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Two new species of *Leucoagaricus* (Agaricaceae) from the Lao People's Democratic Republic

Sysouphanthong P[1,2,3] and Thongklang N[1,2,*]

[1]*Center of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai 57100, Thailand*
[2]*School of Science, Mae Fah Luang University, Chiang Rai 57100, Thailand*
[3]*Biotechnology and Ecology Institute, Ministry of Agriculture and Forestry, P.O. Box 811, Vientiane Capital, Lao PDR*

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Abstract

Two new species of *Leucoagaricus* from Laos are described based on both morphological characteristics and evidence of molecular phylogeny. The first species, *Leucoagaricus flavus*, is well recognized by small and pale yellow to pastel yellow basidiomata; ovoid to ellipsoid basidiospores without a germ pore; clavate basidia; hyaline, clavate to narrowly clavate cheilocystidia; and a cutis pileus covering made up of cylindrical and hyaline elements. Primarily, it is distinguished from other species by its yellow basidiomata. The second species, *Leucoagaricus griseosquamusus*, is recognized by white basidiomata; grey to grayish-brown squamules; ellipsoidal ovoid basidiospores; clavate basidia; clavate to broadly clavate cheilocystidia; a hymeniderm pileus covering made up of a range of ellipsoidal to oblong elements with brown to the dark brown wall. Notably, each species is provided a full description, discussion on related species, field photographs, and line drawing of micro-characteristics. Furthermore, phylogenetic analyses results based on nrITS sequences are provided to show the relationship of each new species.

Keywords – Agaricaceae – Basidiomycota – diversity – distribution – lepiotoid mushroom – phylogeny – Southeast Asia

Introduction

Leucoagaricus (Locq. ex) Singer is a diverse genus of the family Agaricaceae, and it has been estimated to consist of 135 species recently (He et al. 2019). Singer (1986) divided *Leucoagaricus* into six sections viz. *Annulati*, *Rubrotincti*, *Sculpturati*, *Leucoagaricus*, *Piloselli* and *Sphaerocystophori* based on its morphology. Generally, basidiomata of *Leucoagaricus* are small to medium size and lepiotoid or pluteoid shape; a pileus is smooth to squamulose with or without striate margin, lamellae are free, a stipe is smooth to squamulose, an annulus is present or fragile with age. Microscopically; basidiospores are hyaline, smooth or rough wall with or without a germ pore, dextrinoid in Melzer's reagent, metachromatic in Cresyl blue; cheilocystidia are always present; pleurocystidia are present in few species; pileus- and stipe covering are a cutis or a trichoderm; and clamp-connection is absent (Singer 1986, Vellinga 2001, Læssøe & Petersen 2019). *Leucoagaricus* was separated from *Leucocoprinus* by considering more significant, and persistent basidiomata, mostly non-striate cap, absence of a germ pore or without hyaline cover in basidiospore. At the same time, other characteristics are similar to *Leucocoprinus* (Singer 1986).

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Corresponding Author: Naritsada Thongklang – e-mail – naritsada.t@gmail.com

Several molecular studies of both genera showed that they are monophyletic (Vellinga 2004, Vellinga et al. 2011, Liang et al. 2010, Ge et al. 2015, Hussain et al. 2018). However, further studies on phylogenetic relationships might prove the difference between these two genera.

Most species of *Leucoagaricus* were described from temperate zones (Candusso & Lanzoni 1990). Some species were initially described from tropics, e.g., China (Ge 2010, Ge et al. 2015, Liang et el. 2010, Yuan et al. 2014), Pakistan (Hussain et al. 2018, Usman & Khalid 2018), India (Kumar & Manimohan 2009, Latha et al. 2020, Dutta et al. 2021), and Laos (Sysouphanthong et al. 2018).

Laos, a tropical country in Southeast Asia is characterized by highly mountainous areas with the wet monsoon from May to September, and this supports high biodiversity (Bugna 2002, FAO 2000). However, the reports of mushrooms from Laos are rare., In this study, we describe two new species of *Leucoagaricus* from Laos based on both morphology and molecular evidence.

