Neocampanella, a new corticioid fungal genus, and a note on *Dendrothele bispora*

Karen K. Nakasone, David S. Hibbett, and Greta Goranova

Abstract: The new genus *Neocampanella* (Agaricales, Agaricomycetes, Basidiomycota) is established for *Dentocorticium blastanos* Boidin & Gilles, a crustose species, and the new combination, ***Neocampanella blastanos***, is proposed. Morphological and molecular studies support the recognition of the new genus and its close ties to *Campanella*, a pleurotoid agaric. The recently described *Brunneocorticium* is a monotypic, corticioid genus closely related to *Campanella* also. *Brunneocorticium pyriforme* S.H. Wu is conspecific with *Dendrothele bispora* Burds. & Nakasone, and the new combination, ***Brunneocorticium bisporum***, is proposed.

Key words: Dendrothele, dendrohyphidia, Marasmiaceae, sterile white basidiomycete, *Tetrapyrgos.*

Résumé : Les auteurs proposent le nouveau genre ***Neocampanella*** (Agaricales, Agaromycetes, Basidiomycetes, Basidiomycota) établi pour le *Dentocorticium blastanos* Boidin & Gilles, une espèce résupinée ainsi que la nouvelle combinaison, ***Neocampanella blastanos***. Les études morphologiques et moléculaires supportent la délimitation du nouveau genre, ainsi que ses étroites relations avec *Campanella*, un agaric pleurotoïde. Le genre *Brunneocorticium* récemment décrit constitue une entité monotypique corticoïde également apparentée au *Neocampanella*. Le ***Brunneocorticium pyriforme*** S.H. Wu est conspécifique au *Dendrothele bispora* Burds. & Nakasone pour lequel l'on propose la nouvelle combinaison *B. bisporum.*

Mots-clés : Dendrothele, dendrophidia, Marasmiaceae, basidiomycète blanc stériles, *Tetrapyrgos.*

[Traduit par la Rédaction]

Introduction

Corticioid basidiomycetes have simple, reduced fruiting bodies that often appear as thin, crustose areas on bark and woody substrates. This simple morphology belies their boundless variability at the microscopic level. Originally assumed to be closely related, molecular studies show that corticioid species are distributed throughout the Agaricomycetes, formerly the Hymenomycetes or Homobasidiomycetes (Larsson et al. 2004; Binder et al. 2005; Larsson 2007*b*). Many genera of corticioid fungi are defined by just a few morphological traits, but molecular techniques and analyses have repeatedly demonstrated that this simplistic taxonomic approach is woefully inadequate and often misleading. For example, familiar and easily recognized corticioid genera such as *Hyphoderma* (Larsson 2007*a*), *Phanerochaete* (De Koker et al. 2003), *Gloeocystidiellum* (Larsson and Larsson 2003), *Leucogyrophana* (Jarosch and Besl 2001), and *Aleurodiscus* (Wu et al. 2001) were shown to be polyphyletic by molecular methods and analyses.

Introduced in 1907, *Dendrothele* Höhn. & Litsch. is a corticioid genus with discoid or crustose basidiomes with a smooth hymenial surface, occasionally with small, sterile spines, and a monomitic hyphal system. Dendrohyphidia and gloeocystidia are usually present, and basidiospores are globose to allantoid with nonamyloid, smooth, hyaline, thin or thickened walls. Lemke (1964, 1965) included 18 species in his comprehensive study of *Dendrothele* (syn. *Aleurocorticium* P.A. Lemke). In subsequent years, additional species of *Dendrothele* have been described by various authors (Viégas 1945; Burdsall and Nakasone 1983; Gilbertson and Blackwell 1985; Boidin et al. 1986, 1996; Hjortstam 1987, 1997; Greslebin and Rajchenberg 1998; Pouzar 2001; Nakasone 2006; Duhem and Michel 2007). Presently, there are 41 accepted species of *Dendrothele* listed in CortBase (Parmasto et al. 2004).

