

New species of *Boletellus* from Guyana

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Abstract: *Boletellus exiguus* sp. nov. and *Boletellus dicymbophilus* sp. nov. (Boletaceae, Boletales, Basidiomycota) are described as new to science. These boletes were collected from tropical forests dominated by ectomycorrhizal *Dicymbe corymbosa* (Caesalpiaceae) in the Pakaraima Mountains of western Guyana.

Key words: Boletaceae, *Dicymbe*, ectomycorrhizal fungi, Guiana Shield, neotropics

INTRODUCTION

The genus *Boletellus* Murrill (Boletaceae, Boletales, Basidiomycota) encompasses ~ 44 described species worldwide, the majority with tropical distributions (Heinemann and Goossens-Fontana 1954, Snell and Dick 1970, Smith and Thiers 1971, Corner 1972, Horak 1977, Singer 1986, Singer et al 1992, Watling 2001, Halling and Mueller 2005, Ortiz-Santana et al 2007). *Boletellus* has been variably defined, yet all definitions have in common these features: basidiospores that are olivaceous brown in deposit, a yellow hymenophore becoming olivaceous with time and boletoid (i.e. strongly divergent) tube trama. Despite these commonalities individual author concepts vary. Singer (1986) adhered to a broad definition of *Boletellus* by including species with longitudinally winged or ridged spores (sections *Boletellus*, *Chrysen-teroides*, *Ixocephali* and *Dictyopodes*), smooth spores (section *Mirabilis*), spores with imbedded short spines or pits (section *Allospori*) and reticulate spores (section *Retispori*). Heinemann (1951) and Snell and Dick (1970) included species that have spores with imbedded short spines or pits (e.g. *Boletellus purpurascens* Heinem.), smooth spores (e.g. *Boletellus*

mirabilis (Murrill) Singer) as well as those with longitudinally striate spores. Smith and Thiers (1971) argued against Singer's broad concept of the genus and included only species with spores that are longitudinally winged, ridged or striate; by doing so *Boletellus* can be determined easily microscopically and is consistent with the type species' morphology (Smith and Thiers 1971). Corner (1972) and Pegler (1983) also adhered to a narrower definition of *Boletellus* characterized by spores that are longitudinally winged, ribbed, costate or striate.

Here we describe *Boletellus exiguus* sp. nov. and *Boletellus dicymbophilus* sp. nov. discovered in ectomycorrhizal (EM) *Dicymbe* (Caesalpiaceae) forests in Guyana. These two new species are placed in *Boletellus* based on their olivaceous brown, longitudinally ridged basidiospores, dry pilei, tubulose, blue-staining hymenophores and lack of clamp connections.

MATERIALS AND METHODS

Annual collecting expeditions were conducted during the rainy seasons (May–Jul) 1998–1999 in the Upper Ireng River Basin along Guyana's western border with Brazil in the west-central Pakaraima Mountains, and 2000–2005 in the Upper Potaro River Basin ~ 30 km north of the Ireng site. At each site fungi were collected within a 5 km radius of a previously established base camp in forests dominated by *Dicymbe corymbosa* Spruce ex Benth. (Henkel 2003).

Basidiomata were examined in the field for their fresh characteristics. Color was subjectively described and recorded according to Kornerup and Wanscher (1978) with color plates noted in parentheses (e.g. 3C4). Macrochemical spot tests were performed following Singer (1986). Basidiomata were field-dried with silica gel beads.

Microscopic anatomical details were determined on fresh specimens at base camp with an EPOI microscope and in the laboratory with an Olympus BX51 microscope with bright field and phase contrast optics. Fungal tissue of dried specimens was rehydrated and mounted in either H₂O, 3% KOH, or Melzer's reagent. For each taxon a minimum of 20 basidiospores, basidia, cystidia and other structures were measured. Line drawings were made with a drawing tube, inked and scanned. Scanning electron micrographs of basidiospores were obtained with either a Jeol JSM-6400 or Topcon ABT32 scanning electron microscope using 200 kV. Specimens are deposited in these herbaria as indicated: BRG, HSU and NY (Holmgren et al 1990).