Materials & Methods

Mushroom collection and examination

The specimens of *Leucoagaricus* were collected in north Lao (Oudoxay Province) and central Laos (Bolikamxay Province and Vientiane Capital) during the rainy season of 2014–2015. The important ecology notes are locations, forest types, soil type, and substrate. Mushrooms were photographed in the habitat, and their macro characteristics were observed in the laboratory. The important macro characteristics are shape, size, and colour. The color annotations of fresh mushrooms were followed by Kornerup & Wanscher (1990). After macromorphological observation, mushrooms were dried in a hot air dryer at around 40–50°C for 24 hours and deposited at Herbarium National of Laos (HNL) in Biotechnology and Ecology Institute, Ministry of Agriculture and Forestry of Lao PDR. Microscopical characteristics were studied from dry specimens on a microscope. The main characters such as basidiospores, basidia, cystidia, pileus – and stipe coverings were recorded. Spore color was observed in water and 5–10% of KOH. Other chemical reagents that were used to test the reaction of spore walls are Congo red, Cotton blue, Cresyl blue, and Melzer's reagent. The technical term used for the description of mushrooms was following the standard book of Vellinga (2001). Index Fungorum and Facesoffungi numbers were registered as mentioned in Index Fungorum (2022) and Jayasiri et al. (2015).

Phylogenetic study

The dried fungarium specimens were used for DNA extraction following the instructions of the Biospin Fungus Genomic DNA Extraction Kit (Bioer Technology Co., Ltd., Hangzhou, P.R. China). The internal transcribed spacers (ITS) were investigated and using primers ITS1 and ITS4 for polymerase chain reaction (PCR) (Gardes & Bruns 1993, White et al. 1990). Then the PCR products were sent to purify and sequence with Shanghai Sangon Biological Engineering Technology & Services Co., Ltd. The received sequences were edited and contigs assembled in the SeqMan program (DNA Star, Madison, WI, USA). All new sequences were deposited in the National Center for Biotechnology Information (NCBI) (http://www.ncbi.nlm.nih.gov/genbank/).

The new sequences were blasted in the GenBank, and the related sequences to new species and representative sequences of *Leucoagaricus*/*Leucocoprinus* were retrieved from GenBank to combine with new sequences. The dataset consisted of 89 sequences including four new sequences from this study; *Agaricus bisporus* (J.E. Lange) Imbach, *Chlorophyllum molybdites* (G. Mey.) Massee and *Macrolepiota dolichaula* (Berk. & Broome) Pegler & R.W. Rayner were used as outgroups. (Fig. 1). The dataset was aligned in BioEdit software (http://www.mbio.ncsu.edu/BioEdit/bioedit.htm). A Maximum likelihood (ML) analysis was performed in RAxML 7.2.6 (Stamatakis et al. 2008) with the GTRGAMMA model, and the branch support was estimated at over 1000 bootstrap partitions (BP) with the rapid bootstrap option. The Bayesian inferences (BI) analysis was conducted using MrBayes on XSEDE 3.2.7a (CIPRES), and run 10 million generations for the dataset. The best substitution model was defined in MrModelTest v.2.3, and the

best-selected model was GTR + I + G (Nylander 2004).

