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The case of the missing mushroom: a novel bioluminescent species discovered within *Favolaschia* in southwestern China

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Abstract

Seven species of bioluminescent mushrooms belonging to seven genera have been described in the tropical rainforests of China. This study contributes the eighth species, found growing on decaying bamboo in Xishuangbanna Tropical Botanical Garden (XTBG). Morphological characteristics and phylogenetic analyses using internal transcribed spacer (ITS) and ribosomal large subunit (LSU) gene regions placed the species within the genus *Favolaschia.* Comprehensive morphological descriptions, micro and macro photographs, and a phylogenetic tree showing the placement of the new species are provided. This is the second report of bioluminescent *Favolaschia* in China.

Key words: bioluminescent fungi, *Favolaschia xtbgensis,* macrofungi, Yunnan Province

Introduction

Natural bioluminescence is the emission of visible lights from a living organism due to a chemical reaction (Haddock *et al.* 2010). It is widely found across the ocean and terrestrial environments as well as across diverse groups of organisms, including unicellular algae, bacteria (Tanet *et al.* 2019), multicellular fungi (Karunarathna *et al.* 2020; Mishra & Srivastava 2021) and animals (Mensinger 2011; Li *et al.* 2021). At a deeper level, bioluminescence is currently understood as the oxidization of a light-emitting molecule known as luciferin, which is oxidized by an enzyme called luciferase or photoproteins, resulting in an intermediate high-energy substance after which the intermediate subsequently converts into oxyluciferin (Shimomura 2006; Moline *et al.* 2013).

Among identified terrestrial fungi (totalling ~140,000), approximately 100 species belonging to four distantly related lineages, namely Armillaria, Lucentipes, Mycenoid, and Omphalotus, have been recognized as bioluminescent fungi (Kotlobay *et al.* 2018). When luciferins decompose, bioluminescent fungi release green light (~530 nm) from their fruiting bodies or mycelium. Oliveira *et al.* (2012) have found that a single biochemical process is involved across all four bioluminescent monophyletic lineages due to the shared luciferin compound and luciferase enzyme. Numerous studies have suggested that the ecological function of bioluminescence in fungi is to attract insects for spore dispersal, which may be beneficial for fungi growing on the forest floor where wind flow is low (Oliveira *et al.* 2015).

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Favolaschia (Pat.) Pat is a saprobic, generally small, mushroom-like basidiomycetes genus belonging to the family Mycenaceae, which is distributed worldwide with high species diversity. It was reported from a lowland warm-temperate to subtropical and tropical zone (Singer 1974; Johnston *et al.* 2006; Magnago 2013). The name "*Favolaschia"* was first introduced by Patouillard & Lagerheim de (1892) as a section of the genus *Laschia*, and later on it was separated as a new genus. The genus *Favolaschia* comprises 109 species based on existing data in the Species Fungorum (2022) database. Members of this genus are characterised by hymenial pores, a gelatinous trama and consisting of gloeocystidia and acanthocystida (Gillen *et al.* 2012). To date, *F. manipularis* (Corner 1954; Audrey *et al.* 2015) and *F. peziziformis* (Bodensteiner *et al.* 2004) have been reported to have bioluminescence.

There is a long history of macrofungi research in China due to not only their high level of diversity, but also the significance in Chinese food, culture, and traditional medicines (Dai *et al.* 2009; Wu *et al.* 2019). Despite this, only seven bioluminescent mushrooms have been discovered: *Lampteromyces luminescens* M. Zang*, Omphalotus flagelliformis* Zhu L. Yang & B. Feng*, O. mangensis* Jian Z. Li & X.W. Hu*, Filoboletus yunnanensis* P.G. Liu*, Pleurotus Prometheus* (Berk. & M.A. Curtis) Sacc., *Favolaschia manipularis* (Berk.) Teng (Teng 1963) and *Roridomyces viridiluminus* (Dauner *et al.* 2021). In Xishuangbanna Tropical Botanical Garden (XTBG), located in Yunnan Province, southwestern China, there have been several reports of a glowing mushroom in the area, but the species was never sampled or scientifically identified. As a part of our mushroom documentation work in Yunnan Province, we were able to find, collect, and identify this mushroom using morphological and molecular techniques. Our paper introduces this mushroom as a new bioluminescent fungal species belonging to the genus *Favolaschia* from southwest Yunnan Province, which was collected from a dead bamboo stump. This is the second report of the genus *Favolaschia* in China as a bioluminescent fungal genus.

