Mycologia, 106(2), 2014, pp. 307–322. DOI: 10.3852/106.2.307

Cantharellaceae of Guyana II: New species of *Craterellus*, new South American distribution records for *Cantharellus guyanensis* and *Craterellus excelsus*, and a key to the Neotropical taxa

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Abstract: *Craterellus olivaceoluteus* sp. nov. and *Craterellus cinereofimbriatus* sp. nov. are described as new to science. These fungi were collected from Guyana in association with ectomycorrhizal host trees in the genera *Dicymbe* (Fabaceae subfam. Caesalpinioideae) and *Pakaraimaea* (Dipterocarpaceae). *Cantharellus guyanensis* Mont., originally described from French Guiana, is redescribed from recent collections from Guyana, with additional range extensions for the species provided based on material examined from French Guiana, Venezuela, and north central, northeastern and southern Brazil, circumscribing nearly the entire Guiana Shield region and beyond. A new distribution record from French Guiana is provided for *Craterellus excelsus* T.W. Henkel & Aime. Macromorphological, micromorphological and habitat data are provided for the new species and *C. guyanensis* as well as DNA sequence data from the nuclear ribosomal regions of the internal transcribed spacer (ITS) and 28S large subunit (LSU); additional sequence data is provided for *C. guyanensis* and *C. excelsus* specimens collected outside Guyana. The relationships of these taxa within the Cantharellaceae were evaluated with phylogenetic analyses of ITS and LSU sequence data. This work brings the total number of Cantharellaceae species known from Guyana to eight. A key to the *Cantharellus* and *Craterellus* species known from the lowland Neotropics and extralimital montane Central and South America is provided.

Key words: Cantharellales, *Coccoloba*, *Dicymbe*, ectomycorrhizae, Guiana Shield, tropical fungi

Introduction

Wilson et al. (2012) summarized current knowledge of the ectomycorrhizal (ECM) fungal genera *Cantharellus* Adans. ex Fr. and *Craterellus* Pers. (Cantharellaceae, Cantharellales, Agaricomycetes, Basidiomycota) in the Neotropics. Six species originally described in *Cantharellus* were recorded from lowland Neotropical forests; two of them have been transferred to *Craterellus* (Wilson et al. 2012, Yomyart et al. 2012); two additional *Cantharellus* species recently were described from Brazil (Wartchow et al. 2012a, Pinheiro and Wartchow 2013). Two species of *Cantharellus* are known from montane Colombian or Costa Rican *Quercus* forests (Petersen and Mueller 1992, Eyssartier et al. 2003), and one extralimital species from southern South American *Nothofagus* forests (Petersen and Mueller 1992). For *Craterellus*, five species are known from tropical lowland South America when including the new species and combinations described in Wilson et al. (2012). Three additional *Craterellus* species are known from montane Colombian or Costa Rican *Quercus* forests (Wu and Mueller 1995). As currently known, species diversity of these two widely distributed ECM genera

Submitted 26 Apr 2013; accepted for publication 25 Sep 2013.
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is low for the Neotropics, given that > 350 names have been proposed worldwide among the two genera.

Nearly half of the known Neotropical Cantharellaceae diversity resides in the central Guiana Shield region of northeastern South America, where species of *Craterellus*, and to a lesser extent *Cantharellus*, are well represented in primary rainforests dominated by ECM canopy trees of the genus *Dicymbe* (Fabaceae subfam. Caesalpinioideae), *Aldina* (Fabaceae subfam. Papilionoideae) and *Pakaraimaea* (Dipterocarpaceae) (Smith et al. 2011, 2013; Henkel et al. 2012). The synopsis of regional taxa provided by Wilson et al. (2012) indicated that the cantharelloid species known from Guyana were *Cantharellus guyanensis* Mont., *Craterellus pleurotoides* (T.W. Henkel, Aime & S.L. Mill.) A.W. Wilson, *Craterellus excelsus* T.W. Henkel & Aime, *Craterellus atratoides* T.W. Henkel, Aime & A.W. Wilson, *Craterellus strigosus* T.W. Henkel, Aime & A.W. Wilson, *Craterellus atratus* Yomyart et al. and two undescribed morphospecies of *Craterellus*, for a total of eight between the two genera. Here we describe two new species, *Craterellus olivaceoluteus* sp. nov. and *Craterellus cinereofimbriatus* sp. nov. based on material from Guyana, provide a new distribution record for *C. excelsus* from French Guiana, and a new distribution record and redescription of *C. guyanensis* based on numerous collections from Guyana. Additional range extensions and putative host associations are provided for *C. guyanensis* based on material examined from French Guiana, Venezuela and Brazil. Macromorphological, micromorphological and habitat data are provided for *C. olivaceoluteus*, *C. cinereofimbriatus* and *C. guyanensis*, and DNA sequence data from the nuclear ribosomal regions of the internal transcribed spacer (ITS) and 28S large subunit (LSU) are provided for each; additional sequence data is provided for *C. guyanensis* and *C. excelsus* specimens collected outside Guyana. The relationships of these taxa within the Cantharellaceae were assessed with phylogenetic analyses of ITS and LSU sequence data. A key to the *Cantharellus* and *Craterellus* taxa known from the lowland Neotropics and extralimital montane Central and South America is provided.

MATERIALS AND METHODS

Collections.—Collections were made during the May–Jul rainy seasons of 2000–2004, 2006–2010, 2012 and 2013 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, from forests dominated by ECM *Dicymbe corymbosa* Spruce ex Benth. or co-dominated by ECM *D. corymbosa*, *Dicymbe altsonii* Sandw., and *Aldina insignis* (Benth.) Endl. (Smith et al. 2011, Henkel et al. 2012). Additional Guyana collections were made Dec–Jan 2010–2011 and Jun 2012 from the Upper Mazaruni River Basin within a 6 km radius of a base camp at 5° 26′21.3″N; 60°04′43.1″W, 800 m, from forests co-dominated by ECM *Pakaraimaea dipterocarpacea* Maguire & P.S. Ashton and *Dicymbe jenmanii* Sandw. (Smith et al. 2013), and May 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, in monodominant stands of *D. altsonii*. From French Guiana, collections were made in Jan 2011 from Nouragues field station near 4°4′24.0″N, 52° 44′1.0″W, 120 m, and in Jun 2012 from Paracou field station located near 5°16′54.0″N, 52°54′44″W, 10 m. From Venezuela, collections of *C. guyanensis* were made in Jun 2000 on Isla Redonda in Lago Guri near 7° 42′32.30″N, 62°54′01.43″W, 250 m. In French Guiana and Venezuela collections were made in mixed rainforests in proximity to trees of ECM *Neea* spp. (Nyctaginaceae) or lianas of ECM *Coccoloba* (Polygonaceae) species. From northeastern Brazil collections of *C. guyanensis* were made in Pernambuco, Jun 2010, in an Atlantic forest fragment containing ECM *Coccoloba* and *Guapira* (Nyctaginaceae) species at Refúgio Ecológico Charles Darwin near 7° 48′37″S, 34°27′25″W (Costa-Lima 1998, Santiago and Barros 2003, Alves-Araújo et al. 2008, Melo et al. 2011). Paraíba collections were made Apr 2011 at Reserva Ecológica Mata do Pau-Ferro near 6°58′12″S, 35°42′25″W, in an upland wet forest of the Brazilian semiarid zone, where at least two species of ECM *Guapira* occur (Barbosa et al. 2004).

Macromorphological 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. Fungi were field-dried with silica gel. Micromorphological features of fresh specimens were examined with an EPOI field microscope with light optics; dried specimens were examined in the laboratory with an Olympus BX51 microscope with light and phase contrast optics. For basidiospores, basidia, hyphal features and other structures at least 20 individual structures were measured for each specimen examined for all species treated in this study. Rehydrated fungal tissue was mounted in H_2O, 3% KOH, and Melzer's solution. Line drawings were made with tracing paper and modified with Photoshop CS5 (Adobe, San Jose, California). Specimens were deposited in these herbaria: BRG = University of Guyana; HSU = Humboldt State University; PUL = Purdue University; TL = Universite Paul Sabatier, Toulouse; JPB = Universidade Federal da Paraíba, João Pessoa; NY = New York Botanical Garden (Holmgren et al. 1990). Additional specimens of *C. guyanensis* collected by R. Singer (central Brazil) and A. de Meijer (southern Brazil) and *Craterellus orinocensis* Pat. & Gaillard by R.E. Halling (Venezuela) were examined on loan from the Tennessee Fungus Herbarium (TENN).

DNA extraction, amplification, sequencing and phylogenetic analyses.—DNA extraction, polymerase chain reactions (PCR), cloning and sequencing protocols used in this study for newly obtained specimens of *C. guyanensis* and *C. excelsus* were described in Wilson et al. (2012).

For this study, newly generated internal transcribed spacer (ITS) and/or 28S large subunit (LSU) sequences