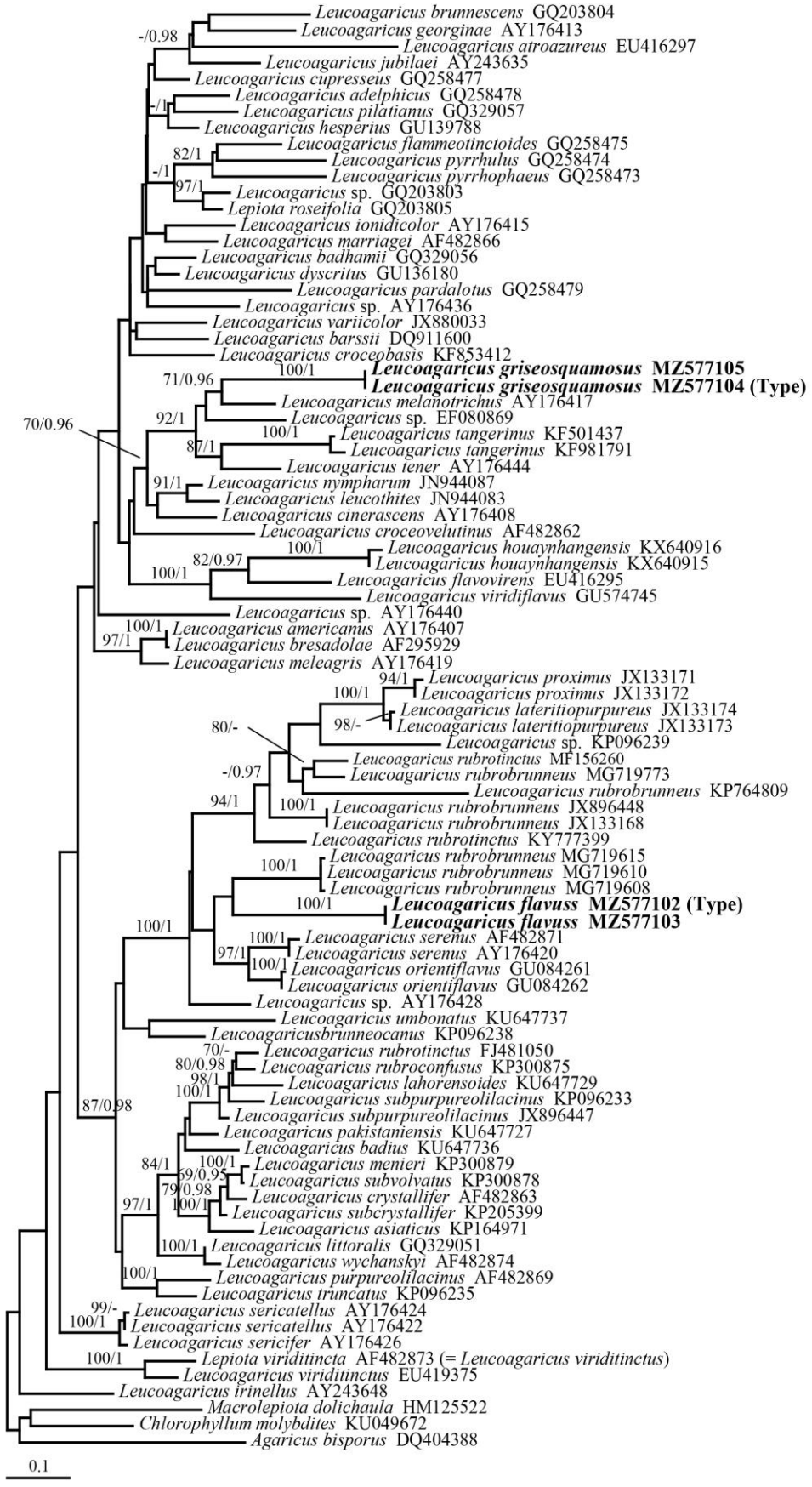

Fig. 1 – Phylogenetic tree based on Maximum Likelihood analysis of nrITS sequences. Bootstrap values ≥ 60% are indicated above the branches, and Bayesian posterior probabilities ≥ 0.95 are

placed above after ML bootstrap values. GenBank accession numbers are given after species names. The new sequences are in bold. *Agaricus bisporus* (J.E. Lange) Imbach, *Chlorophyllum molybdites* (G. Mey.) Massee and *Macrolepiota dolichaula* (Berk. & Broome) Pegler & R.W. Rayner were used as outgroups.

Results

Phylogenetic analyses

Fig. 1 is a Maximum likelihood (ML) phylogenetic tree of *Leucoagaricus*/*Leucocoprinus* species based on nrITS sequences. A total of 89 sequences were analyzed, and the aligned dataset comprised 619 characters (including the gaps). The best RaxML tree with a final likelihood value of -13773.275637 is presented. The matrix had 428 distinct alignment patterns, with 4.17% undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.227051, C = 0.220337, G = 0.231303, T = 0.321309; substitution rates AC = 1.505489, AG = 4.797754, AT = 1.574713, CG = 0.589189, CT = 5.006063, GT = 1.000000; gamma distribution shape parameter α = 0.411001. It was found that two new species were separated from other species. First new species, two sequences of *Leucoagaricus griseosquamosus* were identical and related to *Leucoagaricus melanotrichus* (AY176417) with 70% bootstrap support (BS). Second new species, two sequences of *Leucoagaricus flavus* were identical and the most related to *Leucoagaricus rubrobrunneus* with low BS. The result of the Bayesian analysis was similar to ML, and the Bayesian posterior probabilities (PP) ≥ 0.95 are placed after the ML scores.

Taxonomy

Leucoagaricus flavus Sysouph. & Thongkl. sp. nov. Figs 2–3

Index Fungorum number: IF559485; Facesoffungi number: FoF 10799

Etymology – (Latin) *flavus* = yellow; it refers to as its yellow basidiomata.

Diagnosis – Pale yellow to pastel yellow basidiomata, umbonate to plano-convex pileus and covered with yellow to pastel yellow fibrillose with sulcate margin, free and pale yellow lamellae, cylindrical stipe or slightly tapering upward apex, cuff-liked annulus, ovoid basidiospore without a germ pore, clavate to narrowly clavate cheilocystidia with a short or slightly long appendage, a cutis pileus- and stipe covering and absence of clamp-connections.

