Mycologia, 96(3), 2004, pp. 650–657.

NEW SPECIES OF *CLAVULINA* FROM GUYANA

Jason R. Thacker[1]

Department of Biology, Duke University, Durham, North Carolina 27708

Terry W. Henkel

Department of Biological Sciences, Humboldt State University, Arcata, California 95512

Abstract: Two new species of *Clavulina* are described from rainforests dominated by ectomycorrhizal *Dicymbe* spp. (Caesalpiniaceae) in the Pakaraima Mountains of Guyana. *Clavulina nigricans*, sp. nov. is unique for *Clavulina* in having 4–6 spores per basidium. *Clavulina craterelloides*, sp. nov. has an infundibuliform basidiome, previously unknown in the otherwise coralloid genus *Clavulina*. Macromorphological, micromorphological and habitat data are provided for each taxon, as well as justification for their placement in *Clavulina* based on morphological and molecular features.

Key words: basidiomycetes, coral fungi, Guyana, molecular phylogenetics, neotropics

INTRODUCTION

Clavulina Schröt. (Cantharellales, Basidiomycota) is a genus characterized by branched basidiomata. *Clavulina* traditionally is delimited from other coral fungi by the presence of two-spored basidia with cornute sterigmata (Corner 1950, 1970, Petersen 1988a). Transverse basidial septa formed after basidiospore release also were noted as diagnostic for *Clavulina* by Corner (1950, 1970). Conversely, Petersen (1988) noted that such postpartal septa may be localized on a basidiome or absent entirely and did not include this character in his species descriptions. *Clavulina* currently contains 45 species worldwide, primarily in the tropics (Corner 1950, 1970, Petersen 1983, 1985, 1988, Roberts 1999, Thind and Sharda 1984). Recent molecular studies have shown *Clavulina* to be phylogenetically allied with the Cantharellales (see Hibbett and Thorn 2001).

Coralloid basidiomata and bisterigmate basidia, for the most part, have been good diagnostic features for *Clavulina*. There are records of *Clavulina* spp. with more than two sterigmata per basidium infrequently encountered in otherwise bisterigmate collections (Corner 1950, Petersen 1988). In contrast, *Clavulina amazonensis* Corner regularly possessed 2–4 spores per basidium and was assigned to *Clavulina* due to the presence of incurved sterigmata (Corner 1970, Petersen 1988b). *C. amazonensis* lacked many other features regularly seen in *Clavulina,* such as postpartal basidial septa, inflated hyphae and elongate basidia, and its placement in *Clavulina* has not been verified by molecular phylogenetics. These problems aside, all other species of *Clavulina* recorded to date have coralloid basidiomata and bisterigmate basidia.

Here we present evidence that coralloid basidiomata and bisterigmate basidia are not fully diagnostic for the genus *Clavulina*. Two morphologically distinct species, *C. nigricans* and *C. craterelloides,* are described as new. These fungi are part of an extensive assemblage of *Clavulina* spp. found in ectomycorrhizal *Dicymbe* (Caesalpiniaceae) forests of Guyana (Henkel et al 2002).

MATERIALS AND METHODS

Collections.—Collections were made during May–June rainy seasons of 1998–1999, from the upper Ireng River Basin along Guyana's western border with Brazil in the south-central Pakaraima Mountains (5°05′N, 59°58′W; see Henkel et al 2002). Collections were made during the May–June rainy seasons of 2000–2002 from the upper Potaro River Basin approximately 40 km north of the Ireng site (Henkel 2003). Macroscopic features were described fresh in the field. Colors were described subjectively and coded according to Kornerup and Wanscher (1978). Macrochemical tests were performed according to the methods of Singer (1986). Fungi were field-dried with silica gel (Miller et al 2002).

Micromorphological features from dried specimens were examined with an Olympus BX51 microscope with light and phase-contrast optics. For basidiospores, basidia, cystidia and other structures at least 20 individuals were measured. Rehydrated fungal tissue was mounted separately in H_2O, 3% KOH, and Melzer's solution. Number of sterigmata was assessed with scanning electron microscopy performed on a Phillips XL30 ESEM TMP microscope (FEI Co., Portland, Oregon) after sputter coating with a Hummer V (Anatech, Springfield, Virginia).

Specimens were deposited in these herbaria (Holmgren et al 1990): BRG—University of Guyana; and HSU—Humboldt State University.

Accepted for publication October 6, 2003.

