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Morphological and molecular evidence for a new species of *Leucoagaricus* from China

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A new species, *Leucoagaricus brunneocanus*, is described from southwestern China. It is characterized by a greyish brown to brownish black fibrillose pileus, amygdaliform basidiospores, variably shaped cheilocystidia, and a pileus covering made up of repent to ascending differentiated cylindrical hyphae. Based on morphological and molecular evidences, *La. brunneocanus* was tentatively placed in sect. *Rubrotincti* subsect. *Trichodermi* according to Bon's taxonomical views.

Keywords: Agaricales, lepiotaceous fungi, phylogeny, taxonomy.

The genus *Leucoagaricus* Locq. ex Singer (1948: 35) (Agaricaceae, Agaricales, Basidiomycota) is a widely distributed genus in the world (Singer 1986, Vellinga 2001). According to Index Fungorum (www.indexfungorum.org), about 277 species or varieties have been described within the genus. Taking the rich mycota of China into account, it is reasonable to expect a large number of species of this cosmopolitan genus in China. However, only about 20 species have been reported from China, including more than ten species originally described from China (Mao 1998, Yang et al. 2005, Yang 2007, Ge 2010, Liang et al. 2010, Yuan et al. 2014, Ge et al. 2015).

Previous phylogenetic studies implied that the genera *Leucoagaricus* and *Leucocoprinus* Pat. together form a monophyletic clade (Johnson & Vilgalys 1998, Johnson 1999, Vellinga 2004). Vellinga & Davis (2006) indicated the feasibility of treating the resolved monophyletic *Leucoagaricus*/*Leucocoprinus* clade either as a single large genus, or splitting it into smaller genera. In the study we follow the majority view and regard *Leucoagaricus* and *Leucocoprinus* as separate genera based on morphological characters.

During our study to document the species diversity of *Leucoagaricus* in southwestern China, two interesting collections of *Leucoagaricus* made from the same locality in Sichuan Province were identified as a novel taxon after detailed morphological examinations and molecular evidence based on sequences of the internal transcribed spacer (ITS).

Materials and methods

The specimens are kept in the Herbarium of Cryptogams, Kunming Institute of Botany, Chinese Academy of Sciences (HKAS). Macroscopic characters are based on notes on both fresh and herbarium material. Terminology for descriptive terms follows Vellinga (1988) and colour designations are from Kornerup & Wanscher (1981).

Morphology

For microscopic observations, sections of specimens were cut by hand and mounted in 5 % KOH and Congo red or Melzer's reagent. Basidiospores were also observed in Cresyl blue to test for a metachromatic reaction (Singer 1986). At least 20 elements of each fungal structure (basidia, basidiospores, cheilocystidia, and elements of the pileus covering) per collection were measured. The abbreviation [n/m/p] indicates that measurements were made on n basidiospores in m basidiomata from p collections. Dimensions of basidiospores are given using a notation of the form (a)b–c(d). The range b–c contains a minimum of 90 % of the measured values. Extreme values are given in parentheses. The following abbreviations are used: Q refers to the length/breadth ratio of basidiospores; Q_{av} refers to

Tab. 1. Samples used in this study and their GenBank sequence accession numbers.