Pileus 15–20 mm diam., umbonate, expanding applanate with low umbo, with straight margin; smooth and pale yellow to pastel yellow (3A3–4) at the umbo, breaking around umbo and with concentrically concolorous fibrillose toward the margin, sometimes peeling and with white to the pale yellow fibrillose background; marginal zone fibrillose, concolorous with dish, sulcate and fringed when mature. Lamellae free, pale yellow to pastel yellow (3A3), ventricose, up to 1.5 mm wide, slightly crowded, with 3lamellulae, with a concolorous eroded edge. Stipe 30–35 × 3–5 mm, cylindrical or slightly tapering to apex, with wide base; covered with white to yellowish-white (4A2) fibrillose or soft hair, on yellowish-white (2A2) background. Annulus cuff-liked, fibrillose, concolorous with pileus covering, attached at the middle zone of the stipe. Context in pileus white, thin, up to 2 mm wide; in stipe hollow, concolorous with surface, hollow and with white fibrils in hollow. Smells distinct, soft, flower, fleshy. Taste not observed. Spore print white.

Basidiospores [50,2,2] l × w = 4.8–5.3 × 3.5–4 µm, avl × avw = 5.0 × 3.8 µm, Q = 1.2–1.4, Qav = 1.3, in side-view broadly ellipsoidal ovoid to ellipsoidal ovoid, in frontal view ovoid to ellipsoid, slightly thick-walled, hyaline, without a germ pore, dextrinoid, congophilous, cyanophilous, metachromatic. Basidia 13.0–16 × 6.0–7.5 µm, clavate, hyaline, thin-walled, 4-spored. Pleulocustidia absent. Cheilocystidia 14–42 × 5–10 µm, clavate to narrowly clavate, hyaline, thin-walled. Pileus covering a cutis made up of cylindrical elements, sometimes with narrowly clavate, 15–41 × 3–7 µm, thin-walled, hyaline to pale yellow, with cylindrical and concolorous hyphae, 3–5 µm wide. Stipe covering same as pileus covering, a cutis made up of cylindrical and hyaline elements, 10–35 × 3–5 µm µm wide, thin-walled, with hyaline hyphae, 2–

3.5 µm wide, thin-walled. Clamp connections are absent in all tissues.

Habitat and known distribution – growing solitary, saprotrophic, on humus soil; two samples were found in deciduous and bamboo forests during the rainy season (October to November 2015) of central Laos.

Material examined – Laos, Bolikhamxay Province, Thaphabath District, Tad Xay Waterfall, 14 Oct 2015, P. Sysouphanthong, PS148 (HNL503375, holotype); Vientiane Capital, Xaythany District, Houay Nhang Preserve Forest, 17 Nov 2015, P. Sysouphanthong, PS201 (HNL503428, paratype).

Discussions – *Leucoagaricus flavus* has pale yellow to pastel yellow basidiomata, free and pale yellow to pastel lamellae, white to the yellowish-white stipe, cuff-liked annulus, ovoid basidiospore, clavate to narrowly clavate cheilocystidia and a cutis pileus- and stipe covering. These characters distinctly distinguish the species from other characters. However, there are some species with yellow to yellowish green color that might be confused with *Leucoagaricus flavus*.

Leucoagaricus orientiflavus Z.W. Ge is most similar to *Leucoagaricus flavus* by pastel yellow, light yellow, yellow, or yellowish-white fibrillose pileus; yellowish to yellowish-white stipe surface; white to yellowish-white annulus; amygdaliform basidiospores; clavate to narrowly clavate cheilocystidia and a cutis pileus- and stipe covering. However, *Leucoagaricus orientiflavus* is different from *Leucoagaricus flavus* on larger basidiomata (30–80 mm diam. of pileus), larger basidiospore (6.0–7.5 × 3.0–4.0 µm) and larger basidia (17–24 × 6–7.5 µm) (Ge 2010). Furthermore, analysis of nrITS sequences showed that *Leucoagaricus flavus* and *Leucoagaricus orientiflavus* were clustered, but not identical (Fig. 1).

Leucoagaricus houaynhangensis is different in yellowish-green basidiomata with dark grey to black squamules on pileus and with appendiculate margin, basidiospores with a germ pore, and a trichodarm pileus covering (Sysouphanthong et al. 2018). The analysis of nrITS sequences showed they are not related together (Fig. 1).

