



Coccoloba-associated xerocomoid boletes (*Boletaceae*) from the Caribbean and Mexico: *Tropicoboletus ruborculus* gen. et comb. nov., revision of *Xerocomus coccolobae*, phylogenetic assessment of *Singerocomus guadelupae* comb. nov., and type studies of *Xerocomus caeruleonigrescens*, *X. cuneipes*, and *X. pseudoboletinus* var. *pini-caribaeae*

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Abstract

Only two *Coccoloba*-associated xerocomoid boletes with smooth basidiospores are currently known from the Dominican Republic, namely *Boletus ruborculus* and *Xerocomus coccolobae*. A multilocus phylogenetic analysis of four gene markers (ITS, LSU, *RPB2*, *TEF1*) reveals that *B. ruborculus* forms an autonomous clade in the *Boletaceae* corresponding to a novel genus, which is introduced here as *Tropicoboletus* gen. nov., whereas *X. coccolobae* is confirmed as a member of *Xerocomus* s. str. *Tropicoboletus* is sister to subfamily *Xerocomoideae* in the combined *RPB2/TEF1* *Boletaceae*-wide analysis. Accurate morphological descriptions of the two species based on well-annotated samples are provided, accompanied by color photographs of fresh specimens in habitat and line drawings of their main anatomical features. The holotype collections of *B. ruborculus* and *X. coccolobae* were successfully sequenced and re-examined anatomically. The distribution range of *Tropicoboletus ruborculus* comb. nov. is extended from the original locality in Puerto Rico to the Dominican Republic and Mexico where its presence is reported for the first time. Similarly, the Dominican collections of *X. coccolobae* represent the first documented occurrence of this species for the Island of Hispaniola. Based on molecular and morphological evidence, we conclude that the Belizean species *Xerocomus olivaceus* is conspecific with *X. coccolobae* and is therefore reduced into synonymy. In addition, the holotypes of *Xerocomus caeruleonigrescens*, *Xerocomus cuneipes*, and *Xerocomus pseudoboletinus* var. *pini-caribaeae* were microscopically re-studied, although their exact taxonomic placement remains unresolved in the absence of any phylogenetic inference. Molecular investigation of a paratype of *Boletus guadelupae* resulted in a conspecificity with the recently described *Singerocomus atlanticus* from Brazil, extending the biogeographic coverage of *Singerocomus* to the Caribbean. Accordingly, the new combination *Singerocomus guadelupae* is proposed and *S. atlanticus* is synonymized. Finally, a putative novel *Xerocomus* s. str. species is discovered from the Dominican Republic but not formally described for the time being due to the paucity of material available.

Keywords *Boletales* · Molecular phylogeny · Greater Antilles · Neotropical boletes · Taxonomy

Introduction

Boletes (*Boletaceae*, *Boletales*) are one of the largest and most biodiverse groups of basidiomycetes. They play a vital role in establishing ectomycorrhizal (ECM) association with woody plants and their ecological and economic impact have become increasingly important in the last decades (Singer

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1986; Watling 2008). The rapid progress of molecular phylogenetic techniques applied to the investigation of boletes has recently led to a radical re-assessment of several genera belonging to the hyperdiverse family *Boletaceae*, predominantly with respect to some historically established genera such as *Boletus* Fr., *Leccinum* Gray, *Pulveroboletus* Murrill, *Tylopilus* P. Karsten, *Xerocomus* Quél., etc., which have all been inferred to constitute artificial assemblages of unrelated species as traditionally circumscribed (Binder 1999; Binder and Hibbett 2006; Drehmel et al. 2008; Nuhn et al. 2013; Wu et al. 2014). Particularly, *Boletus* and *Xerocomus* revealed their strong polyphyly, and recently underwent major taxonomic and systematic upsets that facilitated their reciprocal separation and determined a general consensus in their current delimitation (Nuhn et al. 2013; Wu et al. 2014, 2016a, b).

Presently, based on an improved taxonomic resolution derived from advanced molecular phylogenetic inference, *Boletus* s. l. appears to encompass at least twenty-six autonomous monophyletic lineages at the generic rank, focused on previously defined sections or on single species or species-groups (some of which not formally proposed yet), including (1) *Boletus* s. str. (= *Boletus* sect. *Boletus*, corresponding to the *B. edulis* Bull. group, otherwise known as porcini mushrooms); (2) *Butyriboletus* D. Arora & J.L. Frank (= *Boletus* sect. *Appendiculati* Konrad & Maublanc emend. Lannoy & Estadès); (3) *Caloboletus* Vizzini (= *Boletus* sect. *Calopodes* Fr. emend. Lannoy & Estadès); (4) *Retiboletus* Manfr. Binder & Bresinsky (= *Boletus* sect. *Ornatipedes* Singer and sect. *Grisei* Singer); (5) *Suillellus* Murrill (= *B. luridus* Schaeffer complex); (6) *Rubroboletus* Kuan Zhao & Zhu L. Yang (= *B. satanas* Lenz/*B. sinicus* W.F. Chiu complex); (7) *Imperator* G. Koller et al. (= *B. torosus* Fr./*B. rhodopurpureus* Smotlacha complex); (8) *Neoboletus* Gelardi, Simonini & Vizzini (= *B. luridiformis* Rostk. complex); (9) *Imleria* Vizzini (= *B. badius* (Fr.) Fr. complex, corresponding to sect. *Pseudoboleti* Singer p. p.); (10) *Cyanoboletus* Gelardi, Vizzini & Simonini (= *B. pulverulentus* Opat. complex, corresponding to sect. *Subpruinosi* Fr. p. p.); (11) *Baorangia* G. Wu & Zhu L. Yang (= *B. pseudocalopus* Hongo/*B. bicolor* Peck complex, corresponding to sect. *Fragrantes* Lannoy & Estadès p. p. and sect. *Brevitubi* M. Zang p. p.); (12) *Lanmaoa* G. Wu, Zhu L. Yang & Halling (= *B. fragrans* Vittad./*B. carminipes* A.H. Smith & Thiers complex, corresponding to sect. *Fragrantes* p. p.); (13) *Hemileccinum* Šutara (= *B. impolitus* Fr. complex); (14) *Parvixerocomus* G. Wu & Zhu L. Yang (= *B. aokii* Hongo complex); (15) *Crocinoletus* N.K. Zeng, Zhu L. Yang & G. Wu (= *B. rufoaureus* Masee complex); (16) *Exsudoporus* Vizzini, Simonini & Gelardi (= *B. permagnificus* Pöder /*B. frostii* J.L. Russell complex); (17) *Amoenoboletus* G. Wu, E. Horak & Zhu L. Yang (= *B.*

weberi Singer/*B. mcrobbii* (McNabb) G. Stev. complex); (18) *Corneroboletus* N.K. Zeng & Zhu L. Yang (= *B. indecorus* Masee); (19) *Cupreoboletus* Simonini, Gelardi & Vizzini (= *B. poikilochromus* Pöder, Cetto & Zuccherelli); (20) *B. morrisii* Peck; (21) *B. abruptibulbus* Roody, Both & B. Ortiz; (22) *B. lakhanpalii* K. Das, D. Chakr., A. Baghela, S.K. Singh & Dentinger; (23) *B. durhamensis* B. Ortiz, Bessette & McConnell; (24) *B. candidissimus* T.H.G. Pham, A.V. Alexandrova & O.V. Morozova; (25) *B. subsplendidus* W.F. Chiu; and (26) *Butyriboletus hainanensis* N.K. Zeng, Zhi Q. Liang & S. Jiang (*B. hainanensis* complex) (Binder and Bresinsky 2002; Binder and Hibbett 2006; Halling et al. 2007, 2015; Šutara 2008; Zeng et al. 2012, 2014; Gelardi et al. 2013, 2015; Nuhn et al. 2013; Arora and Frank 2014; Vizzini 2014a, b, c, d, e, f; Vizzini et al. 2014; Wu et al. 2014, 2016a, b, 2021; Zhao et al. 2014a, b; Zhu et al. 2014; Das et al. 2015; Ortiz-Santana et al. 2016; Liang et al. 2016; Crous et al. 2019; Bozok et al. 2020; Biketova et al. 2022; Farid et al. 2021).

The heterogeneous *Xerocomus* s. l. was in turn split into twelve independent generic lineages based on molecular evidence: (1) *Xerocomus* s. str. (= *X. subtomentosus* (L.) Quél. complex, corresponding to *Xerocomus* sect. *Subtomentosi* (Fr.) Singer and sect. *Pseudophyllopori* Singer); (2) *Xerocomellus* Šutara (= *X. chrysenteron* (Bull.) Quél. complex, corresponding to *Xerocomus* sect. *Chrysenteri* Blum ex Bon, sect. *Truncati* (A.H. Smith & Thiers) H. Engel & Klofac and sect. *Striatulispori* Redeuilh); (3) *Hortiboletus* Simonini, Vizzini & Gelardi (= *X. rubellus* (Krombh.) Quél. complex); (4) *Rheubarbariboletus* Vizzini, Simonini & Gelardi (= *X. armeniacus* (Quél.) Quél. complex, corresponding to *Xerocomus* sect. *Armeniaci* H. Engel & Klofac); (5) *Pseudoboletus* Šutara (= *X. parasiticus* (Bull.) Quél. complex, corresponding to *Xerocomus* sect. *Parasitici* Singer); (6) *Alessioporus* Gelardi, Vizzini & Simonini (= *X. ichnusanus* Alessio, Galli & Littini complex); (7) *Pulchroboletus* Gelardi, Vizzini & Simonini (= *X. roseoalbidus* Alessio & Littini complex); (8) *Hourangia* Xue T. Zhu & Zhu L. Yang (= *X. cheoi* (W.F. Chiu) F.L. Tai complex); (9) *Singerocomus* T.W. Henkel & M.E. Smith (= *X. inundabilis* Singer complex); (10) *Neotropicomus* A.C. Magnago, Alves-Silva & T.W. Henkel (= *X. parvogracilis* T.W. Henkel & Husbands complex); (11) *X. porophyllus* T.H. Li, W.J. Yan & Ming Zhang; and (12) *X. cyaneibrunnescens* T.W. Henkel & Husbands (Binder 1999; Taylor et al. 2001, 2006; Peintner et al. 2003; Binder and Hibbett 2006; Šutara 2008; Gelardi et al. 2013, 2014; Nuhn et al. 2013; Osmundson et al. 2013; Yan et al. 2013; Wu et al. 2014, 2016b; Zhu et al. 2015; Ariyawansa et al. 2016; Crous et al. 2016, 2019; Das et al. 2016; Henkel et al. 2016; Farid et al. 2017, 2021; Frank et al. 2017, 2020; Loizides et al. 2019; Naseer et al. 2019; Xie et al. 2020; Magnago et al. 2022). Furthermore, an additional generic xerocomoid lineage might be represented by the *X. brasiliensis* (Rick)

Singer complex (corresponding to *Xerocomus* sect. *Brasilienenses* Singer) (Singer 1986; Watling 2008).

It appears clear, however, that additional monophyletic clades are expected to be uncovered as soon as supplementary molecular investigation of poorly known or critical boletoid and xerocomoid taxa will become available in the near future, especially from remote and underexplored areas of the pantropical belt.

Although it has not been as thoroughly investigated as North America and Europe, Mesoamerica has been the object of a large number of mycological contributions published in the past decades which have enhanced our understanding of the neotropical boletes diversity and biogeography with a special emphasis on boletoid or xerocomoid taxa, underpinning the health and functioning of different ecosystems in Mexico, mainland Central America, northern South America, and the Caribbean (e.g., Singer and Fiard 1977; Pegler 1983; Singer et al. 1983; Singer 1988; Halling 1989, 1992, 1997; González-Velázquez and Valenzuela 1993; Gómez 1997; Halling and Mueller 1999, 2002, 2005; García-Jiménez 1999, 2013; Miller et al. 2000; Minter et al. 2001; Halling and Mata 2004; Flores Arzù and Simonini 2000; Franco-Molano et al. 2000; Halling et al. 2004; García-Jiménez 2013; García-Jiménez et al. 2013; Ortiz-Santana et al. 2007; Courtecuisse and Welti 2013; de la Fuente et al. 2018; Flores Arzù 2020). However, most of the neotropical bolete species described to date have been defined based solely on morphological, ecological, or biochemical taxonomic criteria and are in urgent need of phylogenetic reconsideration. Moreover, identification efforts are becoming rather more difficult because several Central American species show a wider distribution throughout the neotropics than previously assumed.

Two xerocomoid smooth-spored ECM bolete species associated with *Coccoloba* (*Polygonaceae*), namely *Boletus ruborculus* T.J. Baroni (Miller et al. 2000) and *Xerocomus coccolobae* Pegler (Pegler 1983), were originally described from the Greater and Lesser Antilles of the Caribbean, respectively. In order to consolidate the taxonomic concept of these two neotropical species, we carefully studied several collections for each species. Furthermore, the DNA of the original material of both species was sequenced for the first time and the holotype specimens re-examined anatomically. In the light of the obtained outcomes, *Tropicoboletus* is described as a new genus to science to accommodate *B. ruborculus*, whereas the generic affiliation of *X. coccolobae* in *Xerocomus* s. str. is corroborated by its phylogenetic placement. Furthermore, type specimens of additional neotropical species, including *Xerocomus pseudoboletinus* var. *pini-caribaeae* Singer, *Xerocomus cuneipes* Pegler, *Xerocomus caeruleonigrescens* Pegler, and *Boletus guadelupae* Singer & Fiard were anatomically re-studied, and the latter species was also phylogenetically investigated.

Materials and methods

Collection site and sampling

Specimens examined were collected in Sosúa, Puerto Plata Province, Dominican Republic and El Morro, Viejo San Juan, Puerto Rico. Dominican Republic samples are deposited at the Herbarium of Jardín Botánico Nacional of Santo Domingo, Dr. Rafael Ma. Moscoso, Dominican Republic (JBSD). The holotype collection of *Xerocomus pseudoboletinus* var. *pini-caribaeae* and a mixed type (holotype/paratype) of *Boletus guadelupae* examined in the present study are deposited at the Field Museum of Natural History, Chicago (F), the holotype of *Boletus ruborculus* is deposited at the New York Botanical Garden (NYBG), while the holotypes of *Xerocomus coccolobae*, *X. cuneipes*, and *X. caeruleonigrescens* and paratype specimens of *B. guadelupae* are all deposited at the Fungarium of the Royal Botanic Gardens Kew (K-M) (acronyms from Thiers 2022). “ANGE,” “MG,” “komille,” and “de la Fuente” refer to the personal herbarium of Claudio Angelini, Matteo Gelardi, Kurt O. Miller, and J.I. de la Fuente, respectively. Fungarium numbers, unless otherwise stated, are cited for all collections from which morphological features were examined. Author citations follow the Index Fungorum, Authors of Fungal Names (www.indexfungorum.org/authorsoffungalnames.htm). Geographic distribution of some studied species have also been checked on MyCoPortal (<https://mycoportal.org>).

Morphological studies

Macroscopic descriptions, macrochemical reactions (30% NH₄OH, 30% KOH), and ecological information, such as habitat notations, time of fruiting, and associated plant communities, accompanied the detailed field notes of the fresh basidiomes. In the field, latitude, longitude, and elevation were determined with a global positioning system (GPS) receiver. Color terms in capital letters (e.g., White, Plate LIII) are from Ridgway (1912). Photographs of collections were taken in the natural habitat using a Nikon Coolpix 8400 camera. Microscopic anatomical features were observed and recorded from revived dried material; sections were rehydrated either in water, 5% potassium hydroxide (KOH), or in ammoniacal Congo red. All anatomical 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 \pm standard deviation (maximum), $Q = \text{length}/\text{width}$ ratio with the extreme values in parentheses, $Q_m = \text{average quotient (length/width ratio)} \pm \text{standard deviation}$ 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 stiptipellis 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, and Melzer’s reagent, respectively. Line drawings of microstructures were traced in free hand based on digital photomicrographs of rehydrated material.

The basidiospores of selected collections (*Tropicobolus ruborculus* NY 577594 and JBSD133073, *Xerocomus coccolobae* K-M000178954 and JBSD133071, *X. cuneipes* K-M000178953, *X. caerulonigrescens* K-M000178955, *Singerocomus guadelupae* K-M000193859, and K-M000193867) were also observed under a Zeiss Ultra-Plus VP FEG-SEM scanning electron microscope (SEM), equipped with Oxford X-Max 80 mm² SDD detector and operated at 2 kV, and a FEI Quanta 650 FEG operated at 5 kV.

DNA extraction, PCR amplification, and DNA sequencing

Genomic DNA for all samples, except for the K-M, NYBG and F specimens, was isolated from 25 mg of dried voucher specimens. DNA extraction and PCR amplification were performed as described by Alvarado et al. (2012). The universal primer pairs ITS1F/ITS4 (White et al. 1990; Gardes and Bruns 1993) and LR0R/LR5 (Vilgalys and Hester 1990; Cubeta et al. 1991) were used for the amplification of the internal transcribed spacer (ITS) and the nuclear large ribosomal subunit (LSU) regions of the nrDNA, respectively. The 6–7 region of the *RPB2* gene (RNA polymerase II second largest subunit) was amplified using the primer pairs brpb2-6F2/brpb2-7R2 (Matheny et al. 2002, 2007). Primers EF1-983F and EF1-1567R (Rehner and Buckley 2005) were used for amplification of the translation elongation factor 1- α (*TEF1*) gene. The PCR products were purified with the Wizard SV Gel and PCR Clean-Up System (Promega, Madison, WI) following manufacturer’s instructions and positive reactions sequenced forward and reverse by MACROGEN Inc. (Seoul, Republic of Korea).

For the K-M, genomic DNA was extracted following an enzymatic digestion and glass-fiber filtration protocol (Dentinger et al. 2010) and for NYBG and F specimens using the NucleoSpin™ Plant II kit. Amplification of the ITS region was performed following standard conditions and using several primer combinations: ITS1F with ITS4B/ITS4/ITS2, ITS3 with ITS4B/ITS4, and ITS8F with ITS6R (White et al. 1990; Gardes and Bruns 1993; Dentinger et al. 2010). Successful amplicons were purified using ExoSAP-IT (USB) and sequenced bidirectionally using BigDye3.1 in a ABI3730 DNA analyzer (Applied Biosystems).

All newly generated sequences were submitted to GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) and their accession numbers are reported in the text, Tables 1, 2, 3, and 4, and Suppl. Mat. Figure 2.

Sequence alignment, dataset assembly, and phylogenetic analysis

Newly generated sequences and sequences retrieved from public databases, GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) and UNITE (<https://unite.ut.ee/>), were combined for phylogenetic reconstructions.

Sequences obtained in this study were checked and assembled using Geneious R11 v.11.1.5 (<https://www.geneious.com>) and Sequencher 5.4.6 (<https://www.genecodes.com/>) programs and preliminary identified using the BLASTn algorithm (Altschul et al. 1990) in GenBank and UNITE. Based on the BLASTn results and recent phylogenetic studies focused on family *Boletaceae* (e.g., Nuhn et al. 2013; Wu et al. 2014, 2016a, b; Gelardi et al. 2015; Henkel et al. 2016; Vadthanarat et al. 2019, 2022; Badou et al. 2022; Magnago et al. 2022), different datasets were constructed with sequences retrieved from GenBank for comparative phylogenetic analysis for each DNA region (Tables 1, 2, 3 and 4). Alignments were generated for ITS, LSU, *RPB2*, and *TEF1* datasets using MAFFT (Katoh et al. 2002) with default conditions for gap openings and gap extension penalties and manually adjusted with Geneious R11 v.11.1.5 (<https://www.geneious.com>). The best-fit models were estimated by the Akaike information criterion (AIC) and the Bayesian information criterion (BIC) using jModelTest v. 2.1.7 (Darriba et al. 2012) to provide a substitution model for each single alignment.

