MYCOSPHERE 15(1): 881–953 (2024) www.mycosphere.org ISSN 2077 7019
Doi 10.5943/mycosphere/15/1/7

ARTICLE

Polyphasic taxonomy clarifies the relationships between *Butyriboletus* and *Exsudoporus*, and new taxa and reports of Boletaceae from China

Wang Y[1,2], Ma YH[3], Wu G[4,5], Yang XY[1], Liu YJ[1], Rao G[1], Dai D[6], Gui XY[1], Tuo YL[1], Wang LY[1], Chen X[7], Zhang B[1*], and Li Y[1,2*]

[1] Engineering Research Center of Chinese Ministry of Education for Edible and Medicinal Fungi, College of Plant Protection, Jilin Agricultural University, Changchun 130118, Jilin, China
[2] College of Plant Protection, Shenyang Agricultural University, Shenyang 110866, Liaoning, China
[3] Institute of Biotechnology and Germplasm Resources, Yunnan Academy of Agricultural Sciences, Kunming 650223, Yunnan, China
[4] CAS Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650201, Yunnan, China
[5] Yunnan Key Laboratory for Fungal Diversity and Green Development, Kunming 650201, Yunnan, China
[6] Institute of Agricultural Applied Microbiology, Jiangxi Academy of Agricultural Sciences, Nanchang 330200, Jiangxi, China
[7] The Administration Bureau of Dr. Sun Yat-sen's mausoleum, Nanjing 210014, Jiangsu, China

Citation – Wang Y, Ma YH, Wu G, Yang XY, Liu YJ, Rao G, Dai D, Gui XY, Tuo YL, Wang LY, Chen X, Zhang B, Li Y 2024 – Polyphasic taxonomy clarifies the relationships between *Butyriboletus* and *Exsudoporus*, and new taxa and reports of Boletaceae from China. Mycosphere 15(1), 881–953, Doi 10.5943/mycosphere/15/1/7

Abstract

The relationships of inter-genus in Boletaceae interested peers for a long time. China benefits from its wide territory and various environments containing plentiful species of Boletaceae. In this study, combining morphology, phylogeny, and biogeography, we discussed in detail the phylogenetic status of *Exsudoporus* and *Butyriboletus* and redivided *Butyriboletus* into three sections. *Exsudoporus* is now treated as a section under *Butyriboletus*. The others are sect. *Butyriboletus* and sect. *Rhodocarnei*. Biogeographical analyses show that *Butyriboletus* originated from East Asia at 23 Mya, with the sect. *Butyriboletus* and the sect. *Exsudoporus* originated at a close time from North and Central America, and East Asia, respectively. Sect. *Rhodocarnei* are from East Asia at 23 Mya. The "long-distance" dispersal is considered to be the highest likelihood of *Butyriboletus* dispersal and allopatric speciation is the major reason for interpreting extant distributions of species. The Land bridge is not the only way for *Butyriboletus* to dispersal to the other continents, especially between Asia and North and Central America. Atmosphere transport also as an important role in shaping the current distribution structure of *Butyriboletus*. According to our research, *Nigroboletus* does not have adequate evidence to warrant a status of genus whether from morphology or phylogeny. *Nigroboletus* was now treated as a synonym of *Xerocomellus*. Meanwhile, we reported 16 new taxa here, one new genus *Niveoboletus* gen. nov., and seven new species *Niveoboletus brunneus* sp. nov., *Rugiboletus caeruloruber* sp. nov., *Cyanoboletus viscidiceps* sp. nov., *Xerocomellus velutinoceps* sp. nov., *Xerocomellus inflatus* sp. nov., *Xerocomellus fuscoscabrosus* sp. nov., and *Hortiboletus sinorubellus* sp. nov., one new section sect. *Rhodocarnei* sect. nov., seven new combinations sect. *Exsudoporus* comb. nov., *Butyriboletus permagnificus* comb. nov., *Xerocomellus roseonigrescens* comb. nov., *Neoboletus luridiceps* comb. nov., *Neoboletus austrinus* comb. nov., *Cyanoboletus gabretae* comb. nov., and *Neoboletus subvelutipes* comb. nov. Additionally, we re-described eight species, five were new

Submitted: 28 November 2023; **Accepted:** 23 April 2024; **Published:** 2 July 2024
***Corresponding Author:** Bo Zhang – e-mail – zhangbofungi@126.com,
Yu Li – e-mail – fungi966@126.com
Accepted by: Samaneh Chaharmiri-Dokhaharani

records for their provinces. For all species, detailed descriptions, photographs, and line-drawing were provided.

Keywords – 16 new taxa – basidiomycota – biogeography – evolution – long-distance dispersal – phylogeny

INTRODUCTION

Expansion and colonization of temperate and boreal forests are facilitated by ectomycorrhizas to an extent. The mutualism they maintain is major reflected in helping plants provide nutrients – photosynthetically fixed carbon, meanwhile, ectomycorrhizas provide nitrogen and water to the host plant (Smith & Read 2008, Wu et al. 2022). As the sexual reproduction organism, ectomycorrhizal fungi have complex structures. One of the major groups, Boletaceae Chevall., is acknowledged in the world because of abundant species and varied morphology.

In recent decades, with the development of molecular technology, the species diversity of Boletaceae are in well studied, and new taxa have been published year after year, especially in East Asia and North America (Li et al. 2011, 2014, Halling et al. 2012a, b, Hosen et al. 2013, Wu et al. 2014, 2023, Zeng et al. 2014, Zhao et al. 2014, Vadthanarat et al. 2018, Zhang & Li 2018, Frank et al. 2020, Garey 2021, Wu et al. 2021, Wang et al. 2022, 2023, Xue et al. 2023). According to the statistics provided by Wu et al. (2023), nearly 100 genera have been reported in the Boletaceae. Furthermore, in the past decade, nearly 370 species have been newly documented in the Mycobank database (https://www.mycobank.org/). Currently, approximately 1200 species are included in Boletaceae. Thereinto, 55 genera and ca. 400 species were reported from China (Wu et al. 2023). China's diverse ecosystems, coupled with endemic phenomena exhibited in numerous boletes, indicate that there are still many boletoid species waiting discovered in the country.

When Wu et al. (2014, 2016) confirmed seven major clades of Boletaceae using four nuclear loci, the phylogenetic framework within Boletaceae came to stability ultimately. Although different clades of orders emerged from different researchers, the seven major clades were universally admitted by global researchers (Zhao et al. 2014, Badou et al. 2022, Vadthanarat et al. 2022, Wang et al. 2023). Contrasting to subfamilies stability, inter- or intra-genus and species defined in some groups are ambiguous, even controversial, e.g. (1) *Porphyrellus* E.-J. Gilbert was certified polyphyletic; (2) *Butyriboletus* D. Arora & J.L. Frank and *Exsudoporus* Vizzini, Simonini & Gelardi intertwined together in phylogenetic relationships; Vizzini (2014) erected *Exsudoporus* to include basidioma stipitate-pileate with distinctly red tinge, red pores and reticulations, bluing context upon exposure and stipe context inamyloid. This action is still in controversy even Biketova et al. (2022) reconfirmed the monophyletic of taxonomic status and redefined Melzer's reaction of the genus stipe context into "varies from inamyloid to amyloid or dextrinoid". The core of the debate was focused on whether *Exsudoporus* is a synonym of *Butyriboletus* or an independent genus (Wu et al. 2016, 2023, Wang et al. 2022); (3) *Suillellus* has been confirmed polyphyletic, species are nested in different *Boletus* s. l. sections. According to Vizzini et al. (2014) and Wu et al. (2016) species of *Suillellus* are delimited by olivaceous pileus, reddish pores, stipe covered with reticulations, and amyloid hyphae of the stipe base. However, such as *Suillellus adalgisae* (Marsico & Musumeci) N. Schwab was described without amyloid hyphae of the stipe base which means not all species in *Suillellus* Murrill., adhere to the genus definition (Vizzini et al. 2014, Wu et al. 2016, Han et al. 2020, Biketova et al. 2022, Wang et al. 2022); (4) the status of *Nigroboletus* was suspended given the morphological description and status in the phylogenetic tree.

Biogeography was founded in the 18th century and constantly introduced new concepts with modern biotechnology development to infer the formation mechanism and distribution pattern of organisms in space and time and to know the driving force for organisms' evolutionary process (Peay & Matheny 2016, Tedersoo 2017). However, compared to animals and plants, the biogeography of macrofungi is still in its infancy. This may be directly caused by the lack of fungal fossils and the difficulty in species delimitations and sampling (Hibbett 2001, Mueller et al. 2001, Han et al. 2018). Recently, the porcini mushrooms, *Strobilomyces* Berk., and several sections in *Amanita* Pers. have

been executed biogeographical analyses, and results showed a uniform palaeotropical origin (Feng et al. 2012, Cai et al. 2014, Sánchez-Ramírez et al. 2015, Han et al. 2018, Codjia et al. 2023). "Host co-migrations at regional levels" and "boreotropical hypothesis" at a global scale are now the most prevailing hypotheses. "Transoceanic or long-distance dispersal" hypothesis does occur, but was assumed rare in fungi (Moyersoen et al. 2003, Moncalvo & Buchanan 2008, Geml et al. 2012). As all know, integrating multiple dimensions, such as biological, ecological, phylogenetic, and phenotype, into one species concept is by no means easy (Taylor et al. 2000, Bakker & Noordeloos 2005, De Queiroz 2007). To understand fungal origin can still better understand their species definitions and more precise high taxonomic status range (He et al. 2019).

In the present study, we refined previous works (Wang et al. 2022, 2023), loaned specimens and gathered from diverse locations throughout China. Our objectives are (1) to provide clarification on the range and phylogenetic status of *Butyriboletus* and *Exsudoporus* as well as their origins; (2) to clarify the phylogenetic relationships between *Nigroboletus* and *Xerocomellus*; (3) to clear *Suillellus* definition and recombination species that do not truly belong to it; and (4) to supplement species diversity within the Boletaceae.

MATERIALS AND METHODS

Samplings and Morphological analyses

Specimens were collected from Yunnan, Jiangsu, Fujian, Henan and Jilin Province, China. Voucher materials were deposited in the Mycology Herbarium of Jilin Agricultural University (HMJAU). Loaned specimens were obtained from the Fungal Herbarium of Hainan Medical University (FHMU), the Herbarium of Microbiology Institute of Guangdong (GDGM) and the Cryptogamic Herbarium (HKAS-KUN) of the Kunming Institute of Botany, Chinese Academy of Sciences. The color of fresh basidiocarps is described according to Kornerup & Wanscher (1978). The tissues of the observed and measured specimens are referred as Wang et al. (2023). The abbreviations of Latin names used in this study: *Baorangia = Ba.*, *Boletellus = Bo.*, *Butyriboletus = B.*, *Cyanoboletus = Cy.*, *Exsudoporus = E.*, *Harrya = H.*, *Heimioporus = He.*, *Hortiboletus = Ho.*, *Niveoboletus = Ni.*, *Royoungia = R.*, *Rugiboletus = Ru.*, *Suillellus = Su.*, *Tylopilus = Ty.*, *Xerocomellus = Xe.*, *Zangia = Z.*.

DNA extraction, PCR amplification, and Sequencing

The NuClean Plant Genomic DNA kits (CWBIO) were used to extract genomic DNA. The primers LROR/LR5 were used for 28S, ITS1/4 for Internal Transcribed Spacer (ITS), 983F/1567R for *tef1-α* (Rehner and Buckley 2005), RPB1-B-F/RPB1-B-R for *rpb1* (Wu et al. 2014), and RPB2-B-F1/RPB2-B-R and PRB2-6F/PRB2-7.1R for *rpb2* (Matheny & Ammirati 2003, Matheny 2005, Wu et al. 2014). The polymerase chain reaction (PCR) procedures were referred to Wu et al. (2014).

Phylogenetic analyses

The new sequences were uploaded to NCBI (https://www.ncbi.nlm.nih.gov/) and other sequences were downloaded from NCBI (Supplementary Table 1). The raw matrixes (ITS, 28S, *tef1*, *rpb1*, *rpb2*) were aligned in Mega 7 (Kumar et al. 2016) and trimed by Bioedit v7.7.1 and TrimAL v1.2 in manual and "strict" or "gappyout" strategies, respectively (Hall 1999, Capella-Gutiérrez et al. 2009). Seven datasets were obtained to execute phylogeny analyses. We concatenated multi-locus datasets by Phylosuite v1.2.1 and conducted a model test in PartitionFinder 2 (Lanfear et al. 2017). The components and best models for matrixes from Dataset I to Dataset VII were listed in Table 1. The Maximum likelihood method (ML) and Bayesian inference phylogenetic analyses (BI) were respectively executed in IQ-Tree 1.6.8 and MrBayes 3.2.6 (Ronquist et al. 2012, Nguyen et al. 2015). ML analyses were conducted using ultra-bootstrap with 20000 replicates. BI analyses were run 10,000,000–30,000,000 generations, and sampled every 2000 generations until the convergence value dropped below 0.01 distinctly. For Dataset I and Dataset VI, BI analyses were run 20,000,000 generations and sampled every 100 generations and 10,000,000 generations and sampled every 100

generations, respectively. The initial 25% of the sampled data were discarded as burn-in. Other parameters were kept at default settings. The software used in the phylogenetic analyses is all in the Integrated tool Phylosuite v1.2.1 (Zhang et al. 2020). Dataset I was used to calculate genetic distances between related genera with the Kimura-2-parameter (K2P) model using MEGA 7 software (Kumar et al. 2016).

Dataset VIII was used to execute fossil calibration to infer divergence times, including an extensive sampling of *Butyriboletus* outgroups. Dataset IX used secondary calibration point at the node age of the tree, as Dataset VIII did.

Calibration strategies and Divergence-time estimations

The secondary calibrations procedure has been used for a long time (Shaul & Graur 2002, Berry et al. 2004). From the last decade, several studies have used it in macrofungi to estimate node ages (Feng et al. 2012, Sánchez-Ramírez et al. 2015, Han et al. 2018, Codjia et al. 2023). We used three calibration points based on fossils for Dataset VIII: (1) *Paleopyrenomycites devonicus* Taylor, Hass, Kerp, M. Krings & Hanlin (ca. 400 Mya) (Taylor et al. 2005); (2) *Quatsinoporites cranhamii* S.Y. Sm., Currah & Stockey (ca. 125 Mya) (Smith et al. 2004); (3) *Archaeomarasmius leggetti* Hibbett, D. Grimaldi & Donoghue (ca. 90 Mya) (Hibbett et al. 1997). For point 1, a normal distribution with a mean of 580 Mya, and standard deviation of 25 Mya; point 2, a normal distribution with a mean of 150 Mya, and standard deviation of 25 Mya; and point 3, a normal distribution with a mean of 100 Mya, and standard deviation of 5 Mya were applied (Lucking et al. 2009, Feng et al. 2012, Han et al. 2018). We removed all introns within *tef1-α, rpb1* and *rpb2* aim to acquire more clear phylogenetic signals. Ultimately, the matrix of Dataset VIII was trim by Bioedit v7.7.1 and TrimAL v1.2 in manual and "strict" strategies, respectively (Hall 1999, Capella-Gutiérrez et al. 2009). We used ModelFinder to infer the best partition models for Dataset VIII (Ronquist et al. 2012).Settings in BEAUti v1.10.4 included Bayesian uncorrelated lognormal relaxed molecular clock and a Yule prior. To reduce the MCMC runs' bias caused by the random startup, we conducted two independent MCMC runs, each for 400 million generations, sampling every 2,000 generations. Generated results were validated by Tracer v1.7.1 to ensure that all parameters meet statistical significance. The sampled trees were combined into a single tree file using LogCombiner 1.8.1 and then summarized using TreeAnnotator 1.8.1 to achieve a maximum clade credibility (MCC) tree. We discarded the first 10% of samples as burn-in. The result was visualized by Figtree v1.4.3. For Dataset IX, sequences of *Butyriboletus*, *Exsudoporus*, and *Rugiboletus* were extensively sampled and the root age of the tree was based on Dataset VIII and the split between *Butyriboletus* & *Exsudoporus* and *Rugiboletus* were assigned age priors. Informations of components and best models for BEAST 1 for Dataset VIII & IX matrixes was shown in Table 2.The root age of the tree was set as a normal distribution, with a mean of 35 Mya, and a standard deviation of 10 Mya. Remained protocols followed the methods in Dataset VIII, but the two independent MCMC runs were executed each for 200 million generations, sampling every 200 generations.

Reconstruction of ancestral state

Five major areas were delimited according to plate tectonic history and the distributions of *Butyriboletus*, *Exsudoporus* and *Rugiboletus*: A = South-Southeast Asia; B = East Asia; C = North and Central America; D = Austria; E = Europe. Each sample is coded from field records and documentation from the literatures. Different models were compared, and the best model DIVALIKE+J was filtered and conducted in BioGeoBEARs in RASP 4.3 based on MCC tree derived from Dataset IX (Yu et al. 2015). Two null models were established using geodispersal probabilities: (1–2) a permissive model with high dispersal rates (1.0) and a restrictive model with low dispersal rates (0.01); (3) a random model with random dispersal rates. All of them were compared to "Boreotropical" model each other based on AIC values, which were calculated using the R package "BioGeoBEARS" (Table 3) (Matzke 2013). Four-time frames of dispersal probabilities were created in the "Boreotropical" model based on the "Boreotropical migration" hypothesis (Fig. 1).

RESULTS

Phylogenetical analyses

The four-locus datasets of *Niveoboletus* (Dataset I) (Zenodo repository Doi: 10.5281/zenodo.10183909) consisted of 109 taxa and 3,154 nucleotide sites. *Parvixerocomus aokii* (Hongo) G. Wu, N.K. Zeng & Zhu L. Yang and *Parvixerocomus pseudoaokii* G. Wu, K. Zhao & Zhu L. Yang were chosen as outgroups (Fig. 2). In the phylogram, our sequences HMJAU68161 and HMJAU68162 were formed a single clade in mild bootstrap (BP) support (79) and robust posterior probability (PP) support (0.91). Although their relationships remain unclear, the average value of genetic distances (0.1193 ± 0.1129) between *Niveoboletus* and *Imleria* Vizzini, *Boletus* L., *Tylopilus* P. Karst., *Porphyrellus* E.-J. Gilbert, *Strobilomyces* Berk., *Tengioboletus* G. Wu & Zhu L. Yang *Xanthoconium* Singer and an undescribed lineage represented by *Tylopilus* sp. HKAS50211 lying in those values (0.1311 ± 0.0225) among the latter eight genera, which can support the clade of *Niveoboletus* as an independent genus.

The four-locus datasets of *Rugiboletus* and *Cyanoboletus* (Dataset II) (Zenodo repository Doi: 10.5281/zenodo.10016248) consisted of 98 taxa and 2,699 nucleotide sites. *Buchwaldoboletus lignicola* (Kallenb.) Pilát, *Chalciporus piperatus* (Bull.) Bataille and *Zangia roseola* (W.F. Chiu) Yan C. Li & Zhu L. Yang were chosen as outgroups (Fig. 3). In the phylogram, our sequences HMJAU68163, HMJAU68164, HMJAU68165, and HMJAU68166 were clustered together with "*Rugiboletus* sp. HKAS55373" in robust support (BP = 100, PP = 1), meanwhile they sister with *Ru. andinus* (Halling) Halling & B. Ortiz in robust support (BP = 100, PP = 1). For HMJAU68168, our sequence formed a single clade sister with clade consisting of *Cy. pulverulentus* (Opat.) Gelardi, Vizzini & Simonini and *Cy. cyaneitinctus* (Murrill) A. Farid, A.R. Franck & J.A. Bolin in mild PP support (0.87) and high BP support (90).

The five-locus datasets of *Hortiboletus* and *Xerocomellus* (Dataset III) (Zenodo repository Doi: 10.5281/zenodo.11100331) consisted of 55 taxa and 2,986 nucleotide sites. *Imleria pallida* (Frost) A. Farid, A.R. Franck & J. Bolin, *I. subalpina* Xue T. Zhu & Zhu L. Yang and *I. obscurebrunnea* (Hongo) Xue T. Zhu & Zhu L. Yang were chosen as outgroups (Fig. 4). In the phylogram, our sequences HMJAU68174, HMJAU68173, HMJAU68175, and HMJAU68176 were cluster together with *Ho. tomentosus* L. Fan, N. Mao & T.Y. Zhao in robust support (BP = 100, PP = 1). HMJAU68177, HMJAU68178–1, HMJAU68178–2, HMJAU68179, HMJAU68180, and HMJAU68181 were cluster together and sister with a sequence named "*Hortiboletus* sp. FHMU2113" in robust support (BP = 98, PP = 1). HMJAU68182–1, HMJAU68182–2, and HMJAU68183 were clustered together and sister with *Ho. arduinus* N.K. Zeng, H.J. Xie & W.F. Lin in robust support (BP = 99, PP = 1). HMJAU68171 and HMJAU68172 were clustered together and sister with *Xe. communis* Xue T. Zhu & Zhu L. Yang in high PP support (0.94) and mild BP support (81). HMJAU68169, HMJAU68170–1 and HMJAU68170–2 were clustered together and sister with a sequence named "*Xerocomellus* sp. HKAS74712" in high support (BP = 97, PP = 1).

The four-locus datasets of *Zangia*, *Royoungia* and *Tylopilus* (Dataset IV) (Zenodo repository Doi: 10.5281/zenodo.10016238) consisted of 115 taxa and 2,907 nucleotide sites. *Harrya moniliformis* Yan C. Li & Zhu L. Yang and *H. chromipes* (Frost) Halling, Nuhn, Osmundson & Manfr. Binder were chosen as outgroups (Fig. 5). In the phylogram, our sequences HMJAU68188–1 and HMJAU68188–2 were cluster together with *Ty. violaceobrunneus* Yan C. Li & Zhu L. Yang in robust support (BP = 100, PP = 1). HMJAU68186 were clustered together with *Z. olivaceobrunnea* Yan C. Li & Zhu L. Yang in robust support (BP = 100, PP = 1). HMJAU68187 was clustered together with *R. reticulata* Yan C. Li & Zhu L. Yang in robust support (BP = 100, PP = 1).

The three-locus datasets of *Boletellus* (Dataset V) (Zenodo repository Doi: 10.5281/zenodo.10016366) Murrill consisted of 43 taxa and 2,036 nucleotide sites. *Heimioporus retisporus* (Pat. & C.F. Baker) E. Horak and *He. subretisporus* (Corner) E. Horak were chosen as outgroups (Fig. 6). In the phylogram, our sequences HMJAU68184 and HMJAU68185 were clustered together with *Bo. putuoensis* Chang Xu, Xu Zhang, Yun-Xia Chen, Rou Xue, Zhi-Fang Le,

Jian-Rui Wang, Yi Li & Nian-Kai Zeng and sister with *Bo*. aff. *putuoensis* FHMU2168 in high support (BP = 92, PP = 0.99).

The four-locus datasets of *Butyriboletus, Exsudoporus* and *Rugiboletus* (Dataset VI) (Zenodo repository Doi: 10.5281/zenodo.10016366) consisted of 64 taxa and 2,930 nucleotide sites. *Baorangia pseudocalopus* (Hongo) G. Wu & Zhu L. Yang, *Gymnogaster boletoides* J.W. Cribb, *Ru. brunneiporus* G. Wu & Zhu L. Yang and *Ru. extremiorientalis* (Lj. N. Vassiljeva) G. Wu & Zhu L. Yang were chosen as outgroups (Fig. 7). In the phylogram, the key characteristics of *Butyriboletus* and *Exsudoporus* were summarized and also listed at the right.

The four-locus datasets of *Suillellus* (Dataset VII) (Zenodo repository Doi: 10.5281/zenodo.10016366) consisted of 68 taxa and 3044 nucleotide sites. Two sequences of *Ba. pseudocalopus* were chosen as outgroups (Fig. 8). Our sequence HMJAU68189 was clustered with *Su. yunnanensis* G. Wu & Zhu L. Yang by robust supports (BP = 100, PP = 1). In the phylogram, *Suillellus* is clearly monophyletic.

Divergence time estimates

Based on Dataset VIII (Zenodo repository Doi: 10.5281/zenodo.10016366), the stem age of Boletales is estimated at 171.59 Mya (122.94–233.34 Mya) and Boletaceae is estimated at 86 Mya (58.26–117.72 Mya) (Supplementary Fig. 1), which overlaps with the divergence time of the Pinaceae and the estimated divergence time of the Boletaceae (Lin et al. 2010, Feng et al. 2012). Analyses of Dataset IX (Zenodo repository Doi: 10.5281/zenodo.10016366) showed that the divergence time of *Butyriboletus* is a young genus originated at ca. 23 Mya (later Oligocene and early Miocene) (Fig. 9). Sect. *Butyriboletus* (Clade A) the youngest clade, originated at ca. 16 Mya, sect. *Exsudoporus* (Clade B), which formerly be recognized as genus *Exsudoporus*, originated at ca. 15 Mya, sect. *Exsudoporus* (Clade C) originated at 17 Mya, and sect. *Rhodocarnei* (Clade D), the oldest clade, originated at ca. 23 Mya. Also, no distinct time differences can be observed between sect. *Exsudoporus* and sect. *Butyriboletus* means that the section status of *Exsudoporus* is more reasonable than the genus status.

Biogeography and Ancestral areas

Butyriboletus is concluded that originated from East Asia, while Clade A and Clade B both originated from North and Central America (Fig. 9). The nearly same diversified time and same originated region further demonstrated the more reliable of treating *Exsudoporus* as a section under *Butyriboletus*. Meanwhile, we rejected the affection of "boreotropical" hypothesis to the dispersal of *Butyriboletus*, because of the young crown age of *Butyriboletus*. Based on the result, the dispersal of *Butyriboletus* between East Asia and North and Central America occurred several times (Figs 9, 10), *viz*. East Asia to North and Central America (ca. 23 Mya and 8 Mya), and from North and Central America to East Asia (ca. 18 Mya and 16 Mya). The recent dispersal events to Europe are also shown from the result (ca. 10 Mya), then dispersal to Asia again from Europe (ca. 7 Mya).

Table 1 Informations of matrixes used in phylogenetic analyses from Dataset I to Dataset VII.

Datasets	Matrixes component	Best models for ITS	Best models for 28S	Best models for *tef1*	Best models for *rpb1*	Best models for *rpb2*
I	28S: 960 bp; *rpb1*: 832 bp; *rpb2*: 720 bp; *tef1*: 642 bp	–	SYM+I+G	TRNEF+I+G	SYM+I+G	TIMEF+I+G
II	28S: 743 bp; *rpb1*: 688 bp; *rpb2*: 663 bp; *tef1*: 575 bp	_	GTR+I+G	SYM+I+G	SYM+I+G	TRNEF+I+G

Table 1 Continued.

Datasets	Matrixes component	Best models for ITS	Best models for 28S	Best models for *tef1*	Best models for *rpb1*	Best models for *rpb2*
III	ITS: 771 bp; 28S: 876 bp; *tef1*: 593 bp; *rpb1*: 816 bp; *rpb2*: 706 bp	GTR + G	TRN+I+G	TRNEF+I+G	TRN+G	SYM+G
IV	28S: 944 bp; *rpb1*: 667 bp; *rpb2*: 721 bp; *tef1*: 575 bp	–	GTR+I+G	TIMEF+I+G	SYM+I+G	K80+G
V	28S: 878 bp; *rpb2*: 707 bp; *tef1*: 451 bp	–	GTR+I+G	K80+I	_	K81+I
VI	28S: 864 bp; ITS: 773 bp; *rpb2*: 711 bp; *tef1*: 582 bp	TVM+G	TRN+I+G	TIMEF+I+G	_	TRNEF+G
VII	28S: 903 bp; *rpb1*: 791 bp; *rpb2*: 719 bp; *tef1*: 631 bp	–	SYM+I+G	TIMEF+I+G	TRNEF+I+G	TRNEF+I+G

Table 2 Informations of matrixes used in BEAST analyses from Dataset VIII to Dataset IX.

Datasets	Matrixes component	Best models for ITS	Best models for 28S	Best models for *tef1*	Best models for *rpb1*	Best models for *rpb2*
VIII	*rpb2*: 369 bp; *rpb1*: 614 bp; *tef1*: 480 bp	–	–	GTR+F+G4	TVMe+G4	SYM+G4
IX	ITS: 568 bp; 28S: 890 bp; *rpb1*: 704 bp; *rpb2*: 707 bp; *tef1*: 551 bp	HKY + F + G4	TN + F + G4	SYM + G4	K2P + G4	SYM + G4

Table 3 Likelihood-ratio test comparison of geodispersal models in *Butyriboletus*.

Models	df	ln-likelihood	AIC
Boreotropical	1	-62.06	130.8
Null			
Permissive with high dispersal	1	-64.04	135
Restrictive except for within-area dispersal	1	-64.04	135

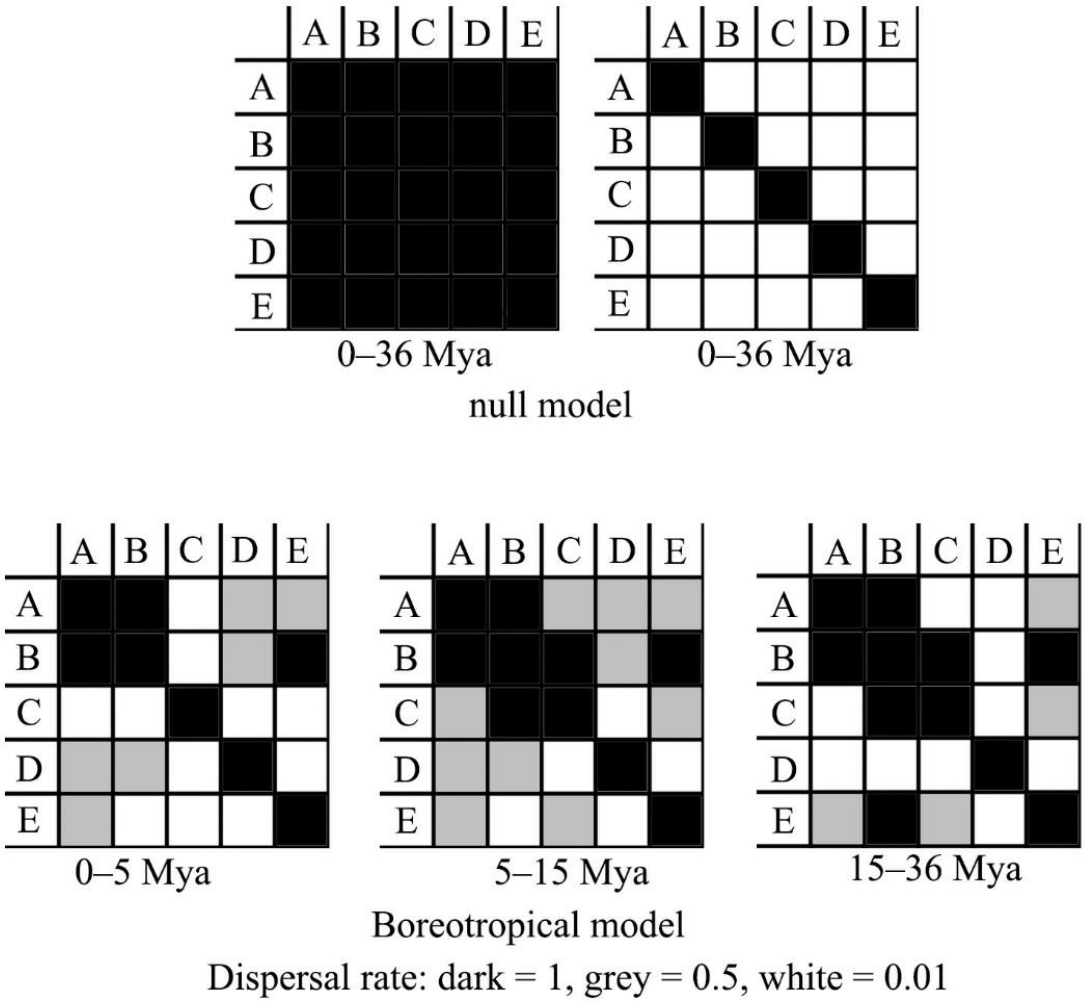


Figure 1 – Geodispersal models in *Butyriboletus* inferred with the DIVALIKE+J model. Two null models of dispersion with different dispersal-rate constraints. The "Boreotropical" model is time structured. A = South-Southeast Asia; B = East Asia; C = North and Central America; D = Austria; E = Europe.

Taxonomy

Niveoboletus Yang Wang, G. Wu, B. Zhang & Y. Li gen. nov.

MycoBank number: MB850507; Facesoffungi number: FoF15040

Type species – *Niveoboletus brunneus* Yang Wang, G. Wu, B. Zhang & Y. Li

Etymology – "Niveo" refers to this genus snow-white hymenophores.

Diagnosis – Distinguished from all other genera of Boletaceae by the following combination of characteristics. A pure white hymenophores which staining light brown when injured, a coarse stipe lacking reticulations, and small and smooth basidiospores.

Basidioma stipitate-pileate with a tubular hymenophore. Pileus hemispherical or convex, tomentose, usually beaded with amber yellow droplets, margin inrolled. Hymenophore decurrent, surface pure white, staining light brown when injured; tubes concolorous with pores. Stipe central, concolorous with pileus, coarse without reticulations, usually beaded with amber yellow droplets,

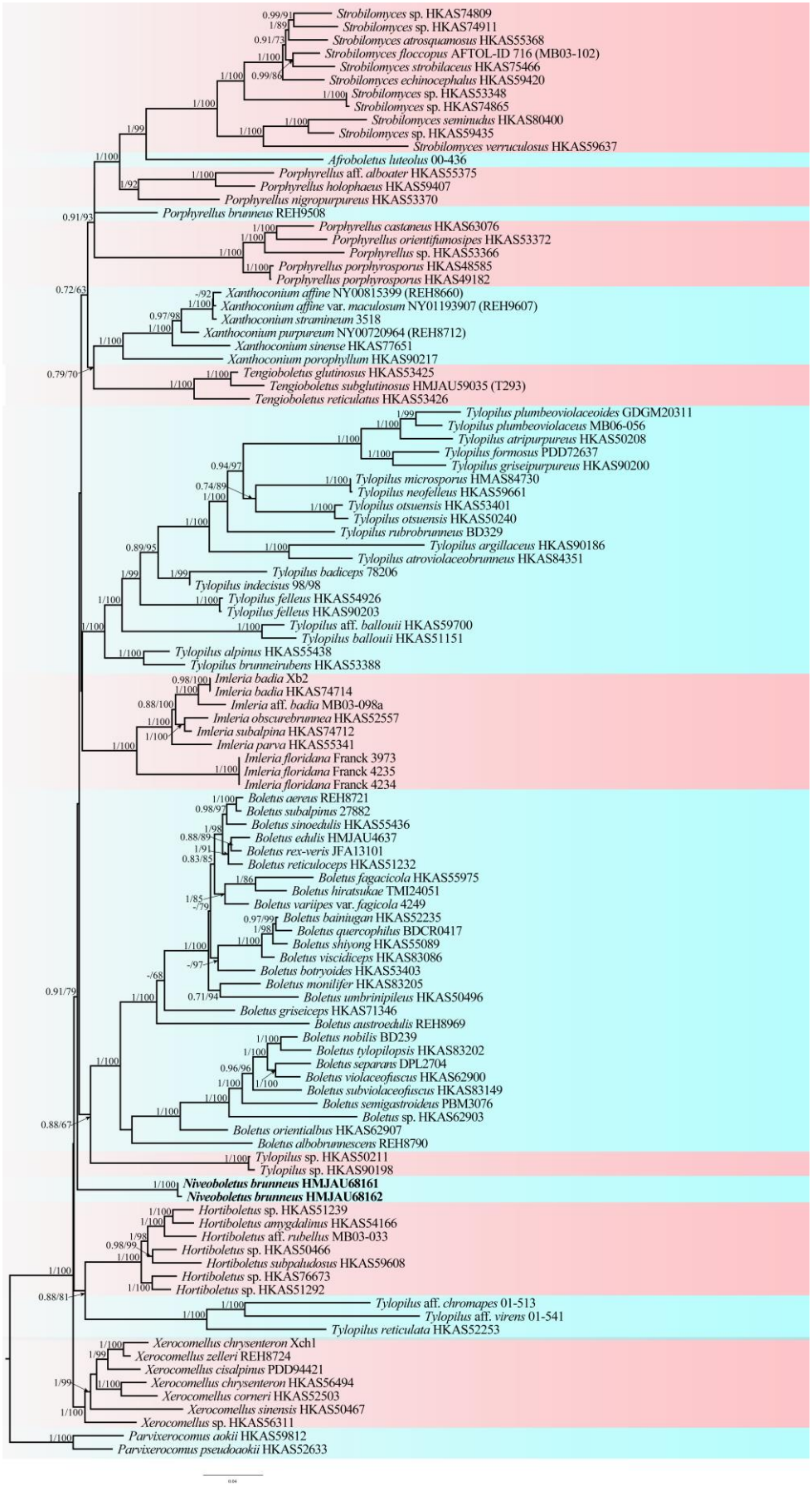


Figure 2 – Phylogenetic relationships of *Niveoboletus* inferred from multi-locus (28S, *tef1-α*, *rpb1*, and *rpb2*) using Bayesian inference and maximum likelihood method (ML tree was shown). The PP

≥ 0.7 and BP ≥ 50 are indicated in the phylogram. Newly formed sequences in this study are indicated in bold.

context at base brown; basal mycelium white. Basidiospores phaseoliform, smooth, thin-walled. Pileipellis an interwoven trichoderm composed of cylindrical hyphae. Clamp connection absent.

Niveoboletus brunneus Yang Wang, G. Wu, B. Zhang & Y. Li sp. nov. Figs 12a–f, 15

MycoBank number: MB850508; Facesoffungi number: FoF15049

Etymology – "brunneus" refers to the brown basidiomes of the species.

Diagnosis – *Niveoboletus brunneus* is characterized by its small and brown basidiomes, snow-white hymenophores turning brownish when injured, coarse not reticulations over the stipe and an interwoven trichodermium pileipellis.

