

Article

Six New Species of *Leucoagaricus* (Agaricaceae) from Northeastern China

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Abstract: Six new species, *Leucoagaricus albosquamosus*, *Leucoagaricus atroviridis*, *Leucoagaricus aurantioruber*, *Leucoagaricus candidus*, *Leucoagaricus centricastaneus* and *Leucoagaricus virens*, collected from northeastern China are described based on morphological characters and molecular evidence. Illustrations of fresh basidiomata and line drawings of key anatomical characters are provided. A phylogenetic tree inferred from internal transcribed spacer (ITS) region and large subunit ribosomal RNA gene (LSU) sequences shows that three of the new taxa are nested within the section *Leucoagaricus* and two of the new taxa are in the subgenus *Sericeomyces*, whereas the other new taxus is clustered with *Leucoagaricus viriditinctus* and *Leucoagaricus irinellus*, forming a clade that does not fit in any known section.



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Keywords: Agaricaceae; phylogeny; six new taxa; taxonomy

1. Introduction

Leucoagaricus Locq. ex Singer is widely distributed [1] and contains approximately 135 species [2], with more tropical species than temperate species [3]. As *Leucoagaricus barsii* (Zeller) Vellinga was an invalid name when Singer designated it as the type species of *Leucoagaricus*, Redhead designated *Leucoagaricus rubrotinctus* (Peck) Singer as the lectotype for this genus instead [4].

Members of *Leucoagaricus* have the following morphological characters: basidiomata slender and fragile to stout fleshy, a smooth or scaly pileal surface with or without an indistinct radiate fringe at the margin, free lamellae, simple annulus, dextrinoid and metachromatic basidiospores, with cheilocystidia, and hyphae without clamp connections [5,6].

Molecular phylogenetic studies show that *Leucoagaricus* is not monophyletic, as species within it are intermixed with those of *Leucocoprinus* Pat. and *Micropsalliota* Höhn. [7–10]. Morphologically, *Leucoagaricus* differs from *Leucocoprinus* in that the pileus of *Leucocoprinus* has obvious striations, and its hymenium has pseudoparaphyses [5]. However, phylogenetic relationships of some species in *Leucoagaricus* and *Leucocoprinus* remain unclear due to a lack of extensive morphological and molecular data [9–11].

Based on morphological observations and molecular phylogenetic analyses, in this study, we describe six new species of *Leucoagaricus* from China.

2. Materials and Methods

2.1. Morphological Studies

Specimens studied were deposited in the Mycological Herbarium of the Chifeng University, Inner Mongolia, China (CFSZ), the Fungal Herbarium of Shenyang Agricultural University (SYAU-FUNGI) and the Herbarium of Cryptogams, Kunming Institute of Botany, Chinese Academy of Sciences (KUN, with HKAS accession numbers) (Table 1). Macroscopic character descriptions were based on fresh material. Color annotations were performed following the procedure of Kornerup and Wanscher [12]. For microscopic observations, sections of specimens were cut and mounted in 5% KOH, then stained with 1% Congo Red reagent. Melzer's reagent was used to test the amyloidity of spores, and Cresyl Blue was used to test for a metachromatic reaction [5,13]. The abbreviation [n/m/p] means n basidiospores were measured from m basidiomata of p specimens. Dimensions for basidiospores are given using (a) b–c (d). The b–c range contains at least 90% of the measured values, and (a) and (d) represent the extreme values whenever present. Q indicates the length/width ratio of a spore in side view, and Q_m stands for the mean value of all basidiospores \pm standard deviation of the samples.

2.2. Molecular Phylogenetics

2.2.1. DNA Extraction, PCR and Sequencing

Total DNA was extracted from dried basidiomata by CTAB method [14]. The phylogenetic tree was reconstructed using internal transcribed spacer (ITS) and large subunit ribosomal RNA gene (LSU) markers [15–17]. Polymerase chain reaction (PCR) was implemented on an ABI 2720 thermal cycler (Applied Biosystems, Foster City, CA, USA). PCR amplification and sequencing procedure followed procedures described in [18]. Specifically, each PCR reaction mixture contained of 1 μ L (25 mmol/L) of each primer, 1 μ L DNA template, 12.5 μ L Biotaq master mix (BioTeke, Beijing, China) and ddH₂O up to 25 μ L. The PCR program was set as follows: pre-denaturation at 95 °C for 5 min; 32 cycles of denaturation at 95 °C for 50 s, annealing at appropriate temperature and time (ITS 52 °C and LSU 50 °C) and extension at 72 °C for 1 min, followed by a final extension at 72 °C for 8 min. The PCR products were purified using a PCR purification combo kit (BioTeke, Beijing, China) and sequenced on an ABI-3730-XL DNA analyzer (Applied Biological Systems, Foster City, CA, USA) using the same primers. The consensus sequences were obtained from forward and reverse primers using SeqMan v. 7.1.0 (DNASTAR, Madison, WI, USA).

2.2.2. Sequence Alignment and Phylogenetic Analyses

Preliminary analysis based on extensive representatives of *Leucoagaricus* and *Leucocoprinus* indicated that the putative new taxa are closely related to taxa in section *Leucoagaricus* and subgenus *Sericeomyces*. Thus, we built the data matrix by incorporating the newly generated sequences with sequences of taxa belonging to the section *Leucoagaricus* and subgenus *Sericeomyces*, as indicated by previous studies [10,11,19–21], along with sequences of representative taxa in other *Leucoagaricus* sections, as well as sequences from representatives of *Leucocoprinus* Pat. and *Micropsalliota* Höhn. *Cystolepiota seminuda* (Lasch) Bon and *Cystolepiota* aff. *seminuda* were designated as outgroup taxa. The sequences were aligned using MAFFT v7.453 [22] and inspected and manually corrected using BioEdit v7.0.9 [23]. TrimAl v.1.4.rev15 [24] was used to remove sites that vaguely aligned. MrModeltest v2.3 [25] predicted that GTR+GAMMA+I was the best model for nucleotide substitution under the Akaike information criterion (AIC). The phylogenetic tree was reconstructed using the Maximum likelihood (ML) and Bayesian inference (BI) methods of RAxML 7.2.6 [26] and MrBayes 3.2.3 [27].

The phylogenetic trees of ITS and LSU were reconstructed, and no potential topology conflicts were found. Thus, phylogenetic analysis was then performed based on the concatenated ITS-LSU dataset using PhyloSuite [28]. For ML analyses, statistical support was calculated with 1000 bootstrap replicates. For BI analyses, we used the GTR+G+I model, and three chains were run for 10 million generations, sampling trees every 100 generations.

The convergence of the chain was determined using Tracer v1.5 (<http://tree.bio.ed.ac.uk/software/tracer/>), accessed on 11 March 2022) to ensure large effective sample size (ESS) values (>200). The resulting phylograms were displayed in FigTree 1.4.3 [29].

