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Leucoagaricus purpurascens, a new species from eastern China based on morphological characteristics and molecular evidence

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Abstract

A new species, *Leucoagaricus purpurascens*, collected from a subtropical region in China, is described based on morphological and molecular data. *Leucoagaricus purpurascens* is characterized by its small basidiomata with purple discolouration when dried, the pileus with distinct umbo, the amygdaliform, ellipsoidal to oblong basidiospores, and the absence of cheilocystidia. A detailed morphological description, line drawings, colour photographs, and a phylogenetic tree showing the phylogenetic placement of the new species are provided.

Keywords: Agaricales, *Leucoagaricus*, phylogeny, taxonomy

Introduction

The genus *Leucoagaricus* Singer (1948), a member of Agaricaceae Chevall., is characterized by the following morphological characteristics: an entire or rarely striate pileus margin, free lamellae, metachromatic basidiospores in cresyl blue, and the absence of clamp-connections and pseudoparaphyses (Singer 1986; Vellinga 2001; Liang *et al.* 2010; Justo *et al.* 2021). These features led to the inclusion of about 130 species within the genus. Phylogenetic studies reveal that species of *Leucoagaricus* and *Leucocoprinus* Pat. intermix within a single clade (Vellinga 2004; Vellinga *et al.* 2011). In this study, we recognize *Leucoagaricus* and *Leucocoprinus* as different genera in the sense of Vellinga (2001) and describe new taxa according to these morphological characters, waiting for generic concepts in this group to be settled. To avoid confusion, we use the abbreviation *La*. for *Leucoagaricus* and *Lc*. for *Leucocoprinus*.

Twenty-three species of *Leucoagaricus* have already been recorded from China, suggesting that the genus is more diverse and speciose in this area (Ge *et al.* 2019). The colour change of basidiomata when bruised or dried is one of the important characteristics in the taxonomy of lepiotaceous fungi (Liang *et al.* 2010). Colour reactions in *Leucoagaricus* are diverse, as certain species display red, lilac, blue or green reactions after drying or bruising. For example, when bruised, *La*. *americanus* (Peck) Vellinga turns yellow at first, then pinkish red (Vellinga 2000), *La*. *ionidicolor* Bellù & Lanzoni changes to lilac on drying (Vellinga 2006), *La*. *purpureoruber* (Z. S. Bi, T. H. Li & G. Y. Zheng) Z. W. Ge & Zhu L. Yang becomes purple or brown when dried (Yang & Ge 2017), *La*. *atroazureus* J. F. Liang, Zhu L. Yang & J. Xu, *La*. *viriditinctus* (Berk. & Broome) J. F. Liang, Zhu L. Yang & J. Xu turns bluish on bruising, and *La*. *flavovirens* J. F. Liang, Zhu L. Yang & J. Xu exhibits a green reaction (Liang *et al.* 2010).

During field surveys in Sheshan National Forest Park (Shanghai, China), we collected a species of *Leucoagaricus* which was morphologically distinct from any known members of lepiotaceous fungi. This taxon is distinguished from all other species by the cream pileus which becomes entirely purple on drying, the absence of cheilocystidia, and the amygdaliform, ellipsoidal to oblong basidiospores. An exhaustive search of the literature, including monographs and papers (Ge 2010; Ge *et al.* 2015; Ge *et al.* 2019; Liang *et al.* 2010; Ma *et al*. 2022; Yang 2007; Yang & Ge 2017; Yu *et al.* 2016; Yuan *et al.* 2014), confirmed the unique nature of this species. In addition, molecular phylogenetic analyses based on two ribosomal DNA markers (ITS and LSU) supported the uniqueness of this taxon. Thus, this taxon is proposed as a new species of *Leucoagaricus,* and detailed descriptions and illustrations are presented.