Materials and methods

Sample collection and herbarium specimen preparation

The fungal fruit bodies of *Favolaschia* were collected from Xishuangbanna Tropical Botanical Garden, Yunnan Province, China during the month of July, 2021. The fruit bodies of *Favolaschia* were observed growing on dead bamboo (*Bambusa polymorpha* Munro) stumps about 5 cm to 30 cm above the ground. The fruit bodies were photographed *in situ* using a Canon 70D camera mounted with a Canon EF 100mm f/2.8L IS USM Macro lens. Two photographs were taken at night with (F=2.8, ISO=3200, shutter speed=1/250 Secs) and without flashlight (F=2.8, ISO=800, shutter speed=107 Secs) to show the physical characteristics of the bioluminescence. After the photographs were taken, fruit bodies were collected and taken to the laboratory in a plastic box and dried in an electric oven at 45 °C until no moisture remained. The dried fruit bodies were stored inside a plastic container and sent to the Kunming Institute of Botany (KIB), Chinese Academy of Sciences for micromorphology and phylogenetic analyses. All dried fruit bodies were deposited in the Kunming Institute of Botany Herbarium (HKAS). Index Fungorum (IF) number was obtained, as explained in Index Fungorum (2022).

Morphological study

Macro-morphological characteristics were described using the terminology of Largent *et al.* (1977), and colours were observed and classified following the protocol of Ridgeway (1912). The conventions of Vellinga (1988) were used to describe the microscopic characteristics. Free-hand sections were made and taken from the dried fruit bodies under a dissecting microscope (OLYMPUS SZ61). The sections were then mounted on a glass slide in 3–5% KOH using 1–3% Congo red for highlighting tissues (Kreisel & Schauer 1987). Microscopic photographs were taken with a Nikon ECLIPSE Ni compound microscope (Nikon, Tokyo, Japan) with a Canon EOS 600D (Tokyo, Japan) DSLR camera fitted on the top. Basidiospores, basidia, cystidia, stipitipellis, and other microscopic structures were photographed, and measurements were taken using the Tarosoft® Image Framework program v. 0.9.7. The size and shape of basidiospores were measured, and the spore quotient [Q = L/W] was calculated using the mean values of the lengths and widths (X_m). The calculation was made from six different fruit bodies, and the mean was taken from 50 different basidiospores (Miettinen & Larsson 2006). Scanning electron microscope (SEM) photography was carried out by sectioning lamellae from dried fruit bodies and mounting them on aluminum stubs with double-sided adhesive tape, coating them with gold palladium alloy, and observing the basidiospores under the SEM (Hitachi S4800) (Cook *et al.* 1997). The photographs were edited in Adobe Photoshop v. 21.0.2.

DNA extraction, PCR amplification, and sequencing

Dried internal tissues of the fruit bodies were used for DNA extraction. Total DNA was extracted using the Biospin Fungus Genomic DNA Extraction Kit (BioFlux®). The ITS and LSU loci were amplified by Polymerase Chain Reaction (PCR). The PCR amplifications were performed in a total volume of 25 μL of PCR mixtures containing 9.5 μL ddH2O, 12.5 μL of PCR master mix, 1 μL of DNA template, and 1 μL of each primer (10 μM). PCR amplification was performed using primer pairs ITS5/ITS4 for internal transcribed spacer rDNA region (ITS1, 5.8S rDNA and ITS2), LROR/LR5 for the nuclear ribosomal large subunit 28S rDNA gene (LSU) (Vilgalys & Hester 1990; White *et al*. 1990; Liu *et al*. 1999). The PCR cycling amplification conditions incorporated slight modifications, such as a hot start of 3 min at 94°C, followed by 35 cycles of 95 °C for 30 s, 55 °C for 1 min, 72 °C for 1 min, and a final extension step at 72 °C for 10 min for both ITS and LSU regions. The sequencing of purified PCR products was carried out by Sangon Biotech (Shanghai) Co., Ltd., Shanghai, China.

Sequence alignment and phylogenetic analyses

The genetic sequences obtained from PCR were entered into a standard BLAST search in the GenBank database in order to verify the primary identity of the novel fungus. The other sequences used in the phylogenetic analyses were obtained from GenBank, and another BLAST search was used to identify sequences with high similarity indices and sequences identified in recently published data (Cortés-Pérez *et al*. 2019; Karunarathna *et al.* 2020). Two strains of *Mycena abramsii* (HMJAU43523 and HMJAU43606) were used as the outgroup taxa. The sequences and their GenBank numbers are listed in Table 1. Sequences were aligned with MAFFT online server (Katoh & Standley 2013) and manually adjusted using BioEdit v. 7.2.5 (Hall 1999). Gaps were treated as missing data. Clade results from Maximum likelihood (ML) analyses were assessed with 1,000 replicates and were executed on the CIPRES web portal (Miller *et al*. 2011) using RAxML-HPC2 on XSEDE v.8.2.8 (Stamatakis 2014) and raxmlGUI v.1.3.1 (Silvestro & Michalak, 2011). The best-fitting substitution model for each single gene partition was determined in MrModeltest v.2.3 (Nylander 2004). Bayesian inference posterior probabilities (PP) with the GTR+I+G model was used for each partition. Bayesian Markov Chain Monte Carlo (MCMC) analyses were conducted in MrBayes v.3.2.2 (Huelsenbeck & Ronquist 2001). The number of generations was set at 1,000,000 with trees sampled every 1000th generations. Based on the tracer analysis, the first-sampled topologies representing 25% of trees were discarded in the burn-in phase. The remaining trees were then used to calculate posterior probabilities (PP) in the majority rule consensus tree (Larget & Simon 1999). Phylogenetic trees and data files were figured in FigTree v.1.4.0 (Rambaut 2012) and edited using Microsoft Office PowerPoint 2009 and Adobe Photoshop v. 21.0.2. Maximum Likelihood bootstrap values (MLBS ≥60%) and posterior probabilities values for BI (PP ≥0.9) are given above each branch.

