ORIGINAL ARTICLE

Tying up loose threads: revised taxonomy and phylogeny of an avian-dispersed Neotropical rhizomorph-forming fungus

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Abstract

Rhizomorpha corynecarpos Kunze was originally described from wet forests in Suriname. This unusual fungus forms white, sterile rhizomorphs bearing abundant club-shaped branches. Its evolutionary origins are unknown because reproductive structures have never been found. Recent collections and observations of *R. corynecarpos* were made from Belize, Brazil, Ecuador, Guyana, and Peru. Phylogenetic analyses of three nuclear rDNA regions (internal transcribed spacer, large ribosomal subunit, and small ribosomal subunit) were conducted to resolve the phylogenetic relationship of *R. corynecarpos.* Results show that this fungus is sister to *Brunneocorticium bisporum*—a widely distributed, tropical crust fungus. These two taxa along with *Neocampanella blastanos* form a clade within the primarily mushroom-forming Marasmiaceae. Based on phylogenetic evidence and micromorphological similarities, we propose the new combination, *Brunneocorticium corynecarpon*, to accommodate this species. *Brunneocorticium corynecarpon* is a pathogen, infecting the crowns of trees and shrubs in the Neotropics; the long, dangling rhizomorphs with lateral prongs probably colonize neighboring trees. Longer-distance dispersal can be accomplished by birds as it is used as construction material in nests of various avian species.

Introduction

Many wood-decaying basidiomycetes produce linear aggregations of vegetative hyphae called cords, strands, or rhizomorphs. Rhizomorphs, as defined here, are fully autonomous vegetative structures that are cords with a differentiated core. In wood-decaying basidiomycetes, rhizomorphs serve an exploratory and exploitative function, interconnecting carbon-rich resources (Boddy 1993). Rhizomorphs produce networks that ramify through soil or litter over considerable distances between individual woody resources (Thompson and Rayner 1983). When a suitable resource is encountered, mycelium originating from the rhizomorph colonizes the substrate and nutrient uptake occurs; these nutrients are then translocated through the rhizomorphs toward the region of extension (Granlund et al. 1985). Rhizomorphs, therefore, are important agents of dispersal for wood-decaying basidiomycetes, allowing the fungus to reach and colonize new resources (Cairney 1991a). Additionally, aggregation into rhizomorphs may protect hyphae against fluctuating conditions in the external environment, including desiccation (Thompson 1984). A rapid diversification of *Armillaria* (Fr.) Staude species (Physalacriaceae, Agaricales, Basidiomycota) coincided with the ability to produce rhizomorphs (Koch et al. 2017), suggesting that the production of these structures could be an adaptive trait.

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Rhizomorphs, however, are not restricted to a subterranean habit; in moist tropical rainforests, they are also found in the tree canopy or subcanopy as a dense tangle of black and brown wiry webs. These aerial rhizomorphs trap falling leaf litter for subsequent nutrient exploitation (Hedger 1990), thus playing a similar role in nutrient acquisition as those in the soil and leaf litter. Species in the Marasmiaceae such as *Marasmius crinis-equi* F. Muell.:Kalchbr., *Marasmius nigrobrunneus* (Pat.) Sacc., and *Crinipellis* Pat. species form these litter-trapping aerial rhizomorph webs (Pegler 1983; Hedger 1990; Hedger et al. 1993).

One conspicuous, yet enigmatic aerial rhizomorph-forming species is *Rhizomorpha corynecarpos* Kunze (Fig. 1a–c), originally described from wet forests in Suriname (Weigelt exsiccata 1828). It hangs from tree branches in the forest canopy in a manner similar to other rhizomorph-producing marasmioid species (Hennings 1904). However, rhizomorphs of *R. corynecarpos* are thick (1–2 mm) and white with abundant club-shaped branches (Fig. 1a–c). Since its original description from Suriname, this fungus has been recorded in Brazil (Berkeley 1856; Hennings 1904) and Guyana (Wakefield 1934), where it was reported to be associated with the crown dieback of trees. Hennings (1904) also noted the presence of this fungus as an important construction material in bird nests, which was subsequently observed by ornithologists in nests of the Guianan streaked antwren (*Myrmotherula surinamensis*) (Sick 1957) and the paradise tanager (*Tangara chilensis*) (Wood et al. 1992).

