-331	A. Bidaud	20/10/2018	*Q. ilex*	France	Ardèche	**MW010167**
	AB 08-10-387	A. Bidaud	27/10/2018	*Q. ilex*	France	Ardèche	**MW010168**
	AB 08-10-388	A. Bidaud	27/10/2018	*Q. ilex*	France	Ardèche	**MW010169**
	AB 08-10-394	E. Bidaud & G. Raffini	31/10/2018	*Q. ilex*	France	Gard	**MW010170**
	AB 99-11-324	P. Pellicier	01/11/1999	*Q. ilex*	France	Hérault	**MW010148**
	XC2013-109	T.E. Brandrud	22/10/2013	*Q. ilex*	France	Hérault	**MW010180**
	FR2012097	F. Richard	25/11/2011	*Q. ilex*, *Q. pubescens*	France	Hérault	**MW010051**

Table 2 (cont.)

GenBankSpecies	Voucher Id	Leg	Collection date	Putative host tree	Country	Locality	GenBank ITS*
Cortinarius subcotoneus (cont.)	SSt13-211	G. Schmidt-Stohn	23/10/2013	*Q. ilex*	France	Hérault	**MW010081**
	GH20131023	G. Hensel	23/10/2013	*Q. ilex*	France	Hérault	**MW010082**
	PML 5411	A. Bidaud	29/10/1992	*Q. ilex*	France	Vaucluse	**MW010131**
	JMB2011112632	J.-M. Bellanger	26/11/2011	*Q. pubescens*, *Q. ilex*, *Pinus*	France	Vaucluse	**MW010069**
	JMB2011112636	J.-M. Bellanger	26/11/2011	*Q. pubescens*, *Q. ilex*, *Pinus*	France	Vaucluse	**MW010066**
	GS7	G. Saar	16/10/2012	*Fagus*	Germany	Baden-Würtemberg	**MW010098**
	GS15	G. Saar	21/10/2012	*Fagus*, *Abies*	Germany	Baden-Würtemberg	**MW010106**
	TUB011826 (as *C. cotoneus*)	NA	NA	NA	Germany	NA	AY669597
	GH20100827	G. Hensel	27/08/2010	*Carpinus*	Germany	Saxony-Anhalt	**MW010088**
	GH20140911a	G. Hensel	11/09/2014	*Quercus*	Germany	Saxony-Anhalt	**MW010111**
	GS6	G. Saar	25/10/2012	*Fagus*, *Quercus*	Germany	Schleswig-Holstein	**MW010097**
	ST42	S. Toninelli	19/10/2014	*Q. ilex*	Italy	Grosseto	**MW010182**
	JDRG08120801	J.D. Reyes	08/12/2008	*Q. suber*, *Cistus ladanifer*	Spain	Jaén	**MW010060**
	JDRG17110810	J.D. Reyes	17/11/2008	*Q. ilex*	Spain	Jaén	**MW010061**
Cortinarius venetus	PML 245 (holotype of *C. venetus* var. *viridis*)	P. Moënne-Loccoz	18/09/1985	*Picea*	France	Haute-Savoie	**MW010118**
	R. Henry 3412 (holotype of *C. pseudovenetus*)	R. Henry	NA	NA	France	NA	**MW010055**
	IB19650108 (as *C. nothoraphanoides*)	M. Moser	15/09/1965	*Pinus*, *Picea*	Austria	Tyrol	**MW010183**
	HMAS268596	NA	NA	NA	China	NA	KX513586
	HMAS274352	NA	NA	NA	China	NA	KX513585
	HMAS274611	NA	NA	NA	China	NA	KX513584
	TAAM128287	A. Kollom	14/09/2001	*Pinus*	Estonia	Hiiu	UDB019877
	TAAM128694	A. Kollom	16/10/2007	*Picea*	Estonia	Järva	UDB015960
	TAAM128704	A. Kollom	16/10/2007	*Picea*	Estonia	Järva	UDB019876
	TU106430	V. Liiv	10/10/2008	Mixed forest	Estonia	Saare	UDB011758
	TU106896	V. Liiv	28/09/2010	Mixed forest	Estonia	Saare	UDB011272
	TU120024	V. Liiv	01/09/2014	*Picea*	Estonia	Tartu	UDB023575
	AB 12-09-62	A. Bidaud	22/09/2012	*Picea*	France	Ain	**MW010178**
	PML 5464/AB 00-08-13	T. Trémont	08/08/2000	*Picea*	France	Ain	**MW010144**
	AB 04-09-251 (as *C.* cf. *nothoraphanoides*)	A. Faurite-Gendron	25/09/2004	*Picea*, *Fagus*	France	Doubs	**MW010154**
	PML 3265 (as *C.* cf. *nothoraphanoides*)	J. Garin	04/10/1992	*Fagus*, *Abies*	France	Drôme	**MW010130**
	PML 5466 (as *C.* cf. *nothoraphanoides*)	A. Bidaud	05/10/1994	*Fagus*, *Pinus*	France	Hautes-Alpes	**MW010145**
	PML 1665	P. Moënne-Loccoz	12/07/1990	*Picea*	France	Haute-Savoie	**MW010123**
	PML 1781 (as *C. pseudovenetus*)	P. Moënne-Loccoz	01/11/1990	*Picea*	France	Haute-Savoie	**MW010124**
	PML 2393 (as *C. pseudovenetus*)	P. Moënne-Loccoz	10/11/1991	*Picea*	France	Haute-Savoie	**MW010126**
	GC18090805	G. Corriol	08/09/2018	*Fagus*, *Abies*	France	Hautes-Pyrénées	**MW010192**
	GC18091404	G. Corriol	14/09/2018	*Abies*	France	Hautes-Pyrénées	**MW010189**
	AB 05-09-65	A. Bidaud	02/09/2005	*Abies*, *Fagus*	France	Isère	**MW010156**
	JMB2013092405	J.-M. Bellanger	24/09/2013	*Fagus*, *Abies*	France	Isère	**MW010110**
	GH20100927	G. Hensel	27/09/2010	*Picea*	Germany	Baden-Würtemberg	**MW010090**
	GS13	G. Saar	11/11/1999	*Abies*, *Picea*, *Pinus*	Germany	Baden-Würtemberg	**MW010104**
	GH20110814	G. Hensel	14/08/2011	*Picea*	Germany	Bavaria	**MW010084**
	TUB 011645 (as *C. venetus* var. *montanus*)	NA	NA	NA	Germany	NA	EF600897
	IB19970371	M. Moser	23/09/1997	*Fagus*	Italy	Abruzzo	UDB001076
	IB19650159 (as *C. nothoraphanoides*)	I. Gruber & M. Moser	19/09/1965	Conifers	Italy	Bolzano	**MW010184**
	MCVE1691	E. Campo	30/09/1993	*Fagus*	Italy	Pordenone	JF907870
	IB19680089 (as *C. nothoraphanoides*)	D. Lamoure & M. Moser	10/09/1968	Conifers	Italy	Trentino	**MW010185**
	2M06	N. Matsushita	04/10/2016	NA	Japan	Iwate	LC373240
	YM2442 (ecto.)	NA	09/2011	*Tsuga*	Japan	Yamanashi	AB848452
	OS580	NA	NA	NA	Norway	Oslo	KC842422
	T42	K. Høiland	05/09/1994	Mixed forest	Norway	Telemark	UDB000134
	MES4179	J. Ballarà & R. Mahiques	30/09/2005	*Pinus*	Spain	Barcelona	**MW010064**
	JDRG20120201	J.D. Reyes	20/12/2002	*Cistus ladanifer*, *Pinus*	Spain	Jaén	**MW010062**

Table 2 (cont.)

GenBankSpecies	Voucher Id	Leg	Collection date	Putative host tree	Country	Locality	GenBank ITS*
Cortinarius venetus (cont.)	JDRG28101801	J.D. Reyes	28/10/2018	*Pinus*, *Quercus*	Spain	Jaén	**MW010206**
	TU105219	A. Kollom	26/09/2011	*Pinus*	Sweden	Fleringe	UDB018218
	AT2004115	A.F.S. Taylor	18/07/2004	Mixed forest	Sweden	Uppsala	UDB000717
Cortinarius viridans	MPU1116859 (holotype)	J.-M. Bellanger & M. Loizides	29/11/2019	*Pinus*, *Cedrus*, *Q. alnifolia*, *Arbutus*	Cyprus	Trooditissa	**MW010202**
	ML81119CV	M. Loizides	09/11/2018	*Pinus*, *Cedrus*, *Q. alnifolia*, *Arbutus*	Cyprus	Trooditissa	**MW010199**
	ML911192CV2	P.-A. Moreau	29/11/2019	*Pinus*, *Cedrus*, *Q. alnifolia*, *Arbutus*	Cyprus	Trooditissa	**MW010203**
	ML911192CV3	P.-A. Moreau	29/11/2019	*Pinus*, *Cedrus*, *Q. alnifolia*, *Arbutus*	Cyprus	Trooditissa	**MW010057**
	ML810192CV	M. Loizides	29/10/2018	*Cedrus*, *Pinus*	Cyprus	Troodos	**MW010198**
Cortinarius betuletorum	TU105268	A. Kollom	05/09/2012	*Picea*, *Pinus*, *Betula*, *Corylus*	Estonia	Võru	UDB018300
Cortinarius colymbadinus	CFP1130 (neotype)	T.E. Brandrud, H. Lindstrom, H. Marklund & S. Muskos	16/08/1992	*Picea*	Sweden	Jämtland	JX127302
Cortinarius olivaceofuscus	TAAM128766	A. Kollom	24/09/2008	Tilia	Estonia	Hiiu	UDB015963
Cortinarius raphanoides	PML 2507	A. Bidaud	20/09/1992	*Betula*	France	Isère	**MW010127**
Cortinarius rubicundulus	O-F-301662	G. Bollingmo	31/08/2012	NA	Norway	Ringerike	UDB036906
Cortinarius rubicundulus aff.	F15898 (as *C. rubicundulus*)	NA	NA	NA	Canada	British Columbia	FJ157080
	TO4 (as *C.* sp.)	NA	NA	NA	Canada	British Columbia	FJ717594
	IB20010177-A5-Sab (as *C. psittacinus*)	U. Peintner & M. Moser	22/09/2001	*Fagus*	Italy	Abruzzo	UDB001106
Cortinarius valgus	LM761 (ecto.)	NA	NA	*Q. robur*	Germany	NA	KM576359
Cortinarius veronicae	PDD68468 (holotype)	K. Soop	21/04/1997	*Nothofagus*	New-Zealand	Canterbury	KC017355
Cortinarius veronicoides	MEL2120747	R.H. Jones	05/06/1999	NA	Australia	Victoria	GQ890324

* In **bold**: sequences newly generated for the present work. NA: not available. The dashed line delimits outgroup sequences.

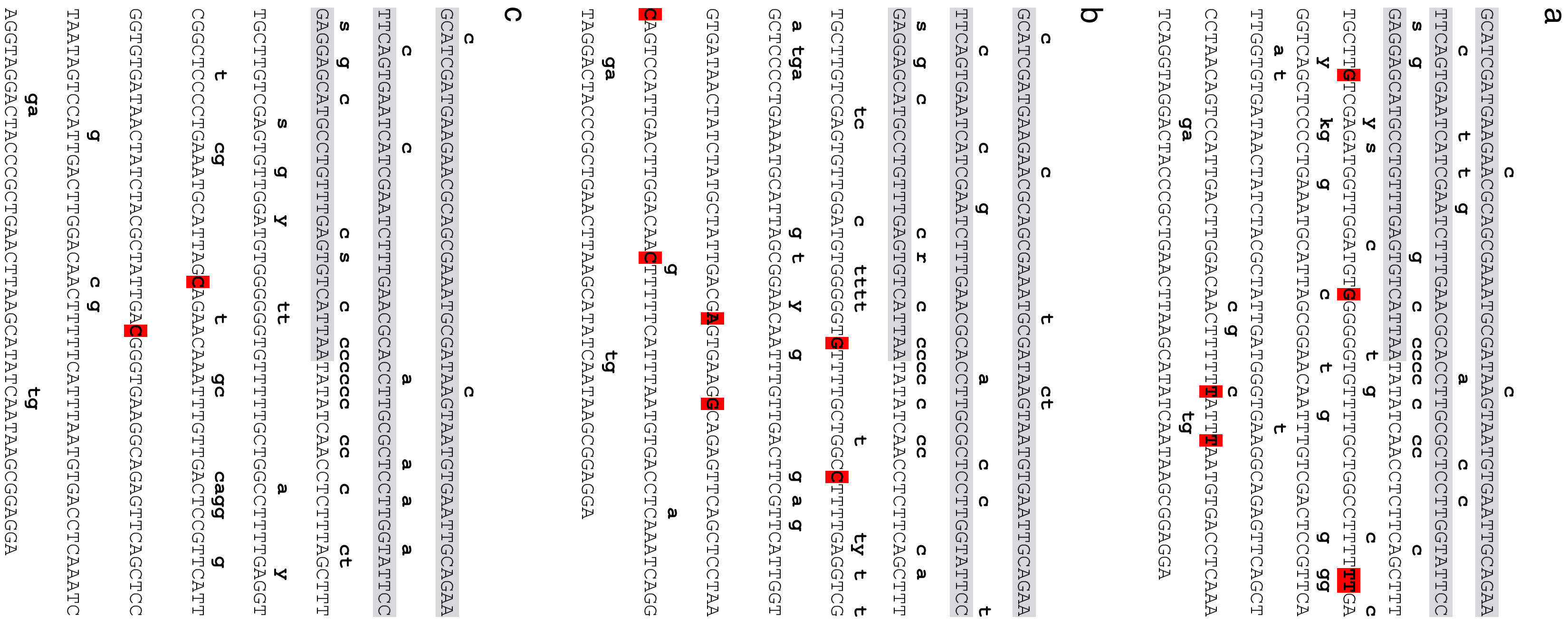

Fig. 1 Mapping of the most frequent intragenomic SNPs along the ITS barcode of three *Cortinarius* species. Consensus sequence of the 5.8S-ITS2 rDNA fragment of the holotypes of: a. *C. pseudovenetus*; b. *C. leproleptopus*; c. *C. xantholamellatus*. Generated by Illumina Miseq sequencing, with SNPs found in at least 0.5 % of the total number of reads within each mOTU indicated as lower case letters above the sequence. Grey and red boxes mark, respectively, the 5.8S rDNA and positions distinguishing each species from their closest neighbour. The number of polymorphic sites is in: a. 48; b. 56; c. 50. Note that the 5.8S rDNA is almost as polymorphic as the ITS2 rDNA and that species diagnostic positions are not (with one exception) touched by these frequent SNPs.

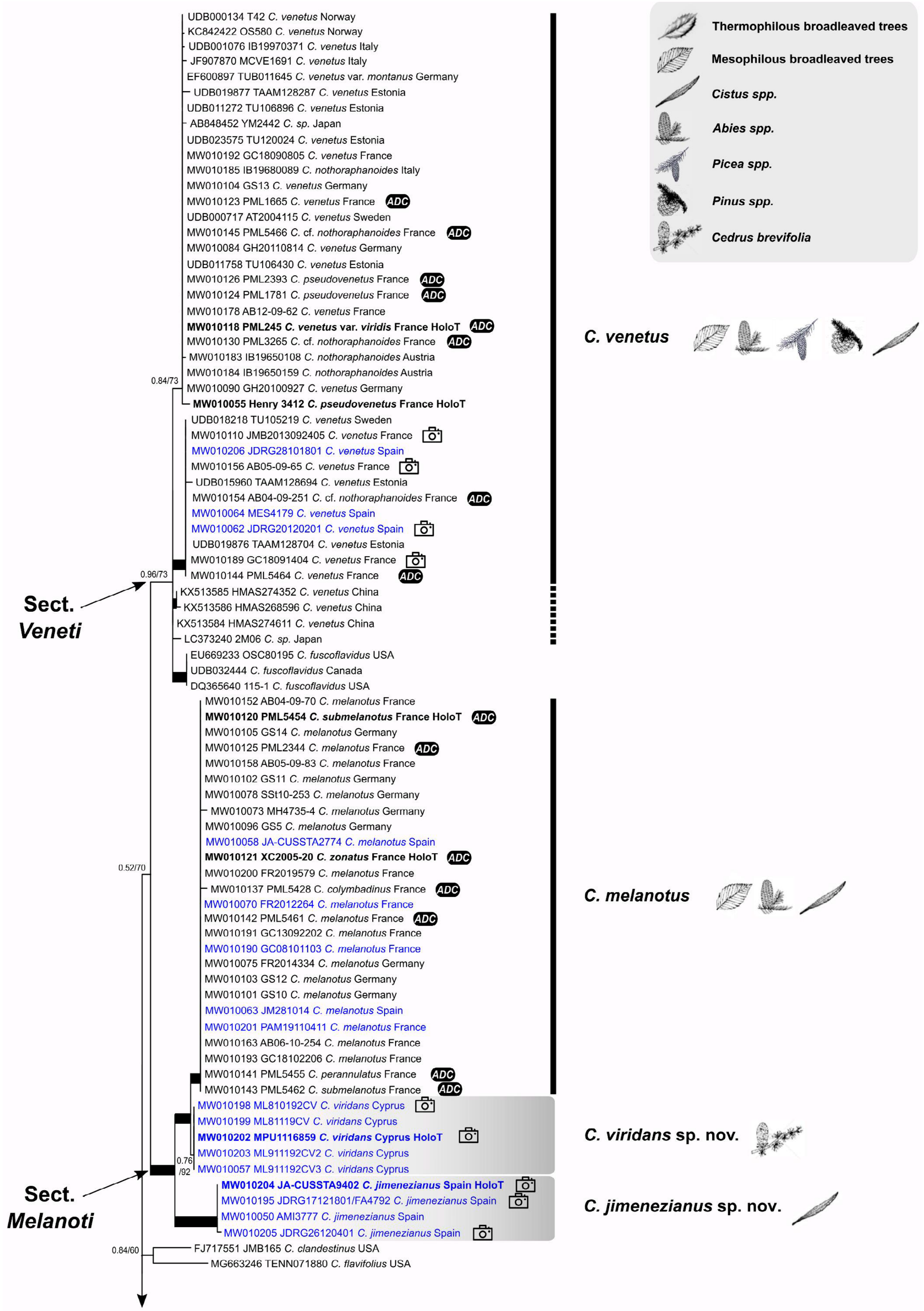

Fig. 2 ITS phylogeny of *Cortinarius* subg. *Leprocybe*. Combined Bayesian and Maximum likelihood analyses of 217 ITS sequences falling in subg. *Leprocybe*, including 11 sequences belonging to sect. *Veronicae*, sect. *Rubicunduli* and other distantly related lineages in the genus. Branches with strong statistical support (SH-aLRT > 0.8 and BPP ≥ 95%) are highlighted as thick lines, others display support values as SH-aLRT/% BPP. *Typus* collections are highlighted in **bold**, those originating from the Mediterranean area (as defined in e.g., Quézel & Médail 2003) are written in blue, those taxonomically described in Bidaud et al. (2005) are marked by '*ADC*' and those illustrated in Fig. 3, 4, 5, 6 and 7 of this study are marked by a camera symbol. Species limits, retained name and major tree hosts for the 11 European species known to date are indicated on the right of each relevant clade, with grey highlight for the three new species here introduced (cf. Taxonomy). Indicated sections are from the companion paper Ammirati et al. 2021.

