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Some new and interesting taxa of *Cortinarius* subgenus *Phlegmacium* from the European Mediterranean Basin

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Abstract: We clarify the taxonomy and nomenclature of several taxa of the genus *Cortinarius* subgenus *Phlegmacium*. To this aim, we have used a combination of morphological and molecular data. The evolutionary relationships of the species were inferred by comparison of the nuITS by means of weighted maximum parsimony, maximum likelihood and two different types of Bayesian methods (with and without a priori alignments). Phylogenetic resolution and support of all or most of the species included in this study and their relationships were possible only when including the phylogenetic signal from ambiguously aligned regions in weighted maximum parsimony analyses (recoded INAASE characters) and when the analysis simultaneously optimized alignment and phylogeny (with BAli-phy). Three species are described as new, *Cortinarius mediterraneensis*, *C. cistoglaucopus* and *C. palazonianus*, and *C. olivaeco-dionysae* is proposed for *C. dionysae* f. *olivaceus*. Descriptions are provided for these taxonomic and nomenclatural novelties, along with discussions of morphological and phylogenetic affinities to closely related taxa. Scanning microphotographs of the basidiospores are provided for the discussed taxa, and color pictures of the basidiomes in their natural habitat are provided for *C. cistoglaucopus*, *C. mediterraneensis* and *C. palazonianus*.

Key words: Agaricales, BAli-Phy, Cortinariaceae, fungal taxonomy, molecular phylogenetics, nuITS

Introduction

Cortinarius (Pers.) Gray is one of the largest genera within the Basidiomycetes with the number of species estimated at ca. 2000 (Kirk et al. 2008) and with a worldwide distribution. Although it is a well known genus, revisions (Garnica et al. 2002; Peintner et al. 2003; Frøslev et al. 2006a, b; Frøslev and Jeppesen 2008; Ortega et al. 2008, 2009; Niskanen et al. 2008, 2009, 2012a, b, 2013; Vila et al. 2008; Suárez-Santiago et al. 2009; Bojantchev 2011a, b; Bojantchev and Davis 2011) have demonstrated that the diversity of the genus is greater than previously thought, which means that numerous new species are still to be expected. But the large number of taxa, together with the lack of reliable microscopic characters and the plasticity of the widely used macro-morphological characters make species delimitation within the genus difficult (Suárez-Santiago et al. 2009). In recent years phylogenetic analyses based on molecular data have proved to be a useful and reliable method for the taxonomic delimitation of numerous species (Peintner et al. 2003; Niskanen et al. 2009, 2011, 2012a, b, 2013; Ortega et al. 2008, 2009; Vila et al. 2008; Suárez-Santiago et al. 2009).

Subgenus *Phlegmacium* includes taxa with fleshy basidiomes exhibiting vivid colors, viscid to glutinous pileus surface and a dry to occasionally glutinous stipe. In recent years many studies have focused on the taxonomy and the evolutionary relationships within this subgenus in Europe (Garnica et al. 2003, 2005, 2011; Richard et al. 2004; Bidaud et al. 2006, 2008; Frøslev et al. 2006a, b; Frøslev and Jeppesen 2008; Vila et al. 2008; Ortega et al. 2009). Warm Mediterranean habitats such as holm oak (*Quecus ilex*) and evergreen oak (*Q. rotundifolia*) woodlands and *Cistus* shrub communities, which were poorly studied in the past, recently have been shown to be rich in *Cortinarius* species, including many *Phlegmacium* taxa (Mahiques 1999, 2001, 2002, 2004, 2006; Richard et al. 2004; Ortega et al. 2008, 2009; Vila et al. 2008).

In the present paper we carry out a study on the taxonomy and molecular species recognition of several taxa belonging to *Cortinarius* subg. *Phlegmacium*, with emphasis on taxa distributed across the European Mediterranean area. For this purpose we have used an integrative approach, based on phylogenetic analyses of the internal transcribed spacer of nuclear ribosomal DNA (nuITS) and morphological and ecological data. As a result of our study, we propose three new species that can be clearly delimited by both morphology and molecular data (*Cortinarius mediterraneensis*, *C. cistoglaucopus* and *C.*

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palazonianus) and one taxon is given specific rank (*C. dionysae* f. *olivaceus*). Our results also support the proposition of the/Aureocistophilus clade, as it appears in our phylogenetic analyses well separated from the/Alluti clade (sensu Garnica et al. 2005), to which it has been traditionally related. The/Aureocistophilus clade includes species that have yellowish pileus, light lamellae, a context that yellows with age or when handled, and a reddish brown reaction to KOH on the pileus surface. It includes several species distributed across the Mediterranean basin and some others in northern and central Europe.

MATERIALS AND METHODS

Taxon sampling.—Morphological and anatomical studies were carried out on specimens from collections in northeastern and southern Iberian Peninsula. The specimens are deposited in the herbarium GDA and personal herbarium of J. Vila, Barcelona, Spain (JVG). The holotypes of *Cortinarius palazonianus* and *C. cistoglaucopus* are deposited in the herbaria LIP. Additional herbarium specimens from these public herbaria were used for comparison: BCN-SCM, GDA, IB, JA-Cussta, TUB; and the personal herbaria of A. Bidaud (AB), J.F. Ammirati (JFA) and G. Saar (SAAR). All specimens examined are in TAXONOMY. Herbaria acronyms, except for personal herbaria, follow Thiers (2013, continuously updated, http://sweetgum.nybg.org/ih/).

For the phylogenetic analyses we used the nuITS for a total of 71 specimens of *Cortinarius*, of which 69 belong to taxa from the subgenus *Phlegmacium* (ingroup). The main objective of this work has been to study the molecular delimitation of three potential new species as well as to further investigate the identity of *C. dionysae* f. *olivaceus*. For this reason we decided to include in our molecular dataset only those taxa with morphological, anatomical and ecological similarities to the taxa that were the focus of our study. Subgenus *Phlegmacium* includes a large number of species, and we decided to not include a wider and more representative taxon sampling of the subgenus also due to methodology. One was the variability we observed in the nuITS. In preliminary alignments (not included in the analyses shown here) the inclusion of more taxa of the subgenus *Phlegmacium* increased the size and number of ambiguously aligned regions due to length variation among sequences. Because ambiguously aligned regions had to be excluded from some of the analyses (i.e. wMP, ML, B1; see *Phylogenetic analyses*), this represented an important loss of phylogenetic signal, which decreased the resolution and confidence of the trees. On the other hand, we restricted the size of the dataset to 71 specimens to be able to successfully analyze it using the software BAli-Phy (i.e. B2; see *Phylogenetic analyses*). The species *C. olivaceofuscus* and *C. tubarius* in subgenus *Dermocybe* were selected as outgroup to root the phylogenetic trees.

A total of 28 nuITS sequences were newly produced for this study; the remaining sequences were retrieved from GenBank (www.ncbi.nlm.nih.gov/) and the UNITE database (unite.ut.ee/; Kõljalg et al. 2005). Voucher information and GenBank and UNITE database accession numbers for specimens included in the phylogenetic analyses are listed (SUPPLEMENTARY TABLE I).

Morphological and anatomical study.—The macroscopic characters were studied from young and mature fresh basidiomes. Terms used in the morphological descriptions follow Vila et al. (2008) and Ortega et al. (2009). Representative collections were photographed in fresh conditions. The color of pileus, stipe and lamellae, and the odor and flavor, were recorded in situ. Color comparisons were made with Kornerup and Wanscher (1973). Macrochemical color reactions were made with 30% KOH solution on fresh basidiomes and/or dried material on the pileus, stipe, bulbipellis and context. Microscopic characters were observed from free-hand radial sections of pileus and longitudinal sections of the lamellae mounted in KOH (2–3%) and Congo red (in 2% NH_4OH). Microscopic examinations were made with a Zeiss optical microscope (2000×) and measurements were made with a 100× oil immersion lens. From each collection we measured 20 spores on lamellae of three different basidiomata when possible and calculated the range of values, including the mean (m.v.), as well as the length : width ratio (Q : L/W). Basidiospore shape and ornamentation were studied with a Leo (Zeiss) model 1539 Gemini field emission scanning electron microscope (FESEM).

