

Standard Paper

High diversity at the small scale: an inventory of foliicolous lichens of Brunei reveals 193 species, including 21 new to science

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Abstract

We present a first comprehensive treatment of the foliicolous lichen biota of Brunei (Brunei Darussalam), a country c. 5765 km² in size located on the northern coast of the island of Borneo. Based on a study of numerous leaves collected from 18 sites, resulting in 1745 individual collections, we identified 193 species in the material, including 21 new to science, raising the number of foliicolous lichens known from Brunei from 27 to 199 taxa. This is one of the highest numbers reported for single countries, after Brazil (455 species), Costa Rica (435), Ecuador (365), Mexico (340), Guyana (296), Australia (238), Bolivia and Colombia (228 each), and Papua New Guinea (213). However, relative to log-transformed area size, Brunei is one of the countries with the highest known foliicolous lichen diversity, having almost half the number of species as Costa Rica within an area little more than 10% of the size of the latter. The foliicolous lichen biota of Brunei has a dominant paleotropical element, clustering with that of Indonesia, Malaysia, the Philippines, Papua New Guinea and Australia. The newly described species are: *Arthonia concentrica* sp. nov., differing from *A. trilocularis* in the circular thallus with concentrically arranged, thinly pruinose ascomata; *Arthonia flavirugosa* sp. nov., differing from *A. flavoverrucosa* in the delicate, light yellowish ridges and the smaller ascospores; *Arthonia tenuilobata* sp. nov., differing from *A. lobulicarpa* in the more delicate lobes, pruinose ascomata and the brown ascospores; *Byssolecania fumosaerulea* sp. nov., differing from *B. fumosonigricans* in the greyish blue outer fringe of the apothecia; *Byssoloma inconspicuum* sp. nov., differing from *B. microcarpum* in the dark brown apothecial disc and the excipulum lacking crystals; *Byssoloma incrustatimurinum* sp. nov., differing from *B. murinum* in the shorter, non-tapering ascospores and the crystals in the excipulum; *Byssoloma subaeruginosum* sp. nov., differing from *B. usambarense* in the dark aeruginous hypothecium and the (olive-)brown thallus; *Chroodiscus lirellicarpus* sp. nov., differing from *C. argillaceus* in the lirellate apothecia; *Chroodiscus minutus* sp. nov., differing from *C. argillaceus* in the very small apothecia; *Echinoplaca septemseptata* sp. nov., differing from *E. tetrapla* in the 7-septate ascospores; *Eremothecella rugosa* sp. nov., differing from *E. calamicola* in the ridged thallus and the longer conidia; *Eremothecella verrucispora* sp. nov., differing from *E. calamicola* in the brown, ornamented ascospores with more numerous septa; *Fellhanera tutongensis* sp. nov., differing from *F. microdiscus* in the 3–7-septate, more elongate, narrower ascospores; *Mazosia bambusiradiata* sp. nov., differing from *M. bambusae* in the radiately arranged thallus verrucae; *Mazosia rugosa* sp. nov., differing from *M. pseudobambusae* in the rugose instead of verrucose thallus surface; *Ocellularia andulauensis* sp. nov., differing from *O. daniiana* in the more delicate, foliicolous thallus and the much smaller ascospores; *Opegrapha albomarginata* sp. nov., differing from all other species of *Opegrapha* with goniocystangia, in the white margin of the goniocystangia; *Phylloporis verrucosula* sp. nov., differing from *P. palmae* in the small perithecia and comparatively narrow ascospores; *Porina riparia* sp. nov., differing from *P. pseudoapplanata* [= *Phyllophiale viridis*] in the finely lacinate thallus with non-radiating photobiont; *Spinomyces rubrotrichoides* sp. nov., differing from other species in the genus in the multiseptate, worm-like ascospores and from *Rubrotricha helminthospora*, with which it agrees in ascospore type, in the entirely whitish, more delicate sterile thallus setae; *Trichothelium subrobinsonii* sp. nov., differing from *T. robinsonii* in the consistently 7-septate ascospores. The following three species are new continental records: *Bapalmuia pallescens* (Paleotropics), *Lyromma palmae* (Paleotropics), and *Tapellaria major* (Paleotropics). We also include two keys: one to foliicolous species of *Arthonia* with 2-septate, pigmented ascospores and one to foliicolous species of *Porina* with *Phyllophiale*-type isidia.

