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A First Phylogenetic Assessment of *Dictyonemo* s.lat in Southwestern North America Reveals Three New Basidiolichens, Described in Honor James D. Lawrey

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A first phylogenetic assessment of *Dictyonema* s.lat. in southeastern North America reveals three new basidiolichens, described in honor of James D. Lawrey

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Abstract. Three species of lichenized basidiomycetes in the *Dictyonema* clade from southeastern North America are described as new to science: *Cyphellostereum georgianum*, *C. jamesianum* and *Dictyonema lawreyi*, all with a crustose-filamentous growth form. Based on ITS sequences, the species form well-supported monophyletic clades in a phylogeny and are represented by at least two specimens each. They are also distinguishable by morphological and anatomical characters. These new findings emphasize the importance of lichenological studies in North America, especially in historically understudied taxonomic groups, such as basidiolichens. This study is dedicated to James D. Lawrey on the occasion of his 70th birthday.

Key words: Lichen systematics, *Hygrophoraceae*, United States, biodiversity

Introduction

The *Dictyonema* clade is the largest group of basidiolichens (Lücking et al. 2017a). It belongs to tribe *Arrheniae*, subfamily *Lichenomphaloideae* and family *Hygrophoraceae* in the order *Agaricales* (Lawrey et al. 2009; Lodge et al. 2014). *Hygrophoraceae* comprises over 600 species, most of which are non-lichenized, except for the *Dictyonema* clade and the genus *Lichenomphalia* (Lodge et al. 2014). Species in the *Dictyonema* clade occur worldwide but the highest diversity is in the Neotropics (Dal Forno et al. 2013; Lücking et al. 2014, 2017b). The clade currently has 137 accepted species in five genera: *Acantholichen*, *Cora*, *Corella*, *Cyphellostereum* and *Dictyonema* (s.str.); however, a few historical genus names that have an uncertain taxonomic status persist (Lücking et al. 2013). All five of the accepted genera occur in the New World, whereas other regions almost exclusively feature *Cyphellostereum* and *Dictyonema*.

Aside from Mexico, the *Dictyonema* clade is sparsely represented in North America. In the 'Cumulative Checklist for the Lichen-forming, Lichenicolous and Allied Fungi of the Continental United States and Canada' (Esslinger 2018), four taxa from this clade are listed: *Cora glabrata* [syn.: *C. pavonia*, *Dictyonema glabratum*, *D. pavonium*], *D. moorei*, *D. phyllogenum* and *D. sericeum*. Two additional names on the list are considered synonyms or misidentifications: *Dictyonema guadalupense* [= *D. sericeum*] and *D. irpicinum* (Esslinger 2018). The genera *Acantholichen*, *Corella* and *Cyphellostereum* were not reported in Esslinger's list but *D. phyllogenum* is now classified in *Cyphellostereum* (Lücking et al. 2013), so this genus is recognized from North America. The taxonomic status of *D. guadalupense* is unclear but certainly it is not a synonym of *D. sericeum* (Lücking et al. 2013). Given that the *Dictyonema* clade has been shown to contain many more species than proposed by Parmasto (1978), including several hundred alone in the

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genera *Cora* and *Dictyonema* (Lücking et al. 2014, 2017b; Dal Forno 2015), it is safe to say that, with the possible exception of *D. moorei*, none of the names listed for North America actually represent an accurate identification of the taxa occurring in this region.

As of February 20th, 2019, the 'Consortium of North American Lichen Herbaria' (CNALH; http://lichenportal.org/) contained 111 records of continental United States specimens identified as *Cora* or *Dictyonema*, with the exception of one misidentification of *Acantholichen*, which we revised. All collections are from the southeastern United States and the majority of them are from Florida (FL, 90 total, 31 in *Cora* and 59 in *Dictyonema*), with a few specimens from North Carolina (NC, 2), South Carolina (SC, 7), Georgia (GA, 4), and Louisiana (LA, 5), all in *Dictyonema*. A single specimen (*Dictyonema* sp.) is mentioned from Texas, and two samples lack information regarding their state provenance. Different names have been applied to identify these specimens: *Cora glabrata* and *C. pavonia* (FL), '*Dictyonema cincinnatum*' (as '*Dichonema cincinnatum*'; FL, SC), *D. glabratum* (FL, ≡ *Cora glabrata*), *D. guadalupense* (FL), *D. irpicinum* (FL, GA), *D. moorei* (FL), *D. pavonium* (FL, ≡ *Cora pavonia*), *D. reticulatum* (SC), *D. sericeum* (FL, GA, LA, NC, SC) and *D. spongiosum* (FL). *Dictyonema sericeum* is also cited for Alabama by Parmasto (1978). These names agree with those included in Esslinger's list (2018), with the exception of *D. spongiosum* and the apparently unpublished name '*Dichonema cincinnatum*', interpreted in CNALH as '*Dictyonema cincinnatum*'. The latter is based on two collections by the same collector (B. M. Davis) from FL and SC and likely a herbarium-working name. It should not be confused with the cyanobacterium *Scytonema cincinnatum* described from France, neither is it derived from the city of Cinncinati in Ohio; rather, the epithet *cincinnatum* (Latin) refers to 'curly hair', i.e. the typical morphology of many filamentous *Dictyonema* species.