[1] Corresponding author. E-mail: jrt1@duke.edu

DNA sequencing.—From two collections each of *C. nigricans* and *C. craterelloides* (including the holotypes), a small piece of fresh basidiome tissue was placed in 500 mL 2× CTAB buffer. DNA was extracted using a chloroform:isoamyl protocol (Zolan and Pukkila 1986). A portion of the nuclear gene coding for the large ribosomal subunit (nuc LSU rDNA) was amplified using the primer pair LROR and LR7 and sequenced with primers LROR, LR3R, LR5 and LR16 (http://www.biology.duke.edu/fungi/mycolab/primers.htm). PCR products were purified with Qiagen QIAquick PCR Purification kit (Qiagen Inc., Chatsworth, California) and sequenced with BigDye Terminators using a 3700 ABI automated DNA sequencer (Applied Biosystems, Foster City, California). Sequences were assembled and edited with Sequencer version 4.1 (Gene Codes, Ann Arbor, Michigan).

Phylogenetic analyses.—The two sequences for each species were found to be identical. The holotype sequence for *C. craterelloides* and *C. nigricans* was deposited in GenBank under accession AY391718 and AY391719, respectively. Sequences initially were assessed using BLAST (Altschul et al 1990) and found to have affinities with cantharelloid fungi. To further assess the phylogenetic affinities of the Guyana taxa, their sequences were aligned with nuc LSU rDNA sequences from these taxa in GenBank: *Auricularia polytricha* (Mont.) Sacc. AF261554, *Cantharellus cibarius* Fr. AY041156, *Cantharellus cinnabarinus* (Schwein.) Schwein. AY041168, *Clavulina cinerea* (Bull.) Schröt. AJ406433, *Clavulina cristata* (Holmsk.) Schröt. AF261553, *Craterellus tubaeformis* (Bull.) Quél. AF287851, *Craterellus cornucopioides* (L.) Pers. AJ279572, *Gomphus novae-zelandiae* Segedin AF261547, *Hydnum rufescens* Pers. AJ406427, *Hydnum repandum* L. AF347095, *Sistotrema brinkmannii* (Bres.) J. Erikss. AJ406430, *Sistotrema niveocremeum* (Höhn. & Litsch.) Donk AJ406429, *Multiclavula corynoides* (Pk.) Petersen U66440, *Multiclavula mucida* (Fr.) Petersen AF287875, *Multiclavula vernalis* (Schwein.) Petersen U66439, and *Ramaria stricta* (Pers.) Quél. AF287887. *Auricularia polytricha, G. novae-zelandiae,* and *R. stricta* were chosen as outgroups based on their phylogenetic placement and short branch lengths relative to the cantharelloid fungi (Hibbett et al 2000). An initial sequence alignment was produced with ClustalW (Thompson et al 1994) and manually optimized in Seaview (Galtier et al 1996). The final alignment was 1200 characters long. Three regions comprising 25, 101 and 133 base pairs were alignable only between *C. cibarius* and *C. cinnabarinus* and were excluded from the analysis. Three regions of 9, 10 and 21 base pairs alignable only between *C. tubaeformis* and *C. cornucopioides* were excluded from analysis. One region of 20 bases alignable only between *Auricularia polytricha, G. novae-zelandiae* and *R. stricta* was excluded from analysis. A total of 42 base pairs of ambiguously aligned regions were excluded from the analysis. A total of 361 unalignable characters were excluded from the analysis, and phylogenetic analysis was performed on the remaining 839 characters.

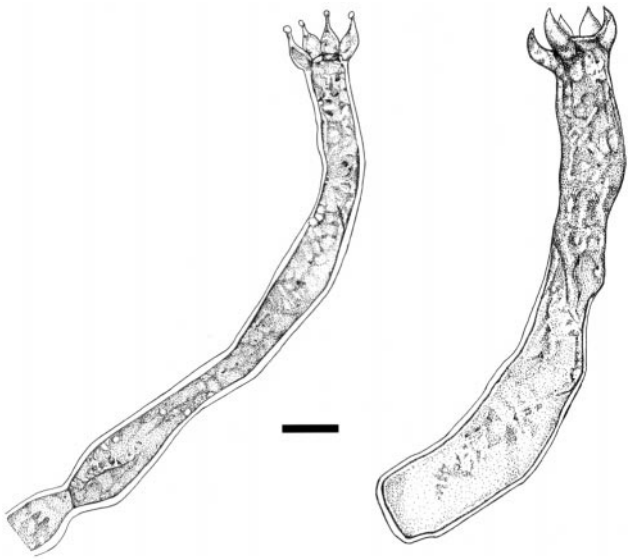
Phylogenetic analyses were performed using maximum-likelihood (ML) and Bayesian metropolis-coupled Markov Chain Monte Carlo (B-MC3) inference. The defaults of each program were used unless otherwise noted. ModelTest 3.06 (Posada and Crandall 1998) selected the TN93+G model with the likelihood ratio test; this model was used for the ML analyses. A corresponding six-parameter gamma model was used in B-MC3 analysis. A heuristic search for the most likely tree and a ML bootstrap analysis were performed in PAUP*4b10 (Swofford 1998). Support for internode placement was estimated using B-MC3 posterior probabilities with a six-parameter gamma model from MrBayes version 3.0 beta 4 (Huelsenbeck and Ronquist 2001), with the first 10 000 generations discarded as the burn-in phase. Trees generated by all three analyses were identical topologically. A Nexus file containing the aligned data and the executable commands for all analyses has been deposited in TreeBase (http://www.treebase.org/treebase/).

