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New species of *Xerocomus* (Boletales) from the Guiana Shield, with notes on their mycorrhizal status and fruiting occurrence

Dillon R. Husbands
Department of Agriculture, Faculty of Agriculture and Forestry, University of Guyana, Georgetown, Guyana

Terry W. Henkel[1]
Department of Biological Sciences, Humboldt State University, Arcata, California 95521

Gregory Bonito
Rytas Vilgalys
Department of Biology, Duke University, Durham, North Carolina 27708

Matthew E. Smith
Department of Plant Pathology, University of Florida, Gainesville, Florida 32611

Abstract: *Xerocomus cyaneibrunnescens*, *Xerocomus potaroensis*, and *Xerocomus parvogracilis* (Boletales, Basidiomycota) are described as new species from the Pakaraima Mountains of Guyana, in the central Guiana Shield region. These boletes occur in neotropical forests dominated by ectomycorrhizal (ECM) trees in the genus *Dicymbe* (Fabaceae subfam. Caesalpinioideae). Each species produced basidiomata during a multi-year plot survey, and each was confirmed as an ECM symbiont with one or more leguminous host plant species in Guyana.

Key words: Basidiomycota, Boletaceae, Boletineae, Caesalpinioideae, ectomycorrhizal fungi, Guyana

Introduction

Species of Boletaceae sensu lato (Boletales, Basidiomycota) are well represented in the ectomycorrhizal (ECM) macromycota associated with the leguminous genus *Dicymbe* (Fabaceae subfam. Caesalpinioideae) in Guyana (Henkel et al. 2012). To date, 28 morphospecies of boletoid fungi have been collected in *Dicymbe*-dominated forests. These species are distributed across eight genera including *Austroboletus* (Corner) Wolfe, *Boletellus* Murrill, *Chalciporus* Bataille, *Fistulinella* Henn., *Phylloporus* Quél., *Pulveroboletus* Murrill, *Tylopilus* P. Karst. and *Xerocomus* Quél. Eighteen of these species, most of which were new to science, have been formally described (Henkel 1999, 2001; Fulgenzi et al. 2007, 2008, 2010; Mayor et al. 2008; Neves et al. 2010). Molecular analysis of roots has confirmed that at least 16 of these boletoid species are ECM associates of *Dicymbe* spp., *Aldina insignis* (Benth.) Endl. (Fabaceae subfam. Papilionoideae), or *Pakaraimaea dipterocarpacea* Maguire & Ashton (Dipterocarpaceae subfam. Pakaraimoideae) (Smith et al. 2011, unpubl).

Xerocomus sensu lato encompasses ~ 160 described species worldwide, many with tropical distributions (Heinemann and Goossens-Fontana 1954; Heinemann 1964; McNabb 1968; Snell and Dick 1970; Corner 1972, 1974; Singer 1986; Singer et al. 1983, 1991; Gomez 1996; Ladurner and Simonini 2003; Ortiz-Santana et al. 2007; Watling 2008; Horak 2011). The genus has been variously defined morphologically over the decades (e.g. Snell and Dick 1970, Singer 1986) and called into question by some American authors (e.g. Smith and Thiers 1971). Within the Boletaceae s.l., both *Xerocomus* s.l. and *Boletus* s.l. have olivaceous brown, smooth basidiospores under light microscopy. *Xerocomus* has been differentiated from *Boletus* by its hymenophoral tubes that are sublamellate near the stipe and adnate to decurrent, subangular to angular, relatively large pores, cylindrical to subequal, thin, usually nonreticulate stipe, parallel to barely divergent (''phylloporoid'') tube trama and trichodermioid, dry pileipellis (e.g. Singer 1986). In lowland ectotrophic forests of the tropics, most boletes encountered with smooth, olivaceous brown basidiospores meet these generic diagnostics for *Xerocomus* and not *Boletus* (e.g. Singer et al. 1983, Horak 2011, Henkel et al. 2012).

While molecular phylogenetic studies of Boletaceae have not confirmed the monophyly of many of the traditional genera, including *Xerocomus* and *Boletus*, neither have they convincingly identified alternative monophyletic generic groups within the family (e.g. Binder and Hibbett 2006, Drehmel et al. 2008). Although some progress has been made in delimiting genera within the Boletaceae using molecular data (Dentinger et al. 2010, Halling et al. 2012, Neves et al. 2012), a full reassessment of *Xerocomus* and *Boletus* will require much further study. This is evidenced by the small number of taxa clustering around the type species *Xerocomus subtomentosus* (L.) Quél. and *Boletus edulis* Bull. in the taxon-extensive nuc-LSU rDNA analysis of Binder and Hibbett (2006, Supplementary Fig. 1). Indeed, two of the new xerocomoid

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[1] Corresponding author. E-mail: twh5@humboldt.edu

species reported here (collections Henkel 8821 and 8850) were unresolved at the generic level in the three-gene phylogenetic analysis of Dentinger et al. (2010, Fig. 4, p 1287). While molecular delimitation of the Boletaceae genera remains elusive, diverse species complexes have been discovered within the north temperate *X. chrysenteron* s.l. and *X. subtomentosus* s.l. (Peintner et al. 2003, Taylor et al. 2006). Šutara (2008) used detailed morphological analyses to erect the segregate genus *Xerocomellus* Šutara. This group includes European *Xerocomus* s.l. species that are morphologically aligned with *X. chrysenteron* s.l. but has not been fully supported by molecular phylogenetic analyses (e.g. Binder and Hibbett 2006, SUPPLEMENTARY FIG. 1).

Here we describe three new species from Guyana: *Xerocomus cyaneibrunnescens*, *Xerocomus potaroensis* and *Xerocomus parvogracilis*. Macromorphological, micromorphological and habitat data are provided for each new species, along with DNA sequence data from the holotypes and other specimens. Each of these species has been studied for many years in Guyana's *Dicymbe* forests. In this light we note their fruiting frequencies in a long-term plot study by Henkel et al. (2012) and their ECM status with native leguminous host plants indicated by molecular and morphological analysis of ECM roots.

MATERIALS AND METHODS

Collections.—They were made during the May–Jul rainy seasons 2000–2002, 2005–2006 and 2008–2010 and the Dec rainy season 2009 from the Upper Potaro River Basin, within a 15 km radius of a permanent base camp at 5°18′04.8″N; 59°54′40.4″W, 710 m (Henkel 2003). Additional collections were made May–Jun 2011 from the Upper Demerara River Basin at Mabura Ecological Reserve, within 2 km of a field station at 5°09′19.0″N; 58°41′58.9″W, 100 m. At Potaro, basidiomata were collected from monodominant forests of *Dicymbe corymbosa* Spruce ex Benth. and other stands containing *D. corymbosa*, *Dicymbe altsonii* Sandw. and *A. insignis*; at Mabura collections were made in *D. altsonii* monodominant stands. Fungi were field-dried with silica gel. Macroscopic features of basidiomata were described fresh in the field. Colors were described subjectively and coded according to Kornerup and Wanscher (1978), with color plates noted in parentheses. Micromorphological features of fresh specimens were examined with an EPOI field microscope with light optics; dried specimens were examined with an Olympus BX51 microscope with light and phase contrast optics. Rehydrated fungal tissue was mounted in H_20, 3% potassium hydroxide (KOH), and Melzer's solution. For holotype collections at least 20 individual basidiospores, basidia and other structures were measured; for additional collections at least five of each structure were measured. Range and mean quotients (Q) of basidiospore length divided by width are included. Outlying measurements observed in less than 5% of a given structure are placed in parentheses. Line drawings were traced from digital photomicrographs and edited with Photoshop CS5 (Adobe, San Jose, California). Scanning electron micrographs (SEM) of basidiospores were obtained with a Topcon ABT32 scanning electron microscope using 200 kV.