Phylogenetic placement of *R. corynecarpos* was unknown because characteristics used in classifying fungi (i.e., sporocarps and spores) are absent. As a result, the genus *Rhizomorpha* Roth has a tangled taxonomic history. The genus was erected for fungal species that produce sterile rhizomorphs (Roth 1791), which is now known to be an assemblage of many non-related fungi in the Ascomycota and Basidiomycota. The type of this genus, *R. fragilis* Roth, forms sterile black rhizomorphs that were shown to be rhizomorphs of an *Armillaria* species (Donk 1962); thus, *Armillaria* and *Rhizomorpha* are synonyms. Stalpers et al. (in press) are proposing to protect *Armillaria* over *Rhizomorpha* since *Rhizomorpha* is the older name and therefore has priority. Currently, there are 117 names of *Rhizomorpha* in Index Fungorum (indexfungorum.org). While some of these species are now known to represent anamorphs of Xylariaceae species and have been transferred into the appropriate genera (i.e., *Rosellinia necatrix* Berl.:Prill.) (Berlese 1892), many others remain undefined.

We used recently collected specimens of *R. corynecarpos* from Belize and Guyana to conduct phylogenetic analyses, resolve the classification for this species, and determine the correct name for it. Given the similar ecological habit of rhizomorphs produced by *R. corynecarpos* and those of species in the Marasmiaceae, we also wanted to explore the hypothesis that these two rhizomorph-forming lineages are closely related. As a result of this study, a new combination, *Brunneocorticium corynecarpon* (Kunze) R. A. Koch, Lodge, Nakasone & Aime, is proposed. Photographic evidence from Brazil, Ecuador, and Peru is also presented as it relates to the ecology, nutritional strategy, and dispersal by birds of *B. corynecarpon*.

Materials and methods

Collections, observations, and microscopy Collecting expeditions across Belize were conducted between 2001 and 2005, where specimens of *R. corynecarpos* were collected in August 2001 at Caves Branch near Belmopan (17° 14′ 0″N, 88° 42′ 42″W at 92 m asl) and in November 2001 at Douglas da Silva, in the Cayo District (15° 58′ 13.65″N, 88° 59′ 31.55″W at 450 m asl), and dried over low heat. Collecting expeditions to the Upper Potaro River Basin in the west-central Pakaraima Mountains of Guyana were conducted during the rainy seasons of May–July 2015–2017 in forests dominated by *Dicymbe corymbosa* Spruce:Benth. and *Dicymbe altsonii* Sandw. (Fabaceae subfam. Caesalpinioideae) (Isaacs et al. 1996; Henkel 2003). Specimens of *R. corynecarpos* were collected within a 15-km radius of a previously established base camp (5° 18′ 04.80″N, 59° 54′ 40.40″W) and field-dried with silica gel. Specimens from Belize are deposited in the Herbarium at the Center for Forest Mycology Research at the Forest Products Laboratory (CFMR) with duplicates at the Forestry Herbarium in Belize (BRH), while specimens from Guyana are deposited in the Kriebel Herbarium (PUL) at Purdue University and the Guyana National Herbarium (BRG). Observations of this fungus were made at the Sani Lodge, Rio Napo, Ecuador, in August 2017; the Manu Biosphere Reserve, Peru, in October 2014; and at the Private Reserve of Natural Heritage, RPPN Cristalino, Mato Grasso, Brazil, in June 2015 and June–July 2017.

Micromorphological features based on dried specimens collected from Belize and Guyana were examined in the laboratory using an Olympus BX43 compound microscope and photographed with a QIClick™ CCD camera. The different layers of the rhizomorphs were sectioned by hand and mounted in water and 1% aqueous Congo red. Hyphal dimensions were measured under a 100× objective.

Molecular methods DNA was extracted from preserved tissue using the Wizard® Genomic DNA Purification Kit (Promega Co., WI, USA). PCR was performed at the following loci: internal transcribed spacer (ITS) region (inclusive of ITS1, 5.8S, and ITS2 regions), using the primer pair ITS1F and ITS4B (Gardes and Bruns 1993), the nuclear ribosomal large subunit DNA (LSU) using the primer pair LSU4B (Aime and Phillips-Mora 2005) and LR6 (Moncalvo et al. 2000), and the nuclear ribosomal small subunit DNA (SSU) using the primer pair NS3 and NS8

Fig. 1 *Brunneocorticium corynecarpon*. **a–c** Rhizomorphs. **d–f** Signs and symptoms of disease. **g** Rhizomorphs incorporated into a nest of a snow-capped manakin, Mato Grasso, Brazil. **h** Rhizomorphs incorporated into a nest of an unknown bird species, Manu Biosphere Reserve, Peru. **i** Bare-necked fruitcrow carrying rhizomorphs, Mato Grasso Brazil. Photo credits: **a** M. Catherine Aime; **b–d**, **h** Susanne Sourell; **e**, **f** Joseph M. Wunderle, Jr.; **g**, **i** Richard C. Hoyer/Birdernaturalist

(White et al. 1990). Reactions included 12.5 μL of Promega PCR Mastermix (Promega Co., WI, USA), 1.25 μL of each primer (at 10 μM), and approximately 20 ng of DNA. The final reaction volume was 25 μL. Uncleaned PCR products were sent to GeneWiz® (South Plainfield, NJ, USA) for sequencing. Sequences were manually edited using Sequencher 5.2.3 (Gene Codes Corporation, MI, USA).

