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Cortinarius* (Basidiomycota, Cortinariaceae) section *Crassispori* revisited: resolving the *C. chevassutii* complex and demystifying *C. variebulbus

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Abstract

Numerous collections made in deciduous and evergreen oak woodlands of Europe allowed us to re-evaluate, both morphologically and molecularly, the systematic position and taxonomic boundaries of *Cortinarius chevassutii* f. *personatus*. This infraspecific taxon and *Cortinarius chevassutii* share the same ecological niche, an identical distribution pattern, and can even co-occur in the same spot, making their distinction quite challenging, morphologically. However, the phylogenetic analysis of our broad dataset supports two reproductively isolated taxa that both deserve the rank of species. According to recent findings, *Cortinarius pseudobulliardoides* is the name to apply to the former *C. chevassutii* f. *personatus*. Based on present knowledge, spore size and average length/width ratio represents the most reliable diagnostic criterion to separate the two species. Additionally, through next generation sequencing (Illumina) of its holotype, we here reveal the phylogenetic position of *Cortinarius variebulbus* within the same sect. *Crassispori*. Recent phylogenetically confirmed collections of this species allow us to document and illustrate this taxon for the first time.

Key words: Phylogeny, taxonomy, ectomycorrhizal, *Telamonia*

Introduction

In recent years, the systematics of *Cortinarius* (Pers.) Gray (1821: 627) has undergone major changes due to DNA sequencing of an increasing number of herbarium collections, including all the putatively new species, as well as the phylogenetic revision of most sections from both hemispheres (Liimatainen *et al.* 2014, Garnica *et al.* 2016, Soop *et al.* 2019, Liimatainen *et al.* 2020). Recently, Liimatainen *et al.* (2022) split the genus *Cortinarius* into 10 genera based on phylogenomic and multi-gene sequence data. *Cortinarius* subgenus *Telamonia* (Fr.) Trog is the most diverse group within the genus and its species are considered taxonomically complex and morphologically challenging (Liimatainen *et al.* 2020). Most of these species are found in the coniferous forests of the Northern Hemisphere (Soop *et al.* 2019).

Knowledge of telamonioid species has increased significantly following the work of Liimatainen *et al.* (2020), that circumscribed no less than 80 phylogenetic sections with their own morphological characteristics. However, this subgeneric organization leaves aside several “lonely riders”, as often informally referred to by *Cortinarius* molecular taxonomists, which do not fit into any recognized section (Bellanger *et al.* 2022b). Furthermore, as these authors acknowledge, some species were not included in the analyses because of short sequences or because they were under study (Liimatainen *et al.* 2020).

Fleshy and grey-brown *Cortinarius* with a bulbous stipe and brownish context are often referred to as “bovinoid” taxa, a group of species actually nesting in several unrelated lineages including, *e.g.*, sect. *Bovini* M.M. Moser, sect. *Sordescentes* Melot, or sect. *Phaeosmi* Liimatainen, Niskanen & Kytövuori (Bellanger *et al.* 2022a). One further such group is *Cortinarius* sect. *Crassispori* Kytöv., Niskanen & Liimatainen, which is dealt with in this article. Section *Crassispori* represents a well-supported clade in a basal position within the “Crown *Telamonias*”, and encompasses species distributed in coniferous and deciduous forests in Europe and North America (Niskanen *et al.* 2020; Liimatainen *et al.* 2020). The three species so far known to belong in section *Crassispori*, *C. chevassutii* Rob. Henry [as ‘*chevassuti*’], in Chevassut & Henry (1982: 37), *C. crassisporus* Kytöv., Niskanen & Liimat., in Niskanen (2014: 1) and *C. duboisensis* Ammirati, Beug, Niskanen & Liimat., in Li *et al.* (2016: 145), share medium to large basidioma size, and a whitish universal veil. Spores can be rather variable in shape: amygdaloid, ellipsoid, obovoid or ovoid to almost subglobose, with dimensions smaller than $13.5 \times 9.0 \mu\text{m}$ (Niskanen *et al.* 2020).

The present work sheds new light on section *Crassispori*, by clarifying the taxonomy of the *C. chevassutii* complex, with the introduction of *C. pseudobulliardoides* Carteret & Reumaux (2012: 274) as a synonym of *C. chevassutii* f. *personatus* Bidaud, in Bidaud *et al.* (2002: 691), and by reporting on *C. variebulbus* Chevassut & Rob. Henry (1982: 42), so far absent from public sequence databases, as an additional member in the section. Updated descriptions and *in situ* photographs of these three species are provided.

Materials and methods

Macro- and micromorphological descriptions

The collections were photographed in the field or in the laboratory and detailed descriptions were made using fresh material. Macrochemical reactions were tested with Guaiac tincture. Micro-anatomical studies were conducted on sections from the pileus, stipe and lamellae, revived and mounted in Congo Red, or in 2 % KOH. Spore measurements were taken from natural deposits on the stipe surface of dry basidiomata, mounted in 2 % KOH and measured under a digital camera Leica ICC50 mounted on a Leica microscope model DMLS. Since it was not always possible to obtain a sufficient quantity of spores from those naturally deposited on the stipe or cortina, a spore preparation from the lamellae was made for each collection in order to achieve a better comparison of spore size across collections. The spore size indicated in the text excludes the apiculus and refers to a 95 % confidence interval in order to exclude aberrant spores. In the descriptions, the number of analyzed collections, basidiomata, and single spores are indicated (in this order) in square brackets. MV refers to the average value, and Q_m to the average length/width quotient ($Q = L/W$). The term «intercarpic variation» here means the variation of spore measurements between specimens from different collections of one species. The 95 % confidence ellipses of spore variation were calculated with the statistical software R (<https://www.r-project.org>). The four-class scale “non-dextrinoid, weakly dextrinoid, moderately dextrinoid and strongly dextrinoid” adopted in this study to classify the dextrinoid reaction of the basidiospores, follows Niskanen (2008). The collected specimens were deposited in the personal herbaria of the authors and at TR (MUSE - Museo delle Scienze di Trento).

Molecular analyses

For the present analysis, 56 collections from France, Germany, Italy, Norway and Spain have been sequenced, including 5 types. Total DNA was extracted and amplified from dried samples using a modified protocol based on Murray & Thompson (1980), or with the REDExtract-N-Amptm Plant PCR Kit (Sigma-Aldrich, St. Louis, MO, USA), following the manufacturer’s instructions. PCR reactions included 35 cycles at a temperature of annealing of 54 °C. The primers ITS1F and ITS4 (White *et al.* 1990, Gardes & Bruns 1993) were used to amplify the ITS rDNA region. Amplicons were purified and Sanger sequenced at Alvalab (Oviedo, Spain) or at Eurofins Genomics (Ebersberg, Germany). The holotype of *C. variebulbus*, unsuccessfully sequenced by the Sanger method, likely due to DNA degradation or contamination by other fungi, was sequenced by an Illumina MiSeq approach, as described in Ševčíková *et al.* (2023).

The chromatograms were manually inspected and edited to optimize indel alignment. The sequences were deposited in GenBank (www.ncbi.nlm.nih.gov/genbank) and the accession numbers are reported in Table 1.

A final dataset of 70 ITS sequences, including the 56 newly generated sequences, 10 public sequences belonging to sect. *Crassispori*, and four *Telamonia* sequences chosen as outgroup, was assembled. Phylogenetic analyses were all performed online at www.phylogeny.lirmm.fr (Dereeper *et al.* 2008) or at <https://ngphylogeny.fr/> (Lemoine *et al.* 2019). Multiple sequence alignment was carried out with MUSCLE 3.7 (Edgar 2004). Fixed indels within *C. chevassutii* and *C. pseudobulliardoides* were coded as transitions to increase resolution of the two clades in Figure 1. Maximum Likelihood (ML) phylogenetic analysis was performed with PhyML 3.0 (Guindon *et al.* 2010). 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. Bayesian inference (BI) of phylogeny was performed using MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003), running 1,000,000 generations. Tree and parameters were sampled every 1,000 generations (1,000 trees), with a burn-in set to 25 % (250 trees). Branch support was assessed by Bayesian posterior probabilities (BPP). Trees were built online using Newick Display 1.6 and edited with Inkscape 0.91 (<https://inkscape.org/fr/>).

TABLE 1. Collections used in phylogenetic analyses and morphological studies. Sequences newly generated from the present work are highlighted in bold in the last column. *This holotype collection has been erroneously identified as n°5357 in Bidaud *et al.* (2002, p. 691), but the material corresponds to that of PML5356, described in the same publication (A. Bidaud, pers. com.).

