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New species and distribution records for *Clavulina* (Cantharellales, Basidiomycota) from the Guiana Shield, with a key to the lowland neotropical taxa

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ABSTRACT

Three new and one previously described species of *Clavulina* (Clavulinaceae, Cantharellales, Basidiomycota) are reported from the central Guiana Shield region from tropical rainforests dominated by ectomycorrhizal trees of the leguminous genus *Dicymbe* (Fabaceae subfam. Caesalpinioideae). We provide morphological, DNA sequence, habitat, and fruiting occurrence data for each species. The new species conform to a generic concept of *Clavulina* that includes coralloid, branched basidiomata with amphigenous hymenia, basidia with two or 2–4 incurved sterigmata and postpartal septa present or absent, and smooth, hyaline, guttulate basidiospores. Placements of the new species in *Clavulina* were corroborated with DNA sequence data from the internal transcribed spacer and large subunit of the nuclear ribosomal repeat, and their infrageneric relationships were examined with phylogenetic analyses based on DNA from the region coding for the second largest subunit of DNA-dependent RNA polymerase II (*rpb2*). To facilitate future studies of the genus in the neotropics, a key is provided for all *Clavulina* species described from the lowland neotropics.

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Introduction

Clavulina Schroet. (Clavulinaceae, Cantharellales, Basidiomycota) is a widely distributed genus of ectomycorrhizal (ECM) fungi that form fleshy, predominantly coralloid basidiomata. Approximately 75 species of *Clavulina* have been described from temperate and tropical forests over much of the world (e.g. Corner 1950, 1970; Thind 1961; Petersen 1967, 1983, 1985, 1988a, 1988b; Thind & Sharda 1984; Roberts 1999; Thacker & Henkel 2004; Henkel *et al.* 2005, 2011; Douanla-Meli 2007; Duhem & Buyck 2007; Trappe & Castellano 2007; Uehling *et al.* 2012). The traditional diagnostic characters for *Clavulina* included coralloid, branched basidiomata with amphigenous hymenia, basidia with two incurved sterigmata and postpartal septa, and smooth, hyaline, guttulate basidiospores (Corner 1950, 1970; Petersen 1988a). *Clavulina* has recently been shown to be morphologically diverse with the description of species with unbranched, infundibuliform or resupinate basidiomata and basidia bearing up to six

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Table 1 – Taxa and accession numbers for sequences used in the phylogenetic analyses.

Taxon	Voucher number	RPB2	Location
Tulasnella violea	GEL 2561	DQ898768	Germany?
Cantharellus appalachiensis	GRSM 77088	DQ898748	Tennessee, USA
Craterellus tubaeformis	TM 0268	DQ898749	Ontario, Canada
Hydnum albomagnum	PBM 2512	DQ234553	Massachusetts, USA
Hydnum repandum	DSH 97-320	AY218489	Massachusetts, USA?
Clavulina cerebriformis	MCA4022	JN228233	Guyana
Clavulina sp.	MB 03-034	DQ366286	Massachusetts, USA
Clavulina cf. cristata	MES426	JN228240	Yunnan, China
Clavulina cf. cinerea	MES427	JN228239	Yunnan, China
Clavulina cinerea	DUKE9351	JN228251	North Carolina, USA
Clavulina cristata	DUKE9312	JN228250	North Carolina, USA
Clavulina cinerea	JKU9	JN228242	California, USA
Clavulina cristata	JKU8	JN228241	California, USA
Clavulina monodiminutiva	TH8738	JN228237	Guyana
Clavulina caespitosa	TH8709	JN228234	Guyana
Clavulina humicola	TH8737	JN228244	Guyana
Clavulina tepurumenga	MCA3116	JN228248	Guyana
Clavulina sprucei	TH9122	JN228236	Guyana
Clavulina sprucei	MCA3989	JN228235	Guyana
Clavulina cf. connata	TH9586	JN228247	Guyana
Clavulina nigricans	TH8284	JN228238	Guyana
Clavulina ornatipes	TH9598	JN228243	California, USA
Clavulina cinereoglebosa	TH8561	JN228246	Guyana
Clavulina effusa	TH9193	JN228245	Guyana
Clavulina amazonensis	TH8742	JN228249	Guyana
Clavulina rosiramea	TH8954	JQ677048	Guyana
Clavulina cirrhata	TH8940	JQ677046	Guyana
Clavulina guyanensis	TH9245	JQ677049	Guyana
Clavulina pakaraimensis	TH9194	JQ677047	Guyana

basidiospores (Thacker & Henkel 2004; Henkel *et al.* 2005; Uehling *et al.* 2012). Molecular systematics studies have confirmed the monophyly of *Clavulina* within the Cantharellales, and supported the placement of morphologically diverse taxa in the genus (Thacker & Henkel 2004; Moncalvo *et al.* 2006; Uehling *et al.* 2012). Recent sporocarp collecting efforts and belowground molecular studies suggest that *Clavulina* is most diverse in the tropics (e.g. Tedersoo *et al.* 2003, 2007, 2008; Moyersoen 2006; Peay *et al.* 2010; Smith *et al.* 2011; Henkel *et al.* 2012).

In the central Guiana Shield region of South America some forests are dominated by ECM trees in the genera *Dicymbe* (Fabaceae subfam. Caesalpinioideae), *Aldina* (Fabaceae subfam. Papilionoideae) or *Pakaraimaea* (Dipterocarpaceae subfam. Pakaraimoideae) (Singer *et al.* 1983; Moyersoen 2006; Degagne *et al.* 2009; Smith *et al.* 2011). In the Upper Potaro Basin of Guyana ECM fungi have been collected in *Dicymbe* forests over the past 14 y, and ~20 of the 174 known species belong to *Clavulina* (Henkel *et al.* 2012). As part of our ongoing effort to document the Guyanese *Clavulina* assemblage we here describe three new species and a new distribution record for *Clavulina cirrhata* (Berk.) Corner, a taxon previously known from a single 1856 collection from the northern Brazilian Amazon (Thacker & Henkel 2004; Henkel *et al.* 2005, 2011; Uehling *et al.* 2012). We provide morphological, DNA sequence, habitat, and fruiting occurrence data for each species. The new species conform to an expanded generic concept of *Clavulina* that includes coralloid, branched basidiomata with amphigenous hymenia, basidia with two or 2–4 incurved sterigmata and often with postpartal septa, and smooth, hyaline, guttulate basidiospores. Generic assignments of the new species were independently assessed with BlastN searches of DNA sequence data from the internal transcribed spacer (ITS) and partial large subunit (28S) of the nuclear ribosomal repeat. Infrageneric relationships were examined with phylogenetic analyses of sequence data from the second largest subunit of DNA-dependent RNA polymerase II (*rpb2*). In order to facilitate further studies, a dichotomous key is provided for all *Clavulina* species known from the lowland neotropics, defined as those species where the type locality is between ~20° North and South and below ~300 m elevation. We excluded species associated with higher elevation ECM hosts because these biomes are similar in some aspects to temperate habitats and can harbour many of the same ECM fungal species (Morris *et al.* 2008; Kennedy *et al.* 2011). Finally, we provide a summary discussion of the exceptional diversity of *Clavulina* in the Guiana Shield. The majority of the *Clavulina* species treated in the key are described from Guyana while others have been described from Argentina, Brazil, Panama, Puerto Rico, Surinam, Trinidad, and Venezuela. We thought it pertinent to include them because growing evidence indicates several neotropical species have extensive range distributions (Tedersoo *et al.* 2010; Henkel *et al.* 2011; Uehling *et al.* 2012), a situation likely applicable to other species.