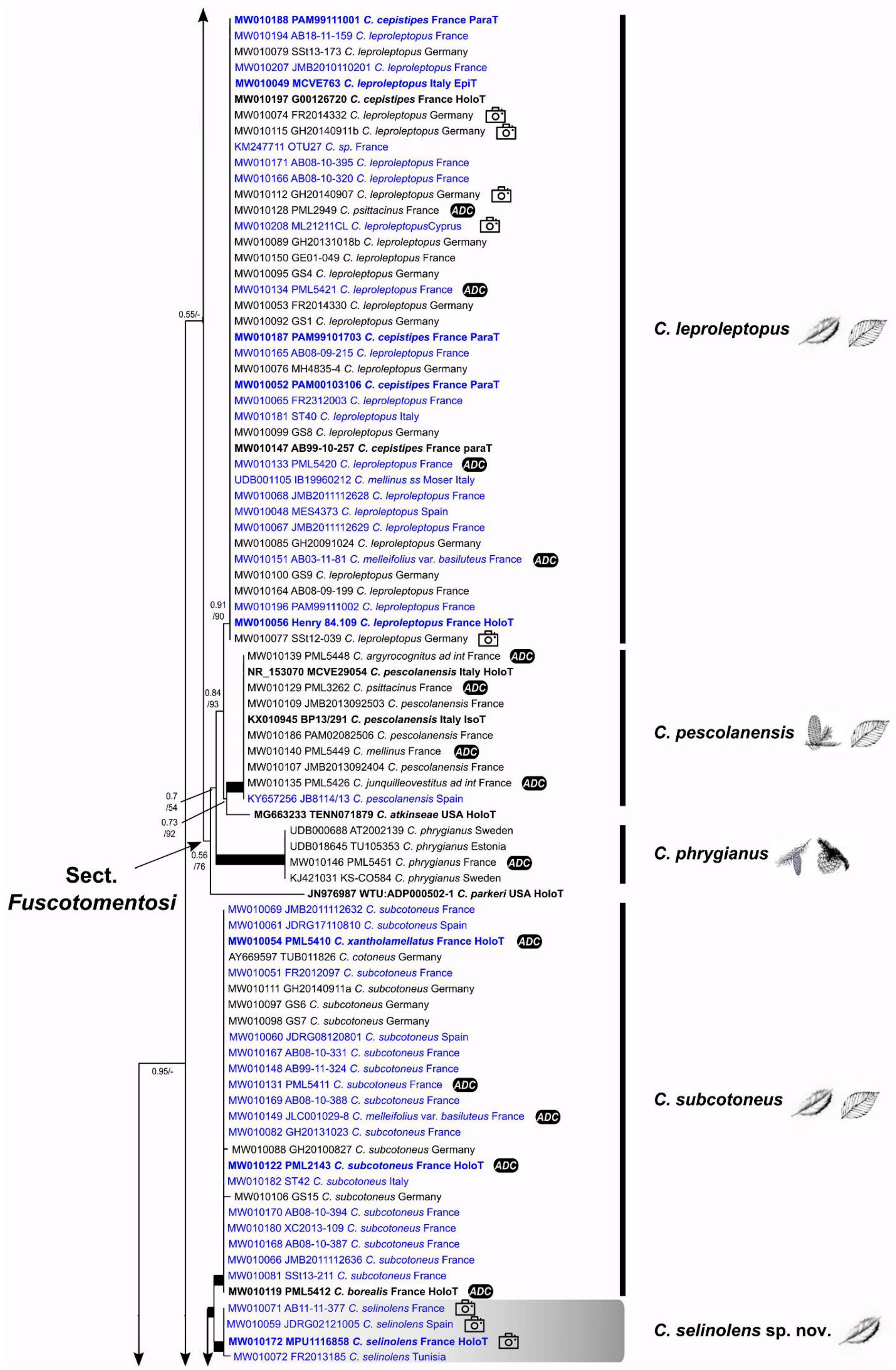
MW010188 PAM99111001 C. cepistipes France ParaT
MW010194 AB18-11-159 C. leproleptopus France
MW010079 SSt13-173 C. leproleptopus Germany
MW010207 JMB2010110201 C. leproleptopus France
MW010049 MCVE763 C. leproleptopus Italy EpiT
MW010197 G00126720 C. cepistipes France HoloT
MW010074 FR2014332 C. leproleptopus Germany
MW010115 GH20140911b C. leproleptopus Germany
KM247711 OTU27 C. sp. France
MW010171 AB08-10-395 C. leproleptopus France
MW010166 AB08-10-320 C. leproleptopus France
MW010112 GH20140907 C. leproleptopus Germany
MW010128 PML2949 C. psittacinus France ADC
MW010208 ML21211CL C. leproleptopusCyprus
MW010089 GH20131018b C. leproleptopus Germany
MW010150 GE01-049 C. leproleptopus France
MW010095 GS4 C. leproleptopus Germany
MW010134 PML5421 C. leproleptopus France ADC
MW010053 FR2014330 C. leproleptopus Germany
MW010092 GS1 C. leproleptopus Germany
MW010187 PAM99101703 C. cepistipes France ParaT
MW010165 AB08-09-215 C. leproleptopus France
MW010076 MH4835-4 C. leproleptopus Germany
MW010052 PAM00103106 C. cepistipes France ParaT
MW010065 FR2312003 C. leproleptopus France
MW010181 ST40 C. leproleptopus Italy
MW010099 GS8 C. leproleptopus Germany
MW010147 AB99-10-257 C. cepistipes France paraT
MW010133 PML5420 C. leproleptopus France ADC
UDB001105 IB19960212 C. mellinus ss Moser Italy
MW010068 JMB2011112628 C. leproleptopus France
MW010048 MES4373 C. leproleptopus Spain
MW010067 JMB2011112629 C. leproleptopus France
MW010085 GH20091024 C. leproleptopus Germany
MW010151 AB03-11-81 C. melleifolius var. basiluteus France ADC
MW010100 GS9 C. leproleptopus Germany
MW010164 AB08-09-199 C. leproleptopus France
MW010196 PAM99111002 C. leproleptopus France
MW010056 Henry 84.109 C. leproleptopus France HoloT
MW010077 SSt12-039 C. leproleptopus Germany
MW010139 PML5448 C. argyrocognitus ad int France ADC
NR_153070 MCVE29054 C. pescolanensis Italy HoloT
MW010129 PML3262 C. psittacinus France ADC
MW010109 JMB2013092503 C. pescolanensis France
KX010945 BP13/291 C. pescolanensis Italy IsoT
MW010186 PAM02082506 C. pescolanensis France
MW010140 PML5449 C. mellinus France ADC
MW010107 JMB2013092404 C. pescolanensis France
MW010135 PML5426 C. junquilleovestitus ad int France ADC
KY657256 JB8114/13 C. pescolanensis Spain
MG663233 TENN071879 C. atkinseae USA HoloT
UDB000688 AT2002139 C. phrygianus Sweden
UDB018645 TU105353 C. phrygianus Estonia
MW010146 PML5451 C. phrygianus France ADC
KJ421031 KS-CO584 C. phrygianus Sweden
JN976987 WTU:ADP000502-1 C. parkeri USA HoloT
MW010069 JMB2011112632 C. subcotoneus France
MW010061 JDRG17110810 C. subcotoneus Spain
MW010054 PML5410 C. xantholamellatus France HoloT ADC
AY669597 TUB011826 C. cotoneus Germany
MW010051 FR2012097 C. subcotoneus France
MW010111 GH20140911a C. subcotoneus Germany
MW010097 GS6 C. subcotoneus Germany
MW010098 GS7 C. subcotoneus Germany
MW010060 JDRG08120801 C. subcotoneus Spain
MW010167 AB08-10-331 C. subcotoneus France
MW010148 AB99-11-324 C. subcotoneus France
MW010131 PML5411 C. subcotoneus France ADC
MW010169 AB08-10-388 C. subcotoneus France
MW010149 JLC001029-8 C. melleifolius var. basiluteus France ADC
MW010082 GH20131023 C. subcotoneus France
MW010088 GH20100827 C. subcotoneus Germany
MW010122 PML2143 C. subcotoneus France HoloT ADC
MW010182 ST42 C. subcotoneus Italy
MW010106 GS15 C. subcotoneus Germany
MW010170 AB08-10-394 C. subcotoneus France
MW010180 XC2013-109 C. subcotoneus France
MW010168 AB08-10-387 C. subcotoneus France
MW010066 JMB2011112636 C. subcotoneus France
MW010081 SSt13-211 C. subcotoneus France
MW010119 PML5412 C. borealis France HoloT ADC
MW010071 AB11-11-377 C. selinolens France
MW010059 JDRG02121005 C. selinolens Spain
MW010172 MPU1116858 C. selinolens France HoloT
MW010072 FR2013185 C. selinolens Tunisia
0.55/-
0.91 /90
0.84 /93
0.7 /54
0.73 /92
0.56 /76
0.95/-
Sect. Fuscotomentosi
C. leproleptopus
C. pescolanensis
C. phrygianus
C. subcotoneus
C. selinolens sp. nov.

Fig. 2 (cont.)

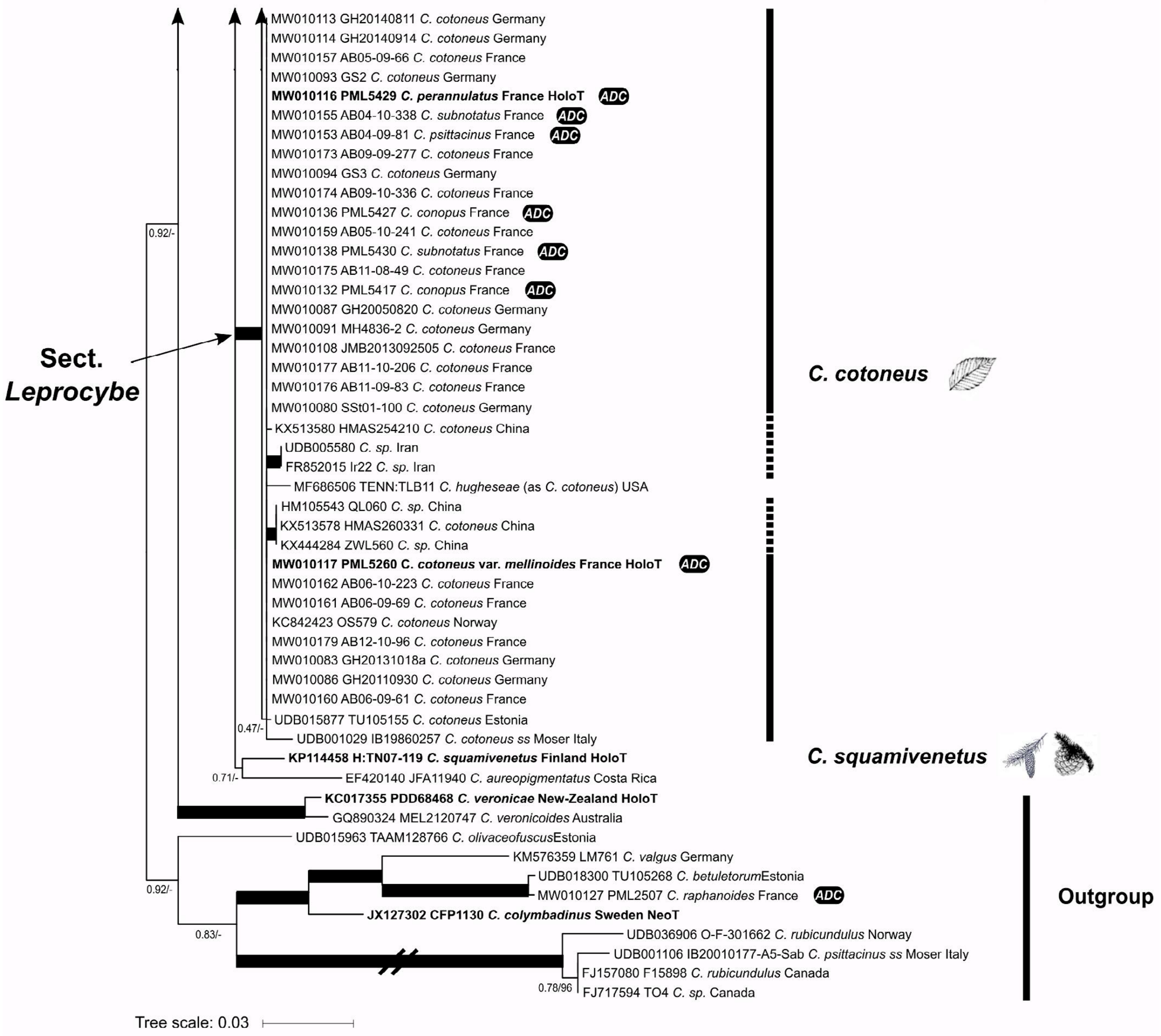

Fig. 2 (cont.)

by merging forward and reverse reads, using the following settings: end-to-end alignment, minimal length of overlap = 10 nt, percentage of identity > 70 %, maximum unaligned sequence ends = 100 %. Full-length sequences were then clustered as molecular Operational Taxonomic Units (mOTUs), using a 98 % identity threshold (Garnica et al. 2016). The *Cortinarius* fraction and taxonomic identity of the most represented species in each dataset were then estimated by Blast analysis of mOTUs. Position and frequency of single nucleotide polymorphisms (SNPs) were recorded for each sample (Fig. 1). The threshold used for mapping the most frequent SNPs was set to 0.5 % within each mOTU, corresponding to 13 occurrences in PML 5410 and 17 occurrences in R. Henry 3412 and R. Henry 84.109. This cutoff is arbitrary, but conservative enough to ensure that mapped SNPs do not result from PCR mutations or sequencing errors. According to reported fidelity of the Phusion^{tm} polymerase (~5 × 10^{-7} error/bp/duplication, McInerney et al. 2014) and the mean error rate of the Illumina Miseq sequencing after quality filtering (0.24 %, Pfeiffer et al. 2018), the number of fake polymorphisms should not exceed one per read. SNPs represented only once in each dataset (singletons) were not considered in statistics about ITS rDNA polymorphism in the three genomes.

RESULTS

Phylogenetic boundaries and species diversity in subg. Leprocybe

At the European scale, the phylogenetic analysis of our ITS dataset resolves 11 supported species in subg. *Leprocybe*, each represented by 1 to 40 sequences (Fig. 2). The minimal phylogenetic distance between them ranges from 5 (*C. cotoneus*/*C. subcotoneus* pair) to 23 (*C. venetus*/*C. cotoneus* pair) differences, representing c. 0.6 % to 3.5 % of sequence divergence, respectively.

Three species, all from the Mediterranean area, are here identified as new to science and described as *C. jimenezianus*, *C. selinolens* and *C. viridans* spp. nov. (Taxonomy). Our sampling efforts yield the first molecular signature, as barcoding sequence, for the historical and well-known taxon *C. melanotus*, so far oddly absent from public ITS sequence databases, and identifies the first confirmed collection of the rare *C. phrygianus* outside northern Europe (see also Ammirati et al. 2021). Our analysis also detects crypticism within *C. venetus*, with two phylogenetically close but distinct European lineages (Fig. 2). Both lineages appear widespread (though only one of those is represented in Spain), but a thorough morphological analysis of collections nesting in these two subclades has failed to

Fig. 3 *Cortinarius venetus*, a genetically polymorphic pan-European greenish species. a–d. *In situ* photography of fresh basidiomata; e. transmitted light microscopy imaging; f. scanning electron microscopy imaging of spores of collections genetically belonging in the smallest subclade depicted in Fig. 2 (from: a. AB 05-09-65; b. JMB2013092405; c, e. GC18091404; d, f. JDRG20120201). — Scale bars: a–d = 5 cm, e = 50 µm, f = 5 µm. — Photos by: a. A. Bidaud; b. J.-M. Bellanger; c, e. G. Corriol; d. J.D. Reyes.

identify any macro-, micro-anatomical, ecological or further biogeographical differences between them. Because the two lineages appear to be fully cryptic based on present data (Fig. 3), we therefore cautiously refrain from proposing a new taxon and tentatively include the two clades within the phylogenetic boundaries of *C. venetus*, at least until some morphological or ecological differences between them can be established (Fig. 2). Eight identified clades overlap with at least one published name, or with a shared and not critical interpretation of a historical binomial (see notes under *C. leproleptopus* and *C. phrygianus*, though), and can thus be readily treated as 'stabilized' species. Overall, the 11 species delineated here allow naming at least eight UNITE species hypotheses (Nilsson et al. 2018; Taxonomy).