Phylogenetic analyses Initial BLAST searches were done with both the ITS and LSU sequences of *R. corynecarpos* to identify the most closely related genera, which included *Brunneocorticium*, *Campanella*, and *Tetrapyrgos*. The final dataset, composed of sequence data from 33 collections, included exemplars from the three closely related aforementioned genera, along with representatives from other genera in the Marasmiaceae. Sequences from the sterile white basidiomycete specimen 3034, closely related to *Campanella* (Vinnere et al. 2005), Agaricales specimen JMCR.34 (Moncalvo et al. 2002), and *Neocampanella blastanos* (Nakasone et al. 2009), were also included. *Anthracophyllum archeri* and *Omphalotus olearius* served as outgroup taxa *fide* Matheny et al. (2006b). Collection information for all specimens and GenBank accession numbers for the included sequences are compiled in Table 1. Sequences

were aligned in Mega 5.0 (Tamura et al. 2011) using the MUSCLE algorithm (Edgar 2004) with refinements to the alignment done manually. Individual gene alignments were concatenated manually after inspection for intergene conflict. PartitionFinder v1.1.0 (Lanfear et al. 2012) was used to determine the best partition strategy and the best models of molecular evolution for both analyses. Phylogenies were reconstructed using maximum likelihood (ML) and Bayesian methods. Maximum likelihood bootstrap analysis for phylogeny and assessment of the branch support by bootstrap percentages (% BS) was performed using RAxML v.2.2.3 (Stamatakis 2006). One-thousand bootstrap replicates were produced. Bayesian analyses for the reporting of Bayesian posterior probability (BPP) support for branches was conducted on a concatenated dataset using the program Mr. Bayes v.3.2.2 (Ronquist et al. 2012). Four simultaneous, independent runs, each with four Markov chain Monte Carlo (MCMC) chains, were initiated and run at a temperature of 0.15 for 20 million generations, sampling trees every 1000 generations until the standard deviation of the split frequencies reached a final stop value of 0.01. We discarded the initial 10% of trees as burn-in and produced a maximum clade credibility tree from the remaining trees using TreeAnnotator; 70% BS and 0.90 BPP represent well-supported lineages. The final alignment and phylogeny can be accessed in TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S22779).

Results

Observations, sequence generation, and phylogenetic analyses Seven collections of *R. corynecarpos* were made in Guyana and two from Belize. Of the seven collections from Guyana, four (MCA 5681, MCA 5803, MCA 6199, and MCA 6225) were made in a 2-km^2 area approximately 1.4 km southwest of basecamp, RAK 247 was made 2.5 km south of basecamp, MCA 5784 was made less than 1 km south from basecamp, and MCA 5856 was made 8 km east of basecamp. All collections from Guyana and one of the two from Belize were sequenced. This fungus was also observed in Brazil, Ecuador, and Peru. Rhizomorphs of *R. corynecarpos* were found incorporated into the nest of a snow-capped manakin (*Lepidothrix nattereri*) in Brazil (Fig. 1g), a purple-throated fruitcrow (*Querula purpurata*) in Ecuador, and an unknown bird species in Peru (Fig. 1h). An observation of the bare-necked fruitcrow (*Gymnoderus foetidus*) gathering *R. corynecarpos* rhizomorphs for nesting material was also made in Brazil (Fig. 1i).