Table 1. Sequences of *Leucoagaricus* newly generated in this study; sequences generated from new species are shown in bold.

| Species | Voucher | GenBank Accession No. | |
|--|---------------------------------|-----------------------|-----------------|
| | | ITS | LSU |
| <i>Leucoagaricus albosquamosus</i> | CFSZ 20662, Holotype | OM976879 | OM976865 |
| <i>Leucoagaricus albosquamosus</i> | CFSZ 22880 | OM976878 | OM976866 |
| <i>Leucoagaricus</i> aff. <i>serenus</i> | HKAS 123090 | OM974302 | OM967221 |
| <i>Leucoagaricus atroviridis</i> | SYAU FUNGI 073, Holotype | OM976852 | OM976868 |
| <i>Leucoagaricus atroviridis</i> | SYAU FUNGI 074 | OM976853 | OM976869 |
| <i>Leucoagaricus aurantioruber</i> | CFSZ 19756, Holotype | OM976875 | OM976863 |
| <i>Leucoagaricus aurantioruber</i> | CFSZ 18372 | OM976874 | OM976862 |
| <i>Leucoagaricus barssii</i> | J. L. Yuan2 | OM974315 | OM967227 |
| <i>Leucoagaricus candidus</i> | CFSZ 20964, Holotype | OM976877 | OM976864 |
| <i>Leucoagaricus candidus</i> | CFSZ 11287 | OM976876 | OM976861 |
| <i>Leucoagaricus centricastaneus</i> | SYAU FUNGI 076, Holotype | OM976855 | OM976871 |
| <i>Leucoagaricus centricastaneus</i> | SYAU FUNGI 075 | OM976854 | OM976870 |
| <i>Leucoagaricus</i> cf. <i>atroazureus</i> | HKAS 123037 | OM974300 | OM967223 |
| <i>Leucoagaricus</i> cf. <i>cinerascens</i> | HKAS 123026 | OM974299 | OM967235 |
| <i>Leucoagaricus</i> cf. <i>dacrytus</i> | HKAS 114897 | OM974301 | OM967219 |
| <i>Leucoagaricus</i> cf. <i>rubrotinctus</i> | HKAS 123038 | OM974306 | OM967224 |
| <i>Leucoagaricus nivalis</i> | HKAS 123041 | OM974308 | OM967225 |
| <i>Leucoagaricus nympharum</i> | HKAS 121785 | OM974312 | OM967233 |
| <i>Leucoagaricus nympharum</i> | HKAS 121801 | OM974311 | OM967234 |
| <i>Leucoagaricus</i> sp. 1 | HKAS 116020 | OM974305 | OM967231 |
| <i>Leucoagaricus</i> sp. 1 | HKAS 123029 | OM974309 | OM967229 |
| <i>Leucoagaricus</i> sp. 2 | HKAS 123028 | OM974313 | OM967228 |
| <i>Leucoagaricus</i> sp. 3 | HKAS 105542 | OM974304 | OM967222 |
| <i>Leucoagaricus</i> sp. 4 | HKAS 123030 | OM974310 | OM967230 |
| <i>Leucoagaricus</i> sp. 6 | HKAS 116134 | OM974307 | OM967232 |
| <i>Leucoagaricus</i> sp. 7 | HKAS 123031 | OM974303 | OM967226 |
| <i>Leucoagaricus</i> sp. 10 | HKAS 123088 | OM974298 | OM967236 |
| <i>Leucoagaricus</i> sp. 11 | HKAS 123089 | — | OM967218 |
| <i>Leucoagaricus subpurpureolilacinus</i> | HKAS 123027 | OM974314 | OM967227 |
| <i>Leucoagaricus virens</i> | CFSZ 19869, Holotype | OM976881 | — |
| <i>Leucoagaricus virens</i> | CFSZ 19794-2 | OM976880 | OM976867 |

Based on the phylogenetic analyses of the combined dataset, the genera *Leucoagaricus*, *Leucocoprinus* and *Micropsalliota* together form a monophyletic clade (BS = 100%, PP = 1.0), consistent with the results of previous studies [10,11,19–21]. However, members of the /leucoagaricus clade (*Leucoagaricus* sensu stricto) and /sericeomyces clade (with the type species of Subgen. *Sericeomyces* nested within) do not mix with members of *Leucocoprinus* or *Micropsalliota* (Figure 1). Together, the /leucoagaricus clade and the /sericeomyces clade form a strongly supported monophyletic clade (BS = 91%, PP = 0.95). Among the five new species, *Leucoagaricus albosquamosus*, *Leucoagaricus atroviridis* and *Leucoagaricus centricastaneus* are nested within the /leucoagaricus clade, and each species had strong bootstrap supports on its own (both BS = 100%, PP = 1.0). *Leucoagaricus aurantioruber* and *Leucoagaricus candidus* are nested in the /sericeomyces clade (Figure 1), in which *Leucoagaricus aurantioruber* formed a distinct clade (BS = 100%, PP = 1.0) sister to *Leucoagaricus rubrobrunneus*, whereas the two collections of *Leucoagaricus candidus* were clustered together with strong bootstrap supports (BS = 100%, PP = 1.0), forming a clade close to an unidentified *Leucoagaricus* species from Italy. The other species, *Leucoagaricus virens*, represented by two collections that clustered together with strong bootstrap supports (BS = 100%, PP = 1.0), is close to *Leucoagaricus viriditinctus* (Berk. & Broome) J.F. Liang, Zhu L. Yang & J. Xu and *Leucoagaricus irinellus* Chalange, forming a clade that does not fit in any known section (Figure 1).

3.2. Taxonomy

Leucoagaricus albosquamosus Y.R. Ma, Z. W. Ge & T.Z. Liu, sp. nov. Figures 2 and 3.

MycoBank: MB 843377

Etymology: from *albo-*(Latin) “white” + “*squamosus*”, as the basidiomata are covered with whitish squamules.