Basidioma small. Pileus 3.3–4 cm in diam., hemispherical or hemispherical and convex at center, margin strongly inrolled, beaded with golden yellow or amber yellow droplets, light brown (6D6), surface tomentose, unchanging color when injured; context firm, orange white (6A2) to greyish orange (6B3), ca. 0.7 cm thick, unchanging color or sometimes erratically staining light brown (6D6) when cut; hymenophore decurrent, surface white (1A1), staining light brown (6D6) when injured, pores irregular, 2–3/mm; tubes concolorous with pores, 0.2–0.3 cm long, changing to light brown (6D6) when injured. Stipe 1.2–1.3 × 4.5–5.5 cm, cylindrical, concolorous with pileus, beaded with golden yellow or amber yellow droplets, surface coarse, turning light brown (6D6) when touched, context light yellow to greyish orange (3A4–6B3), sometimes turning brown (6E4) at base. Basal mycelium white.

Basidiospores (2/2/64) (5.4–) 6.5–6.6–6.8 (–8) × (3–) 3.6–3.7–3.8 (–4.5) μm, Q = 1.42–2.19, Q_m = 1.8 ± 0.17, phaseoliform, hyaline to pale yellow in 5% KOH and ddH_2O, smooth. Basidia 22–46.2 × 3.2–9.2 μm, clavate to elongated clavate, hyaline in 5% KOH and ddH_2O, 2-, 4-spored. Hymenophoral trama boletoid, consisting of hyaline hyphae 3–11.8 μm wide. Pleurocystidia 33.2–63.2 × 3–7.5 μm, subcylindrical, narrowly conical or narrowly lageniform, hyaline in 5% KOH and ddH_2O, thin-walled. Cheilocystidia 41–69.5 × 4.1–7.4 μm, similar to pleurocystidia in shape, hyaline in 5% KOH and ddH_2O, thin-walled. Pileipellis an interwoven trichodermium, composed of cylindrical hyphae, which are hyaline to brownish and covered with yellowish brown granular crustations in ddH_2O, but hyaline and smooth in 5% KOH, occasionally covered with hyaline granular crustations, 3–8.5 μm wide. Stipitipellis sterile, composed of cylindrical hyphae which are yellowish brown and covered with granular crustations in ddH_2O, but hyaline and nearly smooth in 5% KOH, 3–9 μm wide. Reactions not observed in Melzer's in all tissues. Clamp connection absent.

Habitat – Solitary in a broad-leaf forest, dominated by *Castanopsis* sp.

Known distribution – Central China (this study).

Materials examined – China, Jiangxi Province, Jian city, Anfu town, Yangshimu Scenic Area, 03 September 2021, 114°14'39.56" E, 27°31'36.21" N, alt. 537 m, W3351 (HMJAU68162, holotype); Fujian Province, Wuyishan city, Wuyishan mountains national reserve, 17 August 2017, 117°26'45.07" E, 27°25'21.8" N, alt. 588 m, M698 (HMJAU68161).

Notes – This species shares some morphological features with species in the *Boletus* s. str. and *Tylopilus* in robust basidiomata, and nearly white hymenophore. However, it is distinguished from *Boletus* s. str. in morphology by its white and decurrent hymenophores, coarse but no reticulations stipe and light yellow to greyish orange context (Feng 2012). Meanwhile, it differs from *Tylopilus* in having a pileus beaded with amber yellow droplets, context turning to light brown when injured and small and phaseoliform basidiospores. *Tylopilus alpinus* Yan C. Li & Zhu L. Yang can be distinguished by its larger basidiomata, context changing to grayish red when bruised, and larger subfusiform basidiospores. *Niveoboletus brunneus* is also resembles *Ty. balloui* (Peck) Singer, however, it differs from *Ty. balloui* in smaller and phaseoliform basidiospores (Singer 1947, Li & Yang 2021). *Niveoboletus brunneus* somewhat resembles *Imleria* Vizzini. However, it can be distinguished by its hymenophoral surface and context turning light brown erratically when injured, hymenophore

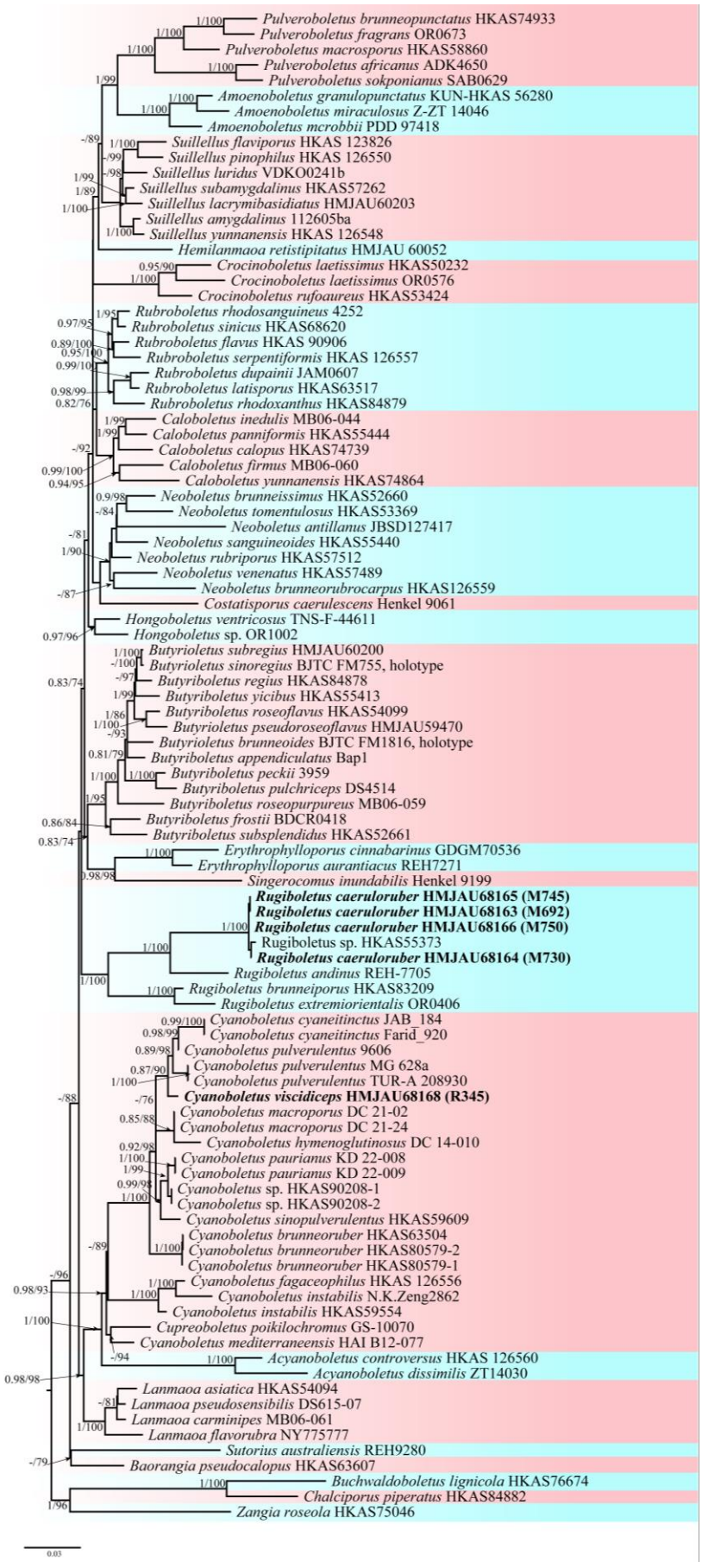


Figure 3 – Phylogenetic relationships of *Rugiboletus Cyanoboletus* inferred from multi-locus (28S, *tef1-α, rpb1*, and *rpb2*) using Bayesian inference and maximum likelihood method (ML tree was

shown). The PP ≥ 0.8 and BP ≥ 80 are indicated in the phylogram. Newly formed sequences in this study are indicated in bold.

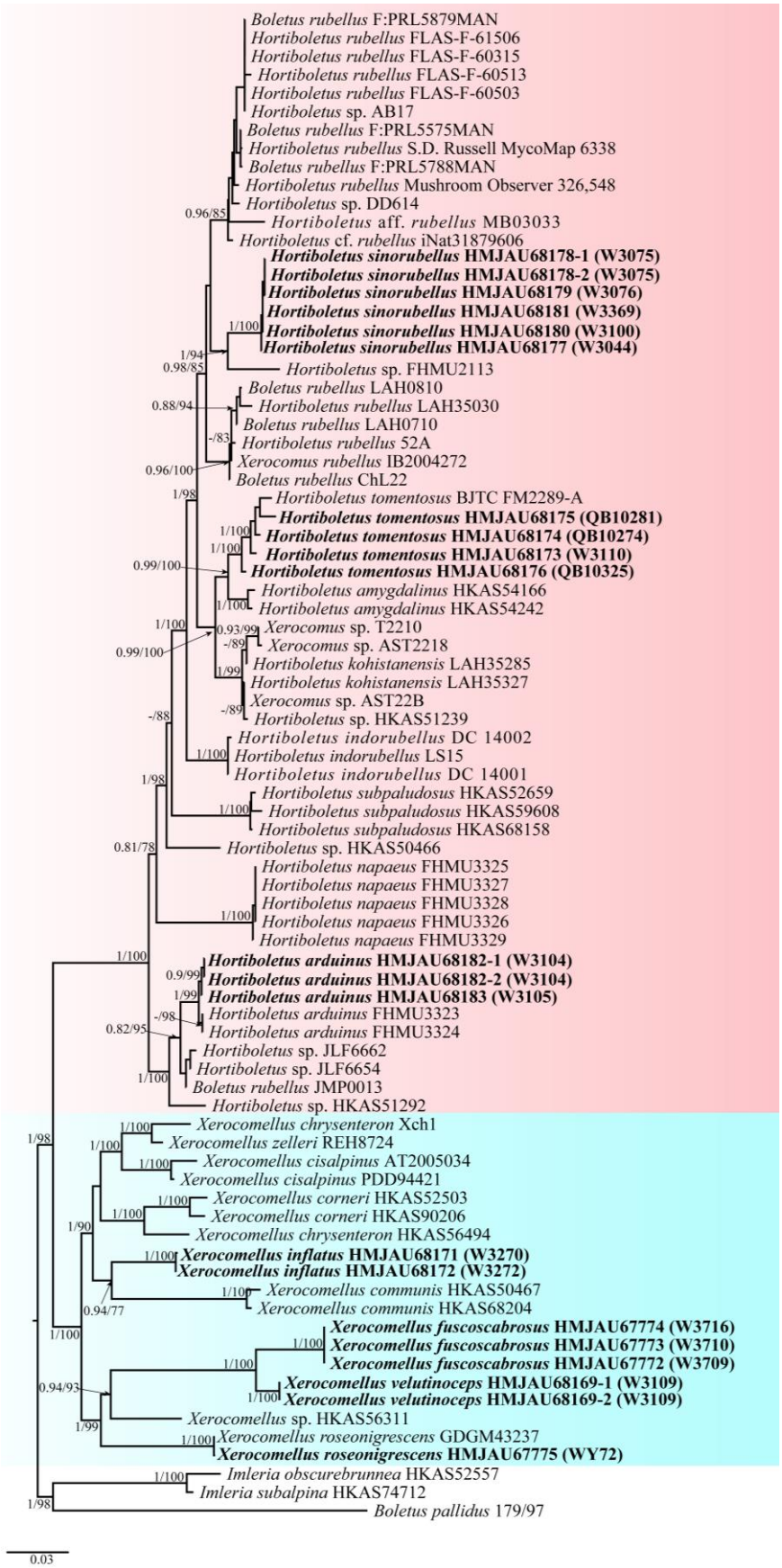


Figure 4 – Phylogenetic relationships of *Hortiboletus* and *Xerocomellus* inferred from multi-locus (28S, *tef1-α*, *rpb1*, and *rpb2*) using Bayesian inference and maximum likelihood method (BI tree was

shown). The PP ≥ 0.8 and BP ≥ 80 are indicated in the phylogram. Newly formed sequences in this study are indicated in bold.

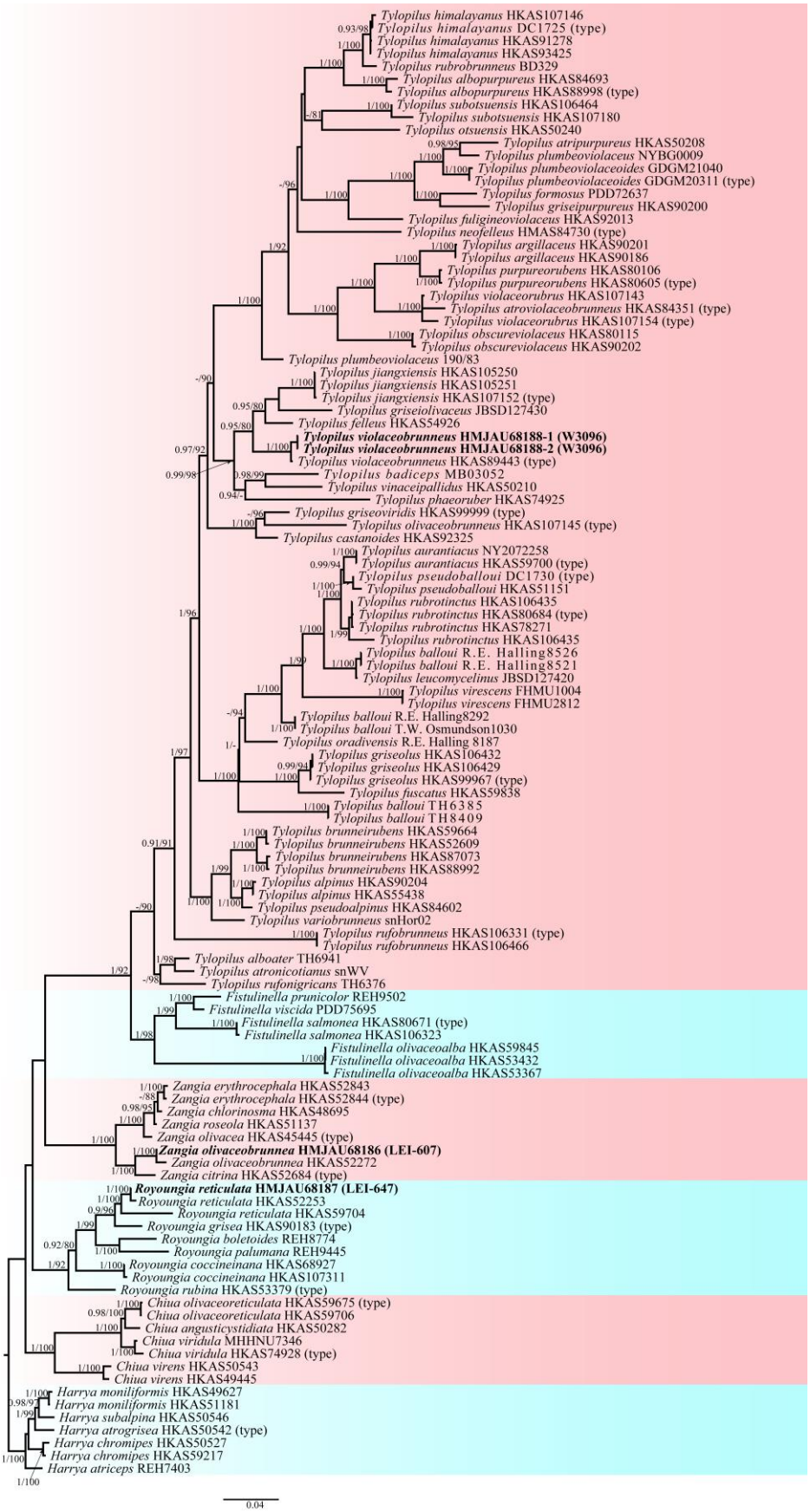


Figure 5 – Phylogenetic relationships of *Zangia*, *Royoungia* and *Tylopilus* inferred from multi-locus

(28S, *tef1-α*, *rpb1*, and *rpb2*) using Bayesian inference and maximum likelihood method (ML tree was shown). The PP ≥ 0.9 and BP ≥ 80 are indicated in the phylogram. Newly formed sequences in this study are indicated in bold.

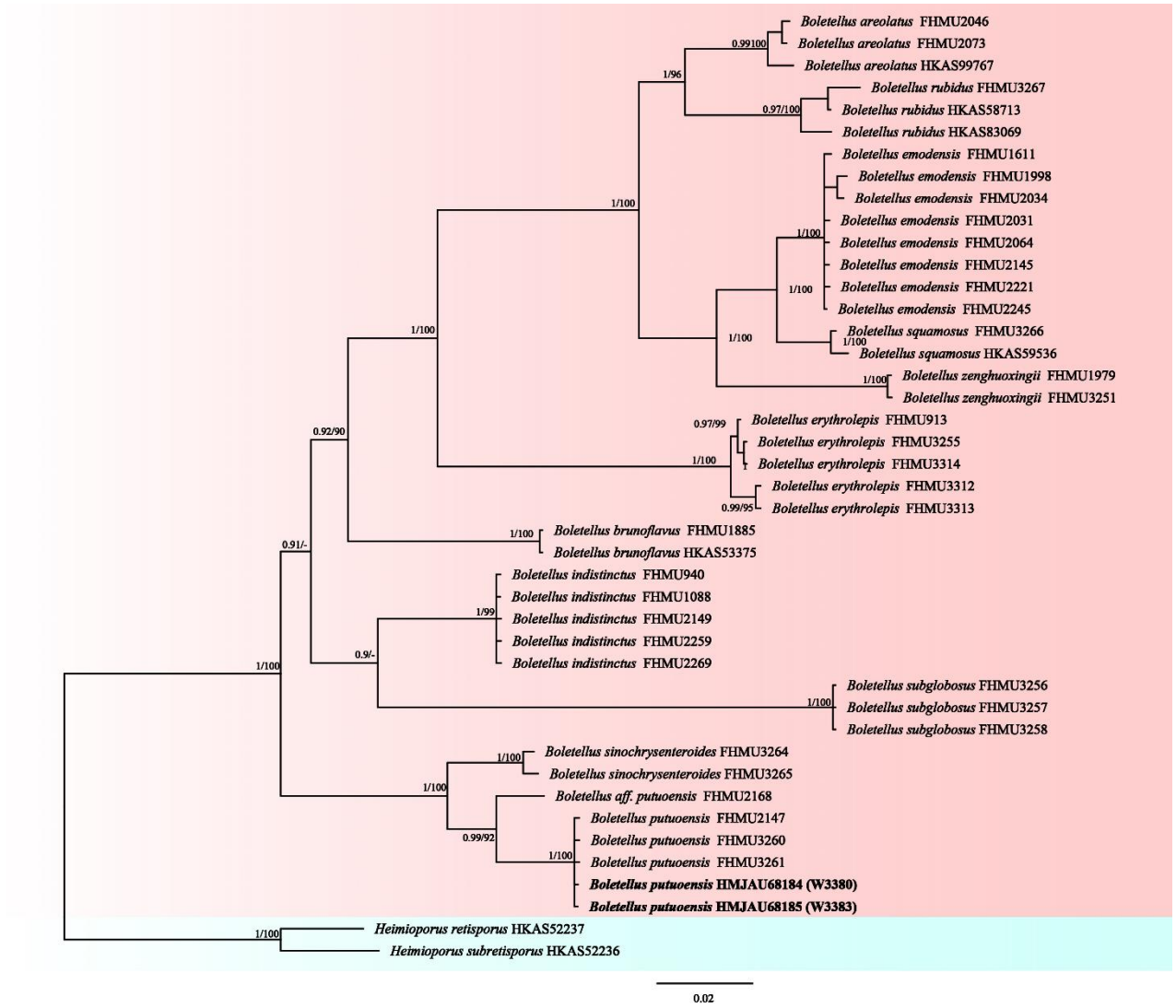


Figure 6 – Phylogenetic relationships of *Boletellus* inferred from multi-locus (28S, *tef1-α*, and *rpb2*) using Bayesian inference and maximum likelihood method (BI tree was shown). The PP ≥ 0.9 and BP ≥ 80 are indicated in the phylogram. Newly formed sequences in this study are indicated in bold.

usually beaded with amber yellow droplets, and basidiospores are very small and ellipsoid (Zhu et al. 2014). Phylogenetically, *Ni. brunneus* formed a single clade.

Rugiboletus caeruloruber Yang Wang, G. Wu, B. Zhang & Y. Li sp. nov. Figs 12g–l, 16

MycoBank number: MB850509; Facesoffungi number: FoF15050

Etymology – "caeruloruber" refers to its basidiomes bluing then red upon exposure.

Diagnosis – Distinguished by the following combination characteristics: pileus hemispherical, entire not rugose, hymenophore light yellow when young, duller when mature. Stipe covered with floccose squamules. Context of pileus and stipe turning blue then red when injured. Basidiospores dextrinoid.

Basidioma medium-sized. Pileus 6–8.5 cm in diam., hemispherical, sterile margin exist, greyish brown (7E3) to brown (7D8); surface dry, tomentose, unchanging color when bruised; context firm, orange white (5A2) to greenish yellow (1A6), up to 1.8 cm thick, in the young stage staining blue when cut, turning red when cut at mature but still bluing near the tubes; hymenophore

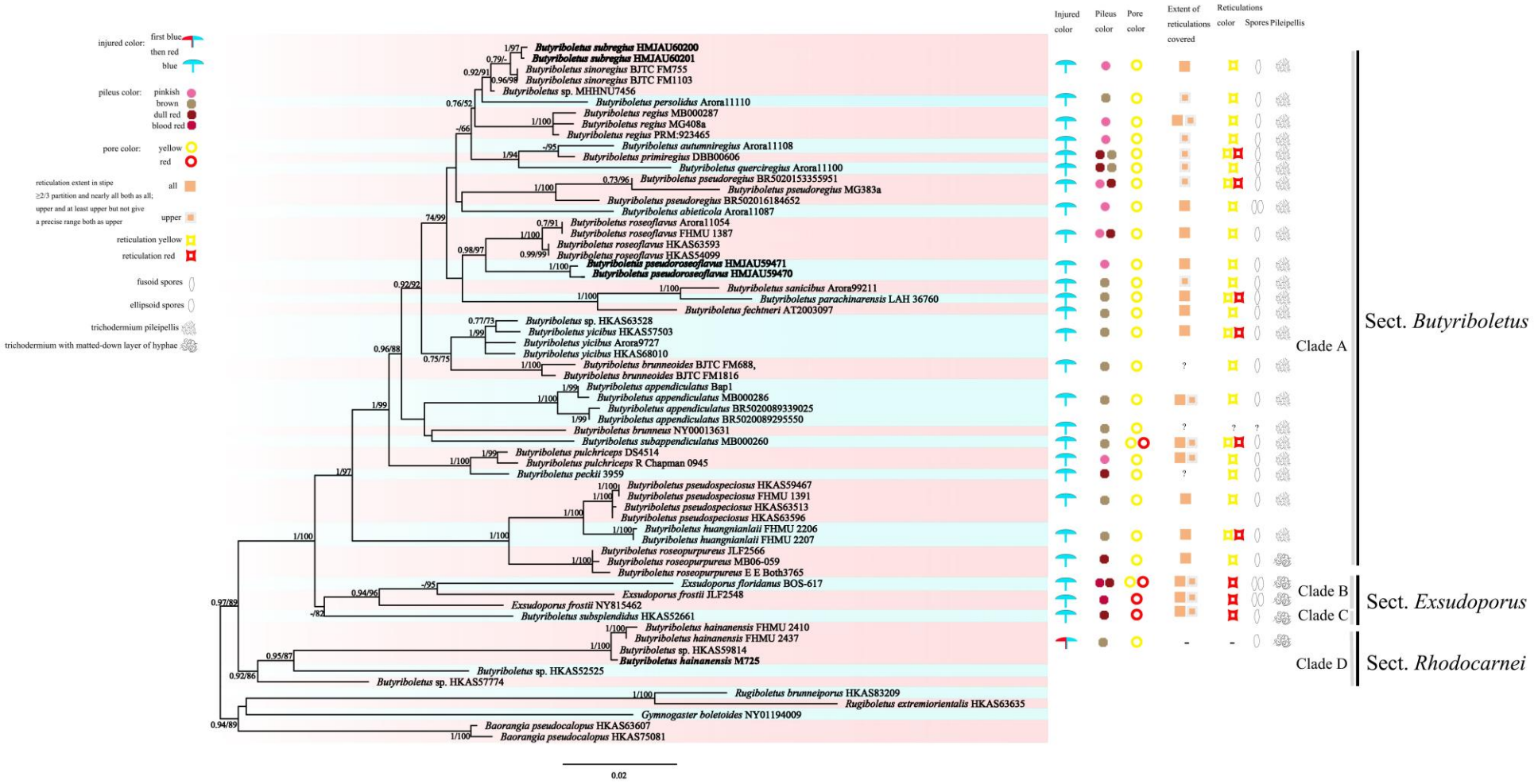


Figure 7 – Phylogenetic relationships of *Butyriboletus* and *Exsudoporus* inferred from multi-locus (28S, *tef1-α*, ITS, and *rpb2*) using Bayesian inference and maximum likelihood method (ML tree was shown). The PP ≥ 0.7 and BP ≥ 50 are indicated in the phylogram with key characteristics listed at the right. Newly formed sequences in this study are indicated in bold.

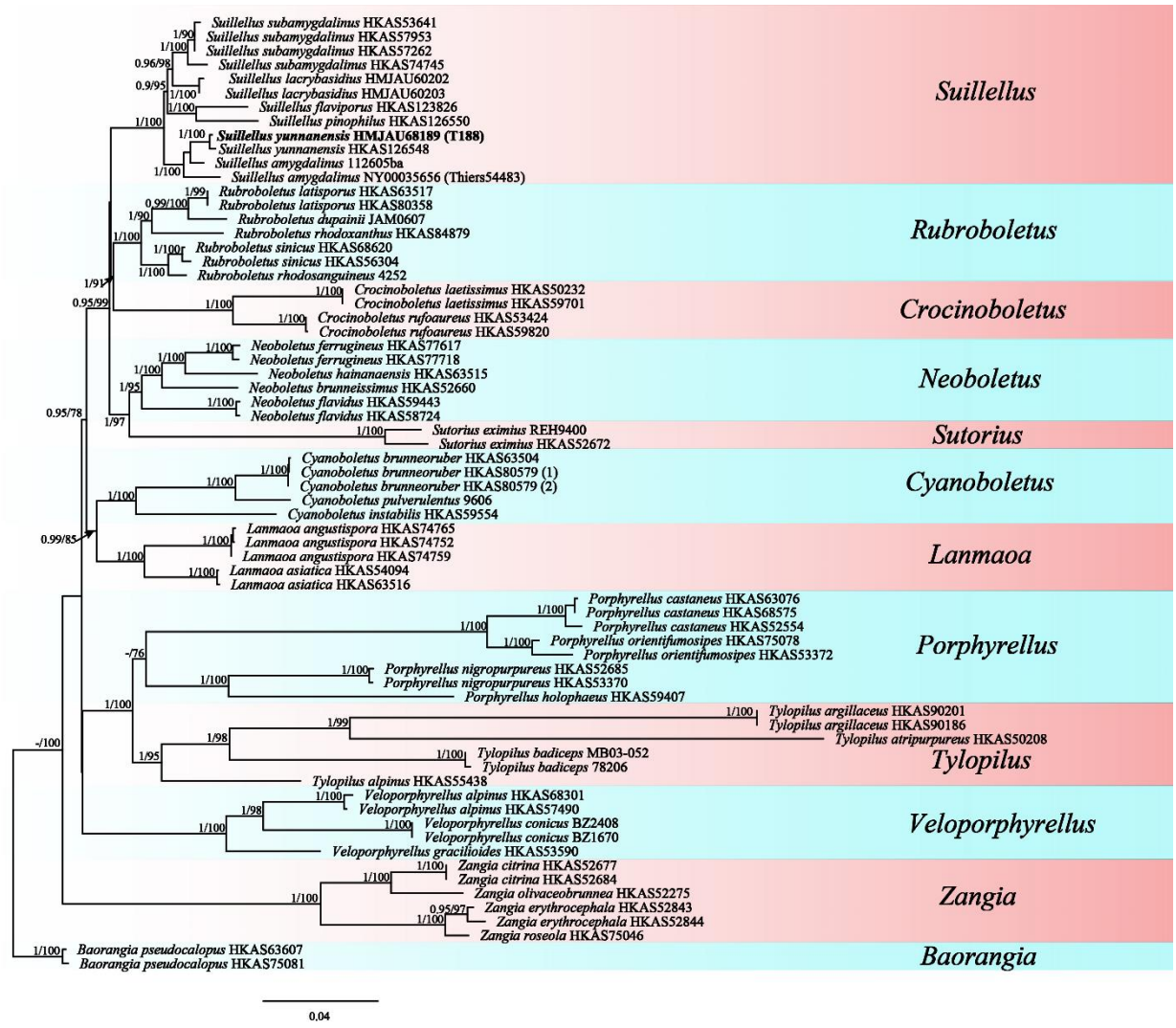


Figure 8 – Phylogenetic relationships of *Suillellus* inferred from multi-locus (28S, *tef1-α*, *rpb1*, and *rpb2*) using Bayesian inference and maximum likelihood method (ML tree was shown). The PP ≥ 0.9 and BP ≥ 70 are indicated in the phylogram with key characteristics listed at the right. Newly formed sequences in this study are indicated in bold.

adnexed, surface greenish yellow (3B6) to yellow (3D8), changing to blue when injured, pores nearly round; tubes greenish yellow (1A6–1B8), 0.8–2.1 cm long, staining blue immediately when bruised. Stipe 1.3–1.7 × 7–9.5 cm, subcylindrical to obclavate, yellowish white (1A2) to greyish yellow, covered with floccose squamules, same color as stipe when young but darker when mature, changing to dark blue when touched, context greenish yellow (1A8) to greyish yellow (4B4), turning blue when injured in the young stage, changing to red at mature. Basal mycelium white.

Basidiospores (4/4/119) (10.5–) 13.8–14–14.3 (–17.8) × (3–) 4.1–4.2–4.3 (–5) µm, Q = 2.63 (3.31)–3.45 (4.40), Q_m = 3.38 ± 0.40, fusiform to elongate ellipsoid or subcylindrical, inequilateral in side view with suprahilar depression, pale brownish yellow in 5% KOH, dextrinoid in Melzer's, smooth. Basidia 17.5–37.1 × 7.5–12.8 µm, clavate or broadly cylindrical, 2-, 4-spored. Hymenophoral trama boletoid, composed of hyaline filamentous hyphae, 3–9 µm wide. Cheilocystidia 27–52 × 4–12.2 µm, fusoid-ventricose, hyaline to pale brown in 5% KOH, thin-walled. Pleurocystidia 23.5–58.2 × 5–11.9 µm, subfusiform or narrow lageniform to lageniform, hyaline in 5% KOH, thin-walled. Pileipellis an interwoven trichodermium, composed of brown hyphae, usually filamentous sometimes slightly inflated, occasionally covered with granular crustation, 2.5–7.3 µm wide. Stipitipellis *Leccinum* type, can up to 265 µm thick, fertile, caulobasidia 16–33 × 5–9 µm, subcylindrical, 2-, 4-spored. Clamp connection absent.

Habitat – Solitary or caespitose in a broad-leaf forest, dominated by *Castanopsis* sp.

Known distribution – Southwest and Central China (this study).

Materials examined – China, Fujian Province, Wuyishan city, Wuyishan mountains national reserve, 20 August 2017, 117°27'2.48" E, 27°25'27.10" N, M745 (HMJAU68165, holotype); 17 August 2017, 117°27'19.33" E, 27°25'26.88" N, alt. 611 m, M692 (HMJAU68163); 19 August 2017, 117°27'2.31" E, 27°25'27.07" N, alt. 672 m, M730 (HMJAU68164); 20 August 2017, 117°27'2.39" E, 27°25'26.95" N, alt. 657 m, M750 (HMJAU68166); Yunnan Province, Jinghong city, 31 July 2008, Bang Feng 262 (HKAS 55373).

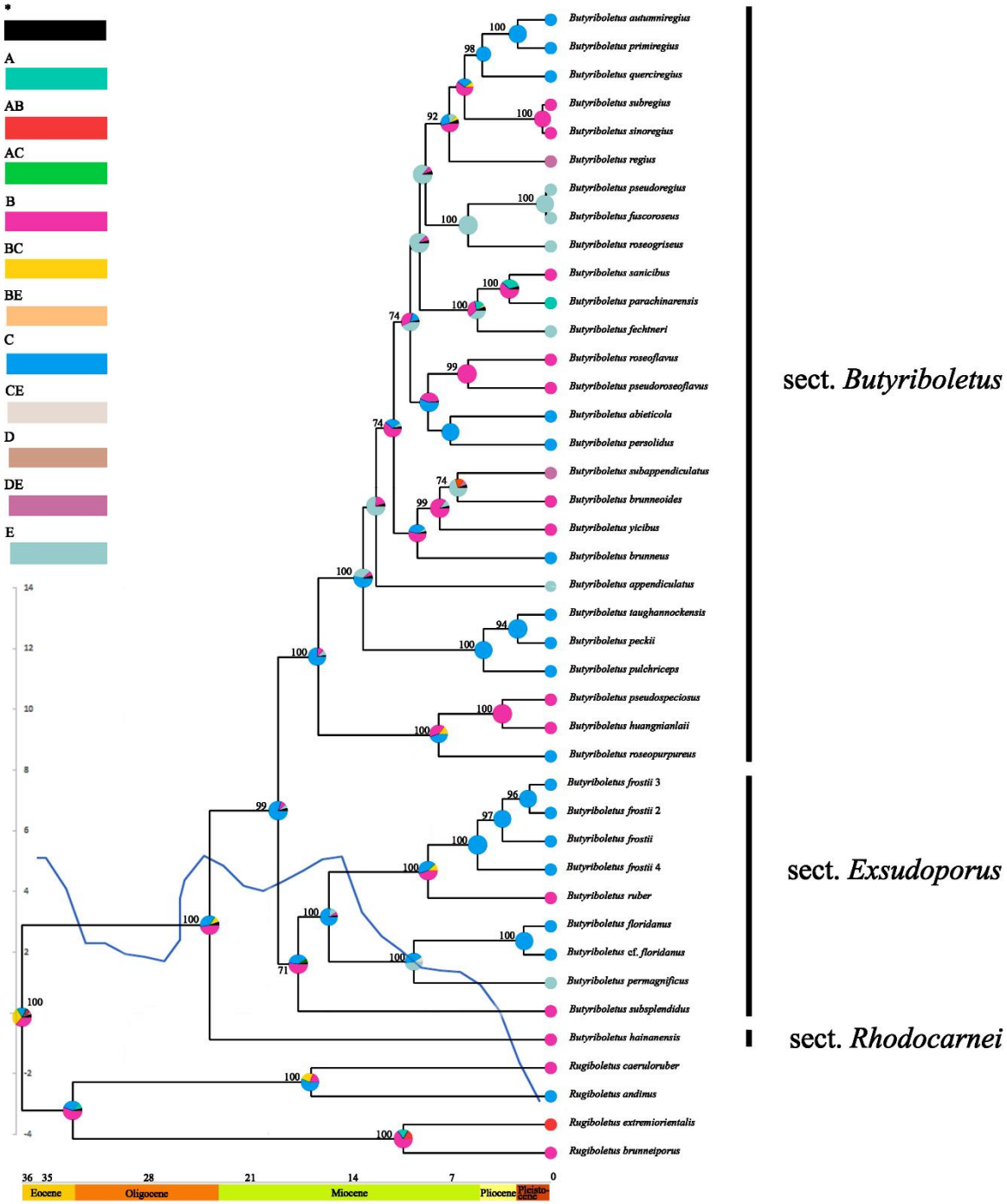


Figure 9 – Chronogram of *Butyriboletus*. The time-scale is set to the mean divergence dates produced in BEAST. Ancestral area reconstruction with pie charts colored by area based on DIVALIKE + J analysis. The blue curve represents global temperature change in geological history according to Zachos et al. (Zachos et al. 2001).

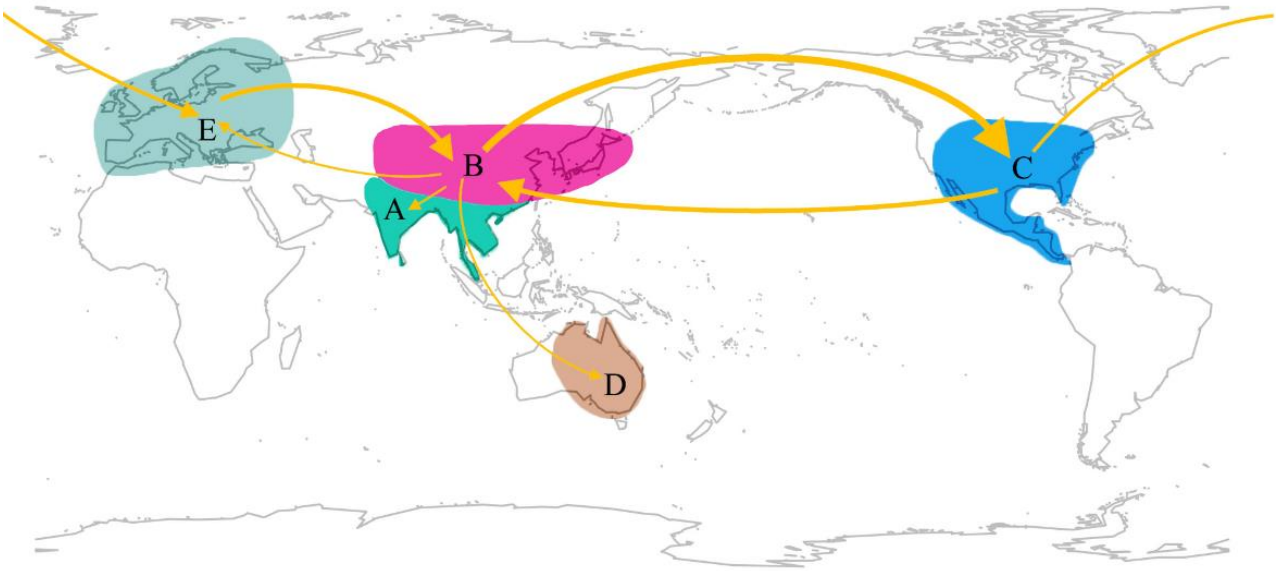


Figure 10 – Dispersal route of *Butyriboletus* illustrated by R (4.3.0, New Zealand). Thickness of lines means the different frequencies of dispersal. Dispersal between East Asia and North and Central America own the most frequencies compared with European and Australia.

