



Critical taxonomic evaluation of selected *Boletellus* species (*Boletaceae*) from the Caribbean

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Abstract

Boletellus and *Aureoboletus* are among the most prominent bolete genera in the family *Boletaceae*. The diversity of these taxa in the Caribbean is high, but their species delimitation is still critical. An inclusive phylogenetic reconstruction of these genera is achieved by sequencing five loci: nuclear ribosomal DNA regions (ITS, LSU) and protein coding genes (*TEF1-α*, *RPB1*, and *RPB2*). Three target species from the Greater Antilles of the Caribbean (Dominican Republic and Puerto Rico) are included in the analysis. The phylogenetic position of these critical taxa is assessed and discussed. Accurate macro- and micromorphological descriptions are provided for *Boletellus ananas*, *B. cubensis*, and *B. domingensis*, accompanied by line drawings of their main microscopical features. *Boletellus cubensis* is documented in detail for the first time from the Dominican Republic and Puerto Rico. Moreover, DNA sequences are successfully generated from isotype specimens of the South American *Boletellus exiguus* (ITS), *B. piakaii* (ITS), the Australian *B. reminiscens* (ITS), and *B. sinapipes* (ITS), as well as from single specimens of the African *B. rubrolutescens* (ITS) and *B. sinochrysenderoides* (ITS, LSU, and *TEF1-α*) from Far Eastern Russia (the first record for that country) and integrated in the phylogeny. Several accessions of five gene markers (ITS, LSU, *TEF1-α*, *RPB1*, and *RPB2*) from five different collections of an unnamed *Aureoboletus* species from Guatemala (Mesoamerica) have also been added to the dataset. In addition, type collections of the 178-year-old material of *B. ananas* and of the infraspecific taxa *B. coccineus* var. *amarus* and *B. ananas* var. *crassotunicatus* are microscopically re-examined, and a revision of their microscopic data is provided. A full description of a couple of recent Australian collections of *Boletellus* cf. *emodensis* is also supplemented as extralimital materials. This study confirms the Caribbean as a hotspot for *Boletaceae* diversity, with the potential to fill many gaps in the global evolutionary history of this family. Our phylogenetic outcomes point towards the need for a genus-wide, revised classification of *Boletellus* and *Aureoboletus*, which is aimed at resolving higher-level infrageneric relationships. However, our results also show that it is still premature to split these potentially polyphyletic genera into smaller units, as long as a more extensive knowledge on critical taxa is lacking and species sampling is incomplete.

Keywords *Boletales* · *Boletellus ananas* · *B. cubensis* · *B. domingensis* · Central America · Multilocus molecular phylogeny · Neotropical boletes · Taxonomy · *Xerocomoideae*

Introduction

Traditional reliance on macro- and micromorphological features for fungal species identification has shown to be untenable due to the high plasticity of these phenotypical traits. Ecological strategies, chemotaxonomy, and particularly the advancement and gradual refinement

of molecular phylogenetic techniques over the past few decades have dramatically transformed our approach to the study of fungal systematics, increasingly resolving the taxonomic boundaries and evolutionary patterns in several lineages distributed across the main orders of the *Agaricomycetes* Doweld (Cao et al. 2021; He et al. 2024). In the *Boletaceae* Chevall., a combined polyphasic approach integrating morphological, ecological, chemotaxonomical, and phylogenetic(omic) data has demonstrated an impressive accuracy in delimiting taxonomic units at species and genus level as well as at higher taxonomic rank

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(subfamilies) (Nuhn et al. 2013; Wu et al. 2014, 2016; Gelardi 2021; Li And Yang 2021; Hyde et al. 2024; Tremble et al. 2024). On the other hand, despite the abundance, remarkable appearance and important ecological roles of boletes, the knowledge of their diversity and distribution, especially in tropical areas, is far from complete.

As part of an ongoing project aimed at monitoring and inventorying the diversity of *Boletales* E.-J. Gilbert in the Greater Antilles of the Caribbean with a special focus on the Dominican Republic and Puerto Rico, *Boletellus* Murrill was chosen as a target genus for further investigation. *Boletellus*, originally introduced by Murrill (1909) and typified by *B. ananas* (M.A. Curtis) Murrill, can be considered among the most species-rich genera in the family *Boletaceae*, boasting more than 65 named species worldwide (<https://www.indexfungorum.org/names/Names.asp>). Its members appear to be characterized, as traditionally established, by very small- to medium-sized basidiomes, mainly with a xerocomoid habit, a dry to more rarely viscid surface, polychromatic and variously ornamented pileus (glabrous, tomentose, verrucose, and squamulose to prominently scaly or sometimes areolate), sometimes with appendiculate velar remnants at margin, adnate to depressed and yellowish olive tubular hymenophore or occasionally with reddish pores, small and roundish to wide and angular pores, dry to viscid and smooth or pruinose, fibrillose-striate, waxy reticulate-alveolate to finely scabrous stipe surface, white to very rarely yellow basal mycelium, presence or absence of a partial veil (sometimes forming an annulus), generally whitish to yellow context, unchanging to more frequently cyanescent (and occasionally rufescent) tissues on bruising, mild taste and olive brown spore print. Microscopically, they share basidiospores generally ellipsoid-fusiform and either smooth-walled or with a versiform exosporial ornamentation (alveolate-reticulate to more frequently longitudinally finely striate or veined, prominently costate to winged with ridges of variable thickness, in some species also with delicate transversal striations on primary ridges), inamyloid or rarely dextrinoid, hymenial cystidia present, pileipellis structure variably arranged (trichoderm, palisadoderm, cutis, hymeniform, celluloderm), hymenophoral trama of the “*Boletus*-type,” absence or rarely presence of clamp connections and primarily or secondarily hemiangiocarpic to gymnocarpic ontogenetic development.

Boletellus species are predominant ectomycorrhizal (ECM) and occur in association mostly with members of the *Fagaceae* and *Pinaceae* in temperate regions but frequently also with *Casuarinaceae*, *Dipterocarpaceae*, *Fabaceae*, *Myrtaceae*, *Polygonaceae*, and possibly other mutualistic plant families (*Sapotaceae*, *Euphorbiaceae*) in tropical areas. *Boletellus* shows a cosmopolitan natural distribution (predominantly in the tropical belt and to a lesser extent in temperate regions, with most of the described taxa distributed in the northern

hemisphere and especially in China, which likely represent the main hotspots of biodiversity of *Boletellus* with a total of 15 species), with the relevant exception of Europe, where the genus has been accidentally introduced with allochthonous species (Murrill 1909; Gilbert 1931; Singer 1945, 1955, 1970, 1986; Heinemann 1951, 1954; Boedijn 1960; Perreau-Bertrand 1961, 1965, 1967; Heim and Perreau-Bertrand 1963; Thiers 1963; Snell And Dick 1970; Smith and Thiers 1971; Corner 1972; Horak 1977, 2011; Baroni and Halling 1980; Pegler and Young 1981; Bi et al. 1982; Singer et al. 1983, 1992; Wen 1985; Zang 1985, 1997; Watling And Gregory 1986; Imazeki et al. 1988; Watling And Hollands 1990; Both 1993; Engel et al. 1996; Chen et al. 1997; Nagasawa 1997; An 1998; Watling and Li 1999; Bessette et al. 2000, 2016; Ortiz-Santana et al. 2007; Watling 2008; Halling and Ortiz-Santana 2009; Zeng And Yang 2011; Henkel et al. 2012; Xue et al. 2023, 2024; Leonard 2024; Wang et al. 2025). In addition, *Boletellus* species are said to be characterized by a relatively long life-cycle (Halling et al. 2007; Watling 2008).

Basidiospore ornamentation is a hallmark of *Boletellus* species and can be considered one of the most important unifying morphological attributes; however, other than the superficially similar eusporial ornamentation, there appears to be very few morphological synapomorphies to rely on for delimiting *Boletellus* as a natural grouping. As a matter of fact, this enlarged genus as historically delimited has been demonstrated to represent, at least in part, a heterogeneous and unnatural assemblage of unrelated entities based on recent multilocus DNA sequence inferences (Binder And Fischer 1997; Binder 1999; Binder And Hibbett 2006; Nuhn et al. 2013; Wu et al. 2014, 2016; Halling et al. 2015) and phylogenomic reconstruction (Tremble et al. 2024). Hence, species in *Boletellus* sect. *Retispori* Singer (with alveolate-reticulate to rugulose-pitted basidiospores) have been confirmed to belong in *Heimioporus* E. Horak (replacing *Heimiella* Boedijn 1951 nom. illegit.) (Horak 2004; Halling et al. 2015; Zeng et al. 2018), whereas species formerly assigned to *Boletellus* sect. *Mirabiles* Singer (with very large and smooth basidiospores), sect. *Dictyopodes* Singer, sect. *Ixocephali* Singer *pro parte* (both with longitudinally ribbed basidiospores), and sect. *Allospori* Singer (with reticulate basidiospores) have recently been segregated and transferred to *Aureoboletus* Pouzar, which is closely related to *Boletellus* (Halling et al. 2015; Zhang et al. 2019; Kuo and Ortiz-Santana 2020; Tremble et al. 2024) within the *Boletaceae* subfamily *Xerocomoideae* Singer (Wu et al. 2014; Xue et al. 2023; Tremble et al. 2024; Li et al. 2025).

At present, *Boletellus* appears to be restricted to the alliance of *B. ananas* and *B. emodensis* (Berk.) Singer (*Boletellus* sect. *Boletellus*, = *B.* sect. *Ananae* Singer) and to the complex of species gravitating around *B. obscurecoccineus* (Höhn.) Singer (core *Boletellus*, according to Halling et al. 2015), along with the *B. chrysenteroides* (Snell) Snell and

B. pseudochrysenteroides A.H. Sm. & Thiers species-complexes (*Boletellus* sect. *Chrysenteroidei* Singer) (Nuhn et al. 2013; Wu et al. 2014, 2016; Halling et al. 2015; Kuo and Ortiz-Santana 2020; Lin et al. 2022; Xue et al. 2022; Tremble et al. 2024; Li et al. 2025; Wang et al. 2025). However, the monophyly of *Boletellus* in its current strict circumscription is weakly supported, although not rejected, and the genus remains paraphyletic (Halling et al. 2015) and likely in need of fragmentation in smaller generic-rank units. The taxonomic placement of *Boletellus elatus* Nagas., *B. jalapensis* (Murrill) E.-J. Gilbert, *B. shichianus* (Teng & L. Ling) Teng and *B. russellii* (Frost) E.-J. Gilbert, as well as that of *Boletus abruptibulbus* Roody, Both & B. Ortiz remains ambiguous and requires a careful re-evaluation (Halling et al. 2015; Zeng et al. 2015; Henkel et al. 2016), but the latter three species have recently been included in *Aureoboletus* (Wu et al. 2016). Similarly, the exact generic position of the neotropical fibulate *Boletellus fibuliger* Singer (Singer et al. 1983), which has not been sequenced to date, presently remains unresolved. Similarly unresolved are several *Boletellus* taxa described from tropical Africa (Beeli 1926; Heinemann 1951, 1954, 1966; Heim and Perreau-Bertrand 1963, 1964; Heinemann and Rammeloo 1990; Watling and Turnbull 1993) and many unnamed *Boletellus* reported only on a morphological basis from Australia (Watling and Gregory 1986, 1991; Watling and Li 1999; Leonard 2024), which might turn out to be misplaced. Relevant progress has been made in the knowledge of the global diversity of *Boletellus* with a number of previously described taxa recently investigated in more depth (Halling and Ortiz-Santana 2009; Halling and Fechner 2011; Zeng and Yang 2011; Ayala-Vásquez et al. 2018; Xue et al. 2023; Wang et al. 2024, 2025). However, in spite of the several new species unveiled in the last twenty-five years (Zang et al. 1999; Zang and Yuan 1999; Wang and Liu 2002; Ortiz-Santana et al. 2007; Fulgenzi et al. 2008; Mayor et al. 2008; Halling et al. 2015; Sato and Hattori 2015; Wu et al. 2016; Barbosa-Silva and Wartchow 2017; Parihar et al. 2018a; Magnago et al. 2019; Lin et al. 2022; Xu et al. 2022; Zhang and Wu 2022; Ayala-Vásquez et al. 2023a, b; Xue et al. 2023, 2024), most of the infrageneric phylogenetic relationships remain poorly resolved owing to the limited species sampling or insufficient genetic variations of the selected DNA loci. Moreover, several other *Boletellus* species are still unclassified, especially from undersampled remote areas (Tremble et al. 2024), and some taxonomic and ecological issues remain ambiguous and in urgent need of assessment. For example, the nutritional mode of *Boletellus* is a moot point.

Even though certain species are undoubtedly strictly ectomycorrhizal (ECM), *Boletellus* was generally regarded as not ECM or otherwise not necessarily or only facultatively ECM (Corner 1972; Pegler and Young 1981; Pegler 1983; Singer 1986; Watling 2008), since it can be found

growing on decayed wood such as debris, dead standing trees or rotten stumps, but also on living trees, thus suggesting a parasitic behavior (Murrill 1909, 1914, 1948, quoting Prof. F.S. Earle). Curiously, specimens are sometimes be found fruiting relatively high from the ground up to shoulder height (Singer 1945; McNabb 1967; Corner 1972; Watling and Hollands 1990; Watling 2008), or even up to two or three meters above the ground or directly on stone walls, especially with respect to *B. ananas* in neotropical regions (Singer 1970; Singer et al. 1983) and to *B. emodensis* s. l. in temperate to tropical regions of eastern Asia (Nagasawa 1997) and Australia (Leonard 2024). On the other hand, the production of basidiomes in elevated positions on woody support structures is not necessarily a prerequisite of saprotrophic nutrition (Rayner et al. 1985; Henkel et al. 2000). However, the controversial status of the trophic mode of *Boletellus* is yet to be addressed with certainty.

A discrete number of *Boletellus* species were described as new or simply recognized from the Caribbean and mainland Central America. Singer et al. (1983), Sommerkamp and Guzmán (1990), Halling (1997), Mata (1999), Flores Arzù and Simonini (2000), Halling and Mueller (2005), Ortiz-Santana et al. (2007), Flores Arzù et al. (2012) and Flores Arzù (2020) reported on the occurrence of a handful of species from Belize, Guatemala, Honduras, Nicaragua, Costa Rica, and Panama. However, the most comprehensive accounts on *Boletellus* s. l. in continental Central America were offered by Singer et al. (1992) and Gómez (1997), with as many as fourteen species and infraspecific taxa being enumerated from this region. Records of *Boletellus* species from both the Greater and Lesser Antilles include the Bahamas islands (Singer et al. 1992; Ortiz-Santana et al. 2007), Cuba (Berkeley and Curtis 1869; Kreisel 1971; Pegler 1983, 1987; Singer et al. 1992; Minter et al. 2001; Ortiz-Santana et al. 2007), Dominican Republic (Minter et al. 2001; Ortiz-Santana et al. 2007; Angelini 2022; Molero Paredes and Nolasco 2023), Guadeloupe (Patouillard 1900; Pegler 1983; Courtecuisse and Welti 2013) and Martinique (Pegler 1983; Courtecuisse and Welti 2013). Nevertheless, *Boletellus* appears to be largely understudied and underrepresented in Mesoamerica.

In order to better decipher the intimate infrageneric relationships, species-level alliances, and biogeographic patterns, a comprehensive multilocus phylogenetic reconstruction of the genus *Boletellus*, substantiated by newly acquired DNA nucleotide sequences including the nuclear ribosomal internal transcribed spacer (ITS), the nuclear ribosomal large subunit (LSU), the translation elongation factor 1- α gene (*TEF1- α*), the largest subunit of RNA polymerase II (*RPB1*), and the second largest subunit of RNA polymerase II (*RPB2*) from multiple species (*B. ananas*, *B. cubensis*, and *B. dominicensis*) yielded in the Dominican Republic and Puerto Rico,

along with related genetic materials previously deposited in public repositories, was carried out.

Type studies are extremely important for understanding the taxonomy of any fungal group. Unfortunately, only a limited number of the described *Boletaceae* species have ITS and LSU sequences of their type specimens stored in RefSeq (NCBI Reference Sequence Database) (Hyde et al. 2024). Accordingly, a thorough re-examination of the type materials of *B. ananas*, *B. coccineus* var. *amarus* (topotype) and *B. ananas* var. *crassotunicatus* Singer (holotype) was also undertaken. We succeeded in sequencing the ITS region of the isotypes of *Boletellus exiguus* T.W. Henkel & Fulgenzi, *B. piakaii* T.W. Henkel & Fulgenzi, *B. reminiscens* Halling & N.A. Fechner and *B. sinapipes* N.A. Fechner, K. Syme, R. Rob. & Halling. Moreover, the multilocus molecular genealogy revealed a putative additional member of *Boletaceae* from continental Central America (Guatemala), whose morphological affinities are still unclear. An ITS sequence was generated from a *Boletellus rubrolutescens* specimen from Cameroon (central Africa); ITS, LSU, and *TEF1-α* sequences were also generated from a Far Eastern single specimen of *Boletellus sinochrysenderoides* N.K. Zeng, R. Xue & Kuan Zhao, which represents the first confirmed record of this species in Russia. Finally, a detailed morphological description of a couple collections of the extralimital *Boletellus* cf. *emodensis* from Queensland, Australia, is supplied for further reference.

Materials and methods

Collection site and sampling

Specimens examined were collected in Sosúa, Puerto Plata Province, Jarabacoa (La Vega Province), Dominican Republic, and in the Municipality of Isabela, Puerto Rico, whereas collections of *Boletellus* cf. *emodensis* were found in the Greater Glider Conservation Area and the Anstead Bushland Reserve, both located in Queensland, Australia. Studied specimens are deposited in BR, JBSD, F, K, LE, MICG, and NY fungaria (according to Index Herbariorum, Thiers 2025) and in the personal fungal collections “ANGE,” “GS,” “MG,” and “MO” maintained by Claudio Angelini, Giampaolo Simonini, Matteo Gelardi, and Kurt O. Miller, respectively. The metadata of most studied collections is given in the following format: COUNTRY, locality, coordinates (DMS), elevation in m, habitat with putative host plants, date (dd Mmm yyyy), leg. = legittur, det. = determinator, collection number (additional collection number—if available). Nomenclatural author citations follow the Index Fungorum (2025). Geographic distribution of the studied species has also been checked

on iNaturalist (2025), MyCoPortal (2025), and Global Biodiversity Information Facility (GBIF) (2025).

Morphological studies

Macroscopic descriptions, macrochemical reactions (30% NH_4OH , 30% KOH), and ecological information, such as habitat notations, time of fruiting and associated plant communities are accompanied by detailed field notes of the fresh basidiomes. In the field, latitude, longitude, and elevation (georeferences) were determined with a Global Positioning System (GPS) receiver. Color terms in capital letters (e.g., White and Plate LIII) are from Ridgway (1912). Photographs of fungal collections were captured in natural habitat using a Nikon Coolpix 8400 camera and a Nikon D3100 camera. Macrochemical tests were carried out on fresh materials. Microscopic features were observed and recorded from revived dried materials; sections were rehydrated either in water, 5% potassium hydroxide (KOH), and anionic solution saturated with Congo red or L4 [7.2 g KOH, 160 mL glycerine, 840 mL dH_2O , 7.6 g NaCl and 5 mL Invadin (Ciba-Geigy), Cléménçon 1972]. All microscopic structures were measured from preparations in anionic Congo red. Colors and pigments were described after examination in water and 5% KOH. Measurements were made at 1000× using a calibrated ocular micrometer (Nikon Eclipse E200 optical light microscope). Basidiospores were measured directly from the hymenophore of mature basidiomes, dimensions are given as (minimum) average ± standard deviation (maximum), Q = length/width ratio with the extreme values in parentheses, Qm = average quotient (length/width ratio) ± standard deviation and average spore volume was approximated as a rotation ellipsoid [$V = (\pi \cdot L \cdot W^2)/6 \pm \text{standard deviation}$]. The notation [n/m/p] indicates that measurements were made on “n” randomly selected basidiospores from “m” basidiomes of “p” collections. The width of each basidium was measured at the widest part, and the length was measured from the apex (sterigmata excluded) to the basal septum. Radial and/or vertical sections of the pileipellis were taken midway between the center and margin of the pileus. Sections of the stipitipellis were taken from the middle part along the longitudinal axis of the stipe. Metachromatic, cyanophilic, and iodine reactions were tested by staining the basidiospores in Brilliant Cresyl blue, Cotton blue in lactophenol (<https://www.titolchimica.it>), and Melzer’s reagent (Imler 1950), respectively. Light micrographs were obtained via Micro Capture 6.9.12 Imaging software using a 5.0 MP digital camera from Diagnostic Instruments. Line drawings of microstructures were traced in free hand based on digital photomicrographs of rehydrated materials.

DNA extraction, PCR amplification, and DNA sequencin

Genomic DNA was extracted using NucleoSpin™ Plant II kit for NY and F samples. The other samples were extracted following the CTAB method (Zolan And Pukkila 1986). Amplification of the internal transcribed spacers of the nrDNA (ITS1 and ITS2) was performed following standard conditions and using several primer pairs: ITS1F with ITS4B/ITS4/ITS2 and ITS3 with ITS4B/ITS4 (White et al. 1990; Gardes And Bruns 1993). The LSU (large subunit) was amplified with the primers LR0R/LR5 and LR0R/LR7 (Cubeta et al. 1991; Hopple And Vilgalys 1999). The protein coding genes *TEF1-α* (transcription elongation factor 1-α), *RPB1* (RNA polymerase II largest subunit), and *RPB2* (RNA polymerase II second largest subunit) were amplified with EF1-983F/EF1-1567R, RPB1-B-F/RPB1-B-R, RPB2-B-F1/RPB2-B-R and bRPB2-6F/bRPB2-7.1R primer pairs (Matheny 2005; Rehner And Buckley 2005; Wu et al. 2014), respectively. Successful amplicons were purified using ExoSAP-IT (USB) and sequenced bidirectionally using BigDye3.1 in a ABI3730 DNA analyzer (Applied Biosystems). Alternatively, PCR products were sent to LGC Genomics (Berlin, Germany) and Microsynth AG (Balgach, Switzerland) for bidirectional sequencing. All produced sequences were checked and edited using Sequencher v. 5.4.6. (Gene Codes Corporation, Ann Arbor, Michigan, USA) or Geneious Prime v. 2025.0.3 (Dotmatics, Bishops Stortford, England, UK).

Sequence alignment, dataset assembly, and phylogenetic analysis

Phylogenetic analyses were carried out with newly generated sequences and sequences retrieved from GenBank (<http://www.ncbi.nlm.nih.gov/>) and UNITE (<http://unite.ut.ee/>). As far as possible, all currently known *Boletellus* and *Aureoboletus* species were included in the analysis, provided sequences were available. Sequences belonging to different loci were first aligned separately using the online version of MAFFT v. 7, for ITS and *RPB1* loci it was worked out with the E-INS-i algorithm and for the LSU, *RPB2*, and *TEF1-α* locus with G-INS-i algorithm, all under default settings (Kato And Standley 2013), then manually corrected and trimmed, and afterwards concatenated in Geneious. Taxa from the *Boletaceae* subfamily *Zangioideae* were chosen as an outgroup based on a phylogenomic analysis of *Boletaceae* (Tremble et al. 2024).

Seven different datasets were generated: Five single-locus alignments and two concatenated 5-loci alignment (ITS + LSU + *RPB1* + *RPB2* + *TEF1-α*). For each alignment, a Maximum Likelihood (ML) tree was calculated with RAXML 8.2.11 (Stamatakis 2014) using 1000 ML bootstrap searches.

The following models were defined for different loci, based on modeltests: ITS = GTR + I + G, LSU = TIM1ef + I + G, *RPB1* = K80 + I + G, *RPB2* = TPM2 + I + G, *TEF1-α* = TrNef + I + G, concatenated = GTR + I + G. Furthermore, Bayesian inference (BI) trees were calculated for each dataset using MrBayes 3.2.7 (Ronquist et al. 2012). BI analyses were performed with the following settings: By GTR + G model, four run with 5 M generations for single-locus and with 10 M for the multi-locus concatenated datasets, sampling every 100 generations, and the 25% burn-in. For the concatenated alignment 5 partitions were defined in both ML and BI analyses. The resulting phylograms were edited using Inkscape 1.3 (<https://inkscape.org/de/>). The root length of the single-locus phylograms was shortened to achieve better displaying options. A total of 45 newly generated sequences (17 ITS, 12 LSU, 2 *RPB1*, 6 *RPB2*, and 8 *TEF1-α*) from 19 specimens corresponding to 10 species were used to elaborate a phylogenetic reconstruction (Table 1). Sequences were submitted to GenBank, and their accession numbers are highlighted in bold in Table 1.

Results

Molecular analysis

As both ML and BI produced similar topologies, only the best ML tree is shown for all single-loci phylogenetic analyses and the multilocus analyses with Posterior probabilities (PP) and Bootstrap support values (BS) reported above the corresponding branches. Significance threshold was set to $PP \geq 0.95$ and $BS \geq 70\%$. Subsignificant support values were annotated in parentheses. Four single-loci phylograms (LSU, *RPB1*, *RPB2*, and *TEF1-α*) are shown as Supplementary Figs. 1, 2, 3, 4. One of the concatenated trees, including more genera of *Boletaceae*, is also shown as Supplementary Fig. 5. All the alignments used for the phylogenetic analyses are provided as Supplementary Files 1, 2, 3, 4, 5, 6, 7. Single-locus trees were built to have a more detailed analysis of clade topology and genealogical concordance species recognition. The multigene phylogram (Fig. 1) analyzed 237 taxa of *Boletellus*, *Aureoboletus*, and the outgroup, and included 5404 sites of 5 loci (ITS = 1–1499, LSU = 1500–2515, *RPB1* = 2516–3383, *RPB2* = 3384–4191, *TEF1-α* = 4192–5404). Not all loci were available for each taxon (see Table 1). The ITS-based tree (Fig. 2) showed the results of 100 taxa included and had 778/1499 (52%) parsimony informative sites, the LSU tree (Supplementary Fig. 1) included 194 taxa of *Boletellus*, *Aureoboletus*, and the outgroup, and 291/1016 (29%) parsimony informative sites, the *RPB1* tree (Supplementary Fig. 2) analyzed 49 taxa and had 418/868 (48%) parsimony informative sites, the *RPB2* tree (Supplementary Fig. 3) 88 taxa with 291/808

Table 1 Taxa, vouchers, countries, GenBank accession numbers and references of the DNA sequences used in the molecular phylogenetic molecular analyses. Sequences in bold were generated in this study

Species	Voucher	Notes	Country	ITS	LSU	<i>RPB1</i>	<i>RPB2</i>	<i>TEF1-α</i>	References
<i>Anthracoporus cystidiatus</i>	HKAS55375	—	China	—	KT990622	KT990969	—	KT990816	Wu et al. (2016)
<i>Anthracoporus cystidiatus</i>	MHHU7312	Holotype	China	NG_153896	MT154710	—	—	—	Li et al. (2021)
<i>Anthracoporus holophaeus</i>	HKAS59407	—	China	—	KT990708	KT991030	KT990506	KT990888	Wu et al. (2016)
<i>Anthracoporus nigropurpureus</i>	HKAS52685	—	China	—	KT990627	KT990973	KT990459	KT990821	Wu et al. (2016)
<i>Anthracoporus nigropurpureus</i>	HKAS53370	—	China	—	KT990628	KT990974	KT990460	KT990822	Wu et al. (2016)
<i>Aureoboletus albipes</i>	FHMU2228 (N.K. Zeng3267)	Holotype	China	—	OP630876	—	—	OP676221	Xue et al. (2023)
<i>Aureoboletus albipes</i>	FHMU2237 (N.K. Zeng3276)	—	China	OP696774	OP630877	—	—	OP676222	Xue et al. (2023)
<i>Aureoboletus auriporus</i>	FLAS-F-60914	—	USA: Florida	MH211684	—	—	—	—	Kaminsky et al. (unpubl.)
<i>Aureoboletus auriporus</i>	BDCR0431	—	Costa Rica	—	HQ161871	HQ161840	—	—	Dentinger et al. (2010)
<i>Aureoboletus betula</i>	MICH:KUO-10030904	—	USA: Ohio	—	MK601736	—	MK766298	MK721090	Kuo and Ortiz-Santana (2020)
<i>Aureoboletus betula</i>	Fire_Survey_616b	—	USA: Tennessee	—	OR253773	—	—	—	Hughes et al. (2025)
<i>Aureoboletus catenarius</i>	HKAS54463	—	China	—	KT990509	KT990890	KT990348	KT990710	Wu et al. (2016)
<i>Aureoboletus catenarius</i>	HKAS54467	—	China	—	KT990510	—	KT990349	KT990711	Wu et al. (2016)
<i>Aureoboletus citriniporus</i>	JLF6091	—	USA: California	MH277496	MH271618	—	—	—	Frank (unpubl.)
<i>Aureoboletus clavatus</i>	FHMU2885 (N.K. Zeng3446)	—	China	—	—	—	—	OP676225	Xue et al. (2023)
<i>Aureoboletus clavatus</i>	GDGM 42962	—	China	—	KR052045	KR052056	—	MK165846	Zeng et al. (2015)
<i>Aureoboletus clavatus</i>	GDGM 42963	Paratype	China	—	KR052046	KR052057	—	KR052054	Zeng et al. (2015)
<i>Aureoboletus conicus</i>	FHMU4730 (N.K. Zeng4276)	Holotype	China	—	OP630878	—	—	—	Xue et al. (2023)
<i>Aureoboletus duplicatoporus</i>	FHMU5068 (Y.Q. Fu104)	—	China	—	—	—	—	OP680532	Xue et al. (2023)
<i>Aureoboletus duplicatoporus</i>	FHMU3335 (N.K. Zeng2417)	—	China	—	—	—	OP680536	—	Xue et al. (2023)
<i>Aureoboletus duplicatoporus</i>	HKAS83115	—	China	—	KT990512	KT990892	KT990351	KT990713	Wu et al. (2016)
<i>Aureoboletus elvirae</i>	MEXU HO 29006	Holotype	Mexico	—	NG_243306	—	OQ938893	—	Ayala-Vásquez et al. (2023a)
<i>Aureoboletus erythraeus</i>	FHMU3144	Holotype	China	NR_173304	MT650076	—	—	MT650114	Wang et al. (2020)
<i>Aureoboletus erythraeus</i>	FHMU1053	—	China	—	MT650074	—	MT650124	MT650112	Wang et al. (2020)
<i>Aureoboletus flaviporus</i>	JLF7121	—	USA: California	MN174799	—	—	—	—	Frank (unpubl.)
<i>Aureoboletus formosus</i>	GDGM 44441	Holotype	China	—	KT291749	—	KT291751	KT291744	Zhang et al. (2015)
<i>Aureoboletus formosus</i>	GDGM 44444	—	China	—	KT291750	—	—	MK165833	Zhang et al. (2015, 2019)
<i>Aureoboletus garciae</i>	MEXU HO 29006	Holotype	Mexico	—	NG_075245	—	—	—	Haelewaters et al. (2020)

