Mycosphere 14(1): 745–776 (2023) www.mycosphere.org ISSN 2077 7019
Article
Doi 10.5943/mycosphere/14/1/9

New taxa of Boletaceae from China

Wu G[1,2#], Li H-J[3#], Horak E[4], Wu K[1,2], Li G-M[1,2], and Yang Z-L[1,2*]

[1]*CAS Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650201, Yunnan, China*
[2]*Yunnan Key Laboratory for Fungal Diversity and Green Development, Kunming 650201, Yunnan, China*
[3]*National Institute of Occupational Health and Poison Control, Chinese Center for Disease Control and Prevention, Beijing 100050, China*
[4]*Schlossfeld 17, Innsbruck A-6020, Austria*

Wu G, Li H-J, Horak E, Wu K, Li G-M, Yang Z-L 2023 – New taxa of Boletaceae from China. Mycosphere 14(1), 745–776, Doi 10.5943/mycosphere/14/1/9

Abstract

China possesses a remarkably rich fungal diversity, particularly among boletes, which can be attributed to its heterogeneous plant communities and varied topography and geography. Despite significant taxonomic efforts, the diversity of bolete species remains inadequately characterized in China, and it is expected that many unexplored taxa are yet to be discovered. Through a combination of morphological observations and molecular phylogenetic analyses, this work identified 12 new taxa of Boletaceae, including two new genera (*Acyanoboletus* and *Hongoboletus*), nine new species (*Acyanoboletus controversus*, *Acyanoboletus dissimilis*, *Cyanoboletus fagaceophilus*, *Neoboletus brunneorubrocarpus*, *Rubroboletus flavus*, *Rubroboletus serpentiformis*, *Suillellus flaviporus*, *Suillellus pinophilus*, *Suillellus yunnanensis*) and one new combination (*Hongoboletus ventricosus*). Detailed illustrations and comparisons with other related species were provided to aid in identification. This study can significantly contribute to our understanding of bolete species diversity in China and allied regions.

Keywords – 12 new taxa – bolete – East Asia – molecular phylogeny – taxonomy

Introduction

In recent years, the species diversity of fungal family Boletaceae Chevall. has been well documented worldwide with detailed data on morphology, molecular phylogeny and ecology, meanwhile a large number of new taxa are discovered especially in Asian and American regions (Neves et al. 2012, Arora & Frank 2014, Henkel et al. 2016, Raspé et al. 2016, Wu et al. 2016a, Wu et al. 2018, Chai et al. 2019, Vadthanarat et al. 2019, Zhang et al. 2019, Li & Yang 2021, Badou et al. 2022, Magnago et al. 2022).

Statistically, until now, in total ca. 100 genera of Boletaceae have been reported, of which 65 were proposed with molecular evidence. About 800 species of Boletaceae were recognized in the world (Kirk et al. 2008). Since 2008, over 370 new species have been additionally described according to MycoBank database. Up to this point, about 1200 species of Boletaceae have been documented globally.

Previous studies have demonstrated varying distribution patterns of boletes. Some of them can be widely distributed in boreal forests from Europe, Asia to North America, such as *Boletus edulis* Bull. and *Strobilomyces strobilaceus* (Scop.) Berk., while many others showed clearly

Submitted 13 January 2023, Accepted 10 May 2023, Published 12 June 2023
Corresponding Author: Zhu-Liang Yang – e-mail – fungi@mail.kib.ac.cn
# These authors contributed equally as first authors to this work

continental endemism such as *Boletus violaceofuscus* W.F. Chiu, *Caloboletus panniformis* (Taneyama & Har. Takah.) Vizzini, *Rubroboletus sinicus* (W.F. Chiu) Kuan Zhao & Zhu L. Yang from East Asia (Zhao et al. 2014a, Zhao et al. 2014b, Cui et al. 2016), *Caloboletus inedulis* (Murrill) Vizzini, *Bothia castanella* (Peck) Halling, T.J. Baroni & Manfr. Binder from North America (Smith & Thiers 1971, Bessette et al. 2000), *Amoenoboletus mcrobbii* (McNabb) G. Wu, E. Horak & Zhu L. Yang and *Ionosporus australis* Khmeln. & Halling from Oceania (Khmelnitsky et al. 2019, Wu et al. 2022), *Afroboletus* Pegler & T.W.K. Young from Africa (Pegler & Young 1981, Han et al. 2018), *Brasilioporus* A.C. Magnago et al., *Binderoboletus* T.W. Henkel & M.E. Sm., *Guyanaporus* T.W. Henkel & M.E. Sm. and *Singerocomus* T.W. Henkel & M.E. Sm. from South America (Magnago et al. 2022). Additionally, a majority of newly-published Boletaceae species have exhibited limited distribution ranges, though further collections and studies may expand their known ranges in the future.

In China, particularly in its southwestern region, the extraordinary plant diversity, intricate terrain and geography, and highly variable climate (Yang 2005, Sun et al. 2017) have greatly fostered the high levels of fungal species diversity and endemism, including within Boletaceae. In total, about 55 genera and 400 species of Boletaceae in China were determined by molecular phylogenetic evidence (Li et al. 2011, Zeng et al. 2013, Wu et al. 2014, Zhao et al. 2014b, Zhu et al. 2014, Zhao et al. 2015, Zhu et al. 2015, Wu et al. 2016a, Wu et al. 2016b, Zeng et al. 2016, Chai et al. 2019, Zhang et al. 2019, Li & Yang 2021, Meng et al. 2021, Fu et al. 2022, Wang et al. 2022, Wu et al. 2022, Zhou et al. 2022), which are account for about 1/2 of global genera and 1/3 of global species in this family. Most of them are endemic to East Asia, and at least half of them is restricted in China based on current knowledge. However, there may still be many new boletoid species waiting to be discovered through systematic explorations and researches in China. In this study, we primarily investigated the new bluing boletes in China, some of which have the potential to be poisonous.

Materials & Methods

Sampling and morphological studies

The samples of target boletes were collected from various regions across China, including the East, Central and Southwest China. All specimens were deposited in the Cryptogamic Herbarium (HKAS) of the Kunming Institute of Botany, Chinese Academy of Sciences. Additionally, certain specimens were duplicated and deposited at National Institute of Occupational Health and Poison Control, Chinese Center for Disease Control and Prevention (abbreviated as NIOHP here). Macroscopic characteristics were recorded from fresh basidiomes. Microscopic structures were observed by using dried material revived in 5% KOH and H_2O under ZEISS Axio Scope.A1 microscope. Sections of the pileipellis were radially taken about midway between the center and margin of the pileus. Sections of the stipitipellis were prepared from longitudinal scalps. All microscopic features were sketched using a drawing tube. For the explanation of basidiospore data, see Wu et al. (2016b).

DNA isolation, PCR, and sequencing

Genomic DNA was extracted from dried materials using the CTAB method (Doyle & Doyle 1987). Fragments of five nuclear loci, including nuc rDNA ITS1-5.8S-ITS2 (ITS), nuc 28S rDNA (nrLSU), translation elongation factor 1-α (*TEF1*), RNA polymerase II largest subunit (*RPB1*) and RNA polymerase II second largest subunit (*RPB2*) were amplified using ITS1F/ITS4, LR0R/LR5, EF1-B-F1 (or EF1-B-F2)/EF1-B-R, RPB1-B-F/RPB1-B-R, RPB2-B-F1 (or RPB2-B-F2)/RPB2-B-R, respectively (Vilgalys & Hester 1990, White et al. 1990, Gardes & Bruns 1993, Wu et al. 2014). PCR procedures and sequencing for these loci followed the protocols described by Wu et al. (2014) and Feng et al. (2012). The new generated sequences were submitted to GenBank (Table 1).

Table 1 Fungal names, collection information, and GenBank accession numbers.

Samples	Voucher numbers	Locality	ITS	nrLSU	EF1	RPB1	RPB2
Acyanoboletus controversus	**HKAS 126560**	**China**	**OQ888701**	**OQ888714**	**OQ873451**	**OQ873469**	**OQ873490**
Acyanoboletus controversus	**HKAS 101248**	**China**		**OQ888715**	**OQ873452**	**OQ873470**	**OQ873491**
Acyanoboletus dissimilis	**ZT14030**	**Malaysia**		**OQ888716**	**OQ873453**	**OQ873471**	**OQ873492**
Amoenoboletus granulopunctatus	HKAS 56280	China		KF112418	KF112265	–	KF112708
Amoenoboletus miraculosus	Z-ZT14046	Malaysia		MW520188	MW566745	–	–
Baorangia major	OR0486	China		–	MG897433	–	MG897443
Baorangia pseudocalopus	HKAS 75081	China		KF112356	KF112168	KF112520	KF112678
Baorangia rufomaculata	4414	USA		KF030248	KF030406	KF030369	–
"*Boletus* cf. *fagicola*"	Mushroom Observer #245071	USA		MH257548	MH337283	–	–
"*Boletus* cf. *subvelutipes*"	Mushroom Observer #206608	USA		MH220333	MH318609	–	–
Boletaceae sp.	JD0693	Burundi		–	MH645591	–	MH645599
Butyriboletus appendiculatus	BR50200892955-50	Belgium		KJ605677	KJ619472	KJ619481	–
Butyriboletus frostii	TENN:SAT1221511	USA		KP055021	KP055018	KP055024	KP055027
Butyriboletus roseoflavus	HKAS 54099	China		KF739665	KF739779	KF739741	KF739703
Butyriboletus ruber	HKAS 106891	China		MN930518	MT063123	MT063118	MT063120
Cacaoporus pallidicarneus	HKAS 52601	China		KF112469	–	KF112552	KF112732
Cacaoporus tenebrosus	OR0654	Thailand		–	MK372275	–	MK372288
Caloboletus aff. *calopus*	HKAS 74739	China		KF112335	KF112166	KF112507	KF112667
Caloboletus panniformis	HKAS 55444	China		KF112334	KF112165	KF112506	KF112666
Caloboletus peckii	Mushroom Observer #246697	USA		MH220330	MH318614	–	–
Chalciporus rubinelloides	HKAS 57362	China		KT990563	KT990759	–	KT990398
Costatisporus cyanescens	Henkel9061	Guyana		LC053662 (Henkel9067)		LC053663	LC053664
Crocinoboletus laetissimus	FHMU2030	China		MK850935	MK850948	–	MK850944
Crocinoboletus rufoaureus	HKAS 53424	China		KF112435	KF112206	KF112533	KF112710
Cupreoboletus poikilochromus	GS-10070	Italy		KT157060	KT157072	KT157066	KT157068
Cyanoboletus bessettei	ARB1393A	USA		–	MW737482	–	MW737457
Cyanoboletus brunneoruber	HKAS 80579_1	China		KT990568	KT990763	KT990926	KT990401
Cyanoboletus cyaneitinctus	Farid 920	USA		MW662579	MW737503	MW737465	–
Cyanoboletus fagaceophilus	**HKAS 123872**	**China**		**OQ888717**	**OQ873454**	**OQ873472**	**OQ873493**

Table 1 Continued.

Samples	Voucher numbers	Locality	ITS	nrLSU	EF1	RPB1	RPB2
Cyanoboletus fagaceophilus	**HKAS 126556**	**China**	**OQ888702**	**OQ888718**	**OQ873455**	**OQ873473**	**OQ873494**
Cyanoboletus fagaceophilus	**HKAS 80691**	**China**		**OQ888719**	**OQ873456**	**OQ873474**	**OQ873495**
Cyanoboletus instabilis	HKAS 59554	China		KF112412	KF112186	KF112528	KF112698
Cyanoboletus pulverulentus	MG 628a	Italy		KT157064	KT157073	–	KT157069
Cyanoboletus sinopulverulentus	HKAS 59609	China		KF112366	KF112193	KF112529	KF112700
Cyanoboletus sp.	HKAS 59418	China		KT990570	KT990765	–	KT990403
Cyanoboletus sp.	HKAS 76850	China		KF112343	KF112187	KF112527	KF112697
Cyanoboletus sp.	HKAS 90208_1	China		KT990571	KT990766	–	KT990404
Cyanoboletus sp.	OR0322	Thailand		–	MH614722	–	MH614768
Erythrophylloporus aurantiacus	REH7271	Costa Rica		–	MH614715	–	MH614761
Erythrophylloporus cinnabarinus	GDGM70536	China		MH374045	MH378802	MH374031	MH374035
Hongoboletus sp.	OR1002	Thailand		–	MH645593	–	MH645601
Hongoboletus ventricosus	**TNS-F-44611**	**Japan**	**OQ888710**	**OQ888732**	–	**OQ873487**	**OQ873507**
Hongoboletus ventricosus	**TNS-F-44612**	**Japan**		**OQ888733**	–	**OQ873488**	**OQ873508**
Hongoboletus ventricosus	**HKAS 122793**	**China**	**OM22031**	**OM219809**	**OM562214**	**OM562216**	**OM562220**
Hongoboletus ventricosus	**HKAS 63598**	**China**		KF112317	KF112152	KF112502	KF112663
Imperator torosus	MB000258	Germany		–	MW566748	–	MW560082
Lanmaoa angustispora	HKAS 74759	China		KM605140	KM605155	KM605167	KM605178
Lanmaoa asiatica	HKAS 63516	China		KT990584	KT990780	KT990935	KT990419
Leccinum scabrum	HKAS 56371	China		KT990587	KT990782	–	KT990423
Neoboletus antillanus	JBSD127417	Dominican Republic		MK388302	–	–	MK488082
Neoboletus brunneissimus	HKAS 52660	China		KF112314	KF112143	KF112492	KF112650
Neoboletus brunneorubrocarpus	**HKAS 126552**	**China**		**OQ888736**	–	–	–
Neoboletus brunneorubrocarpus	**HKAS 126559**	**China**		**OQ888720**	**OQ873457**	**OQ873475**	**OQ873496**
Neoboletus brunneorubrocarpus	**HKAS 76660**	**China**	**OQ888703**	KF112328	KF112180	KF112540	KF112731
Neoboletus erythropus	AF2922	France		–	MG212596	–	MG212638
Neoboletus ferrugineus	HKAS 77617	China		KT990595	KT990788	KT990943	KT990430
Neoboletus flavidus	HKAS 59443	China		KU974139	KU974136	KU974142	KU974144
Neoboletus hainanensis	HKAS 59469	China		KF112359	KF112175	KF112500	KF112669
Neoboletus infuscatus	FHMU3372	China		MW293787	MW307257	–	–
Neoboletus luridiformis	AT2001087	United Kingdom		JQ326995	JQ327023	–	–
Neoboletus magnificus	HKAS 54096	China		KF112324	KF112149	KF112495	KF112654
Neoboletus obscureumbrinus	HKAS 63498	China		KT990598	KT990791	KT990946	KT990433
Neoboletus rubriporus	HKAS 83026	China		KT990601	KT990795	KT990950	KT990437
Neoboletus sanguineoides	HKAS 57766	China		KT990605	KT990799	KT990954	KT990440
Neoboletus sanguineus	HKAS 80849	China		KT990609	KT990803	KT990958	KT990443
Neoboletus sp.	HKAS 50351	China		KF112318	–	KF112516	KF112658
Neoboletus sp.	HKAS 76851	China		KF112321	KF112144	KF112493	KF112651

Table 1 Continued.