Species	Voucher id	Country	Collection date	Associated trees	Genbank ITS
<i>Cortinarius chevassutii</i>	Henry 70955 (holotype, PC)	France	unknown	<i>Quercus ilex</i>	MT934956
<i>Cortinarius chevassutii</i>	Henry 71305 (holotype of <i>C. subsordescens</i> , PC)	France	10/1977	<i>Quercus ilex</i>	MT935527
<i>Cortinarius chevassutii</i>	Henry 82169 (PC)	France	unknown	unknown	MT934957
<i>Cortinarius chevassutii</i>	FR10-SML-1	France	30/10/2010	<i>Quercus ilex</i>	PP919203
<i>Cortinarius chevassutii</i>	JMB2010110109	France	01/11/2010	<i>Quercus ilex</i>	PP919205
<i>Cortinarius chevassutii</i>	Pezilla62	France	23/11/2011	<i>Quercus ilex</i>	PP919204
<i>Cortinarius chevassutii</i>	KS-CO2137	France	23/10/2013	<i>Quercus ilex</i>	PP919221
<i>Cortinarius chevassutii</i>	SSt13-216	France	23/10/2013	<i>Quercus ilex</i>	PP919201
<i>Cortinarius chevassutii</i>	TG2013-163	France	23/10/2013	<i>Quercus ilex</i>	PP919223
<i>Cortinarius chevassutii</i>	TG2013-164	France	23/10/2013	<i>Quercus ilex</i>	PP919224
<i>Cortinarius chevassutii</i>	FA4547	France	10/11/2018	<i>Quercus ilex</i> , <i>Q. pubescens</i>	PP919195
<i>Cortinarius chevassutii</i>	CFP1277a (S)	Hungary	26/10/1994	<i>Quercus</i> spp.	MT934958
<i>Cortinarius chevassutii</i>	MCVE:12546 (as <i>C. diosmus</i>)	Italy	01/10/1995	<i>Quercus ilex</i>	JF907895
<i>Cortinarius chevassutii</i>	TR-gmb01991	Italy	25/10/2009	<i>Quercus pubescens</i>	PP919188
<i>Cortinarius chevassutii</i>	TR-gmb01992	Italy	28/10/2009	<i>Ostrya carpinifolia</i> , <i>Quercus</i> spp.	PP919209
<i>Cortinarius chevassutii</i>	FB26-10-2014	Italy	26/10/2014	<i>Quercus cerris</i>	PP919199
<i>Cortinarius chevassutii</i>	FB10-11-2014	Italy	10/11/2014	<i>Quercus</i> spp., <i>Ostrya carpinifolia</i> , <i>Corylus avellana</i>	PP919198

<i>Cortinarius chevassutii</i>	2809-II	Italy	23/10/2015	unknown	PP919227
<i>Cortinarius chevassutii</i>	TR-gmb01994	Italy	27/10/2022	<i>Quercus ilex</i>	PP919189
<i>Cortinarius chevassutii</i>	KS-CO1611	Spain	28/10/2005	<i>Quercus</i> spp.	PP919220
<i>Cortinarius chevassutii</i>	MES-4613	Spain	05/10/2015	<i>Quercus ilex</i> , <i>Pinus nigra</i>	PP919179
<i>Cortinarius pseudobulliardioides</i>	PC146521 (holotype)	France	05/11/2012	<i>Fagus sylvatica</i> , <i>Carpinus betulus</i>	PP919219
<i>Cortinarius pseudobulliardioides</i>	XC2013-176 (isotype)	France	05/11/2012	<i>Fagus sylvatica</i> , <i>Carpinus betulus</i>	PP919215
<i>Cortinarius pseudobulliardioides</i>	PC5356* (holotype of <i>C. chevassutii</i> f. <i>personatus</i>)	France	01/11/1999	<i>Quercus ilex</i>	MT934959
<i>Cortinarius pseudobulliardioides</i>	PML5357 (paratype of <i>C. chevassutii</i> f. <i>personatus</i>)	France	17/10/1998	<i>Quercus pubescens</i> , <i>Carpinus betulus</i>	PP919214
<i>Cortinarius pseudobulliardioides</i>	JMB2011112612	France	26/11/2011	<i>Quercus pubescens</i> , <i>Pinus halepensis</i>	PP919211
<i>Cortinarius pseudobulliardioides</i>	FR2012257	France	02/11/2012	<i>Quercus ilex</i> , <i>Q. pubescens</i>	PP919213
<i>Cortinarius pseudobulliardioides</i>	JMB2021110608	France	06/11/2021	<i>Quercus ilex</i>	PP919218
<i>Cortinarius pseudobulliardioides</i>	HM 09.10.2010	Germany	09/10/2010	<i>Quercus</i> spp., <i>Carpinus betulus</i>	PP919174
<i>Cortinarius pseudobulliardioides</i>	HM 09.09.2010	Germany	09/09/2010	<i>Quercus</i> spp.	PP919175
<i>Cortinarius pseudobulliardioides</i>	HG2013_071	Germany	12/10/2013	<i>Carpinus betulus</i> , <i>Quercus</i> spp.	PP919176
<i>Cortinarius pseudobulliardioides</i>	HM 03.10.1995	Germany	03/10/1995	<i>Quercus</i> spp., <i>Carpinus betulus</i>	PP919177
<i>Cortinarius pseudobulliardioides</i>	HM 01.10.2007	Germany	01/10/2007	<i>Quercus</i> spp.	PP919178
<i>Cortinarius pseudobulliardioides</i>	HG2014_184	Germany	20/09/2014	<i>Quercus</i> spp., <i>Carpinus betulus</i> , <i>Tilia</i> spp.	PP919182
<i>Cortinarius pseudobulliardioides</i>	HG2014_185	Germany	12/10/2014	<i>Quercus</i> spp., <i>Carpinus betulus</i>	PP919183
<i>Cortinarius pseudobulliardioides</i>	TG2010-035b	Italy	03/10/2010	<i>Quercus pubescens</i> , <i>Ostrya carpinifolia</i> , <i>Fraxinus ornus</i>	PP919222
<i>Cortinarius pseudobulliardioides</i>	MCVE26645	Italy	01/11/2007	<i>Quercus ilex</i>	PP919206
<i>Cortinarius pseudobulliardioides</i>	TR-gmb01993	Italy	13/10/2018	<i>Ostrya</i> , <i>Quercus pubescens</i>	PP919210
<i>Cortinarius pseudobulliardioides</i>	AF-252-2019	Italy	23/10/2019	<i>Quercus ilex</i>	PP919185
<i>Cortinarius pseudobulliardioides</i>	AF-071-2021	Italy	21/11/2021	<i>Quercus ilex</i>	PP919186
<i>Cortinarius pseudobulliardioides</i>	AF-077-2021	Italy	23/11/2021	<i>Quercus ilex</i>	PP919187
<i>Cortinarius pseudobulliardioides</i>	AF-100-2022	Italy	17/11/2022	<i>Quercus ilex</i>	PP919190
<i>Cortinarius pseudobulliardioides</i>	AF-101-2022	Italy	17/11/2022	<i>Quercus ilex</i> , <i>Fraxinus ornus</i>	PP919192
<i>Cortinarius pseudobulliardioides</i>	AF-110-2022	Italy	24/11/2022	<i>Quercus ilex</i> , <i>Fraxinus ornus</i> , <i>Ostrya carpinifolia</i>	PP919191
<i>Cortinarius pseudobulliardioides</i>	TR-gmb01995	Italy	10/12/2022	<i>Quercus ilex</i>	PP919193
<i>Cortinarius pseudobulliardioides</i>	TR-gmb01999	Italy	18/11/2023	<i>Quercus ilex</i>	PP919194

<i>Cortinarius pseudobulliardioides</i>	TEB70-4-14/ DB5559	Norway	25/09/2014	<i>Quercus robur, Tilia cordata</i>	PP919228
<i>Cortinarius pseudobulliardioides</i>	TEB29-09-1996	Norway	29/09/1996	<i>Tilia cordata, Quercus robur</i>	PP919184
<i>Cortinarius variebulbus</i>	Henry4039 (holotype, PC)	France	21/10/1973	<i>Quercus ilex</i>	PP919229
<i>Cortinarius variebulbus</i>	PML4567 (paratype of <i>C. argentatus</i> var. <i>griseobrunneus</i>)	France	04/10/1997	Mixed deciduous trees	PP919216
<i>Cortinarius variebulbus</i>	FR2012204	France	18/10/2012	<i>Quercus ilex</i>	PP919212
<i>Cortinarius variebulbus</i>	TEB469-10	Germany	04/10/2010	<i>Quercus robur, Tilia cordata</i>	PP919180
<i>Cortinarius variebulbus</i>	TEB470-10	Germany	04/10/2010	<i>Quercus robur, Tilia cordata</i>	PP919181
<i>Cortinarius variebulbus</i>	SSt98-216a	Germany	27/09/1998	<i>Quercus</i> spp.	PP919196
<i>Cortinarius variebulbus</i>	SSt98-220b	Germany	28/09/1998	<i>Quercus</i> spp.	PP919197
<i>Cortinarius variebulbus</i>	TM49-07	Germany	07/10/2007	<i>Fagus sylvatica</i>	PP919202
<i>Cortinarius variebulbus</i>	SSt08-175	Germany	04/11/2008	<i>Quercus</i> spp.	PP919200
<i>Cortinarius variebulbus</i>	HM2017-030	Germany	22/09/2014	<i>Quercus</i> spp., <i>Carpinus betulus</i>	PP919225
<i>Cortinarius variebulbus</i>	HM2017-008	Germany	21/10/2016	<i>Tilia</i> spp., <i>Quercus</i> spp.	PP919226
<i>Cortinarius variebulbus</i>	TR-gmb01250	Italy	03/12/2022	<i>Quercus cerris, Ostrya carpinifolia</i>	PP919207
<i>Cortinarius variebulbus</i>	FA4647	Spain	18/11/2018	<i>Quercus ilex, Q. faginea, Pinus pinaster, P. halepensis, Cistaceae</i> spp.	PP919208
<i>Cortinarius variebulbus</i>	FA4772	Spain	06/12/2018	<i>Quercus ilex, Pinus halepensis, Cistaceae</i> spp.	PP919217

Results

The phylogenetic analysis of our ITS dataset resolves seven supported lineages in sect. *Crassispori*, two of which are so far represented by a single environmental sequence and thus cannot yet be taxonomically characterized (Fig. 1). In addition to *C. chevassutii*, *C. crassisporus* and *C. duboisensis*, previously listed in the section (Liimatainen *et al.* 2020), *C. pseudobulliardioides* and *C. variebulbus* are here shown to belong to sect. *Crassispori* as well.