Given the much-revised phylogenetic classification of genera and species in the *Dictyonema* clade (Lücking et al. 2013, 2017b; Dal Forno et al. 2013, 2017; Dal Forno 2015) and that identifications of North American material rely almost entirely on Parmasto's (1978) outdated monograph, virtually nothing is known about the diversity and range of this clade in the United States. The only reported species that might actually be present in North America north of Mexico is the demonstrably widespread *Dictyonema moorei*, which is well characterized by 2–3 rows of cyanobacterial cells inside the fungal sheath. *Dictyonema irpicinum* is restricted to the Paleotropics and *D. guadelupense* likely to the Caribbean, whereas *D. sericeum* and *D. spongiosum* form shelf-like thalli and also appear to be restricted to the Caribbean (Lücking et al. 2013). The genus *Cora* has so far only been found in Florida. and all specimens studied by us belong to a single undescribed species that will be treated in a separate paper.

In order to achieve a more accurate picture of the diversity and taxonomy of filamentous species of *Dictyonema* s.lat. present in North America, we collected fresh material throughout the southeastern United States and obtained molecular data to aid in their classification. We detected three distinct lineages, all new to science – two in the genus *Cyphellostereum* and one in *Dictyonema*, which are described here.

Material and methods

Taxon sampling and phylogenetic analysis. This study is part of a broad systematics study of the *Dictyonema* clade. Most specimens from North America included here were already sequenced and included in prior phylogenetic studies (Dal Forno 2015; Dal Forno et al. 2017). However, to account for newly available ITS sequences not included in previously published datasets, we generated new MAFFT v1.3.7 alignments (Katoh & Toh 2005) on Geneious v11.1.5 (Kearse et al. 2012; File S1 and File S2) and ran new phylogenetic analyses on RAxML-HPC2 on XSEDE (v8.2.10) in the CIPRES portal (Miller et al. 2010), following the same laboratorial and computational procedures as described in Dal Forno (2015) and Dal Forno et al. (2013, 2017). Generated trees were visualized in FigTree v1.4.3 and edited in Photoshop Illustrator. GenBank numbers for the new species are listed in the taxonomy section and in Table S1.

Morphological analysis. Morphological characters were analyzed under a Leica M165 C stereoscope following standard procedures for the group (Lücking et al. 2013). Anatomical thallus characters were investigated by light microscopy using a Leica DM4 B compound microscope, with thallus pieces mounted in tap water. Microscopic measurements were made at 400× and 1000× in water. Images were taken with the aforementioned microscopes with a Leica DFC450 digital camera and processed with Leica Application Suite (LAS) X software. In addition, we used an Olympus DSX 100 compound microscope with Microscope Control v2.1.5 software to generate stacked images.

Results and discussion

Maximum likelihood phylogenetic analysis based on the ITS fungal barcoding marker grouped the sequenced material into three distinct, strongly supported lineages (Figs. 1, 2). Two lineages belong to the genus *Cyphellostereum*, and the two form a strongly supported sister group relationship (Fig. 1), indicating a strong geographic signal for this clade. The closest relative is *C. imperfectum* from Guatemala but this relationship is not well supported. The third lineage is a new species in *Dictyonema* s.str., related to two undescribed species from Brazil and Costa Rica (Fig. 2). The relationship between this new species of *Dictyonema* from the United States and the species from Brazil is not well supported, although the clade with these species and the taxon from Costa Rica is.

Compared to the 111 collections of *Dictyonema* s.lat. listed in CNALH (see above), the eight specimens studied here with molecular data are a small subset covering the easternmost part of the reported distribution range of the *Dictyonema* clade in southeastern North America.