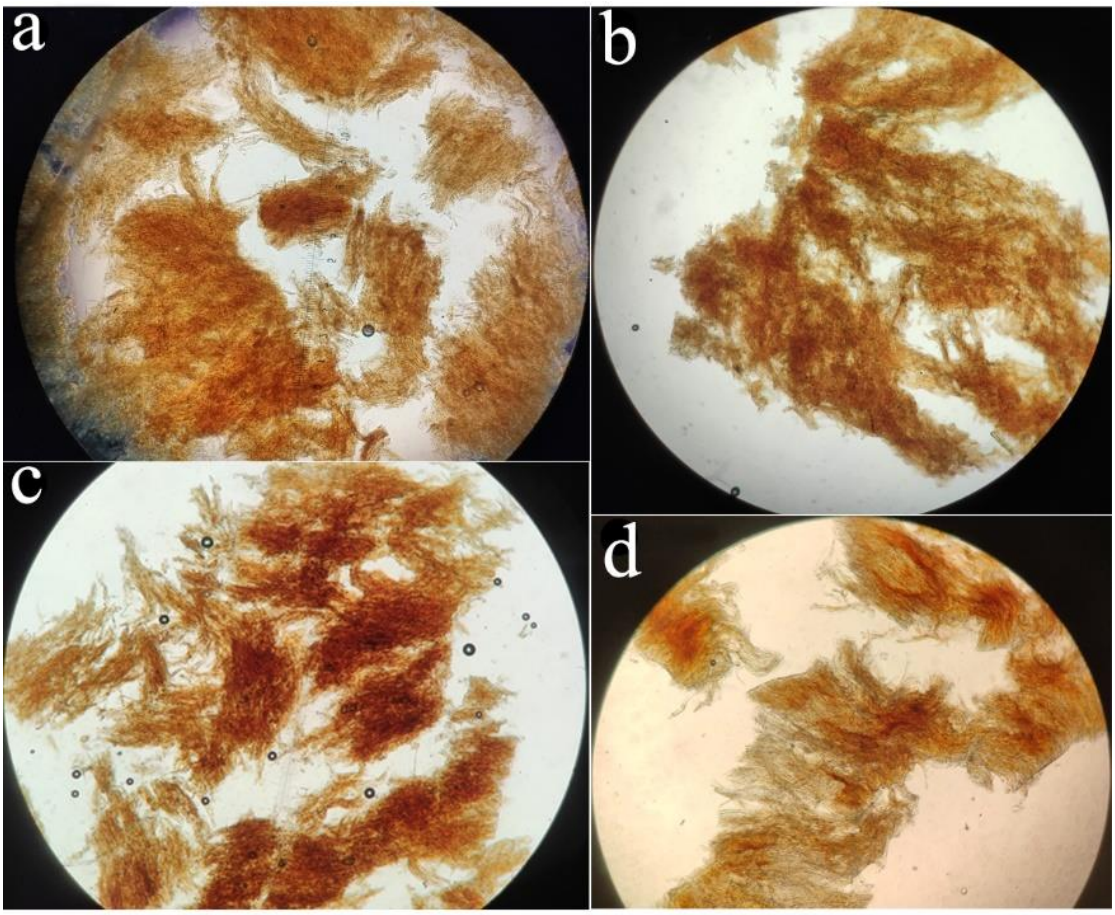


Figure 11 – Dextrinoid reactions of hyphae of stipe context in *Butyriboletus*. a *Butyriboletus hainanensis* HMJAU68167 (M725). b *Butyriboletus roseoflavus* HKAS54099. c *Butyriboletus subregius* (HMJAU60200). d *Butyriboletus ruber* HMJAU68190 (WY91).

Figure 12 – Basidiomata of Boletes. a–d *Niveoboletus brunneus* (a–c from HMJAU68161, d–f from HMJAU68162). g–l *Rugiboletus caeruloruber* (g from HMJAU68163, h–i from HMJAU68164, j–l from HMJAU68165).

Notes – Morphologically, the distinct scabrosities cover on the stipe may misidentify into *Leccinum* Gray. However, the ornamentations on the *Leccinum* are verrucose squamules, not floccose squamules, and the hymenophores of *Leccinum* are whitish. *Hemileccinum* Šutara shares some morphological characteristics with *Ru. caeruloruber*, *viz.* yellow hymenophores, but it can be distinguished by light-colored scabrosities and uncolored context when injured (Šutara 2008). *Leccinellum* Bresinsky & Manfr. Binder differed in context uncolored or turning red then black and pileipellis is an epithelium (Wu et al. 2016). Phylogenetically, *Ru. caeruloruber* sister with *Ru. andinus* (Halling) Halling & B. Ortiz, however, *Ru. andinus* is differs from yellow tinge pileus, context discoloration to blue and basidiospores larger and narrower (Halling & Mueller 2003).

Butyriboletus D. Arora and J. L. Frank, Mycologia 106 (3): 466 (2014)

Synonym – *Exsudoporus* Vizzini, Simonini & Gelardi, Index Fungorum 183: 1 (2014)

Basidiomes medium to large. Basidiomes stipitate-pileate with a tubular hymenophore. Pileus hemispherical, or applanate, glabrous or subtomentosus, usually with brown, blood red, dull red, and pink-rose tinge. Context of pileus pale yellow to yellow, turning to blue or then red and finally black when injured. Hymenophoral surface red or yellow, bluish when injured, tubes yellow, changing to

blue when injured. Stipe covered with reticulations at least at apex, rarely glabrous; reticulations usually yellow, sometimes red. Context of stipe yellow, turning to blue or then red and finally black when injured. Basidiospores ovoid to subfusoid, smooth. Pileipellis an trichoderimum to subcutis, sometimes with gelatinous layer. Clamp connections absent.

Type species – *Butyriboletus appendiculatus* (Schaeffer) D. Arora & J.L. Frank

Figure 13 – Basidiomata of Boletes. a–b *Butyriboletus hainanensis* (HMJAU68167). c–e *Cyanoboletus viscidiceps* (HMJAU68168). f–h *Xerocomellus velutinoceps* (f, h from HMJAU68170, G from HMJAU68169). i–j, m *Hortiboletus tomentosus* (i–j from HMJAU68173, M from HMJAU68176). k–l *Xerocomellus inflatus* (k from HMJAU68171, l from HMJAU68172).

o–p *Xerocomellus fuscoscabrosus* (o from HMJAU67772, p from HMJAU67773). q–s *Xerocomellus roseonigrescens* (HMJAU67775).

Figure 14 – Basidiomata of Boletes. a–c *Hortiboletus sinorubellus* (a–b from HMJAU68177, c from HMJAU68179). d–e *Zangia olivaceobrunnea*. f–g *Royoungia reticulata*. h–i *Suillellus yunnanensis*. j–k *Hortiboletus arduinus* (j from HMJAU68182, k from HMJAU68183). l–m *Boletellus putuoensis* (l from HMJAU68185, m from HMJAU68184). n *Tylopilus violaceobrunneus*.

Key to sections of *Butyriboletus*

1. Stipe nearly glabrous to faint reticulations, context bluish then red finally black when injured……..……...…...sect. *Rhodocarnei*
1. Stipe covered with reticulations at least at upper partition of stipe, context bluish when injured……..……..……2
2. Pileus usually bright red or reddish brown, pores and reticulations red, pileipellis often ixotrichodermium…….……....……..sect. *Exsudoporus*
2. Pores yellow, reticulations usually yellow rarely with red tinge and pileipellis trichodermium……sect. *Butyriboletus*

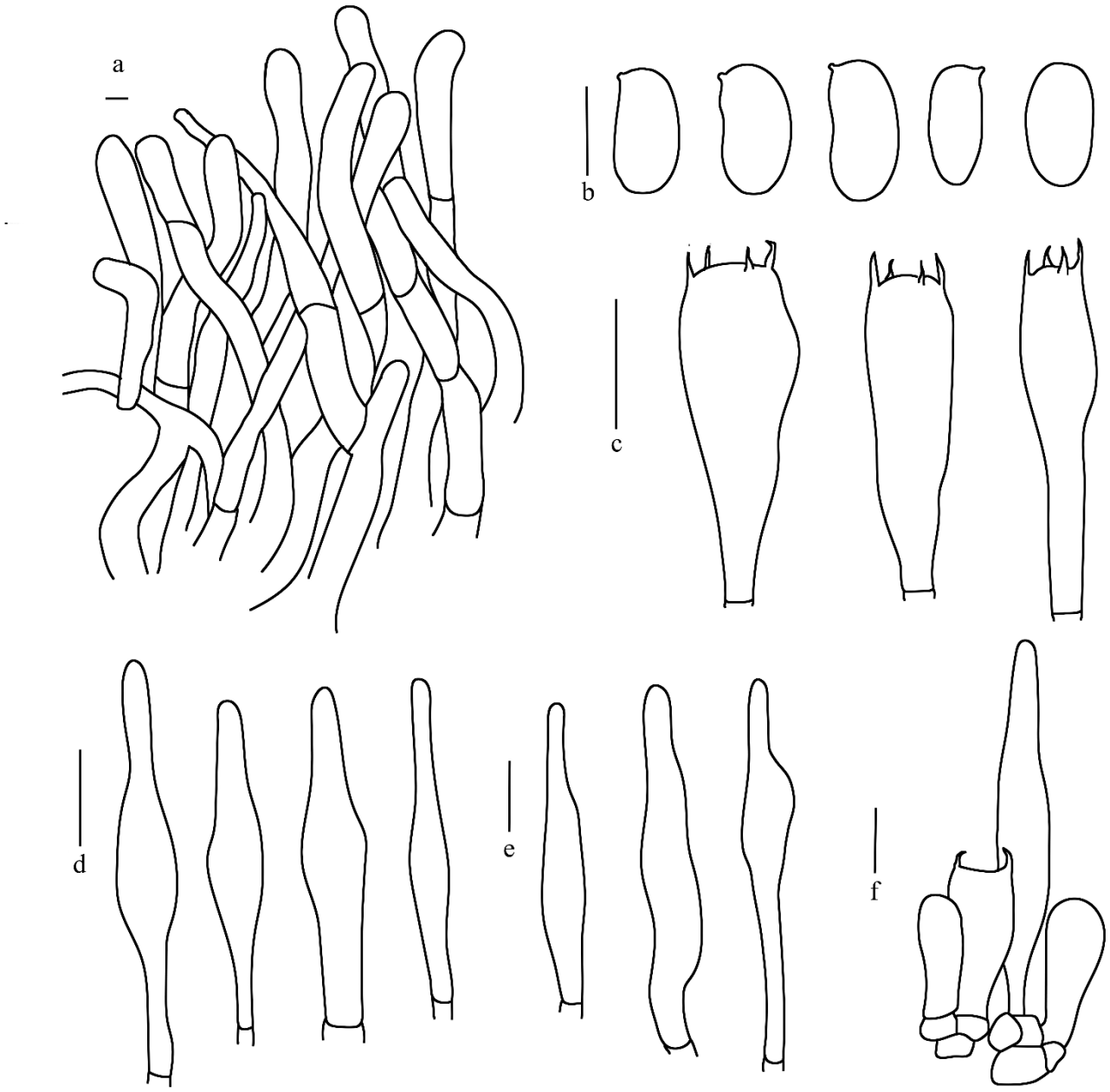


Figure 15 – *Niveoboletus brunneus*. a Pileipellis. b Basidiospores. c Basidia. d Pleurocystidia. e Cheilocystidia. f Basidium, pleurocystidium and basidioles. Scale bars: a, b = 5 μm, c–f = 10 μm.

Butyriboletus* sect. *Butyriboletus

Diagnosis – The section can be distinguished from other sections of *Butyriboletus* in the following combination characteristics: yellow pores rarely red at mature and yellow reticulations at least over the upper partition of stipe, sometimes reddish towards base, basidiospores subfusiform and pileipellis interwoven trichodermium.

Basidiomes stipitate-pileate with a tubular hymenophore. Pileus hemispherical, or applanate, glabrous or subtomentosus, mostly brown, pinkish and reddish. Context light yellow to yellow, bluing or not upon exposure. Hymenophoral surface yellow rarely red at mature, bluing when injured, tubes yellow. Faint or distinctly yellow reticulations at least over the stipe upper partition or sometimes pinkish reticulations at stipe base. Context yellow, turning blue when injured. Basidiospores subfusiform, smooth, pileipellis interwoven trichodermium. Taste mild or slightly spicy.

Type species – *Butyriboletus appendiculatus* (Schaeffer) D. Arora & J.L. Frank

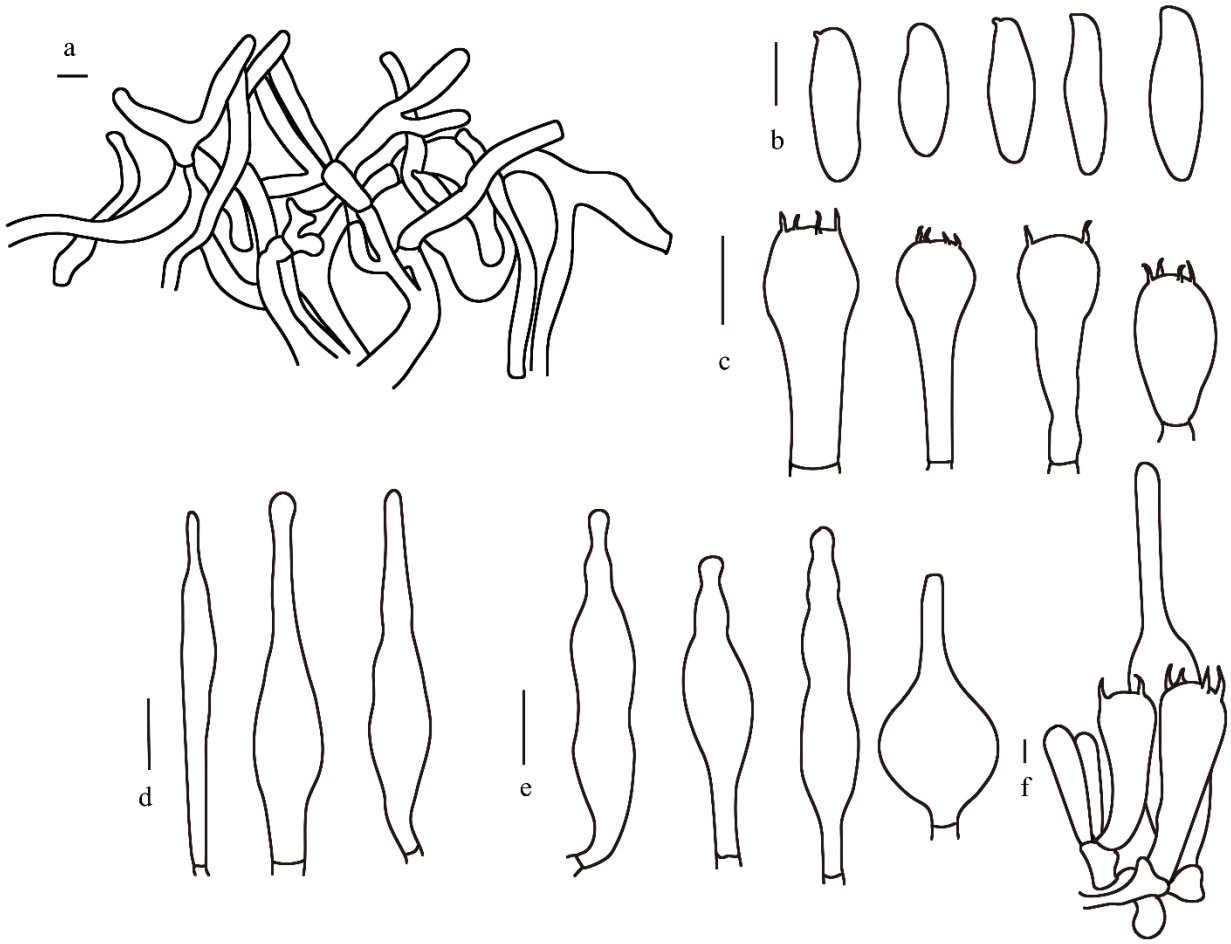


Figure 16 – *Rugiboletus caeruloruber*. a Pileipellis. b Basidiospores. c Basidia. d Pleurocystidia. e Cheilocystidia. f Basidia, pleurocystidium and basidioles. Scale bars: a, b = 5 μm, c–f = 10 μm.

Butyriboletus* sect. *Exsudoporus (Vizzini, Simonini & Gelardi) Yang Wang, G. Wu, B. Zhang & Y. Li comb. & stat. nov.

Basionym – *Exsudoporus* Vizzini, Simonini & Gelardi, Index Fungorum 183: 1 (2014)

MycoBank number: MB850740; Facesoffungi number: FoF16015

Diagnosis – The section can be distinguished from other sections of *Butyriboletus* in the following combination characteristics: red tinge basidiomes, pores and reticulations, often beaded with golden yellow or amber yellow droplets when young and fresh on the hymenophore, and apparently reticulations on the stipe in most instances.

This section primary following the definitions from Biketova et al. (2022). Basidiomes stipitate-pileate with a tubular hymenophore. Pileus hemispherical to applanate, bright blood red, reddish pink or reddish brown, glabrous, sometimes fibrillose, shiny and subviscid when wet, context pale to yellowish, staining blue upon exposure. Hymenophoral surface red to orange-yellow, turning blue when injured, often beaded with golden yellow or amber yellow droplets when young and fresh; tubes yellow to olivaceous-brown, turning blue when injured. Stipe central, solid, whole covered with raised red reticulations but sometimes not obviously and only on upper partition. Context pale yellow to lemon-yellow, staining blue upon exposure. Pileipellis an interwoven (ixo)trichoderm tending to a subcutis; hymenophoral trama "*Boletus*-type". Stipe context varies from inamyloid to amyloid or dextrinoid. Clamp connections absent. Taste mild to acidic.

Type species – *Butyriboletus permagnificus* (Pöder) Yang Wang, G. Wu, B. Zhang & Y. Li

Butyriboletus permagnificus (Pöder) Yang Wang, G. Wu, B. Zhang & Y. Li comb. nov.

MycoBank number: MB850742; Facesoffungi number: FoF16016

Basionym – *Boletus permagnificus* Pöder, Sydowia 34: 151 (1981)

Synonym – *Suillellus permagnificus* (Pöder) Blanco-Dios, Index Fungorum 211: 1 (2015); *Exsudoporus permagnificus* (Pöder) Vizzini, Simonini & Gelardi, Index Fungorum 183: 1 (2014)

Butyriboletus frostii (J.L. Russell) G. Wu, Kuan Zhao & Zhu L. Yang

Basionym – *Boletus frostii* J.L. Russell, Bulletin of the Buffalo Society of Natural Sciences 2: 102 (1874)

Synonym – *Exsudoporus frostii* (J.L. Russell) Vizzini, Simonini & Gelardi, Index Fungorum 183: 1 (2014)

MycoBank number: MB818399

Butyriboletus floridanus (Singer) G. Wu, Kuan Zhao & Zhu L. Yang

Basionym – *Boletus frostii* subsp. *floridanus* Singer, Mycologia 37: 799 (1945)

Synonym – *Boletus floridanus* (Singer) Murrill, Lloydia 11: 23 (1948); *Suillellus floridanus* (Singer) Murrill, Lloydia 11: 29 (1948); *Exsudoporus floridanus* (Singer) Vizzini, Simonini & Gelardi, Index Fungorum 183: 1 (2014)

MycoBank number: MB818398

Butyriboletus ruber (M. Zang) Kui Wu, Gang Wu & Zhu L. Yang

Basionym – *Leccinum rubrum* M. Zang, Acta Botanica Yunnanica 8 (1): 11 (1986)

Synonym – *Boletus kermesinus* Har. Takah., Taneyama & Koyama; Exsudoporus ruber (M. Zang) Gelardi, Biketova & Vizzini

MycoBank number: MB838318

Butyriboletus subsplendidus (W.F. Chiu) Kuan Zhao, G. Wu & Zhu L. Yang

Basionym – *Boletus subsplendidus* W.F. Chiu, Mycologia 40: 222 (1948)

MycoBank number: MB818397

Butyriboletus* sect. *Rhodocarnei Yang Wang, G. Wu, B. Zhang & Y. Li sect. nov.

MycoBank number: MB850741

Etymology – "rhodo-" meaning pinkish red, "carnei" meaning context of basidiomes; "Rhodocarnei" meaning the context turning to blue then red when injured.

Diagnosis – The section can be distinguished from other sections of *Butyriboletus* in the following combination characteristics: context of basidioma discoloring to blue first then red upon exposure, stipe glabrous, or with faint reticulations. Basidiospores smooth, ellipsoid to ovoid.

Basidiomes stipitate-pileate with a tubular hymenophore. Pileus hemispherical, tomentose, context staining blue then red, finally black when injured. Hymenophoral surface concolorous with tubes, yellow, staining blue when injured. Stipe central, surface glabrous or covered with faint reticulations; context staining blue then red, finally black when injured. Basidiospores smooth, ellipsoid to ovoid. Pileipellis an interwoven trichodermium composed of subcylindrical cells. Clamp connections absent in all tissues.

Type species – *Butyriboletus hainanensis* N.K. Zeng, Zhi Q. Liang & S. Jiang

Butyriboletus hainanensis N.K. Zeng, Zhi Q. Liang & S. Jiang Figs 13a–b, 17

Basidiomata medium. Pileus ca. 7 cm in diam., hemispherical, with slightly incurved and appendiculate margin, surface brownish orange (7C5–7C7), tomentose, unchanging color when injured; context firm, ca. 1.2 cm thick, white (1A1), staining blue then gradually red then black when exposed to air. Hymenophore decurrent, surface vivid yellow (2A8) to pastel red (7A5), turning blue when bruised; pores round; tubes ca. 0.4 cm long, yellow. Stipe 1.5–3 × 7–9 cm, subcylindrical, robust, glabrous, vivid yellow (2A8) on the apex, cherry (10B6–10B8) downwards, bluing when bruised; context light yellow (3A4), turning blue then red, finally black when exposed to air. Basal mycelium white.

Basidiospores (53/2/2) (8) 9.1–9.4 (10.5) × (3.9) 4.1–4.2 (4.9) μm, Q = (1.84) 2.2–2.3 (2.53), Q_m = 2.23 ± 0.13, elongated ellipsoid, sometimes ovoid, pale brownish yellow in 5% KOH, smooth. Hymenophoral trama boletoid, hyphae filamentous, 3.5–14.2 μm wide. Basidia clavate, thin-walled, 23–43 × 6.9–10 μm, hyaline to brownish yellow in 5% KOH, 4-spored, scarcely 2-spored. Pleurocystidia 31–57 × 6–9 μm, fusiform or subfusiform, usually brown and seldom hyaline in 5% KOH and ddH_2O, frequently origin from trama. Cheilocystidia 25–49 × 4.9–8 μm, brownish yellow in 5% KOH, similar shape with pleurocystidia, sterile in margin of pores. Pileipellis an interwoven trichodermium, consisting of 1–4 hyaline to brown subcylindrical cells with terminal cells obtuse, 4–15 μm wide. Stipitipellis fertile, caulocystidia share similar shape and color with cheilocystidia. Hyphae of stipe context weakly dextrinoid. Clamp connections absent in all tissues.

Habit – Scattered in the forest dominated by *Castanopsis* sp.

Known distribution – Southern China (this study).

Materials examined – China, Hainan Province, Baisha Country, Yinggeling Nature Reserve, Nankai, alt. 380 m, 31 July 2015, Zeng N.K.2418 (FHMU1548); Fujian Province, Wuyishan Nature Reserve, 117°27'2.04" E, 27°25'26.5764" N, alt. 665 m, 19 August, 2017, M725 (HMJAU68167).

Notes – *Butyriboletus hainanensis* was originally described from Hainan Province, China and now, it was also distributed in Fujian Province, China. Phylogenetically, this species is at the base of *Butyriboletus*, but it differs from other *Butyriboletus* in turning red context when upon exposure, nearly glabrous stipe and ellipsoid or ovoid not fusiform basidiospores. To be noted, the specimens we collected and loaned from FHMU named "FHMU1545" were shown nearly glabrous without reticulations over the stipe even in stereoscope, which is different from the original descriptions of *B. hainanensis* "with faint reticulations" (Liang et al. 2016).

Butyriboletus was amended here to form a broader definition. It now contains species that were formerly placed in *Exsudoporus*. Honestly, some taxonomic alternatives can be chosen when *Exsudoporus* and *B. hainanensis* were successively published based on their phylogenetical status, not only (I) broad circumscription of *Butyriboletus* and divided into three sections *viz*. lower taxonomic status of *Exsudoporus*, but also (II) no taxonomic maneuvers to amend *Butyriboletus* (III) separating Clade C and Clade D (Fig. 7) from *Butyriboletus* and *Exsudoporus* major clade, which mean two new genera will need to be erected and (IV) separating Clade D (Fig. 7) as a new genus, while Clade C will be merged into Clade B (*Exsudoporus*) (Fig. 7) (Vizzini 2014, Liang et al. 2016).

The solution (II) means no measures to treat *Exsudoporus* embedded in the *Butyriboletus* in phylograms (Wu et al. 2016, Biketova et al. 2022, Wang et al. 2022). The advantage is no name changed for Clade A–D (Fig. 7), thus maintaining nomenclature stability. The disadvantage is that *Butyriboletus* henceforth remains nonmonophyletic, which distinctly does not comply with taxonomic decisions.

The solution (III) will introduce two new genera for Boletaceae which currently includes 1200 species but contains nearly 100 genera, and divide *Butyriboletus* into four clades. Advantages are given to every clade a monophyletic origin, which clearly resolves the controversy between *Butyriboletus* and *Exsudoporus*. Meanwhile, preserving the generic name of *Exsudoporus* which loss may raise some concerns about reducing the taxonomic information content of classifications. Disadvantages are promoting the tendency of extreme translations of phylogenetic trees – a single clade represents a separate genus. Especially, the two new genera include only one species, respectively. Furthermore, the two genera do not both obtain well support, the Clade C support was low (-/82) (Fig. 7). The two new genera share some overlapping characteristics with *Butyriboletus* will cause confusion in identification.

The solution (IV) introduces one new genus based on *B. hainanensis*. Advantages are maintaining *Exsudoporus* generic status with few taxonomic names changed and holding on *Butyriboletus* original definition. Disadvantages are the moving of *B. subsplendidus* (Dermek, Lazebn. & J. Veselský) D. Arora & J.L. Frank, which does not comply definition of *Exsudoporus*. The measure will modify original definition of *Exsudoporus*. Meanwhile, it may cause a question – since amending definitions of genus for a convenient classification system is necessary, why be so coy? Furthermore, the tendency of extreme translations of phylogenetic trees still exists.

The solution (I) broad circumscription of *Butyriboletus*, just needs to transfer species of *Exsudoporus* into *Butyriboletus*. This action has already been done by Wu et al. (2016). However, Wu et al. did not further divide into intra-genus taxonomic status. Advantages include simplicity, without an inflated taxonomic framework; the changes relatively stable with enough phylogenetic information were kept for evolutionary history; good backbone support; the "exsudoporus" name was preserved; convenience for nonspecialists to recognize the species range of *Butyriboletus*. Disadvantage is that *Exsudoporus* should be changed to the section under *Butyriboletus*, a few names, *E. permagnificus, E. floridanus, E. frostii*, *E. ruber* should be changed.

To clarify the relationship between *Exsudoporus* and *Butyriboletus*, the core of disputes should be clear. We summarized seven major characteristics of *Butyriboletus* listed in Fig. 7. The etymology of *Exsudoporus* means pores forming exudate droplets when young, however, *E. ruber*, belongs to *Exsudoporus* later by morphological and phylogenetic analyses, show no droplets exist in multiple literature descriptions and our specimens' observations (unpublished). The results mean the droplets exist or not mostly main different characteristics inter-species not inter-genus. Similarly, *Exsudoporus* differs from *Butyriboletus* by the following key characteristics: basidiomes blood red to reddish brown, pores' color different from tubes, distinctly raised and red reticulations over the stipe and interwoven trochodermium tend to subcutis pileipellis. However, reddish brown pileus sometimes still exist in *Butyriboletus* core clade (Clade A), such as *B. primiregius* D. Arora & J.L. Frank, *B. querciregius* D. Arora & J.L. Frank, *B. roseoflavus* (Hai B. Li & Hai L. Wei) D. Arora & J.L. Frank, *B. peckii* (Frost) Kuan Zhao, Zhu L. Yang & Halling and *B. roseopurpureus* (Both, Bessette & Roody) Kuan Zhao, Zhu L. Yang & Halling and *B. subsplendidus* (Clade C) all reported reddish brown pileus. For the red pores, *B. subappendiculatus* in Clade A and *B. subsplendidus* in Clade C show red pores when mature. *Exsudoporus frostii*, as a species with distinctly raised reticulations in *Exsudoporus*, Coker and Beers had reported the different basidiomes unveiled different ornaments of reticulations – the collections of *E. frostii* they found in Highland N. C. showed "stem much less strongly reticulated and only at the top, the lower part of stem delicately streaked longitudinally or only velvety-tomentose, and the smaller, more evenly elliptic spores" (Coker & Beers 1974). Even in the same species, the extent of intensity of reticulations in *Exsudoporus* show an extremely fluctuating. The phenomenon no doubt reduces its taxonomic value.

The red reticulations are also reported in Clade A and C, such as *B. primiregius* D. Arora & J.L. Frank, *B. pseudoregius* (Heinr. Huber) D. Arora & J.L. Frank, *B. huangnianlaii* N.K. Zeng, H. Chai & Zhi Q. Liang and *B. subsplendidus*; sometimes the red reticulations of species are at base *viz*. *B. parachinarensis* Naseer, Davoodian & Khalid, *B. yicibus* D. Arora & J.L. Frank, and *B. subappendiculatus*. Taken together, we can easily know that red reticulations are not uncommon. The trichodermium tends to form a subcutis pileipellis, which is also observed in *Butyriboletus* (Clade A) and *B. hainanensis* (Clade D). The most important characteristics that Farid et al. (2021) and Bozok et al. (2019) focus on are the hyphae of the stipe context amyloid or dextrinoid in Melzer's resolution, which has not yet been reported on the species of *Butyriboletus* (Bozok et al. 2019, Farid et al. 2021). However, we revisited *B. pseudoroseoflavus* Yang Wang, Bo Zhang & Yu Li, *B. roseoflavus* (Hai B. Li & Hai L. Wei) D. Arora & J.L. Frank and *B. subregius* Yang Wang, Bo Zhang & Yu Li in Clade A, and *B. hainanensis* in Clade D, dextrinoid hyphae of stipe context were existing but weakly in *B. hainanensis* (Fig. 11, *B. pseudoroseoflavus* was not shown). As stated above, *Exsudoporus* shares overlapped characteristics with *Buytriboletus* in various key characteristics. Although, listing characteristics to compare different species is not suitable in the framework of Boletaceae because of frequently convergent evolution, the sister clades with affinitive relationships share so many key characteristics that should not erect new genera from a single clade shown on the phylogenetic trees.

Vellinga et al. (2015) tried to supply six guidelines to introduce new genera in fungi to pay attention to the proliferation of genera (Vellinga et al. 2015). Uplifting the number of new genera will continuously segment phylogenetical information, especially to Boletaceae which includes nearly 100 genera. This concern combined five guidelines proposed by authors were adopted by us to choose solution (I) broader circumscription of *Butyriboletus* to include *Exsudoporus*.

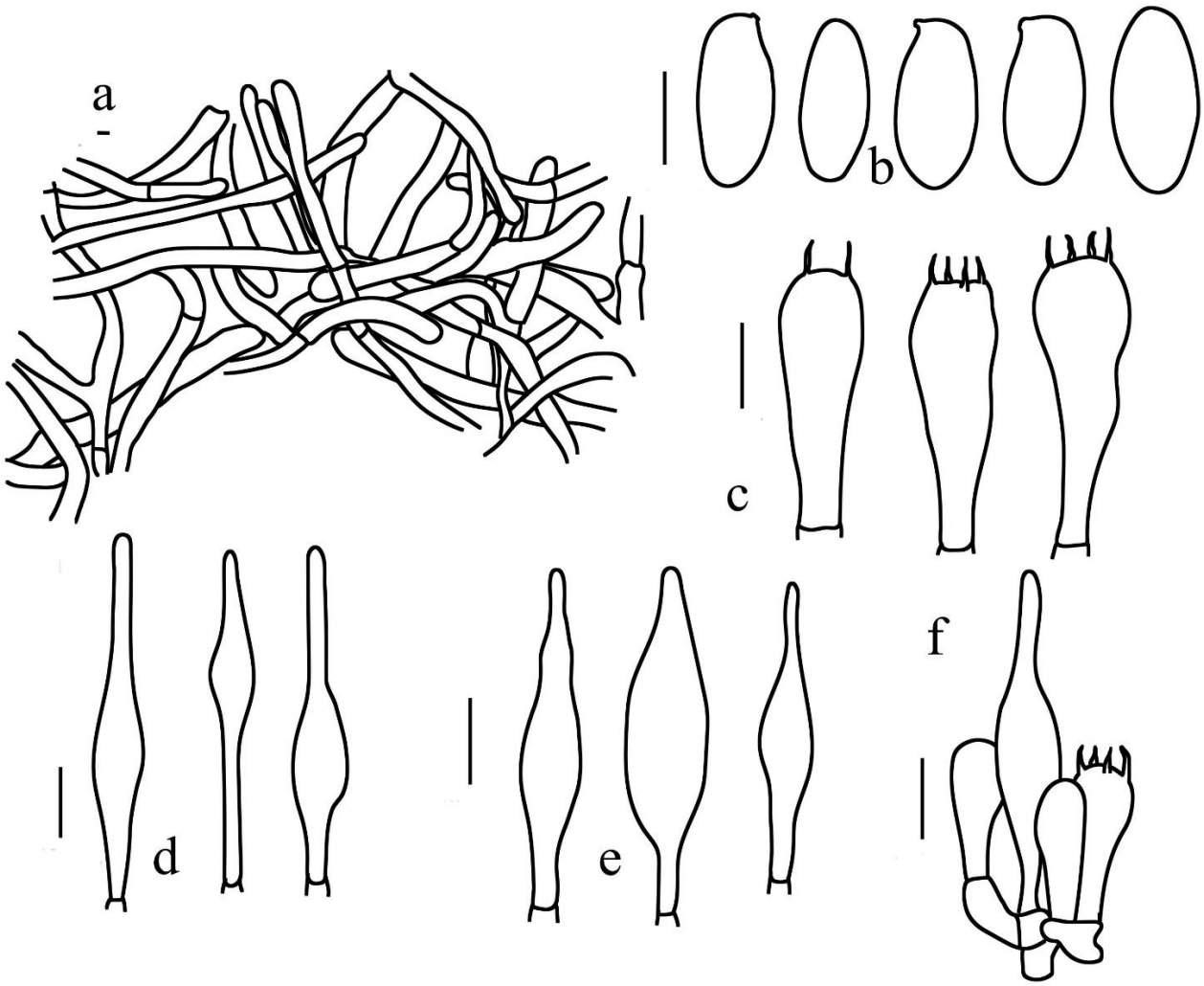


Figure 17 – *Butyriboletus hainanensis*. a Pileipellis. b Basidiospores. c Basidia. d Pleurocystidia. e Cheilocystidia. f Basidia, pleurocystidium and basidioles. Scale bars: a, b = 5 μm, c–f = 10 μm.

Cyanoboletus viscidiceps Yang Wang, G. Rao, B. Zhang & Y. Li sp. nov. Figs 13c–e, 18

MycoBank number: MB850510; Facesoffungi number: FoF15051

Etymology – "*viscidiceps*" refers to its viscid pileus.

Diagnosis – *Cyanoboletus viscidiceps* is closed to *Cy. paurianus* but differs from its colour of stipe and distinctly gelatinous pileus.

Basidioma small. Pileus 4.9 cm in diam., convex, light brown (6D8), glabrous, viscid when wet; context ca. 0.4 cm thick, staining dark blue when cut. Hymenophore decurrent; surface greenish yellow (1B8), bluing when bruised; pores nearly round, tubes concolorous with pore surface, turning dark bluing when injured. Stipe 6.9 × 1.5 cm, central, subcylindrical, glabrous; surface concolorous with pore surface on the apex, and deep red (10C8) downwards, scatter covered with red wart spot, turning dark blue when touched. Basal mycelium white.

Basidiospores (40/1/1) (10.5) 12.2–12.5 (13.9) × (4) 4.8–5.0 (5.8) μm, Q = (2.1) 2.47–2.59 (3.3), Q_m = 2.53 ± 0.19, subfusiform and inequilateral in side view with suprahilar depression, brownish yellow in 5% KOH, smooth. Basidia 22.5–29.2 × 8–12 μm, clavate, 2-, 4-spored. Hymenophoral trama boletoid; hyphae subcylindrical, 5–11.2 μm wide. Pleurocystidia 42–65 × 8–19 μm, fusoid-ventricose, hyaline or brown in 5% KOH, thin-walled. Cheilocystidia 49–64 × 14–17.8 μm, similar to pleurocystidia in shape and color. Pileipellis an ixosubcutis, composed of filamentous hyaline to brown hyphae, 2.5–7 μm wide; terminal cells cylindrical with subacute apex. Stipitipellis fertile, caulocystidia fusoid-ventricose, concolorous with pleurocystidia. Clamp connections absent.