Name	Voucher	Location	accession No.
Chlorophyllum molybdites	DUKE-JJ162	USA, North Carolina	U85309[2]
Lepiota cf. *atrodisca*	UC-ecv3261	USA: California, Humboldt Co.	GU909511[5]
L. cf. *phaeosticta*	TN51705	USA, Tennessee, Great Smoky Mountains	GU903307[5]
Leucoagaricus americanus	UCB-ecv2454	USA, Michigan, Washtenaw Co., Ann Arbor	AY176407[4]
La. asiaticus	LAH10012012	Pakistan, Lahore, Botanical Garden	KP164971
La. atroazureus	HKAS42670	China, Yunnan Prov., Yingjiang Co.	EU416301[8]
La. badhamii	MCVE3047	Italy	GQ329056
La. brunneocanus	HKAS45861	China, Sichuan Prov., Xiangcheng Co.	KP096237[1]
	HKAS45457	China, Sichuan Prov., Xiangcheng Co.	KP096238[1]
La. brunnescens	UC- R. Balsley	USA, New Jersey	GQ203804[9]
La. crystallifer	Huijser-19IX1998	Germany, Baden-Württemberg, Gottenheim	AF482863[4]
La. dacrytus	UC-ecv2010c	USA: New Jersey, Hunterdon Co.	GU903309[5]
La. dyscritus	UC-ecv3532B	USA, California, San Mateo Co.	GU136181
La. flavovirens	HKAS29580	China, Hainan Prov., Ledong Co., Jianfengling	EU416293[8]
La. gaillardii	MCVE16517	Italy	GQ329064
La. griseodiscus	MCVE13719	Italy	GQ329059
La. ionidicolor	L-ecv2280	Netherlands, Limburg Prov., Stokhem	AY176415[4]
La. lateritiopurpureus	VLA M-4729	Russia	JX133174[10]
La. leucothites	HMAS88854	China, Beijin city, Haidian,	EU416308[8]
La. littoralis	MCVE702	Italy	GQ329041
La. marriagei	L-ecv2005	Netherlands, Limburg Prov., Elsloo-Geulle	AF482866[4]
La. melanotrichus	L-ecv2262	Netherlands, Noor-Holland Prov.	AY176417[4]
La. meleagris	L-ecv1990	Netherlands, Noord-Holland Prov., Amsterdam	AY176419[4]
La. nympharum	HMAS99343	China, Tibet, Nyingchi co., Zarao	EU416310[8]
La. orientiflavus	HKAS54260	China, Yunnan Prov., Kunming, Heilongtan	GU084262[7]
La. purpureolilacinus	L-ecv2291	Netherlands, Zeeland Prov.	AF482869[3]
La. rubrobrunneus	LE289431	Russia	JX896448[10]
La. rubrotinctus	VLA M-20287	Russia	JX133167[10]
La. serenus	Bizzi369/98	Italy, Vicenza, Grancona, Val del Gazzo	AY176420[4]
Leucoagaricus sp1	UCB-ecv2561	USA, California, Contra Costa Co.	AY176430[4]
Leucoagaricus sp2	MEL-Thiele2646	Australia	AY176432[4]
Leucoagaricus sp3	UCB-Rogers	USA, Oregon, Lane Co., Eugene	AY176434[4]
Leucoagaricus sp4	PA481	Panama	EF527332[6]
Leucoagaricus sp5	UC-ecv2619	USA, CA, San Mateo Co.	AY243637
Leucoagaricus sp6	UCB-ecv2457	USA: Michigan, Washtenaw Co., Ann Arbor	AY176428[4]
Leucoagaricus sp7	UC-ecv3265	USA: California, Humboldt Co.	GU903302[5]
Leucoagaricus sp8	UC-ecv2375	USA: Oregon, Sinslaw Natn Forest	GU903303[5]
La. subcrystallifer	HKAS49373	China, Sichuan Prov., Luhuo Co.	KP096236[12]
La. sublittoralis	L-ecv2235	Netherlands, Limburg Prov., Elsloo-Geulle	AY176442[4]
La. subpurpureolilacinus	HKAS48285	China, Yunnan Prov., Kunming City, Heilongtan	KP096233[12]
La. tangerinus	HKAS50036	China, Fujian Prov., Sanming, Geshikao	KF501437[11]
La. tener	L-ecv2261	Netherlands, Noor-Holland Prov.	AY176444[4]
La. truncatus	HKAS49288	China, Sichuan Prov., Seda Co.	KP096235[12]
La. vassiljevae	LE 289432	Russia	JX896447[10]
La. viriditinctus	HKAS50033	China, Yunnan Prov., Jinghong, Dadugang	EU419375[8]
La. wychanskyi	L-hah1998	Netherlands, Limburg Prov.	AF482874[3]
Lc. heinemannii	L-ecv2101	Netherlands: Zuid-Holland Prov., Leiden	AF482864
Macrolepiota mastoidea	HKAS50194	China, Jilin Prov, Dunhua City, Huangnihe	HM125531