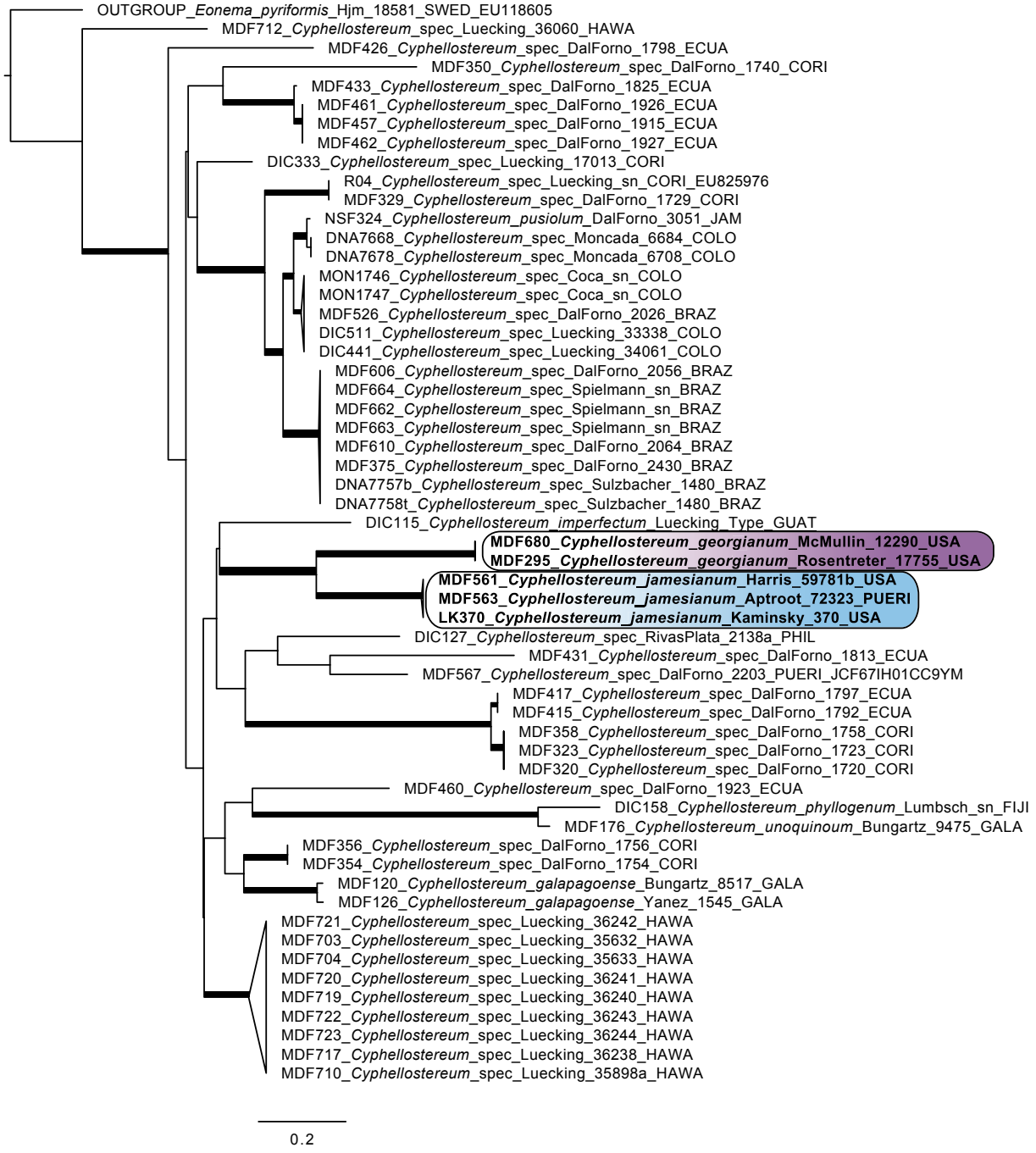

Figure 1. Phylogenetic tree of the genus *Cyphellostereum* inferred by maximum likelihood in RAxML using ITS fungal barcoding (n = 57, alignment 864 bp). Bolded branches have bootstrap values (BS) over 85% and are considered well-supported.

The sequences generated from the North American material did not cluster with the names currently in the 'North American Lichen Checklist' (Esslinger 2018). This supports the notion that the taxa of this clade present in North America do not correspond to the names applied by Parmasto (1978) but likely represent regional endemics. As shown in the species discussion, remarks and figures herein, the three new taxa show distinctive morphologies. These differences may help reassign previously collected material to the current taxonomy. However, there is a notable level of cryptic speciation in *Dictyonema* s.lat. which requires a broader molecular dataset to properly assess the phylogenetic diversity, distribution and morphology of these basidiolichens in North America.

The eight samples included in our study represent three previously unrecognized lineages but they only represent the first step towards a comprehensive study of *Dictyonema* s.lat. in North America. We hope that these results will alert workers to the unrecognized diversity in this clade. Given our prior global sampling, we anticipate that additional new species await discovery in North America, particularly due to the high diversity of unique habitats in this area. This result would be consistent with our detailed studies of *Cora* in the Americas (Lücking et al. 2014, 2017b) and the *Dictyonema* clade in the Galapagos (Dal Forno et al. 2017), which demonstrated that most species in this group are endemic to small areas.

Figure 2. Phylogenetic tree of the genus *Dictyonema* inferred by maximum likelihood in RAxML using ITS fungal barcoding (n = 231, alignment 938 bp). Bolded branches have bootstrap values (BS) over 70% and are considered well-supported. For original tree, see Figure S1.