Samples	Voucher numbers	Locality	ITS	nrLSU	EF1	RPB1	RPB2
Neoboletus thibetanus	HKAS 57093	China		KF112326	–	KF112496	KF112655
Neoboletus tomentulosus	HKAS 53369	China		KF112323	KF112154	KF112509	KF112659
Neoboletus venenatus	HKAS 57489	China		KF112325	KF112158	KF112515	–
Pulveroboletus brunneopunctatus	HKAS 74926	China		KT990621	KT990815	–	KT990456
Pulveroboletus macrosporus	HKAS 58860	China		KF112408	KF112263	KF112543	KF112714
Pulveroboletus ravenelii	REH2565	USA		–	KU665636	–	KU665637
Pulveroboletus subrufus	N.K. Zeng1857 (FHMU)	China		KX453837	KX453855	–	KX453841
Rubroboletus dupainii	JAM 0607	USA		–	KF030413	KF030361	–
Rubroboletus esculentus	HKAS 68679	China		KF112333	KF112147	KF112505	KF112662
Rubroboletus flammeus	FHMU6927	China		OM514334	OM525826	–	OM525824
Rubroboletus flavus	**HKAS 126558**	**China**		**OQ888721**	**OQ873458**	**OQ873476**	–
Rubroboletus flavus	**HKAS 90906**	**China**	**OQ888704**	**OQ888722**	**OQ873459**	**OQ873477**	**OQ873497**
Rubroboletus latisporus	HKAS 63517	China		KP055022	KP055019	KP055025	KP055028
Rubroboletus legaliae	MB-000295	Germany		KY272128	KY272137	KY272131	KY272134
Rubroboletus rhodosanguineus	4252	USA		KF030252	KF030412	–	–
Rubroboletus rhodoxanthus	HKAS 84879	China		KT990637	KT990831	KT990981	KT990468
Rubroboletus satanas	MBinder-BS2	–		AF042015	–	–	AY218473
Rubroboletus serpentiformis	**HKAS 126557**	**China**	**OQ888705**	**OQ888723**	**OQ873460**	**OQ873478**	**OQ873498**
Rubroboletus serpentiformis	**HKAS 126547**	**China**		**OQ888724**	**OQ873461**	**OQ873479**	**OQ873499**
Rubroboletus sinicus	HKAS 56304	China		KJ605673	KJ619483	KJ619482	–
Rugiboletus brunneiporus	HKAS 83009	China		KM605133	KM605146	KM605156	KM605169
Rugiboletus extremiorientalis	HKAS 76663	China		KM605135	KM605147	KM605159	KM605170
Singerocomus atlanticus	ACM1275	Brazil		KY926777	–	–	–
Singerocomus rubriflavus	GAS900	Brazil		KY926779	–	–	–
Suillellus amygdalinus	112605ba	China		JQ326996	JQ327024	KF030360	–
Suillellus amygdalinus	NY00815464	Costa Rica		KT990659	KT990848	KT990997	KT990484
Suillellus flaviporus	**HKAS 126551**	**China**		**OQ888725**	**OQ873462**	**OQ873480**	**OQ873500**
Suillellus flaviporus	**HKAS 123826**	**China**	**OQ888706**	**OQ888726**	**OQ873463**	**OQ873481**	**OQ873501**
Suillellus flaviporus	**HKAS 126554**	**China**		**OQ888727**	**OQ873464**	**OQ873482**	**OQ873502**
Suillellus flaviporus	**HKAS 126555**	**China**		**OQ888728**	**OQ873465**	**OQ873483**	**OQ873503**
Suillellus lacrymibasidiatus	HMJAU 60202	China		OM230174	OM285117	OM285113	OM285115
Suillellus luridus	VDKO0241b	Belgium		–	KT824047	–	KT824014
Suillellus pinophilus	**HKAS 126550**	**China**	**OQ888707**	**OQ888729**	**OQ873466**	**OQ873484**	**OQ873504**
Suillellus queletii	VDKO1185	Belgium		–	MH645598	–	MH645604

Table 1 Continued.

Samples	Voucher numbers	Locality	ITS	nrLSU	EF1	RPB1	RPB2
Suillellus subamygdalinus	HKAS 57262	China		KF112316	KF112174	KF112501	KF112660
Suillellus yunnanensis	**HKAS 126548**	**China**	**OQ888708**	**OQ888730**	**OQ873467**	**OQ873485**	**OQ873505**
Suillellus yunnanensis	**HKAS 126549**	**China**		**OQ888731**	**OQ873468**	**OQ873486**	**OQ873506**
Sutorius aff. *eximius*	REH8594	Costa Rica		JQ327008	JQ327027	–	–
Sutorius australiensis	REH9441	Australia		JQ327006	JQ327032	–	MG212652
Sutorius eximius	REH9400	USA		JQ327004	JQ327029	–	MG212653
Sutorius subrufus	FHMU2004	China		MH879698	MH879728	–	MH879745
Xerocomus subtomentosus	K 167686	United Kingdom		JQ967238	JQ967193	–	–
Zangia erythrocephala	HKAS 75046	China		KF112414	KF112269	KF112579	KF112791

Sequence alignment and molecular phylogenetic analyses

Our target samples were initially blasted in GenBank using nrLSU and *TEF1* sequences and were all finally matched to the major clade "*Pulveroboletus* group" proposed in Wu et al. (2014). Therefore, all generic clades in "*Pulveroboletus* group" were included for this analysis and the corresponding sequences (nrLSU, *TEF1*, *RPB1* and *RPB2*) of two or three representative species for each clade were downloaded from the GenBank. To ensure accuracy in our analysis, all ingroup species, with available and relevant sequences, were included for the genera in which our target samples were likely to cluster. Some genera outside of *Pulveroboletus* group were selected as outgroups. A total of 94 species and 109 specimens were determined for the final analysis. Detailed information of the voucher specimens can be found in Table 1.

The sequences of four genes (nrLSU, *TEF1*, *RPB1* and *RPB2*) in this study were aligned separately by using MAFFT 7.402 with the E-INS-i strategy (Katoh & Standley 2013) and viewed in BIOEDIT 7.0.9 (Hall 1999). These four matrices were well aligned, so all bases were remained. To assess any potential conflicts in the gene tree topologies, single-locus phylogenetic analyses were first done using Maximum Likelihood (ML) in RAXML 8.2.10 (Stamatakis 2014). The sequences of DNA loci without conflicts were then concatenated using PHYUTILITY 2.2 (Smith & Dunn 2008). The best-fitting model of each DNA fragment was evaluated in MODELTEST-NG with default settings except that the option *-s* was set to 3 (Darriba et al. 2019). ITS sequences were provided for the recognition of the species, but were not suitable for the inference of phylogenetic relationships among different genera of the family.

For the multi-gene phylogenetic analyses, both ML analysis and Bayesian Inference (BI) were conducted. In the ML analysis, all parameters were kept at default settings, except the model set as GTRGAMMA, and statistical support was obtained using nonparametric bootstrapping with 1000 replicates. The BI analysis was implemented in MRBAYES 3.2.7 (Ronquist et al. 2012). Two runs and four chains for each were set and run for approximately 40 million generations sampling from the posterior distribution every 100 generations. Other parameters were kept at default settings. The stopval value was set to 0.01 to ensure potential scale reduction factors (PSRF) being close to 1.0 for all parameters indicative of chain convergence (Ronquist et al. 2012). The chain convergence was determined using Tracer v1.5 (http://tree.bio.ed.ac.uk/software/tracer/) to ensure sufficiently large ESS values (≥ 200). Tree samples were then summarized and posterior probabilities (PP) calculated after discarding the first 25% of the samples as burnin. The concatenated sequences of nrLSU and *TEF1* were used to calculate genetic distances between related species or genera with the Kimura-2-parameter (K2P) model using MEGA X software (Kumar et al. 2018).

Results

Phylogenetic analyses

In this study, a total of 10 ITS, 22 nrLSU, 19 *TEF1*, 21 *RPB1*, 20 *RPB2* were newly generated from 22 samples of 10 bolete species. In the four (nrLSU, *TEF1*, *RPB1* and *RPB2*) single-locus phylogenetic analyses, no strongly supported conflict was detected. Therefore, sequences of these four DNA loci were concatenated for the final multi-gene analysis and accounted for 3096 bases. Full alignment of the concatenated data was submitted to TreeBase (ID: 30025). The best-fitting substitution models of the aligned matrices of the four loci were determined as: GTR+I+G for nrLSU, SYM+I+G for *TEF1* and *RPB2*, HKY+I+G for *RPB1*. ML and BI analyses of the concatenated matrix resulted in almost identical topologies, so only ML topology was shown (Fig. 1).

Based on the multi-gene molecular phylogenetic analysis, our target samples formed ten species-level lineages which belonged to six generic clades including two potential new genera (Fig. 1). For the clade of potential new genus, *Hongoboletus*, it currently consisted of two phylogenetic species, and formed a solitary lineage without a sister genus (Fig. 1) receiving moderate bootstrap (BP) and PP support values (100/1.00, 56/-, 57/-) and was reasonably treated as a new genus. For the other clade of potential new genus, *Acyanoboletus*, it was clustered with the known genera *Cacaoporus* Raspé & Vadthanarat, *Cupreoboletus* Simonini, Gelardi & Vizzini, *Cyanoboletus* Gelardi, Vizzini & Simonini and an undescribed lineage represented by Boletaceae sp. JD0693 receiving moderate supports (58/0.99). Although their relationships remain unclear, the genetic distances (0.1046–0.1474) between *Acyanoboletus* and the latter three known genera based on the combined nrLSU and *TEF1* sequences were larger than those (0.0689–0.1218) among *Cyanoboletus*, *Cupreoboletus* and *Cacaoporus*, which can support the clade of *Acyanoboletus* as an independent genus.

Within the genus *Suillellus* Murrill, two potential new species, represented by HKAS 123826 and HKAS 126550 respectively, were clustered together with high support (99/1.00). However, their combined nrLSU and *TEF1* sequences showed distinct levels of genetic variation (0.0323). They were subsequently determined to be closely allied with *Suillellus luridus* (Schaeff.) Murrill. An additional lineage represented by HKAS 126549 was clustered with American species *Suillellus amygdalinus* (Thiers) Vizzini, Simonini & Gelardi with strong support (100/1.00). Within the genus *Rubroboletus* Kuan Zhao & Zhu L. Yang, two potential new species individually represented by HKAS 90906 and HKAS 126547 were clustered with European *Rubroboletus satanas* (Lenz) Kuan Zhao & Zhu L. Yang (82/0.97). In *Neoboletus* Gelardi, Simonini & Vizzini, the potential new species represented by HKAS 76660 was genetically distinct from other members in this genus although its relationship with others was unclear. Within the genus *Cyanoboletus*, there is a potential new species that forms a close cluster with another Chinese species, *C. instabilis* (W.F. Chiu) G. Wu & Zhu L. Yang, with strong support (100/1.00) for their relationship and 97.8% sequence identity based on a combined analysis of nrLSU and *TEF1* sequences.

In general, the newly discovered genera and species have been found to have significant genetic differences from related known species. These differences have been confirmed through morphological analyses, providing strong evidence for their classification as new taxa.

Taxonomy

Acyanoboletus G. Wu & Zhu L. Yang, gen. nov.

MycoBank number: MB 847054; Facesoffungi number: FoF 14133

Type species – *Acyanoboletus controversus* G. Wu & Zhu L. Yang

Etymology – the latin "*A*-" means away or outside, "*Acyanoboletus*" refers to the genus being distinct from *Cyanoboletus*.

Diagnosis – Distinguished from the known genera of Boletaceae by the combination of the following morphological characters: strongly incurved pileal margin when young, pale yellow

context and hymenophore without color changing when bruised, stipe lacking of reticulations, strong unpleasant smell, an intricate trichoderm pileipellis, and smooth basidiospores.

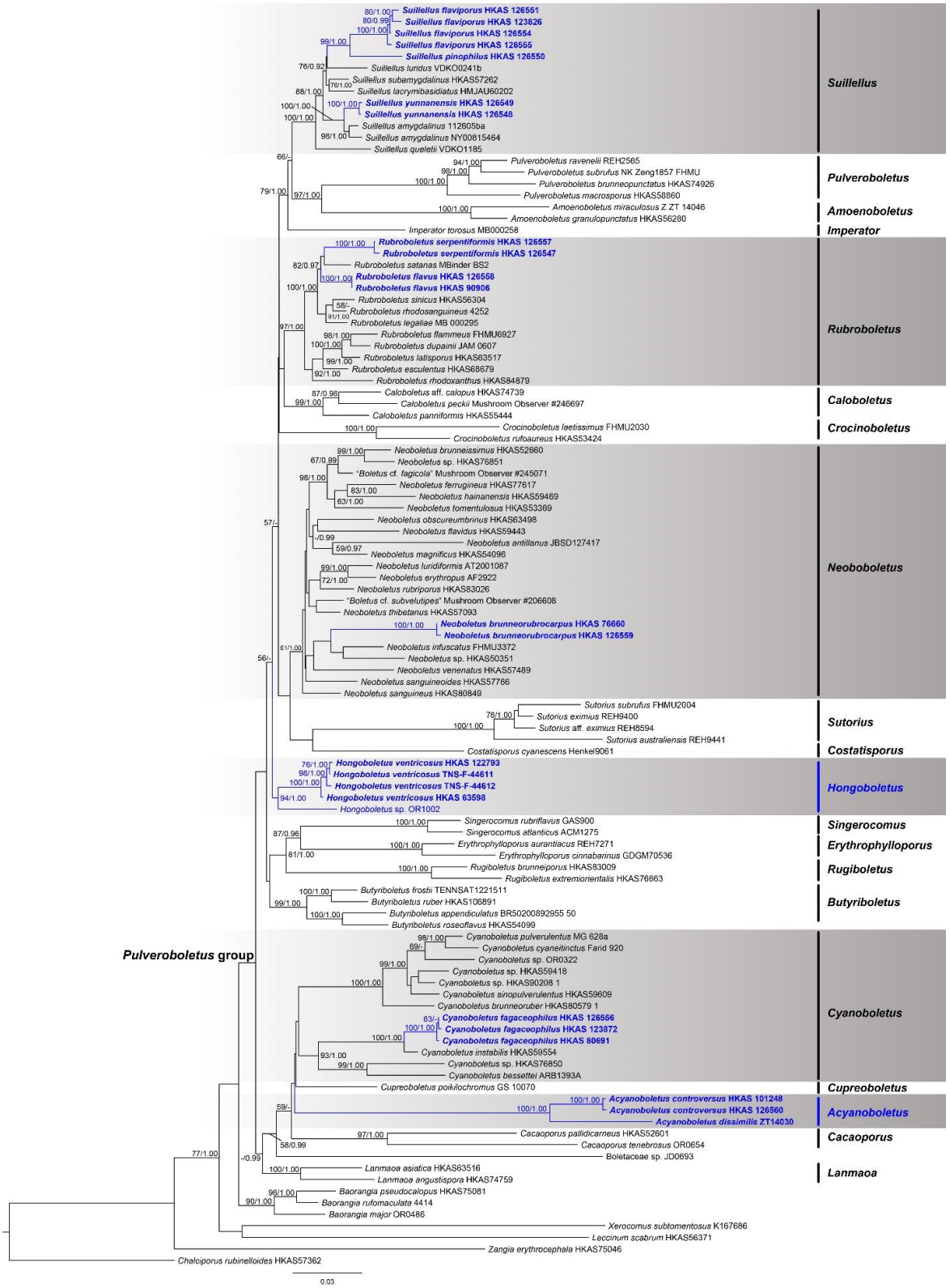

Figure 1 – Maximum likelihood phylogenetic tree of the main clade "*Pulveroboletus* group" of Boletaceae proposed by Wu et al. (2014) inferred from the nucleotide sequences of nrLSU, *TEF1*, *RPB1* and *RPB2*. Bootstrap values (≥ 50%) and posterior probabilities (≥ 0.90) are shown on or beside supported branches. The new taxa proposed in this study are labeled in blue color within a grayish box.

Figure 2 – Fresh basidiomata of new species of Boletaceae from China. a–b *Acyanoboletus controversus* (a: HKAS101248, b: HKAS 126560, holotype). c *Acyanoboletus dissimilis* (ZT 14030). d–f *Hongoboletus ventricosus* (d: HKAS122792, e: HKAS63501, f: HKAS122793). g–i *Cyanoboletus fagaceophilus* (g: HKAS 126556, holotype, h: HKAS80691, i: HKAS123872). j–l *Neoboletus brunneorubrocarpus* (j–k: HKAS76660, holotype, l: HKAS 126552).

Basidiomes stipitate-pileate with a tubular hymenophore. Pileus convex to plano-convex, nearly glabrous to subtomentose, unchanging when touched; context pale yellow, unchanging on exposure. Hymenophoral surface and tubes concolorous, pale yellow, unchanging when bruised. Stipe central, surface nearly glabrous to slightly pruinose, unchanging when touched; context similar to the pileus context, unchanging when bruised. Basidiospores subfusoid, smooth, thin-walled. Pleurocystidia and cheilocystidia lanceolate to narrowly fusoid with short beaks, thin-walled. Pileipellis an interwoven trichoderm composed of entangled and more or less erect hyphae. Clamp connections absent.

Acyanoboletus controversus G. Wu & Zhu L. Yang, sp. nov. Figs 1, 2a–b, 4

MycoBank number: MB 847055; Facesoffungi number: FoF 14135

Etymology – The epithet *controversus* means opposite, refers to the unchanging color of this species on exposure which is different from the blue discoloration of the species in *Cyanoboletus*.

Diagnosis – *Acyanoboletus controversus* is morphologically and phylogenetically close to *A. dissimilis*. The former can be distinguished from the latter by its grayish orange to brownish orange pileus without red tinge, and shorter basidiospores.

Pileus up to 8 cm diam, broadly convex to applanate; surface grayish orange to brownish orange (5A5–5B6), nearly glabrous to subtomentose, incurved at margin when young; context up to

0.8 cm thick, yellowish white to pale yellow (1A2–1A3), unchanging on exposure. Hymenophore sinuate, surface yellowish white to pale yellow (1A2–1A3), unchanging when bruised; tubes up to 8 mm long, concolorous with hymenophoral surface or slightly darker, unchanging when bruised; pores roundish, less than 0.5 mm diam. Stipe 5–7 cm long, up to 1.2 cm diam, firm, solid, subcylindrical, curve; surface pale yellow, light yellow to butter yellow (4A3–4A6), sometimes staining darker when touched, almost glabrous to slightly pruinose; context concolorous with pileal context or slightly darker, firm, unchanging when bruised. Basal mycelium white. Odor like coal gas.

Figure 3 – Fresh basidiomata of new of Boletaceae from China. a–b *Rubroboletus flavus* (HKAS90906, holotype). c–e *Rubroboletus serpentiformis* (c: HKAS 126557, d–e: HKAS 126547, holotype). f–h *Suillellus flaviporus* (f–g: HKAS123826, holotype, h: HKAS 126551). i–j *Suillellus pinophilus* (HKAS 126550, holotype). k–l *Suillellus yunnanensis* (HKAS 126548, holotype).

