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 Dicyme (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, Dicyme, 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). Three additional Craterellus species 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...
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 cantharellloid 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) sequences 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–July 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 co-dominated by ECM *Dicymbe corymbosa* Spruce ex Benth. or co-dominated by ECM *D. corymbosa*, *Dicymbe alsonii* 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 dipterocarpaceae* 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. alsonii*. From French Guiana, collections were made in Jan 2011 from Nouragues field station near 4°44′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 *Neo* 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 Refugio 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 semi-arid 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 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 H2O, 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 = Université 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
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/; Ko¨ljalg 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
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 (Figs. 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; 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,

![Image of basidiomata](image1)

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

![Image of basidiospores](image2)

**Fig. 3.** Basidiospores, basidia and tramal hyphae of *Craterellus olivaceoluteus* (HOLOTYPE; Henkel 9205). Bars = 10 μm.
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 thin; sterigmata (2, 3)4–5–6, (3.7)4.9–5.6 × 1.7–2.5 μm wide at base, 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, devoid of obvious internal contents; wall thin; sterigmata numbers 2–6, cuticular pileipellis with colorless basidiospores, long basidia with variable septation lacking; cells 29.6–101.3 × 4.9–12.4 μm, somewhat inflating. Stipitipellis composed of densely interwoven to subparallel hyphae arranged subanticlinal, with terminal elements often more periclinal, in mass pale brown 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 subanticlinal, 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 hyphal 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 alstonii, Dicymbe jenmani, 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 Dicymbé 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 Dicymbé plot 3, 17 Jul 2009, Henkel 9052 (BRG; HSU); 2.5 km southwest of base camp near Dicymbé 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. alstonii and A. insignis, 6 Jun 2013, Henkel 9757 (BRG; HSU); near Dicymbé 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 Dicymbé plot 3, 20 May 2010, Aime 3980 (BRG; PUL); vicinity of base camp, 1 Jun 2012, Aime 4803 (BRG; PUL); REGION 7 GUUNI-MAZARUNI: Pakaraima Mountains, Upper Mazaruni River Basin, ~ 10 km west of Mt Ayanganna in vicinity of Pegaima savanna in forests dominated by Pakaraimaea dipterocarpaceae and Dicymbe jenmani 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, hynemophore 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 Dicymbé 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 margin and glabrous vs. fuscous brown throughout the 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, inflated pileipellis hyphae with thickened walls (Petersen & Mueller 1992). *Cantharellus lateritus* 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).

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).

![Fig. 4. Basidiomata of *Craterellus cinereofimbriatus* (HOLOTYPE; Henkel 9075). Bar = 10 mm.](image-url)
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 thinly 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 subcuminate 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

Fig. 5. Basidiospores, basidia and tramal hyphae of *Craterellus cinereofimbriatus* (HOLOTYPE; Henkel 9075). Bars = 10 μm.
interwoven to subparallel, anticinal 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 umic 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 SIPARUNE: 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 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 JQ915130; ~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, ~10 km west of Mt Ayanganna in vicinity of Paimaga 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 basidioma 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 pleuris 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 yr.

_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, macro-morphological 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 fulgineous basidioma with fascicles of hairs on the stipe, and much shorter (55–60 vs. 67–104 mm), consistently six-sterigate 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, plant 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)5.4–6.2(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, inamylloid, with many small guttules evenly distributed in epiplasma, 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. Basidia numerous, subcylindrical, densely cyttoplasmic, 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 subpellicles, 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 trama 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...
absent. Stipitpellis a cutis with periclinal terminal elements, these with tannish orange cytoplasmic pigments in KOH; terminal elements and hyphal cells similar to those of the pilepellis. 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 Koate 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. 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.
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

Fig. 7. Basidiospores, basidia and tramal hyphae of *Cantharellus guyanensis* (Henkel 8242). Bars = 10 μm.
species. In addition, molecular phylogenetic analyses including *C. guyanensis* specimens from Guyana, French Guiana, Venezuela and Brazil confirmed their conspecificity (Figs. 1A, B).

While evidence exists for broad geographic distributions of some ECM fungal species in the lowland South American tropics (Wartchow & 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 a further 3000 km southward. *Cantharellus* species known from the lowland South or Guapira in forests dominated by ECM also appears to have broad host-plant range, occurring a further 3000 km southward. *Cantharellus* species known from the lowland South or Guapira in forests dominated by ECM also appears to have broad host-plant range, occurring a further 3000 km southward.

