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New species of *Dictyonema* and *Cyphellostereum* (lichenized *Basidiomycota: Hygrophoraceae*) from tropical Africa and the Indian Ocean, dedicated to the late Hildur Krog

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Abstract: A small collection of lichenized fungi belonging in the *Dictyonema* clade from E Africa and Mauritius, tentatively identified as *D. sericeum*, revealed four species new to science, one in the genus *Cyphellostereum* and three in the genus *Dictyonema* s.str. *Cyphellostereum bicolor* from Mauritius is similar to *C. imperfectum* from Guatemata, but differs in the absence of a persistent white hypothallus and the less compact hyphal sheath of the fibrils, as well as the formation of resupinate hymenophores. *Dictyonema album*, also from Mauritius, belongs in the group of shelf-like morphotypes and is characterized within this group by very loose tufts dominated by sterile hyphae with very loosely arranged cyanobacterial fibrils. *Dictyonema krogiae* from Kenya is another new species in the group with shelf-like thalli and is the first species in this group known to form a distinctly layered thallus, with very compact photobiont layer, loose medulla, and more compact lower cortex. Finally, *Dictyonema tricolor* from Tanzania is a crustose taxon with ascending to erect tufts of densely arranged cyanobacterial fibrils, with the hyphal sheath becoming brown and the tip of the tufts whitish. In addition, *Dictyonema coppinsii* is reported from Mauritius.

Key words: *Agaricales*, basidiolichens, *Basidiomycota*, *Cyphellostereum*, *Dictyonema*, *Hygrophoraceae*, tropical Africa, Indian Ocean, Mascarenes, new species

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Introduction

The systematics, taxonomy and species richness of basidiolichens have long been misunderstood. The genus *Dictyonema* C. Agardh was monographed by Parmasto (1978) with the acceptance of five "lichen" and only two "fungal" species (one with clamps and one without). Parmasto (1978) placed the genus in *Corticiaceae*, whereas later it was reclassified in *Atheliaceae* (Oberwinkler 2001). The *Dictyonema* clade is now known to represent five genera (*Acantholichen* P. M. Jørg., *Cora* Fr., *Corella* Vain., *Cyphellostereum* D. A. Reid and *Dictyonema* s.str.) in subfamily *Lichenomphalinoideae* in *Hygrophoraceae* in the order *Agaricales* (Lawrey & al. 2009; Dal-Forno & al. 2013; Lodge & al. 2014). Within these genera, 60 species are currently recognized, over 250 species are known based on molecular phylogenies, and possibly over 700 are predicted to exist in this lineage (Lücking & al. 2013a, b, 2014a, b; Schmull & al. 2014; Dal-Forno 2015; Dal-Forno & al. 2016). This would place *Hygrophoraceae* among the ten fungal families with the highest number of lichenized species (Jaklitsch & al. 2016). In addition, a novel lineage of cyanobacterial photobionts, namely *Rhizonema* Lücking & Barrie, was discovered in this clade (Lücking & al. 2009, 2014a).

As part of our efforts to critically revise the taxonomy of the *Dictyonema* clade based on these findings, we here describe four new species from tropical Africa (Kenya,

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Tanzania) and the Indian Ocean (Mauritius), collected by Hildur Krog and Einar Timdal between 1972 and 1991. Contrary to the Neotropics, where most of the data for a broad phylogenetic revision of this clade have been obtained so far (Lawrey & al. 2009; Dal-Forno & al. 2013; Lücking & al. 2013a, 2014b; Dal-Forno 2015), very few collections from the Paleotropics have been critically revised. It is therefore not surprising to detect a high number of novelties in a comparatively small set of gatherings. This is also supported by molecular sequence data, which suggests that paleotropical specimens form lineages quite distinct from neotropical taxa, especially in *Cyphellostereum* and *Dictyonema* s.str. (Dal-Forno 2015).