DNA extraction, amplification and sequencing.—Genomic DNA was isolated from 15–30 mg dried herbarium material, with an E.Z.N.A.® Plant DNA Kit (Omega Bio-Tek, USA) following the manufacturer's instructions. The presence of DNA in the isolation was examined with gel electrophoresis. Isolated DNA was resuspended in 100 µL elution buffer.

The entire nuITS region (ITS1, 5.8 S, ITS2) was amplified with primers ITS1F (Gardes and Bruns 1993) and ITS4 (White et al. 1990). Symmetric PCR amplifications were prepared for a final reaction volume of 25 µL with PuReTaq Ready-To-Go™ PCR beads (GE Healthcare, Buckinghamshire, UK), containing 1 µL template genomic DNA. The conditions for the thermo-cycling of the nuITS were: 94 C for 5 min of initial denaturalization linked to 40 cycles at 95 C for 1 min, 57 C for 1 min, and 72 C for 1 min with a final extension of 72 C for 7 min. PCR products were examined with gel electrophoresis and purified with RealClean Spin PCR Clean-up Kit (Durviz S.L., Valencia, Spain). Purified products were sequenced with the same amplification primers (Secugen S.L., Madrid, Spain).

Sequence alignment.—Sequence fragments first were subjected to BLAST queries for a first verification of their identities. They were assembled with MEGA 4.0 (Tamura et al. 2007) and included in a molecular sequence matrix. Sequences were aligned manually with Mesquite 2.75 (Maddison and Maddison 2011). The terminal primers and partial nuclear small (nuSSU) and large (nuLSU) ribosomal subunits were excluded from the analyses. Ambiguously aligned regions (sensu Lutzoni et al. 2000) were delimited manually and excluded from the analyses,

except for the dataset used as input for the Bayesian analyses with software BAli-Phy 2.1.1 (Suchard and Redelings 2006). Alignments were submitted to TreeBASE (http://www.treebase.org; ID number 14837).

Phylogenetic analyses.—Phylogenetic relationships and confidence were inferred with weighted maximum parsimony (wMP) as implemented in PAUP* 4.0b10 for UNIX (Swofford 2002), maximum likelihood (ML) performed in GARLI 2.0 (Zwickl 2006) and two Bayesian analyses with Mr. Bayes 3.2.1 (Ronquist et al. 2012) and BAli-Phy 2.1.1 (Suchard and Redelings 2006).

In the wMP analyses, constant sites were removed from wMP searches and wMP bootstrap analyses (wMP BS). Gaps were treated as a fifth character state. Symmetric step matrices were created for the unambiguously aligned regions (treating ITS1, 5.8S, ITS2 separately) using STMatrix 3.0 (Lutzoni and Zoller, Duke University, http://www.lutzonilab.net/downloads), following the method outlined in Gaya et al. (2011). Phylogenetic signal from the ambiguously aligned regions was recovered without violating positional homology with INAASE 2.3b (Lutzoni et al. 2000). The heuristic search was performed with 1000 random addition sequences (RAS), with tree bisection-reconnection (TBR) branch swapping, MULTREES option in effect and collapsing branches with maximum branch length equal to zero. Branch support for wMP was assessed by bootstrap analyses (Felsenstein 1985) with full heuristic searches. We performed 10 000 bootstrap replicates, using 10 RAS per bootstrap replicate and saving no more than 10 trees per RAS.

Before we analyzed the nuITS with ML as the optimization criterion, we estimated the models of molecular evolution with the Akaike information criterion (AIC; Akaike 1973) as implemented in Modeltest 3.7 (Posada and Crandall 1998). The selected model was TVM+I+G (Posada 2003). GARLI 2.0 was used to estimate the values of substitution rates, proportion of invariable sites and shape parameter of the gamma distribution. We performed searches, setting the program to stop after 5000 generations if no improvement of the Ln likelihood $\leq$ 0.01 was detected, setting a maximum of 500 000 generations. Branch support was calculated with 1000 replicates of ML bootstrapping (ML BS).

The nuITS dataset also was analyzed in a Bayesian framework (B1), with trees sampled with Markov chain Monte Carlo with Metropolis coupling (MCMCMC) as implemented in Mr. Bayes 3.2.1. The analysis was performed assuming the GTR+I+G model (Lanave et al. 1984); this model was chosen based on the AIC implemented in MrModeltest 2.3 (Nylander 2004). Two parallel runs with four independent chains each (three heated chains and one cold chain) were run 10 000 000 generations, with trees sampled every 100 generations. We explored graphically the MCMCMC runs with AWTY online (Wilgenbusch et al. 2004) to check convergence of both independent runs and to ensure that stationarity was reached. We also summarized the parameter values using the SUMP command of MrBayes 3.2.1 and checked that the value of the potential scale reduction factor (PSRF) of all parameters and bipartitions were close to 1.0, meaning that both runs converged. We plotted the log-likelihood scores per generation time with Tracer 1.5 (Rambaut and Drummond 2007, http://beast.bio.ed.ac.uk/Tracer) to determine the number of generations required to reach equilibrium (burn-in). A burn-in sample of the first 25 000 trees was discarded for each run, and the remaining trees (150 000) were used to estimate branch lengths and to calculate posterior probability values (PP) for each clade with the majority rule consensus tree with the SUMT command of MrBayes 3.2.1.

An additional Bayesian analysis was performed (B2) using the software BAli-Phy 2.1.1, which estimates simultaneously alignment and phylogeny (Suchard and Redelings 2006). The nuITS dataset was divided in three partitions (ITS1, 5.8S, ITS2) following the method outlined in Gaya et al. (2011). The settings of the analyses followed the settings developed by Gaya et al. (2011), which established ITS1 and ITS2 to share the same model of evolution (i.e. GTR+G), the same indel model (i.e. RS07) and the same mean branch lengths. The 5.8S partition was analyzed with its own model of evolution (EQU) and branch length estimation, and specifying as indel model the option ''none'', which means that we fixed the alignment for this partition. We ran four independent Markov chains of 30 000 iterations each, sampling the chains every iteration. This number of generations proved to be enough to ensure convergence after calculating the average and the maximum standard deviation of split frequencies (ASDSF, MSDSF respectively) across runs using the executable trees-bootstrap of the BAli-Phy software package. For our analyses, the ASDSF was 0.004—values of ASDSF below 0.01 are considered acceptable to ensure the precision of the estimates of split frequencies (Huelsenbeck and Ronquist 2001)—and the MSDSF was 0.049. Based on the plot of the log-likelihood scores per generation time obtained with Tracer 1.5, the first 3000 samples of each run were discarded and the remaining trees (108 000) were used to compute the majority rule consensus tree.

RESULTS

Alignments and phylogenetic analyses.—The final size of the nuITS alignment for the 71 specimens of *Cortinarius*, including 69 specimens of the subgenus *Phlegmacium* and two outgroup taxa from subgenus *Dermocybe*, was 1404 sites. We excluded 734 sites corresponding to the 5′ and 3′ PCR primer regions, including parts of the nuSSU and nuLSU, as well as 24 ambiguously aligned regions, leaving a dataset of 469 sites. This matrix of 469 sites was analyzed by ML and B1 and included 378 constant characters and 91 variable characters. For the wMP analyses, we excluded the constant sites and included the 24 INAASE characters replacing the 24 ambiguously aligned regions for a final dataset of 115 variable characters, of which 106 were parsimony informative.