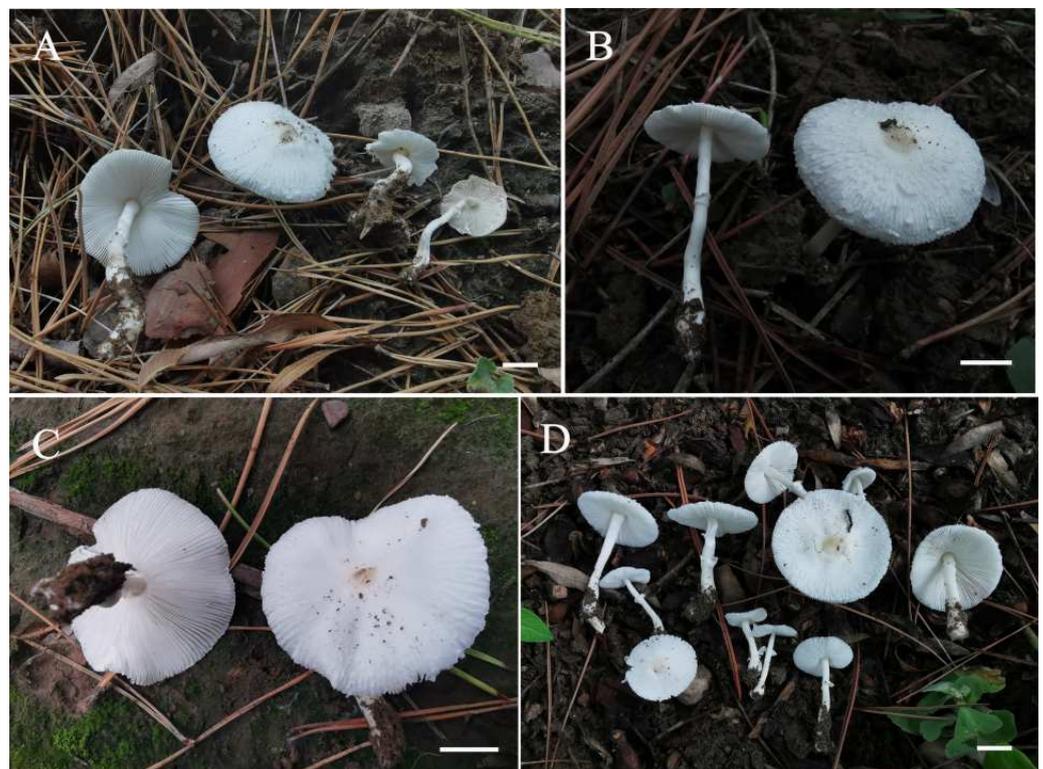


Figure 2. Basidiomata of *Leucoagaricus albosquamosus*. (A,B): CFSZ 20662; (C): CFSZ 22880; (D): CFSZ 22890). Scale bars: 1 cm.

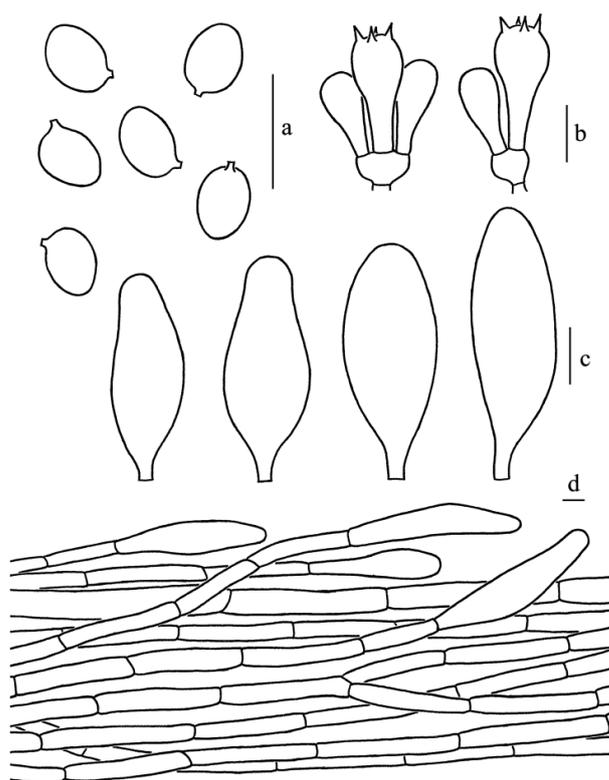


Figure 3. *Leucoagaricus albosquamosus* (CFSZ20662). (a) Basidiospores. (b) Basidia. (c) Cheilocystidia. (d) Elements of pileus squamules. Scale bars: 10 μm .

Diagnosis: *Leucoagaricus albosquamosus* is characterized by its white and somewhat plicate pileus with light brownish center, whitish squamules, broadly ellipsoid to ellipsoid basidiospores, subclavate to subfusiform cheilocystidia and squamules on the pileus composed of hyaline, septate cylindrical hyphae measuring 6–13.5 μm in diameter.

Type: CHINA. Inner Mongolia Autonomous Region: Xibo River Green Belt, Songshan District, Chifeng City, China, 12 August 2019, T.Z. Liu (CFSZ 20662, holotype).
GenBank Acc. No.: ITS = OM976879, LSU = OM976865

Description: Pileus 19–36 mm in diameter; center light brownish (3B3–3B4); somewhat plicate; surface, white (1A1); squamules, white (1A1) to whitish, slightly upturned when mature. Context, white (1A1); no change in color upon bruising. Lamellae, white (1A1), free, crowded, 2–4 mm broad, with lamellulae in 1–2 tiers, with entire edges. Stipe 34–46 \times 3–5 mm, white (1A1), subcylindric, hollow, nearly smooth. Annulus, white (1A1), simple, membranous, located in the middle to upper part of the stipe. Flavor and odor not recorded. Spore print, white.

Basidiospores [65/14/3], 5.0–6.5(7.0) \times 4.0–5.0(5.5) μm , $Q = (1.11)1.22\text{--}1.44(1.50)$, $Q_m = 1.31 \pm 0.08$, broadly ellipsoid to ellipsoid from side view and front view, hyaline, without germ pore, slightly thick-walled (about 0.5 μm), dextrinoid, metachromatic. Basidia, 19.0–23.0 \times 8.5–9.5 μm , clavate, hyaline, thin-walled, four-spored, rarely two-spored; sterigmata, 2.5 μm long. Cheilocystidia, 35.0–47.0 \times 12.5–19.0 μm , subclavate to subfusiform, hyaline. Pleurocystidia, absent. Lamellar trama, trabecular. Squamules on the pileus composed of septate cylindrical hyphae 6–13.5 μm in diameter, hyaline. Stipitipellis composed of hyaline, cylindrical hyphae, 5.0–12.0 μm in diameter. Clamp connections absent in all parts of the basidiomata.

Habitat and Habit: scattered on soil in summer. So far, known only known in Chifeng, Inner Mongolia Autonomous Region.

Other specimens examined: CHINA. Inner Mongolia Autonomous Region: Xibo River Green Belt, Songshan District, Chifeng City, China, 18 August 2020, T.Z. Liu (CFSZ

22880). Inner Mongolia Autonomous Region: Stone park, Songshan District, Chifeng City, 19 August 2020, T.Z. Liu (CFSZ 22890).

Comments: The somewhat plicate pileus of *La. albosquamosus* may suggest that this species be placed in *Leucocoprinus*. Considering *La. albosquamosus* is nested within a strongly supported clade that corresponds to section *Leucoagaricus*, we placed this species within *Leucoagaricus* rather than *Leucocoprinus*. According to phylogenetic analysis (Figure 1), *Leucoagaricus albosquamosus* is a sister taxon to *Leucoagaricus nivalis* (W.F. Chiu) Z. W. Ge & Zhu L. Yang. Together, these two taxa form a sister clade to a clade jointly formed by *Leucoagaricus umbonatus* S. Hussain, H. Ahmad & Afshan and an undescribed species of *Leucoagaricus* [19,30,31].

Leucoagaricus nivalis, originally described in Yunnan, southwestern China, resembles *La. albosquamosus* in its overall white, small basidiomata and subclavate cheilocystidia. However, *La. nivalis* is a white species with narrower amygdaliform basidiospores measuring $6.0\text{--}7.5(9.0) \times (3.0)3.5\text{--}4.5(5.0) \mu\text{m}$ and glabrous to radially fibrillose white pileus [31].