Table 1 (continued)

Species	Voucher	Notes	Country	ITS	LSU	RPB1	RPB2	TEF1- α	References
<i>Aureoboletus gentilis</i>	F-2889	—	Sweden	PQ652902	—	—	—	—	Fritzson and Bravander (unpubl.)
<i>Aureoboletus gentilis</i>	Pug1	—	Germany	—	DQ534635	—	—	KF030399	Binder and Hibbett (2006), Nuhn et al. (2013)
<i>Aureoboletus gentilis</i>	MG372a	—	Italy	—	KF112344	KF112557	KF112741	KF134014	Wu et al. (2014)
<i>Aureoboletus gentilis</i>	ADK4865	—	Belgium	—	—	—	KT823994	KT824027	Raspé et al. (2016)
<i>Aureoboletus glutinosus</i>	GDGM 44733	—	China	—	MH670257	—	MH700231	MH700203	Zhang et al. (2019)
<i>Aureoboletus glutinosus</i>	GDGM 44477	Holotype	China	—	NG_068273	—	MH700229	MH700205	Zhang et al. (2019)
<i>Aureoboletus griseorufescens</i>	GDGM 28490	Holotype	China	—	MH670278	—	MH700241	—	Zhang et al. (2019)
<i>Aureoboletus griseorufescens</i>	ZM131	—	China	—	MH670279	MH700220	MH700242	—	Zhang et al. (2019)
<i>Aureoboletus guangdongensis</i>	FHMu6511 (N.K. Zeng1310-1)	—	China	OM200346	—	—	—	—	Zhang et al. (2022)
<i>Aureoboletus guangdongensis</i>	FHMu3797	—	China	—	—	—	—	OM321040	Zhang et al. (2022)
<i>Aureoboletus innixus</i>	MB03-104	—	USA: Massachusetts	—	KF030239	—	—	KF030400	Nuhn et al. (2013)
<i>Aureoboletus innixus</i>	CFMR:BOS-544	—	USA: New York	—	MK601707	—	MK766270	MK721061	Kuo and Ortiz-Santana (2020)
<i>Aureoboletus longicollis</i>	LE315562	—	Vietnam	MT893598	—	—	—	MW033312	Pham et al. (2020)
<i>Aureoboletus longicollis</i>	FHMu2249 (N.K. Zeng3288)	—	China	OP615084	OP615077	—	—	OP680537	Xue et al. (2023)
<i>Aureoboletus longicollis</i>	FHMu5851 (LWF8)	—	China	—	OP615078	—	—	OP680538	Xue et al. (2023)
<i>Aureoboletus longicollis</i>	HKAS53398	—	China	—	KF112376	KF112625	KF112755	KF112238	Wu et al. (2014)
<i>Aureoboletus marroninus</i>	JXSB2688	—	China	MT712668	—	—	—	—	Chen (unpubl.)
<i>Aureoboletus marroninus</i>	GDGM 43288	Holotype	China	—	NG_057040	—	KT291753	KT291746	Zhang et al. (2015)
<i>Aureoboletus microcarpus</i>	FHMu4716 (N.K. Zeng4464)	—	China	—	OP604279	—	—	—	Xue et al. (2023)
<i>Aureoboletus miniatoaurantiacus</i>	FHMu4964 (N.K. Zeng4709)	—	China	OP629170	OP615086	—	—	OP680539	Xue et al. (2023)
<i>Aureoboletus miniatoaurantiacus</i>	FHMu2038 (N.K. Zeng3077)	—	China	OP629171	OP615087	—	—	OP680540	Xue et al. (2023)
<i>Aureoboletus miniatoaurantiacus</i>	FHMu6977	—	China	OP629172	OP615088	—	—	OP680541	Xue et al. (2023)
<i>Aureoboletus miniatoaurantiacus</i>	KD 22-003	—	India	—	OR349660	—	OR355680	—	Das et al. (2023)
<i>Aureoboletus miniatoaurantiacus</i>	KD 22-004	—	India	—	OR349659	—	OR355681	—	Das et al. (2023)
<i>Aureoboletus minimus</i>	GDGM 44400	Holotype	Vietnam	—	NG_243178	—	—	—	Liu et al. (2024)

Table 1 (continued)

Species	Voucher	Notes	Country	ITS	LSU	<i>RPB1</i>	<i>RPB2</i>	<i>TEF1-α</i>	References
<i>Aureoboletus mirabilis</i>	REH9765	—	USA: California	—	KP327661	—	—	KP327709	Halling et al. (2015)
<i>Aureoboletus mirabilis</i>	HKAS57776	—	China	—	KF112360	KF112624	KF112743	KF112229	Wu et al. (2014)
<i>Aureoboletus nanlingensis</i>	GDGM 44759	—	China	—	MH670276	—	—	MH700206	Zhang et al. (2019)
<i>Aureoboletus nanlingensis</i>	GDGM 46222	—	China	—	MH670275	—	—	—	Zhang et al. (2019)
<i>Aureoboletus nephrosporus</i>	HKAS67931	—	China	—	KT990516	KT990895	KT990357	KT990720	Wu et al. (2016)
<i>Aureoboletus nephrosporus</i>	HKAS74929	Holotype	China	—	NG_057094	KT990896	KT990358	KT990721	Wu et al. (2016)
<i>Aureoboletus ornatipes</i>	FHMU1981 (N.K. Zeng3020)	Holotype	China	—	OP630879	—	OP676224	OP676223	Xue et al. (2023)
<i>Aureoboletus projectellus</i>	AFTOL-ID 713	—	USA: Massachusetts	AY789082	—	AY788850	AY787218	AY879116	Binder et al. (unpubl.)
<i>Aureoboletus projectellus</i>	MICH:KUO-09111014	—	USA: Michigan	—	MK601708	—	MK766271	—	Kuo and Ortiz-Santana (2020)
<i>Aureoboletus projectellus</i>	NY13393	—	USA: New York	—	KP327623	—	—	KP327676	Halling et al. (2015)
<i>Aureoboletus pseudoauriporus</i>	JAB_320	—	—	MW675726	MW675726	MW737508	MW737468	MW737489	Farid et al. (2021)
<i>Aureoboletus pseudoauriporus</i>	Farid_501	—	—	MW675741	MW662576	MW737500	MW737463	—	Farid et al. (2021)
<i>Aureoboletus quercus-spinosae</i>	GDGM 43786	—	China: Tibet	—	KY039969	KY039965	KY039960	MK165838	Zhang et al. (2017)
<i>Aureoboletus quercus-spinosae</i>	GDGM 43755	Holotype	China: Tibet	NR_153561	NG_057121	KY039963	KY039958	MK165836	Zhang et al. (2017)
<i>Aureoboletus raphanaceus</i>	FHMU2166 (N.K. Zeng3205)	—	China	OP629173	OP615089	—	—	—	Xue et al. (2023)
<i>Aureoboletus raphanaceus</i>	FHMU3597 (N.K. Zeng2007)	—	China	OP629174	OP615090	—	OP680545	OP680542	Xue et al. (2023)
<i>Aureoboletus raphanaceus</i>	FHMU5516 (S.D. Yang211)	—	China	—	OP615092	—	—	OP680544	Xue et al. (2023)
<i>Aureoboletus raphanaceus</i>	GDGM 44832	—	China	—	MH670268	MH700218	MH700236	MH700194	Zhang et al. (2019)
<i>Aureoboletus raphanaceus</i>	GDGM 52543	—	China	—	MH670271	—	MH700237	—	Zhang et al. (2019)
<i>Aureoboletus roxanae</i>	DS626-07	—	USA: New York	—	KF030311	KF030381	—	KF030402	Nuhn et al. (2013)
<i>Aureoboletus roxanae</i>	CFMR:BOS-698	—	USA: New York	—	MK601709	—	MK766272	MK721063	Kuo and Ortiz-Santana (2020)
<i>Aureoboletus rubellus</i>	FHMU4877 (N.K. Zeng4592)	—	China	OP696776	OP604280	—	—	OP676226	Xue et al. (2023)
<i>Aureoboletus rubellus</i>	FHMU4453 (Y.Q. Fu002)	—	China	—	OP604281	—	—	OP676227	Xue et al. (2023)
<i>Aureoboletus rugosus</i>	FHMU2766 (G.L. Zhang078)	—	China: Yunnan	OM200347	—	—	—	—	Zhang et al. (unpubl.)
<i>Aureoboletus russellii</i>	CFMR:BOS-716	—	USA: Michigan	—	MK601710	—	MK766273	MK721064	Kuo and Ortiz-Santana (2020)
<i>Aureoboletus russellii</i>	MEN11-031	—	USA: Massachusetts	—	KP327625	—	—	KP327678	Halling et al. (2015)
<i>Aureoboletus sinobadius</i>	LE-F 312680	—	Vietnam	MZ451340	—	—	—	MZ424885	Pham et al. (2021)
<i>Aureoboletus sinobadius</i>	FHMU3117 (N.K. Zeng3494)	—	China	—	OP615107	—	—	OP680546	Xue et al. (2023)

Table 1 (continued)

Species	Voucher	Notes	Country	ITS	LSU	RPB1	RPB2	TEF1- α	References
<i>Aureoboletus solus</i>	FHMU4377 (N.K. Zeng4146-1)	—	China	OP629165	OP615110	—	—	OP680547	Xue et al. (2023)
<i>Aureoboletus solus</i>	FHMU715 (N.K. Zeng1064)	—	China	—	OP615108	—	—	—	Xue et al. (2023)
<i>Aureoboletus</i> sp.	GDGM 24560	—	China	—	—	MN473144	MN549682	—	Zhang et al. (2019)
<i>Aureoboletus</i> sp.	GDGM 26359	—	China	—	—	MN473145	MN549681	MN549670	Zhang et al. (2019)
<i>Aureoboletus</i> sp.	GDGM 44727	—	China	—	—	MN473154	MN549691	—	Zhang et al. (2019)
<i>Aureoboletus</i> sp.	GDGM 49259	—	China	—	MN410706	MN473158	—	—	Zhang et al. (2019)
<i>Aureoboletus</i> sp.	GS10616	—	Guatemala	PX596695	PX596708	—	PX634666	PX549460	This study
<i>Aureoboletus</i> sp.	MICG-5454 (GS10617)	—	Guatemala	—	PX596711	—	—	—	This study
<i>Aureoboletus</i> sp.	MICG-5475 (GS10618)	—	Guatemala	PX596697	PX596712	—	PX634667	PX549463	This study
<i>Aureoboletus</i> sp.	GS11347	—	Guatemala	PX596696	PX596709	PX549457	PX549459	PX549461	This study
<i>Aureoboletus</i> sp.	MICG-6881 (GS11348)	—	Guatemala	PX596698	PX596713	PX549458	PX634668	PX549462	This study
<i>Aureoboletus</i> sp. or <i>A. microcarpus</i>	FHMU4695 (N.K. Zeng4467)	—	China	OM200343	—	—	—	—	Zhang et al. (unpubl.)
<i>Aureoboletus tenuis</i>	FHMU2225 (N.K. Zeng3264)	—	China	OP629160	OP615201	—	—	—	Xue et al. (2023)
<i>Aureoboletus tenuis</i>	HKAS75104	—	China	—	KT990518	KT990897	KT990359	KT990722	Wu et al. (2016)
<i>Aureoboletus thibetanus</i>	AFTOL-450	—	China	DQ200917	AY700189	DQ435800	DQ366279	DQ029199	Matheny et al. (2007); Binder et al. (unpubl.)
<i>Aureoboletus velutipes</i>	GDGM 42608	—	China	—	MH670251	MH700212	MH700227	MH700190	Zhang et al. (2019)
<i>Aureoboletus velutipes</i>	GDGM 44713	Holotype	China	—	NG_068272	MH700213	MH700226	MH700191	Zhang et al. (2019)
<i>Aureoboletus venustus</i>	FHMU4784 (S. Jiang259)	—	China	OP629161	OP615203	—	—	—	Xue et al. (2023)
<i>Aureoboletus venustus</i>	FHMU4776 (S. Jiang256)	—	China	OP629162	OP615204	—	—	OP680548	Xue et al. (2023)
<i>Aureoboletus viscidipes</i>	HKAS77103	—	China	—	KT990519	—	KT990360	KT990723	Wu et al. (2016)
<i>Aureoboletus viscosus</i>	OR0361	—	Thailand	—	—	—	MH614751	MH614703	Vadthananarat et al. (2019)
<i>Aureoboletus yunnanensis</i>	HKAS75050	—	China	—	KT990520	KT990898	KT990361	KT990724	Wu et al. (2016)
<i>Aureoboletus zangii</i>	HKAS74766 (GDGM 44406)	—	China	—	MN204562	KT990900	—	KT990726	Zhang et al. (2019), Wu et al. (2016)
<i>Australopilus palumanus</i>	REH9421	—	Australia: Queensland	—	JX889675	—	—	—	Halling et al. (2012b)
<i>Australopilus palumanus</i>	NY1193865	—	Australia: Queensland	—	—	—	—	MK721067	Kuo and Ortiz-Santana (2020)
<i>Baorangia pseudocalopus</i>	HKAS75081	—	China	—	KF112356	KF112520	KF112678	KF112168	Wu et al. (2014)
<i>Baorangia pseudocalopus</i>	HKAS63607	—	China	—	KY418895	—	—	KY419085	Zhao et al. (2017)
<i>Baorangia rufomaculata</i>	4414	—	USA: New York	—	KF030248	KF030369	—	KF030406	Nuhn et al. (2013)

Table 1 (continued)

Species	Voucher	Notes	Country	ITS	LSU	RPB1	RPB2	TEF1- α	References
<i>Boletellus</i> aff. <i>putuoensis</i>	FHMU2168 (N.K. Zeng3207)	—	China	—	—	—	—	MW925902	Tian et al. (2022)
<i>Boletellus ananas</i>	ANGE1353	—	Dominican Republic	PX587877	PX636316	—	PX634671	—	This study
<i>Boletellus ananas</i>	ANGE986	—	Dominican Republic	PX596690	PX596703	—	PX634670	PX634663	This study
<i>Boletellus ananas</i>	ANGE392	—	Dominican Republic	PX596689	—	—	—	—	This study
<i>Boletellus ananas</i>	NY02072372 (ARB1223)	—	USA: Georgia	—	PX596714	—	PX634669	—	This study
<i>Boletellus ananas</i>	ARB1223	—	USA: Georgia	—	KP327618	—	—	KP327671	Halling et al. (2015)
<i>Boletellus ananas</i>	CFMR BZ3167	—	Belize	—	MK601717	—	MK766279	—	Kuo and Ortiz-Santana (2020)
<i>Boletellus ananas</i>	REH8613	—	Costa Rica	—	KP327629	—	—	KP327682	Halling et al. (2015)
<i>Boletellus ananas</i>	NY815459	—	Costa Rica	—	JQ924336	—	KF112760	KF112308	Wu et al. (2014)
<i>Boletellus ananas</i>	REH8548	—	Belize	—	KP327628	—	—	KP327681	Halling et al. (2015)
<i>Boletellus ananiceps</i>	3794	—	Australia: Victoria	—	KP327666	—	—	KP327712	Halling et al. (2015)
<i>Boletellus ananiceps</i>	REH9484	—	Australia: Queensland	—	KP327655	—	—	KP327705	Halling et al. (2015)
<i>Boletellus areolatus</i>	FHMU2073 (N.K. Zeng3112)	—	China	OP681711	MW826852	—	—	MW925880	Xue et al. (2023)
<i>Boletellus areolatus</i>	HKAS99767	—	China	—	MW826851	—	—	MW925879	Xue et al. (2023)
<i>Boletellus areolatus</i>	FHMU2046 (N.K. Zeng3085)	—	China	—	MT829118	—	MW925938	MW925881	Xue et al. (2023)
<i>Boletellus auro-contextus</i>	TNSF61566	Holotype	Japan	NR_153593	—	—	—	—	Sato and Hattori (2015)
<i>Boletellus auro-contextus</i>	BLT130	—	Japan	AB989020	—	AB999750	AB999783	—	Sato and Hattori (2015)
<i>Boletellus auro-contextus</i>	N.K. Zeng2536	—	China	MT822935	—	—	—	—	Zeng and Jiang (unpubl.)
<i>Boletellus badiovinosus</i>	REH8923	—	Australia: Queensland	—	KP327640	—	—	KP327693	Halling et al. (2015)
<i>Boletellus belizensis</i>	CFMR:BZ429 (JCB2001238)	—	Belize	MN250210	MN250185	—	—	—	Ortiz-Santana et al. (2007)
<i>Boletellus belizensis</i>	CFMR:BZ1564 (BOS218)	—	Belize	MN250209	MN250184	—	—	—	Ortiz-Santana et al. (2007)
<i>Boletellus belizensis</i>	CFMR:BZ316 (TJB9128)	Holotype	Belize	MN250194	MN250169	—	—	—	Ortiz-Santana et al. (2007)
<i>Boletellus brunoflavus</i>	B21061253	—	China	ON364057	ON195936	ON390834	ON390839	ON390828	Lin et al. (2022)
<i>Boletellus brunoflavus</i>	GDGM 87995	—	China	ON364056	ON195935	ON390833	—	ON390827	Lin et al. (2022)
<i>Boletellus brunoflavus</i>	FHMU3249 (N.K. Zeng1271)	—	China	OP681695	MW826894	—	—	—	Xue et al. (2023)
<i>Boletellus brunoflavus</i>	HKAS53375	—	China	—	KF112364	—	KF112748	KF112240	Wu et al. (2014)
<i>Boletellus brunoflavus</i>	FHMU1885 (N.K. Zeng2913)	—	China	—	MW826896	—	MW925949	MW925920	Xue et al. (2023)
<i>Boletellus brunoflavus</i>	GDGM 87996	Holotype	China	ON364059	ON195932	ON390829	ON390835	ON390823	Lin et al. (2022)
<i>Boletellus</i> cf. <i>rubroviolaceus</i>	TH10561	—	Cameroon	MZ351527	—	—	—	—	Koch et al. (unpubl.)

Table 1 (continued)

Species	Voucher	Notes	Country	ITS	LSU	RPB1	RPB2	TEF1- α	References
<i>Boletellus chrysenteroides</i>	3838	—	USA: New York	—	KF030312	KF030383	—	KF030432	Nuhn et al. (2013)
<i>Boletellus chrysenteroides</i>	BD394	—	USA: Minnesota	—	HQ161867	HQ161836	—	—	Dentinger et al. (2010)
<i>Boletellus chrysenteroides</i>	REH9015	—	USA: Pennsylvania	—	KP327645	—	—	—	Halling et al. (2015)
<i>Boletellus chrysenteroides</i>	HKAS105270	—	China	MT520080	—	—	—	—	Zhou (unpubl.)
<i>Boletellus chrysenteroides</i>	iNaturalist # 91541460	—	USA: Indiana	OM809388	—	—	—	—	Russell (unpubl.)
<i>Boletellus chrysenteroides</i>	54/97	—	USA: Massachusetts	DQ534634	DQ534634	—	—	—	Binder and Hibbett (2006)
<i>Boletellus cubensis</i>	ANGE1474	—	Dominican Republic	PX596693	PX596707	—	PX634672	PX634664	This study
<i>Boletellus deceptivus</i>	REH9634	—	Australia: Queensland	—	KP327619	—	—	KP327672	Halling et al. (2015)
<i>Boletellus deceptivus</i>	REH9017	—	Australia: Queensland	—	KP327646	—	—	KP327697	Halling et al. (2015)
<i>Boletellus deceptivus</i>	REH9786	Holotype	Australia: Queensland	—	KP327663	—	—	—	Halling et al. (2015)
<i>Boletellus dicymbophilus</i>	TH8840	—	Guyana	—	HQ161852	HQ161821	—	—	Dentinger et al. (2010)
<i>Boletellus dissiliens</i>	REH9768	—	Australia: Queensland	—	KP327662	—	—	—	Halling et al. (2015)
<i>Boletellus dissiliens</i>	REH9435	—	Australia: Queensland	—	JX889674	—	—	JX889684	Halling et al. (2012a, b)
<i>Boletellus domingensis</i>	ANGE111	—	Dominican Republic	PX596688	PX631442	—	—	—	This study
<i>Boletellus domingensis</i>	ANGE1004	—	Dominican Republic	PX596691	PX596704	—	—	—	This study
<i>Boletellus domingensis</i>	ANGE1332	—	Dominican Republic	PX596692	PX596705	—	PX634673	—	This study
<i>Boletellus domingensis</i>	CFMR DR573 (DJLDR29)	Holotype	Dominican Republic	MN250195	MN250170	—	—	—	Ortiz-Santana et al. (2007)
<i>Boletellus elatus</i>	MHHNU 30660	—	China	MK253770	—	—	—	—	Chen et al. (unpubl.)
<i>Boletellus elatus</i>	RTF0654 (strain117-699)	—	Japan	AB509911	—	—	—	—	Sato et al. 2012
<i>Boletellus elatus</i>	TMI22101	—	Japan	—	KP327620	—	—	—	Halling et al. (2015)
<i>Boletellus elatus</i>	06-204NR	—	Japan	—	KP327621	—	—	—	Halling et al. (2015)
<i>Boletellus emodensis</i>	TNS-F-61549	—	Japan	AB989013	—	—	—	—	Sato and Hattori (2015)
<i>Boletellus emodensis</i>	TNS-F-61564	—	Japan	AB989019	—	—	—	—	Sato and Hattori (2015)
<i>Boletellus emodensis</i>	FHMU1611 (N.K. Zeng2488)	—	China	OP681697	MW826862	—	MW925942	—	Xue et al. (2023)
<i>Boletellus emodensis</i>	FHMU2031 (N.K. Zeng3070)	—	China	OP681702	MW826857	—	—	MW925890	Tian et al. (2022), Xue et al. (2023)

Table 1 (continued)

Species	Voucher	Notes	Country	ITS	LSU	<i>RPB1</i>	<i>RPB2</i>	<i>TEF1-α</i>	References
<i>Boletellus emodensis</i>	FHMU2245 (N.K. Zeng3284)	—	China	OP681704	MW826863	—	MW925940	MW925894	Tian et al. (2022), Xue et al. (2023)
<i>Boletellus emodensis</i>	FHMU2221 (N.K. Zeng3260)	—	China	OP681705	MW826872	—	MW925943	MW925895	Tian et al. (2022), Xue et al. (2023)
<i>Boletellus emodensis</i>	FHMU2154 (N.K. Zeng3193)	—	China	OP681708	MW826866	—	—	—	Xue et al. (2023)
<i>Boletellus emodensis</i>	FHMU2152 (N.K. Zeng3191)	—	China	OP681707	MW826867	—	—	—	Xue et al. (2023)
<i>Boletellus emodensis</i>	FHMU2064 (N.K. Zeng3103)	—	China	OP681703	MW826858	—	—	MW925886	Tian et al. (2022), Xue et al. (2023)
<i>Boletellus emodensis</i>	FHMU892 (N.K. Zeng1340)	—	China	—	MW826871	—	—	—	Xue et al. (2023)
<i>Boletellus emodensis</i>	FHMU1649 (N.K. Zeng2536)	—	China	—	MT829120	—	—	MW925889	Tian et al. (2022), Xue et al. (2023)
<i>Boletellus emodensis</i>	FHMU1904 (N.K. Zeng2934)	—	China	—	MW826860	—	—	—	Xue et al. (2023)
<i>Boletellus emodensis</i>	FHMU1998 (N.K. Zeng3037)	—	China	—	MT829119	—	MW925944	MW925887	Tian et al. (2022), Xue et al. (2023)
<i>Boletellus emodensis</i>	FHMU2034 (N.K. Zeng3073)	—	China	—	MT829121	—	MW925945	MW925888	Tian et al. (2022), Xue et al. (2023)
<i>Boletellus emodensis</i>	FHMU2145 (N.K. Zeng3184)	—	China	—	MW826859	—	—	MW925884	Tian et al. (2022), Xue et al. (2023)
<i>Boletellus emodensis</i>	FHMU2204 (N.K. Zeng3243)	—	China	—	MW826861	—	—	MW925883	Tian et al. (2022), Xue et al. (2023)
<i>Boletellus emodensis</i>	REH8904	—	Australia: Queensland	—	KP327638	—	—	KP327691	Halling et al. (2015)
<i>Boletellus emodensis</i>	REH8742	—	Australia: Queensland	—	KP327633	—	—	KP327686	Halling et al. (2015)
<i>Boletellus erythrolepis</i>	FHMU913 (N.K. Zeng1362)	—	China	—	MW826846	—	—	MW925875	Tian et al. (2022), Xue et al. (2023)
<i>Boletellus erythrolepis</i>	FHMU3255 (S. Jiang78)	Holotype	China	—	MW826909	—	—	MW925927	Tian et al. (2022), Xue et al. (2023)
<i>Boletellus erythrolepis</i>	FHMU3312 (S. Jiang781)	—	China	—	MW826847	—	—	—	Xue et al. (2023)
<i>Boletellus erythrolepis</i>	FHMU3314 (S. Jiang783)	—	China	—	MW826845	—	—	MW925876	Tian et al. (2022), Xue et al. (2023)
<i>Boletellus exiguus</i>	NY1034374	Isotype	Guyana	PX596699	—	—	—	—	This study
<i>Boletellus exiguus</i>	TH8809	—	Guyana	—	HQ161862	HQ161831	—	—	Dentinger et al. (2010)
<i>Boletellus indistinctus</i>	FHMU2149 (N.K. Zeng3188)	—	China	OP681706	MW826875	—	—	MW925909	Tian et al. (2022), Xue et al. (2023)
<i>Boletellus indistinctus</i>	FHMU2259 (N.K. Zeng3298)	—	China	OP681709	MW826874	—	—	MW925915	Tian et al. (2022), Xue et al. (2023)
<i>Boletellus indistinctus</i>	FHMU1088 (N.K. Zeng1624)	—	China	OP681700	MW826873	—	MW925948	MW925912	Tian et al. (2022), Xue et al. (2023)
<i>Boletellus indistinctus</i>	FHMU940 (N.K. Zeng1393)	—	China	OP681696	MW826878	—	—	MW925907	Tian et al. (2022), Xue et al. (2023)

Table 1 (continued)

Species	Voucher	Notes	Country	ITS	LSU	<i>RPB1</i>	<i>RPB2</i>	<i>TEF1-α</i>	References
<i>Boletellus indistinctus</i>	FHMU2269 (N.K. Zeng3308)	—	China	OP681710	MW826876	—	—	MW925906	Tian et al. (2022), Xue et al. (2023)
<i>Boletellus indistinctus</i>	HKAS80681	—	China	—	KT990532	—	KT990368	—	Wu et al. (2016)
<i>Boletellus indistinctus</i>	FHMU886 (N.K. Zeng1333)	—	China	—	MW826880	—	—	MW925916	Tian et al. (2022), Xue et al. (2023)
<i>Boletellus indistinctus</i>	FHMU936 (N.K. Zeng1388)	—	China	—	MW826879	—	—	MW925911	Tian et al. (2022), Xue et al. (2023)
<i>Boletellus indistinctus</i>	FHMU1596 (N.K. Zeng2470)	—	China	—	MT829116	—	—	MW925910	Tian et al. (2022), Xue et al. (2023)
<i>Boletellus indistinctus</i>	FHMU2028 (N.K. Zeng3067)	—	China	—	MT829117	—	—	MW925905	Tian et al. (2022), Xue et al. (2023)
<i>Boletellus indistinctus</i>	FHMU412 (N.K. Zeng649)	—	China	—	MW826881	—	—	—	Xue et al. (2023)
<i>Boletellus indistinctus</i>	HKAS77623	Holotype	China	—	KT990531	—	KT990371	KT990733	Wu et al. (2016)
<i>Boletellus lepidospora</i>	MCA7509	—	Cameroon	MZ351639	—	—	—	—	Koch et al. (unpubl.)
<i>Boletellus lepidospora</i>	TH10574	—	Cameroon	MZ351638	—	—	—	—	Koch et al. (unpubl.)
<i>Boletellus mini-matenebris</i>	ITCV1087	—	Mexico	OR713120	OR713122	—	OQ938894	—	Ayala-Vásquez et al. (2023b)
<i>Boletellus mini-matenebris</i>	MEXU HO 30119 (ITCV1076)	Holotype	Mexico	OR713119	OR713121	—	OQ938895	—	Ayala-Vásquez et al. (2023b)
<i>Boletellus nordestinus</i>	UFRN-Fungos 2726	Holotype	Brazil: Rio Grande do Norte	MG760443	MG760444	—	—	—	Magnago et al. (2019)
<i>Boletellus obscurecoccineus</i>	isolate: 3A3	—	Japan	AB973769	AB973769	—	—	—	Matsuoka and Osono (unpubl.)
<i>Boletellus obscurecoccineus</i>	HKAS134524	—	China	PP806282	—	—	—	—	Wang et al. (unpubl.)
<i>Boletellus obscurecoccineus</i>	REH9038	—	Australia: Queensland	—	KP327649	—	—	KP327700	Halling et al. (2015)
<i>Boletellus obscurecoccineus</i>	REH8741	—	Australia: Queensland	—	KP327632	—	—	KP327685	Halling et al. (2015)
<i>Boletellus obscurecoccineus</i>	REH9061	—	Australia: Queensland	—	KP327650	—	—	KP327701	Halling et al. (2015)
<i>Boletellus obscurecoccineus</i>	REH8782	—	Australia: Queensland	—	KP327634	—	—	KP327687	Halling et al. (2015)
<i>Boletellus paradoxus</i>	BLT136	—	Malaysia	AB989022	—	AB999752	AB999785	—	Sato and Hattori (2015)
<i>Boletellus piakaii</i>	NY01034438	Isotype	Guyana	PX596700	—	—	—	—	This study
<i>Boletellus piakaii</i>	TH8878	—	Guyana	KT339225	—	—	—	—	Smith and Henkel (unpubl.)
<i>Boletellus piakaii</i>	TH8077	—	Guyana	—	HQ161861	HQ161830	—	—	Dentinger et al. (2010)
<i>Boletellus projectellus</i>	AFTOL-ID 713	—	USA	—	AY684158	—	—	—	Binder et al. (unpubl.)
<i>Boletellus pseudochrysenteroides</i>	Mushroom Observer #288188	—	USA: Missouri	—	MH257564	—	—	MH337293	Kudzman and Safonov (unpubl.)

