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, Agaricomycetes, 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, dendrohyphidia, Marasmiaceae, basidiomycète blanc stériles, Tetrapyrgos.

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 Agaricales, formerly the Hymenomycetes or Homobasidiomycetes (Larsson et al. 2004; Binder et al. 2005; Larsson 2007b). 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 2007a), Panerocarphae (De Koker et al. 2003), Gloeocystidiellum (Larsson and Larsson 2003), Leucogrophana (Jarosch and Besl 2001), and Aleurodiscus (Wu et al. 2001) were shown to be polyphyletic by molecular methods and analyses.

Introduced in 1907, Dendrothele Hohn. & 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 Hymenochoetales, 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.
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 blastanosa* 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), *Carpia montagnei* (Berk.) Kuntze, *Criminellis 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.

**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, Fig. S1). The alignment was converted to PHYLIP format (alignment.phylipweb/Home.do) for maximum likelihood (ML) analysis using RAxML version 7.0.4 (Stamatakis 2006; Stamatakis et al. 2008) replicates followed by ML optimization (Stamatakis 2006), five sequences corresponding to the Omphalotaceae sensu Matheny (including *Campanella eberhardtii*) were selected as the outgroup.

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

| New sequences                             | GenBank No.   |
|-------------------------------------------|---------------|
| *Neocampanella blastanosa* FP150016       | FJ663209      |
| Lachnoid species MB02–008                  | FJ663210      |
| **Sequences retrieved from GenBank**       |               |
| Marasmiaceae                              |               |
| Agaricales sp. JMC R34                    | AF261341      |
| *Amylofagellula inflata* PB305/RA          | AY570990      |
| *Branneecorticium bisporum* Wu 9708–292    | DQ679922      |
| *Branneecorticium bisporum* Chen 774       | DQ679921      |
| *Campanella junguhnnii* GEL 4720           | AA406568      |
| *Campanella* sp. MCA 1689                 | AY916668      |
| *Campanella* sp. MCA 2235                 | AY916674      |
| *Campanella* sp. RV 98/79                 | AF261340      |
| *Campanella* sp. RV PR075                 | AF261339      |
| *Chaetocalathus liliputianus* DAOM 175886  | AF261346      |
| *Chaetocalathus liliputianus* C61867       | AY570996      |
| *Chaetocalathus* sp. TENN 3572            | AF261347      |
| *Criminellis campanella* DAOM 17785       | U11916        |
| *Criminellis scabellia* TAA 146345         | AM946340      |
| *Criminellis stipitaria* GLM 45915        | AY247019      |
| *Criminellis stipitaria* PB 302            | AY570997      |
| *Hymenogloea paperyracea* Halling 5013     | AF261344      |
| *Marasmiellus candidus* DED 7489–SFSU      | AY639433      |
| *Marasmiellus palmivorus* DED 6519–SFSU    | AY639434      |
| *Marasmiellus* sp. DMC 027                | EF160084      |
| *Marasmius bekolacongoli* BRNM 691107      | EF160079      |
| *Marasmius bekolacongoli* DMC 005a         | EF160089      |
| *Marasmius haematocephalus* DMC 013        | EF160083      |
| *Marasmius mthalmoyenesis* DMC 011c        | EF160087      |
| *Marasmius oreades* AFTOL-ID 1525          | DQ156126      |
| *Marasmius* sp. DMC 028                    | EF176770      |
| *Marasmius* sp. JEI PR 256                 | AF261342      |
| *Moniliophthora perniciosa*                | AY916737      |
| *Moniliophthora* sp. MCA 2500              | AY916752      |
| Sterile white basidiomycete 3034           | AY445113      |
| *Tetrapyrgos nigripes* DAO M186918         | AF261337      |
| *Tetrapyrgos subendophora* ATCC 42449      | AY445115      |
| *Tetrapyrgos* sp. MCA 2162                 | AY916757      |
| *Tetrapyrgos* sp. TENN 7373                | AF261338      |
| *Tricholomataceae* sp. ATCC 28344          | AY445114      |

