

Outstanding Pinkish Brown-Spored Neotropical Boletes: *Austroboletus subflavidus* and *Fistulinella gloeocarpa* (Boletaceae, Boletales) from the Dominican Republic

Matteo Gelardi^a, Claudio Angelini^{b,c}, Federica Costanzo^a, Enrico Ercole^d, Beatriz Ortiz-Santana^e and Alfredo Vizzini^d

^aAnguillara Sabazia, Italy; ^bPordenone, Italy; ^cNational Botanical Garden of Santo Domingo, Santo Domingo, Dominican Republic; ^dDepartment of Life Science and Systems Biology, University of Turin, Torino, Italy; ^eUSDA Forest Service, Northern Research Station, Center for Forest Mycology Research, Madison, WI, USA

ABSTRACT

The occurrence of *Austroboletus subflavidus* and *Fistulinella gloeocarpa* is documented from the Dominican Republic. The latter species is reported for the first time outside its original locality in Martinique, extending the geographic range for this uncommon pinkish-spored bolete. A detailed morphological description is provided for each species and accompanied by color pictures of fresh basidiomes in habitat and line drawings of the main anatomical features. Both species represent independent lineages within their respective genera based on phylogenetic inference. In addition, *A. subflavidus* clusters in a sister lineage to the core *Austroboletus* clade (*Austroboletus* clade I) here named as *Austroboletus* clade II. In order to confirm the accuracy of species identification, their identity and relationships were subjected to multilocus phylogenetic analyses of three gene markers (ITS, nrLSU, RPB2) including genetic material already available in public databases. *Austroboletus subflavidus* is a widely distributed species in North and Central America, whereas *F. gloeocarpa* is apparently highly localized and seems to appear sparingly in the Dominican Republic, Martinique, and southern Florida. Comparisons with morphologically similar and molecularly inferred allied species are also presented and discussed.

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1. Introduction

With the recent advancement of molecular techniques applied to the study of boletoid mushrooms and related groups (Boletaceae, Boletales), several different generic and infrageneric lineages have been extensively investigated, revealing an extraordinary diversity mainly distributed across temperate, subtropical, and tropical environments of both hemispheres [1–8]. Yet, the increasing number of genera in the Boletaceae has barely been investigated with a molecular approach, thus determining largely unresolved phylogenetic relationships, unclear taxonomic limits, and often revealing a polyphyletic nature in their original circumscription, as in the case of the pinkish brown-spored *Fistulinella* Henn. and *Austroboletus* (Corner) Wolfe.

E.J.H. Corner first introduced *Austroboletus*, typified by *Porphyrellus dictyotus* Boedijn, as a subgenus of his broadly conceived *Boletus* Fr. s. l. to accommodate a number of Malaysian boletes with ornamented basidiospores [9]. A few years later, E. Horak [10] stated that “according to our personal

experience with tropical species of Strobilomycetaceae at least *Heimiella* and subgen. *Austroboletus* have to be considered as good and independent genera within the taxonomic framework of the boletes”. C.B. Wolfe and R.H. Petersen critically reevaluated the infrageneric limits of *Porphyrellus* E.-J. Gilbert s. l. and *Boletus* subgen. *Austroboletus* [11] and shortly after Wolfe [12] upgraded *Austroboletus* to genus rank, providing further insights into the taxonomy and a comprehensive revision of several type specimens. The recognition of *Austroboletus* at the generic rank was subsequently disputed by Corner [13] but accepted and integrated with additional taxa and new combinations by Pegler and Young [14], Singer [15,16], and by Horak [17,18], Watling and Gregory [19], and Singer et al. [20] based on fungal material yielded in Australasia and Latin America. *Austroboletus* currently comprises some 36 species [21] and incorporates taxa assigned by Singer [22] to *Porphyrellus* sect. *Graciles* Singer and sect. *Tristes* Singer and successively placed by Smith and Thiers

[23] in *Tylophilus* sect. *Graciles* A.H. Smith and Thiers.

The genus as presently outlined is characterized from the morphological viewpoint by boletoid fruiting bodies with dry to viscid or even mucilaginous pileus and stipe surfaces, initially whitish or pale cream becoming flesh-pink to vinaceous pink or brownish pink tubular hymenophore at maturity, smooth, furfuraceous-fibrillose to more often markedly reticulate-alveolate, lacerate or lacunose stipe, generally unchanging tissues, flesh-pink, pinkish vinaceous, purplish brown, rust brown to chocolate brown spore print, variously ornamented (finely verrucose or warted to irregularly pitted but also flat-tuberculate to subreticulate) amygdaliform to ellipsoid-fusiform basidiospores, trichoderm or ixotrichoderm pileipellis, bilateral-divergent hymenophoral trama of the “*Boletus*-type”, gymnocarpic, velangiocarpic (primary angiocarpic), or pseudoangiocarpic (secondary angiocarpic) ontogenesis and ectomycorrhizal (ECM) association with several plant families including Fagaceae, Pinaceae, Dipterocarpaceae, Myrtaceae, and caesalpinoid legumes [8,9,12,14,16–18,20,21,24–35], although some species are suspected to be saprotrophic or only facultative ECM [32]. *Austroboletus* appears to be scarcely represented in temperate woodlands of both hemispheres but is particularly diverse throughout the pantropical belt, especially across the neotropical latitudes of Central and northern South America and all along the Australasian region [9,16,18,20,26,30,32–34,36].

Molecular analyses have clearly inferred a distant phylogenetic relationship of *Austroboletus* from *Tylophilus* P. Karsten s. str. and conversely an affinity with other boletoid pinkish-spored genera segregated from *Tylophilus* s. l., such as *Fistulinella* Henn., *Mucilopilus* Wolfe, and *Veloporphyrellus* L.D. Gomez & Singer and possibly with the sequestrate genus *Carolinigaster* M.E. Smith & S. Cruz [5,7,8,31,37–47]. The former three genera, along with *Austroboletus*, have been accommodated in the subfamily Austroboletoidae G. Wu & Zhu L. Yang, as they cluster in an well-delimited grouping with respect to other lineages in the Boletaceae [7]. Despite the increasing number of morphologically and molecularly-based novel species assigned to *Austroboletus* in the last few years from Amazon Colombia [31], India [48,49] and Australia [26], this genus has been shown to represent a polyphyletic unit [5,7,31,37,42]. Moreover, the polyphyly of *Austroboletus* has been further highlighted by the recent separation of the genus *Ionosporus* O. Khmel'nitsky, based on the Malaysian species *Boletus longipes* Masee [41].

Fistulinella, typified by *F. staudtii* Henn., was first recognized by the German mycologist P. Hennings at the beginning of the twentieth century based on material recorded in Cameroon, central Africa [50]. The genus includes the species assigned by Singer [51] to *Porphyrellus* sect. *Pseudotylophili* subsect. *Viscidini* Singer and encompasses at present more than 20 species worldwide [21]. *Fistulinella* is characterized by stipitate-pileate to occasionally sequestrate fruiting bodies having relatively small size, slender and gaunt habit, velate, or evelate, usually viscid to strongly glutinous pileus and stipe surfaces, pileus sometimes scrobiculate, initially whitish becoming pinkish to vinaceous pink or brownish pink tubular hymenophore, slim stipe with a smooth, rarely reticulate but not alveolate-lacunose surface, unchanging tissues, vinaceous pink to reddish brown or rust brown to cocoa brown spore print, narrowly elongate fusoid, inamyloid to dextrinoid, smooth basidiospores, trichoderm to ixotrichoderm or ixocutis pileipellis, strongly gelatinized bilateral-divergent hymenophoral trama of the “*Boletus*-type”, suspected gymnocarpic ontogenesis in some species but probably also velangiocarpic (primary angiocarpic) in others and presumably but not proved ECM association with members of the Polygonaceae, Sapotaceae, Myrtaceae, Euphorbiaceae, Fagaceae, Nothofagaceae, and caesalpinoid legumes in mesophytic and hygrophytic forests ([14,16,20,21,30,32,50,52–58] this study). The biogeographic distribution of *Fistulinella* is more or less overlapping that of *Austroboletus*, the majority of species being distributed in the pantropical belt with only a few extending to temperate regions of both northern and southern hemispheres [16,32]. Despite the longstanding of *Fistulinella*, an unanimous taxonomic interpretation of the genus has never been reached [6,27,56]. From the phylogenetic perspective, *Fistulinella* is inferred to be related to *Austroboletus*, *Mucilopilus*, *Veloporphyrellus*, and apparently *Carolinigaster* [5,7,8,37–39,43,45–47] and it seems to occupy a sister position to the remainder of the Austroboletoidae [5,7,39,41,43,45,47]. On the other hand, preliminary molecular analyses suggested this genus to be polyphyletic [31,37] and accordingly an inclusive revision complemented by further sampling from different geographic regions aiming at a better understanding of its generic boundaries would be urgently needed, especially in relation to morphologically very close smooth-spored genera such as *Mucilopilus* and *Ixechinus* R. Heim ex R. Heim. Moreover Vasco-Palacios et al. [31], and Magnago et al. [42] have stressed that American species belonging in *Fistulinella* cluster in a statistically strongly supported separate clade with respect to those described from Australia and New Zealand, but

it is not until molecular analyses are carried out on the generic type, the African taxon *F. staudtii*, that a taxonomic and geographic delimitation of *Fistulinella* s. str. lineage will be definitely clarified.

In order to reconstruct the phylogeny of *Austroboletus* and *Fistulinella*, nucleotide sequences of three regions, viz., the nuclear ribosomal internal transcribed spacer (ITS) region, large subunit nuclear ribosomal RNA gene (nrLSU) and DNA-directed RNA polymerase II subunit gene (RPB2), were generated in this study from samples of *A. subflavidus* and *F. gloeocarpa* recently recorded in the Dominican Republic (Greater Antilles). Given the limited number of mycological studies undertaken in the island, it is not at all surprising to find out distinctive bolete genera and species that were previously scarcely documented or completely overlooked.

2. Materials and methods

2.1. Collection site and sampling

Specimens examined were collected in Jarabacoa, La Vega Province and Sosúa, Puerto Plata Province, Dominican Republic, and are deposited in the Herbarium of Jardín Botánico Nacional of Santo Domingo, Dr. Rafael Ma. Moscoso, Dominican Republic (JBSD) (acronym from Thiers [59]), while “ANGE” and “MG” refer to the personal herbarium of Claudio Angelini and Matteo Gelardi, respectively. Herbarium numbers 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 and morphological features of the studied species have also been checked on MyCoPortal (<https://mycoportal.org>) and the NYBG Boletineae project (<https://sweetgum.nybg.org/science/projects/boletineae/>), respectively.

2.2. Morphological studies

Macroscopic descriptions, macro-chemical 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 [60]. 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% KOH or in anionic solution saturated with 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 ± 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 [$V = (\pi \cdot L \cdot W^2)/6 \pm \text{SD}$]. The notation [n/m/p] indicates that measurements were made on “n” randomly selected basidiospores from “m” basidiomes of “p” collections. The width of each basidium was measured at the widest part, and the length was measured from the apex (sterigmata excluded) to the basal septum. Radial and/or vertical sections of the pileipellis were taken midway between the center and margin of the pileus. Sections of the stipitipellis were taken from the middle part along the longitudinal axis of the stipe. Metachromatic, cyanophilic, and iodine reactions were tested by staining the basidiospores in Brilliant Cresyl blue, Cotton blue, and Melzer’s reagent, respectively. Line drawings of microstructures were traced in free hand based on digital photomicrographs of rehydrated material.

2.3. DNA extraction, PCR amplification, and DNA sequencing

DNA extraction and PCR amplification were performed from dried basidiomata (Table 1) as described by Vizzini et al. [75]. Primers ITS1F and ITS4 [76,77] were used for the ITS region; primers LR0R and LR5 [78,79] were used for the nrLSU. Amplifications of the RPB2 gene were attempted using the primers bRPB2-6F2, bRPB2-7.1R2, and bRPB2-7R2 [80,81]. 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).

2.4. Sequence alignment, data set assembly, and phylogenetic analyses

The sequences obtained in this study were checked and assembled using Geneious v. 11.1.4 [82] and compared to those available in GenBank by using the Blastn algorithm [83]. Chromatograms were

Table 1. Details of specimens used in the phylogenetic analyses.