The present study[1], Johnson 1999[2], Vellinga et al. 2003[3], Vellinga 2004[4], Vo et al. 2009[5], Ge 2010[6], Liang et al. 2010[7], Vellinga & Balsley 2010[8], Vellinga et al. 2010[9], Malysheva et al. 2013[10], Yuan et al. 2014[11], Ge et al. 2015[12], the others are from Genbank.

the average Q of all basidiospores ± standard deviation.

Molecular identification

DNA was extracted from herbarium materials with a CTAB protocol (Zhou & Liang 2011). Protocols for PCR, sequencing and sequence alignment followed those by Liang et al. (2009). The primers used for the amplification were ITS1 and ITS4 (White et al. 1990). DNA sequences were edited and aligned by Muscle 3.2 (Edgar 2004) and then manually checked and adjusted. Newly produced sequences were deposited in GenBank. The initial BLAST searches in GenBank (Altschul et al. 1990) revealed most similar sequences to the novel taxa are sequence of *La. griseodiscus* (Bon) Bon & Migl., within *La.* sect. *Rubrotincti* Singer subsect. *Trichodermi* M. Bon & Migl. (Bon & Migliozzi 1991). Thus ITS sequences from species within sect. *Rubrotincti* as well as other species reported from China and with grey to brown or dark fibrils were included in the phylogenetic analysis. *Macrolepiota mastoidea* (Fr.) Singer and *Chlorophyllum molybdites* (G. Mey.) Massee were chosen as outgroups. The accession numbers and detailed information of analyzed sequences are in Tab. 1.

The matrix was analyzed using maximum likelihood with the RAxML BlackBox online server (Stamatakis et al. 2008) and MrBayes 3.1 (Huelsenbeck & Ronquist 2005) under a general-time-reversible (GTR) model (nst = 6) following selection of model parameters using the Akaike information criterion (AIC) to determine the best-fit likelihood model with Modeltest 3.7 (Posada & Buckley 2004). All parameters in the ML analysis used the default setting, and statistical support values were obtained using nonparametric bootstrapping with 1000 replicates. The results were subsequently exported to Dendroscope for tree viewing (Huson et al. 2007). Bayesian analyses were run using six chains for 15 million generations and sampling every 1000 generations. The first 1100 iterations were used for the burn-in period. Trees were pooled together and used to generate a 50 % majority-rule consensus tree with branch lengths.

Results

Molecular studies

A dataset including 34 ITS sequences with 836 nucleotide sites was analyzed. Because RAxML and Bayesian analyses resulted in the same topology, only the best Maximum Likelihood tree with bootstrap supports is shown (Fig. 1), Bayesian posterior probability are also displayed with the bootstrap values along the branches.

Bayesian and RAxML phylogenetic analyses showed that sequence of the new species, *La. brunneocanus,* is obviously different from sequences of related species and is sister to a sequence of *La. griseodiscus* and gets strong statistical support (100 % bootstrap and 1.00 Bayesian posterior probability). These two species jointly are sister to *Leucoagaricus* sp. (AY176430) from California, USA.

Taxonomy

Leucoagaricus brunneocanus F. Yu, J.F. Liang & Z.W. Ge, **sp. nov.** – Fig. 2.
MycoBank no.: MB810771

Diagnosis: Pileus grey to greyish brown at centre, with radially grey, brownish grey, greyish brown to brownish black fibrillose or fibrillose-squamulose outwards. Stipe with minute grey brown squamules in lower half. Basidiospores 6–8 × 4–5 µm, amygdaliform, with ventricose adaxial side, not dextrinoid, metachromatic in Cresyl blue. Cheilocystidia variable in shape. Pileus covering with long, radially arranged, repent to ascending hyphae made up of long cylindrical elements. Clamp connections absent.