This paper is dedicated to the late Dr Hildur Krog (1922–2014), who collected lichens on 13 field trips to E Africa and the Indian Ocean. The material was published in a series of taxonomic revisions, often co-authored by Dr T. D. V. Swinscow, with whom she collaborated and often travelled. Their work was summarized in *Macrolichens of East Africa* (Swinscow & Krog 1988).

Material and methods

Specimens were examined with LEICA MS5 and OLYM-PUS SZX12 dissecting microscopes and photographed with a JENOPTIC ProgRes C5 microscope digital camera attached to the latter. Sections of thallus and hymenophore were cut by hand with a razor blade and mounted in tap water for examination with ZEISS Axioscop 2 and VISTA VISION VWR V036 compound microscopes. Secondary chemistry was assessed with standardized methods of thin-layer chromatography (TLC) using solvent system C (Orange & al. 2010).

Results and Discussion

Cyphellostereum bicolor Lücking & Timdal, **sp. nov.** – MycoBank #815880 – Fig. 1.

Holotype: Mauritius, Grand Port, Bambou Mountains, 0.5–1 km NNE of Piton Rouge, 20°20'S, 57°44'E, 250–300 m, epiphytic on tree bark, 12 Nov 1991, *H. Krog & E. Timdal MAU36/02* (O L-21699; isotype: F).

Diagnosis — Differing from *Cyphellostereum imperfectum* Lücking & al. in the absence of a distinct, white hypothallus (not associated with hymenophores) and the loose hyphal sheath around the cyanobacterial filaments.

Description — Thallus epiphytic on tree bark, mostly overgrowing bryophytes (hepatics), appressed filamentous, forming a mat of interrupted patches of densely clustered fibrils connected by a thin to indistinct hypothallus, up to several cm across; fibrils horizontal to irregularly subascending, irregularly oriented, vividly and uniformly aeruginous, intermingled with white patches of densely woven, byssoid hyphae eventually developing into hymenophores. Fibrils in section solitary, not forming agglutinated tufts, each fibril with its own hyphal sheath, 11–14 µm wide, with hyphal sheath c. 2 µm thick, colourless; cyanobacterial filaments composed of 7–9 μ m wide and 5–6 μ m high, aeruginous blue cells lacking tubular fungal hyphae as haustoria; heterocytes sparse, hyaline to yellowish, 6-8 µm wide and 4-6 µm high; hyphal sheath formed by loosely arranged, cylindrical, curved hyphae wrapped around cyanobacterial filaments; hyphae of hypothallus and those associated with fibrils or forming apical setae straight, hyaline, 3-5 µm thick, lacking clamp connections. Hymenophore developed on or underneath white, byssoid areas as irregular, resupinate, effuse patches, patches 0.5-1 mm in diam., \pm flat, with white, smooth surface but often with cracks and interspaces, without distinct margins; hymenophore in section 30–50 µm thick, composed of a woven, strongly hydrophobic layer resting on agglutinated, 4–6 µm thick, generative hyphae emerging from supporting thallus; hymenium forming protruding, palisade-like basidioles, $20-30 \times 5-6 \,\mu\text{m}$; basidia and basidiospores not observed. Chemistry: no substances detected by TLC.

Remarks — Cyphellostereum bicolor forms a striking colour contrast between the aeruginous cyanobacterial filaments and the white hyphal patches developing the hymenophore. It is included in *Cyphellostereum* due to the sheath formed by cylindrical hyphae and the absence of fungal haustoria (Dal-Forno & al. 2013; Lücking & al. 2013a); however, the resupinate hymenophore is more reminiscent of Dictyonema s.str. Another species confirmed in the latter genus based on molecular data, D. huaorani Dal-Forno & al. also lacks jigsaw-puzzleshaped hyphal cells and haustoria (Schmull & al. 2014). Hence, the phylogenetic placement of the new species must be tested with molecular sequence data. Morphologically, it is most similar to C. imperfectum, which differs in the distinct white hypothallus (not associated with hymenophores) and the denser hyphal sheath around the cyanobacterial filaments (Yánez & al. 2012).