The wMP heuristic search resulted in 967 equally parsimonious trees of 502.38 steps (consistency index

[CI] = 0.796, retention index [RI] = 0.946), which were found in one island hit 965 times out of 1000 RAS, in two islands hit three times out of 1000 RAS each, in one island hit two times out of 1000 RAS and in 27 islands where trees were hit only one time out of 1000 RAS. The strict consensus tree of the 967 trees saved during the heuristic search revealed 52 resolved internodes, of which 37 were highly supported (wMP BS ≥ 70%). The ML analysis generated one most likely tree (−ln likelihood = 1399.848878) that recovered 36 nodes, of which 18 were significantly supported (ML BS ≥ 70%).

The 50% majority rule consensus tree of the 150 000 trees from the B1 analyses (performed with MrBayes 3.2.1) was slightly less resolved than the ML tree, with 33 resolved internodes, but better supported with 20 internodes significantly supported (PP ≥ 0.95). The 50% majority rule consensus tree of the 108 000 trees from the B2 analyses (performed with BAli-Phy 2.1.1), however, showed a much more resolved and supported topology compared to B1 and ML, with 50 resolved internodes, of which 44 showed PP ≥ 0.95. Analysis B2 also revealed superior results compared to wMP because, despite a slight decrease of resolved internodes (two less than wMP), it had seven additional supported internodes. Therefore we considered the phylogeny derived from B2 analyses as our best estimate of phylogenetic relationships between the *Cortinarius* species included in this study. Because the four phylogenies were generally congruent, only the B2 tree (FIG. 1) is shown here.

These results have demonstrated that the inclusion of the phylogenetic signal from the ambiguously aligned regions in wMP (as INAASE characters) and also in B2 contributed to a better performance of the analyses in that the resulting topologies are better resolved and supported.

Phylogenetic relationships.—The four analyses recovered with high confidence the new species *Cortinarius mediterraneensis* (see TAXONOMY) as monophyletic. This species appears in the same clade as *Cortinarius subrugulosus*, *C. aureocistophilus*, *C. fulminoides*, *C. inusitatus* and *C. xantho-ochraceus*. Because this clade was recovered in all analyses, with significant support in wMP and B2, and the species included in it share certain morphological features, we propose here its recognition as the/Aureocistophilus clade (see TAXONOMY).

The wMP and B2 analyses recovered with significant support the new species *Cortinarius cistoglaucopus* (see TAXONOMY), which is nested within/Glaucopus-Magicus clade. In both analyses the closest relative to *C. cistoglaucopus* was *C. van-campiae*, but none of them recover this sister relationship as significantly supported. In the B2 tree, specimen *C. glaucopus* 6 had an unexplainable long branch because it is molecularly similar to *C. glaucopus* 1 (i.e. they differ only in positions 415 and 683 on the nuITS alignment). The specimen *C. glaucopus* 8 appeared nested within the *C. magicus* clade. This specimen probably is *C. magicus* that has been misidentified, but the specimen requires revision to confirm this.

All analyses recovered the new species *C. palazonianus* as monophyletic with strong support and also supported its sister relationship with *C. dionysae* within the/Dionysae clade. In addition, the specimens named *C. dionysae* f. *olivaceus* and *C. glaucopus* var. *olivaceus* were nested together with a third specimen, identified as *C. dionysae*, in a clade that was recovered with high confidence by wMP, ML and B2. This clade was clearly separated from the other specimens of *C. dionysae* included in the analyses, which supported the recognition of this forma as a new species (see TAXONOMY).

We also found other relevant results in our tree. The group formed by *Cortinarius camptoros*, *C. lepistoides* and *C. viridocoeruleus* was recovered as monophyletic with significant support in all analyses. Therefore, our molecular phylogenetic results did not fit with the traditional delimitation, based on morphological and anatomical characters, that considers these three taxa as separate species. Thus further studies are needed to better solve the circumscription of this group of taxa. Also we found that specimens *C. multiformis* 1 and 2 were not grouped with the other specimens of *C. multiformis*, which are nested in the/Alluti clade, in any of the phylogenetic analyses, which suggests that they belong to a different species than *C. multiformis*, but the herbarium material must be revised to confirm this.

TAXONOMY

Cortinarius mediterraneensis A. Ortega & Vila, sp. nov. FIGS. 2A, 3A–B

MycoBank MB805897

Type: FRANCE. POQUEROLLES: southern Ferme, under *Pinus halepensis*, *Erica, Arbutus*, 19 Nov 1980, *M. M. Moser* (IB1980618 as *C. multiformis*, HOLOTYPE).

Misapplied names: Cortinarius multiformis sensu Moser et al., Farbatlas Basidiomy 20:125, 2002; *Cortinarius talus* sensu Esteve Raventós et al., Setas Penins Ibérica y Baleares:845, 2007.

Description: Esteve-Raventós et al., Setas Penins Ibérica y Baleares:845, 2007 (as *C. talus*).

Illustration: Moser et al., Farbatlas Basidiomy 20:125, 2002 (as *C. multiformis*); Esteve-Raventós