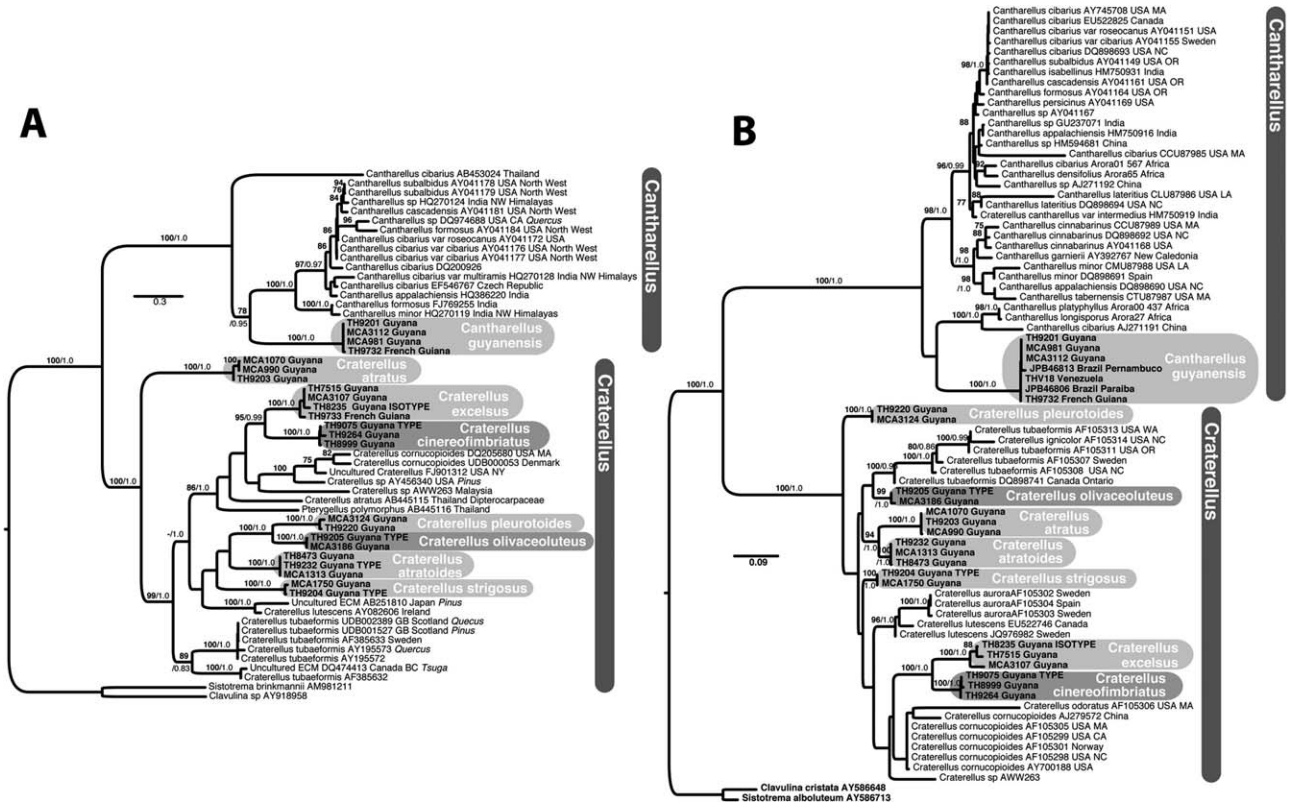

FIG. 1. ITS (A) and LSU (B) maximum likelihood phylogenies from RAxML analysis of *Cantharellus* and *Craterellus* including tropical and north temperate taxa, depicting a clear separation of *Cantharellus* and *Craterellus* within the Cantharellaceae. The new species described here, *C. olivaceoluteus* and *C. cinereofimbriatus*, are nested within *Craterellus*, as are most other Guyanese taxa (in boldface). *Cantharellus guyanensis* from Guyana occurs in *Cantharellus* in a monophyletic clade with specimens from French Guiana (A) and from French Guiana, Venezuela and Brazil (B). The new specimen TH 9732 from French Guiana occurred with Guyanese *C. excelsus* in a well supported clade in (A). Maximum likelihood bootstrap percentages/Bayesian posterior probabilities are at the nodes. Sequences in boldface were originally generated in Wilson et al. (2012) or this study; all other sequences were obtained from GenBank or UNITE.

from *C. guyanensis* specimens from French Guiana, Venezuela and Brazil and a *C. excelsus* specimen from French Guiana were processed and assembled using CodonCode Aligner 3.5.7 (CodonCode Corp., Dedham, Massachusetts, http://www.codoncode.com/). For the new sequences, assembled nucleotide sequence contigs of ITS and LSU regions were used in preliminary BLAST queries of GenBank (www.ncbi.nlm.nih.gov/) and UNITE (unite.ut.ee/; Kõljalg et al. 2005) databases to confirm generic affinities. Along with ITS and LSU sequences from other Guyanese taxa reported in Wilson et al. (2012), additional ITS and LSU sequences of primarily north temperate Cantharellaceae species available on GenBank were assembled into datasets with high intrafamilial inclusivity for phylogenetic analyses. Specimen and GenBank information for all taxa used in this study is provided (SUPPLEMENTARY TABLE I).

Initial alignment of datasets was performed with MUSCLE (Edgar 2004), followed by manual alignments using MacClade 4.07 (Maddison and Maddison 2005). Maximum likelihood (ML) and ML bootstrapping analyses were performed with RAxML (Stamatakis 2006), which was implemented on the CIPRES web portal (Miller et al. 2009) using 1000 bootstrap replicates to generate bootstrap statistics.

Bayesian analyses were performed with MrBayes 3.1.3 (Ronquist and Huelsenbeck 2003) implemented on the CIPRES web portal. These analyses used four chains, sampling every 1000 tree for 10 000 000 generations. All other parameters were used at the default settings. In each analysis, two MCMC analyses were run, which produced two files with ~ 10 000 trees each. The first 1/10th of trees were removed as the burn-in. Both files were combined and a 50% majority rule tree was performed in PAUP* 4.0 (Swofford 2003) to ascertain the Bayesian posterior probabilities for each dataset.

RESULTS

Phylogenetic analyses.—One of the new species described in this study, *Craterellus olivaceoluteus* (*Craterellus* sp. 2 in Wilson et al. 2012), was sister to *C. pleurotoides* in the ITS tree with 100% maximum

FIG. 2. Basidiomata of *Craterellus olivaceoluteus* (HOLOTYPE; *Henkel 9205*). Bar = 10 mm.

likelihood bootstrap (MLB) and 1.0 Bayesian posterior probability (PP) (FIG. 1A). The second new species described here, *Craterellus cinereofimbriatus*, (*Craterellus* sp. 1 in Wilson et al. 2012), was sister to *C. excelsus* in both the ITS and LSU trees (FIG. 1A, 95% MLB and 0.99 PP; and 1B, 100% MLB and 1.0 PP). *Cantharellus guyanensis* sequences from Guyana and French Guiana occurred in a monophyletic group in the ITS tree (FIG. 1A, 100% MLB and 1.0 PP), with the same result for *C. guyanensis* sequences from Guyana, French Guiana, Venezuela and Brazil in the LSU tree (FIG. 1B, 100% MLB, 1.0 PP). These results, along with morphological congruence across the regional specimens of *C. guyanensis*, indicated their conspecificity. The new collection of *C. excelsus* from French Guiana occurred with *C. excelsus* from Guyana in a well supported clade in the ITS analysis (FIG. 1A, 100% MLB, 1.0 PP) and therefore is considered conspecific, corroborated by their identical morphology.

TAXONOMY

Craterellus olivaceoluteus T.W. Henkel, Aime et A.W. Wilson, sp. nov FIGS. 2, 3
MycoBank MB803951

Pileus 12–38 mm broad, 3–17 mm tall, nearly plane to uplifted with broadly undulating margin, broadly centrally depressed but only occasionally perforate, initially dark olive (4F5–5F5) throughout, with age olivaceous brown (4E6–5E6) throughout but transitioning over marginal 1–2 mm to lighter greenish yellow (3A6–3B6) and there somewhat downturned but not inrolled; surface glabrous to slightly radially ridged, under hand lens with a dense, uniform appressed radially fibrillose mat lacking erect elements, moist; margin subentire to finely fimbriate-crenulate;

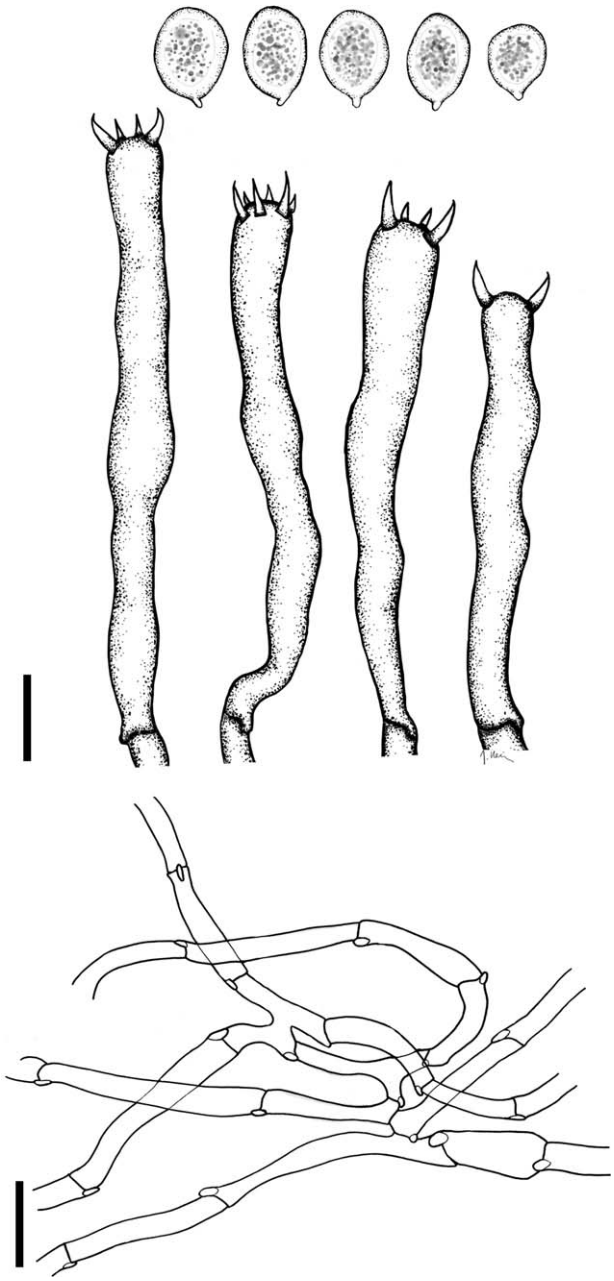

FIG. 3. Basidiospores, basidia and tramal hyphae of *Craterellus olivaceoluteus* (HOLOTYPE; *Henkel 9205*). Bars = 10 μm.

trama concolorous, with age occasionally perforate over hollow stipe. Hymenophore covering entire underside of pileus, with age descending stipe apex somewhat irregularly but there sharply demarcated, rugulose throughout development, this more pronounced with age and hymenial thickening, initially grayish olive (3B2–3B3, 4C3–4D3), with maturity light yellowish olive (near 3A3–3B3), under hand lens densely hispid from basidia. Stipe 22–48(62) mm long, 2–7 mm wide centrally, initially subequal and cylindrical,

with age expanding toward base to 4–8 mm wide, flattening overall and becoming canaliculate, rarely flaring at apex, extreme base rounded, initially olivaceous orange (3A7–3B7) throughout, with age orange (4A7–4A8) over basal two-thirds, olivaceous orange (4B8–4C8) over apical one-third, smooth; basal mycelium wanting; extreme base subtended by thin, off-white subicular mat on organic substrata; trama concolorous, narrowly hollow. Entire basidioma strongly hygrophanous to drab olive-yellow with drying. Primordia filiform-acuminate in youngest stages. Odor mild; flavor mild, chanterelle-like. Basidiospores 8–10(11) × (5.5)6–8 μm (mean = 9.0 × 6.8 μm; n = 60), Q range = 1.3–1.5, Q mean = 1.33, ellipsoid, smooth, hyaline to pale golden yellow in KOH, inamyloid, opaque with uniformly granular contents; wall 0.3 μm thick; hilar appendix 0.7–1 μm long. Basidia (64)70.9–98.8(103.5) × (5.4)7.2–9.6 μm wide centrally, 7.4–10.6(11.1) μm wide at apex, 4.7–7.2(7.9) μm at base, subcylindrical to subclavate, hyaline to very pale yellow in KOH, devoid of obvious contents; wall thin; sterigmata (2, 3)4–5–6, (3.7)4.9–5.2(6.2) μm long, 1.7–2.5 μm wide at base, somewhat curving. Basidioles numerous, cylindrical, with pale yellow granular contents in KOH. Cystidia none. Hymenium in transverse section 114–420 μm thick, olivaceous yellow brown in KOH. Pileipellis a cutis of largely periclinal cylindrical hyphae, 153–224 μm thick, scarcely differentiated from trama, in mass pale yellow in KOH; individual hyphae 4.5–11 μm wide, terminal elements undifferentiated. Pileus tramal hyphae faintly pale brown in KOH, branching frequently, with scattered minute guttules; secondary septation lacking; cells 29.6–101.3 × 4.9–12.4 μm, somewhat inflating. Stipitipellis composed of densely interwoven to subparallel hyphae arranged subanticlinally, with terminal elements often more periclinal, in mass light brown in KOH; individual hyphae pale yellowish brown in KOH, devoid of obvious internal contents; cells 37.0–74.1 × 4.9–7.4 μm; terminal elements undifferentiated and rounded at apex, or rarely slightly inflated near apex and subclavate. Stipe trama hyphae hyaline to faintly yellow in KOH, occasionally branching, occasionally constricted at septum when inflated, devoid of obvious contents or with scattered small guttules; cells 44.5–111.2 × 3.7–11.1 μm. Clamp connections abundant on hyphae of all tissues.