Other lichens collected at the site include *Coccocarpia palmicola* (Spreng.) Arv. & D. J. Galloway, *Parmotrema tinctorum* (Despr. ex Nyl.) Hale, *Phyllopsora breviuscula* (Nyl.) Müll. Arg., *Sticta macrophylla* Bory and *S. weigelii* Isert s.lat.

Dictyonema album Lücking & Timdal, **sp. nov.** – Myco-Bank #815881 – Fig. 2.

Holotype: Mauritius, Savanne, Plaine Champagne, near the viewpoint WNW of Mt Cocotte, 20°26'S, 57°27'E, 650 m, 18 Nov 1991, *H. Krog & E. Timdal MAU57/04* (O L21992; isotype: F).

Diagnosis — Differing from other species in the *Dicty*onema sericeum (Sw.) Berk. & M. A. Curtis group by the

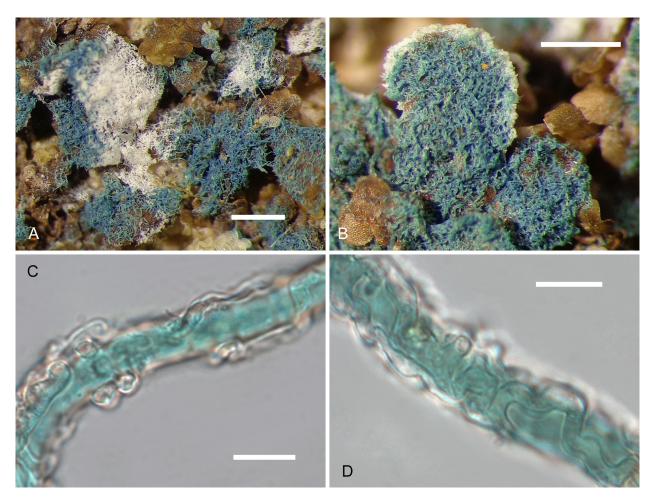


Fig. 1. *Cyphellostereum bicolor* – A, B: thallus fibrils with white basidiocarps and basidiocarp initials; C, D: microscopic view of fibrils with loose hyphal sheath. – Scale bars: A, B = 1 mm; C, D = $10 \mu m$.

combination of irregularly arranged tufts of fibrils that to not form a distinctly layered thallus, being dominated by sterile, straight hyphae with very few associated cyanobacterial fibrils, giving the thallus a whitish appearance.

Description — Thallus epiphytic on shrubs, filamentous, forming semi-circular, adnate to projecting shelves or in basal parts a crust on substrate, up to 10 cm across, composed of numerous imbricate to partially fused lobes c. 1 cm in diam., individual lobes formed by loosely interwoven, ascending to erect, light aeruginous tufts of fibrils with long, white tips; thallus therefore appearing whitish in surface view. Thallus in section 1-2 mm thick, with tufts of fibrils up to 5 mm long from base, not forming a distinct photobiont layer and medulla but instead fibrils connected at base (underside) to a white, loosely woven hypothallus; tufts formed by densely arranged but not agglutinate, sterile, unbranched to sparsely branched hyphae arranged in parallel fashion, up to 0.5 mm thick, intermingled with few (3-8) cyanobacterial fibrils distant from each other, each fibril with its own hyphal sheath, 14-16 µm wide, with hyphal sheath 2-3 µm thick, colourless; cyanobacterial filaments composed of 10-12 µm wide and 3-5 µm high, aeruginous cells penetrated by

tubular fungal hyphae; heterocytes frequent, hyaline, $8-10 \mu m$ wide and $4-6 \mu m$ high; cells of hyphal sheath wavy in lateral outline, $3-5 \mu m$ in diam.; hyphae of hypothallus and those associated with fibrils or forming apical setae straight, hyaline, $4-7 \mu m$ thick, lacking clamp connections. Hymenophore not observed. Chemistry: no substances detected by TLC.