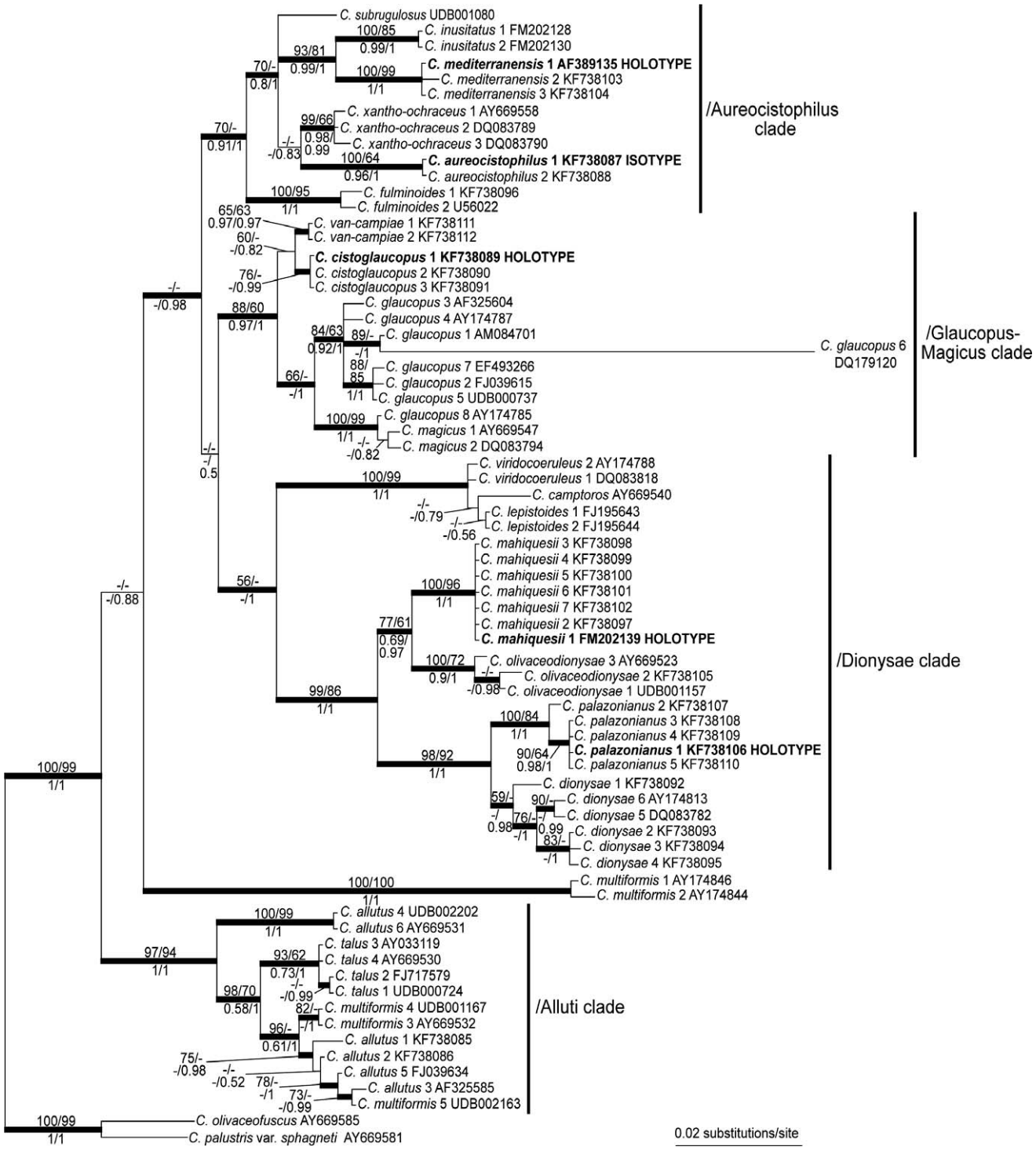

FIG. 1. The Bayesian 50% majority-rule consensus tree inferred from in the BAli-phy (B2) analyses. Numbers above internodes indicate bootstrap support for wMP/ML analyses respectively and numbers under internodes indicate posterior probabilities for B1/B2 analyses respectively. Thicker internodes indicate significant support for at least one statistical method (wMP BS and/or ML BS ≥ 70%; PP B1 and/or PP B2 ≥ 0.95). Type specimens are marked in boldface.

et al., Setas Penins Ibérica y Baleares:845, 2007 (as *C. talus*).

Etymology: The epithet refers to the distribution area of this species.

Pileus 45–90 mm diam, convex or plano-convex, with a not prominent, rounded umbo when young, then flat to flat-depressed with revolute margin when old. Cuticle first glutinous, then becoming dry, yellow

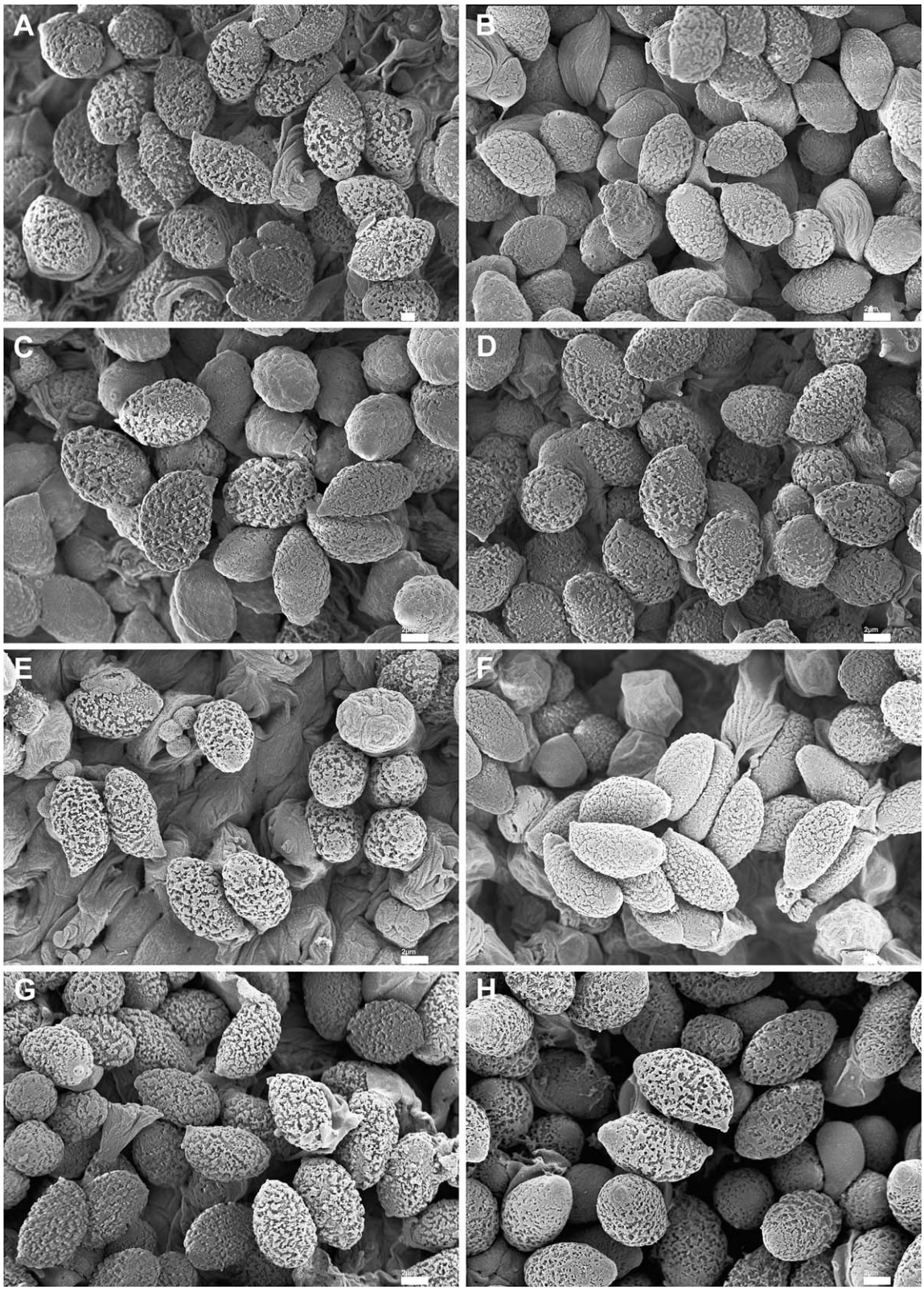

FIG. 2. Scanning (FESEM) micrographs of the spores of (A) *C. mediterraneensis* (IB1980618, HOLOTYPE), (B) *C. aureocistophilus* (JVG 1010123–13, ISOTYPE), (C) *C. fulminoides* (SAAR 8848), (D) *C. subrugulosus* (IB19580092, *C. glaucopus* var. *acyaneus* HOLOTYPE), (E) *C. xantho-ochraceus* (TUB 011861), (F) *C. cistoglaucopus* (LIP JVG 1081108P, HOLOTYPE), (G) *C. olivaceodionysa*e (AB 98–10–253, HOLOTYPE), (H) *C. palazonianus* (LIP JVG 1021217–30, HOLOTYPE).