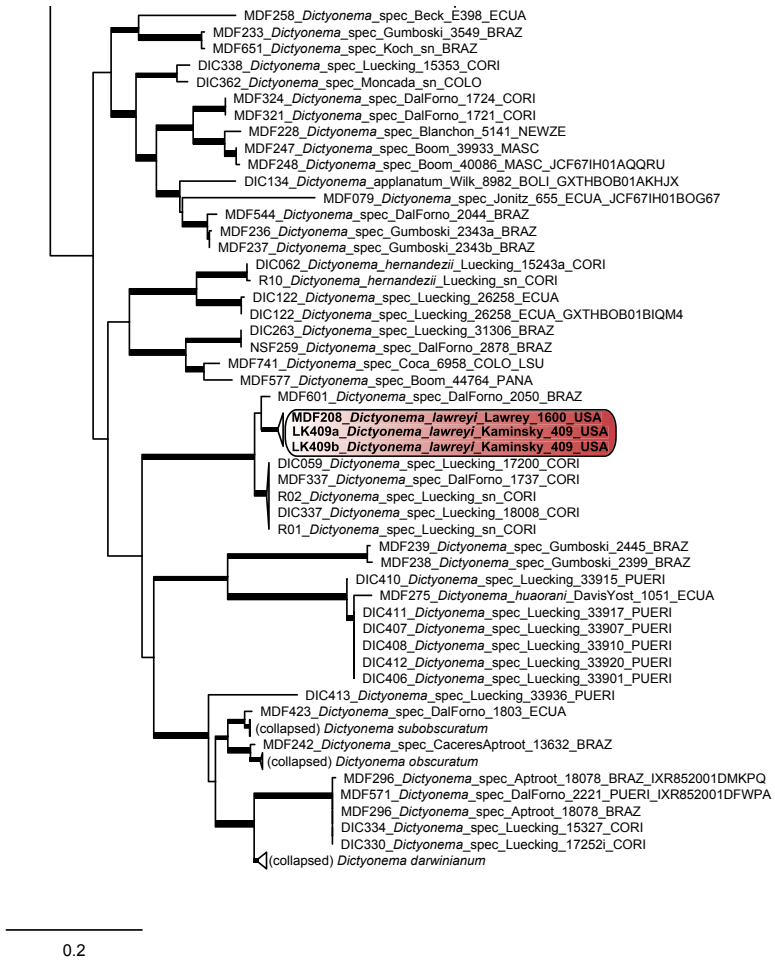

Figure 2. Continued.

Taxonomy

Cyphellostereum georgianum Dal Forno, McMullin & Lücking, sp. nov. (Fig. 3)

MycoBank MB 832378

Diagnosis: Characterized by the opaque, crustose, dark green thallus formed by dense fibrils embedded in an inconspicuous matrix, with abundant corticioid white basidiocarps, and a fungal sheath consisting of irregular, thin, branched hyphae surrounding the cells, partly furnished with clamps.

Type: United States, Georgia, McIntosh County, Harper Lake Park, 31°28′18.9″N (31.47192), 81°36′22.8″W (–81.60632), alt. 25 m (78 ft), on trunk of deciduous tree; 29 March 2013, R. T. McMullin 12290 (CANL – holotype!; US – isotype!).

GenBank ITS barcoding sequences: KY861606 (holotype), KY861529 (paratype)

Description. Thallus epiphytic on tree trunks, crustose-filamentous growth form, developing a continuous mat at 'base', with small irregular elevated thick 'patches' formed by denser fibrils. Upper surface with densely fungal-cyanobacterial fibrils, dark opaque green, with yellowish hue in elevated 'patches' but with bluish 'base'. Thallus composed entirely by cyanobacterial filaments wrapped in fungal sheath; individual cells 7–12.5 µm wide × 5–10 µm high, green to green-bluish, covered by thin elongated fungal cells; heterocytes frequent, pale to bright yellow, 5–7 µm wide × 5–7 µm high, mostly circular; clamp connections observed in loose hyphae forming the thallus and in hymenophore. Hymenophore forming irregular patches, resupinate to corticioid; patches up to 14 mm long and 2 mm wide, white; hymenophore in section up to 100 µm thick, composed of 2–4 µm thick hyphae. Basidioles mostly rounded to clavate, 3–4 µm wide × 12–18 µm high. Basidia and basidiospores not observed.

Etymology. The epithet refers to the state where the type specimens were collected.

Distribution and ecology. Currently only known from the type locality, where it grows on trunks of trees such as *Quercus*. The locality where it was collected has canopy dominated by *Pinus taeda*, with a midstory of *Quercus hemisphaerica*, *Q. geminata*, *Ilex opaca*, *Magnolia grandiflora* and *Carya* sp., and shrub vegetation with *Serrenoa repens*, *Lyonia ferruginea*, *L. lucida* (near wetlands), *Vaccinium arboreum*, *V. tenellum*, *V. stamineum*, *Hamamelis virginiana* and *Ditrysinia fruticosa*.

Remarks. Although possibly originating from a common ancestor, this Georgian species differs from its sister species in South Carolina and Puerto Rico by its dense crustose habit, forming a continuous dark green mat yet with clearly elevated thick patches of dense fibrils, while