Habit – Solitary in the Broadleaf mixed forest dominated by *Quercus mongolica*.

Known distribution – Jilin Province, China (this study).

Material examined – China, Jilin Province, Jian city, Wunvfeng National Forest Park, 16 August 2019, Gu Rao 345 (HMJAU68168, holotype).

Notes – Morphologically, *Cyanoboletus viscidiceps* is somewhat resembled *Cy. paurianus* K. Das & A. Ghosh, and *Cy. sinopulverulentus* (Gelardi & Vizzini) Gelardi, Vizzini & Simonini. However, *Cy. paurianus* is differs in stipe concolorous with pileus and short cystidia only up to 35 μm long (Das et al. 2023). *Cyanoboletus sinopulverulentus* differs from *Cy. viscidiceps* by its pruinose to furfuraceous stipe, larger basidiospores and shorter cystidia (Gelardi et al. 2013). Phylogenetically, *Cyanoboletus viscidiceps* is sister to *Cy. cyaneitinctus* (Murrill) A. Farid, A.R. Franck & J.A. Bolin, however, *Cy. cyaneitinctus* can be distinguished from its dry pileus, larger basidiospores and trichodermium pileipellis (Farid et al. 2021).

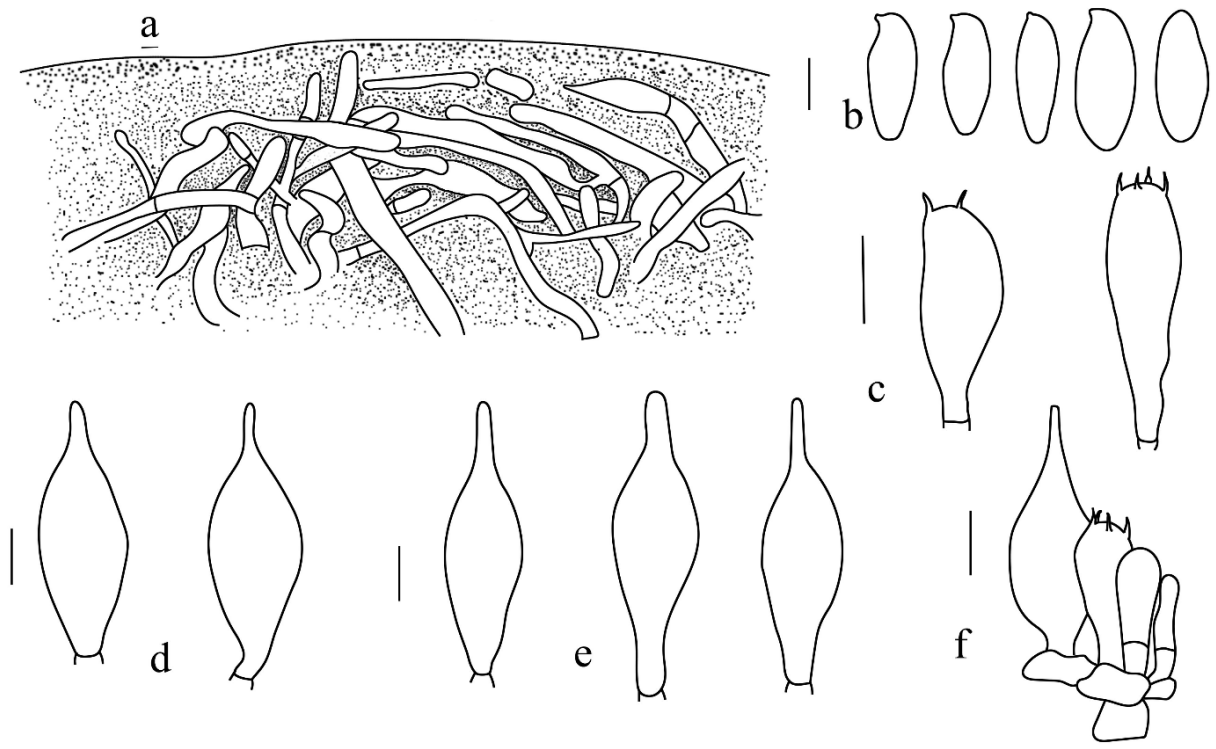


Figure 18 – *Cyanoboletus viscidiceps*. a Pileipellis. b Basidiospores. c Basidia. d Pleurocystidia. e Cheilocystidia. f Basidium, pleurocystidium and basidioles. Scale bars: a, b = 5 μm, c–f = 10 μm.

Xerocomellus Šutara, Czech Mycology 60 (1): 44 (2008)

Synonym – *Nigroboletus* Gelardi, Vizzini, E. Horak, T.H. Li & Ming Zhang, PLoS One 10 (8): e0134295, 6 (2015), syn. nov.

Basidiomes small to medium. Basidiomes stipitate-pileate with a tubular hymenophore, sometimes sequestrate. When basidiomes stipitate-pileate, pileus subapplanate, tomentose or glabrous, usually cracked into squamules at mature; usually with red tinge, rarely brown to black tinge. Context of pileus pallid or pale yellow, unchanging colour or slightly changing to blue to distinctly bluish when injured, rarely changing to deep blue. Surface of hymenophore yellow, turning to blue rarely deep blue when injured; tubes yellow, turning to blue rarely deep blue when injured. Stipe usually covered with longitudinally striate at apex, sometimes with pruinose; context of stipe concolorous with pileal context or deeper downwards. Basidiospores smooth or longitudinally striate, ovoid to subfusoid. Pileus trichodermium to palisadodermium, covered with erratically incrusted. Clamp connections absent.

Type species – *Xerocomellus chrysenteron* (Bull.) Šutara

Xerocomellus velutinoceps Yang Wang, B. Zhang & Y. Li sp. nov. Figs 13f–h, 19

MycoBank number: MB850511; Facesoffungi number: FoF15052

Etymology – "velutinoceps" refers to its pileus velvety.

Diagnosis – Distinguished from other species by its small and red basidiomes, and small basidiospores.

Basidioma very small. Pileus 2.4–2.7 cm in diam., subhemispherical or applanate; surface dry, velvety, distinctly cracked at mature, vivid red (10A8) to brownish red (10D8), staining dark blue when bruised; context 0.3–0.6 cm thick, staining blue when injured. Hymenophore adnate to decurrent; surface light yellow (2A5), bluish when bruised; pores nearly round to angular, 1.5–3/mm; tubes 0.2–0.4 cm long, concolorous with pore surface, changing blue when injured. Stipe 1.8–2.2 × 0.3–0.4 μm, subcylindrical, light yellow (2A5) at apex and base, brownish red (8C8) at middle, staining blue when bruised. Basal mycelium yellowish to yellow.

Basidiospores (59/1/1) (10.2) 11.2–11.6 (13.5) × (4) 4.2–4.4 (5) μm, Q = (2.1) 2.59–2.73 (3.38), Q_m = 2.66 ± 0.24, elongated ellipsoid to fusiform in side view with slight suprahilar depression, brownish yellow, smooth under light microscope. Basidia 25.2–33 × 7.2–10 μm, clavate, hyaline in 5% KOH, thin-walled. Hymenophoral trama intermediate in phylloporoid and boletoid, consisting of filamentous hyphae, 4–15 μm wide. Pleurocystidia 43–73.2 × 8.5–10.8 μm, subfusiform, hyaline to pale brownish in 5% KOH, thin-walled. Cheilocystidia 29–59 × 7.5–18 μm, similar to pleurocystidia in shape and color. Pileipellis a palisadoderm, consisting of 2–4 concatenated, vertically arranged, yellowish brown, slightly or distinctly broadened cells with erratically incrusted; terminal cells subfusiform, 6–15 μm wide, other cells 10–19 μm wide. Stipitipellis fertile. Clamp connections absent.

Habitat – Scattered in the *Quercus* sp. and coniferous mixed forest.

Known distribution – Henan Province, China (this study).

Materials examined – China, Henan Province, Zhumadian City, Biyang County, Madao forest farm Yihe village, 12 July 2021, W3109 (HMJAU68170, holotype); Baiyun Mountains, 11 July 2021, W3086 (HMJAU68169).

Notes – Morphologically, *Xe. velutinoceps* is resembles *Xe. cisalpinus* (Simonini, H. Ladurner & Peintner) Klofac, *Xe. corneri* Xue T. Zhu & Zhu L. Yang, and *Xe. marekii* (Šutara & Skála) Šutara. However, *Xe. velutinoceps* is characterized by *Xe. cisalpinus* by its small basidiomes, pileus without a brown to olive tinge and smaller and narrower basidiospores (Peintner et al. 2003). *Xerocomellus velutinoceps* differs from *Xe. corneri* in pileus without a brown tinge when mature, hymenophores decurrent and smaller basidiospores (Wu et al. 2016). *Xerocomellus marekii* is distinguished from *Xe. velutinoceps* by larger basidiospores can be up to 19 μm extremely (Šutara & Skála 2007). Phylogenetically, the sequence is named "*Xerocomellus* sp. HKAS56311" which was not yet been identified, was clustered with *Xe. velutinoceps*.

Xerocomellus inflatus Yang Wang, B. Zhang & Y. Li sp. nov. Figs 13k–l, 20

MycoBank number: MB850512; Facesoffungi number: FoF15053

Etymology – "inflatus" refers to its terminal cells of pileipellis inflating into subglobose or pyriform.

Diagnosis – Distinguished from other species by its large basidiospores and subglobose or pyriform cells of pileipellis.

Basidiomata small. Pileus 1.8–2.1 cm in diam., hemispherical to applanate; surface dry, velvety when young, distinctly cracked at mature, currant red (10B8) to reddish brown (10D8); context ca. 0.3 cm thick, white (1A1) to light yellow (1A4), bluing when injured. Hymenophore decurrent but slightly depressed around stipe; surface greenish yellow (1A8) when young, duller at mature, staining blue when injured; pores angular, up to 1 mm wide; tubes concolorous with pore surfaces, 0.2–0.3 cm long, turning blue when injured. Stipe 2.6–2.8 cm long, 0.4–0.5 cm wide, subcylindrical to attenuate at base; surface concolorous with hymenophore at apex, covered with velvety, currant red to reddish brown squamules downwards, staining blue when bruised; context white (1A1) to light yellow (1A4), changing to blue when injured. Basal mycelium white or dirty white.

Basidiospores (11.5) 14–14.5 (18) × (4) 4.5–4.7 (5.1) μm, Q = (2.4) 3–3.2 (4.25), Q_m = 3.09 ± 0.37, fusiform in side view with suprahilar depression, yellowish brown, smooth under light micro-

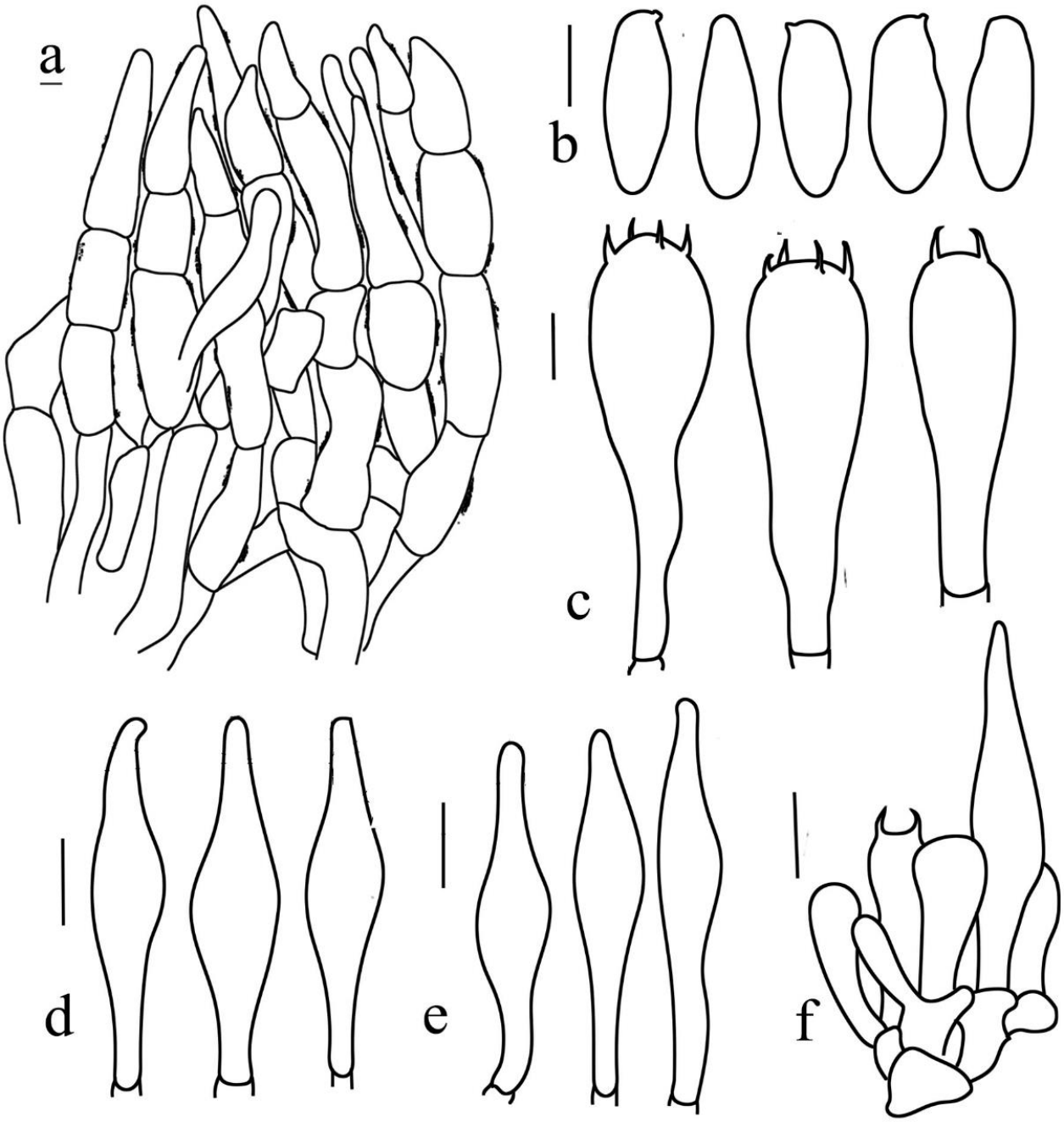


Figure 19 – *Xerocomellus velutinoceps*. a Pileipellis. b Basidiospores. c Basidia. d Pleurocystidia. e Cheilocystidia. f Basidium, pleurocystidium and basidioles. Scale bars: a–c = 5 μm, d–f = 10 μm.

scope. Basidia 22–40 × 7.5–12 μm, clavate, hyaline, thin-walled. Hymenophoral trama intermediate in phylloporoid and boletoid, consisting of filamentous hyphae, 4–14.8 μm wide. Pleurocystidia 30–62 × 8–13 μm, subfusiform or fusiform-ventricose, hyaline to yellowish brown in 5% KOH, thin-walled. Cheilocystidia 31–55.8 × 7.2–11.5 μm, similar to pleurocystidia in shape and color. Pileipellis epithelium, multi cells concatenated, sometimes incrusted; terminal cells subglobose or pyriform, 19–60 × 13–30 μm, hyaline to brown. Clamp connections absent.

Habitat – Solitary in the *Quercus mongolica* forest.

Known distribution – Jilin Province, China (this study).

Materials examined – China, Jilin Province, Jiaohe City, Hongye Valley, General Altar, 19 August 2021, W3272 (HMJAU68172, holotype). 19 August 2021, W3270 (HMJAU68171).

Notes – Morphologically, *Xe. inflatus* is similar to *Xe. cisalpinus*, *Xe. corneri*, and *Xe. dryophilus* (Thiers) N. Siegel, C.F. Schwarz & J.L. Frank. However, *Xe. cisalpinus* is different from

Xe. inflatus by smaller and narrower basidiospores and terminating cells of pileipellis cylindrical and somewhat tapering towards the apex; *Xe. corneri* can be distinguished by smaller basidiospores and Q value, and terminated cells of pileipellis narrower; *Xe. dryophilus* differs in red tinge in the stipe context at down part, smaller basidiospores and gangly hyphae of pileipellis (Thiers 1975, Peintner et al. 2003, Wu et al. 2016).

Phylogenetically, *Xe. inflatus* is sister with *Xe. communis* Xue T. Zhu & Zhu L. Yang, but *Xe. communis* can be distinguished by its dull brown to dull reddish brown pileus, purple context of stipe, smaller basidiospores and Q value, and relatively narrower terminated cells of pileipellis (Wu et al. 2016).

Xerocomellus fuscoscabrosus Yang Wang. B. Zhang & Y. Li sp. nov. Figs 13o–p, 21

MycoBank number: MB851134; Facesoffungi number: FoF15217

Etymology – "fuscoscabrosus" means its surface of pileus with black tint and cracked into scales when mature.

Diagnosis – *Xerocomellus fuscoscabrosus* is characterized by its black tint pileus usually cracked, basidiomes turning blue when injured, and broad cells of pileipellis.

Basidiomes small. Pileus 2–4.2 cm in diam., applanate or slightly depressed at center; surface dry, cracked at mature, violet brown (10E8) to reddish brown (9D8), margin usually relatively pale, vivid red (9A8) to brownish red (9C8); context 0.2–0.4 cm thick, white (1A1), staining blue when injured. Hymenophore decurrent; surface yellow (2A7), bluish when bruised; pores nearly round to angular, 1–3/mm; tubes concolorous with pore surfaces, 0.1–0.4 cm long, turning blue when injured. Stipe 2.6–5.8 cm long, 0.3–0.5 cm wide, subcylindrical; surface concolorous with pileus at apex, then dirty yellow downwards, striate, covered with white pruinose; context yellow (2A7), bluish when injured at apex. Basal mycelium dirty white. Basidiomes without odor.

Basidiospores (10) 10.9–11.2 (12) × (4.5) 5–5.1 (5.8) μm, Q = (1.81) 2.16–2.24 (2.49), Q_m = 2.20 ± 0.21, ovoid to ellipsoid in side view with slightly suprahilar depression, brownish yellow, smooth under light microscope. Basidia 24–36 × 9–13 μm, clavate, hyaline to pale yellow in 5% KOH, thin-walled. Hymenophoral trama intermediate in phylloporoid and boletoid, consisting of filamentous hyphae, 3.5–10.3 μm wide. Pleurocystidia 37–66 × 7–12 μm, subfusiform or fusiform-ventricose, hyaline in 5% KOH, thin-walled. Cheilocystidia 39–71 × 8–12 μm, similar to pleurocystidia in shape and color. Pileipellis a palisadodermium, multi cells concatenated, 8–23 μm wide, sometimes incrusted, brownish yellow. Clamp connections absent.

Habitat – Solitary or scattered in the mixed forest composed by *Quercus mongolica*, *Betula* sp., *Acer* sp., and *Juglans* sp.

Known distribution – Jilin Province, China (this study).

Materials examined – China, Jilin Province, Tonghua city, Huinan county, Sanjiaolong bay, 8 August 2022, 126°26' 24.28" E, 42°19' 55.94" N, alt. 783 m, W3709 (HMJAU67772, holotype); 8 August 2022 W3710 (HMJAU67773); 8 August 2022 W3716 (HMJAU67774).

Notes – Morphologically, *Xe. fuscoscabrosus* is similar to *Xe. cisalpinus, Xe. corneri, and Xe. fennicus* (Harmaja) Šutara. However, *Xe. cisalpinus* is different from *Xe. fuscoscabrosus* by larger basidiospores, and mostly cylindrical cells in the pileipellis; *Xe. corneri* is characterized by its larger basidiospores and Q value, scarcely pleurocystidia; *Xe. fennicus* can be distinguished by its scarcely and larger pleurocystidia, and a pileipellis consisting of cylindrical cells (Peintner et al. 2003, Šutara 2008, Wu et al. 2016).

Phylogenetically, *Xe. fuscoscabrosus* is close to *Xe. velutinoceps*, but the black tint pileus and broader basidiospores and cells in the pileipellis can easily distinguish it from *Xe. velutinoceps*.

Xerocomellus roseonigrescens (Gelardi, Vizzini, E. Horak, T.H. Li & Ming Zhang) Yang Wang, B. Zhang & Y. Li comb. nov. Figs 13q–s, 22

MycoBank number: MB851135

Basionym – *Nigroboletus roseonigrescens* Gelardi, Vizzini, E. Horak, T.H. Li & Ming Zhang, PLoS One 10 (8): e0134295, 6 (2015)

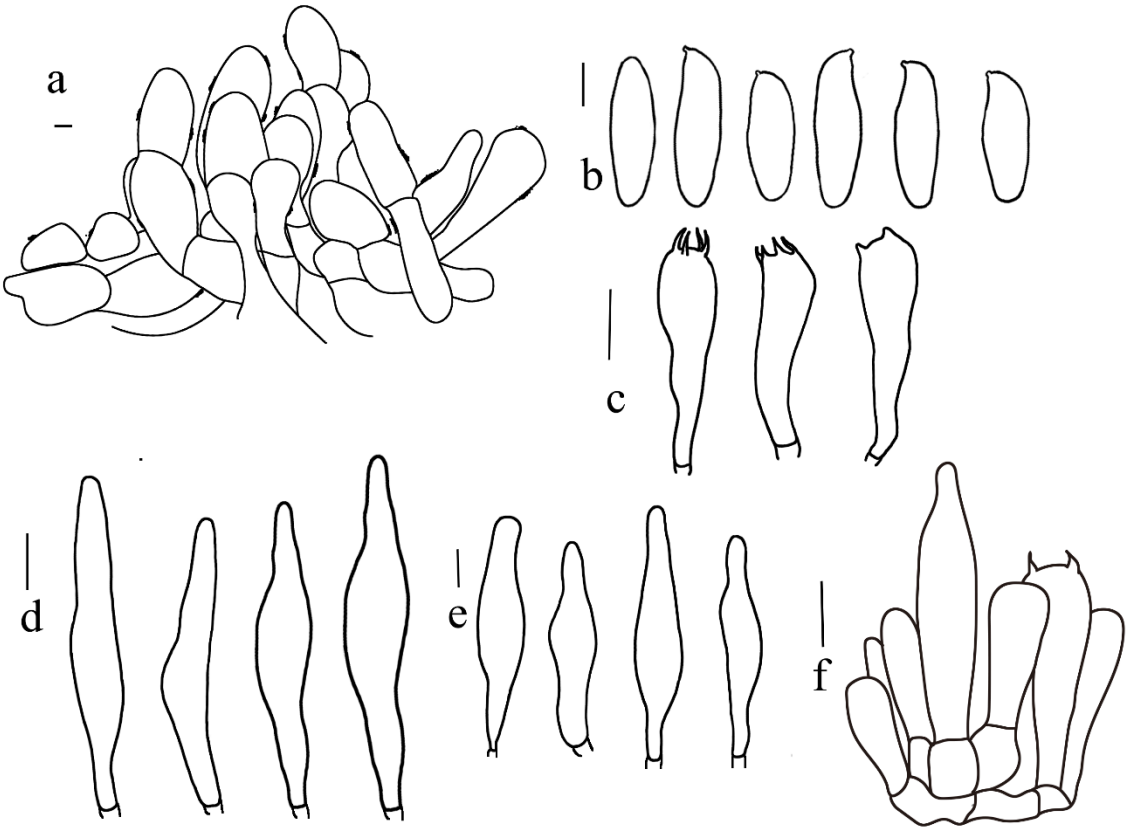


Figure 20 – *Xerocomellus inflatus*. a Pileipellis. b Basidiospores. c Basidia. d Pleurocystidia. e Cheilocystidia. f Basidium, pleurocystidium and basidioles. Scale bars: b = 5 μm, a, c–f = 10 μm.

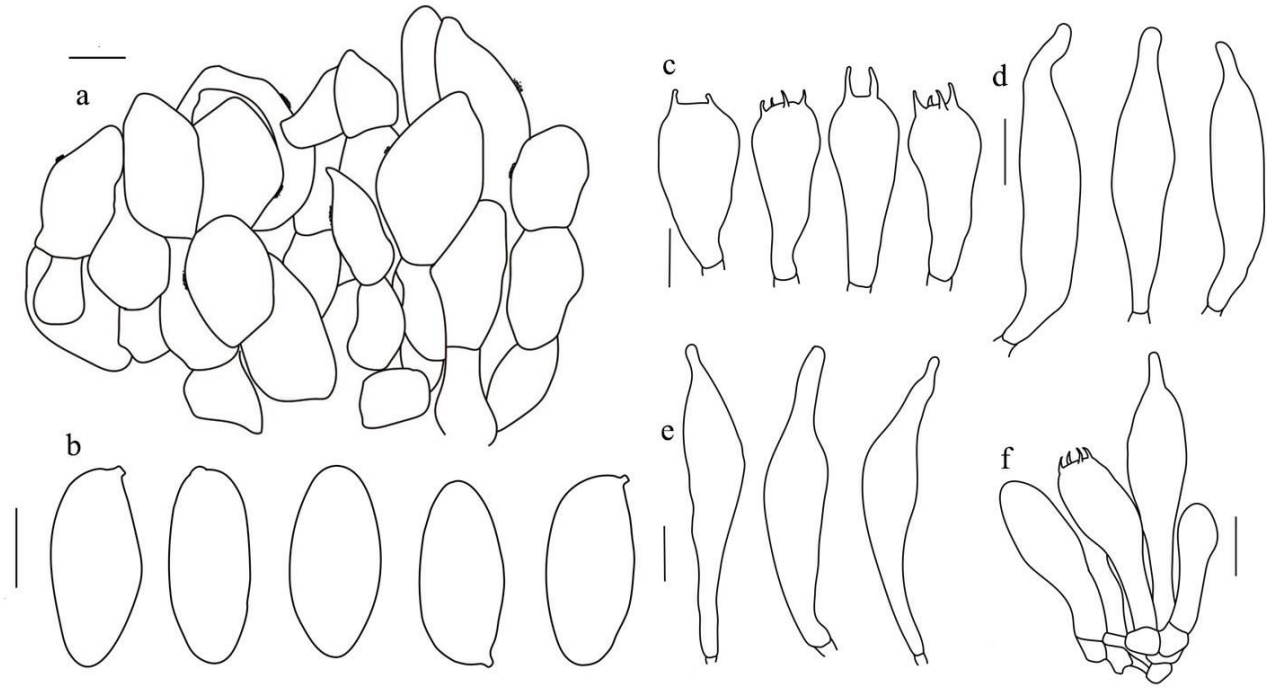


Figure 21 – *Xerocomellus fuscoscabrosus*. a Pileipellis. b Basidiospores. c Basidia. d Pleurocystidia. e Cheilocystidia. f Basidium, pleurocystidium and basidioles. Scale bars: b = 5 μm, a, c–f = 10 μm.

Basidiomes small. Pileus can up to 4.5 cm in diam., applanate; surface dry, tomentose, dark violet (16F3), pink (11A5) at margin; context 0.4–0.5 cm thick, grey (16B1), changing to dark blue upon exposure. Hymenophore adnate with decurrent tooth; surface light yellow (4A5), turning to dark blue when injured; pores irregular to angular, 1.5–2/mm; tubes concolorous with pore surfaces, 0.3–0.4 cm long, turning to dark blue when injured. Stipe 4–4.4 × 0.8–0.9 cm, subcylindrical; surface concolorous with pores, changing to dark blue when bruised; context pastel yellow (1A4), turning to dark blue when injured. Odor indistinct.

Basidiospores (6) 7.8–8.3 (11) × (4.0) 4.7–5.0 (6.8) μm, Q = (1.20) 1.64–1.711 (2.00), Q_m = 1.67 ± 0.19, ovoid to ellipsoid in side view with slightly suprahilar depression, brownish yellow, smooth under light microscope. Basidia 26–35.8 × 7–10.8 μm, clavate, yellow in 5% KOH, thin-walled. Hymenophoral trama intermediate in phylloporoid and boletoid, consisting of filamentous and hyaline to brown hyphae, 4.2–14 μm wide. Pleurocystidia 28–48 × 10.8–16 μm, broadly lageniform or subfusiform, brown, rarely hyaline in 5% KOH, thin-walled. Cheilocystidia 28–50.8 × 11.4–21 μm, similar to pleurocystidia in shape and color. Pileipellis a interwoven trichodermium, consisting of 5–12 μm wide, subcylindrical, pale yellow to brown hyphae, sometimes incrusted. Stipitipellis hymeniform, fertile, caulobasidia can up to 38 μm long, 11.2 μm wide, yellow in 5% KOH; caulocystidia 50–58 × 15–16 μm, similar to pleurocystidia in shape and color. Clamp connections absent.

Habitat – Solitary in the broadleaf forests.

Known distribution – Guangdong and Hunan province, China (this study).

Materials examined – China, Hunan Province, Changsha city, 9 September 2023, WY72 (HMJAU67775); Guangdong Province, Guangzhou, Mount Huolu, Tianlu Lake Forest Park, 23° 13' 35" N, 113° 110' 05" E, alt. 360 m, 14 Sep 2012, M. Zhang, GDGM 43237 (isotype).

Notes – *Xerocomellus roseonigrescens* differs from others in *Xerocomellus* in its dark violet pileus at least at centre, basidiomes discolour to dark blue when bruised, ovoid or ellipsoid basidiospores and cylindrical hyphae of pileipellis.

Nigroboletus is recognized as a junior synonym of *Xerocomellus* here. Gelardi et al. (2015) established this genus from *Xerocomellus* due to the tissues discolor to dull grayish to blackish when exposed, ovoid to ellipsoid basidiospores, a thick lateral stipe stratum measuring 40–100 (160) μm, and cystidia "sometimes with brownish to dark brown, congophilous plaques". However, in our specimens, the basidiomes changed to dark blue when injured, compared to the difference from dark gray to blackish when cut in the original description, which we consider a fluctuation of objective description. Gelardi et al. (2015) highlight that the maximum thickness of *Xerocomellus* is only 40 μm at most, while the lateral stipe stratum in *Nigroboletus* can range from 40–100 (160) μm. The overlapped value of 40 μm and the significant variation of nearly 120 μm in the thickness within a single species suggest that this characteristic should not be considered a reliable factor in distinguishing between the two genera. Furthermore, it should be noted that some species of *Xerocomellus* have not supplied their descriptions about the thickness of their lateral stipe. Cystidia were distinctly observed with brownish to dark brown plasmatic pigment or brownish to dark brown plaques in our specimens but without congophilous plaques. The different specimens show different cystidia, along with congophilous plaques only occasionally appearing in the original description, showing the unreliable of using it to delimit two genera that are sister clades in the phylogenetic tree. The shape of basidiospores was recognized as a key difference between *Nigroboletus* and *Xerocomellus*, but the new species in same major clade (Fig. 4), *Xe. velutinoceps* and *Xe. fuscoscabrosus*, show subfusiform and ovoid to ellipsoid basidiospores, respectively. Combining their other characteristics *viz*. distinctly red tinge pileus, basidiomes turning to blue when injured, cystidia without brownish to dark brown, congophilous plaques, and phylogenetic status with *Nigroboletus*, there remain four choices to choose (I) adopting *Xe. velutinoceps* and *Xe. fuscoscabrosus* as two new species of *Nigroboletus*. However, according to the strict definition of *Nigroboletus*, the two new species distinctly tend to belong to *Xerocomellus*, not *Nigroboletus*, a broader definition of *Nigroboletus* is inevitable. Subsequently, *Nigroboletus* almost entirely overlapped with the definition of *Xerocomellus*. The two sister clades depicted in the phylogenetic tree show many similar key characteristics, suggesting a single genus. (II) holding the genus

Nigroboletus, and accepted the two new species that formed a major clade with *Nigroboletus* as species of *Xerocomellus*. This choice directly caused *Xerocomellus* to be paraphyletic which is unreasonable in taxonomy. (III) erecting status of *Xe*. *velutinoceps* and *Xe*. *fuscoscabrosus* into a new genus to keep the status of *Nigroboletus* which is unreasonable. There are so many typical similarities in *Xe*. *velutinoceps*, *Xe*. *fuscoscabrosus* and *Xerocomellus*, just aim to keep *Nigroboletus* status, one new genus is erected, which abominably exhibits an inflated taxonomic framework. This action has no value in helping the general public to recognize this group, on the other hand, even puts researchers in chaos. (IV) accepting *Nigroboletus* as a junior synonym of *Xerocomellus*. The disadvantage is losing the typical formations of this species. However, according to our results, the low support of the phylogenetic tree in the original literature (Gelardi et al. 2015), and the discriminate characteristics with *Xerocomellus* both cannot warrant as a separate genus. The new species, *Xe*. *fuscoscabrosus* shows a distinctly transitional morphology between *Nigroboletus* and *Xerocomellus*, its ovoid basidiospores and black tint pileus are similar to *Nigroboletus*, but basidiomes bluish upon exposure, the cystidia lack brown pigment and a palisadodermium pileipellis are resembling *Xerocomellus*.

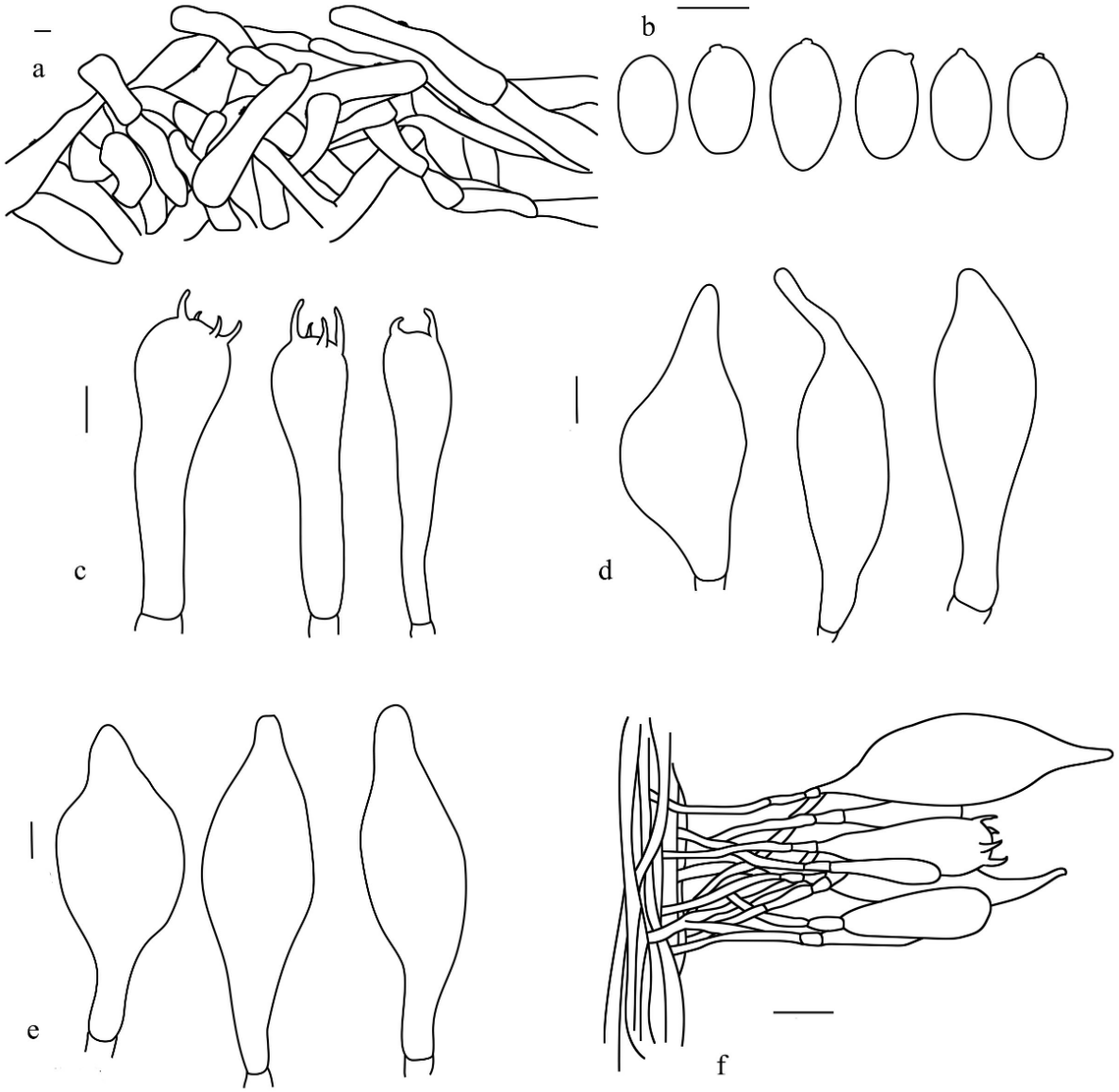


Figure 22 – *Xerocomellus roseonigrescens*. a Pileipellis. b Basidiospores. c Basidia. d Pleurocystidia. e Cheilocystidia. f Stipitipellis. Scale bars: a–e = 5 μm, f = 10 μm.

Taken together, we deem that compulsively treating the *Nigroboletus* clade as a new genus is meaningless, and only causes the loss of phylogenetic information. We adopt solution (IV) that *Nigroboletus* is a junior synonym of *Xerocomellus*.

Hortiboletus sinorubellus Yang Wang, X. Chen, B. Zhang & Y. Li sp. nov. Figs 14a–c, 23

MycoBank number: MB850514; Facesoffungi number: FoF15055

Etymology – "sinorubellus" means similar to *Ho. rubellus*, but now only found in China.

Diagnosis – Distinguished from other species by its cracked pileus at mature, fusiform basidiospores and broader cells of pileipellis.