Materials & methods

Morphological studies

The macroscopic description was based on field notes and photographs. Colour codes refer to Kornerup & Wanscher (1978). Specimens were collected and dried with an electric drier. Materials were deposited in the Herbarium of Kunming Institute of Botany, the Chinese Academy of Sciences (KUN, with HKAS numbers). Microscopic structures were observed under a Leica DM2500 microscope with materials mounted in 5% KOH solution. "*n/m/p*" indicates the size of *n* basidiospores from *m* basidiomata of *p* collections. The size of basidiospores followed *(a)b–c(d)*, where the range *b–c* represents 90% of the measured values, and extreme values (a or d) are given in parentheses. *Q* represents the 'length/breadth ratio' of basidiospores in side view; Q_{av} refers to the average Q of basidiospores ± sample standard deviation.

DNA extraction, PCR and sequencing

Total DNA was extracted from the silica-dried material by the CTAB method (Doyle & Doyle 1987). The nucleotide rDNA regions encompassing the internal transcribed spacers 1 and 2, along with the 5.8S rDNA (ITS) and the D1–D3 domains of nuclear 28S rDNA (LSU), were selected for phylogenetic analyses. Universal primer pairs ITS5/ITS4 (White *et al.* 1990) and LR0R/LR5 (Vilgalys & Hester 1990) were applied to amplify ITS and LSU, respectively. The PCR reactions were performed in an ABI 2720 thermal cycler (Applied Biosystems, Foster City, CA, USA), and the PCR program was as follows: pre-denaturation at 94°C for 5 min; then followed by 35 cycles of denaturation at 94°C for 50 s, annealing at 52°C (ITS) or 50°C (LSU) for 50 s, elongation at 72°C for 60 s; afterward, a final elongation at 72°C for 8 min was included. Six sequences (three ITS and three LSU) were newly generated in this study (TABLE 1).

Molecular phylogenetic analyses

A sequence data matrix of ITS and LSU was prepared for the phylogenetic analysis to infer the systematic position of the described species. In addition to the newly generated sequences, the available sequences of *Leucoagaricus* species described from China, the sequences of *Leucoagaricus* species that exhibit a blue-green discolouration on handling/bruising, as well as sequences of representative species of the genus were incorporated. For broad comparisons, we also included 41 sequences from isolates of genera *Lepiota*, *Leucocoprinus*, and related species (as the outgroups) obtained in previous studies. The sequences used in this study are listed in TABLE 1. DNA sequences were edited and aligned with SeqMan (DNA STAR Package) (Burland 2000) and manually checked and modified. Single-gene alignment was made using the program MAFFT v7.130b (Katoh & Standley 2013), applying the L-INS-I strategy, and manually adjusted in BioEdit v.7.1.3.0 (Hall 1999), ambiguous positions were excluded from the matrix. Gaps were treated as missing data. Since no significant incongruence was detected between phylogenetic trees generated from the ITS and LSU data sets, the alignments of ITS and LSU were concatenated using Phyutility (Smith & Dunn 2008) and analyzed using Maximum Likelihood (ML) and Bayesian inference (BI). *Agaricus bisporus*, *A. campestris,* and *Chlorophyllum molybdites* were selected as outgroups.

ML analyses were performed using RAxML v7.2.6 (Stamatakis *et al.* 2008). A GTRGAMMAI model of evolution was assigned to the data set, and support values were assessed through 1000 rapid bootstrap replicates. The best-fit substitution model used in the Bayesian analysis was determined using the Akaike Information Criterion (AIC) implemented in MrModeltest v2.3 (Nylander 2004). Bayesian Inference (BI) analyses were performed using MrBayes v. 3.2 (Ronquist & Huelsenbeck 2003). Runs were automatically terminated when the average standard deviation of split frequencies fell below 0.01 and ESS values exceeded 200 (Ronquist & Huelsenbeck 2003). Other parameters were kept at their default settings. Tracer v1.5 (http://tree.bio.ed.ac.uk/software/tracer/) was used to assess the chain convergence. The trees were summarized, and posterior probabilities (PP) were obtained by discarding the first 25% of generations as burn-in. The resulting phylograms were displayed in FigTree 1.4.4 (Rambaut 2018).