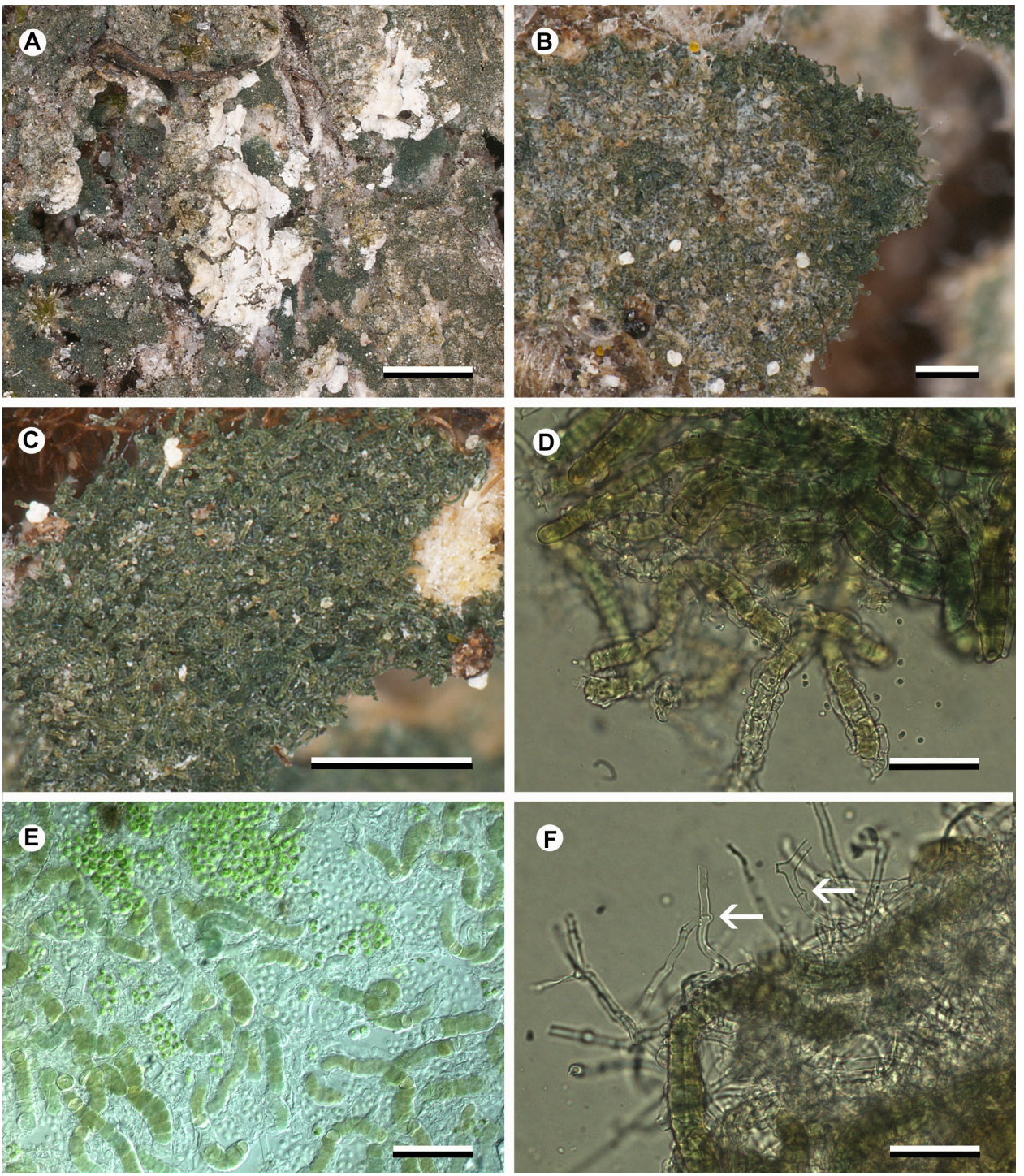

Figure 3. *Cyphellostereum georgianum*. Crustose thallus growing directly on bark and overgrowing bryophytes, with white steroid hymenophores. A–C – general view of thallus observed under dissecting scope. Note reproductive structures, i.e., hymenophores, in A as resupinate white patches; D–F – general view of thallus observed under light microscope. In E, note lichenized fibrils (cyanobacterial cells wrapped in fungal hyphae) and free-living green algae surrounding them. Note clamp connections in F (arrows). Images from specimen collected by T. McMullin 12290 (A–C, E) and from specimen collected by R. Rosentreter 17755 (D, F). Scales: A, B = 2 mm; C = 4 mm; D, F = 30 µm; E = 40 µm.

the sister species has a thinner and more bluish thallus with more defined (separated) fibrils. Close-up observations under a dissecting scope show short yellowish fibrils. The thallus lacks organized layers but parts of it are dominated by a gelatinous matrix formed by photosynthesizing organisms (possibly cyanobacteria and green algae).

Additional specimens examined. United States, Georgia, McIntosh County, Harper Lake Park, 31°28′18.9″N (31.47192), 81°36′22.8″W (–81.60632), alt. 25 m (78 ft), on bark of *Quercus*; 29 March 2013, R. Rosentreter 17755 (SRP – paratype!).

Cyphellostereum jamesianum Dal Forno & Kaminsky, sp. nov. (Fig. 4)

MycoBank MB 832354

Diagnosis: Characterized by the crustose, dark green thallus formed by loose individual fibrils, and a fungal sheath consisting of irregular, thin, branched hyphae surrounding the cells.