Fourteen ITS, 10 LSU, and 12 SSU sequences were generated in this study, ranging from 475 to 825, 807–931, and 713–1780 bp, respectively. After the ends of the individual alignments were trimmed, the size of the aligned datasets was as follows: ITS was 782 bp, LSU was 945 bp, and

SSU was 1677 bp. Seven ITS, five LSU, and five SSU sequences of *R. corynecarpos* were generated from specimens collected over 3 years in Guyana; these specimens share 100% (573/573), 100% (768/768), and 100% (1109/1109) nucleotide identity at ITS, LSU, and SSU, respectively. The specimens from Guyana and the one sequenced specimen from Belize share 98% (560/573 bp), 99% (763/768 bp), and 100% (1109/1 l09 bp) nucleotide identity at ITS, LSU, and SSU, respectively. The alignment was separated into two partitions: (1) ITS and (2) LSU and SSU, implementing the GTR + GAMMA + I model for both partitions for the ML and Bayesian analyses as suggested by PartitionFinder. Two regions of 77 and 56 bp were excluded from the ITS partition due to poor alignment. Both ML and Bayesian analyses of ITS, LSU, and SSU recovered *R. corynecarpos* as sister to *Brunneocorticium bisporum* (Burds. & Nakasone) Nakasone with high statistical significance (94% BS and 0.95 BPP) (Fig. 2). These two species are the sister lineage to *Neocampanella blastanos* (Boidin & Gilles) Nakasone, Hibbett, & Goranova (82% BS and 0.97 BPP). This species is resolved to the tetrapyrgoid lineage of Marasmiaceae *fide* Moncalvo et al. (2002) with high statistical significance (98% BS and 0.98 BPP).

Taxonomy

Brunneocorticium corynecarpon (Kunze) R.A. Koch, Lodge, Nakasone, & Aime, comb. nov., Figures 1, 2, and 3.
    ≡ *Rhizomorpha corynecarpos* Kunze in Weigelt, Exsiccati Surinam: [unnumbered]. 1828.
    ≡ *Rhizomorpha corynephora* Kunze in Weigelt, Exsiccati Surinam: [unnumbered]. 1828 [orthographic variant].
    MycoBank: MB 825519.
    Lectotype (designated here): Surinam[e]. leg. et exsicc. Weigelt 1827, as *R. corynecarpos* Kz. with diagnosis (BPI—910,613).
   **Description:** Sterile basidiomycete without known anamorph or teleomorph, but forming characteristic dangling white, knobby rhizomorphs (Fig. 1a–c) and also occasionally sheathing small branches (Fig. 1d–f). Appressed, translucent-white mycelial fans were observed in Brazil causing a web-blight of young shoots, resulting in a necrosis that progressed from the green stems into the leaf bases and eventually killing the entire shoot (Fig. 1e, f); the pathogenic phase was only observed under very wet conditions. The white knobby rhizomorphs are persistent, dangling from tree and shrub branches, up to a half-meter in length with a hydrophobic surface. The friable crusty outer white layer of the rhizomorph is composed of generative hyphae with clamp connections (Fig. 3a), and amorphous and crystalline materials embedded in a thin sheath of colorless and very narrow (< 0.3-µm diameter) branched hyphae