Goranova (2003) tested the monophyly of *Dendrothele* by sequencing and analyzing nuclear and mitochondrial ribosomal DNA gene regions. She discovered that *Dendrothele* is highly polyphyletic with taxa occurring in 11 lineages distributed among the Hymenochaetales, Russulales, Corticiales, and Agaricales. She concluded that convergence in morphology and habitat occurred repeatedly in this group. In this paper, we investigate one of the lineages in the Agaricales that shows a close relationship to *Campanella* Henn. and describe a new, monotypic genus, *Neocampanella*. Coincidently, Wu et al. (2007) erected a monotypic corticioid genus, *Brunneocorticium* S.H. Wu, which is allied also to *Campanella*. The recently described species, *Brunneocorticium pyriforme* S.H. Wu, from Taiwan and China is determined to be conspecific with *Dendrothele*

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bispora Burds. & Nakasone from Florida. Morphological and ecological diversity in this lineage of Agaricales are discussed.

Materials and methods

Taxon sampling

The nuclear large subunit ribosomal RNA (nLSU rRNA) gene sequence of *Neocampanella blastanos* was used as a BLAST query of the GenBank database (blast.ncbi.nlm.nih.gov/Blast.cgi). Thirty-two of the top-scoring sequences were combined with 9 additional sequences from GenBank, including *Campanella eberhardtii* (Pat.) Singer, *Campanella* sp. (two sequences), *Caripia montagnei* (Berk.) Kuntze, *Crinipellis campanella* (Peck) Singer, *Gymnopus dryophilus* (Bull.) Murrill, *Moniliophthora perniciosa* (Stahel) Aime & Phillips-Mora and *Tetrapyrgos* sp., as well as one unpublished sequence of an undescribed lachnoid species from the Dongling Mountains, generously provided by M. Binder (Table 1). Based on preliminary analyses (not shown) and the higher-level phylogeny of Agaricales of Matheny et al. (2006), five sequences corresponding to the Omphalotaceae sensu Matheny (including *Campanella eberhardtii*) were selected as the outgroup.

DNA extraction, amplification, and sequencing

Goranova (2003) described in detail DNA extraction, amplification, purification, and sequencing procedures followed. These protocols are available as supplementary material[3].

Alignment and phylogenetic analysis

The sequences were aligned with the MAFFT version 6.624b server (align.bmr.kyushu-u.ac.jp/mafft/online/server) using the Q-INS-I algorithm (Katoh and Toh 2008), followed by manual adjustment in MacClade version 4.08 (Maddison and Maddison 2005) (see supplementary data,[3] Fig. S1). The alignment was converted to PHYLIP format and uploaded to the CIPRES Portal version 1.14 at the San Diego Supercomputing Center (8ball.sdsc.edu:8889/cipres-web/Home.do) for maximum likelihood (ML) analysis using RAxML version 7.0.4 (Stamatakis 2006; Stamatakis et al. 2008). The ML analysis used 100 rapid bootstrap (RBS) replicates followed by ML optimization (Stamatakis et al. 2008). The general time reversible (GTR) nucleotide substitution model was employed, with among-site rate heterogeneity modeled with CAT approximation during RBS and the initial ML optimization, switching to the discrete-gamma model with four rate categories during the final ML optimization. A phylogram of the optimal ML tree was produced using FigTree version 1.0 (Rambaut 2006). Maximum parsimony (MP) analyses were conducted using the "portable" version of PAUP* 4.0b10 running in OSX (Swofford 2002). One hundred heuristic MP searches were conducted with the cost of transversions weighted twice that of transitions, with starting trees generated by random taxon

Table 1. Nuclear large subunit ribosomal RNA gene sequences analyzed.