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

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

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

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

**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.
5 (4). Basidioma pale yellow throughout, diminutive; pileus 15–18 mm wide; stipe 15–25 × 2.5 mm; hymenophore smooth; Brazil (Parana). .......... 1

6 (5). Pileus bright red, 30–35 mm wide; stipe pale pinkish orange, light orange, or orangish yellow; basidiospores 3–11 mm; hymenophore light flesh gray, smooth to subrugulose; clamp connections absent; Brazil (Parana). .......... 9 (8).

7 (3). Pileus orangish yellow, 17–52 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

8 (7). Pileus bright orange, 12–25 mm wide; stipe pinkish orange, light orange, or orangish yellow; pileipellis terminal cells thin- or thick-walled; Brazil (Amazonas) .......... Cantharellus amazonensis Wartchow

9 (8). 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.
16. Pileus and stipe dark brown or brownish gray throughout, < 20 mm wide, with scattered or abundant strigose scales. 

17 (16). Pileus dark brown, campanulate to plano-convex, 4–18 mm wide; stipe concolorous, 13–33 × 1–1.5 mm; strigose scales scattered on pileus and stipe; hymenophore brownish gray; basidiospores 8–10 × 6–8 μm; basidia 2–3–4–5-sterigmate; Guyana. 

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. 

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

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. 

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

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

LITERATURE CITED

Alves-Araújo A, Araújo D, Marques J, Melo A, Maciel JR, Uiruapuí J, Pontes T, Lucena MFA, du Bocage AL, Alves M. 2008. Diversity of angiosperms in fragments of Atlantic forest in the state of Pernambuco, northeastern Brazil. Bioremed Biodivers Bioavailab 2:14–26.

Barbosa MRV, Agra MF, Sampaio EVSB, Cunha JP, Andrade LA. 2004. Diversidade florística na Mata do Pau-Ferro, Arecia, Paraíba. In: Pórtio KC, Cabral JJP, Tabarelli M, eds. Brejos de altitude em Pernambuco e Paraíba. História natural, ecologia e conservação. Brasília: Ministério do Meio Ambiente. p 111–122.

Béreau M, Gazel M, Garbaye J. 1997. Les symbiose mycorhizennes des arbres de la forêt tropicale humide de Guyane française. Can J Bot 75:711–716, doi:10.1139/b97-080

Buyck B, Eyssartier G, Kivaisi A. 2000. Addition to the inventory of the genus Cantharellus (Basidiomycota, Cantharellaceae) in Tanzania. Nova Hedwig 71:491–502.

———. Kauff F, Cruaud C, Hofstetter V. 2013. Molecular evidence for novel Cantharellus (Cantharellales, Basidiomycota) from tropical African miombo woodland and a key to all tropical African chanterelles. Fungal Divers 58:282–298, doi:10.1007/s13225-012-0215-4

Corner EFJ, H. 1966. A monograph of cantharelloid fungi. Ann Bot Mem No. 2. Oxford, UK: Oxford Univ. Press. 255 p.

———. 1969. Notes on cantharelloid fungi. Nova Hedwig 18:783–818.

Costa-Lima MLF. 1998. Reserva da biosfera da biosfera da mata Atlântica em Pernambuco: Situação atual, ações e perspectivas. São Paulo: Série Cadernos da Reserva da biosfera. No 12. 43 p.

Dahman M, Danell E, Spatafora JW. 2000. Molecular systematics of Craterellac Cladistic analysis of nuclear LSU rDNA sequence data. Mycol Res 104:388–394, doi:10.1017/S03757990990091380

Edgar R. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res 32:1792–1797, doi:10.1093/nar/gkh340