Table 1 Taxa selected for phylogenetic analysis

Name	Specimen ID	Origin	ITS*	LSU*	SSU*
Agaricales sp.	3034	Australia	AY445119[a]	AY445113[a]	AY445116[a]
Agaricales sp.	JMCR.34			AF261341[b]	
Anthracophyllum archeri	PBM 2201		DQ404387[c]	AY745709[d]	DQ092915[e]
Brunneocorticium bisporum	Chen 774	China		DQ679921[f]	
Brunneocorticium bisporum	Wu 9708–292	China		DQ679922[f]	
Brunneocorticium corynecarpon	FP-150726	Belize	MG717357[g]	MG717346[g]	MG717334[g]
Brunneocorticium corynecarpon	MCA 5681/PUL F22321	Guyana	MG717358[g]		
Brunneocorticium corynecarpon	MCA 5784/PUL F22322	Guyana	MG717359[g]	MG717347[g]	MG717335[g]
Brunneocorticium corynecarpon	MCA 5803/PUL F22323	Guyana	MG717360[g]	MG717348[g]	MG717336[g]
Brunneocorticium corynecarpon	MCA 5856/PUL F22324	Guyana	MG717361[g]	MG717349[g]	MG717337[g]
Brunneocorticium corynecarpon	MCA 6199/PUL F22325	Guyana	MG717362[g]		
Brunneocorticium corynecarpon	MCA 6225/PUL F22326	Guyana	MG717363[g]	MG717350[g]	MG717338[g]
Brunneocorticium corynecarpon	RAK 247/PUL F22327	Guyana	MG717364[g]	MG717351[g]	MG717339[g]
Campanella sp.	MCA 1689	Guyana	AY916670[h]	AY916668[h]	AY916669[h]
Campanella sp.	MCA 3234/PUL F22328	Florida, USA	MG717365[g]	MG717352[g]	
Campanella sp.	MCA 5439/PUL F22329	Guyana	MG717366[g]	MG717353[g]	MG717340[g]
Campanella sp.	RV98/79			AF261340[b]	
Campanella sp.	RV-PR075			AF261339[b]	
Chaetocalathus liliputianus	MCA 485	Puerto Rico	AY916682[h]	AY916680[h]	AY916681[h]
Chaetocalathus cf. columellifer	MCA 2538	Ecuador	AY916686[h]	AY916684[h]	AY916685[h]
Crinipellis sp.	MCA 1527	Guyana	AY916701[h]	AY916699[h]	AY916700[h]
Crinipellis sp.	MCA 2240	Guyana	MG717367[g]	AY916695[h]	
Marasmius aff. crinis-equi	MCA 7492	Cameroon	MG717368[g]	MG717354[g]	MG717341[g]
Marasmius rotula	PBM 2563	New Hampshire, USA	DQ182506[c]	DQ457686[i]	DQ113912[c]
Marasmius sp.	MCA 1708	Guyana	AY916720[h]	AY916718[h]	AY916719[h]
Moniliophthora perniciosa	MCA 2520	Ecuador	AY916743[h]	AY916742[h]	MG717342[g]
Moniliophthora roreri	MCA 2521	Ecuador	MG717369[g]	AY916750[h]	MG717343[g]
Neocampanella blastanos	FP-150016	Puerto Rico		FJ663209[j]	JN368231[j]
Omphalotus olearius	CBS 102282	Slovenia	DQ494681[i]	DQ470816[i]	DQ459374[c]
Tetrapyrgos nigripes	DAOM186918			AF261337[b]	
Tetrapyrgos nigripes	MCA 6925/PUL F22330	Indiana, USA	MG717370[g]	MG717355[g]	MG717344[g]
Tetrapyrgos subdendrophora	DAOM175393			AF042629[k]	
Tetrapyrgos subdendrophora	ATCC 42449	Canada	AY445121[a]	AY445115[a]	AY445118[a]
Tetrapyrgos sp.	MCA 2162	Guyana		AY916757[h]	MG717345[g]
Tetrapyrgos sp.	MEL:2354777	Australia	KP311437[l]	KP311346[l]	

*GenBank accession number for each gene

[a] Vinnere et al. (2005)

[b] Moncalvo et al. (2002)

[c] Matheny et al. (2006a)

[d] Matheny et al. (2004)

[e] Matheny and Hibbett (2005)

[f] Wu et al. (2007)

[g] This study

[h] Aime and Phillips-Mora (2005)

[i] Matheny et al. (2006b)

[j] Nakasone et al. (2009)

[k] Moncalvo et al. (2000)