Guyana specimens were deposited in these herbaria (Holmgren et al. 1990): BRG, University of Guyana; HSU, Humboldt State University; NY, New York Botanical Garden. Type specimens of Malaysian *Xerocomus* and *Boletus* species described by Corner were examined at the Royal Botanic Garden Edinburgh Herbarium (E), and holotypes of Brazilian *Xerocomus* species described by Singer were examined on loan from the herbarium of the Instituto Nacional de Pesquisas da Amazonia (INPA).

Molecular protocols.—Ribosomal DNA sequencing of the ITS and LSU regions for holotype and additional specimens was performed on dried basidioma tissue following the protocols of Dentinger et al. (2010) and Smith et al. (2011). Newly generated sequences were edited in Sequencher 4.1.4 (Gene Codes Corp., Ann Arbor, Michigan), and deposited in GenBank. Accession numbers for these are given under *Specimens examined* for each species. Basidioma ITS rDNA sequences of each new species were subjected to BLASTn queries to assess their closest putative generic relatives in GenBank. Ectomycorrhizal root tips were collected from *D. corymbosa* in 2008 in the Upper Potaro Basin and subjected to the processing and ITS sequencing protocols of Smith et al. (2011). Ectomycorrhiza vouchers matching basidiomata of the species reported here at > 97% for the species-specific ITS region were considered conspecific and examined for the presence of a mantle and Hartig net (e.g. Agerer 1991). Vouchers for species-confirmed ectomycorrhizas are maintained at Humboldt State University.

RESULTS

ITS BLASTn searches of each new species indicated highest matches with species identified as *Xerocomus* on GenBank, although none of searches exceeded 86% similarity. Ectomycorrhiza vouchers TH30812 and TH30826 were > 97% sequence-similar for ITS for *X. cyaneibrunnescens* or *X. potaroensis* respectively and therefore considered conspecific.

TAXONOMY

Xerocomus cyaneibrunnescens T.W. Henkel et Husbands, sp. nov. FIGS. 1–3

MycoBank MB564750

Pileus 30–62(80) mm broad, 8–30 mm tall, convex to broadly convex to plano-convex, tannish brown (5C3–5C5) throughout when young, darkening slightly (6D3–D5) with age, sometimes with darker brown discolorations, evenly rugose throughout, rugosities

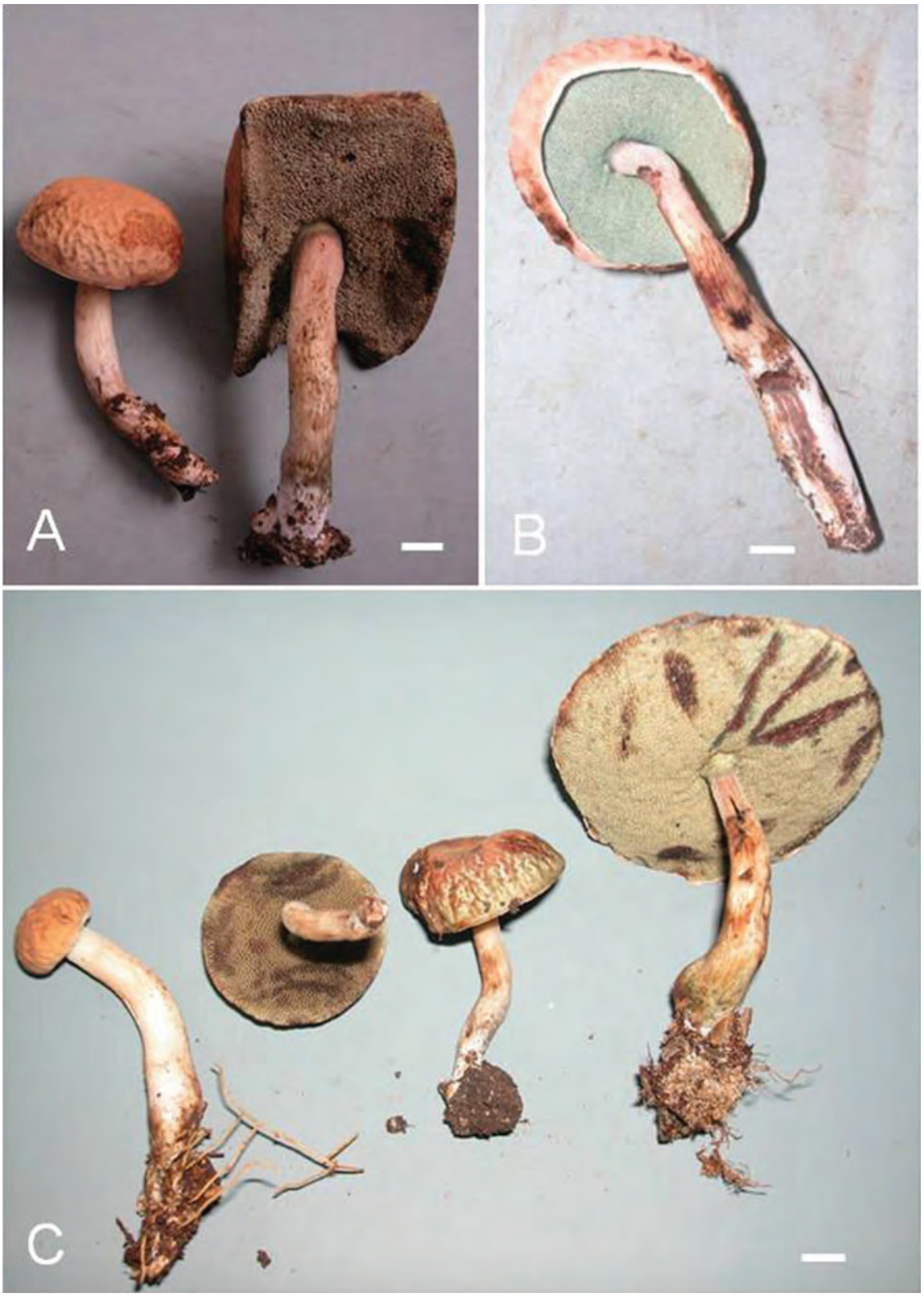

FIG. 1. Basidiomata of *Xerocomus cyaneibrunnescens*. A. HOLOTYPE; *Henkel 9197*. B. *Henkel 9255*, with the young greenish cream tubes and brown staining stipe. C. *Henkel 9601*, developmental series; with blue to brown tube stains on right. Bars =

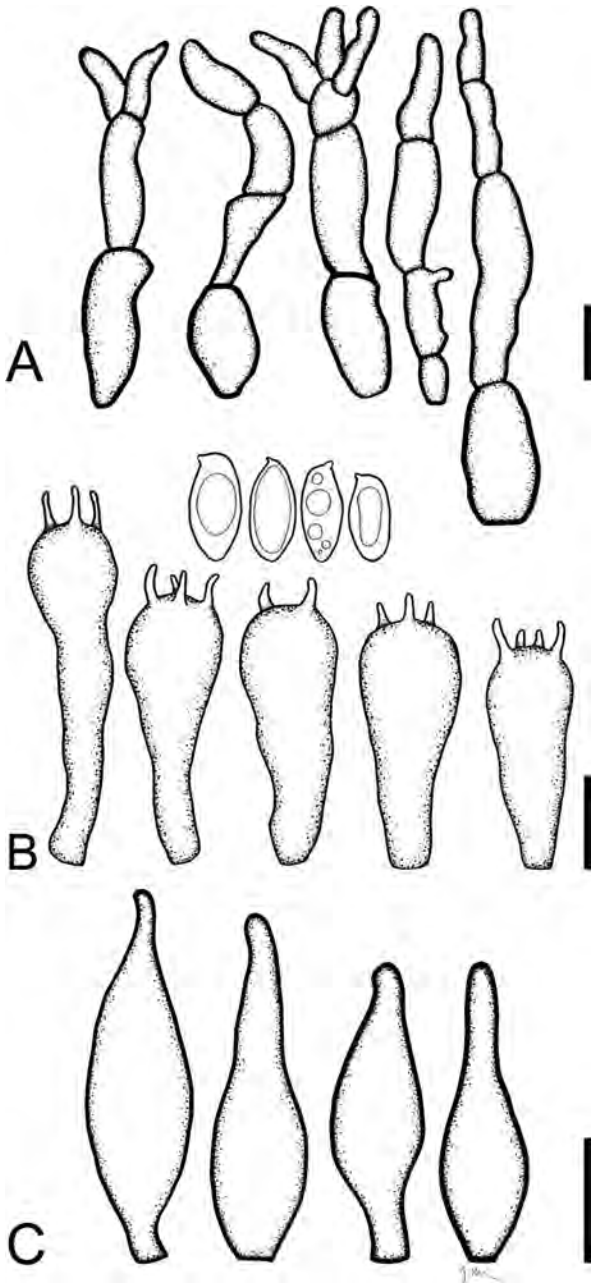

FIG. 2. Microscopic features of *Xerocomus cyaneibrunnescens* (HOLOTYPE; *Henkel 9197*). A. Terminal elements of the pileipellis. B. Basidiospores and basidia. C. Pleurocystidia. Bars = 10 μm.