Four different datasets were assembled to elucidate the phylogenetic placement of the targeting taxa, viz. new genus *Tropicobolus* and the species *Xerocomus coccolobae* and *Boletus guadelupae*. The first dataset focused on family *Boletaceae* and was generated from combined *RPB2* and *TEF1* sequences (Table 1). K80+I+G and TPM1uf+I+G models were chosen for *RPB2* and *TEF1* alignments, respectively. The second and third datasets focused on the genus *Xerocomus* s. str. (LSU sequences, GTR+I+G model),

Table 1 Taxa, locations, vouchers, and accession numbers of the DNA sequences used in the *Boletaceae*-wide phylogenetic analysis inferred from a two-gene dataset (*RPB2* and *TEF1*). Sequences in bold were generated in this study

Taxon	Country	Specimen voucher	<i>RPB2</i>	<i>TEF1</i>
<i>Afroboletus costatisporus</i>	Togo	ADK4644	KT823991	KT824024
<i>Afroboletus luteolus</i>	Togo	ADK4844	MH614748	MH614701
<i>Afroboletus multijugus</i>	Burundi	JD671	MH614747	MH614700
<i>Amoenoboletus granulopunctatus</i>	China	HKAS 80250	MW560080	MW566746
<i>Amoenoboletus mcrobbii</i>	New Zealand	PDD97418	–	MW566744
<i>Amoenoboletus miraculosus</i>	China	ZT14046	–	MW566745
<i>Aureoboletus auriflammeus</i>	USA	CFMR BOS 699	MK766269	MK721060
<i>Aureoboletus catenarius</i>	China	HKAS 54467	KT990349	KT990711
<i>Aureoboletus duplicatoporus</i>	China	HKAS 50498	KF112754	KF112230
<i>Aureoboletus formosus</i>	China	GDGM44441	KT291751	KT291744
<i>Aureoboletus gentilis</i>	Belgium	ADK4865	KT823994	KT824027
<i>Aureoboletus glutinosus</i>	China	GDGM44477	MH700229	MH700205
<i>Aureoboletus innixus</i>	USA	CFMR BOS 544	MK766270	MK721061
<i>Aureoboletus moravicus</i>	Belgium	VDKO1120	MG212615	MG212573
<i>Aureoboletus nephrosporus</i>	China	HKAS 74929	KT990358	KT990721
<i>Aureoboletus projectellus</i>	USA	AFTOL ID 713	AY787218	AY879116
<i>Aureoboletus raphanaceus</i>	China	GDGM53127	MN549706	MN549676
<i>Aureoboletus singeri</i>	Belize	CFMR BOS 468	MK766274	MK721065
<i>Aureoboletus</i> sp.	China	OR0245	MH614749	MH614702
<i>Aureoboletus</i> sp.	Thailand	OR0369	MH614750	MH614703
<i>Aureoboletus tenuis</i>	China	GDGM42601	KT291754	KT291745
<i>Aureoboletus thibetanus</i>	China	AFTOL ID 450	DQ366279	DQ029199
<i>Aureoboletus tomentosus</i>	China	HKAS 90216	KT990355	KT990717
<i>Aureoboletus viscidipes</i>	China	HKAS 77103	KT990360	KT990723
<i>Aureoboletus viscosus</i>	Thailand	OR0361	MH614751	MH614704
<i>Australopilus palumanus</i>	Australia	REH 9433	MK766276	MK721067
<i>Austroboletus dictyotus</i>	Thailand	OR0045	KT823999	KT824032
<i>Austroboletus olivaceoglutinosus</i>	China	HKAS 57756	KF112764	KF112212
<i>Austroboletus</i> sp.	Thailand	OR0891	MH614753	MH614706
<i>Austroboletus subvirens</i>	Thailand	OR0573	MH614752	MH614705
<i>Baorangia major</i>	Thailand	OR0209	MG897441	MG897431
<i>Baorangia major</i>	Thailand	OR0404	MG897442	MG897432
<i>Baorangia major</i>	China	OR0486	MG897443	MG897433
<i>Baorangia pseudocalopus</i>	China	HKAS 75739	KM605179	KJ184570
<i>Boletaceae</i> sp.	China	SV 2022a 1	MZ355903	MW485968
<i>Boletaceae</i> sp.	China	SV 2022a 2	MZ355904	MW485969
<i>Boletellus ananas</i>	Belize	K-M000123769	MH614754	MH614707
<i>Boletellus ananas</i>	Costa Rica	NY815459	KF112760	KF112308
<i>Boletellus areolatus</i>	Japan	TNS F 61444	AB999754	–
<i>Boletellus aurocontextus</i>	Japan	TNS F 61501	AB999770	–
<i>Boletellus emodensis</i>	Thailand	OR0061	KT824003	KT824036
<i>Boletellus emodensis</i>	Japan	TNS F 61564	AB999782	–
<i>Boletellus</i> sp.	Thailand	OR0621	MG212616	MG212574
<i>Boletus aereus</i>	Belgium	VDKO1055	MG212617	MG212575
<i>Boletus albobrunnescens</i>	Thailand	OR0131	KT824006	KT824039
<i>Boletus edulis</i>	Belgium	VDKO0869	MG212618	MG212576
<i>Boletus reticuloceps</i>	China	OR0446	KF112703	MG212577
<i>Boletus rubriceps</i>	USA	MICH KUO 8150719	MK766284	MK721076
<i>Borofutus dhakanus</i>	Thailand	OR0345	MH614755	MH614709

Table 1 (continued)

Taxon	Country	Specimen voucher	<i>RPB2</i>	<i>TEFI</i>
<i>Bothia castanella</i>	USA	MB03-053	–	KF030421
<i>Bothia fujianensis</i>	China	HKAS 82694	–	KM272860
<i>Buchwaldoboletus lignicola</i>	China	HKAS 76674	KF112819	KF112277
<i>Buchwaldoboletus lignicola</i>	Belgium	VDKO1140	MH614756	MH614710
<i>Butyriboletus appendiculatus</i>	Belgium	VDKO0193b	MG212624	MG212582
<i>Butyriboletus floridanus</i>	Belize	BOS 617	MK766287	MK721079
<i>Butyriboletus frostii</i>	USA	NY815462	KF112675	KF112164
<i>Butyriboletus pseudoregius</i>	Belgium	VDKO0925	MG212625	MG212583
<i>Butyriboletus roseoflavus</i>	China	OR0230	KT824007	KT824040
<i>Butyriboletus roseopurpureus</i>	USA	BOTH4497	MG897438	MG897428
<i>Butyriboletus subsplendidus</i>	China	HKAS 50444	KT990379	KT990742
<i>Butyriboletus yicibus</i>	China	HKAS 55413	KF112674	KF112157
<i>Cacaoporus pallidicarneus</i>	Thailand	SV0221	MK372286	MK372273
<i>Cacaoporus tenebrosus</i>	Thailand	SV0223	MK372290	MK372277
<i>Caloboletus calopus</i>	Belgium	ADK4087	KP055030	KJ184566
<i>Caloboletus firmus</i>	Belize	BOS 372	MK766288	MK721080
<i>Caloboletus inedulis</i>	USA	BOTH3963	MG897434	MG897424
<i>Caloboletus radicans</i>	Belgium	VDKO1187	MG212626	MG212584
<i>Caloboletus</i> sp.	Thailand	OR0068	MH614757	MH614711
<i>Caloboletus yunnanensis</i>	China	HKAS 69214	KT990396	KJ184568
<i>Chalciporus africanus</i>	Cameroon	JD517	KT823996	KT824029
<i>Chalciporus piperatus</i>	Thailand	OR0586	KT824009	KT824042
<i>Chalciporus piperatus</i>	Belgium	VDKO1063	MH614759	MH614713
<i>Chalciporus rubinus</i>	Belgium	AF2835	KT823995	KT824028
<i>Chalciporus rubinus</i>	China	OR0139	MH614758	MH614712
<i>Chalciporus</i> sp.	Thailand	OR0363	MH645602	MH645594
<i>Chalciporus</i> sp.	Thailand	OR0373	MH645603	MH645595
<i>Chamonixia brevicolumna</i>	USA	DBG F28707	MK766291	MK721083
<i>Chamonixia caesp. itosa</i>	USA	OSC117571	MK766293	MK721085
<i>Chiua</i> sp.	China	OR0141	MH614760	MH614714
<i>Chiua virens</i>	China	OR0266	MG212627	MG212585
<i>Chiua viridula</i>	China	HKAS 74928	KF112794	KF112273
<i>Crocinoletus laetissimus</i>	Thailand	OR0576	KT824008	KT824041
<i>Crocinoletus rufoaureus</i>	China	HKAS 53424	KF112710	KF112206
<i>Cupreoboletus poikilochromus</i>	Italy	GS10070	KT157068	KT157072
<i>Cyanoboletus brunneoruber</i>	China	OR0233	MG212628	MG212586
<i>Cyanoboletus pulverulentus</i>	Belgium	RW109	KT824013	KT824046
<i>Cyanoboletus sinopulverulentus</i>	China	HKAS 59609	KF112700	KF112193
<i>Cyanoboletus</i> sp.	China	OR0257	MG212629	MG212587
<i>Cyanoboletus</i> sp.	Thailand	OR0322	MH614768	MH614722
<i>Cyanoboletus</i> sp.	Thailand	OR0961	MH614770	MH614724
<i>Erythrophylloporus aurantiacus</i>	Costa Rica	REH7271	MH614761	MH614715
<i>Erythrophylloporus fagicola</i>	Mexico	Garay215	MH614762	MH614716
<i>Erythrophylloporus paucicarpus</i>	Thailand	OR1151	MH614765	MH614719
<i>Erythrophylloporus suthepense</i>	Thailand	SV0236	MH614767	MH614721
<i>Fistulinella prunicolor</i>	Australia	REH9880	MH614771	MH614725
<i>Gymnogaster boletoides</i>	China	NY01194009	KT990406	KT990768
<i>Harrya chromapes</i>	China	HKAS 50527	KF112792	KF112270
<i>Harrya moniliformis</i>	China	HKAS 49627	KT990500	KT990881
<i>Heimioporus australis</i>	Australia	REH9288	–	KP327703

Table 1 (continued)

Taxon	Country	Specimen voucher	<i>RPB2</i>	<i>TEF1</i>
<i>Heimioporus conicus</i>	China	HKAS 53451	KF112805	KF112226
<i>Heimioporus cooloolae</i>	Australia	REH9817	–	KP327710
<i>Heimioporus fruticicola</i>	Australia	REH8962	–	KP327696
<i>Heimioporus gaojiaocong</i>	China	HKAS 80582	KT990409	KT990770
<i>Heimioporus ivoryi</i>	Costa Rica	REH8620	–	KP327683
<i>Heimioporus japonicus</i>	Thailand	OR0114	KT824004	KT824037
<i>Heimioporus japonicus</i>	Thailand	SV0016	MT136766	MT136771
<i>Heimioporus mandarinus</i>	Thailand	OR0218	MG212632	MG212590
<i>Heimioporus subcostatus</i>	Thailand	SV0235	MT136770	MT136775
<i>Hemileccinum depilatum</i>	Belgium	AF2845	MG212633	MG212591
<i>Hemileccinum hortonii</i>	USA	MICH KUO 7050706	MK766377	MK721175
<i>Hemileccinum impolitum</i>	Belgium	ADK4078	MG212634	MG212592
<i>Hemileccinum indecorum</i>	Thailand	OR0863	MH614772	MH614726
<i>Hemileccinum rubropunctum</i>	USA	REH 8501	MK766327	MK721122
<i>Hemileccinum rugosum</i>	China	HKAS 84355	KT990413	KT990774
<i>Hemileccinum</i> sp.	China	HKAS 53421	KF112751	KF112235
<i>Hemileccinum</i> sp.	China	HKAS 59445	KT990414	KT990775
<i>Hemileccinum subglabripes</i>	USA	MICH KUO 7230802	MK766300	MK721092
<i>Hortiboletus amygdalinus</i>	China	HKAS 54166	KT990416	KT990777
<i>Hortiboletus campestris</i>	USA	MICH KUO 8240502	MK766302	MK721094
<i>Hortiboletus rubellus</i>	Belgium	VDKO0403	MH614774	–
<i>Hortiboletus subpaludosus</i>	China	HKAS 59608	KF112696	KF112185
<i>Hourangia cheoi</i>	China	HKAS 52269	KF112773	KF112286
<i>Hourangia microcarpa</i>	China	HKAS 53378	KF112775	KF112300
<i>Hourangia nigropunctata</i>	China	HKAS 57427	KP136978	KP136927
<i>Hourangia pumila</i>	Thailand	OR0762	MH614775	MH614728
<i>Hourangia</i> sp.	China	HKAS 68178	KF112776	KF112301
<i>Hymenoboletus luteopurpureus</i>	China	HKAS 46334	KF112795	KF112271
<i>Imleria badia</i>	Belgium	VDKO0709	KT824016	KT824049
<i>Imleria obscurebrunnea</i>	China	OR0263	MH614776	MH614729
<i>Imleria pallidus</i>	USA	BOTH4356	–	MH614708
<i>Imperator torosus</i>	Germany	MB000258	MW560082	MW566748
<i>Lanmaoa angustispora</i>	China	HKAS 74752	KM605177	KM605154
<i>Lanmaoa asiatica</i>	China	OR0228	MH614777	MH614730
<i>Lanmaoa carminipes</i>	USA	BOTH4591	MG897439	MG897429
<i>Lanmaoa pallidorosea</i>	USA	BOTH4432	MG897437	MG897427
<i>Lanmaoa</i> sp.	Thailand	OR0130	MH614778	MH614731
<i>Lanmaoa</i> sp.	Thailand	OR0370	MH614779	MH614732
<i>Leccinellum cremeum</i>	China	HKAS 90639	KT990420	KT990781
<i>Leccinellum crocipodium</i>	China	HKAS 76658	KF112728	KF112252
<i>Leccinellum griseum</i>	Japan	KPM NC 17832	–	JN378450
<i>Leccinum scabrum</i>	Belgium	VDKO0938	MG212635	MG212593
<i>Leccinum schistophilum</i>	Belgium	VDKO1128	KT824022	KT824055
<i>Leccinum variicolor</i>	Belgium	VDKO0844	MG212636	MG212594
<i>Mucilopilus castaneiceps</i>	China	HKAS 75045	KF112735	KF112211
<i>Neoboletus brunneissimus</i>	China	OR0249	MG212637	MG212595
<i>Neoboletus erythropus</i>	Belgium	VDKO0690	KT824015	KT824048
<i>Neoboletus ferrugineus</i>	China	HKAS 77718	KT990431	KT990789
<i>Neoboletus flavidus</i>	China	HKAS 59443	KU974144	KU974136
<i>Neoboletus hainanensis</i>	China	HKAS 59469	KF112669	KF112175

Table 1 (continued)

Taxon	Country	Specimen voucher	<i>RPB2</i>	<i>TEFI</i>
<i>Neoboletus junquilleus</i>	France	AF2922	MG212638	MG212596
<i>Neoboletus magnificus</i>	China	HKAS 74939	KF112653	KF112148
<i>Neoboletus obscureumbrinus</i>	Thailand	OR0553	MK372294	MK372282
<i>Neoboletus</i> sp.	Thailand	OR0128	MH614781	MH614734
<i>Neoboletus tomentulosus</i>	China	HKAS 53369	KF112659	KF112154
<i>Octaviania asterosperma</i>	Italy	AQUI3899	–	KC552093
<i>Octaviania cyanescens</i>	USA	PNW FUNGI 5603	–	JN378438
<i>Octaviania decimae</i>	Japan	KPM-NC-0017763	–	JN378409
<i>Octaviania tasmanica</i>	Australia	MEL2128484	–	JN378437
<i>Octaviania zelleri</i>	USA	MES270	–	JN378440
<i>Phylloporopsis boletinoides</i>	Dominican Republic	JBSD127413	–	MH588314
<i>Phylloporopsis boletinoides</i>	Dominican Republic	JBSD127414	–	MH588315
<i>Phylloporopsis boletinoides</i>	Belize	CORT 014483	–	MH588316
<i>Phylloporopsis boletinoides</i>	USA	CORT 010991	–	MH588317
<i>Phylloporus bellus</i>	China	OR0473	MH580818	MH580798
<i>Phylloporus brunneiceps</i>	Thailand	OR0050	KT824001	KT824034
<i>Phylloporus castanopsidis</i>	Thailand	OR0052	KT824002	KT824035
<i>Phylloporus maculatus</i>	China	OR0285	MH580820	MH580800
<i>Phylloporus pachycystidiatus</i>	China	HKAS 53422	KF112777	KF112288
<i>Phylloporus pelletieri</i>	Austria	WU18746	MH580821	MH580801
<i>Phylloporus pusillus</i>	Thailand	OR1158	MH580823	MH580803
<i>Phylloporus rhodoxanthus</i>	Austria	WU17978	MH580824	MH580805
<i>Phylloporus rubeolus</i>	China	OR0251	MH580825	MH580806
<i>Phylloporus rubiginosus</i>	China	OR0169	MH580827	MH580808
<i>Phylloporus rubrosquamosus</i>	China	HKAS 52552	KF112780	KF112289
<i>Phylloporus scabripes</i>	Belize	CFMR BOS 621	MK766359	MK721156
<i>Phylloporus</i> sp.	Thailand	OR0896	MH580829	MH580810
<i>Phylloporus subbacillisporus</i>	China	OR0436	MH580831	MH580812
<i>Phylloporus subrubeolus</i>	Thailand	BC022	MH580832	MH580813
<i>Phylloporus yunnanensis</i>	China	OR0448	MG212640	MG212598
<i>Porphyrellus castaneus</i>	China	OR0241	MG212641	MG212599
<i>Porphyrellus nigropurpureus</i>	Benin	ADK3733	MH614782	MH614735
<i>Porphyrellus nigropurpureus</i>	China	HKAS 74938	KF112763	KF112246
<i>Porphyrellus porphyrosporus</i>	Germany	MB97 23	GU187800	GU187734
<i>Porphyrellus</i> sp.	Burundi	JD659	MH614783	MH614736
<i>Porphyrellus</i> sp.	Thailand	OR0222	MH614784	MH614737
<i>Pseudoboletus parasiticus</i>	Germany	Xpa1	–	KF030443
<i>Pulchroboletus sclerotiorum</i>	USA	FLAS F 60333	MF614169	MF614167
<i>Pulchroboletus sclerotiorum</i>	USA	FLAS F 60334	MF614164	MF614165
<i>Pulveroboletus brunneopunctatus</i>	China	HKAS 55369	KT990455	KT990814
<i>Pulveroboletus fragrans</i>	Thailand	OR0673	KT824010	KT824043
<i>Pulveroboletus ravenelii</i>	Togo	ADK4360	KT823990	KT824023
<i>Pulveroboletus ravenelii</i>	Togo	ADK4650	KT823992	KT824025
<i>Pulveroboletus ravenelii</i>	USA	REH2565	KU665637	KU665636
<i>Retiboletus brunneolus</i>	China	HKAS 52680	KF112690	KF112179
<i>Retiboletus fuscus</i>	China	OR0231	MG212642	MG212600
<i>Retiboletus griseus</i>	USA	MB0379	KT823997	KT824030
<i>Retiboletus kauffmanii</i>	China	OR0278	MG212643	MG212601
<i>Retiboletus nigerrimus</i>	China	HKAS 53418	KT990462	KT990824
<i>Retiboletus nigerrimus</i>	Thailand	OR0049	KT824000	KT824033

Table 1 (continued)

