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Taxonomy and phylogeny of the phlegmacioid clade *Camptori* (*Cortinarius* s.l., *Basidiomycota*) in Europe with description of four new species

Geert Schmidt-Stohn¹ · Tor Erik Brandrud² · Jean-Michel Bellanger³ · Günter Saar⁴ · Josep Ballarà⁵ · François Armada⁶ · László Albert⁷ · Tobias Guldberg Frøslev⁸ · Bálint Dima⁹ 

Abstract

In this study, we investigate the phylogeny and taxonomy of the /*Camptori* clade sensu Soop et al. (2019a). Based on combined nrDNA ITS phylogenetic, morphological, and ecological analyses, the clade includes six species in Europe, four of which are described here as new to science: *Cortinarius malavalii*, *C. marklundii*, *C. violaceoserrulatus*, and *C. viridocaelestinus*. We also provide a taxonomic revision of the two known species in the clade, *C. camptoros* and *C. viridocoeruleus*. In its current concept, the /*Camptori* clade is mostly represented in frondose woodlands of southern Europe and none of the species is found in the boreal coniferous zones of Northern Europe. Three species are strictly thermophilous Mediterranean-submediterranean species associated mainly with southern *Quercus* spp., whereas *C. camptoros* is found mainly in montane *Abies* forests, and *C. marklundii* reaches boreonemoral *Tilia-Corylus* sites in S Scandinavia and alpine *Dryas* sites in Spain. An identification key to the species is presented.

Keywords Ectomycorrhiza · Habitat preferences · ITS barcode · Microscopy · *Phlegmacium* · Type studies

Introduction

The huge genus *Cortinarius* has traditionally been divided into 5–8 subgenera (Moser 1967, Brandrud et al. 1990–2018, Jeppesen et al. 2012), of which subgen. *Phlegmacium*, *Telamonia*, and *Dermocybe* are the largest and most well-known, based on morphology. Molecular phylogenetic studies, however, have shown that these entities do not represent unique lineages and need to be emended or more seriously revised to better reflect evolutionary history within the genus (e.g. Peintner et al. 2004, Garnica et al. 2005). Recently,

Liimatainen et al. (2022) have split the genus *Cortinarius* into 10 genera based on genomic and multi-gene sequence data. The new classification, however, is not yet adopted in the current work, which has been submitted before the latter publication.

The traditional subgenus *Phlegmacium*, in particular, encompasses three major clades: /*Phlegmacium* I, II and /*Calochroi* (Stensrud et al. 2014, Garnica et al. 2016, Soop et al. 2019a). For this reason, members of the morphologically based subgenus *Phlegmacium* are nowadays collectively referred to as “phlegmacioid species”. The presently treated

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/Camptori clade s. Soop et al. (2019a) belongs to the major clade Phlegmacium I (Garnica et al. 2016), together with morphologically resembling taxa belonging to /Dionysae clade, sections *Glaucopodes*, *Amoenolentes*, and *Aureocistophili* (Soop et al. 2019a, b). All these groups are characterized by (i) a distinctly duplex structure of pileipellis, including a “sub-cellular” subcutis/hypoderm of inflated elements, and (ii) citriform-amygdaloid spores with verrucose, discrete (little confluent) ornaments. Associated with the pileipellis structure comes also the ability of pilei to get easy water-soaked, exhibiting dark, hygrophanous spots or zones in moist weather (like many telamonioid species).

During the last 10–15 years, the taxonomy of a number of phlegmacoid groups/sections has been extensively revised in Europe on the basis of combined morphological and phylogenetic evidence: sect. *Calochroi* (Frøslev 2007, Frøslev et al. 2007; cf. also Garnica et al. 2009), (sub)section *Elegantiores* (Garnica et al. 2006), sect. *Claricolores* (Brandrud et al. 2013), sect. *Multiformes* (Brandrud et al., 2014a), sect. *Purpurascetes* (Saar et al. 2014), sect. *Riederi* (Brandrud et al. 2018), sect. *Aureocistophili* (Fernández-Brime et al. 2014, Soop et al. 2019b), and subsect. *Varii* (Schmidt-Stohn et al. 2020). Comprehensive taxonomic studies are, however, still lacking for many groups in Europe.

The /Camptori clade, together with the related /Dionysae clade, sect. *Amoenolentes* and sect. *Aureocistophili*, consists of mainly southern, Mediterranean, poorly known species that have been little studied until quite recently. There are hardly any “traces” of Camptori species in classical mycological literature, not even in the *Phlegmacium* monograph of Moser (1961). This situation remained so until *C. viridocoeruleus* was described by Chevassut & Henry (1975) and *C. camptoros* by Brandrud & Melot (1983). Over the years, we have been gradually convinced that these two species were both collective, but clarifying these species complexes with additional phylogenetic methods took a longer time. The revision of /Camptori is presented here with detailed species-level taxonomy, including type studies, based on combined molecular, morphological, and ecological data. Four out of six European Camptori species are here presented as new to science. They are all relatively rare and have restricted distributions in poorly studied regions of Europe, so we find it very likely that further taxa are to be discovered, especially in the Mediterranean region.

Materials and methods

Molecular analyses

A total of 42 Camptori specimens from eight European countries were studied, including the type specimens of *Cortinarius camptoros*, *C. purpuratus*, and

C. viridocoeruleus. Additional eight European and four North American Camptori as well as three outgroup sequences were retrieved from GenBank (Table 1). For most of the DNA extractions as well as the PCR and sequencing of the universal fungal DNA barcode region (Schoch et al. 2012), the ribosomal internal transcribed spacer (ITS1–5.8S–ITS2), we followed the protocols described in Liimatainen et al. (2014), Borovička et al. (2015), Dima et al. (2016), and Brandrud et al. (2018). Primer pairs of ITS1F-ITS4, and alternatively, in case of old type materials ITS1F/ITS2 and ITS3/4 (Gardes & Bruns 1993, White et al. 1990) were used to amplify the whole or partial ITS region. For three specimens (types of *C. camptoros*, *C. purpuratus*, and *C. viridocoeruleus*), the amplicons were sequenced with NGS sequencing on Illumina MiSeq using tagged primers and a setup and bioinformatic approach similar to that in Frøslev et al. (2019). GenBank accession numbers of the sequences used in the phylogenetic analyses are listed in Table 1. Multiple sequence alignment was done in MAFFT v7 (<http://mafft.cbrc.jp/alignment/server>) using the E-INS-I method (Katoh & Standley 2013) with default settings. The alignment was checked and trimmed in SeaView 4 (Gouy et al. 2010). Following Nagy et al. (2012), the phylogenetically informative indels were coded as presence/absence data with FastGap 1.2 (Borchsenius 2009), applying the simple indel coding algorithm (Simmons et al. 2001). The final alignment including nucleotide and binary characters was analysed in RAxML (Stamatakis 2014) and MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003). Maximum likelihood (ML) phylogenetic reconstruction was performed in raxmlGUI (Silvestro & Michalak 2012) using rapid bootstrap analysis with 1,000 replicates. Three nucleotide partitions (ITS1, 5.8S, ITS2) were set to the GTRGAMMA substitution model in addition to one binary partition (indel characters) that was set to default. In the Bayesian inference (BI) phylogeny, the alignment was divided into four partitions (ITS1, 5.8S, ITS2, and indels) as well. The GTR + Γ substitution model was applied to the nucleotide characters, while the two-parameter Markov model was set for the indels. Two independent runs of four Markov chain Monte Carlo (MCMC) were performed each for 5 000 000 generations, sampling every 1000th generation. The first 30% of the trees were discarded as burn-in. For the remaining trees, a 50% majority rule consensus phylogram with posterior probabilities as nodal supports was computed. The best scoring ML tree from Maximum likelihood analysis was further edited in MEGA 7 (Kumar et al. 2016) and Adobe Illustrator CS4 and shown in Fig. 1.

Morphological studies

Fresh material was examined mainly from N, C, W, and S Europe. More collections than those sequenced were studied morphologically, but the character variation described in the

Table 1 *Cortinarius* nrDNA ITS sequences used in the phylogenetic analysis

Species name	Voucher	Country	ITS acc. no.	References
<i>C. anserinus</i>	TUB011436	Germany	AY174807	Garnica et al. (2003)
<i>C. camptoros</i>	Melot 81.359 (holotype)	Germany	ON006470	This study
<i>C. camptoros</i>	TUB011848	Germany	AY669540	Garnica et al. (2005)
<i>C. camptoros</i>	TUB019788	Germany	KJ421043	Garnica et al. (2016)
<i>C. camptoros</i>	TEB901-17	Austria	ON006471	This study
<i>C. camptoros</i>	JB-9819-18	Spain	ON006472	This study
<i>C. camptoros</i>	GS16-5	Germany	MK358087	Soop et al. (2019b)
<i>C. camptoros</i>	GS20-8	Germany	ON006473	This study
<i>C. dionysae</i>	TSJ2000-102	Germany	DQ083782	Frøslev et al. (2005)
<i>C. gracilior</i>	TUB019756	Germany	KJ420995	Garnica et al. (2016)
<i>C. malavalii</i>	MPU927722 (holotype)	France	ON006474	This study
<i>C. malavalii</i>	JB-8503-14	Spain	ON006475	This study
<i>C. malavalii</i>	JMB2011112620	France	ON006476	This study
<i>C. malavalii</i>	JMB2012111401	France	ON006477	This study
<i>C. marklundii</i>	O-F-259458 (holotype)	Norway	ON006478	This study
<i>C. marklundii</i>	SSt13-150	Germany	ON006479	This study
<i>C. marklundii</i>	TEB890-13	Norway	ON006480	This study
<i>C. marklundii</i>	TEB452-17	Norway	ON006481	This study
<i>C. marklundii</i>	JB-9561-18	Spain	ON006482	This study
<i>C. marklundii</i>	JB-9736-18	Spain	ON006483	This study
<i>C. marklundii</i>	CFP1024	Sweden	ON006484	This study
<i>C. marklundii</i>	SSt07-213	Germany	ON006485	This study
<i>C. marklundii</i>	SSt19-145	Germany	ON006486	This study
<i>C. marklundii</i>	XC2012-150	France	ON006487	This study
<i>C. marklundii</i>	TEB358-14	Norway	ON006488	This study
<i>C. marklundii</i>	CFP874	Sweden	ON006489	This study
<i>C. marklundii</i>	AB11-10-202	France	ON006490	This study
<i>C. marklundii</i>	SSt16-083	Sweden	ON006491	This study
<i>C. velicopius</i>	MICH10435 (holotype)	USA	KF732470	Liimatainen et al. (2014)
<i>C. violaceoserrulatus</i>	BP111782 (holotype)	Hungary	ON006492	This study
<i>C. violaceoserrulatus</i>	XC2011-236	France	ON006493	This study
<i>C. violaceoserrulatus</i>	JB-9990-18	Spain	ON006494	This study
<i>C. violaceoserrulatus</i>	JMB2011112640	France	ON006495	This study
<i>C. violaceoserrulatus</i>	DB5689	Hungary	ON006496	This study
<i>C. violaceoserrulatus</i>	CR6374-2018	Spain	ON006497	This study
<i>C. violaceoserrulatus</i>	XC2006-161	France	ON006498	This study
<i>C. violaceoserrulatus</i>	JB-10345-19	Spain	ON006499	This study
<i>C. violaceoserrulatus</i>	Maletti 6-12-2014	Italy	ON006500	This study
<i>C. violaceoserrulatus</i>	OTU32 (as <i>C. sp.</i>)	France	KM247644	Taschen et al. (2015)
<i>C. viridocaelestinus</i>	JA-CUSSTA 9531 (holotype)	Spain	ON006501	This study
<i>C. viridocaelestinus</i>	FA4768	Spain	ON006502	This study
<i>C. viridocoeruleus</i>	Henry3366 (holotype)	France	ON006503	This study
<i>C. viridocoeruleus</i>	TF2000-056 (holotype of <i>C. lepistoides</i>)	Denmark	FJ195643	Frøslev & Jeppesen (2009)
<i>C. viridocoeruleus</i>	Henry84/31 (holotype of <i>C. purpuratus</i>)	France	ON006504	This study
<i>C. viridocoeruleus</i>	SSt13-130	Germany	ON006505	This study
<i>C. viridocoeruleus</i>	SSt20-029	Sweden	ON006506	This study
<i>C. viridocoeruleus</i>	GE02.074 (as <i>C. imperialis</i>)	France	ON006507	This study
<i>C. viridocoeruleus</i>	DB628	Hungary	ON006508	This study