Basidiospores 8.5–10.5 (11) × 4–5 μm [Q = (2.04–)2.1–2.46 (2.63), Q_m = 2.27 ± 0.13], subfusoid and inequilateral in side view, with slight suprahilar depression, subfusoid in face view, pale yellow in 5% KOH, smooth, thin-walled. Basidia 20–29 × 7–10 μm, clavate, 4-spored; sterigmata up to 4 μm long. Cheilocystidia (13) 16–48 (56) × 5–8 (9) μm, common, lanceolate to narrowly fusoid with short beaks, thin-walled. Pleurocystidia 28–68 × 6–10 μm, common, lanceolate to narrowly fusoid with short beaks, thin-walled. Hymenophoral trama intermediate to boletoid; hyphae subcylindrical to cylindrical, 4–10 μm wide. Pileipellis an intricate trichoderm, ca. 150 μm thick, composed of filamentous hyphae 3.5–5 μm wide, thin-walled, with subcylindrical, clavate to ventricose-fusoid terminal cells 12–60 × 3.5–9 μm, thin-walled. Pileal trama composed of interwoven hyphae 3–13 μm wide. Stipitipellis ca. 80 μm thick, hymeniform; terminal cells

17.5–52 × 3.5–12.5 μm, lanceolate, clavate, broadly clavate to ventricose-fusoid. Stipe trama composed of longitudinally arranged parallel thin-walled hyphae 4–10 μm wide. Clamp connections absent.

Known distribution – Southwest China.

Materials examined – China, Yunnan, Malipo County, Malipo Town, Xinhe Village, 1212 m elev., on soil under mixed forest of *Pinus* spp. (*P. kesiya* var. *langbianensis*, etc.) and fagaceous plants (*Quercus*, *Lithocarpus* and *Castanopsis*), 3 August 2018, Si-Peng Jian 168 (HKAS 126560, holotype); Lancang Lahu Autonomous County, Nanling Town, 1160 m elev., on soil under mixed forest of *Pinus* spp. (*P. kesiya* var. *langbianensis*, etc.) and fagaceous plants (*Quercus*, *Lithocarpus* and *Castanopsis*), 1 September 2017, Zhu-Liang Yang 6059 (HKAS 101248).

Notes – Morphologically, species of *Cyanoboletus* differ from *Acyanoboletus controversus* by their distinct blue discoloration in the bruised context and hymenophore (Gelardi et al. 2013, Gelardi et al. 2014, Wu et al. 2016a, Farid et al. 2021).

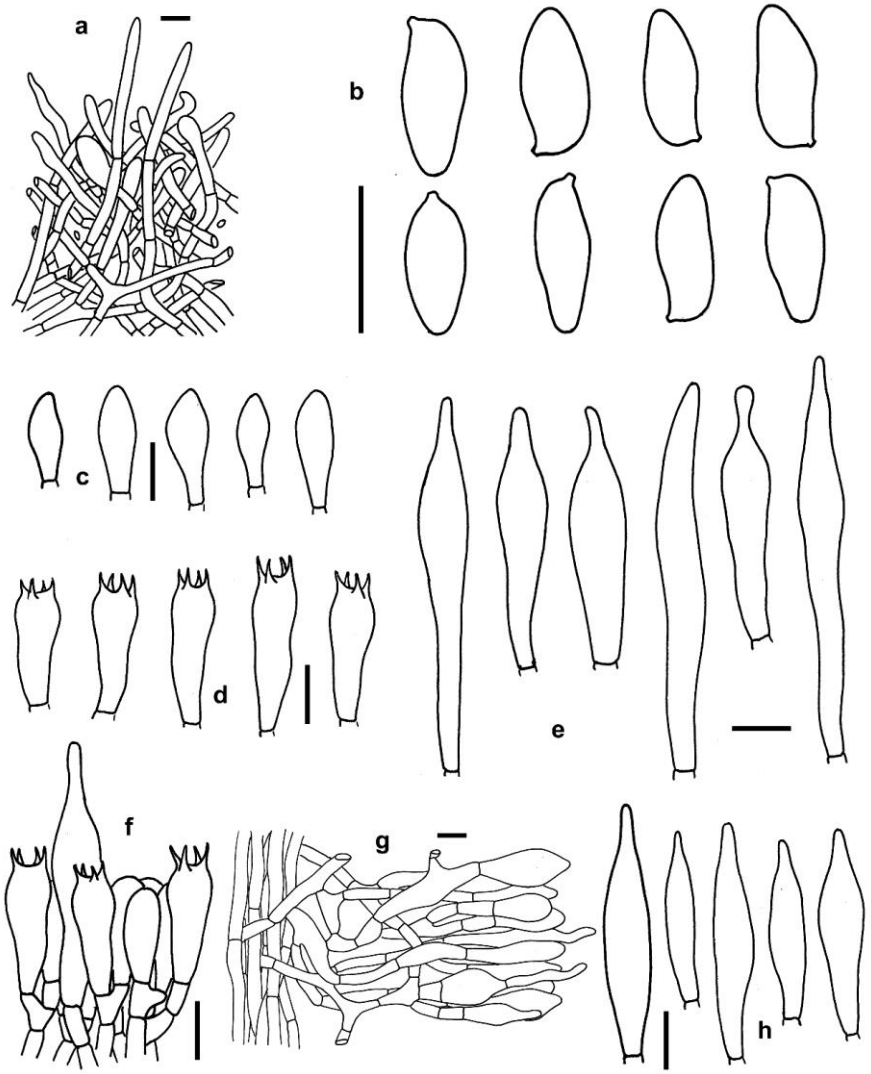

Figure 4 – Microscopic features of *Acyanoboletus controversus* (a–g: HKAS 126560, holotype; h: HKAS101248). a Pileipellis. b Basidiospores. c Cheilocystidia. d Basidia. e Pleurocystidia. f Basidia, pleurocystidium and basidioles. g Stiptipellis. h Cheilocystidia. Scale bars = 10 μm.

Acyanoboletus dissimilis E. Horak & G. Wu, sp. nov. Figs 1, 2c, 5

MycoBank number: MB 848543; Facesoffungi number: FoF 14136

Etymology – The epithet *dissimilis* refers to the morphological characters different from the species *A. controversus*.

Diagnosis – See the diagnosis of *A. controversus*.

Pileus 1–5.5 cm diam, hemispherical with strongly incurved margin, becoming expanded, reddish brown (8D6), pale chestnut brown (5D7–7D2), minutely velutinous, dry; context up to 7 mm, pale yellow (2A2–4A2), unchanging or sometimes slowly becoming pale reddish beige by exposure. Hymenophore emarginate, with short decurrent ribs, surface at first light yellow (3A4–4A4), becoming mustard yellow or pale olive yellow (4D5–4D7) in age, not bluing when bruised; tubes up to 6 mm long, almost concolorous with hymenophoral surface; pores polyedric, 0.5–1 mm diam. Stipe 4–6 cm long, up to 1 cm at apex, gradually tapering towards base, solid, dry, surface pale yellow to light yellow (4A2–4A3) at the apex, concolorous with pileus towards base, minutely tomentose, reticulations absent; context concolorous with pileal context or lighter. Basal mycelium white. Odor strong, unpleasant like pharmacy.

Basidiospores (11) 11.5–13 × 4–5 µm, fusoid and inequilateral in side view, with slight suprahilar depression, fusoid in face view, yellow-brown in 5% KOH, smooth, thin-walled. Basidia 35–45 × 7–9 µm, slender clavate, 4-spored; sterigmata up to 3 µm long. Cheilocystidia (30) 35–55 × 8–10 µm, fusoid, tapering towards obtuse apex, hyaline or with pale yellow plasmatic pigment. Pleurocystidia size and shape like cheilocystidia. Pileipellis a trichoderm composed of cylindrical and obtuse-fusoid cells, with yellow-brown plasmatic pigment, wall not gelatinized. Oleiferous hyphae in subpellis present. Stipitipellis hymeniform; caulocystidia 35–45 × 7–9 µm, shape like cheilocystidia. Clamp connections absent.

Know distribution – Malaysia.

Materials examined – MALAYSIA, Sabah (N-Borneo), Mt Kinabalu, trail to summit, between shelter 1/2, 2230 m elev., on soil in tropical montane fagalean rain forest (dominated by *Lithocarpus-Castanopsis*), 15 June 2013, E. & A. Horak 14030 (ZT 14030, holotype).

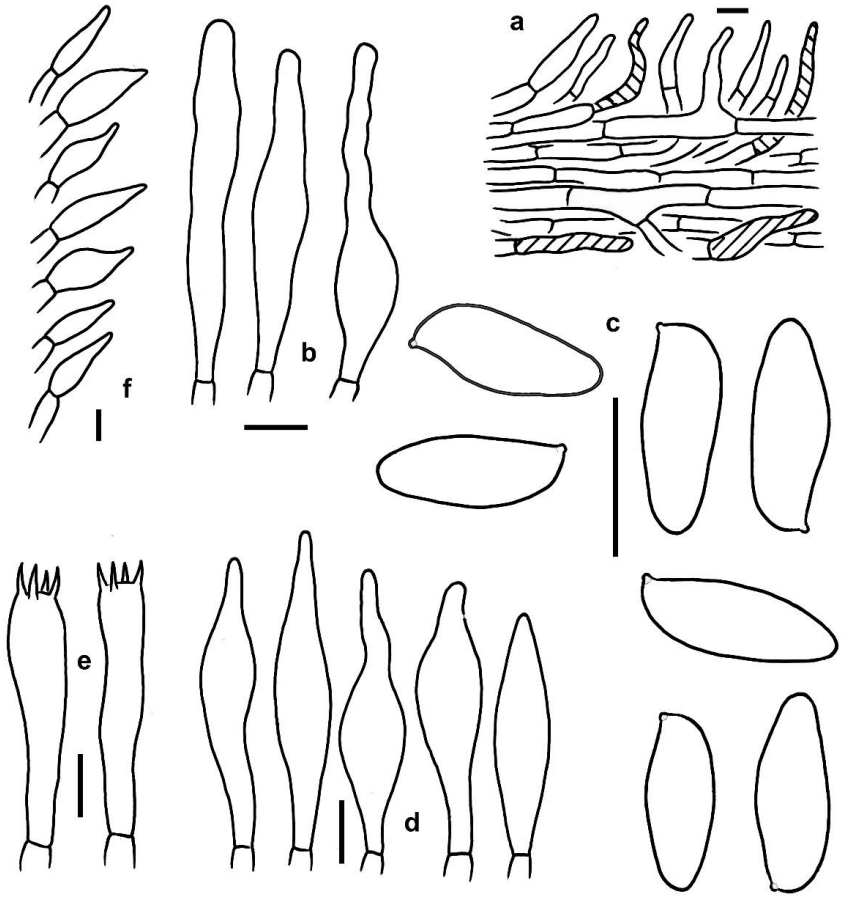

Figure 5 – Microscopic features of *Acyanoboletus dissimilis* (ZT 14030, holotype). a Pileipellis. b Pleurocystidia. c Basidiospores. d Cheilocystidia. e Basidia. f Caulocystidia. Scale bars = 10 µm.

Notes – *Acyanoboletus dissimilis* is distinguished by the strongly incurved pileal margin, non-bluing context when bruised, and strong unpleasant smell. A Malaysian species *Boletus farinolens* Corner was described by Corner (1972) somewhat similar to *A. dissimilis*. However, it is a sad fact that the type material of *B. farinolens* is in rather poor condition and does not allow to examine all essential microscopical characters (Horak 2011). Based on the original description of Corner (1972), *B. farinolens* has a slight blue discoloration in the exposed context and farinaceous smell which are different from those of *A. dissimilis*.

Hongoboletus G. Wu & Zhu L. Yang, gen. nov.

MycoBank number: MB 842439; Facesoffungi number: FoF 14134

Type species – *Hongoboletus ventricosus* (Taneyama & Har. Takah.) G. Wu & Zhu L. Yang

Etymology – *Hongoboletus* (Lat.) is in honor of the late Japanese mycologist Tsuguo Hongo, who made a great contribution to Asian mycology.

Diagnosis – Distinguished from the known genera of Boletaceae by the combination of the following morphological characters: the quick dark-blue discoloration of all parts of basidioma upon exposure, a thick context of pileus but a thin hymenophore, yellow hymenophore surface and tubes, a stout stipe lacking reticulations on the surface, an interwoven trichoderm pileipellis, and smooth basidiospores.

Basidiomes stipitate-pileate with a tubular hymenophore. Pileus convex to plano-convex, nearly glabrous to subtomentose, quickly staining dull blue to blackish blue when touched; context thick, yellowish, quickly staining dull blue to blackish blue on exposure. Hymenophore much thinner than context of pileus. Hymenophoral surface and tubes often concolorous, yellow, quickly staining dull blue to blackish blue when bruised. Stipe central, stout, surface nearly glabrous to pruinose, quickly staining dull blue to blackish blue when touched; context similar to the pileus context, quickly staining dull blue to blackish blue when bruised. Basidiospores subfusoid to ellipsoid, smooth, thin-walled. Pleurocystidia and cheilocystidia subfusoid to narrowly subfusoid. Pileipellis an interwoven trichoderm composed of entangled hyphae. Clamp connections absent.

Hongoboletus ventricosus (Taneyama & Har. Takah.) G. Wu & Zhu L. Yang, comb. nov.

Figs 1, 2d–f, 6

MycoBank number: MB 847056; Facesoffungi number: FoF 14138

Basionym – *Boletus ventricosus* Taneyama & Har. Takah., in Takahashi, Taneyama & Degawa, Mycoscience 54(6): 461 (2013)

Diagnosis – *Hongoboletus ventricosus* is phylogenetically close to an undescribed species represented by *Hongoboletus* sp. OR1002 from Thailand. It is characterized by the quick dark-blue discoloration on all parts of basidiome when bruised, thick context of pileus but thin hymenophore, yellow hymenophoral surface and tubes, a stout stipe lacking of reticulations on the surface, an interwoven trichoderm pileipellis, and smooth basidiospores.

Pileus up to 16 cm diam, convex to broadly convex; surface brownish orange, brownish red, reddish gold to grayish red, nearly glabrous to slightly subtomentose, dry, sterile margin present and often involute; context up to 3 cm thick, light yellow, quickly staining blue then blackish blue on exposure. Hymenophore adnate to depressed, surface light yellow, quickly staining dull blue to blackish blue when bruised; tubes up to 6 mm thick, concolorous with hymenophoral surface, quickly staining dull blue to blackish blue when bruised; pores irregular to angular, 0.5 mm diam. Stipe 6.5–10.7 cm long, 2–3 cm diam, central, broadly obclavate, firm, solid; surface nearly glabrous to pruinose, sometimes longitudinally streaked, pale orange to reddish orange, sometimes pale yellow to butter yellow at the apex; context firm, concolorous with that in pileus, quickly staining dark blue on exposure. Basal mycelium dirty white. Taste mild. Odor indistinct.

Basidiospores (8.5) 9–11 (12.5) × 4–5 (6) μm [Q = (1.7–)1.8–2.44 (2.5), Q_m = 2.16 ± 0.19], ellipsoid to subfusoid and inequilateral in side view, with indistinctive suprahilar depression, ellipsoid to subfusoid in face view, brownish yellow in 5% KOH, smooth, thin-walled. Basidia 32–43 × 9–11.5 μm, clavate, 4-spored, rarely 1-, or 3-spored. Cheilocystidia 34–51× 5.5–7 μm, sparse,

narrowly subfusoid, thin-walled, often with secondary septa. Pleurocystidia 32–68 × 6–10 μm, sparse, narrowly subfusoid, thin-walled. Hymenophoral trama boletoid with hyphae diverging from the central strand to the subhymenium; hyphae subcylindrical to cylindrical, 3–11.5 μm wide. Pileipellis an interwoven trichoderm, ca. 300 μm thick, composed of entangled filamentous hyphae 5–11 μm wide, thin-walled, containing brownish yellow pigments, with subcylindrical to subclavate terminal cells 30–63 × 5–11 μm, sometimes slightly thick-walled (< 1 μm). Pileal trama composed of interwoven hyphae 5–14 μm wide. Stipitipellis ca. 110 μm thick, hymeniform; caulobasidia 28–43 × 9.5–12.5 μm, sparse; other terminal cells 23.5–50 × 7–18 μm, clavate to cystidioid. Stipe trama composed of longitudinally arranged parallel thin-walled hyphae 4–14 μm wide. Clamp connections absent.

Known distribution – Southwest China and Japan.