Keywords: biogeography; epiphylls; Indonesia; lichen biodiversity; Paleotropics

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Introduction

Foliicolous lichens are an ecologically defined group of lichenized fungi that show strong preferences for living leaves as substrata (Santesson 1952; Sérusiaux 1989, 1996; Lücking 2001, 2008). Their highest diversity occurs in tropical and subtropical regions

(Lücking 2003). While the distribution of foliicolous lichens is pantropical, they have been studied most extensively in neotropical rainforests (Lücking 2008). Foliicolous lichens exhibit relatively high diversity, with nearly 1000 species known worldwide (Lücking & Martínez-Colín 2004; Lücking 2008; the present paper). However, recent studies show that lichen diversity has historically been underestimated and that further studies are needed to better understand the taxonomy of these organisms (Sipman & Aptroot 2001; Cáceres *et al.* 2008). Pioneering molecular studies have shown a striking degree of hidden diversity in foliicolous lichens, such as in *Ectolechiaceae*, *Gomphillaceae* and *Strigulaceae* (Wang *et al.* 2020; Jiang *et al.* 2022; Xavier-Leite *et al.* 2022; Lebreton *et al.* 2025). In addition to contributing to biodiversity assessment, foliicolous lichens can provide an insight into broader environmental patterns, such as altitudinal zonation, microclimatic conditions, and disturbance patterns of tropical ecosystems (Lücking 1995, 1997; Martínez-Colín *et al.* 2021).

Lichenological studies have been undertaken to a variable degree in most South-East Asian countries, including India, Thailand, Vietnam, Malaysia, Singapore, Indonesia, the Philippines, southern China and Hong Kong, Taiwan, and Papua New Guinea (Vězda 1977; Aptroot *et al.* 1997; Aptroot & Seaward 1999; Wolseley *et al.* 2002; Aptroot & Sparrius 2006; Singh & Sinha 2010; Sipman 2010; Schumm & Aptroot 2012a, b; Buaruang *et al.* 2017; Joshi *et al.* 2017; Hardini *et al.* 2018; Sinha *et al.* 2018; Jatnika *et al.* 2019; Kistenich *et al.* 2019; Jannah *et al.* 2021). However, the lichen biota of Brunei Darussalam, a small country located in the north of the island of Borneo, is understudied. According to the *Recent Literature on Lichens* (RLL) database (<https://nhm2.uio.no/botanisk/lav/RLL/RLL.HTM>), there is only one known set of lichen collections from the country, most of these representing foliicolous lichens, with 27 species excluding the lichenicolous taxa (Aptroot *et al.* 2003). The *Global Biodiversity Information Facility* (GBIF) results show c. 40 records, mostly the same foliicolous lichens reported by Aptroot *et al.* (2003), except *Coenogonium hypophyllum*, and almost all held at Meise Botanic Garden Herbarium (BR). There are no lichen collections in any of the three registered herbaria in Brunei (BRUN, IBER, UBDH), which limits further study of this group of organisms in the country. To improve this dire situation, we performed broad sampling of foliicolous and also corticolous lichens across the country. In this first contribution, we focus on the foliicolous lichen biota of Brunei Darussalam, presenting a detailed inventory across the country and its common habitat types.

Material and Methods

Study area

The country of Brunei Darussalam experiences a largely aseasonal tropical climate, with an average rainfall of 3386 mm y^{-1} and an average temperature of 27.7 °C (1991–2020 at 50 km $\times$ 50 km resolution) (Harris *et al.* 2020). The climate supports a high diversity and abundance of potential leaf substrata for foliicolous lichens, with 1407 tree species recorded within the country (BGCI 2025). The high tree diversity is found across the seven primary forest types that are recognized within Brunei Darussalam: the mixed dipterocarp, heath, mangrove, peat swamp, montane, beach-type, and freshwater swamp forests. These forests cover 72.1% of the land area according to Brunei Darussalam's report to the United Nations Framework Convention on Climate Change (Brunei Darussalam 2022). To capture the foliicolous lichen diversity across the diverse landscapes for this study, we sampled 18 sites across all four geographical districts (Table 1, Fig. 1).

The inventory was performed using a combination of opportunistic and quantitative sampling to capture the highest possible species richness (Cáceres *et al.* 2008). Sampling and identification work aimed to include rare, inconspicuous, sterile, and cryptic species, which are difficult to capture, yet important for accurately representing species richness (Cáceres *et al.* 2008).