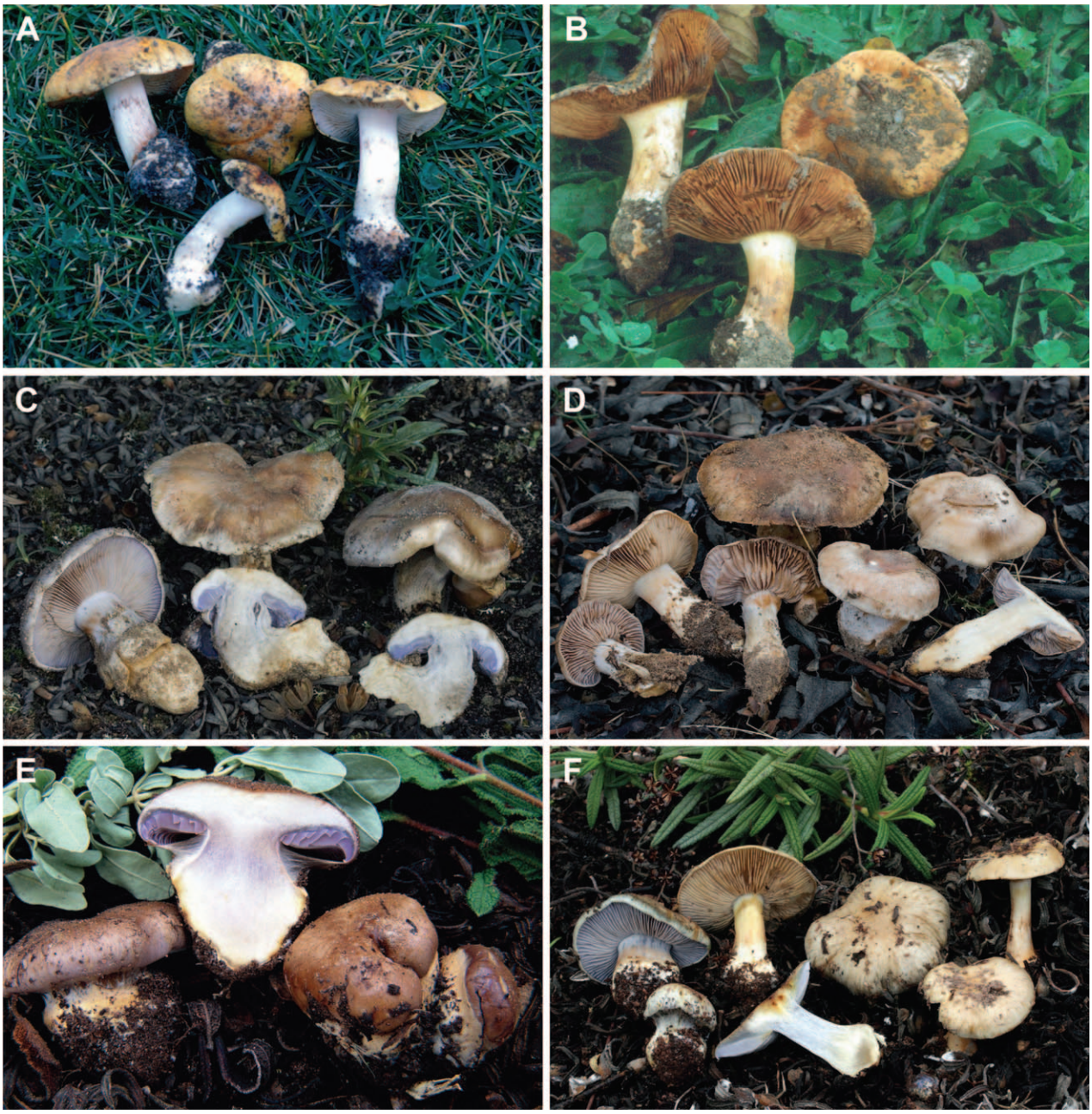

FIG. 3. Basidiome morphology and coloration of (A–B) *C. mediterraneensis,* (C–D) *C. cistoglaucopus* and (E–F) *C. palazonianus*. A. Young and mature basidiomes of *C. mediterraneensis* (JA-Cussta 1606) with a yellow pileus with orange tones in the center, with glutinous cuticle. B. Old specimens of *C. mediterraneensis* (GDA 59132) showing light brown pileus with dry cuticle, and brownish orange lamellae. C. Basidiomes of *C. cistoglaucopus* (LIP JVG 1081108P) showing brownish orange pileus with bluish hues at the margins and bluish lamellae. D. Old basidiomes (JVG 1071208O) showing orange-brown pileus with brownish lamellae. E. Young basidiomes of *C. palazonianus* (JVG 1021126–1) with reddish brown pileus with pale violet in the margins and yellowish hues in the bulb. F. Adult basidiomes of *C. palazonianus* (JVG 1100129–1) with the complete cap surface pale cream and with distinct radial fibrils and one specimen in semihypogeous primordium stage (first row, left).

(3A7–8, 4A4) with orange hues (4B4–6–8), yellowish brown (5C8), and light brown (5D8) in older and dried-damaged specimens; in young basidiomata the whitish, fibrillose universal veil remnants form scarce small patches in the cap, which turn yellowish in older specimens. Lamellae moderately dense, adnate, sinuate, whitish with some pale orange tones (5A2–3) when young, which become orangish (5B8) and finally dun-orange (5–6C–D8); edge entire, irregular or dentate, concolor. Stipe 38–100 × 10–22 mm,

slender, cylindrical, whitish at the beginning of development, soon acquiring light yellow tone (4A3) or orange yellowish (4A–B8), which extends toward the whole surface; bulb 20–38 mm diam, slightly or moderately prominent, poorly marginate, generally rounded, although sometimes it becomes thinner toward the base, becoming turnip-shaped, whitish when young, turning into yellow or orange yellowish with age or when handled. Context whitish, yellowing (2–3A–B7–8, 3A5) when cut or with age. Reaction with 30% KOH light reddish brown (7D7–E7, 8D7) on the cap (tested on dry material). Odor and flavor not distinctive.

Basidiospores 7.2–9.5 × 4.2–5.4 µm (m.v.: 8.2–8.9 × 4.6–5µm), amygdaloid, subcitriform to citriform Q = 1.6–2 (m.v.: 1.75–1.89), with dense, light, moderate or moderate-strong warts (FIG. 2A). Hyphae of universal veil 7 µm wide, hyaline, or yellowish in older basidiomes. Pileipellis duplex. Epicutis thick, the upper layer slightly or moderately gelatinous; hyphae erect or slightly sinuous, 2–5 µm wide, with cylindrical, enlarged or claviform terminal cells, and a yellowish ochraceous vacuolar and encrusted pigment; the lower layer of the epicutis is formed by interwoven, repent hyphae, with yellowish ochraceous encrusted pigment. Hypocutis a dense interwoven repent layer of hyphae, 8–22 µm, with abundant transverse septa, which delimit short cellular elements disposed in ± subcellular structure, with yellowish ochraceous, vacuolar and encrusted pigment. Clamp connections present in all tissues.

Ecology and distribution: In Mediterranean Aleppo pine forests on siliceous soils and in Aleppo pine, Portuguese oak and evergreen oak mixed woodlands on calcareous soils.

Additional specimens examined: SPAIN. GRANADA: Huétor Santillán, Natural Park of the Sierra de Huétor, near forestry house of Peñoncillos, 1300 m, under *Pinus halepensis* and *Quercus rotundifolia*, 14 Nov 1999, *A. Capilla* (GDA 59132). Ibidem, Arroyo de Fardes-Fuente de los Potros, 1300 m, in *Quercus rotundifolia* woodlands with intermixed specimens of *Q. faginea* and *Pinus halepensis*, 1 Nov 2002, *A. Capilla & A. Ortega* (JA-Cussta 1606 as *C. talus*).

Specimens examined for comparison: C. aureocistophilus. ITALY. SARDEGNA: Sassari, Diga del Liscia, under *Cistus monspeliensis*, 3 Dec 1996, *M. Contu* (BCN-SCM 5146). SPAIN. GIRONA: Roses, hillock above Punta Falconera, under *Cistus albidus* and *C. monspeliensis*, 23 Jan 2001, *X. Llimona & J. Vila* (JVG 1010123–13, ISOTYPE). Cadaqués, Cala Jonquet, under *Cistus monspeliensis*, 23 Jan 2001, *X. Llimona & J. Vila* (JVG 1010123–18). *C. fulminoides.* GERMANY. LÖFFINGEN: ''Schwarzwald (mixed coniferous forest)'', *D. Knoch* (SAAR 8848). USA. WYOMING: Teton County, Turpin Meadows Road, 2109 m, mixed conifer subalpine forest (*Picea engelmannii*, *Pinus contorta*, *Abies lasiocarpa*, *Pseudotsuga menziesii*), 13 Aug 1987, *J. Ammirati* (JFA 9541 as *C.* aff. *allutus*). *C. inusitatus.* SPAIN. GRANADA: Huétor Santillán, Natural Park of the Sierra de Huétor, forest track of the Pajareras, 0.5 Km, 1250 m, under *Quercus rotundifolia*, 26 Nov 2006, *A. Ortega* (GDA53699, HOLOTYPE). Ibidem, under *Cistus laurifolius*, 9 Dec 2006, *A. Ortega* (GDA53702). *C. subrugulosus.* AUSTRIA. TIROL: ''Gunglgrün near Imst, beside Forestgarden'', Mid Nov 1958, *M. M. Moser* (IB19580092, HOLOTYPE of *Phlegmacium glaucopus* var. *acyaneum*). *C. xantho-ochraceus.* AUSTRIA. CARINTHIA: Sittersdorf-Jerischach, under *Fagus sylvatica* on calcareous soil, 1 Nov 2003, *G. Saar & T. Münzmay* (TUB 011861 as *C. langei*).