TAXONOMY

Boletellus exiguus T.W. Henkel and Fulgenzi sp. nov.
FIGS. 1–2, 5a, b

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FIG. 1. Basidiomata of *Boletellus exiguus* (HOLOTYPE; Henkel 8696). Bar = 10 mm.

Pileus brunneus, juventute velutinus, postea subtiliter areolatus, 9–33 mm latus. Trama caerulescens ubi exposita. Stipes brunneus, subtiliter longitudinaliter striatus, cartilagineus, apice cum collo rubro, 7–34 × 1–4 mm. Basidiosporae olivaceae in massa, amygdaliformes, longitudinaliter porcatae, 10–15 × 7–9 μm. Fructificatio insidens trunco *Dicymbe* arborum.

HOLOTYPE: Henkel 8696 (BRG; ISOTYPE: HSU, NY; MycoBank No. MB 511183)

Pileus 9–33 (42) mm broad, convex to applanate, dark brown (7D7) throughout when young to

chestnut brown (5D5–5E7) to yellow-tan (4E6) with age, velutinous, becoming finely squamulose and areolate when mature, less so over disk, tacky to dry; margin slightly inrolled when young, irregularly crenulate with age; trama 1–1.2 mm thick at margin, 1–2 mm over tubes, 2–2.5 mm over stipe, dingy-white, bluing rapidly with exposure, solid, less so with age. *Odor* minimal, pleasant; *flavor* mild. *Tubes* 1–2 mm long at margin, 2–7 mm centrally, 2–5 mm at stipe, broadly and shallowly depressed around stipe, of irregular lengths, concolorous with pores, rapidly blue-green (26E7) on exposure; pores lemon yellow (3A7) when young, maturing to olive-yellow (4C7–4C8), rapidly blue-green (26E7) with pressure, with prominent decurrent tooth 2–2.5 mm long, 0.5–2 per mm, subangular, radially elongate near stipe. *Stipe* 7–34 × 1–4 mm, subequal, gradually and slightly flaring to 2–4 mm at apex and base, typically curving outward and upward from *Dicymbe* trunk, cartilaginous, tan (5D6) to maroon-brown (10F6–10D8) throughout, with prominent red (10D8) zone over distal 1–2 mm of apex, darkening slightly with handling, finely longitudinally striate; extreme base with brown tomentum; trama red-maroon (10F6–10F8) in upper half, tan-brown (5D5) below, unchanging.

Basidiospores olivaceous-brown (5F6–6F5) to dark olive-green (3F8) in medium to heavy deposit, 10–15 × 7–9 μm (mean 12.7 × 8.2 μm; n = 20), Q range = 1.2–2, (mean Q = 1.53), olive-golden in H₂O and KOH, inamyloid, amygdaliform, with moderately

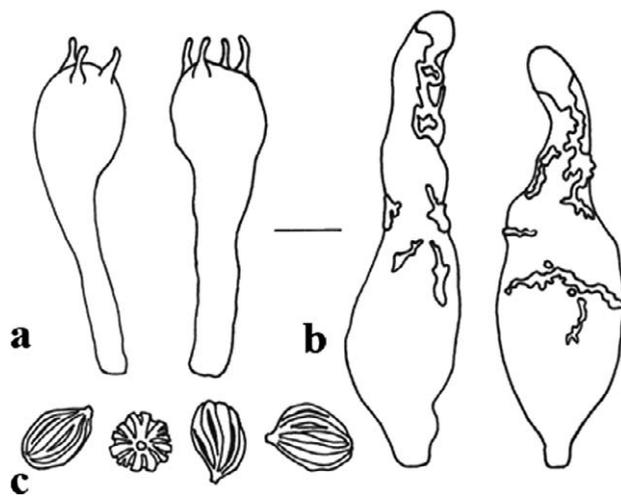


FIG. 2. Microscopic features of *Boletellus exiguus* (HOLOTYPE; Henkel 8696). a. Basidia. b. Pleurocystidia, in Melzer's. c. Basidiospores. Bar = 10 μm.