TABLE 1. DNA sequences used for the phylogenetic analyses.

Taxa	Voucher	Location	GenBank accession numbers	
			ITS	LSU
Agaricus bisporus	RWK-1885	Denmark	AF432886[1]	AY635775[1]
A. campestris	VPI-OKM25665	USA	U85307[2]	U85273[2]
Chlorophyllum molybdites	DUKE-JJ162	USA	U85309[2]	U85274[2]
Lepiota boudieri	HKAS 5803	Jilin, China	EU416280[3]	EU416281[3]
L. brunneoincarnata	HMAS 63488	China	EU416302[3]	EU416303[3]
L. castanea	HKAS 48817	Yunnan, China	EU416282[3]	EU416283[3]
L. clypeolaria	HKAS 5217	Jilin, China	EU416284[3]	EU416285[3]
L. cortinarius	HKAS 46095	Tibet, China	EU416306[3]	EU416307[3]
L. cristata	HKAS 49258	Sichuan, China	EU081937[4]	EU416292[4]
L. cristatoides	Huijser-6116	Netherlands	AY176363[5]	AY176364[5]
L. felina	HKAS 5801	Jilin, China	EU416286[3]	EU416287[3]
L. magnispora	HKAS 8247	Jilin, China	EU416288[3]	EU416289[3]
L. pseudolilacea	HKAS 8288	Jilin, China	EU416304[3]	EU416305[3]
L. subgracilis	HKAS 5802	Jilin, China	EU416290[3]	EU416291[3]
Leucoagaricus albosquamosus	CFSZ 20662	Inner Mongolia, China	OM976879[10]	OM976865[10]
La. albosquamosus	CFSZ 22880	Inner Mongolia, China	OM976878[10]	OM976866[10]
La. amazonicus	HUA_Ortiz 58	Colombia	EU940371[6]	-
La. americanus	UC-ecv2454	USA	AY176407[5]	AF482891[5]
La. atroazureus	HKAS 48453	Hainan, China	EU416297[3]	EU416298[3]
La. atroazureus	HKAS 48450	Hainan, China	EU416299[3]	EU416300[3]
La. atroazureus	HKAS 42670	Yunnan, China	EU416301[3]	-
La. atroviridis	SYAU FUNGI 073	Liaoning, China	OM976852[10]	OM976868[10]
La. atroviridis	SYAU FUNGI 074	Liaoning, China	OM976853[10]	OM976869[10]
La. aurantioruber	CFSZ 19756	Inner Mongolia, China	OM976875[10]	OM976863[10]
La. aurantioruber	CFSZ 18372	Inner Mongolia, China	OM976874[10]	OM976862[10]
La. barssii	L-ecv2268	Netherlands	AF295930[3]	AF482894[5]
La. brunneocanus	HKAS 45457	Sichuan, China	KP096238[9]	-
La. candidus	CFSZ 20964	Inner Mongolia, China	OM976877[10]	OM976864[10]
La. candidus	CFSZ 11287	Inner Mongolia, China	OM976876[10]	OM976861[10]
La. centricastaneus	SYAU FUNGI 076	Liaoning, China	OM976855[10]	OM976871[10]
La. centricastaneus	SYAU FUNGI 075	Liaoning, China	OM976854[10]	OM976870[10]
La. cinerascens	WTU-pbm1830	Hawaii, USA	AY176410[5]	AY176411[5]
La. croceovelutinus	L-ecv2243	Netherlands	AF482862[5]	AF482889[5]
La. crystallifer	Huijser-19IX1998	Germany	AF482863[5]	AY176412[5]
La. pseudopilatianus	Guinberteau-99121300	Greece	AY243632[12]	-
La. flavovirens	HKAS 29580	Hainan, China	EU416293[3]	EU416294[3]
La. flavovirens	HKAS 50024	Yunnan, China	EU416295[3]	EU416296[3]
La. georginae	L-ecv2238	Netherlands	AY176413[5]	AY176414[5]
La. infuscatus	UC-ecv3298	USA	EU141943[7]	-
La. ionidicolor	L-ecv2280	Netherlands	AY176415[5]	AY176416[5]
La. irinellus	Chalange-97082101	France	AY243648[3]	-
La. jubilaei	Guinberteau-99101101	France	AY243635[3]	-