Leucoagaricus umbonatus, a white species originally described in Pakistan, is similar to *La. albosquamosus* in the similarly bulbous stipe base, similarly shaped basidiospores and similarly sized clavate basidia. However, *La. umbonatus* has smaller ventricose to fusiform cheilocystidia ($24\text{--}29 \times 8\text{--}12 \mu\text{m}$) and cutis of radially arranged white fibrils [19].

Leucoagaricus sericifer (Locq.) Vellinga is also similar to *La. albosquamosus* in its white pileus and the shape of the basidiospores. However, *La. sericifer* has oblong amygdaliform to cylindrical amygdaliform basidiospores, as well as more or less lageniform cheilocystidia [6]. Considering the somewhat plicate pileus with squamules, *La. albosquamosus* is somewhat similar to *Leucocoprinus cepistipes* (Sowerby) Pat. However, *Leucocoprinus cepistipes* has small beige–brown to ochraceous brown squamules and lageniform to clavate cheilocystidia, often with apical excrescence [6].

Leucoagaricus atroviridis Y.R. Ma, Z. W. Ge & X.D. Yu, sp. nov. Figures 4 and 5.

Mycobank: MB 843382

Etymology: *atroviridis* (Latin) refers to the bottle-green to dark brown radially fibrillose squamules on the pileus.

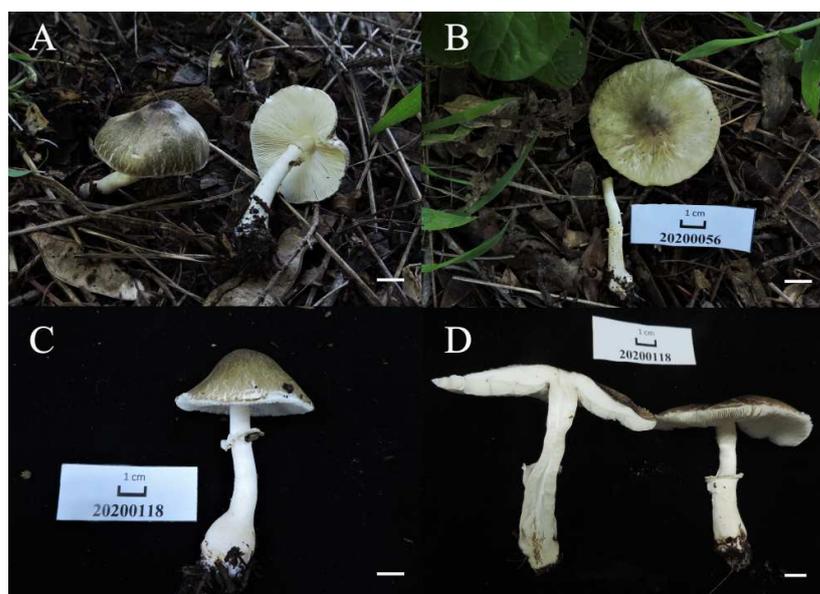


Figure 4. Basidiomata of *Leucoagaricus atroviridis*. (A,B) SYAU FUNGI 073; (C,D) SYAU FUNGI 074. Scale bars: 1 cm.

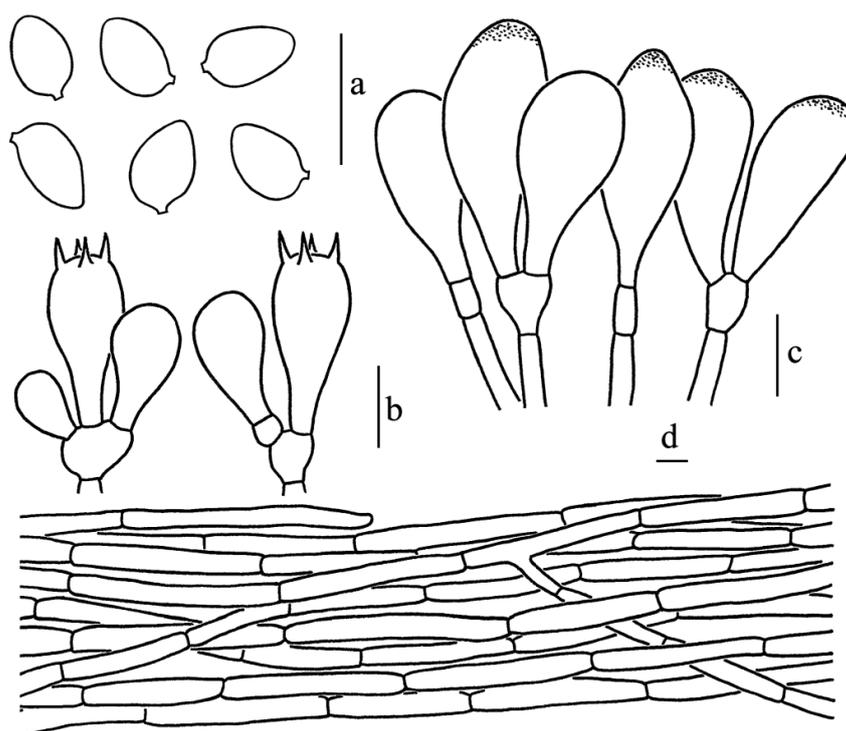


Figure 5. *Leucoagaricus atroviridis* (SYAU FUNGI 073). (a) Basidiospores. (b) Basidia. (c) Cheilocystidia. (d) Elements of pileus squamules. Scale bars: 10 μ m.

Diagnosis: *Leucoagaricus atroviridis* is characterized by bottle-green to dark brown, fibrillose squamules, and broadly clavate cheilocystidia with obvious refractive contents.

Type: CHINA. Liaoning Province: Shenyang, Shenyang Agricultural University, August 2020, X.D. Yu (SYAU FUNGI 073, holotype).

GenBank Acc. No.: ITS = OM976852, LSU = OM976868

Description: Pileus 48–114 mm in diameter, covered with bottle-green (1E7) to dark brown (2F6) radially fibrillose squamules, umbonate. Context, white (1A1), up to 4 mm thick at center, no change in color when bruised. Lamellae-free, crowded, white (1A1), edge finely scalloped. Stipe, 69–73 \times 6–10 mm, white (1A1), smooth, hollow, subcylindrical or attenuate upwards with bulbous base up to 13–16 mm wide. Annulus, white (1A1), located at the middle to upper part of the stipe. Flavor and odor not recorded. Spore print not recorded.

Basidiospores [60/3/2], 5.5–7.0(7.5) \times 4.0–5.0 μ m, $Q = (1.10)1.22\text{--}1.50(1.63)$, $Q_m = 1.36 \pm 0.11$, ellipsoid to ovoid from side view and front view, without germ pore, hyaline, smooth, slightly thick-walled (about 0.5 μ m); dextrinoid, metachromatic. Basidia, 17.0–28.0 \times 7.5–10.0 μ m, clavate, hyaline, four-spored, rarely two-spored; sterigmata, 3.5 μ m long. Cheilocystidia, 21.5–33.5 \times 9.5–15.5 μ m, hyaline, broadly-clavate to broadly fusiform, thin-walled. Some cheilocystidia with obvious refractive contents on the apex. Pleurocystidia absent. Lamellar trama, subregular. Pileus squamules composed of 5.0–8.5 μ m wide subcylindrical repent hyphae with light greenish (30B5) to light brownish (3B3) intracellular pigments. Stipitipellis composed of cylindrical to slightly inflated hyphae, 5.0–11.0 μ m in diameter, hyaline. Clamp connections absent in all parts of the basidiomata.