Taxonomic work

We separated and examined a total of 1763 specimens of foliicolous lichens from the collected material. In most cases, leaves were cut into smaller pieces which were curated separately to highlight particular taxa present on each piece. In selected cases, we kept entire leaves with lists of all species occurring on them, to document high levels of small-scale diversity. Duplicate sets are deposited at the Universiti Brunei Darussalam herbarium (UBDH) and the Herbarium Berolinense (B) of the Botanischer Garten und Botanisches Museum of the Freie Universität Berlin.

Specimens were identified by DAW and RL, with the assistance of BM, during a 4-week visit by DAW to the Botanischer Garten Berlin. For the assessment of morphological features, we used a LEICA Zoom 2000 stereomicroscope. Thin hand-cut sections were studied under a Zeiss Axioskop compound microscope, and all measurements were made on material mounted in water. For microchemical tests, we used Lugol's solution (I), 10% KOH (K), commercial bleach (C) and paraphenylene-diamine crystals dissolved in ethanol (P). Macroscopic images were captured with a Nikon D5300 digital SLR camera using a Nikon AF-S DX Micro NIKKOR 40 mm macro lens with a Raynox digital camera macroscopic lens $\times 4$ attached, and a Cullmann CULight V 220DL LED light source. Microscopic images were taken under $\times 400$ and $\times 1000$ magnification with a Samsung Galaxy A71 mobile phone attached to the PL $\times 10/20$ ocular of the Zeiss Axioskop compound microscope.

For taxonomic identifications, we used keys published in various works (Santesson 1952; Sérusiaux 1985, 1996; Farkas & Vězda 1987; Vězda 1987; Kalb & Vězda 1994; Lücking & Vězda 1998; Kalb *et al.* 2000; Ferraro *et al.* 2001; Sérusiaux & Lücking 2003, 2007; Lücking 2004, 2008; Sparrius 2004; Lücking *et al.* 2006; Sérusiaux *et al.* 2008; McCarthy 2010; Flakus & Farkas 2013; Neuwirth & Stocker-Wörgötter 2017; Naksuwankul & Lücking 2019; Jiang *et al.* 2020, 2022; Wang *et al.* 2021), as well as unpublished keys by RL. Where necessary, specimens were compared to photographed type material, either in the database of RL or on *JSTOR Global Plants* (<https://plants.jstor.org>).

Biogeographic analysis

To place the foliicolous lichen biota of Brunei into context, we established an updated global occurrence database of over 1000 foliicolous lichen species using Lücking (2003) as a base, expanding it with published checklists and inventories of foliicolous lichens from 35 selected countries in the Neotropics, the African Paleotropics, and the eastern Paleotropics (Lücking 1999; Santesson & Lücking 1999; Kalb *et al.* 2000; Lücking & Kalb 2000, 2001; Ferraro *et al.* 2001; Lücking *et al.* 2001; Ferraro 2002; Ferraro & Lücking 2003; Aptroot *et al.* 2003; Farkas 2004, 2014, 2015a; Herrera-Campos *et al.* 2004; Pinokiyo & Singh 2006; Neuwirth 2007; Vězda 2007; Flakus & Lücking 2008; Singh & Pinokiyo 2008; Mateus *et al.* 2011; Breuss 2012; Farkas *et al.* 2012; Flakus 2013; Flakus & Farkas 2013; Van den Broeck *et al.* 2014; Farkas & Flakus 2015; Gupta & Sinha 2016; Jiang *et al.* 2017a, b, 2020, 2022).

The individual country biota was ordinated through a presence/absence data matrix using Principal Coordinate Analysis (PCoA)

Table 1. District, locality, forest type, latitude and longitude of all 18 lichen sampling sites within Brunei Darussalam, sorted by district, sampling strategy and site number. Opp = opportunistic; Qua = quantitative.