[l] Bonito and May (2014)
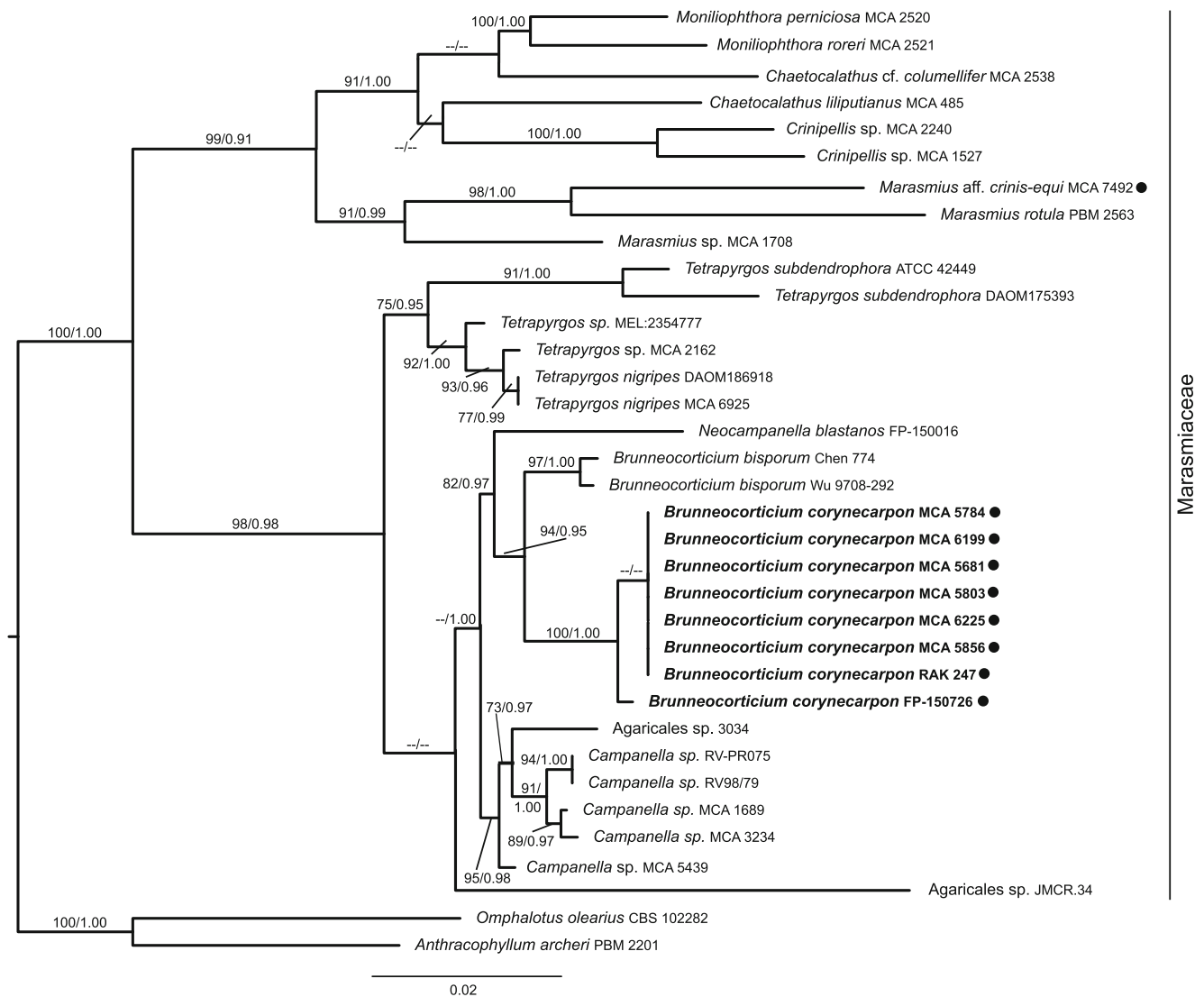
Fig. 2 Maximum-likelihood phylogeny generated from the analysis of three gene regions (ITS, LSU, and SSU) from 33 taxa in the Marasmiaceae (delimited by the black bar) and two outgroup taxa, *Anthracophyllum archeri* and *Omphalotus olearius*, showing a sister relationship of *Brunneocorticium corynecarpon* to *B. bisporum*. Black circles next to the species name indicate known rhizomorph formers. Support values shown above branches represent %BS/BPP; − represents no support

(dendrohyphidia) (Fig. 3b). The inner core of the rhizomorphs, 650–1260 μm in diameter (Fig. 3d), is composed of parallel, thick-walled, pale brown skeletal hyphae 2.2–3.5 μm in diameter, clamp connections rarely seen (Fig. 3c). Growing from tree and shrub branches in wet or seasonally wet tropical forests.

Remarks: The peculiar nodules were interpreted by Kunze to be perithecia as the diagnosis from the lectotype label reads "… cylindrical ramosa flexuosa peritheciisque clavato-subcapitatis divergentibus niveo-lanatis copiosisissimus approximatis." There are two other specimens from Suriname at BPI that may be from the Weigelt exsiccati (BPI—US0456145) or the original collection by Weigelt (Michener collections volume 37 sheet 36, as *R. corynephora* Kze./*Isaria arbuscula* Schw.).

Discussion

Phylogenetic reconstruction Rhizomorphs of *Crinipellis* and *Marasmius* Fr. species are most commonly encountered in tropical forests as masses that form aerial webs in the understory. The rhizomorphs grow gravitropically and intercept leaf litter as it falls (Hedger 1990; Hedger et al. 1993). We observed *B. corynecarpon* forming these similar aerial litter-trapping webs that they may use to supplement their resources beyond the leaves and shoots they have killed (Fig. 1e, f). The placement of *B. corynecarpon* in the Marasmiaceae supports our hypothesis that these canopy rhizomorph-forming fungi are closely related. The inner core of the rhizomorphs of *B. corynecarpon* resembles rhizomorphs of other marasmioid fungi, by being composed of densely packed, thick-walled skeletal