Notes: Cortinarius mediterraneensis also can be clearly separated morphologically from the other taxa of this group: (i) *C. aurocistophilus* has smaller basidiomes, with a pileus up to 50 mm diam, and an attenuated stipe base (Ballarà et al. 2007); (ii) *C. fulminoides* has orange tones in the pileus and the basidiospores are ellipsoid (FIG. 2C) and larger, 8–10 × 4.8–6 µm (m.v.: 9–9.4 × 5.4–5.6 µm) (Münzmay et al. 2009); (iii) *C. subrugulosus* has abundant radial fibrils and white patches of veil on the cap, the bulb is wider and submarginate to marginate and the basidiospores are wider, 8–9.2 × 5.2–6 µm (m.v.: 8.5 × 5.7 µm) (Soop 2004, 2005); (iv) *C. inusitatus* has a pileus with violet and pinkish tones, a universal veil that is well developed, forming scales or patches on the pileus, and has larger basidiospores (8.2–10.8 × 4.5–5.6 µm [m.v.: 9.2 × 5.1 µm]) (Ortega et al. 2009); (v) *C. xantho-ochraceus* also has abundant white veil remnants forming whitish patches on the cap surface, but the bulb is typically marginate and the basidiospores (FIG. 2E) are ellipsoid-amygdaloid or amygdaloid-subcitriform, with moderate warts (Münzmay and Saar 2005, Jeppesen et al. 2012). *C. xantho-ochraceus* (voucher TUB 011861 as *C. langei*) has a negative KOH reaction on pileus, according to Münzmay and Saar (2005). However we have observed in dried material of this same specimen a rusty-tawny KOH reaction.

The only species within the/Aureocistophilus clade with Mediterranean distribution and a similar ecology are *C. inusitatus*, which grows on evergreen oak forests and *Cistus laurifolius* shrubs (Ortega et al. 2009), and *C. aureocistophilus*, which grows under *Cistus* spp. (Ballarà et al. 2007). The remaining species of the/Aureocistophilus clade have a remarkably different ecology in that they live in mixed conifer montane to subalpine forests (*C. fulminoides*, *C. subrugulosus*) and beech woodlands (*C. xantho-ochraceus*).

Cortinarius mediterraneensis morphologically resembles some species from the/Alluti clade (sensu Garnica et al. 2005), such as *C. multiformis* (Fr.) Fr. (= *C. allutus* sensu auct.) or *C. talus* Fr. (= *C. allutus* sensu auct.), because all have (i) a similar habitus, (ii) similar pileus, lamellae and stipe colors and (iii) a similar spore size. Due to these resemblances, two of the three specimens included in our dataset named *C. mediterraneensis* initially were identified as *C. multiformis* (sensu Moser et al. 2002) and *C. talus* (sensu Esteve Raventós et al. 2007). Our molecular phylogenetic results, however, clearly separate *C. mediterraneensis* from taxa of the/Alluti clade, which also is supported by the different ecology and distribution; *C. multiformis* lives in hemiboreal to boreal and, more rarely, temperate coniferous forests and *C. talus* in hemiboreal deciduous woodlands. In addition, the spore morphology is different; basidiospores are ellipsoid-amygdaloid in *C. multiformis* and *C. talus* and amygdaloid- subcitriform-citriform in *C. mediterraneensis*. Other taxa, such as *C. gracilior* (M.M. Moser) M.M. Moser, *C. multiformium* Cons. & Moënne-Locc. and *C. polymorphus* Rob. Henry, also have subcitriform-citriform spores just as *C. mediterraneensis* but, according to Jeppesen et al. (2012), these species have larger spores.

Cortinarius van-campiae Cons., Micologia 2000:115, 2000.

Misapplied name: Cortinarius misermontii sensu Ballará et al., Bull Soc Micol Valenciana 10:78–80, 2005.

Description: Ballarà et al., Bull Soc Micol Valenciana 10:778–880, 2005 (as *C. misermontii*); Fungi non delineati 41–42:65–66, 2007 (as *C. misermontii*); Ortega and Reyes, Micol Veg Med 20:45–62, 2005 (as *C. misermontii*); Consiglio, Micologia 2000:115–117, 2000.

Illustration: Ballarà et al., Fungi non delineati 41–42:198–199, 2007 (as *C. misermontii*).

Specimens examined: SPAIN. GRANADA: La Alcaicería, road from Alhama de Granada to Ventas de Zafarraya, residential area of Prados del Pinar, under *Quercus suber* and *Cistus laurifolius*, on siliceous soil, 3 Dec 2003, *A. Capilla* (GDA 50844). JAÉN: Santa Elena, road to the train station, under *Quercus rotundifolia*, on siliceous soil, 8 Dec 2003, *J. Llavero* (GDA50845).

Notes: In our phylogenetic results (FIG. 1), *Cortinarius van-campiae* is recovered confidently as monophyletic and sister to *C. cistoglaucopus* (new species presented below), from which it can be distinguished based on several macro-morphological features (see *Notes* under *C. cistoglaucopus*). Both species are nested with strong statistical support within the/Glaucopus-Magicus clade, with which they share these characters: (i) pileus surface with abundant radial fibrils in mature basidiomes; (ii) presence of bluish hues on pileus, lamellae, stipe, and trama; and (iii) small or medium-sized basidiospores, with light or moderate ornamentation (FIG. 2F).

The specimens of *Cortinarius van-campiae* originally were identified as *C. misermontii*. After performing the phylogenetic analyses, their nuITS sequences were compared against the GenBank database and revealed that the sequences were exactly the same as the nuITS of the type of *C. van-campiae* (voucher 871, JF907867). Also, the comparison with the unpublished nuITS of the type of *C. misermontii* differed from our specimens of *C. misermontii* by several evolutionary steps (T. Niskanen pers comm). This means that the concept of Iberian authors of *C. misermontii* (Ballarà et al. 2005, 2007; Ortega and Reyes 2005) corresponds to *C. van-campiae*.

Cortinarius cistoglaucopus A. Ortega, Vila, J.C. Campos & Fdez.-Brime, sp. nov. FIGS. 2F, 3C–D MycoBank MB805898

Type: SPAIN. MADRID: El Berrueco, 930 m, under *Cistus laurifolius*, on acidic soil, 8 Nov 2008, *J.C. Campos* (LIP JVG 1081108P HOLOTYPE, ISOTYPE in GDA 59131).

Etymology: The epithet refers to the similarity with *C. glaucopus* and its occurrence in *Cistus* shrubs.

Pileus 35–75 mm diam, hard, fleshy, elastic, convex, trapezoidal to plano-convex, becoming slightly depressed with age; margin slightly incurved when young, straight in mature specimens, lobed and undulated in adult basidiomes. Cuticle smooth, radially fibrillose in old specimens, dry, matt, somewhat separable; variable colors: sometimes it is brownish orange (5C3–5) or grayish brown (5C2) in young specimens, and paler at maturity, when it becomes grayish orange (5–6B2), being lighter toward the margin where it is whitish with some bluish tints (20–22A2), butterfly blue (22A3) or bluish gray (20B1–2) and in other cases it is orange-gray (5B–C2) with reddish gray (8B2) or grayish brown (5C2) tinges when young, becoming brownish gray or orange-brown (5C3–5, D3–5) and light brown (6C3–6) when handled and/or when old; fibrillose universal veil, whitish, evident in young specimens but hardly visible in mature basidiomes. Lamellae dense, sinuate, up to 9 mm wide; pale blue (22A4), sky blue (22A5) or bluish gray (22B3–4) when young, later whitish with grayish beige (20–22B2), and finally becoming brownish (5C–D4–5); edge entire or dentate, concolor or paler. Stipe 35–60 × 11–23 mm, cylindrical, straight or sinuous, bulb up to 25 mm wide, attenuated toward the base, making the stipe

acquire a turnip-shaped aspect or even radicant; surface whitish or whitish gray (20–22B2), in several specimens with bluish hues (22A2) in the upper part. Context of pileus and lower part of the stipe white or whitish gray (22B1), bluish (22A2–3) in the upper part of the stipe and sometimes brownish cream (5A3–B2–4) or brownish ochraceous (5B–C6) in the stipe of older specimens. Reaction with 30% KOH light reddish brown on the context. Odor not distinctive. Flavor pleasant.