New sequences	GenBank No.
Neocampanella blastanos FP150016	FJ663209
Lachnoid species MB02–008	FJ663210
Sequences retrieved from GenBank	
Marasmiaceae	
Agaricales sp. JMCR34	AF261341
Amyloflagellula inflata PB305/RA	AY570990
Brunneocorticium bisporum Wu 9708–292	DQ679922
Brunneocorticium bisporum Chen 774	DQ679921
Campanella junghuhnii GEL4720	AJ406561
Campanella sp. MCA1689	AY916668
Campanella sp. MCA2235	AY916674
Campanella sp. RV-98/79	AF261340
Campanella sp. RV-PR075	AF261339
Chaetocalathus liliputianus DAOM 175886	AF261346
Chaetocalathus liliputianus C61867	AY570996
Chaetocalathus sp. TENN3572	AF261347
Crinipellis campanella DAOM 17785	U11916
Crinipellis scabella TAA146345	AM946420
Crinipellis stipitaria GLM45915	AY207194
Crinipellis stipitaria PB302	AY570997
Hymenogloea papyracea Halling 5013	AF261344
Marasmiellus candidus DED7489-SFSU	AY639433
Marasmiellus palmivorus DED6519-SFSU	AY639434
Marasmiellus sp. DMC 027	EF160084
Marasmius bekolacongoli BRNM691107	EF160079
Marasmius bekolacongoli DMC 005a	EF160089
Marasmius haematocephalus DMC 013	EF160083
Marasmius mbalmayoensis DMC 001c	EF160087
Marasmius oreades AFTOL-ID 1525	DQ156126
Marasmius sp. DMC 028	EF176770
Marasmius sp. JEJ.PR.256	AF261342
Moniliophthora perniciosa	AY916737
Moniliophthora sp. MCA2500	AY916752
Sterile white basidiomycete 3034	AY445113
Tetrapyrgos nigripes DAOM186918	AF261337
Tetrapyrgos subdendrophora ATCC 42449	AY445115
Tetrapyrgos sp. MCA2162	AY916757
Tetrapyrgos sp. TENN7373	AF261338
Tricholomataceae sp. ATCC 28344	AY445114
Omphalotaceae	
Campanella eberhardtii DEH 465	AY639407
Caripia montagnei JMCR143	AF261327
Gymnopus dryophilus RV83/180	AF042595
Lampteromyces japonicus	AF135172
Neonothopanus nambi RV-PR27	AF135175

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[3] Supplementary data for this article are available on the journal Web site (http://botany.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5267. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/eng/ibp/cisti/collection/unpublished-data.html.

addition sequences, MAXTREES set to 1000, and tree bisection–reconnection (TBR) branch swapping. One thousand bootstrapped MP analyses were conducted, with MAXTREES set to 10 and other settings unchanged.

Morphological studies

Freehand sections and squash mounts of basidiomes were examined microscopically in 2% (*w/v*) KOH and 1% (*w/v*) aqueous phloxine or Melzer's reagent (Kirk et al. 2001). Sections were mounted in 0.1% (*w/v*) cotton blue in 60% lactic acid to determine cyanophily of the cell walls (Kotlaba and Pouzar 1964; Singer 1986). Drawings of microscopic features were aided with a camera lucida attachment on an Olympus BH2 compound microscope. *Q* is the ratio of the average length to width measurements of basidiospores (Kirk et al. 2001). Color descriptions were taken from Kornerup and Wanscher (1978), and herbarium designations follow Holmgren and Holmgren (1998).

Results

Molecular analyses

The *N. blastanos* sequence of the 5′-end of the nLSU rRNA obtained was 882 base pairs (bp) in length. The nLSU rRNA sequences retrieved by the BLAST search were all from members of the Agaricales and ranged from 841 bp (*Crinipellis campanella* U11916) to 1447 bp (*Marasmius oreades* DQ156126). The full alignment was 1497 bp long with 198 variable positions and 136 parsimony informative positions. Referring to the phylogeny and classification of Agaricales of Matheny et al. (2006), the ingroup sequences are all members of the Marasmiaceae.

The optimal RAxML tree ($-\log L = -4679.319552$) had 24 nodes in common with the strict consensus of the 706 equally most parsimonious trees (568 steps [ti/tv weighted], CI = 0.558, RI = 0.822; Fig. 1). Both the ML and MP analyses divided the ingroup sequences into two strongly supported major clades (Fig. 1) that are here labeled Marasmiaceae 1 (16 sequences; ML and MP bootstrap = 99%) and Marasmiaceae 2 (21 sequences; ML bootstrap = 98%, MP bootstrap = 96%; Fig. 1).The bipartition separating the ingroup from the five sequences of Omphalotaceae used as the outgroup was also strongly supported (ML and MP bootstrap = 99%; Fig. 1).

Neocampanella blastanos was placed in the Marasmiaceae 1 clade. Within this clade, *N. blastanos* was placed with moderate support (ML bootstrap = 88%, MP bootstrap < 70%) in a group of nine sequences that includes *Brunneocorticium bisporum*, the undescribed lachnoid fungus MB02-008, a "sterile white basidiomycete" isolated from roots of buffalo grass in Australia (Vinnere et al. 2005), *Marasmiellus candidus*, and two isolates of *Campanella* sp. (Fig. 1). The other sequences in the Marasmiaceae 1 clade include an unidentified agaricoid species, three isolates of *Tetrapyrgos* spp., *T. subdendrophora*, and an isolate of *Campanella* sp. (Fig. 1). The Marasmiaceae 2 clade includes additional sequences of *Marasmiellus* and *Marasmius* as well as *Crinipellis*, *Moniliophthora*, *Chaetocalathus*, *Amyloflagellula*, *Hymenogloea*, and an unidentified "Tricholomataceae" species (Fig. 1).