Cortinarius pseudobulliardioides represents the sister clade of *C. chevassutii* and was taxonomically treated as a form of the latter, as *C. chevassutii* f. *personatus*. A sequence of the holotype of this taxon (MT934959, erroneously labeled as PC5357 instead of PC5356, A. Bidaud pers. com.) has been generated by Liimatainen *et al.* (2020), but only included in the supplementary materials 2, preventing the taxon to be positioned relative to *C. chevassutii*. Our analysis reveals that the latter species and its *forma* are in sister clade relationships, distant by five polymorphisms, four of which are fixed (1 SNP + 3 indels, Tab. 2). No sign of gene flow could be detected between the two haplotypes, in spite of their frequent or possible sympatry, supporting complete reproductive isolation of the two taxa. The species rank for *C. chevassutii* f. *personatus* is therefore justified. Recently, the holotype of *C. pseudobulliardioides* has been found to belong to *C. chevassutii sensu lato* (Bidaud *et al.* 2023), and a closer look at our multiple sequence alignment indicated that it belongs to the clade of *C. chevassutii* f. *personatus* (Fig. 1). For that reason, this taxon is treated below as *C. pseudobulliardioides*, the name to be adopted at specific rank (see Taxonomy).

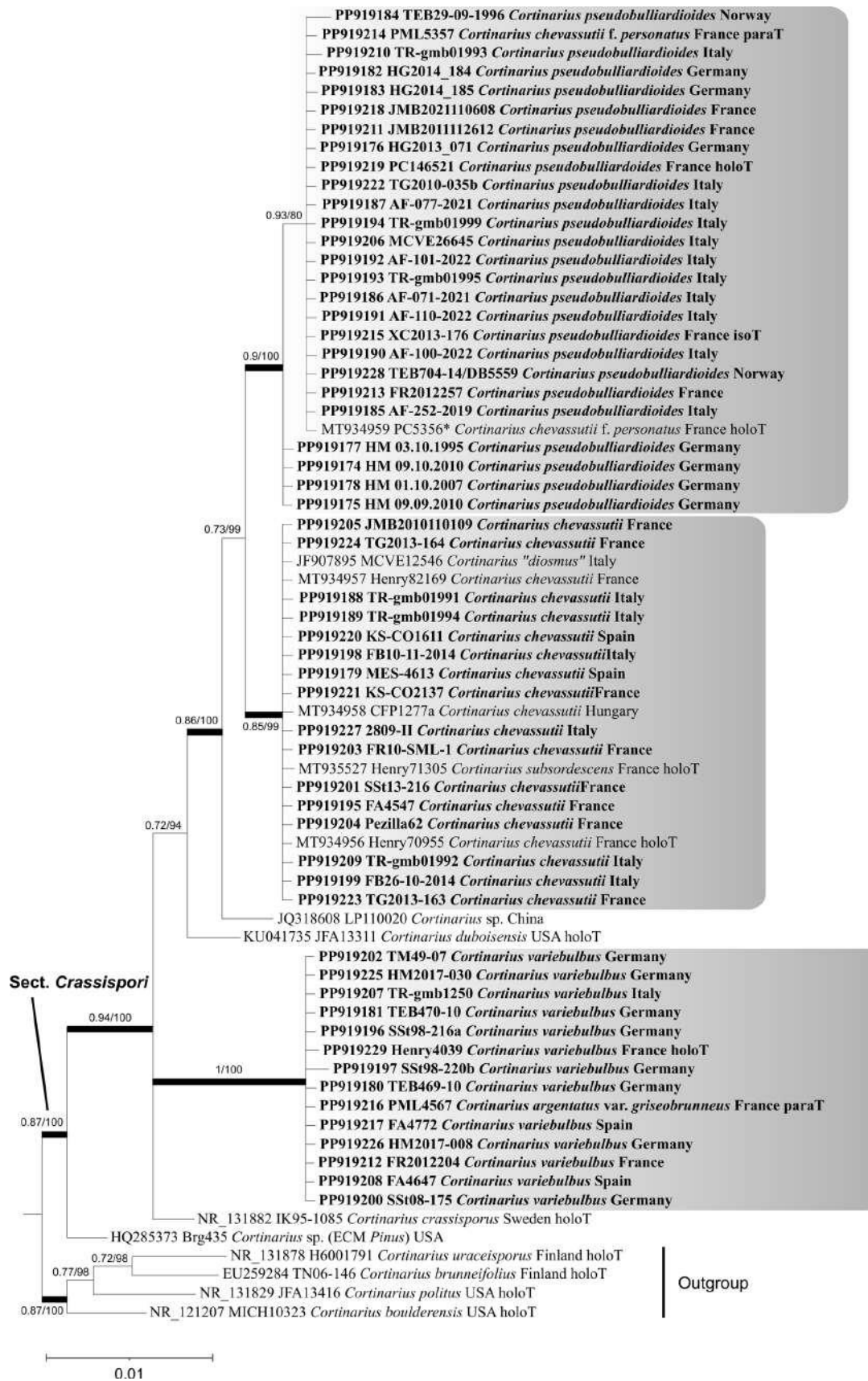


FIGURE 1. ITS phylogeny of section *Crassispori*. Newly generated sequences are highlighted in Bold. Branch support is indicated as SH-aLRT/%BPP values (cf. Materials & Methods), with thickened branches highlighting significant support of both metrics ($\geq 0.82/95$). The three species treated in the Taxonomy section are highlighted in grey boxes. * This holotype collection has been erroneously identified as n°5357 in Bidaud *et al.* (2002, p. 691), but the material corresponds to that of PML5356, described in the same publication (A. Bidaud, pers. com.).

Cortinarius variebulbus was not represented in sequence databases prior to the present work, despite this species having been identified by us for several years as a relative of *C. chevassutii*, both morphologically and phylogenetically. Naming this lineage has been possible thanks to the successful sequencing of the holotype of *C. variebulbus* through an Illumina Miseq approach (cf. Materials & Methods). Phylogenetically, this species is very well resolved and exhibits a rather significant genetic divergence at the ITS locus, consisting of 10 SNPs + 10 indels with respect to its closest relative *C. crassisporus*.

TABLE 2. Distribution of polymorphisms between *Cortinarius pseudobulliardoides* and *Cortinarius chevassutii*. *Blue and bold, fixed polymorphisms in *Cortinarius pseudobulliardoides*.

Species	Voucher	Position in the ITS alignment*						
		85	120	337	353	418	419	420
<i>Cortinarius pseudobulliardoides</i>	TR-gmb01999	-	C	T	C	-	-	-
<i>Cortinarius pseudobulliardoides</i>	AF-101-2022	-	C	T	C	-	-	-
<i>Cortinarius pseudobulliardoides</i>	AF-100-2022	-	C	T	C	-	-	-
<i>Cortinarius pseudobulliardoides</i>	AF-110-2022	-	C	T	C	-	-	-
<i>Cortinarius pseudobulliardoides</i>	TR-gmb01993	-	C	T	C	-	-	-
<i>Cortinarius pseudobulliardoides</i>	XC2013-176	-	C	T	C	-	-	-
<i>Cortinarius pseudobulliardoides</i>	JMB2021110608	-	C	T	C	-	-	-
<i>Cortinarius pseudobulliardoides</i>	FR2012257	-	C	T	C	-	-	-
<i>Cortinarius pseudobulliardoides</i>	JMB2011112612	-	C	T	C	-	-	-
<i>Cortinarius pseudobulliardoides</i>	TR-gmb01995	-	C	T	C	-	-	-
<i>Cortinarius pseudobulliardoides</i>	AF-077-2021	-	C	T	C	-	-	-
<i>Cortinarius pseudobulliardoides</i>	AF-071-2021	-	C	T	C	-	-	-
<i>Cortinarius pseudobulliardoides</i>	MCVE26645	-	C	T	C	-	-	-
<i>Cortinarius pseudobulliardoides</i>	PC5356	-	C	T	C	-	-	-
<i>Cortinarius pseudobulliardoides</i>	PML5357	-	C	T	C	-	-	-
<i>Cortinarius pseudobulliardoides</i>	AF-252-2019	-	C	T	C	-	-	-
<i>Cortinarius chevassutii</i>	MCVE12546	T	-	C	T	A	A	C
<i>Cortinarius chevassutii</i>	JMB2010110109	T	-	C	T	A	A	C
<i>Cortinarius chevassutii</i>	Pezilla62	T	-	C	T	A	A	C
<i>Cortinarius chevassutii</i>	FR10-SML-1	T	-	C	T	A	A	C
<i>Cortinarius chevassutii</i>	MES-4613	T	-	C	T	A	A	C
<i>Cortinarius chevassutii</i>	TR-gmb01994	T	-	C	T	A	A	C
<i>Cortinarius chevassutii</i>	TR-gmb01991	T	-	C	T	A	A	C
<i>Cortinarius chevassutii</i>	Henry70955	T	-	C	T	A	A	C
<i>Cortinarius chevassutii</i>	Henry82169	T	-	C	T	A	A	C
<i>Cortinarius chevassutii</i>	CFP1277a	T	-	C	T	A	A	C
Substitutions				S₁	S₂			
Deletion/insertion (indel)		I₁	I₂				I₃	

Taxonomy

Cortinarius* sect. *Crassispori Kytöv., Niskanen & Liimat., in Niskanen *et al.* (2020), Index Fungorum 439: 6

Type: *Cortinarius crassisporus* Kytöv., Niskanen & Liimat., in Niskanen (2014), Index Fungorum 201: 1.