Table 1 (continued)

Species name	Voucher	Country	ITS acc. no.	References
<i>C. viridocoeruleus</i>	TUB011435	Germany	AY174789	Garnica et al. (2003)
<i>C. viridocoeruleus</i>	CFP907	Germany	ON006509	This study
<i>C. viridocoeruleus</i>	TUB011408	Germany	AY174788	Garnica et al. (2003)
<i>C. viridocoeruleus</i>	TUB023092	Italy	KJ421077	Garnica et al. (2016)
<i>C. viridocoeruleus</i>	TEB985-13	France	ON006510	This study
<i>C. viridocoeruleus</i>	SS04-110	Germany	KJ421183	Garnica et al. (2016)
<i>C. viridocoeruleus</i> cf.	DBB25739	USA	JF742658	GenBank, unpublished
<i>Cortinarius</i> sp.	isolate796 (as <i>C. camptoros</i>)	USA	KX389106	GenBank, unpublished
<i>Cortinarius</i> sp.	JLF8307	USA	MT477099	GenBank, unpublished

taxonomic part is based on the sequenced material. Specimens examined morphologically and sequenced are listed under each species description (see also Table 1); most specimens were examined both macro- and micromorphologically.

The taxonomic descriptions are based on the material studied by the authors. The measurements of macromorphological characters stem from expanded, but never old (and then often aberrant) basidiocarps. The terminology of characters follows Brandrud et al. (1990–2018) and Brandrud (1996).

Microscopic structures were observed partly from fresh material mounted in H₂O, often with a drop of 40% KOH subsequently added, and partly from dried material mounted in H₂O and then KOH.

Basidiospore measurements were made in L4 solution according to Cléménçon (Cléménçon 1972, Erb and Matheis, 1983) at 1000× magnification with the Zeiss microscope Axioskop 40 and the Zeiss Axiocam 208 color on a flat screen with the program ZEN core 3.1.88.0000 from Zeiss. The measurements are based on at least 30 spores from each specimen/basidiocarp; in the descriptions, numbers in square brackets refer (in this order) to the number of collections they originate from, the number of basidiocarps, and the number of spores measured, respectively. Spore measurements are given as follows: length range × width range. *Q* values were calculated as follows: $Q = \text{length} / \text{width}$. MV/MVs indicate “mean value(s)”. To exclude aberrant spores, the given values in the descriptions are based only on spores within the 95% confidence interval.

The photo micrographs of the spores are created with the method of “focus-stacking” (Schmidt-Stohn 2011). About 25 shots with the Zeiss Axiocam 208 color digital camera and the Zeiss Plan-Apochromat 63×/1.40 Oil, each shot with different focus, are combined with the final picture with the Helicon Focus 7.6.6 software. For such small, reproducible focus steps (each about 0.1–0.2 μm in height), a self-made mechanical equipment, coupled with the focusing fine drive of the microscope, is used (any further questions about the equipment, please direct to the first author). For the correction and the

final arrangement of the spores on the plates, Adobe Photoshop version 22.1.0 was used.

The scatter diagrams of the spore dimensions are plotted with Microsoft Excel. For the final presentation, the graphics were copied from Excel and edited with Adobe Photoshop.

Results

Molecular phylogeny

The final dataset is composed of 57 nrDNA ITS sequences. The alignment including the nucleotide and indel characters was 654+54=708 characters long (alignment is included in the 12). Phylogenetic trees from ML and BI analyses showed congruent topologies. The best scoring ML tree is shown in Fig. 1. The /Camptori clade was introduced by Soop et al. (2019a), and the concept is followed here. So far, the circumscription is based mostly on European species and a few North American lineages known from sequence data. The /Camptori clade is well-supported in all phylogenetic analyses (single- and multi-gene as well).

Ten species-level terminal clades were resolved within the /Camptori clade based on our phylogenetic analyses. Four North American lineages (*Cortinarius velicopius* and three yet nameless species) are not treated further in this work. The remaining, moderately to well-supported six clades represent European species. Holotype sequences of *C. camptoros*, *C. lepidoides*, *C. purpuratus*, and *C. viridocoeruleus* clustered into two clades, representing *C. camptoros* and *C. viridocoeruleus*, with *C. purpuratus* and *C. lepidoides* as younger synonyms of the latter name. Four lineages did not match any type sequences, and based on their unique morphological and genetic features, we formally describe them below as *C. malavali*, *C. marklundii*, *C. violaceoserrulatus*, and *C. viridocaelestinus* spp. nov. (see “Taxonomy” part).

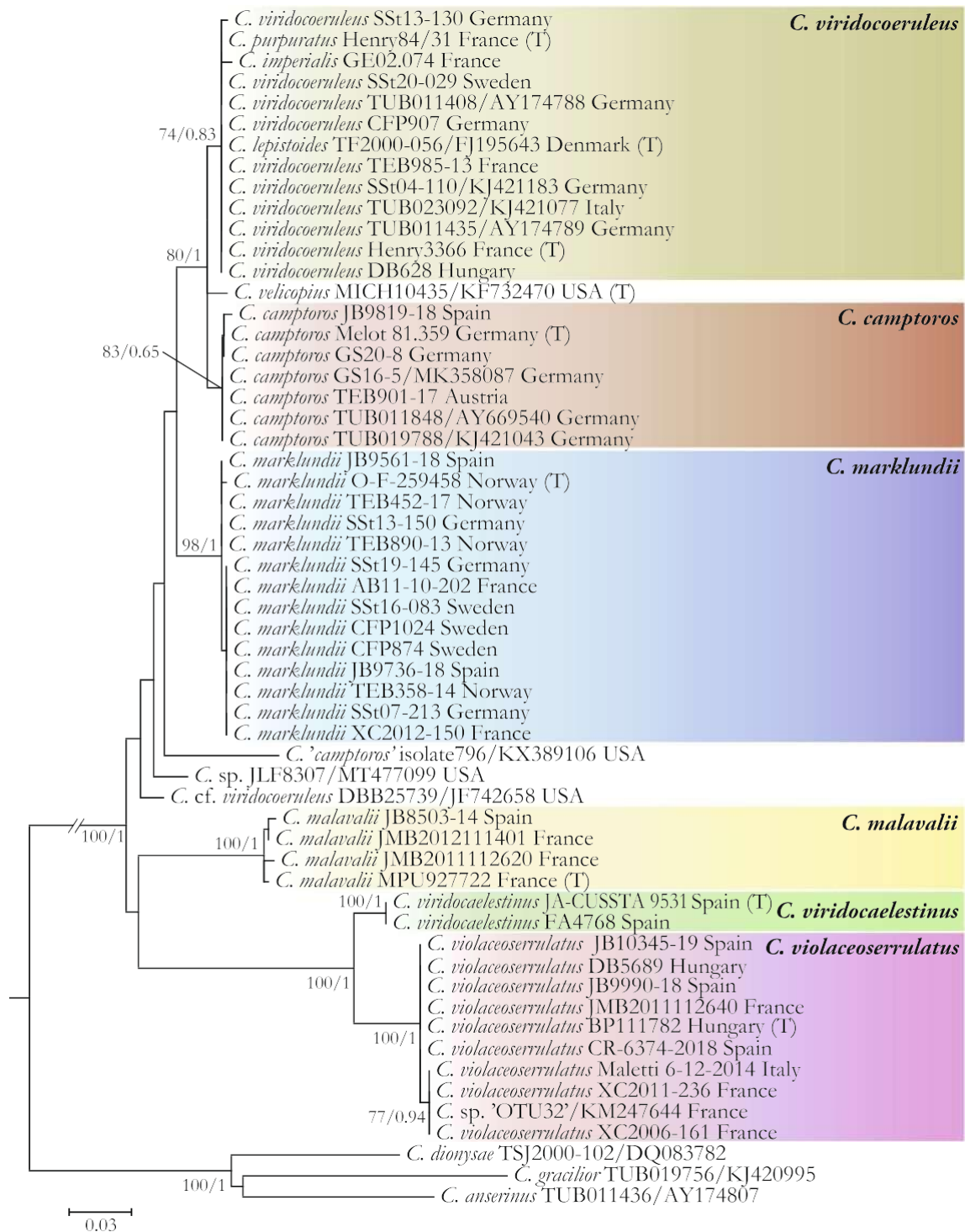


Fig. 1 Maximum likelihood phylogenetic tree of the /Camptori clade of the genus *Cortinarius* based on nrDNA ITS sequence analyses with gap coding. Sequences are labelled with their voucher numbers/GenBank accession numbers and geographical origin. Type sequences are marked

with (T). Species treated in this study are highlighted in colour boxes. ML bootstrap values >70% as well as Bayesian posterior probabilities >0.6 are placed above or below branches. Scale bar indicates 0.03 expected change per site per branch

The minimal phylogenetic distance in the nrDNA ITS region between the six identified species ranges from 6 (*C. camptoros*/*C. viridocoeruleus*) to 36 (*C. malavali*/*C. marklundii*) nucleotide and indel differences,

representing c. 1 to 6% of sequence divergence, respectively. Intraspecific sequence variability is low among the species: 0–2 nucleotide or indel differences, representing maximum of 0.3% of sequence divergence.

Morphological characteristics of the /Camptori clade

The members of the /Camptori clade have some distinctive characters on group level. The pileus is glabrous and often hygrophanous towards margin, or with hygrophanous spots or steaks. The context appears elastic. The lamellae are tinged violaceous blue, often with a pronounced and persistent violaceous edge.

A total of 1113 spores from 26 collections/basidiocarps were measured and partially also documented photographically in this study. The mean values of length (L) \times width (W) for different species fall between 8.7–10.4 \times 5.1–6.2 μm (Table 2). With such narrow ranges, it is hardly possible to calculate statistically significant differences (Fig. 2). Nevertheless, there are clear differences, e.g., between *C. viridocoeruleus* and *C. violaceoserrulatus* (Fig. 3). The shape of the spores is a rather well-characterizing feature of the /Camptori clade as a group, all species possessing distinctly citriform spores with an ornament consisting of isolated to slightly interconnected warts and a more or less visible suprahilar plage (Fig. 4).

The pileipellis is distinctly duplex, with a subcellular subcutis (hypoderm) of inflated, more or less cemented elements, resembling the structure of many telamonioid species, having also similar macrofeatures, i.e. the hygrophanous structure.