Table 1 (continued)

Species	Voucher	Notes	Country	ITS	LSU	<i>RPB1</i>	<i>RPB2</i>	<i>TEF1-α</i>	References
<i>Boletellus puniceus</i>	HKAS77662	—	China	—	—	—	KT990372	—	Wu et al. (2016)
<i>Boletellus putuoensis</i>	W3383	—	China	OR673989	—	OR683477	OR683483	OR683472	Wang et al. (2024)
<i>Boletellus putuoensis</i>	FHMu6959	—	China	ON166671	ON166665	—	ON155835	—	Xu et al. (2022)
<i>Boletellus putuoensis</i>	W3380	—	China	OR673988	OR673998	OR683476	OR683482	OR683471	Wang et al. (2024)
<i>Boletellus putuoensis</i>	FHMu2147 (N.K. Zeng3186)	—	China	—	MW826892	—	—	MW925900	Xue et al. (2023), Tian et al. (2022)
<i>Boletellus putuoensis</i>	FHMu3260 (N.K. Zeng4070)	—	China	—	MW826890	—	—	MW925899	Xue et al. (2023), Tian et al. (2022)
<i>Boletellus putuoensis</i>	FHMu3261 (N.K. Zeng4075)	—	China	—	MW826891	—	—	MW925901	Xue et al. (2023), Tian et al. (2022)
<i>Boletellus putuoensis</i>	FHMu6907	Holotype	China	ON166669	ON166664	—	ON155834	ON155822	Xu et al. (2022)
<i>Boletellus reminiscens</i>	NY01393611	Isotype	Australia: Queensland	PX596702	—	—	—	—	This study
<i>Boletellus reminiscens</i>	REH9284	—	Australia: Queensland	—	KP327651	—	—	KP327702	Halling et al. (2015)
<i>Boletellus rubidus</i>	FHMu3267	—	China	—	MW826849	—	—	MW925877	Xue et al. (2023), Tian et al. (2022)
<i>Boletellus rubidus</i>	HKAS58713	—	China	—	KF112428	—	KF112759	KF112307	Wu et al. (2014)
<i>Boletellus rubidus</i>	HKAS83069	Holotype	China	—	MW826904	—	—	—	Xue et al. (2023)
<i>Boletellus rubrolutescens</i>	BR5020169915682 (NAL374)	—	Cameroon	PX596694	—	—	—	—	This study
<i>Boletellus shoreae</i>	CAL 1688 (AP 6679)	Paratype	India	MH608209	MH608211	—	—	—	Parihar et al. (2018a, b)
<i>Boletellus shoreae</i>	CAL 1684 (AP 6696)	Holotype	India	MH608208	MH608210	—	—	—	Parihar et al. (2018a, b)
<i>Boletellus sinapipes</i>	NY01393539	Isotype	Australia: Queensland	PX596701	—	—	—	—	This study
<i>Boletellus sinapipes</i>	REH9018	—	Australia: Queensland	—	KP327647	—	—	KP327698	Halling et al. (2015)
<i>Boletellus sinapipes</i>	REH9408	—	Australia: Queensland	—	KP327653	—	—	—	Halling et al. (2015)
<i>Boletellus singeri</i>	VB4460	—	Mexico	—	KP327670	—	—	—	Halling et al. (2015)
<i>Boletellus singeri</i>	VB4530	—	Mexico	—	KP327669	—	—	KP327713	Halling et al. (2015)
<i>Boletellus sino-chrysenteroides</i>	FHMu3264	Holotype	China	—	MW826902	—	MW925947	MW925904	Xue et al. (2023), Tian et al. (2022)
<i>Boletellus sino-chrysenteroides</i>	FHMu3265	—	China	—	—	—	MW925946	MW925903	Xue et al. (2023), Tian et al. (2022)
<i>Boletellus sino-chrysenteroides</i>	LE-F 350390	—	Russia: Primorsky Krai	PX628111	PX596710	—	—	PX634665	This study
<i>Boletellus</i> sp.	HKAS122526	—	China	ON794351	—	—	—	—	Wang et al. (2022)

Table 1 (continued)

Species	Voucher	Notes	Country	ITS	LSU	<i>RPB1</i>	<i>RPB2</i>	<i>TEF1-α</i>	References
<i>Boletellus</i> sp.	TAA195080	—	Seychelles	AM412293	—	—	—	—	Tedersoo et al. (2007)
<i>Boletellus</i> sp.	HKAS74888	—	China	—	KF112413	KF112568	KF112747	KF112268	Wu et al. (2014)
<i>Boletellus</i> sp.	HKAS80554	—	China	—	KT990535	—	—	—	Wu et al. (2016)
<i>Boletellus squamosus</i>	HKAS59536	—	China	—	KF112427	—	KF112758	KF112306	Wu et al. (2014)
<i>Boletellus squamosus</i>	FHMU3266 (N.K. Zeng4051)	—	China	—	—	—	—	MW925898	Tian et al. (2022)
<i>Boletellus sub-globosus</i>	FHMU3257	—	China	—	MW826843	—	—	MW925874	Xue et al. (2023), Tian et al. (2022)
<i>Boletellus sub-globosus</i>	FHMU3259 (N.K. Zeng2506)	—	China	—	—	—	—	MW925871	Tian et al. (2022)
<i>Boletellus sub-globosus</i>	FHMU3258 (S. Jiang98)	—	China	—	MW826842	—	—	MW925873	Xue et al. (2023), Tian et al. (2022)
<i>Boletellus sub-globosus</i>	FHMU3257 (S. Jiang99)	—	China	—	MW826843	—	—	MW925874	Xue et al. (2023), Tian et al. (2022)
<i>Boletellus sub-globosus</i>	FHMU3256 (S. Jiang100)	Holotype	China	—	MW826844	—	—	MW925872	Xue et al. (2023), Tian et al. (2022)
<i>Boletellus verruculosus</i>	MHKMU Y.J. Pu 216	—	China	PP189884	PP179427	PP195248	PP195262	PP230538	Xue et al. (2024)
<i>Boletellus verruculosus</i>	MHKMU H.Y. Huang 674	—	China	PP189883	PP179428	PP195251	PP195264	—	Xue et al. (2024)
<i>Boletellus verruculosus</i>	MHKMU H.Y. Huang 682	Holotype	China	PP189882	PP179425	PP195249	PP195261	PP230535	Xue et al. (2024)
<i>Boletellus verruculosus</i>	MHKMU H.Y. Huang 699	—	China	PP189881	PP179426	PP195250	PP195263	PP230536	Xue et al. (2024)
<i>Boletellus verruculosus</i>	MHKMU S. Jiang 414	—	China	PP189885	PP179429	PP195247	PP195260	PP230537	Xue et al. (2024)
<i>Boletellus wen-shanensis</i>	HKAS122938	Holotype	China	—	NG_154028	—	ON007376	—	Zhang and Wu (2022)
<i>Boletellus zenghuoxingii</i>	FHMU3251 (N.K. Zeng2553)	Holotype	China	—	MW826854	—	—	—	Xue et al. (2023)
<i>Boletellus zenghuoxingii</i>	FHMU1979 (N.K. Zeng3018)	—	China	—	MW826855	—	MW925939	MW925878	Xue et al. (2023), Tian et al. (2022)
<i>Butyriboletus appendiculatus</i>	Bap1	—	Germany	—	AF456837	KF030359	—	JQ327025	Binder et al. (2002), Nuhn et al. (2013)
<i>Butyriboletus autumniregius</i>	OSC148262 (Arora11108)	—	USA: California	KC184423	KC184424	—	—	—	Arora and Frank (2014)
<i>Caloboletus calopus</i>	Bc1	—	Germany	—	AF456833	—	—	JQ327019	Halling et al. (2012a)
<i>Caloboletus calopus</i>	BR5020159063805	—	Belgium	KJ605655	KJ184554	—	—	KJ184566	Zhao et al. (2014)
<i>Caloboletus firmus</i>	MB06-060	—	USA: New York	—	KF030278	KF030368	—	KF030408	Nuhn et al. (2013)
<i>Caloboletus firmus</i>	BOS-372 (CFMR BZ-1721)	—	Belize	—	MK601726	—	MK766288	MK721080	Kuo et al. (2020)
<i>Caloboletus firmus</i>	NY00796115	—	—	KJ605656	KJ605678	KJ619473	—	KJ619464	Zhao et al. (2014)
<i>Chiua</i> sp.	HKAS74928	—	China	—	—	MT110407	—	—	Li (unpubl.)
<i>Chiua virens</i>	KPM-NC 22643	—	Japan	OQ220497	—	—	—	—	Orihira (unpubl.)
<i>Chiua viridula</i>	HKAS74928	Holotype	China	—	—	—	KF112794	KF112273	Wu et al. (2014)

Table 1 (continued)

Species	Voucher	Notes	Country	ITS	LSU	<i>RPB1</i>	<i>RPB2</i>	<i>TEF1-α</i>	References
<i>Cyanoboletus brunneoruber</i>	HKAS80579	—	China	—	KT990569	KT990926	KT990401	KT990763	Wu et al. (2016)
<i>Cyanoboletus pulverulentus</i>	9606	—	USA: West Newton	—	KF030313	KF030364	—	KF030418	Nuhn et al. (2013)
<i>Heimioporus australis</i>	REH9288	—	Australia	—	KP327652	—	—	KP327703	Halling et al. (2015)
<i>Heimioporus sinensis</i>	GDGM 45162	Holotype	China	—	NG_073658	—	—	MK165975	Chen et al. (2019)
<i>Hemileccinum impolitum</i>	Bim1	—	Germany	—	AF139715	KF030375	—	JQ327034	Binder and Besl (2000), Nuhn et al. (2013)
<i>Hemileccinum subglabripes</i>	72206	—	USA: Jefferson	—	KF030303	KF030374	—	KF030404	Nuhn et al. (2013)
<i>Hortiboletus amygdalinus</i>	HKAS54166	Holotype	China	—	KT990581	KT990933	KT990416	KT990777	Wu et al. (2016)
<i>Hortiboletus campestris</i>	MICH:KUO-08240502	—	USA: Illinois	—	MK601740	—	MK766302	MK721094	Kuo et al. (2020)
<i>Hortiboletus</i> sp.	HKAS51292	—	China	—	KF112369	KF112181	KF112547	KF112692	Wu et al. (2016)
<i>Hortiboletus subpaludosus</i>	HKAS52659	—	China	—	KT990582	—	KT990417	KT990778	Wu et al. (2016)
<i>Imleria obscurebrunnea</i>	HKAS50477	—	China	KC215206	—	KC215233	KC215241	KC215245	Zhu et al. (2014)
<i>Indoporus shoreae</i>	AP 6697	—	India	MK123977	MK123976	—	MK243368	—	Parihar et al. (2018b)
<i>Indoporus squamulosus</i>	HKAS76299	Holotype	China	—	NG_088124	—	—	MT110334	Li et al. (2021)
<i>Indoporus squamulosus</i>	HKAS107153	—	China	—	—	MT110376	MT110409	MT110335	Li et al. (2021)
<i>Lanmaoa asiatica</i>	HKAS63516	—	China	—	KT990584	KT990935	KT990419	KT990780	Wu et al. (2016)
<i>Lanmaoa borealis</i>	2858	—	USA: New York	—	JQ326998	—	—	JQ327021	Halling et al. (2012a)
<i>Lanmaoa carminipes</i>	MB06-001	—	USA: New York	—	JQ327001	—	—	JQ327022	Halling et al. (2012a)
<i>Lanmaoa pallidiorosea</i>	Mushroom Observer #210760	—	USA: New Jersey	—	MH216001	—	—	MH318610	Kudzman and Safonov (unpubl.)
<i>Lanmaoa pseudosensibilis</i>	DS615-07	—	USA: New York	—	KF030257	—	—	KF030407	Nuhn et al. (2013)
<i>Lanmaoa roseocrispas</i>	ARB92-10	Holotype	USA: Georgia	—	MH036169	—	—	KP327616	
<i>Lanmaoa rubriceps</i>	FHMu1967 (N.K.Zeng3006)	—	China	MH885346	MH879683	—	—	MH879712	Chai et al. (2019)
<i>Lanmaoa sublurida</i>	USF 300104 (Farid_1023)	—	USA: Florida	MW675736	MW662572	MW737498	MW737460	MW737485	Farid et al. (2021)
<i>Lanmaoa sublurida</i>	USF 301506 (Farid 631)	—	USA: Florida	MW675743	MW662578	MW737501	MW737464	MW737487	Farid et al. (2021)
<i>Phylloporus arenicola</i>	JT27954	—	USA	—	JQ003704	—	—	—	Neves et al. (2012)
<i>Phylloporus maculatus</i>	HKAS 59730	—	China	JQ678696	JQ678698	—	JQ678700	JQ967194	Zeng et al. (2012)
<i>Phylloporus maculatus</i>	HKAS 56683	Holotype	China	JQ967253	JQ967210	—	—	JQ967167	Schoch et al. (2014)
<i>Phylloporus maculatus</i>	FHMu3287 (Y. G. Fan2752)	—	China	MW588656	MW588618	—	—	—	Wu et al. (2021)
<i>Phylloporus phaeoxanthus</i>	MAN064	—	Costa Rica	—	JQ003670	—	—	—	Neves et al. (2012)
<i>Phylloporus phaeoxanthus</i> var. <i>simplex</i>	REH7388	—	Costa Rica	—	JQ003671	—	—	—	Neves et al. (2012)

Table 1 (continued)

Species	Voucher	Notes	Country	ITS	LSU	<i>RPB1</i>	<i>RPB2</i>	<i>TEF1-α</i>	References
<i>Phylloporus rhodoxanthus</i>	MAN099	—	USA	—	JQ003676	—	—	—	Neves et al. (2012)
<i>Phylloporus rhodoxanthus</i>	MAN075	—	USA	—	JQ003674	—	—	—	Neves et al. (2012)
<i>Porphyrellus castaneus</i>	HKAS63076	—	China	—	KT990548	KT990916	KT990386	KT990749	Wu et al. (2016)
<i>Porphyrellus castaneus</i>	HKAS52554	Holotype	China	—	KT990697	KT991026	KT990502	KT990883	Wu et al. (2016)
<i>Porphyrellus cyaneotinctus</i>	HKAS80183	—	China	—	MT154718	—	—	MT110340	Li et al. (2021)
<i>Porphyrellus griseus</i>	HKAS82849	Holotype	China	—	NG_088126	—	MT110414	—	Li et al. (2021)
<i>Porphyrellus orientifumosipes</i>	HKAS53372	Holotype	China	—	KT990629	KT990975	KT990461	KT990823	Wu et al. (2016)
<i>Porphyrellus orietifumosipes</i>	HKAS84710	—	China	—	—	—	MT110415	MT110339	Li et al. (2021)
<i>Porphyrellus porphyrosporus</i>	HKAS49182	—	China	—	KT990544	KT990912	KT990383	KT990746	Wu et al. (2016)
<i>Porphyrellus pseudocyaneotinctus</i>	w3088	—	China	—	OP380693	—	—	—	Wang et al. (unpubl.)
<i>Porphyrellus pseudocyaneotinctus</i>	w3085	—	China	—	OP380692	—	—	—	Wang et al. (unpubl.)
<i>Porphyrellus scrobiculatus</i>	HKAS53366	Holotype	China	—	KF112480	KF112610	KF112716	KF112241	Wu et al. (2014)
<i>Pulchroboletus roseoalbidus</i>	MCVC 17577	—	Italy	KJ729490	KJ729503	—	—	—	Gelardi et al. (2014)
<i>Pulchroboletus rubricitrinus</i>	USF Farid335	—	USA: Florida	MF193884	MG026638	—	—	—	Farid et al. (2017)
<i>Pulchroboletus sclerotiorum</i>	FLAS-F- 60333 (ARB1260)	Paratype	USA: Tennessee	MF098659	MF614166	MF614168	MF614169	MF614167	Crous et al. (2019)
<i>Pulchroboletus</i> sp.	ITCV:1170	—	Mexico: Oaxaca	OQ940042	OQ940036	—	OQ938904	—	Zeng et al. (2013)
<i>Sutorius alpinus</i>	HKAS50420	—	China	—	KT990549	KT990917	KT990387	KT990750	Wu et al. (2016)
<i>Sutorius eximius</i>	HKAS91261	—	China	—	—	—	MT110444	—	Li et al. (2021)
<i>Sutorius microsporus</i>	HKAS56291	—	China	—	KF112400	KF112585	KF112803	KF112208	Wu et al. (2014)
<i>Xerocomellus chrysenteron</i>	HKAS56494	—	China	—	KF112357	KF112526	KF112685	KF112172	Wu et al. (2016)
<i>Xerocomellus cisalpinus</i>	PDD94421	—	New Zealand	JQ924296	JQ924322	KF112525	KF112686	KF112171	Wu et al. (2014)
<i>Xerocomellus communis</i>	HKAS50467	Holotype	China	—	KT990670	KT991008	KT990494	KT990858	Wu et al. (2016)
<i>Xerocomellus corneri</i>	HKAS52503	—	China	—	KT990668	KT991006	KT990492	KT990856	Wu et al. (2016)
<i>Xerocomoideae</i> sp.	Mushroom Observer #215764	—	USA: Jug End Reservation	—	MH220316	—	—	MH318611	Kudzman and Safonov (unpubl.)
<i>Xerocomus cisalpinus</i>	PDD94421	—	New Zealand	JQ924296	JQ924322	KF112525	KF112686	KF112171	Wu et al. (2014)
<i>Xerocomus ferrugineus</i>	F014	—	Czechia	—	OR602219	—	—	—	Panek et al. (unpubl.)
<i>Xerocomus magniporus</i>	HKAS59820	—	China	JQ678697	JQ678699	—	JQ678701	JQ967195	Zeng et al. (2012)
<i>Zangia roseola</i>	HKAS52661	—	China	JQ928614	JQ928623	JQ928595	JQ928604	JQ928584	Hosen et al. (2013)





Fig. 1 (continued)

Fig. 1 Phylogram of the best maximum likelihood tree revealed by RAXML from an analysis of the multilocus sequence alignment (ITS, LSU, *RPB1*, *RPB2*, and *TEF1-α*) of the *Aureoboletus/Boletellus* clade. The tree was rooted with taxa from the *Boletaceae* subfamily *Zangioideae* (*Australopilus*, *Chiua*, and *Zangia*). Posterior probabilities (PP) ≥ 0.95 (left) and Bootstrap support values (BS) $\geq 70\%$ (right) are shown above the corresponding branches. Subsignificant support values were annotated in parentheses. Newly sequenced collections are highlighted in blue bold font

(36%) parsimony informative sites, and the *TEF1-α* phylogram (Supplementary Fig. 4) included 149 taxa and 435/1213 (36%) parsimony informative sites. The second concatenated supplementary tree (Supplementary Fig. 5) included 104 taxa and 3887 sites of five loci (ITS = 1–885, LSU = 886–1791, *RPB1* = 1792–2619, *RPB2* = 2620–3342, *TEF1* = 3343–3887).

Delimitation of the genus *Boletellus*

The genus *Boletellus* could be circumscribed in a stricter or broader sense: *Boletellus* s. str. circumscribes a well-supported (multilocus phylogeny, Fig. 1, PP = 0.78, BS = 79%) lineage around the type of the genus, *B. ananas*. The lineages around *B. chrysenteroides*, *B. indistinctus* G. Wu, Fang Li & Zhu L. Yang, *B. brunoflavus* Z.J. Lin, X.X. Huang, Y.S. Liang & L.H. Qiu and *B. dicymbophilus* Fulgenzi & T.W. Henkel are not part of *Boletellus* s. str. The genus *Boletellus* s. l. is only weakly supported (PP = 0.75). In either case, *B. elatus* is not a *Boletellus*, but is closely related to *Aureoboletus* sp. from Guatemala. Moreover, *A. griseorufescens* Ming Zhang & T.H. Li must be reconsidered as a *Boletellus* species.

Delimitation of the genus *Aureoboletus*

The genus *Aureoboletus* is not supported in the multilocus phylogeny (Fig. 1). Based on tree topologies it could be interpreted as one large genus *Aureoboletus* s. l. with basal *A. betula* (Schwein.) M. Kuo & B. Ortiz and *Aureoboletus* sp. from Guatemala. The longest branch in this part of the phylogeny separates *Aureoboletus* s. str. (including the type *A. gentilis*) (PP = 0.99, BS = 75%) from the lineages containing *A. clavatus* and *A. betula/Aureoboletus* sp. Both *Aureoboletus* s. l. and s. str. are well-supported in the *TEF1-α* phylogeny (Supplementary Fig. 4). Reliable support is not provided in any of the other single-locus phylogenies (Fig. 2 and Supplementary Figs. 1, 2, 3).

Phylogenetic position of *Aureoboletus* sp.

Aureoboletus sp. from Guatemala is clearly a sister taxon of *Boletellus elatus* (concatenated phylogeny, ITS, LSU; Figs. 1 and 2 and Supplementary Fig. 1). This lineage has

a marginal and basal position in relation to *Aureoboletus* s. l. In addition, LSU phylogeny reveals a sister-group relationship to *A. miniatoauranticus* (C.S. Bi & Loh) Ming Zhang, N.K. Zeng & T.H. Li, *A. garciae* Ayala-Vásquez & Aguirre-Acosta and *A. conicus* N.K. Zeng, Xu Zhang & Zhi Q. Liang.

Taxonomy

Boletellus ananas (M.A. Curtis) Murrill, *Mycologia* 1 (1): 10. 1909.

Figures 3 and 4

MycoBank MB 100683

Basionym: *Boletus ananas* M.A. Curtis, *American Journal of Arts and Sciences* 2 (6): 351. 1848.

≡ *Suillus ananas* (M.A. Curtis) Kuntze, *Revisio generum plantarum* 3 (3): 535. 1898.

= *Boletus coccineus* Fr., *Epicrisis systematis mycologici*: 423. 1838, *nom. illegit.*, Art. 53.1 (Shenzhen), non *B. coccineus* Bull., *Histoire des champignons de la France* 1 (2): 364. 1791.

= *Strobilomyces coccineus* Sacc., *Sylloge fungorum* 6: 50. 1888.

= *Boletellus coccineus* (Sacc.) Singer, *Beihefte zur Nova Hedwigia* 105: 6. 1992.

? = *Boletus isabellinus* Peck, *Bulletin of the Torrey Botanical Club* 24 (3): 146. 1897, *nom. illegit.*, Art. 53.1 (Shenzhen), non *B. isabellinus* Schwein., *Schriften der Naturforschenden Gesellschaft in Leipzig* 1: 96. 1822.

? = *Boletellus ananas* var. *crassotunicatus* Singer, *Beihefte zur Nova Hedwigia* 77: 152. 1983.

? = *Boletellus coccineus* var. *crassotunicatus* (Singer) Singer, *Beihefte zur Nova Hedwigia* 105: 7. 1992.

? = *Boletellus ananas* var. *minor* Singer, *Beihefte zur Nova Hedwigia* 77: 153. 1983.

? = *Boletellus minor* (Singer) L.D. Gómez, *Revista de Biología Tropical* 44 (Suppl. 4): 69 (1997) ("1996").

? = *Boletellus coccineus* var. *amarus* Singer, *Beihefte zur Nova Hedwigia* 105: 8. 1992.

? = *Boletellus coccineus* var. *minor* (Singer) Singer, J. García & L.D. Gómez, *Beihefte zur Nova Hedwigia* 105: 7. 1992, *nom. illegit.*, Art. 53.1 (Shenzhen).

Type: USA, South Carolina, Society Hill and Santee Canal (Santee River), beside an old log of *Pinus* sp., Jun-Oct 1847, H.W. Ravenel, Curtis 1649 (isotype K-M000141486 [!], ex Herb. Rev. M.J. Berkeley; holotype H.W. Ravenel Herbarium, FH00290409).