*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 Körnerup 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 [it/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 outgroup 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 Tetraprygos 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 pulvulenta, marginibus abruptis. Systema hyphale monomiticum, hyphis fibulatis. Dendrohyphidia praesentia. Cystidia cylindrica, subfusciformia vel capitata. Basidia ephemera, 2 vel 4 sterigmatibus. Basidiospora ellipsoidae vel pyriformes, apiculo prominenti, tenuitunicatia, 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 pulvulent, 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, subfusciform to capitata. 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 capitulate cystidia, and ellipsoid to pyriform basidiospores with a distinct, blunt apiculus. Mature basidia are difficult to observe for they 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 epietus 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 mononitic 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 mononitic hyphal system, whereas Brunneocorticium has a dimitic hyphal system with the brown-pigmented skeletal hyphae dominating the context (see supplementary data, Figs. S5 and S5) and margin. The distinct, sterile brown margin in Brunneocorticium is composed
entirely of skeletal hyphae that develop in advance of the fertile, white hymenium (see supplementary data, 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, includ-
ing *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 *Tetrazygos* 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. Figs. S2 and S3

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

Basidiome resupinate, appressed, widely effuse, beginning as small circular patches, coalescing, up to 70 mm x 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 sub fusiform, capitate, sometimes slightly enlarged at the base, 35–60 μm x 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 x 6–7 μm, with a basal clamp, walls thin, hyaline, smooth, 2-sterigate. Basidiospores often in clusters, pyriform to ellipsoid, tapering slightly toward prominent, blunt apiculus, 11.5–15 μm x 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 September 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.

*Brunneocorticium bisporum* (Burds. & Nakasone) Nakasone, comb. nov. Figure 3, and see supplementary data.

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

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

**SPECIMENS EXAMINED:** Central African Republic. La Maboke, 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

Published by NRC Research Press
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 *Bretiera fantasia*, 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, Yutzuuh, on (corticale) 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 *Dendo­thele 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 asceptate, brown skeletal hyphae, dendrohyphidia, 2-sterigate 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 cat­hymenum 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 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 2007b). 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 monophy-letic 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 clade 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 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 junghuhuii*. Parnasto (1981) described a faint bulge on the abaxial side of some basidiospores of *C. junghuhuii* that suggests a transfer to *Tetrapyrgos* may be appropriate after further study.

**Acknowledgements**

We thank curators Dr. Sheng-Hua Wu (TNM) and Dr. Gaëtan Guignard (LY) for arranging loans used in this study. This study was financially supported by USA National Science Foundation award grants DEB-95-25902 to the State University of New York College at Cortland from the Biotic Surveys and Inventories Program in a joint ven­ture agreement with the US Forest Service, Forest Products
Laboratory, and DEB-0732968, which supports the Assembling the Fungal Tree of Life (AFTOL) project. Dr. Harold H. Burdsall, Jr., Dr. Karl-Henrik Larsson, Dr. Scott Redhead, and an anonymous reviewer provided valuable comments and suggestions to improve this manuscript.

References

Aime, M.C., and Phillips-Mora, W. 2005. The causal agents of witches’ broom and frosty pod rot of cacao (chocolate, Theobroma cacao) form a new lineage of Marasmiaceae. Mycologia, 97(5): 1012–1022. doi:10.3852/mycologia.97.5.1012. PMID: 16596953.

Binder, M., Hibbett, D.S., Larsson, K.-H., Larsson, E., Langer, E., and Langer, G. 2005. The phylogenetic distribution of resupinate forms across the major clades of mushroom-forming fungi (Homobasidiomycetes). Syst. Biodivers. 3(2): 113–157. doi: 10.1017/S1477200005001623.

Boidin, J., and Gilles, G. 1998. Contribution à l’étude des genres Dendrocurticium, Dendrodonia et Dendactochitus (Basidiomycota). Cryptogam., Mycol. 19: 181–202.

Boidin, J., Candousau, F., and Gilles, G. 1986. Bambusicolous fungi from the southwest of France II. Saprobiic Heterobasidiomycetes, resupinate Aphyllophorales and Nidulariales. Trans. Mycol. Soc. Jpn. 27: 463–471.

Boidin, J., Lanquetin, P., and Duhem, B. 1996. Contribution à la connaissance du genre Dendrocurticium (Basidiomycotina, Aphyllophorales). Bull. Trimest. Soc. Mycol. Fr. 112: 87–126.