FIG. 1. Basidiome of *Clavulina nigricans* (holotype, *Henkel 8284*), 1×.

TAXONOMY

Clavulina nigricans Thacker et T.W. Henkel, sp. nov. FIGS. 1–4

Latin diagnosis: Caespites *basidiomatum* 120–190 mm alti, 90–135 mm lati; *rametti singuli* 60–130 mm × 14–45 mm lati, 4–6-plo dichotomi, fasciculis irregularibus coronatis ad apices ramorum terminalium 3–5 mm × 0.5–0.7 mm, apicibus acuminatis; tota basidioma primo ad basim nigrum, supra pallide griseum ad griseum, apicem versus pallescens, ad apices paene album. *Hymenium* maturum pallide ciner-



FIGS. 2–3. Microscopic features of *Clavulina nigricans* (holotype, *Henkel 8284*). Scale bars = 10 μm. 2. 4 and 5-sterigmate basidia.

ascens et tunc hispidum, demum totum nigricans sursum e basi. *Contextus* concolor omnino cavus, 0.3–1.5 mm crassus. *Odor* foetidus; *sapor* farinosus et leniter acer. *Reactiones chemicae*: contextus basalis $FeSO_4$ non reagens. *Basidiosporae* 6–8 × 5–6 μm (median Q = 1.23), subglobosae laeves, in aqua pallide brunneae, in KOH brunneo-griseae, multiguttulatae inamyloideae, pariete 0.4 μm crasso, apiculo 0.2–0.5 μm longo. *Basidia* 80–110 μm longa, ad apicem 5–7 μm, ad basin 3–4 μm lata, cylindrica ad subclavata, guttulis multis et contentis granularibus cinerascentibus; *sterigmata* 5–6.5 μm longa, 1.5–2.5 μm lata cornuta, 4–5 rarius 6 in quoque basidio; *basidiola* multa. *Hyphae tramales non inflatae* 2–3 μm latae laeves hyalinae, nonnullae pigmenta interna brunneo-grisea exhibentes, intertextae; *hyphae tramales inflatae* usque ad 15 μm latae laeves hyalinae. *Fibulae* abundantes.

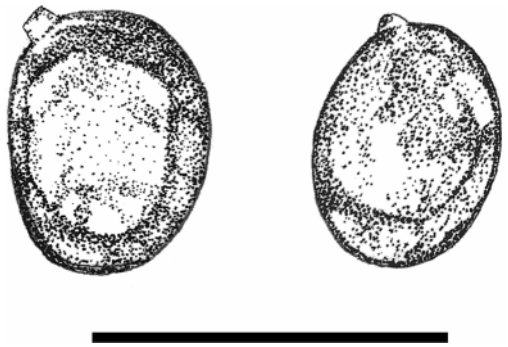


FIG. 3. (continued) Basidiospores.

Basidiomata in dense clusters of basally fused ramets (FIG. 1); entire clusters 120–190 mm tall, 90–135 mm wide; *individual ramets* 60–130 mm × 14–45 mm wide, dichotomously branching 4–6 times; base (below first branching point) 22–45 mm × 3–8 mm, these bases frequently anastomosing to form a semicohesive basal unit; irregularly coronate clusters at apices of terminal branches 3–5 mm × 0.5–0.7 mm; tips acuminate; entire basidiome at first black at the base, light to medium gray above (18D1–18F1), paler toward the apical portion (17B1–17B2 KW), nearly white at the tips. *Hymenium* ripening light gray