Phylogenetic identity of species resolved by Next Generation Sequencing

Our Sanger sequencing attempts failed to produce any sequences for the holotypes of *C. pseudovenetus* (R. Henry 3412), *C. leproleptopus* (R. Henry 84.109) and *C. xantholamellatus* (PML 5410)*, therefore we submitted these three collections to next generation sequencing of the ITS2 domain (Illumina method, cf. Materials and Methods). This powerful method generated more than 12 000 DNA reads out of each sample, of which 68.1 to 81.3 % were full-length fungal sequences of good quality (Table 3). Clustering the latter as molecular Operational

---

* During the drafting of this paper, we were informed that Ammirati et al. (2021) could successfully sequence this material by the classical Sanger method.

Table 3 Illumina sequencing data.

Voucher	R. Henry 3412	R. Henry 84.109	PML 5410
Voucher Id	Holotype of *C. pseudovenetus*	Holotype of *C. leproleptopus*	Holotype of *C. xantholamellatus*
Total nb of reads N0	12189	12709	15542
Nb of paired reads, size- and quality-filtered N1	9908 (81.3 % of N0)	10117 (79.6 % of N0)	10583 (68.1 % of N0)
Nb of *Cortinarius* paired reads, size- and quality-filtered	3521 (28.9 % of N0, 35.5 % of N1)	3688 (29 % of N0, 36.5 % of N1)	2496 (16.1 % of N0, 23.6 % of N1)
Nb and size of mOTUs 98 %	27, 2-4674 sequences	28, 2-3406 sequences	9, 2-4677 sequences
Size of *Cortinarius* mOTU 98 % (frequency rank)	3319 sequences (rank #2, 33.5 % of N1)	3345 sequences (rank #2, 33.1 % of N1)	2405 sequences (rank #3, 22.7 % of N1)
% of *Cortinarius* polymorphic sites, excluding singletons	64.9 % (261/402 sites)	62.6 % (249/398 sites)	60.9 % (245/402 sites)
Taxonomy of the biggest (rank #1) mOTU 98 %	*Aspergillus* sp.	*Aspergillus* sp.	*Cladosporium* sp.
Best Blast hit of the *Cortinarius* mOTU 98 %	EF600897 (*Cortinarius* '*venetus* var. *montanus*')	KM247711 (*Cortinarius* 'sp.')	AY669597 (*Cortinarius* '*cotoneus*')
Revised taxonomy	*C. venetus*	*C. leproleptopus*	*C. subcotoneus*

Taxonomic Units (mOTUs), revealed that traces of *Cortinarius* DNA have been preserved in these three collections but, consistent with our Sanger sequencing attempts, they are heavily contaminated by Ascomycota species. Specifically, 3521, 3688 and 2496 full-length and good-quality sequences of *Cortinarius* have been produced out of R. Henry 3412, R. Henry 84.109 and PML 5410, respectively, representing 16.1 % to 29 % of total reads (Table 3). As expected from the taxonomic history of *C. pseudovenetus* and the phylogenetic position of collections identified as *C. leproleptopus* and *C. xantholamellatus* in our dataset, these three binomials fall in the clades of *C. venetus*, *C. leproleptopus* and *C. subcotoneus*, respectively (see Fig. 2 and Discussion).

Beyond these taxonomic findings, deep sequencing of this material allowed positioning single nucleotide polymorphisms (SNPs) in each individual collection, yielding an unprecedented molecular landscape of the ITS rDNA intragenomic diversity within uncultivated higher Fungi. Excluding singletons from the analysis, which may represent PCR or sequencing artefacts (Materials and Methods), 245 to 261 polymorphic sites out of the ~400 nucleotides of the amplified barcode sequence can be identified in each sample, representing 61 % to 65 % of total amplicon length (Table 3). Mapping the most frequent SNPs within each mOTU identifies 48 to 56 highly polymorphic sites, mostly found in the variable ITS2 domain and its junction to the 5.8S rDNA, but also within the 5.8S rDNA, supposedly much less variable due to structural constraints of the ribosome (Fig. 1). Of note, with one exception (a T in R. Henry 3412), none of the positions distinguishing the three species from their sister species (highlighted in red in Fig. 1) is highly polymorphic, indicating that most diagnostic SNPs in the ITS2 domain have been fixed in the three pairs of sister species, further supporting their reproductive isolation and evolutionary autonomy.

Uncovered synonymies

In an ongoing effort to assign a molecular signature to each of the numerous taxa published in the *ADC*, 37 collections treated in the French monograph are here shown to fall within subg. *Leprocybe*, representing 21 of the 38 taxa included in subsect. *Leprocybe* by Bidaud et al. (2005) (Table 1, Fig. 2). Nineteen of these names unambiguously (but redundantly) fall within the clades of *C. cotoneus*, *C. leproleptopus*, *C. melanotus*, *C. pescolanensis*, *C. subcotoneus* and *C. venetus*, establishing a number of synonyms for these six confirmed species and clarifying long-standing controversies (see Taxonomy). On the other hand, collections of *C. melleifolius* var. *basiluteus* and *C. psittacinus* are represented in two and three clades, respectively, indicating that previous interpretations of these two taxa are ambiguous and in need of revision.

Biogeographical and ecological patterns

Most of the species delineated in our phylogeny appear to be segregated according to putative host plants, biogeography and in some cases substrate specificities, but a couple of taxa revealed to have a broader ecology and distribution than previously thought (Fig. 2). *Cortinarius cotoneus*, *C. subcotoneus*, *C. leproleptopus* and *C. selinolens* are all firmly associated to broadleaved trees (with the interaction of *C. cotoneus* with *Fagaceae* further confirmed by EcM sequences), while *C. pescolanensis*, *C. phrygianus*, *C. squamivenetus* and *C. viridans* seem to be linked to conifers. The latter is notable for its so far exclusive association with the endemic cedar of Cyprus (*Cedrus brevifolia*), occurring on igneous and serpentinized substrates of the Troodos ophiolite. Similarly, the also newly described *C. jimenezianus* from Andalusia (Spain), is unique in this subgenus by its apparently strict association with *Cistaceae* shrubs, as it has so far been exclusively collected under gum rockroses (*Cistus ladanifer*). Based on our expanded molecular sampling, *C. cotoneus*, *C. phrygianus* and *C. squamivenetus* are absent from the Mediterranean region, while *C. jimenezianus*, *C. viridans* and meridional collections of *C. pescolanensis* and *C. venetus* seem to be restricted to the meso-, supra- or oro-Mediterranean zones, where cooler temperatures and more humid conditions exist. *Cortinarius selinolens*, on the other hand, displays strict tropism and a marked preference for xerophilous woodlands of this ecoregion. In contrast to the above, *C. leproleptopus*, *C. melanotus* and *C. subcotoneus* revealed to be widely distributed in warm and dry areas of the Mediterranean but are also found in Germany, associated with a broad range of mesophilous deciduous tree-hosts.

Overall, this study represents an extensive revision of subg. *Leprocybe* of *Cortinarius* in Europe, including the phylogenetic placement of 16 previously unsequenced holotypes, epitypes and paratypes, the molecular confirmation of 23 synonymies, and the description of 3 species new to science.

TAXONOMY

Cortinarius subg. *Leprocybe* M.M. Moser, Z. Pilzk. 35 (3+4): 223. 1969

= *Cortinarius* sect. *Veneti* Konrad & Maubl., Icones Selectae Fungorum VI: 170. 1937, [invalid].

= *Cortinarius* sect. *Leprocybe* M.M. Moser, Z. Pilzk. 35 (3+4): 223. 1969.

= *Cortinarius* subsect. *Leprocybe* Bidaud, Moënne-Locc. & Reumaux, in Bidaud et al., Documents Mycologiques 24 (95): 40. 1994.

Fig. 4 *Cortinarius jimenezianus*, a *Cistus*-associated *Leprocybe* from southern Spain. a–b. *In situ* photography of fresh basidiomata; c. transmitted light microscopy imaging of the suprapellis; d. UV-light fluorescent imaging of a dried specimen; e. scanning electron microscopy imaging of spores; f. sporogram (from: a, e–f. FA4796 (isotype); b. JDRG26120401; d. JDRG17121801/FA4792). — Scale bars: a–b = 5 cm, c = 50 μm, d = 1 cm; e = 5 μm; f = 10 μm. — Photos by: a, c. F. Armada; b. J.D. Reyes.

Type. *Cortinarius cotoneus* Fr., Epicrisis Systematis Mycologici: 289. 1838 [MB 228460].

Basidiomata with yellowish, greenish to olivaceous colours; pileus (20–)40–100 mm, tomentose to fibrillose or squamulose, not or only slightly hygrophanous; stipe cylindrical or clavate, sometimes bulbous; universal veil yellow, olivaceous yellow, olivaceous green or blackish brown; odour usually of radish or parsley; KOH-reaction in most species red to red brown on the flesh; spores subglobose; fluorescent yellow. According to recent phylogenetic studies at the global scale, the subgenus is represented in coniferous and broadleaved forests of the Northern Hemisphere and also includes sect. *Veronicae* and sect. *Persplendidi*, so far represented in Australia and New Zealand (Soop et al. 2019a). In Europe, 11 species can currently be delineated, occurring from southern Spain to Cyprus in the Mediterranean, to Fennoscandia in northern Europe.

Cortinarius jimenezianus Armada & J.D. Reyes, *sp. nov.* — MycoBank MB 837444; Fig. 4

Etymology. Dedicated to Felipe Jiménez, honorary President of the Mycological Society '*Lactarius*' of Jaén.

Diagnosis — Pileus 13–70 mm latus, conico campanulatus, dein applanato convexus, interdum in umbone subdepressus, valde mammosus, carnosus; margine inflexa dein recta. Indumentum siccum, primum leviter lubricosum, dein tomentosum, levis et fulgidum in vetustis basidiomatis; color variabilis, viridis, luteo-olivaceus, brunneo-olivaceum, brunneo-rufus, in margine viridis. Velum universale luteum. Lamellae 3–8 mm latae, adnatae sinuatae, luteae, luteo-olivaceae vel brunneo-olivascentes, dein brunneo-rufae. Stipes 15–90 × 4–8 mm, firmus, plenus et carnosus, ad basim attenuatus, luteo-viridis, ad apicem lutescens, deorsum cremeo-rufus velo luteo-citrino, subannulato praeditus. Cortina tenuis. Mycelium sulphurinum. Caro in pileo brunneo-olivacea, in cortice stipitis luteo-rufescens, in basi brunnea. Odor primum leviter pomaceus, dein raphanicus; sporae ovoideo-subglobosae, vel ellipsoideae, leviter ellipsoidae, laeviter verrucosae vel cristatae (6.8–)7–7.5(–8) × (5.3–)5.5–6.5(–7) µm.

Typus. Spain, Jaén, Parque Natural de Despeñaperros, Santa Elena, Raso de la Venta, 895 m asl, under *Cistus ladanifer* and *Quercus ilex* on acidic soil, 17 Dec. 2018, *F. Armada* & *J.D. Reyes* (holotype, JA-CUSSTA 9402), isotype FA4796 in F. Armada and J.D. Reyes personal herbaria. GenBank ITS MW010204.

Pileus 13–70 mm diam, broadly conical to campanulate at first, gradually expanding to convex or applanate and weakly to moderately umbonate, slightly viscid and finely tomentose when young, but progressively dry and silky or glabrous when ageing, bright olive-green (Ség. 296–301) or greenish yellow to olive-brown (Ség. 315–427), rapidly discolouring reddish brown to dark brown from the centre outwards (Ség. 232). Margin incurved, corrugated when ageing, with persisting greenish hues. *Lamellae* 8 mm wide, bright olive-yellow (Ség. 261–263), then olive-brown (Ség. 216), rather crowded, adnate to emarginate, nearly decurrent, moderately thick. *Stipe* 15–90 × 4–8 mm, rather slender, equal or slightly bulbous and attenuated at the base, entirely hollow when ageing, covered by a cortinoid veil later fleeting to leave a ± well-defined ring-like zone at the apex, greenish yellow or lemon yellow (Ség. 270–320), yellowish in the upper part (Ség. 264), yellowish cream at base (Ség. 185). Cortina concolorous, mycelium sulfur yellow. *Context* olivaceous brown in the pileus (Ség. 435), but olive-cream in the stipe, sometimes with reddish hues at the base (Ség. 296). Fluorescence in UV (360 nm). Smell pleasant when cut, fruity. Taste bitter.

Spores subglobose to ovoid or broadly ellipsoid, dextrinoid, measuring (6.8–)7–7.5(–8) × (5.3–)5.5–6.5(–7) µm (Q = 1.1–1.4; Qm = 1.2), ornamented by coarse, cristate or often truncated warts frequently coalescing to form short discontinuous ridges. Basidia cylindrical, tetrasporic, 30–38 × 7–9.5 µm, with 3 µm long sterigmata. *Marginal cells* 5–14 µm wide, cylindric-clavate to sublageniform, thin walled, septate, on average 30 × 8.5 µm. *Suprapellis* a trichodermium, made up of 3–5 µm wide, parallel hyphae. *Subpellis* composed of allantoid and distinctly inflated hyphae 5–18 (up to 30) µm wide. Pigment both vacuolar and parietal, generally smooth but encrusted in places, dark yellow in the suprapellis, light yellow in the subpellis. Clamp connections present.

Chemical reactions — KOH blood-red on the pileus cuticle, olive (+++) in the pileus and at base of stipe; $AgNO_3$ (+++) greenish yellow in the pileus; Gaiac null in the pileus but ++ in the stipe; Phenolaniline null.

Ecology & Distribution — Fruiting in densely gregarious or fasciculate groups late in the season (December). So far restricted to a few localities of the Parco Natural de Despeñaperros in southern Spain, between 770 m and 915 m asl, under *Cistus ladanifer* on acidic soil.

Other collections studied. Spain, Jaén, Parque Natural de Despeñaperros, Santa Elena, Llano de las Américas, 770 m asl, under *Cistus ladanifer* and *Quercus ilex* on acidic soil, 26 Dec. 2004, *J.D. Reyes*, JDRG26120401; ibid., under *Cistus ladanifer*, 9 Dec. 2014, *A. Mateos Izquierdo*, AMI3777; ibid., Umbria de Magaña, 916 m asl, under *Cistus ladanifer* and *Quercus ilex* on acidic soil, 17 Dec. 2018, *F. Armada* & *J.D. Reyes*, JDRG17121801/FA4792.

Notes — In the field, this species immediately evokes *C. venetus*, especially its variety '*viridis*' (Bidaud et al. 2005), because of the olivaceous-yellow veil. The two species display similarly sized and shaped spores, as well as overall anatomy. However, the flesh of *C. venetus* is not reported as bitter and the latter species fruits under conifers or *Fagus* in Europe, with no confirmed collection in the Mediterranean area prior to this work. *Cortinarius olivaceofuscus*, currently treated in subg. *Dermocybe*, may also superficially resemble *C. jimenezianus*, but the spores of this species are more elongated, measuring 6.5–8 × 4–5 µm (Q = 1.6–1.7) and the ecology is different (associated with *Carpinus*, *Abies* or *Picea* in continental mesophilous forests). Phylogenetically, *C. jimenezianus* is closest to *C. melanotus* and the newly described Cyprian species *C. viridans*, from which it differs by 21 substitutions and indels.

Cortinarius selinolens Bidaud & Bellanger, *sp. nov.* — Fig. 5; MycoBank MB 837445

Etymology. From the Latin names *Petroselinum* (parsley) and *olens* (smelling), referring to the typical odour of the basidiomata of this species.

Diagnosis — Pileus 40–50 mm latus, in centro valde carnosus, convexus dein applanatus, late umbonatus. Margo inflexa vel infracta. Indumentum siccum, non hygrophanum, tomentosum vel squamulosum – squamae in umbone plus minusve hirtae – fusco-brunneum vel umbrino brunneum (Caill. S67–S75) marginem versus olivaceo-brunneum (Caill. P77 usque N79). Lamellae 4–9 mm latae, satis strictae dein distantes, sinuatae-emarginatae, luteo-olivaceae (Caill. N85) dein luteo-olivaceae. Acies integra vel crenulata. Stipes 40–70 × 7–13(–19) µm, plus minusve bulbosus vel subfusiformis, ad apicem albus, luteolus, velo citrino usque ad cortinam brunneo-olivadeam vestitus, ad basim aetate rufescens. Mycelium cremeo-album. Caro in pileo stipitis corticeque alba, ad apicem luteo-olivaceo marmorata, in medulla virido-lutea, ad basim rufescens. Odor petroselini. Sapor dulcis. Sporae (7–)7.5–8.5(–9) × (6–)6.5–7(–7.5) µm ovoideo-globosae, verrucis obtusis praeditae.