broadening and becoming more regular with age, surface under hand lens an erect tomentose mat throughout, with age separating to finely areolate or rivulose toward margin revealing light tan ground, rarely extending over the disk, dry; margin entire with a narrow tan tissue flap; trama subsolid, 1–2 mm at margin, 4–12 mm over tubes, 5–18 mm over stipe, initially off-white, bluing slowly but distinctly especially in older specimens, larval channels brown. Odor mild, boletoid; flavor pleasantly fungoid. Tubes 1–4 mm at margin, 3–10 mm centrally, 2–6 mm at stipe, occasionally sublamellate near stipe, narrowly depressed around stipe, initially cream (3B3–4B3) to light greenish cream (1B3–1C3) or rarely livid light grayish green (29D4, 30C4), maturing darker concolorous and then brownish (4C4–4D4–5D4), staining instantly brown under pressure, becoming distinctively bluish brown within 60 s, eventually to dark brown (~ 6F5–F8); tube edges concolorous, finely roughened under hand lens; pores somewhat stuffed when young, otherwise 1 per mm, initially subisodiametric, subangular at maturity. Stipe 45–107 mm × 5–17 mm, subequal, broadening slightly at base to 9–19 mm, sometimes flaring outward at extreme apex, usually curved, dull tan (5B3–5B4) over upper three-fourths, discoloring brownish where handled, usually with a narrow, well demarcated band that is light grayish green (~ 1C2) to light grayish turquoise (~ 25C3) to rarely brilliant aquamarine blue (24 A3–A4–B4) near extreme apex, 1–1.5 mm wide, with age bluish band becoming progressively darker reddish brown, sometimes subtended by a more reddish zone; upper one-third to two-thirds with distinct low concolorous reticulum more pronounced in mature basidiomata, reticulations discoloring brownish with handling, lower quarter with fine whitish tomentum on tan ground, this coalescing downward into a white, densely matted basal mycelium; trama off-white throughout, fibrous, slowly bluing in older specimens, subsolid.

Basidiospores dark reddish brown (7F7, 8F6–F8) in medium deposit, (9)10–11(13) × 4.5–5(6) μm, Q range (1.8)2–2.5(3) (mean Q = 2.2), broadly subfusiform, smooth, with a shallow suprahilar depression, reddish brown in H_2O, lighter in KOH, inamyloid, uni- to multiguttulate; hilar appendage 0.4–0.5 μm long; wall 0.3–0.5 μm thick; surface under SEM with extremely minute, low ridges, but not distinctly bacilliform. Basidia (22.2)29.6–39.5(46.9) × 7.4–9.9 (12.4) μm, clavate or infrequently narrowly clavate, tapering evenly toward base, hyaline in H_2O and KOH, devoid of refractive content or occasionally granulose and guttulate, these contents olivaceous brown in H_2O, pale gray in KOH; sterigmata (1.2)2.5–2.7(4.9) μm long, two, three or four per basidium. Pleurocystidia infrequent, (34.6)37.1–61.8(76.6) × (7.4)9.9–14.8(17.7) μm, ventricose to ventricose-rostrate to clavate-mucronoid, evenly embedded within or extending 10–22 μm above the hymenial palisade, devoid of contents to occasionally with light gray cytoplasm in KOH, pigment more obvious in H_2O. Cheilocystidia absent. Hymenophoral trama phylloporoid, parallel to barely diverging, in mass olivaceous gray in H_2O, hyaline to faintly yellow in KOH, mediostratum indistinct;

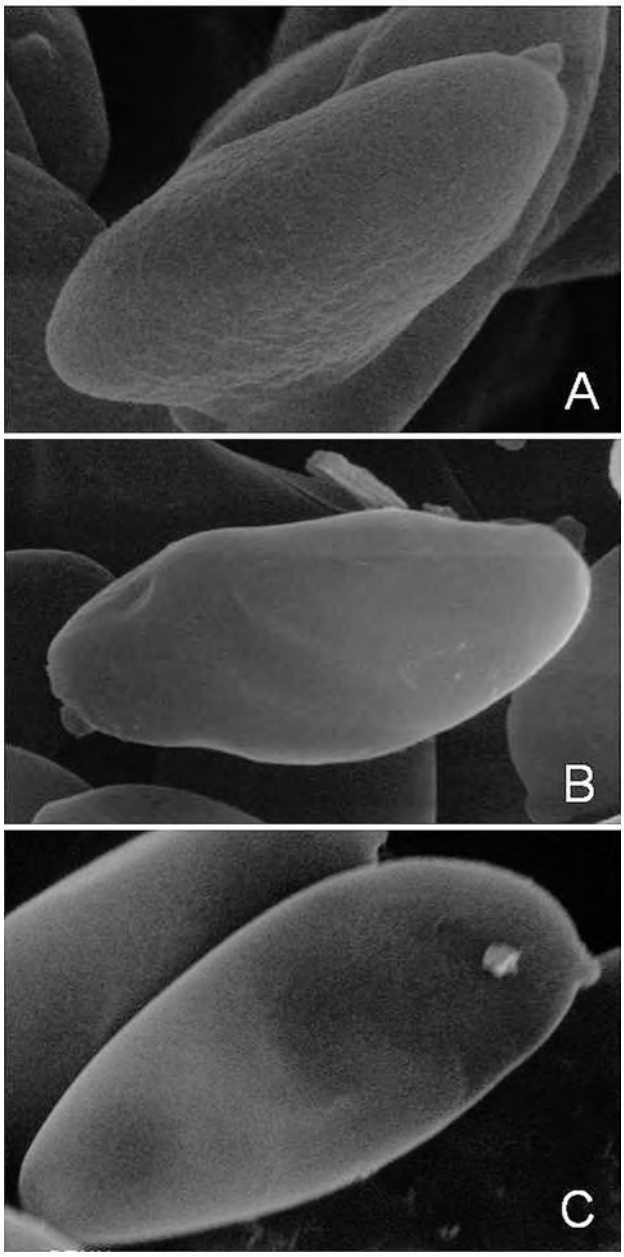

FIG. 3. Scanning electron micrographs of basidiospores of *Xerocomus* species from Guyana. A. *Xerocomus cyaneibrunnescens* (HOLOTYPE; *Henkel 9197*), 10 500×. B. *Xerocomus potaroensis* (*Henkel 8802*), 11 000×. C. *Xerocomus parvogracilis* (HOLOTYPE; *Henkel 9209*) 9500×.

hyphae 4.9–7.4(9.8) µm wide, hyaline in H_2O and KOH, slightly gelatinized in older specimens; conductive hyphae scattered throughout, these 4.9–12.3 µm wide, with opaque, hyaline to pale orange, guttulate cytoplasm. Pileipellis a trichodermial palisade of cylindrical to variously inflated, close-septate hyphae with rounded tips projecting at slightly irregular lengths, often with minute granular external incrustations in faint band-like patterns, granulose-guttulate, in mass orangish brown in H_2O, lighter in KOH, occasionally with short branches from penultimate cells; terminal cells 18.5–37.1(49.4) × (3.7)4.9–10(12.4) µm, cylindrical, obclavate, or subutriform, frequently with irregular nodulose projections; subpellis dense, tannish yellow in KOH. Pileus trama densely interwoven; individual hyphae hyaline, thin walled, devoid of obvious contents, curving and much branched, 4.9–9.9 µm wide, interspersed with frequent opaque, hyaline conductive hyphae, these more concentrated near subpellis. Stipitipellis a trichodermium; terminal elements ventricose, clavate, subglobose, or lageniform, (17.3)24.7–74.1(98.8) × 7.4–19.8(24.7) µm, thin-walled, with pale grayish yellow cytoplasmic contents in KOH, darker in H_2O, occasionally guttulate. Stipe trama in mass with orangish yellow cytoplasmic pigmentation in H_2O, lighter in KOH; individual hyphae 4.9–8.6 µm wide. Clamp connections absent. Macrochemical reactions: 10% NH_4OH yellowish olive on pileus and stipe trama, dark brown instantly on stipe base; 3% KOH dark brown over 30 s on pileus, stipe base, and lower stipe trama, light reddish brown on pileus trama.