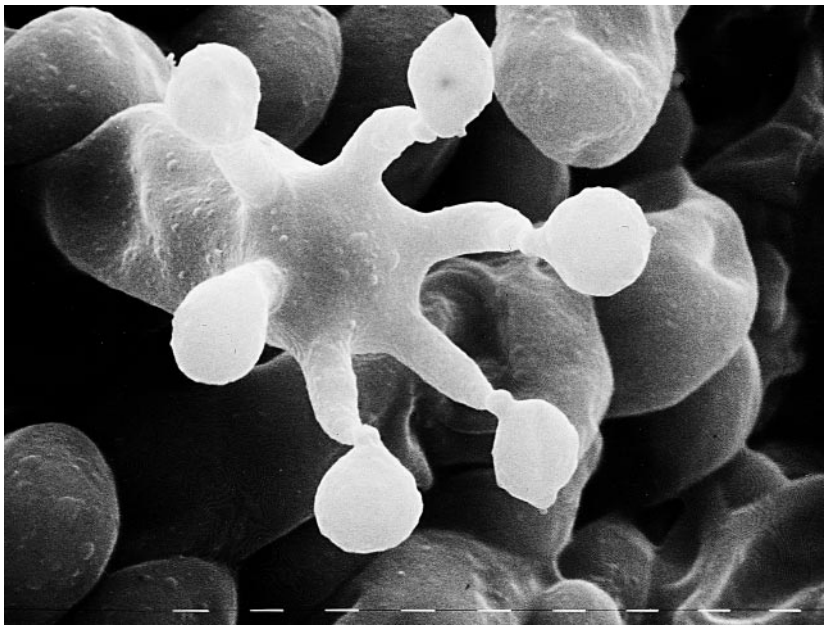


FIG. 4. Scanning electron micrograph of a six-sterigmate basidium with six immature basidiospores, *Clavulina nigricans* (holotype, *Henkel 8284*). Each alternating white scale bar = 1 μm.

and then hispid, eventually entirely black. *Context* concolorous, hollow throughout, 0.3–1.5 mm thick. *Odor* fetid; *taste* mealy and slightly acrid. *Macrochemical reactions:* $FeSO_4$ on basal context nil, KOH and NH_4OH darkening context. *Spore deposit* not obtained.

Basidiospores 6–8 × 5–6 μm (mean Q = 1.23), subglobose, smooth, pale brown in H_2O, brownish-gray in KOH, with numerous opalescent guttules, inamyloid; wall 0.4 μm thick; apiculus 0.2–0.5 μm long (FIG. 3). *Basidia* 80–110 μm long, width at apex 5–7 μm, at base 3–4 μm, cylindrical to subclavate, tapering evenly toward base, with numerous guttules and grayish granular contents; postpartal septa not observed (FIG. 2); *sterigmata* 5–6.5 μm long, 1.5–2.5 μm wide at base, cornute, 4–5(–6) per basidium; *basidioles* numerous. *Uninflated tramal hyphae* 2–3 μm wide, smooth, some with internal, brownish-gray pigments, interwoven. *Inflated tramal hyphae* up to 15 μm wide, smooth, hyaline. *Clamp connections* abundant.

Etymology. Nigricans = ''becoming black'' in Latin.

Habit, habitat and distribution. Occurring singly or scattered on root mat and mineral earth in rainforests dominated by *Dicymbe corymbosa* Spruce ex Benth. and *Dicymbe altsonii* Sandwith; collected during the rainy season (May–July). Known from the type locality in the upper Potaro Basin, as well as the upper Ireng Basin, Guyana.

Specimens examined. GUYANA. REGION 8, POTARO-SIPARUNI: Pakaraima Mountains. Upper Potaro River Basin, 4 km southeast of base camp near confluence with Whitewater Creek, 750 m elevation, under *D. corymbosa,* 14 VI 2001, *Henkel 8284* (HOLOTYPE: BRG; ISOTYPE: HSU); Upper Ireng River Basin, foothills leading to Mount Kukuinang, 1 km west of confluence of Ireng and Sukabi Rivers, 900 m elevation, under *D. altsonii,* 28 V 1998, *Henkel 6754* (BRG, HSU); Upper Ireng River Basin, 1 km west of Kurutuik Falls on adjacent ridges, 750 m elevation, under *D. corymbosa,* 4 VI 1998, *Henkel 6847* (BRG, HSU); Upper Potaro River Basin, 10 km east of Mount Ayanganna, east bank of Potaro River 1 km upstream from confluence with Whitewater Creek, 720 m elevation, under *D. corymbosa,* 6 VI 2000, *Henkel 7440* (BRG, HSU); Pakaraima Mountains, Upper Potaro River Basin, 2 km east of base camp near mouth of Whitewater Creek, 780 m elevation. under *D. corymbosa,* 13 V 2001, *Henkel 8125* (BRG, HSU).

Commentary. *Clavulina nigricans* is a distinctive coral fungus easily recognized in the field by its large, highly branched, gray to black basidiomata and fetid odor. In addition, *C. nigricans* appears restricted to groves of *Dicymbe* trees, which occur in a distinctive, patch-like mosaic in the upper Ireng and upper Potaro River watersheds. This fungus macroscopically does not resemble any currently described *Clavulina* species.