Original name from GenBank	RPB2	nrLSU	ITS	Specimen/voucher	Origin	Reference(s)
<i>Austroboletus</i> aff. <i>fusisporus</i>	KF112766	KF112484	–	HKAS52683	China	Wu et al. [7]
<i>Austroboletus</i> aff. <i>fusisporus</i>	KF112767	KF112486	–	HKAS53461	China	Wu et al. [7]
<i>Austroboletus</i> aff. <i>mutabilis</i>	KF112768	KF112487	–	HKAS53450	China	Wu et al. [7]
<i>Austroboletus</i> aff. <i>rostrupii</i>	–	KJ786636	–	G4357	Guyana	Roy et al. [61]
<i>Austroboletus amazonicus</i>	–	KF714508	–	1839 AMV	Colombia	Vasco-Palacios et al. [31]
<i>Austroboletus amazonicus</i>	–	KF714509	–	1914 AMV	Colombia	Vasco-Palacios et al. [31]
<i>Austroboletus amazonicus</i>	–	NG_058569	NR_153523	HUA2032 AMV	Colombia	Vasco-Palacios et al. [31]
<i>Austroboletus appendiculatus</i>	–	–	KX530028	KCS 1401-CAL_1304	India	Tibpromma et al. [49]
<i>Austroboletus austrovirens</i>	–	–	KP242207	BRI:AQ0794143	Australia	Fechner et al. [26]
<i>Austroboletus austrovirens</i>	KP242133	KP242227	KP242208	BRI:AQ0794171	Australia	Bonito et al. (unpubl.)
<i>Austroboletus austrovirens</i>	KP242131	KP242226	KP242209	BRI:AQ0794609	Australia	Bonito et al. (unpubl.)
<i>Austroboletus austrovirens</i>	–	–	KP242210	BRI:AQ0794622	Australia	Fechner et al. [26]
<i>Austroboletus austrovirens</i>	KP242130	KP242225	KP242211	BRI:AQ0795791	Australia	Fechner et al. [26]
<i>Austroboletus austrovirens</i>	–	–	KP242212	BRI:AQ0796003	Australia	Fechner et al. [26]
<i>Austroboletus austrovirens</i>	KP242113	KP242284	KP012789	MEL:2382920a	Australia	Bonito et al. (unpubl.)
<i>Austroboletus austrovirens</i>	–	–	KP242214	MEL:2382920b	Australia	Fechner et al. [26]
<i>Austroboletus</i> cf. <i>gracilis</i>	–	MN174791	MN174796	JLF6600	USA	Frank (unpubl.)
<i>Austroboletus</i> cf. <i>novae-zelandiae</i>	–	KC552061	–	CD567	Australia	Orihara et al. [62]
<i>Austroboletus</i> cf. <i>subvirens</i>	MH614752	–	–	OR0573	Thailand	Vadthananarat et al. [63]
<i>Austroboletus dictyotus</i>	–	JX901138	–	HKAS59804	China	Hosen et al. [64]
<i>Austroboletus festivus</i>	–	–	KT724085	AMV1800	Colombia	Vasco-Palacios et al. (unpubl.)
<i>Austroboletus festivus</i>	–	KT724095	KT724086	AMV1881	Colombia	Vasco-Palacios et al. (unpubl.)
<i>Austroboletus festivus</i>	–	KY888001	KY886202	FLOR:51599	Brazil	Magnago et al. [42]
<i>Austroboletus festivus</i>	–	–	AB509830	122–549	Japan	Sato et al. (unpubl.)
<i>Austroboletus fusisporus</i>	–	JX889720	JX889719	HKAS75207	China	Hosen et al. [64]
<i>Austroboletus fusisporus</i>	–	MK765810	–	JXSB0351	China ?	Chen (unpubl.)
<i>Austroboletus gracilis</i>	–	–	MH465078	ACAD11344F	Canada	Young et al. [65]
<i>Austroboletus gracilis</i>	–	–	MH167935	Mushroom Observer # 310751	Mexico	Rockefeller (2018, direct submission)
<i>Austroboletus gracilis</i>	–	–	MH979242	NAMA 2017-106	USA	Russell (2018, direct submission)
<i>Austroboletus gracilis</i>	–	EU522815	–	TM03_434	Canada	Porter et al. [66]
<i>Austroboletus gracilis</i>	–	MK601714	–	CFMR BOS-562	USA	Kuo and Ortiz-Santana [5]
<i>Austroboletus gracilis</i> var. <i>flavipes</i>	–	–	–	–	–	–
<i>Austroboletus gracilis</i> var. <i>gracilis</i>	MK766277	MK601715	–	CFMR BOS-547	USA	Kuo and Ortiz-Santana [5]
<i>Austroboletus lacunosus</i>	KP242090	KP242272	KP242161	BRI:AQ0795787	Australia	Bonito et al. (unpubl.)
<i>Austroboletus lacunosus</i>	–	KC552056	KC552014	MEL:2233764	Australia	Orihara et al. [62]
<i>Austroboletus lacunosus</i>	–	KC552057	KC552015	MEL:2265009	Australia	Orihara et al. [62]
<i>Austroboletus lacunosus</i>	–	–	KP191804	PDD:83019	New Zealand	Lebel and Cooper (unpubl.)
<i>Austroboletus lacunosus</i>	–	JX889669	–	REH9146	Australia	Halling et al. [67]

(continued)

Table 1. Continued.

Original name from GenBank	RPB2	nrLSU	ITS	Specimen/voucher	Origin	Reference(s)
<i>Austroboletus mucosus</i>	–	AY612798	–	TH6300	–	Drehmel et al. [3]
<i>Austroboletus mutabilis</i>	KP242097	KP242266	KP242167	BRI:AQ0669270	Australia	Bonito et al. (unpubl.)
<i>Austroboletus mutabilis</i>	KP242098	KP242263	KP242169	BRI:AQ0795793	Australia	Bonito et al. (unpubl.)
<i>Austroboletus mutabilis</i>	KP242099	KP242262	KP242170	BRI:AQ0796266	Australia	Bonito et al. (unpubl.)
<i>Austroboletus neotropicalis</i>	–	JQ924334	JQ924301	NY181457	Costa Rica	Wu et al. (unpubl.)
<i>Austroboletus niveus</i>	–	KC552058	KC552016	MEL:2053830	Australia	Orihara et al. [62]
<i>Austroboletus niveus</i>	KP242109	KP242279	KP242217	Perth 6660703	Australia	Bonito et al. (unpubl.)
<i>Austroboletus niveus</i>	–	JX889668	–	REH9487	Australia	Halling et al. [67]
<i>Austroboletus niveus</i>	–	KP191672	KP191800	PDD:105213	New Zealand	Lebel and Cooper (unpubl.)
<i>Austroboletus niveus</i>	–	KP191673	KP191801	PDD:105246	New Zealand	Lebel and Cooper (unpubl.)
<i>Austroboletus niveus</i>	–	–	KP191802	PDD:81219	New Zealand	Lebel and Cooper (unpubl.)
<i>Austroboletus niveus</i>	–	DQ534622	–	Strain 312	New Zealand	Binder and Hibbett [2]
<i>Austroboletus novae-zelandiae</i>	–	KP242256	KP242175	MEL:2370154	Tasmania (Australia)	Bonito et al. (unpubl.)
<i>Austroboletus novae-zelandiae</i>	–	KP191671	KP191803	PDD:105097	New Zealand	Lebel and Cooper (unpubl.)
<i>Austroboletus novae-zelandiae</i>	–	–	HM060327	PDD:72542	New Zealand	Johnston and Park (unpubl.)
<i>Austroboletus novae-zelandiae</i>	–	DQ534623	–	Strain 50	New Zealand	Binder and Hibbett [2]
<i>Austroboletus occidentalis</i>	–	KC552059	KC552017	MEL:2300518	Australia	Orihara et al. [62]
<i>Austroboletus rarus</i>	KP242086	KP242236	KP242197	BRI:AQ0794045	Australia	Bonito et al. (unpubl.)
<i>Austroboletus rionegrensis</i>	–	–	KY886201	INPA 78693	Brazil	Magnago et al. [42]
<i>Austroboletus roseialbus</i>	–	KY872650	KY872653	Dodd	Australia	Fechner et al. [26]
<i>Austroboletus roseialbus</i>	–	KY872651	KY872652	REH10024	Australia	Fechner et al. [26]
<i>Austroboletus rostrupii</i>	KP242089	–	KP242160	BRI:AQ0795785	Australia	Bonito et al. (unpubl.)
<i>Austroboletus rostrupii</i>	–	–	JN168683	TH8189	Guyana	Smith et al. [68]
<i>Austroboletus</i> sp.	KP242115	KP242235	–	BRI:AQ0794156	Australia	Bonito et al. (unpubl.)
<i>Austroboletus</i> sp.	KP242106	KP242234	KP242215	BRI:AQ0794222	Australia	Bonito et al. (unpubl.)
<i>Austroboletus</i> sp.	KP242087	–	KP242158	BRI:AQ0794242	Australia	Bonito et al. (unpubl.)
<i>Austroboletus</i> sp.	KP242102	KP242259	–	BRI:AQ0794271	Australia	Bonito et al. (unpubl.)
<i>Austroboletus</i> sp.	KP242094	–	KP242159	BRI:AQ0794272	Australia	Bonito et al. (unpubl.)
<i>Austroboletus</i> sp.	–	KP242283	KP242213	MEL:2382826	Australia	Bonito et al. (unpubl.)
<i>Austroboletus</i> sp.	–	–	KY774008	CY13_008	New Caledonia	Carriconde et al. (unpubl.)
<i>Austroboletus</i> sp.	–	–	KY774007	CYMy36L1	New Caledonia	Carriconde et al. (unpubl.)
<i>Austroboletus</i> sp.	–	KF030351	–	DPL7541	USA	Nuhn et al. [6]
<i>Austroboletus</i> sp.	KF112764	KF112383	–	HKAS:57756	China	Wu et al. [7]
<i>Austroboletus</i> sp.	KF112765	KF112485	–	HKAS:59624	China	Wu et al. [7]
<i>Austroboletus</i> sp.	KT990367	KT990527	–	HKAS74743	China	Wu et al. [8]
<i>Austroboletus</i> sp.	–	KY090995	–	LAM 0222	Malaysia	Peay and Lim (unpubl.)
<i>Austroboletus</i> sp.	–	KY091070	–	LAM 0479	Malaysia	Peay and Lim (unpubl.)
<i>Austroboletus</i> sp.	KP242134	KC552060	KP242203	MEL:2305143	New Caledonia	Orihara et al. [62]
<i>Austroboletus</i> sp.	MH614753	–	–	OR0891	Thailand	Vadthananarat et al. [63]
<i>Austroboletus</i> sp.	–	KP191670	KP191805	OTA FUNNZ 2013434	New Zealand	Lebel and Cooper (unpubl.)
<i>Austroboletus</i> sp.	KP242126	KP242277	KP242216	Perth 06658407	Australia	Bonito et al. (unpubl.)
<i>Austroboletus</i> sp.	–	KP242285	–	Perth 7660928	Australia	Bonito et al. (unpubl.)
<i>Austroboletus subflavidus</i>	MT590754	MT580902	MT581525	JBSD130771 (ANGE108 and MG775)	Dominican Republic	This study
<i>Austroboletus subflavidus</i>	MT590755	MT580903	MT581526	JBSD130772 (ANGE388 and MG776)	Dominican Republic	This study
<i>Austroboletus subflavidus</i>	–	MT580901	MT581523	CFMR:DR2859; isolate = TJB-9787	Dominican Republic	This study

(continued)

Table 1. Continued.

Original name from GenBank	RPB2	nrLSU	ITS	Specimen/voucher	Origin	Reference(s)
<i>Austroboletus subflavidus</i>	–	–	MT581524	CFMR:DR592; isolate = DJL-DR-48	Dominican Republic	This study
<i>Austroboletus subflavidus</i>	–	–	MT581522	CFMR:BZ1824; isolate = DJL-BZ-27	Belize	This study
<i>Austroboletus subflavidus</i>	MK766278	MK601716	–	CFMR BZ-3178 BOS-625	Belize	Kuo and Ortiz-Santana [5]
<i>Austroboletus subflavidus</i>	–	MT580900	MT581521	CFMR:BOTH-3463	Florida (USA)	This study
<i>Austroboletus subflavidus</i>	–	–	MH016816	FLAS-F-60635	Florida (USA)	Kaminsky et al. (unpubl.)
<i>Austroboletus subvirens</i>	–	–	AB509915	120-707	Japan	Sato et al. (unpubl.)
<i>Austroboletus subvirens</i>	–	JN378518	–	KPM-NC-0017836	Japan	Orihara et al. [69]
<i>Austroboletus viscidoviridis</i>	KP242128	KP242282	KP242219	Perth 7588682	Australia	Bonito et al. (unpubl.)
<i>Austroboletus viscidoviridis</i>	–	–	KY872649	REH9993	Australia	Fechner et al. [26]
<i>Bothia castanella</i>	–	DQ867117	DQ867110	MB03-053	USA	Halling et al. [70]
<i>Bothia fujianensis</i>	–	KM269193	KM269195	HKAS82694	China	Zeng et al. [71]
<i>Fistulinella campinaranae</i>	–	KY888003	KY886204	FLOR:51608	Brazil	Magnago et al. [42]
<i>Fistulinella campinaranae</i> var. <i>scrobiculata</i>	–	KT724100	KT724090	AMV1513	Colombia	Vasco-Palacios et al. [31]
<i>Fistulinella cinereoalba</i>	–	GQ477439	KT339237	TH8471	Guyana	Fulgenzi et al. [27]
<i>Fistulinella gloeocarpa</i>	MT59076	MT580906	MT581527	JBSD130769 (ANGE969 and MG777)	Dominican Republic	This study
<i>Fistulinella gloeocarpa</i>	–	MT580904	–	CFMR:B4	The Bahamas	This study
<i>Fistulinella gloeocarpa</i>	–	MT580905	–	CFMR:B10	The Bahamas	This study
<i>Fistulinella gloeocarpa</i>	–	–	GQ981503	KM162946	The Bahamas	Bidartondo and Doring (unpubl.)
<i>Fistulinella olivaceoalba</i>	–	MH745969	–	HKAS53432	Vietnam	Crous et al. [37]
<i>Fistulinella olivaceoalba</i>	–	MH718396	NR_163311	LE312004	Vietnam	Crous et al. [37]
<i>Fistulinella prunicolor</i>	MG212630	JX889648	–	REH9502	Australia	Halling et al. [67]
<i>Fistulinella ruschii</i>	–	KY888004	KY886205	FLOR:51609	Brazil	Magnago et al. [42]
<i>Fistulinella ruschii</i>	–	NG_060432	NR_156320	FLOR:51611	Brazil	Magnago et al. [42]
<i>Fistulinella ruschii</i>	–	KY888005	KY886209	ICN 192818	Brazil	Magnago et al. [42]
<i>Fistulinella ruschii</i>	–	MT580907	–	CORT:TJB-8329	United States Virgin Islands	This study
<i>Fistulinella</i> sp.	–	–	KF878352	AMV511	Colombia	Vasco-Palacios et al. [31]
<i>Fistulinella viscida</i>	–	HM624054	–	PDD 25185	New Zealand	Li and Yang (unpubl.)
<i>Fistulinella viscida</i>	–	AF456826	–	Strain 238	–	Binder and Bresinsky [72]
<i>Mucilopilus castaneiceps</i>	KT990391	KT990555	–	HKAS50338	China	Wu et al. [8]
<i>Mucilopilus castaneiceps</i>	KT990385	KT990547	–	HKAS71039	China	Wu et al. [8]
<i>Mucilopilus castaneiceps</i>	KF112735	KF112382	–	HKAS75045	China	Wu et al. [7]
<i>Soliococcus polychromus</i>	–	JQ287643	JX888459	J. Trappe 15399	Australia	Trappe et al. [73]
uncultured <i>Fistulinella</i>	–	–	KT757689	uncultured clone AMV511root	Colombia	Vasco-Palacios et al. (unpubl.)
<i>Veloporphyrellus aff. velatus</i>	KF112733	KF112380	–	HKAS57490	China	Wu et al. [7]
<i>Veloporphyrellus alpinus</i>	–	JX984537	–	KUN:HKAS57490	China	Li et al. [74]
<i>Veloporphyrellus conicus</i>	–	JX984543	–	CFMR:BZ1670	Belize	Li et al. [74]
<i>Veloporphyrellus conicus</i>	MH614792	–	–	REH8510	Belize	Vadthananarat et al. [63]
<i>Veloporphyrellus pantoleucus</i>	–	JX984547	–	F:Gomez21232 basidiocarp1	Costa Rica	Li et al. [74]
<i>Veloporphyrellus pseudovelatus</i>	–	JX984540	–	KUN:HKAS52258	China	Li et al. [74]

(continued)

Table 1. Continued.