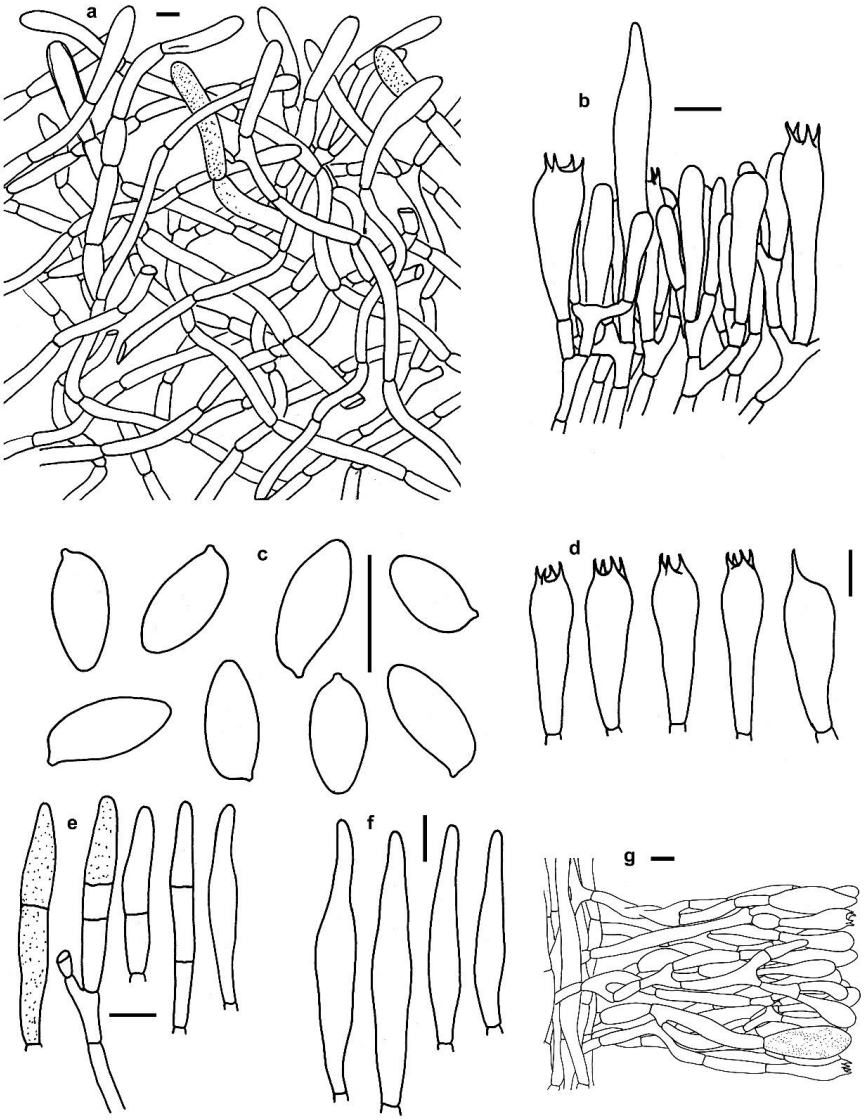

Figure 6 – Microscopic features of *Hongoboletus ventricosus* (HKAS122792). a Pileipellis. b Basidia, pleurocystidium and basidioles. c Basidiospores. d Basidia. e Cheilocystidia. f Pleurocystidia. g Stiptipellis. Scale bars = 10 μm.

Materials examined – China, Yunnan, Yongping County, Bonan Town, Xintian Village, ca. 1800 m elev., on soil in forest of *Pinus yunnanensis*, 27 July 2020, Kui Wu 293 (HKAS 122792); Baoshan Longyang District, 2100 elev., 31 July 2009, Yan-Chun Li 1912 (HKAS 59660);

Kunming City, Ciba free market, 1950 m elev., 13 June 2010, Gang Wu 251 (HKAS 63482); same locality, 14 June 2010, Gang Wu 270 (HKAS 63501), same locality, 10 August 2010, Gang Wu 291 (HKAS 63522); same city, Beichen free market, 10 July 2018, Gang Wu 2643 (HKAS 122793); Nanhua wild mushroom market, 23 August 2010, Gang Wu 366 (HKAS 63598); same locality and date, Gang Wu 367 (HKAS 63599). JAPAN: NAGANO Pref. Kamiminochi-gun, Iizuna-cho, Jizoukubo, 750 m elev., on soil in mixed forest dominated by *Pinus densiflora* and *Quercus serrata*, 27 July 2011, Taneyama, M. (TNS-F-44614, specimen from type locality); NIIGATA Pref. Myokoshi, Hida-iseki Park, 70 m elev., on soil in mixed forest dominated by *Pinus densiflora* and *Quercus serrata*, 8 July 2011, Taneyama, M. (TNS-F-44611).

Notes – *Hongoboletus ventricosus* was originally described as *Boletus ventricosus* from Japan (Takahashi et al. 2013), and commonly seen in wild mushroom markets in central Yunnan of China. By comparing the Chinese samples with Japanese specimens of *Boletus ventricosus*, we phylogenetically and morphologically confirmed that they were conspecific (Fig. 1). On morphology, *Neoboletus flavidus* (G. Wu & Zhu L. Yang) N.K. Zeng, H. Chai & Zhi Q. Liang is somewhat similar to *H. ventricosus* due to their yellow hymenophoral surface, and brown-tinged pileus. However, *N. flavidus* is different in its smaller basidiome, slender stipe and longer basidiospores (10–13 × 4.5–5.5 μm) (Wu et al. 2016a). *Neoboletus obscureumbrinus* (Hongo) G. Wu & Zhu L. Yang and *N. magnificus* (W.F. Chiu) Gelardi, Simonini & Vizzini also resemble *H. ventricosus* because of the brown basidiome and stout stipe, but they have different reddish brown hymenophoral surface and more tomentose pileus surface (Chiu 1948, Hongo 1968, Wu et al. 2016a). Besides, the context in the stipe of *N. obscureumbrinus* is soft-cottony (Wu et al. 2016a) which is different from the firm context of *H. ventricosus*.

Cyanoboletus fagaceophilus G. Wu, Hai J. Li, Zhu L. Yang, sp. nov. Figs 1, 2g–i, 7

MycoBank number: MB 847057; Facesoffungi number: FoF 14137

Etymology – The epithet *fagaceophilus* refers to the preference for fagaceaous host plants of this species.

Diagnosis – *Cyanoboletus fagaceophilus* is phylogenetically and morphologically close to *C. instabilis*. However, the former differs from the latter by its wider basidiospores, more regular (trichoderm to intricate trichoderm) pileipellis with clavate to subfusoid terminal cells, and its association with fagaceous trees.

Pileus 2–6.5 cm diam, convex to broadly convex; surface grayish green (1C5–1D5), brownish orange (6C7), orange white to rose white (6A2–7A2), subtomentose, dry, sometimes incurved at margin; context up to 1.1 cm thick, yellowish white (1A2), slowly staining pale blue on exposure. Hymenophore adnate to sinuate, surface grayish yellow to orange yellow (3B4–3B5, 4B7–4B7), honey yellow to olive yellow (4D6-4D8), staining dull blue when bruised; tubes up to 6 mm long, concolorous with hymenophoral surface, staining dull blue when bruised; pores roundish to ellipsoid, up to 0.5 mm diam. Stipe 2–5 cm long, 0.3–1.2 cm diam, central, sometimes eccentric, firm, solid, subcylindrical, sometimes slightly enlarged downwards; surface concolorous with pileal surface or lighter, covered with pruinose to pubscent squamules; context whitish mixed with hygrophanous color, firm, almost unchanging when bruised. Basal mycelium white.

Basidiospores (7.5) 9–11 (11.5) × 4.5–5.5 μm [Q = (1.5–) 1.8–2.22 (2.40), Q_m = 2.01 ± 0.15], subfusoid, ovoid to ellipsoid and inequilateral in side view, without distinctive suprahilar depression, subfusoid, ovoid to ellipsoid in face view, pale yellow in 5% KOH, smooth, thin-walled. Basidia 27–38 (45) × 8–13 (13.5) μm, clavate, 4-spored, rarely 1-spored; sterigmata up to 4.5 μm long. Cheilocystidia (30.5) 34–68× 4–15 (18) μm, common, lanceolate, narrowly fusoid to ventricose-fusoid with short beaks, thin-walled. Pleurocystidia 40–86 (100) × 6.5–20 μm, scattered, lanceolate, narrowly fusoid to ventricose-fusoid with short beaks, thin-walled. Hymenophoral trama intermediate to boletoid; hyphae subcylindrical to cylindrical, 2–14 μm wide. Pileipellis a trichoderm to an intricate trichoderm, ca. 150 μm thick, composed of filamentous hyphae 3.5–7 μm wide, thin-walled, with subcylindrical, clavate to subfusoid terminal cells 27–68 × 4.5–11.5 μm, thin-walled. Pileal trama composed of interwoven hyphae 2–13 μm wide. Stipitipellis ca. 75

μm thick, hymeniform; terminal cells 22.5–44 × 4.5–17 μm, broadly clavate, clavate to subcylingdrical. Stipe trama composed of longitudinally arranged parallel thin-walled hyphae 3–10 μm wide. Clamp connections absent.

Known distribution – Southwest to South China.

Materials examined – China, Yunnan, Jianshui County, Potou Town, Huiyuan Village, 1320 m elev., on soil in forest dominated by fagaceous plants (*Quercus*, *Lithocarpus* and *Castanopsis*), 2 August 2016, JSPT20160802023 (HKAS 126556, holotype; duplication at NIOHP); Malipo County, Tianbao Town, 1040 m elev., on soil in forest dominated by fagaceous plants (*Quercus*, *Lithocarpus* and *Castanopsis*), 30 July 2017, 532624MF-201-Wu2295 (HKAS 123872). Guangdong, Fengkai County, Heerkou Town, 3 June 2013, Kuan Zhao 266 (HKAS 80691).

Notes – *Cyanoboletus fagaceophilus* is distinguished by a grayish green, orangish white to brownish orange pileus, a yellowish white pileal context slowly staining pale blue when bruised, the yellowish tubes and pores staining dull blue when bruised, a whitish stipe context nearly unchanging when bruised, trichoderm pileipellis, and smooth basidiospores. The allied species *C. instabilis* differs in its narrower basidiospores (9–14 × 4–5 μm), the more interwoven (subcutis) pileipellis with more regular (cylindrical) terminal cells, and the preference for pines (Chiu 1948, Wu et al. 2016a).

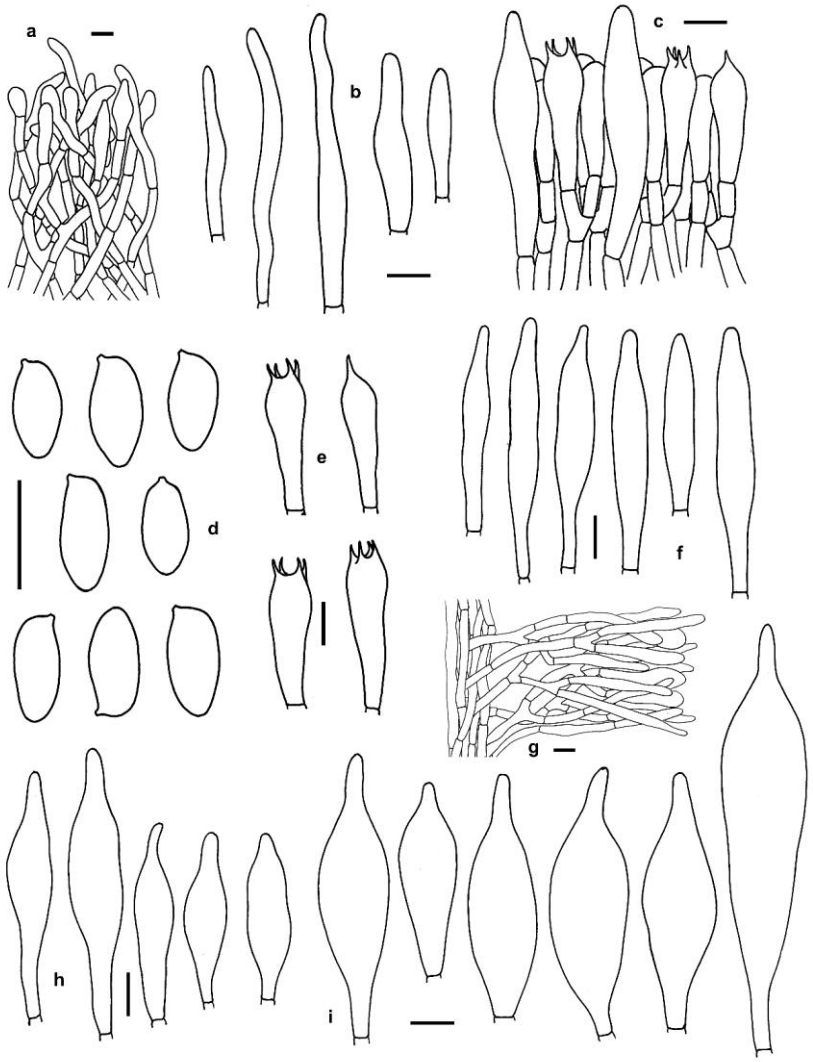

Figure 7 – Microscopic features of *Cyanoboletus fagaceophilus* (a–g: HKAS123872; h–i: HKAS 126556, holotype). a Pileipellis. b Cheilocystidia. c Basidia, pleurocystidia and basidioles. d Basidiospores. e Basidia. f Pleurocystidia. g Stiptipellis. h Cheilocystidia. i Pleurocystidia. Scale bars = 10 μm.

Neoboletus brunneorubrocarpus G. Wu, Hai J. Li, Zhu L. Yang, sp. nov. Figs 1, 2j–l, 8

MycoBank number: MB 847058; Facesoffungi number: FoF 14139

Etymology – The epithet *brunneorubrocarpus* refers to brownish red basidioma of this species.

Diagnosis – *Neoboletus brunneorubrocarpus* may be phylogenetically related to *N. infuscatus* N.K. Zeng, S. Jiang & Zhi Q. Liang, but the former differs from the latter by its darker (reddish brown, brownish red to dark brown) pileus and larger basidiospores.

Pileus up to 8 cm diam, hemispherical, convex to applanate; surface reddish brown, brownish red to dark brown (8D6–8F6, 8C6–8D6), grayish orange to reddish golden (6B6–6C7), glabrous, often shining; context up to 2 cm thick, light yellow to yellow (2A5–2A6), quickly staining dark blue on exposure. Hymenophore adnate to sinuate, surface reddish brown to brownish red (9C8–9D8), reddish orange to grayish orange (7A7–7B7), quickly staining dark blue when bruised; tubes 10 mm thick, maize yellow to grayish yellow (4A6–4B6), quickly staining dark blue when bruised; pores irregular to angular, 0.5 mm diam. Stipe up to 7 cm long, 1.5 cm diam, central, subcylindrical or slightly enlarged downwards, firm, solid; surface background light yellow to light orange (4A4–5A4), covered with dotted squamules and sometimes longitudinal streaks concolorous with pileal surface, quickly staining dark blue when bruised; context firm, concolorous with pileal context, but slowly staining dark blue on exposure. Basal mycelium pale brown to brownish yellowish.

Basidiospores 11.5–14 (14.5) × 4.5–5.5 (6) μm [Q = (2.21–) 2.25–2.80 (2.90), Q_m = 2.49 ± 0.16], subfusoid and inequilateral in side view, without distinctive suprahilar depression, subfusoid in face view, brownish yellowish in 5% KOH, smooth, thin-walled. Basidia 20–34 × 9–13 μm, broadly clavate, 4-spored; sterigmata up to 4 μm long. Cheilocystidia (14) 19–42× 5–9 μm, common, fusoid, sometimes ventricose-fusoid, with short beak or acute apex, thin-walled. Pleurocystidia having two types, type-I (36.5) 39–65 (70) × 8–12.5 (15) μm, scattered, ventricose-fusoid to subfusoid, with short beak or acute apex, thin-walled; type-II (19.5) 22–31 × 9–11.5 μm, broadly clavate with blunt apex. Hymenophoral trama boletoid with hyphae diverging from the central strand to the subhymenium; hyphae subcylindrical to cylindrical, 3.5–11 μm wide. Pileipellis a trichoderm, ca. 150 μm thick, composed of filamentous hyphae 3.5–7.5 μm wide, thin-walled, containing brownish yellow pigments, with subcylindrical to subclavate terminal cells 18–38 × 3–8 μm, slightly thick-walled (< 1 μm). Pileal trama composed of interwoven hyphae 4–12 μm wide. Stipitipellis ca. 50 μm thick, hymeniform; caulobasidia rare; caulocystidia 17.5–36 × 6–12.5 μm, broadly fusoid; other terminal cells 15–25 × 5.5–10.5 μm, clavate to subcylingdrical. Stipe trama composed of longitudinally arranged, parallel, thin-walled hyphae 4–12 μm wide. Clamp connections absent.

Known distribution – Central, Southeast to Southwest China.