Taxon	Country	Specimen voucher	<i>RPB2</i>	<i>TEFI</i>
<i>Rhodactina himalayensis</i>	Thailand	CMU25117	–	MG212603
<i>Rhodactina himalayensis</i>	Thailand	CMU25117	–	MG212602
<i>Rhodactina rostratispora</i>	Thailand	SV0170	MG212645	MG212605
<i>Rossbeevera cryptocyanea</i>	Japan	KPM NC17843	–	KC552072
<i>Rossbeevera griseovelutina</i>	Japan	TNS F 36989	–	KC552076
<i>Rossbeevera pachydermis</i>	New Zealand	KPM NC23336	–	KP222912
<i>Royoungia rubina</i>	China	HKAS 53379	KF112796	KF112274
<i>Rubinosporus auriporus</i>	Thailand	SV0090	MZ355903	MZ355901
<i>Rubinosporus auriporus</i>	Thailand	SV0101	MZ355904	MZ355902
<i>Rubroboletus legaliae</i>	Belgium	VDKO0936	KT824018	KT824051
<i>Rubroboletus rhodosanguineus</i>	USA	BOTH4263	MG897436	MG897426
<i>Rubroboletus rhodoxanthus</i>	China	HKAS 84879	KT990468	KT990831
<i>Rubroboletus satanas</i>	Belgium	VDKO0968	KT824019	KT824052
<i>Rugiboletus andinus</i>	Costa Rica	REH 7705	MK766316	MK721111
<i>Rugiboletus brunneiporus</i>	China	HKAS 83209	KM605168	KM605144
<i>Rugiboletus extremiorientalis</i>	Thailand	OR0406	MG212647	MG212607
<i>Singerocomus inundabilis</i>	Guyana	TWH9199	LC043089	MH645596
<i>Singerocomus rubriflavus</i>	Guyana	TWH9585	–	MH645597
<i>Soliococcus polychromus</i>	Australia	R.E. Halling 9417	–	JQ287644
<i>spongiforma thailandica</i>	Thailand	DED7873	MG212648	KF030436
<i>Strobilomyces echinocephalus</i>	China	OR0243	MG212649	MG212608
<i>Strobilomyces floccopus</i>	Belgium	RW103	KT824011	KT824044
<i>Strobilomyces mirandus</i>	Thailand	OR0115	KT824005	KT824038
<i>Strobilomyces</i> sp.	China	OR0259	MG212650	MG212609
<i>Strobilomyces</i> sp.	Thailand	OR0319	MH614785	MH614738
<i>Strobilomyces</i> sp.	Thailand	OR0778	MG212651	MG212610
<i>Strobilomyces</i> sp.	Thailand	OR1092	MH614786	MH614739
<i>Strobilomyces verruculosus</i>	China	HKAS 55389	KF112813	KF112259
<i>Suillellus luridus</i>	Belgium	VDKO0241b	KT824014	KT824047
<i>Suillellus queletii</i>	Belgium	VDKO1185	MH645604	MH645598
<i>Suillellus subamygdalinus</i>	China	HKAS 57262	KF112660	KF112174
<i>Sutorius australiensis</i>	Australia	REH9441	MG212652	JQ327032
<i>Sutorius eximius</i>	USA	REH9400	MG212653	JQ327029
<i>Sutorius pachypus</i>	Thailand	OR0411	MN067500	MN067484
<i>Sutorius pseudotylopilus</i>	Thailand	OR0378B	MH614787	MH614740
<i>Sutorius rubinus</i>	Thailand	OR0379	MH614788	MH614741
<i>Sutorius ubonensis</i>	Thailand	SV0032	MN067507	MN067491
<i>Tengioboletus glutinosus</i>	China	HKAS 53425	KF112800	KF112204
<i>Tengioboletus reticulatus</i>	China	HKAS 53426	KF112828	KF112313
<i>Tropicoboletus ruborculus</i>	Dominican Republic	JBSD133074 (ANGE1406)	OQ117431	OQ110624
<i>Tropicoboletus ruborculus</i>	Puerto Rico	MO439745-komille277	OQ117432	OQ110625
<i>Tropicoboletus ruborculus</i>	Mexico	JIF-451-ITCV	OQ117433	–
<i>Turmalinea persicina</i>	Japan	KPM NC18001	–	KC552082
<i>Turmalinea yuwanensis</i>	Japan	KPM NC18011	–	KC552089
<i>Tylopilus balloui</i>	Thailand	OR0039	KT823998	KT824031
<i>Tylopilus felleus</i>	Belgium	VDKO0992	KT824020	KT824053
<i>Tylopilus ferrugineus</i>	USA	BOTH3639	MH614789	MH614742
<i>Tylopilus otsuensis</i>	China	HKAS53401	KF112797	KF112224
<i>Tylopilus</i> sp.	Gabon	JD598	MH614790	MH614743
<i>Tylopilus</i> sp.	China	OR0252	MG212654	MG212611

Table 1 (continued)

Taxon	Country	Specimen voucher	<i>RPB2</i>	<i>TEF1</i>
<i>Tylophilus</i> sp.	Thailand	OR0542	MG212655	MG212612
<i>Tylophilus</i> sp.	Thailand	OR1009	MH614791	–
<i>Tylophilus vinaceipallidus</i>	China	OR0137	MG212656	MG212613
<i>Tylophilus violaceobrunneus</i>	China	HKAS 89443	KT990504	KT990886
<i>Veloporphyrellus conicus</i>	Belize	REH8510	MH614792	MH614745
<i>Veloporphyrellus gracilioides</i>	China	HKAS 53590	KF112734	KF112210
<i>Veloporphyrellus pseudovelatus</i>	China	HKAS 59444	–	JX984553
<i>Veloporphyrellus velatus</i>	China	HKAS 63668	–	JX984554
<i>Xanthoconium affine</i>	USA	NY00815399	KT990486	KT990850
<i>Xanthoconium purpureum</i>	USA	MICH KUO 7061405	MK766372	MK721170
<i>Xanthoconium sinense</i>	China	HKAS 77651	KT990488	KT990853
<i>Xerocomellus chrysensteron</i>	Belgium	VDKO0821	KT824017	KT824050
<i>Xerocomellus cisalpinus</i>	Belgium	ADK4864	KT823993	KT824026
<i>Xerocomellus communis</i>	China	HKAS 50467	KT990494	KT990858
<i>Xerocomellus ripariellus</i>	Belgium	VDKO0404	MH614793	MH614746
<i>Xerocomus coccolobae</i>	Dominican Republic	JBSD133071 (ANGE1405)	OQ117434	OQ110626
<i>Xerocomus coccolobae</i>	Dominican Republic	JBSD133068 (ANGE915)	OQ117435	OQ110627
<i>Xerocomus coccolobae</i>	Dominican Republic	JBSD133069 (ANGE965)	OQ117436	OQ110628
<i>Xerocomus</i> aff. <i>coccolobae</i>	Dominican Republic	JBSD133067 (ANGE446)	OQ117437	–
<i>Xerocomus ferrugineus</i>	USA	CFMR BOS 545	MK766375	MK721173
<i>Xerocomus fulvipes</i>	China	HKAS 76666	KF112789	KF112292
<i>Xerocomus magniporus</i>	China	HKAS 58000	KF112781	KF112293
<i>Xerocomus puniceiporus</i>	China	HKAS 80683	KU974146	KU974138
<i>Xerocomus rugosellus</i>	China	HKAS 58865	KF112784	KF112294
<i>Xerocomus</i> sp.	Thailand	OR0053	MH580834	MH580815
<i>Xerocomus</i> sp.	China	OR0237	MH580835	MH580816
<i>Xerocomus</i> sp.	China	OR0443	MH580836	MH580817
<i>Xerocomus spadiceus</i>	USA	MICH KUO 7080702	MK766378	MK721176
<i>Xerocomus subtomentosus</i>	Belgium	VDKO0987	MG212657	MG212614
<i>Xerocomus tenax</i>	USA	MICH KUO 8241404	MK766379	MK721177
<i>Zangia citrina</i>	China	HKAS 52684	–	HQ326872
<i>Zangia olivaceobrunnea</i>	China	HKAS 52272	–	HQ326876
<i>Zangia roseola</i>	China	HKAS 51137	–	HQ326877

and on *X. coccolobae* and allied species (ITS sequences, TrN + I + G model) (Tables 2 and 3). The fourth dataset focused on *Boletus guadelupae* and allied species in *Singerocomus* based on ITS sequences (Table 4), using TPM3uf + G as the best fit model.

For each molecular marker (LSU, *RPB2*, and *TEF1*), three extra single-locus alignments focused on *Boletaceae* were generated by retrieving all available sequences from GenBank (Suppl. Mat. Figures 2–4). GTR + I + G, TIM1 + I + G and TrN + I + G models were chosen for LSU, *RPB2*, and *TEF1*, respectively. The lack of sequences from different loci for the same vouchers prevented us from generating a multilocus analysis.

Phylogenetic analyses were performed using maximum likelihood (ML) with RAxML-NG v. 1.0.1 (Kozlov et al.

2019) and Bayesian Inference (BI) with MrBayes v. 3.2.7a (Ronquist et al. 2012) in the CIPRES science gateway (Miller et al. 2010). ML analyses were performed with 1000 bootstrap replicates (Felsenstein 1985), under the selected evolutionary models to obtain estimates for maximum likelihood bootstrap values (MLB). BI analyses were performed with one cold and three incrementally heated simultaneous Monte Carlo Markov chains (MCMC) run for 10 M generations, under the selected evolutionary models for each unlinked partition. Two simultaneous runs were performed independently. Trees were sampled every 1000 generations, resulting in sampling of 10,001 trees per single run with the first 2500 trees (25%) discarded as burn-in. For the remaining trees of the two independent runs, a majority rule consensus tree showing all compatible partitions

Table 2 Taxa, locations, vouchers, and accession numbers of the nrLSU sequences used in the *Xerocomus* s. str. phylogenetic analysis. Sequences in bold were generated in this study

Taxon	Country	Specimen voucher	nrLSU
<i>Phylloporus pelletieri</i>	United Kingdom	K-M000128205	JQ967215
<i>Phylloporus rubeolus</i>	China	HKAS 52573 holotype	NG_042667
<i>Xerocomus coccolobae</i>	Dominican Republic	JBSD133068 (ANGE915)	OQ102363
<i>Xerocomus coccolobae</i>	Dominican Republic	JBSD133069 (ANGE965)	OQ102364
<i>Xerocomus coccolobae</i>	Dominican Republic	JBSD133071 (ANGE1405)	OQ102365
<i>Xerocomus aff. coccolobae</i>	Dominican Republic	JBSD133067 (ANGE446)	OQ102366
<i>Xerocomus aff. subtomentosus</i>	China	HKAS 58865	KF112389
<i>Xerocomus cf. ferrugineus</i>	USA	Mushroom Observer 429383	MW989502
<i>Xerocomus cf. spacideus</i>	USA	JLF_X15	KU144813
<i>Xerocomus cf. subtomentosus</i>	USA	JLF2777	KU144807
<i>Xerocomus cf. subtomentosus</i>	USA	JLF2784	KU144809
<i>Xerocomus chrysonemus</i>	Spain	JAM0359	KF040544
<i>Xerocomus ferrugineus</i>	USA	CFMR BOS-545	MK601819
<i>Xerocomus ferrugineus</i>	USA	MICH KUO-08100701	MK601820
<i>Xerocomus fraternus</i>	China	HKAS 55328 holotype	NG_059634
<i>Xerocomus fulvipes</i>	China	HKAS 52556	KT990672
<i>Xerocomus lanatus</i>	Germany	MB 95-074	DQ534633
<i>Xerocomus magniporus</i>	China	HKAS 58000	KF112392
<i>Xerocomus magniporus</i>	China	HKAS 59820	JQ678699
<i>Xerocomus microcarpoides</i>	China	HKAS 54753	KT990680
<i>Xerocomus nigromaculatus</i>	Thailand	CMUB39820	KX575653
<i>Xerocomus nothofagi</i>	New Zealand	PDD93823	JQ924320
<i>Xerocomus olivaceus</i>	Belize	CFMR:BZ-3953 TJB-9943 holotype	NG_078682
<i>Xerocomus perplexus</i>	USA	MB00-005	JQ003702
<i>Xerocomus piceicola</i>	China	HKAS 55452	KT990685
<i>Xerocomus puniceiporus</i>	China	HKAS 80683	KU974141
<i>Xerocomus rugosellus</i>	China	HKAS 68292	KT990686
<i>Xerocomus silwoodensis</i>	Albania	JAM0612	KF030323
<i>Xerocomus</i> sp.	China	HCL2021-8-8	OL336491
<i>Xerocomus spadiceus</i> var. <i>gracilis</i>	USA	MB04-022	JQ003703
<i>Xerocomus</i> sp.	China	HKAS 53387	KF112397
<i>Xerocomus</i> sp.	China	HKAS 57339	KT990674
<i>Xerocomus</i> sp.	China	HKAS 57765	KT990675
<i>Xerocomus</i> sp.	China	HKAS 67749	KT990676
<i>Xerocomus</i> sp.	China	HKAS 74927	KF112395
<i>Xerocomus</i> sp.	China	HKAS 75076	KF112387
<i>Xerocomus</i> sp.	China	HKAS76666	KF112390
<i>Xerocomus</i> sp. MAN2011_a	Costa Rica	MAN063	JQ003708
<i>Xerocomus squamulosus</i>	New Zealand	PDD95329	JQ924326
<i>Xerocomus subparvus</i>	China	HKAS 50295 holotype	NG_059631
<i>Xerocomus subparvus</i>	China	HKAS 82814	KT990678
<i>Xerocomus subtomentosus</i>	United Kingdom	K-M000167686	JQ967238
<i>Xerocomus subtomentosus</i>	Finland	IB19980452	AF514831
<i>Xerocomus subtomentosus</i>	China	JXSB1431	MK765844
<i>Xerocomus tenax</i>	USA	REH6871	KF030320
<i>Xerocomus yunnanensis</i>	China	HKAS 68282	KT990691

Table 3 Taxa, locations, vouchers, and accession numbers of the nrITS sequences used in the *Xerocomus* s. str. phylogenetic analysis. Sequences in bold were generated in this study

Taxon	Country	Specimen voucher	nrITS
<i>Xerocomus chrysonemus</i>	United Kingdom	imp0002	DQ066380
<i>Xerocomus coccolobae</i>	Dominican Republic	JBSD133068 (ANGE915)	OQ108300
<i>Xerocomus coccolobae</i>	Dominican Republic	JBSD133069 (ANGE965)	OQ108301
<i>Xerocomus coccolobae</i>	Dominican Republic	JBSD133071 (ANGE1405)	OQ108302
<i>Xerocomus coccolobae</i>	Martinique	K-M000178954 holotype	OQ108303
<i>Xerocomus ferrugineus</i>	Italy	gs1215	DQ066399
<i>Xerocomus ferrugineus</i> f. <i>aurantiiporus</i>	Austria	WU:39588 holotype	NR_171887
<i>Xerocomus illudens</i>	USA	Mushroom Observer #249274	MH230109
<i>Xerocomus illudens</i>	USA	207	OM972478
<i>Xerocomus illudens</i>	USA	MES-3718	ON383381
<i>Xerocomus olivaceus</i>	Belize	CFMR:BZ-3953 TJB-9943 holotype	NR_175148
<i>Xerocomus olivaceus</i>	USA	iNAT:86045660	OM021888
<i>Xerocomus silwoodensis</i>	Italy	MCVE:28973	MH102397
<i>Xerocomus silwoodensis</i>	United Kingdom	K(M):167360	MZ159415
<i>Xerocomus</i> sp.	USA	MUOB:370618	ON180513
<i>Xerocomus spadiceus</i>	USA	JLF3963	KX534077
<i>Xerocomus spadiceus</i>	USA	JLF4012	KX534078
<i>Xerocomus spadiceus</i>	USA	JLF4060	KX534079
<i>Xerocomus subparvus</i>	China	HKAS 105284	MT520093
<i>Xerocomus subparvus</i>	Vietnam	LE315595	MT893600
<i>Xerocomus subtomentosus</i>	USA	Both3312	DQ066413
<i>Xerocomus subtomentosus</i>	Canada	1549a-Q-6103	KM248935

was computed to obtain estimates for Bayesian posterior probabilities (BPP). Significance threshold was set ≥ 0.70 for MLB and ≥ 0.90 for BPP. For all phylogenetic trees, outgroup taxa are indicated in the legend. Pairwise percent identity values (P%I) of the ITS sequences were calculated using Geneious. Alignments are available as Suppl. Mat. Align. 1–4.

Results

Molecular analysis

A total of 33 sequences (12 ITS, 9 LSU, 7 *RPB2*, and 5 *TEF1*) from 12 specimens were newly generated during this study.

We obtained complete ITS sequences from three collections of *Boletus guadelupae*, K-M000193866, K-M000193867, and J.P. Fiard 563A/563B (F, holotype/paratype), the holotype of *Boletus ruborculus* NY 577594 (8253 T.J. Baroni) and an ITS1 sequence from the holotype of *Xerocomus coccolobae* K-M000178954. The holotypes of *Xerocomus cuneipes* K-M000178953 and *X. caeruleonigrescens* K-M000178955 did not yield any amplification.

Both Bayesian and ML analyses produced the same topologies. Therefore, only the ML trees with both MLB

and BPP values are shown (Figs. 1, 2, 3, and 4). The combined *RPB2/TEF1* *Boletaceae*-wide data matrix comprises 285 sequences and is 2067 bp long (Fig. 1, Suppl. Mat. Figure 1 and Table 1). The LSU data matrix of the genus *Xerocomus* comprises a total of 48 sequences and 865 characters (Fig. 2 and Table 2). The ITS data matrix of *X. coccolobae* and allied species comprises 22 sequences and 833 characters (Fig. 3 and Table 3). The ITS data matrix of *B. guadelupae* and allied species (*Singerocomus*) comprises 29 sequences and 870 characters (Fig. 4 and Table 4).

In the combined *RPB2/TEF1* *Boletaceae*-wide analysis (Fig. 1, Suppl. Mat. Figure 1), the subfamilies recognized in recent studies (e.g., Wu et al. 2014; Gelardi et al. 2015; Henkel et al. 2016; Vadthananarat et al. 2019, 2022; Badou et al. 2022) were also recovered. *Xerocomus coccolobae* and *X. aff. coccolobae* are nested in the genus *Xerocomus* s. str. (typified with *X. subtomentosus*). Sequences of *X. olivaceus* from Belize and USA (Florida) (including the holotype NR_175148) cluster with *X. coccolobae* in the same terminal clade (Figs. 2 and 3). The ITS P%I value of the “coccolobae clade” is = 99.7. Collections of *B. ruborculus* from Puerto Rico, the Dominican Republic and Mexico form a strongly supported clade which is sister to subfamily *Xerocomoideae* in the combined *RPB2/TEF1* *Boletaceae*-wide analysis (with only MLB support) and in the single-locus *TEF1* *Boletaceae*-wide analysis

Table 4 Taxa, locations, vouchers, and accession numbers of the nrITS sequences used in the *Singerocomus* (*Pulveroboletus* group) phylogenetic analysis. Sequences in bold were generated in this study

Taxon	Country	Specimen voucher	nrITS
<i>Bothia castanella</i>	USA	MB03-067	DQ867114
<i>Butyriboletus fechtneri</i>	Sweden	AT2003097	KC584784
<i>Butyriboletus regius</i>	Italy	MG408a	KC584789
<i>Butyriboletus yicibus</i>	China	Arora9727	KC184474
<i>Rubroboletus latisporus</i>	China	HKAS 80358 holotype	KJ951990
<i>Rubroboletus sinicus</i>	China	HKAS 68620	KJ951991
<i>Singerocomus atlanticus</i>	Brazil	ACM 527 holotype	KY907177
<i>Singerocomus atlanticus</i>	Brazil	ACM 1275	KY907178
<i>Singerocomus atlanticus</i>	Brazil	BZL 69	KY907181
<i>Singerocomus atlanticus</i>	Brazil	CATO 106	KY907179
<i>Singerocomus atlanticus</i>	Brazil	MJ 105	KY907180
<i>Singerocomus guadelupae</i>	Guadeloupe	(F) J.P. Fiard 563A/B, holotype/paratype	OQ108304
<i>Singerocomus guadelupae</i>	Guadeloupe	K-M000193866	OQ108305
<i>Singerocomus guadelupae</i>	Guadeloupe	K-M000193867	OQ108306
<i>Singerocomus inundabilis</i>	Guyana	Aime 4004	LC043090
<i>Singerocomus inundabilis</i>	Guyana	Henkel 9199	LC043087
<i>Singerocomus inundabilis</i>	Guyana	TH8408	JN021114
<i>Singerocomus inundabilis</i>	Guyana	TH10087	KT380014
<i>Singerocomus inundabilis</i>	Guyana	TH10109	KT380013
<i>Singerocomus rubriflavus</i>	Guyana	BRG 41208 (Henkel 9585) holotype	NR_164253
<i>Singerocomus rubriflavus</i>	Brazil	GAS 900	KY907182
<i>Xerocomus</i> sp.	Colombia	AMV1843	KT354677
<i>Xerocomus</i> sp.	Colombia	AMV1961a	KT354678
<i>Xerocomus</i> sp.	Colombia	AMV1993	KT354679
<i>Xerocomus</i> sp.	Guyana	G1041	KJ786662
<i>Xerocomus</i> sp.	Guyana	G3226	KJ786703
<i>Xerocomus</i> sp.	Guyana	G3268	KJ786708
<i>Xerocomus</i> sp.	Guyana	G3298	KJ786710
<i>Xerocomus</i> sp.	Guyana	G3326	KJ786713

(MLB = 0.77) (Suppl. Mat. Figure 4), whereas the clade occupies an unresolved, uncertain position both in the single LSU and *RPB2* loci of the *Boletaceae*-wide analyses (Suppl. Mat. Figures 2 and 3). The ITS P%I value of the *B. rubrorculus* sequences (JBSD133072-ANGE208 GB acc. n. OQ108295, JBSD133073-ANGE209 GB acc. n. OQ108296, JBSD133074-ANGE1406 GB acc. n. OQ108297, MO439745-komille277 GB acc. n. OQ108298, and NY 577594-TJB 8253 GB acc. n. OQ108299 holotype) is = 99.9.

The ITS sequences of three *B. guadelupae* collections (K-M000193866, K-M000193867, and J.P. Fiard 563A/B, holotype/paratype) cluster together with two *Xerocomus* sp. from Guyana and four *Singerocomus atlanticus* from Brazil (including the holotype KY907177) forming the “guadelupae clade” (Fig. 4). Sequences in this clade share a P%I value of 99.4.

Taxonomy

Xerocomus coccolobae Pegler, Kew Bulletin Additional Series 9: 576. 1983. Figures 5a–d, 6, and 10a, b.