Original diagnosis: *Basidiomata* medium to large-sized. *Pileus* pale brown, brown, grey, grey brown to dark reddish brown, in some species coated by white fibrils, hygrophanous. *Lamellae* at first pale brown, later brown. *Stipe* clavate to bulbous, silky-white fibrillose. Universal veil white, in some species becoming partially pale brown, sparse or forming a couple of incomplete girdles on the stipe. Basal mycelium white. *Context* in pileus pale brown to brown, in stipe brownish white to pale brown, marbled hygrophanous, becoming darker brown at the base with age. *Odour* in lamellae indistinct. *Basidiospores* amygdaloid, ellipsoid, obovoid or ovoid to almost subglobose, $< 13.5 \times 9.0 \mu\text{m}$. Lamellar trama hyphae smooth. In deciduous and coniferous forests.

Cortinarius chevassutii Rob. Henry, in Chevassut & Henry (1982), Doc. mycol. 12(47): 39 (Fig. 2)

= *Cortinarius subsordescens* Rob. Henry (1985), Bull. Soc. mycol. Fr. 101(1): 27

Type:—FRANCE. Gard-Hérault, Vacquières-Nîmes-Montpellier, October 1978 and October 1979, *Quercus ilex*, leg. G. Chevassut, holotype Henry n°70955 in PC herbarium, GenBank ITS MT934956.

Original diagnosis:—*Pileo* (4–10 cm lato) convexo dein convexo-plano, demum plano, tum paulum depresso, margine primo sat involuto, nonnumquam infracto-rugoso, fibrilloso griseascenti. Cute innatis fibrillis in reticulo textis, maculis pruinae griseascentis plenis praecipue insigni; colore autem griseo-brunneo-cinerascenti pallido, dein griseo-fuliginea, demum nigro +/- maculata vel sordescenti. Lamellis (6–8 mm latis) distantibus, sinuato-adnatis vel emarginato-adnatis ex argillaceo-incarnatis mox fulventibus, demum umbrino-fulvis, acie haud integerrimis. Stipite (5–6,5 cm / 10–22 mm) robusto pleno, sat fragili, basi bulboso rotundato marginato, fibrilloso, griseascenti-brunneo. Carne sordide albida vel isabellina, ad basim tandem quoque brunneo-fuliginea. Sporibus ellipsoideo-ovoideo-amygdaliformibus, verruculosis (7,9–8,7/4,3–4,7–5 vel 9,4–10,1/5 μm). Basidiis 4-sp. (33–39/8–8,7 μm). Hyphis fibulatis. Sub Ilicibus sat frequens.

Updated description:—*Pileus* 3–10 (14) cm diam., initially globose to campanulate-convex, later plano-convex to depressed, with a broad obtuse umbo, margin lobed or notched, often fissured, involute in young specimens, then inflexed to straight. Surface dry, hygrophanous, showing a pattern of greyish brown, radial fibrils, occasionally with an overlay of micaceous, radial striae, ground colour greyish white when young, later light ochraceous or brown, at maturity tending to blacken in radially-arranged areas or striae, with whitish, scattered velar remnants occurring especially towards the centre or at margin. *Lamellae* adnate to emarginate, sinuous, fairly well-spaced, argillaceous, later dark brown. Edge eroded, wavy-toothed, concolorous with the faces or whitish. *Stipe* (3)4–7(8) \times 1–2 cm, rather stout, cylindrical, base weakly to distinctly marginate (rarely bulbous, up to 2–3cm), at times bent downwards, fibrillose, initially white, grey-white or concolorous with the pileus; surface dry, crossed by shiny longitudinal fibrils, light-coloured when young, but becoming sordid in old age. Velar remnants whitish, more or less restricted to bulb margin, basal mycelium whitish. *Context* off-white or brownish with red nuances and greyish tinges, more pronounced in stipe base. *Odour* subraphanoid with fruity notes.

Macrochemical reactions KOH not tested, guaiac negative or weakly positive.

Basidiospores [8, 8, 337] $7.3\text{--}9.7 \times 4.6\text{--}5.6 \mu\text{m}$, $MV = 8.5 \times 5.1 \mu\text{m}$, intercarpic variation of $MV = 7.9\text{--}9.1 \times 4.9\text{--}5.3 \mu\text{m}$, $Q = 1.52\text{--}1.82$, $Q_m = 1.67$, intercarpic variation of $Q_m = 1.60\text{--}1.71$, spores yellow-ochre in KOH, mostly elliptic with rounded apex or occasionally slightly tapered, more rarely subamygdaliform or pruniform with a shallow hilar depression. Ornamentation consisting of dense truncate warts, tending to coalesce towards the apex. Plage well-differentiated. Reaction to Melzer's reagent variable, weakly to moderately dextrinoid in most of the collections analyzed (Tab. 3, Figs. 3, 6). *Pileipellis* suprapellis a cutis of subparallel hyphae, 2–7 μm wide, with cylindraceous terminal elements. Pigment brown. Subpellis differentiated, consisting of much broader hyphae, up to 20–25 μm wide; localized presence of yellowish brown intracellular pigment. *Basidia* 20–35 \times 7–9 μm , tetrasporic, cylindro-clavate, hyaline or with greenish-brown intracellular pigment. *Marginal cells* lamellar edge sterile; hairs measuring 20–40 \times 4–6 μm , cylindro-clavate in shape, at times sinuous, either unicellular or two- to three-septate, often with lateral diverticula; terminal element cylindro-clavate (15–20 \times 5–7 μm). *Clamp connections* at all septa.

Habitat and distribution:—Mainly with *Quercus ilex* on calcareous ground, but also with *Q. pubescens* and *Q. cerris*, in mediterranean-submediterranean regions. So far known mainly from western-central Mediterranean regions (France, Italy, Spain), Hungary, and southern temperate outposts in Germany.



FIGURE 2. *Cortinarius chevassutii*, basidiomata. A. coll. TR-gmb01992, Italy (Photo: F. Calledda), B. coll. TG2010-035b, Italy (Photo: G. Turrini), C. coll. FA4547, France (Photo: F. Armada), D. coll. TG2013-164c, France (Photo: G. Turrini), E. coll. TR-gmb01994, Italy (Photo: F. Calledda), F. coll. TR-gmb01991, Italy (Photo: F. Calledda).

Material analysed:—FRANCE. Drôme, Grignan, 10 November 2018, *Quercus ilex* and *Q. pubescens*, leg. F. Armada, FA4547; Hérault, Saint-Martin-de-Londres, 30 October 2010, *Quercus ilex*, leg. F. Richard, FR10-SML-1; Hérault, Mas-de-Londres, 01 November 2010, *Quercus ilex*, leg. J.-M. Bellanger, JMB2010110109; Hérault, Bédarieux, Levas, 23 October 2013, leg. G. Turrini, TG2013-163; ibid., TG2013-164; leg. G. Schmidt-Stohn, SS13-216; ibid., leg. K. Soop, KS-CO2137; Pyrénées-orientales, Pézilla-de-Conflent, 23 November 2011, *Quercus ilex*, leg. E. Taschen, Pezilla62. HUNGARY. Pest, Gödöllő, Domony valley, 26 October 1994, *Quercus* spp., unknown legit, CFP1277a in S herbarium. ITALY. Emilia Romana, Parma, Belvedere fdi Gotra di Albareto, 10 November 2014, *Quercus* spp., *Ostrya carpinifolia*, *Corylus avellana*, leg. F. Bellù, FB10-11-2014; Emilia Romana, Parma, Stabielle di Borgo Val di Taro, 26 October 2014, *Quercus cerris*, leg. F. Bellù, FB26-10-2014; Emilia Romagna, Bettola, Piacenza, 28 October 2018, loc. “Montosero”, mixed forest with *Corylus*, *Quercus cerris*, *Q. pubescens* and *Populus tremula*, leg. F. Calledda, n°01992 in TR-gmb herbarium; Liguria, Massaina, La Spezia, 27 October 2022, loc. “Salterana”, *Quercus ilex*, leg. F. Calledda, n°01994 in TR-gmb herbarium; Lombardy, Cecima, Pavia, 25 October 2009, loc. “Ca del Monte”, forest with *Quercus*

pubescens and *Castanea sativa*, leg. F. Calleda, n°01991 in TR-gmb herbarium; Marche, Monte Catria, 30 November 2015, leg. E. Ludwig, 2809-II; Toscana, San Gimignano, Siena, 01 November 1995, *Quercus ilex*, n°12546 in MCVE herbarium. SPAIN. Castellón, l'Alcalatén, Vistabella del Maestrat, Penyagolosa, Mas de l'Espino, 40°15'37'' N, 0°20'01'' W, 05 October 2015, mixed forest of *Pinus nigra*, *P. sylvestris* and *Quercus ilex*, leg. R. Mahiques, MES-4613; Catalonia, Mas de Carcellara, *Quercus* spp., 28 October 2005, leg. K. Soop, KS-CO1611.