Description of taxa

Neocampanella Nakasone, Hibbett & Goranova, gen. nov.

Basidiomata resupinata, effusa, tenuia, membranacea, laevia vel pulverulenta, marginibus abruptis. Systema hyphale monomiticum, hyphis fibulatis. Dendrohyphidia praesentia. Cystidia cylindrica, subfusiformia vel capitata. Basidia ephemera, 2 vel 4 sterigmatibus. Basidiospora ellipsoideae vel pyriformes, apiculo prominenti, tenuitunicatis, laevibus, hyalinis, acyanophilis, inamyloideis.

TYPUS: *Neocampanella blastanos* (Boidin & Gilles) Nakasone, Hibbett, & Goranova.

ETYMOLOGY: from the Greek *neos* = new + *Campanella*, a genus of Agaricales.

Basidiomata resupinate, effuse, thin, membranous, soft, not gelatinous, smooth to pulverulent, white to pale yellow or orange, margin adnate, more or less abrupt. Hyphal system monomitic, generative hyphae with clamp connections. Dendrohyphidia simple or delicately and finely branched, usually encrusted with tiny hyaline crystals. Cystidia cylindrical, subfusiform to capitate. Basidia ephemeral, more or less cylindrical, bearing 2 or 4 sterigmata. Basidiospores often adherent, ellipsoid or pyriform, often adaxial side slightly flattened, tapering to a prominent, blunt apiculus, with walls thin, hyaline, smooth, acyanophilous, inamyloid.

Neocampanella is characterized by thin, effuse, nongelatinized basidiomes with dendrohyphidia, cylindrical to capitate cystidia, and ellipsoid to pyriform basidiospores with a distinct, blunt apiculus. Mature basidia are difficult to observe for they probably collapse soon after discharging spores. The characteristic spore shape, slightly tapering toward the prominent apiculus, is reminiscent of basidiospores found in species of *Campanella* and related genera. *Neocampanella*, with its corticioid habit and smooth hymenial surface (see supplementary data,[3] Figs. S2 and S3), however, would never be confused with *Campanella*'s pleurotoid form and reticulate lamellae. Dendrohyphidia in the hymenium of *Neocampanella* may be homologous to the Rameales-like structures developed in the pileal epicutis of *Campanella* and allied genera.

Among corticioid taxa, the distinctive pyriform basidiospores of *Neocampanella* are present also in *Brunneocorticium* and *Cylindrobasidium* Jülich. *Cylindrobasidium*, in the Physalacriaceae Corner (Matheny et al. 2006), is characterized by a monomitic hyphal system with clamp connections, abundant, oil-like globules in the hyphae, and thin-walled, fusoid cystidia. Dendrohyphidia are absent in *Cylindrobasidium* but are present in *Neocampanella*, *Brunneocorticium*, and many other genera and species of corticioid fungi. The combination of dendrohyphidia and pyriform basidiospores, however, is unique to *Neocampanella* and *Brunneocorticium*. *Neocampanella* has a monomitic hyphal system, whereas *Brunneocorticium* has a dimitic hyphal system with the brown-pigmented skeletal hyphae dominating the context (see supplementary data,[3] Fig. S5) and margin. The distinct, sterile brown margin in *Brunneocorticium* is composed