Materials and methods

Collections

Most collections were made during the May–Jul. and Dec.–Jan. rainy seasons of 2000–2003 and 2008–2010 from Guyana's Upper Potaro River Basin, within a 10 km radius of a permanent base camp at 5°18′04.8″ N, 59°54′40.4″ W. Additional collections were made in Jun.–Jul. 2011 from the Upper Demerara River Basin at the Mabura Ecological Reserve within a 5 km radius of a base camp at 5°09′19.0″ N, 58°41′58.9″ W. Basidiomata were collected from forests dominated by the ECM canopy trees *Dicymbe corymbosa* and/or *Dicymbe altsonii*. Macroscopic features of basidiomata were described fresh in the field. Colours were described subjectively and coded according to Kornerup & Wanscher (1978), with colour plates noted in parentheses (e.g. 3C3). Fungi were dried in the field with silica gel.

Micromorphology

Micromorphological features of fresh specimens were examined with an EPOI field microscope with light optics; dried specimens were examined with an Olympus BX51 microscope with light and phase contrast optics. For basidiospores, basidia, sterigmata, and hyphal features, rehydrated fungal tissue was mounted in water, 3 % potassium hydroxide (KOH), or Melzer's solution and at least 20 individual structures were measured. Line drawings were made using tracing paper with digital photomicrographs, and edited with Photoshop CS5 (Adobe, San Jose, CA, USA). Specimens of all four species were deposited in each the following herbaria (Holmgren *et al.* 1990): BRG –

University of Guyana, HSU – Humboldt State University, PUL – Purdue University, and NY – New York Botanical Garden, with the destination of specific numbered collections noted in the 'Specimens Examined' sections for each species.

DNA extraction, polymerase chain reactions (PCR), sequencing, and phylogenetic analyses

DNA extractions were performed on dried basidioma tissue for each species reported here. Tissues were homogenized with sterile forceps or a micropestle, and DNA was extracted with the DNeasy Plant Mini Kit (Qiagen, Valencia, CA, USA). The ITS1-5.8s-ITS2 (ITS) and partial large subunit (28S) of the ribosomal DNA were amplified with the forward primers ITS1F and LROR and the reverse primers ITS4B, LR3, LR5F in various combinations with protocols of Vilgalys & Hester (1990), Gardes & Bruns (1993) and Tedersoo *et al.* (2008). The second largest subunit of DNA-dependant RNA polymerase II (*rpb2*) gene was successfully amplified from *Clavulina* specimens using the protocols of Uehling *et al.* (2012). PCR products were viewed on 1.5 % agarose gels stained with SYBR Green I (Molecular Probes, Eugene, Oregon, USA). Amplicons were cleaned with Exonuclease I and shrimp alkaline phosphatase (Glenn & Schable 2005) and sequenced with Big Dye 3.1 (Applied Biosystems, Foster City, CA, USA) with the same primers used for amplification. Sequencing reactions were cleaned and processed on an ABI 3730xl genetic analyzer (Applied Biosystems, Foster City, CA, USA) at the Duke University Genome Sequencing & Analysis Core Facility. Newly generated sequences were edited in Sequencher v.4.1.4 (Gene Codes Corp., Ann Arbor, MI, USA), and deposited in GenBank. Accession numbers and source data for these and other sequences are given in Table 1.

The ITS and 28S rDNA sequences were initially subjected to BlastN algorithm searches in GenBank to confirm the generic placement of our species as indicated by morphological characters. An *rpb2* dataset was then constructed to assess relationships between Guyanese *Clavulina* taxa and their temperate counterparts; this protein coding region provides better resolution in *Clavulina* than 28S and ITS rDNA under phylogenetic analysis (Uehling *et al.* 2012). We included *rpb2* sequences from each of the four species presented here along with those of 20 other *Clavulina* species available on GenBank. Five closely related non-*Clavulina* cantharelloid taxa were included for rooting purposes (Moncalvo *et al.* 2006; Table 1). DNA sequences were compiled in Mesquite 1.1 (Maddison & Maddison 2006) and aligned with MUSCLE (Edgar 2004). The alignment is available on treebase.org under the following link http://purl.org/phylo/treebase/phylows/study/TB2:S13398. Parsimony analysis was performed with the default settings and parsimony bootstrapping with 1000 replicates in PAUP 4.0a112 (Swofford 2002). Maximum likelihood (ML) analysis was performed with the GTR + I + G model with the software package Garli 0.951 (Zwickl 2006). ML bootstrapping was performed with 1000 replicates using the default settings in Garli 0.951.

Results

The ITS and 28S BlastN searches indicated that each of the four species reported here shared highest sequence identity with species of *Clavulina* on GenBank, thereby corroborating our initial generic assignments based on morphology. The maximum parsimony (MP) analysis was based on 787 bp of *rpb2*, utilized 263 parsimony informative characters, and yielded four most parsimonious trees of 1112 steps. Each of these trees supported the placement of the four species in a monophyletic *Clavulina*, within a broad assemblage of neotropical species. The ML analysis produced a phylogeny with a likelihood score of ln −5410.20416, with similar overall topology to the MP trees (results not shown). One of the four most parsimonious MP trees is illustrated in Fig 1, with MP and ML node support generated from 1000 replicates. Based on this phylogeny, the four *Clavulina* species described here occur in a monophyletic *Clavulina* at various positions within a neotropical assemblage and are not closely related to north-temperate taxa.