Type: UNITED STATES, South Carolina, Berkeley County, Francis Marion National Forest along Forest Service Road 204F, 0.25 miles S of McConnel's Landing, 1.3 miles N of jct w/ Forest Service Road 204, 33°14′29″N, 79°31′16″W, alt. ~12 m, on trunk of 4″ diam. oak; 3 December 2013, R. C. Harris 59781 (NYBG – holotype!).

GenBank ITS barcoding sequences: KY861586 (holotype), MN046975 (FL paratype), KY861587 (PR paratype).

Description. Thallus epiphytic on tree trunks, associated with bryophytes, crustose-filamentous growth form, developing a mat of ±individual to slightly interwoven fungal-cyanobacterial fibrils, dark opaque green to green-bluish. Thallus composed entirely of cyanobacterial filaments wrapped in fungal sheath; filament cells 11–13(–14) µm wide × 4–6(–8) µm high, green-bluish, covered by thin elongated fungal cells; heterocytes frequent, pale to bright yellow; clamp connections observed (in fresh material from Puerto Rico). Hymenophore (only one present) in development forming a round patch, resupinated, 0.5 mm long × 0.5 mm wide, white, smooth, flat.

Etymology. This species honors the work of our esteemed colleague, mentor, and friend, Dr. James D. Lawrey, who

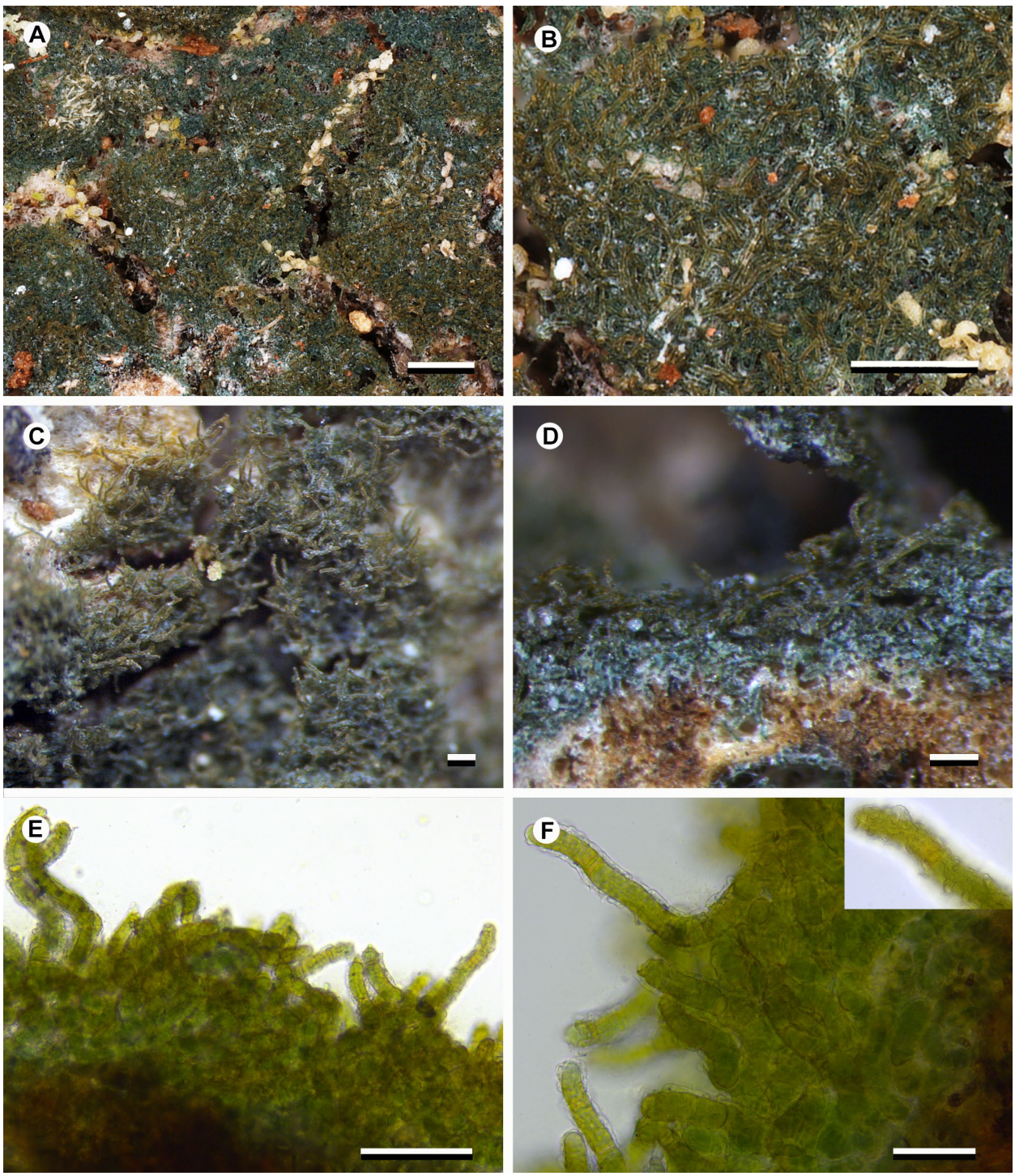

Figure 4. *Cyphellostereum jamesianum*. All images from A. Aptroot 72323. A–C – general view of thallus observed under dissecting scope; E–F – general view of thallus observed under light microscope. Scales: A = 200 µm; B = 400 µm; C–E = 100 µm; F = 50 µm.

contributed to the discovery that the genus *Cyphellostereum* belongs in the *Dictyonema* clade (Lawrey et al. 2009).