Burdsall, H.H., Jr., and Nakasone, K.K. 1983. Species of effused resupinate Aphyllophorales (Basidiomycotina) from the southeastern United States. Mycopath, 17: 253–268.

De Koker, T.H., Nakasone, K.K., Haarhof, J., Burdsall, H.H., Jr., and Janse, B.J.H. 2003. Phylogenetic relationships of the genus Phanerochaete inferred from the internal transcribed spacer region. Mycol. Res. 107(9): 1032–1040. doi:10.1017/ S095375620300827X. PMID: 14563129.

Duhem, B., and Michel, H. 2007. Deux espèces nouvelles de Dendrocurticium. Cryptogam., Mycol. 28: 39–54.

Gilbertson, R.L., and Blackwell, M. 1985. Notes on wood-rotting fungi on junipers in the Gulf Coast region. Mycopath, 24: 325–348.

Goranova, G. 2003. Phylogenetic analyses of rDNA sequences indicate the corticioid genus Dendrocurticium is highly polyphyletic. M.Sc. thesis, Department of Biology, Clark University, Worcester, Mass.

Greslebin, A., and Rajchenberg, M. 1998. Corticioid Aphyllophorales (Basidiomycotina) from the Patagonian Andes forests of Argentina. 3. The genus Dendrocurticium. Mycoyc, 67: 469–486.

Hjortstam, K. 1987. A check-list to genera and species of corticioid fungi (Hymenomycetes). Windahlia, 22: 15–25.

Hjortstam, K. 1997. Dendrocurticium tetraconis, a new corticioid species from Sweden. Windahlia, 22: 13–15.

Holmgren, P.K., and Holmgren, N.H. 1998. Index Herbariorum: A global directory of public herbaria and associated staff [online]. Available from sweetgum.nybg.org/ihf.

Jarosch, M., and Besl, H. 2001. Leucogyrophana, a polyphyletic genus of the order Boletales (Basidiomycotina). Plant Biol. 3(4): 443–448. doi:10.1055/s-2001-16455.

Katoh, K., and Toh, H. 2008. Improved accuracy of multiple ncRNA alignment by incorporating structural information into a MAFFT-based framework. BMC Bioinformatics, 9(1): 212. doi:10.1186/1471-2105-9-212. PMID:18439255.

Kirk, P.M., Cannon, P.F., David, J.C., and Stalpers, J.A. 2001. Ainsworth & Bisby’s dictionary of the fungi. 9th ed. CAB International, Wallingford, UK.

Kromp, A., and Wanscher, J.H. 1978. Methuen handbook of colour. 3rd revised ed. Eyre Methuen, London, UK.

Kotlaba, F., and Pouzar, Z. 1964. Preliminary results on the staining of spores and other structures of Homobasidiomycetes in cotton blue and its importance for taxonomy. Trans. Br. Mycol. Soc. 47: 653–654.

Larsson, K.-H. 2007a. Molecular phylogeny of Hypoderma and the reinstatement of Peniophorea. Mycol. Res. 111(2): 186–195. doi:10.1016/j.mycres.2006.10.002. PMID: 17164083.

Larsson, K.-H. 2007b. Re-thinking the classification of corticioid fungi. Mycol. Res. 111(9): 1040–1063. doi:10.1016/j.mycres.2007.08.001. PMID: 17981020.

Larsson, E., and Larsson, K.-H. 2003. Phylogenetic relationships of russuloid basidiomycetes with emphasis on aphylophoralen taxa. Mycologia, 95(6): 1037–1065. doi:10.2307/3761912.

Larsson, E., Larsson, K., and Köljalg, U. 2004. High phylogenetic diversity among corticioid Homobasidiomycetes. Mycol. Res. 108(9): 983–1002. doi:10.1017/S0953756204000851. PMID:15506012.

Lemke, P.A. 1964. The genus Aleurodiscus (sensu lato) in North America. Can. J. Bot. 42(6): 723–768. doi:10.1139/b64-064.

Lemke, P.A. 1965. Dendrocurticium (1907) vs. Aleurocurticium (1963). Persoonia, 3: 365–367.

Maddison, D.R., and Maddison, W.P. 2005. MacClade 4: analysis of phylogeny and character evolution. Version 4.08. Sinauer Associates, Sunderland, Mass.

