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

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**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.

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 infragenic 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 Boletae family 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 dicytetus* 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 Strobilomyctetaeae 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 Thiern
Austroboletus and molecularly-based novel species assigned to
Despite the increasing number of morphologically
as they cluster in an well-delimited grouping with
subfamily Austroboletoideae G. Wu & Zhu L. Yang,
Legumes 

Dipterocarpaceae, Myrtaceae, and caesalpinoid
plant families including Fagaceae, Pinaceae,
proved ECM association with members of the
Polygonaceae, Sapotaceae, Myrtaceae, Euphorbiaceae,
Nothofagaceae, 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
Tylopilus P. Karsten s. str. and conversely an affinity
with other boletoid pinkish-spored genera segre-
gated from Tylopilus s. l., such as Fistulinella Henn.,
Mucilopilus Wolfe, and Veloporyphyllus L.D. Gomez & Singer and possibly with the sequestrate
(genus to be polyphyletic [31,37] and accordingly an
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 morpho-
logically very close smooth-spored genera such as
Mucilopilus and Ixechnus 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

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. Pseudotylopili subsect.
Viscidini Singer and encompasses at present more
than 20 species worldwide [21]. Fistulinella is char-
acterized by stipitate-pileate to occasionally seque-
strate 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 red-
dish brown or rust brown to cocoa brown spore
print, narrowly elongate fusoid, inamyloid to dextri-
noid, smooth basidiospores, trichoderm to ixotricho-
nder to ixocutis pileipellis, strongly gelatinized
bilateral-divergent hymenophoral trama of the
“Boletus-type”, suspected gymnocarpic ontogenesis
in some species but probably also velangiocarpic (pri-
mary 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 long-
standing 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, Veloporyphyllus, and apparently
Carolinigaster [5,7,37–39,43,45–47] and it seems to
occupy a sister position to the remainder of the
Austroboletoideae [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 morpho-
logically very close smooth-spored genera such as
Mucilopilus and Ixechnus 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

The genus as presently outlined is characterized
from the morphological viewpoint by boletoid fruit-
ing 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 mark-
edly 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