MycoBank MB 109285

= *Xerocomus olivaceus* B. Ortiz & T.J. Baroni, Fungal Diversity 27(2): 382. 2007.

Holotype: Lesser Antilles, Martinique, Morne Aca, on forest floor under *Coccoloba* sp., 26 Aug 1977, leg. J.P. Fiard, K-M000178954 (J.P. Fiard 902A).

Basidiomes small to medium-small. *Pileus* (1.5–) 1.9–7.0 (–8.2) cm broad, at first hemispherical then persistently convex and finally broadly pulvinate-flattened, sometimes slightly depressed at center, 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-lobed, initially slightly involute

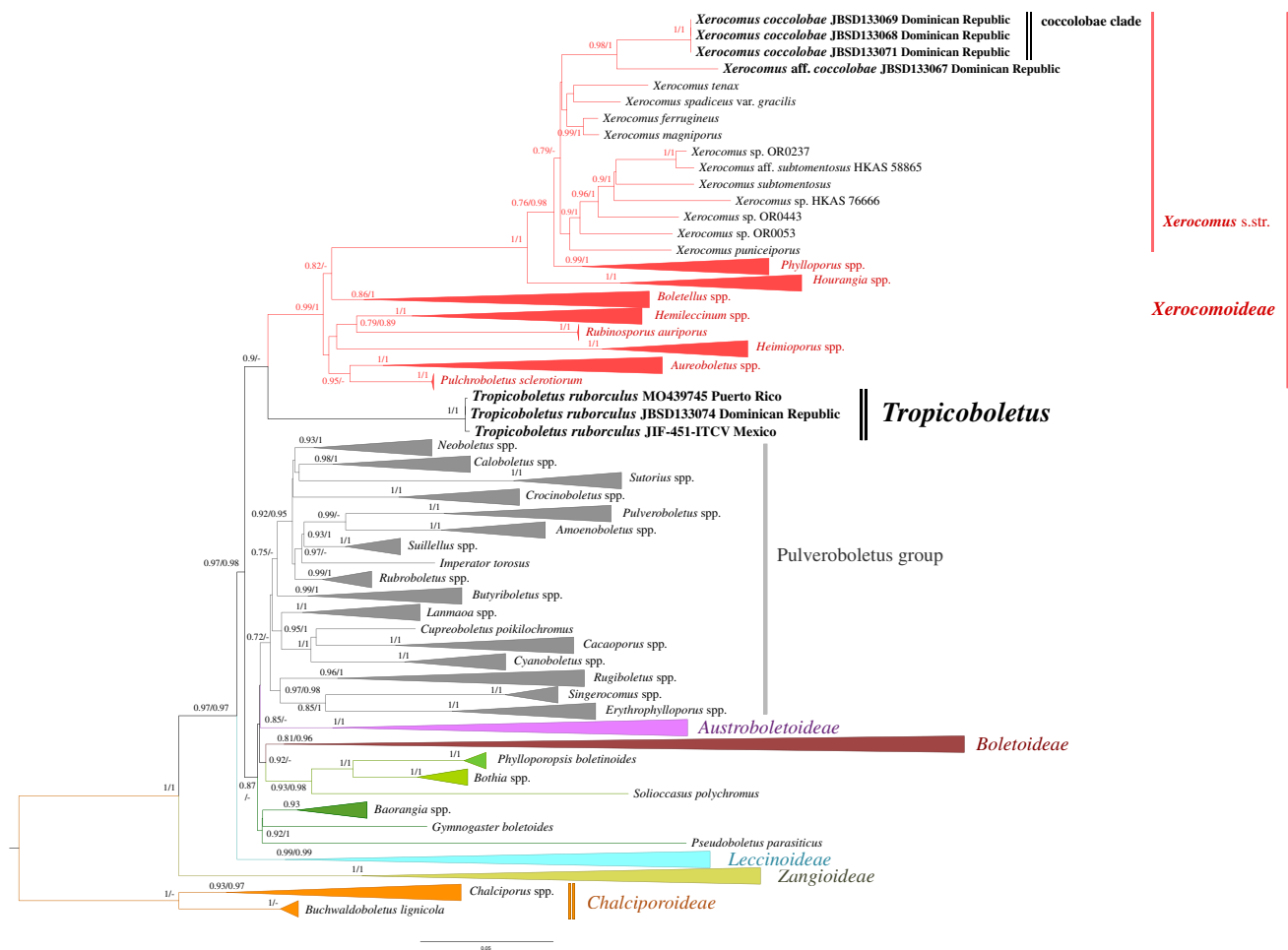


Fig. 1 *Boletaceae*-wide Maximum Likelihood phylogenetic tree inferred from a two-gene dataset (*RPB2* and *TEF1*), showing placement of the new genus *Tropicoboletus*. Maximum likelihood bootstrap support values (MLB ≥ 0.70) and the corresponding Bayesian posterior probabilities (BPP ≥ 0.90) are shown above the supported branches. *Buchwaldoboletus lignicola* and seven *Chalciporus* species (subfamily *Chalciporoideae*) were used as the outgroup taxa. All

taxa belonging to subfamilies *Austroboletoidae*, *Boletoidae*, *Chalciporoideae*, *Leccinoideae*, and *Zangioideae* were collapsed into subfamily clades. All generic clades in the “*Pulveroboletus* group” that were highly supported were also collapsed. In the subfamily *Xerocomoideae* clade, *Xerocomus* s. str. was not collapsed to highlight the position of *X. coccolobae* and *X. aff. coccolobae*. Newly generated sequences are indicated in bold

then curved downwards and finally completely plane or even uplifted, shortly appendiculate and extending beyond the tubes up to 1 mm; surface matt, dry, finely velvety or granulate to coarsely and densely granulate in all developmental stages, usually not cracked but sometimes areolate at maturity and especially in dry weather conditions and then showing a cream color in the cracks (Light Green-Yellow, Green-Yellow, Greenish Yellow, Pl. V); evenly dark brown, bay brown, chestnut brown or purplish brown to less frequently brownish olive to pale brown (Vinaceous-Rufous, Hay’s Russett, Kaiser Brown, Hazel, Liver Brown, Pl. XIV; Pansy Purple, Pl. XII; Dresden Brown, Mars Brown, Pl. XV; Dark Mineral Red, Pl. XXVII; Cacao Brown, Pl. XXVIII; Buffy Olive, Pl. XXX; Fawn Color, Wood Brown, Pl. XL; Light Cinnamon-Drab, Cinnamon-Drab, Pl. XLVI); unchangeable on handling or touching or when injured; subpellis

layer cream yellowish (Light Green-Yellow, Green-Yellow, Greenish Yellow, Pl. V). *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 1.4 cm long), adnate but soon depressed around the stipe apex and decurrent with a tooth, very bright yellow then olive yellow to ochraceous yellow (Lemon Chrome, Light Cadmium, Pl. IV; Wax Yellow, Primuline Yellow, Pl. XVI; Light Viridine Yellow, Greenish Yellow, Green-Yellow, Bright Green Yellow, Viridine Yellow, Oil Yellow, Pl. V; Mustard Yellow, Primuline Yellow, Pl. XVI) at maturity, unchangeable to erratically but moderately to strongly bluing (Paris Blue, Patent Blue, Pl. VIII) when cut, particularly in aged specimens. *Pores* initially forming a flat or concave surface, later irregularly shaped to slightly convex, broad at first then gradually wider with age (up to 2 mm

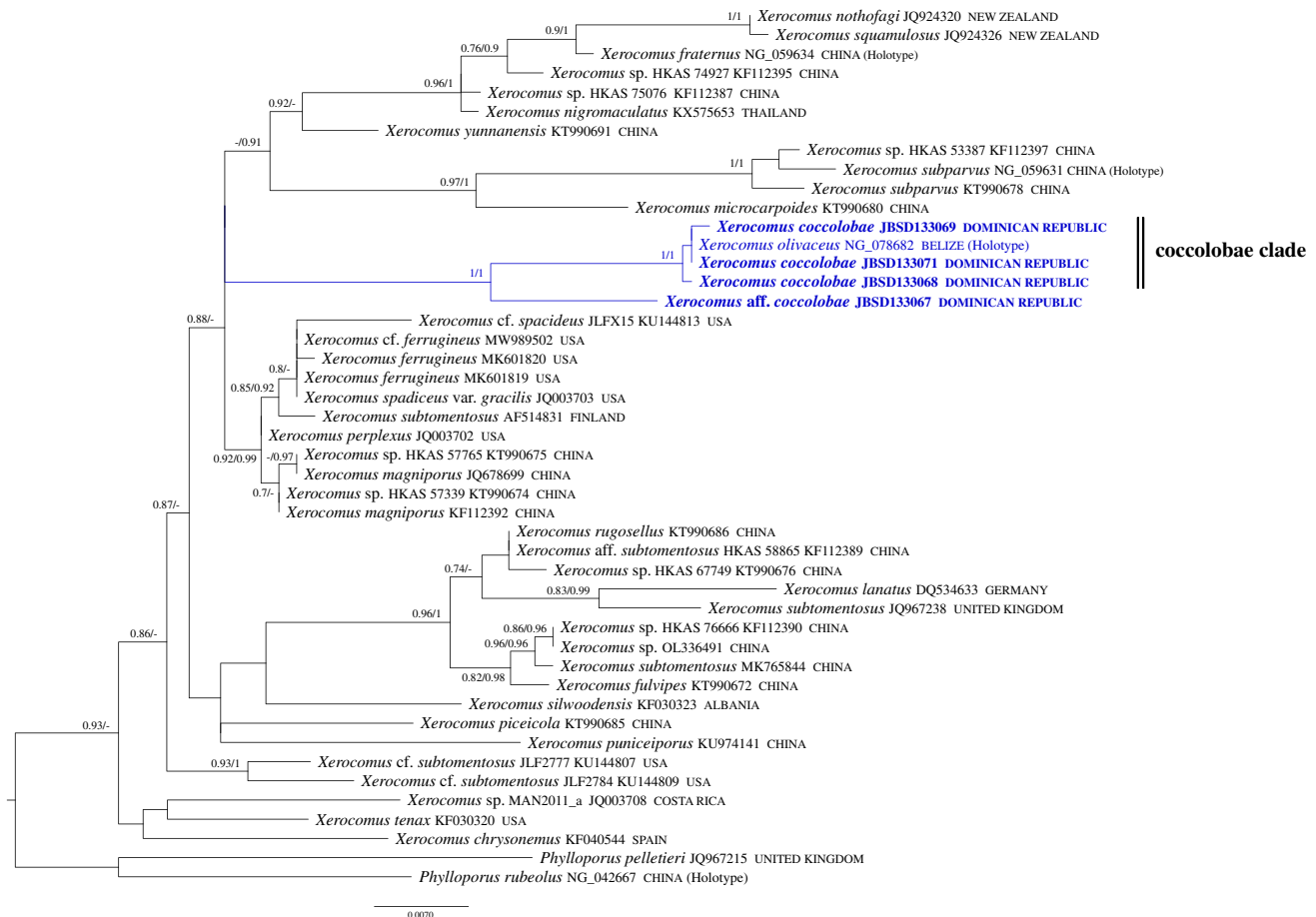


Fig. 2 *Xerocomus* s. str. Maximum Likelihood phylogenetic tree inferred from the LSU dataset, showing the clade of *X. coccolobae* and the undescribed species *X. aff. coccolobae* (JBSD133067). Maximum likelihood bootstrap support values (MLB ≥ 0.70) and the cor-

responding Bayesian posterior probabilities (BPP ≥ 0.90) are shown above the supported branches. *Phylloporus pelletieri* (JQ967215) and *P. rubeolus* (NG_042667) were used as the outgroup taxa. Newly generated sequences are indicated in bold

in diam.), simple, firstly labyrinthine to roundish becoming prominently angular at maturity, stretched and radially arranged towards the stipe, concolorous with the tubes and unchangeable or irregularly bluing (Paris 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* (3.0–) 3.5–5.5 (–7.8) \times 0.4–1.6 (–2.0) cm, as long as or slightly longer or shorter 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 or attenuated from apex down to the base, usually ending with a short taproot at the very base; surface finely to coarsely granulose throughout, with granules more densely arranged in the upper half, devoid of reticulum or ribs, evelate; entirely ornamented by orange-brown, pale brown, brownish olive to chestnut brown granules (Carnelian Red, Vinaceous-Rufous, Cinnamon-Rufous, Hazel, Pl. XIV; Cacao Brown, Pl. XXVIII; Buffy Olive, Pl. XXX;

Fawn Color, Wood Brown, Pl. XL; Light Cinnamon-Drab, Cinnamon-Drab, Pl. XLVI) on a whitish background (White, Pl. LIII) and unfrequently with a narrow purplish brown band (Pansy Purple, Pl. XII) in the upper fourth, unchangeable when pressed; basal mycelium whitish (White, Pl. LIII). *Context* firm and tough when young, later soft textured and eventually flabby in the pileus (up to 2.2 cm thick in the central zone, up to 1.4 cm thick halfway to margin and gradually becoming thinner towards the edge), a little more fibrous in the stipe, at first cream yellowish throughout (Baryta Yellow, Martius Yellow, Picric Yellow, Pl. IV), later very pale yellowish to whitish (Pale Viridine Yellow, Light Green-Yellow, Green-Yellow, Greenish Yellow, Pl. V; White, Pl. LIII) in the pileus and in the connection zone with the stipe, whitish in the stipe (White, Pl. LIII), rarely with scattered pinkish, purplish pink, or pinkish vinaceous spots (Amaranth Purple, Aster Purple, Pansy Purple, Pl. XII), often pale brownish to dirty brown (Citrine, Dark Citrine, Pl. IV; Isabella Color, Light Brownish Olive, Pl. XXX) at the very

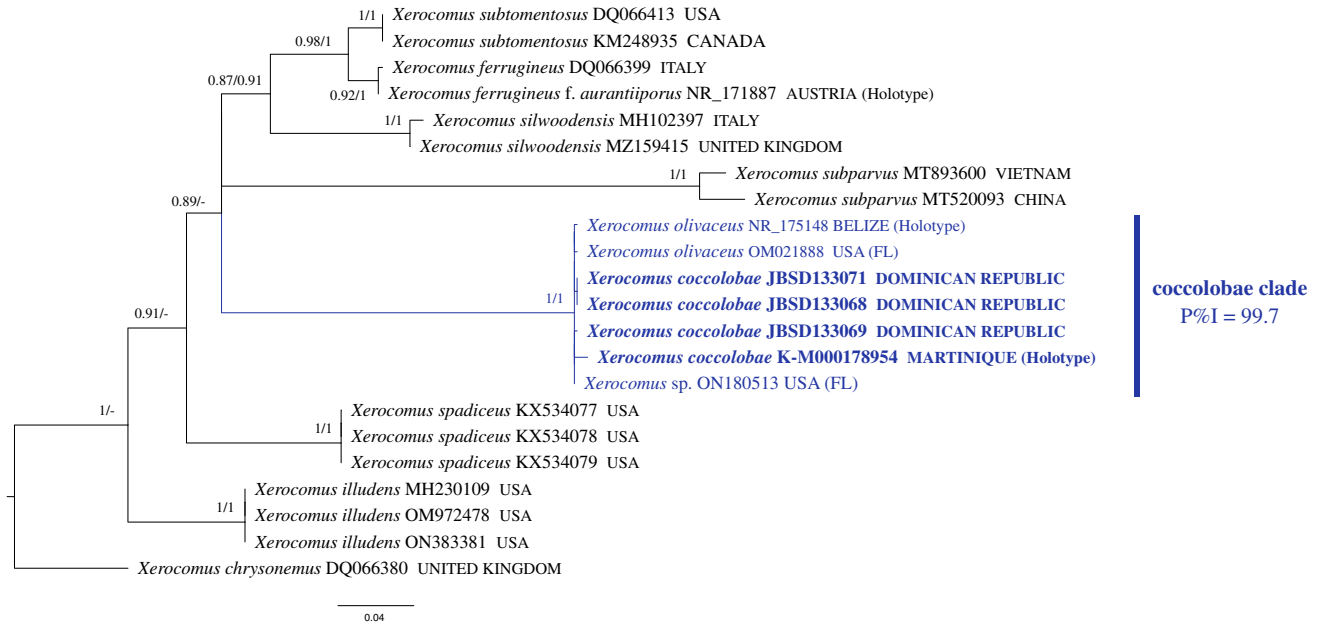


Fig. 3 Selected *Xerocomus* s. str. species Maximum Likelihood phylogenetic tree inferred from the ITS dataset, showing the position of *X. coccolobae* in the genus. Maximum likelihood bootstrap support values (MLB ≥ 0.70) and the corresponding Bayesian posterior prob-

abilities (BPP ≥ 0.90) are shown above the supported branches. *Xerocomus chrysonemus* (DQ066380) was used as the outgroup taxon. Newly generated sequences are indicated in bold

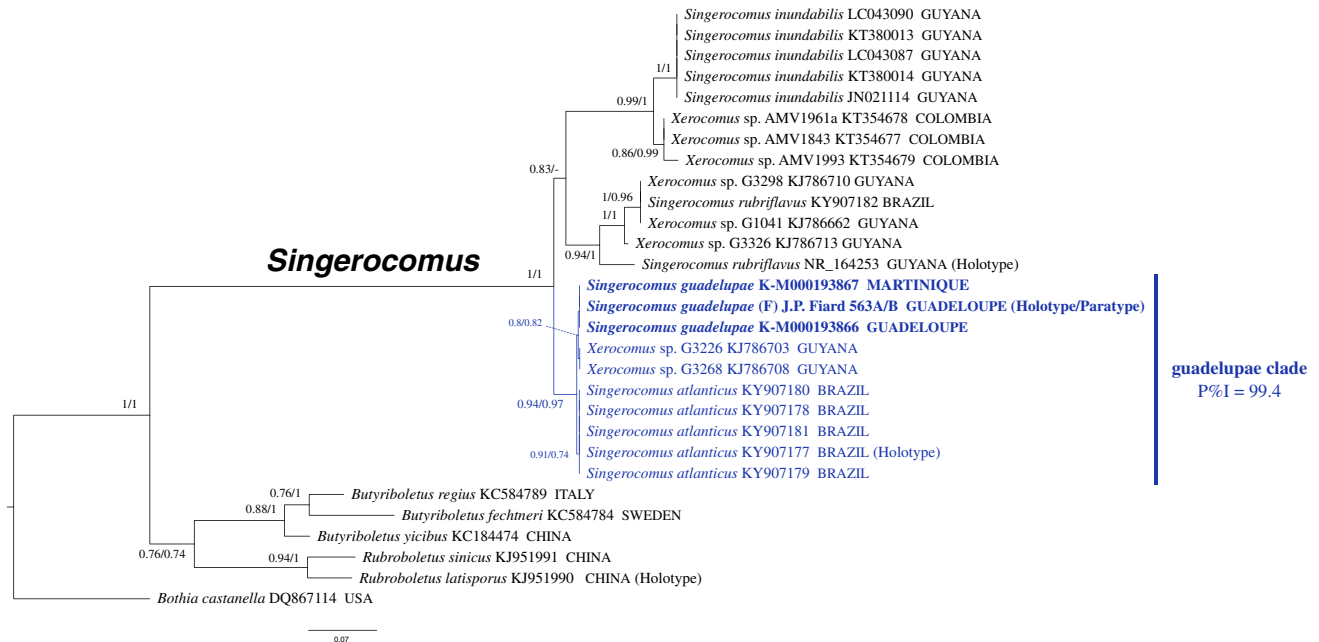


Fig. 4 *Singerocomus* (*Pulveroboletus* group) Maximum Likelihood phylogenetic tree inferred from the ITS dataset, showing the phylogenetic conspecificity of the taxa *Boletus guadelupae* and *Singerocomus atlanticus*. Maximum Likelihood Bootstrap support values (MLB ≥ 0.70) and the corresponding Bayesian posterior probabilities

(BPP ≥ 0.90) are shown above the supported branches. *Butyriboletus* species, *Rubroboletus* species, and *Bothia castanella* (DQ867114) were used as the outgroup taxa. Newly generated sequences are indicated in bold

base; unchangeable to slowly and faintly turning pale blue (Beryl Blue, Pallid Methyl Blue, Pale Methyl Blue, Light Methyl Blue, Pl. VIII) in the pileus context and in the connection zone with the stipe when exposed to air, unchangeable elsewhere; brownish (Auburn, Pl. II; Umber Brown, Pl. III) where eroded by maggots, cream yellowish where eaten by slugs (Light Green-Yellow, Green-Yellow, Greenish Yellow, Pl. V); subhymenophoral layer cream yellowish to pale yellowish (Baryta Yellow, Martius Yellow, Picric Yellow, Pl. IV; Light Green-Yellow, Green-Yellow, Greenish Yellow, Pl. V); exsiccate pale ochraceous on the context, brownish elsewhere (Clay Color, Tawny-Olive, Saccardo's Umber, Pl. XXIX). *Odor* indistinct. *Taste* mild. *Spore print* not obtained. *Macrochemical spot-test reactions*: 30% KOH: bright orange to vinaceous red on pileus surface, pale orange to reddish orange on context and hymenophore; 30% NH₄OH: vinaceous red on pileus surface, none elsewhere.