Habitat and distribution

Most members of the /Camptori clade are thermophilous, with preference for Mediterranean and lowland temperate regions of Europe. Half of the species (*C. malavali*, *C. violaceoserrulatus*, *C. viridicaelestinus*) are seemingly strictly southern *Quercus* associates, whereas *C. viridocoeruleus* has a wider temperate-Mediterranean *Fagus-Quercus* (-*Carpinus*) range. *Cortinarius marklundii* has a peculiar, patchy W European distribution, with core areas in Spain (*Dryas* sites), France-Germany (lowland *Fagus* sites), and S Scandinavia (coastal *Tilia-Corylus* sites). According to present data, *C. camptoros* is restricted to montane *Abies alba* forests in C and S Europe.

Taxonomy

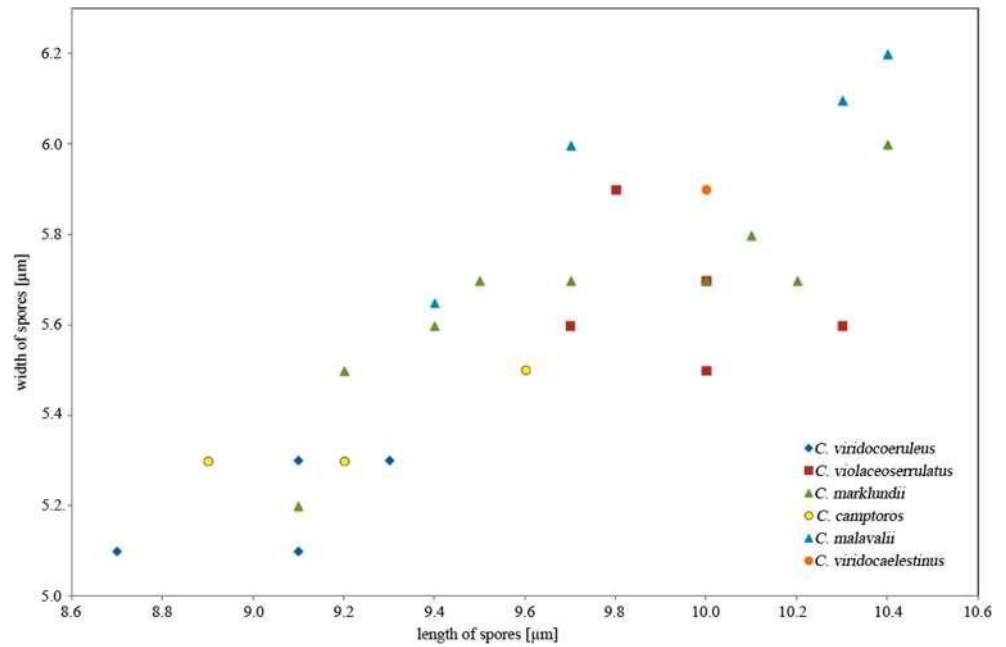
Description of the /Camptori clade

Basidiocarps fleshy and phlegmacioid, pileus glabrous and viscid-glutinous, somewhat elastic (like a *Lyophyllum* sp.), mostly more or less hygrophanous, pileus colours from violaceous-blue, greyish blue, ochraceous yellow, olivaceous brown to vivid ochraceous reddish brown. Lamellae usually tinged violaceous blue to lilaceous when young, often with more or less persistent lilac lamellae edge, otherwise soon fading to greyish brown. Stipe with a (slightly) marginate-bulbous base, glossy, initially violaceous blue, sometimes persistent at apex.

Table 2 Basidiospore characteristics of the species in the /Camptori clade of the genus *Cortinarius*. MV/MVs, mean value(s)

<i>Cortinarius</i> species	<i>n</i> coll.	<i>n</i> basidiocarps	<i>n</i> spores	Length (L) \times width (W) 95% variation (μm); MV	Length (L) \times width (W) total (μm); MV	Variation in MVs (μm)	Q L/W 95% variation; MV	Q L/W total; MV
<i>C. camptoros</i>	3	3	144	8.1–9.3–10.5 \times 4.8–5.4–6.0	7.6–9.3–10.7 \times 4.8–5.4–6.1	8.9–9.6 \times 5.3–5.5	1.56–1.69–1.88	1.48–1.72–1.90
<i>C. viridocoeruleus</i>	4	4	146	8.3–9.1–9.9 \times 4.8–5.2–5.6	7.9–9.1–10.2 \times 4.6–5.2–5.9	8.7–9.3 \times 5.1–5.3	1.56–1.74–1.92	1.55–1.74–2.05
<i>C. marklundii</i>	9	9	387	8.4–9.8–11.0 \times 5.0–5.6–6.2	8.2–9.8–11.5 \times 4.8–5.6–6.5	9.1–10.4 \times 5.2–6.0	1.57–1.73–1.89	1.47–1.73–1.94
<i>C. violaceoserrulatus</i>	5	5	225	8.7–9.9–11.1 \times 5.1–5.7–6.3	8.5–9.9–11.5 \times 5.0–5.7–6.7	9.7–10.3 \times 5.5–5.9	1.54–1.76–1.98	1.34–1.76–2.04
<i>C. malavali</i>	4	4	166	8.8–10.0–11.2 \times 5.4–6.0–6.6	8.7–10.0–11.6 \times 5.1–6.0–7.0	9.4–10.4 \times 5.6–6.2	1.51–1.67–1.83	1.49–1.67–1.95
<i>C. viridicaelestinus</i>	1	1	45	9.0–10.0–11.0 \times 5.5–5.9–6.3	9.2–10.0–11.4 \times 5.4–5.9–6.4	10.0 \times 5.9	1.52–1.70–1.88	1.56–1.70–2.00
Σ	26	26	1113					

Fig. 2 Scatter diagram representing the variation of the basidiospores of the species/ collections in the /Camptori clade of the genus *Cortinarius*. Each dot is the MV of one collection



Universal veil remnants sparse to (rarely) abundant and leaving silvery-whitish patches on pileus surface; sometimes initially with distinct and whitish-bluish volva at bulb margin. Context initially bluish in stipe, becoming ochraceous brown tinged in pileus and bulb.

Basidiospores distinctly citriform, finely to medium coarsely verrucose with isolated and also interconnected warts, mostly clearly visible in the outline of the spores, often with suprahilar plage. Pileipellis duplex, with a distinct, sub-cellular subcutis/hypoderm (resembling that of telamonioid taxa) and above with a thin epicutis of narrow repent-

entangled hyphae. Habitat mainly in temperate-Mediterranean frondose forests.

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

Fig. 5a–d

Mycobank: MB 108801

Holotype: Germany, Baden-Württemberg, Baar, Trossingen, 10 Oct 1981, J. Melot 81.359 (herb. J. Melot). GenBank ON006470 (ITS).

Fig. 3 Scatter diagram representing the variation of basidiospores of *C. viridocoeruleus* and *C. violaceoserrulatus*. Each dot stands for one spore (only values within the 95% confidence interval)

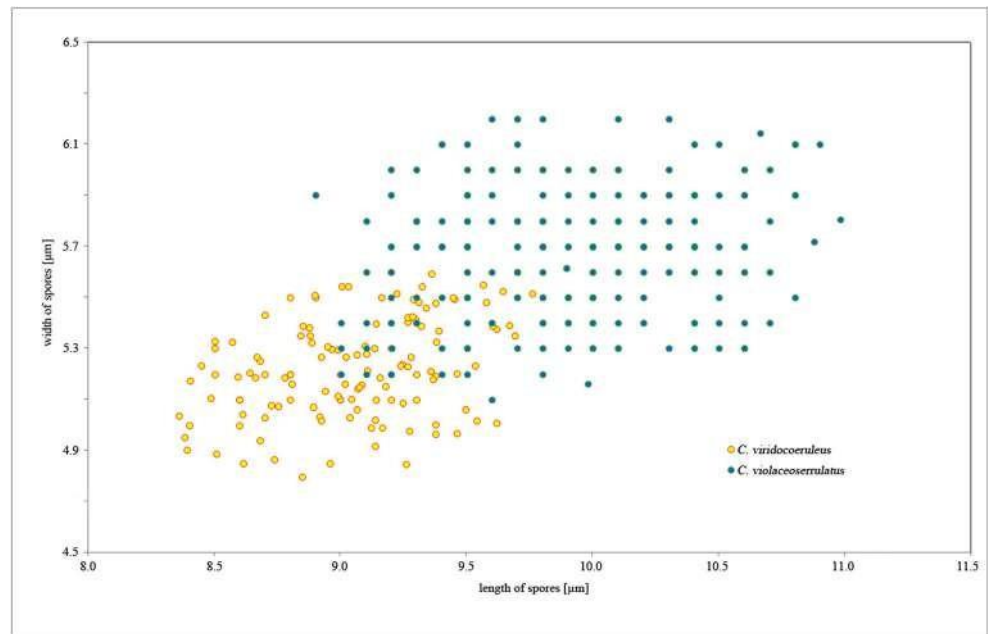


Fig. 4 Basidiospores of selected collections of the species in the /Camptori clade of the genus *Cortinarius*

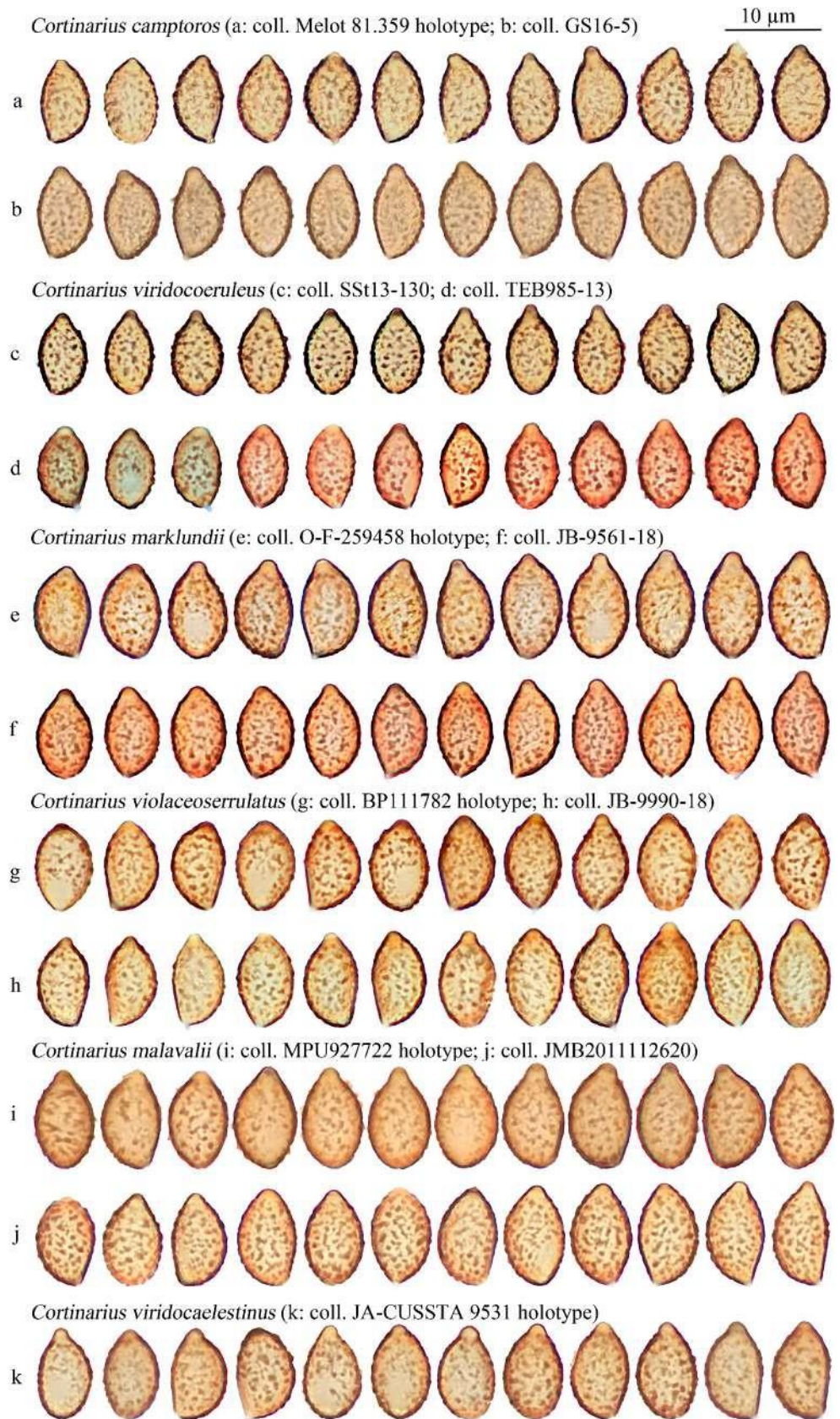


Fig. 5 Basidiocarps of the species in the /Camptori clade of the genus *Cortinarius* (voucher numbers and geographical origin in brackets):