Holotype: Henkel 9205 (BRG; ISOTYPE: HSU; NY)

Habit, habitat and distribution: Solitary or in pairs on humic mat on the forest floor, or on well decayed wood, under *Dicymbe corymbosa*, *Dicymbe altsonii*, *Dicymbe jenmanii*, *Aldina insignis* or *Pakaraimaea dipterocarpacea*; known from the Upper Potaro and Upper Mazaruni River Basins of Guyana.

Etymology: Olivaceous (L. adj. A) = olive green, luteus (L. adj. A) = yellow; referring to the basidioma.

Specimens examined: GUYANA: REGION 8 POTARO-SIPARUNI: Pakaraima Mountains, Upper Potaro River Basin, ~ 15 km east of Mt Ayanganna; old Ayanganna airstrip, 22 May 2000, *Henkel 7411*; vicinity of base camp, 20 Jun 2000, *Henkel 7524* (BRG; HSU); 1.5 km southeast of base camp in *Dicymbe* plot 1, 10 Jun 2004, *Henkel 8678* (BRG; HSU); 1 km southeast of base camp on Benny's ridge, 6 Jul 2008, *Henkel 8913* (BRG; HSU); ~ 2 km southwest of base camp in *Dicymbe* plot 3, 17 Jul 2009, *Henkel 9052* (BRG; HSU); 2.5 km southwest of base camp near *Dicymbe* plot 3, 21 May 2010, *Henkel 9205* (HOLOTYPE BRG; ISOTYPE: HSU; NY), ITS GenBank JQ915109; LSU Genbank JQ915135; ~ 10 km southeast of base camp near Tadang camp, under *D. corymbosa*, *D. altsonii* and *A. insignis*, 6 Jun 2013, *Henkel 9757* (BRG; HSU); near *Dicymbe* plot 3, 24 Jun 2000, *Aime 1356* (BRG; PUL); 5 Jul 2003, *Aime 2316* (BRG; PUL); 4 Jul 2006, *Aime 3186* (BRG; PUL), ITS GenBank JQ915098; LSU GenBank JQ915124; ~ 3 km southwest of base camp in *Dicymbe* plot 3, 20 May 2010, *Aime 3980* (BRG; PUL); vicinity of base camp, 1 Jun 2012, *Aime 4803* (BRG; PUL); REGION 7 CUYUNI-MAZARUNI: Pakaraima Mountains, Upper Mazaruni River Basin, ~ 10 km west of Mt Ayanganna in vicinity of Pegaima savanna in forests dominated by *Pakaraimaea dipterocarpacea* and *Dicymbe jenmanii* on white sand soils; vicinity of base camp, 25 Dec 2010, *Henkel 9539* (BRG; HSU); ~ 200 m south of base camp, 1 Jun 2012, *Henkel 9656* (BRG; HSU); northern vicinity of base camp, 2 Jun 2012, *Henkel 9665* (BRG; HSU).

Commentary: Craterellus olivaceoluteus is easily recognized in the field by its diminutive, pileate-stipitate basidiomata occurring solitarily or in pairs, pileus that is olivaceous brown with greenish yellow margin and centrally depressed but only occasionally perforate, hymenophore that is grayish to yellowish olive, rugulose and sharply demarcated from the stipe apex, stipe that is subequal, orange to olivaceous orange, glabrous, and hollow, basal subiculum that radiates into organic substrata, and filiform-acuminate early primordia. Micromorphologically *C. olivaceoluteus* is characterized by its combination of smooth, colorless basidiospores, long basidia with variable sterigmata numbers 2–6, cuticular pileipellis with undifferentiated, thin-walled terminal elements and abundant clamp connections. Rare fruiting of *C. olivaceoluteus* 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 0.5% of 630 quadrats sampled during the May–Jul rainy seasons over 7 y.

While the well defined pileate-stipitate stature and presence of clamp connections may have led to placement of this species in *Cantharellus* under traditional morphological taxonomy (e.g. Corner 1966), molecular phylogenetic analyses indicated that *C. olivaceoluteus* resides in *Craterellus* (FIG. 1A, B).

The early development of conical primordia with subsequently occasionally perforate pilei in mature basidiomata of *C. olivaceoluteus*, in which the perforation is continuous with the hollow core of the stipe, are consistent with both the traditional concept of *Craterellus* (Corner 1966) and also the modern, in which absence of clamp connections was not considered universal in the genus (Dahlmann et al. 2000).

The sympatric *C. pleurotoides* is remarkably similar to *C. olivaceoluteus* in its olivaceous yellow pileipellis lightening to yellow at the extreme margin, in contrast with the light grayish hymenium, similarly sized and shaped basidiospores, and fruiting on heavily decayed wood (Henkel et al. 2006). *Craterellus pleurotoides* differs fundamentally in its diminutive, strictly pleurotoid basidiomata, and shorter basidia (60–72 vs. 71–99 µm). The striking similarity in coloration and fruiting habit between the two species may reflect relatedness; one of our phylogenetic analyses indicated that *C. olivaceoluteus* and *C. pleurotoides* are sister species (ITS; FIG. 1A).

Craterellus olivaceoluteus is notably similar to a group of north temperate *Craterellus* species that have a well defined pileate-stipitate stature, dark pileus surface and paler hymenophore sharply demarcated from, and contrasting with, a yellowish orange to orange, subequal, glabrous stipe, and clamp connections (i.e. *Craterellus lutescens* [Fr.] Fr., *Craterellus tubaeformis* [Fr.] Quél., and *Craterellus ignicolor* [R.H. Petersen] Dahlman, Danell & Spatafora). Among these species, *C. olivaceoluteus* is most similar to *C. lutescens* but differs in its pileus color and surface texture (olivaceous brown with yellowish green margin and glabrous vs. fuscous brown throughout and fibrillose-floccose), consistently narrower pileus (12–38 mm vs. 20–100 mm), shorter stipe (22–48 mm vs. 50–100 mm), hymenophore color (grayish to yellowish olive vs. yellow to reddish orange) and sterigmata number (4–5–6 vs. 2–3–4) (Corner 1966, p 70–73; Dahlman et al. 2000). *Craterellus olivaceoluteus* differs from *C. tubaeformis* primarily in its lack of well developed hymenophoral gill folds and smaller basidioma, and from *C. ignicolor* in its olivaceous brown vs. dark orange pileus, lack of hymenophoral gill folds, and shorter basidiospores (8–10 vs. 9–13 µm) (Corner 1966, Petersen 1975).

In the greater Neotropics only *Cantharellus xanthoscyphus* R.H. Petersen from Parana, Brazil, has the well defined pileate-stipitate stature, small size, similar general colorations, smooth to rugulose hymenophore, and clamp connections as seen in *C. olivaceoluteus*. *Craterellus olivaceoluteus* can be distinguished from *C. xanthoscyphus* by its broader pileus (12–38 vs. 15–18 mm) with fimbriate vs. lacerate margin, longer stipe (22–48 vs. 15–25 mm), olivaceous brown vs. pale yellow pileus, and lack of strongly inflated pileipellis hyphae with thickened walls (Petersen & Mueller 1992). *Cantharellus lateritius* var. *colombianus* R.H. Petersen from montane Colombian oak woods has yellowish orange pigmentation and a smooth to rugulose hymenophore but differs from *C. olivaceoluteus* in its larger size (up to 80 mm tall), more broadly infundibuliform, imperforate, squamulose pileus, and solid stipe (Petersen & Mueller 1992).

FIG. 4. Basidiomata of *Craterellus cinereofimbriatus* (HOLOTYPE; *Henkel 9075*). Bar = 10 mm.

Among a number of diminutive, clamped Congolian species placed in *Cantharellus* by Heinemann (1958) none have color combinations similar to *C. olivaceoluteus*. *Pseudocraterellus laeticolor* Heinem., also from the Congo, is similar to *C. olivaceoluteus* in basidioma size and subinfundibuliform shape, with overall yellow to orange colorations but differs in its concolorous orange hymenium, smaller basidiospores (6.9–7.9 × 4.6–5.7 vs. 8–10 × 6–8 µm) and unclamped trama hyphae with abundant secondary septation (Heinemann 1958). The widely distributed Paleotropical *Craterellus aureus* Berk. & M.A. Curt. has a yellowish orange pileus and stipe and smooth to rugulose hymenophore but differs fundamentally from *C. olivaceoluteus* in its subglobose basidiospores, orange vs. olivaceous brown pileus and lack of clamp connections (Heinemann 1958). Among species recently described in *Cantharellus* or *Afrocantharellus* from the African or southeastern Asian tropics, none are similar to *C. olivaceoluteus* (e.g. Eyssartier and Buyck 1999; Buyck et al. 2000, 2013; Eyssartier et al. 2009; Tibuhwa et al. 2012).