Basidiomes medium-sized. *Pileus* (4.5–) 5.2–9.8 (–12.0) cm broad, at first hemispherical then persistently convex and finally broadly pulvinate-flattened, sometimes slightly depressed at center, regularly shaped, moderately fleshy, firm at the beginning but progressively softer with age, flabby in old basidiomes; margin even to faintly wavy,

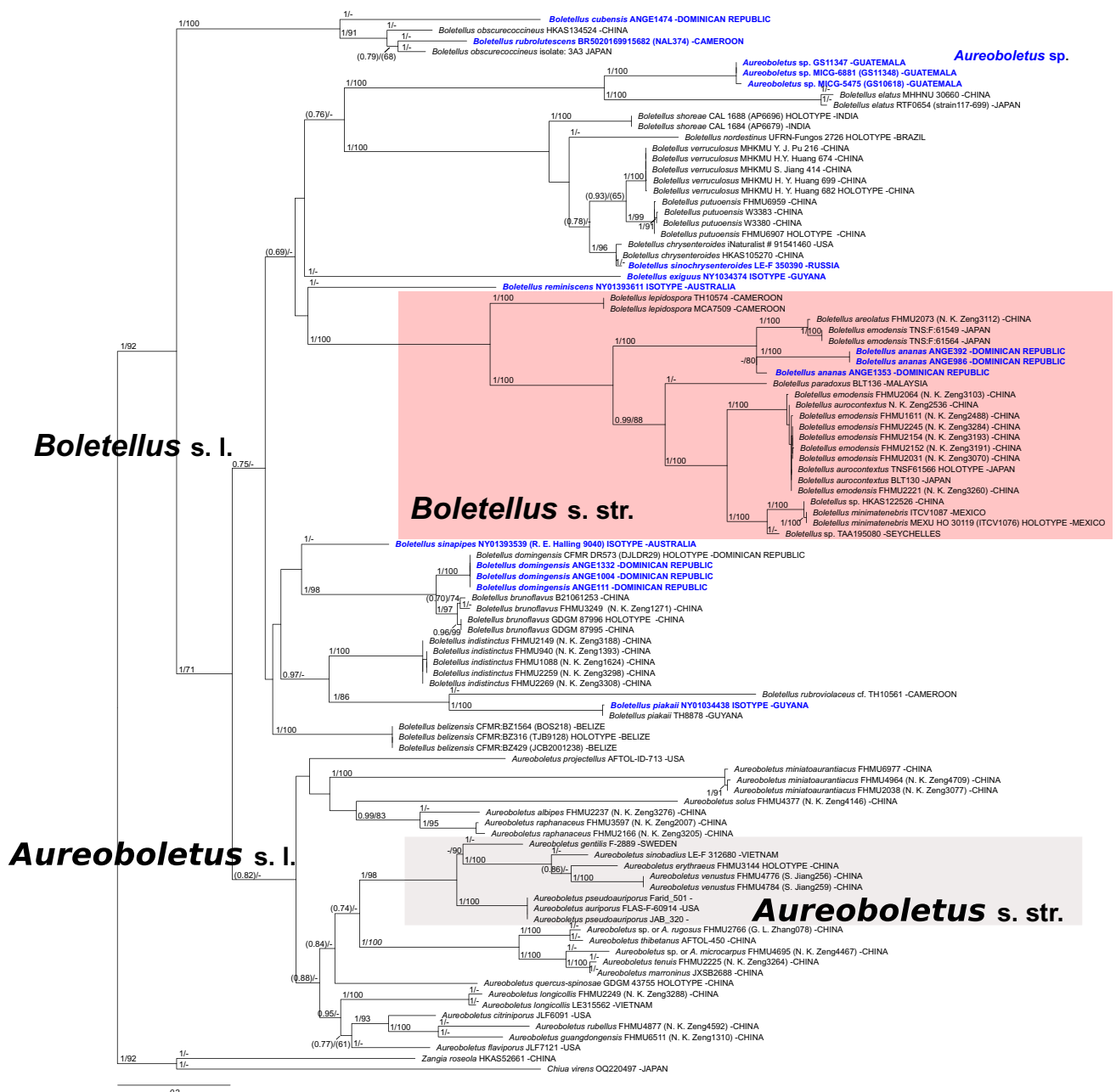


Fig. 2 Phylogram of the best maximum likelihood tree revealed by RAxML from an analysis of the ITS sequence alignment of the *Aureoboletus/Boletellus* clade. The tree was rooted with taxa from the *Boletaceae* subfamily *Zangioideae* (*Chiuia* and *Zangia*). Pos-

initially slightly involute then curved downwards and finally completely plane or even uplifted, distinctly appendiculate with membranaceous velar remnants hanging from the rim and extending beyond the tubes up to 2.0 cm; surface matt, dry, initially velvety-tomentose but soon rupturing into coarse, large, adpressed, irregularly conical to pyramidal, at first erect then progressively prostrate and radially arranged, partly imbricate squamules; variable in color over

terior probabilities (PP) ≥ 0.95 (left) and Bootstrap support values (BS) $\geq 70\%$ (right) are shown above the corresponding branches. Subsignificant support values were annotated in parentheses. Newly sequenced collections are highlighted in blue bold font

time, firstly bright pinkish purple then gradually fading to pastel pink, deep to pale flesh-pink (Tyrian Pink, Mallow Purple, Light Mallow Purple, Amaranth Pink, Mallow Pink, Pale Amaranth Pink, Rose Pink, Pl. XII; Spinel Red, Spinel Pink, Light Rosolane Purple, Pale Rosolane Purple, Pale Rose-Purple, Rosolane Pink, Cameo Pink, Pl. XXVI; Pinkish Vinaceous, Corinthian Pink, Vinaceous, Pale Vinaceous, Livid Pink, Hydrangea Pink, Pl. XXVII) and eventually

Fig. 3 *Boletellus ananas*, basidiomes in habitat. **a, g**: ANGE1353; **b**: ANGE1357; **c-d**: ANGE392; **e-f**: collections lost. Scale bars: 1 cm. Photos by C. Angelini



becoming pinkish gray to dull gray at maturity starting from the center and from squamules tips (Pale Vinaceous, Livid Pink, Hydrangea Pink, Pl. XXVII; Vinaceous-Buff, Light Vinaceous-Fawn, Pale Vinaceous-Fawn, Pale Olive-Buff, Pl. XL) until the surface appears evenly grayish in aged specimens; unchanging on handling or touching; sub-pellis layer between squamules pinkish purple then pale pinkish to whitish (Light Rosolane Purple, Pale Rosolane Purple, Pale Rose-Purple, Rosolane Pink, Cameo Pink, Pl. XXVI; White, Pl. LIII). *Tubes* relatively small at first in side view then increasingly broader with age and initially much shorter than the thickness of the pileus context, at

maturity as long as or slightly longer than the thickness of the context above (up to 1.7 cm long), adnate but soon depressed around the stipe apex and decurrent with a short tooth, pale yellow, lemon yellow to olive yellow and finally ochraceous olive (Empire Yellow, Lemon Chrome, Orange-Citrine, Sulphurine Yellow, Medal Bronze, Pl. IV; Light Greenish Yellow, Pale Greenish Yellow, Greenish Yellow, pl. V; Mustard Yellow, Primuline Yellow, Olive Lake, Old Gold, Buffy Citrine, Pl. XVI) at maturity, turning dark blue (Cerulean Blue, Peacock Blue, Patent Blue, Pl. VIII) when cut. *Pores* initially hidden by a thick, persistent membranaceous single-layered veil emanating from the pileal margin

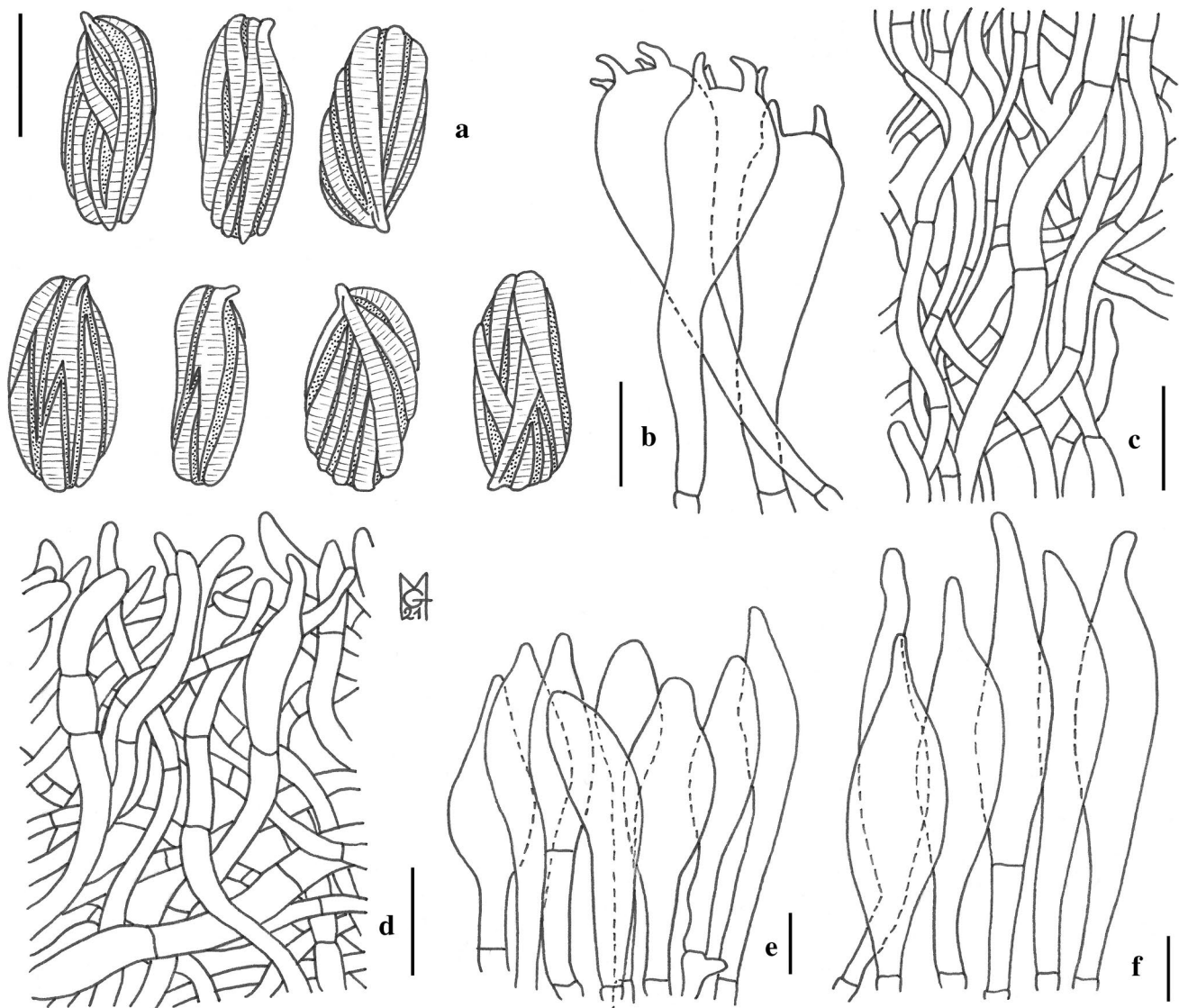


Fig. 4 Microscopic features of *B. ananas* ANGE392 and ANGE1353; **a**: basidiospores; **b**: basidia; **c**: marginal veil; **d**: pileipellis; **e**: cheilocystidia; **f**: pleurocystidia. Scale bars: 10 μ m (**a**, **e–f**); 15 μ m (**b**); 30 μ m (**c–d**). Drawings by M. Gelardi

and consisting of a pinkish then whitish at maturity (Light Rosolane Purple, Pale Rosolane Purple, Pale Rose-Purple, Rosolane Pink, Cameo Pink, Pl. XXVI; Pale Vinaceous, Livid Pink, Hydrangea Pink, Pl. XXVII; White, Pl. LIII), velvety to subsquamulose outer layer and of a pure white (White, Pl. LIII) inner layer, which soon disrupts revealing the fertile tissue underneath; at the beginning forming a flat to slightly convex surface, later moderately convex to ascending; pores at first rather small then gradually wider with age (up to 2 mm in diam.), simple, firstly roundish becoming angular at maturity, slightly stretched and radially arranged towards the stipe, concolorous with the tubes and staining dark blue (Cerulean Blue, Peacock Blue, Patent Blue, Pl. VIII) on bruising or when injured, sometimes with scattered rusty brown (Ferruginous, Pl. XIV; Mikado

Brown, Pl. XXIX) stains at the orifice in aged specimens. *Stipe* (7.0–) 8.0–13.0 (–14.0) $\times$ (1.0–) 1.5–2.5 (–3.0) cm, as long as or more frequently longer than the pileus diameter at maturity, central to slightly off-center, solid, firm, dry, straight or curved to occasionally sinuous, usually cylindrical or gradually and faintly enlarged from apex down to the base, rounded to sometimes swollen or subbulbose at the very base; surface smooth to longitudinally fibrillose, without annulus; evenly whitish (White, Pl. LIII) but pale yellow (Martius Yellow, Baryta Yellow, Pinard Yellow, Pl. IV) at the very apex and with a narrow pinkish purple (Rose Pink, Deep Rose Pink, Pl. XII; Light Rosolane Purple, Pale Rosolane Purple, Spinel Red, Pl. XXVI) band immediately underneath the yellow zone at maturity, faintly turning pale dirty orange (Light Ochraceous-Buff, Ochraceous-Buff, Pl.

XV) when injured, especially in the lower half and more evidently at the base; basal mycelium white (White, Pl. LIII). *Context* firm and tough when young, later soft textured and eventually flabby in the pileus (up to 1.5 cm thick in the central zone, up to 1.0 cm thick halfway to margin and gradually becoming thinner towards the edge), more fibrous in the stipe, pale yellow in the pileus (Baryta Yellow, Pinard Yellow, Pl. IV), whitish in the stipe (White, Pl. LIII), pinkish purple (Tyrian Pink, Mallow Purple, Light Mallow Purple, Amaranth Pink, Mallow Pink, Pale Amaranth Pink, Rose Pink, Pl. XII) underneath the cuticle in young specimens; quickly turning pale blue (Pale Cerulean Blue, Light Cerulean Blue, Cerulean Blue, Pl. VIII; Pale Sulphate Green, Light Sulphate Green, Beryl Green, Pl. XIX) throughout but bruising pale dirty orange to orangish (Light Ochraceous-Buff, Ochraceous-Buff, Ochraceous-Orange, Zinc Orange, Pl. XV) in the cortical layers and especially around the stipe base when exposed to air; vinaceous red (Deep Vinaceous, Corinthian Red, Pl. XXVII) where eroded by maggots; subhymenophoral layer pale yellowish (Baryta Yellow, Pinard Yellow, Pl. IV); exsiccate pileus pinkish beige (Seashell Pink, Pl. XIV; Pale Ochraceous-Salmon, Pl. XV), hymenophore dark brown (Auburn, Pl. I; Liver Brown, Pl. XIV), stipe and context beige (Maize Yellow, Pl. IV; Light Buff, Pl. XV). *Odor* indistinct. *Taste* bitter. *Spore print* dark olivaceous-brown.

Basidiospores [166/8/5] ($13.0\text{--}17.4 \pm 1.8$ (-21.5) $\times$ ($6.0\text{--}7.8 \pm 0.9$ (-11.0) μm , $Q=(1.58\text{--}1.77\text{--}2.91$ (-3.00), $Qm=2.21 \pm 0.25$, $V=578 \pm 183 \mu\text{m}^3$ (including ornamentation), fairly variable in dimension and shape, inequilateral, fusiform or subfusiform to more frequently ellipsoid-fusiform to ellipsoid or broadly ellipsoid in side view, ellipsoid to broadly ellipsoid in face view, occasionally peanut-shaped or irregularly shaped, somewhat tapered towards the proximal end or less frequently towards the distal end, round in axial view, markedly longitudinally ridged (14–16 broad ridges in polar view, each extending for most of the spore length although not reaching the apex but converging and coalesce together, giving the impression of a germ pore) and with fine regular transversal or inclined connecting striations on primary costae, ridges sometimes bifurcate or anastomosing and spiral arranged, moderately high and progressively more prominent with age (up to $0.8 \mu\text{m}$ deep), apex rounded to sometimes slightly truncate and with a somewhat indistinct germ pore, with a moderately pronounced apiculus, usually with an indistinct to shallow suprahilar depression or applanation and with a very slightly pronounced adaxial swelling, moderately thin-walled ($0.3\text{--}0.8 \mu\text{m}$), bright honey yellow in water and 5% KOH, having one, two or three large oil droplets, occasionally pluri-guttulate when mature, inamyloid to very weakly dextrinoid, acyanophilic or very weakly cyanophilic and with a faint metachromatic reaction. *Basidia* 40–71

(-74) $\times$ $11\text{--}18 \mu\text{m}$ ($n=28$), very slender, cylindrical-clavate to clavate, moderately thick-walled ($0.6\text{--}0.9 \mu\text{m}$), predominantly 4-spored but rarely also 1-, 2- or 3-spored, usually bearing relatively short sterigmata ($2\text{--}6 \mu\text{m}$), hyaline to pale yellowish and containing straw-yellow oil guttules in water and 5% KOH, bright yellow (inamyloid) in Melzer's, without basal clamps; basidioles subcylindrical, cylindrical-clavate to clavate, similar in size to basidia. *Cheilocystidia* ($31\text{--}34\text{--}63$ (-67) $\times$ $8\text{--}16$ (-18) μm ($n=30$), common, projecting straight to sometimes flexuous and protruding from the hymenial palisade, cylindrical-fusiform, fusiform, ventricose-fusiform to sublageniform or lageniform, less frequently subclavate, rarely mucronate, sometimes with a secondary septum, with rounded to subacute tip, smooth, moderately thick-walled ($0.3\text{--}0.8 \mu\text{m}$), pale yellowish or with a honey yellow plasmatic pigment in water and 5% KOH, bright yellow (inamyloid) in Melzer's, orthochromatic, without epiparietal encrustations. *Pleurocystidia* $40\text{--}78$ (-93) $\times$ $8\text{--}15 \mu\text{m}$ ($n=17$), relatively infrequent, shape, color and chemical reactions similar to but longer than cheilocystidia. *Pseudocystidia* not observed. *Pileipellis* a trichoderm consisting of strongly interwoven, elongated, filamentous and sinuous, frequently branched hyphae tending to be repent in the outermost layer and thus turning into a cutis not or only partially embedded in gelatinous matter at maturity; terminal elements $14\text{--}96 \times 4\text{--}17 \mu\text{m}$, cylindrical or less frequently bullet-shaped or acorn-shaped, apex rounded-obtuse to sometimes pointed, moderately thick-walled (up to $1 \mu\text{m}$), yellowish to straw yellow in water and 5% KOH, bright yellow to brownish-yellow (inamyloid) in Melzer's, smooth; subterminal elements similar in shape, size and color to terminal elements. *Marginal veil* consisting of subparallel to moderately interwoven, somewhat short, cylindrical, rarely branched, moderately thick-walled (up to $0.8 \mu\text{m}$) non-gelatinous hyphae, $7\text{--}90 \times 4\text{--}12 \mu\text{m}$, pale yellowish to yellowish in water and 5% KOH. *Stipitipellis* a texture of slender, parallel to subparallel and longitudinally running, smooth walled, adpressed hyphae, $3\text{--}11 \mu\text{m}$ wide, hyaline to pale yellowish in water and 5% KOH; the stipe apex covered by a fragmented caulohymenial layer consisting of subcylindrical, subclavate to clavate sterile caulobasidioles, ($24\text{--}27\text{--}50$ (-55) $\times$ $6\text{--}10$ (-12) μm ($n=8$), having a wall up to $0.9 \mu\text{m}$ thick, mixed with elongated filamentous, cylindrical to faintly clavate elements $74\text{--}116$ (-125) $\times$ $7\text{--}12 \mu\text{m}$ ($n=6$); true *caulocystidia* usually not differentiated from caulobasidioles (only a single, ventricose-fusiform caulocystidium observed, $47 \times 15 \mu\text{m}$); caulobasidia uncommon, 1-, 2- and 3-spored, ($41\text{--}47\text{--}61$ (-70) $\times$ $10\text{--}12 \mu\text{m}$ ($n=4$), sterigmata $4\text{--}7 \mu\text{m}$ long, similar in shape, color and size to hymenial basidia. *Lateral stipe stratum* under the caulohymenium absent. *Stipe trama* composed of confusedly and densely arranged, moderately to strongly interwoven, filamentous, smooth, hyaline to pale yellowish in water,

inamyloid hyphae, 2–20 µm broad. *Hymenophoral trama* bilateral divergent intermediate between the “*Boletus*-type” and the “*Phylloporus*-type”, with subparallel to slightly divergent and loosely arranged, gelatinous hyphae (lateral strata hyphae in transversal section not touching each other, (2–) 3–5 (–6) µm apart, 3–16 µm broad), hyaline to very pale yellowish in water and 5% KOH, inamyloid in Melzer’s; lateral strata (20–) 30–50 (–60) µm thick, mediostratum (25–) 30–50 (–60) µm thick, axially arranged, consisting of a tightly adpressed, non-gelatinous bundle of hyphae, 2–7 µm broad; in Congo Red the mediostratum is darker than the lateral strata. *Thromboplerous hyphae* very common, especially in the marginal veil, thick-walled, rarely septate, melanized, with a dense golden yellow to brownish homogeneous content in 5% KOH. *Clamp connections* absent in all tissues. *Ontogenetic development* probably pilangiocarpic.

Edibility probably edible but sometimes reported as inedible.

Ecology and phenology: solitary to more frequently gregarious, mostly growing on stumps or wood debris, but also on soil among litter under 3- and 5-needled *Pinus* species (*P. caribaea* and *P. occidentalis*) in the Dominican Republic. On the island of Hispaniola occurring from late autumn to winter (November to February).

Examined materials: DOMINICAN REPUBLIC, La Vega Province, Jarabacoa, 19°11′12.5″N 70°35′25.5″W, 660 m, 06 Dec 2014, three specimens in all developmental stages growing in a garden on a stump of *Pinus occidentalis*, C. Angelini, ANGE392 (MG721); same loc., a single young specimen growing in a mixed forest on live trunk of *P. occidentalis*, 23 Nov 2017, C. Angelini, ANGE986 (MG814); same loc., two specimens growing on litter under *P. occidentalis*, 18 Nov 2018, C. Angelini, ANGE1068; same loc., six specimens in all developmental stages growing on litter under *P. occidentalis*, 23 Dec 2019, C. Angelini, ANGE1353 (MG852); same loc., a single old specimen growing on litter under *P. occidentalis*, 06 Nov 2019, C. Angelini, ANGE1357 (MG854); same loc., five young to mature specimens growing on litter under *P. occidentalis* and *P. caribaea*, 16 Nov 2020, C. Angelini, ANGE1480 (MG853); same loc., several specimens in all developmental stages growing on litter under *P. occidentalis*, 21 Jan 2020, C. Angelini, collection lost; same loc., a single mature specimen growing on litter under *P. occidentalis*, 28 Feb 2020, C. Angelini, collection lost.

Additional examined materials: *Boletellus ananas* var. *crassotunicatus*: NICARAGUA, Slilma Sia, under *Pinus caribaea*, May 1976, T.H. Ivory, F1030894 (Ivory S/23), holotype. *Boletellus coccineus* var. *amarus*: COSTA RICA, Guanacaste, 7 km north-west of Bagaces, 80 m, under *Quercus oleoides*, Oct 1982, L.D. Gómez, F1052236 (Gómez 18701), topotype.

Additional extralimital sequenced materials: *Boletellus ananas*: USA, Georgia, Camden, Crooked River State Park, 19 Oct 2012, a single mature specimen growing in a mixed woodland with *Quercus virginiana* and *Pinus paluster* on exposed tree roots, A.R. Bessette and A.E. Bessette, NY02072372 (ARB1223).

Phylogenetic position: In the multigene phylogeny (Fig. 1), *Boletellus ananas* taxa fall in a well-supported (PP = 1.00, BS = 99%,) lineage with high heterogeneity, which contains at least two distinct subgroups. The lineage is placed in close proximity to *B. areolatus* and *B. rubidus*.

Notes: *Boletellus ananas*, commonly known with the vernacular name of “pineapple bolete,” is an eye-catching species exhibiting considerable chromatic variation over time. It is easily recognizable by medium to large-sized basidiomes, a conspicuous shaggy pileus consisting of upraised then prostrate and flattened, partly imbricate or irregularly arranged, thick, fibrous, squarrose, coarse, soft squamules with purplish vinaceous-pink then bright rose tones bleaching away in age to pale tan or dull buff starting from scale tips but frequently retaining the reddish pigment between the scales, yellow-olive hymenophore bruising blue when injured and with pores becoming reddish brown in aged specimens, initially covered by a sterile, membranaceous, thick partial veil clasping the stipe, soon radially splitting and projecting with large angular or fimbriate-lacerate, sterile velar lobes attached like a fringe along the pileal margin but not forming an annulus around the stipe, smooth to fibrillose, ringless, pale colored stipe with a reddish belt at the apex, bruising dirty orange especially towards the base, pale yellow context in the pileus and whitish in the stipe, faintly but evenly and rapidly cyanescent on exposure and with a slow dirty orange discoloration localized in the stipe base, mild to bitter taste and dark olive-brown spore print. The most stable and distinctive microscopic feature is the striking basidiospore ornamentation, consisting of longitudinally running, thick ridges. Cross or oblique striations on primary costae of the basidiospores appear as such only when seen under light microscopy, but they look deceptive as they do not constitute a superficial eusporial ornamentation. When observed under SEM, their real nature becomes evident: these veins are tiny perforations running transversally inside the spore wall. In addition, primary costae mostly run longitudinally from pole to pole although they do not reach the apex but rather converge and merge with one another around a circular depression so as to simulate a small germ pore (see Halling et al. 2015: 10). Other reliable microscopic traits include large-sized basidiospores, relatively large basidia, a trichoderm pileipellis consisting of interwoven, filamentous hyphae and a bilateral divergent hymenophoral trama intermediate between the “*Boletus*-type” and the “*Phylloporus*-type” (Curtis 1848; Berkeley and Curtis 1849; Saccardo 1888, as “*Strobilomyces coccineus* Sacc.”; Peck

1889; Murrill 1909, 1914, 1948; Coker And Beers 1943; Singer 1945, 1970; Perreau-Bertrand 1961; Thiers 1963; Horak 1968; Smith and Thiers 1971; García And Castillo 1981; Pegler and Young 1981, as “*B. ananias*”; Singer et al. 1983, 1992 as “*B. coccineus* (Sacc.) Singer”; Weber and Smith 1985; Both 1993; Gómez 1997, perhaps also as “*B. ananiceps* (Berk.) Singer”; Bessette et al. 2000, 2007, 2016, 2019; Flores Arzù And Simonini 2000; Halling And Mueller 2005; Ortiz-Santana et al. 2007, as “*B. coccineus*”; Mayor et al. 2008; Fulgenzi 2009; Magnago 2014; Halling et al. 2015; Ayala-Vásquez et al. 2018, as “*B. coccineus*” and perhaps also as “*B. ananiceps*”; Elliott And Stephenson 2018; Putzke And Putzke 2019; Román Sarabia et al. 2025, also as “*B. coccineus*”; present study).

Ecologically, the exact trophic mode of *B. ananias* is still debated, whether ECM or saprotrophic, and was even suspected by some authors to be parasitic on living plants (Murrill 1909, 1914, 1948; Coker And Beers 1943). Singer (1945) and Thiers (1963), on the contrary, firmly rejected this idea as there appears to be no real evidence of parasitism. This species in its wide concept is currently known to form at least facultative ECM association with a multitude of host plants, predominantly with *Pinaceae*, mostly two-, three-, and five-needled *Pinus* spp. (*P. bahamensis*, *P. caribaea*, *P. occidentalis*, *P. oocarpa*, *P. palustris*, *P. teocote*, etc.), as well as with other ectomycorrhizal-forming phytobionts such as *Quercus* spp. (*Q. catesbaea*, *Q. fusiformis*, *Q. germana*, *Q. humboldtii*, *Q. laurina*, *Q. martinezii*, *Q. oleoides*, *Q. scytophylla*, *Q. virginiana*, etc.) (*Fagaceae*), and leguminous trees such as *Dicymbe* spp. and *Aldina insignis* (*Fabaceae* subfam. *Caesalpinoideae* and *Faboideae*, respectively) and *Pakaraimaea dipterocarpacea* (*Dipterocarpaceae* subfam. *Pakaraimoideae*), but it has been reported also in *Magnolia-Liquidambar* (*Magnoliaceae-Hamamelidaceae*) cloud forests, with *Nectandra coriacea* (*Lauraceae*) and on trunk of the tree fern *Cyathea* (*Cyatheaceae*), in a broad range of habitats from sea level up to 2000 m alt., from late spring to winter (May to February) or even year-round depending on the latitudinal gradient (Singer 1945, 1970; Singer et al. 1983, 1992, as “*B. coccineus*”; Gómez 1997; Franco-Molano And Uribe-Calle 2000; Ortiz-Santana et al. 2007, as “*B. coccineus*”; Mayor et al. 2008; Fulgenzi 2009; Smith et al. 2011, 2013; García-Jiménez 2013, as “*B. coccineus*”; Ayala-Vásquez et al. 2018).

Originally described in the middle of the nineteenth century (Curtis 1848) as *Boletus ananias* M.A. Curtis, the type specimen originated from South Carolina, USA, but limited information is provided by the American author about the original material. *Boletellus ananias* s. l. is widely distributed in North America across the Atlantic southern and south-eastern USA (Virginia, Tennessee and North Carolina south to Florida and west to Texas) (Curtis 1848; Peck 1889; Murrill 1909, 1914, 1948; Coker And Beers 1943;

Singer 1945; Thiers 1963; Weber and Smith 1985; Both 1993; Bessette et al. 2000, 2016, 2019; Halling et al. 2015; Elliott And Stephenson 2018; iNaturalist; MyCoPortal) and Mexico (García And Castillo 1981; Singer et al. 1992, as “*B. coccineus*”; García 1999; García-Jiménez 1999, 2013, as “*B. coccineus*”; Gándara et al. 2014, as “*B. coccineus*”; Ayala-Vásquez et al. 2018, 2023b; Gonzáles-Chicas et al. 2019; Saldivar et al. 2021; Román Sarabia et al. 2025, also as “*B. coccineus*”). In mainland Central America it has been reported from Belize (Ortiz-Santana et al. 2007, as “*B. coccineus*” and “*B. coccineus* var. *amarus* Singer”; Halling et al. 2015), Guatemala (Sommerkamp and Guzmán 1990; Flores Arzù And Simonini 2000; Flores Arzù et al. 2012; Flores Arzù 2020), Honduras (Singer et al. 1992, as “*B. coccineus* var. *amarus* Singer”), Nicaragua (Singer et al. 1983, as “*B. ananias* var. *crassotunicatus* Singer” and “*B. ananias* var. *minor* Singer”, 1992, as “*B. coccineus* var. *crassotunicatus* (Singer) Singer”), Costa Rica (Singer et al. 1983, 1992, as “*B. coccineus*” and “*B. coccineus* var. *amarus*”; Gómez 1997; Halling 1997; Mata 1999; Halling And Mueller 2005; Halling et al. 2015) and Panama (Singer 1955, as “*Strobilomyces pallescens* Cooke & Massee”, 1970; Singer et al. 1983; Singer et al. 1992, as “*B. coccineus* var. *crassotunicatus*”). In the Caribbean, it has been recorded from Cuba (Minter et al. 2001) and the Bahamas islands (Singer et al. 1992, as “*B. coccineus* var. *amarus*”; Ortiz-Santana et al. 2007, as “*B. coccineus* var. *amarus*”). It is also present in northern and north-eastern South America as far south as Colombia (Singer 1970; Halling 1989, 1997; Franco-Molano And Uribe-Calle 2000; Franco-Molano et al. 2000; Vasco-Palacios and Franco-Molano 2013; Vargas And Restrepo 2020), Guyana (Henkel et al. 2004, 2012; Mayor et al. 2008; Fulgenzi 2009) and Brazil (Neves And Capelari 2007, as “*B. ananias* var. *minor*”; Magnago 2014; Putzke And Putzke 2019). Aside from the specimens documented in the present study, several other sightings of *B. ananias* have been made in pine forests of the Dominican Republic, confirming this is one of the most abundant and prolifically occurring bolete species on the island of Hispaniola, as already documented previously by Minter et al. (2001), Ortiz-Santana et al. (2007, as “*B. coccineus*”), Angelini (2022) and Molero Paredes and Nolasco (2023).