Habitat and Habit: solitary in grass in summer. So far, known only in Shenyang, Liaoning Province in northeastern China.

Other specimens examined: CHINA. Liaoning Province: Shenyang, Shenyang Agricultural University, August 2020, X.D. Yu (SYAU FUNGI 074).

Comments: Macroscopically, *Leucoagaricus atroviridis* is characterized by medium to large basidiomata, stipe with a bulbous base and bottle-green to dark brown fibrils.

Phylogenetically, *Leucoagaricus atroviridis* is close to *Leucoagaricus truncatus* Z. W. Ge & Zhu L. Yang and *Leucoagaricus purpureolilacinus* Huijsman (Figure 1). However, *La. purpureolilacinus*, originally described in the Netherlands, has a purplish brown pileus and clavate to subfusiform cheilocystidia [6]. *La. truncatus*, originally described in Sichuan, southwestern China, differs in having a truncated pileus with orange–white to gray–orange squamules and larger basidiospores [11].

Leucoagaricus aurantioruber Y.R. Ma, Z. W. Ge & T.Z. Liu, sp. nov. Figures 6 and 7.

MycoBank: MB 843381

Etymology: *aurantia* (Latin) = orange; *ruber* (Latin) = red, referring to the orange–reddish pileus.



Figure 6. Basidiomata of *Leucoagaricus aurantioruber*. (A,B) CFSZ 18372; (C–E) CFSZ 19756). Scale bars: 1 cm.

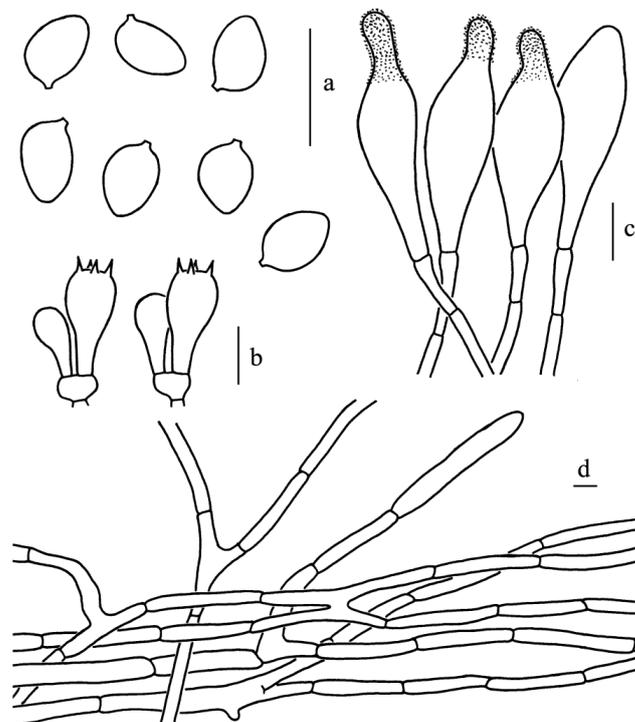


Figure 7. *Leucoagaricus aurantioruber* (CFSZ 19756). (a) Basidiospores. (b) Basidia. (c) Cheilocystidia. (d) Elements of pileus squamules. Scale bars: 10 μ m.

Diagnosis: *Leucoagaricus aurantioruber* is characterized by pileus with minute brown to orange–reddish, radially arranged fibrillose squamules; ellipsoid to ovoid basidiospores; subfusiform cheilocystidia with tiny crystals; and squamules composed of branched, thin-walled hyphae.

Type: CHINA. Inner Mongolia Autonomous Region: Sandaohu, Heilihe National Nature Reserve, Ningcheng County, Chifeng City, 19 August 2018, T.Z. Liu, L. Zhang, Y. Bai (CFSZ 19756, holotype).

GenBank Acc. No.: ITS = OM976875, LSU = OM976863

Description: Pileus 15–24 mm in diameter; at first, nearly hemispherical, umbonate. Surface, orange–reddish (6B7) to orange–brown (6C8), covered with minute brown (6C6) to light orange–reddish (6A4) radially fibrillose squamules; margin, often radially striate; context, white (1A1), up to 3 mm thick at center; no change in color when bruised. Lamellae-free, crowded, white (1A1), thin, 1.5–2 mm wide, with 2–3 tiers of lamellulae, edge finely scalloped. Stipe 33–42 × 2–5 mm, hollow, clavate, attenuate upward, white (1A1), smooth above annulus, slightly fibrillose in lower part. Annulus simple, white (1A1), located in the middle to upper part of the stipe, membranous. Flavor and odor not recorded. Spore print not recorded.

Basidiospores [40/3/2], 6.0–7.5(8.0) × (3.5)4.0–5.0 μm, Q = (1.20)1.30–1.75(2.14), Q_m = 1.54 ± 0.15, ellipsoid to ovoid from side view, ellipsoid from the front view, without germ pore, hyaline, smooth, slightly thick-walled, dextrinoid, metachromatic. Basidia, 16.5–22.0 × 8.0–11.0 μm, clavate, hyaline, four-spored; sterigmata, 4 μm long. Cheilocystidia, 34.5–41.0 × 10.0–14.5 μm, subfusiform, often with a terminal appendage, apex with tiny crystals. Pleurocystidia, absent. Lamellar trama, trabecular. Pileus squamules composed of branched, thin-walled hyphae, 5.0–9.5 μm in diameter. Stipitipellis composed of cylindrical hyphae, 5.5–12.5 μm in diameter, hyaline. Clamp connections absent in all parts of the basidiomata.

Habitat and Habit: solitary to scattered on soil in summer.

Other specimens examined: CHINA. Inner Mongolia Autonomous Region: Sandaohu, Heilihe National Nature Reserve, Ningcheng County, Chifeng City, 21 August 2017, T.Z. Liu (CFSZ 18372).

Comments: *Leucoagaricus aurantioruber* and *Leucoagaricus rubrotinctus* (Peck) Singer are very similar in having orange–reddish pileus. However, *La. aurantioruber* has ellipsoid to ovoid basidiospores and subfusiform cheilocystidia with tiny crystals on the apex [32].

La. rubrobrunneus E.F. Malysheva, Svetash. & Bulakh, originally described in the Russian far east, is similar to *La. aurantioruber* in having subfusiform cheilocystidia, forming a sterile lamellae edge. However, *La. aurantioruber* is distinctly different from *La. rubrobrunneus* in having larger basidiospores and larger pileus (15–24 mm), pileus squamules composed of branched, thin-walled hyphae measuring 5.0–9.5 μm in diameter and cheilocystidia with tiny crystals on the apex [33].