Holotypus. – CHINA, Sichuan Province: Xiangcheng County, 108th ditch, alt. 3000 m, 12 June 2004, *leg.* Z. W. Ge 97 (HKAS 45861).

Description. – Basidiomata small to medium-sized (Fig. 2A). – Pileus 2–5 cm in diam., thin, fragile, plano-convex to applanate with obtuse umbo, centre rather smooth, grey to greyish brown (6E1–10E3), becoming radially fibrillose or fibrillose-squamulose, grey, brownish grey, greyish brown to brownish black (6D1–9E3) outwards. – Lamellae free, crowded, white to cream, with lamellulae of two lengths. – Stipe 4–7 × 0.3–0.4 cm, subcylindrical or attenuate upwards; hollow, whitish, smooth. – Annulus ascending, whitish, with a grey brown, brownish black to black (6E2–9E3) edge. – Context white, thin. – Smell like caramel. – Taste not recorded. – Basidiospores (Fig. 2B) [48/2/2] (5.5)6–8(8.5) × (3.5)4–5 µm [Q = (1.33)1.38–1.88(1.9), Q_{av} = 1.66 ± 0.17], distinctly amygdaliform in side view, narrowed at apex, some with an indistinct apical papilla, with ventricose adaxial side, without germ pore, amygdaliform or ovoid in front view; hyaline, smooth, slightly thick-walled, not dextrinoid, congophilous but turning colours slowly, metachromatic in Cresyl blue. – Basidia 20–27 × 6.5–8 µm, clavate, 4-spored, rarely 2-spored, hyaline. – Cheilocystidia (Fig. 2C) 24–42 × 10–21(30) µm, very variable in shape, from widely clavate to sickle shaped or fusiform, some-