Maekawa, N. 1998. Taxonomic study of Japanese Corticiaceae (Aphyllophorales) IV. Rep. Tottori Mycol. Inst. 36: 1–12.

Matheny, P.B., Curtis, J.M., Hofstetter, V., Aime, M.C., Moncalvo, J.-M., Ge, Z.-W., Yang, Z.-L., Slot, J.C., Ammirati, J.F., Baroni, T.J., Bougheer, N.L., Hughes, K.W., Lodge, D.J., Kerrigan, R.W., Seidl, M.T., Aanen, D.K., DeNitis, M., Daniele, G.M., Desjardins, D.E., Kropp, B.R., Norvell, L.L., Parker, A., Vellinga, E.C., Vilgalys, R., and Hibbett, D.S. 2006. Major clades of Agaricales: a multi locus phylogenetic overview. Mycologia, 98(6): 982–995. doi:10.3852/mycologia.98.6.982. PMID: 17486974.

Moncalvo, J.-M., Vilgalys, R., Redhead, S.A., James, T.Y., Catherine Aime, M., Hofstetter, V., Verduin, S.J.W., Larsen, E., Baroni, J.T., Bougher, N.L., Hughes, K.W., Lodge, D.J., Kerrigan, R.W., and Miller, O.K., Jr. 2002. One hundred and seventeen related taxa with hyphal pegs. Nova Hedwigia, 83(1):99–108. doi:10.1016/S1055-7903(02)00027-1. PMID: 12099793.

Nakasone, K.K. 2006. Dendrocurticium griseocana (Corticiaceae) and related taxa with hyphal pegs. Nova Hedwigia, 83(1): 99–108. doi:10.1017/S095375620500535X.

Parnasto, E. 2001. Notes on the taxonomy and distribution of cotton blue and its importance for taxonomy. Trans. Br. Mycol. Soc. 108(9): 983–1002. doi:10.1017/S0953756204000851. PMID: 15506012.

Pouzar, Z. 2001. Notes on the taxonomy and distribution of Aphyllophorales I. Czech Mycol. 53: 121–131.

Rambaut, A. 2006. FigTree. Version 1.0. Institute of Evolutionary Biology, University of Edinburgh, Edinburgh, Scotland [available from the author: tree.bio.ed.ac.uk/software/figtree].

Ringer, S. 1986. The Agaricales in modern taxonomy. 4th ed. Koeltz Scientific Books, Koenigstein, Germany.

Stamatakis, A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models.
Bioinformatics, 22(21): 2688–2690. doi:10.1093/bioinformatics/btl446. PMID:16928733.
Stamatakis, A., Hoover, P., and Rougemont, J. 2008. A rapid bootstrap algorithm for the RAxML Web servers. Syst. Biol. 57(5): 758–771. doi:10.1080/10635150802429642. PMID:18853362.
Swoford, D.L. 2002. PAUP*. Phylogenetic analysis using parsimony (*and other methods). Version 4. Sinauer Associates, Sunderland, Mass.
Viégas, P.A. 1945. Alguns fungos do Brazil VII–VIII - Cyphellaceae e Thelephoraceae. Bragantia, 5: 253–290.
Vinnere, O., Fatehi, J., Sivasithamparam, K., and Gerhardson, B. 2005. A new plant pathogenic sterile white basidiomycete from Australia. Eur. J. Plant Pathol. 112(1): 63–77. doi:10.1007/s10658-005-2191-y.
Wilson, A.W., and Desjardin, D.E. 2005. Phylogenetic relationships in the gymnopoid and marasmioid fungi (Basidiomycetes, euagarics clade). Mycologia, 97(3): 667–679. doi:10.3852/mycologia.97.3.667. PMID:16392255.
Wu, S.-H., Hibbett, D.S., and Binder, M. 2001. Phylogenetic analyses of Aleurodiscus s.l., and allied genera. Mycologia, 93(4): 720–731. doi:10.2307/3761826.
Wu, S.-H., Wang, D.-M., and Tschen, E. 2007. Brunneocorticium pyriforme, a new corticioid fungal genus and species belonging to the euagarics clade. Mycologia, 99(2): 302–309. doi:10.3852/mycologia.99.2.302. PMID:17682783.