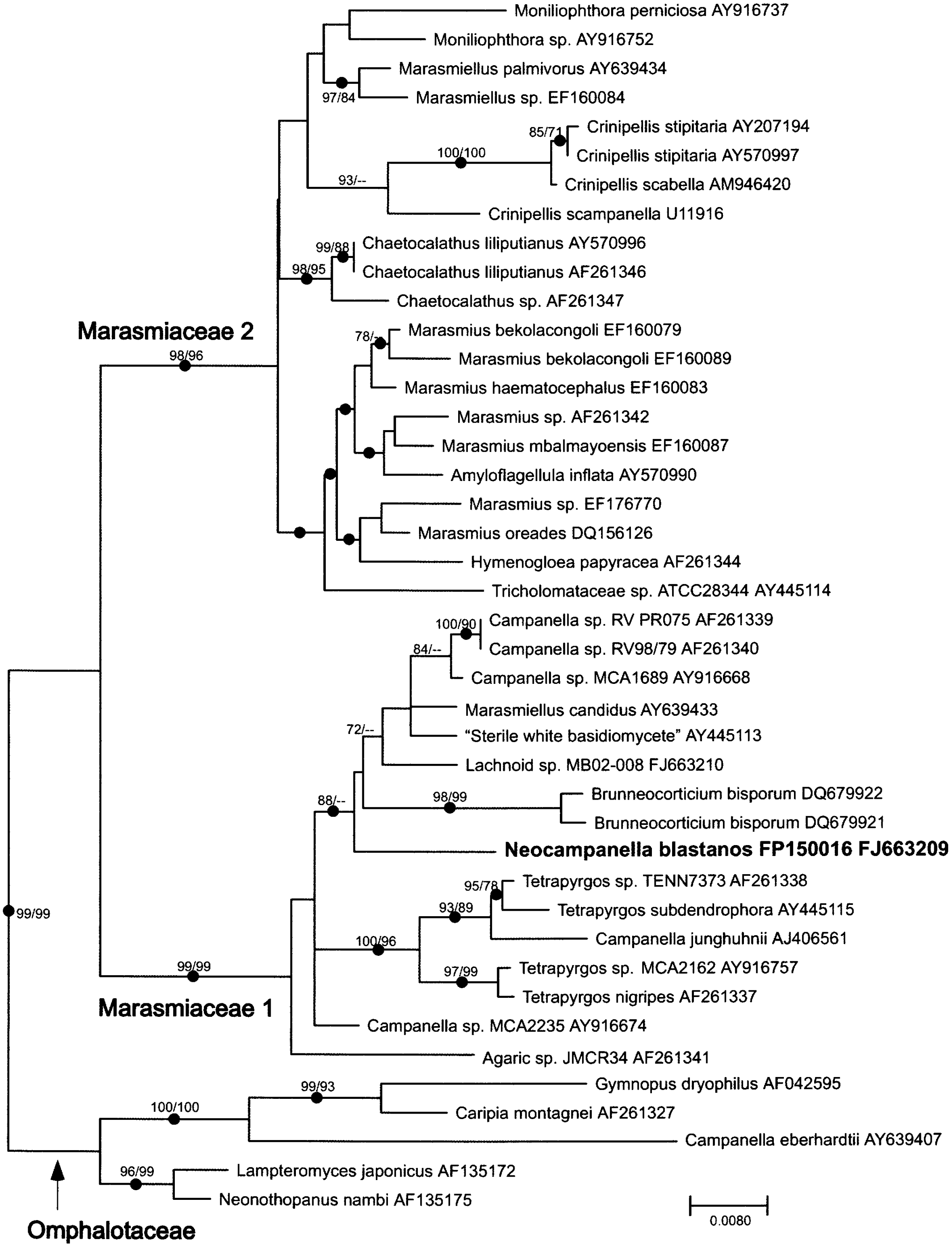


Fig. 1. Phylogenetic placement of *Neocampanella blastanos* based on maximum likelihood (ML) and maximum parsimony (MP) analyses of nuclear large subunit ribosomal RNA gene sequences. This is the optimal tree obtained with ML. Filled dots on branches indicate groups that are also present in the strict consensus of the 706 equally most parsimonious trees. Numbers along branches before slash marks (/) are frequencies from 100 ML bootstrap analyses. Numbers after slash marks are frequencies from 1000 bootstrapped MP analyses. Bootstrap frequencies below 70% are not shown. Group names are discussed in the text. Scale bar units represent numbers of substitutions per site.

entirely of skeletal hyphae that develop in advance of the fertile, white hymenium (see supplementary data,[3] Fig. S4).

Phylogenetic analyses of sequence data from the LSU rRNA gene also support the erection of the new genus *Neocampanella*. The precise placement of *Neocampanella* within the Marasmiaceae 1 clade is not well resolved, but it is strongly supported as a member of that group and it does not appear to be nested within any established genus, including *Brunneocorticium* (Fig. 1). Uncorrected sequence divergence between *Brunneocorticium* and *Neocampanella* is 3.18%. This value exceeds the levels of sequence divergence observed among members of the core *Campanella* and *Tetrapyrgos* clades, which ranged from 0.31% to 2.96% and from 0.27% to 2.7%, respectively, among the taxa.