......*continued on the next page*

TABLE 1 (Continued**)**

Taxa	Voucher	Location	GenBank accession numbers	
			ITS	LSU
La. lacrymans	HKAS 52738	Guangdong, China	KY039574[13]	KY039579[13]
La. leucothites	L-ecv2050	Netherlands	AF482865[8]	-
La. marriagei	L-ecv2005	Netherlands	AF482866[8]	-
La. melanotrichus	L-ecv2262	Netherlands	AY176417[8]	AY176418[8]
La. meleagris	L-ecv1990	Netherlands	AY176419[8]	AF482890[8]
La. naucinus	HMAS 88854	Beijing, China	EU416308[3]	EU416309[3]
La. nivalis	HKAS 82691	Yunnan, China	KY039573[13]	KY039578[13]
La. nympharum	HMAS 99343	Tibet, China	EU416310[3]	EU416311[3]
La. ophthalmus	UC-ecv2716	California, USA	EU141954[7]	-
La. orientiflavus	HKAS 54260	China	GU084262[14]	JN940290[14]
La. paraplesius	UC-ecv3276	California, USA	EU141946[7]	-
La. pilatianus	Guinberteau-99101608	France	AY243626[3]	-
La. purpurascens	**HKAS 123023**	**Shanghai, China**	**OM987458**	**OM987455**
La. purpurascens	**HKAS 123024**	**Shanghai, China**	**OM987459**	**OM987456**
La. purpurascens	**HKAS 123025**	**Shanghai, China**	**OM987460**	**OM987457**
La. purpureolilacinus	L-ecv2291	Netherlands	AF482869[5]	-
La. serenus	Bizzi369/98	Italy	AY176420[5]	-
La. serenus	L-ecv1930	Belgium	-	AY176421[5]
La. sericatellus	L-cb8842	Netherlands	AY176424[5]	AY176425[5]
La. sericifer	L-ecv2116	Netherlands	AY176426[5]	AY176427[5]
La. sinicus	HMAS 60647	Zhejiang, China	DQ182505[13]	NG_027568[13]
La. subcrystallifer	HKAS 49373	Sichuan, China	NR_155320[9]	-
La. sublittoralis	L-ecv2235	Netherlands	AY176442[5]	AY176443[5]
La. subpurpureolilacinus	HKAS 48285	Sichuan, China	NR_155318[9]	-
La. tangerinus	HKAS 50036	Yunnan, China	KF501437[11]	-
La. tener	L-ecv2261	Netherlands	AY176444[5]	AY176445[5]
La. truncatus	HKAS 49288	Sichuan, China	NR_155319[9]	-
La. virens	CFSZ 19869	Inner Mongolia, China	OM976881[10]	-
La. virens	CFSZ 19794	Inner Mongolia, China	OM976880[10]	OM976867[10]
La. viridiflavus	AK80a	India	GU574745[3]	-
La. viriditinctus	HKAS 50033	Yunnan, China	EU419375[3]	EU419376[3]
La. viriditinctus	L0627034	Indonesia	AF482873[8]	-
La. wychanskyi	L-hah1998	Netherlands	AF482874[5]	-
Lc. birnbaumii	NY-EFM549	United Kingdom	U85323[2]	U85288[2]
Lc. brebissonii	L-ecv1784	France	AF482859[5]	AY176446[5]
Lc. cepistipes	NY-EFM518	United Kingdom	U85321[2]	U85286[2]
Lc. cretaceus	C-TL6171	Malaysia	AY176447[5]	-
Lc. cretaceus	L-je9IX1997	Netherlands	-	AY176448[5]
Lc. cf. *fragilissimus*	PA250	Panama	AF079738[1]	-
Lc. cf. *zamurensis*	PA415	Panama	AF079753[1]	AF079671[1]