Materials examined – China: Henan, Neixiang County, Taoyuan Town, Taohuayuan parkland, 450 m elev., on soil in forest dominated by fagaceous plants. 31 July 2010, Xiao-Fei Shi 409 (HKAS 76660, holotype). Guizhou, Meitan County, Shilian Town, 800 m elev., on soil in forest dominated by fagaceous plants (*Quercus*, *Lithocarpus* and *Castanopsis*), 15 September 2015, Hai-Jiao Li 150915-03 (HKAS 126552, duplication at NIOHP). FUJIAN, Wuyishan County, Wutun Town, on soil in forest dominated by fagaceous plants (*Quercus*, *Lithocarpus* and *Castanopsis*), 19 August 2021, GAWYS20210819 (HKAS 126559, duplication at NIOHP)

Notes – *Neoboletus brunneorubrocarpus* is distinguished by the reddish brown pileus with shining surface, a reddish brown to reddish orange hymenophoral surface, maize yellow to grayish yellow tubes staining dark blue when bruised, a stipe covered with dotted squamules and sometimes longitudinal streaks, a trichoderm pileipellis, smooth basidiospores, two types of pleurocystidia (Type I, ventricose-fusoid to subfusoid; Type II, broadly clavate with blunt apex), the preference for the fagaceous host plants. The phylogenetically related species *N. infuscatus* differently has paler (brownish yellow, yellowish brown to pale brown) pileus and smaller basidiospores (8.5–10.5 × 3.5–4.5 μm) (Jiang et al. 2021).

Morphologically, *N. brunneissimus* (W.F. Chiu) Gelardi et al., *N. luridiformis* (Rostk.) Gelardi, Simonini & Vizzini, *N. magnificus*, *Boletus gansuensis* Q.B. Wang et al.,

B. squamulistipes M. Zang and *B. vermiculosus* Peck resemble *N. brunneorubrocarpus*. However, *N. brunneissimus* is distinguishable by its brown basidioma that often lacks a red tinge, narrower basidiospores (10-14 × 4.5-5 μm), and its preference for pines. *Neoboletus magnificus* differs in its stout stipe, narrower basidiospores (10–13 × 4–5 μm) and the preference for pines (Chiu 1948, Wu et al. 2016b). *Neoboletus luridiformis* differs in its longer basidiospores (13–17 × 4–6 μm) and the association with temperate deciduous and coniferous trees, e.g., *Fagus*, *Picea* and *Quercus* spp. primarily in Europe (Alessio 1985, Laessoe & Petersen 2019). *Boletus gansuensis* differs in its wider basidospores (12.0–15.5 × 6–7 μm) and basidia (33–48 × 13–16 μm) and the association with *Betula* sp. (Wang et al. 2003). *Boletus squamulistipes* differs in its brown pileus and hymenophoral surface without red tinge, the shorter basidiospores (9–11.5 × 4–5.5 μm), and its tropical habitat (Zang 1983). *Boletus vermiculosus* differs in its narrower basidia (24–32 × 7–9 μm), shorter pleurocystidia (28–36 × 8–12 μm) and the association with beech in North America (Smith & Thiers 1971).

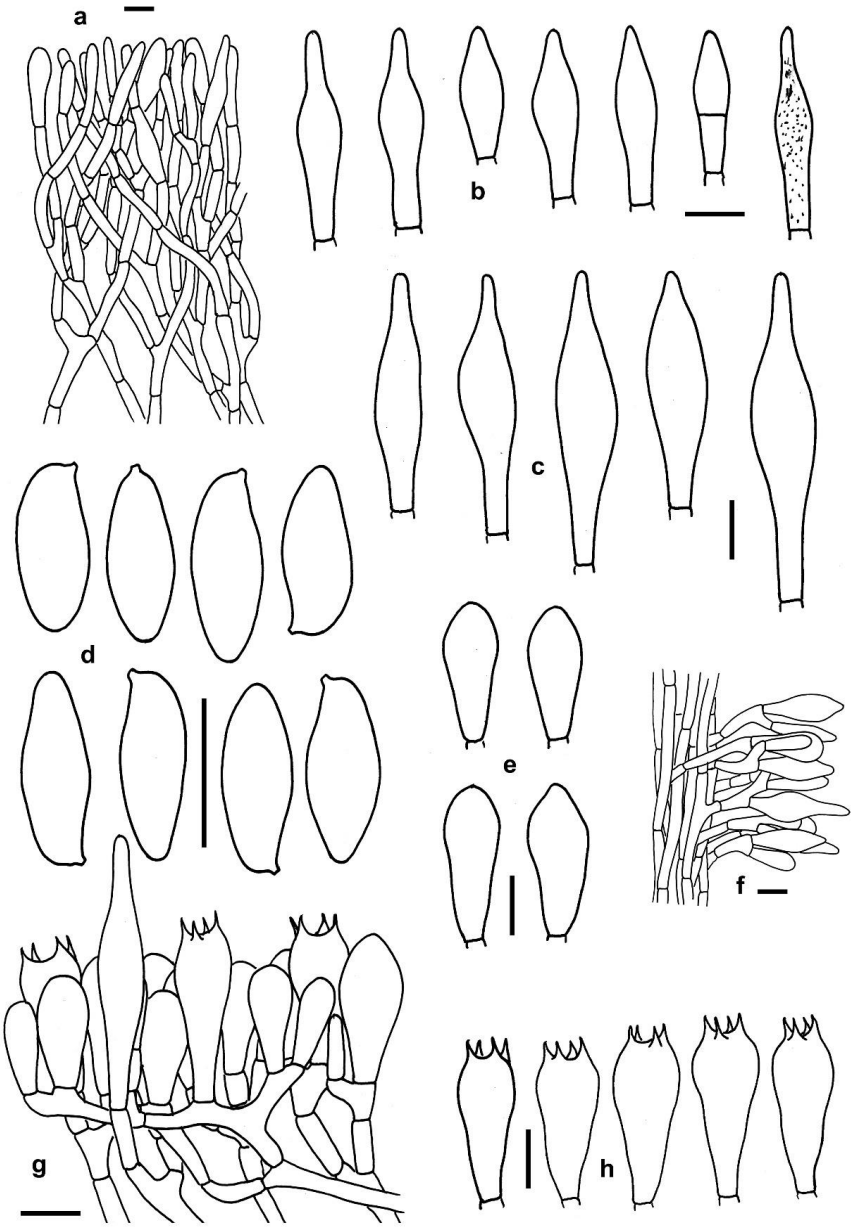

Figure 8 – Microscopic features of *Neoboletus brunneorubrocarpus* (HKAS76660, holotype). a Pileipellis. b Cheilocystidia. c Pleurocystidia, type I. d Basidiospores. e Pleurocystidia, type II. f Stiptipellis. g Basidia, pleurocystidia and basidioles. h Basidia. Scale bars = 10 μm.

Boletus erythropus var. *novoguineensis* Hongo from New Guinea highly resembles to *N. brunneorubrocarpus* on hymenophoral surface color, basidiospore size, and fagaceous host plants (*Castanopsis* spp.) (Hongo 1973). However, the brown to dark brown pileus surface and the far tropical habitat of *Boletus erythropus* var. *novoguineensis* suggests it may differ from *N. brunneorubrocarpus*. Further molecular phylogenetic analysis is required to confirm their relationships. There has been one reported case of gastroenteritis caused by *N. brunneorubrocarpus* in Fujian province, China, indicating its poisonous property.

Rubroboletus flavus G. Wu & Zhu L. Yang, sp. nov. Figs 1, 3a–b, 9

MycoBank number: MB 847059; Facesoffungi number: FoF 14140

Etymology – The epithet *flavus* refers to the yellow hymenophoral surface of this species.

Diagnosis – *Rubroboletus flavus* is phylogentically close to *R. satanas* and *R. serpentiformis*. However, *R. flavus* differs from *R. satanas* by its pale yellow to light yellow hymenophoral surface, larger basidiospores and the association with pine trees. *Rubroboletus flavus* differs from *R. serpentiformis* by its uniformly colored pileus, pale yellow to light yellow hymenophoral surface, pale yellow to pastel yellow reticulations on the stipe surface, and larger basidiospores.

Pileus up to 12 cm diam, subhemispherical to convex, surface birch bark color (6B2) to olive brown (4C3–4D4), sometimes with pink tinge at margin, subtomentose, cracked into small patches in age; context up to 2.5 cm thick, pale yellow to light yellow (2A4–2A5), quickly staining dark blue on exposure. Hymenophore depressed to sinuate, surface and tubes concolorous, pale yellow to light yellow (4A3–4A4), grayish yellow (4B3–4B4), quickly staining dark blue when bruised; tubes up to 15 mm thick, quickly staining dark blue when bruised; pores roundish, 0.5 mm diam. Stipe up to 12 cm long, 2–4 cm diam, central, obclavate, firm, solid; surface pale yellow to pastel yellow (2A2–2A3), almost fully covered with concolorous small-meshed reticulations, sometimes with blackish mildew spot, staining blue when bruised; context firm, concolorous with pileal context, quickly staining dark blue on exposure. Basal mycelium whitish.

Basidiospores (10) 12–16.5 (17) × (5) 5.5–6.5 (7) μm [Q = (1.43–) 1.90–2.76 (2.83), Q_m = 2.26 ± 0.29], subfusoid and inequilateral in side view, with indistinctive suprahilar depression, subfusoid in face view, brownish yellowish in 5% KOH, smooth, thin-walled. Basidia 30–45 × 14–17.5 μm, broadly clavate, 4-spored; sterigmata up to 4 μm long. Cheilocystidia 18.5–36× 6–12 μm, scatterred, broadly clavate, sometimes ventricose-fusoid, with acute apex, occasionally with secondary septum, thin-walled. Pleurocystidia 45–50 ×10.5–16 μm, rare, ventricose-fusoid with short beaks, thin-walled. Hymenophoral trama boletoid with hyphae diverging from the central strand to the subhymenium; hyphae subcylindrical to cylindrical, 4–12 μm wide. Pileipellis a trichoderm, ca. 300–400 μm thick, composed of filamentous hyphae 4–7 μm wide, thin-walled, sometimes clustered into tufts, with narrowly cylindrical terminal cells 27.5–84 × 4–7.5 μm, thin-walled, sometimes surrounded with gelatinized substance. Pileal trama composed of interwoven hyphae 4–12 μm wide. Stipitipellis ca. 75–100 μm thick, hymeniform; caulocystidia common, 36–90 ×6–17 (22) μm. Stipe trama composed of longitudinally arranged parallel thin-walled hyphae 3–13 μm wide. Clamp connections absent.

Known distribution – Southwest to Northwest China.

Materials examined – China, Sichuan, Songpan County, Shili Town, Datun Village, 2930 m elev., on soil in dark coniferous forest (*Abies* spp., *Picea* spp. etc), 19 July 2017, Jian-Wei Liu 112 (HKAS 90906, holotype). GANSU, Diebu County, on soil in dark coniferous forest (*Abies* spp., *Picea* spp. etc), 2 September 2010, Zuo-lin Fu & Kun Huang 17-04 (HKAS 126558)

Notes – *Rubroboletus flavus* is distinguished by a pinkish white to pale red pileus, a pale yellow to light yellow hymenophoral surface quickly staining dark blue when bruised, a pale yellow stipe fully covered with concolorous small-meshed reticulations, a trichoderm pileipellis, smooth basidiospores, a subtropical subalpine or temperate habitat, and the preference for dark coniferous plants (*Picea* or *Abies* spp.).

The phylogenetically related European *R. satanas* differs from *R. flavus* by its orange-red hymenophoral surface, smaller basidiospores (11–13 × 5–6 μm), and its association with temperate

deciduous fagaceous plants (Laessoe & Petersen 2019). *Rubroboletus serpentiformis* differs from *R. flavus* by its snake-skin-like pileal surface, mandarin orange to grayish orange hymenophoral surface, grayish rubious to rubious reticulations on the stipe, and smaller basidiospores (8.5–11 × 4.5–5 μm). As *R. satanas* is a poisonous species, it is highly likely that the closely related species *R. flavus* and *R. serpentiformis* are also inedible, which may result in gastrointestinal symptom.

Morphologically, *R. sinicus* (W.F. Chiu) Kuan Zhao & Zhu L. Yang is somewhat similar to *R. flavus* on the pileus color, while *R. sinicus* is distinguished by its orangish red to blood red hymenophoral surface, red to dark red reticulations on the stipe and smaller basidiospores (7.5–11 × 4.5–5.5 μm) (Chiu 1948, Zhao et al. 2014b).

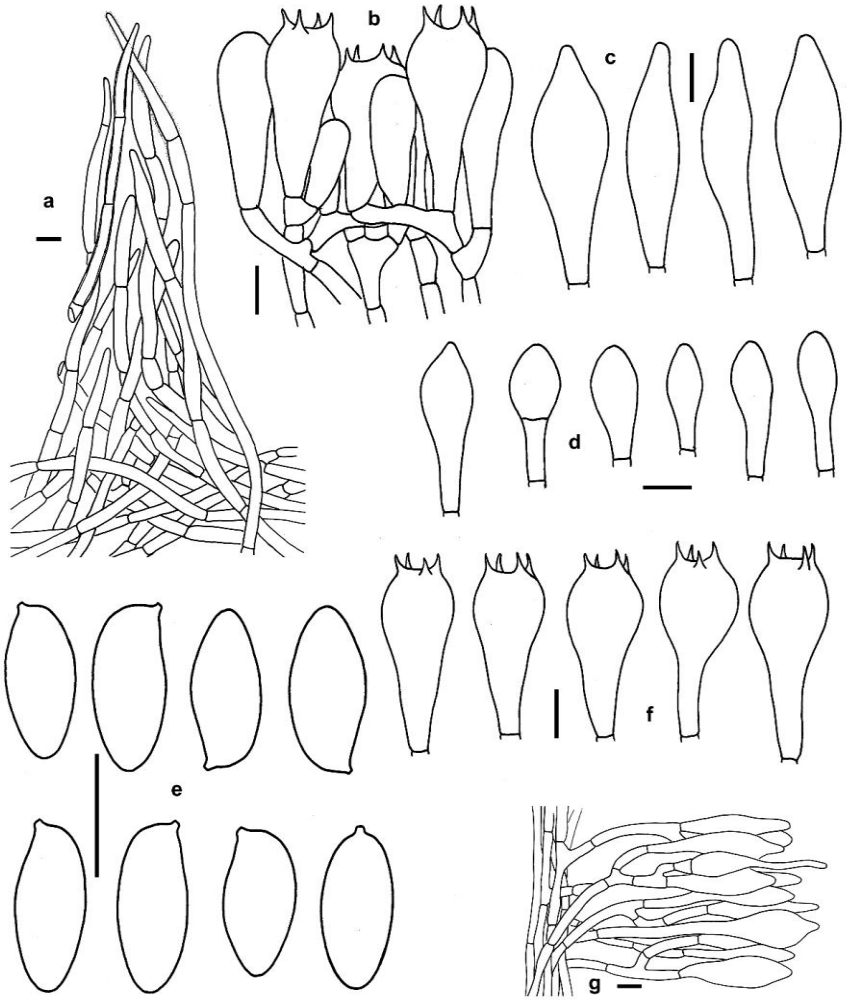

Figure 9 – Microscopic features of *Rubroboletus flavus* (HKAS90906, holotype). a Pileipellis. b Basidia and basidioles. c Pleurocystidia. d Cheilocystidia. e Basidiospores. f Basidia. g Stiptipellis. Scale bars = 10 μm.

Rubroboletus serpentiformis G. Wu, Hai J. Li & Zhu L. Yang, sp. nov. Figs 1, 3c–e, 10

MycoBank number: 847060; Facesoffungi number: FoF 14141

Etymology – The epithet *serpentiformis* refers to the pileal surface of this species similar to snake skin.

Diagnosis – *Rubroboletus serpentiformis* is phylogenetically close to *R. satanas* and *R. flavus*. However, the former differs from the latter by its pale red to reddish white pileus covered with grayish-rubious to rubious snake-skin-patched squamules, slender stipe and smaller

basidiospores. The differences between *R. serpentiformis* and *R. flavus* see the diagnosis and notes of *R. flavus*.

Pileus up to 5–8 cm diam, subhemispheric, convex to broadly convex; surface pale red to reddish white (5A3–8A2), covered with grayish rubious to rubious (12C7–12C8), tomentose squamules, cracked into snake-skin-patches with age; context up to 1.6 cm thick, pale yellow to light yellow (2A4–2A5), quickly staining dark blue on exposure. Hymenophore depressed to sinuate, surface mandarin orange to grayish orange (6B8–6B8), quickly staining dull blue when bruised; tubes 4–5 mm thick, light yellow to butter yellow (4A4–4A5), quickly staining dark blue when bruised; pores roundish, 0.3–0.7 mm diam. Stipe up to 10.5 cm long, up to 2 cm diam, central, subcylindrical, sometimes slightly enlarged downwards, firm, solid; surface pale red to reddish white (5A3–8A2), pale yellow (4A2–4A3) with red tinge, whole or only upper part covered with reticulations and lower part covered with dotted squamules concolorous with pileal tomentose squamules; context firm, slightly darker than pileal context, quickly staining dark blue on exposure. Basal mycelium whitish.