Holotype: Henkel 9197 (BRG; ISOTYPE HSU; NY).

Habit, habitat and distribution: Solitary or scattered around the base and on humic deposits on trunks of *D. corymbosa* trees on lateritic soils; also found in association with *D. altsonii* on sand soils; known from the type locality in the central Pakaraima Mountains and ~ 100 km to the east near Mabura Hill in the lowlands of Guyana.

Etymology: Cyaneus (L. adj. A) = blue; brunnescens (L. adj. B) = becoming brown; referring to the distinctive blue and brown auto-oxidation reactions of the bruised hymenophore.

Specimens examined: GUYANA. REGION 8 POTARO-SIPARUNI: Pakaraima Mountains, Upper Potaro River Basin, within a 15 km radius of Potaro base camp at 5°18′04.8″N, 59°54′40.4″W, 710–750 m; vicinity of base camp, 26 May 2000, *Henkel 7416* (BRG; HSU); 14 Jun 2000, *Henkel 7495* (BRG; HSU); ~ 3.5 km southeast of base camp near *Dicymbe* plot 2, 11 May 2001, *Henkel 8086* (BRG; HSU); ~ 4 km southwest of base camp in *Dicymbe* plot 3, 12 May 2001, *Henkel 8107* (BRG; HSU); ~ 1.5 km southwest of base camp, 26 May 2005, *Henkel 8805* (BRG; HSU), GenBank ITS: JN168785; vicinity of base camp, 31 May 2005, *Henkel 8821* (BRG; HSU), GenBank LSU: HQ161866; RBP1: HQ161835; ATP6: HQ161803; 0.75 km southwest of base camp near Blackwater Point, 10 Jul 2009, *Henkel 9025* (BRG; HSU); ~ 15 km east of Potaro base camp near Tadang base camp in mixed *D. corymbosa-D. altsonii* forest, 19 Dec 2009, *Henkel 9111* (BRG; HSU); ~ 2 km southeast of base camp near *Dicymbe* plot 1, 17 May 2010, *Henkel 9197* (HOLOTYPE BRG; ISOTYPES HSU, NY), GenBank ITS/LSU: JQ751259; ~ 2 km west of base camp near *Dicymbe* masting plots, 3 Jun 2010, *Henkel 9255* (BRG; HSU); REGION 10 UPPER DEMERARA-BERBICE: Mabura Ecological Reserve, field

station at 5°09′19.0″N; 58°41′58.9″W, ~ 100 m; ~ 100 m northwest of Mabura field station in *D. altsonii* monodominant stand 1 on brown sand soils, 20 May 2011, *Henkel 9601* (BRG; HSU). BRAZIL. AMAZONAS: Estrada Manaus-Caracarai km 125, 22 May 1978, *Singer B11015*, *Xerocomus globuliger* Singer!, Holotype (INPA 77399). MALAYSIA. North Borneo, Mount Kinabalu, 19 Aug 1961, *Corner RSNB 1882*, *Xerocomus lucescens* (Corner) E. Horak!, Isotype (E-00085003); 30 Sep 1961, *Corner RSNB 1565*, *Xerocomus pseudochrysenteron* (Corner) E. Horak!, Isotype (E-00085704).

Commentary: *Xerocomus cyaneibrunnescens* is a distinctive bolete recognized in the field by its consistently rugose, ochraceous brown pileus becoming finely areolate to rivulose with age, bluish cream hymenophore staining from brown to blue to dark brown, tan, subequal, apically reticulate stipe with a distinctive greenish to bluish band at the apex in fresh specimens, and habit of fruiting from accumulated humic materials on or around trunks of large *Dicymbe* trees. The species is best disposed in *Xerocomus* s.l. based on the morphological features of hymenophoral tubes that are sublamellate near the stipe and adnate with large, subangular pores, subequal stipe, parallel tube trama, and trichodermioid, dry pileipellis (Singer 1986). While the reddish brown basidiospore deposit is unusual, it has been recorded in other xerocomoid species with parallel tube trama (e.g. *Xerocomus ferruginosporus* [Corner] E. Horak).

Xerocomus cyaneibrunnescens was determined by Smith et al. (2011) to form ectomycorrhizas with the leguminous hosts *D. corymbosa*, *D. altsonii* and *A. insignis* and ranked 31st in frequency out of 118 ECM fungal species recovered using molecular methods from 1140 root tips sampled from 57 trees in the Upper Potaro Basin. Infrequent fruiting of *X. cyaneibrunnescens* in Guyana's *Dicymbe* forests was recorded in a long-term *D. corymbosa* plot study of Henkel et al. (2012), with its basidiomata occurring in 3.3% of 630 quadrats sampled during the May-Jul rainy seasons over 7 y. Ectomycorrhizas of *X. cyaneibrunnescens/D. corymbosa* are illustrated (FIG. 4).

Among *Xerocomus* species described by Singer from the Brazilian Amazon, *X. globuliger* Singer is similar to *X. cyaneibrunnescens* in its brownish, dry, rugose pileus, parallel hymenophoral trama lacking a distinct mediostratum, ventricose-rostrate pleurocystidia, lack of a distinct bluing reaction of the pileipellis with ammonia, and association with leguminous host plants (Singer et al. 1983). *Xerocomus globuliger* can be distinguished from *X. cyaneibrunnescens* by its yellow, unchanging tubes, lack of a stipe reticulum, regularly four-sterigmate basidia, much longer basidiospores (13–17.5 vs. 10–11 μm) that are olivaceous brown and lack of incrusted pileipellis hyphae. *Xerocomus scrobiculatus* Singer resembles *X. cyaneibrunnescens* in its dry, pallid brownish pileus, which lacks a distinct bluing reaction to ammonia, low stipe reticulum, similarly sized basidiospores, hyaline, parallel hymenophoral trama with indistinct mediostratum, and association with leguminous host plants, but differs in its citron yellow tubes, scrobiculate pileus, lack of auto-oxidation reaction of the bruised tubes or exposed trama, presence of a mucronate apex on the olivaceous brown basidiospores, and lack of incrusted pileipellis hyphae (Singer et al. 1983).

Among Malaysian xerocomoid boletes combining the features of *X. cyaneibrunnescens* of dry, dull brown pilei, a weakly reticulate stipe, cyanescent or brunnescent bruising reaction on the tubes, more or less cylindrical pileipellis elements and broadly fusiform basidiospores lacking in olivaceous tones, *X. lucescens* (Corner) E. Horak differs from *X. cyaneibrunnescens* in its more reddish brown pileus, lack of green to bluish coloration in the fresh tubes and stipe apex, persistently cyanescent bruising reaction, presence of cheilocystidia, and regularly cylindrical pileipellis terminal cells (Corner 1972, Horak 2011). *Xerocomus pseudochrysenteron* (Corner) E. Horak differs from *X. cyaneibrunnescens* in its adnate to subdecurrent tubes, reddish brown lower stipe, a more dramatic and intense bluing reaction on the tubes and exposed trama lacking a brunnescent phase, presence of cheilocystidia, and pale brown as opposed to red brown basidiospores. *Xerocomus ferruginosporus* (Corner) E. Horak is one of the few Malaysian taxa with reddish brown basidiospores but differs fundamentally from *X. cyaneibrunnescens* in its much longer, slender fusoid basidiospores (16.5–20 vs. 10–11 μm), white to pale brown tubes with much smaller pores, lack of cyanescent or brunnescent bruising reactions and lack of a distinct stipe reticulation.