TABLE 1. Names, strain numbers and GenBank accession numbers used in the phylogenetic analyses (new taxon is indicated in bold black).

Taxa names	**Culture collection/ Voucher number**	**GeneBank accession numbers**	
		LSU	**ITS**
Favolaschia andina	KG0025	HM246679	HM246678
Favolaschia aurantiaca	FK2047	-	JX987670
Favolaschia auriscalpium	Isolate 5	-	KY649461
Favolaschia austrocyatheae	PDD: 75609	-	NR132809
Favolaschia austrocyatheae	PDD:112220	-	MH578516
Favolaschia brevibasidiata	Cui 6573	-	MZ661794
Favolaschia brevistipitata	Dai 19780	MZ661742	MZ661772
Favolaschia brevistipitata	Dai 19855	MZ661743	MZ661773
Favolaschia brevistipitata	Dai 19856	MZ661744	MZ661774
Favolaschia calocera	BCC36684	MN128539	MN128538
Favolaschia cf. calocera	JM98/186	AF261418	-
Favolaschia cinnabarina	PDD:103392	-	KF727415
Favolaschia cinnabarina	RVPR82	AF261416	-
Favolaschia claudopus	Dai 18656	MZ661735	MZ661775

...continued on the next page

TABLE 1. (Continued)

Taxa names	Culture collection/ Voucher number	GeneBank accession numbers	
		LSU	ITS
Favolaschia cyatheae	PDD75316	-	DQ026256
Favolaschia dealbata	KG0015	HM246677	-
Favolaschia heliconiae	KG0026	HM246680	-
Favolaschia longistipitata	Dai 19799	MZ661739	MZ661784
Favolaschia longistipitata	Dai 19893	MZ661740	MZ661785
Favolaschia longistipitata	Dai 20019	MZ661741	MZ661786
Favolaschia luteoaurantiaca	SP445750	-	NR_132874
Favolaschia macropora	KG0027	HM246682	HM246681
Favolaschia manipularis	Dai 20612	-	MZ801776
Favolaschia manipularis	Dai 20653	-	MZ801777
Favolaschia minima	PDD75430	-	DQ026258
Favolaschia minutissima	Dai 20085	MZ661736	MZ661791
Favolaschia minutissima	Dai 20086	MZ661737	MZ661792
Favolaschia minutissima	Dai 20088	MZ661738	MZ661793
Favolaschia peziziformis	ICMP15757	AY572008	DQ026255
Favolaschia pustulosa	Dai 19892	MT293227	MT292326
Favolaschia sp.	BCC18686	MN093317	MN093316
Favolaschia sp.	4550	-	JX987668
Favolaschia sp.	DUKE3195	-	DQ026236
Favolaschia sp.	DUKE2708	-	DQ026234
Favolaschia sp.	DUKE2876	-	DQ026235
Favolaschia sp.	TH1018	-	DQ026241
Favolaschia sprucei	TH6418	-	DQ026246
Favolaschia tonkinensis	JM98229	-	DQ026247
Favolaschia vararioteca	DUKE4038	-	DQ026244
Favolaschia xtbgensis	**HKAS 121667**	**OL413044**	**OL413048**
Favolaschia xtbgensis	**HKAS 121975**	**OL413035**	**OL413036**
Mycena abramsii	HMJAU43523	MK629350	MH396628
Mycena abramsii	HMJAU43606	MK629355	MH396629

Results

Phylogenetic analyses

The phylogenetic analyses were inferred from ML analyses using a combined ITS and LSU ribosomal DNA data set. For the ITS and LSU regions, 44 taxa distributed in the genus *Favolaschia* with two outgroup taxa in the genus *Mycena*, were aligned and their ends trimmed to create a data set of 1746 (including gaps) base pairs.

In the combined tree (Fig. 2), the final alignment contained 44 strains, with *Mycena abramsii* HMJAU43523 and HMJAU43606 as outgroup taxa. Tree topology of the ML analysis was similar to the BI. The matrix had distinct alignment patterns, with a final ML optimization likelihood value of -6732.817711 (ln). All free model parameters were estimated by the RAxML model, with 529 distinct alignment patterns and 38.84% undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.241693 , C = 0.207448 , G = 0.253528 , T = 0.297330 ; substitution rates AC = 1.454680, AG = 2.974125 , AT = 1.921702 , CG = 0.804913 , CT = 5.523918 , GT = 1.000000; gamma distribution shape parameter alpha = 0.603839; and Tree-Length = 1.072009.