Eyssartier G. 2001. Vers une monographie du genre Cantharellus Adans. Fr. [doctoral dissertation]. Paris: Museum national d’histoire naturelle.
——, Buyck B. 1999. Contributions a un inventaire mycologique du Madagascar 2: Nouveaux taxa dans le genre *Cantharellus*. Mycotaxon 70:203–211.
——, ———, Halling RE. 2003. Une nouvelle chanterelle du Costa Rica: *Cantharellus atrolilacinus* sp. nov. Cryptogamie Mycol 24:21–25.
——, Stubbe D, Walleyn R, Verbeken A. 2009. New records of *Cantharellus* species (Basidiomycota, Cantharellaceae) from Malaysian dipterocarp rainforest. Fungal Divers 36:57–67.
Feibelman TP, Doudrick RL, Gibula WG, Bennett JW. 1997. Phylogenetic relationships within the *Cantharellaceae* inferred from sequence analysis of the nuclear large subunit rDNA. Mycol Res 101:1425–1430, doi:10.1017/S0953756297004115
Heinemann P. 1958. Champignons recoltes au Congo Belge par Madame Goossens-Fontana III. Cantharellineae. Bull Jardin Bot État, Bruxelles 28:335–438.
Henkel TW, Aime MC, Chin M, Andrew C. 2004. Edible mushrooms from Guyana. Mycologist 18:104–111, doi:10.1017/S0269915X04003027
——, ———, Miller SL, Vilgalys R, Smith ME. 2012. Ectomycorrhizal fungal sporocarp diversity and discovery of new taxa in *Dictyhe* monodominant forests of the Guiana Shield. Biodivers Conserv 21:2195–2220, doi:10.1007/s10531-011-0166-1
——, ———, Mehli HK, Miller SL. 2006. *Cantharellus pleurotoides*, a new and unusual basidiomycete from Guyana. Mycol Res 110:1409–1412, doi:10.1016/j.mycres.2006.09.010
——, ———, 2009. *Craterellus excelsus* sp. nov. from Guyana. Mycotaxon 107:201–208, doi:10.5248/107.201
——, ———, ———, Miller SL, Vilgalys R. 2011. Updated floristic inventory of the angiosperms of the Atlantic forest. Kurtziana 37:113–117.
Miller MA, Holder MT, Vos R, Midford PE, Liebowitz T, Chan L, Hoover P, Warnow T. 2009. The CIPRES Portals. http://www.phylo.org/sub_sections/portal
Montagne C. 1854. Cryptogamia guyanensis. Ann Sci Nat Bot Ser 4:91–144.
Patoüillard NT, Gaillard MA. 1888. Champignons du Venezuela et principalement de la region du Haut-Orenoque, recoltes en 1887 par M.A. Gaillard. Bull Soc Mycol Fr 4:7–46.
Petersen RH. 1975. Notes on clavarioid fungi V. A new species of *Cantharellus*. Beih Nova Hedwig 51:183–189.
——, Mueller GM. 1992. New South American taxa of *Amanita* (Amanitaceae, Agaricales) with a key to the lowland Neotropical taxa. Fungal Biol 116:1263–1274, doi:10.1016/j.fungalbiol.2012.09.004
Warnich F. 2012. *Clavulina amazonensis*, an Amazonian fungus discovered in the Atlantic forest. Kurtziana 37:113–117.
———, Maia LC. 2007. The Neotropical Amanita crebre-sulcata Bas: a new citation from northeast Brazil. Hoehnea 34:131–134, doi:10.1590/S2236-8906200700 200001

———, Santos JC, Fonseca MDP. 2012a. Cantharellus amazonensis, a new species from the Amazon. Myco-sphere 3:414–418, doi:10.5943/mycosphere/3/4/4

———, Buyck B, Maia LC. 2012b. Cantharellus aurantio-conspicuus (Cantharellales), a new species from Pernambuco, Brazil. Nova Hedwig 94:129–137, doi:10.1127/0029-5035/2012/0094-0129

Wilson AW, Aime MC, Dierks J, Mueller GM, Henkel TW. 2012. Cantharellaceae of Guyana I. New species, distribution records and a synopsis of known taxa. Mycologia 104:1466–1477, doi:10.3852/11-412

Wu QX, Mueller GM. 1995. The genus Craterellus (Basid-iomycetes, Aphyllophorales) in Costa Rica and Colombia. Doc Mycol 25:487–496.

Yomyart S, Watling R, Phosri C, Piapukiew J, Sihanonth P. 2012. Two interesting cantharelloids from Nan and Kanchanaburi provinces, Thailand. Mycotaxon 122: 413–420, doi:10.5248/122.413