The Congolian *X. sulcatipes* Heinem. & Gooss.-Font. is remarkably similar to *X. cyaneibrunnescens* in the combination of ochraceous, rugose-tomentose pileus becoming areolate toward the margin, grayish green, non-decurrent tubes, yellowish tan stipe with a grayish green apex, cyanescent reaction of the exposed trama, and similarly shaped pleurocystidia, basidia and pileipellis terminal cells. *Xerocomus sulcatipes* can be separated from *X. cyaneibrunnescens* by its longer (12–14.7 vs. 10–11 μm), more fusiform, brown basidiospores, more strongly inflated pileipellis terminal cells (10–20 vs. 4.9–10 μm wide), yellowish stipe with a reddish base, and lack of an auto-oxidation reaction of the bruised hymenophore (Heinemann and Goossens-Fontana 1954).

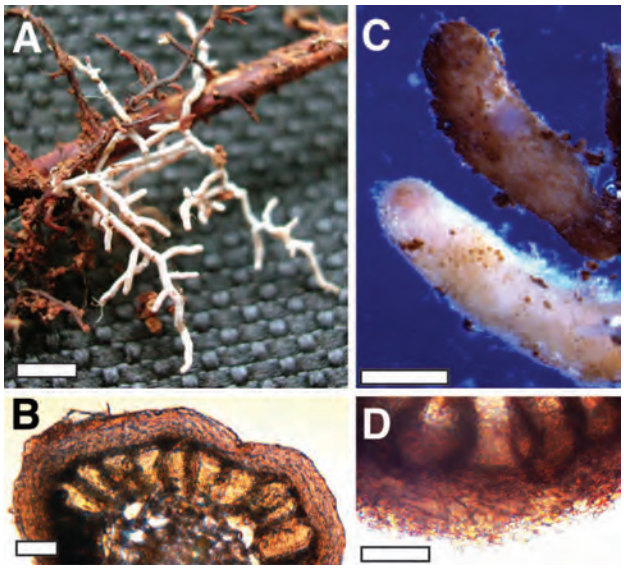

FIG. 4. Ectomycorrhizas of *Xerocomus cyaneibrunnescens* and *Xerocomus potaroensis* formed with *Dicymbe corymbosa*. A. Field photo of elongate, pinnate, smooth, white ectomycorrhizas of *X. cyaneibrunnescens* (voucher TH30812). Bar = 10 mm. B. Transverse section of *X. cyaneibrunnescens* ectomycorrhiza stained in Congo red showing a thick fungal mantle of tightly appressed, prosenchymatous hyphae and Hartig net. Bar = 100 µm. C. Rehydrated ectomycorrhizas of *X. potaroensis* ranging from light yellow when fresh (bottom) to darker, yellowish brown when senescent (top) with loosely associated outer mantle hyphae (voucher TH30826). Bar = 1 mm. D. Transverse section of an *X. potaroensis* ectomycorrhiza stained in Congo red showing the thin mantle with prosenchymatous outer layer, pseudoparenchymatous inner layer, and Hartig net. Bar = 100 µm.

Xerocomus potaroensis T.W. Henkel et Husbands, sp. nov. FIGS. 3, 5, 6

MycoBank MB564751

Pileus 16–52 mm broad, 7–17 mm tall, broadly convex to plano-convex, with age uplifting to nearly plane, initially dark orangish brown (8E8–F8–9F8) to orangish brown (6D8–E8–7D8–E8) with age; surface tomentulose macroscopically, under hand lens a low, dense erect mat contiguous over disk, separating over marginal one-third into fine areoles, revealing light yellow ground; moist; margin entire; trama 0.5–1 mm thick at margin, 2–3 mm over tubes, 4–5 mm above stipe, pale creamish yellow (~ 3A5), brown immediately under pileipellis, unchanging with exposure, suffused with brown streaking with age or around larval channels; subsolid. Odor minimal, indistinctive; flavor somewhat nutty, astringent, like *Boletus edulis*. Tubes 1–2 mm long at margin, 3–6 mm centrally, 2–3 mm at stipe, of slightly varying lengths, usually shallowly and narrowly depressed around stipe and there sublamellate and descending as decurrent teeth contiguous with stipe reticulations, initially dull yellow (3A5–A6–A7) to olivaceous yellow (3B5–B6) at maturity, edges concolorous, slowly and slightly bluing upon pressure, eventually to brown; pores 1–2 per mm, subisodiametric when young, ovate-angular with age. Stipe 25–62 × 3–7 mm, equal, rarely tapered at base, curving, with yellowish brown (6E7–7E7) to orangish brown (8E5–E6) longitudinal striations over lower two-thirds on cream to light yellow ground, striations coalescing upward into a partially anastomosed, irregular low reticulum; lower one-quarter with a pale yellowish bloom grading downward into a dense light yellow (2A2–A3–3A3) tomentum, subtended by aggregations of slender, concolorous hyphal cords and ectomycorrhizas; trama cream-colored, with brown streaking, unchanging on exposure, subsolid.

Basidiospores dark olivaceous brown (4F8, 5F5–F6) in medium deposit, 10–12(14) × 4–5 µm, Q range 2.24–3(3.5) (mean Q = 2.64), subfusiform, with distinct suprahilar depression, olivaceous-brown in H_2O and KOH, inamyloid, smooth, uni- to multiguttulate; hilar appendage 0.3–0.5 µm long; wall 0.2–0.5 µm thick; surface smooth under SEM. Basidia (20)25–34.3 × (6)7.4–9.9 µm, narrowly clavate to clavate, hyaline in H_2O and KOH, devoid of obvious contents or occasionally granulose-guttulate and then pale grayish green in H_2O, two-, three- or four-sterigmate; sterigmata nearly straight, 2–7 µm long. Pleurocystidia abundant, (40)51.9–74.1 × 8.7–12.4(14.8) µm, extending 20–39 µm above the hymenial palisade, broadly clavate-mucronoid, obclavate, or broadly lanceolate with rounded apices, rarely ventricose-rostrate, thin-walled, hyaline or pale grayish in H_2O and KOH, devoid of obvious contents. Cheilocystidia absent. Hymenophoral trama phylloporoid, parallel, mediostratum indistinct, in mass light yellowish gray in H_2O, hyaline in KOH; individual hyphae 4.5–8.6 µm wide, thin walled, devoid of obvious contents, hyaline or faintly gray, weakly gelatinizing; conductive hyphae absent. Pileipellis a trichodermial palisade of inflated cylindrical hyphae continuous with those of the trama; terminal cells narrowly clavate to clavate, occasionally broadly cylindrical or ovate, infrequently branching in groups of two or three from penultimate cell, (17.3)19.8–49.4(66.6) × (7.4)9.9–17.3 µm, yellowish gray in H_2O, nearly hyaline in KOH; subpellis of anticlinal, inflated hyphae and scattered conductive hyphae. Pileus trama interwoven, in mass pale yellow in KOH, hyphae uniformly inflated, branching frequently, 7.4–12.4 µm wide, devoid of obvious contents; conducting hyphae infrequent, opaque, hyaline, 3–5 µm wide. Stipitipellis a trichodermial palisade of

FIG. 5. Basidiomata of *Xerocomus potaroensis* (HOLOTYPE; *Henkel 9260*). Bar = 10 mm.

cylindrical hyphae, in mass with faint tannish yellow to gray in H_2O; terminal cells clavate to occasionally cylindrical-elongate, 24.7–49.4(61.8) × 4.9–9.9(14.8) µm, thin-walled, nearly hyaline in KOH; subpellis of anticlinal short-septate hyphae. Stipe trama in mass dull yellow to gray in H_2O, lighter in KOH; individual hyphae 4.9–9.9 µm wide, thin-walled, irregularly branched, nearly hyaline; conductive hyphae scarce. Clamp connections absent. Macrochemical reactions: 10% NH_4OH instantly and fleetingly blue then immediately to dark burgundy brown on pileus, nil elsewhere; 3% KOH instantly dark burgundy brown on pileus and stipe base, slightly browning pileus and stipe trama.