thick single wall, uniguttulate, with 10–16 longitudinal ridges; ridges < 1 μm tall, occasionally bifurcating, terminating at unequal lengths before the apex and thus leaving a smooth area, all ridges converging at hilar appendage; hilar appendage 0.5–1 μm long. *Basidia* 37–51 \times 12–15 μm , subclavate, tapering gradually to base, hyaline in H_2O and KOH, with numerous refractive globules pale yellow in H_2O , lighter in KOH, with three or four sterigmata; sterigmata 2–4 μm long. *Pleurocystidia* infrequent, 65–85(100) \times 14–20 μm , projecting 27–42 μm above the hymenial palisade, ventricose, thin-walled; wall hyaline in H_2O and KOH, with golden incrustations evident in Melzer's. *Hymenophoral trama* boletoid, strongly divergent; mediostrium 37–54.3 μm wide, of many thin, slightly interwoven hyphae, these hyaline in H_2O , gelatinized and hyaline in KOH, lateral stratum hyphae 6.2–9.8 μm wide, hyaline in H_2O and KOH, nongelatinized. *Pileipellis* a derm consisting of angular cells with tufts of erect inflated terminal cells concentrated in the squamules; tufts 91.4–197.6 μm wide, in mass orange-yellow in H_2O , paler in KOH; terminal cells 19.7–41.2 μm long, cylindrical or ventricose, rarely clavate or mucronate. *Pileus trama* interwoven; individual hyphae 6.1–11 μm wide, light golden in H_2O , hyaline in KOH, regularly septate. *Stipitipellis* a densely interwoven trichodermial palisade of cylindrical elements with inflated terminal cells, in mass golden-orange in H_2O , lighter in KOH; terminal cells projecting 24.7–38.3 μm , cylindrical to ventricose, concentrated on stipe striations. *Stipe trama* of densely interwoven hyphae, these 2–4.9 μm wide, faint golden in H_2O , hyaline in KOH. *Clamp connections* absent. *Macrochemical* reactions: NH_4OH immediately blood-red (9C8) on pileus, then fading within minutes to orange, negative on stipe and pores; KOH red-orange (9B8) on pileus then quickly becoming orange (6B8), red (8D8) on stipe; FeSO_4 negative on pileus, dark blue-green (25F4) on tube mouths then fading to a dark olive-green (26F5), darkening stipe.

Habit, habitat, and distribution. Solitary to scattered among humic accumulations on trunks of large, living *Dicymbe corymbosa* trees; known from the type locality in the Upper Potaro River Basin and adjacent Upper Ireng River Basin of Guyana.

Etymology. Exiguus = small (Latin), referring to the diminutive basidiomata.

Specimens examined. GUYANA. REGION 8 POTARO-SIPARUNI: Pakaraima Mountains, Upper Ireng River Basin; 1.5 km east of confluence of Sukabi and Ireng rivers, lower slope of Mount Kukuinang, elevation 850 m, 6 Jun 1998, *Henkel 6898* (BRG; HSU); west bank of Yuarka Creek, 1 km upstream from confluence with Suruwabaru Creek, elevation 800 m, 31 May 1999, *Henkel 7088* (BRG; HSU), 15 Jun 1999, *Henkel 7208* (BRG; HSU); Upper Potaro River Basin,

within 5 km radius of 5°18'04.8"N, 59°54'40.4"W, elevation 710–750 m; vicinity of Potaro base camp, 26 May 2000, *Henkel 7436* (BRG; HSU); 3 km southwest of Potaro base camp near *Dicymbe* plot 3, 29 Jul 2003, *Henkel 8636* (BRG; HSU); in *Dicymbe* plot 3, 24 Jun 2004, *Henkel 8696* (HOLOTYPE, BRG; ISOTYPE: HSU, NY); 1 km southeast of Potaro base camp, 28 May 2005, *Henkel 8809* (BRG; HSU); 1 km west of Potaro base camp, 30 May 2005, *Henkel 8815* (BRG; HSU).