Craterellus cinereofimbriatus T.W. Henkel, Aime et A.W. Wilson, sp. nov. FIGS. 4, 5

MycoBank MB803952

Pileus 11–43(65) mm broad, 3–10(17) mm tall, planate to uplifted with downturned, sharply undulating

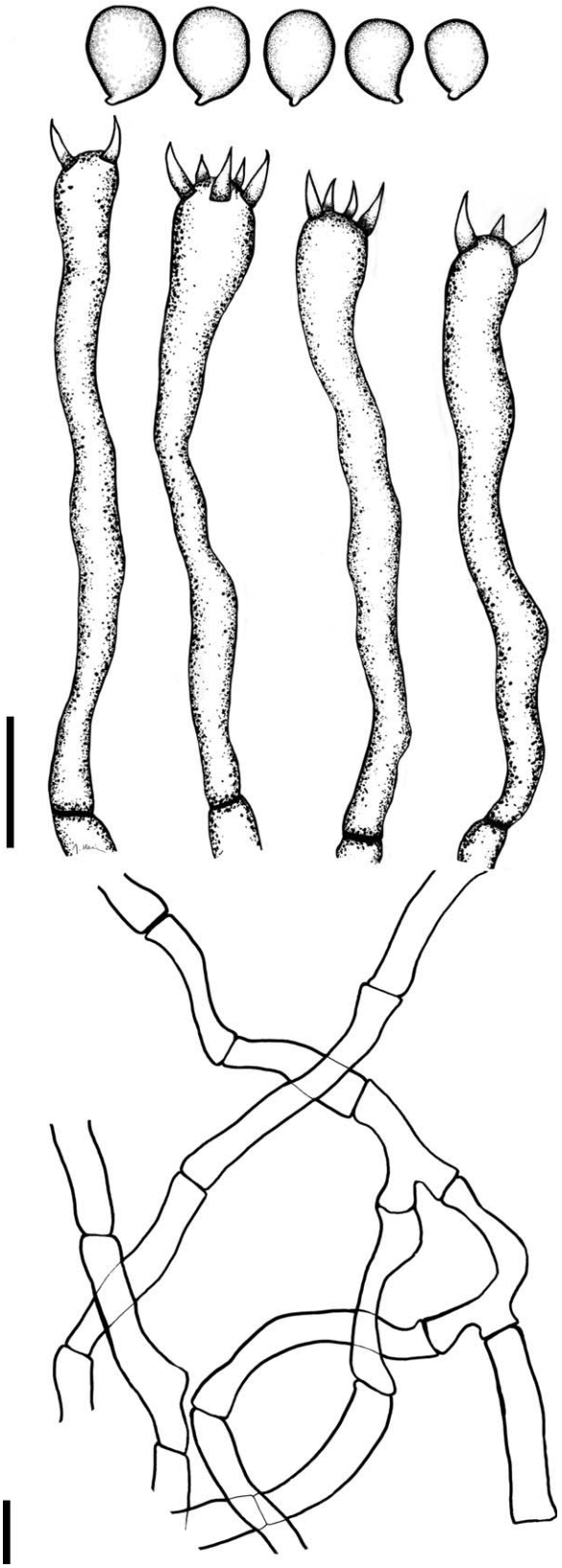

FIG. 5. Basidiospores, basidia and tramal hyphae of *Craterellus cinereofimbriatus* (HOLOTYPE; *Henkel 9075*). Bars = 10 μm.

margin at maturity, broadly and deeply depressed centrally with perforation continuous with hollow stipe, initially grayish brown (5C3–5D5, 5E4–5E5), with age darker brown (5D4, 6F3–6F4 KW), marginal edge lighter gray (5C3, 6C1–6D1), moist; surface glabrous, under hand lens tightly appressed radially fibrillose with scattered, minute suberect scales, extreme edge finely fimbriate-crenulate, splitting irregularly and shallowly with age. Hymenophore covering entire underside of pileus and descending 5–15 mm over apex of stipe and there unevenly and vaguely demarcated from the sterile stipe, light flesh gray (6C1–6C2) to gray with faint bluish cast (15C1–15D1), smooth initially, thickening slightly and subrugulose with age, hispid under hand lens due to projecting basidia, drying to rich yellow. Stipe (17)30–55(72) mm long, 3–11 mm wide, subequal, cylindrical, sometimes enlarging slightly toward base or flaring near apex, light brownish gray (5A2–5A3) to darker concolorous (5D3–5D4) throughout, glabrous, hollow, slightly fused at bases in caespitose clusters; basal mycelium lacking; trama concolorous, hollow centrally. Odor mild, chanterelle-like; flavor pleasant, chanterelle-like, sometimes faintly acrid. Primordia initially filiform-acuminate, extending upward with straight margin. Basidiospores 8.8–11 × (5.5)6–7(7.5) μm (mean = 10.0 × 6.5 μm; n = 80), Q range = 1.3–1.8, Q mean = 1.54, ellipsoid, smooth, pale yellowish gray to light gray in KOH, inamyloid, with minutely granular contents; wall 0.3–0.4 μm thick; hilar appendix 0.8–1 μm long. Basidia (59.3)66.7–103.7(109) × 4.9–7.4 μm (centrally), (5.4)6.2–7.9(9.6) μm wide at apex, (3)3.7–5.4(6.7) μm at base, subcylindrical, wall thin, hyaline to faintly light gray in KOH, devoid of obvious contents; sterigmata (2)3–4–5(6), (3.9)4.9–7.4 μm long, 1.7–2.2(2.5) μm wide at base, somewhat curving. Basidioles numerous, cylindrical, densely guttulate with granular epiplasm, pale yellowish brown in KOH. Cystidia none. Hymenium in transverse section 81.5–395.2 μm thick, yellow in KOH. Pileipellis scarcely differentiated from trama, 265–406 μm thick, of loosely interwoven, curving, irregularly anticlinal hyphae, light grayish brown in mass in KOH, in some sections irregularly and sparsely organized into erect subacuminate fascicles of 15–20 hyphae, fascicles up to 400 μm tall; terminal elements of nearly equal lengths, undifferentiated and rounded at apex; individual hyphae faintly grayish brown in KOH, cells 22–64 × 3.7–6.2 μm. Pileus trama 497–656 μm thick, of tightly interwoven sinuous hyphae, light tannish gray in mass in KOH; individual hyphae branching frequently, somewhat inflating, with scattered minute guttules, faint tannish gray in KOH; cells 34–94 × 3.7–7.4(13.6) μm; secondary septation absent. Stipitipellis composed of tightly packed mass of

interwoven to subparallel, anticlinal hyphae, light tannish brown in mass in KOH; terminal elements of nearly equal lengths, undifferentiated and rounded at apex; individual hyphae faintly tan in KOH, cells 12.4–5.9 × 3.7–6.2 μm. Stipe trama hyphae light grayish brown in mass in KOH; individual hyphae branching occasionally, nearly hyaline in KOH; cells 44.5–61.7 × 4.9–9.9 μm. Clamp connections absent from hyphae of all tissues.

Holotype: Henkel 9075 (BRG; ISOTYPE: HSU; NY)

Habit, habitat and distribution: Solitary or scattered as small caespitose clusters on humic mat under *Dicymbe corymbosa*, *Dicymbe altsonii*, *Dicymbe jenmanii*, *Aldina insignis* or *Pakaraimaea dipterocarpacea*; known from the Upper Potaro and Upper Mazaruni River basins of Guyana.

Etymology: Cinereus (L. adj. A) = light gray, fimbriatus (L. adj. A) = fringed; referring to the light gray basidioma with fringed pileal margin.

Specimens examined: GUYANA: REGION 8 POTARO SIPARUNI: Pakaraima Mountains, Upper Potaro River Basin, ~ 15 km east of Mt Ayanganna; vicinity of base camp, 10 Jun 2000, *Henkel 7475* (BRG; HSU); 2 km southeast of base camp near *Dicymbe* plot 1, 14 May 2001, *Henkel 8137* (BRG; HSU); ~ 4 km southeast of base camp near *Dicymbe* plot 2, 6 Jul 2004, *Henkel 8746* (BRG; HSU); vicinity of base camp, 17 Aug 2007, *Henkel 8873* (BRG; HSU); 0.5 km southeast of base camp in Jordan's plot 5, 6 Jul 2009, *Henkel 8999* (BRG; HSU), ITS GenBank JQ915104, LSU GenBank JQ915130; 2 km southwest of base camp, 26 Jul 2009, *Henkel 9075* (HOLOTYPE BRG; ISOTYPE: HSU; NY), ITS GenBank JQ915105, LSU GenBank JQ915131; 0.75 km west of base camp on line to *Dicymbe* plot 3, 20 May 2010, *Henkel 9202* (BRG; HSU), ~ 1.5 km west of base camp, 23 May 2010, *Henkel 9211* (BRG; HSU); ~ 12 km east of base camp, on *Dicymbe* ridge 0.3 km east of new Ayanganna airstrip, 7 Jun 2010, *Henkel 9264* (BRG; HSU), ITS GenBank JQ915112, LSU GenBank JQ915138; ~ 10 km southeast of base camp near Tadang camp, under *D. corymbosa*, *D. altsonii* and *A. insignis*, 8 Jun 2013, *Henkel 9774* (BRG; HSU); across river from base camp, 2 Jun 2012, *Aime 4811* (BRG; PUL). REGION 7 CUYUNI-MAZARUNI: Pakaraima Mountains, Upper Mazaruni River Basin, ~ 10 km west of Mt Ayanganna in vicinity of Pegaima savanna in forests dominated by *Pakaraimaea dipterocarpacea* and *Dicymbe jenmanii* on white sand soils; vicinity of base camp, 2 Jun 2012, *Henkel 9664* (BRG; HSU). VENEZUELA: AMAZONAS: Atabapo, 9 Aug 1987, *Halling 5462*, *Craterellus orinocensis* Pat. & Gaillard! (TENN 58453).

Commentary: Craterellus cinereofimbriatus is recognized in the field by its light grayish brown, pileate-stipitate, pliant basidiomata tending toward subinfundibuliform and generally 30–65 mm tall, smooth to finely rugulose, flesh gray hymenophore, planate to marginally downturned and undulating, umbilicate to perforate pileus with fimbriate extreme margin that is lighter gray, and regularly hollow stipe. Micromorphologically *C. cinereofimbriatus* is distinguished by its combination of smooth, ellipsoid, pale yellowish gray basidiospores, long, subcylindrical basidia with variable sterigmata 2–6, cuticular pileipellis with undifferentiated, thin-walled terminal elements and lack of clamp connections.

On the basis of its subcoriaceous basidioma with hollow stipe arising from an acuminate primordium with straight margins, *C. cinereofimbriatus* can be identified as a species in *Craterellus* in both the traditional and modern senses (Corner 1966, Feibelman et al. 1997, Dahlman et al. 2000, Wilson et al. 2012). These characters, along with the subinfundibuliform stature, smooth hymenophore, and lack of clamp connections make *C. cinereofimbriatus* morphologically consistent with *Craterellus* sensu lato, despite the recent discovery of several *Craterellus* species in Guyana, which have clamp connections and solid stipes (Wilson et al. 2012). The position of *C. cinereofimbriatus* within *Craterellus* was corroborated by phylogenetic analyses (FIG. 1A, B). Rare fruiting of *C. cinereofimbriatus* 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 only 0.3% of 630 quadrats sampled during the May–July rainy seasons over 7 y.