Basidiospores [171/9/4] (8.3–) 10.7 ± 0.9 (–14.5) × (4.1–) 4.9 ± 0.2 (–5.8) μm, Q = (1.84–) 1.86–2.55 (–2.78), Qm = 2.19 ± 0.16, V = 136 ± 22 μm³, fairly variable in dimension and shape, inequilateral, cylindrical to ellipsoid or broadly ellipsoid, exceptionally nearly ovoid to allantoid in side view, ellipsoid to broadly ellipsoid in face view, smooth under light microscope and SEM, apex rounded, with a short apiculus, usually with a shallow suprahilar depression and with a slightly pronounced adaxial swelling, moderately thick-walled (0.3–0.5 μm), bright yellow colored in water and honey yellow in 5% KOH, having one or less frequently two or three large oil droplets when mature, rarely pluri-guttulate, inamyloid, acyanophilic and staining blue (orthochromatic reaction) in Cresyl blue. *Basidia* (25–) 28–49 (–57) × 10–14 μm (n = 34), cylindrical-clavate to clavate, moderately thick-walled (0.5–0.8 μm), predominantly 4-spored but rarely also 2-spored, usually bearing relatively short sterigmata (2–5 μm), hyaline to pale yellowish and sometimes 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* (40–) 42–68 (–70) × 6–11 (–13) μm (n = 34), very common, decidedly slender, projecting straight to sometimes flexuous, mostly fusiform but also irregularly cylindrical or subcylindrical to sublageniform, rarely showing a narrow and long neck, sometimes multiseptate, 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* (33–) 42–96 (–106) × (5–) 7–14 μm (n = 28), frequent, cylindrical, or subcylindrical to more frequently elongate fusiform or lageniform, rarely showing a narrow and long neck, sometimes multiseptate, longer and slightly broader than but similar in color and chemical reactions

to cheilocystidia. *Pseudocystidia* not observed. *Pileipellis* a trichoderm consisting of moderately to strongly interwoven, frequently branched hyphae which become in the outermost layer a palisadoderm or physalo-palisadoderm of erect subparallel chains of short to moderately slender and restricted at septa, cylindrical hyphae (cylindrocetes), tending to be repent with age and thus turning into a cutis not embedded in gelatinous matter; terminal elements (13–) 15–64 (–82) × 5–24 μm, short cylindrical or irregularly subcylindrical, peanut-shaped, acorn-shaped or bullet-shaped to more frequently cystidioid or elongated lanceolate and then progressively tapering toward the tip, apex rounded-obtuse to pointed, moderately thick-walled (up to 1 μm), hyaline to pale yellowish in water and 5% KOH, mostly smooth but some cells with a scattered but pronounced zebra-like epiparietal brownish pigment in water which tends to be solved in KOH, inamyloid in Melzer's; subterminal elements mostly short cylindrical, size and color similar to terminal elements. *Stipitipellis* a layer of slender, parallel to loosely intermingled and longitudinally running, smooth walled, adpressed hyphae, 3–12 μm wide, hyaline to very pale yellowish in water and 5% KOH; the stipe apex beset by interspersed tufts caulohymenial elements consisting of sterile caulobasidioles, sparse, predominantly 4- and 2-spored, fertile caulobasidia, (28–) 32–35 (–45) × 10–12 μm, sterigmata 2–4 μm long (n = 6) and abundant projecting mostly fusiform to sublageniform but also subcylindrical to mucronate *caulocystidia* similar in color to hymenial cystidia but distinctly shorter, (27–) 32–40 (–45) × 6–10 μm (n = 10), having a wall up to 0.5 μm thick. *Lateral stipe stratum* under the caulohymenium absent. *Stipe trama* composed of confusedly and densely arranged, subparallel to moderately interwoven, filamentous, smooth, inamyloid hyphae, 3–22 μm broad. *Hymenophoral trama* bilaterally divergent of the "Phylloporus-type," with very slightly divergent to nearly parallel and tightly arranged, non-gelatinous hyphae (lateral strata hyphae in transversal section touching or almost touching each other, 0–5 μm apart, 3–16 μm broad), hyaline to very pale yellowish in water and 5% KOH, inamyloid in Melzer's; lateral strata (20–) 25–40 (–50) μm thick, mediostratum (10–) 15–30 (–40) μm thick, axially arranged, consisting of a tightly adpressed, non-gelatinous bundle of hyphae, 3–10 μm broad; in Congo Red the mediostratum is concolorous with the lateral strata. *Thromboplerous hyphae* relatively frequent, thick-walled, rarely septate, melanized, with a golden yellow to brownish homogeneous content in 5% KOH. *Clamp connections* absent in all tissues. *Ontogenetic development* gymnocarpic.

Edibility unknown.

Ecology and phenology: solitary to gregarious, growing on limestone among litter in a seasonally dry and moist



Fig. 5 Basidiomes in habitat. **a–d** *Xerocomus coccolobae*; **a**, **c** JBSD133071 (ANGE1405); **b** JBSD133069 (ANGE965); **d** JBSD133068 (ANGE915). **e–h** *Tropicoboletus ruborculus*; **e**, **g** JBSD133074 (ANGE1406); **f** MO439745 (komille277); **h** JBSD133073 (ANGE209). Photos **a–e**, **g**, **h** by C. Angelini; **f** by K.O. Miller

anthropogenic lowland mixed stand under a large array of neotropical broadleaved trees including *Coccoloba diversifolia* (*Polygonaceae*), which represent its potential ECM host plant. See Parra et al. (2018) for further details on lowland vegetation in the Dominican Republic. Apparently localized in the Dominican Republic. November to December.

Known distribution: Reported to date from both the Lesser and Greater Antilles of the Caribbean (Cuba, Dominican Republic, British Virgin Islands, Martinique),

south-eastern USA (Florida), and Mexico but likely widespread in Mesoamerica. Its occurrence in Brazil appears to be unlikely (see discussion below).

Examined material: DOMINICAN REPUBLIC, Municipality of Sosúa, Puerto Plata Province, loc. cemetery, three km away from the seaside, 19°44'40"N 70°32'21"W, 100 m, 12 Dec 2017, a single aged specimen, C. Angelini, JBSD133068 (ANGE915, MG811); same loc. 01 Dec 2017, four young to mature specimens, C. Angelini, JBSD133069 (ANGE965, MG812); same loc., 16 Dec 2019, a single mature specimen, C. Angelini, JBSD133070 (ANGE1392, MG813); same loc., 14 Dec 2019, three mature specimens, C. Angelini (collection lost); same loc., 16 Dec 2019, five young to mature specimens, one of which growing on an abandoned termites nest, C. Angelini (collection lost); same loc., 23 Nov 2020, several mature specimens, C. Angelini,

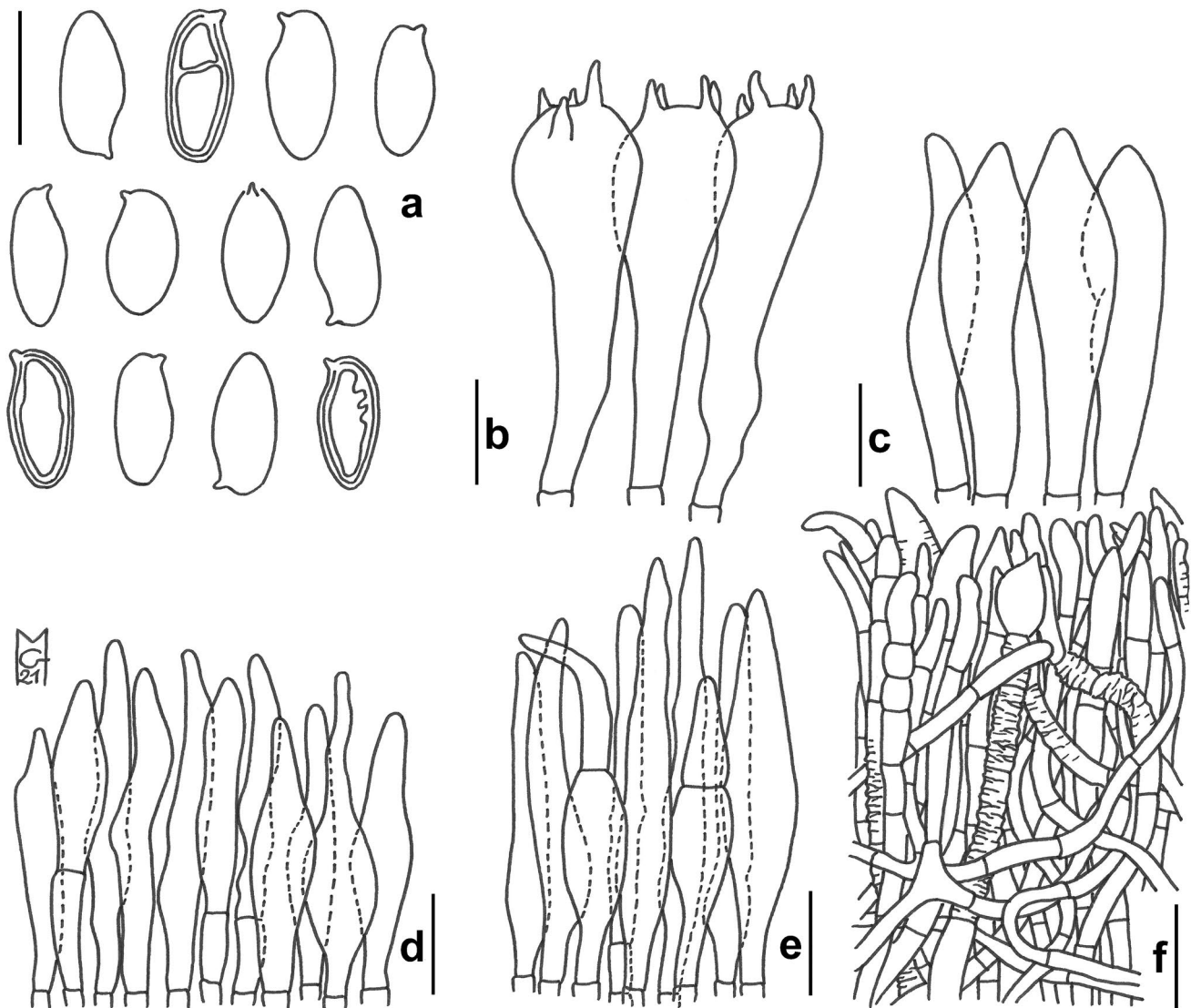


Fig. 6 Microscopic features of *Xerocomus coccolobae*. **a** Basidiospores; **b** basidia; **c** caulocystidia; **d** cheilocystidia; **e** pleurocystidia; **f** pileipellis. Scale bars: 10 µm (**a–c**); 20 µm (**d**, **e**); 40 µm (**f**). Drawings by M. Gelardi

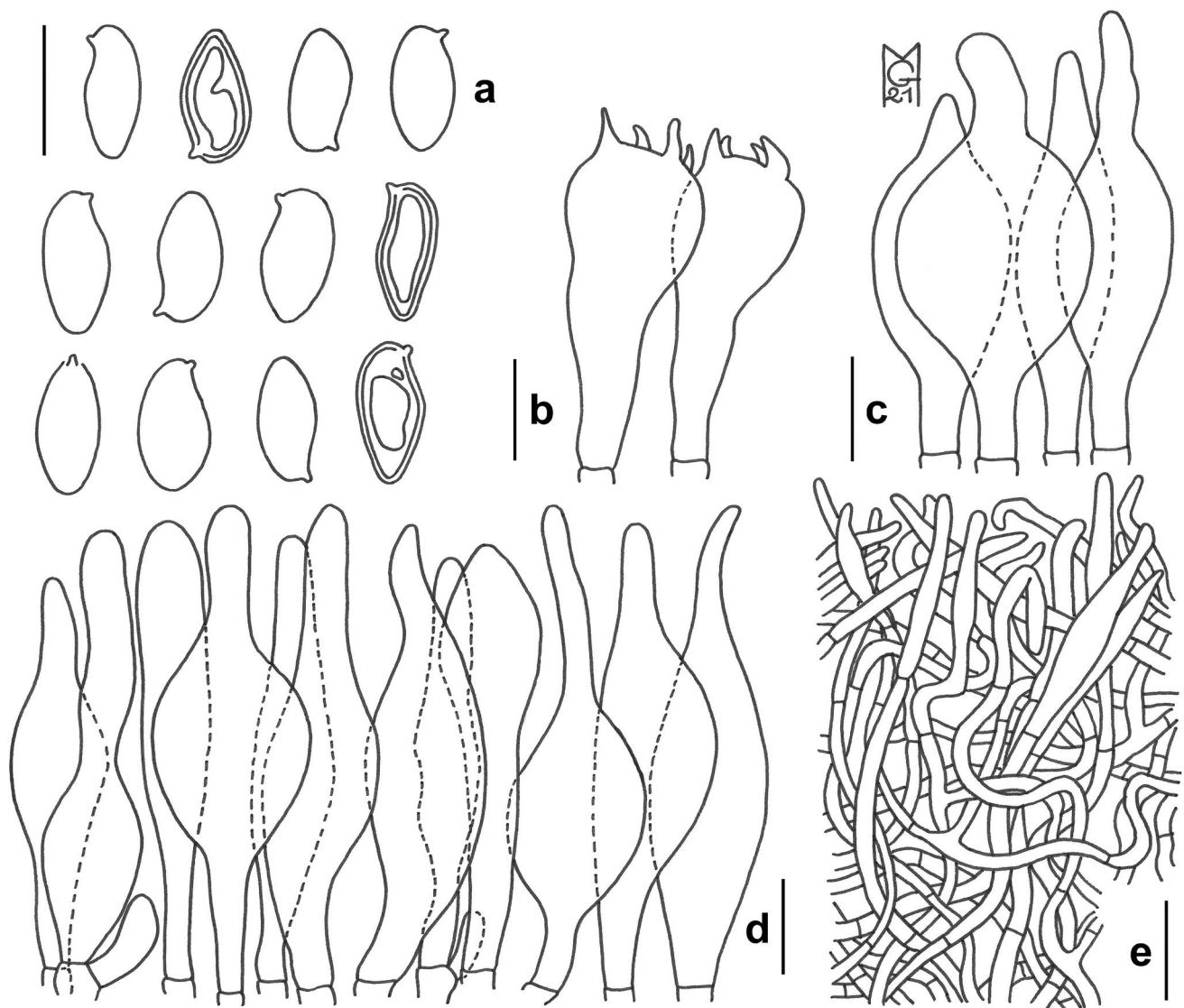


Fig. 7 Microscopic features of *Tropicoboletus rubrorculus*. **a** Basidiospores; **b** basidia; **c** caulocystidia; **d** cheilocystidia and pleurocystidia; **e** pileipellis. Scale bars: 10 μm (**a–d**); 40 μm (**e**). Drawings by M. Gelardi

JBSD133071 (ANGE1405, MG849); MARTINIQUE, Morne Aca, on forest floor under *Coccoloba* sp., 26 Aug 1977, J.P. Fiard, K-M000178954 (J.P. Fiard 902A, holotype).

Additional examined material: Xerocomus aff. *coccolobae*: Dominican Republic, Municipality of Sosúa, Puerto Plata Province, loc. cemetery, three km away from the seaside, 19°44'40"N 70°32'21"W, 100 m, 26 Dec 2014, a single tiny young specimen, C. Angelini, JBSD133067 (ANGE446, MG810). *Xerocomus pseudoboletinus* var. *pini-caribaeae*: BELIZE, Augustine Forest Station, 500 m, under *Pinus caribaea*, 15 Jun 1976, T.H. Ivory, F0002163C (Ivory S-101, holotype). *Xerocomus cuneipes*: MARTINIQUE, Basse Pointe, 50 m, under *Coccoloba uvifera*, 17 Aug 1976, J.P. Fiard, K-M000178953 (J.P. Fiard 710B, holotype).

Notes: We have successfully obtained DNA sequences from the holotype material of *X. coccolobae* (three dried mature specimens), originally found by J.P. Fiard in Martinique and currently preserved at the Royal Botanical Gardens Kew, K-M000178954 (J.P. Fiard 902A) (Fig. 8a) and the anatomical revision of the original specimen produced the following results: basidiospores ellipsoid in side view, smooth under light microscope and SEM (Fig. 10a, b), with a suprahilum depression, apex rounded, golden-yellow, $(8.3\text{--}10.1 \pm 0.9 \text{ (–11.4)} \times (4.3\text{--}4.7 \pm 0.2 \text{ (–5.2)} \mu\text{m}$, $Q = (1.77\text{--}1.99\text{--}2.31 \text{ (2.56)}$, $Q_m = 2.15 \pm 0.16$, $V_m = 119 \pm 16 \mu\text{m}^3$ [32/3/1]; basidia cylindrical-clavate to clavate, $(19\text{--}22\text{--}32 \text{ (–35)} \times 8\text{--}13 \mu\text{m}$ ($n = 10$), sterigmata 2–3 μm long; cheilocystidia fusiform to lageniform, $(24\text{--}29\text{--}49 \text{ (–55)} \times 6\text{--}12 \mu\text{m}$ ($n = 9$); pleurocystidia fusiform, $(30\text{--}$

38–52 (–57) × 7–11 μm ($n = 10$); trichodermal pileipellis of interwoven cylindrical to broadly cylindrical, ocher-yellow to ocher-brown in mass, mainly encrusted hyphae, terminal elements cylindrical but tapering at apex or lageniform, (15–) 21–41 (–50) × (4–) 6–11 (–13) μm ($n = 34$).

With the only exception of the length of hymenial cystidia which appear to be decidedly longer in the Dominican material of *X. coccolobae* when compared with either the protologue or the type revision, the entire overlapping of the remnant morphological, ecological and biogeographic traits of the Dominican Republic collections with the original material described from Martinique by J.P. Fiard (Pegler 1983) coupled with the phylogenetic outcomes allow us to undoubtedly attribute them to the same species. Moreover, the ITS sequence generated from the type material of *X. coccolobae* perfectly match those obtained from the Dominican material, thus confirming their conspecificity. Apart from a nil macrochemical reaction on external surfaces with NH₄OH, there is no other sound morphological or ecological difference, nor molecular evidence for considering *Xerocomus olivaceus* B. Ortiz & T.J. Baroni (Ortiz-Santana et al. 2007) a different species with respect to *X. coccolobae*. The ITS sequence of the holotype material of *X. olivaceus* clearly nested within the terminal clade of *X. coccolobae* and therefore we merge the Belizean bolete into *X. coccolobae* as a later heterotypic synonym.

Key determining features of *X. coccolobae* include small to medium-small sized basidiomes, finely to coarsely granulose, brownish to dark brown or less frequently chestnut brown to purplish brown pileus and stipe surfaces, bright yellow olive tubular hymenophore, whitish basal mycelium, pale yellowish to whitish context usually unchanging to irregularly staining light blue in the pileus-stipe connection zone when damaged, reddish reaction with NH₄OH on pileus cuticle, ellipsoid to broadly ellipsoid, smooth basidiospores, slender pleurocystidia up to 106 μm long, hymenial cystidia (both cheilo- and pleurocystidia) sometimes multiseptate, a palisadoderm pileipellis of cylindrical hyphae, hymenophoral trama of the “*Phylloporus*-type” and the occurrence in lowland xero-mesophytic mixed broadleaved forests in apparent association with *Coccoloba* spp. (*Polygonaceae*) (including *C. uvifera*, *C. diversifolia*, *C. spicata*, *C. swartzii*, *C. pubescens*, etc.) (Pegler 1983; Ortiz-Santana et al. 2007 as “*X. olivaceus*”; this study). Based on our observations, the bluing oxidation of hymenophore and context in *X. coccolobae* is usually absent but sometimes present and quite variable in terms of range and intensity, depending on specimens age and weather conditions. It should therefore be considered a feature of low taxonomic significance. Similarly, pileus and stipe surfaces exhibit a rather considerable color variation at maturity, although always spanning in the range of brown, making the diagnostic value of these chromatic traits overestimated in the past.