Distribution and ecology. This species is known from three localities: two in the southeastern United States and one in Puerto Rico. The type (from South Carolina) was collected in a mature open pine-oak woodland; the Florida specimen is known from old-growth oak-dominated deciduous forest that floods seasonally, and the Puerto Rican specimen from a disturbed forest.

Remarks. This species is sister to *C. georgianum* from Georgia, and both share the crustose-filamentous growth form. However, under a dissecting scope the species are distinct: *C. georgianum* has a thallus organized in dense mats with elevated thick patches of tangled fibrils (Fig. 3), while *C. jamesianum* forms loose, individual to slightly interwoven fungal-cyanobacterial fibrils (Fig. 4).

Additional specimens examined. UNITED STATES, Florida, Sarasota County, Myakka River State Park, off the hiking trail north of the canopy walkway trail; 27°14′39″N, –082°18′W,

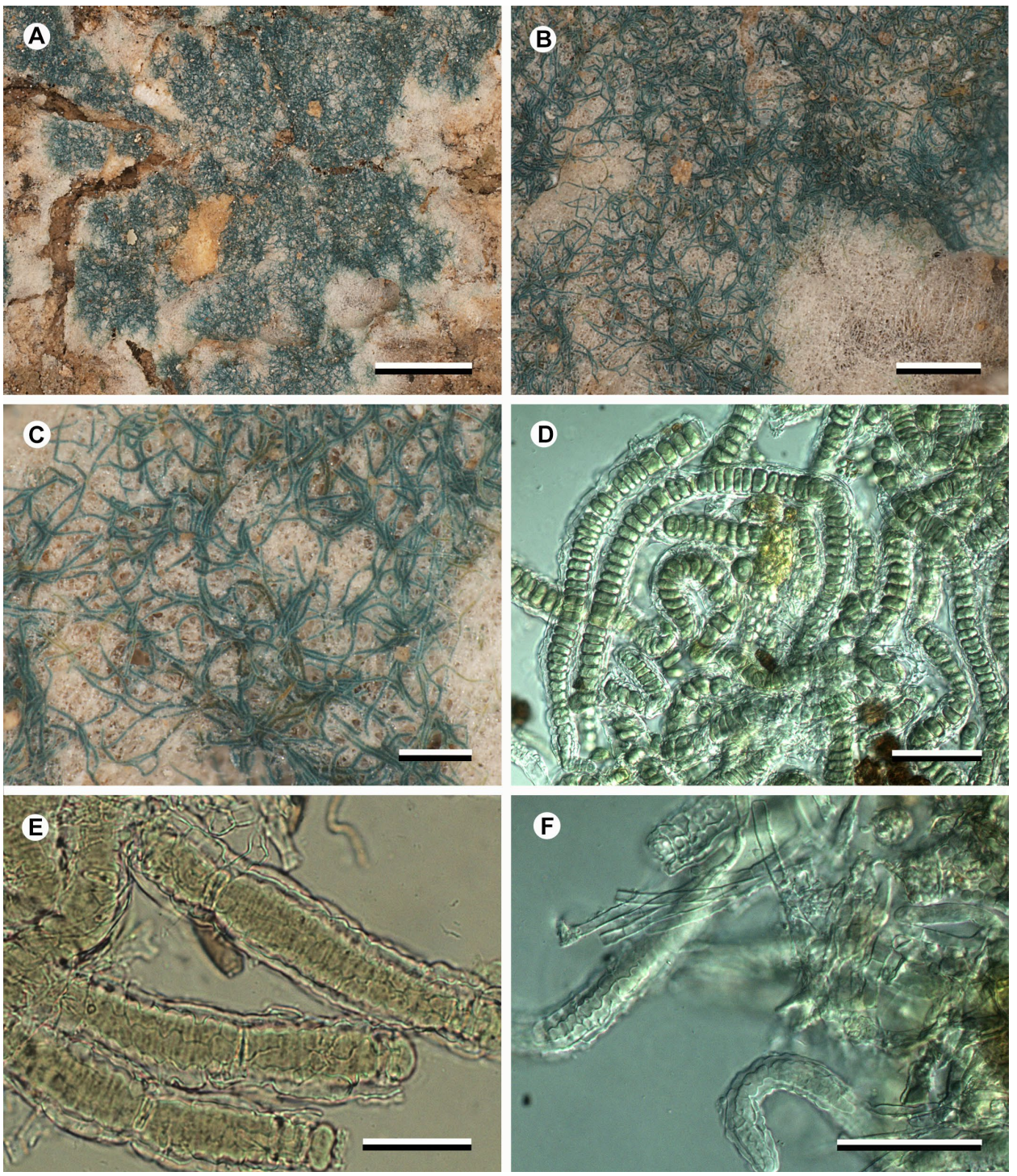

Figure 5. *Dictyonema lawreyi*. All images from J.D. Lawrey 1600 (holotype). Crustose thallus growing directly on bark. A–C – general view of thallus observed under dissecting scope. Note white distinct prothallus and hypothallus; D–F – general view of thallus observed under light microscope. Note jigsaw-puzzle-shaped fungal sheath hyphae. Scales: A, C = 200 µm; B – 500 µm; D, F = 50 µm; E = 25 µm.