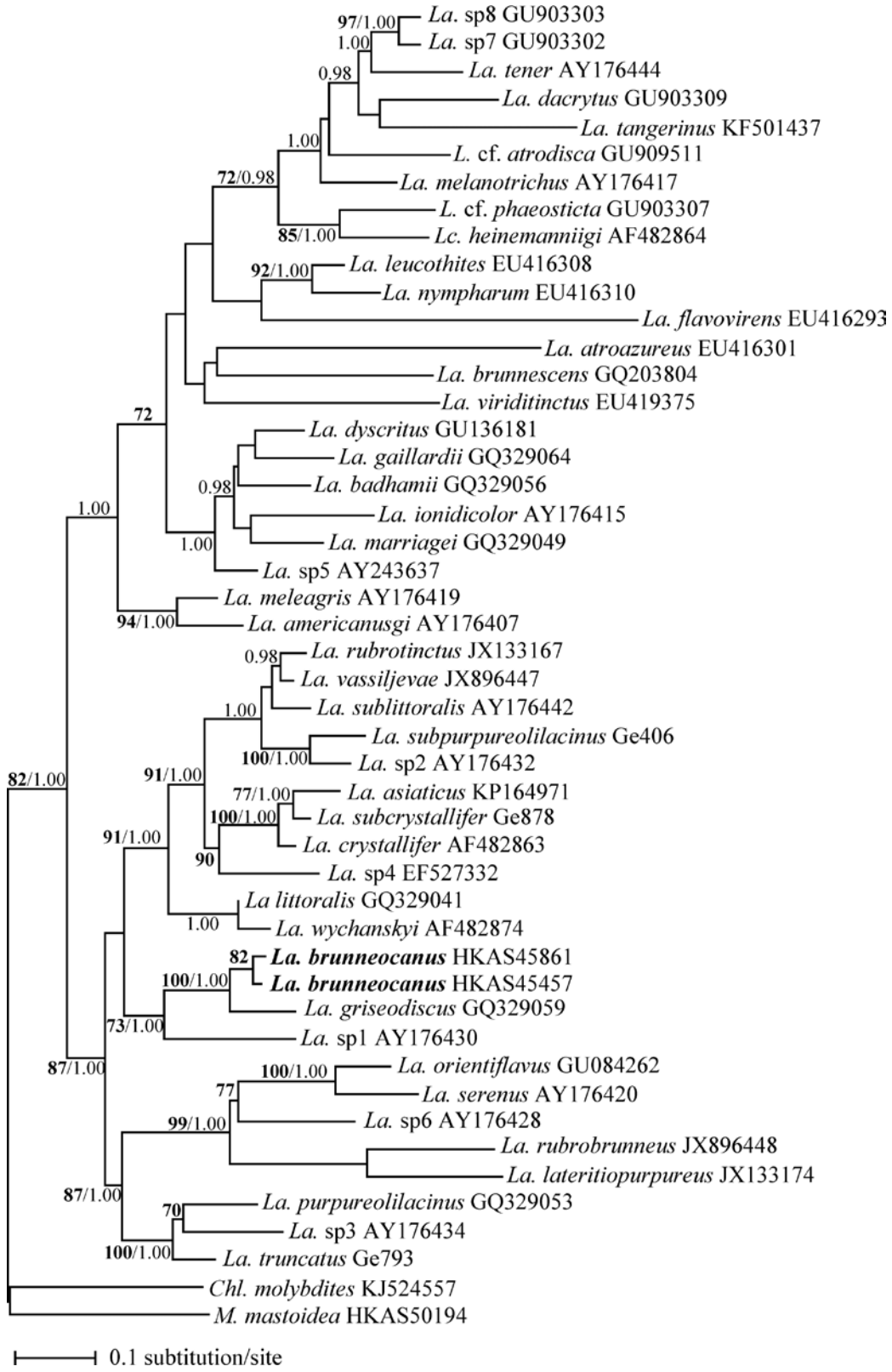

Fig. 1. The best RAxML likelihood tree (–In L 10547.251408) based on the ITS dataset. Support values in bold are RAxML likelihood bootstrap (≥70%). Values in normal type are Bayesian posterior probabilities (≥0.95).