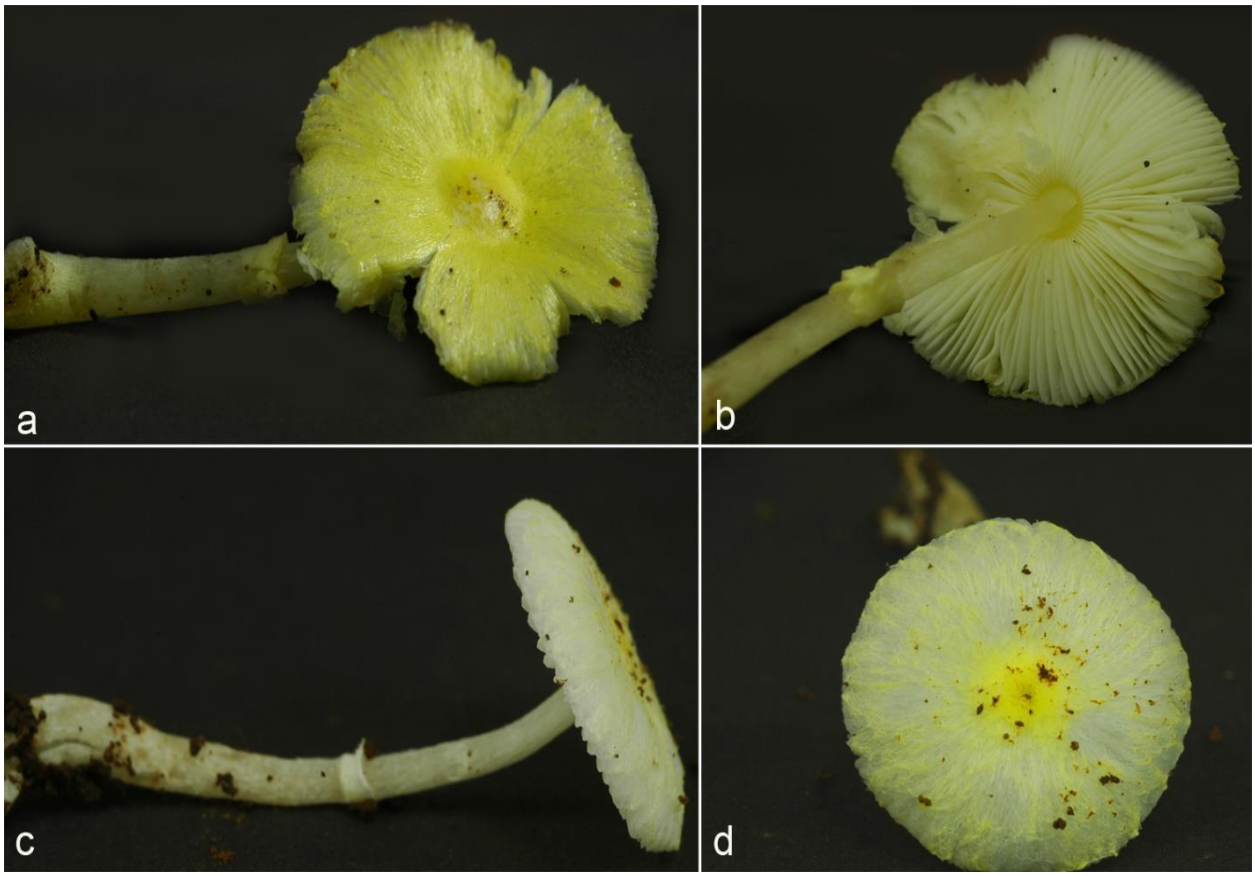

Fig. 2 – Fresh basidiomata of *Leucoagaricus flavus* in situ. a–b (HNL503375, holotype). c–d (HNL503428).