GenBank accession numbers of sequences obtained in this study are in bold face. Sequences obtained from GenBank: [1](Callac & Guinberteau 2005), [2](Johnson 1999), [3](Liang *et al.* 2010), [4](Liang *et al.* 2009), [5](Vellinga 2004), [6](Ortiz *et al.* 2008), [7](Vellinga 2007), [8](Vellinga *et al.* 2003), [9](Ge *et al.* 2015), [10](Ma *et al.* 2022), [11](Yuan *et al.* 2014), [12](Forin *et al.* 2022), [13](Yang & Ge 2017), [14](Ge 2010).

Results

Molecular phylogeny of the datasets

We assembled a combined dataset of ITS and LSU sequences for 78 taxa. The dataset included 1774 nucleotide sites. Phylogenetic trees generated from ML and BI analyses were similar in topology and statistical support values. Therefore, only the tree inferred from the ML analysis is presented (FIGURE 1). The samples collected in this study formed an independent lineage in the trees.

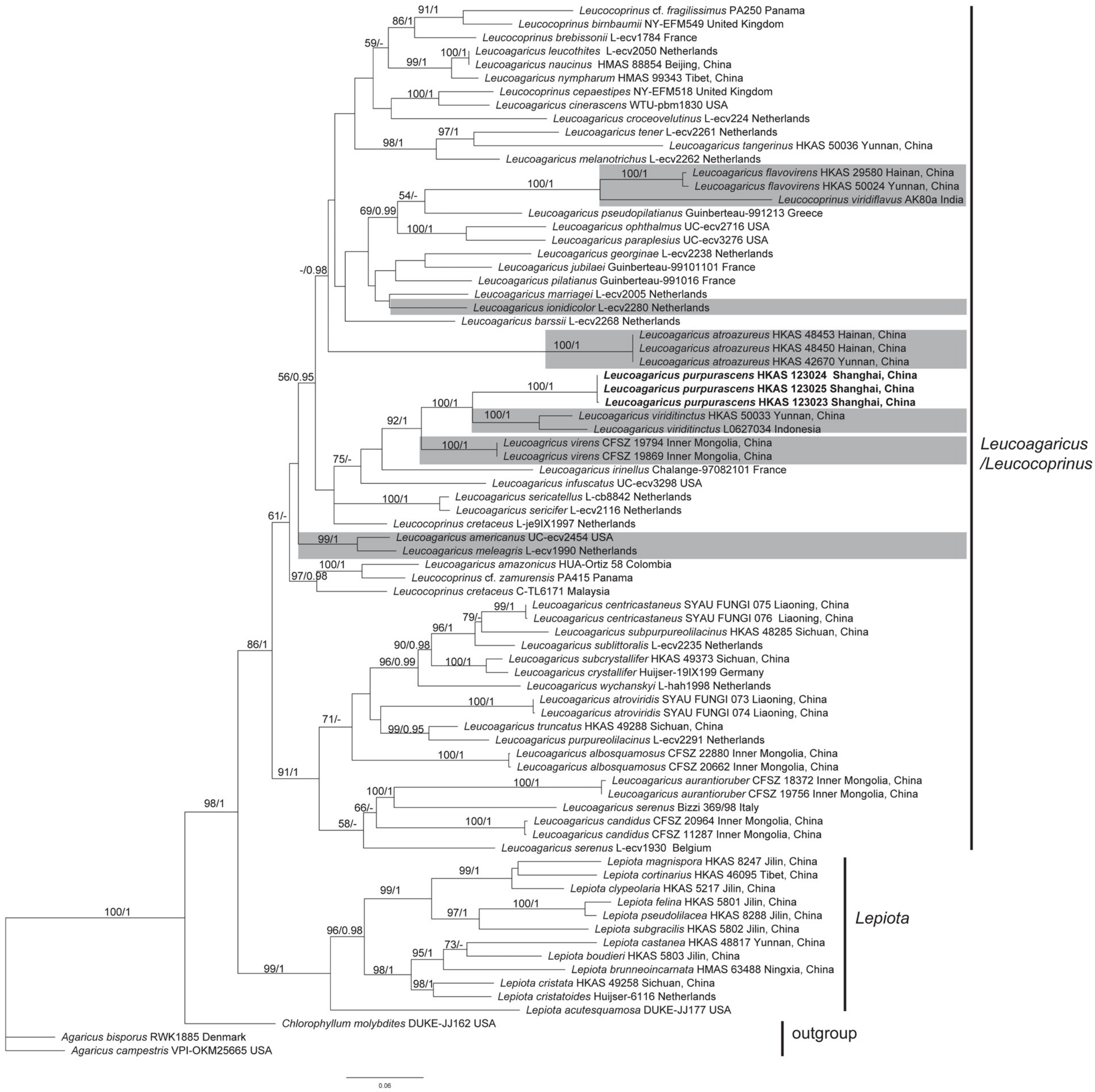

FIGURE 1. Maximum likelihood phylogenetic tree of *Leucoagaricus* inferred from the combined ITS-LSU data set. Bootstrap values >50% for ML and PP >0.95 for BI are shown along the branches. The new species is shown in boldface. The species that change colour on drying or brushing are denoted by the gray boxes.

Taxonomy

Leucoagaricus purpurascens T. Guo & Z. W. Ge, *sp. nov.* FIGURES. 2–3
MycoBank:—MB 845096

Etymology:—"*purpurascens*" means becoming purple, referring to the basidiomata turning purple upon drying.

Diagnosis: Similar to *Leucoagaricus viriditinctus* but differs in the purple changes of basidiomata when dried, larger basidiospores, and the absence of cheilocystidia.

FIGURE 2. Basidiomata of *Leucoagaricus purpurascens*. a. Basidiomata (HKAS 123023, holotype!). b. Dried specimens (HKAS 123023). Bars = 1 cm.