a, b, c, d *C. camptoros* (a Melot 81.359 holotype Germany, b GS16-5 Germany, c JB-9819-18 Spain, d GS20-08 Germany);
 e, f, g, h *C. viridocoenuleus* (e SSt20-029 Sweden, f SSt04-110 Germany, g TEB984-13 France, h TF2000-056, holotype of *C. lepistoides*, Denmark).
 Photos: a J. Melot; b G. Saar; c J. Ballarà; d U. Winkler; e, f G. Schmidt-Stohn; g T.E. Brandrud; h T.S. Jeppesen



Description: compiled from the original diagnosis, as well as from own (sequenced) material. Pileus 30–80 mm, hemispherical, soon plano-convex to broadly umbonate, sometimes irregular, margin involute, finally often split, thin, pronounced and significantly elastic (like *Lyophyllum decastes*), viscid-glutinous, with a greasy appearance, glabrous and glossy when dry, often with a dark, hygrophanous marginal zone or radiate hygrophanous streaks, mature specimens often becoming radially wrinkled upon drying; initially olivaceous grey to grey brown or horn brown, with more ochraceous yellow at centre, often distinctly bicoloured, with ochre to chestnut brown at centre and hygrophanous dark olive grey

at margin, becoming darker olivaceous brown at centre, or centre becoming vividly ochre yellow orange (holotype) or remaining ochraceous brown, at margin discolouring to greyish ochraceous, in places with olive tones or also flamed redbrown and sometimes developing redbrown spots; very thin and fugacious frosty-micaceous veil remnants present at centre when young, sometimes silvery-fibrillose from veil also towards margin. Lamellae normally distant to a little bit more crowded, 4–6 mm broad, broadly emarginate, edge initially irregular wavy-serrulate-fimbriate, first bluish grey to whitish grey, with bluish-violaceous tinge towards edge, often with distinctly and persistently violaceous blue edge, finally

ochraceous to rusty brown. Stipe 40–100 × 9–20 mm, cylindrical with a marginate, not very distinct bulb (up to 25–30 mm wide), initially distinct greyish violet, especially in upper part and at bulb margin, often persistently with bluish tinge, finally discolouring to whitish, and sometimes with brass brown patches. Veil remnants at bulb margin thin but distinct when young, initially greyish blue to whitish, soon disappearing. Basal mycelium whitish or pale bluish. Context fleshy in the centre and thin at margin, in the pileus and the bulb brownish white, sometimes discolouring to yellow orange in the bulb, greyish violet in the entire stipe, often rather persistent, then fading to (greyish) white in the stipe and slightly yellowish in the base of bulb, sometimes saffron yellow discolouring where eaten by larvae in bulb. Odour distinctly earthy, like *C. varicolor*, in the bulb sometimes like honey, taste mild. Macrochemical reactions: negative with KOH in the context, light/pale ochraceous on the basal tomentum and reddish brown on the pileus, negative with Guaiac. Exsiccata with a red-brown pileus and a pale brown stipe. Basidiospores [3, 3, 144], 8.1–10.5 × 4.8–6 μm (MV = 9.3 × 5.4 μm); variation of MVs: 8.9–9.6 × 5.3–5.5 μm; *Q* = 1.56–1.88 (MV = 1.69), brown, distinctly citriform, finely to medium strongly and densely verrucose, warts sometimes isolated but mostly somewhat interconnected, clearly visible in the outline of the spores, suprahilar plage not clearly visible. Lamellar edge partially fertile, with clavate, cylindrical, fusiform or irregularly shaped sterile cells (resembling those of *C. dionysae*). Basidia with granulate-refractive substance.

Pileipellis duplex, epicutis thin, consisting of 2–5 μm wide, more or less hyaline hyphae, here and there with some yellow brown (probably cytoplasmic) pigment. Hypoderm (subcutis) well developed, elements subcellular, 15–30 μm wide, with (chocolate) brown parietal (thick-wall), amber-like pigment, cementing the elements to a compact structure.

Habitat and distribution: Associated with *Abies alba* and probably also *Picea abies* in calcareous, montane coniferous forests. Since lacking from *Phlegmacium*-rich pure *Picea* forests, it seems probable that this species has a strict affinity to the calcareous, mixed *Abies alba* forest type, and that it preferentially forms mycorrhizae with *Abies alba*. *Cortinarius camptoros* is mainly verified from the montane *Abies alba*-*Picea abies*-*Pinus sylvestris* forests of the limestone plateaus of Black Forest, SW Germany, and also from the Eastern Prealps in Austria, as well as one collection from the Pyrenees of NE Spain. There are also finds from the Western Prealps in France (Vercors) as well as from the limestone plateaus of French and Swiss Jura that fit with the present species, but these collections are not verified by sequencing.

Comments: *Cortinarius camptoros* is characterized by its often bicoloured clay grey + ochraceous yellow pileus, turning more vividly reddish brown on exposure, the more or less persistent bluish lamellae edge and its habitat in montane,

calcareous *Abies-Picea* forests of C Europe. The (lilac) blue lamellae edge distinguishes this from *C. marklundii* (described below), which also differs in habitat (associated with *Fagus*, *Tilia*, and *Corylus*), and is phylogenetically well-separated. *Cortinarius marklundii* was included in the initial, wide concept of *C. camptoros* in Brandrud & Melot (1983) but with a separate comment (“Récolte....Norvège... sous feuillus”). See further comments under *C. marklundii*. There is much confusion in the literature around the name *C. camptoros*. Because of our limited knowledge of the *Camptori* species, hitherto most hygrophaneous collections with similar characters have been erroneously identified as *C. camptoros*. For instance, Brandrud et al. (1990–2018), following the initial wide concept of *C. camptoros* in Brandrud & Melot (1983), did not depict the true *C. camptoros* on plate C24 of the CFP (coll. CFP1024), but an undescribed species at that time (here described as *C. marklundii*). Moreover, to our current knowledge, *C. camptoros* is a rare species and considering its initial collective morphological description, it may remain difficult to identify. Habitat may constitute the best distinguishing character, because all sequenced collections of the species originated from sites with coniferous trees (*Abies*, *Picea* and *Pinus*), whereas all other species of the *Camptori* clade are found under broadleaved trees. Most confirmed collections of *C. camptoros* are from a quite restricted geographical area spanning SW Germany to the eastern part of the Black Forest on limestone, and extending to Eastern Austria. There is also one verified collection from the eastern Pyrenees. All other finds mentioned in the literature under the name *C. camptoros* (including varieties or subspecies) outside the *Abies* range must be regarded as (highly) uncertain identifications, if not supported by DNA sequence data. *Cortinarius camptoros* can also be misidentified as *C. viridocoeruleus*. However, *C. viridocoeruleus* usually has more bluish tinges on the pileus when young, and in some stages, it may show pronounced greenish tinges, which is never seen in *C. camptoros*. *Cortinarius viridocoeruleus* displays a different ecology, growing with *Fagus* or *Quercus*. In the protologue of *C. camptoros*, two collections were described from calcareous *Abies alba*, *Picea abies*, and *Pinus sylvestris* forests of the Black Forest region—the type from Trossingen, Baar, and another collection from Neubulach, Calw (W of Stuttgart, Germany) (Brandrud & Melot 1983). Of these, only the type has been sequenced. Later, we have verified the species from more localities in the Black Forest in calcareous coniferous forests with *Abies*. Seven localities from the Black Forest region are reported in Krieglsteiner & Gminder (2010). In these sites, *C. camptoros* often occurs together with other, typical *Abies alba*-associated species such as *C. atrovirens* and *C. dibaphus*, and it seems likely that *Abies* might be the preferred ectomycorrhizal partner of *C. camptoros* too. Based on our observations over many years, *C. camptoros* is one of the rarest phlegmacioid species

in these *Abies*-dominated ecosystems. Consiglio et al. (2007) reported a find of *C. viridocoeruleus* var. *camptoros* (Brandrud & Melot) D. Antonini, M. Antonini & Consiglio under *Pinus sylvestris* and *Quercus ilex* var. *ballota* from Morella, NE Spain. Based on photo and morphological description, it may belong to this species, although this record is from a somewhat deviating habitat. Unfortunately, sequencing attempts on this specimen failed, and the identity of this record remains uncertain. Fernández Sasia & Cadiñanos Aguirre (2000) described a *C. camptoros* f. *fuscoilicis* Cadiñanos from *Quercus faginea* and *Q. ilex* forests of Spain. This has also not been verified by sequencing, and with its quite deviating ecology, it seems highly unlikely to be conspecific with *C. camptoros*. *Cortinarius camptoros* differs from the closest species, *C. viridocoeruleus* (Fig. 1), by 6 substitution and indel positions, representing 1% of sequence divergence in the ITS region.

Additional collections examined: Austria, Niederösterreich, Schneebergdörfel NW, 9 Oct 2017, T.E. Brandrud, I. Krisai-Greilhuber, H. Voglmayr, TEB 901-17 (WU). Germany, Baden-Württemberg, Dunningen, 24 Sept 1995, U. Luhmann, TUB011848; Flözlingen, 9 Oct 2004, G. Saar, TUB019788; Schönbronn, Giffizenmoos, 31 Oct 2016, G. Saar, GS 16-5; Baden-Württemberg, Flözlingen, 17 Oct 2020, U. Winkler, GS 20-08. Spain, Clot Molina, Peguera, Figols, Berguedà, 21 Sept 2018, J. Ballarà, JB-9819-18 (herb. J. Ballarà).

Cortinarius viridocoeruleus Chevassut & Rob. Henry, Doc. Mycol. 5(20): 24 (1975)

Fig. 5e–h

Mycobank: MB 312199

Holotype: France, Hérault, Montpellier, Bois de Maurin, *Quercus ilex*, 19 Nov 1972, G. Chevassut, Henry3366 (PC), GenBank ON006503 (ITS).