The interpretation of *B. ananias* outside its native distribution range in the New World has been controversial. Over the past two centuries, several African, Asian, and Australasian species outwardly resembling *B. ananias* have been misdetermined with that species. Consequently, all reports under the name *B. ananias* from outside the Americas, e.g., from China (including Taiwan) (Chiu 1948, 1957; Teng 1964; Tai 1979; Yeh and Chen 1982; Zang 1985, 1997; Bi et al. 1990, 1994; Chen et al. 1998; Li And Song 2000; Mao 2009), Japan (Imazeki et al. 1970), India (Verma And Pandro 2018), insular and peninsular Malaysia (Corner 1972, 1974; Pegler

1997; Horak 2011; Lee et al. 2012; Tham And Watling 2017), Thailand (Sanmee 2004; Chandrasrikul et al. 2008; Seehanan And Petcharat 2008; Thongklam 2008; Halling et al. 2015; Thongkantha et al. 2021), Vietnam (Perreau-Bertrand And Joly 1964), Australia (Syme 1992; Shepherd And Totterdell 1988; May And Wood 1997), New Caledonia (Heim and Perreau-Bertrand 1963; Corner 1972; Horak And Mouchacca 1998; Horak 2011), and New Zealand (McNabb 1967; Segedin 1987) are almost certainly misapplied and should be referred to *B. emodensis* or any other closely related Asian or Australian species of its complex.

Opinions about the edibility of this species are rather inconsistent. Bessette et al. (2016, 2019) and Ayala-Vásquez et al. (2018) consider it edible, while Bessette et al. (2000) and Elliott and Stephenson (2018) define it as inedible. Henkel et al. (2004) reported contrasting attitudes towards consumption of *B. ananas* s. l. in Guyana. In any case, the tough consistence of the tissues hardly makes this species worthwhile.

The type material of *B. ananas* is housed in both K-M and FH. Because Curtis (1848) actually described this species, the material in FH should be considered the holotype and that in K-M an isotype. To the best of our knowledge, the type material of *B. ananas* (Fig. 5a and b) underwent two revisions over time. The first was carried out by Horak

(1968), the second by Sato and Hattori (2015). The isotype material from South Carolina (USA) (K-M000141486 ex herb. Rev. M.J. Berkeley, dupl. MG1015 isotype) consists of an entire young specimen which is partly covered in mold. Only small fragments of the hymenophore and pileipellis have been processed for the microscopic re-examination and produced the following results: basidiospores ellipsoid-fusiform to ellipsoid or less frequently broadly ellipsoid, $(15.0-19.4 \pm 1.6 (-21.9) \times (7.0-8.4 \pm 0.8 (-10.8) \mu\text{m}$, $Q = (1.89-1.93-2.70 (-3.07)$, $Qm = 2.31 \pm 0.23$, $V = 730 \pm 184 \mu\text{m}^3$ (including ornamentation) [33/1/1], longitudinally ridged (10–14 ridges in polar view, up to 1.2 μm deep) and with very shallow transversal, connecting striations on primary costae, apex rounded to sometimes slightly truncate and with a somewhat indistinct germ pore, inamyloid and cyanophilic; basidia collapsed; cheilo- and pleurocystidia collapsed; pileipellis collapsed. The basidiospores are on average 2 μm longer and 0.6 μm wider than those measured for *B. ananas* in the present study. Unfortunately, the degraded state of the 178-year-old isotype material of *B. ananas* lodged in the Kew Gardens Fungarium prevented a successful DNA extraction and sequencing, either with Sanger or NGS sequencing (Illumina) protocols.

There appears to be a nomenclatural issue related to the correct name to be applied to *Boletellus ananas* (M.A.



Fig. 5 Type materials. **a**, **b**: Isotype collection of *B. ananas* K-M000141486; **c**: Holotype collection of *B. ananas* var. *crassotunicatus* F1030894; **d**: Topotype collection of *B. coccineus* var. *amarus*

F1052236 (taxon reported on the label under the unpublished name *B. ananas* var. *amarus*). Photos **a** and **b** by A. Vizzini, **c** and **d** by T. Yu. Svetasheva

Curtis) Murrill. In a footnote on page 6 in Singer et al. (1992), the authors state: “A more complete knowledge of the boletes of North and Central America makes it not merely possible but nearly certain that the description and illustration of *Boletus coccineus* Fr. Epicrisis p. 423, 1836 provides an earlier name for *B. ananas*.” The most widely used specific epithet for this species is undoubtedly “*ananas*” but according to Singer et al. (1992) *Boletus coccineus* Fr. is the oldest name available and would have priority over the one proposed by M.A. Curtis in 1848. We have carefully checked the original short description of *B. coccineus* by Fries in Epicrisis (Fries 1838) and the original plate by Plumier (1705) which Fries’ protologue refers to and have come to the conclusion there are no reasons to believe it is not conspecific with *B. ananas*, also taking into consideration it was found somewhere in America and that “it is hard to imagine what other species it could possibly represent” (Singer 1945: 126). Nonetheless, *Boletus coccineus* Fr. is illegitimate because the same binomial was proposed earlier by Bulliard (1791) to describe a different species. Consequently, since the basionym of the illegitimate *Boletellus coccineus* is to be considered the legitimate *Strobilomyces coccineus* Sacc. (Saccardo 1888), which is chronologically later than *Boletus ananas* (Curtis 1848), the correct name to be applied to this species is *Boletellus ananas* (M.A. Curtis) Murrill (Mayor et al. 2008; Fulgenzi 2009). Moreover, the unsettlement of the epithet “*ananas*” in favor of “*coccineus*” would determine nomenclatural instability.

The alleged synonymy of *Boletus isabellinus* Peck *nom. illegit.*, originally described by Peck (1897) from Ocean Springs, Mississippi, with *B. ananas* was object of debate with controversial interpretations that have led to conflicting opinions among experts (Both 1993). These two species were considered the same taxon by various authors (Murrill 1909; Singer 1945, 1970; Smith and Thiers 1971). In this regard, Singer wrote: “Murrill also was right in referring *Boletus isabellinus* Peck to *Boletellus ananas* as a synonym. The type specimens at Albany do not leave any doubt as to their identity” (Singer 1945: 126). On the other hand, W.H. Snell firmly excluded such a synonymy based on the re-examination of a co-type of *B. isabellinus*, which was however evidently immature: “There is no resemblance at all between the spores of *B. isabellinus* and *B. ananas*, for the spores of this latter plant are double the size of those of the former (as now available), they are uniformly elliptic-ovoid, and are dark brown and longitudinally striate” (Snell 1933: 230), and he finally came to the opposite conclusion than Singer: “Under any conditions, however, with the specimens at present available, there seems to be no justification for considering *B. isabellinus* the same as *B. ananas*” (Snell 1933: 231). Thus, the question as to whether *B. isabellinus* and *B. ananas* are the same species remains open and, in

this uncertainty, we refrain from taking a position for the time being.

Since modern detailed studies of the types of certain infraspecific taxa of *B. ananas* are not available in the literature, the following descriptions of the microscopic features taken from type collections are provided for comparison. However, not all structures were present for re-examination.

A topotype collection of *B. coccineus* var. *amarus* from Costa Rica (F1052236, Gómez 18701, dupl. MG856, taxon annotated under the unpublished name *B. ananas* var. *amarus*) (Fig. 5c) consists of two entire specimens (one of which young and the other mature) and half of a third mature specimen. Only a small fragment has been processed for the microscopical re-examination: basidiospores ellipsoid to broadly ellipsoid, $(14.0\text{--}) 17.3 \pm 1.3 \text{ (}\pm 20.7\text{)} \times (6.9\text{--}) 9.0 \pm 1.0 \text{ (}\pm 10.7\text{)} \mu\text{m}$, $Q = (1.66\text{--}) 1.70\text{--}2.16 \text{ (}\pm 2.20\text{)}$, $Qm = 1.91 \pm 0.15$, $V = 750 \pm 203 \mu\text{m}^3$ (including ornamentation) [30/1/1], longitudinally ridged (14–16 ridges in polar view, up to 1.2 μm deep) and with transversal, connecting striations on primary costae, apex rounded to sometimes slightly truncate and with a somewhat indistinct germ pore, inamyloid and cyanophilic; basidia mostly collapsed, clavate, $(37\text{--}) 41\text{--}48 \times 12\text{--}17 \text{ (}\pm 20\text{)} \times 3\text{--}5 \mu\text{m}$ ($n = 8$); hymenial cystidia (pleurocystidia mostly collapsed) subfusiform or fusiform to ventricose-fusiform or sublageniform, sometimes with a secondary septum, $(39\text{--}) 44\text{--}64 \text{ (}\pm 72\text{)} \times 9\text{--}12 \text{ (}\pm 14\text{)} \mu\text{m}$ ($n = 10$), moderately thick-walled (0.3–0.7 μm); pileipellis not available for re-examination.

The present re-examination of the topotype material of *B. coccineus* var. *amarus* allowed us to state that no major discrepancies with respect to *B. ananas* var. *ananas* could be located other than the basidiospores, which appear to be slightly broader and more evidently cyanophilic, and the presumably shorter basidia; the remaining microscopical traits of *B. coccineus* var. *amarus* being identical to, or at most with negligible differences, with respect to those of the typical variety (when compared with the statistics of the Dominican material studied here). Of course, we could not appreciate the lacinate-reticulate or tomentose-floccose stipe surface and the very bitter taste from dried material of this variety, as outlined by Singer et al. (1992), Gómez (1997), and Ortiz-Santana et al. (2007). Unfortunately, we failed to obtain good sequences from this topotype collection.

The holotype material of *B. ananas* var. *crassotunicatus* from Nicaragua (F1030894, Ivory S/23, dupl. MG857 isotype, K-M000008239 isotype) (Fig. 5d) consists of a half slice from a mature specimen and a quarter of a pileus. Only a small fragment has been processed for the microscopic re-examination: basidiospores ellipsoid-fusiform to more frequently ellipsoid to broadly ellipsoid, $(14.5\text{--}) 17.4 \pm 1.2 \text{ (}\pm 19.5\text{)} \times (6.0\text{--}) 7.8 \pm 0.7 \text{ (}\pm 9.4\text{)} \mu\text{m}$, $Q = (1.92\text{--}) 1.94\text{--}2.65 \text{ (}\pm 3.05\text{)}$, $Qm = 2.20 \pm 0.23$, $V = 570 \pm 128 \mu\text{m}^3$ (including ornamentation) [30/1/1], longitudinally ridged (12–14 ridges

in polar view, up to 1.2 μm deep) and with transversal, connecting striations on primary costae, apex rounded to sometimes slightly truncate and with a somewhat indistinct germ pore, inamyloid and cyanophilic; basidia collapsed; pleurocystidia collapsed; cheilocystidia of two kinds: 1) subfusiform or fusiform to ventricose-fusiform or sublageniform, sometimes with a secondary septum, $45\text{--}62\text{--}(82) \times 9\text{--}12\text{--}(15) \mu\text{m}$ ($n = 11$), hyaline to pale straw yellow, moderately thick-walled ($0.3\text{--}0.7 \mu\text{m}$), inamyloid; 2) mostly lageniform or sublageniform to rarely fusiform, rarely with a secondary septum, $(36\text{--}) 41\text{--}48\text{--}(55) \times (7\text{--}) 9\text{--}12 \mu\text{m}$ ($n = 8$), staining bright red with Congo red, decidedly thick-walled ($1.2\text{--}2.0 \mu\text{m}$), inamyloid; pileipellis not available for re-examination. Basidiospores measurements perfectly overlap those of the typical *B. ananas* as delimited in the present study. The markedly thick wall of the cheilocystidia (up to 3.7 μm thick) as described in the protologue by Singer et al. (1983) and subsequently reiterated by Gómez (1997), and from which the epithet of this variety of *B. ananas* derives from, is easily visible in one of the two different types of cheilocystidia occurring at pore mouths (although the wall hardly reaches 2 μm in thickness at most based on our observations); this feature, however, has not been observed either in the other kind of cheilocystidia or in the collapsed pleurocystidia. A possible explanation might derive from the apparent different nature of the hymenial cystidia or alternatively because of the very poor state of conservation of the dried material. This variety was also reported from Panama (Singer et al. 1983, 1992, as “*B. coccineus* var. *crassotunicatus*”) and more recently from Brazil (Barbosa-Silva And Wartchow 2017) based on the study of a paratype specimen of *B. ananas* var. *minor* (see below). Since the extraction of DNA from the type specimen failed, it is presently not possible to afford any further conjecture on the taxonomic status of *B. ananas* var. *crassotunicatus*.

Nearctic and neotropical collections of *B. ananas* have long been considered to represent a single taxonomic unit at the species level, although several infraspecific taxa from Central and northern South America were described over time (see above). Conversely, previous outcomes (Lin et al. 2022; Xue et al. 2023; Tremble et al. 2024) and our own results clearly highlight the polyphyly of *B. ananas* and the existence of at least two different cryptic phylogenetic entities within the American *B. ananas* species complex, one corresponding to the true *B. ananas* inhabiting North and Central America (including the Caribbean), which displays a strong heterogeneity and appears to be divided into two different subgroups in the multigene phylogeny (Fig. 1), the other located in north-eastern South America (Guyana) as reported by Mayor et al. (2008), Barbosa-Silva and Wartchow (2017) and Xue et al. (2023). However, morphotypes corresponding to these separate taxa are practically nearly overlapping, with apparently no relevant or stable phenotypic discrepancies upon which to rely for reciprocal separation.

The only reliable differences appear to be the smaller size of the basidiomes (pileus up to 7.4 cm), shorter pleurocystidia (less than 50 μm long), and the occurrence with *Dicymbe* spp., *Aldina insignis*, and *Pakaraimaea dipterocarpaceae* (*Dipterocarpaceae*) in Guyana (Henkel et al. 2004, 2012; Mayor et al. 2008; Fulgenzi 2009; Smith et al. 2011, 2013). Other than host association and geographic distribution, the residual separating features are taxonomically unstable, and the two species coincide in all other respects. Thus, in most cases, only molecular data allow for confident identification.

Boletellus ananas var. *minor* Singer was proposed by R. Singer based on material yielded in the campinarana vegetation of the Brazilian Amazonas and in Nicaragua and was diagnosed as differing from *B. ananas* by smaller basidiomes (pileus up to 3.0 cm diam., stipe 0.4–0.8 cm wide), slightly smaller and less angular pores, and slightly narrower basidiospores ($5.5\text{--}7.5 \mu\text{m}$ broad) (Singer et al. 1983, 1992). Mayor et al. (2008), Fulgenzi (2009), and Magnago (2014) reported to have re-examined the holotype material of *B. ananas* var. *minor* (INPA, Singer B10913), but no detailed information is offered in their respective works. More recently, Barbosa-Silva and Wartchow (2017) carried out a microscopic revision of a paratype specimen of *B. ananas* var. *minor* from Brazil (INPA 102047, Singer B 12137) and reported the presence of thick-walled cheilocystidia which were said to be thin-walled in the original description (Singer et al. 1983, 1992). Accordingly, they concluded that *B. ananas* var. *minor* and *B. ananas* var. *crassotunicatus* were synonyms (Barbosa-Silva And Wartchow 2017). We are currently unable to confirm this hypothesis, nor can we address whether *B. ananas* var. *minor* is the same taxon as the typical *B. ananas* or the unnamed Guyanan species mentioned above, or even a distinct species on its own. An isoparatype collection (including a spore print) of *B. ananas* var. *minor* from Nicaragua (Silma Sia, lowland forest under *Pinus caribaea*, May 1976, M.H. Ivory S/16, Field Museum of Natural History, Chicago, F, paratype) is preserved at RBG Kew Fungarium (K-M000014327).

Boletellus ananas is the most representative species of a tight complex of similar squamose-capped taxa which has a nearly cosmopolitan distribution. Species of the *B. ananas* consortium are morphologically, ecologically, and phylogenetically correlated to one another and often difficult to tell apart. Closely allied species that can be confused with *B. ananas* are *B. ananiceps* (= *Strobilomyces fasciculatus* Cooke 1891 p. p.), *B. areolatus* Hirot. Sato, *B. cremeovellus* Barbosa-Silva & Wartchow, *B. cubensis*, *B. emodensis*, *B. cf. emodensis*, *B. deceptivus* Halling & N.A. Fechner, *B. dissiliens* (Corner) Pegler & T.W.K. Young, *B. immutabilis* (Bouriquet) Perr.-Bertr., *B. paradoxus* (Masse) E.-J. Gilbert, *B. porphyrius* (Pat. & C.F. Baker) E.-J. Gilbert, *B. rubidus* N.K. Zeng, R. Xue, Y.J. Hao & Zhi Q. Liang,

B. squamosus M. Zang, *B. yunnanensis* M. Zang, *B. zenghuoxingii* N.K. Zeng, R. Xue, S. Jiang & Zhi Q. Liang and *Veloporphryrellus africanus* Watling.

Boletellus ananas and *B. ananiceps* (orthographic variant “*B. ananaecephus*”) are lookalikes but phylogenetically distinct (Fig. 1); however, there are apparently few and subtle macromicroscopical and ecological apomorphies affording a clear morphological separation. In *B. ananiceps*, pileus squamules are clay buff to fawn, never pinkish/reddish in any developmental stage (these tints are restricted to the ground between squamules); the basidiospores are slightly longer and narrower [(15.4–) 16–23 (–26) × (6–) 6.5–7.8 (–8.3) μm ($18 \pm 1.5 \times 7.1 \pm 0.7 \mu\text{m}$), $Qm = 2.6$], with 18–22 thinner ridges and, most notably, with smooth ridges (no cross striations), shorter pileipellis terminal cells (27.5–33 μm long), and its distribution is apparently disjunct in Australia and in the neotropics of southern North America (Mexico) and Costa Rica (Berkeley 1873; Saccardo 1888; Cleland And Cheel 1919; Singer 1955, 1990; Perreau-Bertrand 1961; Pegler and Young 1981; Watling And Gregory 1986; Singer et al. 1992; Gómez 1997; May And Wood 1997; Bougher and Syme 1998; Watling and Li 1999; Halling And Fechner 2011; Halling et al. 2015; Ayala-Vásquez et al. 2018; Leonard 2024). The conspecificity of the American samples of *B. ananiceps* (Singer 1990; Singer et al. 1992; Gómez 1997; Ayala-Vásquez et al. 2018) with those from Australia is yet to be confirmed with certainty. Moreover, reports of *B. ananiceps* from China (Bi et al. 1997; Li And Song 2000; Wang 2004) should be attributed to any of the species recently segregated from the *B. emodensis* consortium (Zeng And Yang 2011; Sato And Hattori 2015; Xue et al. 2023). It is worth noting that R. Halling, in a handwritten note dated November 2010 attached to the label of the holotype material of *Strobilomyces ananiceps* Berk. currently housed at RBG Kew, casts some doubts on the identity of this species due to the presence of some spores showing cross-striations on primary ridges.

Boletellus cubensis (see detailed description below) is promptly separated from *B. ananas* by the pileus showing a much less conspicuous ornamentation with an even surface soon disrupting into very finely areolate or subsquamulose patches, the stipe bearing an annulus and sparse cottony, white to grayish floccules in the lower three quarters and the lack of any oxidation reactions. Microscopically, *B. cubensis* exhibits slightly longer basidiospores with a higher number of ridges that are not as broad and raised as those of *B. ananas*, and not transversely veined. In spite of the more or less overlapping geographic distribution of *B. ananas* and *B. cubensis*, they do not grow sympatrically due to different ecological requirements. *Boletellus cubensis* usually lives in lowland habitats and seems to form obligate or at least preferential ECM association with *Coccoloba* spp. (Polygonaceae). In addition, this species is rarer than

B. ananas and much less widespread (Berkeley and Curtis 1869, also as “*Boletus lignatilis*”; Singer 1945, also as “*Boletellus lignatilis*”; Perreau-Bertrand 1965; Pegler and Young 1981; Pegler 1983, 1987, also as “*Boletellus lignatilis*”; Singer et al. 1983, 1992; Gómez 1997, as “*Boletellus lignatilis*”; Ortiz-Santana et al. 2007; de la Fuente et al. 2018; present study).

Boletellus cremeovelosus is easy to tell apart from *B. ananas* based on the complete absence of reddish or pinkish tints, softer, fluffy squamules on pileus surface, non-cyanescent context in the stipe, basidiospores devoid of cross-veins between primary ridges, ECM association with *Coccoloba* spp. and a distribution restricted to the Atlantic Forest of north-eastern Brazil (Barbosa-Silva And Wartchow 2017). Molecular analyses are required to assess the phylogenetic placement of this species.

We presently follow the concept of *B. emodensis* s. str. as outlined by Xue et al. (2023), because their sequences obtained from Chinese collections cluster with a reference voucher from north-eastern India, close to the type locality where *B. emodensis* was originally described (Darjeeling District, West Bengal, eastern Himalaya) (Berkeley 1851). *Boletellus ananas* and *B. emodensis* s. str. exhibit a superficial resemblance and are highly similar in many respects, but they appear heterospecific based on molecular phylogenetic inference and several morphological, ecological, and geographic key features. The latter species differs essentially by a deeper crimson red to dingy reddish purple pileus (more persistent over time although finally fading to pale brown) with smaller, adpressed, verrucose scales, reddish stipe all the way down to the base, stipe base context apparently not rufescent, comparatively longer and slightly broader basidiospores [(17.5–) 18.0–21.5 (–24.5) × 7.5–10 (–11) μm , $Qm = 2.31$] with ridges projecting up to 1.5 μm , and an apparently strict Asian distribution (confirmed molecularly from India, Sri Lanka, China, and Japan) (Berkeley 1851; Pegler and Young 1981; Horak 2011; Sato And Hattori 2015, also as “*B. aurocontextus* Hirot. Sato”; Tibpromma et al. 2017; Xue et al. 2023). Even though three new species, viz. *B. areolatus*, *B. rubidus*, and *B. zenghuoxingii* (in addition to *B. squamosus* and *B. yunnanensis*) have recently been segregated from the *B. emodensis* complex, this species still remains polyphyletic with the discovery of at least two supplementary, unclassified phylogenetic species, one apparently confined to Japan and the other to Australia (*Boletellus* cf. *emodensis*, see detailed description below) (Xue et al. 2023). The binomial *Boletellus floriformis* Imazeki (Imazeki 1952) might become available for the Japanese phylogenetic species cited above, but a thorough re-examination of the type material will be necessary before this name could be applied. Similarly, *Boletus pseudostrobilomyces* W.F. Chiu might turn out to have precedence over any of the aforementioned species’ names recently introduced by

Xue et al. (2023), even though the costate ornamentation on the basidiospores seems to have been neglected (immature specimen?) in the original description (Chiu 1948, 1957). It is also worth noting that several reports of *B. emodensis* s. l. were published from eastern and south-eastern Asia over time (Singer 1945; Corner 1972; Wen 1985; Zang 1985, 1997; Imazeki et al. 1988; Bi et al. 1990, 1994, both as “*B. ananas*”; Hongo And Izawa 1994; Bi et al. 1997, as “*B. ananiceps*”; Chen et al. 1997; Nagasawa 1997; An 1998; Li And Song 2000; Wang 2004; Halling et al. 2007; Seehanan And Petcharat 2008; Thongklam 2008; Mao 2009; Wu et al. 2011; Aryal And Budhathoki 2013, as “*Buchwaldoboletus lignicola* (Kallenb.) Pilát”; Zeng And Yang 2011; Pham And Morozova 2020, as “*B. ananas*”), but in light of modern research it is impossible to determine whether they are referable to the current concept of *B. emodensis* s. str. or to any of the several other taxa of the *B. emodensis* species-complex recently introduced or reviewed by Xue et al. (2023). On the other hand, it appears clear that Sato and Hattori (2015) split local populations of a single entity while describing *B. aurocontextus* from Japan as an independent species and based on a more refined phylogenetic reconstruction this taxon should be synonymized with *B. emodensis* s. str., as most recently outlined by Xue et al. (2023). Conversely, in light of current knowledge the taxonomic status of *Boletellus squamatus* (Berk.) Singer, originally described from the Indian state of Meghalaya (Myrung, Khasi Hills), eastern Himalaya (Berkeley 1852), *B. verrucarius* (Berk.) Singer from the Indian State of Sikkim, eastern Himalaya (Berkeley 1854), and that of *B. annamiticus* (Pat.) E.-J. Gilbert, which was discovered in Vietnam (Rives du Kamly, lectotype) (Patouillard 1909; Zeng And Yang 2011), all three taxa being historically considered closely related to or even treated as later synonyms of *B. emodensis* (see, for example, Singer 1945; Zeng And Yang 2011), should be critically re-evaluated. Considering the striking species diversity in eastern and southeastern Asia, the indiscriminate use of the epithet “*emodensis*” for any taxon of this multitude without deeper investigation is strongly dissuaded. For the same reasons explained above, records of *B. emodensis* outside Asia, e.g. Madagascar (Heim and Perreau-Bertrand 1963), Indonesia (Java) (Boedijn 1960), Papua New Guinea (Horak 1977), Australia (Watling And Gregory 1986; May And Wood 1997; Watling and Li 1999; Young 2005; McMullan-Fisher et al. 2014; Halling et al. 2015), Tasmania (Gates And Ratkovsky 2018), and New Caledonia (Horak And Mouchacca 1998) must evidently be ascribed to different species.

A set of morphological and biogeographic features including a vivid red pileus with small, isolated, upturned scales, a stipe tinged red lengthwise, white context, apparently non-rufescent stipe base context, faintly shorter and broader basidiospores ($16.5 \pm 1.2 \times 9.2 \pm 0.8 \mu\text{m}$, $Q_m = 1.80$) with ridges projecting 1–2 μm , slightly narrower pileipellis

hyphae (up to 11 μm wide) and the occurrence in eastern and south-eastern Asia (China, Japan, Thailand) aid in differentiating *B. areolatus* from *B. ananas* (Sato And Hattori 2015; Xue et al. 2023). This species was tentatively named *B. ananas* in the phylogram by Halling et al. (2015) based on specimens from Thailand.

The recently described *B. rubidus* resembles *B. ananas* but is readily recognized by a more reddish pileus with smaller scales, light pink to pink stipe, apparently non-rufescent stipe base context, smaller basidiospores ($12\text{--}14.5\text{--}15\text{--}16 \times 5\text{--}7\text{--}7.5\text{--}8.5 \mu\text{m}$, $Q_m = 2.1$) and the occurrence in southwestern China (Yunnan Province) and Thailand (Xue et al. 2023; Wang et al. 2025).

In its gross morphology *B. squamosus* is distinguished by brown to brownish pink pileal scales, concolorous or reddish stipe surface, apparently non-rufescent stipe base context, slightly larger basidiospores measuring ($16.5\text{--}17\text{--}21\text{--}22 \times 8\text{--}9\text{--}11 \mu\text{m}$, $Q_m = 1.9$, with ridges projecting 1–1.5 μm and the geographic range which is apparently limited to tropical southern and south-western China (Hainan and Yunnan Provinces) and Thailand (Zang 1985, 1986; Xue et al. 2023). This species was provisionally named *B. emodensis* in the phylogram by Halling et al. (2015) based on specimens from Thailand.

Boletellus yunnanensis resembles *B. ananas* in many respects except for its brownish pileus and stipe, slightly larger basidiospores $18.5\text{--}22.5 \times 9.5\text{--}11 \mu\text{m}$, $Q_m = 2.0$, with ridges projecting 1–1.5 μm and the occurrence in south-western China (Yunnan Province), which are the best clues for identifying this eastern Asian species (Zang 1985, 1986; Xue et al. 2023). However, *B. yunnanensis* is a critical species that has not been sequenced to date. Fresh material is necessary to assess its taxonomic limits and phylogenetic placement.

Xue et al. (2023) introduced *B. zenghuoxingii* as a novel member of the *B. emodensis* consortium, differing from *B. ananas* by the deep red pileus with smaller, erect, conical, and more isolated squamules, apparently non-rufescent stipe base context, slightly larger basidiospores ($17.5\text{--}18\text{--}22 \times 7.5\text{--}8\text{--}9.5\text{--}10 \mu\text{m}$, $Q_m = 2.3$, with ridges projecting 1–1.5 μm , longer pleurocystidia ($83\text{--}103 \times 11\text{--}17 \mu\text{m}$), and the occurrence in southern China (Hainan Province).

The Australian *Boletellus deceptivus* resembles *B. ananas* in general appearance but differs in the brighter and more persistent dark red tint of the pileus, which tends to produce scales towards the margin only and becomes areolate at maturity, slightly smaller basidiospores [$15.3\text{--}17.8\text{--}18.9 \times 6.2\text{--}7\text{--}7.9\text{--}8.4 \mu\text{m}$ ($16.5 \pm 0.8 \times 6.9 \pm 0.4 \mu\text{m}$), $Q_m = 2.4$] which are devoid of apical truncation and rudimentary germ pore, smaller basidia ($25\text{--}32 \times 7\text{--}10 \mu\text{m}$), shorter pleurocystidia (up to 50 μm long), and cheilocystidia (up to 40 μm long), and the occurrence in wet

or dry sclerophyll forests under *Myrtaceae* (*Eucalyptus*, *Lophostemon*, *Leptospermum*, *Melaleuca*, *Syncarpia*), *Casuarinaceae* (*Allocasuarina*), and *Fabaceae* (*Acacia*) in eastern Australia (New South Wales and Queensland) (Halling et al. 2015; Leonard 2024).

In concordance with Halling et al. (2015) and based on the presently examined collections, the Australian *Boletellus* cf. *emodensis* (see detailed description and Discussion below) differs from *B. ananas* by the smaller and more adpressed pileus squamules which are consistently reddish pink over a whitish buff background (soon discoloring pale buff over a reddish pink background in *B. ananas*), reddish stipe lengthwise at least in young specimens and unchanging on handling, basidiospores longer and broader [$(16.8\text{--}19.6 \pm 1.4\text{--}22.8) \times (6.9\text{--}8.9 \pm 0.8\text{--}11.5) \mu\text{m}$, $Qm = 2.20$, $Vm = 824 \mu\text{m}^3$] (at least as far as the Dominican collections of *B. ananas* are concerned), which are constantly devoid of apical truncation and rudimentary germ pore and with primary ridges on average less numerous and obscurely thicker, and generally with less pronounced cross striations, pileipellis mostly consisting of disarticulating cylindrocytes up to $68 \mu\text{m}$ long and the occurrence in Australia in association with *Myrtaceae*, *Fabaceae*, and *Casuarinaceae*. Halling et al. (2015) emphasized the yellowish context in the stipe of *Boletellus* cf. *emodensis* as an additional separating feature, but this trait is unstable because the yellowish tint bleaches whitish in aged or otherwise dehydrated specimens, irrespective of their developmental stage (Halling et al. 2015).