Basidiospores (8) 8.5–11 (12) × 4.5–5 (6) μm [Q = (1.66–)1.76–2.27 (2.36), Q_m = 2.03 ± 0.15], broadly fusoid to ovoid and inequilateral in side view, with slight suprahilar depression, ellipsoid, ovoid to broadly fusoid in face view, yellowish in 5% KOH, smooth, thin-walled. Basidia 30–40 × 9–12 μm, broadly clavate to clavate, 4-spored; sterigmata up to 5 μm long. Cheilocystidia (15.5) 17–32 (35) × (4.5) 5–7 (8) μm, common, lanceolate to narrowly fusoid with acute apex, occasionally clavate, thin-walled. Pleurocystidia 28–53 × 6–10 μm, scattered, lanceolate to subfusoid, with long beak, thin-walled. Hymenophoral trama intermediate to phylloporoid; hyphae subcylindrical to cylindrical, up to 12 μm wide. Pileipellis an intricate trichoderm, ca. 300–500 μm thick, composed of filamentous hyphae 4.5–7.5 μm wide, thin-walled, with subcylindrical, subclavate to subfusoid terminal cells 15–54 × 4–16 μm, thick-walled (often ≤ 2μm, sometimes up to 7 μm). Pileal trama composed of interwoven hyphae 4–13 μm wide. Stipitipellis ca. 40 μm thick between nets, 160 μm on nets, hymeniform; terminal cells 16.5–34 × 4.5–11.5 μm, clavate, broadly fusoid to subcylingdrical. Stipe trama composed of longitudinally arranged parallel thin-walled hyphae 3–8 μm wide. Clamp connections absent.

Known distribution – Southwest China.

Materials examined – China, Yunnan, Pu'er Simao District, Yixiang Town, Dahebian, 1300 m elev., on soil in forest dominated by fagaceous plants (*Quercus*, *Lithocarpus* and *Castanopsis*), 30 June 2017, Gang Wu 2109 (HKAS 126547, holotype); Jianshui County, Panjiang Town, 1660 m elev., on soil in forest dominated by fagaceous plants (*Quercus*, *Lithocarpus* and *Castanopsis*), 3 August 2016, JSPT20160803023 (HKAS 126557, duplication at NIOHP)

Notes – *Rubroboletus serpentiformis* can be recognized by its distinctive features, including its grayish-rubious to rubious tomentose squamules on the pileal surface that become cracked into snake-skin-patches with age, its mandarin orange to grayish orange hymenophoral surface, and its light yellow to butter yellow tubes that quickly stain dark blue when bruised. This species also has a pale red to reddish white stipe that is partially or wholly covered with grayish-rubious to rubious reticulations and dotted squamules, an intricate trichoderm pileipellis, and smooth basidiospores. The phylogenetically related species *R. satanas* differs by a pale gray pileus, a stout stipe, and larger basidiospores (11–13 × 5–6 μm) (Laessoe & Petersen 2019).

Suillellus flaviporus G. Wu, Hai J. Li & Zhu L. Yang, sp. nov. Figs 1, 3f-h, 11

MycoBank number: MB 847061; Facesoffungi number: FoF 14142

Etymology – The epithet *flaviporus* refers to the yellow hymenophoral surface of this species.

Diagnosis – *Suillellus flaviporus* is phylogenetically close to *S. pinophilus*. However, the former differs from the latter by its light yellow to mustard yellow hymenophoral surface, the larger basidiospores and basidia.

Pileus up to 5–11 cm diam, convex to broadly convex; surface cinnamon (6D6), reddish orange, reddish brown to brownish orange (7B7–7C7), subtomentose, dry; context up to 1.2 cm thick, light yellow (3A5), quickly staining dark blue on exposure. Hymenophore adnate to sinuate,

surface and tubes concolorous, light yellow (3A5), wax yellow to mustard yellow (3B5–3B6), quickly staining dull blue when bruised; tubes 8–15 mm thick, concolorous with hymenophoral surface, quickly staining dark blue when bruised; pores irregular to angular, 0.7 mm diam. Stipe up to 11 cm long, up to 1.5 cm diam, central, subcylindrical, sometimes slightly enlarged downwards and tapered at base, firm, solid; surface butter yellow (4A5) to amber yellow (4B6), almost fully covered with grayish red (7B6), orangish red to brownish red (8B7–8C7) reticulations, quickly staining dark blue when bruised; context firm, corn yellow (4A5), orange to golden yellow (5B7–5B8), quickly staining dark blue to blackish blue on exposure. Basal mycelium dirty yellowish white to pale brown.

Basidiospores (10) 11–13.5 × (5.5) 6–7 μm [Q = (1.67–) 1.69–2.19 (2.28), Q_m = 1.92 ± 0.15], broadly fusoid and inequilateral in side view, without distinctive suprahilar depression, ellipsoid, ovoid to broadly fusoid in face view, brownish yellow in 5% KOH, smooth, thin-walled. Basidia (17) 22.5–40 × 13–17 μm, broadly clavate, 2, 3, or 4-spored; sterigmata up to 3 μm long. Cheilocystidia 20–39 × 6–11.5 (18) μm, abundant, narrowly fusoid, thin-walled. Pleurocystidia (35) 39–75 (81) × 9–23 μm, scattered, ventricose-subfusoid, with long beak, thin-walled. Hymenophoral trama boletoid with hyphae diverging from the central strand to the subhymenium; hyphae subcylindrical to cylindrical, 5–10 μm wide. Pileipellis a trichoderm, ca. 160 μm thick, composed of filamentous hyphae 3–10.5 μm wide, thin-walled, with subcylindrical to subclavate terminal cells 18–45 × 5–11 μm, often thin-walled. Pileal trama composed of interwoven hyphae 4–15 μm wide. Stipitipellis ca. 120–170 μm thick, hymeniform; caulobasidia 33–59 × 8–15 μm, sparse; caulocystidia 30–55 × 6.5–10 μm, other terminal cells 13–48 × 3–7 μm, clavate to subcylingdrical. Stipe trama composed of longitudinally arranged parallel thin-walled hyphae 4–10 μm wide. Clamp connections absent.

Known distribution – Southwest to Central China.

Materials examined – China, Yunnan, Malipo County, Donggan Town, Huilong Village, 1470 m elev., on soil in mixed forest dominated by *Pinus yunnanensis* and fagaceous plants (*Quercus*, *Lithocarpus* and *Castanopsis*), 22 June 2017, 532624MF-103-Wu1987 (HKAS 123826, holotype). HUBEI, Enshi City, Baiyangping Town, 862 m elev., on soil in mixed forest dominated by *Pinus massoniana* and fagaceous plants (*Quercus*, *Lithocarpus* and *Castanopsis*), 20 July 2017, Hai-Jiao Li 170720-10 (HKAS 126551, duplication at NIOHP); same locality and date, Zuo-Hong Chen 4 (HKAS 126554); same locality and date, Zuo-Hong Chen 7 (HKAS 126555).

Notes – *Suillellus flaviporus* is distinguished by the whole basidioma quickly staining dark blue when bruised, the concolorous yellow hymenophoral surface and tubes, the butter yellow to amber yellow stipe fully ornamented with grayish red, orangish red to brownish red reticulations, a trichoderm pileipellis, and smooth basidiospores.

The phylogenetcally closed species *S. pinophilus* differs in its brownish orange to light brown hymenophoral surface, the smaller basidiospores (9–12 × 5–6 μm) and basidia (18–27.5 × 10–13.5 μm). *Suillellus luridus* (Schaeff.) Murrill is also phylogenetically related to *S. flaviporus*, but it is different in its orangish red hymenophoral surface, and its association with temperate dediduous oak trees in Europe and North America (Smith & Thiers 1971, Laessoe & Petersen 2019). Morphologically, *Neoboletus flavidus* somewhat resembles *S. flaviporus* with brown basidioma and yellow hymenophore, however, *N. flavidus* is distinguished by its dot-scaled stipe without reticulations on the surface and the narrower basidiospores (10–13 × 4.5–5.5 μm) (Wu et al. 2016a).

Suillellus pinophilus G. Wu, Hai J. Li, Zhu L. Yang, sp. nov. Figs 1, 3i–j, 12

MycoBank number: MB 847062; Facesoffungi number: FoF 14143

Etymology – The epithet *pinophilus* refers to the preference for pine host plants of this species.

Diagnosis – *Suillellus pinophilus* is phylogenetically close to *S. flaviporus*. Their differences see the diagnosis and commentary of *S. flaviporus*

Pileus up to 9 cm diam, convex to broadly convex; surface brownish orange to caramel brown (5C6–6C6), subtomentose, dry; context up to 1 cm thick, pale yellow (2A3–2A4), quickly staining dark blue on exposure. Hymenophore depressed, surface brownish orange to light brown (6C6–7C6), quickly staining blackish blue when bruised; tubes up to 1.8 cm thick, pale yellow (3A3–3A4), quickly staining blackish blue when bruised; pores roundish, 0.5 mm diam. Stipe up to 8 cm long, 1.5 cm diam, central, subcylindrical to slightly obclavate, firm, solid; surface brownish violet (11D7–11D8), mixed with light orange (6A5) tinge, fully covered with concolorous reticulations; context firm, yellowish brown (5E7–5E8) mixed with pale yellow (4A2–4A3) color, staining blue at the apex, almost unchanging on the remaining part. Basal mycelium brown.

Basidiospores 9–12 × 5–6 (7) μm [Q = (1.58) 1.60–2.16 (2.32), Q_m = 1.91 ± 0.16], broadly fusoid, ovoid to ellipsoid and inequilateral in side view, with indistinctive suprahilar depression, broadly fusoid, ovoid to ellipsoid in face view, brownish yellowish in 5% KOH, smooth, thin-walled. Basidia 18–27.5 (36) × 10–13.5 μm, shortly clavate, 4-spored; sterigmata up to 3 μm long. Cheilocystidia 42–58× 10–16 μm, sparse, gourd-shaped to subfusoid with short beak, thin-walled. Pleurocystidia 47–67 × 11–17 μm, sparse, ventricose-fusoid, thin-walled. Hymenophoral trama phylloporoid to intermediate; hyphae subcylindrical to cylindrical, 3.5–12 μm wide. Pileipellis a trichoderm, ca. 150 μm thick, composed of filamentous hyphae 5–8 μm wide, thin-walled, with subcylindrical, subfusoid to broadly fusoid terminal cells 16.5–57.5 × 5–15 μm, thin-walled. Pileal trama composed of interwoven hyphae 7–19 μm wide. Stipitipellis ca. 75 μm thick between nets, 300 μm on nets, hymeniform; terminal cells 10–38 × 5.5–14.6 μm, broadly clavate, broadly fusoid to subcylindrical; caulobasidia present. Stipe trama composed of longitudinally arranged parallel thin-walled hyphae 4–14 μm wide. Clamp connections absent.

Known distribution – Southwest China.

Material examined – China, Yunnan, Dayao County, Longjie Town, Tadi Village, 1958 m elev., on soil in the forest dominated by *Pinus yunnanensis*,13 July 2017, Hai-Jiao Li 170713-05 (HKAS 126550, holotype; duplication at NIOHP)

Notes – Despite being proposed based on only one specimen, this new species can be easily distinguished by several key features. It primarily associates with pine host plants and has a caramel brown to brownish orange basidioma. Its hymenophoral surface and tubes are in different color and both quickly stain dark blue when bruised. The species also has a stipe that is wholly covered with distinct reticulations and has comparatively small basidiospores. Molecular phylogenetic evidence also supported its recognition as a new species. *Suillellus pinophilus* is closely related to *S. flaviporus*, with a solid genetic variation of 0.0323, and comparisons between the two species see notes of *S. flaviporus*.

Suillellus pinophilus is morphologically and phylogenetically related to *S. lacrymibasidiatus* Yang Wang et al. , *S. luridus*, and *S. subamygdalinus* Kuan Zhao & Zhu L. Yang. However, *S. lacrymibasidiatus* was originally described from Xinjiang in Northwest China (Wang et al. 2022), and it can be distinguished from *S. pinophilus* by its larger subamygdaloid to broadly ellipsoid basidiospores (measuring 14.5–15 × 7.5–8 μm), much broader basidia (21–38.5 × 13–20 μm), and lack of pleurocystidia and cheilocystidia (Wang et al. 2022). *Suillellus luridus* is dfferent in its longer basidiospores (11–15 × 5.5–7 μm) and its association with temperate dediduous oak trees in Europe and North America (Smith & Thiers 1971, Laessoe & Petersen 2019). *Suillellus subamygdalinus* differs in its longer basidiospores (12–16 × 5–7 μm) and basidia (34–48 × 8–11 μm) (Wu et al. 2016a).

Morphologically, *Boletus sinensis* (T.H. Li & M. Zang) Q.B. Wang & T.H. Li is also somewhat similar to *S. pinophilus* on brown to ochre yellow pileus. However, *B. sinensis* differs in its reddish brown hymenophoral surface, longer basidiospores (13–19 ×5–6.5 μm) and its tropical habitat (Zang et al. 2001).

Suillellus yunnanensis G. Wu & Zhu L. Yang, sp. nov. Figs 1, 2k–l, 13

MycoBank number: MB 847063; Facesoffungi number: FoF 14144

Etymology – The epithet *yunnanensis* refers to the type locality of this species, namely Yunnan Province of China.

Diagnosis – *Suillellus yunnanensis* is close to *S. amygdalinus*. However, the former differs from the latter by its stipe with prominent reticulations on the surface and distinctively longer basidia.

Pileus up to 3–7 cm diam, hemispherical, convex to broadly convex; surface caramel brown (6C6) to brown (6D7), subtomentose, dry; context up to 1.3 cm thick, pale yellow to light yellow (2A3–2A4), quickly staining blackish blue on exposure. Hymenophore sinuate, surface brownish red to reddish brown (9C7–9D7), quickly staining blackish blue when bruised; tubes up to 0.7 cm thick, light yellow (4A4) to grayish yellow (4C5), quickly staining blackish blue when bruised; pores irregular to angular, 0.3 mm diam. Stipe 6–7 cm long, 0.9–1.5 cm diam, central, subcylindrical, curve, firm, solid; surface brick red to sienna (7D7–7D8), mixed with pinkish color, partially or fully covered with brick red to sienna (7D7–7D8) reticulations, sometimes lower part covered with dotted squamules if no reticulation ornamented, quickly staining blackish blue when bruised; context firm, concolorous with pileal context, quickly staining blackish blue on exposure. Basal mycelium dirty white.

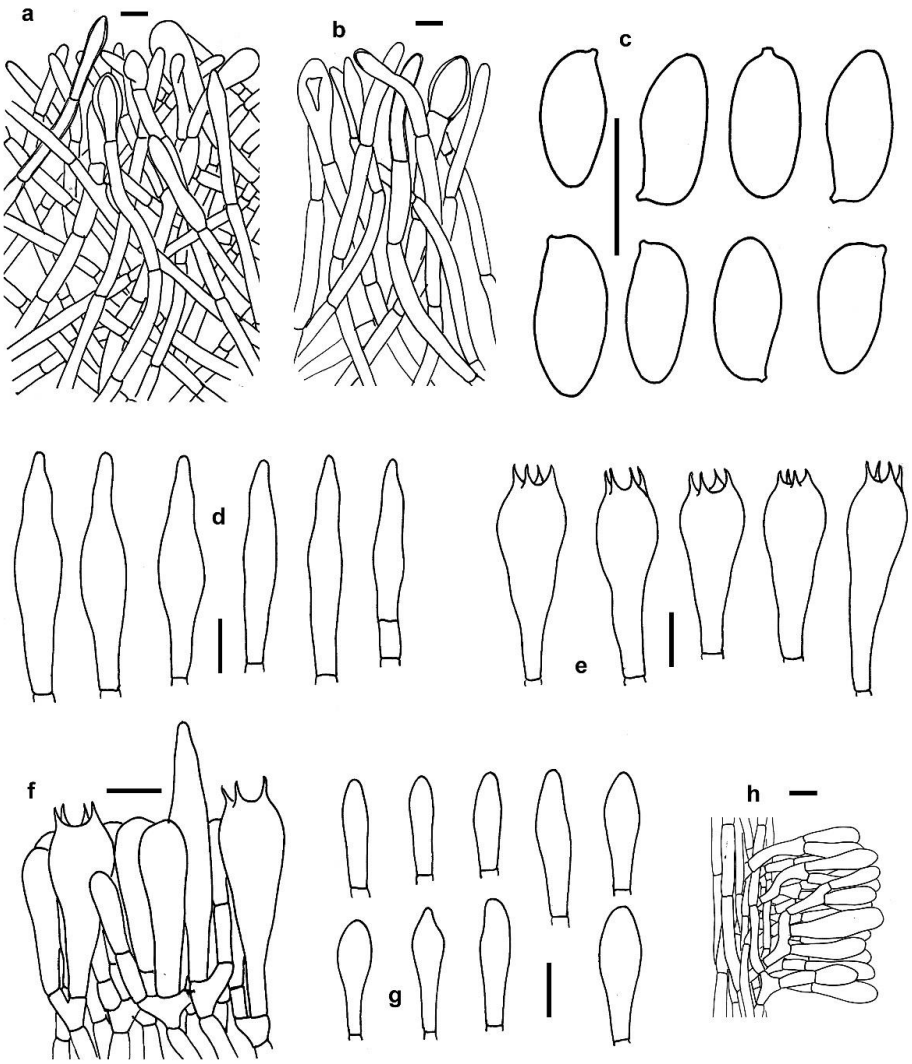

Figure 10 – Microscopic features of *Rubroboletus serpentiformis* (a HKAS 126557; b–h HKAS 126547, holotype). a Pileipellis. b Pileipellis. c Basidiospores. d Pleurocystidia. e Basidia. f Basidia, pleurocystidium and basidioles. g Cheilocystidia; h. Stiptipellis. Scale bars = 10 μm.