Comments:—Recognizing a member of the “*Cortinarius chevassutii* complex” is not too difficult morphologically, because of the unique set of features that characterize them: the marginate/submarginate basal bulb, the silky white veil, the appearance of the pileus and the small- to medium-sized spores. However, the separation of *C. chevassutii sensu stricto* from *C. pseudobulliardoides* (formerly *C. chevassutii* f. *personatus*, see below), without molecular tools, remains challenging. Our analysis of numerous confirmed collections of the two species brought to light that spore shape and length/width Q_m ratio represent the most and probably only reliable diagnostic characters to tell them apart (Tab. 3, Fig. 3). Indeed, although the length values are not much different between the two species (7.1–9.1 μm vs 7.3–9.7 μm , respectively), we observed that the number of spores reaching a length of 10–11 μm was higher in *C. chevassutii*. The average Q_m ratio is consistently higher in *C. chevassutii* (av. $Q_m = 1.67$ vs 1.54), which can be observed also in the scatter plot (Fig. 3). We noted that the spores of *C. chevassutii* are mostly ellipsoid with a rounded apex, whereas those of *C. pseudobulliardoides* are often subamygdaliform with a tapered apex. However, for a certain, unambiguous distinction of these two species, DNA sequencing may remain necessary. Liimatainen *et al.* (2020) have obtained, but not included in their phylogeny, an ITS sequence of the holotype of *C. subsordescens* Rob. Henry, that they listed as a late synonym of *C. chevassutii*; this is confirmed here (Fig. 1). Henry (1985) considered *C. subsordescens* as a species close to *C. chevassutii*, but he distinguished it from the latter by the amygdaliform spore shape and the more marked degree of blackening. Some mycologists later treated this taxon as a variety of *C. chevassutii*, while others synonymized the two names (Fernandez-Sasia & Cadiñanos 2000; Bidaud *et al.* 2002).

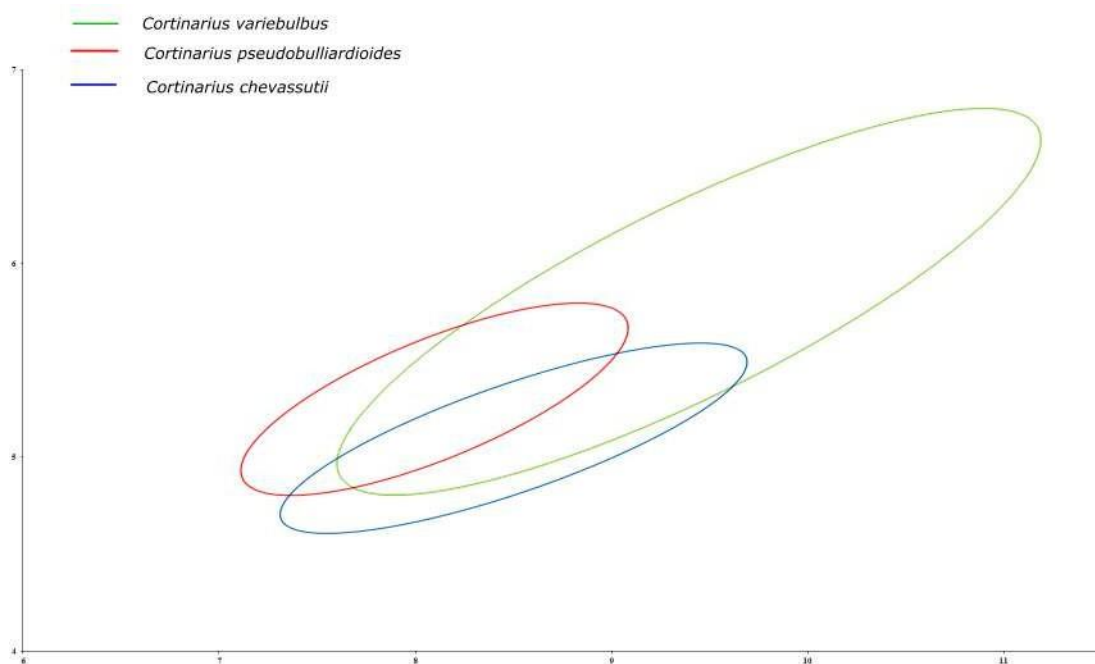


FIGURE 3. Spore size of *Cortinarius chevassutii*, *C. pseudobulliardoides* and *C. variebulbus*. The lines are drawn on the basis of scatter diagrams and contain 95 % of the spore measurements of each species, as reported in Table 3. X/Y axis: length/width of spores (μm).

TABLE 3. *Cortinarius chevassutii*, *Cortinarius pseudobulliardioides* and *Cortinarius variebulbus*, spore measurements.

species	Voucher	N	length (L) × width (W)	length (L) × width (W)	Q L/W total;	Q L/W
			total (µm); MV	95 % variation (µm); MV	MV	95 % variation; MV
<i>Cortinarius chevassutii</i>	TR-gmb01992	45	7.4– 8.4 –10.0 × 4.5– 5.0 –5.8	7.5– 8.4 –9.3 × 4.6– 5.0 –5.4	1.56– 1.67 – 1.74	1.57– 1.67 – 1.77
	TR-gmb01994	45	7.8– 8.6 –9.5 × 4.7– 5.1 –5.5	7.8– 8.6 –9.4 × 4.7– 5.1 –5.5	1.61– 1.69 – 1.78	1.59– 1.69 – 1.79
	MES–4613	45	8.4– 8.8 –10.1 × 4.7– 5.2 –5.6	8.0– 8.8 –9.6 × 4.8– 5.2 –5.6	1.57– 1.70 – 1.80	1.60– 1.70 – 1.80
	MCVE12546	50	8.1– 8.8 –10.1 × 4.8– 5.3 –5.8	7.7– 8.8 –9.9 × 4.8– 5.3 –5.8	1.55– 1.68 – 1.85	1.52– 1.68 – 1.84
	TR-gmb01991	50	8.0– 9.1 –11.1 × 4.8– 5.3 –6.2	7.8– 9.1 –10.4 × 4.8– 5.3 –5.8	1.59– 1.71 – 1.95	1.55– 1.71 – 1.87
	FR10-SML-1	35	7.4– 7.9 –9.1 × 4.5– 4.9 –5.3	7.2– 7.9 –8.6 × 4.5– 4.9 –5.3	1.47– 1.61 – 1.72	1.49– 1.61 – 1.73
	Pezilla62	32	6.9– 8.2 –8.7 × 4.4– 5.0 –5.4	7.5– 8.2 –8.9 × 4.6– 5.0 –5.4	1.51– 1.64 – 1.75	1.52– 1.64 – 1.76
	JMB2010110109	35	7.0– 7.8 –9.5 × 4.4– 4.9 –5.6	6.8– 7.8 –8.8 × 4.5– 4.9 –5.3	1.42– 1.60 – 1.82	1.44– 1.60 – 1.76
	Total	337	6.9– 8.5 –11.1 × 4.4– 5.1 –6.2	7.3– 8.5 –9.7 × 4.6– 5.1 –5.6	1.42– 1.67 – 1.95	1.52– 1.67 – 1.82
<i>Cortinarius pseudobulliardioides</i>	AF-101-2022	20	7.4– 7.8 –8.6 × 4.8– 5.1 –5.4	7.2– 7.8 –8.4 × 4.8– 5.1 –5.4	1.42– 1.54 – 1.65	1.44– 1.54 – 1.64
	AF-100-2022	40	7.6– 8.3 –8.9 × 4.9– 5.2 –5.7	7.7– 8.3 –8.9 × 4.8– 5.2 –5.6	1.47– 1.61 – 1.71	1.49– 1.61 – 1.73
	AF-110-2022	20	7.0– 7.9 –8.6 × 4.8– 5.2 –5.6	7.0– 7.9 –8.8 × 4.8– 5.2 –5.4	1.43– 1.52 – 1.65	1.40– 1.52 – 1.64
	AF-252-2019	36	7.3– 7.9 –8.6 × 4.8– 5.1 –5.5	7.3– 7.9 –8.5 × 4.8– 5.1 –5.4	1.43– 1.54 – 1.69	1.42– 1.54 – 1.66
	AF-071-2021	40	7.5– 8.4 –9.4 × 5.0– 5.4 –5.9	7.5– 8.4 –9.3 × 4.9– 5.4 –5.9	1.41– 1.56 – 1.69	1.44– 1.56 – 1.68
	AF-077-2021	32	7.3– 8.0 –8.6 × 4.9– 5.3 –5.6	7.2– 8.0 –8.8 × 4.9– 5.3 –5.6	1.38– 1.52 – 1.62	1.42– 1.52 – 1.62
	TR-gmb01993	50	6.8– 7.6 –8.2 × 4.7– 5.1 –5.5	7.0– 7.6 –8.2 × 4.8– 5.1 –5.4	1.39– 1.49 – 1.62	1.37– 1.49 – 1.61
	MCVE26645	25	6.9– 7.7 –9.3 × 4.9– 5.3 –6.0	6.7– 7.7 –8.7 × 4.8– 5.3 –5.8	1.30– 1.45 – 1.59	1.31– 1.45 – 1.59
	JMB2011112612	34	7.9– 8.7 –9.3 × 5.1– 5.6 –5.9	8.1– 8.7 –9.3 × 5.2– 5.6 –6.0	1.47– 1.55 – 1.63	1.47– 1.55 – 1.63
	PC5356	30	7.7– 8.4 –9.0 × 4.9– 5.4 –5.9	7.6– 8.4 –9.2 × 4.9– 5.4 –5.9	1.46– 1.55 – 1.65	1.47– 1.55 – 1.63
	FR2012257	38	7.4– 8.1 –8.8 × 5.0– 5.3 –5.8	7.4– 8.1 –8.8 × 4.9– 5.3 –5.7	1.41– 1.54 – 1.67	1.42– 1.54 – 1.66
	TR-gmb01995	20	7.6– 8.2 –8.9 × 5.0– 5.4 –5.7	7.5– 8.2 –8.9 × 5.0– 5.4 –5.8	1.44– 1.51 – 1.63	1.41– 1.51 – 1.61
	JMB2021110608	30	7.4– 8.0 –8.7 × 5.0– 5.4 –5.7	7.3– 8.0 –8.7 × 5.0– 5.4 –5.8	1.40– 1.50 – 1.69	1.38– 1.50 – 1.62