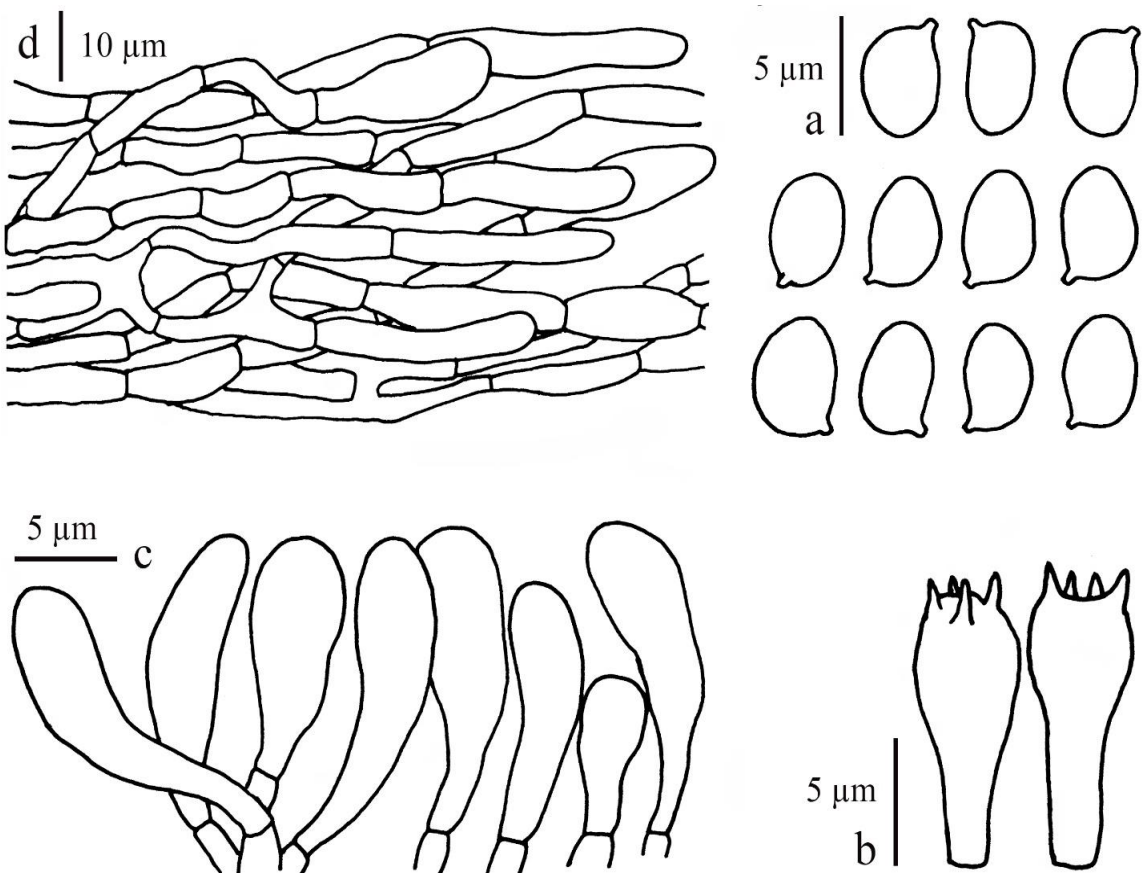

Fig. 3 – Microcharacteristics of *Leucoagaricus flavus* (HNL503375, holotype). a basidiospores. b basidia. c cheilocystidia. d pileus covering.

Other species with yellowish-green basidiomata, *Leucoagaricus sulphurellus* (Pegler) B.P. Akers and *Leucoagaricus viridiflavoides* B.P. Akers & Angels (Akers et al. 2000), but they are different in having brown to greyish-brown pileus covering, presence of pleurocystidia, and bruising blue when touched.

Furthermore, *Leucoagaricus viridiflavus* differs from *Leucoagaricus flavus* in having the darker colour of basidiomata (olive green) and bruising blue, basidiospore with a germ pore, utriform cheilocystidia with short to long appendages (Kumar & Manimohan 2009).

Some yellow species of the genus *Leucocoprinus* are *Leucocoprinus birnbaumii* (Corda) Singer, *Leucocoprinus flavescens* (Morgan) H.V. Sm., *Leucocoprinus flavus* (Beeli) Heinem., *Leucocoprinus flos-sulphuris* (Schnizl.) Cejp and *Leucocoprinus fragilissimus* (Ravenel ex Berk. & M.A. Curtis) Pat. All of them have distinctly long striate on pileus, while it is absent in *Leucoagaricus flavus.*

Leucoagaricus griseosquamosus Sysouph. & Thongkl. sp. nov. Figs 4–5

Index Fungorum number: IF559486; Facesoffungi number: FoF 10800

Etymology – (Latin) *griseus* = grey and (Latin) *squamosa* = *Scales*, the name is referred to greyish scales on the pileus.

Diagnosis – small and white basidiomata, grey to grayish-brown squamose pileus and with sulcate marginal zone, free and white lamellae, cylindrical stipe, cuff-liked annulus, ellipsoidal ovoid basidiospore, clavate basidia, broadly clavate to utriform cheilocystidia, a trichodermal pileus is covering made up of erect of a chain of oblong elements with brown to the dark brown wall, and absence of clam-connections.

Pileus 12–20 mm diam., umbonate, expanding to applanate with low umbo, with straight margin; squamose at umbo toward the margin, grey to grayish-brown (8F1–3), glabrous to slightly coarse and darker at the umbo, on a white background and turning reddish-white (7A2) when

touched; margin with white fibrillose, sulcate when mature. Lamellae free, ventricose, 2–4 mm wide, white, turning reddish-white (7A2) when touched, moderately crowded, with a concolorous eroded edge. Stipe 23–33 × 2.5–3.5 mm, cylindrical, wider at base; covered with white fibrillose on white background, turning reddish-white (7A2) when touched. Annulus cuff-liked, white fibrillose, attached at the upper side of the stipe, fragile or disappearing when mature. The context in pileus white, up to 1 mm wide; in stipe hollow, white, with white fibrils in hollow; both pileus and stipe context turning reddish-white (7A2) when cut. Smell and taste not observed. Spore print white.