Basidiospores 8–9.5 × 4.8–5.2 (–5.5) µm (m.v.: 8.6–8.8 × 4.9–5 µm), ellipsoid Q : L/W = 1.6–1.9 (m.v.: 1.73–1.8), with densely to moderately dense warts (FIG. 2F). Pileipellis duplex. Epicutis thick, the upper layer slightly gelatinous, hyphae erect or slightly sinuous, 3–4(–5) µm wide, with cylindrical, enlarged or claviform terminal cells, and a yellowish cream-colored pigment present, vacuolar and intraparietal; the lower layer of the epicutis is formed by interwoven, repent hyphae, 4–6 µm wide, with yellowish cream or yellowish ochraceous intraparietal pigment. Hypocutis a dense interwoven, repent layer of hyphae, 10–25 µm wide, with abundant transverse septa, which delimit short cellular elements, disposed in a more or less subcellular structure, with a yellowish cream vacuolar pigment. Clamp connections present in all tissues.

Ecology and distribution: Cortinarius cistoglaucopus has a Mediterranean distribution; it occurs under *Cistus* shrubs with thick leaves, mainly *C. laurifolius*, on acidic soil.

Additional specimens examined: SPAIN. SEGOVIA, Cerezo de Arriba, 1130 m, under *Cistus laurifolius*, on acidic soil, 8 Dec 2007, *J. C. Campos* (JVG 1071208O). Ibidem, 15 Dec 2007, *J. C. Campos* (JVG 1071215N).

Notes: Cortinarius cistoglaucopus and *C. van-campiae* (= *C. misermontii* sensu Ballarà et al. 2005) share several morphological traits (i.e. an attenuated to radicant stipe base, pale basidiomes, fibrillose pileus surface and basidiospores), and they also have similar ecology in that both grow on Mediterranean vegetation formations (e.g. cork oak or holm oak forests, *Cistus* shrubs communities). All these similarities led us to consider at first *Cortinarius cistoglaucopus* as a variety of *C. van-campiae*. The phylogenetic results (FIG. 1), however, recover both taxa in two separate, well supported, monophyletic groups, and their sister relationship is weakly supported. An in-depth morphological study revealed that, although they are closely related species, they can be distinguished by these characters: (i) the bulb in *C. van-campiae* is conical and has an evident margin, while in *C. cistoglaucopus* it is not conical and is hardly marginate; (ii) the universal veil is red or reddish in *C. van-campiae* but white or whitish in *C. cistoglaucopus*, which gives the basidiomes a grayish white, grayish cream, ochraceous or brownish ocher color but never with pink-reddish, blood-reddish or red wine hues.

In general the differences among species in section Glaucopodes are small and the separation of species usually is based on a few subtle traits. Thus, taking into account the morphological and molecular differences that we have observed in our collections of *C. van-campiae* and *C. cistoglaucopus*, we think it reasonable to describe *C. cistoglaucopus* as an independent species.

Cortinarius olivaceodionysae A. Ortega, Vila & Fdez.-Brime, stat. nov. and nom. nov. FIG. 2G
MycoBank MB805900

Cortinarius dionysae f. *olivaceus* Rob. Henry in Bidaud et al., Atlas des Cortinaires XVII (2): 1236, 2008, non *Cortinarius olivaceus* Peck, Ann. Rep. N.Y. St. Mus. 24:72, 1872 (1871).

Cortinarius dionysae f. *olivaceus* Rob. Henry, Bull. Soc. Mycol. Fr. 67:238 and 283, 1951 (1952) (nom. inv.).

Type: FRANCE. DOUBS, Cour-Saint-Maurice, 500 m, *Fagus* and *Abies* forest, 7 Oct 1998, *A. Bidaud* (PC AB 98–10–253 HOLOTYPE from *C. dionysae* f. *olivaceus*, HOLOTYPE).

Etymology: The epithet refers to its previous consideration as an olive-colored form of *Cortinarius dionysae*.

Description: Bidaud et al., Atlas des Cortinaires XVII:696, 927, 2008.

Illustration: Bidaud et al., Atlas des Cortinaires XVII:696, 2008.

Macro-morphological description, see Bidaud et al. (2008).

Basidiospores 8.2–10.5 × 5–5.8 µm (m.v.: 9.2–9.6 × 5.4–5.6 µm), amygdaloid, subcitriform to citriform, Q : L/W = 1.5–1.9 (m.v.: 1.7), with moderate to strong ornamentation and ± anastomosing warts (FIG. 2G). Lamellar edges with abundant claviform or pyriform hyaline marginal cells. Pileipellis duplex. Epicutis thick, the upper layer formed by gelatinized, erect or slightly sinuous hyphae, 3–7 µm wide, with cylindrical, enlarged or claviform terminal cells, and a pallid yellowish intracellular pigment; the lower layer of the epicutis is formed by interwoven, repent hyphae, with yellowish encrusted pigment. Hypocutis a dense interwoven, repent layer of hyphae, 10–30 µm wide, with abundant transverse septa, which delimit short cellular elements, disposed in a ± subcellular structure, with encrusted brown-yellowish pigment. With ample clamp connections at septa.

Ecology and distribution: In temperate mixed woodlands of *Fagus sylvatica* and and *Abies* sp., on calcareous soil (Bidaud et al. 2008).

Additional specimens examined: FRANCE. ISÈRE: Tréminis, 950 m., *Fagus* and *Abies* forest, 22 Oct 1998, *A. Bidaud* (AB 98–10–373 as C. *dionysae* f. *olivaceus*).

Notes: In the phylogenetic tree (FIG. 1) the *C. olivaceodionysae* clade, which includes specimens initially identified as *C. dionysae* f. *olivaceus* (AB 98–10–373), *C. dionysae* (UPS AT2003108) and *C. glaucopus* var. *olivaceus* (TUB011856) resp., appears separated from the other *C. dionysae* included in the analyses. The morphology also supports the distinction of *C. olivaceodionysae* by: (i) the presence of olive hues on the pileus instead of the characteristic bluish or violet tones in the pileus of *C. dionysae*; (ii) bulbipellis whitish or cream, never intense yellow as it is in *C. dionysae*.

The molecular phylogeny shows *C. mahiquesii* as the sister taxon of *C. olivaceodionysae*. This molecular proximity also is correlated with several phenotypic similarities: (i) basidiomata size; and (ii) bulbipellis white, lacking yellow tones. However, both species can be easily distinguished because *C. mahiquesii* has: (i) bluish and lilac hues in the pileus; (ii) larger spores, of 10.2–12.4 × 6–6.2 µm, according to Ballarà et al. (2011); and (iii) a different habitat in that *C. mahiquesii* grows under *Cistus* spp. in dry Mediterranean areas.

Cortinarius palazonianus Vila, A. Ortega & Fdez.-Brime, sp. nov. FIGS. 2H, 3E–F

MycoBank MB805899

Type: SPAIN. BARCELONA: Gavà, Ca n'Espinós, 130 m, under *Cistus salviifolius* and *Halimium halimifolium*, in acidic soil, 17 Nov 2002, *J. Vila* and *X. Llimona* (LIP JVG 1021217–30, HOLOTYPE).

Etymology: This species is named in honor of the recently deceased Spanish mycologist Fernando Palazón.