Basidioma small to medium. Pileus 2.3–8 cm in diam., hemispherical to applanate; surface dry, velvety when young, distinctly cracked at mature, currant red (10B8) to vivid red (11A8); context 0.2–0.55 cm thick, yellowish white (2A2) to light yellow (1A4), distinctly or weakly staining blue when exposure. Hymenophore sinuate; surface pale yellow (1A3) when young to greenish yellow (1B5) at mature, staining blue when injured; pores nearly round to labyrinthine, 1.5–4/mm; tubes 0.3–0.7 cm long, concolorous with pore surfaces, turning blue when injured. Stipe 4.5–9.2 cm long, 0.9–1.1 cm wide, subcylindrical to sometimes enlarged at base; surface pastel red (10A4), covered with same color dots at apex when young, longitudinally fibrillose at mature, yellow at base, staining blue when bruised; context light yellow (1A4), turning blue when injured. Basal mycelium dirty white to yellow.

Basidiospores (9) 10.7–11 (14) × (4) 4.4–4.5 (5.9) μm, Q = (1.88) 2.4–2.5 (3.05), Q_m = 2.45 ± 0.2, subfusiform in side view with slight suprahilar depression, brownish yellow, smooth under light microscope. Basidia 24–42 × 8–12 μm, clavate, hyaline in 5% KOH, 2-,4-spored, thin-walled. Hymenophoral trama intermediate in phylloporoid and boletoid, consisting of filamentous hyphae, 4–14 μm wide. Pleurocystidia 33–82 × 6–14 μm, narrowly subfusiform, hyaline to brownish in 5% KOH, thin-walled. Cheilocystidia 27–64 × 6.3–10.3 μm, similar to pleurocystidia in shape and color. Pileipellis a palisadoderm, consisting of 3–7 concatenated, inflated and subcylindrical, brownish yellow cells, with erratically incrusted; terminal cells subfusoid, 15–32 × 10–13.5 μm; the others 24–46 × 12.5–28 μm. Stipitipellis fertile, with terminal cells inflated. Clamp connections absent.

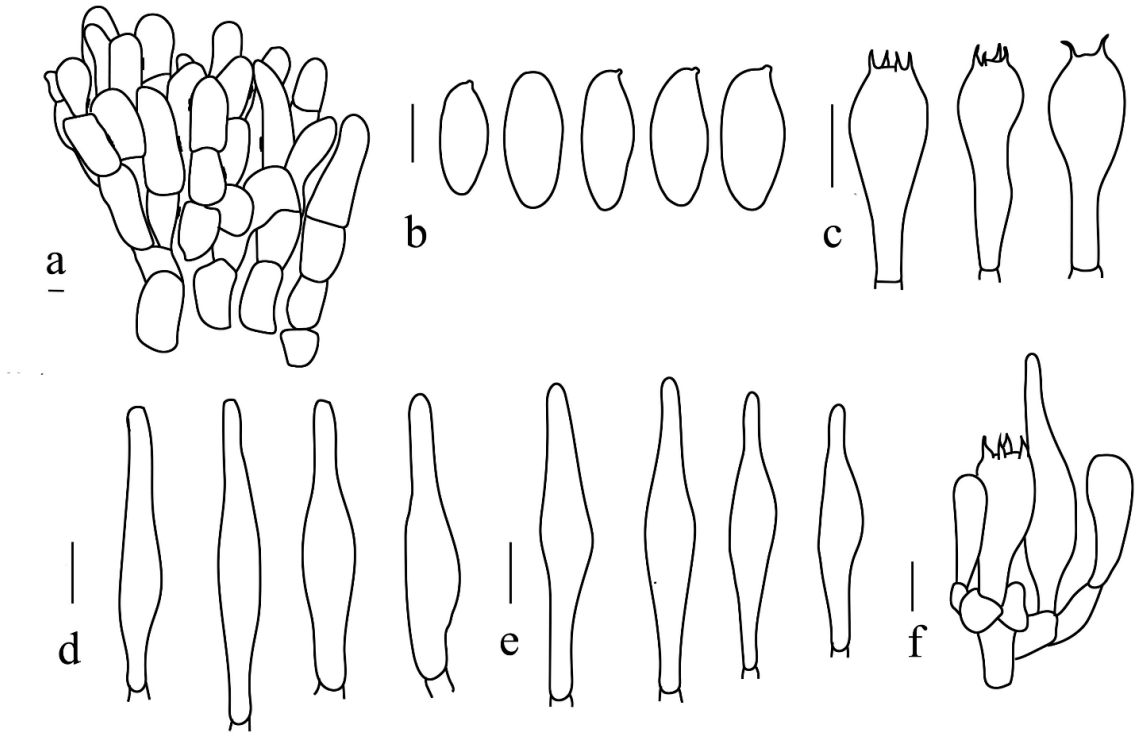


Figure 23 – *Hortiboletus sinorubellus*. a Pileipellis. b Basidiospores. c Basidia. d Pleurocystidia. e Cheilocystidia. f Basidium, pleurocystidium and basidioles. Scale bars: a, b = 5 μm, c–f = 10 μm.

Habitat – Solitary in the coniferous forest or road side.

Known distribution – Henan Province, China (this study).

Materials examined – China, Henan Province, Zhumadian City, Biyang County, Tongshan lake, 11 July 2021, W3044 (HMJAU68177, holotype). Baiyun Moutains, 09 July 2021, W3075 (HMJAU68178), W3076 (HMJAU68179), W3100 (HMJAU68180); Jiangsu Province, Nanjing City, Zijin mountain, 10 September 2021, W3369 (HMJAU68181).

Notes – Morphologically, *Ho. sinorubellus* share some resembles with *Ho. coccyginus* (Thiers) C.F. Schwarz, N. Siegel & J.L. Frank, *Ho. kohistanensis*, and *Ho. subpaludosus*. However, pileus of *Ho. coccyginus* not cracked when mature, context of pileus without discoloration when injured, larger basidiospores can up to 17 μm long, gangly hyphae of pileipellis; *Ho. Kohistanensis*. A. Naseer, S.Sarwar & A.N. Khalid can be distinguished by hymenophores staining brown when injured and ellipsoid basidiospores; *Ho. rubellus* can be characterized by larger basidiospores, longer basidia can up to 53 μm, shorter cystidia and terminated cells of pileipellis broad range from 19–20 μm; *Ho. subpaludosus* differs in having relatively larger basidiospores and narrower hyphae of pileipellis (Peintner et al. 2003, Naseer et al. 2019, Frank et al. 2020).

Phylogenetically, *Ho. sinorubellus* is sister with "*Hortiboletus* sp. N.K. Zeng3152 (FHMU2113)" that still not be identified.

Hortiboletus tomentosus L. Fan, N. Mao & T.Y. Zhao Figs 13i–j, m, 24

Basidioma small. Pileus ca. 2.9 cm in diam., applanate to plano-convex; surface dry, tomentose, sometimes distinctly cracked, yellowish brown (5D8) to orange red (8A8–8C8), darker at center; context 0.4 cm thick, light yellow (1A4), weakly bluing when injured. Hymenophore decurrent but slightly depressed around stipe; surface greenish yellow (1A8) to yellowish brown (5D8), staining blue when injured; pores angular; tubes concolorous with pore surfaces, ca. 0.7 cm long, weakly bluing when injured. Stipe 4.6 cm long, 0.5 cm wide, subcylindrical, enlarged at base; surface deep orange (6A8), longitudinally fibrillose; context concolorous with stipe surface, without discoloration when cut. Basal mycelium yellow.

Basidiospores (8) 9.8–10.4 (13.5) × (4.2) 4.9–5.1 (6.3) μm, Q = (1.67) 2.0–2.1 (2.5), Q_m = 2.03 ± 0.17, ellipsoid to subfusiform in side view with slight suprahilar depression, yellowish brown, dextrinoid, smooth under light microscope. Basidia 23.2–41 × 8.9–12 μm, clavate, hyaline to yellowish, 2-,4-spored, thin-walled. Hymenophoral trama intermediate in phylloporoid and boletoid, consisting of filamentous hyphae, 4–15 μm wide. Pleurocystidia 36–72 × 7–10.2 μm, subfusiform, hyaline in 5% KOH, thin-walled. Cheilocystidia 28–59 × 7–9.8 μm, similar to pleurocystidia in shape and color. Pileipellis a palisadoderm, consisting of 3–5 concatenated, vertically arranged, yellowish brown, slightly or distinctly broadened cells with erratically incrusted, 5.5–13 μm wide; terminal cells subfusiform, apex acute. Stipitipellis sterile. Clamp connections absent.

Habitat – Solitary in the coniferous forest.

Known distribution – Henan, Shanxi and Shaanxi Province, China (this study).

Materials examined – China, Henan Province, Zhumadian City, Biyang County, Madao forest farm, Yihe village, 12 July 2021, W3110 (HMJAU68173, holotype). Shaanxi Province, Qinling mountains, 31 July, 2022, QB10274 (HMJAU68174), QB10281 (HMJAU68175); same location, 1 August, 2022, QB10325 (HMJAU68176).

Notes – Morphologically, *Ho. tomentosus* shares some characteristics with *Ho.kohistanensis*, *Ho. campestris* (A.H. Sm. & Thiers) Biketova & Wasser and *Ho. subpaludosus* (W.F. Chiu) Xue T. Zhu & Zhu L. Yang. However, *Ho. kohistanensis* A. Naseer, S. Sarwar & A.N. Khalid, *Ho. rubellus* (Krombh.) Simonini, Vizzini & Gelardi can be distinguished by browning of hymenophores when injured and broader terminated cells of the pileipellis; *Ho. campestris* is different *Ho. tomentosus* from its larger and amyloid basidiospores; *Ho. subpaludosus* differs from *Ho. tomentosus* in its context distinctly bluing when injured, subfusiform to slender amygdaliform basidiospores and smaller Q value (Smith & Thiers 1971, Wu et al. 2016, Naseer et al. 2019).

Hortiboletus arduinus N.K. Zeng, H.J. Xie & W.F. Lin Figs 14j–k, 25

Basidioma small. Pileus 3.2–4.5 cm in diam., subhemispherical or slightly depressed at center; surface dry, velvety, distinctly cracked at mature, reddish brown to currant red (9D8–10B8); context 0.4–0.5 cm thick, white (1A1) to yellowish white (1A2), staining blue when injured. Hymenophore decurrent to depressed around apex of stipe; surface light yellow (2A5), bluish when bruised; pores irregular, 1.5-2/mm; tubes 0.6–0.7 cm long, concolorous with pore surface, turning blue when injured. Stipe 2.5–7 × 0.4–0.5 cm, subcylindrical and taper at base, madder red (9A7) at upper partition when young, with pastel red (9A4) tinge at mature, light yellow (2A5) downwards; staining blue when bruised; context light yellow (2A4–3A5), turning blue when injured. Basal mycelium yellow.

Basidiospores (50/2/2) (10) 11–11.3 (12.8) × (4) 4.3–4.5 (5.3) μm, Q = (2.2) 2.46–2.57 (2.86), Q_m = 2.52 ± 0.2, fusiform with slight suprahilar depression in side view, brownish yellow, smooth in light microscope. Basidia 31.2–38 × 10–13 μm, clavate, hyaline in 5% KOH, thin-walled, 2-,4-spored. Hymenophoral trama intermediate in phylloporoid and boletoid, consisting of filamentous hyphae 4–14 μm wide. Pleurocystidia 52–95 × 9–14 μm, fusiform-ventricose, hyaline to brownish in 5% KOH, thin-walled. Cheilocystidia 43–85 × 7–14 μm, similar to pleurocystidia in shape and color. Pileipellis an interwoven trichodermium, consisting of 2–5 yellowish brown, more or less broadened cells with erratically incrusted, terminal cells subfusiform, 5.2–17.8 μm wide. Stipitipellis fertile, caluobasidia yellowish, 2-,4-spored. Clamp connections absent.

Habitat – Solitary on *Quercus* sp. forest or coniferous forest.

Known distribution – Zhejiang and Henan Province, China (this study).

Materials examined – China, Henan Province, Zhumadian City, Biyang County, Madao forest farm Yihe village, 12 July 2021, W3104 (HMJAU68182), W3105 (HMJAU68183).

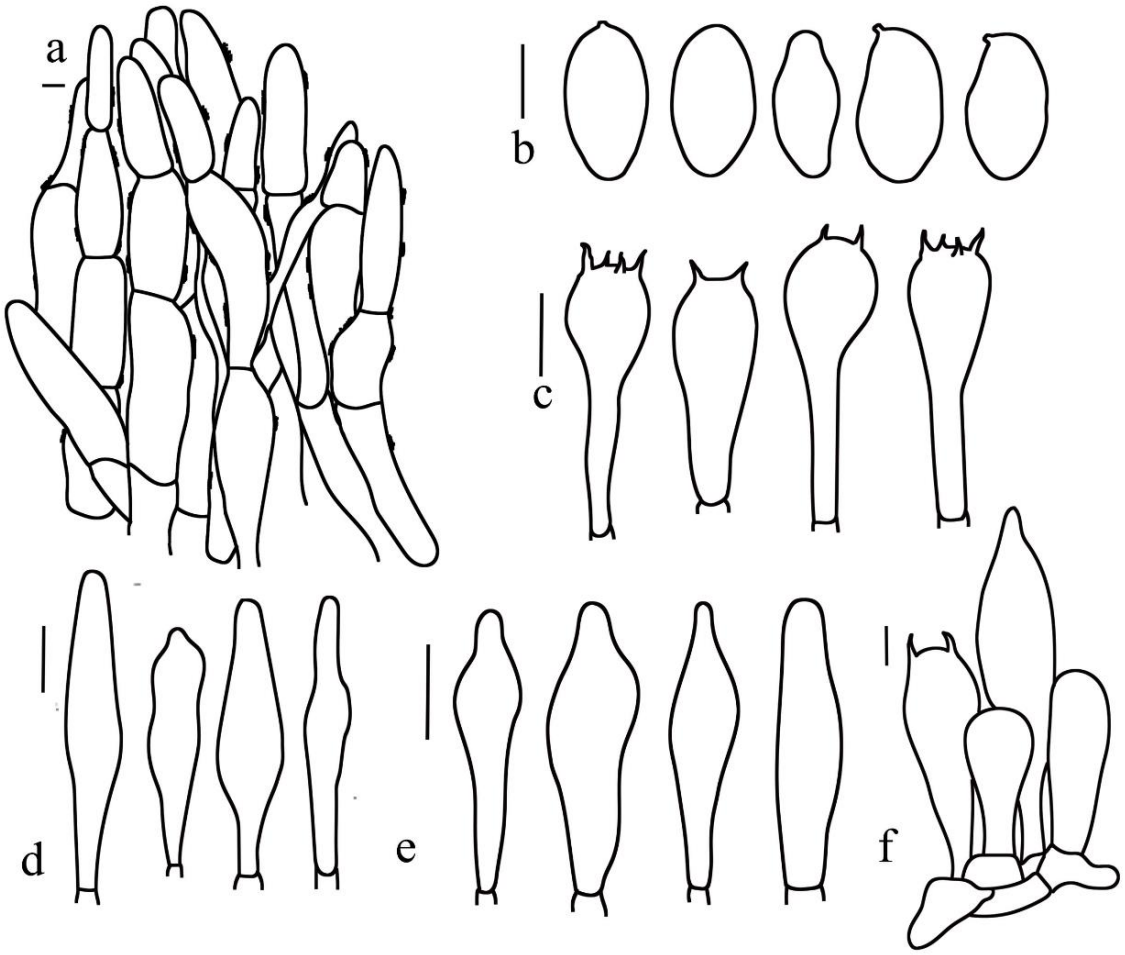


Figure 24 – *Hortiboletus tomentosus*. a Pileipellis. b Basidiospores. c Basidia. d Pleurocystidia. e Cheilocystidia. f Basidium, pleurocystidium and basidioles. Scale bars: a, b, f = 5 μm, c–e = 10 μm.

Notes – *Hortiboletus arduinus* was originally described from Zhejiang Province, China, and now was reported in the Henan Province. Phylogenetically, *Ho. arduinus* cluster with two sequences of unidentified strains and one sequence named "*Boletus rubellus*" which could not be accepted.

Morphologically, *Ho. arduinus* seems like *Ho. bubalinus* (Oolbekk. & Duin) L. Albert & Dima, *Ho*. *coccyginus*, and *Ho*. *rubellus* to an extent. However, *Ho. bubalinus* differs in that its stipe context is pink-red and does not intensely bluing upon exposure. Additionally, it has broader cells of pileipellis; *Ho*. *coccyginus* can be distinguished by its rose-red pileus not cracked, context without discoloration when injured and larger basidiospores; *Ho*. *rubellus* is different from *Ho. arduinus* in carrot-red context and larger basidiospores (Oolbekkink 1991, Peintner et al. 2003, Frank et al. 2020).

Boletellus putuoensis N.K. Zeng, Yi Li, Chang Xu, Xu Zhang & J.R. Wang Figs 14l–m, 26

Baisidioma medium. Pileus 4.1–6.1 cm in diam., hemispherical to applanate; surface dirty yellow (4C3) to olive brown (4E8), dry, tomentose or cracked at mature, context 0.3–0.6 cm thick, white (1A1), staining blue when injured. Hymenophore sinuate; surface greenish yellow (1A8) or deep green (1D8) or greyish green (1C6), staining blue when bruised; pores round, 0.5–1/mm; tubes 1.2–1.7 cm long, concolorous with pores surface, turning blue when exposure. Stipe 4.6–5.9 cm long, 0.6 cm wide, central, subcylindrical, curve, solid; surface concolorous with hymenophoral surface or geranium (11B7) at apex, geranium (11B7) downwards; with densely black dots, sometimes also covered with pale yellow pruinose; context firm, concolorous with stipe surface, changing blue when injured. Basal mycelium dirty white or greyish yellow.

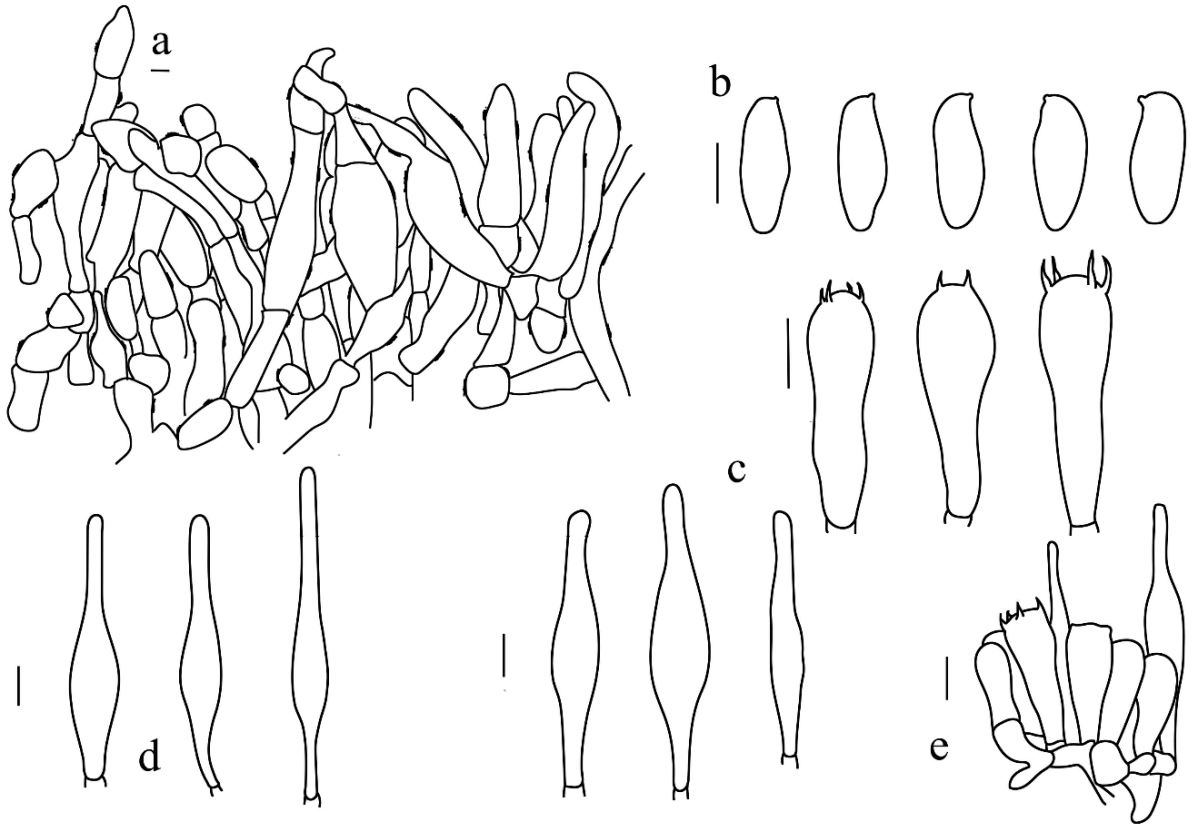


Figure 25 – *Hortiboletus arduinus.* a Pileipellis. b Basidiospores. c Basidia. d Pleurocystidia. e Cheilocystidia. f Basidia, pleurocystidia and basidioles. Scale bars: a, b = 5 μm, c–f = 10 μm.

Basidiospores (60/2/2) 10.4–10.8 (12.5) × (5.80) 7–7.3 (8) μm, Q = (1.27) 1.45–1.50 (1.74), Q_m = 1.48± 0.1, broadly ellipsoid and inequilateral in side view with slightly suprahilar depression, distinctly longitudinally ridged, brown in 5% KOH. Basidia 20–35 × 11.9–16 μm, broadly clavate to lacrymoid, hyaline in 5% KOH, 2-,4-spored, thin-walled. Hymenophoral trama intermediate in phylloporoid and boletoid, consisting of filamentous hyphae, 4–17.2 μm wide. Pleurocystidia 34.5–80 ×

10–25 μm, lageniform to subfusiform, hyaline to brownish in 5% KOH, thin-walled. Cheilocystidia 25–36 × 8–14.2 μm, lageniform or broadly clavate with median constriction, hyaline to brownish in 5% KOH. Pileipellis a trichodermium, composed of inflated or subcylindrical cells, 7.5–20 μm wide, terminal cells subfusoid. Clamp connections absent.

Habitat – Solitary in the broadleaf forest dominated by *Quercus* sp.

Known distribution – Zhejiang, Hainan, Guangdong and Jiangsu Province, China (this study).

Materials examined – China, Jiangsu Province, Nanjing City, Zijin Mountains, 10 September 2021, 118°51'48.24" E, 32°3'36.97" N, alt. 100 m, W3380 (HMJAU68184); 118°51'48.24" E, 32°3'36.97" N, alt. 100 m, W3383 (HMJAU68185).

Notes – *Boletellus putuoensis* was originally described from Zhejiang Province, China, and later reported from Guangdong and Hainan Provinces. Now, it was also distributed in Jiangsu Province, China. Morphologically, *Bo. putuoensis* is similar to *Bo. brunoflavus* Z.J. Lin, X.X. Huang, Y.S. Liang & L.H. Qiu and *Bo. sinochrysenteroides* N.K. Zeng, R. Xue & Kuan Zhao. However, *Bo. brunoflavus* can be distinguished by its larger basidiospores, indistinct ornamentations of basidiospores, and shorter pleurocystidia; *Bo. sinochrysenteroides* differs from *Bo. putuoensis* from its yellow stipe context, and larger basidiospores can measure up to 15.5 μm in length (Lin et al. 2022, Xue et al. 2023).

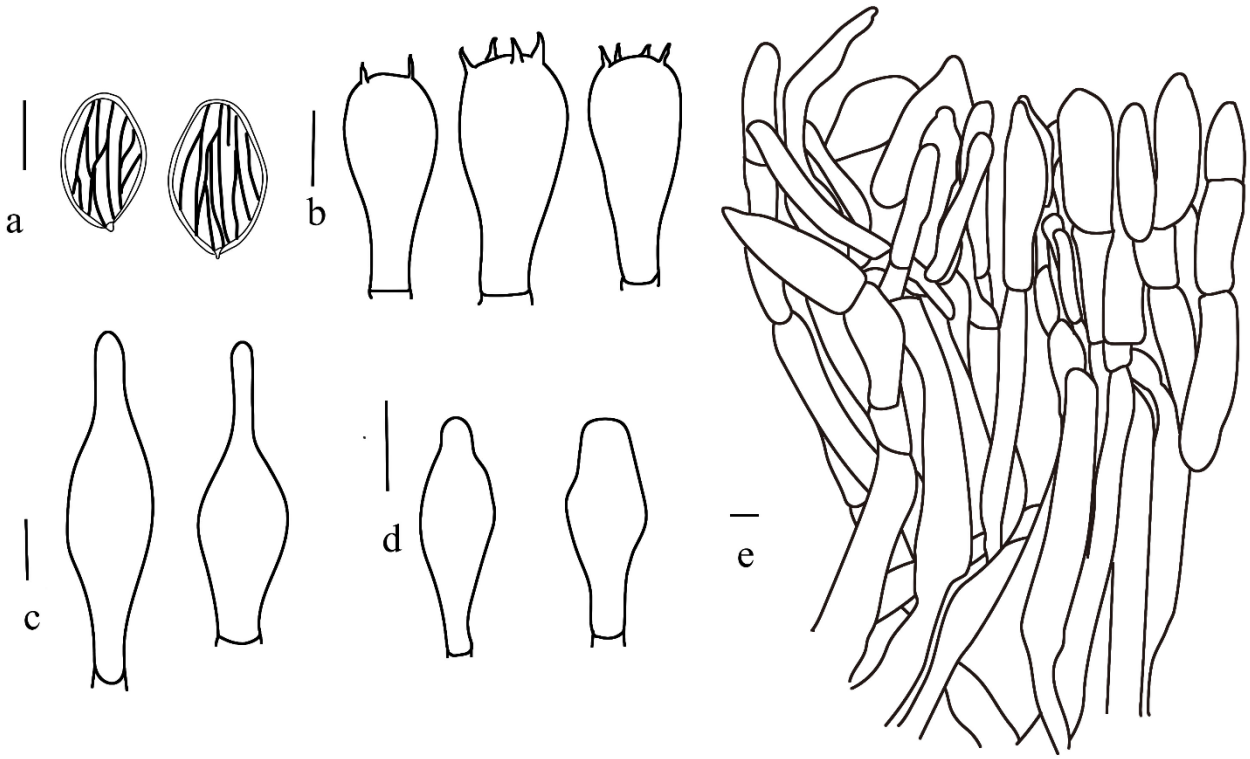


Figure 26 – *Boletellus putuoensis*. a Basidiospores. b Basidia. c Pleurocystidia. d Cheilocystidia. e Pileipellis. Scale bars: a = 5 μm, b–e = 10 μm.

Zangia olivaceobrunnea Yan C. Li & Zhu L. Yang Figs 14d–e, 27

Basidiomata small. Pileus 3–4.6 cm in diam., hemispherical, with narrowly sterile margin, surface brownish red (8C8), viscid when wet, unchanging color when injured; context firm, ca. 0.6 cm thick, yellowish white (1A2), unchanging color when injured. Hymenophore adnexed, surface white (1A1), without color change when injured; pores round; tubes ca.1.5 cm long, white (1A1), unchanging color when injured. Stipe 7.5–8 × 1.4–1.7 cm, obclavate, enlarged downwards, primrose yellow (1A6), but chrome-yellow at base, turning blue asymmetrically when bruised; surface covered with pink-red squamulose; context primrose yellow (1A6) and chrome-yellow at base, slightly asymmetrically bluish when injured. Basal mycelium golden yellow or chrome-yellow.

Basidiospores (11) 12–12.5 (14) × (4.1) 5–5.2 (5.8) μm, Q = (2.1) 2.38–2.5 (3.2), Q_m = 2.44 ± 0.18, elongated ellipsoid to subcylindrical and inequilateral in side view with slight suprahilar depression, pale yellow 5% KOH. Basidia 29–43 × 10.8–13 μm, clavate, 2-,4-spored, hyaline in 5% KOH. Hymenophoral trama boletoid, consist of filamentous hyphae, 3–12.2 μm wide. Pleurocystidia 45–64 × 7.3–11 μm, fusoid-ventricose and usually with long peak, smooth, hyaline in 5% KOH. Cheilocystidia 32–54 × 6–11 μm, subfusiform or ventricose, thin-walled, hyaline in 5% KOH. Pileipellis an entangled hyphoepithelium, outer layer consisting of subcylindrical and hyaline to pale brown hyphae with 3–8 μm wide; inner layer composed of inflated concatenated cells ranged from 19–44 × 11–20 μm. Stipitipellis fertile, caulobasidia 23–35 × 7–9 μm, 2-, 4-spored, pale yellow in 5% KOH. Clamp connections absent in all tissues.

Habitat – Scattered in coniferous forest dominated by *Pinus yunnanensis*.

Known distribution – Yunnan Province, China (this study).

Material examined – China, Yunnan Province, Qujin city, 4 October 2021, LEI–607 (HMJAU68186).

Notes – The micromorphological characteristics of the collections we observed showed some differences in pileipellis descriptions compared to Li et al. (2011), which the hyphae were distinctly suberected and the layer gelatinous. Morphologically, *Zangia olivaceobrunnea* resembles *Z. chlorinosma* (Wolfe et Bougher) Yan C. Li & Zhu L. Yang and *Z. erythrocephala* Yan C. Li & Zhu L. Yang to an extent. However, Z. *chlorinosma* can be distinguished by its pileus without any reddish tinge, and broader basidiospores that can measure up to 7 μm; *Z. erythrocephala* differs from *Z. olivaceobrunnea* in the pale margin of pileus, larger basidiospores that can measure up to 16.5 μm in length and pileipellis as an ixohyphoepithelium (Li et al. 2011). Phylogenetically. *Z. olivaceobrunnea* is sister to *Z. citrina* Yan C. Li & Zhu L. Yang. However, *Z. citrina* differs from *Z. olivaceobrunnea* in pileus context asymmetrically bluish when injured, relatively larger basidiospores and ixohyphoepithelium pileus (Li et al. 2011).

Royoungia reticulata Yan C. Li & Zhu L. Yang Figs 13f–g, 28

Basidioma small. Pileus ca. 3.6 cm in diam., subhemispherical or plano-convex, grayish green (29C6), surface dry, fibrillose; context yellowish white (2A2), without discoloration when injured. Hymenophore depressed around apex of stipe; surface pinkish red (9A2), unchanging color when injured; pores nearly round to angular, ca. 4/mm; tubes 0.7 cm long, concolorous with hymenophoral surface, without discoloration when injured. Stipe 6 × 0.9 cm, obclavate, enlarged at base; surface nearly glabrous, without discoloration when bruised, context light yellow (1A4), chrome-yellow at base, without color change when cut. Basal mycelium golden-yellow.

Basidiospores (39/1/1) (10.1) 11.9–12.5 (13.9) × (4.5) 5.2–5.4 (5.9) μm, Q = (1.9) 2.26–2.36 (2.67), Q_m = 2.31 ± 0.16, elongated ellipsoid to fusoid and inequilateral in side view with slight suprahilar depression, smooth, pale yellow to yellowish brownish in 5% KOH. Basidia 27–43 × 10–15.2 μm, clavate, hyaline in 5% KOH, thin-walled, 2-, 4-spored. Hymenophoral trama boletoid, consisting of 4–14 μm wide filamentous hyphae. Pleurocystidia scarcely, 35–60 × 6–7.2 μm, narrowly fusiform, hyaline in 5% KOH, thin-walled. Cheilocystidia not observed. Pileipellis an interwoven trichodermium, composed of 3.4–7.8 μm wide subcylindrical hyphae, brownish to brown in 5% KOH. Stipitipellis fertile, caulobasidia yellowish. Clamp connections absent in all tissues.

Habit – Scattered in the broadleaf forest dominated by Fagaceae spp.

Known distribution – Yunnan Province, China (this study).

Material examined – China, Yunnan Province, Qujin city, 6 October 2022, LEI-647 (HMJAU68187).

Notes – Morphologically and phylogenetically, *R. reticulata* is closely related to *R. grisea* Yan C. Li & Zhu L. Yang. However, the latter can be distinguished by larger basidiospores and a hyphoepithelium pileus (Wu et al. 2016). Our specimens show a nearly glabrous stipe, which differs from the other specimens collected and described by Li & Yang (2021), meaning ornamentations of the stipe in this species are not stable and vary significantly.

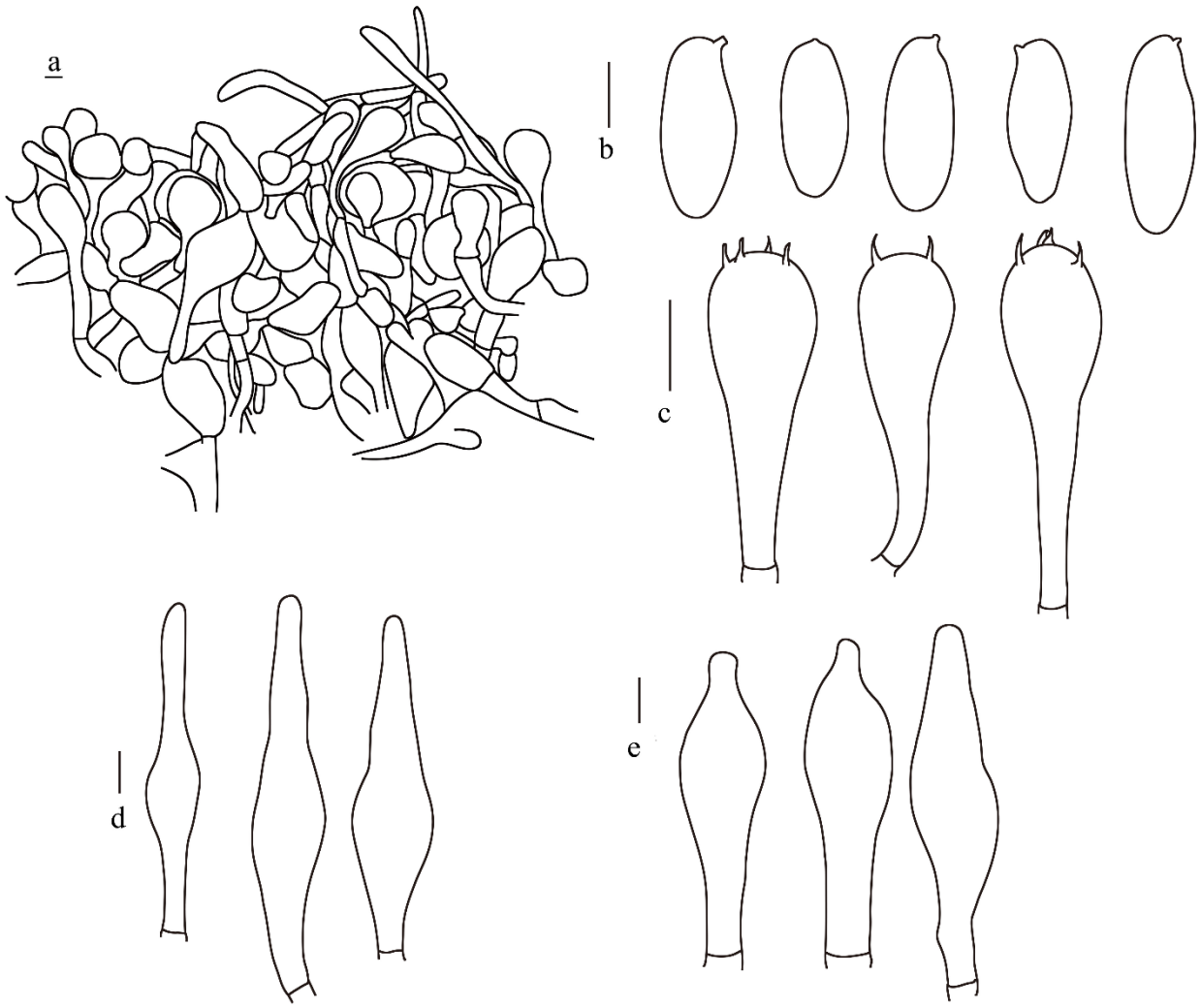


Figure 27 – *Zangia olivaceobrunnea.* a Pileipellis. b Basidiospores. c Basidia. d Pleurocystidia. e Cheilocystidia. Scale bars: a, b = 5 μm, c–e = 10 μm.

Tylopilus violaceobrunneus Yan C. Li & Zhu L. Yang Figs 14n, 29

Basidioma small to medium. Pileus 3–7.1 cm in diam., hemispherical or depress at center when mature, surface dry, tomentose, brownish orange to brownish yellow (5C5–5C7), sometimes margin asymmetrically greyish red (10B5), changing to brown when bruised; context 0.9–1.3 cm thick, white (1A1), unchanging color when exposed to air. Hymenophore adnexed; surface white (1A1), without discoloration when injured; pores nearly round, 3/mm; tubes can up to 0.5 cm long, concolorous with hymenophoral surface, unchanging color when injured. Stipe up to 8.4 cm long, 1.2 cm wide, subfusiform, pale red (10A3) at apex, gradually deepen into brownish red (10C6) at middle, then fading to dull red (10B4) downwards, almost white (1A1) at base, glutinous; covered with distinct reticulations at apex; context white (1A1), without discoloration when injured. Basal mycelium white.

Basidiospores (50/2/1) (8) 9.7–10.2 (12) × (3) 3.4–3.6 (4.9) μm, Q = (2.27) 2.8–3 (3.67), Q_m = 2.89 ± 0.3, fusoid and inequilateral in side view with slight suprahilar depression, smooth, pale yellow in 5% KOH. Basidia 21–30.5 × 8–10 μm, clavate, hyaline in 5% KOH, smooth, thin-walled, 2-,4-spored. Hymenophoral trama boletoid, composed of 2.8–9.5 μm wide filamentous hyphae, hyaline in 5% KOH. Cheilocystidia 20–40 × 5–8.2 μm, subfusiform-ventricose, hyaline in 5% KOH, but usually wine-red in 1% Congo Red solution, thin-walled. Pleurocystidia 30–47 × 6–11 μm, similar to cheilocystidia in shape, hyaline in 5% KOH, but usually wine-red in 1% Congo Red solution. Pileipellis an interwoven trichodermium, consisting of 4–7.3 μm wide subcylindrical hyphae with sometimes terminal cells obtuse, hyaline to brown in 5% KOH. Stipitipellis fertile, caulobasidia brown. Clamp connections absent in all tissues.

Habit – Scattered in the broadleaf forest dominated by *Quercus* sp.