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

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 Austroboletoideae G. Wu & Zhu L. Yang,
as they cluster in a statistically
strongly supported separate clade 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. Khmelnitsky, based on the Malaysian species Boletus
longipes Massee [41].
it is not until molecular analyses are carried out on the generic type, the African taxon *F. staudei*, 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 were collected in Jarabacoa, La Vega Province and Sosúa, Puerto Plata Province, Dominican Republic, and are deposited in the Herbarium of Jardin 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 = length/width ratio with the extreme values in parentheses, Qₘ = average quotient (length/width ratio) ± standard deviation and average spore volume was approximated as a rotation ellipsoid [V = (π.L.W²)/6 ± 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 stipitpellis 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) |
|---------------------------|------|-------|-----|------------------|--------|--------------|
| Austroboletus aff. fusisporus | KF112766 | KF112484 | – | HKASS2683 | China | Wu et al. [7] |
| Austroboletus aff. fusisporus | KF112767 | KF112486 | – | HKASS3461 | China | Wu et al. [7] |
| Austroboletus aff. rostrupii | KF112768 | KF112487 | – | HKASS3450 | China | Wu et al. [7] |
| Austroboletus amazonicus | – | KF714509 | – | 1914 AMV | Colombia | Vasco-Palacios et al. [31] |
| Austroboletus amazonicus | – | NG_08569 | – | RU7352 AMV | Colombia | Vasco-Palacios et al. [31] |
| Austroboletus appendiculatus | – | – | – | – | India | Tibpromma et al. [49] |
| Austroboletus austrovirens | – | – | – | – | Australia | Fechner et al. [26] |
| Austroboletus cf. gracilis | – | JX901138 | – | HKASS9804 | China | Hosen et al. [64] |
| Austroboletus dicyotus festivus | – | KT724085 | – | AMV1800 | Colombia | Vasco-Palacios et al. (unpubl.) |
| Austroboletus fusicosporus festivus | – | KY888001 | – | KY886202 | FLOR:51599 | Brazil | Magnago et al. [42] |
| Austroboletus fusicosporus gracilis | – | JX889720 | JX889719 | HKASS5207 | China | Hosen et al. [64] |
| Austroboletus fusicosporus lacunosus | – | MK768510 | JX889720 | JX889719 | China | ? | Chen (unpubl.) |
| Austroboletus gracilis | – | MK601714 | – | CFMR BOS:562 | USA | Young et al. [65] |
| Austroboletus gracilis | – | – | – | – | Mexico | Rockefeller (2018, direct submission) |
| Austroboletus gracilis var. flavipes | – | – | – | – | New Zealand | Cooper (unpubl.) |
| Austroboletus gracilis var. flavipes | – | EUS228815 | – | TM03_434 | Canada | Porter et al. [66] |
| Austroboletus gracilis var. flavipes | – | MK601714 | – | CFMR BOS:562 | USA | Kuo and Ortiz-Santana [5] |
| Austroboletus lacunosus | KP242090 | KP242272 | KP242161 | BRI:AOQ795787 | Australia | Bonito et al. (unpubl.) |
| Austroboletus lacunosus | – | KC552056 | KC552056 | MEL:2253764 | Australia | Orihara et al. [62] |
| Austroboletus lacunosus | – | KC552057 | KC552057 | MEL:225609 | Australia | Orihara et al. [62] |
| Austroboletus lacunosus | – | – | – | – | New Zealand | Lebel and Cooper (unpubl.) |
| Austroboletus lacunosus | – | JX889669 | – | REH9146 | Australia | Halling et al. [67] |