Holotype:—CHINA. Shanghai: Sheshan National Forest Park, on the ground in an evergreen broad-leaved forest, elev. 40 m, 22 September 2020, *T. Guo 2137* (HKAS 123023!). GenBank: ITS = OM987458; LSU = OM987455.

Description:—Basidiomata (FIGURE 2). *Pileus* 1–2.5 cm diam, when young campanulate, expanding to plano-convex to applanate, umbonate; center light brownish (7C3) to dark brown-red (8E4), elsewhere with light brownish squamules on the whitish (9A1) background; *Context* thin, whitish (9A1); discolours purplish (16B2) to purple (16A4) on drying. *Lamellae* free, whitish to creamy (6A2), crowded, with lamellulae in 1–2 tiers, edge even; discolours purplish (16B2) to purple (16A4) on drying. *Stipe* 2.5–5 × 0.1–0.2 cm, whitish (9A1), slightly attenuate upwards, sometimes slightly curved at the base, smooth, hollow, not brittle; stipe context white; *Annulus* present, sometimes disappearing, with light brownish (6C5) superior edge, membranous. *Odor* none. *Taste* not recorded.

Basidiospores (FIGURE 3) [71/3/3] 8.0–10.0 (10.5) × (4.0) 4.5–6.0 µm (mean 9.2 ± 0.7 × 5.1 ± 0.5 µm), Q = (1.5) 1.6–2.0, Q_{av} = 1.79 ± 0.15, amygdaliform, (sometimes ellipsoidal to oblong) in side view, ovoid in front view, hyaline, smooth, slightly thick-walled (about 0.5 µm), dextrinoid, without germ pore, metachromatic in Cresyl Blue. *Basidia* (24.0) 24.5–31.0 (32.0) × (9.0) 9.5–10.5 (11.0) µm, clavate, four-spored; sterigmata up to 3 µm. *Cheilocystidia and pleurocystidia* not observed. *Lamella trama* subregular, made up of slightly inflated subcylindrical hyphae, hyaline, thin-walled. *Pileus covering* a cutis with radially arranged and sometimes branched repent hyphae, subcylindrical, 7.5–12.5 µm diam, occasionally with brownish yellow pigments on the hyphal wall and in vacuoles. *Stipe covering* a cutis made up of cylindrical hyphae and elements, colourless, (4) 7–10 µm wide. *Clamp connections* not observed.