.....continued on the next page

TABLE 3. (Continued)

species	Voucher	N	length (L) × width (W)	length (L) × width (W)	Q L/W total;	Q L/W
			total (µm); MV	95 % variation (µm); MV	MV	95 % variation; MV
	XC2013-176 (isotype)	34	8.1– 9.1 –10.2 × 5.3– 5.8 –6.1	8.3– 9.1 –9.9 × 5.4– 5.8 –6.2	1.45– 1.58 –1.74	1.44– 1.58 –1.72
	Total	449	6.8– 8.2 –10.2 × 4.7– 5.3 –6.1	7.1– 8.2 –9.1 × 4.8– 5.3 –5.8	1.30– 1.54 –1.74	1.40– 1.54 –1.74
<i>Cortinarius variebulbus</i>	AF-110-2023	25	7.7– 8.2 –9.1 × 5.0– 5.3 –5.7	7.4– 8.2 –9.0 × 4.9– 5.3 –5.7	1.45– 1.55 –1.72	1.41– 1.55 –1.69
	FA4647	35	9.4– 10.1 –11.0 × 5.7– 6.3 –6.9	9.3– 10.1 –10.9 × 5.7– 6.3 –6.9	1.50– 1.62 –1.77	1.52– 1.62 –1.72
	TR-gmb01250	70	7.6– 8.8 –10.6 × 4.6– 5.3 –6.3	7.4– 8.8 –10.2 × 4.5– 5.3 –6.1	1.47– 1.65 –1.87	1.47– 1.65 –1.82
	FA4772	31	9.1– 9.9 –11.0 × 5.7– 6.1 –6.7	9.1– 9.9 –10.7 × 5.7– 6.1 –6.5	1.46– 1.62 –1.78	1.48– 1.62 –1.76
	FR2012204	30	8.6– 9.0 –10.0 × 5.4– 6.0 –6.3	8.2– 9.0 –9.8 × 5.6– 6.0 –6.4	1.40– 1.52 –1.72	1.38– 1.52 –1.66
	PML4567	32	9.6– 10.4 –12.0 × 5.9– 6.3 –7.3	9.4– 10.4 –11.4 × 5.7– 6.3 –6.9	1.52– 1.67 –1.82	1.53– 1.67 –1.81
	Total	223	7.6– 9.4 –12.0 × 4.6– 5.8 –7.3	7.6– 9.4 –11.2 × 4.8– 5.8 –6.8	1.40– 1.61 –1.87	1.44– 1.61 –1.79

Cortinarius pseudobulliardoides Carteret & Reumaux (2012), Bull. Soc. mycol. Fr. 128 (3–4): 274 (Figs. 4, 5)

= *Cortinarius chevassutii* f. *personatus* Bidaud, in Bidaud *et al.* (2002), Atlas des Cortinaires 12: 691

Type:—FRANCE. Eure, under *Fagus sylvatica* and *Carpinus betulus*, on calcareous soil, 05 November 2012, leg. *M. Cerutti*, holotype n°146521 in PC herbarium, isotype XC2013-176 in X. Carteret pers. herb., GenBank ITS PP919219 and PP919215.

Original diagnosis:—*Pileus* (30) 50–70 mm, obtuse convexus, late umbonatus, circa umbonem leviter depressus; margo primum forte involuta, dein lobata, aetate fissa; indumentum lente hygrophanum, udum brunneo-fuscum (Seg. 701-702) vel fere nigrum, marginem versus fibrillosum, interdum rimosum; velum in umbone adpressum, album vel albo-griseum. Lamellae satis confertae, emarginatae-sinuatae, paulum ventriosae, brunneae vel brunneo-rufae; acie alba crenulataque. Stipes 50–70 × 15 mm, satis curtus, bulbosus, cum bulbum ovoideum interdum submarginatum (× 20 mm), fibrillosus, pallidus, fere spurcatus, saepe ad apicem glaucescens. Caro grisea, in stipite obscuriora, inodora. Sporae (7,5) 8–9,5 (10) × 5–5,5 (6) µm, ellipsoideae-subamygdaliformes, satis verrucosae. Habitatio in silvis frondosis calcareis.

Updated description:—*Pileus* 3–12 cm diam., initially globose to campanulate-convex, later plano-convex to depressed, with a broad obtuse umbo, margin lobed or notched, often fissured, involute in young specimens, then inflexed to straight. Surface dry, hygrophanous, showing a pattern of greyish brown, radial fibrils, occasionally with an overlay of radial, micaceous striae, ground colour greyish white when young, later light brown, at maturity tending to blacken in radially arranged areas or striae, with whitish, scattered velar remnants occurring especially towards the center or on the marginal area. *Lamellae* adnate to emarginate, moderately spaced, argillaceous, later russet. Edge eroded, wavy-toothed, concolorous with the faces or whitish. *Stipe* (3)4–7(8) × 0.7–1.5 cm, stout, cylindrical, base weakly to distinctly marginate (rarely bulbous, up to 3 cm at base), at times bent downwards, fibrillose, crossed by shiny longitudinal fibrils, concolorous with the pileus, but becoming sordid in old age; velar remnants whitish, more or less restricted to bulb margin, basal mycelium whitish. *Context* off-white or light brownish with greyish tinges, more pronounced in stipe base. *Odour* subraphanoid. *Macrochemical reactions* KOH not tested, guaiac positive, very slow.

Basidiospores [14, 14, 449] 7.1–9.1 × 4.8–5.8 µm, MV = 8.2 × 5.3 µm, intercarpic variation of MV = 7.6–9,1 × 5.1–5.8 µm, Q = 1.40–1.74, Q_m = 1.54, intercarpic variation of Q_m = 1.45–1.61 ochre-yellow or fulvous in KOH, elliptic or subamygdaliform; apex rounded or tapering; ornamentation variable, consisting of truncate or trapezoidal warts,

PLANCHE II



FIGURE 4. *Cortinarius pseudobulliardiioides*, holotype, reproduced with authorization from Carteret & Reumaux (2012).

isolate or forming short ridges, more prominent and tending to coalesce towards the apex; plage present, but hardly differentiated. Reaction to Melzer's reagent more or less moderately dextrinoid in most collections (Tab. 3, Figs. 3, 6). *Pileipellis* suprapellis a cutis of subparallel hyphae, 3–8 μm wide, with cylindrical terminal elements. Pigment yellowish ochre. Subpellis well-differentiated, consisting of much broader hyphae, up to 25 μm wide; localized presence of brownish intracellular pigment associated with yellowish parietal pigment. *Basidia* 27–40 \times 7–9 μm , tetrasporic, cylindro-clavate, hyaline or with greenish brown intracellular pigment. *Marginal cells* 15–35 \times 3–4 μm , lamellar edge sterile, marginal cells in the form of hyaline, cylindro-clavate or sinuous hairs, either unicellular or two- to three-septate, often with lateral diverticula; terminal element cylindro-clavate (15–20 \times 5–9 μm). *Clamp connections* common at all septa.

Habitat and distribution:—With *Quercus* spp. (including *Q. ilex*), *Carpinus betulus*, *Tilia cordata*, possibly also *Fagus sylvatica* and *Ostrya carpinifolia* on calcareous ground. Mainly in Mediterranean-submediterranean regions, but also in locally thermophilous, temperate sites. So far known only from France, Italy (including Trentino province in N Italy), Germany, and two extreme northern outposts in the Oslofjord area of SE Norway. These Norwegian outposts are from very old, relictual, steep south-facing *Tilia cordata-Quercus robur* forest remnants.



FIGURE 5. *Cortinarius pseudobulliardii*, basidiomata. A. coll. TEB704-14/DB5559, Norway (Photo: B. Dima), B. coll. TR-gmb01993, Italy (Photo: F. Calleda), C. coll. TR-gmb01995, Italy (Photo: F. Calleda), D. coll. AF-252-2019, Italy (Photo: A. Fellin), E. coll. JMB2010110109, France (Photo: J.-M. Bellanger), F. coll. JMB2011112612, France (Photo: J.-M. Bellanger).