(continued)
| Original name from GenBank | RPB2 | nrLSU | ITS | Specimen/voucher | Origin | Reference(s) |
|---------------------------|------|-------|-----|------------------|--------|--------------|
| **Austroboletus mucosus** | –    | AY612798 | –   | TH6300 | – | Drehmel et al. [3] |
| **Austroboletus mutabilis** | KP242097 | KP242266 | KP242167 | BRI:AQ0669270 | Australia | Bonito et al. (unpubl.) |
| **Austroboletus mutabilis** | KP242098 | KP242263 | KP242169 | BRI:AQ0795793 | Australia | Bonito et al. (unpubl.) |
| **Austroboletus mutabilis** | KP242099 | KP242262 | KP242170 | BRI:AQ0796266 | Australia | Bonito et al. (unpubl.) |
| **Austroboletus neotropicalis** | – | JQ924334 | JQ924301 | NY181457 | Costa Rica | Wu et al. (unpubl.) |
| **Austroboletus niveus** | – | KC552058 | KC552016 | MEL:2053830 | Australia | Orihara et al. [62] |
| **Austroboletus niveus** | KP242109 | KP242279 | KP242217 | Perth 6660703 | Australia | Bonito et al. (unpubl.) |
| **Austroboletus niveus** | – | JX889668 | – | REH9487 | Australia | Halling et al. [67] |
| **Austroboletus niveus** | – | KP191672 | KP191800 | PDD:105213 | New Zealand | Lebel and Cooper (unpubl.) |
| **Austroboletus niveus** | – | KP191673 | KP191801 | PDD:105246 | New Zealand | Lebel and Cooper (unpubl.) |
| **Austroboletus niveus** | – | – | KP191802 | PDD:81219 | New Zealand | Lebel and Cooper (unpubl.) |
| **Austroboletus niveus** | – | DQ534622 | – | Strain 312 | New Zealand | Binder and Hibbett [2] |
| **Austroboletus niveus novae-zelandiae** | – | KP242256 | KP242175 | MEL:2370154 | Tasmania (Australia) | Bonito et al. (unpubl.) |
| **Austroboletus niveus novae-zelandiae** | – | KP191671 | KP191803 | PDD:105097 | New Zealand | Lebel and Cooper (unpubl.) |
| **Austroboletus niveus novae-zelandiae** | – | HM060327 | – | PDD:72542 | New Zealand | Johnston and Park (unpubl.) |
| **Austroboletus niveus novae-zelandiae** | – | DQ534623 | – | Strain 50 | New Zealand | Binder and Hibbett [2] |
| **Austroboletus niveus occidentalis** | – | KC552059 | KC552017 | MEL:2300518 | Australia | Orihara et al. [62] |
| **Austroboletus niveus rarius** | KP242086 | KP242226 | KP242197 | BRI:AQ0794045 | Australia | Bonito et al. (unpubl.) |
| **Austroboletus niveus rionegrensis** | – | – | KY886201 | INPA 78693 | Brazil | Magnago et al. [42] |
| **Austroboletus rosealbus** | – | KY872650 | KY872653 | Dodd | Australia | Fechner et al. [26] |
| **Austroboletus rosealbus** | – | KY872651 | KY872652 | REH10024 | Australia | Fechner et al. [26] |
| **Austroboletus rostrupii** | KP242089 | – | KP242160 | BRI:AQ0795785 | Australia | Bonito et al. (unpubl.) |
| **Austroboletus rostrupii** | – | – | JN168683 | TH8189 | Guyana | Smith et al. [68] |
| **Austroboletus sp.** | KP242115 | KP242235 | – | BRI:AQ0794156 | Australia | Bonito et al. (unpubl.) |
| **Austroboletus sp.** | KP242106 | KP242234 | KP242215 | BRI:AQ0794222 | Australia | Bonito et al. (unpubl.) |
| **Austroboletus sp.** | KP242087 | KP242218 | KP242158 | BRI:AQ0794242 | Australia | Bonito et al. (unpubl.) |
| **Austroboletus sp.** | KP242102 | KP242259 | KP242171 | BRI:AQ0794271 | Australia | Bonito et al. (unpubl.) |
| **Austroboletus sp.** | KP242094 | – | KP242159 | BRI:AQ0794272 | Australia | Bonito et al. (unpubl.) |
| **Austroboletus sp.** | – | KP242283 | KP242213 | MEL:2382826 | Australia | Bonito et al. (unpubl.) |
| **Austroboletus sp.** | – | – | KY774008 | CY13_008 | New Caledonia | Carricconde et al. (unpubl.) |
| **Austroboletus sp.** | – | – | KY774007 | CYMy361 | New Caledonia | Carricconde et al. (unpubl.) |
| **Austroboletus sp.** | – | KF030351 | – | DPL7541 | USA | Nuhn et al. [6] |
| **Austroboletus sp.** | KF112764 | KF112383 | – | HKAS57756 | China | Wu et al. [7] |
| **Austroboletus sp.** | KF112765 | KF112485 | – | HKAS59624 | China | Wu et al. [7] |
| **Austroboletus sp.** | KT990367 | KT990527 | – | HKAS574734 | China | Wu et al. [8] |
| **Austroboletus sp.** | – | KY009095 | – | LAM 0222 | Malaysia | Peay and Lim (unpubl.) |
| **Austroboletus sp.** | – | KY091070 | – | LAM 0479 | Malaysia | Peay and Lim (unpubl.) |
| **Austroboletus sp.** | KP242134 | KC552060 | KP242203 | MEL:2305143 | New Caledonia | Orihara et al. [62] |
| **Austroboletus sp.** | MH614753 | – | – | OR0891 | Thailand | Vathvanarath et al. [63] |
| **Austroboletus sp.** | – | KP191670 | KP191805 | OTA | New Zealand | Lebel and Cooper (unpubl.) |
| **Austroboletus sp.** | – | – | – | FUNNZ 2013434 | Australia | Bonito et al. (unpubl.) |
| **Austroboletus sp.** | – | – | – | Australia | Bonito et al. (unpubl.) |
| **Austroboletus subflavidus** | KP242126 | KP242277 | KP242216 | Perth 66608407 | Australia | Bonito et al. (unpubl.) |
| **Austroboletus subflavidus** | KP242285 | KP242285 | KP242216 | Perth 6660928 | Australia | Dominican Republic |
| **Austroboletus subflavidus** | MT590754 | MT580902 | MT581525 | JBSD130771 (ANGE108 and MG775) | Dominican Republic | This study |
| **Austroboletus subflavidus** | MT590755 | MT580903 | MT581526 | JBSD130772 (ANGE108 and MG776) | Dominican Republic | This study |
| **Austroboletus subflavidus** | – | MT580901 | MT581523 | CFMR:DR2859; isolate = TJB-9787 | Dominican Republic | This study |