The hymenium of *Clavulina nigricans* is initially gray and later blackens during active spore production. The only other *Clavulina* species described as turning completely black at maturity is *Clavulina geoglossoides* Corner, which is unbranched to sparingly branched, bisterigmate, with an initially ivory-colored hymenium (Petersen 1988a). Other *Clavulina* species, such as *Clavulina cristata, Clavulina cinerea* and *Clavulina rugosa,* have been reported to turn a dark gray with age but not black. These species are usually cream-colored or light gray at maturity, unlike *C. nigricans.*

Clavulina nigricans is the only known species of *Clavulina* with four or more sterigmata per basidium. A maximum of six have been observed (FIG. 4). Other phenotypic features associated with *Clavulina,* such as inflated, clamped tramal hyphae and cornute sterigmata, were observed in *C. nigricans.*

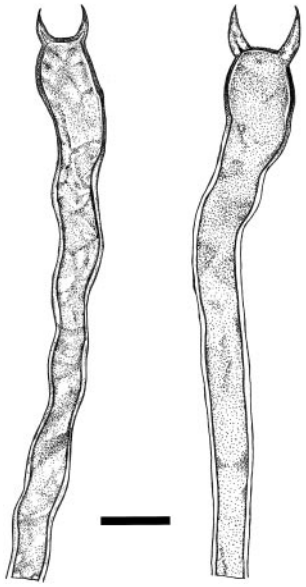
Clavulina craterelloides Thacker et T.W. Henkel, sp. nov. FIGS. 5–7

Latin diagnosis: *Basidiomata* in caespitibus 90–190 mm altis, 18–80 mm latis; *rametti singuli* 80–190 mm alti, 8–22 mm lati; primordia praesentia in formis corporum filiformi-acuminatorum circa basin caespitum; rametti juvenes acuminati clavatique ad apicem rotundantes, apice maturo rumpenti formantique marginem lobatum; ramettus maturus profunde infundibuliformis et cavus in centro, ad basin 5–12 mm latus, ad apicem 17–70 mm latus, parte sterili aurantiaco-brunnea, margine lobato; carne cartilaginea et ad marginem saepe findenti. *Hymenium* maturescens spissescensque modice in areolis irregularibus ad continuis in dimidio superiore colori cinereo-carneo. Superficies interior basidiomatum sterilis, cum exteriore sterili concolor, hispida hygrophana; *contextus* concolor. *Odor* lenis; *sapor* leniter amarus. *Sporae in cumulo* albae. *Reactiones chemicae*: contextus basalis $FeSO_4$ non reagens. *Basidiosporae* (6.5) 7.5–8 × (5.5) 6–7 (7.5) μm (median Q = 1.16), subglobosae ad late ellipsoideae laeves hyalinae inamyloideae, guttulis aliquot indistinctis; pariete 0.5 μm crasso, apiculo 0.5 μm longo. *Basidia* (60) 67–87 (90) μm longa, ad apicem (5) 7.4–8 μm, ad basin 2.7–4.3 μm lata, cylindrica ad subclavata, gloeopora. *Sterigmata* 5–5.5 μm longa, ad basin 2 μm lata subcornuta ad cornuta, 2 in quoque basidio. *Hyphae tramales non inflatae* 2–3 μm latae laeves hyalinae intertextae, saepe gloeoporae, pariete 0.5 μm lato. *Hyphae tramales inflatae* usque ad 15 μm latae laeves hyalinae. *Fibulae* infrequentes in hyphis tramalibus.

Basidiomata in caespitose clusters 90–190 × 18–80 mm (FIG. 5). *Individual ramets* 80–190 × 8–22 mm (centrally); primordia present as filiform-acuminate bodies around base of caespitose clusters; young ramets acuminate and clavate, progressively rounding at apex, with apex rupturing with maturity to form a lobate margin; mature ramet deeply infundibuliform and centrally hollow, apex 17–70 mm across, base 5–

FIG. 5. Basidiomata of *Clavulina craterelloides* (holotype, *Henkel 8234*), 1×.

12 mm wide, non-fertile portion orangish-brown (6D8–6E8), margin lobate and splitting; flesh cartilaginous. *Hymenium* ripening and thickening somewhat in irregular to continuous patches over upper half, becoming grayish flesh (6B3–6B4). Interior basidiome surface sterile and concolorous with infertile exterior, hispid, hygrophanous; *context* concolorous. *Basal mycelium* sparse, cream-colored; subtended by brown ectomycorrhizae. *Odor* mild; *taste* mildly sour.



FIGS. 6–7. Microscopic features of *Clavulina craterelloides* (holotype, *Henkel 8234*). Scale bars = 10 μm. 6. Bisterigmate basidia.