La. bulbiger Justo, Bizzi & Angelini and *La. proximus* are also similar to *La. aurantioruber* in having similarly shaped basidiospores and pileus squamules. However, *La. bulbiger*, originally described in the Dominican Republic, has a yellow–orange pileus, a bulbous stipe base and polymorphic cheilocystidia [21]. *La. proximus* E.F. Malysheva, Svetash. & Bulakh, originally described from the Russian far east, has smaller-sized cheilocystidia measuring 27.0–40.0 × 6.0–14.0 μm [33].

Leucoagaricus rubroconfusus Migl. & Coccia resembles *La. aurantioruber* in having orange fibrillose squamules and ellipsoid to ovoid basidiospores of approximately the same length. However, *La. rubroconfusus* has smaller cheilocystidia without crystals on the apex.

The new species is also similar to *La. japonicus* (Kawam. ex Hongo) Hongo in having ellipsoid or ovoid basidiospores. However, *La. japonicus* has testaceous, scaly pileus; longer basidiospores; and clavate to fusiform cheilocystidia without crystals [5,32,34].

Leucoagaricus candidus Y.R. Ma, Z. W. Ge & T.Z. Liu, sp. nov. Figures 8 and 9.

MycoBank: MB 843379

Etymology: *candidus* (Latin) = white, referring to the almost snow white basidiomata.



Figure 8. Basidiomata of *Leucoagaricus candidus*. (CFSZ 20964). Scale bars: 1 cm.

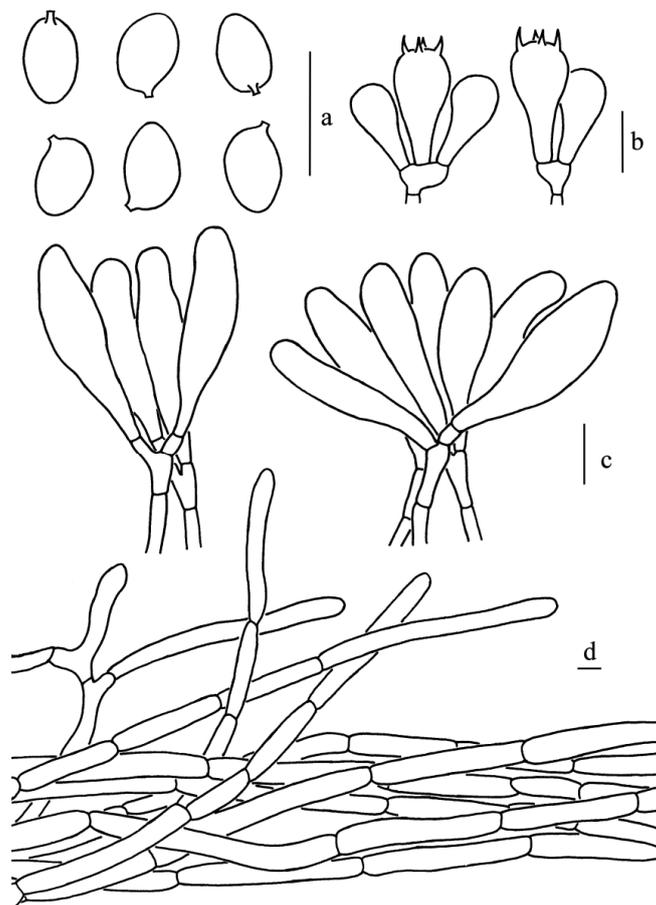


Figure 9. *Leucoagaricus candidus* (CFSZ 20964). (a) Basidiospores. (b) Basidia. (c) Cheilocystidia. (d) Elements of pileus surface. Scale bars: 10 μ m.

Diagnosis: *Leucoagaricus candidus* is characterized by its white basidiomata, white pileus squamules, a margin often with appendiculate white veil remnants and ellipsoid to broadly ellipsoid basidiospores.

Type: CHINA. Inner Mongolia Autonomous Region: Sidaogou, Heilihe National Nature Reserve, Ningcheng County, Chifeng City, 21 August 2019, T.Z. Liu, K. Kang (CFSZ 20964, holotype).

GenBank Acc. No.: ITS = OM976877, LSU = OM976864

Description: Pileus 15–31 mm in diameter, white (1A1), ovoid when young, becoming convex to applanate with age, glabrous to radially fibrillose, margin often with fine

striations when mature, appendiculate with veil remnants. Context: white (1A1), thin, no change in color upon bruising. Lamellae-free, crowded, white (1A1), up to 3 mm in height, edge finely scalloped. Stipe, 27–38 × 3–7 mm, subcylindrical, white (1A1), clavate, hollow, white (1A1) to milk white (1A2), smooth to silky above annulus, with white, minute or fibrillose squamules below annulus. Annulus white (1A1), membranous, located in the middle to upper part of the stipe. Flavor and odor unknown. Spore print not recorded.

Basidiospores [62/5/3], (5.5)6.0–7.5(8.0) × (4.0)4.5–5.0 μm; Q = (1.20)1.33–1.63(1.78), Q_m = 1.46 ± 0.13; ellipsoid in side view, occasionally broadly ellipsoid or elongate; ellipsoid in front view; without germ pore, hyaline, slightly thick-walled (about 0.5 μm); dextrinoid, metachromatic in Cresyl Blue. Basidia, 16.0–20.5 × 7.0–9.5 μm, clavate, hyaline, four-spored. Cheilocystidia, 29.0–42.0 × 8.0–12.5 μm, mostly narrowly clavate, occasionally with a constricted apex. Pleurocystidia, absent. Lamellar trama, trabecular. Pileus surface composed of 5.0–13.0 μm wide repent-hyphae, subcylindrical, thin-walled, hyaline. Stipitipellis composed of subcylindric hyphae, 4.0–8.5 μm in width with yellowish intracellular pigment. Clamp connections absent in all parts of the basidiomata.

Habitat and Habit: solitary to scattered on soil in summer.

Other specimens examined: CHINA. Inner Mongolia Autonomous Region: Daheishan National Nature Reserve, Aohan Banner, Chifeng City, 22 August 2016, T.Z. Liu, S.L. Zhang, Y.X. Yang (CFSZ 11287). Inner Mongolia Autonomous Region: Sidaogou, Heiluhe National Nature Reserve, Ningcheng County, Chifeng City, 22 August 2019, T.Z. Liu, T. Li (CFSZ 20991).

Comments: *Leucoagaricus candidus* is morphologically similar to *Leucoagaricus nivalis*, *Leucoagaricus serenus* (Fr.) Bon & Boiffard and *Leucoagaricus sericifer* on the overall whitish to white basidiomata. However, *La. candidus* differs from them by having ellipsoid to broadly ellipsoid basidiospores and a pileus surface composed of wider hyphae (5.0–13.0 μm). In addition, both *La. serenus* and *La. sericifer* were originally described in Europe and are widespread in Europe [6,31,35].

Two white European species, *La. subvolvatus* (Malencon & Bertault) Bon and *La. menieri* (Sacc.) Singer, are also similar to *La. candidus* in the overall white basidiomata and similar basidiospores. However, *La. subvolvatus* has white to cream pileus and cheilocystidia with crystals at the apex [32]; *La. menieri* has fragile and sericeous pileus and cheilocystidia with crystals at the apex [32].