The combined ITS and LSU phylogenetic analyses reveal that the new species, *Favolaschia xtbgensis*, differs from the closely related *Favolaschia* sp. BCC 18686 with strong statistical support values (94% BS and 0.98 PP), confirming it as a distinct taxon.

Taxonomy

Favolaschia xtbgensis Karunarathna & Nimalrathna *sp. nov.* Figs. 1,3

Index Fungorum number: IF559348

Etymology*:* The species epithet "xtbgensis" refers to the place "Xishuangbanna Tropical Botanical Garden" where the type species was collected.

Holotype*:—HKAS121667*

***Diagnosis*:—**This new species can be distinguished from other taxa in the genus *Favolaschia* by white to grayish lilac, translucent, smooth and spongy pileus; 1 × 2 mm size 180–200 pores in hymenophore; 8.2–10.4 × 6.1–8.2 µm size basidiospores; 30–44 × 10–13 µm size basidia and the absence of cheilocystidia and pleurocystidia.

Pileus 5–12 mm diam., plano-convex, surface white to grayish lilac, translucent, smooth, spongy, margin not entire. *Hymenophore* poroid, outermost pores close to the margin are smaller than the center, mostly hexagonal, pores 1 × 2 mm in size, 180–200 in number/hymenophore. *Stipe* concolorous with pileus, short, 2–4 mm long, 1–2 mm in diameter, lateral, eccentric, cylindric, surface smooth. *Context* white and thin. Spore print white.

Luminescence. Emitting soft green light in the fruit bodies, spore print and the mycelium of the fruit bodies (Fig. 1B).

Basidiospores 8.2–10.4 × 6.1–8.2 µm (Q =1.27, total number of spores examined = 50), subglobose, white, spore surface rough, large oil drop inside. *Basidia* (Fig. 3A) 30–44 × 10–13 µm, clavate, 4 spored, sterigmata 6–7 × 1–2µm. *Hymenophore edge* fertile, cheilocystidia and pleurocystidia absent. Gloeocystidia and Acanthocystida absent. *Pileal trama* (Fig. 3B) composed of thin-walled, gelatinized, filamentous hyphae, 7–10 µm in diameter, branched. Clamp-connections present.

Ecology and distribution*:*—Caespitose, growing up to 20–30 fruit bodies, Southwest China (Yunnan Province, Menglun City), June to September.

Material examined*:*—CHINA. Yunnan Province, Menglun City, 26°54'50.58"N 99°46'50.76"E, elev. 550 m, on dead bamboo, 21 July 2021, Thilina Nimalrathna (HKAS121667, **holotype**).

Additional specimen examined:—CHINA. Yunnan Province, Menglun City, 26°54'50.58"N 99°46'50.76"E, elev. 550 m, on dead bamboo, 22 July 2021, Thilina Nimalrathna (HKAS 121975, **paratype**).

FIGURE 1. Fruit bodies of *Favolaschia xtbgensis* in the field, at night. A. Photographed with the aid of a flashlight. B. Photographed in complete darkness. Scale bars: A, B=10 mm.