This is the first verified report of *X. coccolobae* from the Dominican Republic. *Xerocomus coccolobae* has so far been reported from the Caribbean (Cuba, Dominican Republic, British Virgin Islands, and Martinique) and from Mexico (Veracruz, Quintana Roo, Yucatan) (Pegler 1983; García-Jiménez 1999; Minter et al. 2001; Ortiz-Santana et al. 2007; de la Fuente et al. 2018, 2020). According to the present outcomes, the distribution of *X. coccolobae* should also be extended to south-eastern USA (Florida) in association with *Coccoloba uvifera*. However, the exact area of occupancy of *X. coccolobae* is currently indefinite but based on the current known distribution and host association it is plausible to claim that its geographical range may correspond with that of the plant genus *Coccoloba*, which is an important constituent of the coastal mixed vegetation communities of neotropical lowland ecosystems and that most likely represents its ECM plant associate.

An additional collection *Xerocomus* aff. *coccolobae* JBSD133067 (ANGE446, MG810), consisting of a single very young specimen that was firstly identified as *X. coccolobae*, turned out to occupy a sister position to the main clade of *X. coccolobae* (Figs. 1 and 2). This fruiting body might represent a novel member of *Xerocomus* s. str., although it morphologically recalls *X. hypoxanthus* Singer (see below). Additional mature specimens will be required to assess its taxonomy.

Watling and de Meijer (1997) introduced *Xerocomus* cf. *coccolobae* from Brazil (State of Paraná), later published by de Meijer (2008) as *X. basius* de Meijer & Watling, differing from the Central American *X. coccolobae* by the innately fibrillose-squamulose, olive brown to yellowish brown pileus, reddish stipe, negative reaction with NH₄OH on pileus surface, narrower basidiospores [7.8–11.0 (–12.0) × 3.0–4.0 μm], smaller basidia (22–28 × 6–8 μm), more dispersed, smaller hymenial cystidia (30–40 × 5–9 μm), absence of caulocystidia, a pileipellis structure consisting of interwoven, non-encrusted, narrower hyphae (4.5–13 μm broad) and the occurrence in mixed, dense ombrophilous montane forests, presumably in association with unknown angiosperms (Watling and de Meijer 1997; de Meijer 2008). This species has been quoted in a number of Brazilian fungal checklists (de Meijer 2001, 2006, both as “*Xerocomus* sp. A”; Neves and Capelari 2007, as “*X. cf. coccolobae*”; Sulzbacher et al. 2013, as “*X. aff. coccolobae*”; Magnago 2014, as “*X. coccolobae*”; Putzke and Putzke 2019, as “*X. cf. coccolobae*”).

The possibility of confusion with any of the numerous similar *Xerocomus* s. str. species cannot be ruled out. A certain morphological affinity exists between *X. coccolobae* and other xerocomoid taxa occurring in the same geographical macro-region, such as *X. hypoxanthus*, *X. cuneipes*, and *X. pseudo-boletinus* var. *pini-caribaeae*.



Fig. 8 Type materials. **a** Holotype collection of *Xerocomus coccolobae* K-M000178954 (J.P. Fiard 902A); **b** holotype collection of *Xerocomus pseudoboletinus* var. *pini-caribaeae* M.H. Ivory S/101 (F); **c** holotype collection of *Boletus ruborculus* NY 577594 (TJB 8253); **d** holotype collection of *Xerocomus cuneipes* K-M000178953 (J.P. Fiard 710B); **e** authentic collections of *Boletus guadelupae* K-M000193859, K-M000193860 (J.P. Fiard 563B, isoparatype), and K-M000193861; **f** holotype/paratype collection of *Boletus guadelupae* J.P. Fiard 563A (labeled as “Fiard 563”) and J.P. Fiard 563B (F); **g** holotype collection of *Xerocomus caeruleonigrescens* K-M000178955 (J.P. Fiard 905A). Photos **a, d, e, g** by A. Yu. Bike-tova; **b, c, f** by T. Yu. Svetasheva

The pan-American *X. hypoxanthus* resembles *X. coccolobae* in its general appearance but is easily separated based on the yellowish stipe with a granulose-furfuraceous bright yellow apex, yellow basal mycelium, blue-green reaction with NH_4OH on pileus, and deep blue to brown reaction with KOH , longer basidiospores [(8.2–) 11–14 (–15.5) \times (3.2–) 4.2–5.2 μm , $12.4 \pm 1.1 \times 4.6 \pm 0.3$, $Q_m = 2.6$] and the growth under various frondose trees and conifers (*Quercus*, *Pinus* but also *Coccoloba*) and on very decayed woody debris and sawdust or trunks of palmetto. This species is known from south-eastern USA, continental Central America, the Caribbean, and is apparently allochthonous with introduced plants in South America (Brazil) (Singer 1946; Singer and Digilio 1960; Pegler 1983; Singer et al. 1983; Both 1993; Gómez 1997; Bessette et al. 2000, 2016, 2019; Pers. Obs.). The ITS sequence OL342399 (PLN 11-MAR-2022) named *Xerocomus hypoxanthus* voucher DUKE:0351605, USA: South Carolina, Mountain Rest (Stallman, J., Johnson, J., Roy, B., Lodge, D., Sheehan, B. and Russell, S. direct submission), shares 99.76% with OL342390 *Boletaceae* sp. voucher DUKE:0352590, 99.75% with *Cyanoboletus bessettei* A.R. Bessette, L.V. Kudzma & A. Farid voucher ARB1393A (MW675737) and ARB1393B (MW675738). It represents *Cyanoboletus bessettei*.

Xerocomus cuneipes is superficially very similar to *X. coccolobae* and shares with the latter species the same habitat and putative ECM association with *Coccoloba*. The revision of the holotype material (which consists of four mature specimens), originally found by J.P. Fiard in Martinique and currently preserved at the Royal Botanical Gardens Kew, K-M000178953 (J.P. Fiard 710B) (Fig. 8d) resulted as follows: basidiospores ellipsoid-fusiform to ellipsoid with suprahilar depression and sometimes with a shallow abaxial depression close to the distal end, rounded apex, pale golden-yellow, smooth under light microscope and SEM (Fig. 10c), measuring (10.3–) 11.4 \pm 0.7 (–13.0) \times (4.9–) 5.3 \pm 0.2 (–5.7) μm , $Q = (1.96\text{--}) 2.01\text{--}2.30$ (–2.49), $Q_m = 2.15 \pm 0.14$, $V_m = 168 \pm 20 \mu\text{m}^3$ [35/2/1]; basidia clavate to broadly clavate, (19–) 22–33 (–38) \times 10–13 (–15) \times 2–3 μm ($n = 13$), sterigmata 2–3 μm long; cheilocystidia rare, lanceolate, lageniform with a thin neck to occasionally mucronate, (35–) 42–59 (–63) \times 10–14 μm ($n = 4$); pleurocystidia variable in shape, fusiform to ventricose fusiform or lageniform, occasionally narrowly ovate, some with

a secondary septum, (22–) 26–53 (–66) \times (6–) 8–14 (–16) μm ($n = 19$); pileipellis a trichoderm of interwoven filamentous to cylindrical, umber-brown in mass, mainly non-incrusted hyphae or with a fine granular incrustation, terminal elements cylindrical to cystidioid with pointed apex, (23–) 38–64 (–89) \times (7–) 9–14 (–18) μm ($n = 33$); hymenophoral trama of the “*Phylloporus*-type”. These data match those provided in the protologue of *X. cuneipes* (Pegler 1983). *Xerocomus cuneipes* can be discriminated from *X. coccolobae* by the smaller size (pileus up to 2.8 cm broad, stipe up to 2.4 \times 0.4 cm), a stipe distinctly tapered at base and with a deep vinaceous brown tint in the lower half, abundant yellow basal mycelium, slightly larger basidiospores [(11.0–) 11.7 \pm 0.5 (–12.5) \times (4.5–) 5.3 \pm 0.4 (–6.0) μm , $Q_m = 2.2$] and shorter basidia (22–26 \times 11–12 μm) (Pegler 1983). *Xerocomus cuneipes* in addition to the Lesser Antilles (Martinique) where it was firstly described (Pegler 1983) was repeatedly reported from Mexico (García-Jiménez 1999; García-Jiménez and Garza-Ocañas 2001; de la Fuente et al. 2018, 2020) but not found in the Dominican Republic to date. Unfortunately, we were unable to generate DNA sequences from the type specimen of *X. cuneipes* due to its poor condition; however, according to morphological traits, it might be an additional representative of *Xerocomus* s. str. Moreover, since morphological and ecological traits of *X. cuneipes* mostly overlap those of *X. coccolobae*, a possible conspecificity of these two taxa cannot be ruled out. However, until further evidence is provided, we presently prefer to maintain them separate.

The holotype material of *X. pseudoboletinus* var. *pini-caribaeae*, originally collected in Belize by M.H. Ivory and housed at the Field Museum of Natural History, Chicago (F) (M.H. Ivory S/101, dupl. MG860), which consists of a single mature specimen (Fig. 8b), has been studied for a more accurate comparison with *X. coccolobae* and the anatomical re-examination produced the following results: basidiospores elongated fusiform to ellipsoid-fusiform in side view, ellipsoid-fusiform to ellipsoid in face view, with a short apiculus and a shallow suprahilar depression, apex rounded, (11.3–) 12.7 \pm 0.8 (–14.4) \times (4.6–) 5.2 \pm 0.4 (–6.0) μm , $Q = (1.98\text{--}) 2.17\text{--}2.93$ (–2.95), $Q_m = 2.43 \pm 0.21$, $V = 184 \pm 32 \mu\text{m}^3$ [30/1/1], smooth, inamyloid; hymenial elements (basidia, pleurocystidia, and cheilocystidia) collapsed; hymenophoral trama bilateral divergent of the “*Phylloporus*-type”; pileipellis a trichoderm of mostly collapsed interwoven filamentous to broadly cylindrical, smooth hyphae with terminal elements 3–17 μm wide. The basidiospores measurements as resulted from the present re-examination of the type material are not in accordance with the original description, as they are much shorter when compared with the size provided by Singer et al. (1983) for *X. pseudoboletinus* var. *pini-caribaeae*: “11.5–17.5 (–20) \times 4.5–5.8 (–6.8) μm , most frequently about 15–15.5 \times 5–5.5 μm ” (p. 80). In addition, the collecting date reported on the box containing the holotype sample

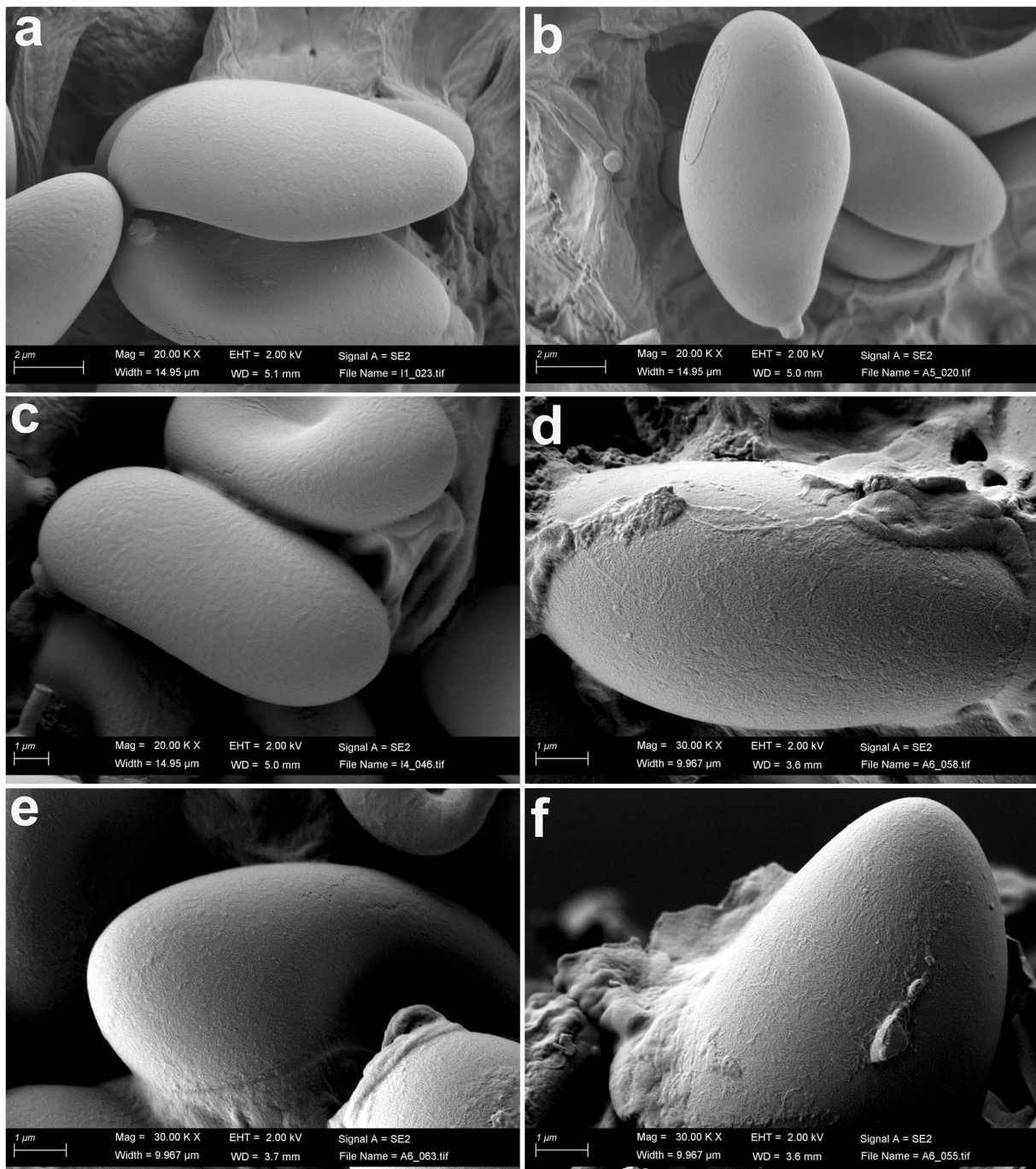


Fig. 9 Basidiospores from selected collections under SEM. **a, b** *Xerocomus coccolobae* (K-M000178954, holotype; JBSD133071, respectively); **c** *Xerocomus cuneipes* (K-M000178953, holotype); **d–f** *Xero-*

comus caeruleonigrescens (K-M000178955, holotype). Photos by A. Yu. Biketova and B. Dobrić

(16 Nov 1976) (Fig. 8b) is also different from that reported in the protologue (15 Jun 1976) which probably refers to another collection (M.H. Ivory S/378) from Puerto Cabezas, Nicaragua (Singer et al. 1983). Unfortunately, we were unable to successfully extract and amplify DNA from the holotype of *X. pseudoboletinus* var. *pini-caribaeae*. *Xerocomus*

pseudoboletinus var. *pini-caribaeae* was said to differ from the type (var. *pseudoboletinus*) in larger basidiospores and exclusive association with pines (although the type variety can also associate with pine trees) (Singer et al. 1983), but based on the aforementioned revision the actual existence of var. *pini-caribaeae* should be carefully evaluated. There

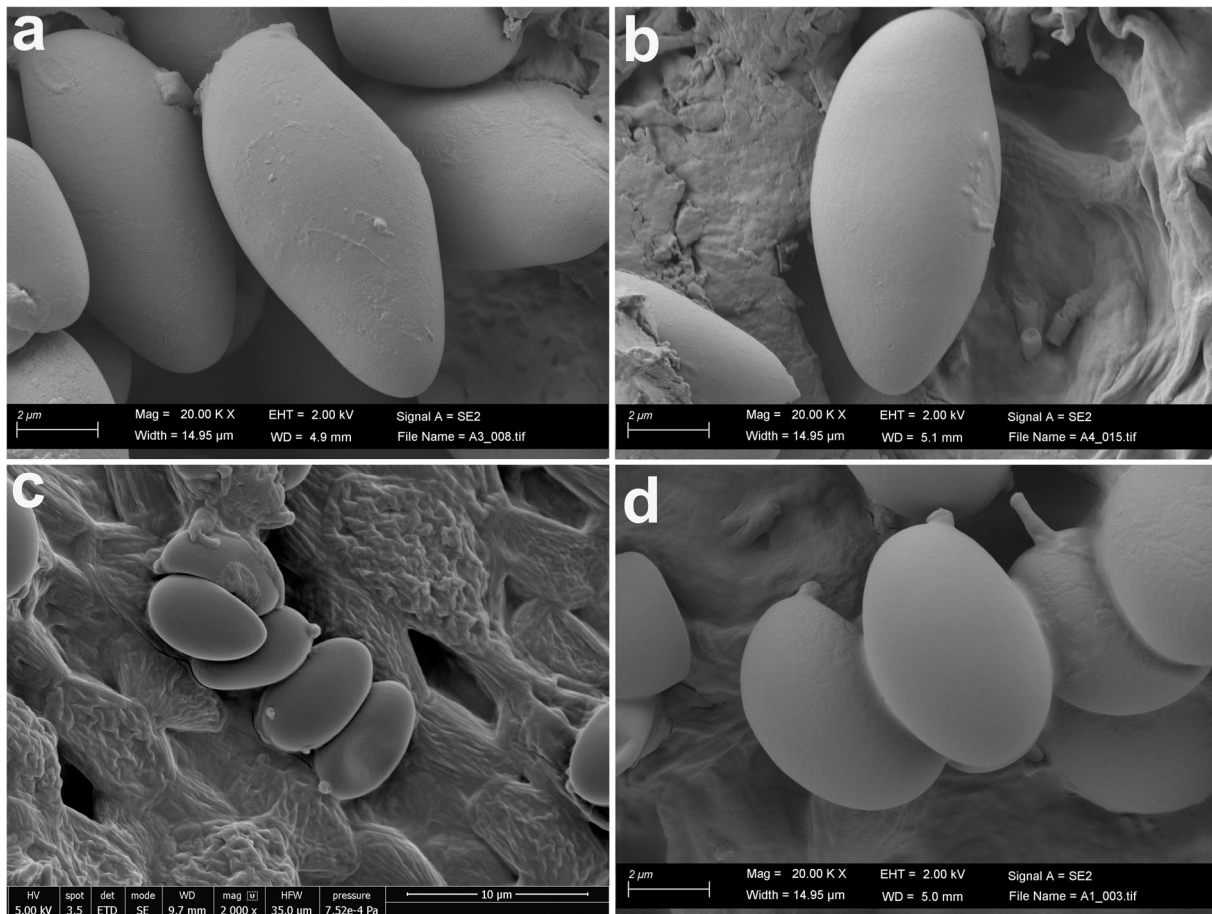


Fig. 10 Basidiospores from selected collections under SEM. **a, b** *Tropicoboletus ruborculus* (NY 577594, holotype; JBSD133073, respectively); **c, d** *Singerocomus guadelupae* (K-M000193867,

K-M000193859, respectively). Photos **a, b, d** by A. Yu. Biketova and B. Dobrić; **c** by I.S. Druzhinina

is no doubt, however, that *X. coccolobae* and *X. pseudoboletinus* var. *pini-caribaeae* represent two different taxa, the latter differing in larger dimension of the basidiomes (pileus up to 12 cm diam., stipe up to 12 × 2.8 cm), predominantly reddish brown color of the pileus and bright yellow of the stipe, longer and slightly broader basidiospores, a trichoderm to ixotrichoderm pileipellis of interwoven, narrower hyphae (up to 13–15 μm broad), a blue-green reaction with NH₄OH on pileus and an overall brown reaction with KOH, and different ECM host trees (*P. caribaea* and *P. clausa*) (Singer et al. 1983; Gómez 1997). *Pinus caribaea* Morelet is a not uncommonly encountered pine tree in montane forests of the Dominican Republic; however, the Caribbean pine is not at all present along the sea-shore areas where *C. coccolobae* occurs. The known distribution of *X. pseudoboletinus* extends from south-eastern USA to Central and/or South America (Singer et al. 1983; Both 1993; Gómez 1997; MyCoPortal). It is to be noted that in Both (1993) the type material of *X. pseudoboletinus* var. *pini-caribaeae* is incorrectly cited from Nicaragua.

Finally, the generic type *X. subtomentosus* (L.) Quél. is reminiscent of *X. coccolobae* but is promptly distinguished by the larger size (pileus up to 25 cm broad, stipe up to 12 × 4 cm), finely tomentose pileus, pale yellowish context with flesh pink hues in the lower third of the stipe, yellowish and usually coarsely ribbed or roughly pseudo-reticulate stipe, blue-green reaction with NH₄OH on pileus surface, slightly longer basidiospores [(9.7–) 12.2 ± 0.9 (–17.2) × (3.8–) 4.8 ± 0.3 (–5.9) μm, Qm = 2.5] with bacillate ornamentation under SEM, trichodermal pileipellis consisting of narrow filamentous hyphae (terminal elements averaging 40 × 12 μm), more ventricose hymenial cystidia (up to 21 μm broad), ECM association with broad-leaved trees (mainly *Fagaceae* and *Betulaceae*) and the occurrence in Europe in warm to temperate woodlands (Engel et al. 1996; Lannoy and Estadès 2001; Ladurner and Simonini 2003; Watling and Hills 2005; Taylor et al. 2006; Muñoz et al. 2008; Šutara 2008; Šutara et al. 2009; Knudsen and Taylor 2012; Galli 2013; Klofac and Krisai-Greilhuber 2020; Pers. obs.).