Basidiospores [75,3,3] l × w = 6.0–7.5 × 4.0–4.5 µm, avl × avw = 6.4 × 4.2, Q = 1.4–1.7, Qav = 1.5, in side-view ellipsoidal ovoid to oblong ovoid, in frontal view ovoid to oblong, slightly thick-walled, hyaline, dextrinoid, congophilous, cyanophilous, metachromatic. Basidia 14–17 × 7–8 µm, clavate, hyaline, thin-walled, 4-spored. Pleurocystidia absent. Cheilocystidia 14–25 × 7–11 µm, short clavate to clavate, sometimes fusiform, often septate, hyaline, slightly thick-walled. Pileus covering trichodermal made up of erect chains of ellipsoidal to oblong elements, 10–25 × 5–7.5 µm, with depression at septate, branched, with intracellular and parental brown to dark brown pigments, slightly thick-walled. Stipe covering a cutis made of cylindrical to narrowly clavate elements, 17.5–30 × 5.5–7.5 µm, hyaline, thin-walled, with hyaline hyphae, 2.5–10 µm wide. Clamp connection absent in all tissues.

Fig. 4 – Fresh basidiomata of *Leucoagaricus griseosquamosus*. a (HNL501781, holotype). b (HNL501986). c–d (HNL503430).