Neocampanella blastanos (Boidin & Gilles) Nakasone, Hibbett & Goranova, comb. nov. Figure 2 and see supplementary data,[3] Figs. S2 and S3

≡*Dentocorticium blastanos* Boidin & Gilles, Cryptog. Mycol. 19(3): 193. 1998

Basidiome resupinate, appressed, widely effuse, beginning as small circular patches, coalescing, up to 70 mm × 30 mm, thin, up to 180 µm thick, membranous, soft, white, light yellow (4A3), greyish yellow (4B3), orange white (5A2), or pale orange (5A3), smooth, porulose, or subpulverulent, lacking cracks, not reacting to KOH; margin more or less distinct, abrupt, or rapidly thinning out. Hyphal system monomitic, generative hyphae with clamp connections. Subicular hyphae 2–3 µm diameter, nodose septate, walls thin, hyaline, typically encrusted with a thin layer of hyaline crystals. Subhymenium not observed. Hymenium a dense palisade of dendrohyphidia, cystidia, and basidia. Dendrohyphidia simple or highly branched, sometimes knobby, 20–45 µm long, 1–2.5 µm diameter, with a basal clamp connection, walls thin, hyaline, encrusted with a thin layer of adherent, hyaline crystalline material. Cystidia cylindrical to subfusiform, capitate, sometimes slightly enlarged at the base, 35–60 µm × 5–9 µm, apex 4–10 µm diameter, with a basal clamp connection, walls thin, hyaline, smooth. Basidia collapsing soon after maturity, cylindrical, sometimes slightly enlarged at the base, occasionally with lateral knobs, 30–35 µm × 6–7 µm, with a basal clamp, walls thin, hyaline, smooth, 2-sterigmate. Basidiospores often in clusters, pyriform to ellipsoid, tapering slightly toward prominent, blunt apiculus, 11.5–15 µm × 5.5–7 µm, Q = 2.0–2.1, sometimes developing a short germination peg, walls thin, hyaline, smooth, acyanophilous, not reacting in Melzer's reagent.

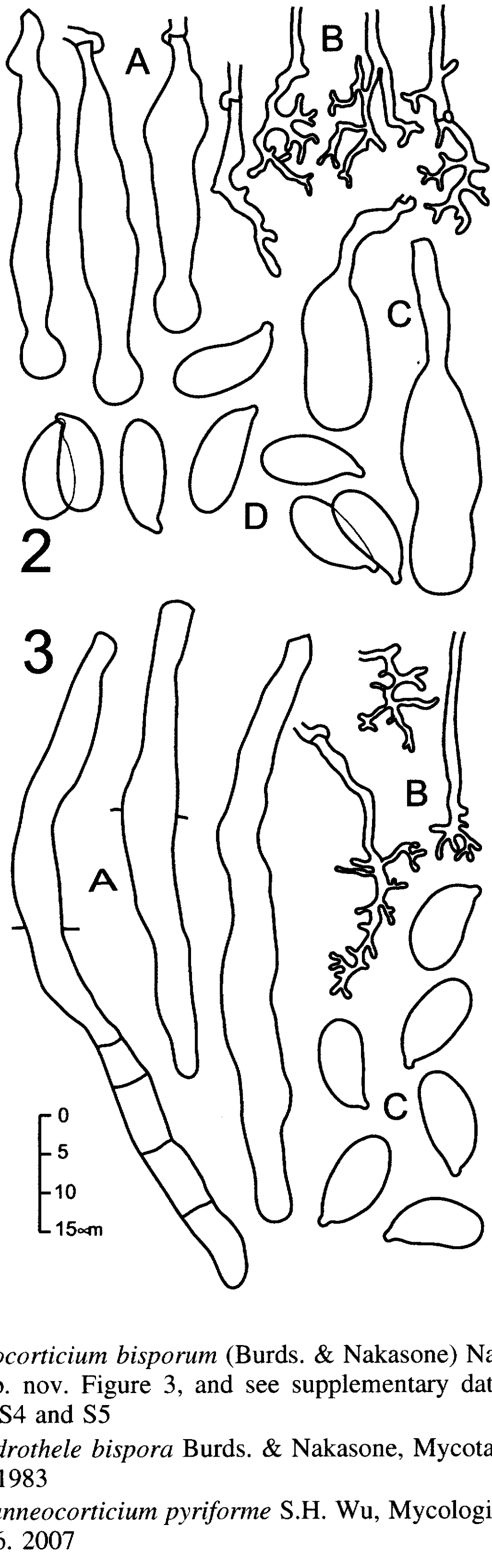
HABITAT: on wood and bark of small hardwood twigs.