Tropicoboletus Angelini, Gelardi & Vizzini, **gen. nov.**
Mycobank MB847064.

Etymology: the epithet refers to the occurrence of this genus in the tropical belt.

Basidiomata pileate-stipitate with poroid hymenophore, epigeal, evelate, small-sized with a xerocomoid silhouette; pileus convex to applanate, subtomentose to glabrous; hymenophore adnate to depressed around the stipe, yellow to olive-brown; stipe solid, dry, longitudinally finely fibrillose, reticulum absent; basal mycelium yellow; context firm, whitish but pale cream-yellowish in the pileus; tissues unchangeable or turning light blue slowly and erratically when injured or exposed; taste mild to slightly sour; spore print olive-brown; sordid green reaction with ammonia on pileus cuticle; basidiospores smooth, ellipsoid-fusiform; pleuro-, cheilo and caulocystidia present; trichodermal pileipellis; hymenophoral trama bilateral-divergent of the “*Phylloporus*-type”; lateral stipe stratum present, of the “boletoid type”; clamp connections absent; ontogenetic development gymnocarpic; geographic distribution in the tropical belt. According to the phylogenetic analysis of the combined *TEF1* and *RPB2* sequences the genus is sister to subfamily *Xerocomoideae*.

Type: *Boletus ruborculus* T.J. Baroni.

Tropicoboletus ruborculus (T.J. Baroni) Angelini, Gelardi & Vizzini, **comb. nov.** Figures 5e–h, 7, and 9a, b
Mycobank MB847066.

Basionym: *Boletus ruborculus* T.J. Baroni, *Mycologia* 92 (3): 563. 2000.

Holotype: Greater Antilles, Puerto Rico, Arecibo, Barrio Dominguito, Mata de Platano Private Reserve, under *Coccoloba* sp., 08 Nov 1996, leg. T.J. Baroni, S.A. Cantrell and F. Bird, NY 577594 (Baroni TJB 8253, PR-1926).

Basidiomes small. *Pileus* (2.2–) 2.8–4.5 (–4.7) cm broad, at first hemispherical then persistently convex and finally broadly pulvinate-flattened, sometimes slightly depressed at center, 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-lobed, initially slightly involute then curved downwards and finally completely plane or even uplifted, shortly appendiculate and extending beyond the tubes up to 1 mm; surface matt, dry, finely tomentose but later smooth and glabrous and then slightly greasy with moist weather, not cracked; somewhat variable in color, ranging from flesh-pink to purplish pink or pinkish vinaceous to vinaceous red (Hermosa Pink, La France Pink, Shrimp Pink, Pl. I; Safrano Pink, Orient Pink, Pl. II; Venetian Pink, Alizarine Pink, Acajou Red, Vandyke Red, Pl. XIII; Deep Vinaceous, Dark Vinaceous, Pl. XXVII) but progressively fading with

age becoming pinkish gray, pinkish brown, brownish pink to grayish or pale grayish brown (Light Vinaceous-Fawn, Vinaceous-Fawn, Fawn Color, Army Brown, Buffy Brown, Pl. XL; Purple-Drab, Vinaceous-Drab, Pl. XLV; Light Cinnamon-Drab, Cinnamon-Drab, Light Drab, Pl. XLVI; Pale Mouse Gray, Light Mouse Gray, Olive Gray, Mouse Gray, Pl. LI; Storm Gray, Pl. LII) starting from the center, although tending to retain pinkish hues towards the peripheral zone even in senescence, always paler at margin, outer rim usually whitish (White, Pl. LIII); slowly reddening (Pomegranate Purple, Bordeaux, Pl. XII; Deep Vinaceous, Dark Vinaceous, Pl. XXVII) on handling or touching or more obviously when injured; subpellis layer reddish violet (Rose Pink, Pale Amaranth Pink, Mallow Pink, Pl. XII). *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 0.6 cm long), adnate but soon depressed around the stipe apex and decurrent with a short tooth, pale yellow to olive yellow and finally brownish olive (Buff Yellow, Pl. IV; Greenish Yellow, Bright Green Yellow, Oil Yellow, Javel Green, pl. V; Primuline Yellow, Pl. XVI; Raw Sienna, Pl. III) at maturity, unchangeable to erratically turning very light blue (Pale Blue-Green, Tyrolite Green, Pl. VII) when cut. *Pores* initially forming a concave surface, later flat then slightly convex, broad at first then gradually wider with age (up to 2 mm in diam.), simple, firstly roundish becoming prominently angular at maturity, stretched and radially arranged towards the stipe, concolorous with the tubes and unchangeable or irregularly and very slowly and faintly bluing (Pale Blue-Green, Tyrolite Green, Pl. VII) 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* (2.3–) 2.6–5.8 (–9.0) × 0.5–1.0 (–1.3) cm, slightly longer than or as long as 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 swollen or conversely attenuated from apex down to the base, usually ending with a short taproot at the very base; surface longitudinally finely fibrillose throughout, non-reticulate, evelate; whitish to pale yellowish (White, Pl. LIII; Baryta Yellow, Pinard Yellow, Pl. IV) in the upper third, whitish (White, Pl. LIII) elsewhere but irregularly streaked or mottled bright flesh-pink, pinkish vinaceous or purplish pink to purplish red (Hermosa Pink, La France Pink, Shrimp Pink, Pl. I; Safrano Pink, Orient Pink, Pl. II; Venetian Pink, Alizarine Pink, Acajou Red, Vandyke Red, Pl. XIII), with a pale yellow to yellow (Baryta Yellow, Pinard Yellow, Picric Yellow, Pale Lemon Yellow, Pl. IV) basal tomentum, unchangeable or faintly reddening (Pomegranate Purple, Bordeaux, Pl. XII; Deep Vinaceous, Dark Vinaceous, Pl. XXVII) to rarely very slowly and faintly bluing (Pale

Blue-Green, Tyrolite Green, Pl. VII) when pressed; basal mycelium yellow (Pale Lemon Yellow, Lemon Yellow, Pl. IV). *Context* firm and tough when young, later soft textured and eventually flabby in the pileus (up to 0.9 cm thick in the central zone, up to 0.7 cm thick halfway to margin and gradually becoming thinner towards the edge), a little more fibrous in the stipe, whitish, pale cream to very pale yellowish (White, Pl. LIII; Baryta Yellow, Pl. IV) in the pileus but cream to pale yellowish (Baryta Yellow, Pinard Yellow, Pl. IV) upon the tubes and upper fourth of the stipe, pinkish violet (Rose Pink, Pale Amaranth Pink, Mallow Pink, Pl. XII) underneath the cuticle, more or less evenly bright flesh-pink, purplish pink or pinkish vinaceous to vinaceous red (Hermosa Pink, La France Pink, Shrimp Pink, Strawberry Pink, Peach Red, Pl. I; Safrano Pink, Orient Pink, Grenadine Pink, Grenadine, Pl. II; Venetian Pink, Alizarine Pink, Old Rose, Pl. XIII) in the rest of the stipe but pale brownish to dirty brown (Medal Bronze, Dark Citrine, Pl. IV; Isabella Color, Light Brownish Olive, Pl. XXX) at the very base; very slowly and faintly turning pale blue (Pale Blue-Green, Pl. VII; Pale Blue, Light Cerulean Blue, Cerulean Blue, Pl. VIII) upon the tubes and more sporadically in the connection zone with the stipe when exposed to air, occasionally bluing all over the pileus context, unchangeable or nearly so elsewhere; yellowish (Pinard Yellow, Pl. IV) to dark vinaceous red (Pomegranate Purple, Bordeaux, Pl. XII; Deep Vinaceous, Dark Vinaceous, Pl. XXVII) where eroded by maggots, whitish to pale flesh-pink where eaten by slugs (Hermosa Pink, La France Pink, Pl. I; White, Pl. LIII); subhymenophoral layer pale yellowish (Baryta Yellow, Pinard Yellow, Pl. IV); exsiccate pale ochraceous on the context, brownish elsewhere (Clay Color, Tawny-Olive, Saccardo's Umber, Pl. XXIX). *Odor* indistinct. *Taste* mild to slightly sour. *Spore print* olive-brown. *Macrochemical spot-test reactions*: 30% KOH: vinaceous red on pileus surface; 30% NH₄OH: with vapors greenish black on pileus surface.

Basidiospores [189/12/7] (6.5–) 10.4 ± 0.9 (–13.0) × (3.5–) 5.0 ± 0.3 (–6.0) μm, Q = (1.53–) 1.60–3.00 (–3.25), Q_m = 2.07 ± 0.17, V = 138 ± 23 μm³ (a single anomalous spore measured 14.0 × 6.0 μm), inequilateral, ellipsoid to ellipsoid-fusiform in side view, broadly ellipsoid to ellipsoid or nearly ovoid in face view, smooth under light microscope and SEM, apex rounded, with a short apiculus, usually with a shallow suprahilar depression and with a pronounced adaxial swelling, moderately thick-walled (0.3–0.6 μm), straw yellow colored in water and honey yellow in 5% KOH, having one or two large oil droplets when mature, rarely pluri-guttulate, inamyloid to very weakly dextrinoid, acyanophilic and staining blue (orthochromatic reaction) in Cresyl blue. *Basidia* 25–40 × 10–13 μm (n = 27), cylindrical-clavate to clavate, moderately thick-walled (0.3–0.6 μm), predominantly 4-spored but rarely also 2- or 3-spored, usually bearing relatively short sterigmata (2–5 μm), hyaline to

pale yellowish and sometimes 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* (31–) 38–60 × (7–) 10–20 μm (n = 29), common, moderately slender, projecting straight to sometimes flexuous, fusiform to more frequently ventricose-fusiform or ampullaceous and usually showing a narrow and long neck but also sublageniform to lageniform, rarely subcylindrical or subclavate, 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* (34–) 36–59 (–61) × (7–) 9–18 (–20) μm (n = 18), relatively frequent, shape, size, color, and chemical reactions similar to cheilocystidia. *Pseudocystidia* not observed. *Pileipellis* a trichoderm consisting of strongly interwoven, elongated, filamentous and sinuous to less frequently slightly enlarged, 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; terminal elements 35–137 × (2–) 3–14 (–17) μm, particularly long and slender, cylindrical to rarely cystidioid, apex rounded-obtuse, moderately thick-walled (up to 1 μm), hyaline to more often straw yellow in water and 5% KOH, some cells with a scattered brownish vacuolar pigment in water which tends to be solved in 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, 3–17 μm wide, hyaline to yellowish in water and 5% KOH; the stipe apex covered by a well-developed caulohymenial layer consisting of sterile caulobasidioles, sparse, predominantly 2- and 1-spored, fertile caulobasidia, (25–) 28–38 (–42) × 8–12 μm, sterigmata 2–4 (–6) μm long (n = 10) and abundant projecting *caulocystidia* similar in size, shape, and color to hymenial cystidia, (28–) 31–47 (–54) × 10–19 (–22) μm (n = 10), having a wall up to 1 μm thick. *Lateral stipe stratum* under the caulohymenium present and well differentiated from the stipe trama, of the “boletoid type”, at the stipe apex a (25–) 30–80 (–90) μm thick layer consisting of divergent, inclined and running towards the external surface, loosely intermingled and rarely branched hyphae remaining separate and embedded in a gelatinous substance. *Stipe trama* composed of confusedly and densely arranged, subparallel to moderately interwoven, filamentous, smooth, inamyloid to barely dextrinoid hyphae, 2–8 (–10) μm broad. *Hymenophoral trama* bilaterally divergent of the “*Phylloporus*-type”, with very slightly divergent to nearly parallel and tightly arranged, non-gelatinous hyphae (lateral strata hyphae in transversal section touching or almost touching each other, 0–4 μm apart, 4–13 μm broad), hyaline to very pale yellowish in water and 5% KOH, inamyloid in Melzer's;

lateral strata (15–) 20–30 (–40) μm thick, mediostratum (10–) 15–35 (–40) μm thick, axially arranged, consisting of a tightly adpressed, non-gelatinous bundle of hyphae, 3–9 μm broad; in Congo Red the mediostratum is concolorous with or at most slightly darker than the lateral strata. *Thromboplerous hyphae* very abundant especially in the hymenophore, thick-walled, rarely septate, melanized, with a golden yellow to brownish homogeneous content in 5% KOH. *Clamp connections* absent in all tissues. *Ontogenetic development* gymnocarpic.

Edibility unknown.

Ecology and phenology: solitary to gregarious, growing on limestone among litter in a seasonally dry and moist anthropogenic lowland mixed stands under a large array of neotropical broadleaved trees including *Coccoloba* spp. (*C. uvifera*, *C. diversifolia*, *C. pubescens*, *C. spicata*, etc.) (*Polygonaceae*), which represent its putative ECM host trees. See Parra et al. (2018) for further details on lowland vegetation communities in the Dominican Republic. November and December.

Known distribution: It is known to date only from Mexico and the Greater Antilles of the Caribbean (Dominican Republic and Puerto Rico) but almost certainly also occurring in Belize and neighboring countries of mainland Central America. Apparently localized and infrequent.

Examined material: DOMINICAN REPUBLIC, Municipality of Sosúa, Puerto Plata Province, cemetery, three km away from the seaside, 19°44'40"N 70°32'21"W, 100 m, 16 Dec 2013, a single mature specimen, C. Angelini, JBSD133072 (ANGE208, MG808); same loc., 19 Dec 2013, five mature specimens, C. Angelini, JBSD133073 (ANGE209, MG809); same loc., 14 Dec 2019, three young to mature specimens, C. Angelini (collection lost); same loc., 23 Nov 2020, six mature specimens, C. Angelini, JBSD133074 (ANGE1406, MG850); same loc., 22 Nov 2020, a single young specimen, C. Angelini, JBSD133075 (ANGE1479, MG851); PUERTO RICO, Viejo San Juan, El Morro, along the Camino Escénico, 18°28'17"N 66°07'23"W, 22 Nov 2020, three mature specimens, K.O. Miller, MO439745 (komille277); Arecibo, Barrio Dominiguito, Mata de Platano Private Reserve, under *Coccoloba* sp., 08 Nov 1996, T.J. Baroni, S.A. Cantrell and F. Bird, NY 577594 (Baroni TJB 8253, PR-1926, holotype); MEXICO, Quintana Roo, Santa Elena, close to rio Hondo in the vicinity of the borderline with Belize, 12 Oct 2019, J.I. de la Fuente, JIF-451-ITCV (de la Fuente 451).

Notes: *Tropicoboletus* is a novel genus segregated from the polyphyletic *Boletus* s.l. Multilocus phylogenetic analysis clearly resolved *Boletus ruborculus* with strong statistical support in a monophyletic lineage sister to subfamily *Xerocoideae* (Fig. 1). The isolated phylogenetic placement of *Tropicoboletus* justifies its recognition as an independent genus.

There does not appear to be one exclusive morphological trait that could serve alone to separate *Tropicoboletus* from similar genera in the *Boletaceae*; however, a combined set of features allows a prompt circumscription of this new genus. The only known species *T. ruborculus* can be recognized, even in the field, with reasonable certainty as it is easily distinguished by a combination of macro-morphological characters: basidiomes with a diminutive size and xerocoid silhouette, flesh-pink, pinkish red or vinaceous red to brownish red pileus and stipe surfaces, yellowish olive tubular hymenophore, slowly and erratically bluing tissues on exposure, vivid yellow basal mycelium, a sordid green reaction on pileus surface with ammonia vapors and the occurrence in lowland mixed broadleaved tropical woodlands in probable association with *Coccoloba* spp. In addition, some anatomical key features integrating macroscopic identification include ellipsoid-fusiform, smooth basidiospores, predominantly and distinctly ventricose-fusiform to ampullaceous hymenial cystidia, a trichodermal pileipellis and the hymenophoral trama of the “*Phylloporus*-type” (Miller et al. 2000; this study). Beside the peculiar ecosystem where this bolete resides, the distinctive and conspicuous yellow basal mycelium is the most reliable diagnostic attribute for a proper recognition of the species in the field. This clear-cut feature, however, has not been previously emphasized. In the protologue of *B. ruborculus* (Miller et al. 2000) nothing is said about the color of the basal mycelium, either because its importance was underestimated or because it was simply overlooked. The association with *Coccoloba* species is most likely but not yet confirmed by direct observation of the ectomycorrhizae. Interestingly, specimens collected in Puerto Rico under *C. uvifera* (including the type specimen) exhibit a brighter red pileal surface when compared to basidiomes occurring with *C. diversifolia* from the Dominican Republic, but they are otherwise identical from both morphological and phylogenetic aspects.

Confident identification of *T. ruborculus* is also reinforced in the present study by the availability of additional verified samples recently yielded in Puerto Rico and Mexico which were placed in the same clade as the Dominican vouchers. However, just a handful of collections of this rare species are presently known from the neotropics, making *T. ruborculus* a sparingly encountered species. Prior to the present study, *T. ruborculus* resulted unnoticed from Mexico and the Dominican Republic as this species was known only from the type locality in Puerto Rico (Miller et al. 2000). Presumably, it is native to Central America and most likely widespread throughout the neotropics but to what extent is the actual distribution range of *T. ruborculus* remains to be determined. One might hypothesize that the distribution of this species roughly overlaps with that of *Coccoloba*, which appears to represent its alleged strict symbiotic partner.

For the sake of completeness, a careful re-examination of the holotype material of *B. ruborculus* (which consists of a single mature specimen divided in half) originally collected in Puerto Rico and housed at the New York Botanical Garden (NY 577594, TJB 8253, dupl. MG855) (Fig. 8c) has been carried out, resulting in the following anatomical data: basidiospores ellipsoid-fusiform, ellipsoid to broadly ellipsoid, smooth under light microscope and SEM (Fig. 9a, b), measuring $(9.0\text{--}10.5 \pm 0.6 \text{ (}\text{--}12.0)\text{)} \times (4.8\text{--}5.3 \pm 0.3 \text{ (}\text{--}6.0)\text{)} \mu\text{m}$, $Q = (1.63\text{--}1.76\text{--}2.18 \text{ (}\text{--}2.22)\text{)}$, $Q_m = 1.98 \pm 0.13$, $V = 155 \pm 22 \mu\text{m}^3$ [30/1/1], cylindrical-clavate to clavate or occasionally sphaeropedunculate basidia, $28\text{--}33 \text{ (}\text{--}36)\text{)} \times 10\text{--}13$ ($n=6$), sterigmata $2\text{--}3 \mu\text{m}$ long, rare and mostly collapsed, subfusiform or fusiform to subclavate hymenial cystidia (pleurocystidia), $37\text{--}50 \times 6\text{--}9 \mu\text{m}$ ($n=3$) and a trichodermal pileipellis of interwoven filamentous to broadly cylindrical, smooth hyphae with terminal elements $3\text{--}15 \text{ (}\text{--}19)\text{)} \mu\text{m}$ wide. These data almost perfectly match those provided by T.J. Baroni (Miller et al. 2000) for *B. ruborculus* in the protologue. Furthermore, we successfully generated an ITS sequence from the holotype of *B. ruborculus* (GB acc. n. OQ108299) which shares a P%I=99.9 with other sequences of *B. ruborculus* obtained in the present study (GB acc. n. OQ108295–OQ108298), therefore confirming their conspecificity.

Despite its resemblance with several other red-colored xerocomoid boletes, macro- and micro-morphological features of *T. ruborculus* are reliable and compelling enough to allow a clear-cut delimitation from lookalikes such as *Boletus guadelupae* and *Xerocomus caeruleonigrescens*, which grow in the same ecosystem in alleged association with various species of *Coccoloba*.

In the present study, we have generated ITS sequences from three different *B. guadelupae* collections: J.P. Fiard 563A/B (F) (holotype/paratype, see below), K-M000193866 (D.N. Pegler 2981) and K-M000193867 (D.N. Pegler 2745). Based on the resulting phylogenetic tree (Fig. 4), *B. guadelupae* is clearly nested in *Singerocomus*, forming a strongly supported lineage (MLB 0.94, PP 0.97) which is sister to a clade containing *S. inundabilis* (Singer) T.W. Henkel & Husbands and *S. rubriflavus* T.W. Henkel & Husbands. Sequences of the recently described *S. atlanticus* A.C. Magnago (including the holotype KY907177) cluster in the same clade of *B. guadelupae*, sharing a P%I=99.4 and thus indicating there are contaxic. The following new combination is therefore required:

Singerocomus guadelupae (Singer & Fiard) Gelardi, Biketova, Martinez-Suz & Vizzini, **comb. nov.**

Mycobank MB847067.