Holotype: *Henkel 9260* (BRG; ISOTYPES HSU; NY).

Habit, habitat and distribution: Solitary to scattered on humic mat of forest floor under *D. corymbosa* and *D. altsonii* on lateritic soils; known only from within a 15 km radius of the type locality in the Upper Potaro River Basin of Guyana.

Etymology: Potaroensis (-ensis Latin adj. B) = adjectival suffix indicating origin or place, referring to the type locality of the species in the Upper Potaro River Basin of Guyana.

Specimens examined: GUYANA. REGION 8 POTARO-SIPARUNI: Pakaraima Mountains, Upper Potaro River Basin, within 15 km radius of Potaro base camp at 5°18′04.8″N, 59°54′40.4″W, 710–750 m; vicinity of base camp, 26 May 2000, Henkel 7421 (BRG; HSU); ~ 1.5 km southwest of base camp on line to *Dicymbe* plot 3, 26 May 2005, *Henkel 8802* (BRG; HSU), GenBank ITS/LSU: JN168784; ~ 1 km west of base camp near *Dicymbe* masting plots, 30 May 2005, *Henkel 8817* (BRG; HSU); vicinity of base camp, 2 Jul 2006, *Henkel 8866* (BRG; HSU); ~ 15 km east of Potaro base camp in mixed *D. corymbosa-D. altsonii* forest, ~ 400 m southwest of Tadang base camp at root sampling site 17, 30 Dec 2009, *Henkel 9177* (BRG; HSU); ~ 2 km southeast of Potaro base camp near *Dicymbe* plot 1, 17 May 2010, *Henkel 9196* (BRG; HSU); ~ 10 km east of Potaro base camp, ~ 1.5 km east of Ayanganna airstrip in mixed *D. corymbosa/D. altsonii* forest, 6 Jun 2010, *Henkel 9260* (HOLOTYPE BRG; ISOTYPE HSU;

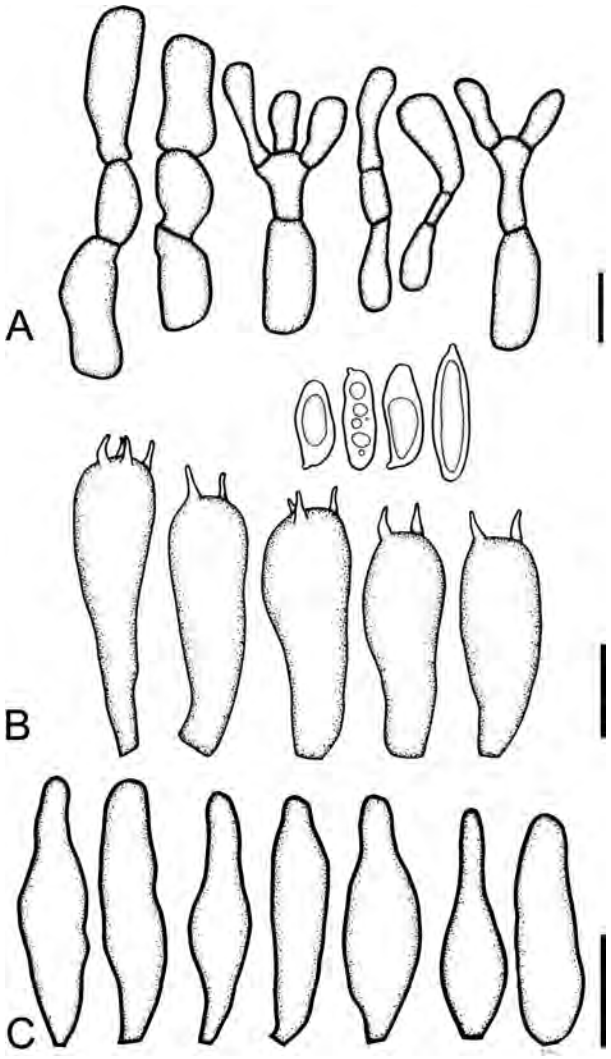

FIG. 6. Microscopic features of *Xerocomus potaroensis* (HOLOTYPE; *Henkel 9260*). A. Terminal elements of the pileipellis. B. Basidiospores and basidia. C. Pleurocystidia. Bars = 10 μm.

NY), GenBank ITS/LSU: JQ751260. MALAYSIA: North Borneo, Mount Kinabalu, 30 Jun 1961, *Boletus havilandii* Corner!, Isotype (E-00084971).

Commentary: *Xerocomus potaroensis* is recognized in the field by its small to medium sized basidiomata with orangish brown, tomentulose pileus, dull yellow to olivaceous, slightly bluing hymenophore that is sublamellate and adnate to slightly subdecurrent at the stipe, the stipe with orangish brown striations and apical reticulations on creamish ground, and light yellow basal mycelium with abundant concolorous hyphal cords. The fleetingly blue to burgundy brown NH_4OH reaction on the pileus is also distinctive. The species is best disposed in *Xerocomus* s.l. based on the morphological features of hymenophoral tubes that are sublamellate near the stipe and adnate with angular pores, subequal, relatively thin stipe, olivaceous brown, smooth basidiospores, parallel tube trama, and trichodermioid, dry pileipellis (Singer 1986).

Xerocomus potaroensis was confirmed by Smith et al. (2011) as forming ectomycorrhizas with the leguminous hosts *D. corymbosa*, *D. altsonii* and *A. insignis*, and ranked ninth in frequency out of 118 ECM fungal species recovered using molecular methods from 1140 root tips sampled from 57 trees in the Upper Potaro Basin. The frequent occurrence of *X. potaroensis* in Guyana's *Dicymbe* forests was corroborated in a long-term *D. corymbosa* plot study of Henkel et al. (2012), with basidiomata occurring in 11.6% of 630 quadrats sampled during the May–Jul rainy seasons over 7 y. Ectomycorrhizas of *X. potaroensis*/*D. corymbosa* are illustrated (FIG. 4).

Among neotropical boletes *X. belizensis* B. Ortiz & T.J. Baroni resembles *X. potaroensis* in its overall basidioma dimensions and general colorations, pale cream-colored pileus trama unchanging on exposure, irregular upper stipe reticulum, and similar basidiospore and basidium shapes and dimensions (Ortiz-Santana et al. 2007). *Xerocomus belizensis* is differentiated from *X. potaroensis* by its caespitose fruiting habit, more yellowish brown pileus that is rimose-areolate over the disk and lacks the instantly blue to burgundy brown NH_4OH reaction, basidiospores that are regularly four-sterigmate, slender, more fusoid pleurocystidia, and cylindrical pileipellis terminal elements that are more narrow (4–12 vs. 9.9–17.3 μm) and lacking in the terminal branching seen in *X. potaroensis*. *Xerocomus pseudoboletinus* (Murr.) Singer from Florida and Belize resembles *X. potaroensis* in general macromorphology and presence of a blue or green flash with NH_4OH on the pileus but is separated by its entirely pruinose, non-reticulate stipe, white basal mycelium, shorter pleurocystidia (25.8–64 vs. 51.9–74.1 μm) and presence of dermatobasidia on the stipe (Singer 1945, Ortiz-Santana et al. 2007). *Xerocomus hemixanthus* Singer from Florida, USA, is another small, brown bolete with subadnate hymenophore and reticulate stipe with pale yellow basal mycelium, but differs from *X. potaroensis* in its shorter pleurocystidia (27–38 vs. 51.9–74.1 μm), persistently blue pileipellis reaction to NH_4OH, nearly globose pileipellis terminal cells and presence of abundant cheilocystidia (Singer 1945). The sympatric *X. amazonicus* var. *amazonicus* Singer, also known from Brazil, is suggestive of *X. potaroensis* in its overall basidioma size, concolorous brownish pileus and stipe, and yellow hymenophore, but differs in its more reddish brown pileus which reacts persistently blue with NH_4OH, lack of any color change of the