Original name from GenBank	RPB2	nrLSU	ITS	Specimen/voucher	Origin	Reference(s)
<i>Veloporphyrellum velatus</i>	–	JX984546	–	KUN:HKAS63668	China	Li et al. [74]
<i>Veloporphyrellum vulpinus</i>	–	MN511171	MN511178	LE315547	Viet Nam	Crous et al. [37]

Newly obtained sequences are in bold.

examined and manually edited for accuracy. Newly acquired sequences were submitted to GenBank (<http://www.ncbi.nlm.nih.gov/genbank/>) and samples with accession numbers are listed in bold typeface in Table 1. Homologous sequences from vouchered specimens and from environmental samples were selected and retrieved from GenBank (see Table 1).

Alignments were generated for the ITS, nrLSU, and RPB2 datasets with MAFFT [84] with default conditions for gap openings and gap extension penalties. Alignments were then manually adjusted and concatenated using Geneious v. 11.1.4 [82]. We estimated the best fit substitution model for each single alignment using the Bayesian information criterion (BIC) with jModelTest 2 [85] and therefore selected the TIM1 + G, TIM2 + G, and K80 + G models for nrLSU, ITS, and RPB2, respectively. The ITS dataset was not partitioned. A combined nrLSU/ITS/RPB2 analyses focused on the Austroboletoidae as circumscribed by Wu et al. [7,8] was performed. Sequences of *Austroboletus betulae* [3,86] were not included in the analyses because the species was recently inferred to belong in *Aureoboletus* Pouzar within the subfamily Xerocomoideae [5]. *Bothia* and *Solioccasus* sequences were used as outgroup according to Wu et al. [7,8] and Magnago et al. [42]. Phylogenetic trees were constructed with Bayesian inference (BI) and Maximum likelihood (ML) criteria. The partitioned BI was performed with MrBayes v. 3.2.7a [87] 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 10001 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 was computed to obtain estimates for Bayesian posterior probabilities (BPPs). Partitioned ML analyses were performed using RAxML v. 7.3.2 [88] with 1000 bootstrap replicates [89] and the GTRGAMMA model of sequence evolution. Support values from bootstrapping runs (MLB) were mapped on the best ML tree using the “-f a” option of RAxML and “-x 12345” as

a random seed to invoke the novel rapid bootstrapping algorithm. BI and ML analyses were run on the CIPRES Science Gateway [90]. BPP values ≥ 0.95 and MLB values $\geq 70\%$, are reported in the resulting tree (Figure 1). Lower values are exceptionally represented inside parentheses. Branch lengths were estimated as mean values over the sampled trees. Pairwise percent identity values (P %IV) of the ITS sequences were calculated using Geneious v. 11.1.4 [82]. Alignments and phylogenetic trees are available at TreeBASE (www.treebase.org) under ID 26454.

3. Results

3.1. Molecular analyses

Both Bayesian and Maximum Likelihood analyses produced comparable topologies and therefore only Bayesian trees with BPP and MLB values are shown (Figure 1). The nrLSU dataset comprised 92 accessions and 974 characters. The ITS dataset included 76 taxa and 1397 characters. The RPB2 dataset is composed of 39 taxa and 527 characters. The combined dataset comprised 122 specimens (Table 1). The genera *Austroboletus* and *Fistulinella*, as currently morphologically circumscribed, are polyphyletic, as well as *Veloporphyrellum* (Figure 1). Two major strongly supported sister clades were recognized in *Austroboletus*, herein named as I (BPP = 1; MLB = 93%), including the type species *A. dictyotus*, and II (BPP = 1; MLB = 95%). *Austroboletus festivus*, *A. gracilis*, and *A. rionegrensis* are independent evolutionary lineages outside *Austroboletus*. The sequences of *A. subflavidus* form a separate clade (BPP = 1; MLB = 99%) within major clade II. P%IV of the ITS sequences of the *A. subflavidus* clade is 97.3.

Most *Fistulinella* sequences cluster in a clade strongly supported only by the Bayesian analyses (BPP = 1; MLB = 65%) also including *F. gloeocarpa*. *Fistulinella prunicolor* and *F. viscida* fall outside the *Fistulinella* clade. The two *Fistulinella gloeocarpa* collections show a P%IV of 99.4.

3.2. Taxonomy

Austroboletus subflavidus (Murrill) Wolfe, *Bibliotheca Mycologica* 69: 67. 1979 (“1980”) Figures 2 and 3.

MYCOBANK MB 118437

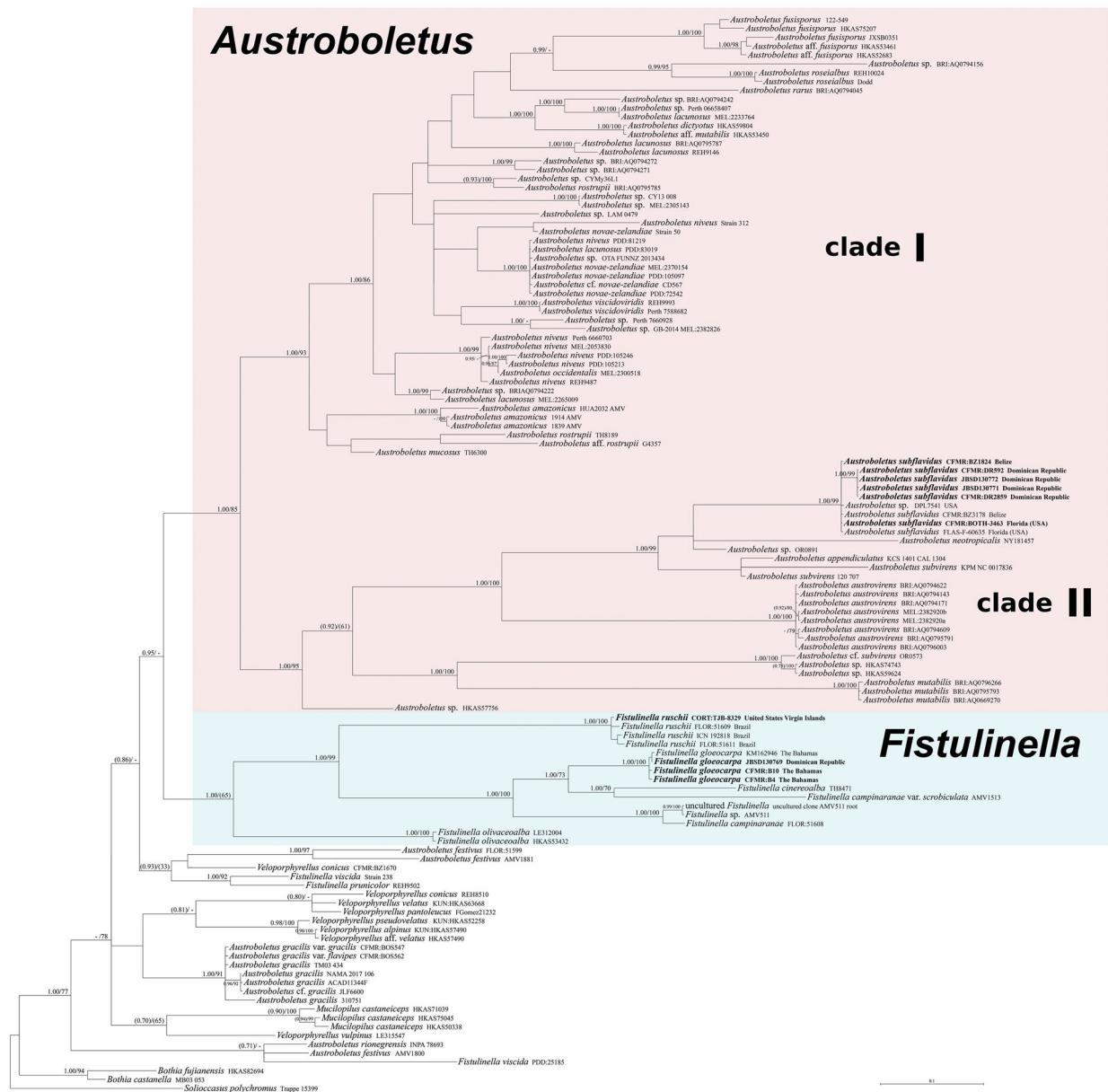


Figure 1. Phylogeny of the genera in Austroboletales based on a Bayesian and Maximum likelihood inference analyses of a combined matrix of three nuclear gene regions (nrLSU, ITS, and RPB2). Bayesian posterior probability (BPP) values (in bold) ≥ 0.95 and Maximum likelihood bootstrap (MLB) values $\geq 70\%$ are shown on the branches. Lower values are exceptionally represented inside parentheses. Newly sequenced collections are in bold.

Basionym: *Tylophilus subflavidus* Murrill, Mycologia 30 (5): 521. 1938.

≡ *Boletus subflavidus* (Murrill) Murrill, Mycologia 30 (5): 525. 1938

≡ *Boletellus subflavidus* (Murrill) Snell, Mycologia 33 (4): 422. 1941.

≡ *Porphyrellus subflavidus* (Murrill) Singer, Farlowia 2 (1): 120. 1945.

Holotype: USA, Florida, Gainesville, under *Pinus* sp., 14 Aug 1937, W.A. Murrill, **15862** (FLAS); **neotype** designated by C.B. Wolfe [12]: USA, Florida, Gainesville, 11 Jul 1938, E. West, Arnold and W.A. Murrill (NY, **isoneotype**: FH); authentic material also preserved in NY and FLAS [91].

Basidiomes small. **Pileus** (1.4) 2.1–5.0 (5.5) cm broad, at first hemispherical then persistently convex

to nearly applanate, not depressed at center, regularly to hardly unevenly shaped by shallow depressions, moderately fleshy, firm at the beginning but progressively softer with age; margin obtuse, steady to faintly wavy-lobed, slightly involute then curved downwards, sterile and not or only a little extending beyond the tubes (up to 1 mm); surface matt, dry, very finely tomentose, soon disrupted and appearing typically areolate with age and showing the whitish (White, Pl. LIII) context beneath, rarely not cracked; cuticle patches color ranging from whitish, ivory, beige or pale cream yellowish (White, Pl. LIII; Maize Yellow, Martius Yellow, Pl. IV; Marguerite Yellow, Pl. XXX; Naphtalene Yellow, Straw Yellow, Pl. XVI) to ochraceous or pale ochraceous-olive (Deep Olive-Buffer, Dark Olive-Buffer, Pl. XL;

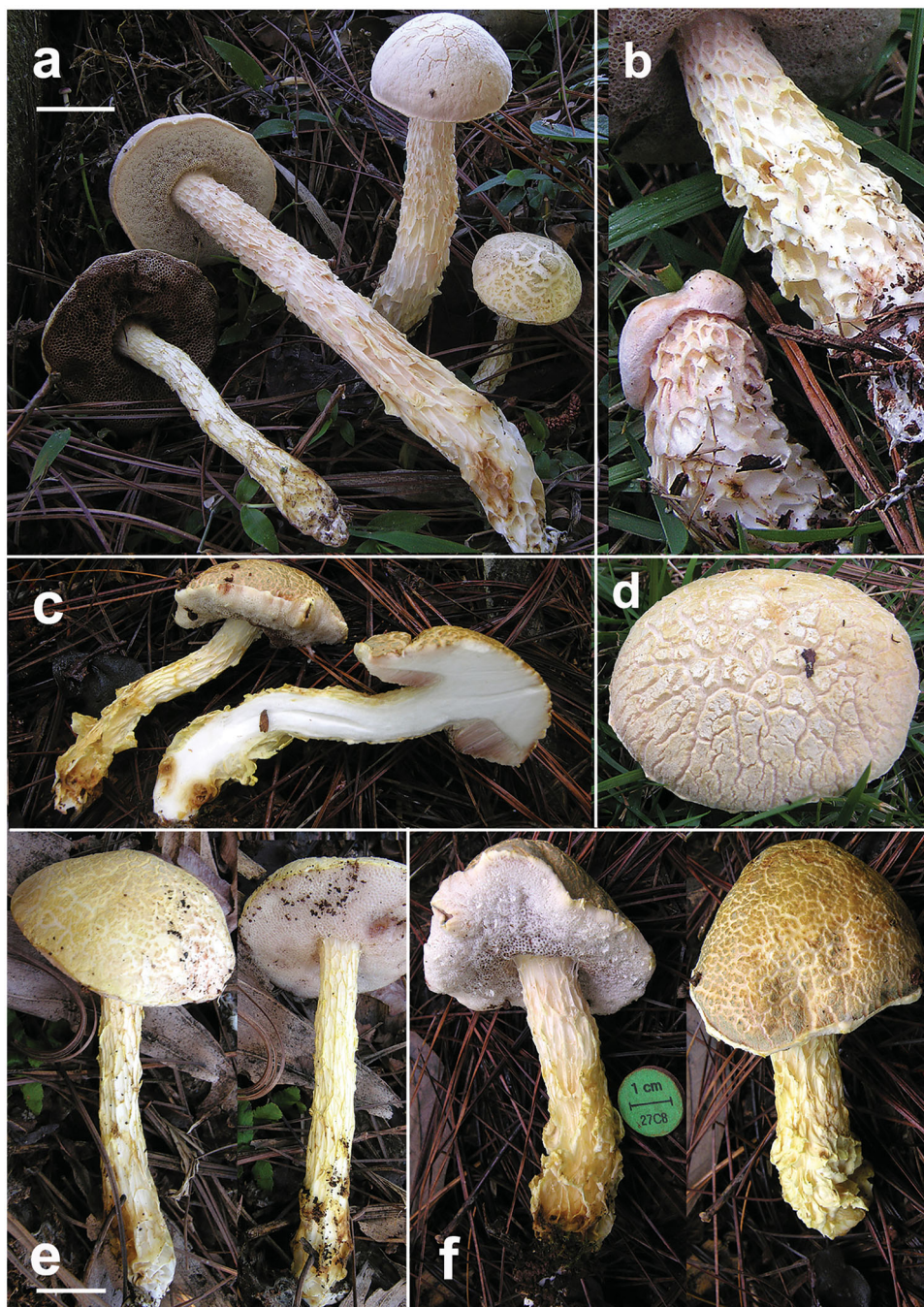


Figure 2. *Austroboletus subflavidus* basidiomes in habitat. (a) JBSD130773 (ANGE1145); (b–d) close up of the stipe, context, and pileus, respectively (b, d: JBSD130774, ANGE1146; c: JBSD130771, ANGE108); (e) JBSD130772 (ANGE388); (f) JBSD130771 (ANGE108). Scale bars: 1 cm. Photos by C. Angelini.