Craterellus cinereofimbriatus most closely resembles the sympatric *C. excelsus* in its drab, light gray to gray brown colorations overall, broadly undulating pileal margin at maturity, consistently smooth hymenophore, hollow stipe, and similarly sized and shaped basidia and basidiospores (Henkel et al. 2009). *Craterellus cinereofimbriatus* can be distinguished for *C. excelsus* by its consistently shorter basidiomata (30–60 vs. 60–135 mm) that occur solitarily or in small caespitose clusters as opposed to the frequent, large caespitose clusters of *C. excelsus*, more narrow central pileal perforation leading to a less broadly infundibuliform, more defined pileate-stipitate stature and regularly fimbriate-crenulate vs. smooth extreme pileal margin. These subtle, but discernable, macromorphological differences between *C. cinereofimbriatus* and *C. excelsus* were corroborated by molecular phylogenetic analyses, in which these taxa resolved as sister species within *Craterellus* (FIG. 1A, B).

Among the few *Craterellus* species described elsewhere from the lowland South American tropics, *C. orinocensis* resembles *C. cinereofimbriatus* in basidioma size and general coloration but differs in its more fully infundibuliform, brownish fuliginous basidioma with fascicles of hairs on the stipe, and much shorter (55–60 vs. 67–104 μm), consistently six-sterigmate basidia (Patouillard and Gaillard 1888, Corner 1966, Singer et al. 1983). Examination of a collection identified as *C. orinocensis* from Atabapo,

Venezuela (*Halling 5462*, TENN 058453) corroborated differences with *C. cinereofimbriatus* in the former's broader infundibuliform stature and decidedly smaller basidiospores (6.2–8.6 × 4.9–6.9 vs. 8.8–11 × 6–7 μm).

Craterellus verrucosus Massee from Malaysia has the caespitose habit, short basidioma with a light gray hymenium, thin, pliant context, and basidiospores similar in size to those of *C. cinereofimbriatus*. *Craterellus verrucosus* can be distinguished from *C. cinereofimbriatus* by its fuscous fuliginous to black, verrucose stipe base, rugulose hymenium, somewhat shorter, subclavate basidia (55–95 μm), and more inflated trama hyphae (up to 25 μm wide; Corner 1966).

Among the described varieties of *Craterellus cornucopioides* (L.) Pers., the north temperate *C. cornucopioides* var. *cornucopioides* (L.) Pers. is similar to *C. cinereofimbriatus* in its caespitose basidiomata and basidia approaching 100 μm long but can be distinguished by its regularly bisterigmate basidia and fuliginous black basidiomata with cinereous hymenia (Corner 1966). The European *C. cornucopioides* var. *flavicans* Sacc. and *C. cornucopioides* var. *roseus* R. Heim are distinguished by light yellow or rosaceous hymenia respectively. In the Paleotropics *C. cornucopioides* var. *mediosporus* Corner from Malaysia has up to six-sterigmate basidia and basidiospores similar in size to those found in *C. cinereofimbriatus* but is distinguished by its fuliginous black basidiomata (Corner 1966). *Craterellus cornucopioides* var. *parvisporus* Heinem. from the Congo has smaller basidiospores (6.8–8.5 × 4.3–6 μm) than *C. cinereofimbriatus*, regularly four-sterigmate basidia, and blackish brown basidiomata (Heinemann 1958).

Pseudocraterellus sinuosus (Fr.) Corner is superficially similar to *C. cinereofimbriatus* in basidioma stature and coloration and has been recorded from the Guiana Shield region (Corner 1969) but is easily distinguished by its copiously secondarily septate hyphae forming moniliform rows of cells in the trama (Corner 1966).

Cantharellus guyanensis Mont. Ann Sci Nat Bot Ser 4:107. 1854. FIGS. 6, 7

Pileus 10–35(60) mm wide, 5–12(25) mm tall, broadly convex to plano-convex to plane and then broadly depressed centrally, margin inrolled to downcurved throughout development, with advanced age uplifted, broadly undulating, and splitting irregularly, initially deep, bright orange (5A8–6A8–7A8), concolorous throughout development, eventually lightening to yellow-orange (5A6–5A7) throughout, glabrous, moist; surface under hand lens a dense, low, erect tomentum; extreme margin subcrenulate; trama creamish orange, solid. Hymenophore of well defined ridges, these subclose, subthick, decurrent, forking once near margin or further back, with 1–3 lamellulae, orangish cream (4A3–4A4, 5A3–5A4), with age and hymenial thickening fusing superficially and increasingly intervenose; edges concolorous, smooth, minutely hispid under hand lens. Stipe 30–62 mm long, 3–12 mm broad, equal, slightly attenuating at extreme base, more rarely enlarged at base, or flaring slightly at apex, pinkish orange (6A3) to light orange (4A4–5A4, 6A4–6A5) throughout, smooth, with fine whitish bloom under hand lens, occasionally with minute concolorous scales at apex, sometimes nearly white over basal one-third; basal mycelium a dense white bloom, with mycelial wefts descending into organic substrata; trama in section creamish orange, solid, rarely centrally hollow over basal half. Primordia initially broadly conical, light orange with white bloom, 1–7 mm tall, with a distinct inrolled pileal limb. Odor minimal, mildly fungoid; flavor pleasant, chanterelle-like, with subastringent sharpness. Edible and choice, although not traditionally used by the Patamona Amerindians in Guyana (Henkel et al. 2004). Basidiospores 7–9.2(10.2) × (4)4.5–6.2(7.1) μm (mean = 8.2 × 5.2 μm; n = 80), Q range = (1.3)1.4–1.8(2), Q mean = 1.6, ellipsoid, with rather pronounced abaxial depression, smooth, hyaline in KOH, inamyloid, with many small guttules evenly distributed in epiplasm, occasionally uniguttulate; wall 0.3–0.4 μm thick; hilar appendix 0.9–1 μm long. Basidia (44.5)49.4–81.5(96.3) × (4.9)5.4–7.4 μm (centrally), 7.4–9.9 μm wide at apex, (3.7)4.9–5.4(6.2) μm at base, subcylindrical to subclavate, hyaline to faintly grayish in KOH, devoid of obvious contents, occasionally minutely granulose; sterigmata 3–4–5–6, (3.7)4.9–7.4 μm long, 1.5–2.5 μm wide at base, somewhat curving. Basidioles numerous, subcylindrical, densely cytoplasmic, pale yellowish brown in KOH. Cystidia none. Hymenium in transverse section 44–96 μm thick, in mass yellowish orange in KOH. Pileipellis a cutis of interwoven periclinal inflated hyphae, scarcely differentiated from subpellis, pale tannish orange in mass in KOH, hyphae nearly hyaline individually; terminal cells broadly cylindrical, rarely obclavate, inflated, often constricted one or more times centrally, apex rounded, (29)57.1–94.4(154) × 8.4–14.9 μm, walls noticeably thickened to near 1 μm; penultimate cells inflated, (26)54.7–99.4(135) × (7)8.9–14.9(25) μm; subpellis hyphae occasionally with minute external encrustations. Pileus tramal hyphae smooth, hyaline in KOH, branching occasionally, somewhat inflating, unconstricted at septa, devoid of obvious internal contents; cells 22.2–98.8 × 2.5–9.9(12.4) μm; secondary septation

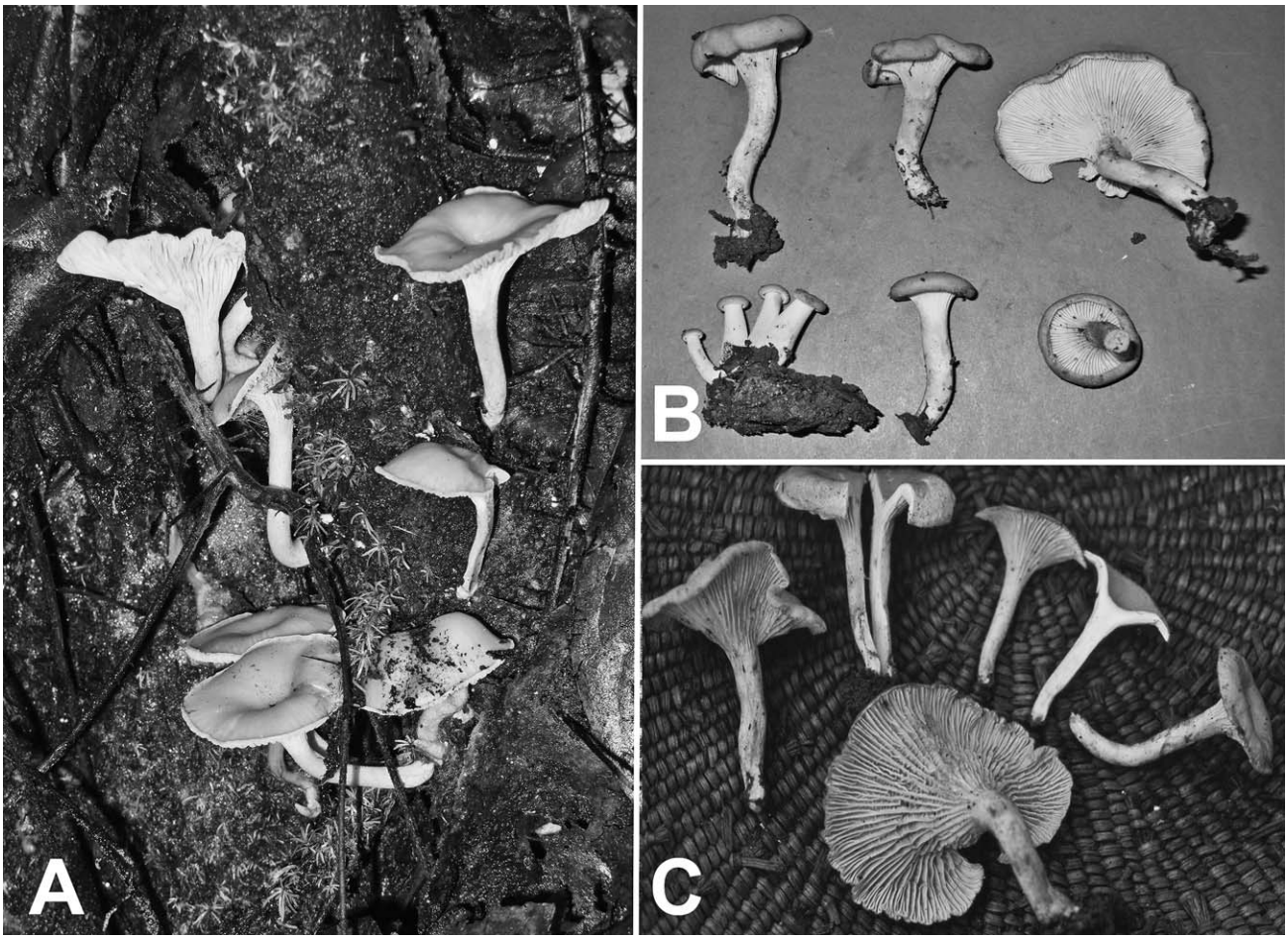

FIG. 6. Basidiomata of *Cantharellus guyanensis* Mont. A. Field habit, on humic deposits on lower trunk of *Dicymbe corymbosa* (Caesalpinioideae), Upper Potaro Basin, Guyana, *Henkel 9201*. B. French Guiana, *Henkel 9732*. C. Venezuela, *Henkel V-18*. All images × 0.75.

absent. Stipitipellis a cutis with periclinal terminal elements, these with tannish orange cytoplasmic pigments in KOH; terminal elements and hyphal cells similar to those of the pileipellis. Stipe tramal hyphae smooth, hyaline to faintly yellow in KOH, occasionally branching and constricted at septum, devoid of obvious contents or with scattered guttules; cells 44.5–111.2 × 3.7–11.1 µm. Clamp connections abundant on hyphae of all tissues.