Remarks — This new species has the gross morphology of the Dictyonema sericeum group, with shelf-like, filamentous lobes (Lücking & al. 2013a). Within that group, it belongs in a complex of species with irregularly arranged tufts of fibrils that do not form a distinctly layered thallus, very different from, for instance, D. krogiae described below. The gross morphology is somewhat reminiscent of the non-shelf forming D. tricolor, also described below, but the internal anatomy of the tufts is quite distinct in D. album, being dominated by sterile, straight hyphae with very few associated cyanobacterial fibrils, giving the thallus a whitish appearance. Such an anatomy is not known from any of the currently recognized species in the D. sericeum group (Lücking & al. 2013a, b) and is probably an adaptation to exposed microsites.

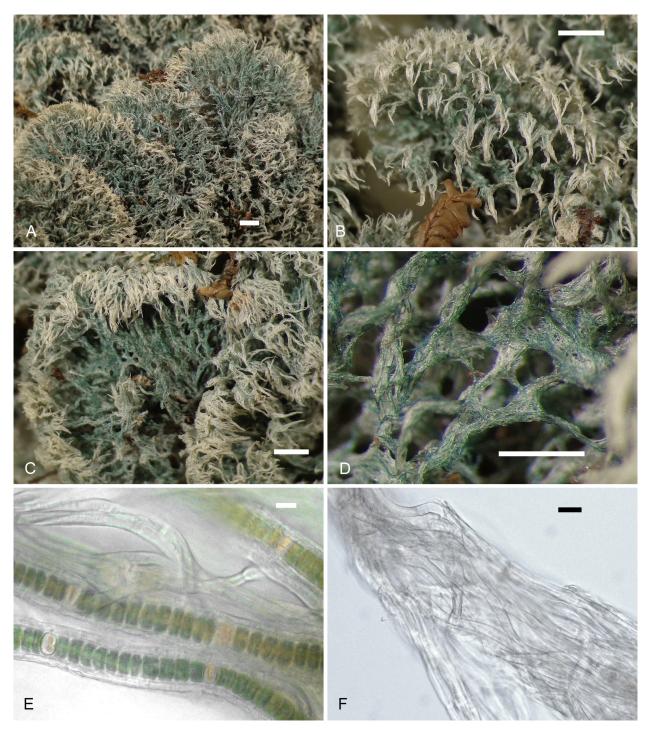


Fig. 2. *Dictyonema album* – A–D: thallus fibrils (enlarged in D); E, F: microscopic view of fibrils with hyphal sheath and associated hyphal tufts. – Scale bars: A-D = 1 mm; E, F = 10 µm.

Other species collected in the forest near the type specimen of *Dictyonema album* include *Bulbothrix suffixa* (Stirt.) Hale, *Pannaria santessonii* Swinscow & Krog, *Sticta macrophylla*, *Usnea baileyi* (Stirt.) Zahlbr., *U. himantodes* Stirt. and *U. rubicunda* Stirt. At the other site, *D. album* was collected together with *Crocynia molliuscula* (Nyl.) Nyl., *Hypotrachyna microblasta* (Vain.) Hale, *Leioderma erythrocarpum* (Delise ex Nyl.) D. J. Galloway & P. M. Jørg., *Pannaria multifida* P. M. Jørg., P. ramosii Vain., Parmeliella endoferruginea Aptroot, Phyllopsora buettneri (Müll. Arg.) Zahlbr., P. confusa Swinscow & Krog, P. porphyromelaena (Vain.) Zahlbr., P. swinscowii Timdal & Krog, Pseudocyphellaria argyracea (Delise) Vain., Psoroma sphinctrinum (Mont.) Nyl., Sticta tomentosa (Sw.) Ach. and S. weigelii s.lat.