Primuline Yellow, Olive Lake, Buffy Citrine, Pl. XVI; Ecu Olive, Light Yellowish Olive, Isabella Color, Buffy Olive, Pl. XXX); not staining on handling or when injured; subcuticular layer white (White, Pl. LIII). *Tubes* at first thin then increasingly broader, initially shorter or as long as but later longer than the thickness of pileus context (up to 1.4 cm long), adnate at first but soon deeply depressed around the stipe apex, whitish (White, Pl. LIII) at first to pale flesh-pink (Flesh-Pink, Venetian Pink, Pl. XIII; Pale Salmon Color, Pl. XIV; Pale Purplish Vinaceous, Pale Grayish Vinaceous, Pl. XXXIX), then pinkish lilac (Pale Lavender Violet,

Pale Mauve, Mauvette, Light Mauve, Pl. XXV; Light Pinkish Lilac, Pl. XXXVII; Pale Brownish Vinaceous, Pl. XXXIX) and finally brownish pink to dirty brownish (Sorghum Brown, Hay's Brown, Light Seal Brown, Pl. XXXIX), unchangeable when cut. *Pores* initially forming a flat surface, later convex to ascendant, at first small then gradually wider (up to 1 mm in diam.), simple, roundish to barely angular at maturity, concolorous with or slightly paler than tubes and very slowly and faintly darkening (Purplish Vinaceous, Livid Brown, Pl. XXXIX) on bruising or when injured, occasionally beaded by scattered watery droplets. *Stipe* (2.9) 4.5–7.5 (10.2)

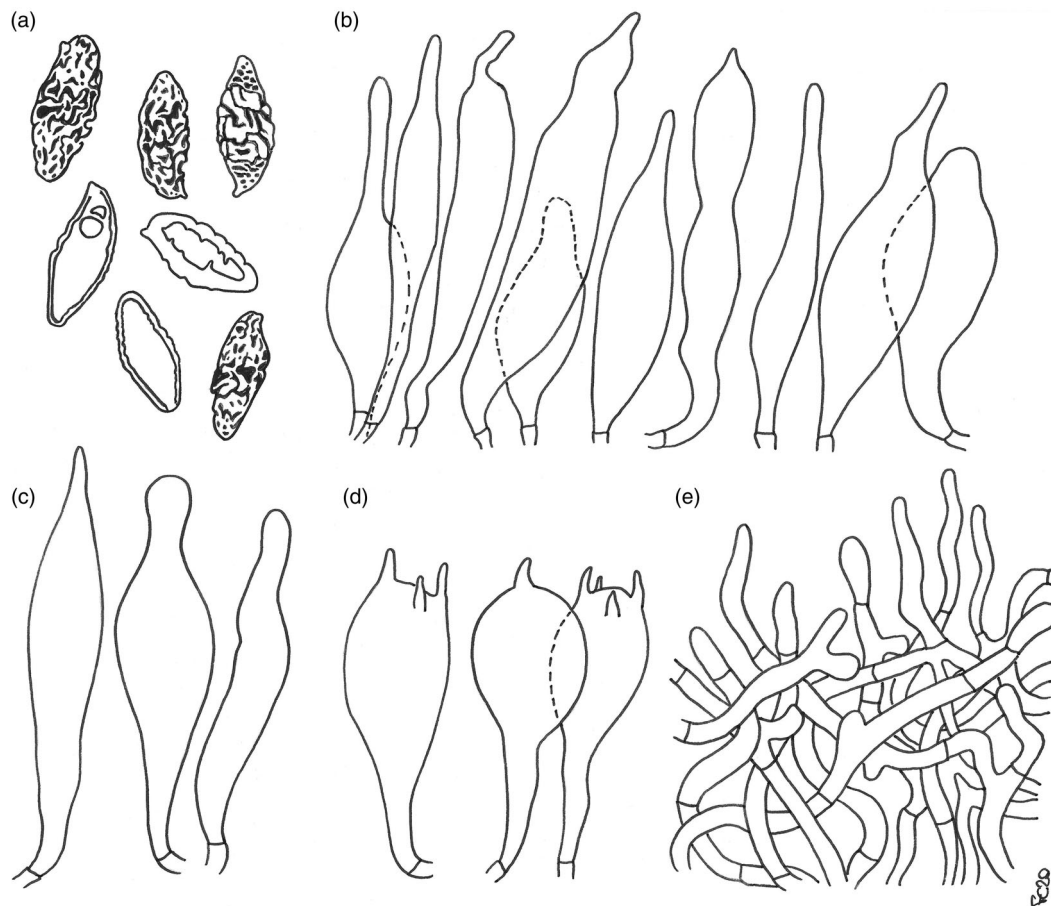


Figure 3. *Austroboletus subflavidus*. Micromorphological features; (a) basidiospores; (b) cheilo- and pleurocystidia; (c) caulocystidia; (d) basidia; (e) elements of the pileipellis. Scale bars: 10 μm (a–d); 20 μm (e). Drawings by F. Costanzo.

\times (0.4) 0.6–1.8 (2.0) cm, constantly longer than pileus diameter, central to slightly off-center, solid, firm, dry but decidedly viscid with moist weather, straight or curved, cylindrical to more frequently gradually swollen toward the base, ending with a short taproot at the very base, apparently evelate; surface prominently reticulate to deeply reticulate-alveolate throughout, reticulate pattern consisting of longitudinally stretched, waxy anastomosing ribs, increasingly coarser and more prominent to distinctly folded toward the base; whitish (White, Pl. LIII) to ivory or beige (Maize Yellow, Pl. IV; Marguerite Yellow, Pl. XXX) in the upper three fourth, pale cream yellowish to ochraceous (Martius Yellow, Pl. IV; Naphtalene Yellow, Straw Yellow, Pl. XVI; Primuline Yellow, Pl. XVI) downwards, usually with pale brown (Chamois, Pl. XXX; Sudan Brown, Pl. III) spots or shades at the stipe base, reticulum concolorous to pale cream yellowish (Martius Yellow, Pl. IV; Naphtalene Yellow, Straw Yellow, Pl. XVI), unchangeable when pressed; basal mycelium white (White, Pl. LIII). *Context* firm when young, later soft textured and eventually flabby in the pileus (up to 2.2 cm thick in the central zone), a little more fibrous in the stipe, white (White, Pl. LIII) throughout, usually with pale brown (Chamois, Pl.

XXX; Sudan Brown, Pl. III) spots or shades at the stipe base; unchangeable when exposed to air; subhymenophoral layer white (White, Pl. LIII); exsiccate pileus beige to pale olive brown (Maize Yellow, Pl. IV; Marguerite Yellow, Pl. XXX; Dark Olive-Buff, Pl. XL), hymenophore dull brown (Dull Brown, Pl. XXX), stipe and context beige (Maize Yellow, Pl. IV; Marguerite Yellow, Pl. XXX). *Odor* indistinct to faintly fruity. *Taste* bitter. *Spore print* not obtained. *Macrochemical spot-test reactions*: 30% KOH: none; 25% NH_4OH : pinkish on pileus, none on context.

Basidiospores [122/7/4] (13.1) 15.9 ± 1.15 (19.5) \times (5.5) 7.0 ± 0.58 (8.7) μm , $Q = (1.76) 1.87\text{--}2.61$ (2.68), $Q_m = 2.26 \pm 0.16$, $V = 416 \pm 89 \mu\text{m}^3$ (including ornamentation), inequilateral, ellipsoid-fusiform, ellipsoid to broadly ellipsoid in side view, broadly ellipsoid to amygdaliform in face view, distinctly verrucose in central part by disruption of the outer wall, minutely pitted or furrowed to form irregular isolated, short rounded-tuberculate warts, or sinuous confluent meandering ridges 0.1–0.7 μm high, becoming progressively less pronounced toward both the apex and the distal end which appear minutely perforate-punctate or porose to nearly smooth, apex rounded, with a short apiculus and usually with a less ornamented suprahilar

applanation or shallow depression, often with a shallow abaxial depression close to the distal end and with an adaxial swelling, moderately thick-walled (0.5–1.0 μm), honey yellow colored in water, and 5% KOH, having one, less frequently two or three large oil droplets when mature, rarely pluri-guttulate, inamyloid to faintly dextrinoid, strongly cyanophilic, and with a weak metachromatic reaction. *Basidia* 27–49 (51) \times 12–19 μm ($n=18$), subclavate to clavate or broadly clavate, moderately thick-walled (0.3–0.8 μm), predominantly 4-spored but also 1-, 2-, or 3-spored, usually bearing relatively short sterigmata (2–5 μm) (sterigmata up to 6 μm long in 1-spored basidia), hyaline to pale yellowish and seldom containing scattered straw-yellow oil guttles in water and 5% KOH, bright yellow (inamyloid) in Melzer's, without basal clamps; basidioles faintly clavate to clavate, similar in size to basidia. *Cheilocystidia* (33) 35–65 (70) \times 7–10 (12) μm ($n=12$), uncommon, moderately slender, projecting straight to sometimes flexuous, irregularly cylindrical or cylindrical fusiform to fusiform with a narrow and long neck, sometimes mucronate, less frequently ventricose fusiform, with rounded to subacute tip, smooth, moderately thick-walled (0.5–0.8 μm), hyaline to pale yellowish in water and 5% KOH, bright yellow (inamyloid) in Melzer's, without epiparietal encrustations. *Pleurocystidia* (36) 43–69 (73) \times 8–12 μm ($n=9$), infrequent, size, shape, color, and chemical reactions similar to cheilocystidia, occasionally lageniform, subclavate, mucronate to subcapitate. *Pseudocystidia* not recorded. *Pileipellis* a trichoderm consisting of strongly interwoven, elongated, frequently branched, filamentous and sinuous to cylindrical hyphae not to moderately embedded in gelatinous matter; terminal elements 27–100 \times 4–15 μm , long and slender, filamentous and sinuous or short cylindrical to cystidioid, apex rounded-obtuse to more rarely pointed, thick-walled (up to 1.3 μm), hyaline to pale straw yellow in water and 5% KOH, golden yellow (inamyloid) in Melzer's, smooth to occasionally ornamented by a very subtle granular epiparietal encrustation; 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, 2–11 μm wide, hyaline to very pale yellowish in water and 5% KOH; the stipe apex covered by a layer 300–400 μm thick of strongly entangled filamentous and sinuous, frequently branched hyphae 2–6 μm broad, having a wall up to 0.3 μm thick, heavily embedded in gelatinous matter, giving rise in the outermost part to a well-developed caulohymenial layer consisting of caulobasidioles, projecting *caulocystidia* similar in shape, size, color and

chemical reactions to hymenial cystidia, (50) 53–57 \times (8) 10–14 μm ($n=5$), having a wall up to 0.8 μm thick and very sparse caulobasidia mostly 1-, 2-, and 3-spored, 44–51 \times 10–14 μm , sterigmata up to 6 μm long ($n=3$). *Lateral stipe stratum* under the caulohymenium usually absent or not differentiated from the underlying layer but occasionally present, of the "boletoid type", 30–40 μm thick and consisting of divergent, inclined and running toward the external surface, loosely intermingled and branched hyphae remaining separate and heavily embedded in a gelatinous substance. *Stipe trama* composed of densely arranged, subparallel to moderately interwoven, filamentous, smooth, inamyloid hyphae, 3–16 μm broad. *Hymenophoral trama* bilateral divergent of the "Boletus-type", with slightly to strongly divergent, recurved-arcuate and loosely arranged, not-branched, distantly septate and generally not restricted at septa, gelatinous hyphae (lateral strata hyphae in transversal section not touching each other, (3) 4–8 (9) μm apart, 3–10 μm broad), hyaline to very pale yellowish in water and 5% KOH, inamyloid in Melzer's; lateral strata (20) 30–40 (50) μm thick, mediostratum (15) 20–30 (40) μm thick, axially arranged, consisting of a tightly adpressed, non-gelatinous bundle of hyphae, 3–8 μm broad, more frequently septate; in Congo Red the mediostratum is darker than the lateral strata. *Oleipherous hyphae* scattered although more frequently observed in the hymenium and basal stipe trama, golden yellow in 5% KOH and Melzer's. *Clamp connections* absent in all tissues. *Ontogenetic development* probably gymnocarpic.

Edibility unknown.

Ecology and phenology: solitary to scattered or gregarious, growing on soil among litter in association with *Pinus occidentalis* in the Dominican Republic. Elsewhere associated with other pine trees (*P. palustris*, *P. caribaea*, etc.) and oaks (*Quercus marilandica*, *Q. minima*, *Q. laurifolia*, *Q. virginiana*, *Q. oleoides*, *Q. humboldtii*, etc.). Apparently uncommon at least in the Dominican Republic, fairly common to infrequent or occasional elsewhere. June to January.

Known distribution: eastern North America, eastern, and south-eastern USA (New Jersey south to Florida and west to Texas) down into the Gulf coastal plain and Mexico, Belize and Costa Rica in mainland Central America south to Colombia in northern South America, in the Greater Antilles Islands of the Caribbean reported from the Dominican Republic.

Examined material: DOMINICAN REPUBLIC, La Vega Province, Jarabacoa, Buena Vista, 19°11'09.3"N 70°35'16.9"W, 660 m, 22 Dec 2013, a single mature specimen, under *P. occidentalis*, C.

Angelini (JBSD130771, ANGE108, and MG775); same loc., 06 Dec 2014, a single middle-aged specimen, C. Angelini (JBSD130772, ANGE388, and MG776); same loc., Golf Club, 19°11'12.5"N 70°35'25.5"W, 800 m, 03 Jan 2020, several specimens in all developmental stages, C. Angelini (JBSD130773 and ANGE1145); same loc., 03 Jan 2020, three specimens two of which mature and the other one a primordium, C. Angelini (JBSD130774 and ANGE1146).

Comments: Originally described from northern Florida as a member of *Tylophilus* by Murrill [92], the species was then recombined in *Boletellus* Murrill by Snell [93] and subsequently transferred to *Porphyrellus* E.-J. Gilbert by Singer [94]. Some decades later Wolfe [12] placed it in *Austroboletus* where it is currently retained based on morphological and molecular inference.