Material analysed:—FRANCE. Gard, Roquedur, 02 November 2012, *Quercus ilex* and *Quercus pubescens*, leg. J.-M. Bellanger, FR2012257; Hérault, Murviel-lès-Montpellier, 01 November 1999, *Quercus ilex*, leg. A. Faurite-Gendron, n°5356* in PC herbarium (holotype of *C. chevassutii* f. *personatus*); Isère, Saint-Marcel-Bel-Accueil, 17 October 1998, *Quercus pubescens* and *Carpinus betulus*, leg. J. Garin, PML5357 (paratype of *C. chevassutii* f. *personatus*); Vaucluse, Cadenet, 26 November 2011, forest with *Quercus pubescens* and *Pinus halepensis*, leg. J.-M. Bellanger, JMB2011112612; Vaucluse, Saignon, 06 November 2021, *Quercus ilex*, leg. J.-M. Bellanger, JMB2021110608. GERMANY. Sachsen-Anhalt, Freyburg, FND Kleine Probstei, 01 October 2007, *Quercus* spp., *Carpinus betulus*, leg. M. Huth, HM 01.10.2007; *ibid.*, 03 October 1995, *Quercus* spp., leg. M. Huth, HM 03.10.1995; Sachsen-Anhalt, Freyburg, Müncheroda, Langer Berg, 09 October 2010, *Quercus* spp., leg. M. Huth, HM 09.10.2010; Sachsen-Anhalt, Freyburg, Balgstädt, NSG Tote Täler, 09 September 2010, *Quercus* spp., leg. M. Huth, HM 09.09.2010; Sachsen-Anhalt, NSG Müncheberg, 12 October 2013, *Quercus* spp., *Carpinus betulus*, leg. G. Hensel, HG2013_071; Sachsen-Anhalt, Freyburg, Müncheroda, Schäper Holz, 12 October 2014, *Quercus* spp., *Carpinus betulus*, leg. G. Hensel & M. Huth, HG2014_185; Sachsen-Anhalt, Klosterhäseler, Metzenholz, 20 September 2014, *Quercus* spp., *Tilia* spp., *Carpinus betulus*, leg. G. Hensel & U. Täglich, HG2014_184. ITALY. Liguria, Genoa, Chiavari, 10 December 2022, loc. “Le Grazie”, *Quercus ilex*, leg. F. Calleda & F. Boccardo, n°01995 in TR-gmb herbarium; Liguria, Genoa, Camogli, Parco di Portofino, 18 November 2023, loc. “Portofino Vetta”, forest with *Quercus ilex*, leg. F. Calleda, n°01999 in TR-gmb herbarium (not studied); Lombardy, Varzi, Pavia, 13 October 2018, loc. “Cella”, forest with *Ostrya carpinifolia* and *Quercus pubescens*, leg. F. Calleda, n°01993 in TR-gmb herbarium; Trentino-Alto Adige, Bolzano, Settequerce, 03 November 2013, leg. G. Turrini, TG2010-035b; Trentino-Alto Adige, Trentino, Madruzzo, 23 October 2019, loc. “Castel Toblino”, thermophilic forest with *Quercus ilex* and *Ruscus aculeatus*, leg. A. Fellin, AF-252-2019; *ibid.*, 21 November 2021, AF-071-2021; *ibid.*, 23 November 2021, AF-077-2021; *ibid.*, 17 November 2022, AF-100-2022 and AF-101-2022, thermophilic forest with *Quercus ilex* and *Fraxinus ornus*; Trentino-Alto Adige, Trentino, Riva del Garda, 24 October 2022, loc. “monte Brione”, forest with *Quercus ilex* and *Q. pubescens*, leg. A. Fellin, AF-110-2022; Veneto, Treviso, Cordignano, 01 November 2007, loc. “Villa di Villa”, forest with *Quercus ilex*, leg. E. Campo, n°26645 in MCVF herbarium. NORWAY. Telemark, Bamble, Stokkevann east, 25 October 2014, leg. T.E. Brandrud & B. Dima, TEB704-14/DB5559; Telemark, Porsgrunn, Blekebakken nature reserve, 29 September 1996, leg. T.E. Brandrud, TEB29-09-1996.

Comments:—This species has been treated by some mycologists as part of *C. chevassutii* s. l., and is better known by others as *Cortinarius chevassutii* f. *personatus* (Bidaud *et al.* 2002). We show here that this taxon deserves the species rank, based mainly on the well-supported phylogenetic differences, but also on some small differences in spore shape (see above). French mycologists introduced *C. chevassutii* f. *personatus* because of some distinctive “key features”, such as the vigorous positive reaction to guaiac on the context (“...Carne ope gaiaco intense cyanea...”), the size of the basidiomata (“*A typo differ statura majore pileus usque 110 mm side...*”) and the peculiar, strongly fibrillose appearance of the pileus, which is obvious in plate 405 of the Atlas des Cortinaires 12 (Bidaud *et al.* 2002). Such morphological features, regarded by the authors as diagnostic, are here judged ineffectual in the separation of the two taxa. All collections of the present species that we studied displayed some phenotypic plasticity for what concerns basidioma size and pileus appearance (Fig. 5), which can also be assessed by comparing the published illustrations of *Cortinarius chevassutii* f. *personatus* in the Atlas des Cortinaires 12, pl. 405 (Bidaud *et al.* 2002) and of *C. pseudobulliardiioides* in the Bull. Soc. mycol. Fr., 128(3–4), pl. II (Carteret & Reumaux 2012, reproduced above in Fig. 4). As to the reaction to guaiac, a test conducted on fresh material revealed that its discriminating usefulness is rather weak, since the two taxa show a wide variation in positive reactions to the reagent, with often a long response time. In summary, according to our observations, the alleged macro-morphological differences between *C. chevassutii* and its *forma personatus*, here treated under the name *C. pseudobulliardiioides* regarding pileus, lamellae and stipe colors or the surface texture of the pileus are not easy to establish objectively, being elements of an intergrading continuum. Therefore, telling the two species apart in the field is very difficult and a reliable identification can be attained only through careful microscopy and in some cases only with sequence data. The two species are known from different countries in Europe, show an almost identical distribution pattern and certainly were confused in the past. Moreover, the two populations cover the same ecological niche represented by thermophilic deciduous forests and are associated with the same host trees (Chevassut & Henry 1982; Brandrud *et al.* 1998; Bidaud *et al.* 2002), coexisting sympatrically in the same environments. Of the three other known members of sect. *Crassispori*, only *C. variebulbus* presents risks of confusion with *C. pseudobulliardiioides* (see below), as both *C. crassisporus* and *C. duboisensis* are conifer species with different spores and without a marginate-bulbous stipe. The former displays a transcontinental distribution in boreal or hemiboreal conifer forests of Alaska and Fennoscandia (Niskanen 2014; von Bonsdorff *et al.* 2015), the latter is a West North American species occurring in woodlands including *Pinus ponderosa* Douglas ex C. Lawson, *Abies grandis* (Douglas ex D. Don) Lindl. and *Quercus garryana* Dougl. (Li *et al.* 2016).

Cortinarius variebulbus Chevassut & Rob. Henry (1982), Doc. mycol. 12(47): 41 (Fig. 7)

= *Cortinarius argentatus* var. *griseobrunneus* Bidaud & Reumaux, in Bidaud *et al.* (2002), Atlas des Cortinaires 12: 691, *pro parte*

Type:—FRANCE. Vaucluse, near Avignon, 21 October 1973, *Quercus ilex*, leg. G. Chevassut, Henry n°4039 in PC herbarium, GenBank ITS PP919229.

Original diagnosis:—*C. variebulbus* n. sp. *C. acutibulbus* sat similis sed stipes et sporas diversas. Pileo (2.5–4 cm lato) e convexo vel convexo-obtuso demum plano, immo deformiter explanato, sicco, griseoalbidis fibrillis innatis, subargenteis subvirgato, griseo-fusco, griseascente, demum disco fucescente vel nigricante, alibi sordescente. Lamellis (5–7 mm latis) emarginatis, fulvis. Stipite (2.5–4 cm/8–12 mm) curto, nunc subaequali nunc clavato-bulboso marginato vel submarginato, nunc recto, cylindrico, abulboso, tantum linea dubia circumdato nunc fusoido-connato-abulboso), semper ad basim attenuato (sed non acuto), albido-fibrilloso, valde cortinato-velato (usque ad bulbum fibrilloso. Carne pallida, pallide ochracea vel pallide isabellina, inodora, dulci. Sub ilicibus gregatim.

Updated description:—*Pileus* 4–7 cm diam., globose to conical-convex, at maturity plano-convex, with a broad, obtuse umbo. Pileal margin inflexed or slightly involute, occasionally with whitish velar remnants. Pileus surface mostly dry, hygrophanous, with darker innate fibrils, whitish silvery when young, with age becoming a milky coffee color or spotted fulvous-brown, especially on handling or rubbing. *Lamellae* moderately spaced, slightly intervenose, intercalated with short lamellulae, adnate to emarginate, light clay-coloured, then rusty ochre, finally cinnamon, edge wavy, concolorous or whitish towards the pileus margin. *Stipe* 3–6 × 1–2 cm, rather stout, cylindrical, base either clavate or with an oblique, submarginate bulb, somewhat enlarged (up to 3.5 cm) and roundish in shape, whitish or subconcolorous with the pileus when young, with fibrillose universal velar remnants resting more or less on bulb margin. Cortinate remnants whitish. *Context* whitish or pale ochraceous in the stipe. *Odour* faintly raphanoid, with a sweetish fragrant component. *Macrochemical reactions* reaction to guaiac positive, very slow, setting in after at least 5 minutes.