Taxonomy

Clavulina rosiramea Uehling, T.W. Henkel et Aime, **sp. nov.** Figs 2, 3
MycoBank 564665

Voucher material

Holotype *Henkel 8954* (Holotype BRG; Isotype HSU)

Description

Basidiomata coralloid, rare, solitary or in pairs on litter mats under *Dicymbe corymbosa*; individual basidiomata 42–90(115) mm tall, monopodial or branching one to three times near apex, 10–15 mm wide across branches; stipe dark orangish-brown (6C8), glabrous, with minute longitudinal striations; hymenium amphigenous, covering upper one-third of branches, initially pale pinkish orange (6C3–6C4) to pale pink (6B3–6B4) when mature, thickening and becoming sharply demarcated from sterile stipe with age, in transverse section 0.3–1.3 mm thick; branch tips sub-acuminate, rounding with hymenial thickening. *Odour* minimal; *taste* not obtained. *Basidiospores* (6.5)7–9(10) × (6)7–8(9) μm (mean Q = 1.12), subglobose to somewhat rounded triangular in adaxial view, tapering evenly towards the hilar appendage, smooth, hyaline to pale cream in water, hyaline in KOH, inamyloid, with one irregularly angular, translucent guttule; wall 1 μm thick; hilar appendage 0.5–0.75(1) μm long. *Basidia* (30)33–45(54) μm long, subcylindric to slightly clavate, tapering downward over lower one-fourth, width 6–8 μm at apex, 5–7 μm centrally, 3–4 μm at base, hyaline with uniform oleiferous content, postpartal septa absent; sterigmata cornute, 3.5–5(6) μm long, two per basidium, consistently with prominent central constriction. *Basidioles* numerous. *Cystidia* absent. *Tramal hyphae* smooth, lacking obvious internal contents, hyaline, uninflated; cells 30–50 μm × 3–10 μm. *Clamp connections* absent.

Etymology

Roseus (Latin adj. A) = pink, ramus (Latin s.m. II) = branching, referring to the pink hymenium and sparsely branched basidiomata characteristic of this species.

Habit, habitat, and distribution

Clavulina rosiramea is rarely encountered late in the May–Jul. rainy season, and fruits solitarily or in pairs on the litter mat of the forest floor under *D. corymbosa*; known only from the type locality in the Upper Potaro River Basin of Guyana.

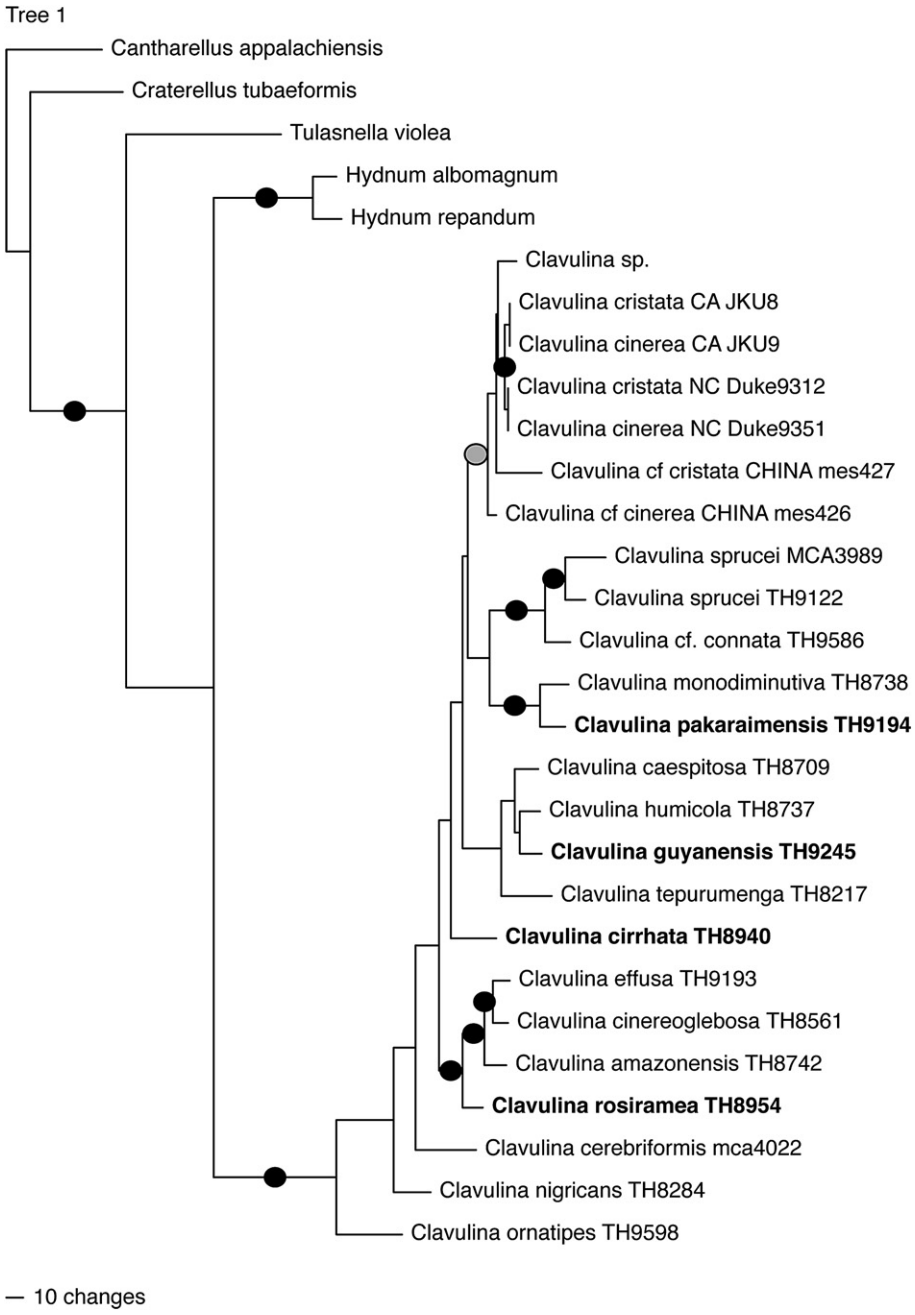

Fig 1 – Rooted MP phylogeny depicting phylogenetic relationships of *Clavulina* species and other Cantharellales taxa based on *rpb2* sequences. *Clavulina* species reported here are shown in bold text. The black nodes indicate bootstrap support greater than 75 for MP and ML; grey nodes indicate support greater than 75 for MP only.

Commentary

Clavulina rosiramea is recognized in the field by its monopodial to sparsely branched basidioma with an orangish-brown stipe contrasting with the pale pink hymenium. These features along with the micromorphology are consistent with placement of the species in *Clavulina*. The *rbp2* phylogenetic analysis indicated placement of *C. rosiramea* in a well-supported subclade with three other *Clavulina* species, in a broader assemblage of neotropical species (Fig 1). The perceived rarity of *C. rosiramea* in Guyana's *Dicymbe* forests was corroborated in a long-term *D. corymbosa* plot study of Henkel *et al.* (2012), with basidiomata occurring in only 2.5 % of 630, 100 m^2 quadrats sampled over 7 y.

Other *Clavulina* species with pale pink hymenia include *Clavulina puiggarii* (Speg.) Corner and *Clavulina castaneipes* (G.F. Atkinson) Corner (Corner 1950). These species have either a whitish or pale pink stipe whereas *C. rosiramea* has an orangish-brown stipe. Another orange-stiped *Clavulina* species known from Guyana, *Clavulina kunmudlutsa* T.W. Henkel & Aime, is easily differentiated from *C. rosiramea* by its much

Fig 2 – Basidiomata of *Clavulina rosiramea* (Holotype; *Henkel* 8954). Bar = 20 mm.