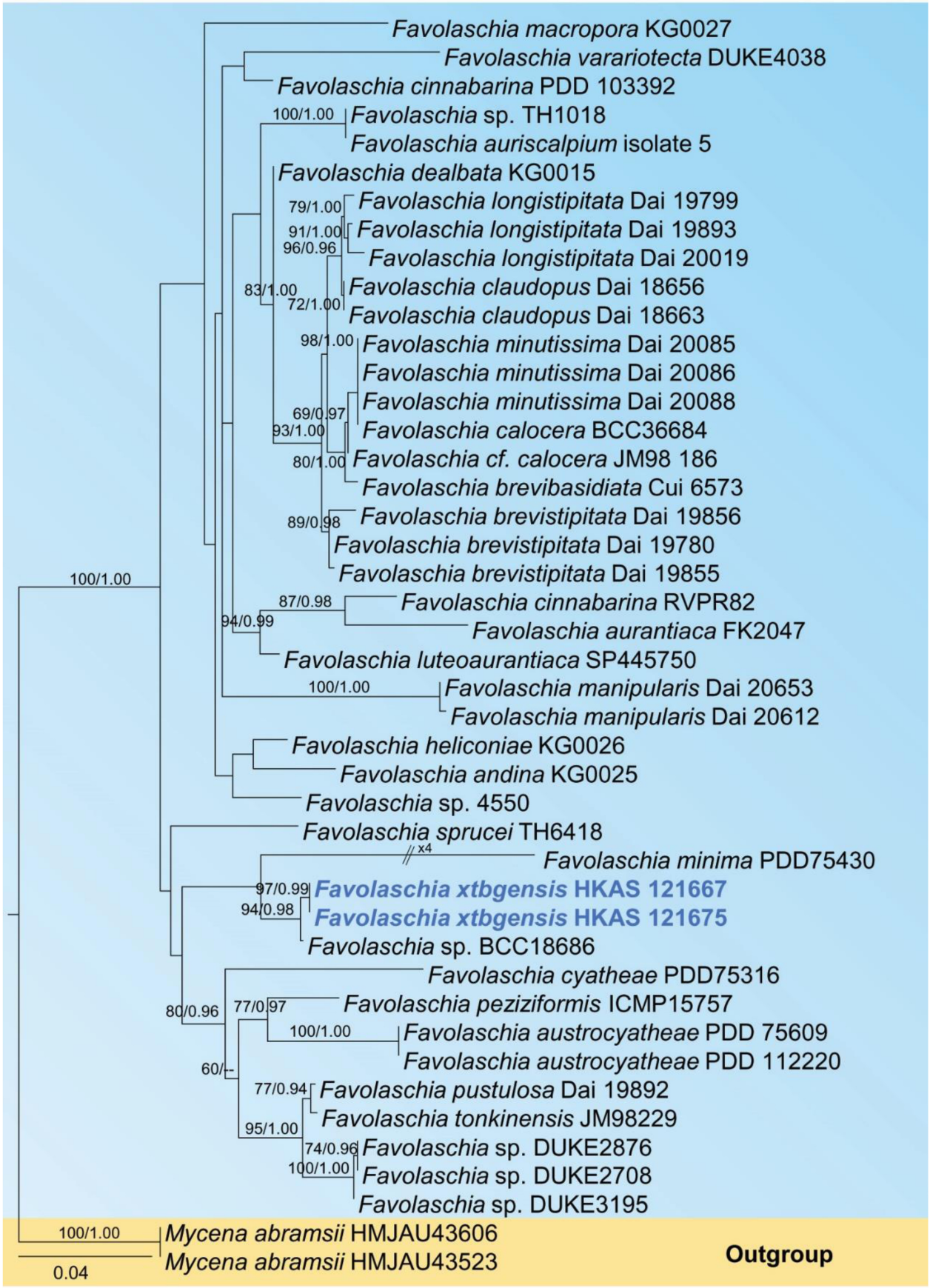

FIGURE 2. Maximum Likelihood tree generated using RAxML based on combined ITS and LSU sequence data. MLBS Bootstrap support values for maximum likelihood (≥60%) and posterior probability values (PP) for BI (≥0.90 PP) are given above each branch. The new species is shown in bold blue. The tree is rooted to *Mycena abramsii* (HMJAU43606, HMJAU43523).