Habitat and distribution:—Gregarious or scattered in the subtropical evergreen broad-leaved forest; currently only known from the type locality.

Additional specimens examined:—CHINA. Shanghai City, Sheshan National Forest Park, on the roadside in a subtropical evergreen broad-leaved forest, elev. 35 m, 4 August 2021, *T. Guo 2323* (HKAS 123024); same locality, 4 August 2021, *T. Guo 2324* (HKAS 123025).

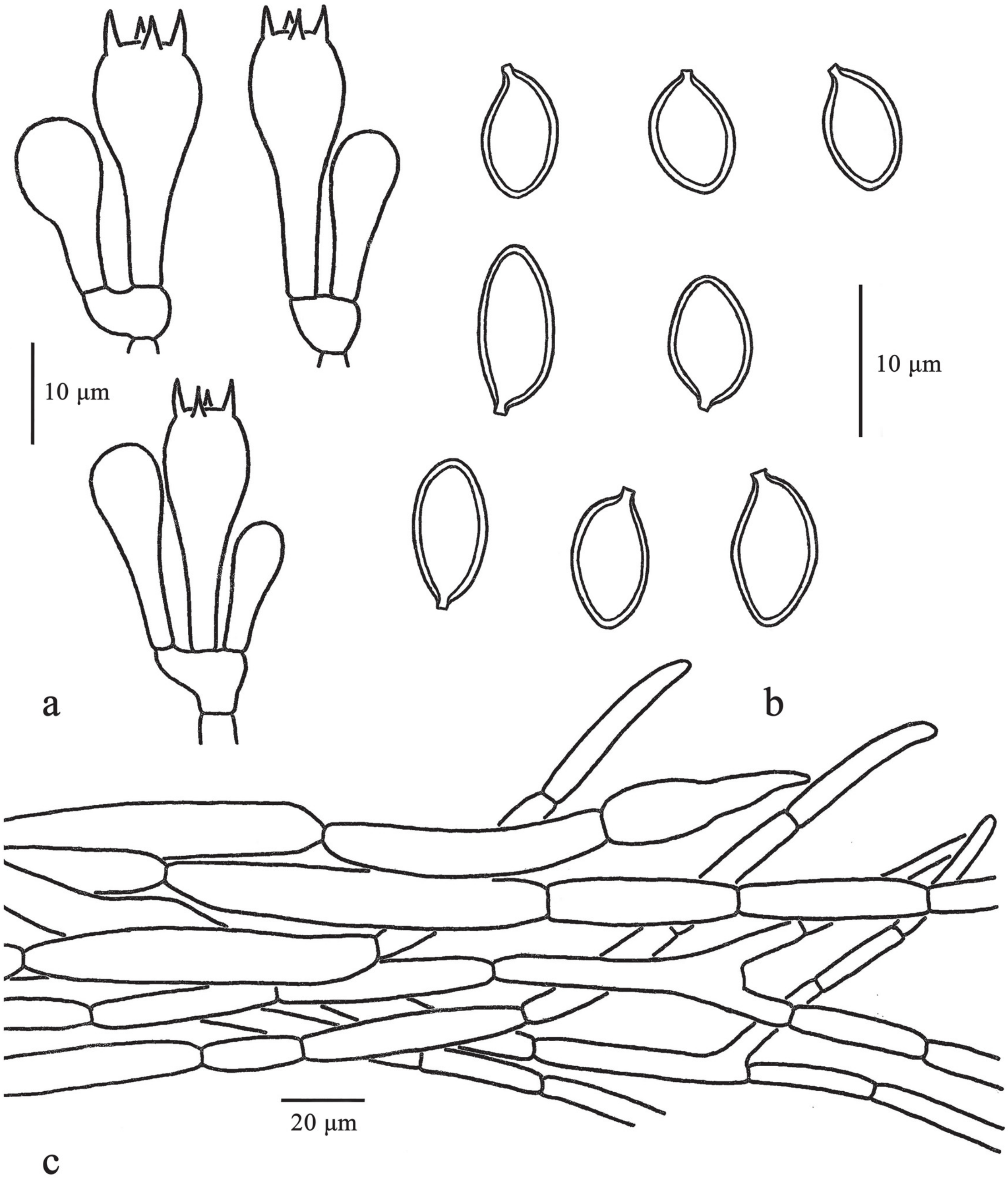

FIGURE 3. Microscopic characteristics of *Leucaoagricus purpurascens* (HKAS 123023, holotype). a. Basidia; b. Basidiospores; c. Pileipellis.

Discussion

The species newly described in this study, *La. purpurascens*, is characterized by the purple changes of basidiomata when dried, its umbonate pileus covered with light brownish squamules, absence of cheilocystidia, and the relatively larger basidiospores (FIGURES 2–3). Phylogenetic evidence also suggests that *La. purpurascens* differs from its close relatives (FIGURE 1).

Cheilocystidia are typically present in species of *Leucoagaricus*. However, it is reported that broadly clavate to pyriform cheilocystidia were observed in some collections of *La. vinditinctus,* although no cheilocystidia were observed from its type specimen (Liang *et al.* 2010). In the present study, repeated observations of the lamella edges of *La. purpurascens* collections only found narrowly clavate to clavate cells (19.0–27.0 × 6.0–8.5 [10.0] µm) intermixed with mature basidia. These narrowly clavate to clavate cells are smaller than basidia (24.5–31.0 × 9.5–10.5 µm), suggesting these narrowly clavate to clavate cells are young basidia instead of cheilocystidia and indicating the absence of cheilocystidia of this species.