Typus. France, Gard, Rousson, Serre des Pastres, 250 m asl, under *Quercus ilex* on calcareous soil, 31 Oct. 2008, *A. Bidaud* & *J. Chabrol* (holotype, MPU1116858), isotype AB 08-10-396 in A. Bidaud personal herbarium. GenBank ITS MW010172.

Pileus 40–50 mm diam, at first hemispherical to convex, gradually expanding to plano-convex with a broad, pronounced and somewhat flattened at the top umbo, very thick-fleshed towards the middle; margin roughly incurved. Cuticle dry, non-hygrophanous, finely tomentose to squamulose, more densely squamulose and dark grey-brown or umber-brown in the centre (Caill. S67–S75), paler olive-brown to brown towards the margin (Caill. P77 to N79). *Lamellae* 4–9 mm wide, sinuate-emarginate, moderately crowded and straw-yellow to olive-yellow

Fig. 5 *Cortinarius selinolens*, a quercophilous Mediterranean *C. melanotus* lookalike. a–b. *In situ* photography of fresh basidiomata; c. transmitted light microscopy imaging of the suprapellis; d. UV-light fluorescent imaging of a dried specimen; e. scanning electron microscopy imaging of spores; f. sporogram (from: a, c, f. AB 08-10-396 (isotype); b, e. JDRG02121005; d. AB 11-11-377/JMB2011112503). — Scale bars: a–b = 5 cm, c = 30 µm, d = 1 cm; e = 5 µm; f = 10 µm. — Photos by: a, c. A. Bidaud; b. J.D. Reyes.

(Caill. N85) when young, becoming more distant and olivaceous brown at maturity, with smooth or crenate edges. *Stipe* 40–70 × 7–13(–19) mm, at first squat and strongly clavate, soon becoming more elongated and cylindrical, dirty white and with rusty-brown cortina remnants in the upper part, straw-coloured to yellowish and often with brown or ochraceous stains below; base remaining bulbous (onion-shaped) to subfusiform and extensively brown- to reddish stained with age. Veil fibrillose, lemon-yellow, soon fleeting, leaving streaks of olive-brown or rusty-brown cortinoid remnants on the stipe. Basal mycelium whitish cream. *Context* whitish in pileus and cortex of the stipe, yellowish green in centre, and reddish at the base. Fluorescence in UV (360 nm). Odour of parsley.

Spores ovoid to subglobose, dextrinoid, measuring (7–)7.5–8.5(–9) µm × (6–)6.5–7(–7.5) µm (Q = 1.1–1.3; Qm = 1.2), with fine obtuse warts, some coalescing to form short isolated ridges; hilar appendage 1–1.5 µm long. Basidia tetrasporic, clavate, 29–36 × 8–9 µm; sterigmata 4–5 µm long. *Marginal cells* clavate, 5–7 µm wide, intermixed with tufts of 8–11 µm wide clavate or subcapitate hairs. *Suprapellis* rather thin, made up of erected bundles of 10–20 µm wide, septate hyphae, terminating in 28–60 µm long acute elements. *Subpellis* poorly developed, made up of short septate cells, 10–15 µm long, radially arranged. Vacuolar pigment olive-yellow and parietal pigment brown-yellow, generally smooth but encrusted by places.

Chemical reactions — KOH olive-yellow in the pileus, vinaceous-pink at base, on pileipellis venetian-red or blackish in the centre, mahogany-brown on margin; AgNO$_3$ sulfur-yellow in the context; Gaiac, Phenolaniline, Tl4, Metol: null.

Ecology & Distribution — Fruiting solitary or gregariously during autumn and winter; so far restricted to thermophilous *Quercus ilex* or *Arbutus unedo* woodlands of the western Mediterranean region.

Other collections studied. France, Hérault, Notre-Dame-de-Londres, 250 m asl, under *Quercus ilex* on calcareous soil, 25 Nov. 2011, *J.-M. Bellanger* & *A. Bidaud*, AB 11-11-377/JMB2011112503. – Spain, Jaén, Parque Natural de Sierra Mágina, Cambil, 1150 m asl, under *Quercus ilex* on calcareous soil, 2 Dec. 2010, *J.D. Reyes*, JDRG02121005. – Tunisia, Jendouba, Souk el Jema, under *Arbutus unedo*, 1 Nov. 2010, *F. Richard*, FR2013185.

Notes — The relatively stout habitus and markedly bulbous stipe base of this species may evoke *C. cotoneus* in the field, but the latter has larger spores and, as shown in the present work, seems to be absent from the Mediterranean. Because of its similar colours, *C. phrygianus* can also be compared with *C. selinolens*, but the flesh of this rare species is odourless, its spores are considerably smaller (5.5–6.5 × 4.5–5 µm) and the ecology is different, typically found in association with *Pinus* on calcareous soil (Niskanen & Kytövuori 2012). Conversely, *C. subcotoneus* and *C. leproleptopus* occur in thermophilous Mediterranean woodlands like *C. selinolens*, but they are different morphologically and can hardly be confused with this species. Due to the parsley scent and scaly pileus, *C. selinolens* is morphologically closer to *C. melanotus*, but the stipe of the latter species is usually less bulbous and covered by a brown veil, the pileus displays more obvious greenish hues, and spores are smaller, measuring 6.5–7.5(–8) × 5–5.5(–6) µm (Niskanen & Kytövuori 2012). Phylogenetically, *C. selinolens* is sister to *C. subcotoneus*, from which it differs by 5 substitutions and 2 indels.

Cortinarius viridans Bellanger & Loizides, *sp. nov.* — Fig. 6; MycoBank MB 837446

Etymology. Viridans [Adj.] = green, referring to the olivaceous hues and greenish tinges of basidiomata.

Diagnosis — Pileus 20–60(–70) mm latus parvus vel medius, tomentoso-fibrillosus vel squamulosus, brunneo-olivaceus. Lamellae ochraeco-luteae. Stipes ad basim acuminatus, apicem versus cortina aurantio-brunnea egregie subannulatus. Sporae ovoideae vel subglobosae, verrucis truncatis, saepe curte cretatis, 6.5–7.5(–8) × 5.5–6.5(–7) µm. Ex insula Cypro sub Cedrus brevifolia, in solo vulcanico.

Typus. Cyprus, Trooditissa, 1400 m asl, under *Cedrus brevifolia* on igneous, acidic soil, 29 Nov. 2019, *J.-M. Bellanger* & *M. Loizides* (holotype, MPU1116859), isotype ML911192CV1 in M. Loizides personal herbarium. GenBank ITS MW010202.

Pileus 20–60(–70) mm diam, hemispherical to campanulate at first, gradually expanding to convex but usually maintaining a broad, flattened umbo, dry, coarsely and densely tomentose to fibrillose when young, becoming more distinctly fibrillose-squamulose with age, occasionally silky and adpressly squamulose, umber-brown, greenish brown or olive-brown (Ség. 277–278 to Ség. 283–295); fibrills dark brown to olive-grey, often black towards the centre; margin persistently incurved, not significantly expanding or undulating, not hygrophanous, frequently with remnants of cortina attached. *Lamellae* 2–4 mm wide, olive-yellow, gradually becoming ochre-yellow and finally tobacco-brown, adnate to adnexed or somewhat emarginate at maturity, moderately thick; edges smooth, concolorous or slightly paler. *Stipe* 40–70 × 10–30 mm, clavate to ventricose and typically deeply rooting into the substrate, slightly bulbous or attenuated towards the base, covered in a cortinoid veil later fleeting to leave a thick annular zone at the apex; pure white above the annular zone, dirty white or straw-coloured below and usually covered in conspicuous, brownish, fibrillose or squamulose bands; cortina thick, abundant, brown to orange in colour; basal mycelium white. *Context* straw-coloured or concolorous with the stipe. Fluorescence in UV (360 nm). Smell at first weakly raphanoid, but then fruity when cut, somewhat reminiscent of apricots. Taste mild, fungoid.

Spores subglobose to ovoid, sometimes also broadly ellipsoid, measuring 6.5–7.5(–8) × 5.5–6.5(–7) µm (Qm = 1.2), without a germ pore, ornamented by coarse truncated warts frequently coalescing to form short, discontinuous ridges; hilar appendage poorly developed, < 1 µm long, often inconspicuous. *Basidia* tetrasporic, measuring 28–42 × 6–8 µm, irregularly cylindrical to clavate, thick-walled, with granular or vacuolar content and a basal clamp; sterigmata acute, 3–5 µm long. *Marginal cells* abundant, similar in size and shape to the basidia, with a basal clamp. *Hymenophoral trama* composed of non-dextrinoid, ± parallel, hyaline and thick-walled hyphae 4–18 µm wide, often somewhat constricted at the septa; septa frequently clamped. *Suprapellis* composed of periclinal, subhyaline to brown (KOH) cylindrical or allantoid (inflated) hyphae 6–17 µm wide, often terminating in clavate or somewhat attenuated and slightly ascending hyphal ends, sometimes coarsely encrusted; most septae with clamps. *Subpellis* extensively gelatinized in parts, composed of tightly packed, poorly differentiated hyphae. Clamp connections frequent throughout, but sometimes inconspicuous.

Chemical reactions — KOH brown or vinaceous-brown on the pileus and stipe; Gaiac instantly reddish purple (+++) on the pileus; Phenolaniline null.

Ecology & Distribution — Fruiting gregariously or in fasciculate clusters between late October and December, on serpentine and igneous substrates under *Cedrus brevifolia*. Rare, known only from a couple of localities on the island of Cyprus, at high elevations ranging from 1400 m to 1600 m asl.

Other collections studied. Cyprus, Troodos, 1600 m asl, under *C. brevifolia* on serpentine soil, 29 Oct. 2018, *M. Loizides*, ML810192CV; Trooditissa, 1400 m asl, under *C. brevifolia* on igneous, acidic soil, 9 Nov. 2018, *M. Loizides*, ML81119CV; ibid., 29 Nov. 2019, *P.-A. Moreau*, ML911192CV2 and ML911192CV3.

Notes — Considering its unique ecological niche and biogeographical distribution, this rare species can hardly be confused with other species in the field. Provided the ectomycorrhizal

Fig. 6 *Cortinarius viridans*, a Cyprian endemic *Leprocybe* associated with *Cedrus brevifolia*. a–b. *In situ* photography of fresh basidiomata; c. transmitted light microscopy imaging of the suprapellis; d. UV-light fluorescent imaging of a dried specimen; e. scanning electron microscopy imaging of spores; f. sporogram (from: a, c. ML911192CV1 (isotype); d–f. ML810192CV). — Scale bars: a–b = 5 cm, c = 50 µm, d = 1 cm; e = 5 µm; f = 10 µm.— Photos by: a. P.-A. Moreau; b–c. M. Loizides.

association with *Cedrus* is confirmed by sequencing of the root tips in the future, *C. viridans* would represent the first report of an endemic Basidiomycota species associated with an endemic tree-host in the Mediterranean. From a morphological perspective, *C. viridans* closely resembles *C. melanotus*, both macromorphologically and microanatomically. However, the latter species usually displays a pileus which is more tomentose than fibrillose, with more prominent dark scales towards the center, and has an odour of parsley. *Cortinarius selinolens* is also similar, but produces stouter basidiomata, also with a parsley odour, and has larger spores measuring (7–)7.5–8.5(–9) × (6–)6.5–7(–7.5) µm. This species also has a very different ecology and is so far known only from thermo-Mediterranean *Quercus ilex* and *Arbutus unedo* matorral in the western Mediterranean. *Cortinarius phrygianus* can also superficially resemble *C. viridans*, but has much smaller spores measuring 5.5–6.5 × 4.5–5 µm, and a completely different ecology (see below). So far, none of the above species have been documented in Cyprus, with *C. leproleptopus* being the only other member of subg. *Leprocybe* currently represented on the island. Phylogenetically, *C. viridans* is not polymorphic at the ITS locus and is sister to *C. melanotus*, with 4 substitutions and 2 indels further distinguishing the two species.

Cortinarius cotoneus Fr., Epicrisis Systematis Mycologici: 289. 1838 — MycoBank MB 228460. UNITE SH1503798.08FU (1.5 %)

≡ *Dermocybe cotonea* (Fr.) Ricken, Die Blätterpilze 1: 160. 1915.

= *Cortinarius perannulatus* Bidaud, in Bidaud et al., Atlas des Cortinaires 15: 1031. 2005.

= *Cortinarius cotoneus* var. *mellinoides* Bidaud, Moënne-Locc. & Reumaux, in Bidaud et al., Atlas des Cortinaires 15: 1031. 2005.

= *Cortinarius subannulatus* Jul. Schäff. & M.M. Moser, Beih. Sydowia 1: 226. 1957, p.p.

= *Cortinarius subnotatus* Fr., Epicrisis Systematis Mycologici: 290. 1838, *sensu* Bidaud et al. 2005, p.p.

= *Cortinarius psittacinus* M.M. Moser, Z. Pilzk. 35: 245. 1969, *sensu* Bidaud et al. 2005, p.p.

= *Cortinarius conopus* (Pers.) Hlaváček, Mykol. Sborn. 64 (5): 247. 1987, *sensu* Bidaud et al. 2005, p.p.

Typus. Sweden, Gotland, Vallstena sn, Alvena lindängar, broad-leaved deciduous forest, calcareous soil (*Corylus*, *Quercus*, *Tilia*), 1 Oct 1990, coll. Brandrud et al., CFP1032 (neotype, F44846 in S, designated in Ammirati et al. 2021).

Selected descriptions — Niskanen & Kytövuori 2012: 765; Bidaud et al. 2005: f. 763 & 763bis (as *C. cotoneus* var. *mellinoides*); Brandrud et al. 1992: B01.

Selected illustrations — Bidaud et al. 2005: Pl. 561 (PML 5429, as *C. perannulatus*), Pl. 570 (PML 5260, as *C. cotoneus* var. *mellinoides*), Pl. 572 (PML 5417, PML 5427, as *C. conopus*), Pl. 573 (PML 5430, AB 04-10-338, as *C. subnotatus*), Pl. 574 (AB 04-09-81, as *C. psittacinus*).

Notes — As here phylogenetically circumscribed, *C. cotoneus* is a broadly distributed species likely associated to *Fagaceae* trees, present in continental and northern Europe. The taxonomic study of North American *Leprocybe* performed in the companion paper reveals that the species is present in North America. However, the unique sequence so far published from the New World and annotated as *C. cotoneus*, MF686506, actually belongs to a distinct species (*C. hugheseae*, cf. Ammirati et al. 2021). European sequences are remarkably conserved at the ITS locus (not considering UDB001029, that displays signs of poor quality, data not shown and Fig. 2), but the clade also includes slightly divergent sequences from northern Iran and China. A deeper taxon sampling in central and eastern Asia will be necessary to clarify the extent of gene flow within this lineage, and thus identify species boundaries across the Eurasiatic transect. An unexpected outcome of our analyses is the apparent absence of this species in the Mediterranean area, as all collections identified as *C. cotoneus* in Spain, Italy or southern France turned out to belong to *C. subcotoneus*, or to the newly described *C. selinolens*. Considering this updated biogeography, the usually robust habitus of the species and its large spores, *C. cotoneus* can hardly be misidentified by field taxonomists. The present study shows that *C. perannulatus* and *C. cotoneus* var. *mellinoides*, both published in the *ADC* in 2005, are conspecific with *C. cotoneus*. In the same monograph, several collections described as distinct species, namely *C. conopus*, *C. psittacinus* and *C. subnotatus*, are also here shown to be later synonyms of this species. An old collection identified as *C. subannulatus* by Moser (IB19990237) also falls in this clade (U. Peintner & R. Kuhnert, pers. comm.), indicating that the latter binomial may also represent a late synonym of *C. cotoneus*. In its revised boundaries, this species is closest to *C. selinolens* and *C. subcotoneus*, and differs from each one of them by 5 substitutions.

Cortinarius leproleptopus Chevassut & Rob. Henry, Doc. Mycol. 19 (73): 47. 1988 — Fig. 7; MycoBank MB 134786. UNITE SH1662309.08FU (1 %)

≡ *Cortinarius leptopus* Reumaux, in Bidaud et al., Atlas des Cortinaires 15: 1031. 2005, [illeg.].

? = *Cortinarius leproleptopus* var. *basiluteus* Chevassut & Rob. Henry, Doc. Mycol. 24 (94): 57. 1994.

= *Cortinarius melleifolius* var. *basiluteus* (Chevassut & Rob. Henry) Bidaud & Reumaux, in Bidaud et al., Atlas des Cortinaires 15: 1031. 2005, p.p.

= *Cortinarius cepistipes* A. Favre & P.-A. Moreau, Rivista di Micologia 1: 17. 2001.

= *Cortinarius mellinus* Britzelm., Bot. Centralbl. 62 (10): 308. 1895, *sensu* Moser 1969, p.p.

= *Cortinarius psittacinus* M.M. Moser, Z. Pilzk. 35: 245. 1969, *sensu* Bidaud et al. 2005, p.p.

Typus. France, Hérault, Quissac, under *Quercus ilex*, 19 Nov. 1984, *G. Chevassut* (holotype, R. Henry 84.109 in PC), isotype R. Henry 84.110 in PC, paratypes Chev. 3341, 3342 in PC. GenBank ITS MW010056. – Italy, Reggio Emilia, Castelnuevo ne' Monti, Borra del Prato, under *Castanea sativa*, *Quercus pubescens*, *Fagus sylvatica* and *Pinus sylvestris*, 9 Oct. 1994, *G. Consiglio* & *B. Bigazzi*, E.C. 94190 (epitype, MCVE763). GenBank ITS MW010049.