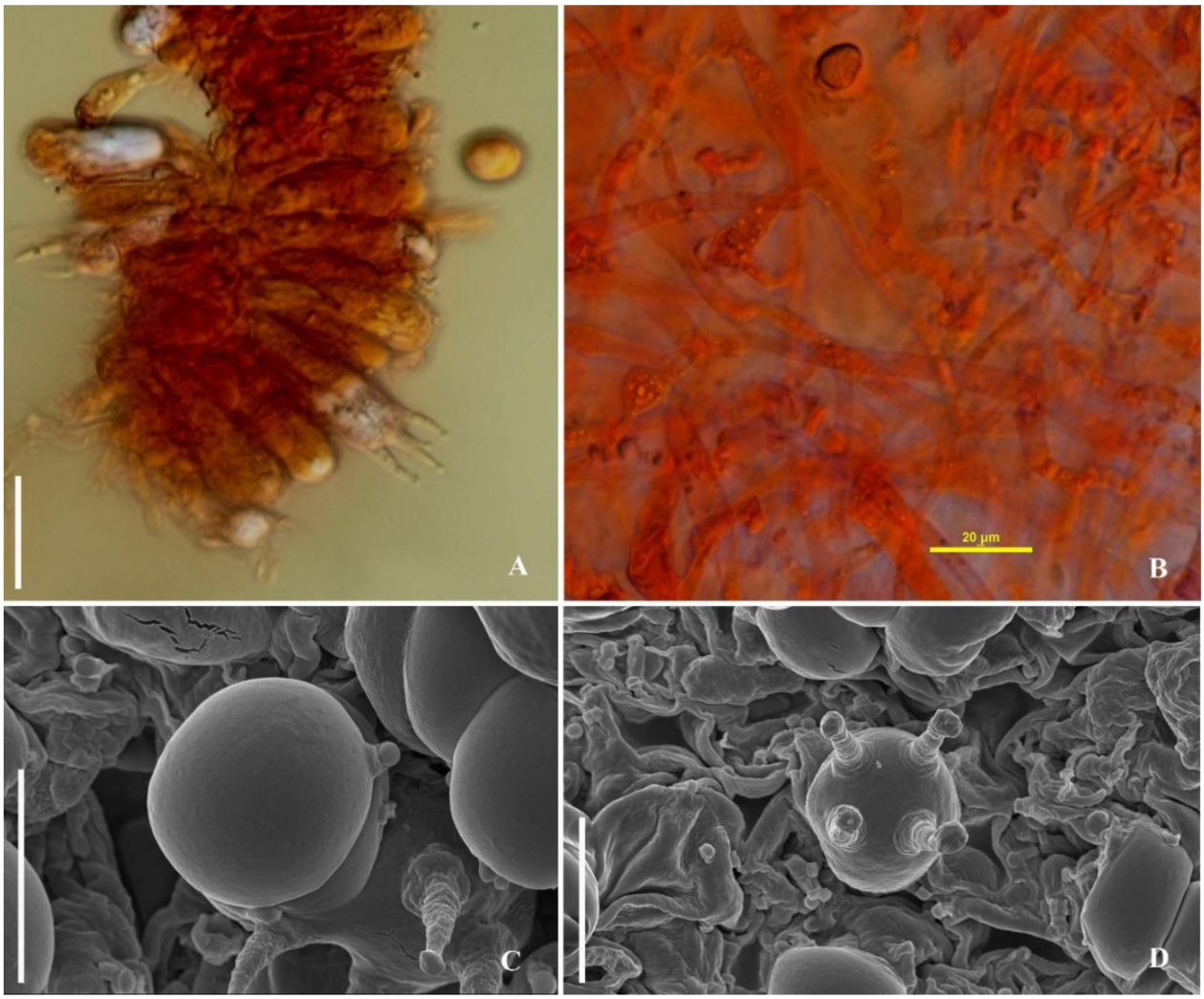

FIGURE 3. Microscopic structures of *Favolaschia xtbgensis* (HKAS121667, holotype). A. Hyphae at edge of pores showing basidia. B. Hyphae of pileus cortex. C. Basidiospores under SEM. D. Upper view of a basidium with sterigmata and young basidiospores under SEM. Scale bars: A=20 µm; C, D=10 µm.

Discussion

Since most of the species in the genus *Favolaschia* lack sequence data in GenBank, we compared the species described in the monograph of Singer (1945) with our new species, and found that *Favolaschia tonkinensis* is morphologically similar to our new species.

Favolaschia xtbgensis sp. nov. is a look alike with *F. tonkinensis* (Singer1945; Krishnendu *et al.* 2014; Zhang & Dai 2021), in having a pileus of similar diameter (*F. xtbgensis* = 5–12 mm, *F. tonkinensis*= 7.5–9 mm) and a white to grayish lilac, translucent, smooth and spongy surface. Moreover, both have smaller outermost pores closer to the margin than center, but *F. tonkinensis* has smaller pores that are 0.8 mm in size and higher (200–250) in number/hymenophore (Krishnendu *et al.* 2014). However, the size of basidiospores is slightly larger in *F. tonkinensis* (8–12.5 × 7–10.5µm) (Singer 1945; Johnston *et al.* 2006), with subglobose, white spores, and moreover, *F. tonkinensis* contains a smooth spore surface versus the rough spore surface of *F. xtbgensis*. *Favolaschia xtbgensis* is similar to *F. tonkinensis* with its 4-spored basidia, but *F. tonkinensis* has smaller basidia (35.7–39.6 × 7.88–8.27 µm) and larger sterigmata (7.88–8.27 × 3.15–3.55 µm). Furthermore, *F. xtbgensis* is phylogenetically distinct from *F. tonkinensis* (Fig. 2). A synopsis table showing the characteristics of *Favolaschia* species reported from China is shown below in Table 1.

TABLE 2. Morphological features of *Flavolaschia* species reported from China.