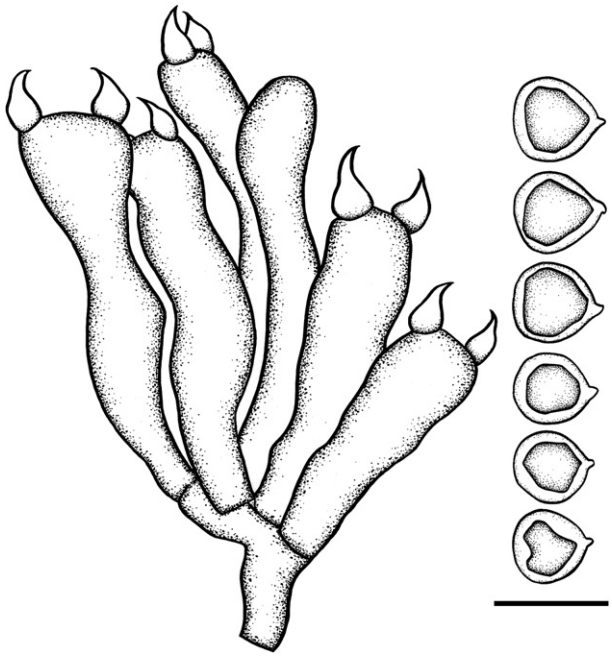

Fig 3 – Basidia and basidiospores of *Clavulina rosiramea* (Holotype; *Henkel* 8954). Bar = 10 μm.

taller (75–160 mm), highly branched basidiomata with a greyish orange mature hymenium (Henkel *et al.* 2011). The Brazilian *Clavulina panurensis* (Berk.) Corner has basidiomata that branch 4–5 times and an ochraceous orange hymenium, in contrast to the minimal branching and pink hymenium of *C. rosiramea* (Corner 1950).

Specimens examined

Guyana: *Region 8 Potaro-Siparuni*: Pakaraima Mountains (Upper Potaro River Basin, within a 4 km radius of base camp at 5°18′04.8″ N, 59°54′40.4″ W), alt. 710–750 m; vicinity of base camp, 18 Jul. 2000, *Henkel 7652* (BRG; HSU); 3 km southeast of base camp in *Dicymbe* plot 1, 18 Jul. 2003, *Aime 3141* (BRG; PUL); 3 km southeast of base camp in *Dicymbe* plot 1, 18 Jul. 2003, *Henkel 8574* (BRG; HSU); ~3 km southwest of base camp in *Dicymbe* plot 3, 20 Jul. 2008, *Henkel 8954* (Holotype: BRG; Isotype: HSU), ITS Genbank JQ677064, 28S Genbank JQ677044, *rpb2* GenBank JQ677048.

Clavulina guyanensis Uehling et T.W. Henkel, **sp. nov.** Figs 4, 5
MycoBank 564684

Voucher material

Holotype *Henkel 9245* (Holotype BRG; Isotypes HSU, NY)

Description

Basidiomata coralloid, solitary or in clustered pairs on litter mat in *Dicymbe* forest; individual basidiomata 34–100 mm tall × 10–32 mm across branches, branching 2–5 times towards apex, polychotomous at the base and irregularly dichotomous towards branch apices; branches round to flattened and canaliculate below branch points, tips acuminate when young, becoming rounded with age and hymenial thickening; stipe 20–45 mm × 2.5–4 mm, finely fibrillose with shallow longitudinal striations visible under hand lens, light brown (6D5–6E5) to vinaceous brown (7F8–8F8) with maturity, often with mycophagy-exposed tannish brown (5B4–5C4) trama; hymenium appearing initially above first branching point and extending below it with maturity and then sharply demarcated from the stipe, amphigenous, greyish brown (10F3–10F4), hispid under hand lens, thickening slightly with age, 0.2–0.5 mm thick in transverse section. *Odour* pleasant, cantharelloid; *taste* nutty and fruity. *Basidiospores* (7)8–9(10) × (6.5)7–9 μm (mean Q = 1.07), subglobose, smooth; hyaline in water, yellowish grey in KOH, inamyloid, with one large oleiferous guttule; wall 1 μm thick; hilar appendage 0.75–1 μm long. *Basidia* (39)48–60(70) μm long, subcylindric to subclavate, 6–8 μm wide at apex, 5–7 μm wide centrally, 3–4 μm wide at base; postpartal septa present in ~60 % of basidia examined, these 12–20 μm below basidial apex, basidia constricted at septa and evacuated and flaccid above, with bluish grey refractive contents in lower half; sterigmata cornute, (4)5–6.5(7) μm long, two per basidium. *Basidioles* numerous. *Cystidia* absent. *Tramal hyphae* smooth, lacking obvious internal contents, hyaline, uninflated; cells 35–40 × 7–12 μm. *Clamp connections* abundant.

Fig 4 – Basidiomata of *Clavulina guyanensis*. (A) Holotype; *Henkel* 9245. (B) Mature basidiomata with mycophagy-damaged stipes (*Henkel* 9257). Bars = 10 mm.

Etymology

Guyanensis (–ensis Latin adj. B) = adjectival suffix indicating origin or place, referring to the currently known distribution of the species in Guyana.

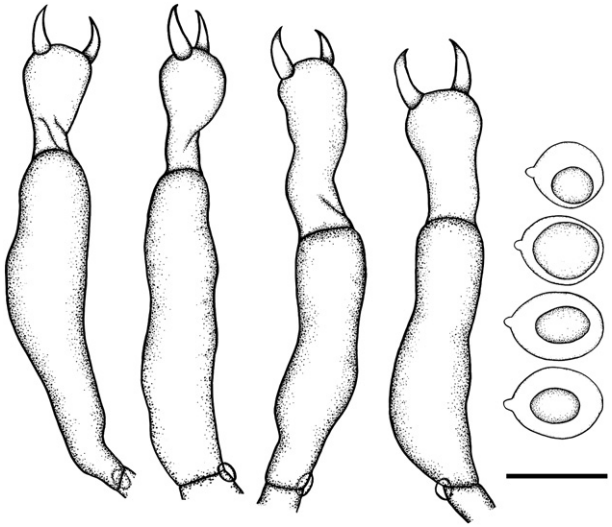

Fig 5 – Basidia and basidiospores of *Clavulina guyanensis* (Holotype; *Henkel* 9245). Bar = 10 μm.

Habit, habitat, and distribution

Clavulina guyanensis is rare and fruits solitarily to scattered on the litter mat under *D. corymbosa* on lateritic soils or under *Dicymbe altsonii* on sand soils; known from type locality in the Upper Potaro River Basin of Guyana and ~100 km eastward into the lowlands near Mabura Hill.

Commentary

Clavulina guyanensis is recognized in the field by its branched basidiomata with a deep vinaceous brown stipe, contrasting greyish brown hymenium, and frequent mycophagy damage revealing the tan brown trama. These features along with the micromorphology are consistent with placement of the species in *Clavulina*. The *rpb2* phylogenetic analysis indicated that *C. guyanensis* occurs within an assemblage of neotropical *Clavulina* species (Fig 1). The perceived rarity of *C. guyanensis* in Guyana's Upper Potaro Basin was corroborated in a long-term *D. corymbosa* plot study of Henkel *et al.* (2012), with basidiomata occurring in only 2.2 % of 630, 100 m^2 quadrats sampled over 7 y.