DISTRIBUTION: Puerto Rico, Central African Republic, Réunion (Boidin and Gilles 1998).

SPECIMENS EXAMINED: Puerto Rico. Luquillo Municipio, B. O. Sabana, ridge above chicken farm along Rio Sabana (18°21′0″N, 66°44′4″W), altitude 75 m above sea level, on bark and wood of hardwood branch, 30 June 1996, K.K. Nakasone, FP 150016 (CFMR). Central African Republic. Savane de Bébé, sur *Hibiscus owariense*, au sol, 13 Septembre 1967, J. Boidin, LY 5897 (LY).

Neocampanella blastanos is characterized by a thin, effuse, white basidiome with capitate cystidia, dendrohyphidia, and pyriform basidiospores. This is a rare species but probably occurs worldwide in subtropical to tropical regions. Microscopically, *N. blastanos* compares favorably with the holotype of *Campanella elongatispora* Singer (Argentina, Jujuy, Lagunas de Yala, 11 February 1965, R. Singer T4025 at F) with respect to the capitate cystidia and pyriform basidiospores.

Figs. 2–3. Fig. 2. *Neocampanella blastanos*, FP150016: A, cystidia; B, dendrohyphidia; C, immature basidia; D, basidiospores. Fig. 3. *Brunneocorticium bisporum*, from paratype Wu 9708–292: A, septate cystidia; B, dendrohyphidia; C, basidiospores.



Brunneocorticium bisporum (Burds. & Nakasone) Nakasone, comb. nov. Figure 3, and see supplementary data,[3] Figures S4 and S5

≡ *Dendrothele bispora* Burds. & Nakasone, Mycotaxon 17: 253. 1983

=*Brunneocorticium pyriforme* S.H. Wu, Mycologia 99(2): 306. 2007

SPECIMENS EXAMINED: Central African Republic. La Maboké, sur branchette, 8 Mai 1965, J. Boidin, LY 5360 (LY). China. Yunnan, Hsishuangpanna, Green Stone Forest Park, on (corticate) branch of angiosperm, 18 August 1997, S.H. Wu and

S.Z. Chen, Wu 9708–292 (TNM). Guadeloupe. Près Saint Sauveur, rive de Grand Etang, sur branchettes mortes en l'air de *Psychotria berteroana*, 10 Octobre 1976, J. Boidin LY 8189 (LY). Mauritius. Maurice Island, parc aux oiseaux de Casella, sur tronc vivant et sur branche morte de *Britera fantesia*, 6 Mars 1995, J. Boidin LY 16100 (LY). Réunion. Anse des Cascades, sur gros bois mort au sol, 18 Mars 1995, J. Boidin, LY 16197 (LY); sur arbuste vivant, same date and collector, LY16195 (LY). Taiwan. Taitung, Green Island, Yutzuhu, on (corticate) branch of *Murraya paniculata*, 9 April 1998, S.Z. Chen 774 (TNM, holotype of *Brunneocorticium pyriforme*). United States. Florida, Alachua County, Hatchet Creek, on *Taxodium distichum*, 27 July 1972, H.H. Burdsall, Jr. 6762 (CFMR, holotype of *Dendrothele bispora*).

Voucher specimens of the *B. pyriforme* DNA sequences used in this study were examined morphologically and confirmed to be conspecific with *D. bispora*. For descriptions and illustrations, see Burdsall and Nakasone (1983), Boidin et al. (1996), Maekawa (1998), and Wu et al. (2007). This species is characterized by a yellowish white to grayish brown, effuse basidiome with distinct, sterile, brown margins and a smooth hymenial surface. Microscopically, it has a dimitic hyphal system with clamped generative hyphae and aseptate, brown skeletal hyphae, dendrohyphidia, 2-sterigmate basidia, and pyriform basidiospores with a distinct apiculus. Average basidiospore size for three specimens, 9–15 spores, range 11.9–12.5 μm × 6.4–6.7 μm, Q = 1.80–1.90. Cylindrical cystidia with adventitious septa were found in the Chinese specimen only. The colorless dendrohyphidia are often obscured by encrusting hyaline crystals and were overlooked by Wu et al. (2007). Mature basidia were rare and probably developed in a catahymenium as reported by Boidin et al. (1996). It occurs primarily on corticate branches of angiosperms and rarely on gymnosperms. Originally described from the United States in Florida, *B. bisporum* has a pantropical distribution.