Habit, habitat and distribution: In Guyana, in small to large troops on humic mat of forest floor in *Dicymbe*-dominated stands or on humic deposits on lower trunks of *Dicymbe corymbosa*, preferentially on sandy soils; more rarely under *Dicymbe* or *Aldina* on lateritic soils; known from the Upper Potaro and Upper Mazaruni Basins of Guyana and 100 km to the east in the lowlands of the Mabura Hill region; also known from French Guiana, Venezuela, and north central, northeastern and southern Brazil in association with putative nyctaginaceous or polygonaceous ECM host plants.

Specimens examined: GUYANA: REGION 8 POTARO-SIPARUNI: Pakaraima Mountains, Upper Potaro River Basin, ~ 15 km east of Mt Ayanganna; vicinity of base camp, 10 Jun 2000, *Henkel 7488* (BRG; HSU); 3 km southwest of base camp near *Dicymbe* plot 3, 4 Jun 2001, *Henkel 8242* (BRG; HSU); 1.5 km southeast of base camp near *Dicymbe* plot 1, 17 May 2010, *Henkel 9201* (BRG; HSU), ITS GenBank JQ915106, LSU GenBank JQ915132; ~ 10 km southeast of base camp near Tadang camp, under *D. corymbosa*, *D. altsonii* and *A. insignis*, 6 Jun 2013, *Henkel 9762* (BRG; HSU); old Ayanganna airstrip, 20 May 2000, *Aime 981* (BRG; HSU; PUL), ITS GenBank JQ915099, LSU GenBank JQ915125; ~ 2 km southwest of base camp near *Dicymbe* plot 3, 27 Jun 2006, *Aime 3112* (BRG; HSU; PUL), ITS GenBank JQ915093, LSU GenBank JQ915122; ~ 2.5 km southeast of base camp in *Dicymbe* plot 1, 16 May 2010, *Aime 3947* (BRG; PUL); REGION 7 CUYUNI-MAZARUNI: Pakaraima Mountains, Upper Mazaruni River Basin, ~ 6 km west of Mt Ayanganna, 3.8 km east of Pegaima base camp on west bank of Koatse Creek, under *D. corymbosa* on white sand soils, 31 Dec 2010, *Henkel 9577* (BRG; HSU). REGION 10 UPPER DEMERARA-BERBICE: Mabura Ecological Reserve; ~ 100 m northwest of Mabura

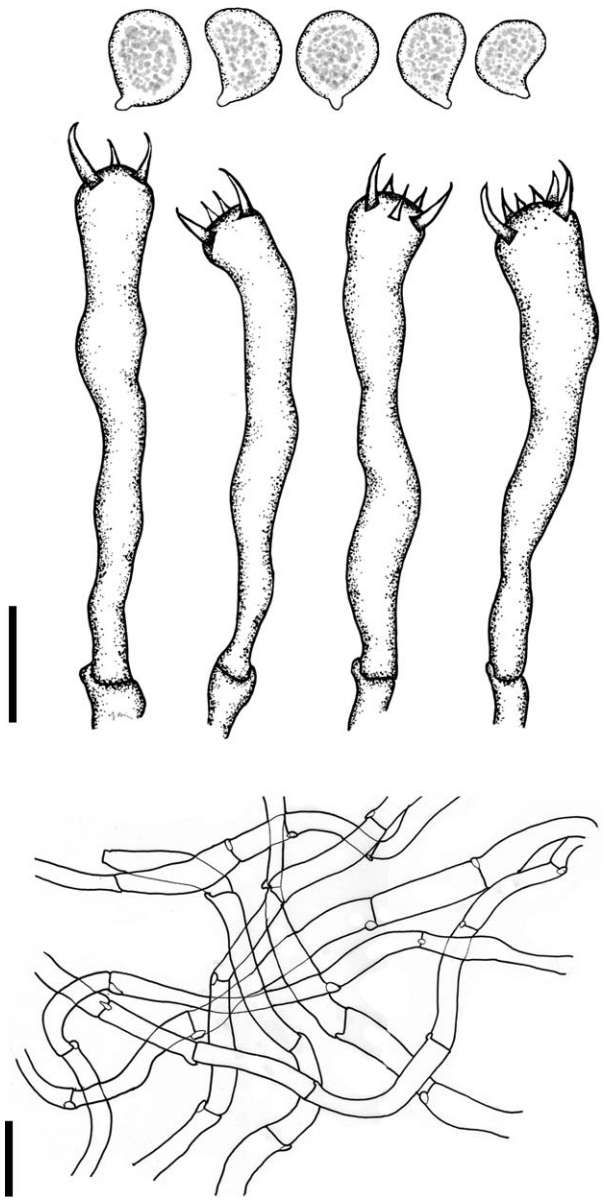

FIG. 7. Basidiospores, basidia and tramal hyphae of *Cantharellus guyanensis* (*Henkel 8242*). Bars = 10 μm.

field station in *D. altsonii* monodominant stand No. 1 on brown sand soils, 24 May 2011, *Henkel 9607* (BRG; HSU). VENEZUELA: BOLIVAR: Caroni River Basin, Lago Guri; Isla Redonda under *Coccoloba* sp., 4 Jul 2000, *Henkel V-18* (HSU), LSU GenBank KC897657; 5 Jul 2000, *Henkel V-20* (HSU). FRENCH GUIANA: Nouragues Field Station, on small plateau close to inselberg camp, 24 Jun 2011, *Roy G178* (TL), LSU GenBank 878735; Paracou Field Station, plot 15 near tree No. 786, 26 Jun 2012; *Henkel 9732* (TL; HSU), ITS GenBank KC878733, KC897654, LSU GenBank KC878734, KC897656. BRAZIL: AMAZONAS: Manaus-Caracarai road, in campina forest, Apr 1977, *Singer 43724* (TENN 43724); PARANA: Campina Grande do Sul, Parque Marumbi, in native forest, 18 Apr 1991, *de Meijer 1944* (TENN 57222); PERNAMBUCO: Igarassu, Refúgio Ecológico Charles Darwin, 30 Jun 2010, *Pereira* s.n. (JPB46813), LSU GenBank KC897658; PARAIBA: Areia, Reserva Ecológica Mata do Pau-Ferro, 30 Apr 2011, *Wartchow 01/2011* (JPB46806), LSU GenBank KC897659.

Commentary: Key macromorphological characters allowing field recognition of *C. guyanensis* include the well defined pileate-stipitate stature, the yellow-orange to orange pileus with downturned margin and rarely exceeding 40 mm diam, the orangish cream, well defined, lamelloid hymenophore, and subequal, light orange, solid stipe. In addition the preference for sand-rich soils and fruiting habit in medium to large troops has been observed regularly in Guyana and also in French Guiana and Venezuela. While rare fruiting of *C. guyanensis* 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 0.8% of 630 quadrats sampled during the May–July rainy seasons over 7 y; these study plots were located on lateritic soils, whereas the species has been observed fruiting and collected much more frequently in *Dicymbe* forests on sand soils.

Micromorphologically *C. guyanensis* is distinguished by the ellipsoid, smooth, hyaline to yellowish basidiospores with granular-guttulate cytoplasm, relatively short (generally < 80 μm) basidia with 3–4–5–6 sterigmata, abundant clamp connections on hyphae of all tissues, and a cuticular pileipellis with broadly cylindrical terminal elements with thickened walls. Overall, material from Guyana agrees well with the type description of *C. guyanensis*, from French Guiana, provided by Montagne (1854) and a modern revision of the type specimen (Eyssartier 2001) except that the purplish orange tints in the developing pilei recorded in the type have never been observed in the numerous collections from Guyana or in the recent collections *Roy G178* and *Henkel 9732* from French Guiana. In addition, the hollow stipe recorded by Montagne is rarely seen in the Guyana material.

Specimens of *C. guyanensis* from French Guiana, Venezuela and Brazil examined for this study agree well with the Guyana material across the pertinent character set, with some minor variations. The French Guiana collection (*Henkel 9732*) varied from the Guyana material in its more subglobose basidiospores (mean Q = 1.3 vs. 1.6). The Brazilian collection (*Singer 43724*) had slightly more ellipsoid basidiospores (mean Q = 1.8 vs. 1.6) and somewhat shorter basidia (41–57 vs. 49.4–81.5 μm). The two Venezuelan collections (*Henkel THV-18*, *THV-20*), as well as an additional southern Brazilian specimen (*de Meijer 1944*), were identical to the Guyana material in all characters. Minor variations between specimens notwithstanding, the morphological character package shared by specimens examined from across the Guiana Shield argue strongly for a single regional

SUPPLEMENTARY TABLE I. *Cantharellaceae* taxa, specimen ID and GenBank numbers for sequences used in phylogenetic analyses