Commentary. *Boletellus exiguus* is recognized in the field by its diminutive size, the chestnut-brown, squamulose and finely areolate pileus, irregularly angular pores that are lemon-yellow when young, rapidly blue-staining hymenophore, a red zone at the apex of a small curving stipe, and the habit of fruiting alone or in small groups on *Dicymbe* trunks. The masses of humus that accumulate between the epicormic shoots and roots of mature *Dicymbe* trees appear to be a required site for fruiting of *B. exiguus* and are known to harbor abundant ectomycorrhizae (Woolley et al 2007). A similar fruiting habit has been noted elsewhere for other *Boletellus* spp. (e.g. *Boletellus emodensis* [Berk.] Singer, *Boletellus ananas* [M.A. Curt.] Murrill; Corner 1972, Singer et al 1983) and also is recorded here for *Boletellus dicymbophilus* sp. nov. Microscopically *B. exiguus* is distinguished by having three or four sterigmate basidia with numerous pale yellow refractive globules, pleurocystidia with golden incrustations in Melzer's, and a pileipellis of angular cells with tufts of erect inflated terminal elements.

Boletellus exiguus is best disposed infragenerically in *Boletellus* section *Chrysenteroidei* Singer based on the absence of red tints on the pileus, the general lack of viscosity and the absence of a marginal veil (Snell and Dick 1970, Singer 1986). The diminutive size of *B. exiguus* is similar to that of the boletelloid *Boletus ridiculus* Corner from Malaysia; *B. ridiculus* however can be distinguished from *B. exiguus* by its longer basidiospores (16–21 μm vs. 10–15 μm) and shorter pleurocystidia (40–60 μm vs. 65–85[100] μm) (Corner 1972). The distinctive red zone at the stipe apex of *B. exiguus* resembles the red annular band of *Boletellus cubensis* (Berk. & M.A. Curt.) Singer from the eastern Caribbean, but *B. exiguus* lacks an annulus; *B. cubensis* is also markedly larger (pileus 20–60 mm vs. 9–42 mm diam, stipe 30–70 mm vs. 7–34 mm long; Pegler 1983, Singer et al 1983). Among Congolian *Boletellus* spp. none are phenotypically close to *B. exiguus* (Heinemann and Goossens-Fontana 1954). Other members of *Boletellus* that deviate from strictly 4-sterigmate basidia are *Boletellus jalapensis* (non sensu Murrill) Gilbert, and *Boletellus obscurecoccineus* (Höhn) Singer, but otherwise these species do not phenotypically resemble *B. exiguus* (Corner 1972, Singer et al 1983).



FIG. 3. Basidiomata of *Boletellus dicymbophilus* (Henkel 8818). Bar = 10 mm.

Boletellus dicymbophilus Fulgenzi and T.W. Henkel
sp. nov. FIGS. 3–4, 5c

Pileus porphyreus, convexus vel planus, rugosus, velutinus, postea subtiliter areolatus, 19–48 mm latus; trama alba, immutabilis. Stipes brunneus, longitudinaliter striatus, ad tactum atrans, 41–60(81) × 4–7 mm. Basidiosporae olivaceo-brunneae in massa, amygdaliformes, longitudinaliter porcatae, 12–15 × 8–11 μm. Fructificatio insidens trunco *Dicymbe* arborum.