(continued)
| Original name from GenBank | RP2  | nrLSU | ITS | Specimen/voucher | Origin | Reference(s) |
|---------------------------|------|-------|-----|------------------|--------|--------------|
| Austroboletus subflavidus | –    | –     | MT581524 | CFMR:DRS92; isolate = DJL-DR-48 | Dominican Republic | This study |
| Austroboletus subflavidus | –    | –     | MT581522 | CFMR:BZ1824; isolate = DJL-BZ-27 | Belize | This study |
| Austroboletus subflavidus | MK766278 | MK601716 | – | CFMR:DRS92; isolate = DJL-DR-48 | Belize | Kuo and Ortiz-Santana [5] |
| Austroboletus subflavidus | –    | MT580900 | MT581521 | CFMR:BOTH-3463 | Florida (USA) | This study |
| Austroboletus subflavidus | –    | –     | MH016816 | FLAS-F-6035 | Florida (USA) | Kaminsky et al. (unpubl.) |
| Austroboletus subvirens   | –    | –     | AB059915 | 120-707 | Japan | Sato et al. (unpubl.) |
| Austroboletus subvirens   | –    | –     | MT581522 | CFMR:BZ1824; isolate = DJL-BZ-27 | Belize | This study |
| Austroboletus subvirens   | –    | –     | MT580900 | CFMR:BOTH-3463 | Florida (USA) | This study |
| Austroboletus subvirens   | –    | –     | MK766278 | CFMR:BOTH-3463 | Florida (USA) | This study |
| Fistulinella cinereocarpa | MT59076 | MT580906 | MT581527 | JBSD130769 (ANGE969 and MG777) | Dominican Republic | This study |
| Fistulinella cinereocarpa | –    | MT580904 | –     | CFMR:B84 | The Bahamas | This study |
| Fistulinella cinereocarpa | –    | MT580905 | –     | CFMR:B100 | The Bahamas | This study |
| Fistulinella cinereocarpa | –    | –     | GQ981503 | HKAS53432 | Vietnam | Crous et al. [37] |
| Fistulinella cinereocarpa | –    | –     | MH718396 | LE312004 | Vietnam | Crous et al. [37] |
| Fistulinella cinereocarpa | MG212630 | JX889648 | –     | REH9502 | Australia | Halling et al. [67] |
| Fistulinella ruschii     | –    | NG_060432 | NR_156320 | FLOR:51609 | Brazil | Magnago et al. [42] |
| Fistulinella ruschii     | –    | KY888005 | KY888006 | FLOR:51611 | Brazil | Magnago et al. [42] |
| Fistulinella ruschii     | –    | –     | KF112733 | KF112380 | China | Wu et al. [8] |
| Fistulinella ruschii     | –    | –     | JQ287643 | JX888459 | Costa Rica | Li et al. [74] |
| Fistulinella ruschii     | –    | –     | AF456826 | Strain 238 | – | Binder and Bresinsky [72] |
| Fistulinella sp.         | –    | –     | KF873352 | AMV511 | Colombia | Vasco-Palacios et al. [31] |
| Fistulinella sp.         | –    | –     | HM624054 | PDD 25185 | New Zealand | Li et al. (unpubl.) |
| Fistulinella sp.         | –    | –     | JX889648 | REH9502 | Australia | Halling et al. [67] |
| Fistulinella sp.         | –    | –     | KF112733 | KF112380 | China | Wu et al. [8] |
| Fistulinella viscidoviridis | –    | –     | JQ287643 | JX888459 | Costa Rica | Li et al. [74] |
| Fistulinella viscidoviridis | –    | –     | KF112733 | KF112380 | Brazil | Li et al. [74] |
| Fistulinella viscidoviridis | –    | –     | JX984547 | F:Gomez21232 basidiocarp1 | Costa Rica | Li et al. [74] |
| Fistulinella viscidoviridis | –    | –     | JX984540 | KUNHKAS52258 | China | Li et al. [74] |
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 Austroboletoideae as circumscribed by 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 GTR+GAMMA 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 ≥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 Veloporphyrellus (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. gloeo-carpa. Fistulinella prunicolor and F. viscosa 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
Basionym: *Tylopilus 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); neo-