Selected illustrations — This study: Fig. 7; Bidaud et al. 2005: Pl. 574 (PML 5420, 5421), Pl. 575 (PML 2949, as *C. psittacinus*); Consiglio et al. 2004: B8; Favre & Moreau 2001: 19, 21 (as *C. cepistipes*) and 22.

Emended description — *Pileus* 20–60(–80) mm diam, convex-campanulate with an incurved margin when young, entirely covered with squamous fibrils, golden yellow to greenish yellow on fresh basidiomata, becoming honey-rusty with age, red to reddish brown with KOH. *Lamellae* adnate or emarginated, rather spaced, concolorous. *Stipe* 50–80 × 5–12 mm, cylindrical, clavate or clearly bulbous (up to 30 mm diam), fibrillous, yellowish, naked or covered variable amounts of a yellow partial veil. *Context* yellowish, odour of raw potato, of radish or dusty-earthy, with weak or null reaction to KOH.

Spores ovoid to subglobose 6–8.5(–9.5) × 5.5–7 µm (Q = 1.1–1.4), ornamented by almost isolated warts. *Suprapellis* hymenodermic or trichodermic, made up of parallel bundles of hyphae 3–12 mm wide, more or less erected. *Subpellis* usually well developed, pseudoparenchymatous, made up of cylindrical elements up to 100 × 20 µm.

Ecology & Distribution — Solitary or gregarious, fruiting rather late in the autumn under broadleaved trees of the *Fagaceae* family, occurring mostly, but not exclusively, on calcareous soils, from Mediterranean *Quercus ilex*, *Q. pubescens*, *Q. alnifolia* or *Castanea sativa* woodlands to ± thermophilous *Q. robur* and

Fig. 7 *Cortinarius leproleptopus*, a pan-European yellowish *Leprocybe. In situ* photography of fresh basidiomata from: a–d. Germany; e. Cyprus. Note the green-olivaceous tinges on some German collections, absent from the original diagnosis describing Mediterranean collections. Reaction to KOH on the flesh and pileus is shown in c and d (from: a. GH20140907; b. FR2014332; c. GH20140911b; d. SSt12-039; e. ML21211CL). — Scale bars = 5 cm.— Photos by: a. G. Hensel; b. M. Huth; c. M. Huth & G. Hensel; d. G. Saar; e. M. Loizides.

Fagus sylvatica forests in continental regions. So far confirmed in Cyprus, France, Germany, Italy and Spain.

Notes (see also 'Discussion' for further comments) — This species has been originally described as a yellow, strictly meridional *Leprocybe* without greenish tones, but with a cylindrical stipe and an ecology restricted to thermophilous and calcareous *Quercus* woodlands of the Mediterranean area (Chevassut & Henry 1988). As revised here, *C. leproleptopus* is more polymorphic and displays a much broader distributional and ecological range. In particular, the stipe can be cylindrical to neatly bulbous and may be glabrous or covered by abundant yellow veil remnants. The dominant colour of basidiomata is yellow, but greenish hues may be present on the pileus and lamellae of some fresh collections (Fig. 7). Microscopically, the hyphae of the hypodermis are usually well differentiated and spores rarely exceed 8.5 × 7 µm. This species is indeed present in the western Mediterranean region (Spain, France, Italy), but also occurs considerably further east, in Cyprus and north, in the French Alps as well as Germany. The conspecificity of *C. leproleptopus* var. *basiluteus* with the present species is likely, but cannot be ascertained because no original material of this taxon could be traced and sequenced. From a phylogenetic point of view, *C. leproleptopus* is remarkably stable at the ITS locus (0 differences between the 40 available sequences) and differs from its sister species *C. pescolanensis* by 6 substitutions.

Cortinarius melanotus Kalchbr., in Fries, Hymenomycetes Europaei (Upsaliae): 365. 1874 — MycoBank MB 219634

≡ *Gomphos melanotus* (Kalchbr.) Kuntze, Revis. Gen. Pl. (Leipzig) 2: 854. 1891.

= *Cortinarius submelanotus* Bidaud, in Bidaud et al., Atlas des Cortinaires 15: 1032. 2005.

= *Cortinarius zonatus* Reumaux, in Bidaud et al., Atlas des Cortinaires 15: 1033. 2005.

= *Cortinarius colymbadinus* Fr., Epicrisis Systematis Mycologici: 289. 1838, *sensu* Bidaud et al. 2005.

Typus. Kalchbrenner, Icones selectae Hymenomycetum Hungariae 3, 1875, t. 27, f. 2 (holotype, iconotype). See also Ammirati et al. (2021).

Selected descriptions — Niskanen & Kytövuori 2012: 766; Consiglio et al. 2006: D128; Bidaud et al. 2005: f. 756, f. 756bis (as *C. submelanotus*), f. 759 (as *C. zonatus*); Brandrud et al. 1998: D56.

Selected illustrations — Bidaud et al. 2005: Pl. 558 (PML 5428, as *C. colymbadinus*), Pl. 559 (PML 5461), Pl. 560 (PML 5454, as *C. submelanotus*, PML 2344), Pl. 563 (PML 5455, as *C. perannulatus*, XC 2005-20, as *C. zonatus*).

Notes — Prior to the present work, no ITS sequence of this historical species was publicly available. Our dataset shows that, as currently interpreted by taxonomists, *C. melanotus* is confirmed in Spain and is not rare in France and Germany. Since this species was described from Central Europe and is reported in Fennoscandia (Fries 1874, Brandrud et al. 1998, Niskanen & Kytövuori 2012), it is probably present throughout most of the continent (Table 2, Fig. 2). *Cortinarius melanotus* is often claimed to be associated with *Abies* or *Pinus* spp. in calcareous soils (Brandrud et al. 1998, Niskanen & Kytövuori 2012, Eyssartier & Roux 2017). However, the clade includes several collections from broadleaved woodlands and at least some fruiting on acidic soils (Bidaud et al. 2005; Table 2). The unveiled conspecificity of *C. submelanotus* with *C. melanotus* in the present work, was already suspected by Bidaud et al. (2005) who considered their new species as a putative variant of *C. melanotus*. The colour of veil remnants on the stipe (brown vs yellow), should thus not be overemphasised in taxonomic terms, since collections with both velar colours nest in the same clade. However, the placement of *C. zonatus* in the latter was less expected and indicates that the species can occasionally produce odourless basidiomata with crown-like colours on the pileus. The interpretation of *C. colymbadinus* by the French authors of the *ADC* also falls in this clade, but this binomial has recently been neotypified and is now assigned to a distinct lineage of subg. *Telamonia* (Dima et al. 2014; Fig. 2). Phylogenetically, *C. melanotus* displays limited polymorphism at the ITS locus, with 4 variable sites, and is separated from its closest species *C. viridans* by 4 substitutions and 2 indels.

Cortinarius pescolanensis Picillo & Marchionni, Micologia e Vegetazione Mediterranea 31 (1): 63. 2016 — MycoBank MB 816349. UNITE SH1662079.08FU (1 %)

= *Cortinarius mellinus* Britzelm., Bot. Centralbl. 62 (10): 308. 1895, *sensu* Bidaud et al. (2005).

= *Cortinarius psittacinus* M.M. Moser, Z. Pilzk. 35: 245. 1969, *sensu* Bidaud et al. (2005), p.p.

= *Cortinarius junquilleovestitus* Bidaud, in Bidaud et al., Atlas des Cortinaires 15: f. 765. 2005, [invalid].

= *Cortinarius argyrocognitus* Bidaud, in Bidaud et al., Atlas des Cortinaires 15: f. 767. 2005, [invalid].

Typus. ITALY, Molise, Pescopennataro, Fonte della Gallina, under *Abies alba* with some *Fagus sylvatica* trees on basic soil, 14 Oct. 2012, *B. Picillo* & *M. Marchionni* (holotype, MCVE29054), isotype BP13/291 in B. Picillo personal herbarium. GenBank ITS KX010944/NR_153070 and KX010945.

Selected descriptions — Ballarà et al. 2017: 39; Picillo & Marchionni 2016: 63; Bidaud et al. 2005: f. 765 (as *C. junquilleovestitus*), f. 767 (as *C. argyrocognitus*), f. 768 (as *C. mellinus*).

Selected illustrations — Ballarà et al. 2017: 40; Picillo & Marchionni 2016: 64; Bidaud et al. 2005: Pl. 572 (as *C. junquilleovestitus*), Pl. 575 (PML 3262, as *C. psittacinus*), Pl. 576 (as *C. argyrocognitus*), Pl. 577 (PML 5449, as *C. mellinus*).

Notes — This taxon was recently published from Italy but had been repeatedly described under different names in the *ADC*, namely *C. mellinus*, *C. junquilleovestitus ad int* and *C. argyrocognitus ad int*. All phylogenetically confirmed collections of *C. pescolanensis* so far originate from mountainous forests of France, Italy and Spain, dominated by *Abies* spp., more or less mixed with scattered *Fagus* or *Pinus* trees, and occurring exclusively on calcareous bedrock (Table 2 and data not shown). Basidiomata are intermediate in size between *C. venetus* and *C. cotoneus*, while the pileus and the veil are predominantly ochraceous-orange in colour, lacking green hues, and the pileus center is distinctly darker by persistent dark scales. Phylogenetically, the species is remarkably stable at the ITS locus (1 polymorphic position) and differs from its closest neighbour *C. leproleptopus* by 6 substitutions.

Cortinarius phrygianus (Fr.) Trog, Verzeichnis schweizerischer Schwämme (1844) — MycoBank MB 152271. UNITE SH1662078.08FU (1 %)

≡ *Cortinarius sublanatus* var. *phrygianus* Fr., Epicrisis Systematis Mycologici: 283. 1838.

≡ *Cortinarius phrygianus* Fr., Hymenomycetes Europaei (Upsaliae): 365. 1874.

≡ *Gomphos phrygianus* (Fr.) Kuntze, Revis. Gen. Pl. (Leipzig) 2: 854. 1891.

= *Cortinarius arenatus* (Pers.) Fr., Epicrisis Systematis Mycologici: 283. 1838, *sensu* Melot in Brandrud et al. (2014).

Typus. Sweden. Darlana, Rättvik sn, Enån, coniferous forest, *Pinus*, 14 Sept. 1988, coll. Brandrud et al., CFP774 (neotype F44888 in S, designated in Ammirati et al. 2021).

Selected descriptions — Niskanen & Kytövuori 2012: 766; Bidaud et al. 2005: f. 738; Brandrud et al. 1990: A30.

Selected illustrations — Soop et al. 2019a: f. 3d; Bidaud et al. 2005: Pl. 541; Brandrud et al. 1990: A30.

Notes — This iconic but rare Friesian species has been reported by Nordic authors to be largely confined to Fennoscandia (Brandrud et al. 1990). Consistently, it has so far been confirmed only from dry *Pinus* or *Picea* woodlands of Sweden and Estonia. A few older reports from Austria, Germany and Switzerland do exist, but in the absence of molecular analysis, they may refer to different species, especially *Cortinarius melanotus* (Brandrud & Bendiksen 2014). In France, *C. phrygianus* has been first interpreted by Henry (1977) as a rare species fruiting in broadleaved forests of the eastern part of the country. The authors of the *ADC* named this latter taxon *C. hirtipes* and instead applied *C. phrygianus* to a single collection from the Ain department (Bidaud et al. 2005), here found to be conspecific with the Swedish and Estonian sequenced material (Table 2, Fig. 2). Such finding represents the first confirmation of *C. phrygianus* outside Nordic European countries, and incidentely yields some credit to previous, non-sequenced continental reports. The collection of this species described in 1990 in the *CFP* has been lately renamed as *C. arenatus* (Brandrud et al. 2014: plate A30), a binomial variously interpreted by previous authors (Bidaud et al. 2005). We tentatively ascribe the better-known name *C. phrygianus* to the present taxon, until the synonymy of the two names is fully established. In the field, the species can only be confused with *C. melanotus*, which shares similar macro-morphology, although the latter usually displays more obvious greenish hues, typically smells of parsley and has larger spores measuring 6.5–7.5(–8) × 5–5.5(–6) µm vs 5.5–6.5 × 4.5–5 µm (Niskanen & Kytövuori 2012). Phylogenetically, *C. phrygianus* is remarkably stable at the ITS locus and well separated from all other known species in the subgenus (e.g., 19 substitutions and 9 indels relative to *C. leproleptopus*). More collections of this species are, however, needed to better understand its natural variability, at molecular, morpho-anatomical as well as ecological levels.

Cortinarius squamivenetus Kytöv., Liimat. & Niskanen, Index Fungorum 196 (1): 2. 2014 — MycoBank MB 550843. UNITE SH2122528.08FU (< 0.5 %).

Typus. Finland, Koillismaa, Kuusamo, Oulanka National Park, Camping pale, Puukkorinne rich mixed forest (*Picea*, *Pinus*, *Populus*), 1 Sept. 2007, *T. Niskanen*, *I. Kytövuori* & *K. Liimatainen*, TN 07-119 (holotype in H), isotype in NY. GenBank ITS KP114458.

Selected description — Liimatainen 2014: 2.

Selected illustration — Cf. Ammirati et al. (2021).

Notes — This species was so far known only from the northern boreal zone of Finland, where it fruits early in the autumn in coniferous forests on calcareous ground. Ammirati et al. (2021) describe two additional collections from Quebec (Canada). No photographic representation of *C. squamivenetus* has been published to date, but judging from descriptions, this taxon would be mostly similar to *C. venetus*, from which it would differ by black appressed fibrillose scales and slightly smaller spores (6.4 × 5.5 µm vs 7 × 5.8 µm, on average). A broader taxon sampling of this species is obviously necessary, to better understand the full range of its morpho-anatomical variability and precise its ecological/biogeographical range. From an evolutionary perspective, it is difficult to position *C. squamivenetus* relative to other species solely by ITS phylogeny, because in the phylogram depicted in Fig. 2, it lies in an unsupported basal position, with more than 20 differences with other clades (e.g., 15 substitutions and 7 indels relative to *C. venetus*).

Cortinarius subcotoneus Bidaud, Atlas des Cortinaires 15: 1032. 2005 — MycoBank MB 357354. UNITE SH1856985.08FU (0.5 %)

= *Cortinarius borealis* Bidaud, in Bidaud et al., Atlas des Cortinaires 15: 1031. 2005.

= *Cortinarius xantholamellatus* Bidaud, in Bidaud et al., Atlas des Cortinaires 15: 1033. 2005.

? = *Cortinarius sublanatus* var. *xanthophyllus* Maire, Fungi Catalaunici: Contributions à l'étude de la Flore Mycologique de la Catalogne: 104. 1933.

= *Cortinarius melleifolius* var. *basiluteus* (Chevassut & Rob. Henry) Bidaud & Reumaux, in Bidaud et al., Atlas des Cortinaires 15: 1031. 2005, p.p.

Typus. France, Drôme, La Roche-Saint-Secret, 350 m asl, under *Quercus pubescens* in calcareous soil, 9 Nov. 1990, *A. Bidaud*, PML 2143 (holotype in PC). GenBank ITS MW010122.

Selected descriptions — Bidaud et al. 2005: f. 762 (as *C. borealis*), f. 764 (including *C. xantholamellatus*).

Selected illustrations — Bidaud et al. 2005: Pl. 567 (as *C. borealis*), Pl. 570, Pl. 571 (as *C. xantholamellatus*), Pl. 578 (JLC001029-8, as *C. melleifolius* var. *basiluteus*).

Notes — This taxon has been initially defined as a *C. cotoneus*-like species with different veil remnants on the stipe and slightly smaller spores. Our analyses provide an additional important difference between the two species, biogeographical in nature: while *C. cotoneus* seems to be absent from the Mediterranean area, *C. subcotoneus* is almost exclusively fruiting in this ecoregion, with the notable exception of a few German localities. The species is closely associated with *Quercus* spp. in meridional localities and with *Fagaceae* in Germany. The synonymy of *C. subcotoneus* with *C. xantholamellatus*, *C. borealis* and one published collection of *C. melleifolius* var. *basiluteus*, all unravelled here, indicates that yellow pigments can occasionally be present in basidiomata, at least veil and lamellae, and that, in rare cases, some blue hues can be detected at the top of the stipe. Bidaud et al. (2005) proposed that *C. xantholamellatus* may be conspecific with *C. sublanatus* var. *xanthophyllus*, a variant described by R. Maire from Spain under *Quercus suber* and *Castanea sativa*, on acidic soil. However, no collection of *C. subcotoneus* has so far been confirmed outside calciphilous *Quercus* woodlands in the Mediterranean area, casting some doubt on such a synonymy. Phylogenetically, the species is moderately polymorphic, with 3 identified substitutions and 2 indel positions, and can be distinguished from its sister species *C. selinolens* by 5 substitutions and 2 indels.

Cortinarius venetus (Fr.) Fr., Epicrisis Systematis Mycologici: 291. 1838 — Fig. 3; MycoBank MB 143469. UNITE SH1855806.08FU (0.5 %) + SH1856058.08FU (0.5 %)

≡ *Agaricus raphanoides* (var.) *b venetus* Fr., Observ. Mycol. 2: 76. 1818.

≡ *Dermocybe veneta* (Fr.) Ricken, Die Blätterpilze 1: 162. 1915.