Known distribution –Shandong, Yunnan and Henan Province, China (this study).

Material examined – China, Henan Province, Zhumadian city, Biyang county, 113°33'15.01" E, 32°52'6.73" N, alt. 415 m, 10 July 2021, W3096 (HMJAU68188).

Notes – *Tylopilus violaceobrunneus* was originally described from Shandong Province, China, and then reported from Yunnan Province. In the present study, it has also been found distributed in Henan Province, China. Morphologically, *Tylopilus violaceobrunneus* is similar to *Ty. albopurpureus* Yan C. Li & Zhu L. Yang and *Ty. atripurpureus* (Corner) E. Horak, Malay Fores Rec in its purple tingle on the stipe. However, brown pileus and reticulations covered on the apex of stipe of *T. violaceobrunneus* can easily help distinguish it from *Ty. albopurpureus* and *Ty. atripurpureus* (Li & Yang 2021). *Tylopilus himalayanus* D. Chakr., K. Das & Vizzini is different from context turning to red when injured, hymenophore yellowish when young, stipe nearly glabrous, basidiospores larger and the pileipellis a palisadoderm (Chakraborty et al. 2018). *Tylopilus olivaceobrunneus* Yan C. Li & Zhu L. Yang differs from *Ty. violaceobrunneus* in larger pores, a glabrous stipe, larger basidia (up to 58 μm) and wider hyphae of the pileipellis (Li & Yang 2021).

Phylogenetically, *Ty. violaceobrunneus* sister with the clade of *Ty. felleus* (Bull.) P. Karst., *Ty. griseiolivaceus* Angelini, Gelardi, Costanzo & Vizzini and *Ty. jiangxiensis* Yan C. Li & Zhu L. Yang. However, *Ty. felleus* is distinguished from other species by its enlarged stipe base and distinct larger basidiospores; *Ty. griseiolivaceus* differs from *Ty. violaceobrunneus* in distinctly fibrillose pileus when mature, glabrous stipe surface, and smaller basidiospores; *Ty. jiangxiensis* differs in very small to small basidioma, rufescent discoloration when injured, glabrous stipe surface, and a trichodermium pileipellis consisting of collapse hyphae (Gelardi et al. 2019, Zhao et al. 2020, Li & Yang 2021).

Suillellus yunnanensis G. Wu & Zhu L. Yang Figs 14h–i, 30

Basidioma medium. Pileus up to 7.5 cm diam., hemispherical, with narrow appendiculate margin; surface Persian orange (6A7), dry, tomentose, context up to 1 cm thick, staining blue when injured. Hymenophore sinuate; surface brownish orange (7C8), turning blue when bruised; pores round; tubes up to 0.8 cm long, bluing when injured. Stipe 11 cm long, 1 cm wide, central, subcylindrical; surface orange red (8A8) at apex, brownish red (9C8) downwards, dull red (10C5) at base, staining blue when bruised; covered with reticulations, especially at 2/3 upper partition, lower 1/3 partition velvety; context staining blue when injured. Basal mycelium dirty white to brown.

Basidiospores (11.2) 12.6–13.0 (14.8) × (4.8) 5.1–5.2 (5.8) μm, Q = (2.07) 2.5–2.6 (2.79), Q_m = 2.5 ± 0.16, subfusiform in side view with indistinctive suprahilar depression, brownish yellow in 5% KOH, smooth, thin-walled. Basidia 21–30 × 9.2–11 μm, clavate or broadly clavate, hyaline in 5% KOH, 2-, 4-spored. Cheilocystidia 27–46 × 6.2–11 μm, narrowly fusiform, hyaline to yellowish in 5% KOH. Pleurocystidia 32–64 × 7–12.8 μm, similar to cheilocystidia in shape and color. Hymenophoral trama boletoid, consisting of filamentous hyphae, 3.5–8.2 μm wide. Pileipellis an interwoven trichodermium, composed of brownish yellow and cylindrical hyphae, sometimes slightly inflated, 4–9 μm wide, smooth, thin-walled. Stipitipellis fertile, caulobasidia 26–34.5 × 9.5–11.5 μm, yellowish in 5% KOH. Hyphae of the flesh in the stipe base amyloid in Melzer's reagent. Clamp connections absent.

Habitat – Solitary in the *Quercus mongolica* forest.

Known distribution –Southwest and Northeast China (this study).

Material examined – China, Jilin Province, Jian city, Wunvfeng National Forest Park, alt. 900 m, 9 August 2019, Yong-Lan Tuo 188 (HMJAU68189).

Notes – *Suillellus yunnanensis* was originally described from Yunnan Province, China. Herein, this species was found in Jilin Province, China, suggesting this species has a wider distribution than expected. Phylogenetically, *Suillellus yunnanensis* is related to *Su. amygdalinus* (Thiers) Vizzini, Simonini & Gelardi, but it differs from distinct reticulations that covered nearly whole stipe (Thiers 1975, Vizzini et al. 2014).

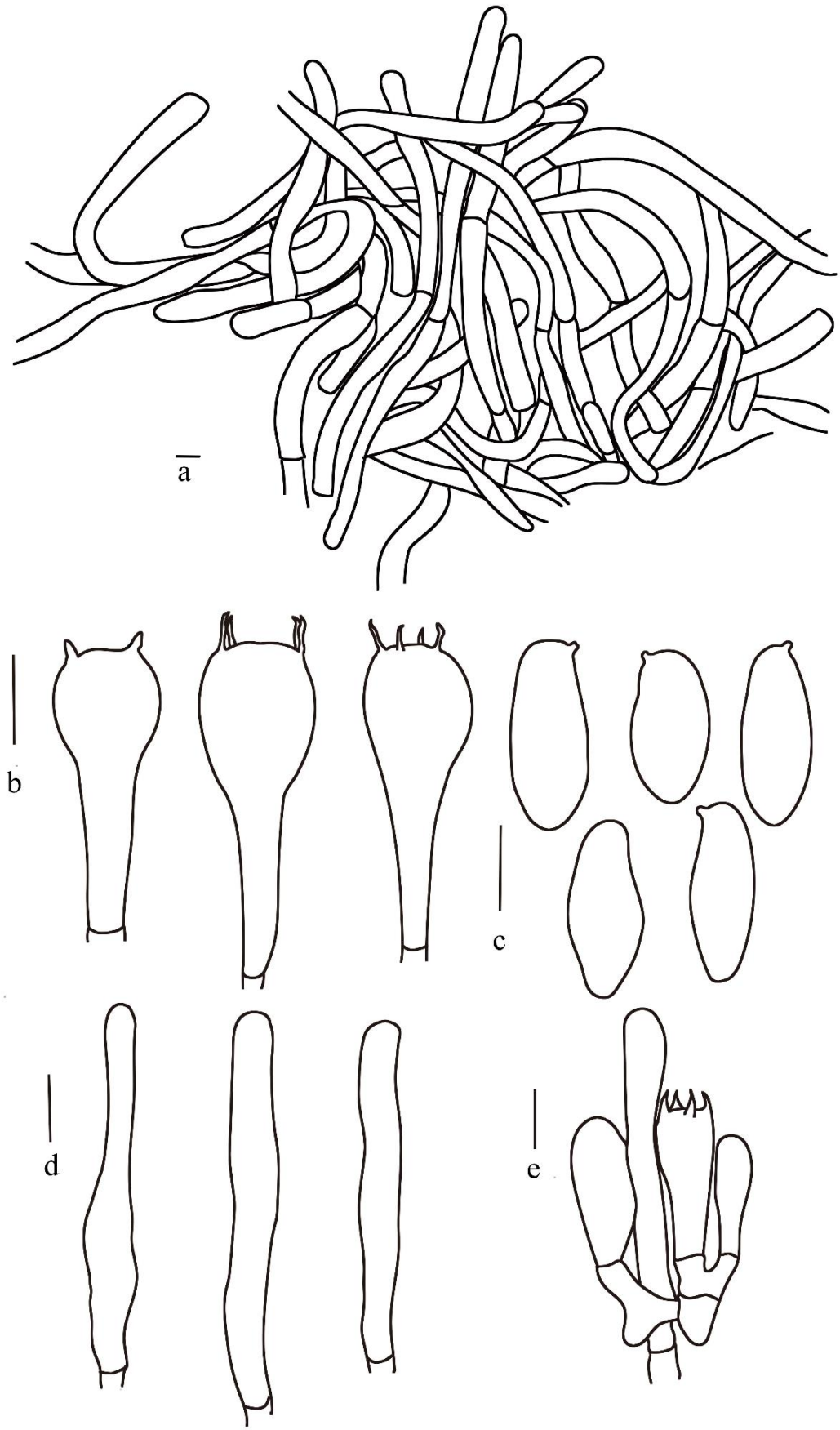


Figure 28 – *Royoungia reticulata.* a Pileipellis. b Basidiospores. c Basidia. d Pleurocystidia. e Basidium, pleurocystidium and basidioles. Scale bars: a, c = 5 μm, b, d, f = 10 μm.

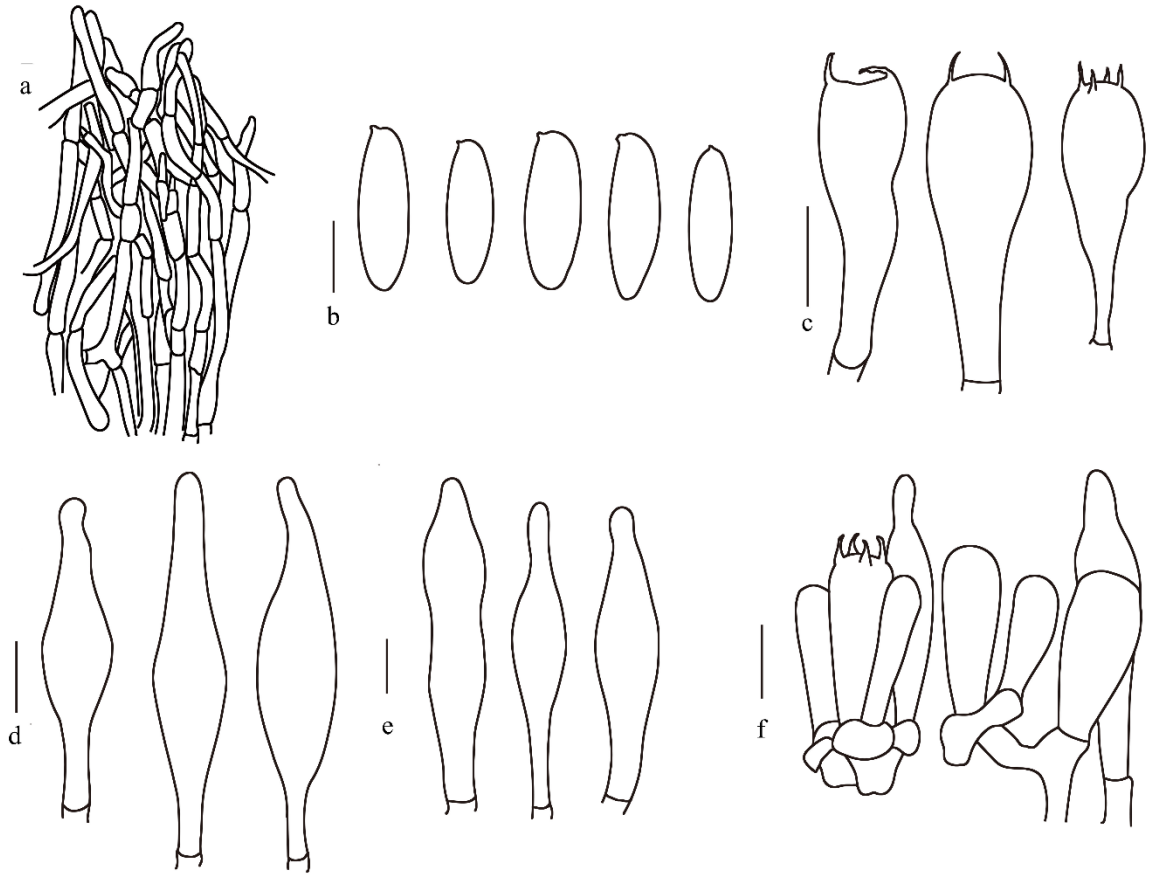


Figure 29 – *Tylopilus violaceobrunneus.* a Pileipellis. b Basidiospores. c Basidia. d Pleurocystidia. e Basidium, pleurocystidia and basidioles. Scale bars: a, b, d, e = 5 μm, c, f = 10 μm.

Morphologically, *Su. yunnanensis* shares some resemble with *Su. subamygdalinus* Kuan Zhao & Zhu L. Yang, and *Su. pinophilus* G. Wu, Hai J. Li, Zhu L. Yang. However, Su. *pinophilus* is different *Su. yunnanensis* from indistinct discoloration on the stipe and smaller basidiospores; *Su. subamygdalinus* differs from *Su. yunnanensis* in its surface with red tingle, white basal mycelium, and lager basidiospores and usually found in the forests of *Betula, Picea* and *Salix* in subalpine areas (Wu et al. 2016, 2023).

Neoboletus luridiceps (Murrill) Yang Wang, B. Zhang & Y. Li, comb. nov.

MycoBank number: MB850844; Facesoffungi number: FoF16011

Basionym – *Boletus luridiceps* Murrill, in Florida, Lloydia 8: 289 (1946)

Notes – *Boletus luridiceps* was proposed by Murill (1945) and has not been reported up to now. This species has brown to yellowish brown pileus, nearly dark but turning to dark-fulvous hymenophores at mature, context turning blue upon exposure, and glabrous stipe with red punctations. Based on these characteristics that comply with the definition of *Neoboletus* Gelardi, Simonini & Vizzini, we transfer *Boletus luridiceps* to *Neoboletus luridiceps* as a new combination.

Neoboletus austrinus (Singer) Yang Wang, B. Zhang & Y. Li, comb. nov.

MycoBank number: MB850845; Facesoffungi number: FoF16012

Basionym – *Boletus austrinus* Singer, in Mycologia, 37:797–799 (1945)

Notes – *Boletus austrinus* was proposed by Singer (1945) and then transferred to *Suillellus* by Murill (1948). This species has brownish purple pileus, red pores, purplish brown or vinaceous furfuraceous squama covered over yellow apex of the stipe with downwards vinaceous strigose at base and yellow context bluish upon exposure. All of these characteristics correspond to the *Neoboletus*. Based on this, we transfer *Boletus austrinus* to *Neoboletus austrinus* as a new combination.

Cyanoboletus gabretae (Pilát) Yang Wang, B. Zhang & Y. Li, comb. nov.

MycoBank number: MB850846; Facesoffungi number: FoF16013

Basionym – *Boletus gabretae* Pilát, in Ceská Mykologie, 22:167 (1968)

Notes – *Boletus gabretae* was proposed by Pilát (1968) and then reported by Kallio (1984) in Finland. It is noticeable by mycologists in conspicuous deep blue color when basidiomes were handled or cut. It was transferred to *Suillellus* by Blanco-Dios (2015). However, according to the original description, the hyphae of stipe context are not amyloid which does not accord with the definition of *Suillellus*. Based on its instantly and intensely deep bluish upon exposure and yellow hymenophore, we transfer it to *Cyanoboletus gabretae* as a new combination. Although, the reticulations of stipe were rarely in the *Cyanoboletus* and usually present in the *Butyriboletus*, *Cyanoboletus poikilochromus* (Pöder, Cetto & Zuccher.) M. Carbone, D. Puddu & P. Alvarado still share the distinct reticulations, but *Butyriboletus* with no intensely deep blue when injured.

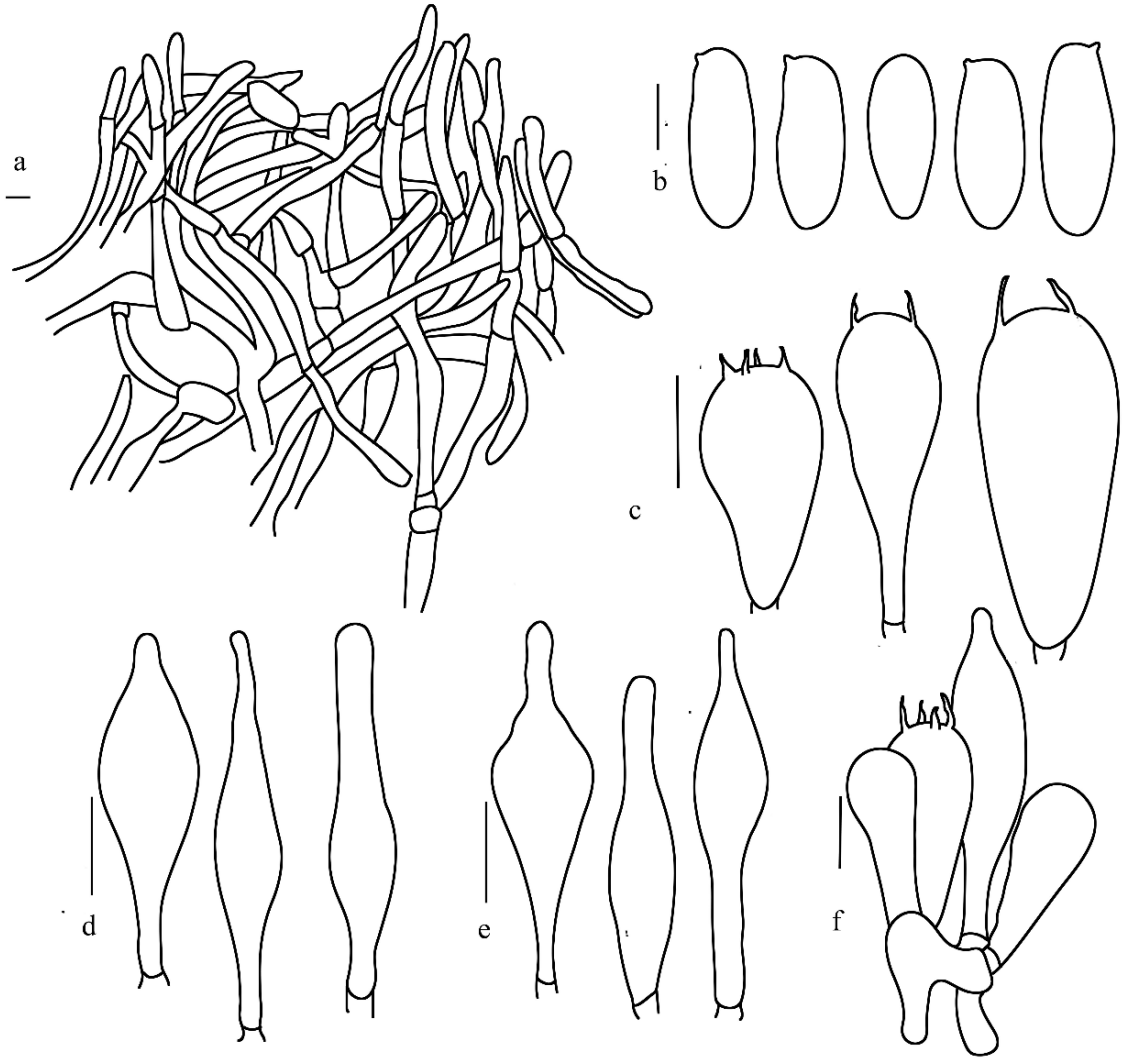


Figure 30 – *Suillellus yunnanensis.* a Pileipellis. b Basidiospores. c Basidia. d Pleurocystidia. e Cheilocystidia. f Basidium, pleurocystidium and basidioles. Scale bars: a, b = 5 μm, c–f = 10 μm.

Neoboletus subvelutipes (Peck) Yang Wang, B. Zhang & Y. Li, comb. nov.

MycoBank number: MB850847; Facesoffungi number: FoF16014

Basionym – *Boletus subvelutipes* Peck, in Bulletin of the New York State Museum, 2:142 (1889)

Notes – *Boletus subvelutipes* was proposed by Peck (1889), and Smith & Thiers (1971) redescribed the species. Meanwhile, Murrill (1948) transfered it to *Suillellus*. However, “all hyphae

nonamyloid" do not comply with the definition of *Suillellus*. Based on its tawny to cinnamon pileus, red pores, "stipe surface evenly furfuraceous to punctate" without reticulations, red strigosity at the base and basidiomes turning blue when injured, we transfer it to *Neoboletus subvelutipes* as a new combination.

DISCUSSION

Our study reassessed the relationships of *Exsudoporus* and *Butyriboletus*, in contrast to the findings of Biketova et al. (2022), Farid et al. (2021), and Bozok et al. (2019), and we subscribe to the view of Wu et al. (2016), Chai et al. (2019), and Kuo et al. (2020) that *Butyriboletus* including *Exsudoporus*. *Nigroboletus* was treated as a synonym of *Xerocomellus* based on our observations on type specimens and relationships of phylogenetic trees. Meanwhile, we reported eight new taxa, one new section, and seven new combinations, and redescribed eight species, in which some morphological characteristics differ from the original description.

The rapid development of molecular technology incontrovertibly facilitated steps of modern taxonomy that reflected in fungi are many new high taxonomic units were erected or amended (Wu et al. 2014, Cui et al. 2018, He et al. 2023). Meanwhile, the fact researchers should face is blowing up the number of new taxa, especially in genus status. In most cases, the new genus can help clarify relationships between some genera that have been debated since the beginning of morphological observations, as done by Buck et al. (2008), Šutara et al. (2008) and Li et al. (2011). However, sometimes for the consistency and convenience in nomenclature, a new genus erected was not so necessary, as discussed by Justo (2014) and Halling et al. (2015). *Exsudoporus* and *Butyriboletus* were two genera both described in 2014, but the *Exsudoporus* was established later. Vizzini et al. (2014) assumed it differ from *Butyriboletus* in blood red to reddish brown pileus, and red pores and reticulations. However, through detailed morphological comparison, these morphologies evidently cannot support it as a single genus. The reddish-brown pileus overlaps some *Butyriboletus* species with a brown pileus, which dims into reddish brown at maturity. Although rarely, red pores were also observed in *Butyriboletus*, especially in *B. hainanensis*, the base group (Clade D) of *Butyriboletus* (Clade A–D). Red reticulations have also been reported in some *Butyriboletus* species. He (2019) employed divergence time as an additional criterion to resolve high-rank taxonomic problems in Basidiomycota. Following them, in our study, we tried to clarify the relationships and dispel disputation between *Butyriboletus* (now sect. *Butyriboletus*) and *Exsudoporus* (now sect. *Exsudoporus* Clade B). Results showed that both of them derived from North and Central America and with close time 16 Mya and 15 Mya, respectively. The sister groups (take *B. subsplendidus* together) with intimate phylogenetic relationships and now have sole original region and almost the same time of origin undoubtedly cannot reject being merged into one genus treatment. Based on those, we treated *Exsudoporus* as a section under *Butyriboletus* which represents species mostly red in basidiomes, and divided *Butyriboletus* into three sections. This treatment balanced the typical differences in morphology and monophyly in phylogenetic trees. To some extent, the name *Exsudoporus* retained settled the concern about a more reasonable alteration of taxonomic systems caused by the loss of a particular generic name. Boletaceae, currently, have nearly 100 genera for 1200 species, which has astonished some researchers (Vellinga et al. 2015, Kuo & Ortiz-Santana 2020, Hyde et al. 2023). In this circumstance, a new genus introduced in Boleteceae, should be more prudent. In the future, a consistent and prevailing principle should be invoked for new higher taxonomic units erected. For now, the six guidelines proposed by Vellinga et al. (2015) should be followed for a long time.

The estimated divergence from Dataset IX indicated that the origin time of *Butyriboletus* is ca. 23 Mya, which is too young for the "Boreotropical migration" hypothesis and too old for "Host comigrations at regional levels". Based on those findings, we have adopted the "long-distance dispersal" hypothesis as the more likely cause to explain the current biogeographical structure of *Buytriboletus*. In view of the multi-dispersal events arising between East Asia and North and Central America (Fig. 10), we assumed that several pathways, not just a single one, affected the dispersal of *Butyriboletus*, *viz*. Beringia is not the only channel for the dispersal of *Butyriboletus*. The last dispersal from East Asia to North and Central America (Fig. 9), distinctly did not rely on the Beringia. The

atmospheric transport has been shown to be very helpful in the spread of plant pathogens, and in this aspect, the dispersal of *Butyriboletus* may also be under the help (Schmale III & Ross 2015). Another strong evidence is the complete absence of *Butyriboletus* records in Siberia and Canada so far, which suspiciously if the multi-dispersal with the help of Beringia, this circumstance cannot be understood. Extensive collections are necessary in the future, and perhaps the conclusion will be modified. However, currently, migration through Beringia is not the sole dispersal style in *Butyriboletus*. At ca. 12 Mya (Fig. 9), *Butyriboletus* dispersed to Europe which we would like to assume relied on the broken North Atlantic Land Bridge, then from Europe returned to East Asia again. An interesting phenomenon that merits attention is the radiational evolution of species in *Butyriboletus* most appear with the decline of temperature, which complied with its now temperate zone group definition. Every new dispersal to a continent is usually accompanied by a small flourishing of species and radiational diversification. Combined with the decline in temperature causing the range of hosts to shrink, we hypothesized that the long-distance dispersal and colonization in local hosts may facilitate the endemism of *Butyriboletus*, subsequently contributing to the diversification of *Butyriboletus*. The allopatric speciation may be the major factor contributing to the diversity of *Butyriboletus*. This speculation corresponds to the biogeographical structure of extant species. Although, according to our results, the dispersal probabilities between Asia and Europe are less than between Asia and North and Central America, which seems unreasonable in distance. For this reason, we speculate that the different extent of investigations in Europe and America may obscure the explanation of dispersal events. Based on the Sequence No. KC416635 from the NCBI, *Butyriboletus regius* (Krombh.) D. Arora & J.L. Frank was also thought to be found in Australia. However, given the submitter did not provide the host information, we cannot reject the probability that this species dispersal with european migrations or commercial activity. Meanwhile, we did not find the records of *Butyriboletus* from Africa and South America, where the records of species that exist may revise our speculations. We hope further discovery from those regions in the future can make the origin and dispersal of *Butyriboletus* more clear.

Nigroboletus has now been reclassified as a junior synonym of *Xerocomellus* here based on morphological and phylogenetic analyses. The two new species (*Xe. fuscoscabrosus* and *Xe. velutinoceps*) belong to the major clade of *Nigroboletus* help us clarify the relationships between *Nigroboletus* and *Xerocomellus*, especially *Xe. fuscoscabrosus*, which reveals a distinct transition of morphology intermediate between *Nigroboletus* and *Xerocomellus*. *Nigroboletus* was established based on the single clade in the phylogenetic tree. However, with the new species of this clade being reported, the morphological features of *Nig. roseonigrescens* (now *Xe. roseonigrescens*) were concluded to be only an exception. This circumstance reminds us that extreme translation of the single clade from phylogenetic trees and terrifically strict delimiting of the range in high rank taxonomic units will finally cause meaningless inflated taxonomic units. Any processing of higher taxa performed in Boletaceae or other families should be considered whether the results of this study provide the researcher with a more concise framework and a more convenient pathway to understand the group or not.

It is worth mentioning that, future studies require to pay characters such as different basidiomes in different habitats may exhibit significant variations in morphology, sometimes to an extreme extent. In our collections, the pileipellis of *Z. olivaceobrunnea* showed entangled hyphoepithelium that is different from the anticlinal and nearly parallel hyphae in the original description. In *R. reticulata*, which is named for its conspicuous reticulations over stipe, but showed nearly glabrous in our collections. The ornamentations of stipe may be unstable in some groups. The future identification shows be more careful to employ this feature to divide species. As given in Vizzini et al. (2014) said, overstressing some characteristics such as stipe ornamentations (presence/absence of reticulum) in delimiting species is improper, and may cause over-segmentation of species. For taxonomy, combining multi-features, including ecology, phylogeny, morphology, and biogeography, will be a tendency in the future.

According to Vizzini et al. (2014), Wang et al. (2022), and Wu et al. (2023), *Suillellus* is a monophyletic genus that one conspicuously feature is dextrinoid hyphae in the stipe base. In this study, based on original descriptions, we recombined four species that do not comply with the

definition of *Suillellus* and aim to make *Suillellus* clearer in phylogenetic status. However, some species within this genus are rarely reported and have brief descriptions, making it difficult for us to determine their status, for example, *S. adalgisae* and *S. hypocarycinus*. For those species, the new materials discovered in the region of type specimens reported are important.

The new taxa of Boletaceae are continuously being described from China, which means various and abundant species in Boletaceae, and a rich diversity of resources in China. Conducting extensive and in-depth investigations in China is necessary and urgent.

ACKNOWLEDGEMENTS

The authors thank Dr. Zhu-Liang Yang and Dr. Wen-Zhang Ma at Kunming Institute of Botany, Chinese Academy of Sciences, Dr. Tai-Hui Li and Dr. Ming Zhang at Microbiology Institute of Guangdong, and Prof. Nian-Kai Zeng at Hainan Medical University for the help in the loaning process of specimens and Mrs. Fei-Yang Chen for the help in the collection of specimens HMJAU68190. We are also grateful for the Cryptogamic Herbarium of the Kunming Institute of Botany, Chinese Academy of Sciences, Herbarium of Microbiology Institute of Guangdong and Fungal Herbarium of Hainan Medical University loaning specimens. This work was financed by the Natural Science Foundation of China (No. 31970020), the Jilin Province Science and Technology Development Plan Project (No. 20230202119NC); Research on the Creation of Excellent Edible Mushroom Resources and High Quality & Efficient Ecological Cultivation Technology in Jiangxi Province (20212BBF61002), The Scientific and Technological Tackling Plan for the Key Fields of Xinjiang Production and Construction Corps (No. 2021AB004); and the "111" program (No. D17014).

REFERENCES

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.

Bakker HC, Noordeloos ME. 2005 – A revision of European species of *Leccinum* Gray and notes on extralimital species. Persoonia: Molecular Phylogeny and Evolution of Fungi 18(4), 511–574.

Berry PE, Hahn WJ, Sytsma KJ, Hall JC et al. 2004 – Phylogenetic relationships and biogeography of *Fuchsia* (Onagraceae) based on noncoding nuclear and chloroplast DNA data. American Journal of Botany 91(4), 601–614.

Blanco Dios JB. 2015 – Nomenclatural Novelties. Index Fungorum (211). http://www.indexfungorum.org/Names/IndexFungorumPublicationsListing.asp (Accessed on January 19, 2024).

Biketova AY, Gelardi M, Smith ME, Simonini G et al. 2022 – Reappraisal of the Genus *Exsudoporus* (Boletaceae) Worldwide Based on Multi–Gene Phylogeny, Morphology and Biogeography, and Insights on *Amoenoboletus*. Journal of Fungi 8(2), 101.

Bozok F, Assyov B, Taşkın H. 2019 – First records of *Exsudoporus permagnificus* and *Pulchroboletus roseoalbidus* (Boletales) in association with non–native Fagaceae, with taxonomic remarks. Phytologia Balcanica 25(1).

Buyck B, Hofstetter V, Eberhardt U, Verbeken A et al. 2008 – Walking the thin line between *Russula* and *Lactarius*: the dilemma of Russula subsect. Ochricompactae. Fungal Diversity 28, 15–40.

Cai Q, Tulloss RE, Tang LP, Tolgor B et al. 2014 – Multi–locus phylogeny of lethal amanitas: Implications for species diversity and historical biogeography. BMC Evolutionary Biology 14(1), 1–16.

Capella-Gutiérrez S, Silla-Martínez JM, Gabaldón T. 2009 – trimAl: a tool for automated alignment trimming in large–scale phylogenetic analyses. Bioinformatics 25(15), 1972–1973.

Chai H, Liang ZQ, Xue R, Jiang S et al. 2019 – New and noteworthy boletes from subtropical and tropical China. MycoKeys (46), 55.

Chakraborty D, Vizzini A, Das K. 2018 – Two new species and one new record of the genus *Tylopilus* (Boletaceae) from Indian Himalaya with morphological details and phylogenetic estimations.

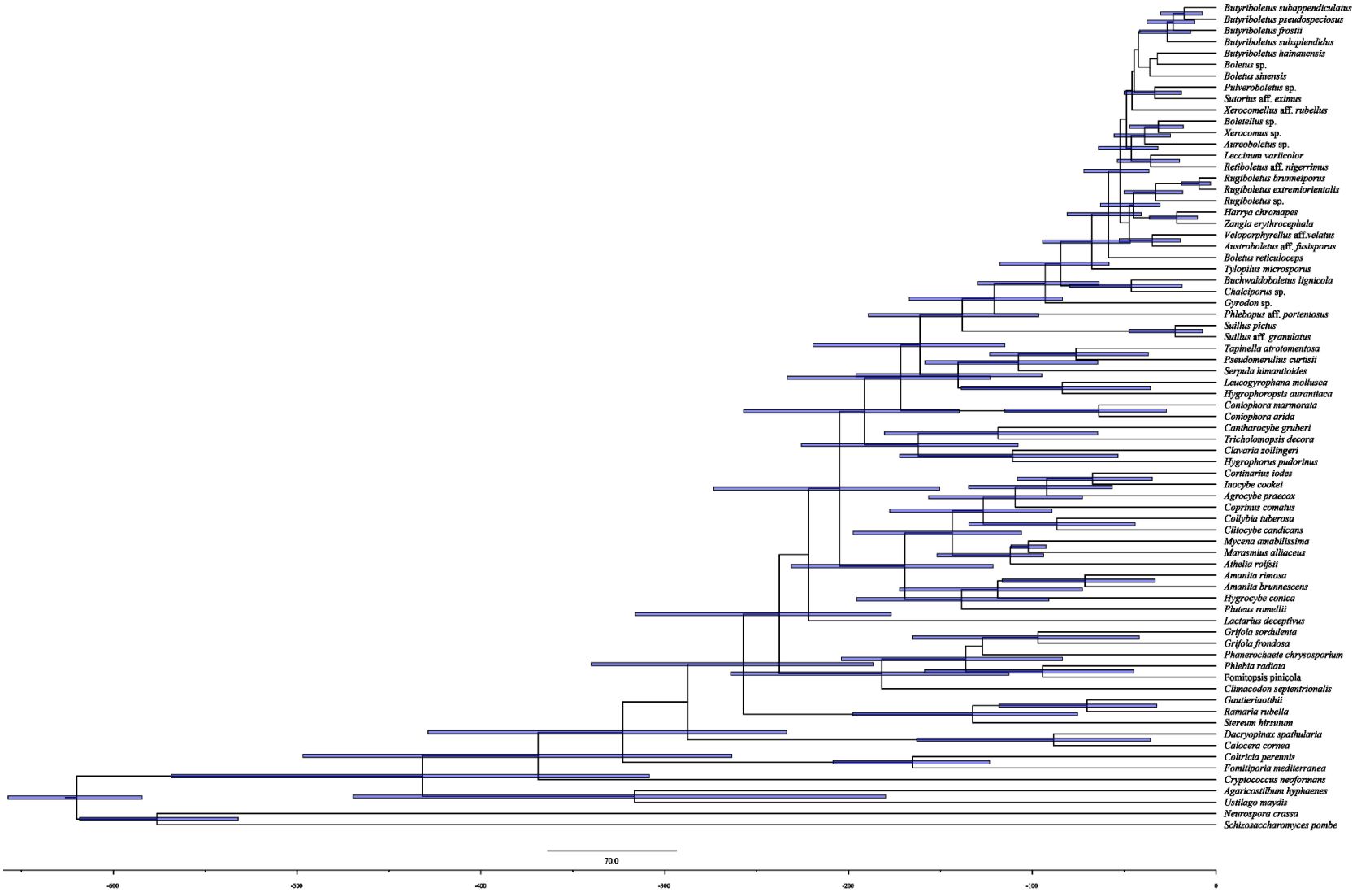
MycoKeys (33), 103.
Codjia JEI, Sánchez-Ramírez S, Ebika STN, Wu G et al. 2023 – Historical biogeography and diversification of ringless *Amanita* (section *Vaginatae*) support an African origin and suggest niche conservatism in the Americas. Molecular Phylogenetics and Evolution 178, 107644.
Coker WC, Beers AH. 1974 – The Boleti of North Carolina. Courier Corporation.
Cui YY, Cai Q, Tang LP, Liu JW, Yang ZL. 2018 – The family Amanitaceae: molecular phylogeny, higher–rank taxonomy and the species in China. Fungal Diversity 91, 5–230.
Das K, Ghosh A, Chakraborty D, Datta S, Bera I et al. 2023 – Four novel species and two new records of boletes from India. Journal of Fungi 9(7), 754.
De Queiroz K. 2007 – Species concepts and species delimitation. Systematic biology 56(6), 879–886.
Dios JBB. 2015 – *Nomenclatural Novelties* [Online]. Available: http://www.indexfungorum.org/Names/IndexFungorumPublicationsListing.asp (Accessed on August 11, 2023).
Farid A, Bessette AE, Bessette AR, Bolin JA 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. 2012 – Molecular phylogeny and biogeography of *Boletus* L. s.s. and *Hydnum* L. dissertation, Kunming Institute of Botany, Kunming.
Feng B, Xu J, Wu G, Zeng NK et al. 2012 – DNA sequence analyses reveal abundant diversity, endemism and evidence for Asian origin of the porcini mushrooms. PLoS One 7(5), e37567.
Frank J, Siegel N, Schwarz C, Araki B, Vellinga E. 2020 – *Xerocomellus* (Boletaceae) in western North America. Fungal Systematics and Evolution 6(1), 265–288.
Gelardi M, Angelini C, Costanzo F, Dovana F et al. 2019 – *Tylopilus griseiolivaceus* sp. nov. and *T. leucomycelinus* (Boletaceae) revisited from the Dominican Republic within a comprehensive phylogeny of *Tylopilus* s. str. Mycological Progress 18, 1039–1056.
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, Ercole E, Horak E et al. 2015 – Circumscription and taxonomic arrangement of *Nigroboletus roseonigrescens* Gen. Et Sp. Nov., a new member of Boletaceae from tropical South–Eastern China. PLoS ONE 10(8): e0134295.
Geml J, Timling I, Robinson CH, Lennon N et al. 2012 – An arctic community of symbiotic fungi assembled by long-distance dispersers: phylogenetic diversity of ectomycorrhizal basidiomycetes in Svalbard based on soil and sporocarp DNA. Journal of Biogeography 39(1), 74–88.
Hall TA. 1999 – BioEdit: a user–friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic acids symposium series: Oxford, 95–98.
Halling RE, Fechner N, Nuhn M, Osmundson T et al. 2015 – Evolutionary relationships of *Heimioporus* and *Boletellus* (Boletales), with an emphasis on Australian taxa including new species and new combinations in *Aureoboletus*, *Hemileccinum* and *Xerocomus*. Australian Systematic Botany 28(1), 1–22.
Halling RE, Mueller GM. 2003 – *Leccinum* (Boletaceae) in Costa Rica. Mycologia 95(3), 488–499.
Halling RE, Nuhn M, Fechner NA, Osmundson TW et al. 2012a – *Sutorius*: a new genus for *Boletus eximius*. Mycologia 104(4), 951–961.
Halling RE, Nuhn M, Osmundson T, Fechner N et al. 2012b – Affinities of the *Boletus chromapes* group to *Royoungia* and the description of two new genera, *Harrya* and *Australopilus*. Australian Systematic Botany 25(6), 418–431.
Han L, Wu G, Horak E, Halling R et al. 2020 – Phylogeny and species delimitation of *Strobilomyces* (Boletaceae), with an emphasis on the Asian species. Persoonia: Molecular Phylogeny and Evolution of Fungi 44, 113.
Han LH, 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(1), 201–212.
He MQ, Zhao RL, Hyde KD, Begerow D et al. 2019 – Notes, outline and divergence times of Basidiomycota. Fungal diversity 99(1), 105–367.
He ZM, Chen ZH, Bau T, Wang G S et al. 2023 – Systematic arrangement within the family Clitocybaceae (Tricholomatineae, Agaricales): phylogenetic and phylogenomic evidence, morphological data and muscarine-producing innovation. Fungal Diversity 123(1), 1–47.
Hibbett DS. 2001 – Shiitake mushrooms and molecular clocks: historical biogeography of *Lentinula*. Journal of Biogeography 28(2), 231–241.
Hibbett DS, Grimaldi D, Donoghu MJ. 1997 – Fossil mushrooms from Miocene and Cretaceous ambers and the evolution of Homobasidiomycetes. American Journal of Botany 84(7), 981–991.
Hosen MI, Feng B, Wu G, Zhu XT et al. 2013 – *Borofutus*, a new genus of Boletaceae from tropical Asia: phylogeny, morphology and taxonomy. Fungal Diversity 58, 215–226.
Hyde KD, Abdel-Wahab MA, Abdollahzadeh J, Abeywickrama PD et al. 2023 – Global consortium for the classification of fungi and fungus-like taxa. Mycosphere, 14(1).
Justo A. 2014 – The taxonomy of Turkey Tails (*Trametes*) and related polypores: One genus or too many. Mycophile 54(4), 8–10.
Kallio P. 1984 – *Boletus gabretae* in Finland. Karstenia 24, 77–78.
Kornerup A, Wanscher JH. 1978 – Methuen handbook of colour.
Kumar S, Stecher G, Tamura K. 2016 – MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. Molecular biology and evolution 33(7), 1870–1874.
Kuo M, Ortiz–Santana B. 2020 – Revision of leccinoid fungi, with emphasis on North American taxa, based on molecular and morphological data. Mycologia 112(1), 197–211.
Lanfear R, Frandsen PB, Wright AM, Senfeld T, Calcott B. 2017 – PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Molecular biology and evolution 34(3), 772–773.
Li YC, Li F, Zeng NK, Cui YY, Yang ZL. 2014 – A new genus *Pseudoaustroboletus* (Boletaceae, Boletales) from Asia as inferred from molecular and morphological data. Mycological Progress 13, 1207–1216.
Li YC, Yang ZL. 2021 – The boletes of China: *Tylopilus* s.l. Springer.
Li YC, Feng B, Yang ZL. 2011 – *Zangia*, a new genus of Boletaceae supported by molecular and morphological evidence. Fungal Diversity 49, 125–143.
Lin CP, Huang JP, Wu CS, Hsu CY et al. 2010 – Comparative chloroplast genomics reveals the evolution of Pinaceae genera and subfamilies. Genome Biology and Evolution 2, 504–517.
Liang ZQ, An DY, Juang S, Su MS, Zeng NK. 2016 – *Butyriboletus hainanensis* (Boletaceae, Boletales), a new species from tropical China. Phytotaxa 267(4), 256–262.
Lin ZJ, Huang XX, Liang YS, Qiu LH. 2022 – *Boletellus brunoflavus* sp. nov. (Boletaceae, Basidiomycota) from Baiyun Mountain, Guangzhou, China. Phytotaxa 567(3), 245–256.
Lucking R, Huhndorf S, Pfister DH, Plata ER, Lumbsch HT. 2009 – Fungi evolved right on track. Mycologia 101(6), 810–822.
Matheny PB. 2005 – Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (*Inocybe*; Agaricales). Molecular phylogenetics and evolution 35(1), 1–20.
Matheny PB, Ammirati JF. 2003 – *Inocybe angustispora*, *I. taedophila*, and *Cortinarius aureifolius*: an unusual inocyboid *Cortinarius*. Mycotaxon 88, 401–407.
Matzke NJ. 2013 – BioGeoBEARS: BioGeography with Bayesian (and likelihood) evolutionary analysis in R scripts, CRAN: The Comprehensive R Archive Network, Berkeley, CA. https://rdrr.io/cran/BioGeoBEARS/ (Accessed on October 21, 2023).
Moncalvo JM, Buchanan PK. 2008 – Molecular evidence for long distance dispersal across the Southern Hemisphere in the *Ganoderma applanatum* – australe species complex (Basidiomycota). Mycological research 112(4), 425–436.
Moyersoen B, Beever RE, Martin F. 2003 – Genetic diversity of *Pisolithus* in New Zealand indicates