Austroboletus subflavidus is readily distinguished among congeneric species based on the small to medium-sized basidiomes (pileus up to 11 cm diam. and stipe up to 14.5 cm long and 5 cm wide), pileus surface dry and becoming rimose-areolate with age, whitish beige or pale cream yellowish to ochraceous olive, occasionally with a pale pinkish tinge, pinkish hymenophore, slender, deeply reticulate-alveolate, whitish beige to yellowish stipe usually showing brownish shades or patches at the base, white context and basal mycelium, unchanging tissues on bruising or injury, bitterish to bitter taste, ellipsoid-fusiform to amygdaliform, strongly cyanophilic basidiospores which are minutely pitted forming short round-warted or meandering fissured-ridged medial ornamentation and becoming rugulose-punctate to nearly smooth proximally and distally, trichoderm pileipellis consisting of filamentous to cylindrical hyphae and the occurrence in temperate to tropical environments in association with Fagaceae and Pinaceae [12,14,24,25,29,51,92,94–99]. In mainland regions *A. subflavidus* is usually found under a wide array of pine (belonging to both *Pinus* subgen. *Pinus* and *P.* subgen. *Strobus*) and oak trees [20,29,94,96,98,100]. In the Dominican Republic, it appears to be associated exclusively with five-needled *P. occidentalis* in mountain woodlands ([29]; this study).

When compared with congeneric American species, *A. subflavidus* is practically unmistakable but reveals a slight resemblance with other extralimital pale colored *Austroboletus*, such as *A. niveus* (G. Stev.) Wolfe, *A. eburneus* Watling & N.M. Greg., *A. roseialbus* Fechner, Bonito, Lebel, & Halling and *A. appendiculatus* Semwal *et al.*

Confident morphological identification criteria for distinguishing *A. niveus* from *A. subflavidus* include viscid pileus and stipe surface with age,

slightly longer and narrower, elongate subfusiform to cylindrical basidiospores [(14.5) 17–19 (21.8) × (4) 4.5–6.0 (6.8) μm] with a very subtle granular punctate, rugulose ornamentation distributed over the entire surface, lageniform, broader hymenial cystidia (52–75 × 12–23 μm), no staining reaction with NH₄OH on pileus and the occurrence with *Agathis* (Araucariaceae), *Nothofagus* (Nothofagaceae), *Eucalyptus*, and *Leptospermum* (Myrtaceae) in Oceania (Australia including Tasmania and New Zealand) [12,14,19,34,36,101–105]. A color picture of *A. niveus* (incorrectly named *A. eburneus*) taken by R.E. Halling in Queensland has recently been published in Mikšík [106].

Austroboletus eburneus is separated from *A. subflavidus* by the non-areolate pileus surface, elongate fusiform to cylindrical subfusiform, narrower basidiospores [(14.5) 15.5–17.5 (19) × 4.4–5.5 μm] with an overall very slightly granular-punctate, rugulose ornamentation and the occurrence in Australia in association with *Allocasuarina littoralis* (Casuarinaceae) and *Eucalyptus* spp. (Myrtaceae) [19,34].

The recently described *A. roseialbus* barely recalls *A. subflavidus* phenotypically in the general appearance but is easily discriminated on account of the generally smaller size (pileus 3–5 cm broad), viscid-glutinous pileal surface, slimmer (5–7 mm wide) and sticky stipe with cottony surface showing a delicately reticulate pattern, smaller basidiospores (11.2–14 × 6.3–7 μm, $Q_m = 1.8$) with an alveolate-reticulate equatorial ornamentation, smaller basidia (28–35 × 10–14 μm) and the occurrence on the other side of the Pacific Ocean in wet sclerophyll forests under Myrtaceae and Casuarinaceae in New South Wales, Australia [26].

Finally, *A. appendiculatus* differs from *A. subflavidus* by the pale brown pileus surface, yolk yellow or golden yellow to pale orange stipe, mild taste, slightly shorter basidiospores (14.2–16.5 × 7.3–9.1 μm, $Q_m = 1.83$), clavate to subclavate or subventricose, larger caulocystidia (40–70 × 11–20 μm) and the occurrence under *Shorea robusta* (Dipterocarpaceae) in India [49].

Fistulinella gloeocarpa Pegler, Kew Bulletin Additional Series 9: 591. 1983 Figures 4 and 5.

MYCOBANK MB 124413

Holotype: Lesser Antilles, Martinique, Terreville, on soil in secondary mesophytic forest, 200 m, 10 Oct 1975, J.P. Fiard, 611 A, B (K)

Basidiomes small. *Pileus* (1.5) 2.0–5.0 (5.5) cm broad, at first hemispherical then persistently convex and finally broadly pulvinate-flattened, sometimes slightly depressed at center, regularly to hardly unevenly shaped by shallow depressions, moderately fleshy, firm at the beginning but progressively softer with age, flabby in old basidiomes; margin obtuse,

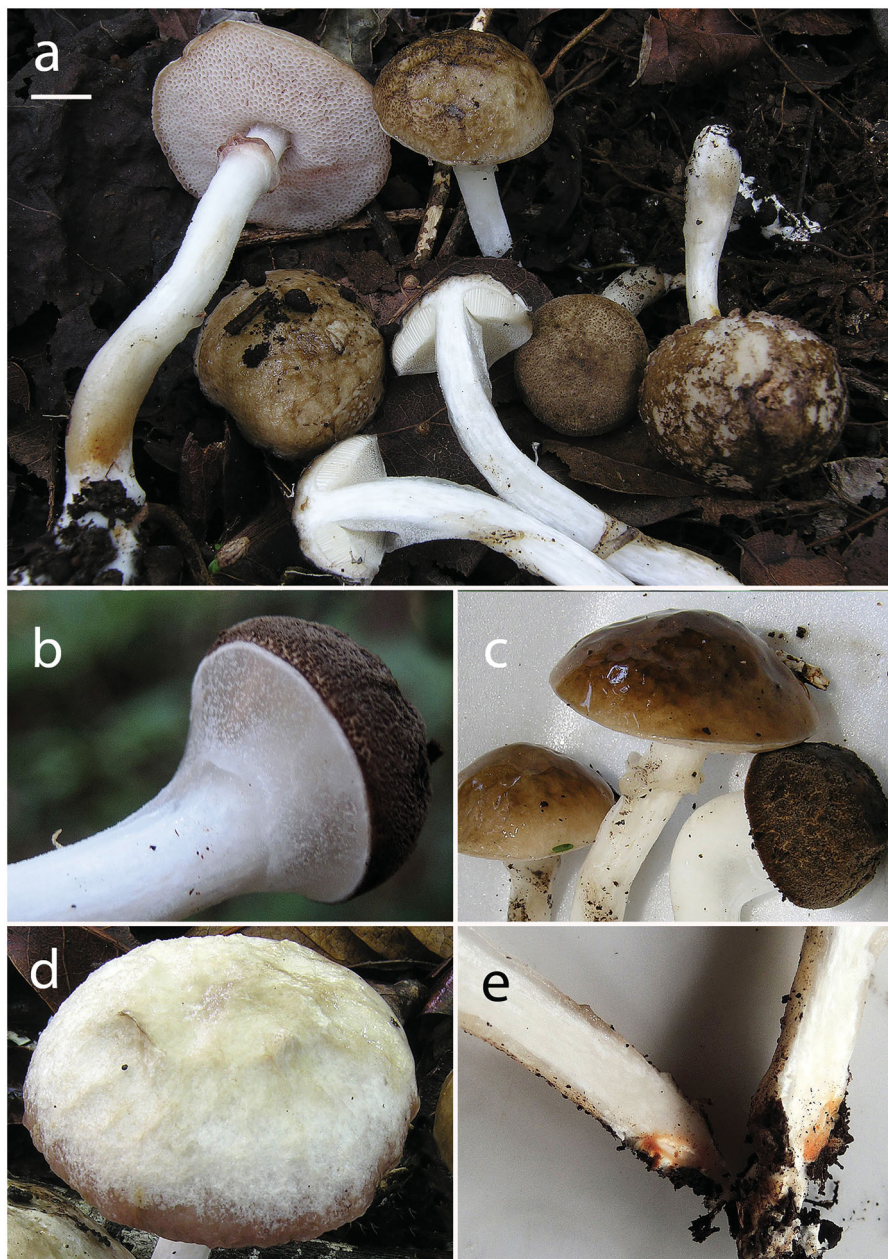


Figure 4. *Fistulinella gloeocarpa* basidiomes in habitat. (a) JBSD130769 (ANGE969); (b–d) details of the pileus in various stages of age (b: JBSD130769, ANGE969; c, d: JBSD130770, ANGE970); (e) close up on the pinkish ochraceous spots in the context of the stipe base, JBSD130769 (ANGE969). Scale bars: 1 cm. Photos by C. Angelini.

steady to faintly wavy-lobed, initially slightly involute soon curved downwards and finally nearly completely plane, not or only a little extending beyond the tubes; surface matt, in the early developmental stages with an innermost gelatinous pellicle underlying a dry, very finely rugulose-granulose outermost layer, later progressively smooth and glabrous, sometimes hammered to delicately wrinkled or coarsely ridged-reticulate (scrobiculate) due to the coagulation of the gelatinous layer, always strongly glutinous with age, irrespective of the weather conditions, not cracked; cuticle decidedly variable in color depending on the weather, ranging from pure white, whitish or pale grayish white to pale brownish gray (White, Pl. LIII; Pale Drab-Gray, Light Grayish Olive, Light Drab, Drab, Pl. XLVI) when

rainy but typically darker, mouse gray or slate gray to brown, dark brown or blackish brown (Mouse Gray, Deep Mouse Gray, Iron Gray, Pl. LI; Sudan Brown, Antique Brown, Argus Brown, Raw Umber, Pl. III; Buckthorn Brown, Dresden Brown, Mummy Brown, Pl. XV; Dark Mouse Gray, Blackish Mouse Gray, Plate LI) when dry, in young specimens always with a narrow white (White, Pl. LIII) marginal rim; not staining on handling or when injured; subcuticular layer white (White, Pl. LIII) to mouse gray or slate gray (Mouse Gray, Deep Mouse Gray, Iron Gray, Plate LI). *Tubes* at first thin then increasingly broader and decidedly longer than the thickness of the pileus context (up to 1.8 cm long), adnexed to deeply depressed around the stipe apex to nearly free, whitish (White, Pl. LIII) at first then

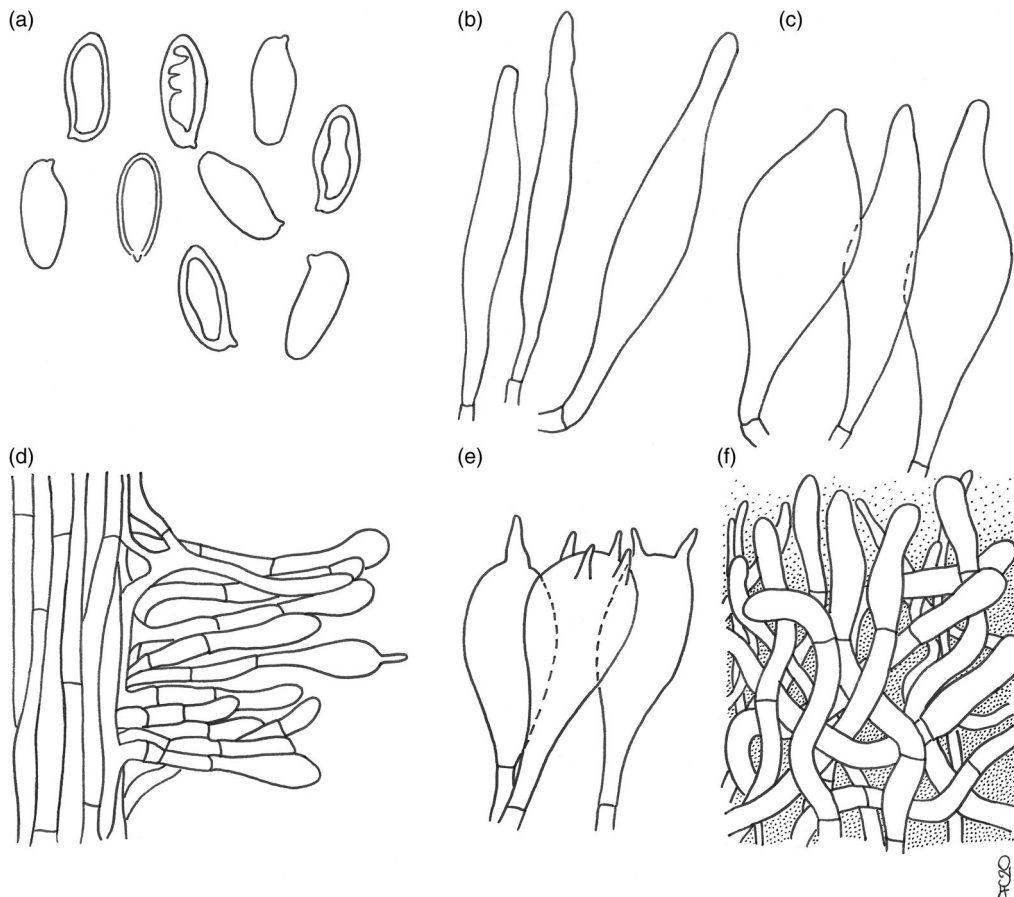


Figure 5. *Fistulinella gloeocarpa*. Micromorphological features; (a) basidiospores; (b) cheilocystidia; (c) pleurocystidia; (d) stipitipellis; (e) basidia; (f) elements of the pileipellis. Scale bars: 10 μ m (a–c, e); 20 μ m (d, f). Drawings by F. Costanzo.

whitish pink to pale flesh-pink, light pinkish lilac (Light Buff, Pl. XV; Seashell Pink, Pale Salmon Color, Pl. XIV; Flesh-Pink, Chatenay Pink, Pl. XIII; Pale Purplish Vinaceous, Pale Grayish Vinaceous, Pl. XXXIX; Light Pinkish Lilac, Pl. XXXVII; Brownish Vinaceous, Deep Brownish Vinaceous, Pl. XXXIX) at maturity and further darkening up to cocoa brown (Sayal Brown; Wood Brown, Pl. XL) in old fruiting bodies, unchangeable when cut. *Pores* initially hidden by a thick, colorless, glutinous veil which soon disrupts revealing the fertile tissue underneath; at the beginning forming a flat surface, later slightly convex to ascendant, at first relatively small then gradually wider (up to 2 mm in diam.), simple, roundish to barely angular at maturity, concolorous with the tubes and not staining on bruising or when injured. *Stipe* (3.0) 5.0–7.5 (8.0) \times (0.4) 0.6–1.1 (1.3) cm, usually longer than or less frequently as long as the pileus diameter at maturity, central to slightly off-center, solid, firm, straight or curved, cylindrical to more frequently slightly swollen toward the base, ending with a short taproot at the very base; entirely enveloped by a thick, colorless, glutinous membrane which soon disrupts in velar remnants forming an ascending, persistent glutinous annulus located in the upper part of the stipe, eventually becoming cocoa brown (Sayal