HOLOTYPE: Henkel 8616 (BRG; ISOTYPE: HSU, NY; MycoBank No. MB 511184)

Pileus 19–48 (82) mm broad, convex to planoconvex, red-brown (8E8–9E8–9F5) when immature, becoming brown (6E6–6F6) and then orange-tan (6C6) to yellow-tan (4C6) with age, rugulose to rugose throughout, velutinous, finely areolate with age (under lens), moist, margin slightly inrolled and entire; trama 1–3 mm thick at margin, 2–5 mm over tubes, 3–7 mm above stipe, white to cream, slightly browning with exposure, solid. *Odor* indistinct; *flavor* mild. *Tubes* 1–6 mm long at margin, 5–13 mm centrally, 4–8 mm at stipe, narrowly and shallowly depressed around stipe, with short decurrent tooth 1–2 mm long, concolorous with pores, instantly bluing (26E8) on exposure, eventually darkening to brown; pores progressing from yellow (4A7–4B7) to orange-yellow (4C8–5D8) to dark yellow (4A8–5B8), rapidly blue-green (26E7) with pressure, 0.5–1.5 per mm,

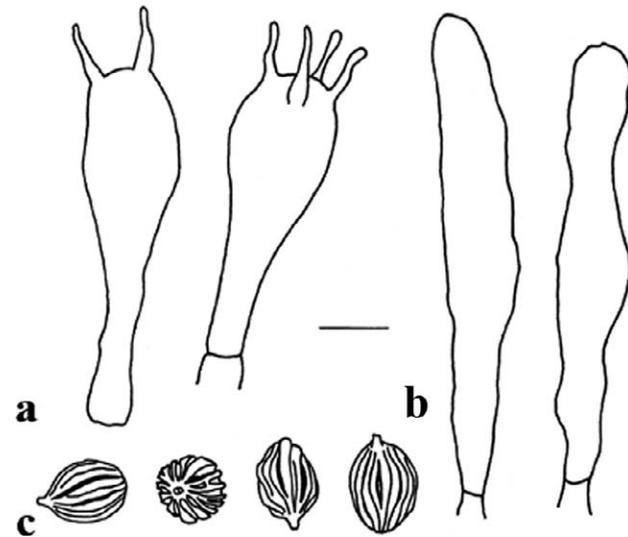


FIG. 4. Microscopic features of *Boletellus dicymbophilus* (HOLOTYPE; Henkel 8616) a. Basidia. b. Pleurocystidia. c. Basidiospores. Bar = 10 μm.

isodiametric to angular with age. *Stipe* 41–60 (81) × 4–7 mm, equal, slightly enlarging at extreme base, red-brown (9D7–9E7) throughout, with handling becoming brown (7F6–7F7) to dark brown (8F5), finely longitudinally striate throughout, striations minutely pubescent (under lens), subreticulate at apex, base with brown (8F5) strigose hairs on lower 4–20 mm; trama brown (6E7–6F7) throughout to dark brown (7F7) to red-brown (8E4), unchanging, solid.

Basidiospores olive (4D6) to olivaceous brown (4F5) in light to heavy deposit; 12–15 × 8–11 μm (mean = 13 × 9 μm; n = 25), Q range 1.2–1.7 (mean Q = 1.37), golden-olive in H₂O and KOH, inamyloid, amygdaliform, usually uniguttulate, with 7–10 longitudinal ridges; ridges < 1 μm tall, dichotomously forked, occasionally nonforked, terminating in unequal lengths near apex, at extreme base all ridges converging at hilar appendage; hilar appendage 1–1.5 μm long. *Basidia* 43–48 × 12–15 μm, clavate, thin-walled, hyaline in H₂O and KOH, with numerous refractive globules, these light golden in H₂O, lighter in KOH; with 2, 3 or 4 sterigmata. *Pleurocystidia* frequent, 33–56 × 7–12 μm, projecting 22–49 (57) μm beyond the hymenial palisade, arising from the subhymenium, cylindrical to narrowly clavate; thin-walled, hyaline in H₂O and KOH, with minute amber incrustations at basal and apical portions evident in Melzer's and H₂O. *Hymenophoral trama* boletoid, strongly divergent; mediostatum 37–59.3 μm wide, of thin, slightly anastomosing hyphae, golden-orange in H₂O, gelatinized and lighter in KOH; lateral stratum hyphae 1.2–2.5 μm wide, hyaline in H₂O and KOH, nongelatinized. *Pileipellis* a two-layered trichodermial palisade, in mass golden in H₂O,