= *Cortinarius pseudovenetus* Rob. Henry, Bull. Soc. Mycol. France 77 (2): 116. 1961.

= *Cortinarius venetus* var. *montanus* M.M. Moser, Z. Pilzk.: 25. 1970.

= *Cortinarius venetus* var. *viridis* Moënne-Locc., in Bidaud et al., Atlas des Cortinaires 15: 1033. 2005.

= *Cortinarius nothoraphanoides* (ined.) M.M. Moser, Guida alla determinazione dei funghi (Polyporales, Boletales, Agaricales, Russulales): 374. 1986, [invalid].

Typus. Sweden, Uppland, Uppsala-näs sn, Dalkarlskärret, coniferous forest (*Pinus*, *Picea*), 18 Aug. 1986, Lindström et al., CFP112 (neotype, F44498 in S, designated in Ammirati et al. 2021).

Selected descriptions — Niskanen & Kytövuori 2012: 766; Bidaud et al. 2005: f. 760 (as *C. pseudovenetus*), f. 760bis (as *C.* cf. *nothoraphanoides*), f. 761 (as *C. venetus* and *C. venetus* var. *viridis*); Consiglio et al. 2004: B193; Brandrud et al. 1990: A15.

Selected illustrations — This study: Fig. 3; Bidaud et al. 2005: Pl. 564 (PML 2393, as *C. pseudovenetus*), Pl. 565 (PML 1781, as *C. pseudovenetus*, PML 1665), Pl. 566 (PML 245, as *C. venetus* var. *viridis*), Pl. 567 (PML 3265, PML 5466, AB 04-09-251, as *C.* cf. *nothoraphanoides*).

Notes — As revised here, *C. venetus* is a European species occurring as two haplotypes currently lacking biogeographical, ecological or morpho-anatomical distinguishing features (Fig. 2, 3). The species fruits under coniferous trees or *Fagus* and produces relatively small basidiomata that usually display obvious green hues on the pileus (from green yellowish to olive-brown), with a hygrophanous tendency unusual in the subgenus and frequent ochraceous oxidation when ageing. This species delivers spores of 7 × 5.8 µm on average but one collection studied by us yielded smaller spores of 5.4–6.5 × 4.7–5.2 µm, in addition to displaying atypical red staining of the stipe base (GC18091404, Fig. 3c, e). Risk of confusion exists with the newly described *C. jimenezianus* in southern Spain, where the two species co-occur. The late fruiting of the latter, in addition to its bitter taste and association with rockroses should provide sufficient clues in distinguishing the two lookalikes. Our work further establishes the synonymy of *C. pseudovenetus* with *C. venetus* and supports the varietal rank of *C. venetus* var. *viridis*, indicating that the extent of green hues on young basidiomata and that of oxidation in older ones, should not be granted too much taxonomic value. Consistent with the reported synonymy of *C. pseudovenetus* with *C. venetus* var. *montanus* (Bidaud et al. 2005), a short sequence of the holotype of this variety could be obtained and falls within the *C. venetus* clade as well (U. Peintner & R. Kuhnert, pers. comm.). Lastly, authentic material of *C. nothoraphanoides* (ined.) and 3 collections published in the *ADC* as *C.* cf. *nothoraphanoides*, belong to the same clade, strongly suggesting that this invalidly published binomial actually represents a synonym of *C. venetus*. From an evolutionary point of view, *C. venetus* is closest to several East Asiatic sequences and to the western North American *C. fucoflavidus* (cf. Ammirati et al. 2021).

DISCUSSION

Revisiting species boundaries in subgenus Leprocybe

Until the simultaneous publication of *Cortinarius Flora Photographica CFP* (Brandrud et al. 1990) and the *Atlas des Cortinaires ADC* in the late 20th century (Moënne-Loccoz & Reumaux 1990), taxonomic boundaries within subg. *Leprocybe* (= sect. *Veneti*) were for the most part consensual. These two major contemporary monographs were built upon rather opposing views of species concepts, and authors adopted contrasting taxonomic choices to delimit species within this lineage. As a result, only four species were accepted in the *CFP* (Brandrud et al. 1990, 1992, 1998), as opposed to 38 taxa in the *ADC* (Bidaud et al. 2005). The four names included in the *CFP*, *C. cotoneus*, *C. melanotus*, *C. phrygianus* and *C. venetus*, are typified in the companion paper of this study (Ammirati et al. 2021), with sequenced collections from the *CFP* monograph corresponding with the four clades as delineated here. In marked contrast, the phylogenetic identity of the *ADC* taxa remained entirely unresolved prior to the present work, with the exception of *C. raphanodiabolicus sensu ADC*, which has been recently synonymised with *C. sciophylloides* in subg. *Telamonia* (Liimatainen et al. 2017).

Our sequencing efforts on this taxonomically valuable material, allowed us to phylogenetically position 21 of these 38 taxa within subg. *Leprocybe* (Table 1, Fig. 2). In addition, we could demonstrate that *C. raphanoides sensu ADC*, as well as *C. squamulosus sensu ADC* and *C. ignipes sensu ADC*, belong, respectively, to sect. *Brunneotincti* of subg. *Telamonia* (Fig. 2), and dermocyboid lineages unrelated to subg. *Leprocybe* (data not shown). Conversely, it is here confirmed that *C. phrygianus*, treated in sect. *Pholidei* in the *ADC* but in sect. *Veneti* in Funga Nordica, actually belongs to subg. *Leprocybe* (Fig. 2). The remaining 13 taxa described by the French authors in the lineage and still lacking a molecular signature are *C. alutaceoolivascens*, *C. cotoneus*, *C. depexus*, *C. depexus* var. *luminosus*, *C. raphanoides* var. *carnecyaneus*, *C. fulvoraphanoides*, *C. leptopus*, *C. melleifollius*, *C. notatus*, *C. pseudodecoloratus*, *C. subannulatus*, *C. sublanatoides* and *C. valgus* (Bidaud et al. 2005). Considering nonetheless the phylogenetic positioning of successfully sequenced collections, and especially those of *C. raphanoides* and *C. raphanodiabolicus* in subg. *Telamonia*, it seems unlikely that any of these phylogenetically unresolved taxa represent additional biological species in subg. *Leprocybe*.

Controversy over Cortinarius leproleptopus finally settled

One of the main questions we sought to answer in the present study, concerns the phylogenetic identity of *C. leproleptopus* and *C. cepistipes*. The former, described by Chevassut & Henry in 1988, is a striking yellow species fruiting under evergreen oaks in thermophilous woodlands of the Mediterranean, resembling a slender *C. cotoneus* without olivaceous tinges and with smaller spores. A few years later, the same authors introduced the variety *basiluteus*, occurring in the same habitat, but displaying a more bulbous stipe covered at its base with conspicuous remnants of a yellow cortina (Chevassut & Henry 1994). However, following additional harvests of both taxa in their original area of distribution and further collections from the French Alps, Favre & Moreau (2001) concluded that the taxon is chimeric. After revising the type material of both *C. leproleptopus* and of var. *basiluteus*, these authors argued that the diagnosis and the conserved material actually correspond to two distinct species, which can be mostly separated by the extent of development of the hypodermis. For the one represented by the exsiccata (exhibiting a banal filamentous hypodermis), they published a revised description out of a collection from the French Provence (PAM99111002), and epitypified the name with an Italian collection by G. Consiglio (MCVE763/E.C. 94190), while for the one described in the protologue (with a more differentiated hypodermis) and most new harvests of theirs, they introduced the new name *C. cepistipes*.

This move prompted strong criticism from the authors of the *ADC* (Bidaud et al. 2005), who rejected the analysis of Favre & Moreau and controversially introduced a new (but invalid) binomial, *C. leptopus*, in an attempt to reinstate the original species-concept described by Chevassut & Henry under a different name. The *ADC* authors also considered *C. cepistipes* to be a later synonym of *C. psittacinus*, a species that features a subcellular hypodermis as well. Favre & Moreau (2006) subsequently pointed out that *C. leptopus* is indeed invalid, because it was based on the same type as *C. leproleptopus*, and also contested the synonymy of *C. cepistipes* with *C. psittacinus*. Nonetheless, the controversy over the autonomy of *C. cepistipes* and the status of var. *basiluteus*, persisted to this day, as original material from both taxa remained unsequenced. The conspecificity demonstrated here of (i) the holotype and epitype of *C. leproleptopus*, (ii) the holotype and four paratypes of *C. cepistipes*, (iii) PAM99111002, and (iv) the two published collections of *C. leproleptopus sensu ADC*, establishes that *C. leproleptopus* and *C. cepistipes* are conspecific, with nomenclatural priority laying with the former binomial. Additional collections from diverse habitats and geographical regions sequenced for the present work, also illustrate considerable ecological plasticity for this species, significantly extending its distribution range to the eastern limits of the Mediterranean basin (Cyprus) and continental Europe (Germany).

In contrast, the taxonomic status of *C. leproleptopus* var. *basiluteus* remains uncertain, since both collections cited in the original diagnosis by Chevassut & Henry (1994), the holotype n° 3594 and the paratype n° 91.83, could unfortunately not be located. A third authentic collection annotated '*C. leproleptopus* var. *basiluteus*' exists in the two French mycologists' private herbaria, but its voucher id 'Holot. Hry 84109' is cited in the protologue of the type and is thus nomenclaturally linked to var. *leproleptopus*, not var. *basiluteus*. Favre & Moreau (2001) could not explain this oddity but cite *C. leproleptopus* var. *basiluteus* as a synonym of *C. leproleptopus*. Four years later, considering the colour of the pileus and the shape of the stipe, the authors of the *ADC* recombined the taxon as *C. melleifolius* var. *basiluteus*, and added two collections to support their interpretation: AB 03-11-81 and JLC001029-8 (Bidaud et al. 2005). Unfortunately, this material belongs to two distinct clades, *C. leproleptopus* and *C. subcotoneus*, respectively (Table 2, Fig. 2), making this taxon chimeric and too ambiguous to be reliably interpreted based on current data. However, given the remarkable morphological plasticity unveiled here in *C. leproleptopus*, the possibility that this variant represents yet another phenotype of the former, seems highly probable.

A question indirectly raised by this long-standing debate finally needs to be addressed and finds here a partial answer: what is *Cortinarius psittacinus*? The three collections cited in the *ADC* under this name fall in three distinct clades (*C. cotoneus*, *C. leproleptopus* and *C. pescolanensis*; Table 1, Fig. 2), indicating that, as pointed out by Favre & Moreau (2006), the authors of the *ADC* had a mixed interpretation of Moser's species. But so did Moser himself, it seems. Indeed, although the holotype of *C. psittacinus* could unfortunately not be sequenced (R. Kuhnert & U. Peintner, pers. comm.), the plate illustrating the species in the Farbatlas (n° 110, Moser & Jülich 2000) undoubtedly represents a member of subg. *Leprocybe*, akin to *C. cotoneus* and *C. leproleptopus*. However, the only available sequence of this species, obtained from an Italian harvest from Moser himself (UDB001106), falls in sect. *Rubicunduli*, in sister clade relationship to *C. rubicundulus* (Fig. 2). At first glance, this finding comes as a surprise, because this species is phylogenetically unrelated to subg. *Leprocybe* (Garnica et al. 2005, Stensrud et al. 2014, Soop et al. 2019a) and, from a morphoanatomical point of view, displays only superficial resemblance to members of this lineage. However, although included in subg. *Phlegmacium* by some contemporary authors (Bidaud et al. 1999), *C. rubicundulus* is treated in subg. *Leprocybe* by Moser (1978), or in a wide concept of subg. *Cortinarius* by Nordic mycologists (Brandrud et al. 1990). In their typical forms, *C. rubicundulus* and *C. leproleptopus* are easily distinguished from one-another, at least by the strong and rapid yellowing of basidiomata upon bruising and obvious bundles of cystidia on gill edges for the former. The two species may be confused in the field, however, since they can both be found in the same *Fagaceae* woodlands, share the same stout habit and squamulose pilei and, when ageing, they may both develop rusty-brown colours. It is also worth noting that the Italian sequenced collection does not actually belong to *C. rubicundulus*, but to a closely related clade (referred to as *C.* aff. *rubicundulus* in Fig. 2), of which no morphological description or representation are available. Thus, we can only speculate as to whether Moser actually misidentified a slightly deviating collection of *C. rubicundulus*, or collected a cryptic, sister species of the latter possibly lacking some of the obvious diagnostic differences with *C. leproleptopus.* In the current state of knowledge though, *C. psittacinus* does not qualify as an earlier name for *C. leproleptopus*, nor do older binomials such as *C. conopus*, *C. depexus*, *C. notatus* or *C. subnotatus*, all matching some features of *C. leproleptopus*, but also those of *C. cotoneus* and other confirmed species in the subgenus (Favre & Moreau 2001, Bidaud et al. 2005).

Mediterranean Leprocybe: ecological patterns and specificities

A striking pattern emerging from the results of the present study is the strict Mediterranean distribution of three previously undescribed species, each of them defined by highly specialised ecological preferences (habitat, specificity). *Cortinarius jimenezianus* is so far known only from matorral on siliceous soils in southern Spain, where it appears to occur in exclusive association with *Cistus ladanifer*. *Cistaceae* shrubs are prominent components of the Mediterranean biome, often hosting very specific ectomycorrhizal fungi, including several species of *Cortinarius* (Henry & Contu 1986, Vila & Llimona 2006, Ortega et al. 2007, Loizides & Kyriakou 2011, Loizides 2016). This highly specialised ecological niche, formed in heavily eroded and degraded Mediterranean landscapes, is replaced by *Helianthemum* heathlands in northern latitudes, where a different group of *Cortinarius* species thrive in treeless communities in association with perennial plants of genus *Helianthemum* (Barden 2007, Henrici 2010, 2011, Kibby 2015, Dima et al. 2016). Although a limited number of species appear to overlap between these two ecosystems (e.g., *C. cisticola*, *C. decipiens*), the majority of *Cortinarius* diversity in Mediterranean *Cistus* matorral is distinctly different from that of *Helianthemum* heathlands (Liimatainen & Ainsworth 2018). Considering the morphological similarity between *C. jimenezianus* and *C. venetus*, Mediterranean collections assigned to the latter species fruiting near rockroses (e.g., those reported in Bidaud et al. 2007), should be carefully re-examined and sequenced, in order to confirm their phylogenetic identity.

Cortinarius selinolens is in all likelihood associated to *Quercus ilex*, even though a single collection of this species originates from a pure *Arbutus unedo* woodland in Tunisia. Trees of the *Ericaceae* family are known to form arbutoid mycorrhizae (AM) with a broad range of EcM fungi, often acting as 'substitute' hosts for pine- or oak-associated fungi (Molina & Trappe 1982, Kennedy et al. 2012). Consistent with this pattern, three additional *Cortinarius* species (*C. luteocingulatus*, *C. natalis* and an unknown species akin to *C. luteoperonatus*), as well as several Basidiomycota typically linked to thermophilous *Quercus* forests, were also collected in the same Tunisian forest together with *C. selinolens* (F. Richard, pers. comm.). Like some Mediterranean collections of *C. venetus* may in fact reveal to belong to *C. jimenezianus*, reports of *C. melanotus* from sclerophyllous woodlands (e.g., Ortega et al. 2007), may actually refer to *C. selinolens* instead, due to some morphological similarities and, more importantly, a reported odour of parsley.

Cortinarius viridans has so far been exclusively collected under *Cedrus brevifolia*, the endemic cedar of Cyprus, on igneous and serpentine substrates of the Troodos ophiolite. The unique geographical position, altitudinal range and insular character of Cyprus, have contributed in shaping a diverse range of ecosystems and associated fungal diversity, reflected in high numbers of putatively endemic or range-restricted species (Crous et al. 2017, 2018, Loizides et al. 2016, 2019, 2020, Vidal et al. 2019). Ultramafic bedrocks, from which serpentines are derived, often support unique and highly specific plant communities (Whittaker 1954, Brooks 1987), but it is less clear whether these iron-rich, nutrient-poor substrates can act as a strong abiotic filter to EcM and AM fungi (Branco 2010, Southworth et al. 2014, Kohout et al. 2015). Interestingly, *Cortinarius* species have been shown to dominate EcM lineages found in ultramafic soils of New Caledonia (Carriconde et al. 2019), and it is thus possible that the highly specialised ecological and pedoclimatic preferences of *C. viridans*, are indicative of a narrowly endemic distribution of this species confined within the Troodos ophiolitic massif. The taxonomic autonomy of *Cedrus brevifolia* relative to *C. lebani* has been controversial but it is postulated that the former represents recently diverging populations of the latter, supporting an ongoing speciation process in Cyprus (Bou Dagher-Kharrat et al. 2006, Eliades et al. 2011, Jasinska et al. 2012). Further sampling for possible *Leprocybe* occurrences under *C. lebani* in nearby Lebanon as well as in igneous and serpentine-associated ecosystems at a continental scale, will be necessary to confirm this hypothesis in the future.

The neglected Mediterranean hotspot – an emerging area of interest

Besides these novelties, our findings suggest that the Mediterranean functions as a major ecological filter in this lineage, with most species being either absent from this ecoregion, or tightly linked to it. This was somewhat unexpected because many meridional species in the genus occur both in Mediterranean *Quercus ilex* forests and in relatively thermophilous deciduous forests of much northern continental Europe (Brandrud 2000), pretty much like *C. leproleptopus*, *C. melanotus* and *C. subcotoneus*. Such ecological plasticity has been the root of much taxonomic confusion in the past, including the controversial interpretations of extra-Mediterranean collections of *C. leproleptopus*, because Mediterranean species were *a priori* assumed to be distinct from their extra-Mediterranean counterparts, and phenotypic polymorphism was often interpreted as diagnostic features. In *Cortinarius*, such bias is not rare and is responsible, for instance, for the failure to recognize *C. haasii* (extra-Mediterranean) in *C. aurantiorufus* (Mediterranean), when the latter species was first introduced (Bidaud et al. 2001, Frøslev et al. 2007, Bellanger 2015).