Brown; Wood Brown, Pl. XL) due to spore discharge; very finely pruinose to smooth and glabrous, devoid of reticulum; white (White, Pl. LIII) throughout but usually with cream yellowish, ochraceous yellow (Martius Yellow, Pl. IV; Naphtalene Yellow, Straw Yellow, Pl. XVI; Primuline Yellow, Pl. XVI) to bright flesh-pink (Light Coral Red, Pl. XIII; Salmon Color, Apricot Buff, Pl. XIV) spots or shades at the stipe base, unchangeable when pressed; basal mycelium white (White, Pl. LIII), rhizomorphs brownish (Mikado Brown, Pl. XXIX). *Context* firm when young, later soft textured and eventually flabby in the pileus (up to 0.7 cm thick in the central zone), a little more fibrous in the stipe, white (White, Pl. LIII) throughout but in young specimens with a mouse gray or slate gray (Mouse Gray, Deep Mouse Gray, Iron Gray, Plate LI) band just beneath the cuticle, with cream yellowish, ochraceous yellow (Martius Yellow, Pl. IV; Naphtalene Yellow, Straw Yellow, Pl. XVI; Primuline Yellow, Pl. XVI) to bright pinkish (Light Coral Red, Pl. XIII; Salmon Color, Apricot Buff, Pl. XIV) spots or shades at the stipe base; unchangeable when exposed to air; subhymenophoral layer white (White, Pl. LIII); exsiccate pileus dull grayish to brownish (Pale Drab-Gray, Light Grayish Olive, Light Drab, Drab, Pl. XLVI), hymenophore flesh-pink to cocoa brown

(Sayal Brown; Wood Brown, Pl. XL), stipe and context whitish to beige (White, Pl. LIII; Maize Yellow, Pl. IV; Marguerite Yellow, Pl. XXX). *Odor* indistinct. *Taste* mild. *Spore print* cocoa brown (Sayal Brown; Wood Brown, Pl. XL). *Macrochemical spot-test reactions*: 30% KOH: staining wine red everywhere; 25% NH₄OH: none.

Basidiospores [70/7/3] (10.3) 12.8 ± 1.00 (16.2) \times (4.5) 5.3 ± 0.34 (6.4) μm , $Q = (2.00) 2.03\text{--}2.75$ (2.84), $Q_m = 2.40 \pm 0.17$, $V = 193 \pm 35 \mu\text{m}^3$, inequilateral, ellipsoid fusiform to fusiform in side view, ellipsoid to ellipsoid fusiform in face view, smooth, apex rounded, with a short apiculus, usually with a shallow suprilar depression and a slightly pronounced adaxial swelling, moderately thin-walled (0.3–0.5 μm), straw yellow colored in water and 5% KOH, having one, less frequently two or three large oil droplets when mature, rarely pluri-guttulate, inamyloid, strongly cyanophilic and with an ortochromatic reaction. *Basidia* (21) 23–38 (40) \times 10–14 μm ($n = 20$), subclavate to clavate, moderately thick-walled (0.3–0.8 μm), predominantly 4-spored but also 1-, 2-, or 3-spored, usually bearing relatively short sterigmata (2–5 μm) (sterigmata up to 8 μm long in 1-spored basidia), hyaline to pale yellowish and seldom containing scattered straw-yellow oil guttles in water and 5% KOH, bright yellow (inamyloid) in Melzer's, without basal clamps; basidioles cylindrical-clavate, faintly clavate to clavate, similar in size to basidia. *Cheilocystidia* (37) 39–56 (60) \times 5–9 μm ($n = 13$), common, moderately slender, projecting straight to sometimes flexuous, irregularly cylindrical or cylindrical fusiform to narrowly fusiform, 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* (32) 36–58 (65) \times (6) 8–13 μm ($n = 10$), infrequent, color, and chemical reactions similar to but with a different shape, fusiform to ventricose fusiform or lageniform and broader than cheilocystidia. *Pseudocystidia* not recorded. *Pileipellis* an ixotrichoderm consisting of interwoven, elongated, frequently branched, filamentous and sinuous to cylindrical, disarticulating and easily detached hyphae heavily embedded in gelatinous matter; terminal elements 22–135 \times (4) 5–22 μm , long and slender, filamentous and sinuous to large cylindrical or sausage-shaped, apex rounded-obtuse, thick-walled (up to 2 μm), hyaline to very pale yellowish in water and 5% KOH, golden yellow (inamyloid) in Melzer's, smooth to sometimes ornamented by a very subtle granular epiparietal encrustation; 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, 5–10 μm wide, hyaline to very pale yellowish in water and 5% KOH; the stipe apex covered by a layer 100–150 μm thick of strongly entangled filamentous and sinuous, frequently branched hyphae 2–5 μm broad, having a wall up to 0.3 μm thick, heavily embedded in gelatinous matter, giving rise in the outermost part to disrupted tufts of projecting parallel to subparallel and anticlinally arranged, septate hyphae; terminal elements short cylindrical to irregularly cylindrical or subclavate to peanut-shaped or acorn-shaped, 15–54 \times 7–10 μm , occasionally filamentous and up to 80 \times 4 μm , apex rounded-obtuse; caulohymenial elements not differentiated or nearly so, caulobasidia infrequent, mostly 1- and 2-spored, 35–45 \times 7–10 μm , sterigmata up to 7 μm long ($n = 6$), caulocystidia not observed. *Lateral stipe stratum* absent. *Stipe trama* composed of confusedly and densely arranged, subparallel to moderately interwoven, filamentous, smooth, inamyloid hyphae, 4–22 μm broad. *Hymenophoral trama* bilateral divergent of the "Boletus-type", with slightly to strongly divergent, recurved-arcuate and loosely arranged, not-branched, distantly septate and generally restricted at septa, gelatinous hyphae (lateral strata hyphae in transversal section not touching each other, (4) 5–12 (15) μm apart, 5–12 μm broad), hyaline to very pale yellowish in water and 5% KOH, inamyloid in Melzer's; lateral strata (20) 30–80 (90) μm thick, mediostratum (10) 20–40 (50) μm thick, axially arranged, consisting of a tightly adpressed, non-gelatinous bundle of hyphae, 2–8 μm broad, more frequently septate; in Congo Red the mediostratum is darker than the lateral strata. *Oleiferous hyphae* scattered although more frequently observed in the basal stipe trama, golden yellow to brownish in 5% KOH and Melzer's. *Clamp connections* absent in all tissues. *Ontogenetic development* probably hemiangiocarpic (monovelangiocarpic) due to the presence of a thick, glutinous and colorless, universal veil enveloping the entire basidiomes.

Edibility unknown.

Ecology and phenology: gregarious, growing on limestone among litter in a seasonally dry and moist anthropized lowland mixed stand under a large array of neotropical broadleaved trees including *Coccoloba diversifolia* (Polygonaceae) and (in Martinique) perhaps also with *Haematoxylum* sp. (Caesalpinoideae), which represent its possible ECM host trees. See Parra et al. [107] for further details on lowland vegetation in the Dominican Republic. Apparently localized in the Dominican Republic. August to March.

Known distribution: to date only known from both the Lesser and Greater Antilles islands of the Caribbean (Martinique, the Bahamas and the

Dominican Republic) and in all probability in south-eastern USA (Florida) in tropical environment (see 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, 01 Dec 2017, several specimens in all developmental stages, C. Angelini (JBSD130769, ANGE969, and MG777); same loc., 02 Dec 2017, several specimens in all developmental stages, C. Angelini (JBSD130770, ANGE970, and MG778); same loc. 28 Mar 2020, a single mature specimen, C. Angelini (ANGE1147).

Comments: Macro-morphologically, anatomically, and ecologically, samples in this study almost perfectly match the description of *Fistulinella gloeocarpa* described by Pegler [55] from Martinique (Lesser Antilles) based on material mostly collected by J.P. Fiard and by Pegler. This species can be recognized on account of the following combination of characters: small basidiomes (pileus up to 5.5 cm diam.), pileus surface at first dry and rugulose-granulose to progressively smooth, sometimes hammered to finely wrinkled-reticulate or scrobiculate and then strongly glutinous with age, ranging from whitish, grayish or grayish brown to dark brown or blackish brown, white to pinkish hymenophore covered by a thick, colorless and glutinous veil in early developmental stages, smooth, glutinous, white stipe usually showing yellowish ochraceous shades or patches at the base and with a persistent glutinous annulus at maturity, white context and basal mycelium, unchanging tissues on bruising or injury, mild taste, cocoa brown spore deposit, reddish staining reaction with KOH on all tissues, ellipsoid-fusiform, smooth, strongly cyanophilic basidiospores, ixotrichoderm pileipellis consisting of filamentous to cylindrical hyphae and the occurrence in low-elevation neotropical environments in alleged association with *Coccoloba diversifolia* (this plant was found at the collection sites in both Martinique and the Dominican Republic) and *Haematoxylum* sp. ([55]; this study).

A considerable amount of specimens collected in the field in the Dominican Republic has given us the opportunity to recognize reliable discriminating features for separating *F. gloeocarpa* from a number of morphological lookalikes occurring in Central and northern South America, such as *F. jamaicensis* (Murrill) Singer, *F. venezuelae* (Singer & Digilio) Singer, *F. mexicana* Guzmán, *F. campinaranae* Singer, *F. cinereoalba* Fulgenzi & T.W. Henkel and *F. ruschii* A.C. Magnago.

Fistulinella jamaicensis is separated from *F. gloeocarpa* by its tiny basidiomes (pileus up to 1.8 cm diam., stipe 3 cm long, 3.5 mm wide), somewhat

areolate pileus surface, smaller basidiospores [(9.5) 10–11 (12) × (4) 4.8–5 (5.2) μm, $Q_m = 2.0$], shorter hymenial cystidia (20–30 × 10–12 μm) with apical ampullaceous neck and apparently an absence of veils [20,22,108,109]. Lewis and Cibula [110] and more recently Bessette et al. [95] provided a re-description of *F. jamaicensis* from southern USA emphasizing characters such as a pileus up to 4.5 cm diam., pinkish or brownish pink than grayish to grayish brown pileus with amber-yellow spots in age, stipe often with brownish scales and spores 8.5–14.5 × 4.5–6.5 μm. Given the several morphological discrepancies when a comparison is made with the original description by Murrill [108], we suspect it does not represent the same taxon.

Fistulinella venezuelae differs by the whitish to yellowish pileus at the margin with yellow ochraceous to tawny center, ochraceous-ferruginous tints in the upper part of the stipe at maturity and pale yellowish to brownish gray mealy punctuations in the lower portion, white context with a pale ochraceous peripheral zone, absence of velar covering, weakly bitterish taste, elongate fusiform-cylindrical, much longer basidiospores [(12) 14.5–21.5 × 4.5–6 (6.5) μm, $Q_m = 3.2$], generally longer hymenial cystidia (up to 93 μm long) usually exhibiting a long and slender neck, a cutis pileipellis with markedly narrower filamentous hyphae [(2) 3.5–10.5 μm wide] and growth in mountain environment in doubtful association with *Alnus acuminata* in Venezuela or in lowland vegetation in the Lesser Antilles (Martinique, Dominica) [14,20,51,55,111–113]. Additional collections of *F. venezuelae* have been made in Puerto Rico, Virgin Islands, and French Guyana (MycPortal).

Guzmán described *F. mexicana* from evergreen lowland cloud forests in the Yucatan peninsula, southern-eastern Mexico [52] in putative association with *Coccoloba* spp. [114]. This species is distinguished from *F. gloeocarpa* by the yellowish brown or grayish, irregularly areolate pileus surface, presence of a colorless mucilaginous volva at the stipe base, slightly shorter basidiospores (8.1–12.2 × 4.1–5.9 μm), smaller, clavate pleurocystidia (24–43 × 5–8 μm), cheilocystidia none, cylindrical-globose caulocystidia (35–48 × 12–16 μm), narrower pileipellis hyphae (2.5–6.5 μm wide) and sometimes with an apparently lignicolous growth [20,30,52,114,115]. This species has most recently been listed for the Mexican state of Quintana Roo by de la Fuente et al. [114].

Even if outwardly very similar, *F. campinaranae* and its var. *scrobiculata* Singer can be discriminated from *F. gloeocarpa* by the presence of a membranous but fugacious whitish ring on the stipe, slightly narrower, dextrinoid basidiospores [(11.5) 12–15

(18) × (3) 4–5 (6) μm, $Q_m = 3.3$], narrower pileipellis hyphae (3.4–10 μm broad), narrower hyphae of lateral stratum (2–6 μm wide) in the hymenophoral trama and the occurrence on rotting wood and decayed stumps or less frequently on humus-sandy soil in Brazilian Amazonian caatinga and campinarana vegetation, in lowland Colombian rainforests dominated by *Pseudomonotes* (Dipterocarpaceae) and along the Brazilian coastal Atlantic Forest (Bahia) under leguminous trees (Fabaceae) [20,31,42,57,116]. This species is also separated from *F. gloeocarpa* based on molecular inference [42]. Regrettably, efforts for extracting DNA from either the holotype collection (not located at INPA) and paratype samples resulted unsuccessful [42].

Fistulinella gloeocarpa and *F. cinereoalba* are two look-alike species and phylogenetically most closely related to each other, being sister species in the molecular analysis (Figure 1). The latter species, however, can be unraveled based on the stipe base devoid of yellowish ochraceous spots, very finely squamulose stipe surface, hymenophore and stipe turning brownish when injured, decidedly longer and slightly narrower, variably dextrinoid basidiospores [12.4–19.8 (24.8) × 3.7–4.9 (6) μm, $Q_m = 3$], aciculate to cylindrical, narrower pleurocystidia (37–61 × 3.7–6.2 μm), narrower pileipellis hyphae (2.4–7 μm broad), narrower hyphae of lateral stratum (2–6 μm wide) in the hymenophoral trama and the occurrence in Guyana in association with *Dicymbe corymbosa* (Fabaceae subfamily Caesalpinioideae) and along the coastal Atlantic Forest in Brazil (Bahia) [27,116–118]. Magnago [118] reports much broader pleurocystidia (43–76 × 10–17 μm) for the Brazilian collections.