Additional specimen examined — MAURITIUS: Savanne, along the road between Mt Cocotte and Bassin Blanc,

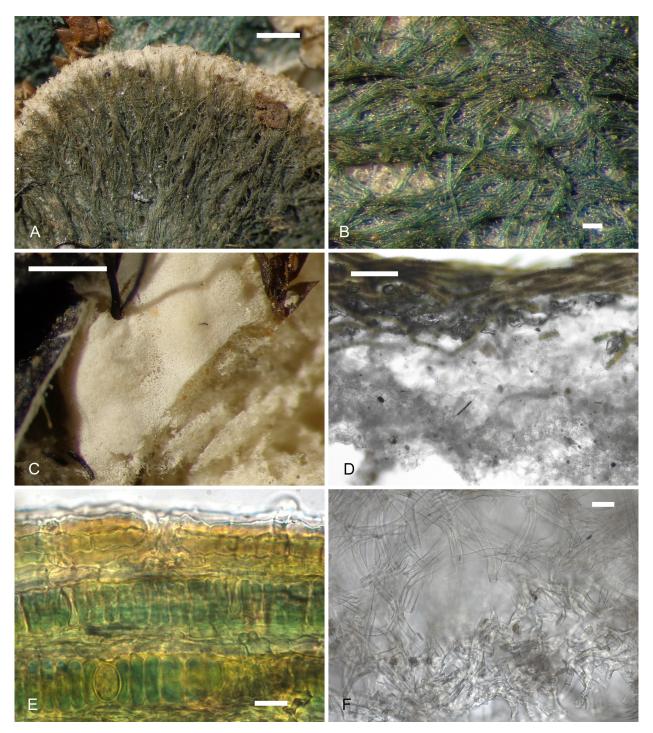


Fig. 3. *Dictyonema krogiae* – A, B: thallus fibrils (enlarged in B); C: basidiocarp; D–F: microscopic sections of thallus showing photobiont (filament) layer (E) and medulla and lower "cortex" enlarged (F). – Scale bars: A, C = 1 mm; B, D = 0.1 mm; E, F = $10 \mu m$.

20°26'S, 57°28'E, 550–580 m, 18 Nov. 1991, *H. Krog & E. Timdal MAU58/03* (O L-22008).

Dictyonema krogiae Lücking & Timdal, **sp. nov.** – MycoBank #815882 – Fig. 3.

Holotype: Kenya, Central Province, Kirinyaga District, Mount Kenya, 2 km N of Irangi Forest Station, near river Ena, 00°20'S, 37°28'E, 2000 m, moist deciduous forest, on trees, 9 Feb 1972, *H. Krog K48/102* (O L-1305; iso-type: F).

Diagnosis — Differing from *Dictyonema ligulatum* (Kremp.) Zahlbr. by the lack of clamp connections and the filaments being arranged in dense, parallel, radiating lines, and generally from other species in the *D. sericeum* group in the distinctly layered thallus, including a dense photobiont layer and a loose lower cortex.

Description — Thallus epiphytic on trees, intermingled with other lichens (Parmotrema A. Massal.) and bryophytes (Frullania Raddi), filamentous, forming semi-circular, adnate to projecting shelves up to 10 cm across, with single lobes 1-6 cm wide, composed of densely arranged, horizontally radiating and parallel, dark aeruginous fibrils without or with indistinct interspaces resting on a thick, byssoid, irregularly interwoven medulla (hypothallus), visible as narrow, c. 0.5 mm wide line along margin, strongly contrasting with aeruginous fibrils. Thallus in section 400–500 µm thick, ecorticate, with a fully exposed, well-defined photobiont layer, 100-150 µm thick, a distinct medulla of very loosely woven hyphae, 200-300 µm thick, and a lower "cortex" of more densely woven hyphae, c. 50 µm thick; photobiont layer composed of numerous, periclinally arranged, parallel fibrils formed by cyanobacterial filaments wrapped in a closed hyphal sheath of jigsaw-puzzle-shaped cells; fibrils 15-20 µm wide, with hyphal sheath 2-3 µm thick, colourless or olive-brown towards thallus centre; cyanobacterial filaments composed of 12-15 µm wide and 5-7 µm high, aeruginous green cells penetrated by tubular fungal hyphae; heterocytes sparse, hyaline to yellowish, 11-13 µm wide and 4-6 µm high; cells of hyphal sheath wavy in lateral outline, 3-5 µm in diam., in surface fibrils and towards thallus margin often shallowly verrucose-papillose; hyphae of medulla, lower "cortex" (hypothallus) and white bordering line (prothallus) straight, much branched, 4-6 µm thick, lacking clamp connections. Hymenophore sparsely developed as soft, irregular, resupinate, effuse patches on underside, patches 0.5–1 mm in diam., slightly convex, with whitish, smooth surface and without distinct margins; hymenophore in section 70-150 µm thick, composed of a paraplectenchymatous layer resting on strongly agglutinated, 4-6 µm thick, generative hyphae emerging from supporting thallus; hymenium composed of numerous, palisade-like basidioles and scattered basidia; basidioles $20-30 \times 5-6 \mu m$; basidia $30-40 \times 5-7 \mu m$, 4-sterigmate; basidiospores (only few seen) ellipsoid, non-septate, hyaline, $7-10 \times 3-4 \mu m$. Chemistry: no substances detected by TLC.