Boletellus dissiliens, originally collected in Singapore, looks superficially like *B. ananas* but is distinguished easily based on basidiomes constantly devoid of bright pinkish or reddish tints which are replaced by overall grayish buff, tan-buff to buff-white or drab pinkish-tan colors, pileus not truly squamose but somewhat matted subtomentose and breaking up into large flat, felt-like patches, smaller basidiospores [$(13\text{--}14\text{--}17.5\text{--}18.5) \times (4.9\text{--}5.2\text{--}7\text{--}8.4) \mu\text{m}$, on average $15.9 \times 7.1 \mu\text{m}$, $Qm = 2.2$], vesiculose to utriform, much broader ($18\text{--}30 \mu\text{m}$ wide) hymenial cystidia and the occurrence in southern and south-eastern Asia (India, Singapore) with *Fagaceae* (*Quercus*), *Dipterocarpaceae* (*Shorea*), and *Arecaceae* (*Oncospermum*) debris, and presumably in Australia with *Myrtaceae*, *Casuarinaceae*, and *Fabaceae* (Corner 1972; Pegler and Young 1981; Harsh And Bisht 1982; May And Wood 1997; Horak 2011; Halling et al. 2015; Sato And Hattori 2015; Tham And Watling 2017; Verma And Pandro 2018; Semwal et al. 2022; Lee And Choong 2023; Leonard 2024). However, the conspecificity of the Australian samples of *B. dissiliens* with the original material from south-east Asia is yet to be molecularly demonstrated because the type of *B. dissiliens* has not been sequenced to date.

Boletellus paradoxus, originally described from Singapore, is separated from *B. ananas* by smaller-sized

basidiomes (pileus 6–7 cm diam., stipe 4–5 $\times$ 0.5–0.6 cm), umber-brown pileus and stipe and different geographic distribution (Massee 1909; Singer 1955; Pegler and Young 1981). This is a critical species which has never been sequenced to date. It has been considered a later heterotypic synonym of *B. emodensis* by Corner (1972, see also handwritten notes made by the same E.J. Corner and dated 24 Aug 1970, accompanying the holotype and isotype materials of *Strobilomyces paradoxus* Massee lodged at Kew, K-M000178931a-b), and Horak (2011) based on basidiospores size and ornamentation. Fresh material is urgently needed to assess its taxonomic and phylogenetic boundaries. Sato and Hattori (2015) included sequences from an umber-capped collection of *Boletellus* cf. *paradoxus* found in a lowland mixed dipterocarp forest in Sarawak, Malaysian Borneo, forming an independent species-level lineage (Sato And Hattori 2015; Xue et al. 2023; present study). Whether this voucher collection is conspecific with *B. paradoxus* from Singapore has not yet been clarified either.

Another southeastern Asian species, *B. porphyrius*, originally described from the Singapore Botanic Garden, essentially differs from *B. ananas* by smaller-sized basidiomes (pileus 3.5–4.5 cm diam., stipe 6–9 $\times$ 0.6–0.8 cm), umber brown stipe surface, darkening context on exposure, slightly longer basidiospores ($17.5\text{--}21 \times 7.5\text{--}9.5 \mu\text{m}$), and different geographic distribution (Patouillard And Baker 1918; Saccardo 1925; Singer 1945, 1955; Perreau-Bertrand 1961; Horak 2011). This is also a critical species which has been generally regarded as conspecific with *B. emodensis* (Boedijn 1960; Corner 1972; Horak 2011), but it should be re-evaluated in the light of the recent segregation of the *B. emodensis* species-complex (Xue et al. 2023). Boedijn (1960) recorded this taxon in Java, Indonesia, opting to place it under synonymy with *B. emodensis*.

Boletellus immutabilis is a rare and poorly known species described by Bouriquet from Madagascar as a member of *Strobilomyces* Berk. (Bouriquet 1946), later recombined in *Boletellus* by Heim and Perreau-Bertrand (1963) after a revision of the type material. According to Heim and Perreau-Bertrand (1963), *B. immutabilis* is a member of the *B. ananas* aggregate but differs from this species by the red pileus, entirely reddish stipe, shorter basidiospores ($12.5\text{--}13.2\text{--}16.8\text{--}18 \times 6\text{--}7.2\text{--}8 \mu\text{m}$ lacking cross striations on primary ridges, occurrence under introduced *Eucalyptus* sp., and different geographic distribution (Bouriquet 1946; Heim and Perreau-Bertrand 1963). Phylogenetic affiliations of *B. immutabilis* with related species are presently unknown.

The similar-looking African taxon *Veloporphyrillus africanus*, which is unquestionably a member of the *B. ananas*/*B. emodensis* consortium based on preliminary unpublished molecular phylogenetic studies (Hampe, in litt.), shows several morphological features in parallel with *B. ananas*, including a squamulose pileus with

an appendiculate margin, olivaceous hymenophore and cyanescent context. However, it is separated by the buff to pale brown pileus and stipe surfaces, smaller basidiospores [(11.8–) 12.7–13 (–14.2) $\times$ 4.4–4.8 (–5.2) μ m], smaller basidia (23–25 $\times$ 12.5–14 μ m), smaller hymenial cystidia (pleurocystidia 26–27.5 $\times$ 5–6.5 μ m, cheilocystidia 19.5–26.5 $\times$ 5–6.5 μ m), and the occurrence in tropical African miombo woodlands in association with caesalpinoid legumes of the family *Fabaceae* (*Brachystegia*, *Isoberlinia*), *Uapaca* (*Phyllanthaceae*), *Marquesia*, and *Monotes* (*Dipterocarpaceae*) (Watling And Turnbull 1993; Kamou et al. 2017; Vanié-Léabo et al. 2017; Piepenbring et al. 2020). The description and related illustrations of *Boletellus pustulatus* (Beeli) E.J. Gilbert offered by Niemälä et al. (2021) from eastern tropical Africa (Tanzania) are most likely to be referred to *V. africanus*. Strangely, in the protologue, the basidiospores were said to be smooth walled (Watling And Turnbull 1993) as opposed to the general rule of ridged ornamentation found in all closely related *Boletellus* species. We cannot exclude that the dried specimen examined by Watling and Turnbull (1993) might be immature and still devoid of eusporial ornamentation, but future investigations of the type specimen and additional samples will be necessary to address this inconsistency, which prompted an incorrect generic placement.

Boletellus cubensis (Berk. & M.A. Curtis) Singer, Farlowia 2 (1): 127. 1945.

Figures 6, 7a–d, and 8

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Basionym: *Boletus cubensis* Berk. & M.A. Curtis, Journal of the Linnean Society 10: 304. 1869 (“1868”).

≡ *Suillus cubensis* (Berk. & M.A. Curtis) Kuntze, Revisio generum plantarum 3 (2): 535. 1898.

= *Boletus lignatilis* Berk. & M.A. Curtis, Journal of the Linnean Society 10: 303. 1969 (“1868”).

= *Boletellus lignatilis* (Berk. & M.A. Curtis) L.D. Gómez, Revista de Biología Tropical 44 (suppl. 4): 68. 1997 (“1996”).

? = *Boletus guadalupensis* Pat., Bulletin de la Société Mycologique de France 16: 177. 1900.

Type: Greater Antilles, Cuba, on the ground, October, C. Wright, Wright (Curtis) 344 (holotype K-M000178411; ex Herb. Rev. M.J. Berkeley isotype M.A. Curtis Herbarium, FH00543126; isotype NY65200).

Basidiomes small to medium-sized. **Pileus** (2.0–) 4.4–7.2 (–7.5) cm broad, at first hemispherical then persistently convex or rarely subconical and finally broadly pulvinate-flattened, sometimes slightly depressed at center, regularly to less frequently unevenly shaped by shallow depressions, moderately fleshy, firm at the beginning but progressively softer with age, flabby in old basidiomes; margin even to faintly wavy, initially slightly involute then curved downwards and

finally completely plane or even uplifted, distinctly appendiculate with white (White, Pl. LIII) and bluing (Patent Blue, Pl. VIII) velar remnants hanging from the rim, extending beyond the tubes up to 6 mm; surface matt, dry, tomentose and not dissociated at first but soon becoming minutely cracked-areolate to subsquamulose; somewhat variable in color, ranging from uniformly pale flesh-pink, deep flesh-pink to reddish pink or pinkish vinaceous to reddish purple, vinaceous red or dark garnet red (Shrimp Pink, La France Pink, Pl. I; Safrano Pink, Orient Pink, Orange Pink, Pl. II; Flesh-Pink, Chatenay Pink, Old Rose, Eugenia Red, Acajou Red, Pompeian Red, Vandyke Red, Pl. XIII; Aster Purple, Pansy Purple, Pl. XII; Light Corinthian Red, Dark Vinaceous, Corinthian Red, Pl. XXVII) but squamules progressively fading with age becoming reddish brown, olivaceous brown or grayish brown to dark brown (Dark Olive Buff, Citrine-Drab, Buffy Brown, Army Brown, Olive-Brown, Pl. XL; Light Cinnamon-Drab, Cinnamon-Drab, Light Drab, Drab, Grayish Olive, Pl. XLVI; Olive Gray, Mouse Gray, Pl. LI) starting from the center, although always retaining reddish tints towards the peripheral zone even in senescence; unchanging to slowly reddening (Pomegranate Purple, Bordeaux, Pl. XII; Deep Vinaceous, Dark Vinaceous, Pl. XXVII) on handling or touching or more obviously when injured; subpellis layer between cracks whitish to pale cream or pale pinkish (White, Pl. LIII; Martius Yellow, Pl. IV, Shrimp Pink, La France Pink, Pl. I; Rose Pink, Pl. XII). **Tubes** wide at first in side view then increasingly broader with age and as long as or slightly longer than the thickness of the pileus context (up to 1.0 cm long), adnexed but soon deeply depressed around the stipe apex and decurrent with a short tooth, pale yellow to olive yellow and finally ochraceous olive (Pinard Yellow, Citrine, Dark Citrine, Pl. IV; Light Green-Yellow, Light Greenish Yellow, Greenish Yellow, Bright Green Yellow, Oil Yellow, Javel Green, pl. V; Primuline Yellow, Olive Lake, Yellowish Citrine, Pl. XVI) at maturity, unchangeable when cut. **Pores** initially covered by a thick, double-layered veil consisting of a pinkish (Rose Pink, Pale Amaranth Pink, Mallow Pink, Light Mallow Purple, Pl. XII), membranaceous inner layer underlying a pure white (White, Pl. LIII), cottony outer layer, which soon disrupts revealing the fertile tissue underneath; at the beginning forming a flat to slightly convex surface, later moderately convex to ascending; pores broad at first then gradually wider with age (up to 2 mm in diam.), simple, firstly labyrinthine becoming prominently angular at maturity, stretched and radially arranged towards the stipe, concolorous with the tubes and not staining on bruising or when injured, sometimes with scattered rusty brown (Ferruginous, Pl. XIV; Mikado Brown, Pl. XXIX) stains at the orifice in aged specimens. **Stipe** (4.8–) 6.6–9.5 (–10.8) $\times$ (0.6–) 0.8–1.7 (–2.2) cm, as long as or more frequently longer than the pileus diameter at maturity, central to slightly off-center, solid, firm, dry, straight or curved to occasionally sinuous, gradually and faintly swollen from apex

Fig. 6 *Boletellus cubensis*, basidiomes in habitat. **a-e, g**: collection lost; **f**: MO 401056. Scale bars: 1 cm. Photos by C. Angelini (a-e, g) and K.O. Miller (f)



down to the base which is sometimes subbulbose, occasionally cylindrical or subcylindrical, usually ending with a short taproot at the very base; surface smooth to finely pruinose at apex and with an ample and persistent, soft, cottony, whitish annulus becoming dark olive brown with age due to spore discharge; underneath the ring nearly entirely ornamented by minute cottony, whitish to pale gray (White, Pl. LIII; Pallid Mouse Gray, Pale Mouse Gray, Light Mouse Gray, Olive Gray, Pl. LI) floccules longitudinally or irregularly arranged (ephemeral remnants of an alleged universal veil) on a smooth background; evenly yellowish (Martius Yellow, Baryta Yellow, Pinard Yellow, Pl. IV) above the ring in very

young specimens but soon retaining the yellow tint only at the extreme apex, elsewhere with an abruptly bright flesh-pink, pinkish vinaceous or reddish pink to reddish purple, vinaceous red or garnet red background (Hermosa Pink, La France Pink, Shrimp Pink, Geranium Pink, Begonia Rose, Pl. I; Safrano Pink, Orient Pink, Pl. II; Flesh-Pink, Chatenay Pink, Venetian Pink, Alizarine Pink, Old Rose, Eugenia Red, Acajou Red, Pompein Red, Vandyke Red, Pl. XIII; Aster Purple, Amaranth Purple, Pansy Purple, Pl. XII; Light Corinthian Red, Dark Vinaceous, Corinthian Red, Pl. XXVII), becoming gradually lighter downwards, white at base (White, Pl. LIII), unchangeable or faintly reddening (Amaranth Purple,

Fig. 7 *Boletellus cubensis*, basidiomes in habitat. **a-d**: ANGE1474 (a: macrochemical staining with 30% KOH; b: basidiome growing on wood; c: basidiome growing on stone); *Boletellus* aff. *emodensis*, basidiomes in habitat **e**: MG602; **f**: MG598. Scale bars: 1 cm. Photos by C. Angelini (a-d) and M. Gelardi (e, f)



Pomegranate Purple, Pl. XII) when pressed but typically turning dark blue (Patent Blue, Pl. VIII) on the ring; basal mycelium white (White, Pl. LIII). *Context* firm and tough when young, later soft textured and eventually flabby in the pileus (up to 0.8 cm thick in the central zone, up to 0.4 cm thick half-way to margin and gradually becoming thinner towards the edge), a little more fibrous in the stipe, whitish to pale cream (White, Pl. LIII; Martius Yellow, Pl. IV) in the pileus, pale cream to yellowish (Baryta Yellow, Pinard Yellow, Empire Yellow, Lemon Chrome, Pl. IV) in the connection zone with the stipe or down to the upper third of the stipe but white elsewhere and pure white at the very base (White, Pl. LIII),

pinkish red (Rose Pink, Pale Amaranth Pink, Mallow Pink, Light Mallow Purple, Pl. XII) underneath the cuticle and the stipe cortex; typically unchangeable throughout or occasionally slowly and faintly turning pale blue (Pale Blue-Green, Pl. VII; Pale Blue, Pale Cerulean Blue, Light Cerulean Blue, Pl. VIII) erratically in the pileus of aged specimens when exposed to air; yellowish (Pinard Yellow, Pl. IV) to pale vinaceous red (Light Corinthian Red, Pl. XXVII) where eroded by maggots; subhymenophoral layer cream to pale yellowish (Baryta Yellow, Pinard Yellow, Pl. IV); exsiccate pileus reddish brown to dark brown (Garnet Brown, Claret Brown, Pl. I; Argus Brown, Pl. III), hymenophore olivaceous to olivaceous

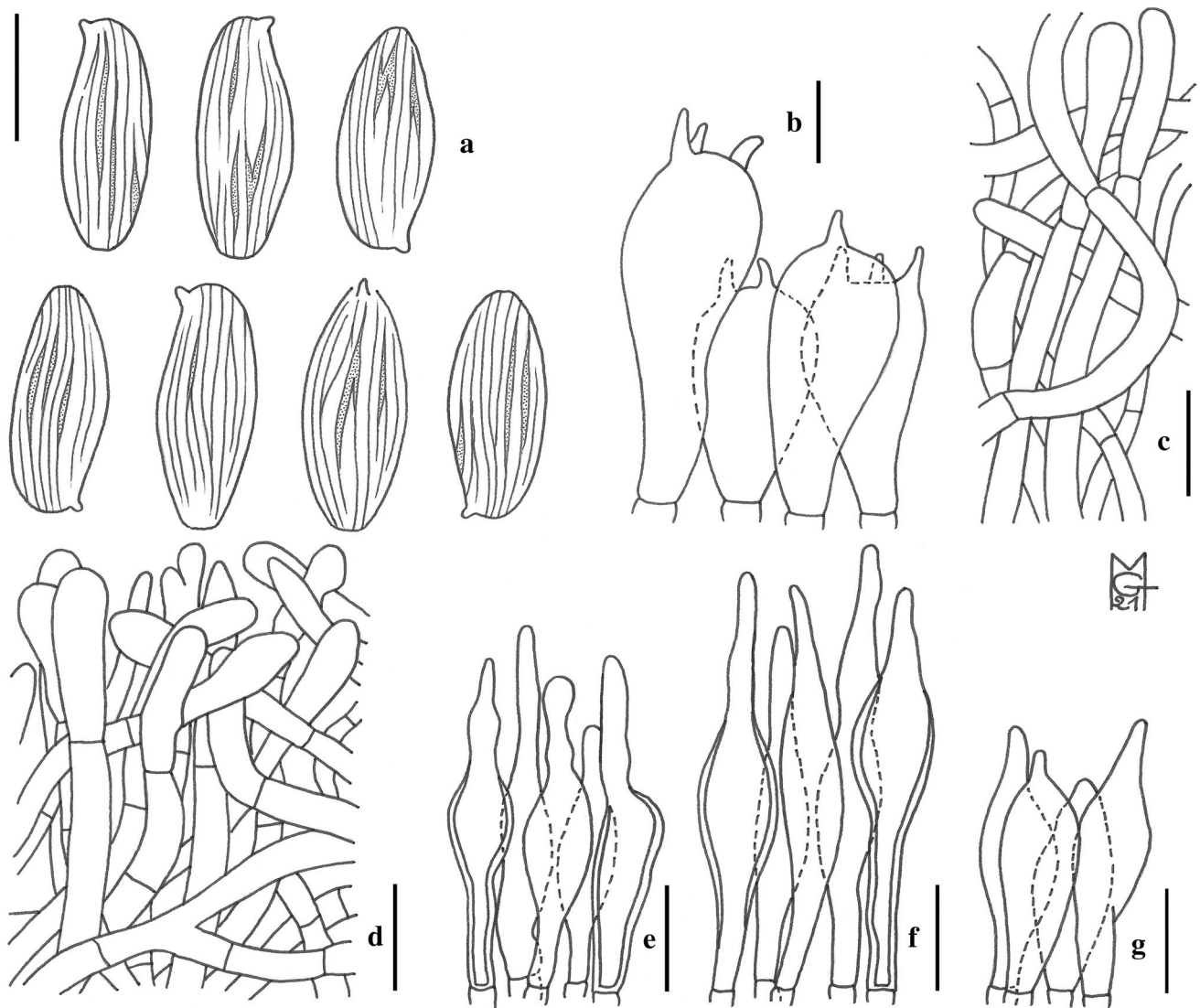


Fig. 8 Microscopic features of *B. cubensis* ANGE1474 and MO 401056; **a**: basidiospores; **b**: basidia; **c**: marginal veil; **d**: pileipellis; **e**: cheilocystidia; **f**: pleurocystidia; **g**: caulocystidia. Scale bars: 10 μ m (a–b); 20 μ m (c–g). Drawings by M. Gelardi

brown (Olive-Ocher, Brownish Olive, Pl. XXX), stipe beige to reddish brown or dark brown (Maize Yellow, Pl. IV; Marguerite Yellow, Pl. XXX; Garnet Brown, Pl. I; Argus Brown, Pl. III) and context beige to yellowish (Maize Yellow, Pl. IV; Light Orange-Yellow, Pl. III). *Odor* indistinct. *Taste* decidedly bitter. *Spore print* dark olivaceous-brown. *Macrochemical spot-test reactions*: 30% KOH: orange to vinaceous red on pileus surface, yellowish orange to bright orange on context and hymenophore; 30% NH_4OH : greenish on pileus surface, none elsewhere.

Basidiospores [102/7/3] $(14.5\text{--}18.5 \pm 1.6 \text{ (} -22.8) \times (6.4\text{--}7.9 \pm 0.5 \text{ (} -9.3) \mu\text{m})$, $Q = (1.95\text{--}2.06\text{--}2.65 \text{ (} -2.71)$, $Qm = 2.35 \pm 0.15$, $V = 612 \pm 125 \mu\text{m}^3$ (including ornamentation), inequilateral, fusiform or subfusiform to ellipsoid-fusiform in side view, ellipsoid-fusiform to

ellipsoid in face view, round in axial view, longitudinally faintly ridged (16–22 narrow ridges in polar view although not reaching the apex and coalesce together, giving the impression of a germ pore) and devoid of transversal connecting striations on primary costae, ridges low, continuous or sometimes bifurcate and forming only very shallow furrows but progressively more prominent with age (up to 0.4 μm deep), apex rounded to very frequently truncate (truncation up to 2 μm wide) and with a somewhat indistinct germ pore, with a moderately pronounced apiculus, usually with distinct suprahilar depression or applanation and with a very slightly pronounced adaxial swelling, moderately thin-walled (0.3–0.8 μm), bright honey yellow in water and 5% KOH, having one or less frequently two or three large oil droplets, occasionally pluri-guttulate when

mature, inamyloid, cyanophilic and with a faint metachromatic reaction. *Basidia* 24–45 (–48) $\times$ 13–17 (–19) μm ($n=24$), short to more rarely long clavate, moderately thick-walled (0.6–1.0 μm), predominantly 3-spored but rarely also 2- or 1-spored (4-spored basidia not observed), usually bearing relatively short sterigmata (2–6 μm), hyaline to very pale yellowish and containing straw-yellow oil guttules in water and 5% KOH, bright yellow (inamyloid) in Melzer's, without basal clamps; basidioles cylindrical-clavate to clavate, similar in size to basidia. *Cheilocystidia* (36–) 40–67 (–70) $\times$ 7–13 μm ($n=24$), very common, projecting straight to rarely flexuous and protruding from the hymenial palisade, fusiform or ventricose-fusiform to sublageniform but always inflated in the middle part and showing a narrow and often sinuous, long neck, with rounded to subacute tip, smooth, moderately to decidedly thick-walled (0.3–2.0 μm), staining bright red in Congo red, very pale yellowish in water and 5% KOH, bright yellow (inamyloid) in Melzer's, orthochromatic, without epiparietal encrustations. *Pleurocystidia* 58–90 (–93) $\times$ 9–15 μm ($n=24$), very frequent, shape, color and chemical reactions similar to but longer and slightly broader than cheilocystidia. *Pseudocystidia* not observed. *Pileipellis* a trichoderm consisting of subparallel to moderately or strongly interwoven, usually short cylindrical to filamentous, rarely branched hyphae not embedded in gelatinous matter; terminal elements 15–95 $\times$ 4–14 μm , cylindrical or irregularly cylindrical to more frequently cylindrical-clavate or subclavate, apex usually inflated and rounded-obtuse, moderately thick-walled (up to 1.2 μm), pale pinkish in water and 5% KOH, bright yellow to golden yellow (inamyloid) in Melzer's, smooth to sometimes ornamented by a subtle granular or zebra-like epiparietal encrustation; subterminal elements cylindrical, similar in size and color to terminal elements; thromboplerous hyphae abundant. *Marginal veil* consisting of moderately to strongly interwoven, filamentous to somewhat short cylindrical, sometimes branched, thin-walled (up to 0.5 μm) non-gelatinous hyphae, 22–80 $\times$ 4–15 μm , hyaline to pale yellowish in water and 5% KOH. *Stipitipellis* a texture of slender, parallel to subparallel and longitudinally running, smooth walled, adpressed hyphae, 2–10 μm wide, hyaline to pale yellowish in water and 5% KOH; the stipe apex covered by a fragmented caulohymenial layer mostly consisting of subclavate to clavate sterile caulobasidioles, fusiform or ventricose-fusiform to sometimes mucronate *caulocystidia*, (27–) 33–52 (–56) $\times$ 8–16 μm ($n=18$), having a wall up to 1.0 μm thick and irregularly cylindrical, cylindrical-clavate to subclavate, 1- or 2-spored *caulobasidia*, (28–) 30–50 (–58) $\times$ 10–13 (–16) μm ($n=12$), sterigmata 3–5 μm long, similar in shape, color and size to hymenial basidia. *Lateral stipe stratum* under the caulohymenium absent. *Stipe trama* composed of confusedly and densely arranged, moderately to strongly interwoven, filamentous, smooth, hyaline to

pale yellowish in water, inamyloid hyphae, 2–15 μm broad. *Hymenophoral trama* bilaterally divergent of the “*Boletus*-type” or at most intermediate between the “*Boletus*-type” and the “*Phylloporus*-type”, with moderately divergent and slightly recurved-arcuate, loosely arranged, often branched, restricted at septa, gelatinous hyphae (lateral strata hyphae in transversal section not touching each other, (2–) 4–10 (–12) μm apart, 4–12 μm broad), hyaline to very pale yellowish in water and 5% KOH, inamyloid in Melzer's; lateral strata (10–) 15–50 (–60) μm thick, mediostratum (10–) 15–25 (–30) μm thick, axially arranged, consisting of a tightly adpressed, non-gelatinous bundle of hyphae, 3–10 μm broad; in Congo Red the mediostratum is darker than the lateral strata. *Thromboplerous hyphae* infrequent but very common in the pileipellis, thick-walled, rarely septate, melanized, with a dense golden yellow to brownish homogeneous content in 5% KOH. *Clamp connections* absent in all tissues. *Ontogenetic development* presumably metavelangiocarpic due to the contemporaneous presence of an araneose universal veil and a membranaceous partial veil emanating from pileal margin hyphae.

Edibility unknown but most likely edible and apparently not disagreeable.

Ecology and phenology: solitary to more frequently gregarious but with a disperse growth, after abundant rains in coastal limestone hills, mainly among litter, rarely on wood at the base of stumps or on stones, under a large array of neotropical broadleaved trees including *Coccoloba diversifolia* (*Polygonaceae*), which represent its possible ECM host trees. See Parra et al. (2018) for further details on lowland vegetation in the Dominican Republic. Occurring from late autumn to winter (November to January).

Examined materials: DOMINICAN REPUBLIC, Puerto Plata Province, Municipality of Sosúa, loc. cemetery, three km away from the seaside, 19°44'40"N 70°32'21"W, 100 m, 29 Nov 2020, twelve specimens in all developmental stages growing on litter of a coastal deciduous forest under *Coccoloba diversifolia*, C. Angelini, ANGE1474 (MG858); same loc., 14 Dec 2019, three mature specimens growing on litter under *C. diversifolia*, C. Angelini, collection lost; PUERTO RICO: Municipality of Isabela, limestone hills along highway PR-113 near 'La Cara del Indio', 18°28'59.16"N 66°57'46.44"W, 71 m, 30 Jan 2020, several basidiomes scattered at the base of *Coccoloba diversifolia* in coastal limestone hills, K.O. Miller, MO401056 (MG865).

Phylogenetic position: The whole lineage (*Boletellus subglobosus* complex, Fig. 1) is strongly supported (PP = 1.00, BS = 100%) and contains *B. subglobosus* N.K. Zeng, R. Xue, S. Jiang & Zhi Q. Liang, *B. obscurecoccineus* (Höhn.) Singer, *B. puniceus* (W.F. Chiu) X.H. Wang & P.G. Liu, along with *B. cubensis*.

Notes: *Boletellus cubensis* was originally described from Cuba in the second half of the nineteenth century

by Berkeley and Curtis (1869) but seems not to have been circumscribed adequately for more than a hundred years, until Pegler (1983) and subsequently Singer et al. (1992) re-described it in detail based on new findings from the Lesser Antilles and Mexico, respectively.

This species is one of the several handsome, brightly colored taxa which fall into the *B. ananas* aggregate based on morphological appearance. The pinkish to vinaceous red or dark reddish purple then olivaceous brown to grayish brown pileus surface which soon disrupts into very finely areolate patches or a subsquamulose pattern with appendiculate velar remnants at the margin, the ring-bearing concolorous stipe which is usually swollen towards the base to subbulbose and with sparse cottony, white to grayish flocules overlaying the lower three quarters of the length, the yellow-olive hymenophore with angular pores at maturity, the white to pale yellowish context, the white basal mycelium and the non-discoloring tissues are an unmistakable combination of field characters for recognizing this species in habitat. Trustworthy microscopic features include mostly subfusiform, longitudinally faintly and narrowly ridged basidiospores lacking cross-striations and usually truncate at the apex, displaying a cyanophilic and a slight metachromatic reaction, a trichodermal pileipellis of intertwined cylindrical hyphae and a hymenophoral trama bilaterally divergent of the “*Boletus*-type” (Berkeley and Curtis 1869, also as “*Boletus lignatilis*”; Singer 1945, also as “*Boletellus lignatilis*”; Perreau-Bertrand 1965; Pegler and Young 1981; Pegler 1983, 1987, also as “*Boletellus lignatilis*”; Singer et al. 1983, 1992; Gómez 1997, as “*Boletellus lignatilis*”; Ortiz-Santana et al. 2007; de la Fuente et al. 2018; present study). An additional distinctive morphological attribute is the oxidation of the veil, which is the only part of the fungus turning blue upon injury. One last point is worth of attention, the predominantly 3-spored basidia which might constitute another meaningful feature, albeit its diagnostic value should be tested on a greater number of collections to be properly evaluated. However, this unusual microscopic feature could be an apomorphic trait apparently solely occurring in the presently examined collections, as it has never been reported earlier. With the exclusion of the three-spored basidia cited above, no major discrepancies have been noted by comparing our Dominican and Puerto Rican materials with the descriptions provided in previous works. Gómez (1997) and de la Fuente et al. (2018), however, indicated the presence of transverse veins between primary ridges in the basidiospore ornamentation of *B. cubensis*, but in all other consulted literature (including our own observations), this feature is clearly excluded.