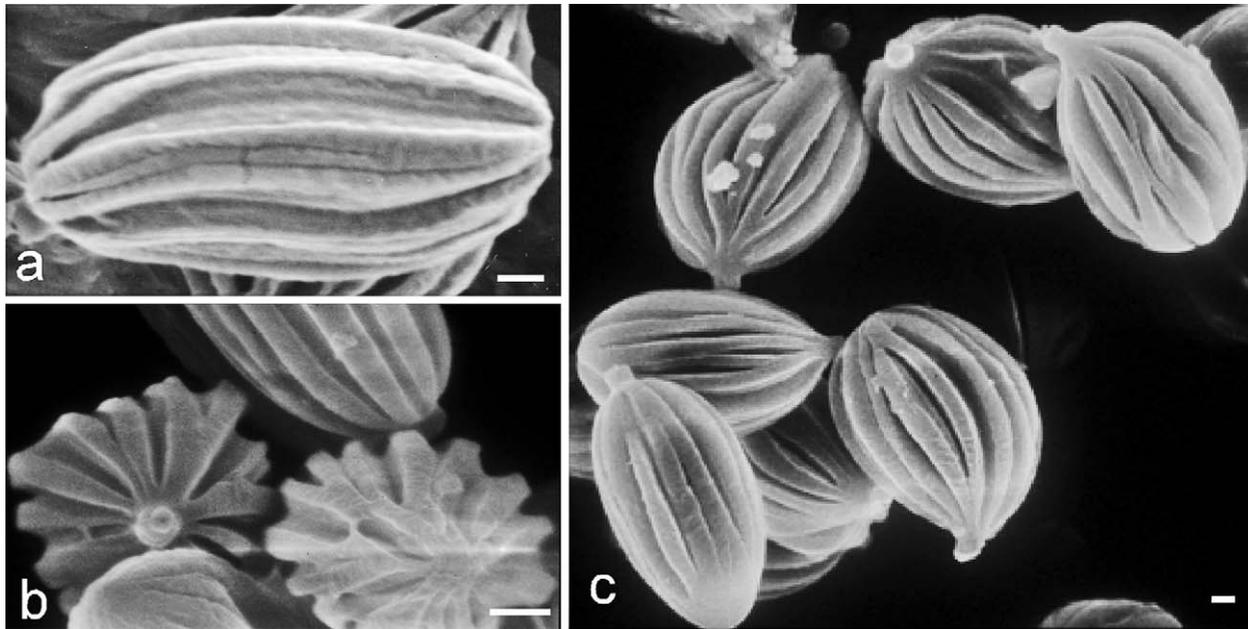


FIG. 5. Scanning electron micrographs of basidiospores of *Boletellus* species from Guyana. a. *Boletellus exiguus* (HOLOTYPE; Henkel 8696), $\times 6700$. b. *Boletellus exiguus* (Henkel 8809), $\times 8900$. c. *Boletellus dicymbophilus* (Henkel 8824), $\times 3200$. Bar = 1 μm .