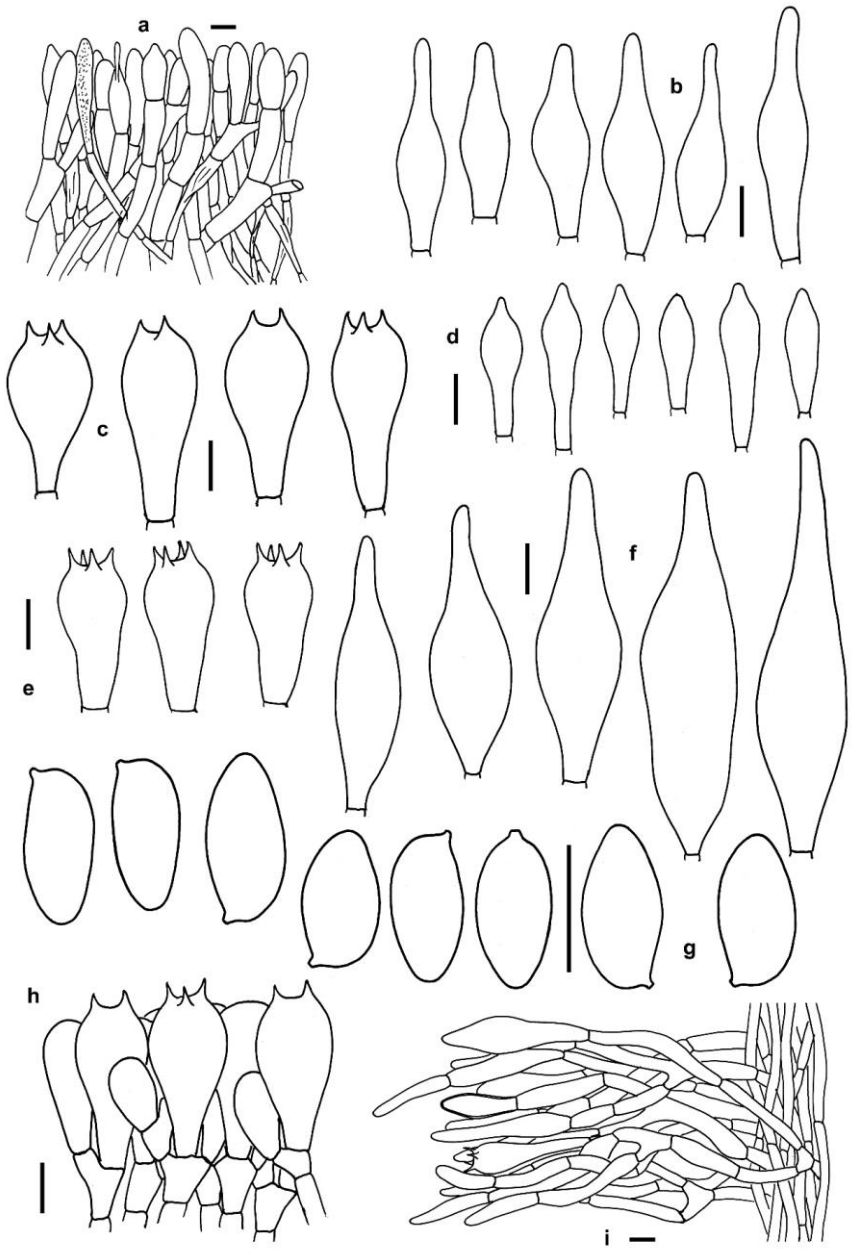

Figure 11 – Microscopic features of *Suillellus flaviporus* (HKAS 123826, holotype; a–g, fruitbody 1; e–f, fruitbody 2). a Pileipellis. b Pleurocystidia. c Basidia. d Cheilocystidia. e Basidia. f Pleurocystidia. g Basidiospores. h Basidia and basidioles. i Stiptipellis. Scale bars = 10 μm.

Basidiospores 12–14 (15) × 5–6.5 (7) μm [Q = (2.0) 2.03–2.5 (2.7), Q_m = 2.24 ± 0.16], broadly fusoid to subfusoid and inequilateral in side view, with indistinctive suprahilar depression, ellipsoid to subfusoid in face view, brownish yellow in 5% KOH, smooth, thin-walled. Basidia 34–62 (70) × 8–14 μm, clavate, 4-spored, rarely 2-spored; sterigmata up to 4 μm long. Cheilocystidia 18–48× 5–7.5 μm, common, narrowly fusoid with acute apex, thin-walled. Pleurocystidia 43–70 × 7–9 μm, sparse, narrowly fusoid, slightly thick-walled (< 0.5 μm). Hymenophoral trama boletoid with hyphae diverging from the central strand to the subhymenium; hyphae subcylindrical to cylindrical, 2–10 μm wide. Pileipellis a trichoderm to slight ixotrichoderm, ca. 150 μm thick, composed of entangled filamentous hyphae 3–7 μm wide, slightly thick-walled (≤ 1 μm), with subcylindrical to subfusoid terminal cells 20.5–42.5 × 5–7.5 μm, slightly thick-walled (≤ 1 μm), often imbedded in gelatinized substance. Pileal trama composed of interwoven hyphae 4–11 μm wide. Stipitipellis ca. 75 μm thick, hymeniform; caulocystidia 21–48 × 6.5–11.5 μm, common; caulobasidia 22.5–35 × 9.5–11 μm, sparse; other terminal cells 15–34 × 5–8.5 μm, subcylindrical

with acute apex. Stipe trama composed of longitudinally arranged parallel thin-walled hyphae 3–13 μm wide. Clamp connections absent.

Known distribution – Southwest China.

Materials examined – China, Yunnan, Kunming City, Kunming Botanic Garden, 1950 m elev., on soil in forest dominated by fagaceous plants (*Quercus*, *Lithocarpus* and *Castanopsis*), 5 July 2018, Gang Wu 2639 (HKAS 126548, holotype); same locality, 2 September 2020, Gang Wu 3014 (HKAS 126549).

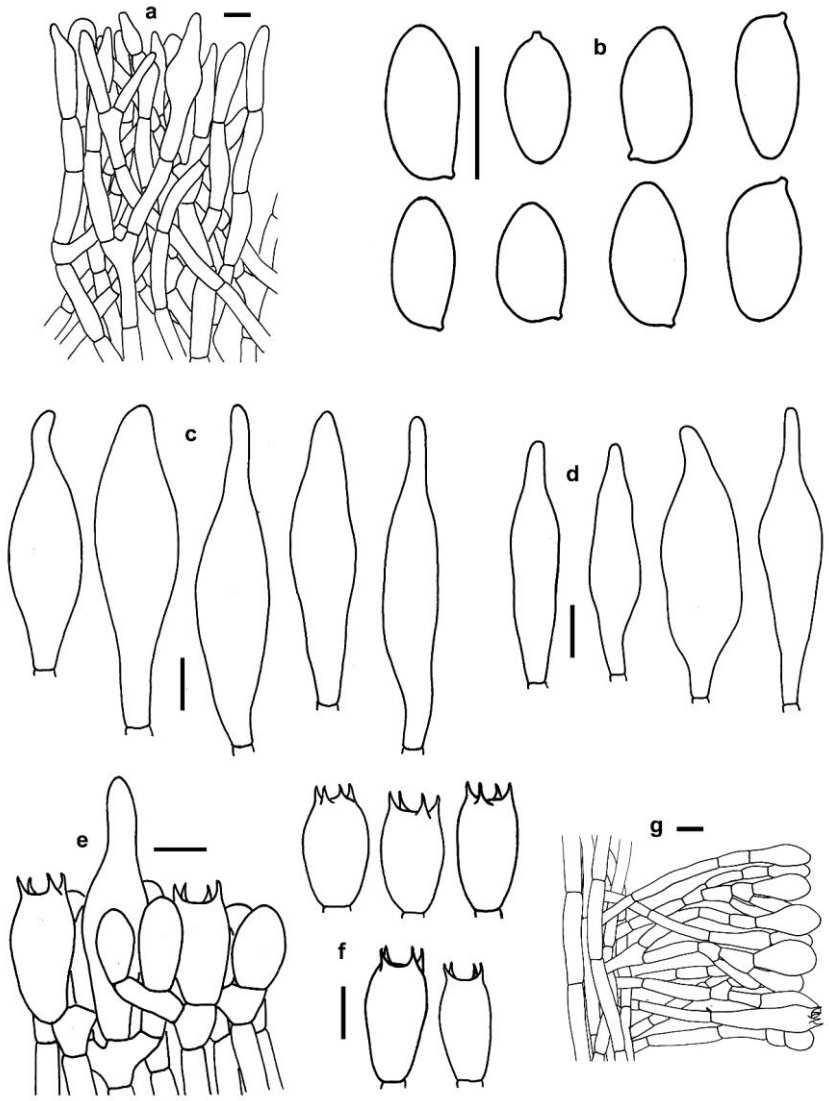

Figure 12 – Microscopic features of *Suillellus pinophilus* (HKAS 126550, holotype). a Pileipellis; b Basidiospores. c Pleurocystidia. d Cheilocystidia. e Basidia, pleurocystidium and basidioles. f Basidia. g Stiptipellis. Scale bars = 10 μm.

Notes – *Suillellus yunnanensis* is distinguished by the whole basidioma staining blackish blue quickly when bruised, the caramel brown to brown pileus, the reddish brown hymenophoral surface and light yellow tubes, the stipe wholly covered with distinct reticulations, a trichoderm to ixotrichoderm pileipellis, smooth basidiospores, and the preference for the fagaceous host plants. The phylogenetically related species *S. amygdalinus* differs in its equal to ventricose stipe covered with granulose or tomentose squamules, but without distinct reticulations, and its shorter basidia (30–35× 9–11 μm) (Thiers 1965).

By comparing ITS sequences of *S. yunnanensis* with available ITS sequences in GenBank, the best hit was *S. mendax* (Simonini & Vizzini) Vizzini, Simonini & Gelardi with 95.42% identity.

Suillellus mendax is distinguished by its larger Q value of basidiospores (2.6–2.8), smaller basidia (24.9–30.5 × 9.5–12.7 μm) and wider cystidia (Pleurocystidia: 60.0–69.1×11.1–12.9 μm, Cheilocystidia: 40.2–62.4 × 10.2–13.3 μm) (Vizzini et al. 2014).

The Chinese species *S. subamygdalinus*, *S. lacrymibasidiatus* and *S. pinophilus* somewhat resemble *S. yunnanensis*. However, all of them differ in their Pinaceae hosts. In addition, *S. subamygdalinus* differs in its subtomentose pileus more or less tinged with red color, and its preference for subalpine niche (Wu et al. 2016a); *S. lacrymibasidiatus* differs in its wider basidiospores (14.5–15 × 7.5–8 μm), the shorter but broader basidia (21–38.5 × 13–20 μm), lack of pleurocystidia and cheilocystidia, and its temperate distribution (Wang et al. 2022); *S. pinophilus* differs in its smaller basidiospores (9–12 × 5–6 μm).

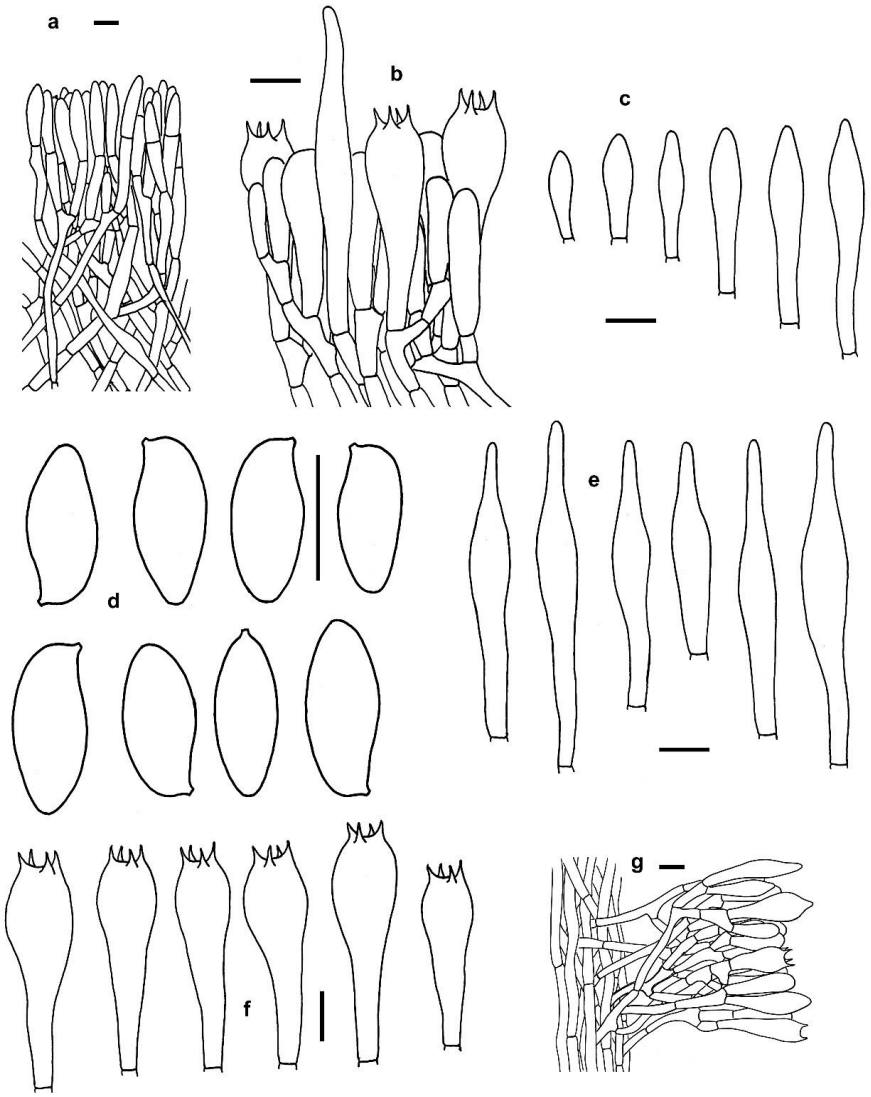

Figure 12 – Microscopic features of *Suillellus yunnanensis* (HKAS 126548, holotype). a Pileipellis. b Basidia, pleurocystidium and basidioles. c Cheilocystidia. d Basidiospores. e Pleurocystidia. f Basidia. g Stiptipellis. Scale bars = 10 μm.

Discussion

China's diverse regions, ranging from tropical to temperate zones, contribute to its high species diversity across all kingdoms of life, including fungi. In the past decades, Chinese mycologists had made their greatest efforts to uncover the fungal diversity in China, and boletes received high attention because of their edibility (Chiu 1948, Bi et al. 1982, Ying & Ma 1985, Chen

et al. 1997, Li & Song 2000, Zang 2006). By molecular techniques, more and more new taxa of boletes were found in China (Wu et al. 2016a, Chai et al. 2019, Zhang et al. 2019, Li & Yang 2021, Fu et al. 2022, Wang et al. 2022). Based on evidence from morphology, ecology, and molecular phylogeny, this study identified two new genera, nine new species, and one new combination of Boletaceae.

The new genus *Hongoboletus* phylogenetically represented a solitary clade and was clustered with a clade comprising the genera *Amoenoboletus* G. Wu, E. Horak & Zhu L. Yang, *Caloboletus* Vizzini, *Costatisporus* T.W. Henkel & M.E. Sm., *Crocinoboletus*, *Imperator* Koller et al., *Neoboletus*, *Pulveroboletus* Murrill, *Rubroboletus* Kuan Zhao & Zhu L. Yang, *Suillellus*, and *Sutorius* Halling, Nuhn & N.A. Fechner (this study, Wu et al. 2016a). Among these genera, *Neoboletus*, *Imperator*, *Rubroboletus*, and *Suillellus* are morphologically similar to *Hongoboletus* because of the dark-colored basidiomes and bluing reaction on exposure. However, all of them morphologically differs from *Hongoboletus* by its often brown to reddish brown hymenophoral surface (Smith & Thiers 1971, Alessio 1985, Zhao et al. 2014b, Wu et al. 2016a, Wu et al. 2016b). Moreover, the genera *Imperator*, *Rubroboletus* and *Suillellus* are different in the reticulated stipe, and *Neoboletus* is distinguished by the squamulose stipe surface and a more regular trichoderm pileipellis (Zhao et al. 2014b, Wu et al. 2016a). Morphologically, *Hongoboletus* is also similar to the genera *Lanmaoa* G. Wu & Zhu L. Yang and *Baorangia* G. Wu & Zhu L. Yang, which often have thick context and thin hymenophore (Wu et al. 2016b). However, *Lanmaoa* and *Baorangia* differ in the lighter and slower blue discoloration of context when bruised, and are phylogenetically distinct from *Hongoboletus* (Wu et al. 2016a, Wu et al. 2016b, Chai et al. 2018, Phookamsak et al. 2019).