It can be found growing on soil among litter as well as on rotten wood or woody debris in neotropical forests but also in gardens and parks from summer to winter (August to January). Although not unquestionably associated with

Coccoloba diversifolia and *C. uvifera* (Polygonaceae), it is expected to be found under additional *Coccoloba* species and other members of the Polygonaceae and Sapotaceae (de la Fuente et al. 2018). It is also reported under *Lysiloma* (Fabaceae subfam. Mimosoideae) (Singer et al. 1992) and from a mixed stand of *Coccoloba diversifolia* and *Quercus virginiana* Mill. in the Everglades National Park, Florida (iNaturalist 2025).

This uncommon bolete has hitherto been reported with certainty from Florida (iNaturalist 2025) and Mexico (Singer et al. 1992; Ortiz-Santana et al. 2007; de la Fuente et al. 2018, 2020; iNaturalist) in North America, Cuba (Berkeley and Curtis 1869; Singer et al. 1992; Minter et al. 2001; Ortiz-Santana et al. 2007), Dominican Republic (Angelini 2022; present study), and Puerto Rico (iNaturalist; present study) in the Greater Antilles, Saint Kitts e Nevis (iNaturalist 2025), Martinique and Guadeloupe (Pegler 1983) in the Lesser Antilles of the Caribbean, and Belize (Ortiz-Santana et al. 2007), Honduras (GBIF) and Costa Rica (Gómez 1997; Ortiz-Santana et al. 2007) in continental Central America. It is highly predictable that its distribution may extend to the South Atlantic and Gulf Coast States, to several other islands of the West Indies as well as to other countries of mainland Central America. Collections of *B. cubensis* recorded in GBIF from French Guyana might belong to a different species. Prior to this study, *B. cubensis* was not described in detail from either the Dominican Republic or Puerto Rico.

Boletellus lignatilis (Berk. & M.A. Curtis) L.D. Gómez is identical to *B. cubensis* in all essential morphological features and is unanimously considered a synonym of the latter species (Singer 1945, 1970; Pegler 1983, 1987; Ortiz-Santana et al. 2007).

The phylogenetic position of *B. cubensis* is confirmed in the genus *Boletellus*. A sister relationship is inferred with *B. obscurecoccineus* (Höhn.) Singer and *B. subglobosus* based on multilocus, ITS, LSU, and *TEF1-α* phylogenies (Figs. 1 and 2, Supplementary Figs. 1, 4), consistent with the outcomes of other recent molecular studies (Lin et al. 2022). Additionally, the ITS sequence from a *Boletellus rubrolutescens* Heinem. & Rammeloo collection (Cameroon, BR5020169915682 (NAL374)) clustered with two *B. obscurecoccineus* collections (Fig. 2), suggesting a possible conspecificity between the two taxa.

The type material of *B. cubensis* is housed in K-M, FH, and NY. Because Berkeley and Curtis (1869) described this species, the material in K-M should be considered the holotype and those in FH and NY as isotypes. We believe it is not necessary to re-examine the type materials of either *B. cubensis* (Wright (Curtis) 344, K-M000178411, holotype) or *B. lignatilis* (Wright (Curtis) 6, K-M000178409, holotype), both stored in Kew, since this task was already accomplished by David N. Pegler some 37 years ago (Pegler 1987) and the results of his revision are perfectly congruent with the

microscopic data obtained from our Dominican and Puerto Rican collections. In addition, at the time of Pegler's type revisions, the original material of *B. lignatilis* was already heavily infected by molds and certain microscopic features were not discernible (Pegler 1987). Various attempts to extract DNA from the holotype of *B. cubensis* did not yield the expected results. Unfortunately, both types are too old and in poor condition for molecular studies and the holotype sequencing of *B. cubensis* failed.

Following Singer (1945, 1970), Pegler (1983), Singer et al. (1983), and Gómez (1997), *Boletus guadalupensis* Pat. almost certainly represents an immature specimen of *B. cubensis* and should therefore be considered conspecific (cfr. also Murrill 1910, 1914). Alternatively, it is not to be completely ruled out that Patouillard's species might be a younger stage of *B. ananas* due to the presence of appendiculate velar remnants on pileus margin, as previously surmised by Singer et al. (1983). Mature and fresh material of *B. guadalupensis* would be desirable to solve the matter.

A number of species, namely, *Boletellus ananas*, *B. ananiceps*, *B. emodensis* s. l., and *B. deceptivus*, can be mistaken for *B. cubensis*. For a comparison between *B. cubensis* and *B. ananas*, see under the latter species.

Boletellus emodensis aggregate (including *B. areolatus*, *B. emodensis* s. str., *B. rubidus*, *B. squamosus*, *B. yunnanensis*, and *B. zenghuoxingii*) is easy to set apart from *B. cubensis* based on a more or less coarsely squamulose to scaly pileus, ringless stipe with a pink to pinkish brown or reddish tint throughout, cyanescent context on exposure, basidiospores with cross-striations on primary ridges, occurrence in association with members of the Fagaceae and Pinaceae, and a strict Asian distribution (Berkeley 1851; Corner 1972; Pegler and Young 1981; Imazeki et al. 1988; Chen et al. 1997; Thongklam 2008; Horak 2011; Wu et al. 2011; Zeng And Yang 2011; Sato And Hattori 2015; Tibpromma et al. 2017; Xue et al. 2023).

A less pigmented pileus exhibiting a pinkish to pale reddish ground color underlying large, coarse and dull tan squamules, smooth stipe, cyanescent tissues upon bruising, rufescent stipe base context, narrower basidiospores [(15.4–) 16–23 (–26) × (6–) 6.5–7.3 (–8.3) μm (18 ± 1.5 × 6.8 ± 0.7 μm), $Qm = 2.6$], smaller hymenial cystidia (40–43 × 10–11 μm), shorter pileipellis terminal cells (27.5–33 μm long) and different host trees (*Myrtaceae* in Australia, *Fagaceae* in the neotropics) allow a prompt separation of *B. ananiceps* from *B. cubensis* (Berkeley 1873; Saccardo 1888; Cleland And Cheel 1919; Singer 1955; Perreau-Bertrand 1961; Pegler and Young 1981; Watling And Gregory 1986; Singer et al. 1992; Gómez 1997; Bougher and Syme 1998; Watling and Li 1999; Halling And Fechner 2011; Halling et al. 2015; Ayala-Vásquez et al. 2018).

Boletellus deceptivus differs from *B. cubensis* by the squamulose pileus surface with upturned then repent,

coarse, pyramidal scales, fibrillose stipe lacking both annulus and cottony floccules, cyanescent hymenophore and context which also turns dirty orange-brown towards the base on exposure, slightly smaller basidiospores [15.3–17.8 (–18.9) × (6.2) 7–7.9 (–8.4) μm (16.5 ± 0.8 × 6.9 ± 0.4 μm), $Qm = 2.4$] with broader and more pronounced longitudinal ridges and with evident cross striations, smaller, four-sterigmate basidia (25–32 × 7–10 μm), shorter pleurocystidia (up to 50 μm long) and cheilocystidia (up to 40 μm long), and the occurrence in wet or dry sclerophyll forests under *Myrtaceae* (*Eucalyptus*, *Lophostemon*, *Leptospermum*, *Melaleuca*, *Syncarpia*), *Casuarinaceae* (*Allocasuarina*), and *Fabaceae* (*Acacia*) in eastern Australia (New South Wales and Queensland) (Halling et al. 2015; Leonard 2024).

Boletellus domingensis B. Ortiz & Lodge, Fungal Diversity 27: 276. 2007.

Figures 9 and 10

Mycobank MB 511046

Holotype: Greater Antilles, Dominican Republic, Santiago province, Las Placetas, near San José de las Matas, under *Pinus occidentalis*, 28 Jan 1998, D.J Lodge, DJL-DR-29, DR 573 (CFMR, holotype; JBSD, isotype).

Basidiomes small-sized. **Pileus** (1.9–) 3.2–5.0 (–5.6) cm broad, at first hemispherical then persistently convex and finally broadly pulvinate-flattened, regularly to unevenly shaped by shallow depressions, moderately fleshy, firm at the beginning but progressively softer with age, flabby in old basidiomes; margin even to faintly wavy, initially curved downwards and finally completely plane or even uplifted, shortly appendiculate and extending beyond the tubes up to 1 mm; surface matt, dry to slightly greasy in wet weather, initially finely velvety and not dissociated but soon becoming minutely cracked-areolate, especially in dry weather conditions and then showing a whitish color in the cracks (White, Pl. LIII); evenly ochraceous-brown, brown to bay brown or dark brown (Sudan Brown, Brussels Brown, Raw Umber, Pl. III; Buckthorn Brown, Cinnamon-Brown, Dresden Brown, Pl. XV; Rood's Brown, Vandyke Brown, Pl. XXVIII; Snuff Brown, Saccardo's Umber, Bister, Sepia, Pl. XXIX; Drab Olive-Buff, Duffy Brown, Olive-Brown, Pl. XL); unchangeable on handling or touching or when injured; subpellis layer whitish (White, Pl. LIII). **Tubes** wide at first in side view then increasingly broader with age and as long as or slightly longer or shorter than the thickness of the pileus context (up to 1.1 cm long), adnate but soon deeply depressed around the stipe apex and decurrent with a tooth, yellow then olive yellow (Pale Lemon Yellow, Lemon Yellow, Lemon Chrome, Pl. IV; Citrin Yellow, Strontian Yellow, Pl. XVI; Light Viridine Yellow, Greenish Yellow, Green-Yellow, Bright Green Yellow, Oil Yellow, Yellowish Oil Green, Pl. V; Citron Yellow, Amber Yellow, Pl. XVI) at maturity, turning blue (Italian Blue, Paris Blue,

Fig. 9 *Boletellus domingensis*, basidiomes in habitat. **a-c, e**: ANGE1332 (**a**: macrochemical staining with 30% KOH); **d**: ANGE1004. Scale bars: 1 cm. Photos by C. Angelini



Patent Blue, Pl. VIII) when cut. *Pores* initially forming a flat surface, later irregularly shaped to slightly convex or ascending, broad at first then gradually wider with age (up to 3 mm in diam.), simple, firstly labyrinthine becoming prominently angular at maturity, stretched and radially arranged towards the stipe, concolorous with the tubes and discoloring blue (Italian Blue, Paris Blue, Patent Blue, Pl. VIII) on bruising or when injured, occasionally with scattered rusty brown (Ferruginous, Pl. XIV; Mikado Brown, Pl. XXIX) stains at the orifice in aged specimens. *Stipe* (3.2–) 3.5–6.0 (–6.3) × (0.4–) 0.7–1.0 (–1.2) cm, as long as or slightly longer than the pileus diameter at maturity, central to slightly off-center, solid, firm, dry, straight or

curved to occasionally sinuous, cylindrical, subcylindrical to gradually and faintly enlarged from apex down to the base, usually rounded or less frequently ending with a short taproot at the very base; surface smooth or pruinose to very finely fibrillose throughout, devoid of reticulum or ribs, evenate; pale yellow (Martius Yellow, Baryta Yellow, Pinard Yellow, Pl. IV) at the very apex and with a narrow vinaceous red (Deep Vinaceous, Corinthian Red, Pl. XXVII) band immediately underneath the yellow zone, uniformly brown, dark brown to blackish brown (Sudan Brown, Brussels Brown, Raw Umber, Pl. III; Buckthorn Brown, Cinnamon-Brown, Dresden Brown, Mummy Brown, Pl. XV; Rood's Brown, Vandyke Brown, Pl. XXVIII; Snuff Brown,

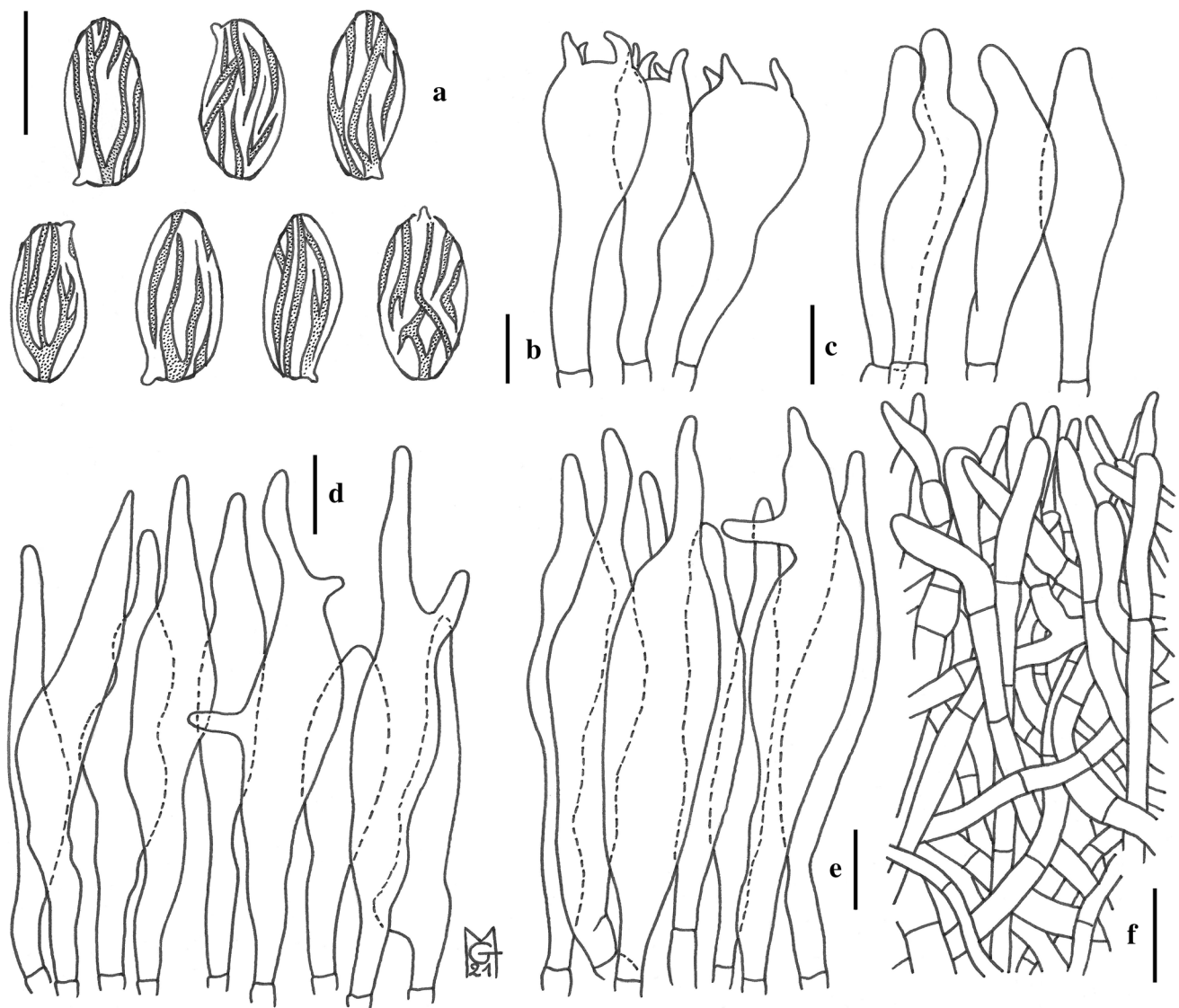


Fig. 10 Microscopic features of *B. domingensis* ANGE111, ANGE1004 and ANGE1332; **a**: basidiospores; **b**: basidia; **c**: caulocystidia; **d**: cheilocystidia; **e**: pleurocystidia; **f**: pileipellis. Scale bars: 10 µm (a-e); 20 µm (f). Drawings by M. Gelardi

Saccardo's Umber, Bister, Sepia, Pl. XXIX; Drab Olive-Buff, Duffy Brown, Olive-Brown, Clove Brown, Pl. XL; Dark Grayish Brown, XLV) elsewhere, unchangeable when pressed; basal mycelium whitish to whitish gray (White, Pl. LIII; Light Gull Gray, Pl. LIII). *Context* firm and tough when young, later soft textured and eventually flabby in the pileus (up to 1.3 cm thick in the central zone, up to 0.7 cm thick halfway to margin and gradually becoming thinner towards the edge), more fibrous in the stipe, at first whitish in the pileus and upper third of the stipe (White, Pl. LIII), later whitish only in the pileus, elsewhere evenly purple red or dark vinaceous red (Aster Purple, Dahlia Purple, Pansy Purple, Bordeaux, Pl. XII) but fading with age dull brownish red to pale dirty brown (Army Brown, Pl. XL; Olive Lake, Pl. XVI; Tawny Olive, Pl. XXIX; Isabella Color, Pl.

XXX); turning pale blue to blue (Beryl Blue, Pallid Methyl Blue, Pale Methyl Blue, Light Methyl Blue, Peacock Blue, Pl. VIII) in the pileus context and more intensely (Patent Blue, Pl. VIII) in the connection zone with the stipe when exposed to air, unchangeable elsewhere; subhymenophoral layer whitish (White, Pl. LIII); exsiccate pileus and stipe in various shades of brown (Chamois, Isabella Color, Light Brownish Olive, Pl. XXX), hymenophore dark brown (Auburn, Pl. I; Liver Brown, Pl. XIV), context beige to yellowish (Maize Yellow, Pl. IV; Cream Buff, Pl. XXX). *Odor* indistinct. *Taste* mild. *Spore print* not obtained. *Macrochemical spot-test reactions*: 30% NH_4OH : vinaceous red on pileus surface.

Basidiospores [136/7/4] (11.1–) 14.0 ± 0.8 (–16.4) $\times$ (5.4–) 6.9 ± 0.5 (–8.8) µm, $Q = (1.76\text{--}) 1.82\text{--}2.41$

(−2.48), $Qm = 2.02 \pm 0.12$, $V = 357 \pm 66 \mu\text{m}^3$ (including ornamentation), inequilateral, ellipsoid-fusiform or ellipsoid to less frequently broadly ellipsoid in side view, ellipsoid to broadly ellipsoid in face view, round in axial view, longitudinally irregularly ridged (10–12 broad ridges in polar view but not reaching the apex and coalesce together, giving the impression of a germ pore), without transversal connecting striations on primary costae, ridges often bifurcate or anastomosing, moderately high and appearing progressively more prominent with age (up to 0.8 μm deep), apex rounded and with a somewhat indistinct germ pore, with a short apiculus, usually with a shallow to markedly pronounced suprahilar depression or applanation and with an adaxial swelling, relatively thin-walled (0.3–0.5 μm), honey yellow colored in water and 5% KOH, having one, two or three large oil droplets when mature, rarely pluri-guttulate, inamyloid, acyanophilic and with an ortochromatic reaction. *Basidia* 37–53 (−57) $\times$ 9–18 μm ($n = 29$), cylindrical-clavate to clavate, moderately thick-walled (0.3–0.8 μm), predominantly 4-spored but frequently also 1-, 2- or 3-spored, usually bearing relatively short sterigmata (2–5 μm), hyaline to pale yellowish and containing straw-yellow oil guttules in water and 5% KOH, bright yellow (inamyloid) in Melzer's, without basal clamps; basidioles faintly clavate to clavate, similar in size to basidia. *Cheilocystidia* (40–) 42–77 (−80) $\times$ 8–12 (−14) μm ($n = 28$), relatively common, moderately slender, projecting straight to sometimes flexuous and protruding from the hymenial palisade, irregularly cylindrical, cylindrical-fusiform, narrowly fusiform or fusiform and showing a narrow and long neck, occasionally short lageniform, not infrequently bifurcate or even diverticulate, with rounded to subacute tip, smooth, moderately thick-walled (0.5–1.0 μm), hyaline to pale yellowish in water and 5% KOH, bright yellow (inamyloid) in Melzer's, without epiparietal encrustations. *Pleurocystidia* (47–) 50–82 (−85) $\times$ 7–16 μm ($n = 23$), infrequent, shape, color and chemical reactions similar to but on average slightly longer and broader than cheilocystidia. *Pseudocystidia* not observed. *Pileipellis* a trichoderm consisting of moderately to strongly interwoven, mostly short cylindrical hyphae (cylindrocytes), infrequently branched, tending to become erect in the outermost layer and not embedded in gelatinous matter; terminal elements 25–68 $\times$ 3–13 (−17) μm , cylindrical, cystidioid, mostly attenuated towards the tip or occasionally slightly enlarged, apex rounded-obtuse to pointed, moderately thick-walled (up to 1 μm), yellowish to brownish in water, hyaline to pale yellowish but some elements with straw yellow plasmonic pigment and 5% KOH, inamyloid in Melzer's, smooth; subterminal elements similar in shape, size and color to terminal elements. *Stipitipellis* a layer of slender, parallel to loosely intermingled and longitudinally running, smooth walled, adpressed hyphae, 4–17 μm wide, hyaline to very pale yellowish in water and 5% KOH; the stipe apex

covered by a fragmented caulohymenial layer consisting of sterile caulobasidioles, very sparse to common, 1-, 2-, 3- and 4-spored fertile caulobasidia, (37–) 40–50 $\times$ 11–16 μm ($n = 10$), sterigmata 3–5 μm long, having a wall up to 1 μm thick, and uncommon projecting *caulocystidia* similar in shape and color to hymenial cystidia but distinctly shorter, (30–) 37–44 (−48) $\times$ 8–12 μm ($n = 9$), having a wall up to 1 μm thick; in mature specimens long and sinuous filamentous hyphae, 3–9 μm broad and up to 130 μm long, are sometimes found intermixed with caulohymenial elements. *Lateral stipe stratum* under the caulohymenium generally present although sometimes absent or not well differentiated from the stipe trama, of the “boletoid type”, at the stipe apex a (20–) 30–40 (−50) μm thick layer consisting of divergent hyphae, inclined and running towards the external surface, loosely intermingled and branched, remaining separate and embedded in a gelatinous substance. *Stipe trama* composed of confusedly and densely arranged, moderately to strongly interwoven, filamentous, smooth, inamyloid hyphae, 4–20 μm broad. *Hymenophoral trama* bilateral divergent of the “*Phylloporus*-type” or at most intermediate between the “*Phylloporus*-type” and the “*Boletus*-type”, with subparallel to slightly divergent and densely arranged, typically restricted at septa, not or only slightly gelatinous hyphae (lateral strata hyphae in transversal section not touching each other or nearly so, (1–) 2–6 (−7) μm apart, 2–15 μm broad), hyaline to very pale yellowish in water and 5% KOH, inamyloid in Melzer's; lateral strata (20–) 30–40 (−50) μm thick, mediostratum (20–) 30–40 (−50) μm thick, axially arranged, consisting of a tightly adpressed, more frequently septate, non-gelatinous bundle of hyphae, 2–6 μm broad; in Congo Red the mediostratum is concolorous or faintly darker than the lateral strata. *Thromboplerous hyphae* infrequent, thick-walled, rarely septate, melanized, with a dense golden yellow to brownish homogeneous content in 5% KOH. *Clamp connections* absent in all tissues. *Ontogenetic development* gymnocarpic.

Edibility unknown, not tested for edibility but presumed to be edible although of indifferent quality. Caution is recommended.

Ecology and phenology: solitary to more frequently gregarious, growing on soil among litter but often also on decaying wood or at the base of standing stumps under five-needled pine species (*P. occidentalis*) (*Pinaceae*). Late autumn to winter (November to February).

Examined materials: DOMINICAN REPUBLIC, La Vega Province, Jarabacoa, 19°11' 12.5"N 70°35' 25.5"W, 660 m, 22 Dec 2013, five mature specimens growing on litter under *P. occidentalis*, C. Angelini, ANGE111 (MG861); same loc., a single mature specimen growing on litter under *P. occidentalis*, 28 Nov 2017, C. Angelini, ANGE1004 (MG862); same loc., three mature specimens, 23 Nov 2017, C. Angelini, ANGE1016-2 (MG863); same loc., two young

Boletellus pictiformis and *B. flocculosipes* are very similar to each other and they are closely related to *B. domingensis*. Both species, however, differ from *B. domingensis* by the coarsely scaly-squamulose to shaggy pileus and stipe surfaces, bright yellow context, slightly smaller basidiospores [(12–) 12.5–13.7 (–15.5) $\times$ 5.5–6.8 (–7) μ m], smaller basidia (25–39 $\times$ 9–14 μ m), shorter hymenial cystidia [(23–) 30–60 $\times$ 9–14 μ m], and the occurrence in mesophytic hammock under hardwoods (*Quercus* and *Carya*) in south-eastern USA, Mexico and perhaps Venezuela (Murrill 1943; Singer 1945, 1970, as “*B. pictiformis* var. *fallax*”; Perreau-Bertrand 1965; Singer et al. 1983, as “*B. fallax* (Singer) Singer”, 1992; Both 1993; García-Jiménez 1999, 2013; García 1999; Bessette et al. 2000, also as “*B. fallax*”; Ayala-Vásquez et al. 2018; Saldivar et al. 2021). A broader pileus (up to 14 cm diam.) and a black staining reaction with NH_4OH also differentiates *B. flocculosipes* from *B. domingensis* (Singer 1945, 1970; Singer et al. 1983, 1992; Bessette et al. 2000), whereas *Boletellus pictiformis* is additionally separated from *B. domingensis* by the reddish pore surface (Murrill 1943; Singer 1945, 1970; Singer et al. 1983, 1992; Bessette et al. 2019). As already suggested by Singer et al. (1992), *B. pictiformis* var. *fallax* sensu Thiers (1963) might be *B. pseudochrysenteroides*. Singer et al. (1992) questioned about a presumed conspecificity of *B. pictiformis* and *B. flocculosipes* due to their strict morphological affinities, but this issue presently remains unaddressed.

In field characteristics *B. domingensis* approaches the North American *B. pseudochrysenteroides* and the central American *B. belizensis* B. Ortiz & T.J. Baroni in many respects. *Boletellus pseudochrysenteroides* is easily separated from *B. domingensis* on the basis of larger size (pileus up to 10 cm diam., stipe up to 9 $\times$ 1.4 cm), evenly pinkish red pileus surface fading olivaceous brown with age, reddish stipe bruising blue intensely when injured and with copious golden yellow basal mycelium, smaller basidiospores [11–14 (–15) $\times$ 5.5–7 (–8) μ m], smaller basidia [20–28 (–36) $\times$ 8–10 (–12) μ m], shorter cheilocystidia (28–37 $\times$ 7–11 μ m) and pleurocystidia [36–48 (–56) $\times$ 9–13 μ m] and the occurrence under hardwoods in eastern North America (Both 1993; Smith and Thiers 1971; Smith et al. 1981; Singer et al. 1992; Bessette et al. 2000, 2016; Kuo And Methven 2014). This species has also been reported from Mexico (García et al. 1986; Singer et al. 1992; García-Jiménez 1999, 2013; Ayala-Vásquez et al. 2018).

Among Central American *Boletellus* species, *B. domingensis* is also similar to *B. belizensis* (B. Ortiz & T.J. Baroni) which is separated by the reddish brown pileus, creamy-ochraceous basal mycelium, evenly golden yellow context bruising deep blue throughout on exposure, slightly smaller basidiospores (12–14.4 $\times$ 5.6–7.2 μ m), narrower basidia (36–48 $\times$ 10–12 μ m), smaller cheilocystidia (41–49 $\times$ 6–9 μ m), and pleurocystidia (37–58 $\times$ 5–9 μ m), longer caulocystidia (20–89 $\times$ 9–13 μ m) and the association

with *Quercus* spp., exclusively in mainland Central America (Belize, Guatemala) (Ortiz-Santana et al. 2007; Flores-Arzú, pers. obs.). Given several morphological affinities, a possible conspecificity of *B. belizensis* with *B. pseudochrysenteroides* is highly probable, as also suggested by molecular inferences (Zhang and Wu 2022; Xue et al. 2023; present study, Fig. 1). Should, in the years to come, *B. belizensis* turn out to be the same species as *B. pseudochrysenteroides*, the latter binomial would take precedence.

Boletellus minimatenebris (Nom. inval., Arts F.5.2, 40.5; Madrid, Turland et al. 2025) has most recently been described from Mexico (Ayala-Vásquez et al. 2023b). When compared to *B. domingensis*, it has smaller-sized basidiomes (pileus 1.0–3.4 cm diam., stipe 2.5–4.7 $\times$ 0.5–0.8 cm), non-cracking pileal surface, smaller pores (up to 0.5 mm wide), brown basal mycelium, blackish-brown reaction with NH_4OH on pileus, shorter basidia [30–33 (–38) $\times$ 12–13 μ m], and a putative association with *Quercus elliptica* Née in mixed *Quercus-Pinus* forests (Ayala-Vásquez et al. 2023b).

The eastern Asian *B. brunoflavus* is macromorphologically very similar to *B. domingensis*, but it is readily distinguished microscopically by the much smaller basidiospores [(9–) 10–12.5 (–13) $\times$ 4–5 μ m, $Qm=2.4$], smaller basidia (22–36 $\times$ 6–11 μ m), shorter and slightly narrower cheilocystidia (30–41 $\times$ 8–10 μ m) and pleurocystidia (28–56 $\times$ 9–12 μ m) and the occurrence under two-needled *Pinus massoniana* Lamb. and fagaceous trees in south-eastern and southern China (Fujian, Guangdong and Hainan Provinces) (Lin et al. 2022; Xue et al. 2023). In the original description of *B. brunoflavus*, the basidiospores are reported as being even much smaller [(6.1–) 6.4–8.2 (–8.9) $\times$ (2–) 2.3–3.3 (–3.6) μ m, $Qm=2.6$] (Lin et al. 2022), probably because of wrong measurements.