Eponymy — This new species is dedicated to Hildur Krog for her invaluable contributions to African lichenology.

Remarks — The shelf-like filamentous forms of *Dicty*onema were assigned to only two species by Parmasto (1978), presumably with the single difference of presence (*D. ligulatum*) vs absence (*D. sericeum*) of clamp connections. Molecular phylogenetic and morphological studies showed that a number of different species are present in this apparently monophyletic complex, separated by details in their thallus morphology and anatomy (Dal-Forno & al. 2013; Dal-Forno 2015). Among these, thus far three species are known with their cyanobacterial fibrils arranged in a narrow, compact, well-defined photobiont layer resting on a well-defined medulla, resulting in a uniformly blue-green colour contrasting with the white prothallus and hypothallus: the paleotropical D. ligulatum and D. scabridum (Vain.) Lücking with clamp connections and the latter additionally with finger-like thallus outgrowths (Lücking & al. 2013a), and the recently described, neotropical D. huaorani (Schmull & al. 2014); the latter resembles D. ligulatum morphologically but lacks clamp connections and also lacks the jigsaw-puzzleshaped hyphal sheath cells and the tubular haustoria penetrating the cyanobacterial filaments typical of the other two species. Dictyonema krogiae comes morphologically closest to D. ligulatum, but lacks clamp connections and the filaments are arranged in dense, parallel, radiating lines, whereas in D. ligulatum they are irregularly oriented and leave small interspaces. The distinctly developed layers in D. krogiae, including a dense photobiont layer and a loose lower cortex, are not known from any other species in this morphotype.

The type locality was apparently very rich in lichens and Hildur Krog made at least 191 collections there. It is the holotype locality of Phyllopsora confusa (Swinscow & Krog 1981). Other species collected include Anzia afromontana R. Sant., Bulbothrix meizospora (Nyl.) Hale, Crocodia clathrata (De Not.) Trevis., Dirinaria applanata (Fée) D. D. Awasthi, Flavoparmelia caperata (L.) Hale, Hypotrachyna costaricensis (Nyl.) Hale, H. endochlora (Leight.) Hale, H. microblasta, H. neodissecta (Hale) Hale, H. osseoalba (Vain.) Y. S. Park & Hale, H. rockii (Zahlbr.) Hale, H. subfatiscens (Kurok.) Swinscow & Krog, H. sublaevigata (Nyl. ex Tuck.) Hale, Kroswia crystallifera P. M. Jørg., Leprocaulon arbuscula (Nyl.) Nyl., Nephroma tropicum (Müll. Arg.) Zahlbr., Pannaria fulvescens (Mont.) Nyl., Parmelinella wallichiana (Taylor) Elix & Hale, Parmotrema arnoldii (Du Rietz) Hale, P. cooperi (J. Steiner & Zahlbr.) Sérus., P. cryptoxanthum (Abbayes) Hale, P. direagens (Hale) Hale, P. eunetum (Stirt.) Hale, P. hababianum (Gyeln.) Hale, P. nilgherrense (Nyl.) Hale, P. sancti-angelii (Lynge) Hale, P. subarnoldii (Abbayes) Hale, P. umbrosum (Krog & Swinscow) Krog & Swinscow, Phyllopsora chlorophaea (Müll. Arg.) Zahlbr., P. porphyromelaena, Punctelia neutralis (Hale) Krog, Ramalina calcarata Krog & Swinscow, R. pusiola Müll. Arg., Sticta cyphellulata (Müll. Arg.) Hue and Usnea exasperata (Müll. Arg.) Motyka.