Spore deposit white. Edible when cooked. *Macrochemical reactions*: $FeSO_4$ on basal context nil.

Basidiospores (6.5) 7.5–8 × (5.5) 6–7 (7.5) μm (mean Q = 1.16), subglobose to broadly ellipsoid, smooth, hyaline, inamyloid, with several ill-defined guttules; spore wall 0.5 μm thick; apiculus 0.5 μm long (FIG. 7). *Basidia* (FIG. 8) (60) 67–87 (90) μm long, (5) 7.4–8 μm wide at apex, 2.7–4.3 μm wide at base, cylindrical to subclavate, tapering evenly toward base, slightly curving, gloeoporous; post-partal septa not observed (FIG. 6). *Sterigmata* 5–5.5 μm long, 2 μm wide at base, subcornute to cornute, 2 (or rarely 3) per basidium. *Uninflated tramal hyphae* 2–3 μm wide, smooth, hyaline, interwoven, often gloeoporous; wall 0.5 μm wide. *Inflated tramal hyphae* up to 15 μm wide, smooth, hyaline. *Clamp connections* infrequently observed.

Etymology. The infundibuliform stature of this fungus is suggestive of the genus *Craterellus*.

Habit, habitat and distribution. Occurring as scat-

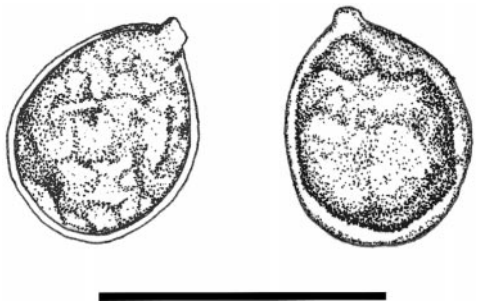


FIG. 7. (continued) Basidiospores.

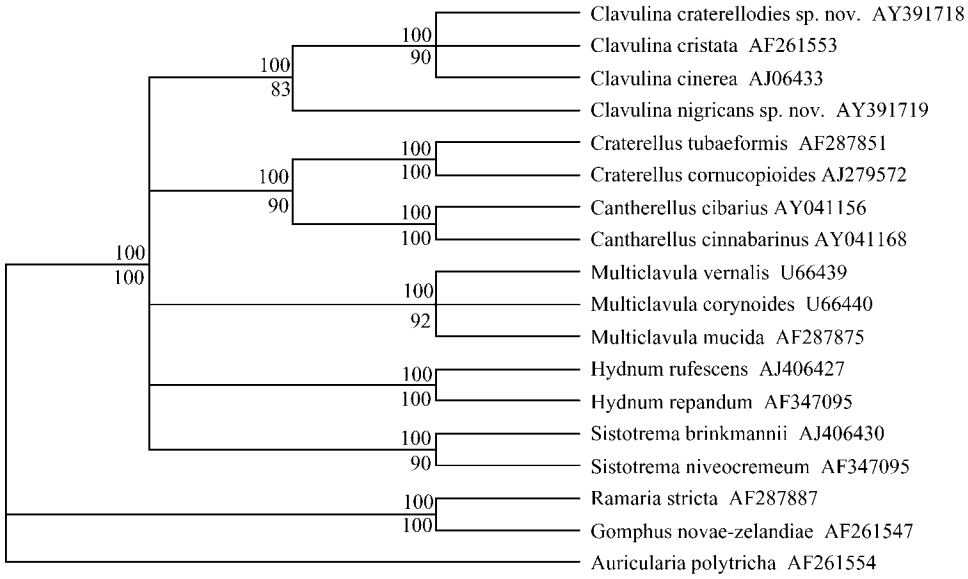


FIG. 8. A cladogram showing the position of *Clavulina craterelloides* sp. nov. and *Clavulina nigricans* sp. nov. within the Cantharellales based on an alignment of nuclear large-subunit rDNA sequences. The topology was rooted with *Auricularia polytricha* and includes outgroups *Ramaria stricta* and *Gomphus novae-zelandiae* Bayesian support values are shown above and maximum-likelihood bootstrapping values below internodes. Polytomies are shown where internodes did not receive either 95% Bayesian posterior probability or a maximum-likelihood bootstrap value of ≥70.

tered caespitose clusters on mineral earth in forests dominated by *D. corymbosa* and *D. altsonii*; infrequently occurring in much higher densities locally; collected during the May–July rainy season. Known from the type locality in the upper Potaro Basin and adjacent upper Ireng Basin, Guyana.