In some regards, *F. gloeocarpa* is also similar to *F. ruschii*, however, corroborative features for distinguishing the latter species include the tomentose and mostly dry, chestnut brown to orange-brown pileus surface, cream pinkish stipe, NH_4OH staining reddish orange and yellow on pileus and stipe, respectively, longer and narrower basidiospores [14–18 (22) × 4–5 μm, $Q_m = 3.4$], presence of broadly cylindrical, multiseptate pleurocystidia, narrower pileipellis hyphae (4–11 μm broad), narrower hyphae of lateral stratum (4–7 μm wide) in the hymenophoral trama and the occurrence along the Brazilian coastal Atlantic Forest under caesalpinoid legumes (Fabaceae) and the Virgin Islands of the Caribbean ([118] as “*F. rhytidocystidiata* Magnago & M.A. Neves *ad int.*”, [42]; this study). Based on morphological resemblance and preliminary phylogenetic inference (Figure 1) it appears quite possible that *F. ruschii* and *F. venezuelae* might represent the same taxon (collection TJB-8329 was formerly identified by T.J. Baroni as *F. venezuelae*). Should this

conspecificity be confirmed, *F. venezuelae* would have priority over *F. ruschii* having been described previously than the latter species but further studies are needed to elucidate their taxonomic relationships.

4. Discussion

The bulk of *Austroboletus* based on the data mining and phylogenetic inference (Figure 1) indicates there is a core for the genus, including the type species (clade I). A very small number of species (including *A. subflavidus*) attributed to *Austroboletus* that fall outside the core (clades I and II), suggesting polyphyly, need a closer look and further analyses. Accordingly, the disposition of *A. subflavidus* ultimately results uncertain, nonetheless we feel that any transfer to either a new genus or a new subgenus (corresponding to clade II) would at present be premature.

Macro- and micro-morphological features of Dominican samples of *A. subflavidus* studied herein consistently match those retrievable in the aforementioned available literature but they display, as already pointed out by Ortiz-Santana et al. [29] based on Dominican and Belizean material, generally smaller dimensions and perhaps minor anatomical differences with regard to the North American populations, probably due to geographic distance and different hosts or dissimilar climatic conditions.

Concerning biogeography, *A. subflavidus* shows a broad distribution, spanning from warm temperate to subtropical Atlantic regions of eastern, southeastern USA and Mexico south to the neotropical countries of continental and insular Central America [12,20,25,29,96] and northern South America [31]. All reports of *A. subflavidus* from outside its natural distribution range in the western hemisphere (see, among others, [119–121]) should be carefully re-assessed.

As far as the genus *Fistulinella* is concerned, since it was first described from Martinique [55] *F. gloeocarpa* has not anymore been recollected elsewhere, albeit Vasco-Palacios et al. [31] suggested a possible occurrence in lowland *Pseudomonotes* (Dipterocarpaceae) forests in Colombian Amazonia but did not provide any convincing evidence. Accordingly, the present account is the only documented record of *Fistulinella gloeocarpa* from outside the Lesser Antilles and the first from the Dominican Republic. Indeed, genetic material generated in this study match with a sequence deposited in GenBank (GQ981503, collection KM162946) and obtained by D.J. Lodge from the Bahamas islands, further widening the distribution range of *F. gloeocarpa*. Moreover, three additional molecularly

unconfirmed records of this species have been spotted under *Coccoloba diversifolia* in Florida by J. Bolin (JAB211) and by Alan R. Franck (4662) in 2018 and published online in the mycological website Mushrooms Observer (https://mushroomobserver.org/observer/show_observation/359000).

Unfortunately, it has not been possible to either reexamine the holotype material or paratype collections made by Pegler in Martinique in the '70s preserved at the Royal Botanic Gardens Kew (K). On the other hand, no major morphological discrepancies can be observed when comparing the Dominican collections with the original description [55], despite its evident morphological variability. As a matter of fact, depending on the weather conditions and developmental stages, basidiomes of *F. gloeocarpa* may be extremely mutable concerning their morphological appearance. The most variable characters are the texture and color of the pileal surface; the surface is initially dark colored and finely rugulose-granulose but tends to become much paler, smooth, glutinous, and often typically rugulose-scrobiculate. Neither in the original diagnosis nor in the comments of *F. gloeocarpa* mention is made about the presence of yellowish ochraceous spots at the stipe base [55]. However, a yellowish patch is clearly visible in one of the two color photographs (Pl. 19E-F) accompanying the original description, indicating that this chromatic trait was simply overlooked by Pegler. Likewise Pegler [55] did not report the presence of a ring on the stipe of *F. gloeocarpa* but it might have been removed accidentally by handling or simply gone unnoticed. However, the presence of a thick, persistent glutinous annulus obviously reflects an angiocarpic ontogenetic development and may determine, in addition to the mucilaginous volva reported for *F. mexicana* Guzmán (see below), an emendation of the diagnostic traits of *Fistulinella*, which was thought to be devoid of veils in all its representatives [16,32,55]. It would be advisable, however, to propose such an emendation only when the taxonomic limits of *Fistulinella* are better clarified.

In spite of the fact that morphological differences seem to justify specific separation of *F. gloeocarpa* from the several closely allied species occurring in the same geographic macro-region, some of them (*F. jamaicensis*, *F. mexicana*, and *F. venezuelae*) are still lacking molecular confirmation and further research will be required to confirm their autonomous taxonomic status and mutual phylogenetic relationships. Especially *F. jamaicensis* and *F. mexicana* might finally turn out to be conspecific with *F. gloeocarpa* given morphological affinities and geographic proximity, but until sequenced material from Jamaica and Mexico is not available for

comparison, it will be advisable to maintain these taxa as separate entities.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

References

- [1] Binder M. Zur molekularen Systematische der Boletales: Boletineae und clerodermatineae subordo nov [PhD dissertation]. Regensburg: Nat Fak III-Biol Vorkl Med, Universität Regensburg; 1999.
- [2] Binder M, Hibbett DS. Molecular systematics and biological diversification of Boletales. *Mycologia*. 2006;98(6):971–981.
- [3] Drehmel D, James T, Vilgalys R. Molecular phylogeny and biodiversity of the boletes. *Fungi*. 2008;1(4):17–23.
- [4] Halling RE, Fechner N, Nuhn M, et al. Evolutionary relationships of *Heimioporus* and *Boletellus* (Boletales), with an emphasis on Australian taxa including new species and new combinations in *Aureoboletus*. *Aust Syst Bot*. 2015;28(1):1–22.
- [5] Kuo M, Ortiz-Santana B. Revision of leccinoid fungi, with emphasis on North American taxa, based on molecular and morphological data. *Mycologia*. 2020;112(1):197–211.
- [6] Nuhn ME, Binder M, Taylor AFS, et al. Phylogenetic overview of the Boletineae. *Fungal Biol*. 2013;117(7–8):479–511.
- [7] Wu G, Feng B, Xu JP, et al. Molecular phylogenetic analyses redefine seven major clades and reveal 22 new generic clades in the fungal family Boletaceae. *Fungal Divers*. 2014;69(1):93–115.
- [8] Wu G, Li YC, Zhu XT, et al. One hundred noteworthy boletes from China. *Fungal Divers*. 2016; 81(1):25–188.
- [9] Corner E.J.H. *Boletus* in Malaysia. Singapore: Government Printing Office; 1972.
- [10] Horak E. *Boletellus* and *Porphyrellus* in Papua New Guinea. *Kew Bull*. 1977;31(3):645–652.

- [11] Wolfe CB, Jr, Petersen RH. Taxonomy and nomenclature of the supraspecific taxa of *Porphyrellus*. *Mycotaxon*. 1978;7:152–162.
- [12] Wolfe CB, Jr. *Austroboletus* and *Tylopilus* subg. *Porphyrellus*, with emphasis on North American taxa. *Bibliotheca Mycologica*. 69. Berlin Stuttgart: Cramer; 1980.
- [13] Corner EJH. *Boletus longipes* Masee, a critical Malaysian species. *Garden's Bulletin*, Singapore. 1980;33(2):290–296.
- [14] Pegler DN, Young TWK. A natural arrangement of the Boletales, with reference to spore morphology. *Trans Br Mycol Soc*. 1981;76(1):103–146.
- [15] Singer R. Notes on bolete taxonomy – III. *Persoonia*. 1981;11(3):269–302.
- [16] Singer R. *The Agaricales in modern taxonomy*, 4th ed. Koenigstein: Koeltz Scientific Books; 1986.
- [17] Horak E. Supplementary remarks to *Austroboletus* (Corner) Wolfe (Boletaceae). *Sydowia*. 1980;33:71–87.
- [18] Horak E. Mycogeography in the South Pacific region: Agaricales, Boletales. *Austral J Bot*. 1983; 10:1–41.
- [19] Watling R, Gregory NM. Observations on the boletes of the Cooloola Sandmass, Queensland and notes on their distributions in Australia. *Proc Roy Soc Queensl*. 1986;97:97–128.
- [20] Singer R, Araujo I, Ivory MH. The ectotrophically mycorrhizal fungi of the neotropical lowlands, especially central Amazonia (litter decomposition and ectomycorrhiza in Amazonian forests 2. *Beihefte Zur Nova Hedwigia*. 1983;77:1–352.
- [21] He MQ, Zhao RL, Hyde KD, et al. Notes, outline and divergence times of Basidiomycota. *Fungal Divers*. 2019;99(1):105–367.
- [22] Singer R. The Boletineae of Florida with notes on extralimital species. II. The Boletaceae (Gyroporoideae). *Farlowia*. 1945b;2(2):223–303.
- [23] Smith AH, Thiers HD. *The boletes of Michigan*. Ann Arbor (MI): University of Michigan Press; 1971.
- [24] Bessette AE, Roody WC, Bessette AR. *North American boletes. A color guide to the fleshy pored mushrooms*. Syracuse (NY): Syracuse University Press; 2000.
- [25] Bessette AE, Roody WC, Bessette AR. *Boletes of Eastern North America*. Syracuse (NY): Syracuse University Press; 2016.
- [26] Fechner N, Bonito G, Bougher NL, et al. New species of *Austroboletus* (Boletaceae) in Australia. *Mycol Progress*. 2017;16(8):769–775.
- [27] Fulgenzi TD, Halling RE, Henkel TW. *Fistulinella cinereoalba* sp. nov. and new distribution records for *Austroboletus* from Guyana. *Mycologia*. 2010; 102(1):224–232.
- [28] Halling RE, Osmundson TW, Neves MA. *Austroboletus mutabilis* sp. nov. from northern Queensland. *Muelleria*. 2006;24:31–36.
- [29] Ortiz-Santana B, Lodge DJ, Baroni TJ, et al. Boletes from Belize and the Dominican Republic. *Fungal Divers*. 2007;27:247–416.
- [30] Singer R, García J, Gómez LD. The Boletineae of Mexico and Central America III. *Beihefte Zur Nova Hedwigia*. 1991;102:1–99.
- [31] Vasco-Palacios AM, Lopez-Quintero CA, Franco-Molano AE, et al. *Austroboletus amazonicus* sp. nov. and *Fistulinella campinaranae* var. *scrobiculata*, two commonly occurring boletes from a forest dominated by *Pseudomonotes tropenbosii* (Dipterocarpaceae) in Colombian Amazonia. *Mycologia*. 2014;106(5):1004–1014.
- [32] Watling R. *A manual and source book on the boletes and their allies*. Synopsis Fungorum. 24. Oslo: Fungiflora; 2008.
- [33] Watling R, de Meijer AR. Macromycetes from the State of Paraná, Brazil 5. Poroid and lamellate boletes. *Edinburgh J Bot*. 1997;54(2):231–251.
- [34] Watling R, Li TH. *Australian boletes. A preliminary survey*. Edinburgh: Royal Botanic Garden Edinburgh; 1999.
- [35] Ying JZ. Notes on the genus *Austroboletus* in China. *Agarica*. 1985;6(12):80–89.
- [36] McNabb RFR. The Strobilomycetaceae of New Zealand. *N Z J Bot*. 1967;5(4):532–547.
- [37] Crous PW, Luangsa-Ard JJ, Wingfield MJ, et al. *Fungal planet description sheets: 785–867*. *Persoonia*. 2018;41:238–417.
- [38] Crous PW, Wingfield MJ, Lombard L, et al. *Fungal planet description sheets: 951–1041*. *Persoonia*. 2019;43:223–425.
- [39] Farid A, Gelardi M, Angelini C, et al. *Phylloporus* and *Phylloboletellus* are no longer alone: *Phylloporopsis* gen. nov. (Boletaceae), a new smooth-spored lamellate genus to accommodate the American species *Phylloporus boletinoides*. *Fungal Syst Evol*. 2018;2:341–359.
- [40] Henkel TW, Obase K, Husbands D, et al. New Boletaceae taxa from Guyana: *Binderoboletus segoi* gen. and sp. nov., *Guyanaporus albipodus* gen. and sp. nov., *Singerocomus rubriflavus* gen. and sp. nov., and a new combination for *Xerocomus inundabilis*. *Mycologia*. 2016;108(1):157–173.
- [41] Khmelnitsky O, Davoodian N, Singh P, et al. *Ionosporus*: a new genus for *Boletus longipes* (Boletaceae), with a new species, *I. australis*, from Australia. *Mycol Progress*. 2019;18(3):439–451.
- [42] Magnago AC, Neves MA, da Silveira BRM. *Fistulinella ruschii*, sp. nov., and a new record of *Fistulinella campinaranae* var. *scrobiculata* for the Atlantic Forest, Brazil. *Mycologia*. 2017;109(6): 1003–1013.
- [43] Orihara T, Smith ME. Unique phylogenetic position of the African truffle-like fungus, *Octaviania ivoryana* (Boletaceae, Boletales), and the proposal of a new genus, *Afrocastellanoa*. *Mycologia*. 2017; 109(2):323–332.
- [44] Smith ME, Amses KR, Elliott TF, et al. New sequestrate fungi from Guyana: *Jimtrappea guyanensis* gen. sp. nov., *Castellanea pakaraimophila* gen. sp. nov., and *Costatisporus cyanescens* gen. sp. nov. (Boletaceae, Boletales. *IMA Fungus*. 2015;6(2):297–317.
- [45] Sulzbacher MA, Orihara T, Grebenc T, et al. *Longistriata flava* (Boletaceae, Basidiomycota) – a new monotypic sequestrate genus and species from Brazilian Atlantic Forest. *MycKeys*. 2020; 62:53–73.
- [46] Zhao K, Wu G, Yang ZL. A new genus, *Rubroboletus*, to accommodate *Boletus sinicus* and its allies. *Phytotaxa*. 2014;188(2):61–77.
- [47] Zhao K, Wu G, Halling RE, et al. Three new combinations of *Butyriboletus* (Boletaceae). *Phytotaxa*. 2015;234(1):51–62.