= *Cortinarius purpuratus* Rob. Henry, Bull. trimest. Soc. mycol. Fr. 101(1): 28 (1985), MycoBank: MB 105185. *Holotype*: France, Henry84/31 (PC)

= *Cortinarius lepistoides* T. S. Jeppesen & Frøslev, Mycotaxon 106: 474 (2009). MycoBank: MB 512356. *Holotype*: Denmark, Jutland, Vosnæs havskov, 30 Sept 2000, TF2000-56 (C).

Description: compiled from the protologue, Frøslev & Jeppesen (2009), Eyssartier (2004), and own findings. Pileus 30–100 mm, hemispherical, then plano-convex, slightly glutinous, glabrous and glossy when dry, often somewhat radially wrinkled upon drying, some specimens towards margin at about half the diameter distinctly innately fibrillose (it is uncertain if these structures are remnants of a superficial veil or from deeper, dark fibres), violaceous blue to violaceous grey (especially towards margin), sometimes with radiate hygrophanous streaks when young, soon becoming more greyish with a greyish brown centre and sometimes rusty

spots, with an altogether ± hygrophanous appearance, mostly with a very thin but often clearly visible frosty veil. Single collections from Mediterranean areas develop also greenish tinges. Lamellae crowded, emarginate or almost adnexed at the stipe, edge initially irregular wavy, first greyish-blue to lavender-blue with a distinctly and remaining violaceous edge, finally ochraceous brown with a tendency to turn rusty brown. Stipe 40–80 × 8–18 mm, with a marginate bulb (up to 40 mm), initially greyish-blue to lavender-blue as the young lamellae and finally discolouring whitish from below, with violaceous blue veil at bulb margin. Context white in pileus and bulb but distinctly violaceous blue in the stipe, soon fading whitish in the stipe and slightly yellowish in the bulb. Odour distinctly earth-like, resembles *C. varicolor*; also a malt/honey-like component noted, especially in the bulb. Macrochemical reactions: KOH yellow brown or red brown on pileus and in pileus context, somewhat weaker in stipe and bulb. Basidiospores [4, 4, 146], 8.3–9.9 × 4.8–5.6 μm (MV = 9.1 × 5.2 μm); variation of MVs: 8.7–9.3 × 5.1–5.3 μm; Q = 1.56–1.92 (MV = 1.74), brown, distinctly citriform, medium strongly and densely verrucose, warts sometimes isolated but mostly interconnected, clearly visible in the outline of the spores, suprahilar plage sometimes clearly visible. Lamellar edge more or less fertile, with sterile cells scattered to sometimes more abundant (in contradiction to Eyssartier 2004). Pileipellis duplex, cutis thin, consisting of 10–15 layers of 2–4 μm wide hyphae, granular intracellular pigment. Hypoderm well developed, consisting of up to 30 μm wide hyphae with a yellow-brown parietal pigment.

Habitat and distribution: Associated mainly with *Fagus sylvatica*, but also with *Quercus* spp., *Carpinus* and possibly *Corylus* on calcareous or base rich, loamy soils. *Cortinarius viridocoeruleus* occurs mainly in temperate deciduous forests and is known from Denmark, France, Germany, Hungary, Italy, and Sweden. Mediterranean-submediterranean collections are only verified from Montpellier-Bédarieux area (Hérault) of S France (most reports from S Europe of *C. viridocoeruleus* apparently belong to other species).

Comments: As with *C. camptoros*, many references to *C. viridocoeruleus* (partly also as “*viridocoeruleus*” or “*viridicaeruleus*”) can be found in the literature (e.g. Ballarà et al. 2011, Consiglio et al. 2007, Soop 2017). Unfortunately, these records can most often not be unambiguously interpreted without associated DNA sequence data. However, from our wide selection of sequence-verified collections, we can assemble a precise image of what *C. viridocoeruleus* is. Majority of the photos and descriptive notes from different localities in Europe converge to a quite uniform and consistent representation of this most characteristic and easily recognizable species in the group. This revised concept is well expressed by Frøslev et al. (2009) in the protologue of *C. lepistoides*: a medium to large *Phlegmacium* with a violaceous blue to violaceous grey pileus covered partly by a frost-like, white veil, first greyish-

blue to lavender-blue lamellae with a distinctly and persisting violaceous edge and a mostly sharp margined bulb with violaceous blue veil at margin. According to the priority rules, *C. lepistoides* is a later synonym of *C. viridocoeruleus*. *Cortinarius lepistoides* was published because at that time, the authors thought that the name *C. viridocoeruleus* applied to the species we here describe as *C. viridocaelestinus*. The protologue and original description of *C. viridocoeruleus* (Chevassut & Henry 1975) are, however, somewhat in contradiction to the uniform circumscription of the species as it emerges from our synthesis. The French authors describe the pileus as “vividly uniform green then slightly fulvous to tawny in the centre”. Moreover, the line drawing accompanying the protologue (assumingly of the holotype; loc. cit. Fig. 1) depicts a small, delicate species, with stipe not wider than 5 mm, and with very atypical spores. One can say that colours should not be overestimated in this group and that the basidiocarp size and slenderness may be influenced by local ecological constraints. Consistent with this, almost all collections of this species studied by us are from temperate, continental regions and were growing with *Fagus* and possibly *Carpinus* or *Corylus*, whereas the holotype originates from *Quercus ilex* Mediterranean woodlands of the Montpellier area. However, one of our sequenced collections was found in such a habitat in Bédarieux, 75 km West from Montpellier, and it did display greenish tinges and a less robust habit when compared to extra-Mediterranean material. There is another explanation though, for these observed contradictions. Chevassut & Henry (1975) indicated that their species was known (by Chevassut) from two sites near Montpellier, so it is possible that their concept was not pure, including both *C. viridocoeruleus* and one or more morphologically similar Camptori species. Consistent with this hypothesis, Henry (1976)—only one year after *C. viridocoeruleus*—described *C. versicolorum* which he distinguished from the former, mostly by less vivid green tinges, concolorous and smooth lamellae edge, and a stouter habit. Most later authors placed these two names in synonymy (Bidaud et al. 2008, Eyssartier & Roux 2011) and Chevassut himself later admitted that *C. versicolorum* probably represents a simple form of *C. viridocoeruleus*, if not simply identical (Chevassut 1991). Considering what we now know about the morphological features and distribution of Camptori species in the Mediterranean area, it seems likely that Chevassut had in hands *C. viridocoeruleus*, *C. malavali*, and *C. violaceoserrulatus*, but it also seems very likely that he and Henry would not have been able to discriminate them with the limited taxonomic tools of the pre-sequencing era. It is remarkable though that their descriptions of *C. viridocoeruleus* and *C. versicolorum* collectively include all necessary elements to describe the three aforementioned Mediterranean Camptori. We thus conclude that the two names published in 1975 and 1976 are probably both collective and partly redundant. Regardless of the observed contradictions, the

successful sequencing of the holotype of *C. viridocoeruleus* nomenclaturally links this name to the present species. Unfortunately, original material of *C. versicolorum* could not be located, preventing us to confidently associate this name to either of the three Mediterranean clades.

One collection belonging to the *C. viridocoeruleus* cluster (GE02.074, Southwest France, Dordogne; see Fig. 1) was initially identified as *C. imperialis* Bidaud by Eyssartier (2004), suggesting that this name might have represented a later synonym of *C. viridocoeruleus*. The description and the photo of this collection indeed show great similarities with other sequenced collections of *C. viridocoeruleus*, however, the original description of *C. imperialis* shows less similarities with this species (see pl. 100 in Bidaud et al. 1993). Bidaud placed the species in Sect. *Caerulescentes*, and furthermore it was described as being associated with *Picea* and depicted as having amygdaliform to subamygdaliform basidiospores. Therefore, *C. imperialis* is very unlikely a Camptori species, a conclusion that Frøslev et al. (2009) draw too, when comparing it to *C. lepistoides*. The sequence of the holotype of *C. purpuratus* Rob. Henry clusters also with *C. viridocoeruleus* (Fig. 1). This species was described by Henry (1985) as resembling those of sect. *Purpurascetes*, lacking the typical purple reaction with T14. It is not easy to get an exact impression of *C. purpuratus* because there are no illustrations of basidiocarps or basidiospores in the protologue. Bidaud et al. (1993) later produced a more complete description of this species, based on a collection ecologically, morphologically and microscopically compatible with *C. viridocoeruleus*, but unfortunately it was not sequenced. According to the priority rules, *C. purpuratus* is here included as a later synonym of *C. viridocoeruleus*. *Cortinarius viridocoeruleus* differs from the closest species, *C. camptoros* (Fig. 1), by 6 substitution and indel positions, representing 1% of sequence divergence in the ITS region.

Additional collections examined: Denmark, Jylland, Vosnæs Havskov, 30 Sept 2000, T. Frøslev, T.S. Jeppesen, TF2000-056 (*C.*, holotype of *C. lepistoides*). France, Hérault, Bédarieux, Levas, *Quercus ilex*, 23 Oct 2013, T.E. Brandrud, TEB985-13 (O); Dordogne, Notre-Dame-de-Sanilhac, route de Phébus, under *Carpinus* with a few *Quercus* on calcareous soil, 4 Oct 2002, G. Eyssartier, GE02.074 (PC). Germany, Schleswig-Holstein, Bad Malente-Gremsmühlen, Dieksee, 07 Oct 2004, G. Schmidt-Stohn, SSt04-110 (herb. Schmidt-Stohn); Mecklenburg-Vorpommern, Plau, Ziegeleiteich, 4 Oct 2013, G. Schmidt-Stohn, SSt13-130 (herb. Schmidt-Stohn); Bayern, Main-Spessart, Karlstadt, Karlsburg NW, 4 Oct 1989, H. Marklund et al., CFP907 (TEB 43-89) (S). Eschweiler, *Quercus* spp., *Fagus sylvatica*, 3 Oct 2001, B. Oertel, F. Röger, TUB 011408. Hungary, Pest County, Visegrádi Mts, 11 Nov 2003, L. Albert, B. Dima, DB628. Sweden, Öland, Halltorps Hage, 25 Sept 2020, G. Schmidt-Stohn, SSt20-029 (herb. G. Schmidt-Stohn).

Cortinarius violaceoserrulatus, L. Albert, Dima, Schmidt-Stohn, C. Rossi & Ballarà, sp. nov.

Fig. 6a–d

Mycobank: MB 843228

Holotype: Hungary, Budapest, Mt Széchenyi-hegy, L. Albert, 23 Nov 2014, AL 14/441 (BP111782); GenBank ON006492 (ITS).

Etymology: the epithet refers to the serrulate/crenulated lamellae edge which is beautifully and persistently violaceous.

Diagnosis: *Cortinarius violaceoserrulatus* differs from other species in the /Camptori clade from the ochraceous to yellow ochraceous pileus with whitish, thick veil patches, the bluish-lilac serrulate lamellae edge, in combination with paler (greyish) lamellae, and the basidiospores $MV \geq 9.7 \times 5.5 \mu\text{m}$.