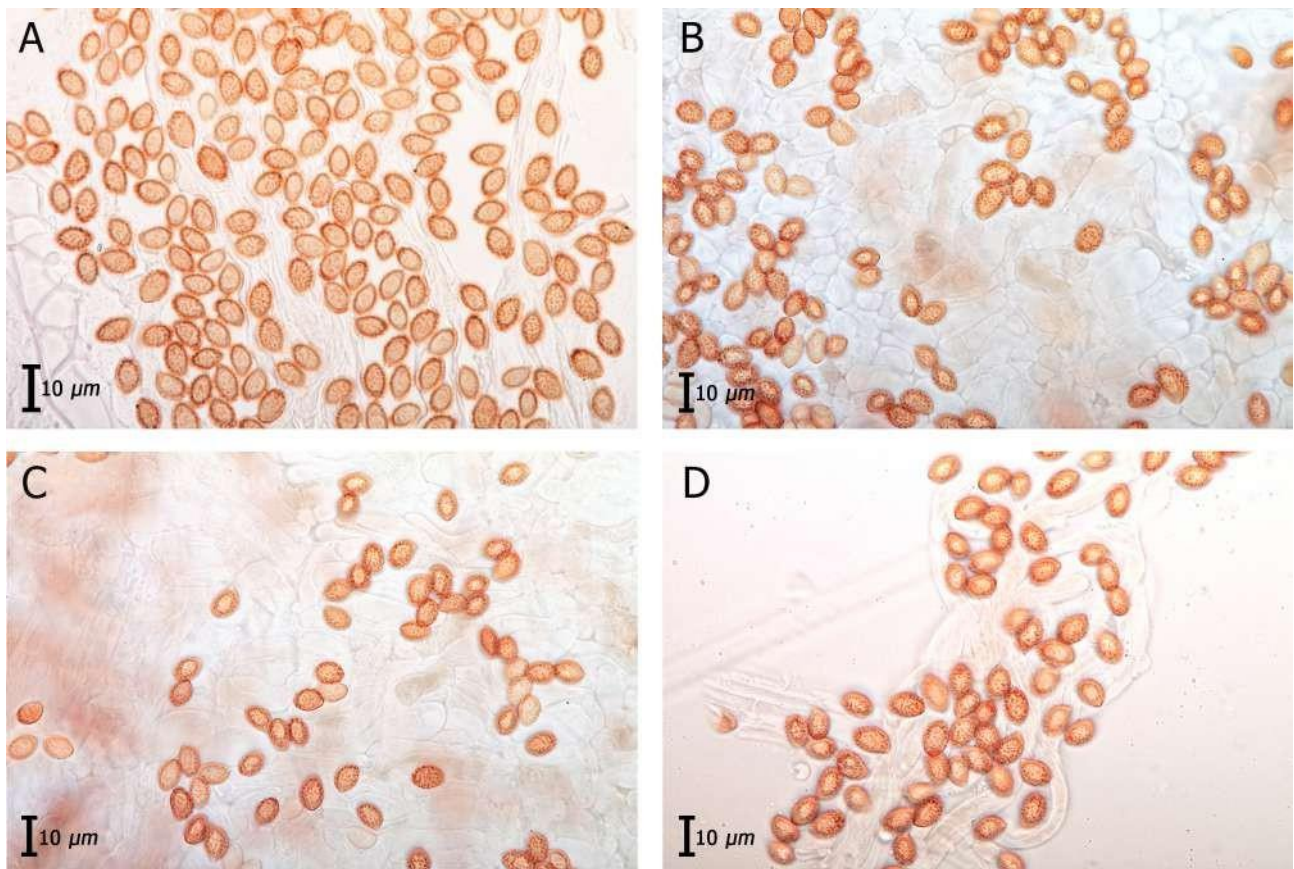


FIGURE 6. Basidiospores of *Cortinarius chevassutii*, *Cortinarius pseudobulliardiioides* and *Cortinarius variebulbus*. (Photos G. Boerio). A. *Cortinarius chevassutii*, coll. TR-gmb01992; B. *Cortinarius pseudobulliardiioides*, coll., TR-gmb01993. C. *Cortinarius pseudobulliardiioides*, coll. TR-gmb01999. D. *Cortinarius variebulbus*, coll. TR-gmb01250.

Basidiospores [6, 6, 223] $7.6\text{--}11.2 \times 4.8\text{--}6.8 \mu\text{m}$, $MV = 9.4 \times 5.8 \mu\text{m}$, intercarpic variation of $MV = 8.2\text{--}10.4 \times 5.3\text{--}6.3 \mu\text{m}$ $Q = 1.44\text{--}1.79$, $Q_m = 1.61$, intercarpic variation of $Q_m = 1.52\text{--}1.67$, predominantly elliptic-subamygdaliform, subovoid in front view, coarsely and densely warted, warts forming trapezoidal plaques, here and there catenulate or coalescing into short ridges, ornamentation generally more prominent towards the apex. Apex rounded or weakly tapering. Plage well differentiated. Spores more or less moderately or strongly dextrinoid to Melzer's reagent (Tab. 3, Figs. 3, 6). *Pileipellis* Suprapellis a cutis of thin, cylindrical hyphae, $3\text{--}9 \mu\text{m}$ wide; subpellis well-differentiated, made up of broader, short-celled hyphae, $15\text{--}20 \mu\text{m}$ wide. Pigment intracellular and parietal, yellowish brown. *Basidia* $27\text{--}42 \times 7\text{--}12 \mu\text{m}$, narrowly clavate, clamped, hyaline or with brownish yellow intracellular pigment in KOH. *Marginal cells* Lamellar edge partially sterile; marginal cells consisting of sinuous, basidioliform, cylindro-clavate cells, interspersed with basidia, mostly unicellular, occasionally with a median septum and/or lateral diverticulum, terminal element cylindro-clavate ($12\text{--}30 \times 3\text{--}10 \mu\text{m}$). *Clamp connections* common at all septa.

Habitat and distribution:—With *Quercus* spp. (incl. *Q. ilex*), *Carpinus betulus* and *Tilia cordata* on calcareous ground, mainly in Mediterranean-submediterranean and warm thermophilous regions; known from France, Italy, Spain and thermophilous sites in Germany, north to the limestone plateau of Huy.

Material analysed:—FRANCE. Drôme, Saint-Justin, 04 October 1997, mixed deciduous trees, leg. A. Bidaud, PML4567 (paratype of *Cortinarius argentatus* var. *griseobrunneus*); Gard, Montdardier, 18 October 2012, *Quercus ilex*, leg. F. Richard, FR2012204. GERMANY. Sachsen-Anhalt, Huy, Huysburg east, 04 October 2010, leg. T.E. Brandrud & G. Schmidt-Stohn, TEB469-10; *ibid.*, TEB470-10; Sachsen-Anhalt, Freyburg, Kleine Probstei, NSG Tote Täler, 22 September 2014, *Quercus* spp., *Carpinus betulus*, leg. M. Huth, HM2017-030; *ibid.*, 21 October 2016, *Tilia* spp., *Quercus* spp., HM2017-008; Sachsen-Anhalt, Dingelstedt, Huy, 28 September 1998, *Quercus* spp., leg. G. Schmidt-Stohn, SSt98-220b; *ibid.*, 04 November 2008, SSt08-175; Nordrhein-Westfalen, Wachendorf, 07 October 2007, *Fagus sylvatica*, leg. T. Münzmay, TM49-07; Freyburg, Tote Täler, 04 November 2008, leg. G. Schmidt-Stohn, SSt08-175; Huy, Dingelstedt, 27 September 2008, leg. G. Schmidt-Stohn, SSt98-216a. ITALY. Trentino-Alto Adige, Trento, 03 December 2022, loc. “Dosso S. Rocco”, mixed forest with *Quercus cerris*, *Q. pubescens* and *Ostrya carpinifolia*, leg. A. Valdagni, n°01250 in TR-gmb herbarium; *ibid.*, 24 October 2020, AV-011-2020 (not sequenced); *ibid.*, 22 November 2023, leg. A. Fellin, AF-110-2023 (not sequenced); *ibid.*, 23 November 2023, leg. A. Valdagni, AF-111-2023 (not sequenced). SPAIN. Jaén, Cambil, Sendero Gibrálberca, 1150 m asl, 18 November 2018, *Quercus ilex*, *Q. faginea*, *Pinus Pinaster*, *P. halepensis* and various *Cistaceae* spp., leg. F. Armada & J.D. Reyes, FA4647; Granada, Jàtar, Loma del Cura, 1000 m asl, 06 December 2018, *Quercus ilex*, *Pinus halepensis* and various *Cistaceae* spp., leg. F. Armada & M.-J. Díaz de Haro, FA4772.

Comments:—*Cortinarius variebulbus* is the third taxon in the *C. chevassutii* complex, characterized by the presence of a more or less abruptly bulbous stipe base. This species seems, however, to display the least marginated bulbous stipe when compared to *C. chevassutii* and *C. subbulliardoides*, with some specimens with a more clavate-bulbous than a clearly marginate-bulbous stipe base. The spores of *C. variebulbus* are also, on average, slightly larger than those produced by the two other species (see Fig. 3).

This taxon, together with *C. chevassutii* and *C. acutibulbus* Chevassut & Rob. Henry (1982: 40), was originally placed in subgenus *Phlegmoloma* Rob. Henry, introduced for a few *Telamonia* species displaying morphological characters normally found in *Phlegmacia*, including a marginate-bulbous stipe (Henry 1991). This species is characterized by medium-sized basidiomata, a pileus covered with silvery, innate, radially-arranged fibrils, tending to become greyish on a beige background, which give the surface a sparkly appearance in mature specimens, and a stipe flaring into a marginate or submarginate bulb decorated with abundant velar remnants. In the protologue, Henry compares this species to *C. acutibulbus*, differentiating the two species by differences in the shape of the bulb and spore shape and size. The examination of these micromorphological features in our phylogenetically confirmed collections of *C. variebulbus* shows that most spores have an ellipsoid or subamygdaliform shape, while some others are ovoid in front view. Spore size was also found to be more variable and overall larger than what was reported in the protologue (Tab. 3, Figs. 3, 6 vs Henry 1991). This suggests some phenotypic plasticity within *C. variebulbus*, and careful measurements of the spores of additional sequenced collections of this species will be welcome in the future to better assess the actual variability in spore size. In the meantime, and in the absence of reference sequence for *C. acutibulbus*, the synonymy of this species with *C. variebulbus* remains dubious. The sequence of one paratype (PML4567) of *Cortinarius argentatus* var. *griseobrunneus* Bidaud & Reumaux in Bidaud *et al.* (2002: 691) is here shown to belong to *C. variebulbus* (Fig. 1). The lack of available sequence for the holotype of this infraspecific taxon prevents strong conclusions to be made about its conspecificity with *C. variebulbus* but in any case, the latter binomial would have priority at specific rank.



FIGURE 7. *Cortinarius variebulbus*, basidiomata. A. coll. AF-110-2023, Italy (Photo: A. Fellin). B. coll. TR-gmb01250, Italy (Photo: A. Valdagni). C. coll. FA4772, Spain (Photo: F. Armada). D. coll. FA4647, Spain (Photo: F. Armada). E. coll. SS198-216a, Germany (Photo: G. Schmidt-Stohn). F. coll. SS108-175, Germany (Photo: G. Schmidt-Stohn). Bar: 1cm (A).

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