It becomes apparent from the results of the present study, that in the absence of a wide phylogenetic taxon sampling from both Mediterranean and continental ecoregions, it is virtually impossible to draw reliable taxonomic conclusions on the ecological, morphological and distributional boundaries of such versatile polymorphic species. Moreover, the evolutionary history of subg. *Leprocybe* as unfolding here, suggests that the Mediterranean has been, and probably still is, a key area of species radiation within this lineage (Fig. 8), confirming that this often-neglected ecoregion is indeed a remarkable hotspot of diversity for higher Fungi. Such findings are of paramount significance in the broader context of climate change, as Mediterranean ecosystems are forecasted to undergo dramatic changes due to accelerated climate warming, including mass aridification, desertification, extensive loss of habitat, shifts in biodiversity composition and perhaps even mass species extinctions (Giorgi 2006, IPCC 2007, Giorgi & Lionello 2008, Richard et al. 2011, Ágreda et al. 2015, Büntgen et al. 2015, Loizides et al. 2019).

Next generation sequencing of old type material – what future in fungal taxonomy?

Nomenclatural instability has hampered fungal taxonomy for decades. The advent of molecular phylogenetic tools at the turn of the millennium, has revolutionised our ability to resolve cryptic or poorly understood species, but still failed to stabilise taxonomy, prompting some scientists to controversially advocate abandoning fungal nomenclature altogether (Money 2013). The inability to reliably assign a single Linnaean binomial to molecularly identified biological species, can be mostly attributed to two fundamental problems:

1. the insufficient representation of type collections in public sequence databases, to which names are legitimately attached; and
2. the inherent difficulties to identify species limits by phylogenetic methods, especially when using the cheap and straightforward ITS rDNA barcoding method (Kiss 2012).

By its ability to sort out original DNA from contamination DNA, next generation sequencing addresses these two shortcomings and is thus expected to soon integrate into the fungal taxonomist's toolbox. First, as demonstrated here and in another recent work (Forin et al. 2018), old and heavily contaminated herbarium material can be 'salvaged' by deep sequencing, due to the potent sensitivity of the method, which is several magnitudes higher than that of Sanger sequencing. Generating and publishing ITS barcodes of ancient holotypes conserved in European and North American fungaria, will undoubtedly mark a milestone in stabilizing fungal taxonomy, as old and previously ambiguous names will be unequivocally deciphered and made available for currently recognised clades. Second, by documenting the intragenomic diversity of the ITS barcode for analysed species, NGS allows selecting SNPs relevant for defining species limits. Indeed, the limited number of nucleotide differences between two closely related clades is often difficult to translate into an informative taxonomy, such as for instance trying to interpret between two recently derived species and a single polymorphic one, the two often representing competing options in the absence of any other criterion. Because polymorphisms tend to fix between two populations upon their reproductive isolation, documenting genetic flow at polymorphic sites is crucial in the decision-making process. In Sanger sequencing of diploid organisms, heterozygocities represent hallmarks of genetic flow between two haplotypes and, as such, they disqualify concerned sites for species diagnosis. However, insufficient sampling, the iterative and stochastic nature of the PCR that tend to asymmetrically amplify alleles over cycles, and excessive data processing of public sequences (Selosse et al. 2016), all converge to mask heterozygocities. The ITS polymorphisms unveiled by NGS at the individual genome scale, alleviate this issue and provide an efficient alternative in disqualifying variable sites for species limit delineation.

Beyond these obvious benefits for fungal taxonomy, the molecular landscape of the ITS allelic diversity within a single fungal genome yields data out of reach of classical Sanger sequencing, of interest to better understand the complex mechanisms of concerted evolution (Eickbush & Eickbush 2007). This process is responsible for sequence homogenization of the multiple alleles of DNA arrays such as the rDNA cistron within individual genomes, limiting sequence variation at the intraspecific scale. However, just a handful of studies have addressed this evolutionary mechanism in fungi and only a very recent one reports on higher Fungi (Tremble et al. 2020). Deciphering how concerted evolution controls the allelic diversity of multiple copy

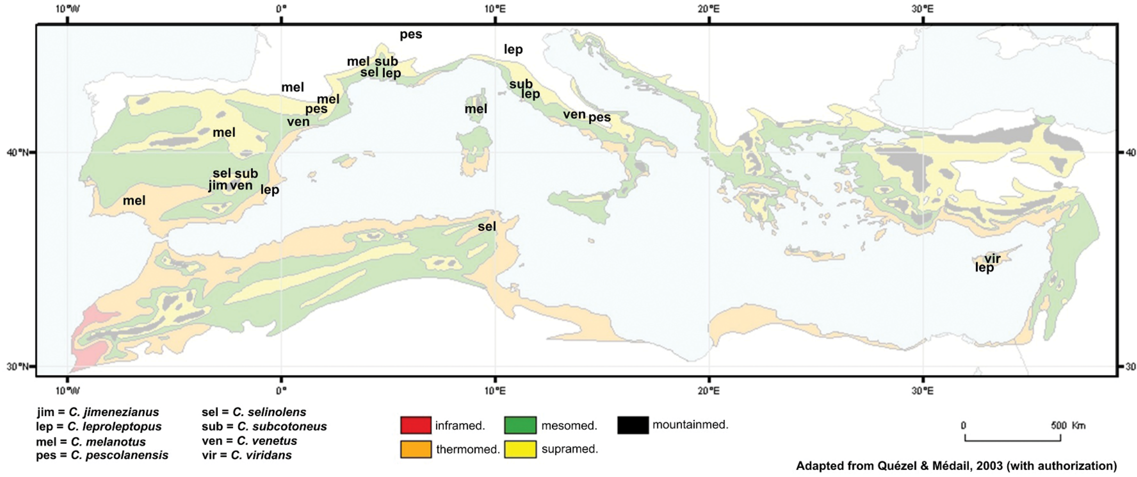

Fig. 8 Biogeographical distribution of *Leprocybe* species in the Mediterranean. Mapping of sequenced collections of the eight confirmed species in subg. *Leprocybe* around the Mediterranean basin. Colours delimit vegetation types in the Mediterranean, as defined in Quézel & Médail (2003). Note that *C. pescolanensis* is present in a single locality within the area, at high elevations, and that *C. cotoneus*, *C. phrygianus* and *C. squamivenetus* are so far not represented in the Mediterranean.

genes in these organisms, and how the process is modulated (or not) by environmental cues, certainly represents a promising research avenue. Although such research lays beyond the scope of the present work, the high intragenomic ITS polymorphism unveiled here in three species of *Cortinarius* was unexpected and contrasts with observations in yeast strains maintained in the lab (Ganley & Kobayashi 2011). However, it is consistent with what has been reported in plant pathogenic fungi and, more recently in *Boletus edulis* (Simon & Weiß 2008, Tremble et al. 2020), suggesting that concerted evolution may be relaxed in some or all lineages of uncultured higher fungi. More work will shed light on the regulatory pathways controlling this universal evolutionary process in Basidiomycota, in relation to relevant ecological constraints.

Key to species

1. In boreal coniferous forests 2
1. In continental or mountainous mesophilous forests, absent from the Mediterranean 3
1. In Mediterranean ecosystems 9

2. Average spore size < 6 × 5 µm, conspicuous brown veil bands on stipe . . . . *C. phrygianus*
2. Average spore size > 6 × 5 µm, conspicuous brown scales on pileus . . . . *C. squamivenetus*

3. Slender species (S > 4) 4
3. Stout species (S < 4)* 5

4. Brown scales on pileus, never hygrophanous, olivaceous-brown dominating hues, parsley odour typical or at least frequent . . . . *C. melanotus*
4. Smooth and often hygrophanous pileus, green dominating hues, odour of parsley absent . . . . *C. venetus*

5. In deciduous forests 6
5. In coniferous forests 8

6. Average spore size > 8.5 × 7 µm. . . . . *C. cotoneus*
6. Average spore size < 8.5 × 7 µm. 7

7. Average spore size = 8 × 6.5 µm, olivaceous-brown dominating hues . . . . *C. subcotoneus*
7. Average spore size = 7.5 × 6 µm, yellow dominating hues . . . . *C. leproleptopus*

8. Average spore size < 6 × 5 µm, conspicuous brown veil bands on stipe . . . . *C. phrygianus*
8. Average spore size > 6 × 5 µm, meridional . . . . *C. pescolanensis*

9. Known from Cyprus, under *Cedrus brevifolia* . *C. viridans*
9. Known from Spain, under *Cistus ladanifer* 10
9. Ecology different 11

10. Flesh bitter, cespitose or densely gregarious . . . . *C. jimenezianus*
10. Flesh mild, solitary to gregarious, rarely cespitose . . . . *C. venetus*

11. *Abies*-dominated, supra-mediterranean ecosystems . . . . *C. pescolanensis*
11. Ecology different 12

12. Stout species (S < 4) 13
12. Slender species (S > 4) 15

13. Average spore size < 8 × 6 µm, yellow dominating hues . . . . *C. leproleptopus*
13. Average spore size > 8 × 6 µm, olivaceous-brown dominating hues 14

14. Scaly pileus and parsley odour, evoking *C. melanotus* . . . . *C. selinolens*
14. Tomentose pileus and rapahanoid odour, evoking *C. cotoneus* . . . . *C. subcotoneus*

15. Brown scales on pileus, never hygrophanous, olivaceous-brown dominating hues, parsley odour frequent . . . . *C. melanotus*
15. Smooth and often hygrophanous pileus, green dominating hues, never with an odour of parsley . . . . . . *C. venetus*

Acknowledgements This work is dedicated to Georges Chevassut (1923–2003) and Fernand Trescol (1925–1993), who devoted their life to describe the diversity of *Cortinarius* in French Mediterranean ecosystems. Their pioneering work in the pre-DNA era has inspired many contemporary mycologists, including some authors of the present study. This work has been initiated by the generous gift of German collections from Gunnar Hensel, Manfred Huth, Günter Saar and Geert Schmidt-Stohn. The authors are grateful to these colleagues, as well as to the following ones for providing us with material analysed in the present work: Josep Ballarà, Tor Erik Brandrud, Rafael Mahiques Santandreu, Antonio Mateos Izquierdo, Jose Mora Gómez, Pierre-Arthur Moreau, Alberto Pérez Puente, Franck Richard, Luis Romero de la Osa, Nicolas Suberbielle and Stefano Toninelli. We also warmly thank Philippe Clerc from G, as well as Regina Kuhnert and Ursula Peintner from IB, for sending us precious material and unpublished sequences. Preparation of samples for sequencing was performed at the GEMEX facility of the Functional and Evolutive Ecology Center (CEFE) of Montpellier (Head: Marie-Pierre Dubois). Illumina deep sequencing was performed at the GENSEQ facility of the Labex CeMEB of Montpellier (Head: Eric Desmarais & Frédérique Cerqueira). Finally, we warmly thank the two referees for their thorough and constructive reviewing of our manuscript.

REFERENCES

Ágreda T, Águeda B, Olano JM, et al. 2015. Increased evapotranspiration demand in a Mediterranean climate might cause a decline in fungal yields under global warming. Global Change Biology 21 (9): 3499–3510.

Ammirati J, Barlow TE, Seidl M, et al. 2012. Cortinarius parkeri, a new species from the Pacific Northwest of North America. Botany 90: 327–335.

Ammirati J, Liimatainen K, Bojantchev D, et al. 2021. Cortinarius subgenus Leprocybe, unexpected diversity and significant differences in species compositions between western and eastern North America. Persoonia 46: 216–239.

Anisimova M, Gil M, Dufayard JF, et al. 2011. Survey of branch support methods demonstrates accuracy, power, and robustness of fast likelihood-based approximation schemes. Systematic Biology 60: 685–699.

Ballarà J, Mahiques R, Garrido-Benavent I. 2017. Estudi de Cortinariaceae del Parc natural Cadí-Moixeró (IV). Moixeró 9: 20–49.

Barden N. 2007. Helianthemum grasslands of the Peak District and their possible mycorrhizal associates. Field Mycology 8 (4): 119–126.

Bellanger J-M. 2015. Les cortinaires calochroïdes: une mise au point taxinomique. Documents mycologiques 36: 3–34.

Bellanger J-M, Bidaud A, Moreau P-A. 2018. Qu'est-ce que Cortinarius parasuaveolens? Documents mycologiques 37: 39–51.

Bellanger J-M, Moreau P-A, Corriol G, et al. 2015. Plunging hands into the mushroom jar: a phylogenetic framework for Lyophyllaceae (Agaricales, Basidiomycota). Genetica 143: 169–194.

Bidaud A, Bellanger J-M, Carteret X, et al. 2017. Atlas des Cortinaires, pars XXIV. Éditions Fédération mycologique Dauphiné-Savoie. Marlioz.

Bidaud A, Moënne-Loccoz P, Reumaux P. 1994. Validitates. Documents myco logiques 24 (95): 40.

Bidaud A, Moënne-Loccoz P, Reumaux P. 1999. Atlas des Cortinaires, pars IX. Éditions Fédération mycologique Dauphiné-Savoie. Marlioz.

Bidaud A, Moënne-Loccoz P, Reumaux P. 2001. Atlas des Cortinaires, pars XI. Editions Fédération mycologique Dauphiné-Savoie. Marlioz.

Bidaud A, Moënne-Loccoz P, Reumaux P., et al. 2005. Atlas des Cortinaires, Pars XV. Éditions Fédération mycologique Dauphiné-Savoie. Marlioz.

Bidaud A, Ortega A, Vila J. 2007. Tres Cortinarius, seccion Leprocybe del area mediterranea de la peninsula iberica. Micologia e Vegetazione Mediterranea 22 (1): 41–49.

Bödeker IT, Clemmensen KE, De Boer W, et al. 2014. Ectomycorrhizal Cortinarius species participate in enzymatic oxidation of humus in northern forest ecosystems. New Phytologist 203 (1): 245–256.

Bou Dagher-Kharrat M, Mariette S, Lefèvre F, et al. 2006. Geographical diversity and genetic relationships among Cedrus species estimated by AFLP. Tree Genet Genomes 3: 275–285.

Branco S. 2010. Serpentine soils promote ectomycorrhizal fungal diversity. Molecular Ecology 19 (24): 5566–5576.

---

* cf. Materials and Methods.

Brandrud TE. 2000. Some distribution patterns of Cortinarius subgenus Phlegmacium species in Europe. The Journal of the J.E.C. 2: 49–70.

Brandrud TE, Bendiksen E. 2014. Sandfuruskogog sandfuru-skogsopper. Viktige områder for biologisk mangfold. NINA Rapport 1042, Oslo.

Brandrud TE, Lindström H, Marklund H, et al. 1990. Cortinarius Flora Photographica. Vol. I (French version). Cortinarius HB, Sweden.

Brandrud TE, Lindström H, Marklund H, et al. 1992. Cortinarius Flora Photographica. Vol. II (French version). Cortinarius HB, Sweden.

Brandrud TE, Lindström H, Marklund H, et al. 1994. Cortinarius Flora Photographica. Vol. III (French version). Cortinarius HB, Sweden.

Brandrud TE, Lindström H, Marklund H, et al. 1998. Cortinarius Flora Photographica. Vol. IV (French version). Cortinarius HB, Sweden.

Brandrud TE, Lindström H, Marklund H, et al. 2014. Cortinarius Flora Photographica. Vol. V (French version). Cortinarius HB, Sweden.

Britzelmayr M. 1895. Materialien zur Beschreibung der Hymenomyceten 5. Botanisches Centralblatt 62 (10): 305–313.

Brooks RR. 1987. Serpentine and its vegetation: A multidisciplinary approach. Ed Dioscorides Press, Portland.

Büntgen U, Egli S, Galván JD, et al. 2015. Drought-induced changes in the phenology, productivity and diversity of Spanish fungi. Fungal Ecology 16: 6–18.

Cailleux A. 1981. Code des couleurs des sols. Boubée, Paris.

Carriconde F, Gardes M, Bellanger J-M, et al. 2019. Host effects in high ectomycorrhizal diversity tropical rainforests on ultramafic soils in New Caledonia. Fungal Ecology 39: 201–212.

Chevassut G, Henry R. 1975. Six cortinaires méditerranéens nouveaux du chêne vert dans le Bas-Languedoc. Documents mycologiques 5 (20): 23–36.

Chevassut G, Henry R. 1988. Cortinaires nouveaux ou rares de la région Languedoc-Cévennes (3ème note - suite n°2). Documents mycologiques 19 (73): 45–62.

Chevassut G, Henry R. 1994. Cortinaires nouveaux ou rares de Languedoc-Cévennes (Pars 4). Documents Mycologiques 24 (94): 57–62.

Chevassut G, Trescol F. 1986. Un nouveau Phlegmacium Scauri (Cortinarius auricilis) abondant dans la chênaie verte méditerranéenne française. Documents mycologiques 16 (63–64): 67–74.

Cheype J-L. 2014. Contribution à la connaissance des champignons de la haute vallée de l'Arve (Haute-Savoie). Bulletin mycologique et botanique Dauphiné-Savoie 214: 16–18.