Taxon name	Pileus	Stipe	Trama	Basidia	Basidiospores	Cystidia	Pileipellis/ Stipitipellis	Reference
Favolaschia brevibasidiata Q.Y. Zhang & Y.C. Dai	Pileus 2–7 × 1.5–4 mm, apricot-orange when fresh, orbicular, cream buff when dry; pileal surface slightly undulated in a reticulate pattern matching the pores below, sometimes faintly pruinose when dry.	Stipe obvious, laterally attached, concolorous with pileus, cylindrical or tapered to a slightly wider base, sometimes curved, very finely velutinate under a lens, 2–8 mm long.	Hyphae subparallel along tubes, partly branched, strongly gelatinized, hyaline, thin-walled, some slightly inflated, 2–4(–6) µm in diameter.	23–30 × 8–10 µm, few fusoid, cylindric or clavate, contain some guttules, 2–spored, sterigmata 1.5–4 µm long; basidioles in shape similar to basidia, but slightly smaller.	10–12(–13.5) × 6–7.8(–8) µm, L = 11.33 µm, W = 6.9 µm, Q = 1.64 (n = 30/1), ellipsoid to broadly ellipsoid, hyaline, thin-walled, smooth, with some guttules, faintly IKI+, CB−.	Gloeocystidia present at the edges of pores, in hymenium and pileipellis, slightly thick-walled, smooth, contents dense and yellow-orange, those in hymenium clavate to ventricose, 25–36 × 10–18 µm; those at the pore edges more or less the same size as those in pileipellis, clavate, cylindrical or subglobose, 13–36 × 10–22 µm. Acanthocysts at the edges of pores and in pileipellis, slightly thick-walled, contents dense and yellow-orange, clavate, short vesiculose to pyriform-elongated, 15–47 × 9–12 µm.	Pileipellis comprising a palisade of acanthocysts and gloeocystidia. Hyphae in stipe parallel along stipe, slightly thick-walled, some inflated, 3–6(–11) µm in diameter. Clamp connections absent.	Zhang & Dai (2021)
Favolaschia longistipitata Q.Y. Zhang & Y.C. Dai	Pileus 2–12 × 1.5–8 mm, flabelliform to subcircular, lemon-chrome when fresh, becoming curry yellow when dry; pileal surface slightly undulated in a reticulate pattern matching the pores below, sometimes faintly pruinose when dry.	Stipe obvious, laterally attached, concolorous with pileus, cylindrical or tapered to a slightly wider base, sometimes curved, very finely velutinate under a lens, 4–12 mm long.	Hyphae subparallel along tubes, strongly gelatinized, partly branched, hyaline, thin-walled, some slightly inflated, 2–4(–6) µm in diameter. Pileipellis comprising a palisade of acanthocysts and gloeocystidia. Hyphae in stipe parallel along stipe, slightly thick-walled, some slightly inflated, 2–4(–7) µm in diameter.	32–47 × 9–13 µm, cylindric or clavate, few fusoid, contain some guttules, 2–spored, sterigmata 4–6 µm long; basidioles in shape similar to basidia, but slightly smaller	(9–)9.8–13 × 6–8 µm, L = 11.31 µm, W = 6.72 µm, Q = 1.62–1.74 (n = 120/4), ellipsoid to oblong, hyaline, thin-walled, smooth, with some guttules, faintly IKI+, CB−.	Gloeocystidia present at the edges of pores, in hymenium and pileipellis, slightly thickwalled, smooth, contents dense and yellow-orange, those in hymenium pyriform, 25–45 × 10–12 µm; those at pore edges more or less the same size as those in pileipellis, subglobose or ventricose, 20–40 × 6–21 µm. Acanthocysts at the edges of pores and in pileipellis, slightly thick-walled, contents dense and yellow-orange, elongated to irregular shaped, 16–42 × 5–13 µm.	Pileipellis comprising a palisade of acanthocysts and gloeocystidia. Hyphae in stipe parallel along stipe, slightly thick-walled, some slightly inflated, 2–4(–7) µm in diameter.	Zhang & Dai (2021)

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TABLE 2. (Continued)

Taxon name	Pileus	Stipe	Trama	Basidia	Basidiospores	Cystidia	Pileipellis/ Stipitipellis	Reference
Favolaschia manipularis	Pileus 0.3–2.5 cm in diam., conico-campanulate to convex with conical umbo, translucently reticulate, hygrophanous, white pruinose, whitish, greyish to hyaline when moist, purely white to yellowish when dried up.	Stipe 20–65 × 0.5–3 mm, hollow, hyaline to white, completely white, pruinose, cylindrical, thickened in the base.	Hyphae of the cortical layer of the stipe 3–8 µm wide, clamped, with diverticulate terminal cells.	Basidia 16–18 × 6–8 µm, narrowly clavate, clamped, with up to 6 µm long sterigmata.	Basidiospores 6–8 × 4–5 µm, Q = 1.2–1.6, smooth, white, ellipsoid to broadly ellipsoid and amyloid.	Cheilocystidia 51–75 × 7–13 µm, sterile lamella edge, lageniform, subcylindrical or subclavate, mostly diverticulate or irregularly branched in the apex, simple lageniform with more or less developed neck. Pleurocystidia not visible. Pileocystidia 25–34 × 8–11 µm, abundant, irregularly shaped, lageniform to subclavate, with excrescences. Caulocystidia 24–39 × 6–8 µm, abundant, irregularly shaped.	Pileipellis hyphae 5–16 µm wide, clamped, with diverticulate terminal cells.	Teng (1963)
Favolaschia minutissima Q.Y. Zhang & Y.C. Dai	Pileus 2–4 × 1–3 mm, reniform to suborbicular, apricot-orange when fresh, becoming cream buff when dry; pileal surface slightly undulated in a reticulate pattern matching the pores below, sometimes faintly pruinose when dry.	Stipe often scarcely developed, laterally attached, concolorous with pileus, short and curved, cylindric, very finely velutinate under a lens, 0.5–4 mm long.	Hyphae subparallel along tubes, strongly gelatinized, partly branched, hyaline, thin-walled, some slightly inflated, 2–4(–6) µm in diameter. Pileipellis comprises a palisade of acanthocysts and gloeocystidia. Hyphae in stipe parallel along stipe, slightly thick-walled, some slightly inflated, 2– 4(–7) µm in diameter.	25–37 × 7–9.5 µm, clavate, few fusoid, contain some guttules, 2–spored, sterigmata 5–7 µm long; basidioles in shape similar to basidia, but slightly smaller	(6–)7.5–11(–11.5) × (4.8–)5–7.2(–7.8) µm, L = 9.16 µm, W = 6.10 µm, Q = 1.46–1.56 (n = 90/3), broadly ellipsoid to ovoid, hyaline, thin-walled, smooth, with some guttules, faintly IKI+, CB−	Gloeocystidia present at the edges of pores, in hymenium and pileipellis, slightly thick-walled, smooth, contents dense and yellow-orange, those in hymenium clavate to vesiculose, 30–42 × 10–12.5 µm; those at the pore edges more or less the same size as those in pileipellis, pyriform, subglobose or ventricose, 20–48 × 10–26 µm. Acanthocysts at the edges of pores, in hymenium and pileipellis, slightly thick-walled, contents dense and yellow-orange, clavate to oblong, 9–45 × 7–12 µm.	Pileipellis comprising a palisade of acanthocysts and gloeocystidia. Hyphae in stipe parallel along stipe, slightly thick-walled, some slightly inflated, 2– 4(–7) µm in diameter.	Zhang & Dai (2021)