Dictyonema tricolor Lücking & Timdal, **sp. nov.** – MycoBank #815883 – Fig. 4A–D.

Holotype: Tanzania, Southern Highlands, Iringa District, Lulando Forest at NE edge of Mufindi escarpment, 08°36'S, 35°37'E, 1450 m, low montane rain forest, on trees, Apr 1989, *H. Krog 3T23/001* (O L-153734).

Diagnosis — Differing from *Dictyonema coppinsii* Lücking & al. in the tricolored, regularly ascending tufts of fibrils and from *D. galapagoense* A. Yánez & al. also in the much more robust thallus and the presence of fungal haustoria.

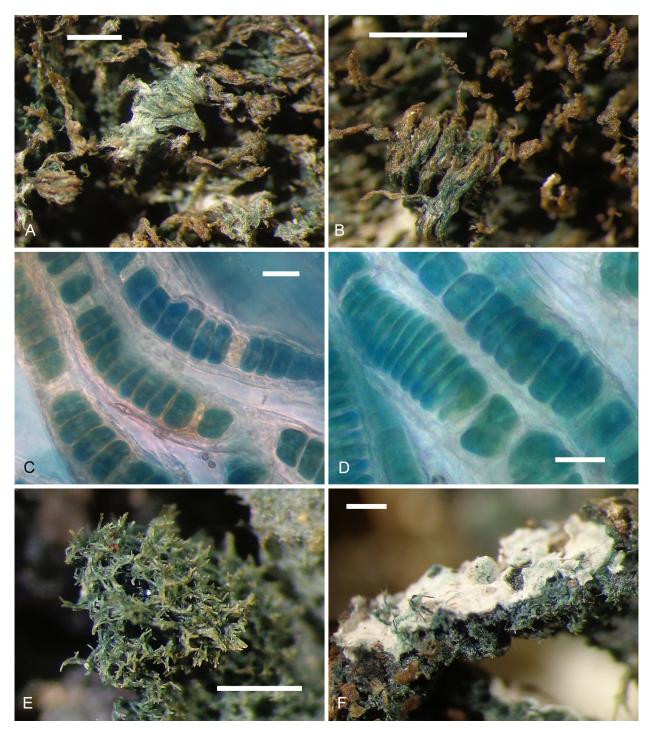


Fig. 4. A–D: *Dictonema tricolor*; A, B: thallus fibrils enlarged; C, D: microscopic view of fibrils with dense hyphal sheath. – E, F: *Dictonema coppinsii*; E: thallus fibrils; F: basidiocarp. – Scale bars: A, B, E, F = 1 mm; C, D = 10 μ m.

Description — Thallus epiphytic on tree bark, filamentous with ascending to erect fibrils, forming a \pm continuous mat with fibrils evenly dispersed or clustered, up to several cm across; fibrils ascending from a basal, white, densely interwoven, opaque hypothallus, aeruginous with tips or upper part becoming white or (dark) brown, often oriented into same direction, accompanied by irregular strands of white, densely packed hyphae, forming tufts up to 3 mm long and 0.3 mm wide. Fibrils in section forming tufts composed of 5-15 individual, strongly agglutinated fibrils, each fibril with its own hyphal sheath, $15-18 \mu m$ wide, with hyphal sheath $2-3 \mu m$ thick, colourless or becoming brown towards apex of fibrils, at tips often minutely and shallowly papillose; fibrils often ending in prolonged setae formed by agglutinate, straight hyphae not associated with photobiont filaments; cyanobacterial filaments composed of $10-12 \mu m$ wide and $4-6 \mu m$ high, aeruginous blue