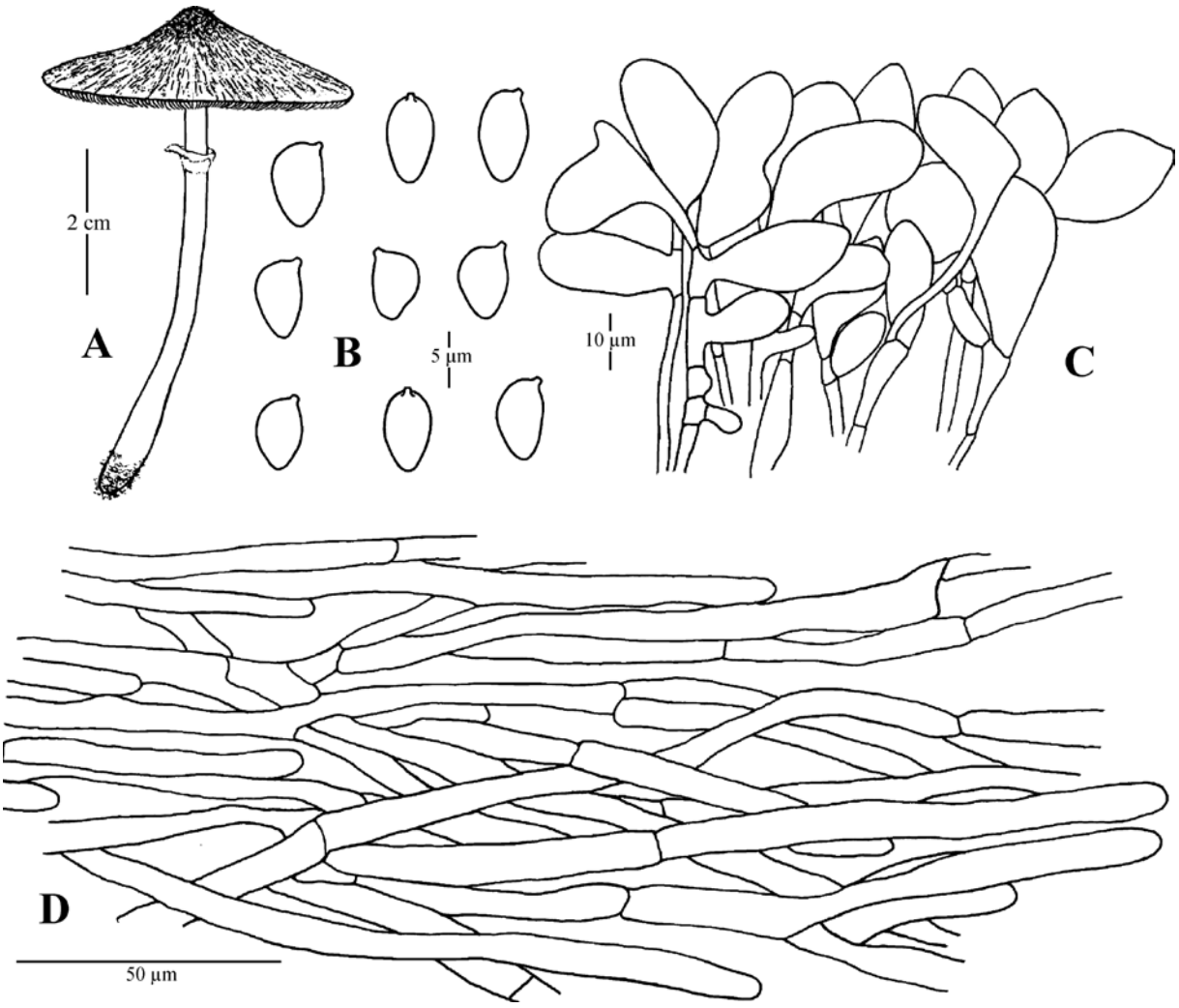

Fig. 2. *Leucoagaricus brunneocanus*. **A.** Basidioma. **B.** Basidiospores. **C.** Cheilocystidia. **D.** Pileus covering. (A, B and D from holotype, C from HKAS 45457) .

times a bit strangulate or flexuous, or with a papilla at the apex, often linked in chains, and densely arranged into sterile lamella edge. – Pleurocystidia absent. – Pileus covering (Fig. 2D) with long, radially arranged, repent to ascending hyphae made up of long cylindrical elements; terminal elements 50–128 × 5–10 µm, cylindrical, sometimes differentiated, thin-walled, with pale greyish brow to dark brown intracellular pigments. – Clamp connections absent.

Etymology. – Brunneus (Latin) = brown; canus (Latin) = grey; named due to its brown grey fibrillose pileus.

Habitat and distribution. – Solitary, saprotrophic and terrestrial, on the ground under thorny shrub vegetation of *Caragana* and *Rosa* at high altitude in summer in southwestern China.

Additional specimens examined. – Type locality, 10 July 2004, *leg.* Zhu L.Yang 3972 (HKAS 45457).

Notes. – *Leucoagaricus brunneocanus* is well characterized by its grey brown fibrillose pileus, amygdaliform basidiospores with a narrow apex, variably shaped cheilocystidia, and a pileus covering made up of repent to ascending, differentiated cylindrical hyphae. Based on a grey to greyish brown pileus and differentiated terminal elements of the pileus covering, we tentatively place *La. brunneocanus* in sect. *Rubrotincti* subsect. *Trichodermi* (Bon & Migliozzi 1991) according to Bon's (1996) taxonomical views.

Leucoagaricus brunneocanus is morphologically very similar to the French species *La. griseodiscus* (Bon 1996), which has a darker or blackish pileus centre, a slightly clavate stipe, narrowly utriform to

lecythiform, sometimes branched, capitate cheilocystidia, ovoid or amygdaliform basidiospores with narrow and elongated apex, and a pileus covering with a few short elements at the base. Our phylogenetic analyses include an Italian collection identified as *La. griseodiscus,* and show that the two species have a close phylogenetic relationship, but the nrITS sequences clearly distinguish the two species: the similarity of sequences between the two collections is only 93 %.