Species	ID	Date	Location	ITS	28S
Original sequences used in this study and Wilson et al. 2012					
Cantharellus guyanensis	MCA3112	2006	Guyana	JQ915096	JQ915122
Cantharellus guyanensis	MCA981	2000	Guyana	JQ915099	JQ915125
Cantharellus guyanensis	TH9201	2010	Guyana	JQ915106	JQ915132
Cantharellus guyanensis	TH9732	2012	French Guiana	KC897654	KC897656
Cantharellus guyanensis	THV-18	2000	Venezuela		KC897657
Cantharellus guyanensis	JPB46813	2010	Brazil, Pernambuco		KC897658
Cantharellus guyanensis	JPB46806	2011	Brazil, Paraiba		KC897659
Craterellus atratoides (type)	TH9232	2010	Guyana	JQ915111	JQ915137
Craterellus atratoides	MCA1313	2000	Guyana	JQ915093	JQ915119
Craterellus atratoides	TH8473	2002	Guyana	JQ915103	JQ915129
Craterellus atratus	MCA1070	2000	Guyana	JQ915092	JQ915118
Craterellus atratus	TH9203	2010	Guyana	JQ915107	JQ915133
Craterellus atratus	MCA990	2000	Guyana	JQ915100	JQ915126
Craterellus excelsus (isotype)	TH8235	2001	Guyana	JQ915102	JQ915128
Craterellus excelsus	MCA3107	2006	Guyana	JQ915095	JQ915121
Craterellus excelsus	TH7515	2000	Guyana	JQ915101	JQ915127
Craterellus excelsus	TH9733	2012	French Guiana	KC897655	
Craterellus strigosus (type)	TH9204	2010	Guyana	JQ915108	JQ915134
Craterellus strigosus	MCA1750	2001	Guyana	JQ915094	JQ915120
Craterellus pleurotoides	MCA3124	2006	Guyana	JQ915097	JQ915123
Craterellus pleurotoides	TH9220	2010	Guyana	JQ915110	JQ915136
Craterellus olivaceoluteus (type)	TH9205	2010	Guyana	JQ915109	JQ915135
Craterellus olivaceoluteus	MCA3186	2006	Guyana	JQ915098	JQ915124
Craterellus cinereofimbriatus	TH8999	2009	Guyana	JQ915104	JQ915130
Craterellus cinereofimbriatus (type)	TH9075	2009	Guyana	JQ915105	JQ915131
Craterellus cinereofimbriatus	TH9264	2010	Guyana	JQ915112	JQ915138
Cantharellus platyphyllus	Arora00-437	2000	Chisipite, Harare, Zimbabwe, Africa		JQ915113
Cantharellus cibarius	Arora01-567	2001	Zambia, Africa		JQ915114
Cantharellus longisporus	Arora27		Near Harare, Zimbabwe, Africa		JQ915115
Cantharellus densifolius	Arora65		Chimanimani, Zimbabwe, Africa		JQ915116
Craterellus sp	AWW263		Kuala Pilah, Negeri Sembilan, Malaysia	JQ915091	JQ915117
Genbank ITS sequences					
Cantharellus appalachiensis			India	HQ386220	
Cantharellus cascadensis			USA Northwest	AY041181	
Cantharellus cibarius			Thailand	AB453024	
Cantharellus cibarius				DQ200926	
Cantharellus cibarius			Czech Republic	EF546767	
Cantharellus cibarius var cibarius			USA Northwest	AY041176	
Cantharellus cibarius var cibarius			USA Northwest	AY041177	
Cantharellus cibarius var multiramis			India, NW Hi	HQ270128	
Cantharellus cibarius var roseocanus			USA, Northwest	AY041172	
Cantharellus formosus			USA Northwest	AY041184	
Cantharellus formosus			India	FJ769255	
Cantharellus minor			India, NW Himalayas	HQ270119	
Cantharellus sp			USA, CA	DQ974688	
Cantharellus sp			India, NW Himalayas	HQ270124	
Cantharellus subalbidus			USA Northwest	AY041178	
Cantharellus subalbidus			USA Northwest	AY041179	
Cantharellus tubaeformis			GB, Scotland	UDB001527	

SUPPLEMENTARY TABLE I. Continued

Species	ID	Date	Location	ITS	28S
Cantharellus tubaeformis			GB, Scotland	UDB002389	
Craterellus cornucopioides			Denmark	UDB000053	
Craterellus cornucorpioides			USA, MA	DQ205680	
Craterellus lutescens			Ireland	AY082606	
Craterellus sp			USA	AY456340	
Craterellus tubaeformis				AF385632	
Craterellus tubaeformis			Sweden	AF385633	
Craterellus tubaeformis				AY195572	
Craterellus tubaeformis				AY195573	
Uncult ECM			Japan	AB251810	
Uncult Craterellus			USA, NY	FJ901312	
UncultECM			Canada, British Columbia	DQ474413	
Clavulina sp (OUTGROUP)				AY918958	
Sistotrema brinkmannii (OUTGROUP)				AM981211	
GenBank LSU sequences					
Cantharellus appalachiensis	GRSM77088		Smokies, TN		DQ898690
Cantharellus appalachiensis			India		HM750916
Cantharellus cascadensis			USA, OR		AY041161
Cantharellus cibarius	GRSM77029		Smokies, TN		DQ898693
Cantharellus cibarius			China		AJ271191
Cantharellus cibarius			USA, MA		AY745708
Cantharellus cibarius			USA, MA		CCU87985
Cantharellus cibarius			Canada		EU522825
Cantharellus cibarius var cibarius			Sweden		AY041155
Cantharellus cibarius var roseocanus			USA, OR		AY041151
Cantharellus cinabarinus	GRSM77031		Smokies, TN		DQ898692
Cantharellus cinnabarinus			USA		AY041168
Cantharellus cinnabarinus			USA, MA		CCU87989
Cantharellus formosus			USA, OR		AY041164
Cantharellus garnierii			New Caledonia		AY392767
Cantharellus isabellinus			India		HM750931
Cantharellus lateritius	GRSM77030		Smokies, TN		DQ898694
Cantharellus lateritius			USA, LA		CLU87986
Cantharellus minor			USA, LA		CMU87988
Cantharellus minor			Spain		DQ898691
Cantharellus persicinus			USA		AY041169
Cantharellus sp			China		AJ271192
Cantharellus sp					AY041167
Cantharellus sp			India		GU237071
Cantharellus sp			China		HM594681
Cantharellus subalbidus			USA, OR		AY041149
Cantharellus tabernensis			USA, MA		CTU87987
Craterellus aurora			Sweden		AF105302
Craterellus aurora			Sweden		AF105303
Craterellus aurora			Spain		AF105304
Craterellus cornucopioides			USA, NC		AF105298
Craterellus cornucopioides			USA, CA		AF105299
Craterellus cornucopioides			Norway		AF105301
Craterellus cornucopioides			USA, MA		AF105305
Craterellus cornucopioides			China		AJ279572
Craterellus cornucopioides			USA		AY700188
Craterellus ignicolor			USA, NC		AF105314
Craterellus lutescens			Canada		EU522746
Craterellus odoratus			USA, MA		AF105306
Craterellus tubaeformis			Sweden		AF105307

SUPPLEMENTARY TABLE I. Continued

Species	ID	Date	Location	ITS	28S
Craterellus tubaeformis			USA, NC		AF105308
Craterellus tubaeformis			USA, OR		AF105311
Craterellus tubaeformis			USA, WA		AF105313
Craterellus tubaeformis			Canada, Ontario		DQ898741
Clavulina cristata (OUTGROUP)					AY586648
Sistotrema alboluteum (OUTGROUP)					AY586713

species. In addition, molecular phylogenetic analyses including *C. guyanensis* specimens from Guyana, French Guiana, Venezuela and Brazil confirmed their conspecificity (FIG. 1A, B).

While evidence exists for broad geographic distributions of some ECM fungal species in the lowland South American tropics (Wartchow and Maia 2007, Menolli et al. 2009, Henkel et al. 2011, Uehling et al. 2012, Wartchow 2012), *C. guyanensis* constitutes the first case of an individual species being documented over a geographical area circumscribing nearly the entire Guiana Shield region, with a N-S distribution of ~ 1200 km, and E-W of ~ 2500 km. Consideration of the de Meijer specimen from Parana in southern Brazil would extend the known distribution of *C. guyanensis* a further 3000+ km southward. *Cantharellus guyanensis* also appears to have broad host-plant range, occurring in forests dominated by ECM *Dicymbe* or *Aldina* spp. in Guyana and in mixed, non-ectotrophic rainforests in spatial proximity to trees or lianas of ECM *Coccoloba*, *Guapira* or *Neea* spp. in French Guiana, Venezuela and northeastern Brazil (e.g. Béreau et al. 1997, Terborgh et al. 2006, Alves-Araújo et al. 2008). Potential host plants for Singer's collection from north central Brazilian campina forest include ECM *Aldina* spp. and possibly *Glycoxylon inophyllum* (Mart. ex Miq.) Ducke (Sapotaceae) (Singer et al. 1983), as also noted in Singer's personal communication to RH Petersen included with the specimen housed at TENN.

Until recently *C. guyanensis* was one of the few valid *Cantharellus* species known from the lowland South American tropics (Wartchow et al. 2012a, Wilson et al. 2012). Three new Brazilian species have since come to light that deserve comparison with *C. guyanensis*. *Cantharellus aurantioconspicuus* Wartchow & Buyck from the Atlantic coastal forest of Brazil is similar to *C. guyanensis* in its well defined pileate-stipitate habit, overall orange coloration, well developed lamellate hymenophore, and basidiospore and basidium sizes and dimensions, but differs in its more robust stature with a consistently broader pileus (25–90 mm vs. 10–35 mm) and lack of thickened walls in the pileipellis terminal cells (Wartchow et al. 2012b). *Cantharellus amazonensis* Wartchow from near Manaus in the central Brazilian Amazon has similarly small basidiomata (30–35 mm diam) but differs fundamentally in its bright red pileus, non-anastomosing lamellae, primarily six-sterigmate basidia (vs. 3–4–5–6) and lack of thickened walls in the pileipellis terminal cells (Wartchow et al. 2012b). *Cantharellus protectus* Wartchow & FGB Pinheiro, recently described from the Brazil's Atlantic coastal forest, is exceedingly similar to *C. guyanensis* in basidioma stature and size, predominantly yellow-orange pileus and well defined lamellate-intervenose hymenophore but differs in its darker orange vs. pinkish orange to light orange stipe, consistently smaller basidiospores (5.5–7.5 × 3.5–5 µm vs. 7–9.2 × 4.5–6.2 µm), shorter basidia (36–58 vs. 49.4–81.5 µm) that are predominantly six-sterigmate, and slightly thickening walls (to 0.5 µm) in the pileipellis terminal cells (Pinheiro and Wartchow 2013).

Craterellus excelsus T.W. Henkel & Aime Mycotaxon 107:202. 2009.

Specimen examined: FRENCH GUIANA: Paracou Field Station, mixed forest plot 15 near tree No. 786, 26 Jun 2012, *Henkel 9733* (HSU; TL), ITS GenBank KC897655.

Commentary: Craterellus excelsus, previously known only from the type locality in Guyana, recently was collected in French Guiana. The French Guiana material agrees well both macro- and microscopically with *C. excelsus* (Henkel et al. 2009) and appears conspecific in the ITS phylogenetic analysis (FIG. 1A). The record of *C. excelsus* from French Guiana is a significant range extension of ~ 500 km eastward for the species and likely a host extension because basidiomata were collected close to ECM *Coccoloba* lianas. The species was known previously only from *Dicymbe*-dominated forests in Guyana.