14 m; old-growth oak-dominated seasonally flooded hardwood forest, on oak; 16 January 2018, L. Kaminsky 370 (FLAS, US – paratypes!). PUERTO RICO, Utuado, Río Abajo State Forest, ~65 km WSW of San Juán and 15 km S of Arecibo, access road in forest beyond camp ground; 18°19′N, 66°43′W, 380 m; lowland evergreen and seasonal evergreen wet forest on karst, disturbed primary and old-growth secondary forest, on tree bark; 20 February 2014, A. Aptroot 72323 (US, ABL, F, UPR – paratypes!).

Dictyonema lawreyi Dal Forno, Kaminsky & Lücking, sp. nov. (Fig. 5)

MycoBank MB 832355

Diagnosis: A turquoise appressed-filamentous *Dictyonema* with a well-developed, arachnoid, white prothallus and loosely arranged and prostrate turquoise filaments resting on a white hypothallus.

Type: United States, Florida, Marion County, Ocala National Forest, 2.2 miles N of Florida Highway 40 on Florida Highway 19, Mormon Branch on E side of road, 29°12′N, 81°39′W, on *Magnolia*, 2 January 1996; J. D. Lawrey 1600 (US – holotype!; GMUF – isotype!).

GenBank ITS barcoding sequences: KY861507 (holotype), MN046973 (paratype).

Description. Thallus epiphytic on tree trunks, with crustose-filamentous growth form, white hypothallus extending to form distinct prothallus with continuous, fine mat of turquoise fibrils on top. Upper surface with very loosely interwoven and irregular fungal-cyanobacterial fibrils. Patches up to 5 cm long, ±continuous. Thallus composed mainly of cyanobacterial filaments wrapped in fungal sheath; filament cells 12–17.5 µm wide × 3–8 µm high, green-bluish, covered by jigsaw-puzzle-shaped fungal cells; heterocytes rare, mostly hyaline to sparsely pale yellow, 8–10 µm wide × 4–5 µm high; clamp connections not observed. Immature hymenophore possibly present, forming resupinate, irregular, small white patches, but hymenium was observed.

Etymology. This species is also dedicated to Dr. James D. Lawrey, whose pioneering work helped to redefine the circumscription of the genus *Dictyonema* s.str. (Lawrey et al. 2009) and who is the collector of the holotype specimen.

Distribution and ecology. This species is known from three specimens, all epiphytic in hardwood forests in Florida. The specimen from Ordway-Swisher was collected where an oak-dominated deciduous forest begins to intergrade with pine.

Remarks. This species is a typical-looking appressed-filamentous *Dictyonema*, but the color more resembles species belonging to the *Cyphellostereum imperfectum* group. However, anatomically it is clearly a *Dictyonema* due to the presence of jigsaw-puzzle-shaped fungal cells wrapping around the cyanobacterial cells. The species from Brazil, which appears in Figure 2 as the sister species (without support), and the species from Costa Rica that together form a well-supported clade with *Dictyonema lawreyi*, are also crustose-filamentous with a clear white prothallus. Nonetheless, both (unnamed) species are dark green and the fibrils are very distinct: the Brazilian species forms dense mats of packed interwoven fibrils, while the Costa Rican species form small tufts of interwoven erect fibrils. Under a microscope these morphologies differ greatly from *D. lawreyi*, which has sparse, loosely interwoven, bright turquoise fibrils resting on a white hypothallus.

Additional specimens examined. UNITED STATES, Florida, Putnam County, Ordway-Swisher Biological Station, Southeast of Lake Suggs. Habitat: deciduous hardwood forest. At edge of deciduous hardwood forest and longleaf pine habitat boundary. 29.684450°, –82.013689°, 29 m; on base of *Quercus*, 15 December 2016, L. Kaminsky 409 (FLAS, US – paratypes!). Note: One of the sequences for this specimen is short (159bp) and therefore not submitted to GenBank. However, this sequence is available in the alignment of File S2.

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Supplementary electronic material

Figure S1. Phylogenetic tree of the genus *Dictyonema* inferred by maximum likelihood in RAxML using ITS fungal barcoding (n = 231, alignment 938 bp). Tree visualized in FigTree v1.4.3 and edited in Photoshop Illustrator. Download file

Table S1. List of specimens included in this study. Download file

File S1. MAFFT alignment generated on Geneious used to generate the phylogenetic tree of the genus *Cyphellostereum* (n = 57, alignment 864 bp). Download file

File S2. MAFFT alignment generated on Geneious used to generate the phylogenetic tree of the genus *Dictyonema* (n = 231, alignment 938 bp). Download file

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