multiple long-distance dispersal from Australia. New Phytologist 160(3), 569–579.
Mueller GM, Wu QX, Huang YQ, Guo SY et al. 2001 – Assessing biogeographic relationships between North American and Chinese macrofungi. Journal of biogeography 28(2), 271–281.
Murrill WA. 1945 – More fungi from Florida. Lloydia 8, 263–290.
Murrill WA. 1948 – Florida boletes. Lloydia 11(1), 21–35.
Naseer A, Sarwar S, Khalid AN, Healy R, Smith ME. 2019 – *Hortiboletus kohistanensis* (Boletaceae), a new bolete species from temperate and subalpine oak forests of Pakistan. Phytotaxa 388(3), 239–246.
Nguyen LT, Schmidt HA, Von Haeseler A, Minh BQ. 2015 – IQ–TREE: a fast and effective stochastic algorithm for estimating maximum–likelihood phylogenies. Molecular biology and evolution 32(1), 268–274.
Oolbekkink G. 1991 – The taxonomic value of the ornamentation of spores in 'the *Xerocomus*–group'of *Boletus*. Persoonia: Molecular Phylogeny and Evolution of Fungi 14(3), 245–273.
Peay KG, Matheny PB. 2016 – The biogeography of ectomycorrhizal fungi – a history of life in the subterranean. Molecular mycorrhizal symbiosis, 341–361.
Peck CH. 1889 – *Boleti of the United States.* University of the State of New York.
Peintner U, Ladurner H, Simonini G. 2003 – *Xerocomus cisalpinus* sp. nov., and the delimitation of species in the *X. chrysenteron* complex based on morphology and rDNA–LSU sequences. Mycological Research 107(6), 659–679.
Pilát A. 1968 – *Boletus gabretae* sp. nov. bohemica ex affinitate Boleti junguillei (Quél.) Boud.
Rehner SA, Buckley E. 2005 – A Beauveria phylogeny inferred from nuclear ITS and EF1–α sequences: evidence for cryptic diversification and links to *Cordyceps teleomorphs*. Mycologia 97(1), 84–98.
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.
Sánchez-Ramírez S, Tulloss RE, Amalfi M, Moncalvo JM. 2015 – Palaeotropical origins, boreotropical distribution and increased rates of diversification in a clade of edible ectomycorrhizal mushrooms (*Amanita* section *Caesareae*). Journal of Biogeography 42(2), 351–363.
Schmale III DG, Ross SD. 2015 – Highways in the sky: Scales of atmospheric transport of plant pathogens. Annual review of phytopathology 53, 591–611.
Shaul S, Graur D. 2002 – Playing chicken (*Gallus gallus*): methodological inconsistencies of molecular divergence date estimates due to secondary calibration points. Gene 300(1–2), 59–61.
Singer R. 1945 – New Bolataceae from Florida (a preliminary communication). Mycologia 37(6), 797–799.
Singer R. 1947 – The Boletoideae of Florida with notes on extralimital species III. The American Midland Naturalist 37(1), 1–135.
Smith AH, Thiers HD. 1971 – The Boletes of Michigan. Bulletin of the Torrey Botanical Club 99(3).
Smith S, Read D. 2008 – Mycorrhizal Symbiosis, 3rd editio Edn. Cambridge, MA: Academic Press.
Smith SY, Currah RS, Stockey RA. 2004 – Cretaceous and eocene poroid hymenophores from Vancouver Island, British Columbia. Mycologia 96(1), 180–186.
Šutara J. 2008 – *Xerocomus* s.l. in the light of the present state of knowledge. Czech Mycology 60(1), 29–62.
Šutara J, Skála E. 2007 – *Boletus marekii*, a new species with truncate spores from the *Boletus chrysenteron* group. Czech Mycology 59, 11–24.
Taylor JW, Jacobson DJ, Kroken S, Kasuga T et al. 2000 – Phylogenetic species recognition and species concepts in fungi. Fungal genetics and biology 31(1), 21–32.
Taylor TN, Hass H, Kerp H, Krings M, Hanlin R. 2005 – Perithecial ascomycetes from the 400 million year old Rhynie chert: an example of ancestral polymorphism. Mycologia 97(1), 269–285.

Tedersoo L. 2017 – Biogeography of mycorrhizal symbiosis. Springer.
Thiers HD. 1975 – California mushrooms-A field guide to the boletes.
Vadthanarat S, Raspé O, Lumyong S. 2018 – Phylogenetic affinities of the sequestrate genus *Rhodactina* (Boletaceae), with a new species, *R. rostratispora* from Thailand. MycoKeys (29), 63.
Vadthanarat S, Raspé O, Lumyong S. 2022 – *Rubinosporus auriporus* gen. et sp. nov. (Boletaceae: xerocomoideae) from tropical forests of Thailand, producing unusual dark ruby spore deposits. Journal of Fungi 8(3), 278.
Vellinga EC, Kuyper TW, Ammirati J, Desjardin DE et al. 2015 – Six simple guidelines for introducing new genera of fungi. IMA fungus 6(2), A65–A68.
Vizzini A. 2014 – Nomenclatural Novelties. Index Fungorum (183). http://www.indexfungorum.org/Names/IndexFungorumPublicationsListing.asp (Accessed on October 29, 2023).
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 Y, Tuo YL, Wu DM, 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.
Wang Y, Wang LY, Dai D, Qi ZX et al. 2023 – Boletaceae in China: Taxonomy and phylogeny reveal a new genus, two new species, and a new record. Frontiers in Microbiology 13, 1052948.
Wu G, Feng B, Xu J, Zhu XT 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, Li HJ, Horak E, Wu K et al. 2023 – New taxa of Boletaceae from China. Mycosphere 14(1), 22.
Wu, G, Li YC, Zhu XT, Zhao K et al. 2016 – One hundred noteworthy boletes from China. Fungal Diversity 81(1), 25–188.
Wu G, Miyauchi S, Morin E, Kuo A et al. 2022 – Evolutionary innovations through gain and loss of genes in the ectomycorrhizal Boletales. New Phytologist 233(3), 1383–1400.
Wu LL, Liang ZQ, Su MS, Fan YG et al. 2021 – Updated taxonomy of Chinese *Phylloporus* (Boletaceae, Boletales): six new taxa and four redescribed species. Mycological Progress 20, 1243–1273.
Xue R, Zhang X, Xu C, Xie H et al. 2023 – The subfamily Xerocomoideae (Boletaceae, Boletales) in China. Studies in Mycology 106, 95–197.
Yu Y, Harris AJ, Blair C, He X. 2015 – RASP (Reconstruct Ancestral State in Phylogenies): a tool for historical biogeography. Molecular phylogenetics and evolution 87, 46–49.
Zachos J, Pagani M, Sloan L, Thomas E, Billups K. 2001 – Trends, rhythms, and aberrations in global climate 65 Ma to present. science 292(5517), 686–693.
Zeng NK, Wu G, Li YC, Liang ZQ, Yang ZL. 2014 – *Crocinoboletus*, a new genus of Boletaceae (Boletales) with unusual boletocrocin polyene pigments. Phytotaxa 175(3), 133–140.
Zhang D, Gao F, Jakovlić I, Zou H et al. 2020 – PhyloSuite: an integrated and scalable desktop platform for streamlined molecular sequence data management and evolutionary phylogenetics studies. Molecular ecology resources 20(1), 348–355.
Zhang M, Li TH. 2018 – *Erythrophylloporus* (Boletaceae, Boletales), a new genus inferred from morphological and molecular data from subtropical and tropical China. Mycosystema 37(9), 1111–1126.
Zhao K, Wu G, Yang ZL. 2014 – A new genus, *Rubroboletus*, to accommodate *Boletus sinicus* and its allies. Phytotaxa 188(2), 61–77.
Zhao K, Zhang FM, Zeng QQ, Han LH, Li YC. 2020 – *Tylopilus jiangxiensis*, a new species of *Tylopilus* s. str. from China. Phytotaxa 434(3), 281–291.
Zhu XT, Li YC, Wu G, Feng B et al. 2014 – The genus *Imleria* (Boletaceae) in East Asia. Phytotaxa 191(1), 81–98.

Supplementary materials



Supplementary Figure 1 – Chronogram and estimated divergence times of *Boletales*, *Butyriboletus* and *Rugiboletus* generated from molecular clock analysis using the *tef1-α*, *rpb1* and *rpb2* data.

Supplementary Table 1 Sequences used in this study. Newly generated sequences are shown in black bold.

Taxon	Voucher	Locality	28S	ITS	*TEF1*	*rpb1*	*rpb2*
Acyanoboletus controversus	HKAS 126560	China	OQ888714	–	OQ873451	OQ873469	OQ873490
Acyanoboletus dissimilis	ZT14030	Malaysia	OQ888716	–	OQ873453	OQ873471	OQ873492
Afroboletus luteolus	00-436	Africa	KF030238	–	KF030397	KF030392	–
Agaricostilbum hyphaenes	CBS7811		–	–	AY788845	AY780933	AY879114
Agrocybe praecox	AFTOL-ID728		–	–	DQ516069	DQ385876	DQ061276
Amanita brunnescens	AFTOL-ID673		–	–	AY788847	AY780936	AY881021
Amanita rimosa	HKAS77336	China	–	–	–	KJ466622	KJ481958
Amoenoboletus granulopunctatus	HKAS 56280	China	KF112418	–	MW566747	–	MW560081
Amoenoboletus mcrobbii	PDD 97418	New Zealand	MW520184	–	MW566744	–	–
Amoenoboletus miraculosus	Z-ZT 14046	Malaysia	MW520188	–	MW566745	–	–
Athelia rolfsii	Sr_471	India	–	–	–	JN790642	JN790645
Aureoboletus sp.	HKAS57581	China	–	–	KF112560	KF112746	KF112233
Austroboletus aff. *fusisporus*	HKAS52683	China	–	–	KF112571	KF112766	KF112213
Baorangia pseudocalopus	HKAS63607	China	KF112355	–	KF112167	KF112519	KF112677
Baorangia pseudocalopus	HKAS75081	China	KF112356	–	KF112168	KF112520	KF112678
Boletellus aff. *putuoensis*	N.K. Zeng3207 (FHMU2168)	China	–	–	MW925902	–	–
Boletellus areolatus	N.K. Zeng3085 (FHMU2046)	China	MT829118	–	MW925881	–	MW925938
Boletellus areolatus	N.K. Zeng3112 (FHMU2073)	China	MW826852	OP681711	MW925880	–	–
Boletellus areolatus	KUN-HKAS99767	China	MW826851	–	MW925879	–	–
Boletellus brunoflavus	N.K. Zeng2913 (FHMU1885)	China	MW826896	–	MW925920	–	MW925949
Boletellus brunoflavus	KUN-HKAS53375	China	KF112364	–	KF112240	–	KF112748
Boletellus emodensis	N.K. Zeng2488 (FHMU1611)	China	MW826862	OP681697	–	–	MW925942
Boletellus emodensis	N.K. Zeng3037 (FHMU1998)	China	MT829119	–	MW925887	–	MW925944
Boletellus emodensis	N.K. Zeng3070 (FHMU2031)	China	MW826857	OP681702	MW925890	–	–
Boletellus emodensis	N.K. Zeng3073 (FHMU2034)	China	MT829121	–	MW925888	–	MW925945

Supplementary Table 1 Continued.

Taxon	Voucher	Locality	28S	ITS	*TEF1*	*rpb1*	*rpb2*
Boletellus emodensis	N.K. Zeng3103 (FHMU2064)	China	MW826858	OP681703	MW925886	–	–
Boletellus emodensis	N.K. Zeng3184 (FHMU2145)	China	MW826859	–	MW925884	–	–
Boletellus emodensis	N.K. Zeng3260 (FHMU2221)	China	MW826872	OP681705	MW925895	–	MW925943
Boletellus emodensis	N.K. Zeng3284 (FHMU2245)	China	MW826863	OP681704	MW925894	–	MW925940
Boletellus erythrolepis	N.K. Zeng1362 (FHMU913)	China	MW826846	–	MW925875	–	–
Boletellus erythrolepis	S. Jiang78 (FHMU3255)	China	MW826909	–	MW925927	–	–
Boletellus erythrolepis	S. Jiang78-1 (FHMU3312)	China	MW826847	–	–	–	–
Boletellus erythrolepis	S. Jiang78-2 (FHMU3313)	China	MW826848	–	–	–	–
Boletellus erythrolepis	S. Jiang78-3 (FHMU3314)	China	MW826845	–	MW925876	–	–
Boletellus indistinctus	N.K. Zeng1393 (FHMU940)	China	MW826878	OP681696	MW925907	–	–
Boletellus indistinctus	N.K. Zeng1624 (FHMU1088)	China	MW826873	OP681700	MW925912	–	MW925948
Boletellus indistinctus	N.K. Zeng3188 (FHMU2149)	China	MW826875	OP681706	MW925909	–	–
Boletellus indistinctus	N.K. Zeng3298 (FHMU2259)	China	MW826874	OP681709	MW925915	–	–
Boletellus indistinctus	N.K. Zeng3308 (FHMU2269)	China	MW826876	OP681710	MW925906	–	–
Boletellus putuoensis	N.K. Zeng3186 (FHMU2147)	China	MW826892	–	MW925900	–	–
Boletellus putuoensis	N.K. Zeng4070 (FHMU3260)	China	MW826890	–	MW925899	–	–
Boletellus putuoensis	N.K. Zeng4075 (FHMU3261)	China	MW826891	–	MW925901	–	–

Supplementary Table 1 Continued.

Taxon	Voucher	Locality	28S	ITS	*TEF1*	*rpb1*	*rpb2*
Boletellus rubidus	FHMU3267	China	MW826849	–	MW925877	–	–
Boletellus rubidus	KUN-HKAS58713	China	KF112428	–	KF112307	–	KF112759
Boletellus rubidus	KUN-HKAS83069	China	MW826904	–	–	–	–
Boletellus sinochrysenteroides	K. Zhao998 (FHMU3264)	China	MW826902	–	MW925904	–	MW925947
Boletellus sinochrysenteroides	K. Zhao925 (FHMU3265)	China	MW826901	–	MW925903	–	MW925946
Boletellus sp.	HKAS59536	China	–	–	KF112622	KF112758	KF112306
Boletellus squamosus	N.K. Zeng4051 (FHMU3266)	China	MW826856	–	MW925898	–	–
Boletellus squamosus	KUN-HKAS59536	China	KF112427	–	KF112306	–	KF112758
Boletellus subglobosus	S. Jiang100 (FHMU3256)	China	MW826844	–	MW925872	–	–
Boletellus subglobosus	S. Jiang99 (FHMU3257)	China	MW826843	–	MW925874	–	–
Boletellus subglobosus	S. Jiang98 (FHMU3258)	China	MW826842	–	MW925873	–	–
Boletellus zenghuoxingii	N.K. Zeng3018 (FHMU1979)	China	MW826855	–	MW925878	–	MW925939
Boletellus zenghuoxingii	N.K. Zeng2553 (FHMU3251)	China	MW826854	–	–	–	–
Boletus aereus	REH8721	USA	KF030339	–	KF030426	KF030377	–
Boletus albobrunnescens	REH8790	Thailand	HQ161879	–	–	HQ161877	–
Boletus austroedulis	REH8969	Australia	HQ161847	–	–	HQ161816	–
Boletus bainiugan	HKAS52235	China	KF112457	–	KF112203	KF112587	KF112705
Boletus botryoides	HKAS53403	China	-	–	KT990738	–	KT990375
Boletus edulis	HMJAU4637	China	KF112455	–	KF112202	KF112586	KF112704
Boletus fagacicola	HKAS55975	China	JN563853	–	–	JN563879	–
Boletus griseiceps	HKAS71346	China	JQ172789	–	–	JQ172792	–
Boletus hiratsukae	TMI24051	Japan	JQ172788	–	–	JQ172793	–
Boletus monilifer	HKAS83205	China	KM820806	–	–	KM820816	–
Boletus nobilis	BD239	USA	EU232002	–	–	EU231993	–
Boletus orientialbus	HKAS62907	China	JN563856	–	–	JN563873	–
Boletus pallidus	179/97	USA	–	DQ534564	KF030424	KF030396	–

Supplementary Table 1 Continued.

Taxon	Voucher	Locality	28S	ITS	*TEF1*	*rpb1*	*rpb2*
Boletus quercophilus	BDCR0417	Costa Rica	EU232001	–	–	EU231995	–
Boletus reticuloceps	HKAS51232	China	KT990537	–	KT990739	KT990906	KT990376
Boletus reticuloceps	HKAS57671	China	–	–	KF112648	KF112703	KF112201
Boletus rex-veris	JFA13101	USA	EU232005	–	–	EU231998	–
Boletus rubellus	ChL22	Poland	–	KX438318	–	–	–
Boletus rubellus	LAH0810	Pakistan	–	KJ802929	–	–	–
Boletus rubellus	LAH0710	Pakistan	–	KJ802928	–	–	–
Boletus rubellus	JMP0013	USA	–	EU819460	–	–	–
Boletus rubellus	F:PRL5575MAN	USA	–	GQ166888	–	–	–
Boletus rubellus	F:PRL5788MAN	USA	–	GQ166883	–	–	–
Boletus rubellus	F:PRL5879MAN	USA	–	GQ166876	–	–	–
Boletus semigastroideus	PBM3076	New Zealand	KF030352	–	KF030430	KF030384	–
Boletus separans	DPL2704	USA	KF030329	–	KF030431	KF030385	–
Boletus shiyong	HKAS55089	China	JN563849	–	–	JN563869	–
Boletus sinensis	HKAS76851	China	–	–	KF112493	KF112651	KF112144
Boletus sinoedulis	HKAS55436	China	JN563854	–	–	JN563863	–
Boletus sp.	HKAS62903	China	JN563855	–	KF112220	JN563875	–
Boletus sp.	HKAS59554	China	–	–	KF112528	KF112698	KF112186
Boletus subalpinus	27882	USA	KF030340	–	KF030427	KF030379	–
Boletus subviolaceofuscus	HKAS83149	China	KM820808	–	–	KM820818	–
Boletus tylopilopsis	HKAS83202	China	KM820809	–	–	KM820824	–
Boletus umbrinipileus	HKAS50496	China	JN563846	–	–	JN563864	–
Boletus variipes var. *fagicola*	4249	USA	JQ327014	–	JQ327017	KF030378	–
Boletus violaceofuscus	HKAS62900	China	JN563859	–	KF112219	JN563876	KF112762
Boletus viscidiceps	HKAS83086	China	KM820810	–	–	KM820825	–
Buchwaldoboletus lignicola	HKAS76674	China	KF112350	–	KF112277	KF112642	KF112819
Buchwaldoboletus lignicola	HKAS76674	China	–	–	KF112642	KF112819	KF112277
Butyriboletus abieticola	Arora11087	USA	KC184413	KC184412	–	–	–
Butyriboletus appendiculatus	Bap1		AF456837	KJ419923	JQ327025	–	–
Butyriboletus appendiculatus	BR50200893390-25	Belgium	KT002609	KT002598	KT002633	–	–
Butyriboletus appendiculatus	BR50200892955-50	Belgium	KJ605677	KJ605668	KJ619472	–	KP055030
Butyriboletus appendiculatus	MB000286	Germany	KT002610	KT002599	KT002634	–	–
Butyriboletus autumniregius	Arora11108	USA	KC184424	KC184423	–	–	–
Butyriboletus brunneus	NY00013631	USA	KT002611	KT002600	KT002635	–	–

Supplementary Table 1 Continued.

Taxon	Voucher	Locality	28S	ITS	*TEF1*	*rpb1*	*rpb2*
Butyriboletus fechtneri	AT2003097		KF030270	KC584784	–	–	–
Butyriboletus floridanus	BOS 617, BZ 3170	Belize	MK601725	MN250222	MK721079	–	MK766287
Butyriboletus frostii	JLF2548	USA	–	KC812303	–	–	–
Butyriboletus frostii	NY815462	Costa Rica	JQ924342	–	KF112164	–	KF112675
Butyriboletus frostii	BDCR0418	Costa Rica	HQ161855	–	–	HQ161824	–
Butyriboletus frostii	NY815462	Costa Rica	–	–	–	KF112675	KF112164
Butyriboletus hainanensis	N.K. Zeng 1197 (FHMU 2410)	China	KU961651	KU961653	–	–	KU961658
Butyriboletus hainanensis	N.K. Zeng 2418 (FHMU 2437)	China	KU961652	KU961654	KU961656	–	KX453856
Butyriboletus hainanensis	N.K. Zeng 2418 (FHMU 2437)	China	–	–	–	KX453856	KU961656
Butyriboletus huangnianlaii	N.K. Zeng 3245 (FHMU 2206)	China	MH879688	MH885350	MH879717	–	MH879740
Butyriboletus huangnianlaii	N.K. Zeng 3246 (FHMU 2207)	China	MH879689	MH885351	MH879718	–	MH879741
Butyriboletus parachinarensis	LAH 36760		NG_088158	MT825245	–	–	–
Butyriboletus peckii	3959	USA	JQ326999	–	JQ327026	–	–
Butyriboletus persolidus	Arora11110	USA	–	KC184444	–	–	–
Butyriboletus primiregius	DBB00606	USA	KC184451	–	–	–	–
Butyriboletus pseudoregius	BR50201618465-02	Belgium	KT002613	KT002602	KT002637	–	–
Butyriboletus pseudoregius	BR50201533559-51	Belgium	KT002614	KT002603	KT002638	–	–
Butyriboletus pseudoregius	MG383a	Italy	–	KC184458	–	–	–
Butyriboletus pseudoroseoflavus	HMJAU59471 (R383)		OL587852	OL604165	OL739123	–	OL739125
Butyriboletus pseudospeciosus	HKAS59467	China	KF112331	–	KF112176	–	KF112672
Butyriboletus pseudospeciosus	HKAS63513	China	KT990541	–	KT990743	–	KT990380
Butyriboletus pseudospeciosus	HKAS63596	China	KT990542	–	KT990744	–	KT990381
Butyriboletus pseudospeciosus	N.K. Zeng 2127 (FHMU 1391)	China	MH879687	MH885349	MH879716	–	–
Butyriboletus pseudospeciosus	HKAS63513	China	–	–	KT990909	KT990380	KT990743
Butyriboletus pulchriceps	R. Chapman 0945	USA	KT002615	KT002604	KT002639	–	–
Butyriboletus pulchriceps	DS4514	USA	KF030261	–	KF030409	KF030376	–
Butyriboletus querciregius	Arora11100	USA	–	KC184461	–	–	–

Supplementary Table 1 Continued.

Taxon	Voucher	Locality	28S	ITS	*TEF1*	*rpb1*	*rpb2*
Butyriboletus regius	MB000287	Germany	KT002616	KT002605	KT002640	–	–
Butyriboletus regius	MG408a		KC584790	KC584789	–	–	–
Butyriboletus regius	PRM:923465	Czech Republic	KJ419931	KJ419920	–	–	–
Butyriboletus regius	HKAS84878	Germany	MT264910	–	MT269659	MT269660	MT269661
Butyriboletus roseoflavus	Arora11054	China	KC184435	KC184434	–	–	–
Butyriboletus roseoflavus	HKAS63593	China	KJ184559	KJ909517	KJ184571	–	–
Butyriboletus roseoflavus	N.K. Zeng 2123 (FHMU 1387)	China	MH879686	MH885348	MH879715	–	–
Butyriboletus roseoflavus	HKAS54099	China	KF739665	–	KF739779	KF739741	KF739703
Butyriboletus roseopurpureus	E.E. Both3765	USA	KT002617	KT002606	KT002641	–	–
Butyriboletus roseopurpureus	JLF2566	USA	KC184467	KC184466	–	–	–
Butyriboletus roseopurpureus	MB06-059	USA	KF030262	–	KF030410	KF030372	–
Butyriboletus sanicibus	Arora99211	China	KC184470	KC184469	–	–	–
Butyriboletus sp.	MHHNU7456	China	KT990539	–	KT990741	–	KT990378
Butyriboletus sp.	HKAS52525	China	KF112337	–	KF112163	–	KF112671
Butyriboletus sp.	HKAS57774	China	KF112330	–	KF112155	–	KF112670
Butyriboletus sp.	HKAS59814	China	KF112336	–	KF112199	–	KF112699
Butyriboletus sp.	HKAS63528	China	KF112332	–	KF112156	–	KF112673
Butyriboletus subappendiculatus	MB000260	Germany	KT002618	KT002607	KT002642	–	–
Butyriboletus subappendiculatus	HKAS84880	Germany	–	–	KT002630	–	KT002642
Butyriboletus subregius	HMJAU60200 (T95)	China	OM237339	OM237336	OM285111	–	OM285109
Butyriboletus subregius	HMJAU60201 (T198)	China	OM237340	OM237337	OM285112	–	OM285110
Butyriboletus subsplendidus	HKAS52661	China	KF112339	–	KF112169	KF112512	KF112676
Butyriboletus subsplendidus	HKAS50444	China	–	–	KT990908	KT990379	KT990742
Butyriboletus yicibus	Arora9727	China	KC184475	KC184474	–	–	–
Butyriboletus yicibus	HKAS57503	China	KT002620	KT002608	KT002644	–	–
Butyriboletus yicibus	HKAS68010	China	KT002619	KJ909521	KT002643	–	–
Butyriboletus yicibus	HKAS55413	China	KF112338	–	KF112157	KF112511	KF112674
Butyrioletus brunneoides	BJTC FM1816, holotype	China	OL721747	–	OL799255	–	OL771223

Supplementary Table 1 Continued.

Taxon	Voucher	Locality	28S	ITS	*TEF1*	*rpb1*	*rpb2*
Butyrioletus pseudoroseoflavus	HMJAU59470	China	OL587853	–	OL739124	–	OL739126
Butyrioletus sinoregius	BJTC FM755, holo-type	China	OL721748	–	OL799252	–	OL771224
Caloboletus calopus	HKAS74739	China	KF112335	–	KF112166	KF112507	KF112667
Caloboletus firmus	MB06-060	USA	KF030278	–	KF030408	KF030368	–
Caloboletus inedulis	MB06-044	USA	JQ327013	–	JQ327020	KF030362	–
Caloboletus panniformis	HKAS55444	China	KF112334	–	KF112165	KF112506	KF112666
Caloboletus yunnanensis	HKAS74864	China	KF112415	–	KF112200	KF112508	KF112679
Calocera cornea	GEL5359		–	–	AY701526	AY536286	AY881019
Cantharocybe gruberi	AFTOL-ID1017		–	–	DQ435808	DQ385879	DQ059045
Chalciporus piperatus	HKAS84882	Germany	KT990562	–	KT990758	–	KT990397
Chalciporus sp.	HKAS53400	China	–	–	–	KF112821	KF112279
Chiua angusticystidiata	HKAS50282	China	KT990554	–	KT990754	MT110408	KT990390
Chiua olivaceoreticulata	HKAS59675 (type)	China	KT990699	–	KT990884	–	–
Chiua olivaceoreticulata	HKAS59706	China	KT990593	–	KT990787	KT990941	KT990428
Chiua virens	HKAS50543	China	KT990550	–	KT990751	KT990918	MT110452
Chiua viridula	MHHNU7346	China	KT990561	–	–	–	KT990394
Chiua viridula	HKAS74928 (type)	China	KF112483	–	KF112273	KF112583	KF112794
Clavaria zollingeri	AFTOL-ID563		–	–	AY857988/AH01 4578	AY780940	AY881024
Climacodon septentrionalis	AFTOL-ID767		–	–	AY864873	AY780941	AY885151
Clitocybe candicans	AFTOL-ID541		–	–	DQ447891	DQ385881	DQ408149
Collybia tuberosa	AFTOL-ID557		–	–	AY857982	AY787219	AY881025
Coltricia perennis	AFTOL-ID 447		–	–	–	AY218526	AY885147
Coniophora arida	MUCL30844		–	–	GU187457	GU187779	GU187685
Coniophora marmorata	MUCL31667		–	–	GU187448	GU187780	GU187688
Coprinus comatus	AFTOL-ID626		–	–	AY857983	AY780934	AY881026
Cortinarius iodes	AFTOL-ID285		–	–	AY857984	AY536285	AY881027
Costatisporus caerulescens	Henkel 9061	Guyana	–	–	–	LC053663	LC053664
Crocinoboletus laetissimus	OR0576	Thailand	–	–	KT824041	–	KT824008
Crocinoboletus laetissimus	HKAS50232	China	KT990567	–	KT990762	KT990925	–
Crocinoboletus laetissimus	HKAS59701	China	KF112436	–	–	–	KF112711
Crocinoboletus rufoaureus	HKAS53424	China	KF112435	–	KF112206	KF112533	KF112710
Crocinoboletus rufoaureus	HKAS59820	China	KF112434	–	–	KF112532	KF112709

Supplementary Table 1 Continued.

Taxon	Voucher	Locality	28S	ITS	*TEF1*	*rpb1*	*rpb2*
Cryptococcus neoformans	CBS918	JN989412	–	–	JN989412	JN989346	EF211741
Cupreoboletus poikilochromus	GS-10070	Italy	KT157060	–	KT157072	KT157066	KT157068
Cyanoboletus brunneoruber	HKAS63504	China	KF112368	–	KF112194	KF112531	KF112702
Cyanoboletus brunneoruber	HKAS80579 (1)	China	KT990568	–	KT990763	KT990926	KT990401
Cyanoboletus brunneoruber	HKAS80579 (2)	China	KT990569	–	KT990764	KT990927	KT990402
Cyanoboletus cyaneitinctus	JAB_184		MW662584	–	–	MW737504	MW737467
Cyanoboletus cyaneitinctus	Farid_920		MW662579	–	–	MW737503	MW737465
Cyanoboletus fagaceophilus	HKAS 126556	China	OQ888718	–	OQ873455	OQ873473	OQ873494
Cyanoboletus hymenoglutinosus	DC 14-010	India	KT860060	–	–	–	–
Cyanoboletus instabilis	HKAS59554	China	KF112412	–	KF112186	KF112528	KF112698
Cyanoboletus macroporus	DC 21-02	India	OQ860239	–	–	–	ON364552
Cyanoboletus macroporus	DC 21-24	India	OQ860241	–	–	–	OQ876894
Cyanoboletus mediterraneensis	HAI B12-077	Israel	OM801212	–	–	–	–
Cyanoboletus paurianus	KD 22-008	India	OQ859920	–	–	–	OQ914389
Cyanoboletus paurianus	KD 22-009	India	OQ859919	–	–	–	OQ914388
Cyanoboletus pulverulentus	MG 628a	Italy	KT157064	–	–	–	KT157069
Cyanoboletus pulverulentus	TUR-A 208930	Italy	MZ265200	–	–	–	MZ277230
Cyanoboletus pulverulentus	9606	USA	KF030313	–	KF030418	KF030364	–
Cyanoboletus sinopulverulentus	HKAS59609	China	KF112366	–	KF112193	KF112529	KF112700
Cyanoboletus sp.	HKAS90208-2	China	–	–	KT990767	–	KT990405
Cyanoboletus sp.	HKAS90208-1	China	KT990571	–	KT990766	–	KT990404
Dacryopinax spathularia	GEL5052		–	–	–	AY786054	AY881020
Erythrophylloporus aurantiacus	REH7271	Costa Rica	–	–	MH614715	–	MH614761
Erythrophylloporus cinnabarinus	GDGM70536	China	MH374045	–	MH378802	MH374031	MH374035
Fistulinella olivaceoalba	HKAS59845	China	MT154768	–	MT110369	MT110405	MT110443
Fistulinella olivaceoalba	HKAS53432	China	MT154769	–	MT110370	–	–
Fistulinella olivaceoalba	HKAS53367	China	KF112439	–	KF112304	KF112615	KF112790
Fistulinella prunicolor	REH9502	Australia	JX889648	–	JX889690	–	–
Fistulinella salmonea	HKAS80671 (type)	China	MT154766	–	–	MT110404	–
Fistulinella salmonea	HKAS106323	China	MT154767	–	MT110368	–	–
Fistulinella viscida	PDD75695	New Zealand	MW114854	–	–	–	–
Fomitiporia mediterranea	Michael Fischer 3/22		–	–	–	AY803748	AY885149
Fomitopsis pinicola	MB03-036		–	–	–	AY786056	AY885152

Supplementary Table 1 Continued.