Leucoagaricus fulgineodiffractus Bellù & Lanzoni (Bellù &Lanzoni 1988), originally described from Italy, differs from *La. brunneocanus* by its dark brown to blackish-brown, radially splitting pileus surface, larger ovoid or amygdaliform spores (7–8.5 × 4–5 µm), narrower clavate cheilocystidia (30–40 × 8–10 µm) and fusiform terminal elements of the pileus covering (Candusso &Lanzoni 1990, Bon 1996). *Leucoagaricus brunneocingulatus* (Orton) M. Bon (Bon 1976) is distinguished by a red-brown pileus, almost bulbous at stipe base, a brown-rimmed annulus, smaller basidiospores (5–6 × 3.5–4 µm) with a pointed and elongated apex, and fusiform or clavate cheilocystidia.

Leucoagaricus tener (Bon 1996) differs in fresh basidiomata exuding drops on a stipe and pileus, a pileus with radially brown fibrils and slightly sulcate in marginal zone, fading orange when touched, and cylindrical to narrowly clavate cheilocystidia, while *La. dacrytus* Vellinga (Vellinga & Balsley 2010) differs in the golden drops exuded on the basidiocarp surface, relatively small spores (5.9–7.4 × 2.9–4.1 µm), the narrowly clavate cheilocystidia, and the cutis-like pileus covering. *La. fuligineodiscus* P. Mohr & Daehncke, a species in sect. *Rubritincti* subsect. *Rubrotincti* from Germany, has ivory to brown pileus, bulbous stipe base, ellipsoid basidiospores with rounded apex, and cylindrical, clavate or bottle-shaped cheilocystidia, often with a few crystals at the apex (Mohr & Ludwig 2004).

Leucoagaricus melanotrichus (Malençon & Bertault) Trimbach (Trimbach 1975) has a grey pileus and variable shaped cheilocystidia (Bon 1996, Vellinga 2001). This species was placed in sect. *Leucoagaricus* by Bon (1996), a position not supported by the molecular evidence (Vellinga 2004). Morphologically, it is distinguished from *La. brunneocanus* by its dark grey pileus with a purplish or greenish hue, ellipsoid to oblong spores with straight adaxial side in side-view, short clavate to short handle-capitate cheilocystidia, irregularly arranged cylindrical elements of pileus covering with not differentiated terminal elements while *La. melanotrichus* var. *fuligineobrunneus* Bon & Boiffard (Bon & Boiffard 1978) differs from the new species by having small fragile basidiomata (1–2 cm), a stipe with an ochraceous base, and ellipsoid to oblong basidiospores with straight adaxial side (Bon 1996). Other species in section *Leucoagaricus*, such as *La. atrofibrillosus* Singer from Chile, *La. atroalbus* P. Mohr & Daehncke and *La. brunneosquamulosus* P. Mohr & Daehncke from Germany, possess similar pileus colour. However, these species were placed in section *Leucoagaricus* based on pileus covering with not differentiated terminal elements. In addition *La. atrofibrillosus* is distinguished by its shorter and narrower ellipsoid basidiospores (6.6–7.2 × 3.7–3.8 µm) (Singer 1969). *La. atroalbus* differs in larger elongated ovoid to ellipsoid basidiospores (8–10.5 × 3.5–4 µm) and cylindrical, clavate or fusiform cheilocystidia while *La. brunneosquamulosus* in grey brownish pileus with ochre spots, larger oval basidiospores with rounded apex (8–10 × 5.5–6.5 µm), and narrowly clavate or narrowly fusiform cheilocystidia with constricted or capitate apex (Mohr & Ludwig 2004).

Several other dark species are also worth noting here, such as *Lepiota atrodisca* Zeller (Zeller 1938), *L. fusciceps* Hongo (Hongo 1973), and *L. phaeosticta* Morgan (Morgan 1906) and *Leucocoprinus heinemannii* Migl. (Migliozzi 1987); their black pileus covering easily distinguishes them from *La. brunneocanus*.

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