cells penetrated by tubular fungal hyphae; heterocytes frequent, hyaline to yellowish, 10–13 μ m wide and 4–6 μ m high; cells of hyphal sheath wavy in lateral outline, 3–5 μ m in diam.; hyphae of hypothallus and those associated with fibrils or forming apical setae straight, hyaline, 4–6 μ m thick, lacking clamp connections. Hymenophore not observed. Chemistry: no substances detected by TLC.

Remarks — This new species represents a morphotype with filaments that are ascendant to erect, being somewhat intermediate between entirely appressed taxa and those forming semi-circular shelves. Thus far, only a few described species represent this morphotype. Among these, the European Dictyonema coppinsii has uniformly blue-green tufts of fibrils that are irregular to (sub-) erect (Lücking & al. 2014a). Dictyonema galapagoense also forms (sub-)erect tufts of fibrils but is much more delicate and lacks fungal haustoria, so the photobiont filaments are much narrower, with more or less squared cells (Yánez & al. 2012). The new species forms a distinct colour contrast between the aeruginous fibrils visible from the base and the either brown or white colour of the apical portions of the tufts. The specimen was first published as D. sericeum by Krog (2000).

Other lichens collected at this site include Canoparmelia texana (Tuck.) Elix & Hale, Heterodermia casarettiana (A. Massal.) Trevis., Hypotrachyna costaricensis, H. horrescens (Taylor) Krog & Swinscow, Parmeliella pannosa (Sw.) Müll. Arg., Parmotrema amaniense (J. Steiner & Zahlbr.) Krog & Swinscow, P. cooperi, P. hololobum (Hale) Hale, Phyllopsora dolichospora Timdal & Krog, P. furfuracea Zahlbr., P. martinii Swinscow & Krog, P. porphyromelaena, Pseudocyphellaria aurata (Ach.) Vain., Rimelia cetrata (Ach.) Hale & A. Fletcher and Usnea baileyi.

Dictyonema coppinsii Lücking & al. in Lichenologist 46: 262. 2014. – Fig. 4E, F.

Remarks — This species was recently described for the W European taxon previously known under the invalid name "*Dictyonema interruptum*". The material from Mauritius agrees in all characters with the material from Europe, but molecular data from fresh material are needed to confirm this considerable range extension. Other species collected at the site include *Coccocarpia pruinosa* Arv., *C. smaragdina* Pers., *Lobaria patinifera* (Taylor) Hue, *Parmotrema tinctorum*, *Physma byrsaeum* (Ach.) Tuck., *Pyxine subcinerea* Stirt., *Rimelia reticulata* (Taylor) Hale & A. Fletcher, *Sticta dichotoma* Bory, *S. weigelii* s.lat. and *Usnea rubicunda*.

Specimens examined — MAURITIUS: Grand Port, Mt des Créoles, 20°23'S, 57°40' E, 320–360 m, 12 Nov 1991, *H. Krog & E. Timdal MAU35/10* (F, O L-21661).

Conclusions

The present findings show underline the notion that the *Dictyonema* clade, including the genera *Acantholichen*, *Cora*, *Corella*, *Cyphellostereum* and *Dictyonema* s.str., is highly diverse with a large proportion of regional and local endemics. This diversity was not previously recognized and material from Africa had mostly been labelled *D. sericeum*. The fact that only few collections of *Dictyonema* resulted from the field trips made by Dr Krog and her colleagues, but these few gatherings yielded almost exclusively new taxa, shows that this enigmatic group of lichens remains undercollected and that African wet ecosystems may harbour a large number of unrecognized species in this clade.

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