Leucoagaricus centricastaneus Y.R. Ma, Z. W. Ge & X.D. Yu, sp. nov. Figures 10 and 11.

MycoBank: MB 843380

Etymology: centri- = center; *castaneus* (Latin) = chestnut, refers to the almost chestnut in the center of the pileus.



Figure 10. Basidiomata of *Leucoagaricus centricastaneus*. (A) SYAU FUNGI 072; (B,C) SYAU FUNGI 075; (D) SYAU FUNGI 076). Scale bars: 1 cm.

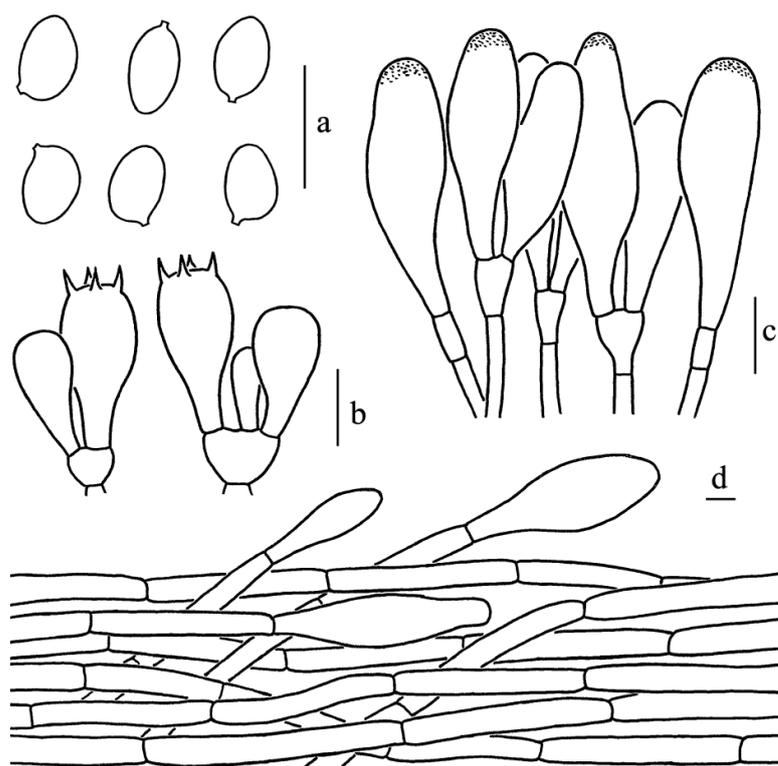


Figure 11. *Leucoagaricus centricastaneus* (SYAU FUNGI 076). (a) Basidiospores. (b) Basidia. (c) Cheilocystidia. (d) Elements of pileus squamules. Scale bars: 10 μm .

Diagnosis: *Leucoagaricus centricastaneus* is characterized by its pileus with orange-brown, yellow-brown or red-brown floccose squamules, ovoid to ellipsoid basidiospores and clavate to fusiform cheilocystidia with refractive contents on the apex.

Type: CHINA. Liaoning Province: Shenyang, Shenyang Agricultural University, August 2020, X.D. Yu (SYAU FUNGI 076, holotype).

GenBank Acc. No.: ITS = OM976855, LSU = OM976871

Description: Pileus, 43–62 mm in diameter; slightly umbonate, covered with orange-brown (5B6), yellow-brown (3B6) or red-brown (9D7–9D8) floccose squamules. The color of the squamules washes out towards the margin. Context, white (1A1); fleshy, no change in color when bruised. Lamellae-free, white (1A1), crowded, up to 3 mm, edge finely scalloped. Stipe, 47–73 \times 3–6 mm; white (1A1), nearly smooth or slightly fibrillose, enlarged to subclavate toward base. Annulus, simple; white (1A1), membranous, located in the middle to upper part of the stipe. Flavor and odor not recorded. Spore print not recorded.

Basidiospores, [60/3/2], (5.0)5.5–7.0(7.5) \times (4.0)4.5–5.0 μm ; $Q = (1.20)1.22\text{--}1.44(1.50)$; $Q_m = 1.32 \pm 0.09$; ovoid to ellipsoid in side view; ellipsoid in front view; dextrinoid, metachromatic in Cresyl Blue, without germ pore, hyaline, slightly thick-walled (about 0.5 μm). Basidia, 17.5–24.0 \times 8.5–10.5 μm ; clavate, hyaline, four-spored; sterigmata, 2.5 μm long. Cheilocystidia, 28.5–43.5 \times 9.0–15.0 μm ; clavate to broadly clavate, at times fusiform, hyaline, forming clusters. Some cheilocystidia have obvious refractive contents at the apex. Pleurocystidia, absent. Lamellar trama, trabecular. Pileus squamules made up of subcylindrical septate hyphae 6.5–10.5 μm in diameter, with terminal elements barely differentiated, narrowly clavate to slightly fusiform (42.0–72.5 \times 12.5–24.0 μm). Stipitipellis composed of subcylindrical to long ellipsoid hyphae, 5.5–13.0 μm in diameter, hyaline. Clamp connections absent in all parts of the basidiomata.

Habitat and Habit: solitary in grass in summer. So far, known only in Shenyang, Liaoning Province in northern China.

Other specimens examined: CHINA. Liaoning Province: Shenyang, Shenyang Agricultural University, August 2020, X.D. Yu (SYAU FUNGI 075). Liaoning Province: Shenyang, Shenyang Agricultural University, August 2020, X.D. Yu (SYAU FUNGI 072).

Comments: *Leucoagaricus centricastaneus* is very close to *Leucoagaricus lahorensis* Qasim, T. Amir & Nawaz and *Leucoagaricus lahorensiformis* S. Hussain, H. Ahmad, Afshan & Khalid in the phylogenetic analysis (Figure 1). All three species have subclavate cheilocystidia. However, *La. lahorensis* and *La. lahorensiformis*, originally described in Pakistan, have a differently colored pileus (orange, orange–reddish or reddish–brown) and amygdaliform to ellipsoid basidiospores, and the cheilocystidia of *La. lahorensis* has no refractive contents on the apex [19,36].

Leucoagaricus japonicus, *Leucoagaricus rubrotinctus* (Peck) Singer and *Leucoagaricus vassiljevae* E.F. Malysheva, Svetash. & Bulakh are similar to *La. centricastaneus* in having similarly shaped cheilocystidia. However, the cheilocystidia of these species have no refractive contents on the apex [32–34]. In addition, *La. japonicus*, originally described in Japan, has a testaceous, scaly pileus; longer cheilocystidia; and amygdaliform basidiospores [34]. *La. rubrotinctus*, originally described in the United States, has an orange–reddish pileus and larger amygdaliform basidiospores [32]. *La. vassiljevae*, described in the Russian far east, has appressed red–brown or crimson–brown fibrils and broadly clavate basidia [33].

Leucoagaricus virens Y.R. Ma, Z. W. Ge & T.Z. Liu, sp. nov. Figures 12 and 13.

Mycobank: MB 843378

Etymology: from “*virens*” (Latin), referring to the dark green to light green reaction of basidiomata when bruised or dried.