Fig. 3 Micromorphological features of *B. corynecarpon*. **a** Generative hypha with a clamp, indicated by the arrow. **b** Dendrohyphidia. **c** Thick-walled, skeletal hyphae from the inner core of a rhizomorph. **d** Rhizomorph cross section. Scale bars: **a**–**c** = 10 μm, **d** = 200 μm
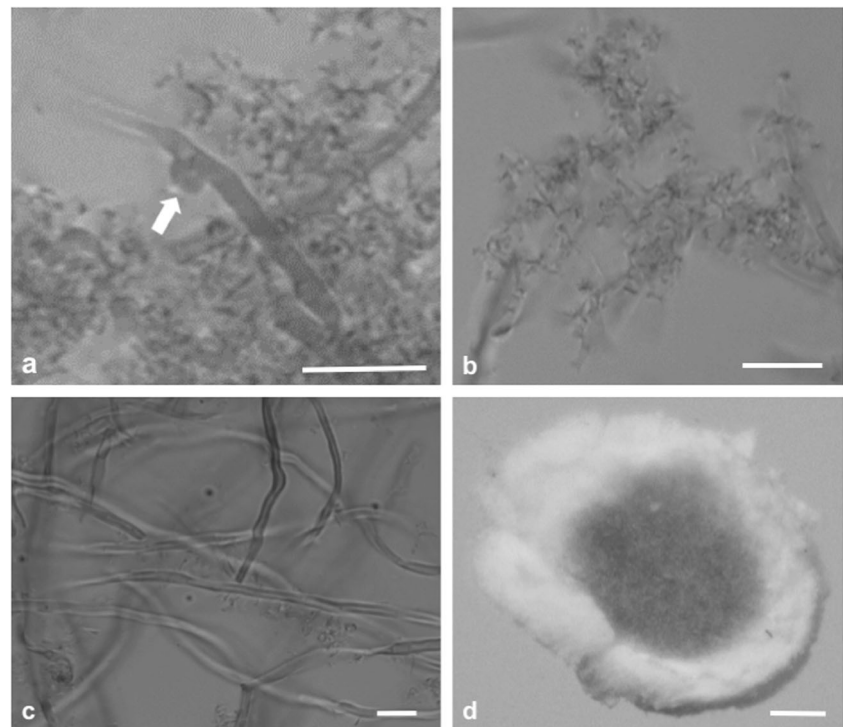
hyphae (Cairney 1991b), suggesting that these structures are homologous within this family. While we included only one other known rhizomorph-forming species in our phylogeny, *M. crinis-equi*, many of the other species in *Marasmius* sect. *Marasmius*, subsect. *Sicciformes* produce abundant rhizomorphs (Antonín 2007). At least three other species, including *M. crinis-equi*, *M. nigrobrunneus* (Hedger et al. 1993), and *M. guyanensis* (R. A. Koch, personal observation), are known to produce litter-trapping networks. Besides genera in the Marasmiaceae, other known rhizomorph-forming genera include *Micromphale* (Hedger et al. 1993) and *Armillaria* (Koch et al. 2017), which all belong in the Marasmiineae (Dentinger et al. 2016). Phylogenetic placement of *B. corynecarpon* within the Marasmiineae is consistent with what is known about this suborder, in that one of the characteristics is production of vegetative rhizomorphs in many of the members (Dentinger et al. 2016).

Our phylogenetic analysis also revealed *B. corynecarpon* as sister to *B. bisporum*. Whereas *B. corynecarpon* forms sterile rhizomorphs and lack basidia, *B. bisporum* is a crust fungus fruiting on living trunks or fallen branches that produces basidia in a hymenium (for description, see Burdsall and Nakasone (1983), Boidin et al. (1996) as *Dendrothele bispora*, and Wu et al. (2007) as *Brunneocorticium pyriforme*). Although *B. bisporum* lacks rhizomorphs, it does develop brown, thick-walled skeletal hyphae in the subiculum of the sporocarp that are similar to the thick-walled skeletal hyphae found in the rhizomorph core of *B. corynecarpon*. Both species have clamped generative hyphae. In addition, dendrohyphidia in the hymenium are heavily encrusted in *B. bisporum* and

similar structures were observed encasing the rhizomorphs in *B. corynecarpon*. These morphological similarities, coupled with the phylogenetic analyses, support the transfer of *Rhizomorpha corynecarpos* into *Brunneocorticium*. Phylogenetic divergence between the collections of *B. corynecarpon* from Guyana and Belize (Fig. 2) suggests that specimens from these two countries could represent different species. However, we treat them as tentatively conspecific at this time given the lack of additional characters that would support these as distinct species.

Pathogenicity We observed *B. corynecarpon* killing native shrubs and trees in Belize, Guyana, Peru (Fig. 1d), Suriname, and Brazil (Fig. 1e, f). Mycelium fully encases the outer cortex of infected stems (Fig. 1d–f) and can spread to the leaves (Fig. 1e, f). The characteristic rhizomorphs of *B. corynecarpon* grow out of infected twigs and are likely used as a means of further spreading this disease. The possible pathogenicity of *B. bisporum* should be tested given the morphological similarities and the phylogenetic proximity to *B. corynecarpon*.