Pileus 20–80 mm diam, subglobose in semihypogeous primordium stage, later hemispherical, convex, plano-convex, or plane, sometimes depressed at center in older specimens. Cuticle is variably colored: in subhypogeous primordium stage light blue (22A3–4), sky blue (22A4), pastel blue (22A5) or pastel violet (18A4), in young specimens is brown (7E4–7), reddish brown (8E4–7), light brown (7D7–8), or orange-brown (6,7C7–8) with tinges of pale blue (22A3), light blue (22A4), or pale violet (15,16,17,18A2–3) toward the margin (although this violet-bluish tinges progressively disappear with the age), then the cuticle becomes flesh-colored (6B2,3) and maize yellow (4B4–5) at the center and pale yellowish cream (4A2) or pale orange-cream (5A2) toward the margin, and finally the complete cap surface is pale cream (4,5A2) in adult basidiomes; this color persists in the dried specimens; with abundant and evident radial fibrils, yellowish (4A3,4) veil remnants present toward the margin. Lamellae dense, adnate, sinuate or emarginated; light blue (22A4–5) or blue (22A6), soon pale blue (20A2–3) or pale violet (18A2), again light violet (18A4–5); edge entire or serrulate, concolor or slightly paler. Stipe 30–85 × 12–25 mm, stocky or slender, with a strongly marginate bulb in young specimens, which becomes scarcely marginate and ± rounded, turnip-shaped with development; light blue (22A3–4) only in the upper part, whitish in the rest of the stipe and yellowish (4A4–5) in the bulb. Context whitish, violet (18, 19A4–5–6) in the cap (over the lamellae) and in the upper part of stipe, yellowing toward the bulb. Reaction with KOH 30% brownish in the context. Odor and flavor markedly floury.

Basidiospores 9.5–10.5 × 5.2–5.8 µm (m.v.: 10.1 × 5.5 µm), subcitriform to citriform, Q : L/W = 1.64–2.02 (m.v.: 1.78), with moderate to strong ornamentation and ± anastomosing warts (FIG. 2G). Lamellar edges with abundant claviform or pyriform hyaline marginal cells. Pileipellis duplex. Epicutis thick, the upper layer formed by gelatinized, erect or slightly sinuous hyphae, 2–4 µm wide, with cylindrical, enlarged or claviform terminal cells; the lower layer of the epicutis is formed by interwoven, repent hyphae, with brown-yellowish encrusted pigment. Hypocutis consisting of a dense interwoven, repent layer of hyphae, 8–20 µm, with abundant transverse septa, which delimit short cellular elements, disposed in a ± subcellular structure, with encrusted ochraceous yellowish pigment. Clamp-connections present in all tissues.

Ecology and distribution: In Mediterranean *Cistaceae* shrubs (*Cistus albidus*, *C. monspeliensis*, *C. salviifolius*, *Halimium halimifolium*) and cork oak (*Quercus suber*) and evergreen oak forests.

Additional specimens examined: SPAIN. BARCELONA: Gavà, Ca n'Espinós, 130 m, under *Cistus salviifolius* and *Halimium halimifolium*, in acidic soil, 26 Nov 2002, *J. Vila & X. Llimona* (JVG 1021126–1). Ibidem, under *Cistus monspeliensis* and *Halimium halimifolium*, in acidic soil, 19 Jan 2010, *J. Vila & X. Llimona* (JVG 1100119–7). Ibidem, 29 Jan 2010, *J. Vila & X. Llimona* (JVG 1100129–1). Tiana, Ermita de l'Alegria, 170 m, under *Cistus albidus*, in acidic soil, 17 Dec 2002, *J. Vila & X. Llimona* (JVG 1021217–27). GIRONA: Riells de Montseny, 510 m, under *Quercus ilex* and *Castanea sativa*, in acidic soil, 29 Oct 2000, *J. Vila & C. Gutiérrez* (JVG 1001029–2). GRANADA: Huétor Santillán, Natural Park of the Sierra de Huétor, forest track of the Pajareras, 0.5 Km, 1250 m, under *Quercus rotundifolia* and *Cistus laurifolius* on siliceous soil, 29 Dec 2006, *A. Ortega* (GDA 59133).

Notes: All specimens included in the phylogenetic analyses named *Cortinarius palazonianus* form a well supported clade in all phylogenetic analyses performed, showing that this is a well defined taxon, not only morphologically but also molecularly. The clade

C. palazonianus has a sister relationship with *C. dionysae*, which reveals a more variable nuITS; it is recovered only as a well supported clade in analysis B2. *Cortinarius palazonianus* and *C. dionysae* are similar because both have farinaceous odor and citriform spores and grow in dry Mediterranean communities, on siliceous soils. However *C. palazonianus* can be distinguished from *C. dionysae* by these characters: (i) basidiome with semihypogeous development; (ii) less robust habitus and a slender stipe; and (iii) blue or violet hues in young specimens in the pileus and lamellae.

Another taxon closely related to *C. palazonianus* is *C. mahiquesii*, which has not only farinaceous odor and citriform spores, but the basidiomes also develop semihypogeously and have ephemeral blue or violet hues in the pileus and lamellae. Both species also grow in Mediterranean *Cistaceae* shrubs, although *C. mahiquesii* exclusively grows in these communities while *C. palazonianus* can grow also in cork oak and evergreen oak forests. Both taxa can be clearly distinguished by these characters: (i) *C. palazonianus* lacks gray-olive tinges in the pileus and *C. mahiquesii* never has yellowish tinges in the bulb; and (ii) *C. mahiquesii* has a remarkably different structure of the epicutis, which has a tendency to become a trichoderm, formed by flexuose and straight terminal elements (see Vila et al. 2008).

DISCUSSION

/Aureocistophilus clade.—The phylogeny obtained in this study (FIG. 1) recovered a well supported clade that includes these species: *Cortinarius subrugulosus* Bidaud & Armada (= *C. glaucopus* var. *acyaneus* [M.M. Moser] Nézdojm.; *C. parherpeticus* sensu Soop), *C. aureocistophilus* Vila, Contu & Llimona, *C. fulminoides* M.M. Moser (= *C.* aff. *allutus* sensu Ammirati, JFA 9541), *C. inusitatus* A. Ortega, Bidaud, Suár.-Sant. & Vila, *C. mediterraneensis* A. Ortega & Vila and *C. xantho-ochraceus* P.D. Orton. Ortega et al. (2009) recovered a similar clade formed by the species *C. allutus* U56022 (= *C. fulminoides* 2 in our study), the *C. inusitatus* clade, *C. multiformis* (= *C. mediterraneensis* 1 in our study) and the *C. langei* clade (= *C. xantho-ochraceus* clade in our study). Although this clade was recovered in Ortega et al. (2009) with high statistical support (i.e. bootstrap value = 97) and it grouped taxa that share macroscopic and microscopic features, the authors did not propose to recognize it. Therefore we propose here to name it the/Aureocistophilus clade.

The species belonging to this clade grow in typical Mediterranean formations as Aleppo pine (*Pinus halepensis*), Portuguese oak (*Quercus faginea*), and evergreen oak woodlands, and *Cistus* shrub communities, as well as in temperate montane forests (under *Fagus sylvatica*, *Picea* spp., and *Pinus sylvestris*). The combination of characters that circumscribe this group is: (i) pileus yellowish, yellowish-orange, or yellowish-ochraceous (except for *Cortinarius inusitatus*, which is reddish violet or grayish violet, with yellowish olive hues toward the margin); (ii) universal veil remnants abundant on cap surface; (iii) lamellae light (whitish, cream or pale pinkish); (iv) context yellowing with age and manipulation, and odor and taste not distinctive; (v) KOH (30%) reaction blood red or dark brick on the cap; and (vi) spores m.v.: 8.3–9.4 × 4.6–5.7 µm ellipsoid, subamygdaloid, amygdaloid, subcitriform, or citriform, with light or moderate ornamentation (FIGS. 2A–E).

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