Boletellus domingensis is also reminiscent of the most recently described *B. sinochrysenteroides* from China. However, the stipe becoming finely squamulose in age, evenly yellow context turning blue throughout on exposure, presence of cross-striations on primary ridges on the basidiospores, shorter basidia (28–37 $\times$ 11.5–15 μ m), shorter cheilocystidia (23–42 $\times$ 8.5–13.5 μ m), and pleurocystidia (37–60 $\times$ 10–16.5 μ m), and the occurrence under fagaceous trees in eastern China (Jiangxi and Zhejiang Provinces) (Xue et al. 2023; present study) allow an easy discrimination from *B. domingensis*.

The recently described Chinese *B. verruculosus* L.P. Tang & R. Xue is easy to set apart from *B. domingensis* based on the stipe surface beset by small warty scales, yellowish basal mycelium, slightly smaller basidiospores [(10–) 10.5–14.5 (–16) $\times$ (5–) 5.5–7 μ m, $Qm=2.05$], shorter cheilocystidia (29–49 $\times$ 9.5–16.5 μ m), shorter pleurocystidia (32–58 $\times$ 10–18 μ m), an epithelioid pileipellis consisting of chains of subglobose to broadly subcylindrical cells up to 19.5 μ m wide with shorter terminal elements

(15–36 × 3.5–12 µm) and a distribution in Yunnan Province (south-western China) (Xue et al. 2024).

Finally, another similar species occurring in the Dominican Republic is *Xerocomus coccolobae* Pegler. However, this taxon differs dramatically from *B. domingensis* by its finely to coarsely and densely granulose pileus and stipe surfaces, pale brownish to dirty brown context only at the very stipe base, unchangeable to erratically and faintly bluing context on exposure, smooth-walled, smaller basidiospores [(8.3–) 8.8–11.6 (–14.5) × (4.1–) 4.7–5.1 (–5.8) µm, $Qm = 2.2$], pleurocystidia up to 106 µm long and the occurrence in lowland xero-mesophytic mixed broadleaved forests in association with *Coccoloba diversifolia*, but also with other *Coccoloba* spp. (including *C. uvifera*, *C. spicata*, *C. swartzii*, *C. pubescens*, etc.) across its natural distribution range in the Caribbean and tropical North America (Florida, Mexico) (Pegler 1983; Ortiz-Santana et al. 2007, as “*Xerocomus olivaceus* B. Ortiz & T.J. Baroni”; Gelardi et al. 2023).

Extralimital species

Boletellus cf. *emodensis*

Fig. 7e and f

Basidiomes medium to medium-large sized. *Pileus* (4.2–) 6.8–9.5 (–12.0) cm broad, at first hemispherical then persistently convex or more rarely broadly pulvinate-flattened, regularly to faintly irregularly shaped, moderately fleshy, firm at the beginning but progressively softer with age, flabby in old basidiomes; margin even to faintly wavy, initially slightly involute then curved downwards and remaining so with age, distinctly appendiculate with membranaceous velar remnants hanging from the rim and extending beyond the tubes up to 1.3 cm; surface matt, dry, covered by relatively small and tightly adpressed, irregularly conical to pyramidal, at first erect then progressively prostrate and radially arranged, partly imbricate squamules, up to 1.0 × 0.8 cm; squamules reddish purple or vinaceous red to reddish-pink (Rhodamine Purple, Mallow Purple, Light Mallow Purple, Amaranth Pink, Mallow Pink, Pale Amaranth Pink, Rose Pink, Pl. XII; Rosolane Purple, Spinel Pink, Liseran Purple, Rose-Purple, Pale Rose-Purple, Rosolane Pink, Cameo Pink, Pl. XXVI; Dark Vinaceous, Vinaceous, Pale Vinaceous, Livid Pink, Hydrangea Pink, Pl. XXVII) over a whitish beige background (Olive-Buffer, Pale Olive-Buffer, Pl. XL; White, Pl. LIII); unchanging on handling or touching; subpellis layer between squamules whitish (White, Pl. LIII). *Tubes* relatively small at first in side view then increasingly broader with age and as long as the thickness of the context above (up to 3.4 cm long), depressed around the stipe apex and decurrent with a long tooth, yellow to olive yellow and finally brownish olive (Empire Yellow, Lemon Chrome, Sulphurine Yellow, Pl. IV; Oil Yellow, Light Greenish Yellow, Pale

Greenish Yellow, pl. V; Mustard Yellow, Primuline Yellow, Old Gold, Pl. XVI) at maturity, turning blue (Peacock Blue, Patent Blue, Pl. VIII) when cut. *Pores* initially hidden by a thick, persistent membranaceous single-layered, velvety to subsquamulose veil emanating from the pileal margin, reddish then pale pinkish at maturity (Rhodamine Purple, Mallow Purple, Light Mallow Purple, Amaranth Pink, Mallow Pink, Pale Amaranth Pink, Rose Pink, Pl. XII; Rosolane Purple, Spinel Pink, Liseran Purple, Rose-Purple, Pale Rose-Purple, Rosolane Pink, Cameo Pink, Pl. XXVI), which soon disrupts revealing the fertile tissue underneath; at the beginning forming a concave then flat to convex surface; pores at first rather small then gradually wider with age (up to 3 mm in diam.), simple, firstly roundish soon becoming angular, slightly stretched and radially arranged towards the stipe, concolorous with the tubes and staining blue (Peacock Blue, Patent Blue, Pl. VIII) on bruising or when injured, sometimes with scattered rusty brown (Ferruginous, Pl. XIV; Mikado Brown, Pl. XXIX) stains at the orifice in aged specimens. *Stipe* (10.5–) 13.0–14.5 (–20.5) × (0.9–) 1.1–2.8 (–3.0) cm, decidedly longer than the pileus diameter in all stages of development, central, solid, firm, dry, slender, somewhat tough, straight or curved to occasionally sinuous, cylindrical to cylindrical-fusoid or gradually and faintly tapering from apex down to the base but swollen at the very base, moderately rooting; surface entirely longitudinally fibrillose, without annulus; evenly reddish purple to pinkish red (Rhodamine Purple, Mallow Purple, Light Mallow Purple, Amaranth Pink, Mallow Pink, Pale Amaranth Pink, Rose Pink, Pl. XII; Magenta, Rosolane Purple, Spinel Pink, Liseran Purple, Rose-Purple, Pale Rose-Purple, Rosolane Pink, Cameo Pink, Pl. XXVI; Dark Vinaceous, Vinaceous, Pale Vinaceous, Livid Pink, Hydrangea Pink, Pl. XXVII) in the upper three quarters of the stipe, this tint tending to reduce to the upper half or even to the apical portion with age, yellow-ochraceous to drab gray-ochraceous (Pale Pinkish Buff, Pl. XXIX; Cartridge Buff, Pl. XXX; Pale Olive-Buffer, Olive-Buffer, Pl. XL; Pale Smoke Gray, Pl. XLVI) elsewhere, not staining when injured; basal mycelium whitish (White, Pl. LIII). *Context* firm and tough when young, later soft textured and eventually flabby in the pileus (up to 3.5 cm thick in the central zone), more fibrous in the stipe, pale cream yellowish in the pileus (Baryta Yellow, Pinard Yellow, Pl. IV), whitish in the stipe (White, Pl. LIII) but pale orange to dirty orange (Light Ochraceous-Buffer, Ochraceous-Buffer, Ochraceous-Orange, Zinc Orange, Ochraceous-Tawny, Buckthorn Brown, Pl. XV) towards the base; quickly and more or less uniformly turning blue (Pale Cerulean Blue, Light Cerulean Blue, Cerulean Blue, Peacock Blue, Pl. VIII; Sky Blue, Yale Blue, Olympic blue, Blanc's Blue, Pl. XX) in the pileus and the connection zone with the stipe when exposed to air but soon fading whitish beige (White, Pl. LIII), unchangeable

elsewhere; subhymenophoral layer pale yellowish (Baryta Yellow, Pinard Yellow, Pl. IV); exsiccate pileus, stipe and context beige (Maize Yellow, Pl. IV; Light Buff, Pl. XV), hymenophore dark brown (Auburn, Pl. I; Liver Brown, Pl. XIV). *Odor* weak, agreeable. *Taste* mild. *Spore print* brown. *Macrochemical spot-test reactions*: 30% NH_3 : brownish on pileus and stipe, no response on context and hymenophore; 30% KOH: brownish on pileus, vinaceous red to reddish brown on stipe, yellowish orange to vinaceous red on context but olive green towards the stipe base, vinaceous brown on hymenophore; FeSO_4 : sordid olive green to bluish green everywhere.

Basidiospores [68/3/2] $(16.8\text{--}) 19.6 \pm 1.4 \text{ (}\text{--}22.8\text{)} \times (6.9\text{--}) 8.9 \pm 0.8 \text{ (}\text{--}11.5\text{)} \mu\text{m}$, $Q = (1.90\text{--}) 1.93\text{--}2.44 \text{ (}\text{--}2.46\text{)}$, $Qm = 2.20 \pm 0.12$, $Vm = 824 \pm 136 \mu\text{m}^3$ (including ornamentation) (a single anomalous spore measured $27.0 \times 10.0 \mu\text{m}$), fairly variable in dimension, inequilateral, elongate cylindrical, ellipsoid-fusiform to ellipsoid or less frequently broadly ellipsoid in side view, ellipsoid to broadly ellipsoid in face view, round in axial view, markedly longitudinally ridged (10–14 broad ridges in polar view and apparently running full length and reaching the apex) and with regular transversal or inclined, sometimes inconspicuous connecting striations on primary costae, ridges occasionally bifurcate or anastomosing, moderately high and progressively more prominent with age (up to $1.0 \mu\text{m}$ thick), apex rounded, never truncate nor with an indistinct germ pore, with a short apiculus, usually with a shallow suprahilar depression or appplanation and with a very slightly pronounced adaxial swelling, thick-walled ($0.3\text{--}0.5 \mu\text{m}$), dark honey yellow colored in water and 5% KOH, having one, two or three large oil droplets, rarely pluri-guttulate when mature, inamyloid, acyanophilic and with a faint metachromatic reaction. *Basidia* $40\text{--}55 \times 13\text{--}19 \mu\text{m}$ ($n = 12$), relatively short, cylindrical-clavate to clavate, moderately thin-walled ($0.3\text{--}0.5 \mu\text{m}$), predominantly 4-spored but also 1-, 2- or 3-spored, usually bearing relatively short sterigmata ($2\text{--}6 \mu\text{m}$), hyaline to pale yellowish and containing straw-yellow oil guttules in water and 5% KOH, bright yellow (inamyloid) in Melzer's, without basal clamps; basidioles subcylindrical, cylindrical-clavate to clavate, similar in size to basidia. *Cheilocystidia* $35\text{--}59 \times 10\text{--}13 \mu\text{m}$ ($n = 3$), infrequent, projecting straight to sometimes flexuous and protruding from the hymenial palisade, fusiform, ventricose-fusiform with a long neck to sublageniform or lageniform, with rounded to subacute tip, smooth, moderately thick-walled ($0.3\text{--}0.8 \mu\text{m}$), hyaline to pale yellowish in water and 5% KOH, bright yellow (inamyloid) in Melzer's, without epiparietal encrustations. *Pleurocystidia* $(30\text{--}) 40\text{--}62 \text{ (}\text{--}65\text{)} \times 8\text{--}15 \text{ (}\text{--}19\text{)} \mu\text{m}$ ($n = 11$), relatively common, sometimes with a secondary septum or occasionally multiseptate, shape, color and chemical reactions similar to cheilocystidia. *Pseudocystidia* not recorded. *Pileipellis* a trichoderm consisting of subparallel

to moderately strongly interwoven, mostly short cylindrical (cylindrocetes), frequently branched and easily detachable hyphae intermixed with scattered filamentous and sinuous elements, initially erect then tending to be repent in the outermost layer and thus turning into a cutis not embedded in a gelatinous matter at maturity; terminal elements $18\text{--}68 \times 4\text{--}18 \mu\text{m}$, cylindrical, cystidioid, bullet-shaped or acorn-shaped, apex rounded-obtuse to sometimes pointed, moderately thin-walled (up to $0.5 \mu\text{m}$), hyaline to yellowish in water and 5% KOH, bright yellow to orange (inamyloid to barely dextrinoid) in Melzer's, smooth to occasionally encrusted by a subtle zebra-pattern epiparietal pigment; subterminal elements similar in shape, size and color to terminal elements. *Marginal veil* not observed. *Stipitipellis* a texture of slender, parallel to subparallel and longitudinally running, smooth walled, adpressed hyphae, $3\text{--}16 \mu\text{m}$ wide, hyaline to pale yellowish in water and 5% KOH; the stipe apex covered by a fragmented caulohymenial layer consisting of subcylindrical, subclavate to clavate sterile *caulobasidioles*, $(15\text{--}) 24\text{--}29 \text{ (}\text{--}33\text{)} \times 5\text{--}12 \mu\text{m}$ ($n = 8$), having a wall up to $0.7 \mu\text{m}$ thick; *caulocystidia* not differentiated from *caulobasidioles*; *caulobasidia* not observed. *Lateral stipe stratum* under the caulohymenium absent. *Stipe trama* composed of confusedly and densely arranged, moderately to strongly interwoven, filamentous, smooth, yellowish pink in water and pale yellowish in KOH 5%, inamyloid hyphae, $3\text{--}20 \mu\text{m}$ broad. *Hymenophoral trama* bilateral divergent intermediate between the "Boletus-type" and the "Phylloporus-type", with subparallel to slightly divergent and loosely arranged, restricted at septa, gelatinous hyphae (lateral strata hyphae in transversal section not touching each other, $(2\text{--}) 3\text{--}5 \text{ (}\text{--}7\text{)} \mu\text{m}$ apart, $3\text{--}16 \mu\text{m}$ broad), hyaline to very pale yellowish in water and 5% KOH, inamyloid in Melzer's; lateral strata $(15\text{--}) 20\text{--}30 \text{ (}\text{--}40\text{)} \mu\text{m}$ thick, mediostratum $(10\text{--}) 15\text{--}30 \text{ (}\text{--}40\text{)} \mu\text{m}$ thick, axially arranged, consisting of a tightly adpressed, more frequently septate, non-gelatinous bundle of hyphae, $2\text{--}9 \mu\text{m}$ broad; in Congo Red the mediostratum is darker than the lateral strata. *Thromboplerous hyphae* infrequent, observed mostly in the pileipellis, with a dense golden yellow to brownish pigment in 5% KOH. *Clamp connections* absent in all tissues. *Ontogenetic development* probably mixangiocarpic.

Edibility unknown but most likely edible although not recommended as it may be confused with untested allied species.

Ecology and phenology: solitary to more frequently gregarious, mostly growing on wood but also on soil among litter in dry sclerophyll forests under a large array of myrtaceous trees including *Eucalyptus racemosa*, *E. microcorys*, *E. tereticornis*, *E. intermedius*, *Corymbia citriodora*, *C. maculata*, *Melaleuca* spp., etc. (Myrtaceae) and *Allocasuarina littoralis* (Casuarinaceae). Halling et al. (2015) and Leonard (2024) reported this species to

also occur under *Angophora*, *Leptospermum*, *Lophostemon*, *Syncarpia* (Myrtaceae), *Acacia* (Fabaceae) and *Callitris* (Cupressaceae) in Australia.

Examined materials: AUSTRALIA, Queensland, Brisbane, Alexandra Hills, Greater Glider Conservation Area, 27°13'29"S 153°13'9"E, 60 m, 20 Apr 2014, several specimens in various developmental stages, some growing on soil, others on woody substrate at the base of living trees, all partially dehydrated due to dry weather conditions, on sandy soil in a subtropical coastal dry sclerophyll woodland dominated by *Allocasuarina littoralis*, *Eucalyptus racemosa*, *E. microcorys* and *Corymbia citriodora* with the presence of *Melaleuca quinquinervia*, *Acacia* sp., *Banksia* sp. and other tropical broadleaved trees, M. Gelardi, MG598; Queensland, Brisbane City Council, Anstead Bushland Reserve, Moggil Conservation Park, 27°31'58"S 152°51'29"E, 60 m, 21 Apr 2014, two partially dehydrated mature specimens, along a trackside in a dry sclerophyll woodland dominated by *Corymbia maculata*, *Eucalyptus tereticornis* and *E. intermedius* with the presence of *Melaleuca* sp., M. Gelardi, R.E. Halling, J. Dearnaley, N. Fechner, T.W. May, D. Leemon, S. Nuske, K. Schwabenbauer, L. Irinyi, S. Abell, J. Wixted, L. Francis, M. Elliott, R. Robinson and M. Thompson, MG602.

Additional extralimital materials: *Aureoboletus* sp.: GUATEMALA, Departamento de Santa Rosa, Pueblo Nuevo Viñas, Aldea El Cuje, 14°14'50"N, 90°28'47"W, 1156 m, 27 Jun 2018, G. Simonini and R. Flores-Arzù, GS10616, MICG-5454 (GS10617) and MICG-5475 (GS10618); same loc., 14°14'50"N, 90°28'47"W, 1156 m, 10 June 2021, R. Flores-Arzù, same loc., 14°14'50"N, 90°28'47"W, 1156 m, R. Flores-Arzù, MICG-6793; same loc., 14°14'50"N, 90°28'47"W, 1156 m, 21 Aug 2018, R. Flores-Arzù, MICG-6023; same loc., 14°14'33"N 90°28'09"W, 1104 m, 10 Jun 2021, lower part of an oak forest, R. Flores-Arzù, MICG-6002 and MICG-6003; same loc., 14°15'05"N, 90°28'17"W, 1264 m, 07 Jul 2023, oak forest without the presence of coffee plants, R. Flores-Arzù (GS11347); Departamento de Guatemala, Concepción Pinula, Finca Pangea, 14°30'23"N, 90°21'10"W, 1603 m, 09 Jul 2023, a single specimen collected under oak trees, R. Flores-Arzù, MICG-7036; Departamento de Guatemala, San José Pinula, Finca Las Nubes, 14°33'50"N, 90°20'02"W, 2327 m, 22 Jun 2022, a single specimen collected on exposed soil in a pine-cypress-oak forest, B. Dentinger, MICG-7093;

Boletellus exiguus T.W. Henkel & Fulgenzi: GUYANA, Region 8 Potaro-Siparuni, Pakaraima Mountains, Upper Potaro River Basin, 3 km southwest of Potaro base camp in *Dicymbe* plot 3, 5°18'04"N 59°54'40"W, 710–750 m, 24 Jun 2004, growing in humic accumulations on a trunk of large, living *Dicymbe corymbosa* tree, NY1034374 (T.W. Henkel 8696, isotype);

Boletellus piakaii T.W. Henkel & Fulgenzi: GUYANA, Region 8 Potaro-Siparuni, Pakaraima Mountains, Upper Potaro River Basin, near Potaro base camp in *Dicymbe* plot 1, 5°18'04"N 59°54'40"W, 710–750 m, 02 Jul 2004, growing on root mat in *Dicymbe corymbosa* forest, NY1034438 (T.W. Henkel 8728, isotype);

Boletellus reminiscens Halling & Fechner: AUSTRALIA, Queensland, Wide Bay District, Great Sandy National Park, Fraser Island, Pile Valley Walking track, from Central Station to Pile Valley, 25°28'34"S 153°3'20"E, 100 m, 12 Feb 2009, growing on sandy soil in wet sclerophyll forest dominated by *Myrtaceae* with *Syncarpia* and *Lophostemon*, legit. and det. N. Fechner, A.M. Young and R.E. Halling, NY1393611 (R.E. Halling 9063, isotype);

Boletellus rubrolutescens Heinem. & Rammeloo: CAMEROON, Route Foumban, Koudoun, 5°39'27"N 10°54'84"E, 922 m, 07 Nov 2011, growing on soil in a gallery forest under *Uapaca* sp., legit. A.L. Njouonkou, det. A. de Kesel, BR5020169915682 (NAL374); *Boletellus sinapipes* Fechner, K. Syme, R. Rob. & Halling: AUSTRALIA, Queensland, Wide Bay District, Great Sandy National Park, Fraser Island, road from Central Station to Lake McKenzie, 25°28'40"S 153°2'51"E, 109 m, 09 Feb 2009, growing gregarious on sandy soil under *Eucalyptus*, *Syncarpia* and *Lophostemon*, legit. and det. R.E. Halling, NY1393539 (R.E. Halling 9040, isotype);

Boletellus sinochrysenteroides: RUSSIA, Primorsky Krai, Ussuriysky District, vicinity of Kamenushka village, 43°36'58"N 132°14'14"E, 24 Aug 2021, a single mature specimen growing in a lowland mixed forest with *Quercus mongolica*, *Pinus koraiensis*, *Abies holophylla*, etc., legit. D. Pogostina, det. T.Yu. Svetasheva and A.Yu. Biketova, LE-F 350390.

Discussion

The genus *Boletellus* has long been not well delimited from the morphological viewpoint. Various contrasting interpretations of the generic limits of this species-rich group of boletes have been offered by different authors over the past decades in several taxonomic treatments (Gilbert 1931; Heinemann 1954; Thiers 1963; Snell and Dick 1970; Smith and Thiers 1971; Corner 1972; Pegler and Young 1981; Singer et al. 1983, 1992; Singer 1986; Imazeki et al. 1988; Both 1993; Engel et al. 1996; Nagasawa 1997; Bessette et al. 2000; Ortiz-Santana et al. 2007; Watling 2008; Halling and Ortiz-Santana 2009; Horak 2011).

In the present study, we address various issues. DNA analyses were instrumental in classifying previously under-sampled *Boletellus* species and resolve their interspecific relationships. The identity of the studied collections was confirmed after bioinformatic analysis based on multilocus

molecular data (ITS, LSU, *RPB1*, *RPB2*, and *TEF1- α*) (Fig. 1) and morphological investigation. Our molecular outcomes are congruent with those obtained by previous investigations based on world-scale sampling (Halling et al. 2015), and the polyphyletic nature of *Boletellus* is reaffirmed and corroborated by molecular inference. In concordance with earlier studies, the phylogenetic placement of *B. ananas*, *B. cubensis* and *B. domingensis* is confirmed in the genus *Boletellus* s. l.

The genus *Boletellus* s. l. as currently defined is clearly polyphyletic. *Boletellus* s. str. could be re-defined based on the well-supported lineage containing the type species of the genus, *B. ananas*. Several species would need to be excluded and taxonomically re-assessed, like *B. elatus*, *B. exiguus* and *A. betula*. Further detailed studies are needed to address these issues.

In order to advancing knowledge of the phylogenetic relationships within *Boletellus* and refine the taxonomy of collective or poorly known species with greater confidence, some American taxa have been investigated in depth. Morphological descriptions of *B. ananas*, *B. cubensis*, and *B. domingensis* have been sharpened and their taxonomic limits refined as never before. Of great interest is the species alliance gravitating around the pair *B. ananas* and *B. emodensis*, a species-rich group with large, deeply costate basidiospores showing a mostly pantropical distribution. Species of this alliance are polymorphic and superficially similar to one another at first glance, yet they constitute separate and independent entities. Particularly, *B. ananas* is an iconic and showy American bolete with a unique appearance which has long been misinterpreted in the mycological literature of the eastern hemisphere. Contrary to the Asian, heterogeneous *B. emodensis* species-complex, which has most recently been largely disentangled with an increasing number of novel taxa being described (Sato And Hattori 2015; Xue et al. 2023) (see notes under *B. ananas*), the American *B. ananas* still awaits to be properly revisited. As a matter of fact, this name has been consistently misapplied in eastern and south-eastern Asia as well as in Australasia. Based on available knowledge *B. ananas* appears to be confined to the American continent. However, molecular phylogenetic analysis support this species in its current delimitation as polyphyletic, with accessions actually clustering in at least two independent, distantly related terminal clades representing two separate species occurring in America, one of which (*B. ananas* s. str., although showing a high heterogeneity, see Fig. 1) with a wide geographic distribution spanning through south-eastern North America, Central America and the Caribbean south to northern South America, the other (*B. ananas* s. l.) apparently restricted to northeastern South America (Guyana). The independent position of the clade containing the sequences of the Guyanese *B. ananas* is not shown in the present work due to the very long branches

which produced disturbance in the phylogenetic reconstruction, but it is clearly visible in the study by Xue et al. (2023). In the absence of clear-cut delimiting features other than phylogenetic inference and different distribution range, we believe it premature to propose a taxonomic novelty and are confident that American specialists, who are more familiar and experienced with this unnamed species, will take care of formally describing the cryptic novel taxon in the future.

We performed microscopic revisions of the isotype material of *B. ananas*, the holotype of *B. ananas* var. *crassotunicatus*, and of a topotype collection of *B. coccineus* var. *amarus*. Regrettably, all type specimens proved challenging for molecular study, and various attempts to yield DNA from these samples were unsuccessful. Data are still insufficient to determine whether the aforementioned varieties are really conspecific with *B. ananas* s. str.

Although somewhat peripheral to the subject of the present work, we mention the first molecularly confirmed record of *Boletellus sinochrysenderoides* from Far East Russia. In addition, for a matter of completeness and for enabling a better comparison, especially with respect to *B. ananas*, we have decided to include a well-annotated description of two overseas collections of *Boletellus* cf. *emodensis* recently gathered by the first author in the surrounding of Brisbane, Queensland, eastern Australia. It is unfortunate that repeated attempts to extract DNA from both samples resulted in being unsuccessful, and we were therefore not able to acquire any sequences, but based on gross morphology matching the Australian materials of *B. emodensis* as recently delimited by Halling et al. (2015) and Leonard (2024), we are confident enough in their provisional identification. However, it appears clear that *B. emodensis* is a collective species (Xue et al. 2023) and that the Australian collections previously assigned to that name represent a new, yet undescribed taxon. Despite this, due to the limited number of collections examined in the present study and to the fact that we were unable to obtain good sequences from them, we currently refrain from introducing a new species. An alternative option to describing a novel taxon would be to reinstate the old names *Boletellus pallescens* (Cooke & Massee) E.-J. Gilbert (holotype collection preserved at RBG Kew, K-M000164982 and K-M000158693, previously re-examined by E. Horak in 1966 and 2010 and R.E. Halling in 2008 according to handwritten notes in the original spreadsheet). Other available names would be *B. rufescens* (Cooke & Massee) Singer (holotype collection preserved at Kew, K-M000158692, previously re-examined by E. Horak in 1975 and R.E. Halling in 2009 according to handwritten notes in the original spreadsheet), *B. ligulatus* (Cooke) Singer and *Strobilomyces fasciculatus* (holotype collection preserved at RBG Kew, K-M000164979, previously re-examined by E. Horak in 2010). *Boletellus pallescens* and *B. rufescens* were originally introduced from Brisbane

(Queensland), while *B. ligulatus* and *S. fasciculatus* were described from Victoria. They might all be possible candidates for naming this Australian species, but taxonomic and nomenclatural implications should be carefully pondered. Leonard (2024), for instance, suspected *B. pallescens* to be conspecific with *B. ananiceps*.

It is all but easy to separate *Boletellus* from *Aureoboletus* (Klofac and Gelardi 2025). Historical morphological features which were considered to be diagnostic to discriminate against these genera are extremely heterogeneous and currently untenable based on molecular delimitation. Size, shapes, colors, surfaces texture, presence/absence of a partial veil, oxidation reactions, microscopic traits, ecology, and distribution range are largely overlapping across species assigned to both genera. There is no specific attribute that can be used to undisputedly separate *Boletellus* from *Aureoboletus*, including spore ornamentation. As stated above, ornamented basidiospores are shared by all *Boletellus* species, nonetheless eusporial ornamentation can also be observed in a few *Aureoboletus* species (*A. shichianus* (Teng & L. Ling) G. Wu & Zhu L. Yang, *A. betula*, *A. longicollis* (Ces.) N.K. Zeng & Ming Zhang, *A. wusangongii* N.K. Zeng, H.Z. Qin, W.F. Lin & L.G. Hu (= *A. pseudorsellii* D.F. Sun, R. Hua, F. Zhou & J.B. Zhang, see Qin et al. 2024 and Zhou et al. 2025, etc.), which exhibit longitudinally ridged, nodulose-verrucose or reticulate basidiospores. Several *Aureoboletus* species have viscid to glutinous pileus and stipe surface, which are usually not observed in *Boletellus*, however, *Aureoboletus* species with consistently dry surfaces are also known (Klofac and Gelardi 2025). Similarly, *Aureoboletus* species are mostly non-cyanescent, but with some relevant exceptions (Zhang et al. 2019; Xue et al. 2023). From the molecular perspective, *Boletellus* and *Aureoboletus* are sister genera, but their reciprocal distance is still obscure, and clear-cut phylogenetic and taxonomic boundaries are yet to be assessed.

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Author contribution MG, CA, and AV conceived the study; CA and KOM conducted sampling and provided materials; MG and FC performed the microscopic analyses; LRH, TYS, UP, and AYB performed the laboratory experiments and generated sequences; LRH analysed the sequence data and produced the phylotrees; MG made microscopy drawings; AV, CA, and MG prepared the photoplates; LRH, AV, and AYB edited the phylotrees and arranged the tables. MG wrote the manuscript with contributions from all authors. All authors agreed with the submission of the manuscript.

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Data availability Sequence data have been deposited in GenBank as given in Table 1 and alignments as Supplementary files.

Declarations

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests The authors declare no competing interests.

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