Wu et al. (2007) showed, using partial LSU rRNA gene sequences, that *B. bisporum* (as *B. pyriforme*) is embedded in the Agaricales and related to *Marasmiellus candidus* and *Tetrapyrgos subdendrophora*. Our results confirm this and place *Brunneocorticium* in the Marasmiaceae 1 clade with *Neocampanella*, *Campanella*, and *Tetrapyrgos* (Fig. 1).

Discussion

Recent molecular studies have established that crustose, corticioid species are distributed throughout the Agaricales (Binder et al. 2005; Larsson et al. 2004; Larsson 2007*b*). The results of our study confirm and expand on these prior observations. Morphological and molecular studies show that the monotypic, corticioid genera *Neocampanella* and *Brunneocorticium* are closely related to the pleurotoid genera *Campanella* and *Tetrapyrgos*. Although the species samples were small, previous studies showed that *Campanella* and *Tetrapyrgos* were distinct, monophyletic sister clades (Moncalvo et al. 2002; Aime and Phillips-Mora 2005; Matheny et al. 2006). Our results confirm that *Tetrapyrgos* is monophyletic, but *Campanella* appears to be polyphyletic. The first indication that *Campanella* may not be monophyletic came from Wilson and Desjardin's (2005) phylogenetic study of gymnopoid and marsmioid agarics, which showed that *Campanella eberhardtii* did not cluster with *Tetrapyrgos* and *M. candidus* but was in a sister clade, with *Marasmiellus ramealis* (Bull.) Singer, to *Rhodocollybia*. In the present study, *Campanella eberhardtii* was found to be more closely related to the outgroup Omphalotaceae (sensu Matheny) than to the other *Campanella* species of the ingroup Marasmiaceae.

A comparative discussion of *Campanella*, *Tetrapyrgos*, *Marasmiellus*, and allied genera is beyond the scope of this study. However, general observations on the similarities and differences among the corticoid genera, *Neocampanella* and *Brunneocorticium*, and the agaricoid genera, *Campanella* and *Tetrapyrgos*, may be useful. These four genera are included in the Marasmiaceae 1 lineage and display a wide range of phenotypes. Besides the obvious basidiome form differences, crustose versus pileate, the dimitic hyphal system with brown pigmented skeletal hyphae of *Brunneocorticium* is contrasted with monomitic hyphal systems of the other genera. The gelatinous context of *Campanella* is unlike the membranous texture of the corticioid taxa, and the unusual tetrahedral basidiospores of *Tetrapyrgos* are unique in Marasmiaceae 1.

Although morphological differences are striking in the genera of the Marasmiaceae 1 clade, some notable morphological similarities include pyriform to fusiform basidiospores found in *Campanella*, *Neocampanella*, and *Brunneocorticium*, and hymenial cystidia with a bulbous apex present in *Neocampanella* and some *Campanella* species. Dendrohyphidia developed in the hymenium of the corticioid genera may be homologous to the diverticulate pileocystidia or hyphae of the pileipellis in the agaricoid genera.

In addition to phenotypic differences among species in the Marasmiaceae 1 clade, nutritional requirements differ also. Most species are saprobic on decayed logs and branches or stems of woody grasses. Sterile white basidiomycete 3034, however, was shown to be pathogenic on 12 plant species in Australia (Vinnere et al. 2005).

Several inconsistent results in Fig. 1 deserve comment. First, *Marasmiellus candidus* is included within the Marasmiaceae 1 clade. Wilson and Desjardin (2005) discussed this anomaly and noted that *M. candidus* and species in section *Candidi* are morphologically distinct from other *Marasmiellus* species. Second, species within the *Tetrapyrgos* clade have basidiospores that are tetrahedral in shape or have a distinct lateral bulge, except for *Campanella junghuhnii*. Parmasto (1981) described a faint bulge on the abaxial side of some basidiospores of *C. junghuhnii* that suggests a transfer to *Tetrapyrgos* may be appropriate after further study.

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