Taxon	Voucher	Locality	28S	ITS	*TEF1*	*rpb1*	*rpb2*
Gautieriaotthii	AFTOL-ID466		–	–	AY864865	AY218486	AY883434
Grifola frondosa	DSH s.n.		–	–	AY864876	AY786057	AY885153
Grifola sordulenta	TENN55054		–	–	AY864877	AY786058	AY885154
Gymnogaster boletoides	NY01194009 (REH9455)	China	KT990572	–	KT990768	–	KT990406
Gyrodon sp.	HKAS57588	China	–	–	KF112640	KF112817	KF112275
Harrya atriceps	REH7403	Costa Rica	JX889662	–	JX889702	–	–
Harrya atrogrisea	HKAS50542 (type)	China	KT990694	–	KT990880	KT991024	KT990499
Harrya chromapes	HKAS50527	China	–	–	KF112580	KF112792	KF112270
Harrya chromipes	HKAS50527	China	KF112437	–	KF112270	KF112580	KF112792
Harrya chromipes	HKAS59217	China	HQ326931	–	HQ326864	MT110406	MT110451
Harrya moniliformis	HKAS49627	China	KT990695	–	KT990881	KT991025	KT990500
Harrya moniliformis	HKAS51181	China	KT990591	–	KT990785	KT990939	KT990426
Harrya subalpina	HKAS50546	China	KT990692	–	KT990879	KT991022	MT110450
Heimioporus retisporus	HKAS52237	China	KF112347	–	KF112228	–	KF112806
Heimioporus subretisporus	HKAS52236	China	KF112346	–	KF112227	–	KF112807
Hemilanmaoa retistipitatus	HMJAU 60052	china	OP380695	–	OP495816	OP495812	OP495814
Hongoboletus sp.	OR1002	Thailand	–	–	MH645593	–	MH645601
Hongoboletus ventricosus	TNS-F-44611	Japan	OQ888732	–	–	OQ873487	OQ873507
Hortiboletus aff. *rubellus*	MB03-033	USA	KF030294	–	KF030419	KF030371	–
Hortiboletus amygdalinus	HKAS54242	China	KT990580	–	KT990776	–	KT990415
Hortiboletus amygdalinus	HKAS54166	China	KT990581	–	KT990777	KT990933	KT990416
Hortiboletus arduinus	FHMU3323	China	MT646432	–	MT646447	–	–
Hortiboletus arduinus	FHMU3324	China	MT646439	–	MT646448	–	–
Hortiboletus cf. *rubellus*	iNat31879606	USA	–	MN498119	–	–	–
Hortiboletus indorubellus	DC 14–002	India	–	KT319647	–	–	–
Hortiboletus indorubellus	LS15	Pakistan	MK002872	MK002767	–	–	–
Hortiboletus indorubellus	DC 14–001	India	KU566807	–	–	–	–
Hortiboletus kohistanensis	AST22 (LAH35285)	Pakistan	–	MG988193	–	–	–
Hortiboletus kohistanensis	AST48 (LAH35327)	Pakistan	MG988187	MG988192	–	–	–
Hortiboletus napaeus	N.K. Zeng1863 (FHMU3325)	China	MT646438	MT646445	MT646449	–	–
Hortiboletus napaeus	N.K. Zeng2272 (FHMU3326)	China	MT646433	MT646440	MT646450	–	–

Supplementary Table 1 Continued.

Taxon	Voucher	Locality	28S	ITS	*TEF1*	*rpb1*	*rpb2*
Hortiboletus napaeus	N.K. Zeng2520 (FHMU3327)	China	MT646434	MT646441	–	–	–
Hortiboletus napaeus	N.K. Zeng2736 (FHMU3328)	China	MT646435	MT646442	MT646451	–	–
Hortiboletus napaeus	N.K. Zeng2887 (FHMU3329)	China	MT646436	MT646443	MT646452	–	–
Hortiboletus rubellus	SJ113 (LAH35030)	Pakistan	–	KX907539	–	–	–
Hortiboletus rubellus	FLAS-F-61506	USA	–	MH211937	–	–	–
Hortiboletus rubellus	FLAS-F-60315	USA	–	MF153033	–	–	–
Hortiboletus rubellus	FLAS-F-60513	USA	–	MH211664	–	–	–
Hortiboletus rubellus	FLAS-F-60503	USA	–	MH211661	–	–	–
Hortiboletus rubellus	Mushroom Observer 326,548	USA	–	MH802590	–	–	–
Hortiboletus rubellus	S.D. Russell Myco-Map 6338	USA	–	MK560106	–	–	–
Hortiboletus rubellus	52A	Spain	–	MN652008	–	–	–
Hortiboletus sp.	N.K. Zeng3152 (FHMU2113)	China	MT646437	MT646444	MT646446	–	–
Hortiboletus sp.	DD614	USA	MH203598	MH168538	–	–	–
Hortiboletus sp.	JLF6662	USA	MN294425	MN306135	–	–	–
Hortiboletus sp.	JLF6654	USA	MN294424	MN306134	–	–	–
Hortiboletus sp.	AB17	USA	–	MH796997	–	–	–
Hortiboletus sp.	HKAS51292	China	KF112369	–	KF112181	KF112547	KF112692
Hortiboletus sp.	HKAS76673	China	KF112370	–	KF112182	KF112548	KF112693
Hortiboletus sp.	HKAS50466	China	KF112372	–	KF112183	KF112549	KF112694
Hortiboletus sp.	HKAS51239	China	KF112425	–	KF112184	KF112550	KF112695
Hortiboletus subpaludosus	HKAS52659	China	KT990582	–	KT990778	–	KT990417
Hortiboletus subpaludosus	HKAS68158	China	KT990583	–	KT990779	KT990934	KT990418
Hortiboletus subpaludosus	HKAS59608	China	KF112371	–	KF112185	KF112551	KF112696
Hygrocybe conica	PBM918		–	–	–	AY803747	AY883425
Hygrophoropsis aurantiaca	AFTOLID714		–	–	AY858961	AY786059	AY883427
Hygrophorus pudorinus	AFTOL-ID1723		–	–	DQ447912	DQ472725	DQ447891
Imleria aff. *badia*	MB03-098a	USA	KF030355	–	KF030423	KF030393	–
Imleria badia	Xb2	Germany	KF030357	–	KF030422	–	–

Supplementary Table 1 Continued.

Taxon	Voucher	Locality	28S	ITS	*TEF1*	*rpb1*	*rpb2*
Imleria badia	HKAS74714	China	KF112375	–	–	KF112609	–
Imleria obscurebrunnea	HKAS52557	China	KC215220	KC215207	KC215243	KC215225	KC215234
Imleria subalpina	HKAS74712	China	KC215218	KC215208	KC215246	KC215230	KC215239
Imleria floridana	Franck 3973	USA	MN584687	–	MN584684	MN584678	MN584681
Imleria floridana	Franck 4234	USA	MN584688	–	MN584685	MN584679	MN584682
Imleria floridana	Franck 4235	USA	MN584689	–	MN584686	MN584680	MN584683
Imleria parva	HKAS 55341	China	KC215216	–	KC215252	KC215229	KC215238
Inocybe cookei	AFTOL-ID520		–	–	DQ447915	DQ385884	DQ435790
Lactarius deceptivus	AFTOL-ID 682		–	–	AY864884	AY803749	AY885158
Lanmaoa angustispora	HKAS74765	China	KF112322	–	KF112159	KF112521	KF112680
Lanmaoa angustispora	HKAS74752	China	KM605139	–	KM605154	KM605166	KM605177
Lanmaoa angustispora	HKAS74759	China	KM605140	–	KM605155	KM605167	KM605178
Lanmaoa asiatica	HKAS54094	China	KF112353	–	KF112161	KF112522	KF112682
Lanmaoa asiatica	HKAS63516	China	KT990584	–	KT990780	KT990935	KT990419
Lanmaoa carminipes	MB06-061	USA	–	–	–	KF030363	–
Lanmaoa flavorubra	NY775777	Costa Rica	JQ924339	–	KF112160	–	KF112681
Lanmaoa pseudosensibilis	DS615-07	USA	KF030257	–	KF030407	–	–
Leccinum variicolor	HKAS57758	China	–	–	KF112591	KF112725	KF112251
Leucogyrophana mollusca	DAOM138006	USA	–	–	GU187468	GU187817	–
Marasmius alliaceus	AFTOL-ID556		–	–	AY860526	AY786060	AY883430
Mycena amabilissima	AFTOL-ID1686		–	–	DQ447926	DQ474121	GU187727
Neoboletus antillanus	JBSD127417	Dominican Republic	MK388302	–	–	–	MK488082
Neoboletus brunneissimus	HKAS52660	China	KF112314	–	KF112143	KF112492	KF112650
Neoboletus brunneorubrocarpus	HKAS 126559	China	OQ888720	–	OQ873457	OQ873475	OQ873496
Neoboletus hainanaensis	HKAS63515	China	KT990614	–	KT990808	KT990964	KT990449
Neurospora crassa	MUCL 19026		–	–	XM_959004	XM_952013	XM_959775
Parvixerocomus aokii	HKAS59812	China	KF112378	–	KF112266	KF112597	–
Parvixerocomus pseudoaokii	HKAS52633	China	KF112379	–	KF112267	KF112598	KF112736
Phanerochaete chrysosporium	FPL5175		–	–	AY864880	AY854086	AY885155
Phlebia radiata	AFTOL-ID 484		–	–	AY864881	AY218502	AY885156
Phlebopus aff. *portentosus*	HKAS52855	China	–	–	KF112647	KF112822	KF112282
Pluteus romellii	AFTOL-ID625		–	–	AY862187	AY786063	AY883433
Porphyrellus aff. *alboater*	HKAS55375	China	KT990622	–	KT990816	KT990969	–

Supplementary Table 1 Continued.

Taxon	Voucher	Locality	28S	ITS	*TEF1*	*rpb1*	*rpb2*
Porphyrellus brunneus	REH9508	Australia	JX889646	–	JX889688	–	–
Porphyrellus castaneus	HKAS52554	China	KT990697	–	KT990883	KT991026	KT990502
Porphyrellus castaneus	HKAS63076	China	KT990548	–	KT990749	KT990916	KT990386
Porphyrellus castaneus	HKAS68575	China	KT990560	–	–	–	–
Porphyrellus holophaeus	HKAS59407	China	KT990708	–	KT990888	KT991030	KT990506
Porphyrellus nigropurpureus	HKAS52685	China	KT990627	–	KT990821	KT990973	KT990459
Porphyrellus nigropurpureus	HKAS53370	China	KT990628	–	KT990822	KT990974	KT990460
Porphyrellus orientifumosipes	HKAS75078	China	KF112481	–	KF112242	–	KF112717
Porphyrellus orientifumosipes	HKAS53372	China	KT990629	–	KT990823	KT990975	KT990461
Porphyrellus porphyrosporus	HKAS48585	China	KT990543	–	KT990745	KT990911	KT990382
Porphyrellus porphyrosporus	HKAS49182	China	KT990544	–	KT990746	KT990912	KT990383
Porphyrellus sp.	HKAS53366	China	KF112480	–	KF112241	KF112610	KF112716
Pseudomerulius curtisii	REH8912	USA	–	–	GU187474	GU187796	GU187731
Pulveroboletus africanus	ADK4650	Togo	–	–	KT824025	–	KT823992
Pulveroboletus brunneopunctatus	HKAS74933	China	KF112407	–	KF112262	KF112545	KF112713
Pulveroboletus fragrans	OR0673	Thailand	–	–	KT824043	–	KT824010
Pulveroboletus macrosporus	HKAS58860	China	KF112408	–	KF112263	KF112543	KF112714
Pulveroboletus sokponianus	SAB0629	Benin	–	–	MH983002	–	MH983003
Pulveroboletus sp.	HKAS58860	China	–	–	KF112543	KF112714	KF112263
Ramaria rubella	PBM2408		–	–	–	AY786064	AY883435
Retiboletus aff. *nigerrimus*	HKAS59699	China	–	–	JQ928592	JQ928603	JQ928582
Royoungia boletoides	REH8774	Australia	JX889660	–	JX889701	–	–
Royoungia coccineinana	HKAS68927	China	KT990508	–	–	KT990889	KT990347
Royoungia coccineinana	HKAS107311	China	MW114848	–	MW165271	–	MW165287
Royoungia grisea	HKAS90183 (type)	China	KT990546	–	–	KT990914	–
Royoungia palumana	REH9445	Australia	JX889652	–	JX889693	–	–
Royoungia reticulata	HKAS 52253	China	NG_059623	–	KT990786	KT990940	KT990427
Royoungia reticulata	HKAS59704	China	KT990594	–	–	KT990942	MT110445
Royoungia reticulata	HKAS49445	China	KT990557	–	KT990757	KT990924	KT990393
Royoungia rubina	HKAS53379 (type)	China	MT154776	–	KF112274	–	KF112796
Rubroboletus dupainii	JAM0607	USA	KF030251	–	KF030413	KF030361	–
Rubroboletus flavus	HKAS 90906	China	OQ888722	–	OQ873459	OQ873477	OQ873497
Rubroboletus latisporus	HKAS63517	China	KP055022	–	KP055019	KP055025	KP055028

Supplementary Table 1 Continued.

Taxon	Voucher	Locality	28S	ITS	*TEF1*	*rpb1*	*rpb2*
Rubroboletus latisporus	HKAS80358	China	KP055023	–	KP055020	KP055026	KP055029
Rubroboletus rhodosanguineus	4252	USA	KF030252	–	KF030412	–	–
Rubroboletus rhodoxanthus	HKAS84879	Germany	KT990637	–	KT990831	KT990981	KT990468
Rubroboletus serpentiformis	HKAS 126557	China	OQ888723	–	OQ873460	OQ873478	OQ873498
Rubroboletus sinicus	HKAS68620	China	KF112319	–	KF112146	KF112504	KF112661
Rubroboletus sinicus	HKAS56304	China	KJ605673	–	KJ619483	KJ619482	KP055031
Rugiboletus andinus	REH-7705	Costa Rica	–	–	MK721111	–	MK766316
Rugiboletus brunneiporus	HKAS83209		KM605134	–	KM605144	–	KM605168
Rugiboletus brunneiporus	HKAS83209	China	KM605134	–	KM605144	KM605158	KM605168
Rugiboletus brunneiporus	HKAS68586	China	–	–	KF112534	KF112719	KF112197
Rugiboletus extremiorientalis	HKAS63635	China	KF112403	–	KF112198	–	KF112720
Rugiboletus extremiorientalis	OR0406	Thailand	–	–	MG212607	–	MG212647
Rugiboletus extremiorientalis	HKAS74754	Thailand	–	–	KT990982	KT990469	KT990832
Rugiboletus sp.	HKAS55373	China	KF112362	–	KF112303	KF112588	KF112804
Rugiboletus sp.	HKAS55373	China	–	–	KF112588	KF112804	KF112303
Schizosaccharomyces pombe	Strain972		–	–	NM_001021568	NM_001018498	NM_001022750
Serpula himantioides	30528	Belgium	–	–	GU187480	GU187808	GU187748
Singerocomus inundabilis	Henkel 9199	Guyana	–	–	–	LC043088	LC043089
Stereum hirsutum	AFTOL-ID 492		–	–	AY864886	AY218520	AY885159
Strobilomyces atrosquamosus	HKAS55368	China	KT990648	–	KT990839	KT990989	KT990476
Strobilomyces echinocephalus	HKAS59420	China	KF112463	–	KF112256	KF112600	KF112810
Strobilomyces floccopus	AFTOL-ID 716 (MB03-102)	–	AY684155	–	AY883428	AY858964	AY858963
Strobilomyces seminudus	HKAS80400	China	KT990646	–	KT990834	KT990984	KT990471
Strobilomyces sp.	HKAS74809	China	KF112459	–	KF112254	KF112599	KF112808
Strobilomyces sp.	HKAS74911	China	KF112460	–	KF112255	KF112601	KF112809
Strobilomyces sp.	HKAS53348	China	KF112462	–	KF112257	KF112602	KF112811
Strobilomyces sp.	HKAS74865	China	KF112467	–	KF112258	KF112603	KF112812
Strobilomyces sp.	HKAS59435	China	KF112464	–	–	KF112605	KF112814
Strobilomyces strobilaceus	HKAS75466	China	KT990644	–	KT990836	KT990986	KT990473
Strobilomyces verruculosus	HKAS59637	China	KT990645	–	KT990838	KT990988	KT990475
Suillellus amygdalinus	112605ba	USA	JQ326996	–	JQ327024	KF030360	–

Supplementary Table 1 Continued.

Taxon	Voucher	Locality	28S	ITS	*TEF1*	*rpb1*	*rpb2*
Suillellus amygdalinus	NY00035656 (Thiers54483)	USA	KT990650	–	KT990840	KT990990	KT990477
Suillellus flaviporus	HKAS 123826	China	OQ888726	–	OQ873463	OQ873481	OQ873501
Suillellus lacrybasidius	HMJAU60202 (W3194)	China	OM230174	OM237315	OM285117	OM285113	OM285115
Suillellus lacrybasidius	HMJAU60203 (W3229)	China	OM230172	OM237338	OM285116	–	OM285114
Suillellus luridus	VDKO0241b	Belgium	–	–	KT824047	–	KT824014
Suillellus pinophilus	HKAS 126550	China	OQ888729	–	OQ873466	OQ873484	OQ873504
Suillellus subamygdalinus	HKAS57262	China	KF112316	–	KF112174	KF112501	KF112660
Suillellus subamygdalinus	HKAS53641	China	KT990651	–	KT990841	KT990991	KT990478
Suillellus subamygdalinus	HKAS57953	China	KT990652	–	KT990842	KT990992	–
Suillellus subamygdalinus	HKAS74745	China	KT990653	–	KT990843	KT990993	KT990479
Suillellus yunnanensis	HKAS 126548	China	OQ888730	–	OQ873467	OQ873485	OQ873505
Suillus aff. *granulatus*	HKAS57622	China	–	–	KF112646	KF112824	KF112281
Suillus pictus	AFTOL-ID717		–	–	AY858965	AY786066	AY883429
Sutorius aff. *eximus*	HKAS56291	China	–	–	KF112585	KF112803	KF112208
Sutorius australiensis	REH9280	Australia	JQ327005	–	JQ327031	–	–
Sutorius eximius	REH9400	USA	JQ327004	–	JQ327029	–	–
Sutorius eximius	HKAS52672	China	KF112399	–	KF112207	KF112584	KF112802
Sutorius ferrugineus	HKAS77617	China	KT990595	–	KT990788	KT990943	KT990430
Sutorius ferrugineus	HKAS77718	China	KT990596	–	KT990789	KT990944	KT990431
Sutorius flavidus	HKAS59443	China	KU974139	–	KU974136	KU974142	KU974144
Sutorius flavidus	HKAS58724	China	KU974140	–	KU974137	KU974143	KU974145
Sutorius rubriporus	HKAS57512	China	KF112327	–	KF112151	KF112498	KF112656
Sutorius sanguineoides	HKAS55440	China	KF112315	–	KF112145	KF112499	KF112652
Sutorius tomentulosus	HKAS53369	China	KF112323	–	KF112154	KF112509	KF112659
Sutorius venenatus	HKAS57489	China	KF112325	–	KF112158	KF112515	KF112665
Tapinella atrotomentosa	7897	USA	–	–	GU187488	GU187813	GU187757
Tengioboletus glutinosus	HKAS53425	China	KF112341	–	KF112204	KF112578	KF112800
Tengioboletus reticulatus	HKAS53426	China	KF112491	–	KF112313	KF112649	KF112828
Tengioboletus subglutinosus	HMJAU59035 (T293)	China	OL588197	–	OL739118	OL739120	OL739122
Tricholomopsis decora	AFTOL-ID537		–	–	DQ447943	DQ408112	DQ029195

Supplementary Table 1 Continued.

Taxon	Voucher	Locality	28S	ITS	*TEF1*	*rpb1*	*rpb2*
Tylopilus aff. *chromapes*	01-513	Africa	JX889672	–	JX889682	–	–
Tylopilus aff. *virens*	01-541	Africa	JX889677	–	JX889687	–	–
Tylopilus alboater	TH6941	USA	AY612832	–	–	–	–
Tylopilus albopurpureus	HKAS84693	China	MT154739	–	MT110352	MT110390	MT110425
Tylopilus albopurpureus	HKAS88998 (type)	China	MT154740	–	MT110353	MT110391	MT110426
Tylopilus alpinus	HKAS90204	China	KT990643	–	–	MT110389	–
Tylopilus alpinus	HKAS55438	China	KF112404	–	KF112191	KF112538	KF112687
Tylopilus argillaceus	HKAS90201	China	KT990588	–	KT990783	–	–
Tylopilus argillaceus	HKAS90186	China	KT990589	–	KT990784	–	KT990424
Tylopilus atripurpureus	HKAS50208	China	KF112472	–	KF112283	KF112620	KF112799
Tylopilus atronicotianus	snWV	USA	KF030293	–	–	–	–
Tylopilus atroviolaceobrunneus	HKAS84351	China	KT990625	–	KT990819	–	–
Tylopilus aurantiacus	NY2072258	Thailand	EU430740	–	–	–	–
Tylopilus aurantiacus	HKAS59700 (type)	China	KF112458	–	KF112223	KF112619	KF112740
Tylopilus badiceps	MB03-052	USA	KF030336	–	–	–	–
Tylopilus badiceps	78206	USA	KF030335	–	KF030429	–	–
Tylopilus balloui	R.E. Halling8526	Belize	EU430736	–	–	EU434336	–
Tylopilus balloui	R.E. Halling8521	Belize	EU430735	–	–	EU434339	–
Tylopilus balloui	TH6385	Guyana	AY612823	–	–	–	–
Tylopilus balloui	TH8409	Guyana	HQ161873	–	–	HQ161842	–
Tylopilus balloui	R.E. Halling8292	USA	EU430734	–	–	–	–
Tylopilus balloui	T.W. Osmund-son1030	USA	EU430737	–	–	EU434338	–
Tylopilus brunneirubens	HKAS59664	China	KT990709	–	MT110349	MT110387	MW165290
Tylopilus brunneirubens	HKAS87073	China	MT154737	–	MT110350	–	MT110423
Tylopilus brunneirubens	HKAS88992	China	MT154738	–	MT110351	MT110388	MT110424
Tylopilus brunneirubens	HKAS52609	China	KT990626	–	KT990820	KT990972	–
Tylopilus brunneirubens	HKAS53388	China	KF112405	–	KF112192	KF112539	KF112688
Tylopilus castanoides	HKAS92325	China	MT154723	–	MW165267	–	–
Tylopilus felleus	HKAS54926	China	KF112411	–	HQ326866	KF112575	KF112737
Tylopilus felleus	HKAS90203	China	KT990545	–	KT990747	KT990913	KT990384
Tylopilus formosus	PDD72637	New Zealand	HM060319	–	–	–	–
Tylopilus formosus	PDD72637	New Zealand	HM060319	–	–	–	–
Tylopilus fuligineoviolaceus	HKAS92013	China	MT154721	–	MT110341	MT110382	MT110416

Supplementary Table 1 Continued.

Taxon	Voucher	Locality	28S	ITS	*TEF1*	*rpb1*	*rpb2*
Tylopilus fuscatus	HKAS59838	China	MW114857	–	–	–	–
Tylopilus griseiolivaceus	JBSD127430	–	MN115801	–	–	–	–
Tylopilus griseipurpureus	HKAS90200	China	KT990624	–	KT990818	KT990971	KT990458
Tylopilus griseolus	HKAS106432	China	MT154734	–	MT110347	MT110386	–
Tylopilus griseolus	HKAS106429	China	MT154735	–	MT110348	MW165281	–
Tylopilus griseolus	HKAS99967 (type)	China	MT154736	–	MW165266	–	MW165284
Tylopilus griseoviridis	HKAS99999 (type)	China	MW114856	–	–	–	–
Tylopilus himalayanus	HKAS107146	China	MT154741	–	–	–	–
Tylopilus himalayanus	HKAS91278	China	MT154742	–	MT110354	MT110392	MT110427
Tylopilus himalayanus	HKAS93425	China	MT154743	–	MT110355	MT110393	–
Tylopilus himalayanus	DC17–25 (type)	India	MG799328	–	–	–	–
Tylopilus indecisus	98/98	USA	AF456820	–	–	–	–
Tylopilus jiangxiensis	HKAS107152 (type)	China	MT154731	–	–	–	–
Tylopilus jiangxiensis	HKAS105250	China	MN304779	–	MN304797	MN304785	MN304791
Tylopilus jiangxiensis	HKAS105251	China	MN304780	–	MN304798	MN304786	MN304792
Tylopilus leucomycelinus	JBSD127420	Dominican Republic	MN115803	–	–	–	MN095210
Tylopilus microsporus	HKAS59661	China	–	–	KF112614	KF112798	KF112225
Tylopilus neofelleus	HMAS84730 (type)	China	KM975494	–	–	–	–
Tylopilus neofelleus	HKAS59661	China	KF112450	–	KF112225	KF112614	KF112798
Tylopilus obscureviolaceus	HKAS80115	China	MT154730	–	MT110345	MT110385	MT110422
Tylopilus obscureviolaceus	HKAS90202	China	KT990623	–	KT990817	KT990970	KT990457
Tylopilus olivaceobrunneus	HKAS107145 (type)	China	MT154722	–	–	–	–
Tylopilus oradivensis	R.E. Halling 8187	Costa Rica	EU430732	–	–	EU434342	–
Tylopilus otsuensis	HKAS53401	China	KF112449	–	KF112224	KF112613	KF112797
Tylopilus otsuensis	HKAS50240	China	KT990553	–	KT990753	KT990921	–
Tylopilus phaeoruber	HKAS74925	China	KF112473	–	KF112222	KF112577	KF112739
Tylopilus plumbeoviolaceoides	GDGM21040	China	MT154720	–	–	–	–
Tylopilus plumbeoviolaceoides	GDGM20311	China	KM975498	–	–	–	–
Tylopilus plumbeoviolaceus	NYBG0009	USA	KY432825	–	–	–	–
Tylopilus plumbeoviolaceus	190/83	USA	AF457405	–	–	–	–
Tylopilus plumbeoviolaceus	MB06-056	USA	KF030350	–	KF030439	KF030395	–
Tylopilus pseudoalpinus	HKAS84602	China	MW114855	–	MW165268	–	–
Tylopilus pseudoballoui	DC17–30 (type)	India	MG799327	–	–	–	–

Supplementary Table 1 Continued.

Taxon	Voucher	Locality	28S	ITS	*TEF1*	*rpb1*	*rpb2*
Tylopilus pseudoballoui	HKAS51151	China	KT990590	–	MW165265	–	KT990425
Tylopilus purpureorubens	HKAS80106	China	MT154726	–	MT110343	–	–
Tylopilus purpureorubens	HKAS80605 (type)	China	MT154727	–	MT110344	–	MT110420
Tylopilus rubrobrunneus	BD329	USA	HQ161876	–	–	HQ161845	–
Tylopilus rubrotinctus	HKAS106435	China	MW114852	–	–	–	–
Tylopilus rubrotinctus	HKAS106435	China	MW114851	–	–	–	–
Tylopilus rubrotinctus	HKAS78271	China	MT154732	–	MT110346	–	MW165291
Tylopilus rubrotinctus	HKAS80684 (type)	China	MT154733	–	MW165264	–	MW165283
Tylopilus rufobrunneus	HKAS106331 (type)	China	MT154714	–	MT110337	MT110380	MT110413
Tylopilus rufobrunneus	HKAS106466	China	MT154715	–	MT110338	MT110381	–
Tylopilus rufonigricans	TH6376	Guyana	AY612835	–	–	–	–
Tylopilus sp.	HKAS50211	China	KT990552	–	KT990752	KT990920	KT990389
Tylopilus sp.	HKAS90198	China	KT990559	–	–	–	–
Tylopilus subotsuensis	HKAS106464	China	MT154724	–	MT110342	MT110383	MT110418
Tylopilus subotsuensis	HKAS107180	China	MW114847	–	–	–	–
Tylopilus variobrunneus	snHor02	–	KF030316	–	–	–	–
Tylopilus vinaceipallidus	HKAS50210	China	KF112431	–	KF112221	KF112576	KF112738
Tylopilus violaceobrunneus	HKAS89443 (type)	China	KT990702	–	KT990886	KT991028	KT990504
Tylopilus violaceorubrus	HKAS107143	China	MT154728	–	–	–	–
Tylopilus violaceorubrus	HKAS107154 (type)	China	MT154729	–	–	–	MW165286
Tylopilus virescens	FHMU1004	China	MG365898	–	MG365904	–	–
Tylopilus virescens	FHMU2812	China	MG365895	–	–	–	–
Ustilago maydis	PBM2469		–	–	KP322928	AY485636	AY885160
Veloporphyrellus aff. *velatus*	HKAS57490	China	–	–	KF112555	KF112733	KF112209
Veloporphyrellus alpinus	HKAS68301	China	JX984538	–	JX984550	–	–
Veloporphyrellus alpinus	HKAS57490	China	KF112380	–	KF112209	KF112555	KF112733
Veloporphyrellus conicus	BZ2408	Belize	JX984545	–	–	–	–
Veloporphyrellus conicus	BZ1670	Belize	JX984543	–	JX984555	–	–
Veloporphyrellus gracilioides	HKAS53590	China	KF112381	–	KF112210	KF112556	KF112734
Xanthoconium affine	NY00815399 (REH8660)	USA	KT990661	–	KT990850	KT990999	KT990486
Xanthoconium affine var. *maculosum*	NY01193907 (REH9607)	USA	KT990660	–	KT990849	KT990998	KT990485
Xanthoconium porophyllum	HKAS90217	China	KT990662	–	KT990851	KT991000	KT990487

Supplementary Table 1 Continued.

Taxon	Voucher	Locality	28S	ITS	*TEF1*	*rpb1*	*rpb2*
Xanthoconium purpureum	NY00720964 (REH8712)	USA	KT990663	–	KT990852	KT991001	–
Xanthoconium sinense	HKAS77651	China	KT990664	–	KT990853	KT991002	KT990488
Xanthoconium stramineum	3518	USA	KF030353	–	KF030428	KF030386	–
Xerocomellu aff. *Rubellus*	HKAS51239	China	–	–	KF112550	KF112695	KF112184
Xerocomellus chrysenteron	Xch1	Germany	AF050647	–	KF030415	KF030365	–
Xerocomellus chrysenteron	HKAS56494	China	KF112357	–	KF112172	KF112526	KF112685
Xerocomellus cisalpinu	AT2005034	Finland	KF030354	–	KF030417	KF030367	–
Xerocomellus cisalpinus	PDD94421	New Zealand	JQ924322	–	KF112171	KF112525	KF112686
Xerocomellus communis	HKAS68204	China	KT990671	–	KT990859	KT991009	KT990495
Xerocomellus corneri	HKAS90206	Philippines	KT990669	–	KT990857	KT991007	KT990493
Xerocomellus corneri	HKAS52503	China	KT990668	–	KT990856	KT991006	KT990492
Xerocomellus sinensis	HKAS50467	China	KT990670	–	KT990858	KT991008	KT990494
Xerocomellus sp.	HKAS56311	China	KF112340	–	KF112170	KF112524	KF112684
Xerocomellus zelleri	REH8724	USA	KF030271	–	KF030416	KF030366	–
Xerocomus rubellus	IB2004272	Austria	–	EF644119	–	–	–
Xerocomus sp.	T2210	Pakistan	–	MG988195	–	–	–
Xerocomus sp.	AST2218	Pakistan	–	MG988194	–	–	–
Xerocomus sp.	AST22B	Pakistan	MG988189	–	–	–	–
Xerocomus sp.	HKAS76666	China	–	–	KF112631	KF112789	KF112292
Zangia chlorinosma	HKAS48695	China	HQ326939	–	–	MW165274	–
Zangia citrina	HKAS52677	China	HQ326940	–	HQ32687	–	–
Zangia citrina	HKAS52684	China	HQ326941	–	HQ326872	–	–
Zangia erythrocephala	HKAS52843	China	HQ326943	–	–	–	–
Zangia erythrocephala	HKAS52844	China	HQ326944	–	–	–	–
Zangia erythrocephala	HKAS75046	China	–	–	KF112579	KF112791	KF112269
Zangia olivacea	HKAS45445 (type)	China	HQ326945	–	HQ326873	MW165275	–
Zangia olivaceobrunnea	HKAS52272	China	HQ326948	–	HQ326876	MW165279	MW165289
Zangia olivaceobrunnea	HKAS52275	China	HQ326947	–	HQ326875	–	–
Zangia roseola	HKAS75046	China	KF112414	–	KF112269	KF112579	KF112791
Boletellus putuoensis	**HMJAU68184 (W3380)**	**China**	**OR673998**	**OR673988**	**OR683471**	**OR683476**	**OR683482**
Boletellus putuoensis	**HMJAU68185 (W3383)**	**China**	**–**	**OR673989**	**OR683472**	**OR683477**	**OR683483**

Supplementary Table 1 Continued.

Taxon	Voucher	Locality	28S	ITS	*TEF1*	*rpb1*	*rpb2*
Butyriboletus hainanensis	**HMJAU68167 (M725)**	**China**	**OR673991**	**–**	**OR683467**	**–**	**–**
Cyanoboletus viscidiceps	**HMJAU68168 (R345)**	**China**	**OR673995**	**–**	**OR683468**	**OR683473**	**OR683479**
Hortiboletus arduinus	**HMJAU68182 (W3104)**	**China**	**OR704333**	–	**OR663931**	**OR663945 & OR663946**	**OR573951**
Hortiboletus arduinus	**HMJAU68183 (W3105)**	**China**	**OR704334**	–	**OR663932**	**OR663947**	**OR573952**
Hortiboletus tomentosus	**HMJAU68173 (W3110)**	**China**	**OR704335**	–	**OR663935**	**OR663949**	**–**
Hortiboletus tomentosus	**HMJAU68174 (QB10274)**	**China**	**OR704336**	–	**OR663923**	**OR663939**	**OR573957**
Hortiboletus tomentosus	**HMJAU68175 (QB10281)**	**China**	–	–	**OR663924**	**–**	**OR573958**
Hortiboletus tomentosus	**HMJAU68176 (QB10325)**	**China**	**OR704337**	–	**OR663925**	**OR663940**	**–**
Hortiboletus sinorubellus	**HMJAU68177 (W3044)**	**China**	**OR704327**	–	**OR663926**	**OR663941**	**OR573948**
Hortiboletus sinorubellus	**HMJAU68178 (W3075)**	**China**	**OR704328**	–	**OR663927**	**OR663942 & OR663943**	**–**
Hortiboletus sinorubellus	**HMJAU68179 (W3076)**	**China**	**OR704329**	–	**OR663928**	**–**	**OR573949**
Hortiboletus sinorubellus	**HMJAU68180 (W3100)**	**China**	**OR704331**	–	**OR663930**	**OR663944**	**OR573950**
Hortiboletus sinorubellus	**HMJAU68181 (W3369)**	**China**	–	–	**OR663938**	**–**	**OR573956**
Niveoboletus brunneus	**HMJAU68162 (W3351)**	**China**	**OR673997**	**–**	**OR683470**	**OR683475**	**OR683481**
Niveoboletus brunneus	**HMJAU68161 (M698)**	**China**	**OR673994**	**–**	**OR683466**	**–**	**OR683478**
Royoungia reticulata	**HMJAU68187 (LEI-647)**	**China**	**OR554117**	**–**	**OR566410**	**OR566414**	**OR566417**
Rugiboletus caeruloruber	**HMJAU68163 (M692)**	**China**	**–**	**OR558328**	**–**	**OR566422**	**OR566424**

Supplementary Table 1 Continued.

Taxon	Voucher	Locality	28S	ITS	*TEF1*	*rpb1*	*rpb2*
Rugiboletus caeruloruber	**HMJAU68164 (M730)**	**China**	**–**	**OR558329**	**OR566419**	**–**	**–**
Rugiboletus caeruloruber	**HMJAU68165 (M745)**	**China**	**OR554014**	**OR558330**	**OR566420**	**OR566423**	**OR566425**
Rugiboletus caeruloruber	**HMJAU68166 (M750)**	**China**	**–**	**OR558331**	**OR566421**	**–**	**OR566426**
Suillellus yunnanensis	**HMJAU68189 (T188)**	**China**	**OR673996**	**–**	**OR683469**	**OR683474**	**OR683480**
Tylopilus violaceobrunneus	**HMJAU68188 (W3096)**	**China**	**OR554118**	**OR575630**	**OR566411 & OR566412**	**OR566415**	**OR566418**
Xerocomellus inflatus	**HMJAU68171 (W3270)**	**China**	**OR704332**	–	**OR663936**	**OR663950**	**OR573954**
Xerocomellus inflatus	**HMJAU68172 (W3272)**	**China**	**OR704326**	–	**OR663937**	**OR663951**	**OR573955**
Xerocomellus velutinus	**HMJAU68169 (W3086)**	**China**	**OR704330**	–	**OR663929**	**–**	**–**
Xerocomellus velutinus	**HMJAU68170 (W3109)**	**China**	–	–	**OR663933 & OR663934**	**OR663948**	**OR573953**
Xerocomellus fuscoscabrosus	**HMJAU67772 (W3709)**	–	–	–	**OR828573**	–	–
Xerocomellus fuscoscabrosus	**HMJAU67773 (W3710)**	–	**OR828568**	–	**OR828572**	**OR828575**	–
Xerocomellus fuscoscabrosus	**HMJAU67774 (W3716)**	–	**OR828569**	**OR828565**	**OR828574**	–	**OR828576**
Xerocomellus roseonigrescens	**HMJAU67775 (WY72)**		**OR828570**	**OR828566**	**OR828571**	–	–
Zangia olivaceobrunnea	**HMJAU68186 (LEI-607)**	**China**	**OR554116**	**OR575629**	**OR566409**	**OR566413**	**OR566416**