Among sympatric *Clavulina* species from Guyana with branching basidiomata with grey colours, *Clavulina tepurumenga* T.W. Henkel & Aime differs from *C. guyanensis* in being regularly caespitose, with usually taller basidiomata that can be broader across branches (40–166 mm *vs.* 80–100 mm) and in lacking vinaceous brown tones in the stipe (Henkel *et al.* 2011). *Clavulina pakaraimensis* sp. nov. (described below)

has shorter basidiomata (21–70 mm *vs*. 80–100 mm) that are densely caespitose with a flesh brown stipe rather than vinaceous brown as in *C. guyanensis*. *Clavulina guyanensis* is also macroscopically similar to *Clavulina urnigerobasidiata* R.H. Petersen from New Zealand, but differs in its lack of cystidia, which are copiously present in the latter (Petersen 1988a). *Clavulina mutabilis* R.H. Petersen from North Carolina, USA, has a branched basidioma with vinaceous grey hymenium but differs from *C. guyanensis* in its white stipe and shorter basidia (30–50 *vs*. 48–60 μm; Petersen 1967).

Specimens examined

Guyana: *Region 8 Potaro-Siparuni* (Pakaraima Mountains, Upper Potaro River Basin, within a 10 km radius of base camp at 5°18′04.8″ N, 59°54′40.4″ W), alt. 710–750 m; 2 km southeast of base camp in vicinity of *D. corymbosa* plot 2 on lateritic soils, 1 Jun. 2010, *Henkel* 9245 (Holotype: BRG; Isotype: HSU, NY), ITS GenBank JQ677056, *rpb2* GenBank JQ677049; 1.5 km east of Ayanganna airstrip, 7 Jun. 2010, *Henkel* 9257 (BRG; HSU), ITS GenBank JQ677057. *Region 10 Upper Demerara-Berbice* (Mabura Ecological Reserve, base camp located at 5°09′19.0″ N; 58°41′58.9″ W), alt. ~100 m; 1 km northwest of Mabura field station, under *D. altsonii* on white sand soils, 24 May 2011, *Uehling* 19 (BRG; HSU), ITS GenBank JQ677058; 100 m northwest of Mabura field station in *D. altsonii* monodominant stand 1 on brown sand soils, 28 May 2011, *Uehling* 28 (BRG; HSU), ITS GenBank JQ677055.

Clavulina pakaraimensis Uehling, T.W. Henkel et Aime, **sp. nov.**
Figs 6, 7
MycoBank 564685

Voucher Material

Holotype *Henkel* 9194 (Holotype BRG; Isotypes HSU, NY).

Description

Basidiomata coralloid, gregarious in caespitose clusters on litter mat in *Dicymbe* forest; clusters 21–70 mm tall × 10–32 mm wide across branches; individual basidiomata 17–70 mm × 7–20 mm across branches, branching 3–6 times towards apex, dichotomous at oblique angles basally and polychotomous towards apices, branches flattening, thickening, and twisting with age, branch tips sharply acuminate when young to rounded with age; stipe 8–20 × 2–5 mm, flesh brown (6B3–6C3) to pinkish grey (9D4–9D5) with age, glabrous; hymenium amphigenous, initiating above first branching point and extending below it with maturity, dissipating towards stipe without sharp demarcation, greyish flesh (9D2), hispid under hand lens, thickening slightly with age, 0.4–0.6 mm thick in transverse section. *Odour* pleasant, cantharelloid; *taste* nutty and fruity. *Basidiospores* (6.5)7–8(9) × (5.5)6–7(7.5) μm (mean Q = 1.21), subglobose, smooth, hyaline in water, pale cream in KOH, inamyloid, with one large guttule; wall 1 μm thick; hilar appendage 0.5–1.0 μm long. *Basidia* (30)37–56(62) μm long, subcylindric, tapering slightly downward over lower half, width 5–7 μm at apex, 5–6 μm centrally, 4–5 μm at base, guttulate-cytoplasmic; post-partal septa present in ~30 % of basidia examined, these 7–15 μm below basidial apex, with basidium constricted at septum, evacuated and collapsed in upper half, guttulate-cytoplasmic in lower half; sterigmata cornute, (4)4.5–6(7) μm long, 2–3(4) per basidium. *Basidioles* numerous, with dense granular cytoplasm near apex. *Cystidia* absent. *Tramal hyphae* smooth, lacking obvious internal contents, hyaline, uninflated; cells 17–37 × 2.5–7.5 μm. *Clamp connections* abundant.

Etymology

Pakaraimensis (–ensis Latin adj. B) = adjectival suffix indicating origin or place, referring to the species' type locality in the Pakaraima Mountains of Guyana.

Habit, habitat, and distribution

Clavulina pakaraimensis fruits frequently in gregarious caespitose clusters on the forest floor litter mat under *D. corymbosa*; known only from type locality in the Upper Potaro River Basin of Guyana.

Commentary

Clavulina pakaraimensis is recognized in the field by its frequently occurring, gregarious, highly branched, caespitose, uniformly flesh grey, medium-sized basidiomata in *D. corymbosa* forest. These features along with the micromorphology are consistent with placement of the species in *Clavulina*. The *rpb2* phylogenetic analysis indicated that *C. pakaraimensis*

Fig 6 – Basidiomata of *Clavulina pakaramensis* (Holotype; *Henkel* 9194). Bar = 20 mm.

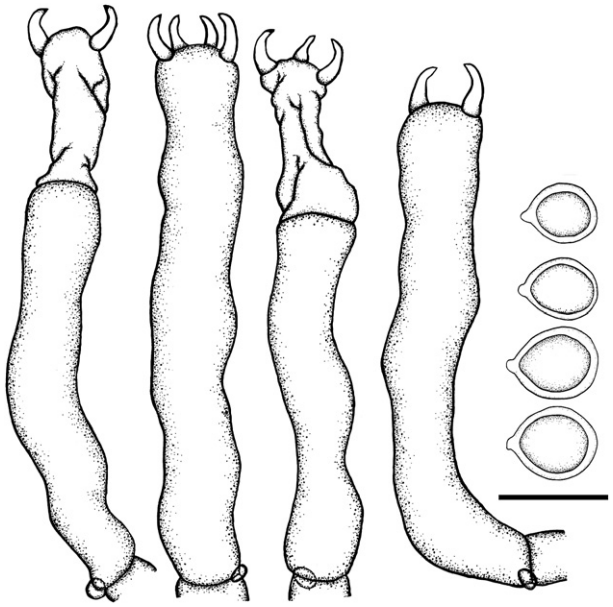

Fig 7 – Basidia and basidiospores of *Clavulina pakaraimensis* (Holotype; *Henkel* 9194). Bar = 10 μm.