...continued on the next page

TABLE 2. (Continued)

Taxon name	Pileus	Stipe	Trama	Basidia	Basidiospores	Cystidia	Pileipellis/ Stipitipellis	Reference
Favolaschia calocera R.Heim	Pileus 5–20 mm diam., convex, typically lobed on both sides of the stipe creating a reniform shape, surface slightly undulate in a reticulate pattern matching the pores below, when fresh glabrous, orange to pale orange, when dry sometimes faintly pruinose, brownish orange or orange.	Stipe 1.2–15 × 0.8–2.5 mm, laterally attached, cylindrical or tapered to a slightly wider base, sometimes curved depending on position of fruit body on substrate, concolorous with pileus, glabrous, sometimes faintly pruinose when dry		Basidia 28–35 × 6–10 µm, obclavate, tapered slightly towards the base, 2-spored, sterigmata 8.5–14 µm long.	Spores 9–12.5 × 6.5–8.5 µm, broadly ellipsoid or broadly ovoid, bilaterally symmetrical in face view, asymmetrical in side view, apex broadly rounded, base broadly rounded or broadly conical, hilum truncate or obtuse, excentrally oriented, wall smooth, hyaline,	Gloeocystidia cylindric to clavate, walls slightly thickened, contents dense and yellow-orange; those amongst the basidia cylindric, 8.5–12.5 µm, those on the pore edges and in the pileipellis broad-clavate, 11–25 µm diam. Acanthocysts on edges of pores and in pileipellis, 35–52 × 8.5–14 µm, cylindric to subclavate, apex rounded or broadly rounded, typically tapering to a narrow base, wall hyaline, with numerous rod-shaped diverticula	Pileipellis comprises a palisade of acanthocysts and gloeocystidia. Clamp connections lacking.	Johnston *et al.* (2006)
Favolaschia pustulosa (Jungh.) Kuntze	Pileus 5–85 mm diam., spherical, subspherical, or reniform in outline, convex, surface slightly undulate in a reticulate pattern matching the pores below, when fresh white, somewhat translucent, glabrous, when dry pale yellow-brown to brown, often somewhat powdery in appearance.	Stipe present or absent, when present up to 5 × 1–6 mm, attached laterally, concolorous with pileus, glabrous, lacking basal mycelium		Basidia 25–35 × 5.5–8 µm, 4-spored, obclavate, tapered towards the obtuse base, sterigmata 3–6 µm long.	Spores 7.5–10 × 5–7 µm, broadly ellipsoidal, apex broadly rounded, base broadly rounded or broadly conical with distinct hilar appendage, wall smooth, hyaline, amyloid. Cortex of hyaline, loosely interwoven hyphae 5–10 µm diam., widely spaced in gelatinous matrix; gloeoporous hyphae lacking		Pileipellis barely differentiated from cortex, hyphae slightly more densely interwoven and a few with free ends; edges of pores similar in structure, sterile, barely differentiated from trama	Johnston *et al.* (2006)
Favolaschia tonkinensis	Pileus 7.5–9 mm diam., plano-convex, surface white, translucent, soft, spongy, covered with a thick gelatinous matrix, margin entire.	Stipe almost sessile, 2 1 mm in diameter, lateral, eccentric, cylindric, surface smooth.	Pileal trama composed of thin-walled filamentous hyphae, 11.82 3.94 µm, embedded in thick gelatinous matrix, inamyloid. Clamp-connexions and	Basidia 35.7–39.6 7.88–8.27 µm, cylindro clavate, 4 spored, tetrasterigmatic, sterigmata 7.88–8.27 3.15–3.55 µm.	Spores (7.88–)9.45–9.85(–10.24) (7.09–)7.88–8.67(–9.85) µm [Q =1.09, total number of spores examined=30], subglobose, white, smooth, amyloid, granular contents present	Cheliocystidia and pleurocystidia absent.		Krishnendu *et al.* (2014), Zhang & Dai (2021)

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