- [48] Das K, Dentinger BTM. *Austroboletus olivaceoglutinosus*, a new mushroom species from Sikkim, India with a distinctive green, glutinous pileus. *Kew Bull.* 2015;70(1):15.
- [49] Tibpromma S, Hyde KD, Jeewon R, et al. Fungal diversity notes 491–602: taxonomic and phylogenetic contributions to fungal taxa. *Fungal Divers.* 2017;83(1):1–261.
- [50] Hennings P. Beiträge zur Flora von Afrika. XXI. Fungi Camerunenses Novi. III. Botanische Jahrbücher Für Systematik. 1901;30:39–57.
- [51] Singer R. Strobilomycetaceae (Basidiomycetes). *Flora Neotropica* 5. New York (NY): Hafner; 1970.
- [52] Guzmán G. El género *Fistulinella* Henn. (= *Ixechnus* R. Heim) y las relaciones florísticas entre México y África. *Boletín de la Sociedad Mexicana de Micología.* 1974;8:53–63.
- [53] Horak E. Synopsis generum Agaricalium (Die Gattungstypen der Agaricales). Waber-Bern: Kommissionsverlag Druckerei Büchler; 1968.
- [54] Horak E. Revision of Malaysian species of Boletales s. l. (Basidiomycota) described by E. J. H. Corner (1972, 1974). Kuala Lumpur: Malayan Forest Records; 2011.
- [55] Pegler DN. Agaric flora of the Lesser Antilles. *Kew Bulletin Additional Series.* London: HMSO; 1983.
- [56] Redeuilh GL, Soop K. Nomenclature et taxinomie des genres affines à *Fistulinella* (Boletaceae) et *Fistulinella lutea* sp.nov. de Nouvelle Zélande. *Bulletin de la Société Mycologique de France.* 2006;122(4):291–304.
- [57] Singer R. Notes on bolete taxonomy – II. *Persoonia.* 1978;9(4):421–438.
- [58] Watling R. Australian boletes: their diversity and possible origins. *Aust Syst Bot.* 2001;14(3):407–416.
- [59] Thiers B. Index Herbariorum: a global directory of public herbaria and associated staff. New York botanical garden's virtual herbarium. <http://sweetgum.nybg.org/ih/>. Accessed 10 July 2020.
- [60] Ridgway R. Color standards and color nomenclature. Washington (DC): Self-published; 1912.
- [61] Roy M, Schimann H, Braga-Neto R, et al. Diversity and distribution of ectomycorrhizal fungi from Amazonian lowland white-sand forests in Brazil and French Guiana. *Biotropica.* 2016;48(1):90–100.
- [62] Orihara T, Lebel T, Ge Z-W, et al. Evolutionary history of the sequestrate genus *Rossbeevera* (Boletaceae) reveals a new genus *Turmalinea* and highlights the utility of ITS minisatellite-like insertions for molecular identification. *Persoonia.* 2016;37:173–198.
- [63] Vadthananarat S, Lumyong S, Raspé O. *Cacaoporus*, a new Boletaceae genus, with two new species from Thailand. *MycKeys.* 2019;54:1–29.
- [64] Hosen MI, Feng B, Wu G, et al. *Borofutus*, a new genus of Boletaceae from tropical Asia: phylogeny, morphology and taxonomy. *Fungal Divers.* 2013;58(1):215–226.
- [65] Young AP, Evans RC, Newell R, et al. Development of a DNA barcoding protocol for fungal specimens from the E.C. Smith Herbarium (ACAD). *Northeast Nat.* 2019;26(3):465–483.
- [66] Porter TM, Skillman JE, Moncalvo JM. Fruiting body and soil rDNA sampling detects complementary assemblage of Agaricomycotina (Basidiomycota, Fungi) in a hemlock-dominated forest plot in southern Ontario. *Mol Ecol.* 2008;17(13):3037–3050.
- [67] Halling RE, Nuhn M, Osmundson T, et al. Affinities of the *Boletus chromapes* group to *Royoungia* and the description of two new genera, *Harrya* and *Australopilus*. *Aust. Systematic Bot.* 2012;25(6):418–431.
- [68] Smith ME, Henkel TW, Aime CM, et al. Ectomycorrhizal fungal diversity and community structure on three co-occurring leguminous canopy tree species in a neotropical rainforest. *New Phytol.* 2011;192(3):699–712.
- [69] Orihara T, Smith ME, Shimomura N, et al. Diversity and systematics of the sequestrate genus *Octaviania* in Japan: two new subgenera and eleven new species. *Persoonia.* 2012;28:85–112.
- [70] Halling RE, Baroni TJ, Binder M. A new genus of Boletaceae from eastern North America. *Mycologia.* 2007;99(2):310–316.
- [71] Zeng NK, Su MS, Liang ZQ, et al. A geographical extension of the North American genus *Bothia* (Boletaceae, Boletales) to East Asia with a new species *B. fujianensis* from China. *Mycol Progress.* 2015;14(1):6.
- [72] Binder M, Bresinsky A. *Retiboletus*, a new genus for a species-complex in the Boletaceae producing retipolides. *Feddes Repert.* 2002;113(1–2):30–40.
- [73] Trappe JM, Castellano MA, Halling RE, et al. Australasian sequestrate fungi 18: *Soliococcus polychromus* gen. & sp. nov., a richly colored, tropical to subtropical, hypogeous fungus. *Mycologia.* 2013;105(4):888–895.
- [74] Li YC, Ortiz-Santana B, Zeng NK, et al. Molecular phylogeny and taxonomy of the genus *Veloporphyrellus*. *Mycologia.* 2014;106(2):291–306.
- [75] Vizzini A, Consiglio G, Marchetti M, et al. Insights into the Tricholomatineae (Agaricales, Agaricomycetes): a new arrangement of Biannulariaceae and *Callistosporium*, Callistosporiaceae fam. nov., *Xerophorus* stat. nov., and *Pleurocollybia* incorporated into *Callistosporium*. *Fungal Diversity.* 2020;101(1):211–259.
- [76] Gardes M, Bruns TD. ITS primers with enhanced specificity for basidiomycetes-application to the identification of mycorrhizae and rusts. *Mol Ecol.* 1993;2(2):113–118.
- [77] White TJ, Bruns TD, Lee S, et al. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In Innis MA, Gelfand DH, Sninsky J, et al., editors. *PCR protocols: a guide to methods and applications.* San Diego (CA): Academic Press; 1990. pp. 315–322.
- [78] Rehner SA, Samuels GJ. Taxonomy and phylogeny of *Gliocladium* analysed from nuclear large subunit ribosomal DNA sequences. *Mycol Res.* 1994;98(6):625–634.
- [79] Vilgalys R, Hester M. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *J Bacteriol.* 1990;172(8):4238–4246.
- [80] Liu YJ, Whelen S, Hall BD. Phylogenetic relationships among Ascomycetes: evidence from an

- RNA polymerase II subunit. *Mol Biol Evol.* 1999; 16(12):1799–1808.
- [81] Matheny PB, Wang Z, Binder M, et al. Contributions of *rpb2* and *tef1* to the phylogeny of mushrooms and allies (Basidiomycota, Fungi). *Mol Phylogenet Evol.* 2007;43(2):430–451.
- [82] Kearse M, Moir R, Wilson A, et al. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics.* 2012;28(12):1647–1649.
- [83] Altschul SF, Gish W, Miller W, et al. Basic local alignment search tool. *J Mol Biol.* 1990;215(3):403–410.
- [84] Katoh K, Misawa K, Kuma K, et al. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Res.* 2002;30(14):3059–3066.
- [85] Darrriba D, Taboada GL, Doallo R, et al. jModelTest 2: more models, new heuristics and parallel computing. *Nat Methods.* 2012;9(8):772
- [86] Binder M, Fischer M. Molekularbiologische Charakterisierung der Gattungen *Boletellus* und *Xerocomus*: *Xerocomus pruinosus* (Fr. & Hoek) Quel. und verwandte Arten. *Bollettino Del Gruppo Micologico G Bresadola.* 1997;40(2–3):79–90.
- [87] Ronquist F, Teslenko M, van der Mark P, et al. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst Biol.* 2012;61(3):539–542.
- [88] Stamatakis A. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics.* 2006; 22(21):2688–2690.
- [89] Felsenstein J. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution.* 1985; 39(4):783–791.
- [90] Miller MA, Pfeiffer W, Schwartz T. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 November 2010, New Orleans; 2010. p. 1–8.
- [91] Halling RE. An annotated index to species and infraspecific taxa of Agaricales and Boletales described by William A. Murrill. *Mem New York Bot Garden.* 1986;40:1–120.
- [92] Murrill WA. New boletes. *Mycologia.* 1938;30(5):520–525.
- [93] Snell WH. The genera of the Boletaceae. *Mycologia.* 1941;33(4):415–423.
- [94] Singer R. The Boletineae of Florida with notes on extralimital species. I. The Strobilomycetaceae. *Farlowia.* 1945;2(1):97–141.
- [95] Bessette AE, Bessette AR, Lewis DP. *Mushrooms of the Gulf Coast States: A field guide to Texas, Louisiana, Mississippi, Alabama, and Florida.* Austin (TX): University of Texas Press; 2019.
- [96] Both EE. *The boletes of North America. A compendium.* Buffalo (NY): Buffalo Museum of Science; 1993.
- [97] Grand LF, Moore RT. Scanning electron microscopy of basidiospores of species of Strobilomycetaceae. *Can J Bot.* 1971;49(8):1259–1261.
- [98] Thiers HD. The bolete flora of the Gulf coastal plain. I. The Strobilomycetaceae. *J Elisha Mitchell Sci Soc.* 1963;79:32–41.
- [99] Weber NS, Smith AH. *A field guide to southern mushrooms.* Ann Arbor (MI): University of Michigan Press; 1985.
- [100] Trappe JM. Fungus associates of ectotrophic mycorrhizae. *Bot. Rev.* 1962;28(4):538–606.
- [101] Gates G, Ratkowsky D. *A field guide to Tasmanian fungi.* 3rd ed. Hobart: Tasmanian Field Naturalists Club; 2018.
- [102] McKenzie EHC, Buchanan PK, Johnston PR. Checklist of fungi on *Nothofagus* species in New Zealand. *N Z J Bot.* 2000;38(4):635–720.
- [103] Segedin BP. An annotated checklist of agarics and boleti recorded from New Zealand. *N Z J Bot.* 1987;25(2):185–215.
- [104] Stevenson G. *The Agaricales of New Zealand. I. Boletaceae and Strobilomycetaceae.* Kew Bull. 1962;15(3):381–385.
- [105] Taylor GM. *Mushrooms and toadstools in New Zealand.* Mobil New Zealand Nature Series. Wellington: AH & AW Reed; 1981.
- [106] Mikšík M. *Hřibovité Houby Evropy.* Praha: Vydalo nakladatelství Svojtka & Co; 2017.
- [107] Parra AL, Angelini C, Ortiz-Santana B, et al. The genus *Agaricus* in the Caribbean. Nine new taxa mostly based on collections from the Dominican Republic. *Phytotaxa.* 2018;345(3):219–271.
- [108] Murrill WA. A new *Boletus* from Jamaica. *Mycologia.* 1910;2(6):305–305.
- [109] Saccardo PA, Trotter A. *Supplementum Universale, Pars VIII. Sylloge Fungorum omnium hucusque cognitorum 21.* Patavia; 1912.
- [110] Lewis DP, Cibula WG. Studies on Gulf Coast Agarics (Basidiomycota: Agaricaceae): notes on some interesting and rare species. *Texas J Sci.* 2000;52:65–78.
- [111] Dennis RWG. *Fungus flora of Venezuela and adjacent countries.* Kew Bulletin Additional Series 3. Kew: Royal Botanic Garden; 1970.
- [112] Singer R, Digilio APL. Las boletáceas de Sudamérica tropical. *Lilloa.* 1960;30:141–164.
- [113] Wolfe CB. Jr. *Mucilopilus*, a new genus of the Boletaceae, with emphasis on North American taxa. *Mycotaxon.* 1979;10(1):116–132.
- [114] de la Fuente JI, García-Jiménez J, López CY, et al. An annotated checklist of the macrofungi (Ascomycota, Basidiomycota, and Glomeromycota) from Quintana Roo, Mexico. *CheckList.* 2020;16(3):627–648.
- [115] Wolfe CB. Jr A taxonomic evaluation of the generic status of *Ixechinus* and *Mucilopilus* (Ixechineae, Boletaceae). *Mycologia.* 1982;74(1):36–43.
- [116] Putzke J, Putzke MTL. *Cogumelos (fungos Agaricales) no Brasil - Ordens Boletales (Boletaceae e Paxillaceae), Polyporales (Polyporaceae/Lentinaceae), Russulales (Russulaceae) e Agaricales (Cortinariaceae, Inocybaceae, Pluteaceae e Strophariaceae).* São Gabriel. 2019;2.
- [117] Fulgenzi TD. *Systematics of Boletaceae from the Guiana Shield [thesis].* Arcata (CA): Humboldt State University; 2009.
- [118] Magnago AC. *Taxonomia e sistemática de Boletaceae (Boletales) para o Brasil [Dissertação*

- Pós-Graduação]. Florianópolis: Universidade Federal de Santa Catarina; 2014.
- [119] May TW, Wood AE. Catalogue and bibliography of Australian macrofungi 1. Basidiomycota. In: Fungi of Australia, vol. 2A. Canberra: CSIRO Publishing; 1997.
- [120] Thongklam S. Diversity of boletes in some national parks of upper northern Thailand [PhD dissertation]. Chiang Mai: Chiang Mai University; 2008.
- [121] Watling R, Hollands R. Boletes from Sarawak. Notes from the Royal Botanic Garden, Edinburgh. 1990;46(3):405–422.