Fig 8 – Basidiomata of *Clavulina cirrhata* (Berk.) Corner (*Henkel* 8940). Bar = 20 mm.

occurs in a well-supported subclade with one other *Clavulina* species, in a broader assemblage of neotropical species (Fig 1). The relatively high frequency of *C. pakaraimensis* in Guyana's *Dicymbe* forests was indicated by its status as one of the most commonly fruiting *Clavulina* species in a long-term *D. corymbosa* plot study of Henkel *et al.* (2012), with basidiomata occurring in 12.4 % of 630, 100 m^2 quadrats sampled over 7 y.

The overall pinkish brown to flesh grey colouration of *C. pakaraimensis* is unique among described *Clavulina* species. The sympatric *C. tepurumenga* has grey, highly branched, caespitose basidiomata, but is differentiated from *C. pakaraimensis* by its regularly taller basidiomata (40–166 *vs.* 17–70 mm), greyish brown *vs.* flesh brown to pinkish grey stipe, purplish grey *vs.* pinkish grey hymenium, and bisterigmate *vs.* 2–4 sterigmate basidia (Henkel *et al.* 2011). *Clavulina ornatipes* (Peck) Corner is dark fuscous brown and has shorter basidia in contrast to *C. pakaraimensis* (20–36 *vs.* 37–56 μm respectively; Corner 1950). *Clavulina complanata* Corner from Australia has salmon pink basidiomata but is distinguished from *C. pakaraimensis* by its lack of any brown tones in the stipe and shorter basidiospores (5.2–7 *vs.* 7–8 μm respectively; Corner 1950). The north-temperate *Clavulina cinerea* (Bull.) J. Schröt. has off-white to grey, profusely branched basidiomata but has a cream-coloured stipe and lacks any pinkish tones (Corner 1950).

Specimens examined

Guyana: *Region 8 Potaro-Siparuni* (Pakaraima Mountains, Upper Potaro River Basin, within a 4 km radius of base camp at 5°18′04.8″ N, 59°54′40.4″ W), alt. 710–750 m; 2–4 km southwest of base camp, 8 Jun. 2001, *Henkel* 8254 (BRG; HSU), ITS GenBank JQ677052; 2–4 km southwest of base camp, 27 Jun. 2006, *Aime* 3118 (BRG; PUL), ITS-28S GenBank JQ677051; 1–2 km southeast of base camp, 16 May 2010, *Henkel* 9194 (Holotype: BRG; Isotype: HSU, NY), ITS-28S GenBank JQ677051, *rpb2* GenBank JQ677047; 1.5 km west of base camp, 23 May 2010, *Henkel* 9212 (BRG; HSU), ITS GenBank JQ677053; 2 km southeast of base camp, 1 Jun. 2010, *Henkel* 9244 (BRG; HSU), ITS GenBank JQ677054.

Clavulina cirrhata (Berk.) Corner, A monograph of *Clavaria* and allied genera. 311. 1950 Figs 8, 9

Synonym: *Clavaria cirrhata* Berk., Hook. J. Bot. 8:275. (1856).

Description

Basidiomata coralloid, in Guyana in troops of caespitose clusters on litter mat in *D. corymbosa* forest; clusters 70–140 mm tall, 50–75 mm across branches; individual basidiomata 43–140 mm tall × 24–58 mm across branches, branching 3–6 times dichotomously to more polychotomously upward, length between branch points decreasing markedly upward towards apices, branches flattening and twisting

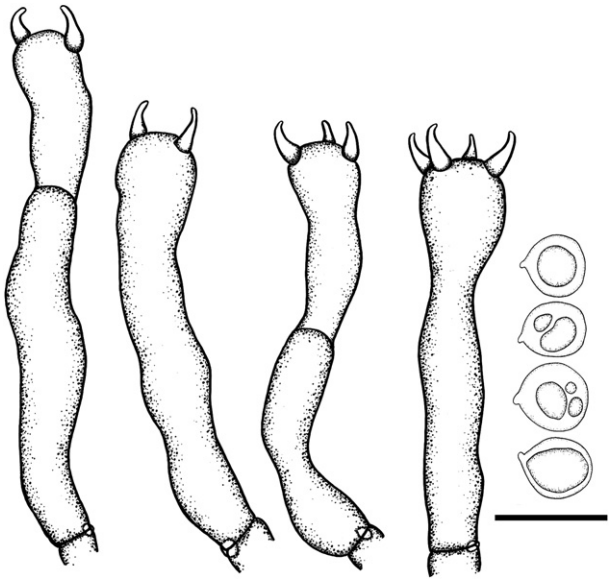

Fig 9 – Basidia and basidiospores of *Clavulina cirrhata* (*Henkel* 8940). Bar = 10 μm.

progressively with age, canaliculate beneath branch points, with many short, abortive acuminate side branches along main axes; apices crenate, with acuminate tips of irregular lengths, these rounding with hymenial thickening; stipe 15–28 × 5–8 mm, pale cream (3A2–3A3), with shallow longitudinal striations and irregular pits; hymenium extending downward immediately below first branching point and there faintly to strongly demarcated from stipe, nearly amphigenous but with more prominent thickening on downward-facing branch sides and there 0.5–1 mm thick, hispid under hand lens, creamy white (3A2–3A3) to pale orangish cream (4A3–4A4, 4B4) with age. *Odour* mildly fragrant, floral; *taste* sweet, somewhat nutty to farinaceous. *Basidiospores* (5.5) 6–7.5(8) × 5.5–6.5(7.5) μm (mean Q = 1.13), nearly globose, slightly flattened on distal adaxial side, smooth, hyaline in water, bluish grey in KOH, inamyloid, with one to several large guttules; wall 1 μm thick; hilar appendage 0.5–1.0 μm long. *Basidia* (30)35–53(61) μm long, subclavate, widening over apical one-fourth and there somewhat bulbous, otherwise tapering evenly towards base, width 6–8 μm at apex 5–7 μm centrally, 3.5–5 μm at base, with finely granulose contents with finely granulose contents, post-partal septum present in ~50 % of basidia examined, these 10–20 μm below basidial apex, basidium slightly constricted immediately above post-partal septum, somewhat evacuated and flaccid above septum, cytoplasmic below; sterigmata cornute, (3.5)4–5(6) μm long, 2–3(4) per basidium. *Basidioles* numerous. *Cystidia* absent. *Tramal hyphae* smooth, lacking obvious internal contents, hyaline, uninflated; cells 30–50 μm long × 2.5–10 μm wide. *Clamp connections* abundant.

Habit, habitat, and distribution

In Guyana *C. cirrhata* fruits frequently from the humus/mineral soil interface of the forest floor, in troops of caespitose clusters covering several square metres in *D. corymbosa* and *D. altsonii* forest; known from the Upper Potaro River Basin and Mabura Hill area of Guyana, and the northcentral Brazilian Amazon.