Description: Pileus 40–80 mm, convex then applanate, margin incurved, becoming wavy in mature specimens, viscid, smooth to slightly radially fibrillose, often wrinkled, hygrophanous, especially at the margin, with persistent, almost always with thick whitish veil patches at the centre,

Fig. 6 Basidiocarps of the species in the /Camptori clade of the genus *Cortinarius* (voucher numbers and geographical origin in brackets):

a, b, c, d *C. marklundii* (a SSt13-150 Germany, b JB-9727-18 Spain, c TEB354-14 holotype Norway, d TEB452-17 Norway); e, f, g, h *C. violaceoserrulatus* (e AL14/441 holotype Hungary, f JMB2011112640 France, g CR6374-2018 Spain, h JB9990-18 Spain); Photos: a G. Schmidt-Stohn; b J. Ballarà; c, d B. Dima; e L. Albert; f J.M. Bellanger; g C. Rossi; h J. Ballarà



entirely pale olive greenish when young, then yellow-ochraceous to ochraceous-yellow and later olivaceous brown, greyish ochre, ochraceous brown, sometimes with darker brownish spots. Lamellae crowded, emarginate to adnate, 4–5 mm wide, edge distinctly irregular crenulate to almost serrulate, pale (bluish) grey when young (in Mediterranean collections conspicuously blue colour were also observed), later greyish brown to finally rusty brown, with persistently violaceous blue edge. Stipe 50–100 × 8–12 mm, cylindrical, with a rounded marginated bulb (up to 20 mm wide), fibrillose to almost smooth towards apex, pale violaceous blue at the apex but sometimes also the whole stipe especially when young, whitish to greyish ochraceous with age. Cortina sparse and fugacious. Basal mycelium white. Context firm, thin, elastic as in other species of the group, whitish, more or less violaceous in the cortex, finally slightly yellowing especially in the bulb cortex. Taste mild, slightly sour, odour faintly earth-like. Macrochemical reactions: KOH brownish on the pileus, ochraceous brown in the context. Basidiospores [5, 5, 225], 8.7–11.1 × 5.1–6.3 μm (MV = 9.9 × 5.7 μm); variation of MVs: 9.7–10.3 × 5.5–5.9 μm; $Q = 1.54–1.98$ (MV = 1.76), brown, distinctly citriform, finely to medium strongly and densely verrucose, warts isolated but also interconnected, clearly visible in the outline of the spores, suprahilar plage often clearly visible. Pileipellis duplex, epicutis thin, consisting of 2–5 μm wide, more or less hyaline, gelified hyphae, occasionally with some yellow brown (probably cytoplasmatic) pigment. Hypoderm (subcutis) well developed, of subcellular, inflated elements 15–25 μm wide, with yellow, parietal (thick-wall) pigment, and a weak yellowish cytoplasmatic pigmentation.

Habitat and distribution: Widespread, known from various southern European countries (France, Italy, Spain) in thermophilous frondose forests dominated by *Quercus ilex*, while the type locality is from Hungary, where it grows in warm calcareous sites with *Quercus pubescens*.

Comments: In the past, *C. violaceoserrulatus* was mostly included in a wide concept of *C. viridocoeruleus*. Mainly through molecular genetic analysis, we now realize that there are actually three species hidden in this aggregate. Therefore, it seems obvious that Chevassut had a broader concept of his *C. viridocoeruleus*, most likely including—besides *C. viridocoeruleus* s. str.—the newly established species *C. violaceoserrulatus* and *C. malavalii*. In his ecological papers, Chevassut mentioned *C. viridocoeruleus* as one of the frequent phlegmacia in *Quercus ilex* forests around Montpellier, fruiting together with *C. aurilicis* and *C. quercilicis*. This ecology matches *C. malavalii* and *C. violaceoserrulatus* much better than *C. viridocoeruleus*, which is apparently very rare in that region (only one recent find near Bédarioux). *Cortinarius violaceoserrulatus* is known from France, Hungary, Italy, and Spain, in transition between the more northerly distributed *C. viridocoeruleus* (with most

collections known from Sweden, Denmark and Germany) and the currently only southern (France, Spain) *C. malavalii*. *Cortinarius violaceoserrulatus* grows in calcareous, thermophilic forests, an assemblage also stated by Chevassut for his Mediterranean collections of *C. viridocoeruleus* sensu lato. Therefore, *C. violaceoserrulatus* is perhaps more frequent in the Montpellier area than *C. viridocoeruleus* and *C. malavalii*. With regard to morphology, *C. violaceoserrulatus* is apparently easily distinguishable from *C. viridocoeruleus* and from *C. malavalii*. Almost all collections of *C. violaceoserrulatus* display distinct white velum patches on the pileus, whereas *C. malavalii* has no or only traces of such a velum. Generally, *C. viridocoeruleus* has no such velum patches but more often a distinct, very characteristic frosty whitish velum. Moreover, the colours of the three species are somewhat different. In many collections of *C. violaceoserrulatus*, ochraceous-yellow to yellow-ochraceous tinges are clearly visible, and generally, the basidiocarps make a rather bright impression whereas *C. malavalii* is usually more green olivaceous, ochraceous-brown to yellow brown and is generally darker. Only a single collection of *C. violaceoserrulatus* from the Mediterranean area showed greenish tinges. In contrast to most collections of *C. viridocoeruleus*—especially those from northern regions in Sweden, Denmark, and Germany—young and fresh *C. violaceoserrulatus* has vividly violaceous blue or violaceous grey colours in lamellae edges, particularly towards pileus margin, and soon becomes greyish with a greyish brown centre. *Cortinarius violaceoserrulatus* forms a sister clade to *C. viridocaelestinus* (Fig. 1), from which it differs by 21 substitution and indel positions, representing 4% of sequence divergence in the ITS region.

Additional collections examined: France, Vaucluse, Cadenet, La Royère, under *Q. ilex* and *Q. pubescens*, calcareous soil, 26 Nov 2011, J.-M. Bellanger JMB201112640 (herb. J.-M. Bellanger); Essone, Cheptainville under *Fagus sylvatica* on calcareous soil, 12 Dec 2011, R. Challenge, XC2011-236; Region Ile-de-France, in deciduous forest, 30 Oct 2006, X. Carteret, XC2006-161; Hungary, Budapest, Csillebérc, 13 Nov 2014, L. Albert, B. Dima, DB5689 (herb. ELTE); Italy, Livorno, Piombino, Mediterranean forest, 6 Dec 2014, M. Maletti, Maletti 6-12-2014 (herb. M. Maletti); Spain, Cadiz, Grazalema, Llanos de Rabel, calcareous forest with *Quercus ilex* f. *ballota* and *Q. faginea*, 3 Dec 2018, C. Rossi, CR6374-2018 (herb. C. Rossi, G. Schmidt-Stohn); Berguedà, Montmajor, Comarmada, calcareous *Quercus ilex* forest with *Buxus sempervirens*, 11 Nov 2018, J. Ballarà, JB-9990-18 (herb. J. Ballarà, G. Schmidt-Stohn), calcareous *Q. ilex* and *Q. humilis* forest, 2 Dec 2019, J. Ballarà, JB-10345-19 (herb. J. Ballarà).

Cortinarius marklundii Brandrud, Dima, Saar, Schmidt-Stohn & Ballarà, sp. nov.

Fig. 6e–h

Mycobank MB 843229

Holotype: Norway, Oppland, Gjøvik, Biri, Eriksrud nature reserve, T.E. Brandrud & B. Dima, 4 Sept 2014, TEB354-14 (O-F-259458), GenBank ON006478 (ITS). *Isotype*: DB5427 (herb. ELTE).

Etymology: the name is in honour to the late photographer of *Cortinarius Flora Photographica*, Hans Marklund, Härnösand, Sweden.

Diagnosis: *Cortinarius marklundii* is characterized by the initially olivaceous (green) grey, more or less hygrophanous pileus, bluish lamellae and stipe, and more or less citriform spores. The species can be distinguished from close taxa based on the soon redbrown discolouring pileus, the lack of a bluish-lilac lamellae edge, and its association with *Tilia*, *Fagus*, and *Dryas*.

Description: Pileus 4–8 cm, (hemi-)spherical, then plano-convex (to broadly umbonate), sometimes irregular, somewhat elastic (like a *Lyophyllum* sp.), viscid-glutinous, glabrous and glossy when dry, often with a dark, hygrophanous marginal zone or with radiate hygrophanous streaks, mature specimens often become radially wrinkled upon drying; initially olivaceous (greenish)grey, even bluish grey tinged at incurved margin when very young, but this tinge fades instantly (on exposure), soon discolouring more vivid ochraceous redbrown from centre, often bicoloured, ochre brown at centre and hygrophanous dark olive grey at margin, finally fulvous or chestnut brown at centre and paler ochraceous yellow brown towards margin, sometimes with redbrown spots. Often with very thin and fugacious frosty-micaceous veil remnants at centre when young, rarely with silvery white veil patches, sometimes radially silvery-fibrillose towards margin. Lamellae crowded, emarginate to adnexed, edge initially irregular wavy-serrulate to white fimbriate, when very young (deep) greyish violet, soon becoming paler, sometimes almost grey, with paler to whitish edge (edge never persistently bluish), finally ochraceous (-rusty) brown. Stipe 3–6(–7) × 0.8–1.6 cm, with a marginate bulb (up to 3 cm wide), initially pale to distinct greyish violet, especially in upper part, usually soon discolouring to whitish, and finally sometimes with brass brown patches. Veil remnants at bulb margin rather thin but distinct and almost volva-like when very young, soon disappearing, initially greyish white or often with a distinctly but very fugacious bluish tinge, soon tinged ochre yellow. Basal mycelium whitish (or when young with a bluish tinge, which usually disappears instantly on exposure). Context white in pileus and bulb, initially greyish violet in the stipe (most distinct at apex, and towards surface, in places concentrated to hygrophanous spots/streaks), soon fading whitish in the stipe and becoming yellowish tinged elsewhere, even brownish in the base of bulb, rather strongly brownish where damaged by insect larvae. Odour earth-like *C. varicolor*, and with a component of bread dough, or more of honey/malt-like, especially in the bulb. Macrochemical reactions: KOH

somewhat red brown on pileus, brownish in context. Basidiospores [9, 9, 387], 8.4–11.0 × 5.0–6.2 μm (MV = 9.8 × 5.6 μm); variation of MVs: 9.1–10.4 × 5.2–6.0 μm; $Q = 1.57$ – 1.89 (MV = 1.73), brown, distinctly citriform, finely to medium strongly and densely verrucose, warts sometimes isolated but mostly interconnected, clearly visible in the outline of the spores, suprahilar plage often clearly visible. Lamellar edge often more or less sterile, with clavate, cylindrical or irregularly shaped sterile cells. Pileipellis duplex, epicutis thin, consisting of 2–5 μm wide, more or less hyaline hyphae. Hypoderm (subcutis) well developed, elements subcellular, 15–30 μm wide, with brown parietal (thick-wall), amber-like pigment, cementing the elements into a compact layer.

Habitat and distribution: Associated with *Tilia cordata* (and *Corylus avellana*) in S Scandinavia, with *Fagus sylvatica* in Central/Western Europe, and with *Dryas octopetala* in the Spanish Pyrenees. *Cortinarius marklundii* is known from few, scattered sites in calcareous *Fagus* forests of Germany and France. Larger, but fragmented populations are found in relict calcareous *Tilia* woodlands (often in scree areas with limestone/shale gravel) of the Oslofjord-Vänern-Gotland areas of S Scandinavia. Finally, the species is also recorded from calcareous alpine *Dryas* sites of the Pyrenees.