lighter in KOH; terminal cells $42\text{--}76.6 \times 12.4\text{--}24.7 \mu\text{m}$, most inflated and of variable shapes, oblong, cylindrical, napiform, vesiculate, to occasionally bluntly ventricose; penultimate cells interwoven, less inflated, hyaline in H_2O and KOH, inamyloid. *Pileus trama* interwoven; hyphae $6.2\text{--}12.4 \mu\text{m}$ wide, thin-walled, faint golden in H_2O , hyaline in KOH, regularly septate, with external dark burgundy acerose crystals evident in KOH, Melzer's, and H_2O . *Stipitipellis* an interwoven trichodermial palisade of cylindrical elements giving rise to inflated terminal cells, in mass golden in H_2O , lighter in KOH; terminal cells $40\text{--}66.7 (77) \times 4.9\text{--}7.4 \mu\text{m}$ wide, thin-walled, cylindrical to aciculate; hyaline in H_2O and KOH, inamyloid. *Stipe trama* of densely packed longitudinal hyphae, these $5\text{--}10 \mu\text{m}$ wide, hyaline in H_2O and KOH, with external dark burgundy acerose crystals evident in KOH, Melzer's and H_2O . *Clamp connections* absent. *Macrochemical reactions*: NH_4OH burgundy on pileus, orange on pileus trama, burgundy on stipe base trama; KOH burgundy to orange on pileus, dark orange on pileus trama, burgundy on stipe base trama.

Habit, habitat, and distribution. Solitary or in groups of 2–3 among humic accumulations on trunks of large, living *Dicymbe corymbosa* trees; known only from the type locality in the Upper Potaro River Basin of Guyana.

Etymology. *Dicymbophilus* = *Dicymbe* loving (Greek), referring to the exclusive fruiting habit on *Dicymbe* trunks.

Specimens examined. GUYANA. REGION 8 POTARO-SIPARUNI: Pakaraima Mountains, Upper Potaro River, within 5 km radius of $5^\circ 18' 04.8''\text{N}$, $59^\circ 54' 40.4''\text{W}$, elevation 710–750 m; Ayanganna airstrip, 20 May 2000, Henkel 7405 (BRG; HSU); *Dicymbe* plot 2, 8 May 2000, Henkel 7455 (BRG; HSU); *Dicymbe* plot 2, 10 May 2000, Henkel 7480 (BRG; HSU); *Dicymbe* plot 2, 23 Jun 2000, Henkel 7851 (BRG; HSU); vicinity of Potaro base camp, 2 May 2001, Henkel 8011 (BRG; HSU); *Dicymbe* plot 1, 18 May 2001, Henkel 8152 (BRG; HSU); vicinity of Potaro base camp, 25 Jul 2003, Henkel 8616 (HOLOTYPE, BRG; ISOTYPE: HSU, NY); vicinity of Potaro base camp, 5 Jul 2004, Henkel 8733 (BRG; HSU); vicinity of Potaro base camp, 31 May 2005, Henkel 8818 (BRG; HSU); 1.5–2 km southeast of Potaro base camp, 1 Jul 2005, Henkel 8824 (BRG; HSU); 0.5–1 km west of Potaro base camp, 3 Jun 2005, Henkel 8829 (BRG; HSU); 2 km southeast of Potaro base camp, 5 Jun 2005, Henkel 8840 (BRG; HSU).

Commentary. *Boletellus dicymbophilus* is distinctive due to its dark red-brown, rugose pileus that becomes lighter with maturation, its subequal, dark brown, longitudinally striate stipe, the yellow to olive-yellow, blue-staining hymenophore, lack of a bluing reaction of the exposed trama and habit of fruiting singly or in groups of 2–3 on *D. corymbosa* trunks. Microscopically *B. dicymbophilus* is distinguished by its 2–4 sterigmate basidia with numerous pale yellow refractive globules, cylindrical to narrowly clavate pleurocystidia with amber encrusting pigments evident in H_2O and Melzer's, a 2-layered palisadic pileipellis of variously shaped terminal elements, a palisadic stipitipellis of variably shaped cylindrical elements and the presence

of external burgundy acerose crystals in the pileus and stipe trama.