Commentary

Clavulina cirrhata is recognized in the field in Guyana by its large, highly branching, and twisting, white basidiomata developing pale orange hymenia and occurrence in large troops of caespitose clusters in the immediate vicinity of *Dicymbe* trees. The *rpb2* phylogenetic analysis indicated that *C. cirrhata* occurs in an unresolved position within an assemblage of neotropical species (Fig 1). In a long-term *D. corymbosa* plot study of Henkel *et al.* (2012) basidiomata of *C. cirrhata* occurred in 6.8 % of 630, 100 m^2 quadrats sampled over 7 y.

Berkeley (1856) originally described the species as *Clavaria cirrhata* from a single collection from the Brazilian Amazon, and with subsequent combination into *Clavulina* by Corner (1950). The Guyana material is consistent macro- and micromorphologically with published descriptions of *C. cirrhata*. Salient corroborating features include the large, pale cream basidiomata with a dichotomous to polychotomous, flattening and twisting branching pattern, accentuated development of orangish cream hymenia on downward-facing branch sides, and the basidiospore, basidium, and tramal hyphae morphology and dimensions. The discovery of *C. cirrhata* in Guyana constitutes a range extension for the species of nearly 1000 km northeastward from the Brazilian Amazon into the Guiana Shield. Similar regional distributions have recently been demonstrated for *Clavulina amazonensis* Corner and *Clavulina sprucei* (Berk.) Corner (Henkel *et al.* 2011).

The north-temperate *C. cristata* (Holmsk.) J. Schröt and *C. rugosa* (Bull.) J. Schröt. resemble *C. cirrhata* in having large, nearly white, much-branched basidiomata. However, both lack the pale orangish cream mature hymenium of *C. cirrhata* and have longer basidiospores (7–11 or 9–14 μm, respectively, *vs.* 6–7.5 μm). The Nepalese *Clavulina alta* Balfour-Browne is another large white *Clavulina* species superficially resembling *C. cirrhata*, but lacks a pale orangish cream mature hymenium and has decidedly longer basidiospores (9.5–14 *vs.* 6–7.5 μm; Balfour-Browne 1968).

Specimens examined

Guyana: *Region 8 Potaro-Siparuni* (Pakaraima Mountains, Upper Potaro River Basin, within a 10 km radius of base camp at 5°18′04.8″ N, 59°54′40.4″ W), alt. 710–750 m; 2 km south of base camp, 14 Jul. 2008, *Henkel 8940* (BRG; HSU; NY), ITS GenBank JQ677059, *rpb2* Genbank JQ677046; 1 km west of base camp, 7 Jul. 2009, *Henkel 9002* (BRG; HSU), ITS GenBank JQ677060; 2.5 km southwest of base camp, 21 May 2010, *Henkel 9207* (BRG; HSU), ITS GenBank JQ677062; 1.5 km east of Ayanganna airstrip, 7 Jun. 2010, *Henkel 9266* (BRG; HSU), ITS GenBank JQ677061. *Region 10 Upper Demerara-Berbice* (Mabura Ecological Reserve, field station located at 5°09′19.0″ N, 58°41′58.9″ W), alt. ~100 m; 4.5 km northwest of field station, 3 Jun. 2011, *Uehling 33* (BRG; HSU), ITS GenBank JQ677063.

A key to *Clavulina* species known from the lowland neotropics

1. Basidiomata resupinate (crust-like) or effuso-coralloid (with crust-like and upright branching portions)……2

Basidiomata coralloid or infundibuliform (funnel shaped)……4

2. (1) Basidiomata off-white to yellowish cream and entirely resupinate, hymenium cerebriform, undulating and somewhat pitted, individual basidiomata small (0.3–0.5 mm in diameter), Guyana…… ***Clavulina cerebriformis*** Uehling, T. W. Henkel & Aime

Basidiomata grey with fleshy-orange tones, entirely resupinate or effuso-coralloid……3

3. (2) Basidiomata entirely resupinate, somewhat erumpent but never erect-coralloid, fusing and patch-like directly on humic debris on tree trunks, Guyana…… ***Clavulina cinereoglebosa*** Uehling, T.W. Henkel & Aime

Basidiomata effuso-coralloid, with fertile hymenium on both resupinate and upright branching portions, in troops on organic matter on ground, Guyana…… ***Clavulina effusa*** Uehling, Henkel & Aime

4. (1) Basidiomata infundibuliform (funnel shaped), caespitose, and large (90–190 × 18–80 mm), stipe orange brown, hymenium off-white to cream, Guyana, Ecuador…… ***Clavulina craterelloides*** Thacker & T. W. Henkel

Basidiomata coralloid, either unbranched or branched……5

5. (4) Basidiomata unbranched……6

Basidiomata branched……11

6. (5) Basidiomata tall (75–200 mm), densely caespitose, apices sharply acuminate, stipe golden brown, hymenium greyish cream to greyish cream with age, Guyana……
……*Clavulina caespitosa* T. W. Henkel, Meszaros & Aime

Basidiomata shorter (under 100 mm tall), fruiting either singly, in clusters, or in troops, hymenium and stipe colours not as above……7

7. (6) Stipe dark purplish brown and hymenium bluish grey……8

Stipe orange or brown but not purplish; hymenium pinkish grey, light orange brown, or drab brown but not bluish grey-
……9

8. (7) Basidiomata 56–100 mm tall, fruiting from the mineral soil singly or rarely in small clusters, clamp connections frequent, Guyana…… *Clavulina dicymbetorum* T. W. Henkel, Meszaros & Aime

Basidiomata 17–55 mm tall, fruiting on humic mats in medium to large troops, clamp connections absent, Guyana…… *Clavulina griseohumicola* T. W. Henkel, Meszaros & Aime

9. (7) Basidiomata mostly greater than 30 mm tall (23–70 mm), lacking clamp connections, basidiomata with a brown stipe and light orange brown hymenium, Guyana……
…… *Clavulina humicola* T. W. Henkel, Meszaros & Aime

Basidiomata mostly less than 30 mm tall (8–35), clamp connections occasional, with buffy brown or orangish tan base and drab brown or pinkish grey hymenium……10

10. (9) Basidiomata with buffy brown base and drab brown hymenium, 10–20 mm tall, fruiting singly or in clusters of 2–3, clamp connections frequent, Puerto Rico……
Clavulina pilosa Corner

Basidiomata with dull orangish tan base and pinkish grey hymenium, 8–35 mm tall, always fruiting in large troops, clamp connections occasional, Guyana……
…… *Clavulina monodimunitiva* T. W. Henkel, Meszaros & Aime

11. (5) Basidiomata light coloured; with orange, white or cream stipe and pale pink, white, cream or pale yellow hymenium……
……12

Basidiomata dark coloured; with brown black, grey, or maroon base, and brown or grey hymenium……20

12. (11) Basidiomata with orange tones; orange stipe and pale pink or orange hymenium……13

Basidiomata entirely lacking orange tones; with pale pink, white, or cream stipe and hymenium……16