Specimens examined. GUYANA. REGION 8, POTARO-SIPARUNI: Pakaraima Mountains. Upper Potaro River Basin, 3 km southwest of base camp on Potaro River, 1 km upstream from confluence with Whitewater Creek, 750 m elevation, under *D. corymbosa,* 2 VI 2001, *Henkel 8234* (HOLOTYPE: BRG; ISOTYPE: HSU); upper Potaro River Basin, vicinity of base camp 1 km upstream from confluence with Whitewater Creek, 720 m elevation, under *D. corymbosa,* 2 VII 2002, *Henkel 8520* (BRG, HSU).

Commentary. Clavulina craterelloides is recognized easily in the field by the large, rich orange-brown, infundibuliform, caespitose basidiomata restricted to groves of *Dicymbe* trees. There are no records of other *Clavulina* species with an infundibuliform shape and smooth hymenophore, features otherwise indicative of *Craterellus*. While the type species for *Craterellus, C. cornucopioides,* is bisterigmate, most other species of *Craterellus* are not (Corner 1966). The two cornute sterigmata (or rarely three) per basidium and inflated hyphae present in *C. craterelloides* are indicative of *Clavulina*. In addition, basidiome development in *C. craterelloides* is more suggestive of *Clavulina* than *Craterellus*. Whereas *Craterellus* basidomata are infundibuliform with incurved margins from early development (Corner 1966), *C. craterelloides* is coralloid with an unruptured, acuminate apex when young, expanding and rupturing in age to become infundibuliform.

PHYLOGENETIC ANALYSES AND DISCUSSION

FIGURE 8 shows the results of the phylogenetic analyses. All supported internodes received both a ML bootstrap value ≥70 and B-MC3 posterior probability ≥95%. If no internode received support from either ML bootstrapping or B-MC3 analysis, the topology at this node is shown as a polytomy. Despite the unusual morphological features of *C. nigricans* and *C. craterelloides,* both ML bootstrapping and B-MC3 phylogenetic analysis of nuclear LSU sequences provided clear support for a "*Clavulina*" clade containing *C. nigricans, C. craterelloides, C. cristata* and *C. cinerea* (FIG. 8). The genera *Craterellus, Hydnum, Multiclavula* and *Sistotrema* also received high bootstrap and posterior-probability support values. Relationships among the cantharelloid genera were not resolved in this analysis.

A clade with *C. cinerea, C. craterelloides* and *C. cristata* also received high support in both ML and B-MC3 bootstrapping analysis, showing *C. nigricans* to be clearly basal to these three taxa. A case could be made that *C. nigricans* should be placed in its own genus, sister to *Clavulina*. However, the basal position of *C. nigricans* likely could be an artifact of insufficient taxon sampling. The authors therefore have taken the more conservative view of placing *C. nigricans* in *Clavulina*.

With the discovery of *C. nigricans* and *C. craterelloides,* there are no inviolate phenotypic characters

delimiting *Clavulina*. The presence of four-, five- and even six-spored basidia in *C. nigricans* rendered bisterigmate basidia as no longer diagnostic for *Clavulina* (Corner 1950). Postpartal basidial septa, already questioned by Petersen (1988) as diagnostic for *Clavulina,* were not observed in either *C. nigricans* or *C. craterelloides*. The cornute sterigmata present in most *Clavulina* species are also found in *Craterellus* (Corner 1966). The lack of consistent, definitive morphological features to describe *Clavulina* contrasts with the molecular studies that suggested that species of *Clavulina,* including these newly described species from Guyana, form a monophyletic clade within the Cantharellales (this study, Pine et al 1999, Hibbett et al 2000).

As the neotropical macromycota increasingly is explored, it is evident that many taxa depart from traditional morphology-based generic concepts (Henkel et al 2000, Miller et al 2001, Miller et al 2002). In such cases, molecular tools are useful for resolving the taxonomic affinities of these fungi.

ACKNOWLEDGMENTS

This research was made possible by grants from the National Geographic Society's Committee for Research and Exploration, the Smithsonian Institution's Biological Diversity of the Guianas Program and the A.W. Mellon Foundation to T.W. Henkel, NSF Grant DEB9708035 to R. Vilgalys and NSF Grant DBI-0098534 to the Duke SEM laboratory. The authors wish to thank M. Catherine Aime for field observations, François Lutzoni for advice on phylogenetic tree reconstruction, Rytas Vilgalys for early review of the manuscript, Cheryl Sinkiewicz for line drawings, Mark Garland for latin diagnoses, Megan Saunders for aid in digital imaging and Leslie Eibest for aid in SEM microscopy. Field assistance was provided in Guyana by Mimi Chin, Christopher Andrew, Leonard Williams and Benny Cheong. Research permits were granted by the Guyana Environmental Protection Agency and the Ministry for Amerindian Affairs. This paper is No. 76 in the Smithsonian Institution's Biological Diversity of the Guianas Program publication series.