Figure 12. Basidiomata of *Leucoagaricus virens*. (A–C) CFSZ 19869. Scale bars: 1 cm.

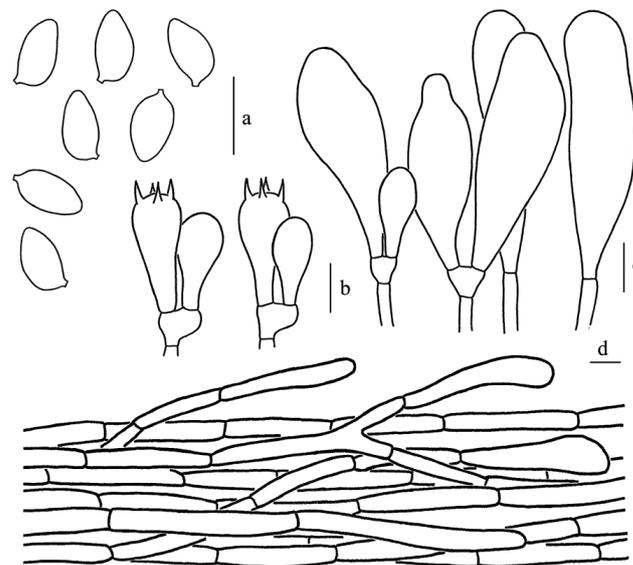


Figure 13. *Leucoagaricus virens* (CFSZ19869). (a) Basidiospores. (b) Basidia. (c) Cheilocystidia. (d) Elements of pileus squamules. Scale bars: 10 μ m.

Diagnosis: *Leucoagaricus virens* is characterized by dark green (27E6) to light green (27B3) changes of pileus when bruised or dried; amygdaliform to ellipsoid basidiospores; and narrowly clavate, clavate to fusiform cheilocystidia.

Type: CHINA. Inner Mongolia Autonomous Region: Sandaohu, Heilihe National Nature Reserve, Ningcheng County, Chifeng City, 21 August 2018, T.Z. Liu and Y.X. Chen (CFSZ 19869, holotype).

GenBank Acc. No.: ITS = OM976881, LSU = OM976867 (CFSZ19794-2)

Description: Pileus, 7–13 mm in diameter; at first, nearly campanulate, becoming convex with age; center slightly umbonate, sometimes margin with inconspicuous striations; surface, whitish (1A2) to yellowish (2A3), covered with brown (6C3) to grey–brown (6E3), fibrillose, more or less radially arranged squamules; the central umbo is uniformly colored. The surface of the pileus discolours dark green (27E6) to light green (27B3) when bruised or dried. Context, thin; 1–2 mm, white (1A1), becoming dark green to light green when bruised or dried. Lamellae-free, crowded, white (1A1), slightly ventricose, with entire edges; discolours dark green to light green where bruised or dried. Stipe, 37–50 × 1–3 mm; subcylindrical, hollow, light yellowish brown (4B3), nearly smooth. Annulus, white (1A1), membranous, located at the upper part of the stipe. Flavor and odor not recorded. Spore print not observed.

Basidiospores [60/3/2], (7.5)8.0–10.0(10.5) × (4.0)4.5–5.0(5.5) μm; Q = (1.50)1.60–2.10(2.13); Q_m = 1.85 ± 0.14; amygdaliform to elongate in side view; ellipsoid to elongate in front view; without germ pore, hyaline, slightly thick-walled (about 0.5–1.0 μm), dextrinoid, metachromatic in Cresyl Blue. Basidia, 16.5–27.5 × 8.5–10.0 μm; clavate, hyaline, four-spored; sterigmata, 4.5 μm long. Cheilocystidia, 27.5–52.0 × 9.5–17.0 μm; narrowly clavate to clavate, sometimes fusiform, hyaline, thin-walled. Pleurocystidia, absent. Lamellar trama, trabecular. Pileus squamules composed of loosely arranged subcylindrical hyphae with light brown (3B4) intracellular and extracellular pigments; terminal elements barely differentiated, subcylindrical to narrowly clavate (31.5–53.5 × 8.0–13.0 μm). Stipitipellis composed of hyaline, subcylindrical hyphae, 4.5–11.5 μm in diameter. Clamp connections absent in all parts of the basidiomata.

Habitat and Habit: solitary to scattered on soil in summer. So far, known only in Chifeng, Inner Mongolia Autonomous Region, China.

Other specimens examined: CHINA. Inner Mongolia Autonomous Region: Sandaohu, Heilihe National Nature Reserve, Ningcheng County, Chifeng City, 20 August 2018, T.Z. Liu, L. Zhang and Y. Bai (CFSZ 19794-2).

Comments: Basidiomata of *Leucoagaricus virens* turn dark green to light green when bruised or dried. This feature is similar to those of *Leucoagaricus viriditinctus* (Berk. & Broome) J.F. Liang, Zhu L. Yang & J. Xu, and *Leucoagaricus flavovirens* J.F. Liang, Zhu L. Yang & J. Xu. *La. viriditinctus* is also similar to *La. virens* in the overall appearance of basidiomata. However, *La. viriditinctus*, a species originally described in Sri Lanka, has a light blue to dark blue context when bruised or dried, and its cheilocystidia are broadly clavate to pyriform [37].

Leucoagaricus virens is also similar to *La. flavovirens*, a species originally described in China. Both species have amygdaliform to ellipsoid basidiospores and squamules composed of subcylindrical hyphae. However, *La. flavovirens* has bluish green (27A7–8) changes of basidiomata when bruised [37].

Leucocoprinus viridiflavus (Petch) E. Ludw. also has this feature. *Lc. viridiflavus* is similar to *La. virens* in having olive (1E4–1E5) to dark olive (2F8) changes of basidiomata on exposure of context. However, *Lc. viridiflavus* have germ pore and utriform, ventricose or broadly clavate cheilocystidia [38].

Leucoagaricus atroazureus J.F. Liang, Zhu L. Yang & J. Xu and *La. caeruleus* (Peck) J.F. Liang, Zhu L. Yang & J. Xu, both described in southern China, are also similar to *La. virens* in having white context, brownish squamules on the pileus and similarly shaped basidiospores. However, *La. atroazureus* has smaller basidiospores (5.5–8.0 × 3.5–5.5 μm)

and dark blue changes of basidiomata when bruised or dried; *La. caerulescens* has clavate to broadly clavate cheilocystidia and bluish green changes of basidiomata when dried [37].

4. Discussion

Based on morphological and molecular data, in this study, we described six new species of *Leucoagaricus* from northeastern China, with three species in section *Leucoagaricus*, two in subgenus *Sericeomyces* and one within a clade not belonging to any currently recognized section. The taxonomy of *Leucoagaricus* has been a focus worldwide in recent years, with many new taxa described around the world [11,19–21,37,39,40]. However, as shown in Figure 1, there are putative new species to be described that are represented by a single collection (e.g., HKAS 123028, HKAS 105542, HKAS 123030 and HKAS 116134). With additional field work carried out and additional collections documented, more new taxa are expected to be described.

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Data Availability Statement: Data can be found within the manuscript.

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