13. (12) Basidiomata with brownish orange stipe and light pink hymenium, sparsely branched, Guyana
……*Clavulina rosiramea*

Basidiomata with orange stipe and orange hymenium, variously branching……14

14. (13) Basidiomata with greyish orange hymenium and contrasting white branch tips……
……*Clavulina amazonensis* Corner

Basidiomata with orange hymenium and concolourous branch tips……15

15. (14) Basidiomata 75–120 (160) mm tall, basidia 47–69(77) μm long, basidiomata with dull orange to brownish orange stipe and light pinkish orange hymenium maturing to pale greyish orange, branches cylindrical, Guyana……
……*Clavulina kunmudlutsa* T. W. Henkel & Aime

Basidiomata 50 mm tall, basidia 36–50 μm long, basidiomata with pale ochraceous orange stipe and hymenium, branches stout and flattened, Brazil, Venezuela……*Clavulina panurensis* (Berk.) Corner

16. (12) Basidiomata with white stipe and pink hymenium, up to 45 mm tall, sparsely branching, Argentina, Brazil, Trinidad……
……*Clavulina puiggarii* (Speg.) Corner

Basidiomata with hymenium that is white, cream, pale orange or pale yellow but not pink, stipe white or cream, variously branching……
……17

17. (16) Basidiomata less than 50 mm tall, with white stipe and white hymenium……18

Basidiomata more than 50 mm tall, stipe cream-coloured, hymenium with pale orange or pale yellow tones, 70–140 mm tall, basidia 2–3(4) sterigmate, Brazil, Guyana……*Clavulina cirrhata* (Berk.) Corner

18. (17) Basidiomata fruiting directly from mineral soil, lacking basal mycelial patch, Brazil, Guyana……
……*Clavulina connata* (Berk.) Corner

Basidiomata fruiting in elevated positions on litter, arising from a distinct basal mycelial patch ……
……19

19. (18) Basidiomata less than 15 mm tall, basidiospores 9.5–11 × 5–6 μm, basal disc membranous, hymenium unilateral, Brazil……*Clavulina delicia* (Berk.) Corner

Basidiomata usually greater than 15 mm tall (9–48 mm), basidiospores 8–10 × 7–8 μm, basal disc byssoid (thread-like), hymenium amphigenous, Brazil and Guyana……*Clavulina sprucei* (Berk.) Corner

20. (11) Basidiomata extremely large (120–190 mm tall), with black stipe, dark grey hymenium becoming ash grey to black upon maturity, in dense caespitose clusters, Guyana…
…… *Clavulina nigricans* Thacker & T. W. Henkel

Basidiomata smaller (usually less than 100 mm tall), with brown, maroon, or grey stipe and brown or grey hymenium, fruiting variously……
……21

21. (20) Basidiomata with golden brown stipe, apparently without grey tones in the hymenium, up to 25 mm tall, Surinam……*Clavulina chondroides* (Berk.) Corner

Basidiomata with greyish brown, vinaceous brown, or pinkish brown stipe, hymenium some shade of grey, >25 mm tall..
……22

22. (21) Basidiomata with distinct vinaceous brown stipe, brownish grey hymenium, fruiting singly or in pairs, 42–100 mm tall, Guyana……
……*Clavulina guyanensis*

Basidiomata pinkish or greyish brown but not vinaceous brown, hymenium pinkish or purplish grey, usually fruiting in troops or caespitose clusters……23

23. (22) Basidiomata with pinkish brown stipe and light pinkish grey hymenium, 21–70 mm tall, fruiting in small troops, Guyana……*Clavulina pakaraimensis*

Basidiomata with greyish brown stipe and lilac to purple grey hymenium, 40–166 mm tall, fruiting in caespitose clusters……*Clavulina tepurumenga* T. W. Henkel & Aime

Discussion

The work of Corner and others in the palaeotropics along with the recent descriptions of numerous new *Clavulina* species from Guyana have altered the old notion that the genus is primarily temperate (Corner 1950, 1970; Thind 1961; Petersen 1967, 1983, 1985, 1988a, 1988b; Thind & Sharda 1984; Roberts 1999; Thacker & Henkel 2004; Henkel *et al.* 2005, 2011; Douanla-Meli 2007; Duhem & Buyck 2007; Trappe & Castellano 2007; Uehling *et al.* 2012). Currently ~75 *Clavulina* species have been described worldwide, about 40 of these appear to have tropical distributions, with nearly half from the central Guiana Shield region. While several morphospecies from Guyana remain to be described, the four *Clavulina* species treated here bring the number of named species from Guyana to 18. Of these 15 are currently only known formally from Guyana, and three were previously described from elsewhere in the South American tropics. In addition to the singularly high number of sympatric species, the Guiana Shield is the only region thus far known that has *Clavulina* species exhibiting basidioma macromorphologies ranging from the typical branched coralloid to monopodial, infundibuliform, effuso-coralloid, or resupinate (Corner 1950; Petersen 1988a; Uehling *et al.* 2012). Recent belowground molecular studies in Guyana have also documented a number of *Clavulina* species on ECM roots as yet undiscovered as sporocarps (Smith *et al.* 2011, in press). Based on these combined reports we estimate that there are at least 40 species of *Clavulina* in Guyana.

Some *Clavulina* species occurring in Guyana have much broader regional distributions (Henkel *et al.* 2011). *Clavulina amazonensis* and *Clavulina sprucei* are known from ~1000 km away in Brazil (Corner 1950; Henkel *et al.* 2011; Petersen 1988b), as is *Clavulina cirrhata* reported here. *Clavulina rosiramea* has an ITS sequence 97 % similar to that of an ECM root tip from a *Neea* host plant in Ecuador (ITS GenBank FN557546; Tedersoo *et al.* 2010) suggesting a broad trans-Amazonian distribution for the species. *Clavulina craterelloides* was originally described from Guyana (Thacker & Henkel 2004) but was recently reported from Cuyabeno, Ecuador, indicating a similarly large range for the species (Læssøe & Petersen 2008; D.J. Lodge personal communication).

Given the emerging picture of *Clavulina* prevalence across the South American tropics, as well as the numerous species known from Australasia, one may hypothesize a Gondwanan origin for *Clavulina* (Petersen 1988a; Smith *et al.* 2011). More representative sampling of all regions of the distribution will be necessary to provide sufficient evidence to address such a hypothesis. Analyses comparing the currently accessible neotropical and temperate collections suggest that, at the least, *Clavulina* may be an ancestrally tropical lineage. Kennedy *et al.* (2012) recently analyzed a *Clavulina* ITS dataset including sequences from voucher specimens, root tips, and soil samples from tropical and temperate locations. Their phylogenetic analysis identified a primarily temperate monophyletic *Clavulina* clade that exhibited a speciation rate nearly 2.6 times higher than the tropical lineages distributed across the rest of the cladogram. Such results argue for further studies of the genus in a historical biogeographic context, which in turn may enhance understanding of global evolutionary patterns in ECM fungi.

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