bruised hymenophore, bright livid yellow basal mycelium, shorter pleurocystidia (24–34 vs. 51.9–74.1 μm) and presence of cheilocystidia and fasciculate caulocystidia (Singer et al. 1983; Husbands and Henkel unpubl data). *Xerocomus spadiceus* var. *gracilis* (A.H. Sm. & Thiers) L.D. Gomez, known from Michigan, USA, and Costa Rica, is similar to *X. potaroensis* in overall basidioma stature and colorations, dull yellow, weakly cyanescent hymenophore, the unique blue to reddish brown NH_4OH reaction on the pileus, and a number of micromorphological features, but is differentiated from *X. potaroensis* by its dull yellow brown pileus, lack of stipe reticulations, bright yellow basal mycelium, regularly four-sterigmate basidia, shorter pleurocystidia (32–50 vs. 51.9–74.1 μm), and presence of cheilocystidia and caulocystidia (Smith and Thiers 1971, Gomez 1996).

The Bornean *Boletus havilandii* Corner is similar to *X. potaroensis* in its overall stature, orange brown to red brown pileus and concolorous stipe, dull yellow to olivaceous pores, yellowish upper stipe reticulum, similarly sized, broadly cylindrical pileipellis terminal cells, and parallel tube trama, but differs in its longer (12–16.5(18) vs. 10–12(14) μm), more fusiform basidiospores, longer basidia (35–40 vs. 25–34.2 μm) and presence of clavate cheilocystidia (Corner 1972, Horak 2011). Among Congolian boletes *X. spinulosus* Heinem. & Gooss.-Font. and *X. subspinulosus* Heinem. each combine the orangish to reddish brown pileus and stipe colors, dull yellow to olivaceous, adnate to subdecurrent hymenophore bruising slightly blue, and relatively low Q basidiospores seen in *X. potaroensis*; both can be differentiated from *X. potaroensis* by their much larger pileus widths (60–120 and 80–130 mm respectively), presence of cheilocystidia, and lack of apical stipe reticulations and yellow basal mycelium (Heinemann and Goossens-Fontana 1954, Heinemann 1964).

Xerocomus parvogracilis T.W. Henkel & Husbands, sp. nov. FIGS. 3, 7, 8

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Pileus 14–36 mm broad, 3–10 mm tall, convex to broadly convex to plano-convex, dull coppery brown (6D5–6E5–E6, D5–E5) throughout, lighter concolorous (5C4–C5) toward margin, subglabrous to finely rugulose throughout, under hand lens with low erect brown tomentum separating into minute areoles toward margin revealing light tan (4A1–A2) ground, dry to subviscid when wet; margin entire; trama subsolid, 0.5 mm thick at margin, 2–3 mm over tubes, 3–5 mm above stipe, white to pale cream-colored (5A1–A2), unchanging. Odor slightly musty or fruity, fungoid; flavor mild, indistinctive. Tubes 1–2.5 mm at margin, 3–5 mm centrally, 1–3 mm at stipe, narrowly and fairly deeply depressed at stipe and there sublamellate and slightly decurrent (0.5–1 mm), drab olivaceous cream (4A5–B5) to dull olive (4C4–C5) with maturity, browning slightly upon pressure, of equal lengths, edges smooth; pores 1.5–2 per mm, isodiametric to subangular with age. Stipe 16–45 mm × 2–4 mm, equal, nearly concolorous (6D4–D5, 6E7–F7), usually with well-defined olivaceous cream band at extreme apex, lighter at extreme base with faint white bloom, glabrous macroscopically, under hand lens minutely scurfy-fibrillose and faintly longitudinally striate; trama white to pale yellow, unchanging, solid.

Basidiospores olivaceous brown (4D6–4E5–E6) in moderate deposit, 11–14(15) × 4–5(6) μm, Q range 2.4–3(3.3) (mean Q = 2.7), subfusiform, with distinct suprahilar depression, olivaceous brown in H_2O and KOH, inamyloid, smooth, uni- to multiguttulate; hilar appendage 0.1–0.2 μm long; wall 0.3–0.5 μm wide; surface smooth under SEM. Basidia 22.2–32.1 × (7.4)9.9–11.1(12.4) μm, clavate to broadly clavate, hyaline in H_2O and KOH, devoid of obvious contents or variously granulose-guttulate, two- or four-sterigmate; sterigmata 2–4(5) μm long. Pleurocystidia infrequent to scattered, (30)37.1–64.2(74.1) × 9.9–14.8 μm, ventricose-rostrate, occasionally narrowly so, or clavate-mucronoid, extending 12–30 μm above the hymenial palisade, thin-walled, hyaline to pale grayish in H_2O and KOH, devoid of obvious contents. Cheilocystidia absent. Hymenophoral trama parallel, non-gelatinizing, in mass with pale yellowish gray cytoplasmic pigmentation in H_2O, lighter in KOH; mediostratum indistinct; individual hyphae thin walled, 4.9–7.4(9.9) μm wide; conductive hyphae sparsely scattered throughout, opaque, hyaline, irregularly branched, 2.5–4.9(9.9) μm wide. Pileipellis a trichodermial palisade with polymorphic terminal cells, these dacryoid, globose-mucronoid, ventricose, obclavate, ovate, or lanceolate, (14)22.2–61.2(86.5) × 9.9–19.8(27.2) μm, with light yellowish gray internal pigment in H_2O, nearly hyaline in KOH; subpellis undifferentiated. Pileus trama loosely interwoven; individual hyphae inflated, 8.6–12.4 μm wide, faintly yellow in H_2O, hyaline in KOH; conductive hyphae scattered, opaque, hyaline, irregularly branched, 2.5–4.9 μm wide, more concentrated near the pileipellis. Stipitipellis a trichodermial palisade, in mass faint yellowish grey in H_2O; terminal cells clavate to occasionally ventricose, 27.2–42 × (4.9)7.4–12.4 μm, nearly hyaline in KOH; subpellis anticlinal. Stipe trama in mass with faint yellowish gray cytoplasmic pigmentation in

FIG. 7. Basidiomata of *Xerocomus parvogracilis* (HOLOTYPE; *Henkel 9209*). Bar = 10 mm.

H_2O, nearly hyaline in KOH; individual hyphae thin-walled, 3.7–7.4 µm wide, hyaline, irregularly branched; conductive hyphae infrequent, 2.5–4.9(9.9) µm wide, opaque, pale yellow. Clamp connections absent. Macrochemical reactions: 10% NH_4OH burgundy brown on pileus instantly, lighter brown on stipe, nil on trama; 3% KOH dark brown instantly on pileus, lighter brown on stipe, nil or slightly yellowing pileus and stipe trama.

Holotype: *Henkel 9209* (BRG; ISOTYPE HSU; NY).

Habit, habitat and distribution: Solitary on humic deposits on trunks of *D. corymbosa* on lateritic soils or on litter mat at base of *D. altsonii* on white sand soils; known from the type locality in the Upper Potaro Basin and ~ 100 km to the east near Mabura Hill in the lowlands of Guyana.

Etymology: Parvus (L. adj. A) = small; gracilis (L. adj. B) = thin, slender, referring to the small pileus and thin, slender stipe of the species.