Comments: *Cortinarius marklundii* is characterized by the pileus soon discolouring vividly ochre red-brownish, lamellae lacking a (persistently) violaceous blue edge, and being associated with *Tilia*, *Fagus*, and *Dryas*. The bluish-violaceous colours are generally weaker or more fugacious than on the other species in the group; the pileus hardly shows any bluish tinges, and veil remnants at bulb margin rarely show bluish (and then very fugacious) tinges. *Cortinarius marklundii* was initially included in the wide concept of *C. camptoros* in Brandrud & Melot (1983). In that paper, the morphology of the type and another collection from *Abies-Picea* forests of the Black Forest, Germany, were described in detail, as well as that of a collection from calcareous *Tilia-Corylus* forest of Langesund, outer Oslofjord, Norway. The latter represents *C. marklundii*. In its revised delimitation, *C. camptoros* is a Central European, montane species of calcareous *Abies-Picea* forests, that can be distinguished from *C. marklundii* by distinct lilac lamellae edges, less warm pileus colours and by a phylogenetic distance of 15 substitution and 4 indel differences representing 3% of sequence divergence in the ITS region (Fig. 1). With its *Tilia* forest populations in S Scandinavia, *C. marklundii* is the only species of the /Camptori clade that occurs in N Europe. *Cortinarius marklundii* was first depicted in *Cortinarius, Flora Photographica* in 1994 (Brandrud et al. 1990–2018; plate C24; as *C. camptoros*), with material from a calcareous, *Tilia*-dominated woodland meadow at Gotland, Sweden. Later, in Brandrud (1999) and in Brandrud & Bendiksen (2001: Fig. 5, as *C. camptoros*), this species was mentioned as a *Tilia*-associated variant of the *C. camptoros* s. str.

Subsequently, records of this species were published from a number of calcareous lime forests in Norway, in national reports (see, e.g., Brandrud et al., 2014b, 2016, 2020), always as *C. camptoros*. It is now recorded from 19 localities in SE Norway, from the Oslofjord area, north to Lake Mjøsa (sequence-verified from 4 collections). In S Sweden, it is known from approx. 20 localities, mainly from Gotland, Öland and near Lake Vänern, Kinnekulle (sequence-verified from 3 localities). In Norway and Sweden, it occurs mainly in calcareous *Tilia* forests or semi-open woodlands with *Tilia*, but apparently also in *Corylus* thickets without *Tilia*. These S Scandinavian *Tilia-Corylus* localities seem to host the largest European populations of the species. The calcareous *Tilia* forests are regarded as old relicts from warm periods (6000–8000 BP) after the ice age where such *Tilia* forests had a much wider distribution and were much more widespread in temperate Europe (cf. Brandrud 1999). Elsewhere in Europe, the species displays a western distribution, so far confirmed from a few sites in Germany, France, and Spain. In Germany and France, the species is found in rich *Fagus* forests, in shady sites with more leaf-litter/humus, making the soil more humid than many of the *Tilia* scree sites. Specimens from *Fagus* populations may look a little different, with a more pronounced hygrophanous marginal zone, and a less vivid reddish-brown oxidized, discoloured pileus (centre) (see Fig. 6g), but phylogenetically they are identical. The Spanish localities are alpine *Dryas* heaths in the eastern Pyrenees. In the Pyrenees, *Fagus* woodlands often constitute the uppermost subalpine forests, and it is likely that the species also has populations in the *Fagus* woodlands adjacent to the *Dryas* sites. In the exposed *Dryas* sites, the species becomes vividly reddish-brown-ochraceous brown. The species seems restricted to Europe, but should be expected to occur also further East in Europe, in association with *Tilia* or *Fagus*. *Cortinarius marklundii* forms a sister clade to the *C. viridocoeruleus-C. camptoros-C. velicopius* clade. The most similar species is *C. viridocoeruleus* (Fig. 1), from which it differs by 17 substitution and indel positions, representing 3% of sequence divergence in the ITS region.

Additional collections examined: France, Somme, Forêt de Creuse, calcareous broadleaved tree forest with *Quercus*, *Fagus*, 22 Oct 2012, X. Carteret, XC2012-150 (herb. X. Carteret); Ain, Valserhône, Mussel, loamy-calcareous *Fagus* forest, R. Fillion & A. Bidaud, 17 Oct 2011, AB11-10-202 (herb. R. Fillion & A. Bidaud). Germany, Sachsen-Anhalt, Ufrungen, Seeberge, calcareous *Fagus* forest, 10 Oct 2013, G. Schmidt-Stohn & G. Hensel, SS13-150 (herb. G. Schmidt-Stohn); Mecklenburg-Vorpommern, Plau am See, Ziegeleiteich, loamy forest with *Quercus*, *Carpinus*, *Corylus*, and *Fagus*, 16 Oct 2019, G. Schmidt-Stohn, SS19-145 (herb. G. Schmidt-Stohn); Thüringen, Bad Frankenhausen/Kyffhäuser, Ichstedter Lindenallee, *Tilia* on base rich ground, 9 Oct 2007, G. Schmidt-Stohn, SS07-213 (herb. G. Schmidt-

Stohn). Norway, Oppland, Gjøvik, Biri, Eriksrud NR, 4 Sept 2014, T.E. Brandrud, B. Dima, TEB358-14 (O), DB 5423 (ELTE); Akershus, Asker, Bjerkås NR (Bjerkås IV), 4 Sept 2017, T.E. Brandrud, B. Dima, TEB452-17 (O), DB6411 (ELTE); Telemark, Porsgrunn, Klevstrand, 9 Oct 2013, T.E. Brandrud, TEB890-13 (O). Spain, Berguedà, Saldes, Serra Encija, Refugi, 10 Sept 2018, J. Ballarà, JB-9736-18 (herb. J. Ballarà); Berguedà, Saldes, Serra Encija, Serrat Voltor, 2 Sept 2018, J. Ballarà, JB-9561-18 (herb. J. Ballarà). Sweden, Gotland, Vallstena, Alvena lindaräng, 29 Sept 1990, H. Marklund et al., CFP1024 / TEB 28-90 (S); Västergötland, Kinnekulle, H. Marklund et al., CFP874 (S); Öland, Ekerum, Halltorps Hage, lövängar with *Tilia* and *Corylus*, 8 Sept 2016, G. Schmidt-Stohn, SS16-083 (herb. G. Schmidt-Stohn).

Cortinarius malavali Bellanger & Ballarà, sp. nov.

Fig. 7a–c

MycoBank: MB 843230

Holotype: France, Hérault, Montpellier, CNRS “route de Mende” campus, under *Quercus ilex*, calcareous soil, 13 Nov 2012, J.-M. Bellanger, P. Geniez, JMB2012111303 (MPU927722), GenBank ON006474 (ITS).

Etymology: Dedicated to the French mycologist Jean-Claude Malaval, who devoted decades of his life to fungal diversity and keeps transmitting his vast knowledge to young naturalists.

Diagnosis: A rather stout member of the /Camptori clade, featuring green-olivaceous tinges on the pileus, contrasting with blue stipe when fresh, greyish to light lilac lamellae with concolorous edges, in *Quercus* woodlands of the Mediterranean area.

Description: Pileus 30–80 mm, hemispherical to convex, then expanded, often with a low umbo, hygrophanous, radially wrinkled with age, often bicoloured and marbled when fresh, dominated by green olivaceous tinges but distinctly warmer yellow orange towards the centre, dehydrating as more uniformly ochraceous colours upon rapid fading of greenish hues, often with rust brown spots or streaks. Lamellae moderately crowded, sinuate, grey to pale brown with faint lilac hues, edge crenulate, whitish. Stipe 40–75 × 9–18 mm, with conspicuous marginated bulb (15–32 mm), violaceous blue when young or after handling, towards base colouring orange brown. Veil not abundant but breaking into white, silky patches on the pileus surface, persisting in mature basidiocarps. Cortina abundant, whitish. Context firm, rubber-like as other species in the group, whitish in the pileus and stipe centre, blue violaceous in cortex, orange cream at base. Taste mild and odour faint. Macrochemical reactions: KOH reddish on the pileus, ochraceous cream on the context. Basidiospores [4, 4, 166], 8.8–11.2 × 5.4–6.6 µm (MV = 10.0 × 6.0 µm); variation of MVs: 9.4–10.4 × 5.6–6.2 µm; Q = 1.51–1.83 (MV = 1.67), brown, distinctly citriform, finely to medium strongly and densely verrucose, warts sometimes

Fig. 7 Basidiocarps of the species in the /Camptori clade of the genus *Cortinarius* (voucher numbers and geographical origin in brackets): a, b, c *C. malavali* (a JMB2012111303 holotype France, b JMB2011112620 France, c JMB 2012111301bis paratype France, not sequenced); d, e, f *C. viridocaelestinus* (d JA-CUSSTA 9531 holotype Spain, e FA 4768 paratype Spain, f FA 4689 paratype Spain, not sequenced). Photos: a, b, c J.-M. Bellanger; d, e, f F. Armada



isolated but mostly somewhat interconnected, often clearly visible in the outline of the spores, suprahilar plage often clearly visible. Basidia 4-spored $32\text{--}36 \times 8\text{--}10 \mu\text{m}$. Lamellar edge with elements $7\text{--}10 \mu\text{m}$ wide, clavate to cylindrical. Pileipellis duplex, epicutis of gelified $2\text{--}5 \mu\text{m}$ wide, yellowish hyphae with claviform terminal elements. Hypoderm (subcutis) subcellular, of inflated elements $8\text{--}26 \mu\text{m}$ wide with yellow thick walls and a yellowish, intracellular pigmentation. *Exsiccata* brownish brick.

Habitat and distribution: Mediterranean calcareous *Quercus ilex* forests. Known from South France and Southeast Spain.

Comments: This species was probably described by Henry as *C. versicolorum* (Henry 1976). However, this binomial cannot safely be applied to the present taxon because it may also refer to *C. violaceoserrulatus* (see comments under *C. viridocoeruleus*). Unfortunately, the type material of *C. versicolorum* could not be found and sequenced to firmly link it to either of the three species currently represented in *Quercus* woodlands of the Montpellier area. *Cortinarius*

malavali differs mostly by greyish lamellae, with only faint lilac hues and concolorous smooth edges from *C. violaceoserrulatus*, which has conspicuously blue colour on lamellae that persists longer on edges when dehydrating. Based on our limited sampling of *C. malavali*, the species also seems slightly stouter than *C. violaceoserrulatus* and differently coloured, more greenish-olivaceous and with less yellow hues on the pileus. *Cortinarius viridocaelestinus* grows in the same habitats but is so far only known from mountainous *Q. ilex* forests of southern Spain. Furthermore, *C. viridocaelestinus* produces shorter and semi-hypogeous basidiocarps with a combination of very distinctive features that should prevent any confusion: conspicuous and uniform green hues on the pileus, green translucent context contrasting with blue lamellae edges and abundant, thick veil remnants on the pileus. *Cortinarius viridocoeruleus* is more distantly related to *C. malavali* (Fig. 1) but in the Mediterranean area, one collection of *C. viridocoeruleus* from the Montpellier area (TEB984-13, Fig. 5g) is morphologically very similar to *C. malavali*, making confusions possible. Like most

Camptori species, the greenish colours of *C. malavali* rapidly vanish on drying, and turn ochraceous with brown to rusty streaks, and then the species becomes hard to identify. We believe collections illustrated by Consiglio (1995: 14–16) and Palazón (2001: 454) under the name *C. viridicoeruleus* may actually represent *C. malavali*. *Cortinarius malavali* occupies an isolated position in the phylogeny of the /Camptori clade, differing from its most similar relatives, *C. marklundii*, by 36 substitution and indel positions, and from *Cortinarius* sp. from USA (JF742658), by 35 substitution and indel positions, representing 6% of sequence divergence in the ITS region.