There is at least one other known pathogenic aerial rhizomorph-forming species in the Marasmiaceae, *M. crinis-equi*, which is the causal agent of horse-hair blight. The disease is spread from infected twigs to healthy twigs by rhizomorph extension in the canopies of tree crops like tea (Hu 1984). Additionally, several distantly related basidiomycete species in the Cantharellales that produce arboreal rhizomorphic cord systems are also the causal agents of tree

and shrub diseases, including thread blight caused by *Rhizoctonia noxia* (Donk) Oberw., R. Bauer, Garnica, & Kirschner (Ceratobasidiaceae, Cantharellales) and several related species previously assigned to *Ceratobasidium* or *Thanatephorus* (Ceresini et al. 2012; Gónzalez et al. 2016). As with rhizomorph-forming agaric fungi, cords of arboreal *Rhizoctonia* species are also used for dispersal (Burt 1918).

It is possible that adaptations to the litter-trapping nutritional strategy of these rhizomorph-forming species have made them effective pathogens. For instance, the rhizomorphs of *M. crinis-equi* emit defoliation-inducing volatiles; these volatiles cause leaves to drop, which subsequently become trapped in the aerial webs (Su et al. 2011) or held fast by rhizomorph attachments (byssi) made prior to abscission, although leaf necrosis has also been observed with attachments by this species (Hedger et al. 1993). Su et al. (2011) hypothesized that inducing defoliation is adaptive for *M. crinis-equi* because it is easier to obtain nutrients from detached leaves. While volatile production is unknown in *B. corynecarpon* and other aerial rhizomorph-forming species, future studies should examine whether it employs a similar strategy to *M. crinis-equi* for nutrient acquisition.

Ecology and dispersal While the presence of clamp connections in the generative hyphae is evidence that this fungus is dikaryotic, a sporulating morph has never been observed from the earliest documenters of *B. corynecarpon* (Hennings 1904; Wakefield 1934) to modern researchers, and therefore still remains unknown or nonexistent. Given the sister relationship with a crust species, it is possible that *B. corynecarpon* also forms this type of sporocarp. In the Pakaraima Mountains, an area where extensive collecting and sequencing of saprotrophs has occurred during the last 15 years (Henkel et al. 2012), no likely sporocarps have ever been found for this species. Placement of *B. corynecarpon* rhizomorphs in moist chambers, with preservation of samples every 2 h for 24 h, failed to induce sporulation. This fungus has only been observed and collected in wet tropical forests, an ecosystem with a substantial and constant production of leaf litter (Golley 1983)—the resource aerial rhizomorph-forming fungi utilize (Hedger 1990; Hedger et al. 1993). One hypothesis for why litter-trapping fungi do not often sporulate is that tropical rainforests have a substantial litter layer, which may favor rhizomorph production; therefore, there may be greater selection for the production of long-lived rhizomorphs and against spore production as a means for spreading fungal inoculum (Cairney 1991a).

We encountered strands of *B. corynecarpon* being carried by or incorporated into the nests of Neotropical birds (Fig. 1g–i); thus, birds have the ability to act as a dispersal vector for *B. corynecarpon*. With an effective dispersal strategy of its vegetative structures that utilizes birds, *B. corynecarpon* may not need to rely on spore production as a means for dispersal.

Incorporation of rhizomorphs into bird nests has been previously reported for *Marasmius* rhizomorph-forming species (see Aubrecht et al. 2013, and citations within). Adaptive advantages for the birds that incorporate these structures into their nests remains speculative; experimental evidence showed that marasmioid rhizomorphs take up significantly less water compared to other grassy fibers that may be used in bird nests, which Freymann (2008) hypothesized could be beneficial to birds in the tropics, where wet or cold nests provide a substrate for pathogens (Singleton and Harper 1998). Additionally, marasmioid rhizomorphs are longer than other fibers available to birds to use for nest construction (Freymann 2008). Consistent with the aforementioned characteristics of marasmioid rhizomorphs, rhizomorphs of *B. corynecarpon* have a hydrophobic outer layer and have been found up to 50 cm long. Finally, marasmioid rhizomorphs produce biochemical agents, like antibiotics, so another benefit to using rhizomorphs could be the release of active substances when they come into contact with nestlings (Aubrecht et al. 2013). However, the production of active biochemical agents remains to be tested in *B. corynecarpon*.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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