**type** designated by C.B. Wolfe [12]: USA, Florida, Gainesville, 11 Jul 1938, E. West, Arnold and W.A. Murrill (NY, **isocation**: 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 planate, 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; Naftalene Yellow, Straw Yellow, Pl. XVI) to ochraceous or pale ochraceous-olive (Deep Olive-Buff, Dark Olive-Buff, Pl. XL;
Primuline Yellow, Olive Lake, Buffy Citrine, Pl. XVI; Ecru 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 Lavander 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 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.
× (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; unchangeable when exposed to air; subhymenophoral layer white (White, Pl. LIII); exciscate 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% NH₄OH: pinkish on pileus, none on context.

Basidiospores [122/7/4] (13.1) 15.9 ± 1.15 (19.5) × (5.5) 7.0 ± 0.58 (8.7) μm, Q = (1.76) 1.87–2.61 (2.68), Qₘ = 2.26 ± 0.16, V = 416 ± 89 μm³ (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

**Figure 3. Austroboletus subflavidus.** Micromorphological features; (a) basidiospores; (b) chello- and pleurocystidia; (c) caulocystidia; (d) basidia; (e) elements of the pileipellis. Scale bars: 10 μm (a–d); 20 μm (e). Drawings by F. Costanzo.
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 pluriguttulate, inamyloid to faintly dextrinoid, strongly cyanophilic, and with a weak metachromatic reaction. Basidia 27–49 (51) × 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 guttules in water and 5% KOH, bright yellow (inamyloid) in Melzer’s, without basal clamps; basidioles faintly clavate to clavate, similar in size to basidia. Cheilocystidia (33) 35–65 (70) × 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) × 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 × 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 caulobasidioides, projecting caulocystidia similar in shape, size, color and chemical reactions to hymenial cystidia, (50) 53–57 × (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 × 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 Tylopilus by Murrill [92], the species was then recombined in Boletellus by Snell [93] and subsequently transferred to Tylopilus Florida as a member of Boletellus. The species was then recombined in Tylopilus. 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 brownish shades or patches at the base, white hymenophore, slender, deeply reticulate-alveolate, olive, occasionally with a pale pinkish tinge, pinkish surface dry and becoming rimose-areolate with age, and stipe up to 14.5 cm long and 5 cm wide), pileus (3.5–5.0 (5.5) cm broad), viscid-pileal surface with age, flabby in old basidiomes; margin obtuse, unevenly shaped by shallow depressions, moderately slightly depressed at center, regularly to hardly finally broadly pulvinate-flattened, sometimes 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, rugulate 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 Mikšik [106].