Additional collections examined: France, Hérault, Montpellier, CNRS “route de Mende” campus, under *Quercus ilex*, calcareous soil, 17 Nov 2011, J.-M. Bellanger, P. Geniez, JMB201111701 (herb. J.-M Bellanger); *ibid*, 13 Nov 2012, JMB2012111303bis (paratype, herb. J.-M Bellanger); *ibid*, 14 Nov 2012, JMB2012111401 (herb. J.-M Bellanger); Vaucluse, Cadenet, La Royère, under *Q. ilex* and *Q. pubescens*, calcareous soil, 26 Nov 2011, J.-M. Bellanger, JMB2011112620 (herb. J.-M Bellanger). Spain, Barcelona, Berguedà, Montmajor, Mare de Deu del Bosc, under *Q. ilex*, 19 Oct 2014, J. Ballarà, JB-8503-14 (herb. J. Ballarà).

Cortinarius viridocaelestinus Armada & Bellanger, sp. nov.

Fig. 7d–f

Mycobank MB 843231

Holotype: Spain, Andalusia, Granada, Huétor de Santillán, Arroyo Palacios, under *Quercus ilex*, *Q. faginea* and a few scattered *Pinus halepensis* and *P. pinaster*, 1290–1320 m asl, F. Armada & M.-J. Díaz de Haro, 24 Nov 2018, JA-CUSSTA 9531 (JA), isotype FA4680 (herb. F. Armada), GenBank ON006501 (ITS).

Etymology: From the two Latin adjectives *viridis*, meaning green and *caelestinus*, meaning sky-blue and also referring to god’s kingdom.

Diagnosis: A semi-hypogeous member of the /Camptori clade, with green, hyaline hues on pileus and in the context, with initially sky-blue lamellae and a thick, conspicuous white veil.

Description: Pileus 32–50 mm, convex then applanate, often depressed towards the centre in mature specimens, viscid and covered by stuck clumps of earth, smooth to slightly wrinkled, hygrophanous, almost uniform pastel-green to glaucous bottle-green on young basidiocarps, persisting but mixed with brown or grey-brown hues when ageing, with paler margin. Lamellae crowded, adnate to sinuate, 5 mm wide, initially sky-blue then turning pinkish cream on faces when ageing, but the bluish tinges persisting longer on edges that are crenulate. Stipe 26–48 × 10–15 mm, with a rounded marginate bulb (up to 24 mm wide), fibrillose to almost smooth towards top, concolorous to lamellae but rapidly turning green-yellowish from the base. Mycelium

white. Veil thick, membranous, white, persisting on the pileus centre as a unique patch or as a few smaller but conspicuous fragments, covering the outer surface and margin of the bulb by a thick white layer. Cortina abundant, whitish, rapidly collapsing along the whole stipe, turning ochraceous to rusty-brown from spores when ageing. Context firm, elastic like other species in the group, bottle-green hyaline in the pileus, bulb and stipe centre, whitish elsewhere, yellowing with age. Taste mild, not farinaceous, odour faint of pastry when cut. Macrochemical reactions: KOH pinkish-brown to foxy-brown on the pileus, foxy-brown on yellowing parts of the context. Basidiospores [1, 1, 45], 9.0–11.0 × 5.5–6.3 μm (MV = 10.0 × 5.9 μm); Q = 1.52–1.88 (MV = 1.70), brown, distinctly citriform, rarely amygdaloid, finely to medium strongly and densely verrucose, warts sometimes isolated but mostly interconnected, clearly visible in the outline of the spores, suprahilar plage often clearly visible. Basidia 4-spored 25–35 × 8.5–13.5 μm. Lamellar edge with marginal elements, 6–15 μm wide, clavate to cylindrical or more inflated to subglobose, shortly septate (2–3 segments), clamped. Pileipellis made of a layer of weakly gelified, 0.5–3 μm wide hyphae, topping poorly differentiated hyphae mixed with wider, up to 7–8 μm wide hyphae, with parietal to finely encrusted yellow pigmentation. Hypoderm elements sausage-like, up to 26 μm wide. Clamps present and numerous everywhere.

Habitat and distribution: So far only known from a single locality in montane *Quercus* woodlands near Granada, Spain. Late autumn.

Comments: *Cortinarius viridocaelestinus* is a remarkable species so far only known from two collections from the type locality. Nevertheless, we here describe it as new, because it displays a combination of morphological features that should prevent any confusion with other members of the /Camptori clade. Furthermore, it constitutes a phylogenetically unique clade, sister to *C. violaceoserrulatus*, from which it differs by 21 substitution and 3 indel positions. In macromorphological terms, the placement in /Camptori is straightforward because of the rubber-like context, the hygrophanous pileus, and the green and blue colours. However, the extent, persistence, and hyaline aspect of green hues on the pileus but also in the context, which is not blue, is unique to this species. The thick and conspicuous white veil and semi-hypogeous fruiting are also remarkable in the clade and should by themselves prevent any misidentification in the field. However, more collections of *C. viridocaelestinus* will be necessary to appreciate the stability of these spectacular features and better circumscribe its ecological requirements.

Additional collection examined: Spain, Andalusia, Granada, Huétor de Santillán, Arroyo Palacios, under *Quercus ilex*, *Quercus faginea* and a few scattered *Pinus halepensis* and *Pinus pinaster*, 1290–1320 m asl, 24 Nov 2018, F. Armada & M.-J. Díaz de Haro, FA 4689 (paratype, herb. F. Armada—not sequenced); *Parque Natural Sierras de Tejeda, Almijara y Alhama*, Játar, Loma

del Cura, under *Quercus ilex* and a few scattered *Pinus halepensis* and *Pinus pinaster* with numerous *Cistaceae*, 1024 m, 6 Dec 2018, F. Armada & M.-J. Díaz de Haro, FA4768 (herb. F. Armada).

Key to species of the /Camptori clade

- 1 Associated with *Abies*, probably also *Picea* or *Pinus* *C. camptoros*
- 1* Associated with frondose trees such as *Quercus*, *Fagus*, *Tilia*, *Corylus* 2
- 2 Pileus predominantly ochraceous to yellow ochraceous, with \pm thick whitish veil patches, MV of spores $\geq 9.7 \times 5.5 \mu\text{m}$ (for Mediterranean coll. see also 5*) *C. violaceoserrulatus*
- 2* Pileus more redbrown, ochre brown, chestnut brown or predominantly violaceous blue to violaceous grey especially when fresh 3
- 3 Pileus often distinctly innately fibrillose, initially predominantly violaceous blue to violaceous grey especially when fresh and wet, then greyish to greyish brown, often with a thin but clearly visible frosty veil, MV of spores $\leq 9.3 \times 5.3 \mu\text{m}$ *C. viridocoeruleus*
- 3* Pileus redbrown, ochre brown or chestnut brown to glaucous bottle-green, without such a clearly visible frosty veil but possibly with velum patches on pileus. 4
- 4 Associated with deciduous trees, mainly *Fagus*, *Tilia* or also *Dryas octopetala* (Spain) from temperate regions, pileus glabrous and glossy, not innately fibrillose, first olivaceous grey, soon ochraceous redbrown and finally fulvous to chestnut brown *C. marklundii*
- 4* Associated with sclerophyllous *Quercus* species, so far only known from Mediterranean areas in France and Spain, pileus not glossy, often radially wrinkled or covered by sticked clumps of earth. 5
- 5 Rather stout species with pileus up to 8 cm, pileus with green-olivaceous tinges contrasting with the blue stipe when fresh, pileus later more uniformly ochraceous, often with rust brown spots or streaks, without conspicuous veil remnants *C. malavali*
- 5* Rather small, semi-hypogeous, species with pileus 3–5 cm, covered by sticked clumps of earth, uniform pastel-green to glaucous bottle-green when young, then brown or grey-brown, with a thick, membranous, white, persisting veil on the pileus centre as a unique patch or smaller but conspicuous fragments *C. viridocaelestinus*

Discussion

In the present study of the /Camptori clade, we describe four species as new in addition to the two already existing ones, *C. camptoros* and *C. viridocoeruleus*. All of the new species, except *C. viridocaelestinus*, have previously been included in

the wide concept of *C. camptoros* or *C. viridocoeruleus*, respectively. Due to limited and overlapping morphological differentiation between the species, and a rather limited material available, insights from molecular genetic methods have been necessary to resolve the taxonomy, although the amplification and sequencing of the nrDNA ITS region in this group have been particularly difficult. Also, the ecological differentiation combined with molecular data has shown to be important taxonomic character. Although most species are southern and strictly associated to thermophilous, frondose trees, one species deviates from this pattern, being mainly associated with *Abies alba* in C or S Europe. Our phylogenetic analysis shows that all collections from coniferous trees (*Abies alba*, *Picea abies* and possibly also *Pinus* spp.) fall into one phylogenetic unit, together with the type of *C. camptoros* Brandrud & Melot. Originally, *C. camptoros* was treated in a wider concept including *C. marklundii*, which we show here is a species associated to deciduous trees. Looking at the original labels of the sequenced specimens assigned on morphological identification, the name *C. viridocoeruleus* appears in three different clades, representing *C. viridocoeruleus* (assessed by the holotype sequence) and the two new species *C. violaceoserrulatus* and *C. malavali*. Therefore, *C. viridocoeruleus* has frequently been treated collectively. Our study also shows that *C. viridocoeruleus* is apparently rarer in S Europe than the other two species. However, at the European scale, *C. viridocoeruleus* and *C. marklundii* are apparently the most widespread Camptori species. Both are distributed from SW Europe north to the southernmost Scandinavia. It should be noted that none of the Camptori species known so far does occur in the vast boreal coniferous zone of N Europe. Whereas *C. viridocoeruleus* is preferentially a temperate *Fagus* forest species, *C. marklundii* has its major distribution in calcareous *Tilia-Corylus* forests of SE Norway and S/C Sweden, but occurs also in *Fagus* forests of Germany, and in (sub)alpine *Dryas* heaths of Spain. These *Dryas* populations might be old relict (remnant) populations from former *Fagus* forests, and the S Scandinavian populations are apparently old relict site of 6000–7000-year-old *Tilia* forests. Finally, *C. viridocaelestinus* is so far known only from the type locality and with its outstanding features, it seems easily distinguishable from all the other species.

However, it must be pointed out that our knowledge of the Camptori clade still remains limited. This study is the first large-scale attempt to disentangle this group. All the six currently known species are rare or very rare, and so we did not have enough collections of each species for more sound conclusions. Therefore, we would not be surprised if further species in this group will show up. But we hope that the present study will be a solid basis for future additions.

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Author contribution All authors contributed to the study conception and design as well as to material preparation, data collection, and discussions. Molecular lab work was performed by B. Dima, J.M. Bellanger, and T.G. Frøslev. Phylogenetic analyses were performed by B. Dima. Macroscopic analyses were done by all authors. Microscopic analyses and statistics were done by G. Schmidt-Stohn. The manuscript was written by G. Schmidt-Stohn, J.M. Bellanger, T.E. Brandrud, and B. Dima. All authors commented on the manuscript as well as read and approved the final version.

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Availability of data and material MycoBank, GenBank

Code availability Not applicable

Declarations

Conflict of interest The authors declare no competing interests.

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