Boletellus dicymbophilus is best disposed infragenerically in *Boletellus* section *Chrysenteroidei* Singer based on the dry pileus lacking red tints and the absence of a marginal veil (Snell and Dick 1970, Singer 1986). Nonbluing trama has also been reported for *Boletellus longicollis* (Ces.) Pegler & Young, *B. obscurecoccineus* (Corner 1972) and *B. cubensis* (Berk. & M.A. Curtis) Singer (Pegler 1983, Singer et al 1983); although only *B. longicollis* from Malaysia and Japan is otherwise phenotypically similar to *B. dicymbophilus*, with dark brown rugose pilei, but the former has a well developed, white, gelatinous appendiculate veil (Corner 1972, Imazeki et al 1988). Other members of *Boletellus* that deviate from strictly 4-sterigmate basidia are *B. jalapensis*, *Boletellus ivoryi* Singer and *B. obscurecoccineus*, but each differs from *B. dicymbophilus*; for example *B. jalapensis* has longer basidiospores (15–25 vs. 12–15 μm) and *B. obscurecoccineus* longer pleurocystidia (65–130 vs. 33–56 μm ; Corner 1972, Singer et al 1983). *Boletellus dicymbophilus* is similar to *Boletellus pustulatus* (Beeli) Gilbert from tropical Africa in basidioma stature, basidiospore size, and the presence of a 2-layered palisadic pileipellis of variously shaped hyphal elements. However *B. pustulatus* possesses ventricose-rostrate pleurocystidia, cheilocystidia and a bluing reaction in the exposed trama (Heinemann and Goossens-Fontana 1954, Watling and Turnbull 1992).

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LITERATURE CITED

- Corner EJH. 1972. *Boletus* in Malaysia. Singapore: Botanic Gardens.
- Halling RE, Mueller GM. 2005. Common Mushrooms of the Talamanca Mountains, Costa Rica. New York: New York Botanical Gardens Press.
- Heinemann P, Goossens-Fontana M. 1954. Flore iconographique des champignons du Congo. In: Fascicle 3. Boletineae. Brussels: Le jardin Botanique de l'Etat. p 51–78.
- Henkel TW. 2003. Monodominance in the ectomycorrhizal *Dicymbe corymbosa* (Caesalpiniaceae) from Guyana. J Tropic Ecol 19:417–437.
- Holmgren PK, Holmgren NH, Barnett LC. 1990. Index Herbariorum. Part I: the herbaria of the world. Reg Veg 120:1–693.
- Horak E. 1977. *Boletellus* and *Porphyrellus* in Papua New Guinea. Kew Bulletin 31:645–652.
- Imazeki R, Otani Y, Hongo T. 1988. Fungi of Japan. Tokyo: Yama-Kei Publishing Co. Ltd.
- Kornerup A, Wanscher JH. 1978. Methuen handbook of colour. 3rd ed. London: Eyre Methuen Ltd.
- Ortiz-Santana B, Lodge DJ, Baroni TJ, Both EE. 2007. Boletes from Belize and the Dominican Republic. Fungal Divers 27:247–416.
- Pegler DN. 1983. Agaric flora of the Lesser Antilles. Kew Bull Add Ser 9:1–668.
- Singer R, Araujo I, Ivory MH. 1983. The ectotrophically mycorrhizal fungi of the neotropical lowlands, especially Central America. Beih Nov Hedweg 77:1–352.
- . 1986. The Agaricales in modern taxonomy. 4th ed. Koenigstein, Germany: Koeltz Scientific Books.
- , Garcia J, Gomez LD. 1992. The Boletineae of Mexico and Central America IV. Beih Nov Hedweg 105: 1–49.
- Smith AH, Thiers HD. 1971. The Boletes of Michigan. Ann Arbor: University of Michigan Press.
- Snell WH, Dick EA. 1970. The Boleti of Northeastern North America. Lehre, Germany: J. Cramer.
- Watling R. 2001. Australian boletes: their diversity and possible origins. Aust Syst Bot 14:407–416.
- , Turnbull E. 1992. Boletes from South and East Central Africa I. Edinburgh J Bot 49:343–361.
- Woolley LP, Henkel TW, Sillett SC. 2007. Reiteration in the tropical monodominant tree *Dicymbe corymbosa* (Caesalpiniaceae) and its potential adaptive significance. Biotropica 40:32–42.