The new genus *Acyanoboletus* was found to be clustered in a clade with moderate support (52/0.97), consisting of *Cyanoboletus*, *Cupreoboletus*, *Cacaoporus*, and an unresolved lineage represented by "Boletaceae sp. JD0693." However, the relationships between these genera within the clade remain unclear. Notably, *Acyanoboletus* exhibited high genetic variations with *Cyanoboletus*, *Cupreoboletus*, and *Cacaoporus*, ranging from 0.1046 to 0.1474. By conducting additional morphological comparisons, *Cyanoboletus* and *Cupreoboletus* can be distinguished from *Acyanoboletus* based on their blue discoloration in the bruised context and hymenophore (Gelardi et al. 2014, Gelardi et al. 2015, Wu et al. 2016a), and *Cacaoporus* is different in its chocolate dark brown basidioma (Vadthanarat et al. 2019). In general, *Acyanoboletus* is reasonably treated as an independent genus.

All of the newly proposed species in this study are the blue-staining boletes, with the exception of the species belonging to *Acyanoboletus*. Among them, *Rubroboletus flavus*, *R. serpentiformis*, *Suillellus flaviporus*, *S. pinophilus*, and *S. yunnanensis* are likely to be inedible due to the fact that many other species within the genera of *Rubroboletus* and *Suillellus* are commonly classified as poisonous mushrooms and can lead to gastrointestinal disorders. Some examples of such poisonous species include *Rubroboletus satanas*, *S. luridus*, and others (Lange & Hora 1963). Moreover, *Neoboletus brunneorubrocarpus* has been responsible for one case of poisoning reported in Fujian Province, China. Therefore, it is not recommended to consume these new species.

Despite the recent publications of a significant number of new bolete taxa in China, with approximately 400 recorded species in the region, there are still many more boletes to be discovered. These include not only new species, but also some known species that were published decades ago but had been largely ignored, such as *Boletus citrifragrans* W.F. Chiu & M. Zang, *Boletus minutus* W.F. Chiu, *Boletus subgriseus* Z.S. Bi, and others. Therefore, it is crucial to conduct more extensive and in-depth investigations and comprehensive taxonomic work on boletes in China.

Acknowledgement

The authors thank Prof. Zuo-Hong Chen at Hunan Normal University, Dr. Kuan Zhao, Mr. Jian-Wei Liu, Mr. Si-Peng Jian, Mr. Shi-Bin Jiao at Kunming Institute of Botany, Chinese

Academy of Sciences (KIB), Mr. Zuo-Lin Fu and Mr. Kun Huang at Institute of Forestry Science, Bailongjiang Forestry Administration, Gansu Province, Ms. Yan-Fen Qian, Ms. Ji Gao, Ms. Qian Fang, Ms. Yan-Fang Qi, Ms. Jian-Mei Zhang, Mr. Xiao-Gang Tan, at Jianshui CDC, Yunnan Province for collecting specimens, and thank the TNS Herbarium for loaning specimens. The authors are also grateful to the editor and anonymous reviewers for their constructive suggestions. This work was financed by National Natural Science Foundation of China under grant numbers 31970015 and 32270025, Yunnan Young & Elite Talents Project (YNWR-QNBJ-2018-266), Yunnan Xingdian Talents Support Plan - Science and Technology Leading Talents Program (202305AB350004), CAS "Light of West China" Program, Natural Science Foundation of Yunnan Province for Excellent Young Scholars (202301AW070011), Natural Science Foundation of Yunnan Province (202201AT070128).

References

Alessio C. 1985 – Fungi Europaei 2: *Boletus* Dill. ex L. (sensu lato) Libreria editrice Biella Giovanna, Saronno.

Arora D, Frank JL. 2014 – Clarifying the butter boletes: a new genus, *Butyriboletus*, is established to accommodate *Boletus* sect. *Appendiculati*, and six new species are described. Mycologia 106(3), 464–480.

Badou SA, Furneaux B, De Kesel A, Khan FK et al. 2022 – *Paxilloboletus* gen. nov., a new lamellate bolete genus from tropical Africa. Mycological Progress 21(1), 243–256.

Bessette A, Roody WC, Bessette AR. 2000 – North American boletes: a color guide to the fleshy pored mushrooms. Syracuse University Press, New York.

Bi Z-S, Lu D-J, Zheng G-Y. 1982 – Basidiomycetes from Dinghu Mountain of China. II. Some species of Boletaceae (1). Acta Botanica Yunnanica 4(1), 55–64.

Chai H, Liang Z-Q, Jiang S, Fu X-L, Zeng N-K. 2018 – *Lanmaoa rubriceps*, a new bolete from tropical China. Phytotaxa 347(1), 71–80.

Chai H, Liang Z-Q, Xue R, Jiang S et al. 2019 – New and noteworthy boletes from subtropical and tropical China. Mycokeys 46, 55–96.

Chen CM, Huang HW, Yeh KW. 1997 – The boletes of Taiwan (VII). Taiwania 42(3), 174–179.

Chiu W-F. 1948 – The boletes of Yunnan. Mycologia 40(2), 199–231.

Corner EJH. 1972 – *Boletus* in Malaysia. Botanic Gardens, Singapore.

Cui Y-Y, Feng B, Wu G, Xu J, Yang Z-L. 2016 – Porcini mushrooms (*Boletus* sect. *Boletus*) from China. Fungal Diversity 81(1), 189–212.

Darriba D, Posada D, Kozlov AM, Stamatakis A et al. 2019 – ModelTest-NG: a new and scalable tool for the selection of DNA and protein evolutionary models. Molecular Biology and Evolution 37(1), 291–294.

Doyle JJ, Doyle JL. 1987 – A rapid DNA isolation procedure for small quantities of fresh leaf tissue. Phytochemical Bulletin 19, 11–15.

Farid A, Bessette A, Bessette A, Bolin J et al. 2021 – Investigations in the boletes (Boletaceae) of southeastern USA: four novel species and three novel combinations. Mycosphere 12(1), 1038–1076.

Feng B, Xu J, Wu G, Hosen MI et al. 2012 – DNA sequence analyses reveal abundant diversity, endemism and evidence for Asian origin of the porcini mushrooms. PLoS One 7(5), e37567.

Fu H-Y, Li T, Fan L. 2022 – Two new species of *Butyriboletus* from China. Phytotaxa 544(2), 207–219.

Gardes M, Bruns T. 1993 – ITS Primers with enhanced specificity for Basidiomycetes: Application to the identification of mycorrhizae and rusts. Molecular Ecology 2(2), 113–118.

Gelardi M, Simonini G, Ercole E, Davoli P, Vizzini A. 2015 – *Cupreoboletus* (Boletaceae, Boletineae), a new monotypic genus segregated from Boletus sect. Luridi to reassign the Mediterranean species B. poikilochromus. Mycologia 107(6), 1254–1269.

Gelardi M, Vizzini A, Ercole E, Voyron S et al. 2013 – *Boletus sinopulverulentus*, a new species from Shaanxi Province (central China) and notes on *Boletus* and *Xerocomus*. Sydowia 65(1), 45–57.
Gelardi M, Vizzini A, Simonini G. 2014 – *Cyanoboletus*. Index Fungorum 176, 1.
Hall TA. 1999 – BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. In: Nucleic Acids Symposium Series, 1999. pp. 95–98.
Han L-H, Feng B, Wu G, Halling RE et al. 2018 – African origin and global distribution patterns: Evidence inferred from phylogenetic and biogeographical analyses of ectomycorrhizal fungal genus *Strobilomyces*. Journal of Biogeography 45, 201–212.
Henkel TW, Obase K, Husbands D, Uehling JK et al. 2016 – New Boletaceae taxa from Guyana: *Binderoboletus segoi* gen. and sp. nov., *Guyanaporus albipodus* gen. and sp. nov., *Singerocomus rubriflavus* gen. and sp. nov.,and a new combination for *Xerocomus inundabilis*. Mycologia 108(1), 157–173.
Hongo T. 1968 – Notulae Mycologicae (7): auctore. Memoirs of Shiga University 18, 34–39.
Hongo T. 1973 – Enumeration of the Hygrophoraceae, Boletaceae and Strobilomycetaceae. Bull Nat Sci Mus Tokyo 16, 537–557.
Horak E. 2011 – Revision of Malaysian species of Boletales s.l. (Basidiomycota) described by EJH Corner (1972, 1974). Malayan Forest Records 51, 1–283.
Jiang S, Mi H-X, Xie H-J, Zhang X et al. 2021 – *Neoboletus infuscatus*, a new tropical bolete from Hainan, southern China. Mycoscience 62(3), 205–211.
Katoh K, Standley DM. 2013 – MAFFT Multiple sequence alignment software version 7: Improvements in performance and usability. Molecular Biology and Evolution 30(4), 772–780.
Khmelnitsky O, Davoodian N, Singh P, Raspé O et al. 2019 – *Ionosporus*: a new genus for *Boletus longipes* (Boletaceae), with a new species, *I. australis*, from Australia. Mycological Progress 18(3), 439–451.
Kirk PM, Cannon PF, Minter D, Stalpers JA. 2008 – Dictionary of the Fungi, 10th edn. CAB International, Wallingford.
Kumar S, Stecher G, Li M, Knyaz C, Tamura K. 2018 – MEGA X: Molecular Evolutionary Genetics Analysis across Computing Platforms. Molecular Biology and Evolution 35(6), 1547–1549.
Laessoe T, Petersen JH. 2019 – Fungi of temperate Europe. Volume I. Princeton University Press, Princeton and Oxford.
Lange M, Hora FB. 1963 – Collins' guide to mushrooms and toadstools. Collins, London.
Li T-H, Song B. 2000 – Chinese boletes: a comparison of boreal and tropical elements. Tropical mycology, 1–9.
Li Y-C, Yang Z-L. 2021 – The boletes of China: *Tylopilus* s.l. Science Press, Beijing.
Li Y-C, Feng B, Yang Z-L. 2011 – *Zangia*, a new genus of Boletaceae supported by molecular and morphological evidence. Fungal Diversity 49(1), 125–143.
Magnago AC, Alves-Silva G, Henkel TW, da Silveira RMB. 2022 – New genera, species, and combinations of Boletaceae from Brazil and Guyana. Mycologia 114(3), 607–625.
Meng X, Wang G-S, Wu G, Wang P-M et al. 2021 – The genus *Leccinum* (Boletaceae, Boletales) from China based on morphological and molecular data. Journal of Fungi 7(9), 732.
Neves MA, Binder M, Halling R, Hibbett D, Soytong K. 2012 – The phylogeny of selected *Phylloporus* species, inferred from NUC-LSU and ITS sequences, and descriptions of new species from the Old World. Fungal Diversity 55(1), 109–123.
Pegler D, Young T. 1981 – A natural arrangement of the Boletales, with reference to spore morphology. Transactions of the British Mycological Society 76(1), 103–146.
Phookamsak R, Hyde KD, Jeewon R, Bhat DJ et al. 2019 – Fungal diversity notes 929–1035: taxonomic and phylogenetic contributions on genera and species of fungi. Fungal Diversity 95(1), 1–273.

Raspé O, Vadthanarat S, De Kesel A, Degreef J et al. 2016 – *Pulveroboletus fragrans*, a new Boletaceae species from Northern Thailand, with a remarkable aromatic odor. Mycological Progress 15(4), 38.
Ronquist F, Teslenko M, Van Der Mark P, Ayres DL et al. 2012 – MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic biology 61(3), 539–542.
Smith AH, Thiers HD. 1971 – The boletes of Michigan. University of Michigan Press, Ann Arbor.
Smith SA, Dunn CW. 2008 – Phyutility: a phyloinformatics tool for trees, alignments and molecular data. Bioinformatics 24(5), 715–716.
Stamatakis A. 2014 – RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30(9), 1312–1313.
Sun H, Zhang J, Deng T, Boufford DE. 2017 – Origins and evolution of plant diversity in the Hengduan Mountains, China. Plant Diversity 39(4), 161–166.
Takahashi H, Taneyama Y, Degawa Y. 2013 – Notes on the boletes of Japan 1. Four new species of the genus *Boletus* from central Honshu, Japan. Mycoscience 54(6), 458–468.
Thiers HD. 1965 – California Boletes. I. Mycologia 57(4), 524–534.
Vadthanarat S, Lumyong S, Raspé O. 2019 – *Cacaoporus*, a new Boletaceae genus, with two new species from Thailand. Mycokeys 54, 1–29.
Vilgalys R, Hester M. 1990 – Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. Journal of Bacteriology 172(8), 4238–4246.
Vizzini A, Simonini G, Ercole E, Voyron S. 2014 – *Boletus mendax*, a new species of *Boletus* sect. *Luridi* from Italy and insights on the *B. luridus* complex. Mycological Progress 13(1), 95–109.
Wang Q-B, Li T-H, Yao Y-J. 2003 – A new species of *Boletus* from Gansu Province, China. Mycotaxon 88, 439–446.
Wang Y, Tuo Y-L, Wu D-M, Gao N et al. 2022 – Exploring the relationships between four new species of boletoid fungi from Northern China and their related species. Journal of Fungi 8(3), 218.
White TJ, Bruns T, Lee S, Taylor J. 1990 – Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis M, Gelfand D, Sninsky J, White T (eds.) PCR protocols: a guide to methods and applications, vol 18. Academic Press, San Diego. pp. 315–322.
Wu G, Feng B, Xu J, Zhu X-T et al. 2014 – Molecular phylogenetic analyses redefine seven major clades and reveal 22 new generic clades in the fungal family Boletaceae. Fungal Diversity 69, 93–115.
Wu G, Lee SML, Horak E, Yang Z-L. 2018 – *Spongispora temasekensis*, a new boletoid genus and species from Singapore. Mycologia 110(5), 919–929.
Wu G, Li M-X, Horak E, Yang Z-L. 2022 – Phylogenetic analysis reveals the new genus *Amoenoboletus* from Asia and New Zealand. Mycologia 114(1), 144–156.
Wu G, Li Y-C, Zhu X-T, Zhao K et al. 2016a – One hundred noteworthy boletes from China. Fungal Diversity 81, 25–188.
Wu G, Zhao K, Li Y-C, Zeng N-K et al. 2016b – Four new genera of the fungal family Boletaceae. Fungal Diversity 81, 1–24.
Yang Z-L. 2005 – Diversity and biogeography of higher fungi in China. In: Xu JP (ed.) Evolutionary genetics of fungi. Horizon Bioscience, Norfolk. pp. 35–62.
Ying J-Z, Ma Q-M. 1985 – New taxa and records of the genus *Strobilomyces* in China. Acta Microbiologica Sinica 4(2), 95–102.
Zang M. 1983 – A tentative subdivision and two new species of *Boletus* from Yunnan, China. Mycosystema 2(1), 12–17.
Zang M. 2006 – Flora fungorum sinicorum. Vol. 22, Boletaceae (I). Science Press, Beijing, China.

Zang M, Li T-H, Petersen RH. 2001 – Five new species of Boletaceae from China. Mycotaxon 80, 481–488.
Zeng N-K, Liang Z-Q, Wu G, Li Y, Yang Z-L. 2016 – The genus *Retiboletus* in China. Mycologia 108(2), 363–380.
Zeng N-K, Tang L-P, Li Y-C, Bau T et al. 2013 – The genus *Phylloporus* (*Boletaceae*, *Boletales*) from China: morphological and multilocus DNA sequence analyses. Fungal Diversity 58(1), 73–101.
Zhang M, Li T-H, Wang C-Q, Zeng N-K, Deng W-Q. 2019 – Phylogenetic overview of *Aureoboletus* (Boletaceae, Boletales), with descriptions of six new species from China. Mycokeys 61, 111–145.
Zhao K, Wu G, Feng B, Yang Z-L. 2014a – Molecular phylogeny of *Caloboletus* (*Boletaceae*) and a new species in East Asia. Mycological Progress 13(4), 1127–1136.
Zhao K, Wu G, Halling RE, Yang Z-L. 2015 – Three new combinations of *Butyriboletus* (Boletaceae). Phytotaxa 234(1), 51–62.
Zhao K, Wu G, Yang Z-L. 2014b – A new genus, *Rubroboletus*, to accommodate *Boletus sinicus* and its allies. Phytotaxa 188(2), 61–77.
Zhou F, Gao Y, Song H-Y, Hu H-J et al. 2022 – *Retiboletus atrofuscus* (Boletaceae, Boletales), a new species from China. Archives of Microbiology 204(7), 381.
Zhu X-T, Li Y-C, Wu G, Feng B et al. 2014 – The genus *Imleria* (Boletaceae) in East Asia. Phytotaxa 191(1), 81–98.
Zhu X-T, Wu G, Zhao K, Halling RE, Yang Z-L. 2015 – *Hourangia*, a new genus of Boletaceae to accommodate *Xerocomus cheoi* and its allied species. Mycological Progress 14(6), 37.