In the phylogram (FIGURE 1), *La. purpurascens* is sister to *La. viriditinctus*. These two jointly form a sister clade with *La. virens* Y. R. Ma, Z. W. Ge & T. Z. Liu. However, *La. viriditinctus* differs from *La. purpurascens* by presenting dark blue changes of basidiomata when bruised or dried, smaller basidiospores (7.0–8.5 × 4.0–5.0 μm), and having broadly clavate to pyriform cheilocystidia and mainly from tropical regions (Liang *et al.* 2010; Retnowati 2015), while *La. virens*, described from a temperate region, differs from *La. purpurascens* in having clavate to broadly clavate cheilocystida, and presenting dark green to light green reaction when the basidiomata were bruised or dried (Ma *et al.* 2022).

Morphologically, *La. purpurascens* also resembles *La. atrosquamulosus* (Hongo) Z. W. Ge & Zhu L. Yang (Yang & Ge 2017). However, *La. atrosquamulosus* can be distinguished from *La*. *purpurascens* by its larger basidiomata, blackish brown squamules on the pileus, the presence of cheilocystida and smaller basidiospores (5–7 × 3.5–4 μm). Several other *Leucoagaricus* and *Leucocoprinus* species with bruising reactions exist in China, viz. *La*. *atroazureus*, *La*. *flavovirens* J. F. Liang, Zhu L. Yang & J. Xu, *La*. *virens* Y. R. Ma, Z. W. Ge & T. Z. Liu, and *Lc. viridiflavus* (Petch) E. Ludw. However, these species display blue or green reactions and have cheilocystidia (Ge *et al.* 2019; Ma *et al.* 2022). *Leucoagaricus purpureoruber* also stains purple on drying, but it has larger basidiomata, clavate to fusiform cheilocystidia and basidiospores with an apical germ pore (Yang & Ge 2017).

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