LITERATURE CITED

Altschul SF, Gish W, Miller W, Myers EW, Lipman DJ. 1990. Basic local alignment search tool. J Mol Biol 215(3): 403–10.

Corner EJH. 1950. A monograph of *Clavaria* and allied genera. Oxford University Press. London: Oxford University Press. 701 pp.

———. 1966. A monograph of cantharelloid fungi. Oxford University Press. London: Oxford University Press. 255 p.

———. 1970. Supplement to "A monograph of *Clavaria* and allied genera." Beih Nova Hedwigia 33:1–299.

Galtier N, Gouy M, Gautier C. 1996. SeaView and Phylo_win, two graphic tools for sequence alignment and molecular phylogeny. Comput Applic Biosci 12:543–548.

Henkel TW. 2003. Monodominance in the ectomycorrhizal *Dicymbe corymbosa* (Caesalpiniaceae) from Guyana. J Trop Ecol 19(4):417–437.

Henkel TW, Terborgh JT, Vilgalys R. 2002. Ectomycorrhizal fungi and their leguminous hosts in the Pakaraima Mountains of Guyana. Mycol Res 106(5):515–531.

Henkel TW, Aime MC, Miller SL. 2000. Systematics of pleurotoid Russulaceae from Guyana and Japan, with notes on their ectomycorrhizal status. Mycologia 92(6):1119–1132.

Hibbett DS, Thorn RG. 2001. Basidiomycota:Homobasidiomycetes. In: McLaughlin DJ, McLaughlin EG, Lemke PA, eds. The Mycota. Vol. VII. Systematics and evolution. Berlin: Springer Verlag.

Hibbett DS, Gilbert LB, Donoghue MJ. 2000. Evolutionary instability of ectomycorrhizal symbioses in basidiomycetes. Nature 407:506–508.

Holmgren PK, Holmgren NH, Barnett LC. 1990. Index herbariorum. Part I. The herbaria of the world. New York: New York Botantical Garden. 693 p.

Huelsenbeck JP, Ronquist F. 2001. MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17(8): 754–755.

Kornerup A, Wanscher JH. 1978. Methuen handbook of color. London: Eyre Methuen. 252 p.

Miller OK, Henkel TW, James TY, Miller SL. 2001. *Pseudotulostoma,* a remarkable new volvate genus in the Elaphomycetaceae from Guyana. Mycol Res 105(10):1268–1272.

Miller SL, Aime MC, Henkel TW. 2002. The Russulaceae of the Pakaraima Mountains of Guyana. I. New species of pleurotoid *Lactarius*. Mycologia 94:545–553.

Petersen RH. 1983. Notes on clavarioid fungi XVIII. A preliminary outline of *Clavulina* in Southeastern Australia. Nova Hedwigia 37:19–35.

———. 1985. Notes on clavarioid fungi. XX. New taxa and distributional records in *Clavulina* and *Ramaria*. Mycologia 77(6):903–919.

———. 1988a. The clavarioid fungi of New Zealand. Wellington: DSIR Science Information Publishing Centre, Department of Scientific and Industrial Research. 170 p.

———. 1988b. Notes on clavarioid fungi. XXII. Three interesting South American collections. Mycologia 80: 571–576.

Pine EM, Hibbett DS, Donoghue MJ. 1999. Phylogenetic relationships of cantharelloid and clavarioid Homobasidiomycetes based on mitochondrial and nuclear rDNA sequences. Mycologia 91(6):944–963.

Posada D, Crandall KA. 1998. MODELTEST: testing the model of DNA substitution. Bioinformatics 14(9):817–818.

Roberts P. 1999. Clavarioid fungi from Korup National Park, Cameroon. Kew Bull 54:517–539.

Swofford DL. 1998. PAUP*: Phylogenetic Analysis Using Parsimony (*and other methods). Version 4.0b10. Sunderland, Massachusetts: Sinauer.

Thompson JD, Higgins DG, Gibson TJ. 1994. Clustal W: improving the sensitivity of progressive multiple sequence

alignment through sequence weighting, positions-specific gap penalties and weight matrix choice. Nucleic Acids Res 22:4673–4680.

Thind KS, Sharda RM. 1984. Three new species of clavarioid fungi from Himalayas. Indian Phytopath 37:234–240.

Vilgalys R. 2002. Conserved primer sequences for PCR amplification and sequencing from nuclear ribosomal RNA. ⟨http://www.biology.duke.edu/fungi/mycolab/primers.htm⟩. Accessed 4 Nov 2002.

Zolan ME, Pukkila PJ. 1986. Inheritance of DNA methylation in *Coprinus cinereus*. Mol Cell Biol 6(1):195–200.