KEY TO LOWLAND NEOTROPICAL *CANTHARELLUS* AND *CRATERELLUS* SPECIES, WITH EXTRALIMITAL CENTRAL AND SOUTH AMERICAN TAXA[4]

1. Basidioma colors bright; pale yellow, olivaceous yellow or brown, golden yellow, yellowish orange, orange, to bright red; clamp connections always present 2

[4] Additional references not cited elsewhere in the text: Singer 1963; Wu and Mueller 1995; Eyssartier et al. 2003.

1. Basidioma colors somber; violet brown, grayish brown, dark brown, or black; clamp connections present or absent 10
2 (1). Basidiomata pleurotoid, 7–23 mm wide; stipe absent or lateral, Guyana . . . . . *Craterellus pleurotoides* (T.W. Henkel, Aime & S.L. Mill.) A.W. Wilson
2. Basidiomata pileate-stipitate; stipe central . . . 3
3 (2). Hymenophore smooth to rugulose, stipe hollow or solid 4
3. Hymenophore with well developed, lamella-like ridges, stipe solid 7
4 (3). Stipe hollow, olivaceous orange to orange, 22–48 × 2–7 mm; pileus olivaceous brown with greenish yellow margin, 12–38 mm wide; hymenophore grayish olive; Guyana . . . . . *Craterellus olivaceoluteus* T.W. Henkel, Aime & A.W. Wilson
4. Stipe solid; pileus pale yellow, golden yellow, yellowish orange, orange, or bright red . . . 5
5 (4). Basidioma pale yellow throughout, diminutive; pileus 15–18 mm wide; stipe 15–25 × 2.5 mm; hymenophore smooth; Brazil (Parana). . . . . *Cantharellus xanthoscyphus* G.M. Mueller & R.H. Petersen
5. Pileus golden yellow, orange, or orange-brown . . . 6
6 (5). Pileus orange to orange-brown, finely fibrillose, 17–22 mm wide; stipe white, 10–15 × 10 mm; hymenophore off-white to white, rugulose; Argentina (Neuquen), in *Nothofagus* forests . . . . . *Cantharellus nothofagorum* G.M. Mueller & R.H. Petersen
6. Pileus golden yellow to orange, with brownish gray squamules, 20–80 mm wide; stipe pale orangish white, 30–50 × 5–8 mm diam; hymenophore pale orangish white, smooth to rugulose; Colombia (Pasto), in montane *Quercus* forests . . . . . *Cantharellus lateritius* var. *colombianus* R.H. Petersen
7 (3). Pileus bright red, 30–35 mm wide; stipe pale yellow to yellowish orange, up to 60 × 4 mm; hymenophore yellowish to pale orange, strongly lamellate, not anastomosing or intervenose; Brazil (Amazonas) . . . . . *Cantharellus amazonensis* Wartchow
7. Pileus yellow-orange or orange, hymenophore lamellate and intervenose 8
8 (7). Pileus orange with reddish orange disk, 25–90 mm wide; stipe bright orange or pale cream, 28–64 × 8–20 mm; hymenophore pale yellow to cream; basidiospores 7–9 × 4–5 µm (mean Q = 1.7); basidia 60–85 × 8–9.5 µm; pileipellis terminal cells thin-walled; Brazil (Pernambuco) . . . . . *Cantharellus aurantioconspicuus* Wartchow & Buyck
8. Pileus orange, yellow-orange, or orange-yellow throughout, generally < 62 mm wide; stipe pinkish orange, light orange, or orangish yellow; pileipellis terminal cells thin- or thick-walled; basidiospore mean Q < 1.7 9
9 (8). Pileus orangish yellow, 17–52 mm wide; stipe orangish yellow, 30–60 × 4–9 mm; hymenophore orangish yellow; basidiospores 5.5–7.5 × 3.5–5 µm (mean Q = 1.5); basidia 36–58 × 5–8 µm; pileipellis terminal cells with walls ≤ 0.5 µm thick; Brazil (Paraiba) . . . . . *Cantharellus protectus* Wartchow & F.G.B. Pinheiro
9. Pileus bright orange to yellowish orange, 10–35(60) mm wide; stipe pinkish orange to light orange, 30–62 × 3–12 mm; hymenophore orangish cream; basidiospores 7.2–9.2 × 4.5–6.2 µm (mean Q = 1.6); basidia 49–81 × 5.4–7.4 µm; pileipellis terminal cells with walls 1 µm thick; Guyana, French Guiana, Venezuela (Bolivar), Brazil (Amazonas, Paraiba, Parana, Pernambuco) . . . . . *Cantharellus guyanensis* Mont.
10 (1). Hymenophore with well developed, lamella-like ridges 11
10. Hymenophore smooth, rugulose, or rugose 12
11 (10). Pileus violet brown to nearly black over disk, 20–60 mm wide, imperforate; stipe whitish lilac, 30–50 × 6–10 mm, solid; hymenophore creamish yellow to pale orange; clamp connections present; Costa Rica, in montane *Quercus* forests . . . . . *Cantharellus atrolilacinus* Eyssartier, Buyck & Halling
11. Pileus black to dark grayish brown, 12–60 mm wide, perforate; stipe black overall, grayish at base, 30–80 × 4–11 mm, hollow; hymenophore dark gray with pinkish tint; clamp connections absent; Colombia, Costa Rica, in montane *Quercus* forests . . . . . *Craterellus boyacensis* Singer
12 (10). Basidioma with well defined pileus and stipe; pileus imperforate or narrowly perforate; stipe solid or hollow; clamp connections present or absent 13
12. Basidioma infundibuliform, trumpet-like; pileus broadly perforate; stipe hollow; clamp connections absent 18
13 (12). Pileus narrowly perforate; stipe hollow. 14
13. Pileus imperforate; stipe solid 15
14 (13). Pileus dark grayish brown with light grayish tan margin, 5–22 mm wide; stipe concolorous, 25–70 × 1.5–3 mm; hymenophore light bluish gray, smooth to rugulose; clamp connections present; Guyana . . . . . *Craterellus atratoides* T.W. Henkel, Aime & A.W. Wilson
14. Pileus grayish brown with light gray margin, 11–45(65) mm wide; stipe light brownish gray, 30–55(72) × 3–11 mm; hymenophore light flesh gray, smooth to subrugulose; clamp connections absent; Guyana . . . . . *Craterellus cinereofimbriatus* T.W. Henkel, Aime & A.W. Wilson
15 (13). Pileus black or dark grayish brown, planate to upturned at maturity, 12–25 mm wide; stipe

gray, 20–37 × 1–4 mm; hymenophore gray, smooth, adnate; clamp connections absent; trama hyphae with abundant secondary septa; lowland Suriname; Colombia, Costa Rica, in montane *Quercus* forests . . . *Pseudocraterellus sinuosus* (Fr.) Corner

15. Pileus brownish gray, dark brown, or brown with off-white margin, campanulate to plano-convex at maturity; hymenophore decurrent, smooth to rugulose; clamp connections present; secondary septa absent 16

16 (15). Pileus brown or light brown with off-white margin, surface glabrous or with few strigose scales, 9–32 mm wide; stipe light to dark brown, 8–30 × 1–2, with scattered strigose scales; hymenophore light gray; basidiospores 9–10(11) × 7–9 μm; basidia (2)3–4–5-sterigmate; Guyana; Brazil (Rio de Janeiro) . . . . . *Craterellus atratus* (Corner) Yomyart et al.

16. Pileus and stipe dark brown or brownish gray throughout, < 20 mm wide, with scattered or abundant strigose scales 17

17 (16). Pileus dark brown, campanulate to plano-convex, 4–18 mm wide; stipe concolorous, 13–33 × 1–1.5 mm; strigose scales abundant on pileus and stipe; hymenophore brownish gray; basidiospores 8–10 × 6–8 μm; basidia 2–3–4–5-sterigmate; Guyana . . . . . *Craterellus strigosus* T.W. Henkel, Aime & A.W. Wilson

17. Pileus brownish gray, plano-convex, 11–15 mm wide; stipe gray, 12–20 × 2 mm; strigose scales scattered on pileus and stipe; hymenophore gray; basidiospores 7.3–9 × 6–6.5 μm;basidia (4–5)6-sterigmate; Brazil (Amazonas) . . . *Cantharellus hystrix* Corner

18 (12). Basidiomata < 31 mm tall, < 36 mm broad across apex, dark grayish brown throughout; hymenophore smooth; basidia regularly four-sterigmate; Costa Rica, in montane *Quercus* forests . . . . . *Craterellus costaricensis* Qui X. Wu

18. Basidiomata > 45 mm tall, overall gray brown, dark brown, or black; hymenophore smooth or smooth to rugulose; basidia not regularly four-sterigmate 19

19 (18). Basidiomata black or very dark brown, 45–100 mm tall, 30–50 mm wide across apex; hymenophore blackish gray, smooth to rugulose; sterile base concolorous; basidiospores 11–15 × 7–10 μm; basidia two-sterigmate; Colombia (Cundimarca), Costa Rica, in montane *Quercus* forests . . . . . *Craterellus fallax* A.H. Sm.

19. Basidiomata grayish brown; basidiospores ≤ 12 μm long; basidia not regularly two-sterigmate 20

20 (19). Basidiomata light grayish brown, 60–135 mm tall, 25–70 mm wide across apex; hymenophore grayish cream to light gray, smooth; basidiospores 9–12 × 6.5–9 μm; basidia 2–6-sterigmate; Guyana, French Guiana . . . . . *Craterellus excelsus* T.W. Henkel & Aime

20. Basidiomata dark grayish brown, 60–80 mm tall, 20–30 wide across apex; hymenophore violaceous gray, smooth to rugulose; basidiospores 6–9 × 5–7 μm; basidia regularly six-sterigmate; Venezuela (Amazonas)..... . . . . *Craterellus orinocensis* Pat. & Gaillard

ACKNOWLEDGMENTS

The authors thank the following for financial support: National Science Foundation DEB-0918591 and the National Geographic Society's Committee for Research and Exploration to TWH, NSF DEB-0732968 to MCA and the Chicago Botanic Garden for preliminary molecular analyses. French Guiana fieldwork was supported by Investissements d'Avenir grants of the ANR (CEBA: ANR-10-LABX-0025). Dillon Husbands functioned as Guyanese local counterpart and assisted with field collecting, descriptions and specimen processing. Additional field assistance in Guyana was provided by M. Chin, C. Andrew, V. Joseph, P. Joseph, F. Edmund and L. Edmund. Eliane Louisanna provided expert field and lab assistance in French Guiana. Sophie Manzi and Pierre-Arthur Moreau provided technical assistance in France. John Terborgh facilitated field work in Venezuela in 2000. Shawnee Gowan provided lab assistance at Humboldt State. Ron Petersen provided access to specimens at TENN. Two anonymous reviewers provided very useful comments on earlier versions of the manuscript. Research permits were granted by the Guyana Environmental Protection Agency. This paper is No. 198 in the Smithsonian Institution's Biological Diversity of the Guiana Shield Program publication series.

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