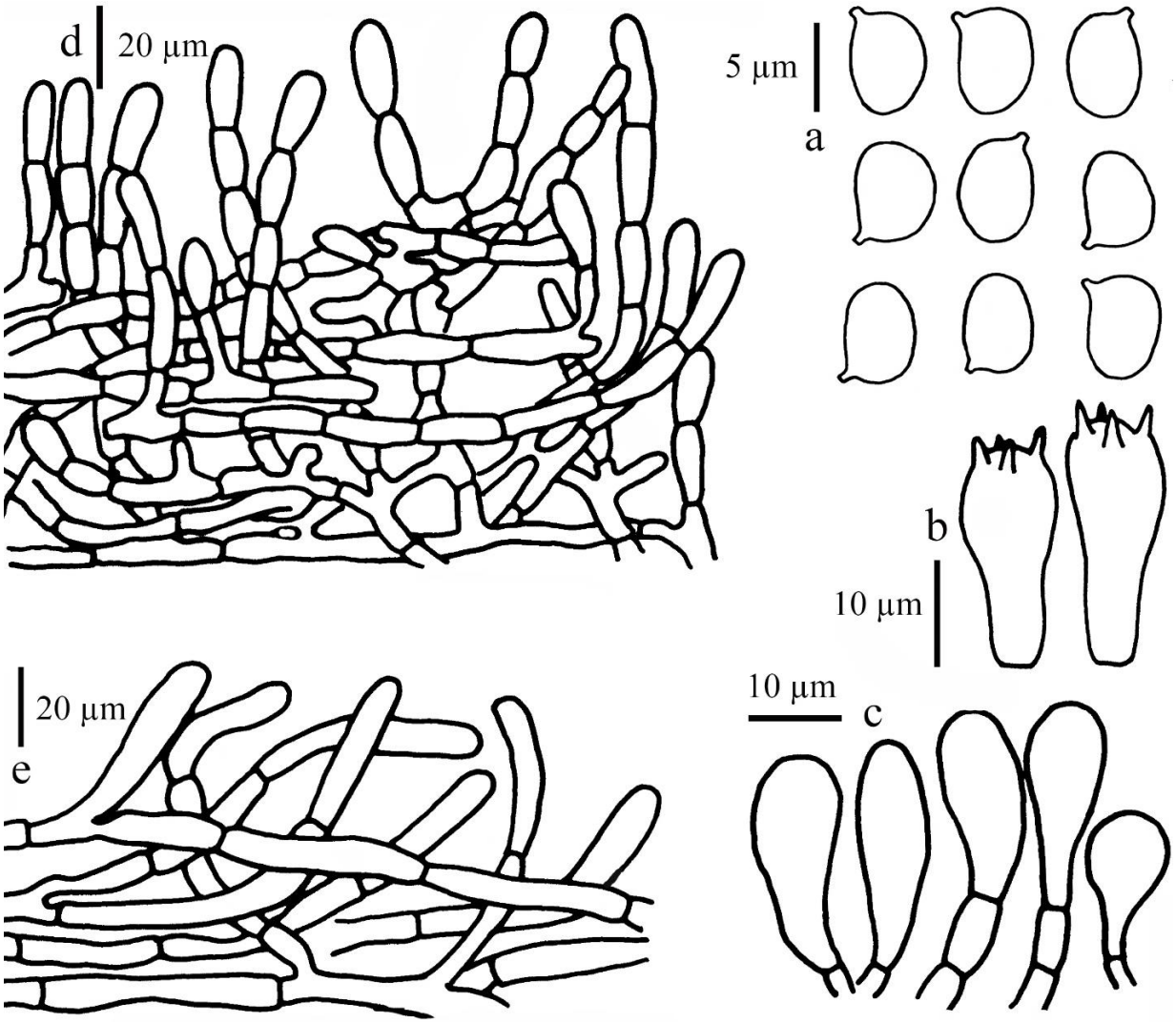

Fig. 5 – Microcharacteristics of *Leucoagaricus griseosquamosus* (HNL501781, holotype). a basidiospoes. b basidia. c cheilocystidia. d pileus covering. e stipe covering.

Habitat and known distribution – growing solitary or with few basidiomata, saprotrophic and terrestrial on soil; found in deciduous forests during the rainy season of central and northern Laos.

Material examined – Laos, Oudomxay Province, Xay District, Houay HoumValley, collected date 23 Jun 2014, P. Sysouphanthong, PS2014-110 (HNL501781, holotype); *ibidem*, 08 Jul 2014, P. Sysouphanthong, PS2014-315 (HNL501986, paratype); Vientiane Capital, Xaythany District, Houy Nhang Preserve Forest, 17 Nov. 2015, P. Sysouphanthong, PS203(HNL503430, paratype).

Discussions – *Leucoagaricus griseosquamosus* is commonly recognized by small and white basidiomata, squamose and grey to grayish-brown pileus, white lamellae, cylindrical and white fibrillose stipe, cuff-liked annulus, ovoid basidiospores, broadly clavate to utriform cheilocystidia and a trichodermal pileus covering, a cutis stipe covering. There are few species with grey color that are similar to *Leucoagaricus griseosquamosus*.

Firstly; the European species, *Leucoagaricus melanotrichus* (Malençon & Bertault) Trimbach is the most similar to *Leucoagaricus griseosquamosus* by morphology; the type species was from Morocco, and described as *Lepiota melanotricha* Malençon & Bertault (Malençon & Bertault 1970). *Leucoagaricus melanotrichus* has a grey to dark grey background with purplish-brown squamulose fibrils on pileus, 15–20 μm mm diam.; stipe is white and with grey to the dark grey annulus; spores are ellipsoidal subamygdaliform, 6.0–7.5 × 3.8–5 μm; basidia are clavate, 23–26 × 7–9 μm; cheilocystidia are clavate to narrowly clavate, 25–45 × 7–13 μm; and a trichodermal pileus covering (Candusso & Lanzoni 1990). However, *Leucoagaricus griseosquamosus* is

different in grey to grayish-brown squamose pileus with white background, white annulus, shorter basidia (14–17 × 7–8 µm), shorter cheilocystidia (14–25 × 7–11 µm) and sometimes with septate, and basidiomata are turned reddish-white when touched. Furthermore, the result from NCBI BLAST of the type species of *Leucoagaricus griseosquamosus* (MZ577104) showed that lacking identical species, and the analysis of nrITS sequence showed that two new sequences of *Leucoagaricus griseosquamosus* are identical, and are clustered with *Leucoagaricus melanotrichus* (AY176417) with low bootstrap support (Fig. 1).

Secondly, *Leucocoprinus heinemannii* Migl. is a species having black to dark grey fibrillose squamules on white background, but different from *Leucoagaricus griseosquamosus* by having distinctly sulcate-striate on pileus margin, and the species are known from temperate Europe (Birkebak 2010, Salom & Siquier 2017, Migliozzi & Zecchin 1998).

Furthermore, *Lepiota atrodisca* Zeller is similar to *Leucoagaricus griseosquamosus* by having mouse grey to sooty black squamules on pileus and almost striate and splitting margin, white lamellae, equal and white stipe, superior and white annulus with blackish margin, ellipsoid-ovoid basidiospores (7 × 4 µm) and clavate cheilocystidia (Zeller 1938). However, *Lepiota atrodisca* has some similar characteristics and lacking clamp-connection; although it is placed in the genus *Lepiota*.

Phylogenetically, *Leucoagaricus tangerinus* Y. Yuan & J.F. Liang is close to *Leucoagaricus griseosquamosus*. However, *Leucoagaricus tangerines* is distinguished by having light orange to brownish-yellow fibrillose on pileus (Yuan et al. 2014).

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