Clericuzio M, Dovana F, Bellanger J-M, et al. 2017. Cortinarius parasuaveolens (= C. pseudogracilior): new data and a synonymy of a very poorly known species of section Calochroi. Sydowia 69-2017–0213.

Comandini O, Contu M, Rinaldi AC. 2006. An overview of Cistus ectomycorrhizal fungi. Mycorrhiza 16: 381–395.

Consiglio G. 2012. Il Genere Cortinarius in Italia, parte sesta. Associazione Micologica Bresadola. Fondazione Centro Studi Micologici, Trento.

Consiglio G, Antonini D, Antonini M. 2003. Il Genere Cortinarius in Italia, parte prima. Associazione Micologica Bresadola. Fondazione Centro Studi Micologici, Vicenza.

Consiglio G, Antonini D, Antonini M. 2004. Il Genere Cortinarius in Italia, parte seconda. Associazione Micologica Bresadola. Fondazione Centro Studi Micologici, Vicenza.

Consiglio G, Antonini D, Antonini M. 2006. Il Genere Cortinarius in Italia, parte quarta. Associazione Micologica Bresadola. Fondazione Centro Studi Micologici, Vicenza.

Consiglio G, Moënne-Loccoz P. 2004. Cortinarius multiformium, sp. nov. Rivista di Micologia 47 (4): 324.

Crous PW, Wingfield MJ, Burgess TI, et al. 2017. Fungal Planet description sheets 625–715. Persoonia 39: 270–467.

Crous PW, Wingfield MJ, Burgess TI, et al. 2018. Fungal Planet description sheets 716–784. Persoonia 40: 240–393.

Dereeper A, Guignon V, Blanc G, et al. 2008. Phylogeny.fr: robust phylogenetic analysis for the non-specialist. Nucleic Acids Research 36: W465–W469.

Dima B, Liimatainen K, Niskanen T, et al. 2014. Two new species of Cortinarius, subgenus Telamonia, sections Colymbadini and Uracei, from Europe. Mycological Progress 13: 867–879.

Dima B, Lindström H, Liimatainen K, et al. 2016. Typification of Friesian names in Cortinarius sections Anomali, Spilomei, and Bolares, and description of two new species from northern Europe. Mycological Progress 15 (9): 903–919.

Edgar RC. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32: 1792–1797.

Eickbush TH, Eickbush DG. 2007. Finely orchestrated movements: evolution of the ribosomal RNA genes. Genetics 175: 477–485.

Eliades NGH, Gailing O, Leinemann L, et al. 2011. High genetic diversity and significant population structure in Cedrus brevifolia Henry, a narrow endemic Mediterranean tree from Cyprus. Plant Systematics and Evolution 294: 185–198.

Eyssartier G, Roux P. 2017. Guide des champignons – France et Europe – 4e edition. Ed Belin, Paris.

Favre A, Moreau P-A. 2001. Investigazioni intorno a Cortinarius leproleptopus Chevassut & R. Henry. Rivista di Micologia 44 (1): 15–26.

Favre A, Moreau P-A. 2006. Rêves, délires et chimères: commentaires sur l'Atlas des Cortinaires, pars XV. Bulletin mycologique et botanique Dauphiné-Savoie 183: 55–60.

Forin N, Nigris S, Voyron S, et al. 2018. Next generation sequencing of ancient fungal specimens: The case of the Saccardo mycological herbarium. Frontiers in Ecology and Evolution 6: 129.

Fries EM. 1818. Observationes Mycologicae 2. Copenhagen.

Fries EM. 1838. Epicrisis Systematis Mycologici. Uppsala.

Fries EM. 1874. Hymenomycetes europaei. Upsaliae.

Frøslev TG, Jeppesen TS, Læssøe T, et al. 2007. Molecular phylogenetics and delimitation of species in Cortinarius section Calochroi (Basidiomycota, Agaricales) in Europe. Molecular Phylogenetics and Evolution 44: 217–227.

Ganley ARD, Kobayashi T. 2011. Monitoring the rate and dynamics of concerted evolution in the ribosomal DNA repeats of Saccharomyces cerevisiae using experimental evolution. Molecular Biology and Evolution 28 (10): 2883–2891.

Gardes M, Bruns TD. 1993. ITS primers with enhanced specificity for basidiomycetes. Application to the identification of mycorrhizae and rusts. Molecular Ecology 2: 113–118.

Garnica S, Schön ME, Abarenkov K, et al. 2016. Determining threshold values for barcoding fungi: lessons from Cortinarius (Basidiomycota), a highly diverse and widespread ectomycorrhizal genus. FEMS Microbiology Ecology 92 (4): fiw045.

Garnica S, Weiß M, Oertel B, et al. 2005. A framework for a phylogenetic classification in the genus Cortinarius (Basidiomycota, Agaricales) derived from morphological and molecular data. Canadian Journal of Botany 83: 1457–1477.

Gelman A, Rubin DB. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7: 457–511.

Giorgi F. 2006. Climate change hot-spots. Geophysical Research Letters 33 (8): L08707.

Giorgi F, Lionello P. 2008. Climate change projections for the Mediterranean region. Global and Planetary Change 63 (2): 90–104.

Guindon S, Lethiec F, Duroux P, et al. 2010. PHYML online – a web server for fast maximum likelihood-based phylogenetic inference. Nucleic Acids Research 33 (Web server issue): W557–559.

Henrici A. 2010. Notes & records. Field Mycology 11 (2): 69–70.

Henrici A. 2011. Notes & records. Field Mycology 12 (1): 34–36.

Henry R. 1961. Cortinaires rares ou nouveaux du Doubs, du Jura et des Vosges. Bulletin de la Société Mycologique de France 77 (2): 116.

Henry R. 1977. Nouveau regard sur les cortinaires. Bulletin de la Société Mycologique de France 93 (3): 342–343.

Henry R, Contu M. 1986. Description d'une nouvelle espèce xéro-thermophile, Cortinarius xerophilus sp. nov. Documents mycologiques 16 (63–64): 63–65.

Hlaváček J. 1987. Mykologický sbornik 64 (5): 247.

Intergovernmental Panel on Climate Change [IPCC]. 2007. The physical science basis, Working Group I. Contribution to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change: 996. Cambridge University Press, Cambridge.

Jasinska AK, Boratynska K, Sobierajska K, et al. 2012. Relationships among Cedrus libani, C. brevifolia and C. atlantica as revealed by the morphological and anatomical needle characters. Plant Systematics and Evolution 299: 35–48.

Kalchbrenner C. 1875. Icones selectae Hymenomycetum Hungariae 3: 37–50.

Kennedy PG, Smith DP, Horton TR, et al. 2012. Arbutus menziesii (Ericaceae) facilitates regeneration dynamics in mixed evergreen forest by promoting mycorrhizal fungal diversity and connectivity. American Journal of Botany 99 (10): 1691–1701.

Kibby G. 2015. Fungal portraits No. 64: Cortinarius bolaris. Field Mycology 16: 111–112.

Kiss L. 2012. Limits of nuclear ribosomal DNA internal transcribed spacer (ITS) sequences as species barcodes for Fungi. Proceedings of the National Academy of Sciences of the United States of America 109 (27): E1811.

Kohout P, Doubková P, Bahram M, et al. 2015. Niche partitioning in arbuscular mycorrhizal communities in temperate grasslands: a lesson from adjacent serpentine and nonserpentine habitats. Molecular Ecology 24 (8): 1831–1843.

Konrad P, Maublanc A. 1937. Icones Selectae Fungorum VI. Lechevalier, Paris.

Kuntze O. 1891. Revisio Generum Plantarum 2. Leipzig.

Kuyper TW. 1986. A revision of the genus Inocybe in Europe. I. Subgenus Inosperma and the smooth-spored species of subgenus Inocybe. Persoonia Supplement Volume 3.

Liimatainen K. 2014. Nomenclatural novelties. Index Fungorum 196 (1): 2.

Liimatainen K, Ainsworth AM. 2018. Fifteen Cortinarius species associated with Helianthemum in Great Britain: results of a DNA-based analysis. Field Mycology 19 (4): 119–135.

Liimatainen K, Carteret X, Dima B, et al. 2017. Cortinarius section Bicolores and section Saturnini (Basidiomycota, Agaricales), a morphogenetic overview of European and North American species. Persoonia 39: 175–200.

Loizides M. 2016. Macromycetes within Cistaceae-dominated ecosystems in Cyprus. Mycotaxon link page 131: 255–256.

Loizides M, Alvarado P, Polemis E, et al. 2020. Multiple evolutionary origins of sequestrate species in the agaricoid genus Chlorophyllum. Mycologia 112: 400–422.

Loizides M, Bellanger J-M, Assyov B, et al. 2019. Present status and future of boletoid fungi (Boletaceae) on the island of Cyprus: Cryptic and threatened diversity unravelled by ten-year study. Fungal Ecology 41: 65–81.

Loizides M, Bellanger J-M, Clowez P, et al. 2016. Combined phylogenetic and morphological studies of true morels (Pezizales, Ascomycota) in Cyprus reveal significant diversity, including Morchella arbutiphila and M. disparilis spp. nov. Mycological progress 15: 39.

Loizides M, Kyriakou T. 2011. Fungi of the Cistus Maquis. Field Mycology 12: 14–22.

Mahiques R, Ballará J, Salom JC, et al. 2018. Morphogenetic diversity of the ectomycorrhizal genus Cortinarius section Calochroi in the Iberian Peninsula. Mycological Progress 17 (7): 815–831.

Maire R. 1933. Fungi Catalaunici: Contributions à l'étude de la Flore Mycologique de la Catalogne: 1–120.

Martin F, Kohler A, Murat C, et al. 2016. Unearthing the roots of ectomycorrhizal symbiosis. Nature Reviews Microbiology 14: 760–773.

McInerney P, Adams P, Hadi MZ. 2014. Error rate comparison during polymerase chain reaction by DNA polymerase. Molecular Biology International, Article ID 287430.

Médail F, Myers N. 2004. Mediterranean basin. In: Hotspots revisited: Earth's biologically richest and most endangered terrestrial ecoregions, pp. 144e147.

Médail F, Quézel P. 1997. Hot-spots analysis for conservation of plant biodiversity in the Mediterranean basin. Annals of the Missouri Botanical Garden 84 (1): 112e127.

Moënne-Loccoz P, Reumaux P. 1990. Atlas des Cortinaires, pars I. Éditions Fédération mycologique Dauphiné-Savoie, Annecy.

Molina RJ, Trappe JM. 1982. Lack of mycorrhizal specificity by the ericaceous hosts Arbutus menziesii and Arctostaphylos uva-ursi. New Phytologist 90: 495–509.

Money NP. 2013. Against the naming of fungi. Fungal Biology 117 (7–8): 463–465.

Moser M. 1969. Cortinarius Fr. Untergattung Leprocybe subgen. nov., Die Rauhköpfe. Zeitschrift für Pilzkunde 35 (3): 213–248.

Moser M. 1970. Cortinarius Fr., untergattung Leprocybe subgen. nov. Die Rauhköpfe. Vorstudien zu einer monographie. Zeitschrift für Pilzkunde 36 (1–2): 37–57.

Moser M. 1978. Die Röhrlinge und Blätterpilze, 4th edition. In: Gams H (ed), Kleine Kryptogamenflora IIb/2. Fischer Verlag, Stuttgart.

Moser M. 1986. Guida alla determinazione dei funghi (Polyporales, Boletales, Agaricales, Russulales).

Moser M, Jülich W. 2000. Farbatlas Der Basidiomyceten, Lfg 18. 110 pl.

Myers N, Mittermeier RA, Mittermeier CG, et al. 2000. Biodiversity hotspots for conservation priorities. Nature 403 (6772): 853e858.

Nilsson RH, Larsson KH, Taylor AFS, et al. 2018. The UNITE database for molecular identification of fungi: handling dark taxa and parallel taxonomic classifications. Nucleic Acids Research 47 (D1): D259–D264. https://doi.org/10.1093/nar/gky1022.

Niskanen T, Kytövuori I. 2012. Subgen. Cortinarius sect. Veneti Konrad & Maubl. In: Knudsen H, Vesterholt J (eds), Funga Nordica Vol. 2, Agaricoid, boletoid, clavarioid, cyphelloid and gastroid genera: 765–766. Nordsvamp, Copenhagen.

Niskanen T, Kytövuori I, Bendiksen E, et al. 2012. Cortinarius (Pers.) Gray. In: Knudsen H, Vesterholt J (eds), Funga Nordica Vol. 2, Agaricoid, boletoid, clavarioid, cyphelloid and gastroid genera: 762–885. Nordsvamp, Copenhagen.

Niskanen T, Liimatainen K, Kytövuori I, et al. 2016. Cortinarius subgenus Callistei in North America and Europe – type studies, diversity, and distribution of species. Mycologia 108 (5): 1018–1027.

Ortega A, Mahiques R. 1995. Contribución al estudio del genero Cortinarius en España Peninsular. I. Cryptogamie Mycologie 16 (4): 243–275.

Ortega A, Suárez-Santiago VN, Reyes JD. 2008. Morphological and ITS identification of Cortinarius species (section Calochroi) collected in Mediterranean Quercus woodlands. Fungal Diversity 29: 73–88.

Ortega A, Vila J, Bidaud A, et al. 2007. Notes on four mediterranean Cortinarius fruiting in sclerophilous and heliophilous plant ecosystems. Mycotaxon 101: 137–147.

Peintner U, Moncalvo JM, Vilgalys R. 2004. Toward a better understanding of the infrageneric relationships in Cortinarius. Mycologia 96 (5): 1042–1058.

Pellitier PT, Zak DR. 2017. Ectomycorrhizal fungi and the enzymatic liberation of nitrogen from soil organic matter: why evolutionary history matters. New Phytologist 217 (1): 68–73.

Pfeiffer F, Gröber C, Blank M, et al. 2018. Systematic evaluation of error rates and causes in short samples in next-generation sequencing. Scientific Reports 8: 10950.

Picillo B, Marchionni M. 2016. Cortinarius pescolanensis (Basidiomycota, Cortinariaceae), una nuova specie dal Molise (Italia). Micologia e Vegetazione Mediterranea 31 (1): 61–74.

Prosser SW, deWaard JR, Miller SE, et al. 2015. DNA barcodes from century-old type specimens using next-generation sequencing. Molecular Ecology Resources 16 (2): 487–497.

Quézel P, Médail F. 2003. Écologie et biogéographie des forêts du bassin méditerranéen. Elsevier, Paris.

Richard F, Roy M, Shahin O, et al. 2011. Ectomycorrhizal communities in Mediterranean forest ecosystem dominated by Quercus ilex: season dynamics and response to drought in the surface organic horizon. Annals of Forest Science 68 (1): 57–68.

Ricken A. 1915. Die Blätterpilze. Weigel, Leipzig.

Ronquist F, Huelsenbeck JP. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574.

Schäffer J, Moser M. 1957. Beihefte zur Sydowia 1: 226.

Séguy E. 1936. Code universel des couleurs. Encyclopédie Pratique du Naturaliste 30. Lechevalier, Paris.

Selosse M-A, Vincenot L, Opik M. 2016. Data processing can mask biology: towards better reporting of fungal barcoding data? New Phytologist 210 (4): 1159–1164.

Simon UK, Weiß M. 2008. Intragenomic variation of fungal ribosomal genes is higher than previously thought. Molecular Biology and Evolution 25 (11): 2251–2254.

Smith SE, Read D. 2010. Mycorrhizal symbiosis. Academic Press, Boston (ed), Amsterdam.

Soop K, Dima B, Cooper JA, et al. 2019a. A phylogenetic approach to a global supraspecific taxonomy of Cortinarius (Agaricales) with an emphasis on the southern mycota. Persoonia 42: 261–290.

Soop K, Schmidt-Stohn G, Dima B, et al. 2019b. Cortinarius subgenus Phlegmacium sect. Aureocistophili in Europe. The Journal of the J.E.C. 21: 33–54.

Southworth D, Tackaberry LE, Massicotte HB. 2014. Mycorrhizal ecology on serpentine soils. Plant Ecology & Diversity 7 (3): 445–455.

Stensrud Ø, Orr R, Reier-Røberg K. 2014. Phylogenetic relationships in Cortinarius with focus on North European species. Karstenia 54: 57–71.

Suárez-Santiago VN, Ortega A, Peintner U, et al. 2009. Study on Cortinarius subgenus Telamonia section Hydrocybe in Europe, with especial emphasis on Mediterranean taxa. Mycological Research 113: 1070–1090.

Tedersoo L, Nara K. 2010. General latitudinal gradient of biodiversity is reversed in ectomycorrhizal fungi. New Phytologist 185: 351e354.

Tremble K, Suz LM, Dentinger DTM. 2020. Lost in Translation: population genomics and long-read sequencing reveals relaxation of concerted evolution of the ribosomal DNA cistron. Molecular Phylogenetics and Evolution 148: 106804.

Trog JG. 1844. Verzeichnis schweizerischer Schwämme. Bern, Switzerland.

Vidal JM, Alvarado P, Loizides M, et al. 2019. A phylogenetic and taxonomic revision of sequestrate Russulaceae in Mediterranean and temperate Europe. Persoonia 42: 127–185.

Vila J, Llimona X. 2006. Noves dades sobre el component fúngic de les comunitats de Cistus de Catalunya II. Revista Catalana de Micologia 28: 167–207.

White TJ, Bruns T, Lee S, et al. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, et al. (eds), PCR Protocols: a guide to methods and applications: 315–322. Academic Press, New York.

Whittaker RH. 1954. The ecology of serpentine soils. Ecology 35 (2): 258–288.