Austroboletus eburneus is separated from A. subflavidus by the non-areolate pileus surface, elongate fusiform to cylindric subfusiform, narrower basidiospores [(14.5) 15.5–17.5 (19) × 4.4–5.5 μm] with an overall very slightly granular-punctate, rugulate 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, Qm = 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, Qm = 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 gloecaropa 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,
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 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.
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, colorless with the tubes and not staining on bruising or when injured. Stipe (3.0) 5.0–7.5 (8.0) × (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).

Figure 5. Fistulinella gloeocarpa. Micromorphological features; (a) basidiospores; (b) cheilocystidia; (c) pleurocystidia; (d) stipitpellis; (e) basidia; (f) elements of the pileipellis. Scale bars: 10 μm (a–c, e); 20 μm (d, f). Drawings by F. Costanzo.
(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). Macromorphological spot-test reactions: 30% KOH: staining wine red everywhere; 25% NH₄OH: none.

Basidiospores [70/7/3] (10.3) 12.8 ± 1.00 (16.2) × (4.5) 5.3 ± 0.34 (6.4) μm, Q = (2.00) 2.03–2.75 (2.84), \( Q_w = 2.40 ± 0.17, V = 193 ± 35 \mu m^3 \), 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 suprahilar 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, inamylloid, strongly cyanophilic and with an orthochromatic reaction. Basidia (21) 23–38 (40) × 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 (2–5μm) (sterigmata up to 8 μm long in 1-spored basidia), hyaline to pale yellowish and seldom containing scattered straw-yellow oil guttules in water and 5% KOH, bright yellow (inamylloid) in Melzer’s, without basal clamps; basidioles cylindrical-clavate, faintly clavate to clavate, similar in size to basidia. Cheilocystidia (37) 39–56 (60) × 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 (inamylloid) in Melzer’s, without epiparietal encrustations. Pleurocystidia (32) 36–58 (65) × (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 × (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 (inamylloid) 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. Stipitpellis 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, septic hyphae; terminal elements short cylindrical to irregularly cylindrical or subclavate to peanut-shaped or acorn-shaped, 15–54 × 7–10 μm, occasionally filamentous and up to 80 × 4 μm, apex rounded-obtuse; caulohymenial elements not differentiated or nearly so, caulobasidia infrequent, mostly 1- and 2-spored, 35–45 × 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, inamylloid 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, inamylloid 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. (Caesalpinioideae), 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. cinereoulba* Fulgenzi & T.W. Henkel and *F. ruschia* 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) 4.8–5.2 μm, Qm = 2.0], shorter hymenial cystidia (20–30 × 10–12 μm) with apical ampullaceous neck and apparently an absence of veil [20,22,108,109]. Lewis and Cibula [110] and more recently Besette 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, Qm = 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 (MycoPortal).

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 check 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) \times (3) 4–5 (6) \mu m, Q_m = 3.3], narrower pileipellis hyphae (3.4–10 \mu m broad), narrower hyphae of lateral stratum (2–6 \mu m wide) in the hymenophoral trama and the occurrence on rotten 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) [27,116]. This species is also separated from *F. ruschii* 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. cinereocolba_ 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 ochreous 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) \times 3.7–4.9 (6) \mu m, Q_m = 3], aciculate to cylindrical, narrower pleurocystidia (37–61 \times 3.7–6.2 \mu m), narrower pileipellis hyphae (2.4–7 \mu m broad), narrower hyphae of lateral stratum (2–6 \mu m 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 \times 10–17 \mu m) 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_{4}OH staining reddish orange and yellow on pileus and stipe, respectively, longer and narrower basidiospores [14–18 (22) \times 4–5 \mu m, Q_m = 3.4], presence of broadly cylindrical, multiseptate pleurocystidia, narrower pileipellis hyphae (4–11 \mu m broad), narrower hyphae of lateral stratum (4–7 \mu m 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-scorbulate. 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. gloeocapa 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).

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