Basionym: *Boletus guadelupae* Singer & Fiard, Bulletin de la Société Mycologique de France 92(4): 445. 1976 (“1977”).

\equiv *Xerocomus guadelupae* (Singer & Fiard) Pegler, Kew Bulletin Additional Series 9: 575. 1983.

$=$ *Singerocomus atlanticus* A.C. Magnago, Acta Botanica Brasiliica 32 (2): 3. 2018.

Holotype: Lesser Antilles, Guadelupe, Matouba, Basse Terre, 700 m, 31 Jul 1975, leg. J.P. Fiard, J.P. Fiard 563A (labeled as “Fiard 563”), F.

Examined material: GUADELUPE, Trace de Sofaia, 250 m, on soil, twigs, and rotting roots in forest, 25 Jul 1975, J.P. Fiard, K-M000193860 (isoparatype); same locality (F, J.P. Fiard 563B paratype, or J.P. Fiard 563A/563B mixed holotype/paratype); same locality, on forest soil and decayed trunk in lower mountain rainforest, 23 Aug 1975, J.P. Fiard, K-M000193859 (original collection number unknown!); Basse Terre, Courbayre, Morne Cadet, 300 m, 09 Oct 1977, D.N. Pegler, K-M000193866 (D.N. Pegler 2981). MARTINIQUE, Plateau Perdrix, on the ground and among fallen leaves in forest at start of rains, 05 Jul 1976, J.P. Fiard, K-M000193861 (J.P. Fiard 563C); Absalon, Clark Ravine, 15 Sep 1977, D.N. Pegler, K-M000193867 (D.N. Pegler 2745).

Additional examined material: *Xerocomus caeruleonigrescens*: MARTINIQUE, Morne Aca, solitary on the forest floor, 250 m, 28 Aug 1977, J.P. Fiard, K-M000178955 (J.P. Fiard 905A, holotype).

Singerocomus guadelupae is delimited from *T. ruborculus* by the presence of an olivaceous yellow pruina covering pileus surface in the early developmental stage, white to whitish yellow basal mycelium, unchanging tissues on bruising or exposure, a blue reaction with NH_4OH and a yellow reaction with KOH on the pileus, considerably smaller, broadly ellipsoid to ovoid basidiospores [$(6.0\text{--}7.3 \pm 0.3 \text{ (}\text{--}9.0)\text{)} \times (3.3\text{--}4.5 \pm 0.2 \text{ (}\text{--}6.0)\text{)} \mu\text{m}$, $Q_m = 1.6$] which are smooth, fusoid to lageniform or ventricose-rostrate, narrower hymenial cystidia ($34\text{--}62 \times 4\text{--}11 \mu\text{m}$) which are sometimes thick-walled (up to $2.7 \mu\text{m}$ thick) and narrower caulocystidia ($31\text{--}43 \times 6\text{--}9.8 \mu\text{m}$) (Singer and Fiard 1977; Pegler 1983; Singer et al. 1983; Magnago et al. 2018, as “*Singerocomus atlanticus*”). *Singerocomus guadelupae* may establish ECM association with *Polygonaceae*, *Nyctaginaceae*, and *Fabaceae* and to date it has been reported from both the Greater and Lesser Antilles (Cuba, Martinique, Guadelupe, Dominica) and from all along the Atlantic Forest in Brazil (Singer and Fiard 1977; Pegler 1983; Singer et al. 1983; Minter et al. 2001; Magnago et al. 2018, as “*Singerocomus atlanticus*”; Putzke and Putzke 2019) but has not as yet been found in the Dominican Republic. Having been confirmed as a member of *Singerocomus*, *S. guadelupae* broadens the biogeographic range of the genus to the Caribbean. For additional considerations on type collections of *B. guadelupae*, see below. The anatomical study of the authentic specimen K-M000193859 of *B. guadelupae* collected in Guadelupe

by J.P. Fiard and lodged at the Royal Botanic Gardens Kew (K-M) resulted as follows: basidiospores broadly ellipsoid to ovoid in side view, smooth under light microscope and SEM (Fig. 9d), with an indistinct suprahilar depression and rounded apex, pale golden-yellow, $(6.4\text{--}7.2 \pm 0.5 \text{ (} -8.4) \times (4.1\text{--}4.5 \pm 0.3 \text{ (} -5.4) \mu\text{m}$, $Q = (1.32\text{--}1.49\text{--}1.69 \text{ (} -1.80)$, $Q_m = 1.59 \pm 0.10$, $V_m = 80 \pm 15 \mu\text{m}^3$ [33/3/1]; basidia cylindrical-clavate to clavate, $28\text{--}35 \text{ (} -41) \times 8\text{--}11 \mu\text{m}$ ($n = 12$), sterigmata $2\text{--}3 \mu\text{m}$ long; cheilo- and pleurocystidia fusiform to lageniform, cheilocystidia $(40\text{--}43\text{--}55 \text{ (} -58) \times (7\text{--}9\text{--}12 \mu\text{m}$ ($n = 10$); pleurocystidia $(22\text{--}31\text{--}53 \text{ (} -60) \times 6\text{--}10 \mu\text{m}$ ($n = 10$); trichodermal pileipellis of interwoven filamentous to cylindrical, reddish in mass, smooth to rarely encrusted hyphae, terminal elements cylindrical but tapering at apex, $(14\text{--}19\text{--}40 \text{ (} -66) \times 4\text{--}9 \text{ (} -12) \mu\text{m}$ ($n = 33$). These microscopic data are consistent with those reported for *B. guadelupae* in the protologue (Singer and Fiard 1977).

A re-examination of the anatomical features of the holotype material of *X. caeruleonigrescens* K-M000178955 (J.P. Fiard 905A), originally found in Martinique and consisting of a single mature specimen (Fig. 8g), produced the following results: basidiospores ellipsoid to broadly ellipsoid without suprahilar depression, golden-yellow, smooth under light microscope and with very finely bacillate (rodlet) encrustation on most of the surface under SEM, although some smooth patches may occur [Fig. 10d–f; similar to those of *X. ferrugineus* (Schaeff.) Alessio (see Šutara 2008, Fig. 2, for comparison)], measuring $(10.3\text{--}11.2 \pm 0.6 \text{ (} -13.0) \times (5.0\text{--}6.0 \pm 0.3 \text{ (} -6.6) \mu\text{m}$, $Q = (1.65\text{--}1.74\text{--}2.01 \text{ (} -2.19)$, $Q_m = 1.87 \pm 0.13$, $V_m = 211 \pm 29 \mu\text{m}^3$ [33/1/1]; basidia cylindrical-clavate to clavate, $25\text{--}30 \text{ (} -32) \times 9\text{--}12 \mu\text{m}$ ($n = 12$), sterigmata $2\text{--}3 \mu\text{m}$ long; cheilocystidia fusiform to clavate, $(29\text{--}31\text{--}40 \text{ (} -43) \times 6\text{--}10 \mu\text{m}$ ($n = 6$); pleurocystidia fusiform to lageniform with elongated neck, with pale yellow content, $(29\text{--}35\text{--}52 \text{ (} -54) \times 6\text{--}12 \mu\text{m}$ ($n = 12$); pileipellis a palisadoderm of interwoven cylindrical to broadly cylindrical, umber-brown in mass hyphae, some with ochre-brownish content, terminal elements cylindrical with rounded apex, $(13\text{--}23\text{--}36 \text{ (} -43) \times (4\text{--}6\text{--}8 \mu\text{m}$ ($n = 33$); hymenophoral trama of the “*Phylloporus*-type”. These data are consistent with those provided in the protologue of *X. caeruleonigrescens* (Pegler 1983). *Xerocomus caeruleonigrescens* is separated from *T. ruborculus* by the smaller size of the fruiting bodies (pileus 2.5 cm diam., stipe 3.3×0.4 cm), tissues bruising deep bluish black throughout, slightly larger basidiospores [$(10.0\text{--}11.3 \pm 0.8 \text{ (} -13.0) \times (5.2\text{--}6.0 \pm 0.4 \text{ (} -6.5) \mu\text{m}$, $Q_m = 1.9$] which are finely bacillate under SEM, smaller basidia ($25\text{--}28 \times 9\text{--}11 \mu\text{m}$), narrower hymenial cystidia ($40\text{--}50 \times 9\text{--}11 \mu\text{m}$) and a palisadoderm pileipellis with shorter and narrower terminal cells ($21\text{--}65 \times 5\text{--}7 \mu\text{m}$) (Pegler 1983). This species has also been reported from Mexico (García-Jiménez 1999; García-Jiménez and Garza-Ocañas 2001; de la Fuente et al. 2018, 2020). Unfortunately,

various attempts to sequence and amplify the ITS region of the holotype material of *X. caeruleonigrescens* resulted unsuccessful and therefore we could not determine the exact phylogenetic placement of this taxon.

The pine-associated *Boletus caribaesus* (Singer) Singer, originally introduced as a subspecies of *Boletus rubellus* Krombh. (= *Hortiboletus rubellus* (Krombh.) Simonini, Vizzini & Gelardi), differs from *T. ruborculus*, aside from the different ECM host tree (*Pinus caribaea*), by larger-sized basidiomes (pileus up to 15 cm broad, stipe up to 3.5 cm wide), yellow context discoloring dark blue throughout on exposure, whitish basal mycelium, an indistinct reaction on pileus surface with NH_4OH , slightly longer basidiospores [$(9.0\text{--}9.5\text{--}14.2 \text{ (} -14.5) \times (4.0\text{--}4.2\text{--}6.5 \mu\text{m}$], smaller cheilocystidia ($20\text{--}23 \times 6.5\text{--}7 \mu\text{m}$), narrower pleurocystidia ($23\text{--}70 \times 7.5\text{--}11 \mu\text{m}$) and caulocystidia ($29\text{--}45 \times 8\text{--}11 \mu\text{m}$), narrower pileipellis hyphae (up to $7 \mu\text{m}$ wide), hymenophoral trama of the “*Boletus*-type” and sometimes by the tendency to develop sterile gasteroid basidiomes (carpo-phoroidism) (Singer 1945, 1947; Singer et al. 1983). This species occurs from south-eastern USA (Florida) south to continental Central America (Belize) (Singer 1945, 1947; Singer et al. 1983). Presently unknown from the Dominican Republic.

Molecular separation of *T. ruborculus* from the European *H. rubellus* is morphologically substantiated by the presence in this latter taxon of larger-sized basidiomes (pileus up to 12 cm broad, stipe up to 12×3 cm), a reddish stipe surface turning blue on handling, a more constant and intense bluing of pileal context when exposed, a dirty ochraceous yellow stipe context which usually exhibits carrot orange to flame red tiny punctuations at the very base, a negative to pale yellow reaction with NH_4OH on the pileus, slightly longer basidiospores [$(9.2\text{--}12.0 \pm 0.9 \text{ (} -15.1) \times (3.8\text{--}5.2 \pm 0.4 \text{ (} -6.7) \mu\text{m}$, $Q_m = 2.3$], narrower hymenial cystidia ($40\text{--}60 \times 8\text{--}13 \mu\text{m}$), a physalo-palisadoderm pileipellis of subparallel, broader hyphae, and the occurrence preferably on woodland edges, grassy clearings, tracksides, cultivated lands or similar rural environments, mainly in association with *Fagaceae* (*Quercus*, *Castanea*, *Fagus*) (Engel et al. 1996; Lannoy and Estadès 2001; Ladurner and Simonini 2003; Peintner et al. 2003; Watling and Hills 2005; Muñoz et al. 2008; Šutara et al. 2009; Knudsen and Taylor 2012; Galli 2013; Klofac and Krisai-Greilhuber 2020; Pers. obs.). In addition, *H. rubellus* is phylogenetically very distantly related to *T. ruborculus* (Wu et al. 2016a, b).

More collections of *T. ruborculus* are surely needed for a better taxonomic understanding of the generic limits of *Tropicoboletus* and a more accurate knowledge of its ecology and geographic distribution patterns in Mesoamerica. Furthermore, future extensive research in undersampled ecological niches might uncover additional members of *Tropicoboletus*, especially from the paleotropics.

Clarification on type collections of *Boletus guadelupae*

There appears to be much confusion with dates and collection numbers of the type specimens of *B. guadelupae*. Based on data provided in the protologue (Singer and Fiard 1977), the holotype was collected in Basse Terre, Matouba, Guadelupe, 31 Jul 1975 (collection number not specified), whereas J.P. Fiard 563B (collected in Trace de Sofaia, Guadelupe, 25 Jul 1975) is designated as paratype, both collections having been deposited at the Field Museum of Natural History, Chicago (F).

In Singer et al. (1983), the collection number of the holotype from Matouba is specified as J.P. Fiard 563C. This is inconsistent with the information reported in Pegler (1983), where the holotype collection from Matouba is reported under the number J.P. Fiard 563A (with a wrong date “July 1075”) and strangely enough the type is said to be housed at K-M instead of F as previously reported in Singer and Fiard (1977). This is another contradictory information which can be explained by the fact that the type was later duplicated at K-M. However, according to ICN rules, there cannot be two holotypes of the same species deposited at two different official herbaria. Therefore, we must assume that part of J.P. Fiard 563A was housed at F (labeled as “Fiard 563” and representing the holotype as reported in the protologue and based on the collection date provided by Pegler) and part at K-M (representing an isotype, but see below). The same thing probably happened to the paratype J.P. Fiard 563B, which was split between F and K-M. We have also been able to retrieve J.P. Fiard 563C (K-M000193861) at K-M (Fig. 8e), but unlike what written by Singer et al. (1983) this sample originates from Martinique and is dated 05 Jul 1976. Consequently, J.P. Fiard 563C cannot be considered the holotype and the type data reported in Singer et al. (1983) are evidently wrong. Likewise, the specimen K-M000193860 (which is referred to as J.P. Fiard 563B on 25 Jul 1975, heavily infected by *Hypomyces* sp.) housed at the Royal Botanic Gardens Kew as the holotype of *B. guadelupae* is not the holotype nor an isotype but a simple isoparatype (Fig. 8e). We are not able to address why the letter “B” after Fiard’s collection number was handwritten modified as “A” in the accompanying label (Fig. 8e), but no doubt the correct number is the original J.P. Fiard 563B. Another authentic specimen K-M000193859, which was collected by Fiard on 23 Jul 1975 and not mentioned in the protologue, has a wrong collection number (J.P. Fiard 563B, again with the label handwritten modified by replacing the letter “A” with the letter “B” after Fiard’s collection number) (Fig. 8e), but it can be neither J.P. Fiard 563B nor J.P. Fiard 563A, because these vouchers were collected on 25 Jul 1975 and 31 Jul 1975, respectively. Accordingly, the original collection number of K-M000193859 presently remains unknown. K-M000193861 (J.P. Fiard 563C) (Fig. 8e) from Martinique is an additional authentic collection.

With regard to the type material preserved at F, which consists of three fragmented dried specimens (Fig. 8f), it is clearly visible that the upper right label (coll. Fiard 563B) refers to the paratype (although the date 25 Aug 1957 is obviously incorrect) while the bottom left label (Fiard 563, dated 31 Jul 1975) refers to the holotype. Unfortunately, it is impossible to know which of the two collections the dried specimens refer to. We are inclined to believe that the specimens refer to the holotype collection, but we have no proof to demonstrate it. One might hypothesize that J.P. Fiard 563A and J.P. Fiard 563B could have mixed into a single bag, so as to become a sole collection (this would explain the presence of two labels in the same packet). On the other hand, considering all material of *B. guadelupae* presently housed in the Fungarium of the Kew Gardens, we must conclude that an isotype of this species has never been deposited at K-M, since none of the available collections is dated 31 Jul 1975, unless we accept that the type at F is a mixture of the holotype and paratype specimens, in this case K-M000193860 would actually represent the isotype of *B. guadelupae*.

Notes on basidiospore ornamentation of *Xerocomus* s. str. under SEM

According to Šutara (2008), species of the genera *Xerocomus* and *Phylloporus* Quél. have bacillate spore ornamentation under SEM. Heinemann et al. (1988) were the first to observe such ornamentation in *X. subtomentosus* (bacillate) and *X. ferrugineus* (bacillate or roughened to smooth). The bacillate ornamentation of the basidiospores of *X. subtomentosus*, *X. chrysonemus* A.E. Hills & A.F.S. Taylor, *X. silwoodensis* A.E. Hills, U. Eberh. & A.F.S. Taylor, and *X. doodhcha* K. Das, D. Chakr., Baghela, S.K. Singh & Dentinger is detectable under $\times 6$ K – $\times 15$ K magnification, while that of *X. ferrugineus* can be observed with $\times 30$ K or higher magnification (Oolbekkink 1991; Šutara 2008; Das et al. 2016). Based on the current study, *X. coccolobae* has smooth basidiospores under SEM, as well as *X. cuneipes* (a single specimen K-M000178953), which has not yet been proven genetically to be a member of *Xerocomus* s.str. (Fig. 10c). A single specimen of *Xerocomus caeruleonigrescens* (K-M000178955), which has not been successfully sequenced, showed a finely bacillate (rodlet) encrustation which was observed on most of the basidiospore surface, although some patches appeared to be smooth (Fig. 10d–f).

This kind of incrustation can be explained by hydrophobin (surface active protein) coating of basidiospores and has similar rodlet pattern to assembled Class I hydrophobins on aerial hyphae of *Schizophyllum commune* Fr. and pileus surface of *Agaricus bisporus* (J.E. Lange) Imbach (Wösten et al. 1993; Lugones et al. 1996). Hydrophobins of mushroom-forming

fungi (*Agaricomycetes*) are far from being well studied (Li et al. 2021). So far, *Pisolithus tinctorius* (Mont.) E. Fisch. (putative *P. albus* (Cooke & Masee) Priest), *Suillus luteus* (L.) Roussel, and *Paxillus involutus* (Batsch) Fr. are the only species of the order Boletales where hydrophobins, which are predominantly produced during ectomycorrhiza formation, were formally detected and characterized (Tagu et al. 1996; Duplessis et al. 2001; Rineau et al. 2017). However, there is no information on basidiospore coat hydrophobins in Boletales in the available literature. They likely play an important role in spore protection and germination, as it has been shown in anamorphic fungi (Cai et al. 2021).

Additional remarks on some *incertae sedis* genera

In the combined *RPB2/TEF1* phylogeny focused on the whole family *Boletaceae*, we recovered a well-supported clade (MLB = 0.93, PP = 0.98) containing *Soliococcus* Trappe, Osmundson, Manfr. Binder, Castellano & Halling, *Bothia* Halling, T.J. Baroni & Manfr. Binder and *Phylloporopsis* Angelini, A. Farid, Gelardi, M.E. Smith, Costanzo & Vizzini (provisionally named “*Bothia* clade” in Farid et al. 2018), and another clade with no statistical support comprising *Pseudoboletus* Šutara, *Gymnogaster* J.W. Cribb and *Baorangia* G. Wu & Zhu L. Yang (Fig. 1). All these genera are currently settled in the *Boletaceae* but with an uncertain phylogenetic placement (*incertae sedis*). The “*Bothia* clade” might represent an additional subfamily within the *Boletaceae*, although the only known synapomorphy of this grouping appears to be the cyanophily of the basidiospore wall as previously highlighted by Farid et al. (2018). On the other hand, *Pseudoboletus*, *Gymnogaster* and *Baorangia* do not appear to be strictly related to one another from morphological, ecological, or trophic standpoints and their phylogenetic close proximity could be only artifactual. Obviously, further investigation on morphological, ecological, and chemical features and additional molecular loci will be required to better clarify the taxonomic boundaries of these genera and their reciprocal phylogenetic relationships. Accordingly, we believe it is premature to introduce formal ranks for these two groups of genera and we therefore refrain from proposing new subfamilies for the time being.

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Author contribution All authors contributed to the study, conception, and design. Claudio Angelini, Kurt O. Miller, Javier Isaac de la Fuente, and Jesús García Jiménez collected specimens and contributed to the morphological work and descriptions. Matteo Gelardi and Alona Yu. Biketova performed microscopical descriptions. Matteo Gelardi made the line drawings. Enrico Ercole and Alfredo Vizzini did the molecular lab work and performed the phylogenetic analyses. Alona Yu. Biketova, Laura M. Suz, Tatiana Yu. Svetasheva, Kurt O. Miller, Javier Isaac de la Fuente, and Jesús García Jiménez provided some DNA sequences. Matteo Gelardi and Alfredo Vizzini wrote the manuscript, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability Sequence data are deposited in GenBank. The datasets generated and analyzed during the current study are in the tables or available from the corresponding author upon request.

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication Informed consent was obtained from all individual participants included in the study.

Competing interests The authors declare no competing interests.

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