Specimens examined: GUYANA. REGION 8 POTARO-SIPARUNI: Pakaraima Mountains, Upper Potaro River Basin, within 5 km radius of Potaro base camp at 5°18′04.8″N, 59°54′40.4″W, 710–750 m; vicinity of base camp, 23 Jun 2000, *Henkel 7544* (BRG; HSU); 27 Jul 2000, *Henkel 7681* (BRG; HSU); ~ 3 km southwest of base camp on line to *Dicymbe* plot 3, 8 Jun 2001, *Henkel 8252* (BRG; HSU); 2 km east-southeast of base camp in Lance plot 1, 5 Jun 2005, *Henkel 8836* (BRG; HSU); 300 m southeast of base camp on Benny's ridge, 8 Jun 2005, *Henkel 8850* (BRG; HSU); GenBank ITS: JQ751263; LSU: HQ161865; RBP1: HQ161834; ATP6: HQ161802; vicinity of base camp, 2 Jul 2006, *Henkel 8864* (BRG; HSU); 1.5 km west of base camp in vicinity of *Dicymbe* masting plots, 23 May 2010, *Henkel 9209* (HOLOTYPE BRG; ISOTYPE HSU; NY), GenBank ITS: JQ751261; LSU: JQ751262. REGION 10 UPPER DEMERARA-BERBICE: Mabura Ecological Reserve, field station located at 5°09′19.0″N; 58°41′58.9″W, ~ 100 m; 1.4 km west-northwest of Mabura field station in *D. altsonii* monodominant stand 2 on white sand soils, 25 May 2011, *Henkel 9614* (BRG; HSU). MALAYSIA: North Borneo, Mount Kinabalu; 21 Feb 1964, *Corner RSNB 5403B, Boletus sepiola* Corner!, Isotype (E-00088002); 8 Apr 1964, *Corner RSNB 8172*, *Xerocomus dispersus* var. *dispersus* (Corner) E. Horak!, Isotype (E-00084565); 5 May 1964, *Corner RSNB 8668*, *Xerocomus raphanolens* (Corner) E. Horak!, Isotype (E-00086542); Pahang, Fraser's Hill, 23 May 1930, *Corner s.n. 23*, *Xerocomus microcarpioides* (Corner) E. Horak!, Isotype (E-00085029).

Commentary: Xerocomus parvogracilis is a small, elegant bolete recognized in the field by its coppery brown, smooth to finely rugulose pileus < 36 mm diam, narrow, cylindrical concolorous stipe lacking in reticulations, dull olivaceous mature hymenophore and unchanging trama. The species is best disposed in *Xerocomus* s.l. based on the morphological features of hymenophoral tubes that are sublamellate near the

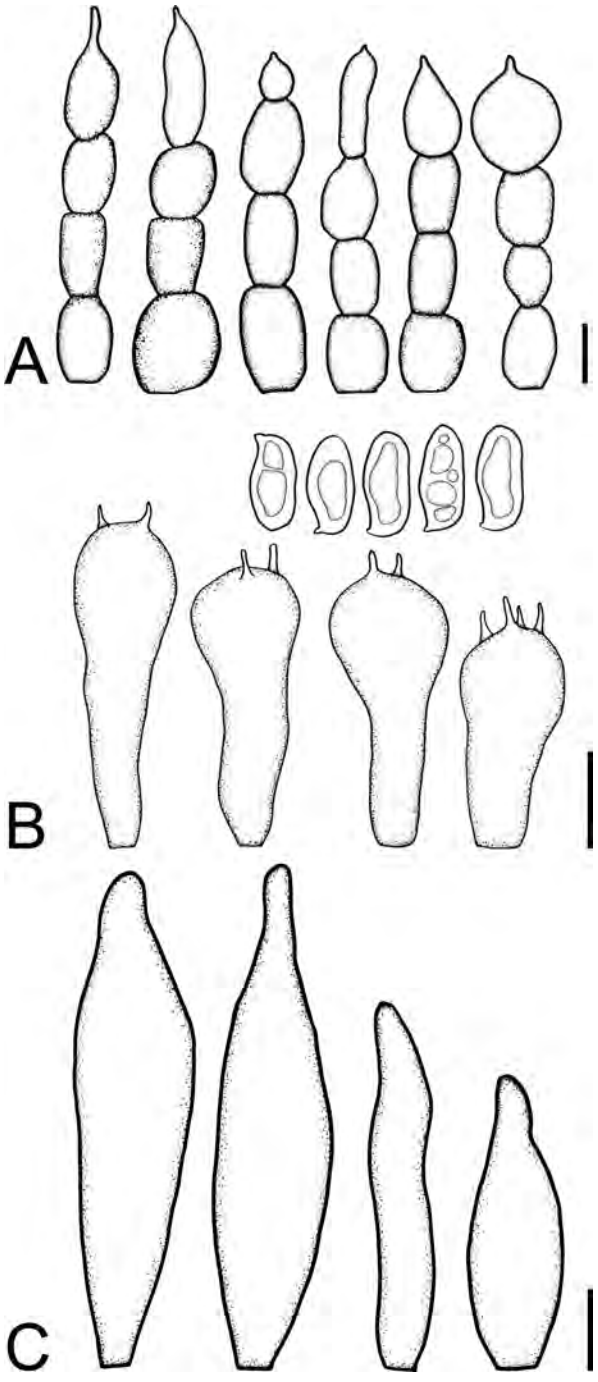

FIG. 8. Microscopic features of *Xerocomus parvogracilis* (HOLOTYPE; *Henkel 9209*). A. Terminal elements of the pileipellis. B. Basidiospores and basidia. C. Pleurocystidia. Bars = 10 μm.

stipe and adnate to subdecurrent with subangular pores, equal, thin stipe, olivaceous brown, smooth basidiospores, parallel tube trama, and trichodermioid, dry pileipellis (Singer 1986). In a long-term *D. corymbosa* plot study basidiomata of *X. parvogracilis* were relatively rare, occurring in 3.3% of 630 quadrats sampled during the May–Jul rainy seasons over 7 y (Henkel et al. 2012). The species has been confirmed by molecular analysis of roots as an ECM symbiont of *D. corymbosa* (Henkel and Smith unpubl data).

Several Malaysian xerocomoid taxa described by Corner combine the salient features present in *X. parvogracilis* of pileus < 36 mm diam, slender stipe, basidiospores > 11 um long, and moniliform pileipellis elements with inflated terminal cells. Examination of type specimens at E and published descriptions indicated differences at the species level for each (Corner 1972, Horak 2011). *Boletus sepiola* Corner differs from *X. parvogracilis* primarily in its strongly divergent hymenophoral trama and cyanescent tubes and trama. *Xerocomus dispersus* var. *dispersus* (Corner) E. Horak differs from *X. parvogracilis* in its greater pileus width (26–60 vs. 14–36 mm), bright yellow pores, presence of cheilocystidia, and pileipellis elements with dark brown cytoplasmic pigment and lacking the great variability in shape of the terminal cells as seen in *X. parvogracilis*. *Xerocomus microcarpioides* (Corner) E. Horak is remarkably similar to *X. parvogracilis* in its small pileus, thin stipe and overall colorations, but differs fundamentally in its pileipellis of entangled, entirely moniliform hyphae lacking in inflated, variably shaped terminal cells. *Xerocomus raphanolens* (Corner) E. Horak has a strikingly similar pileipellis structure to that of the *X. parvogracilis*, including the wide range of shapes of the inflated terminal cells but differs in having very long, slender fusoid basidiospores (18–20 vs. 11–15 μm), abundant clavate cheilocystidia, and in lacking pleurocystidia.

Xerocomus latisporus Heinem. from the Congo is quite similar to *X. parvogracilis* in its small brown, tomentose pileus, narrow, cylindrical concolorous stipe lacking reticulations, and unchanging trama, but is differentiated by its wider, more ellipsoid basidiospores (6.1–7.2 vs. 4–5 μm), longer basidia (43–50 vs. 22–32 μm) that are regularly four-sterigmate, and lanceolate, longer (70–90 vs. 37.1–64.2 μm) pleurocystidia (Heinemann 1964).

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