Site	District	Locality	Forest type	North	East
Opp-03	Belait	Wasai Telingan, Teraja	Mixed dipterocarp	114.466204	04.372007
Opp-04	Belait	Wasai Teraja	Mixed dipterocarp	114.448030	04.341376
Opp-06	Belait	Jalan Labi Mixed Dipterocarp Forest	Mixed dipterocarp	114.476389	04.580278
Opp-07	Belait	Jalan Badas	Peat swamp	114.420556	04.560278
Opp-09	Belait	Andulau Forest Reserve	Mixed dipterocarp	114.522290	04.655550
Opp-11	Belait	Jalan Labi Heath Forest	Heath	114.467438	04.475669
Qua-01	Belait	Andulau Forest Reserve	Mixed dipterocarp	114.522290	04.655550
Qua-03	Belait	Jalan Labi Heath Forest	Heath	114.467438	04.475669
Qua-04	Belait	Jalan Labi Mixed Dipterocarp Forest	Mixed dipterocarp	114.476389	04.580278
Qua-08	Belait	Wasai Telingan, Teraja	Mixed dipterocarp	114.466204	04.372007
Qua-09	Belait	Wasai Teraja	Mixed dipterocarp	114.448030	04.341376
Opp-01	Brunei Muara	Bukit Dadap	Secondary	114.894568	04.863550
Opp-02	Brunei Muara	Sungai Brunei	Mangrove	114.960227	04.866498
Opp-14	Brunei Muara	Old Growth Kerangas Plot, Universiti Brunei Darussalam	Heath	114.897300	04.974700
Opp-17	Brunei Muara	Bukit Tempayan Pisang	Secondary	115.045223	05.012201
Opp-19	Brunei Muara	Shabandar Hills	Secondary	114.852227	04.954794
Qua-07	Brunei Muara	Old Growth Kerangas Plot, Universiti Brunei Darussalam	Heath	114.897300	04.974700
Opp-10	Temburong	Betayan	Mixed dipterocarp	115.103089	04.702775
Opp-13	Temburong	Batu Apoi	Mixed dipterocarp	115.220705	04.682650
Opp-15	Temburong	Kampong Tamada	Mixed dipterocarp	115.079835	04.548629
Opp-22	Temburong	Ulu Temburong National Park	Mixed dipterocarp	115.160084	04.551892
Opp-23	Temburong	Pulau Selirong	Mangrove	115.105000	4.8944444
Qua-02	Temburong	Betayan	Mixed dipterocarp	115.103089	04.702775
Qua-05	Temburong	Batu Apoi	Mixed dipterocarp	115.220705	04.682650
Qua-10	Temburong	Kampong Tamada	Mixed dipterocarp	115.079835	04.548629
Opp-08	Tutong	Taman Kulimambang, Tasek Merimbun	Mixed dipterocarp	114.671905	04.594094
Opp-18	Tutong	Tutong Kerangas	Heath	114.585727	04.742889
Qua-06	Tutong	Tutong Kerangas	Heath	114.585727	04.742889

and cluster analysis. Jaccard's distance measure was used to quantify dissimilarities with two dimensions retained ($k = 2$). Eigenvalues were extracted and plotted to evaluate the proportion of variation explained by each axis. The same Jaccard dissimilarity matrix was used for cluster analysis with the complete linkage method. Country biota were grouped by shape and colour into broad biogeographical regions (red circles represent Afrotropics, green triangles represent Asia, yellow squares represent Neotropics, and purple diamonds represent Oceania). The analyses were performed in R Studio v. 4.4.2 using the *vegan* package for ordination methods for community ecology, and the *ggplot2*, *ggrepel* and *dendextend* packages for visualization (Galili 2015; Wickham 2016; Slowikowski 2024; Oksanen *et al.* 2022; R Core Team 2024).

Results and Discussion

We identified a total of 193 species in 55 genera and 17 families in the material studied (Table 2; Supplementary Material File S1). This

includes 21 species described below as new to science, in the genera *Arthonia*, *Byssolecania*, *Byssoloma*, *Chroodiscus*, *Echinoplaca*, *Eremothecella*, *Fellhanera*, *Mazosia*, *Ocellularia*, *Opegrapha*, *Phylloporis*, *Porina*, *Spinomyces* and *Trichothelium*, and three new continental records: *Bapalmuia pallescens* (Paleotropics), *Lyromma palmae* (Paleotropics) and *Tapellaria major* (Paleotropics).

Of the 27 taxa reported by Aptroot *et al.* (2003), the following six were not found in the present material: *Chroodiscus mirificus* (Kremp.) R. Sant., *C. aff. mirificus* (with larger ascospores), *Loflammia epiphylla* (Fée) Lücking & Vězda, *Opegrapha cf. lambinonii* Sérus., *Porina aff. lucida* R. Sant. (with longer, 13-septate ascospores) and *Spinomyces albostrigosus* (R. Sant.) Xavier-Leite *et al.*. The total number of foliicolous species known from Brunei is thus raised from 27 to 199, an increase of 172 taxa. Higher numbers are known only from Brazil (455 species), Costa Rica (435), Ecuador (365), Mexico (340), Guyana (296), Australia (238), Bolivia and Colombia (228 each), and Papua New Guinea (213). However, due to its small size, Brunei currently has the highest species density

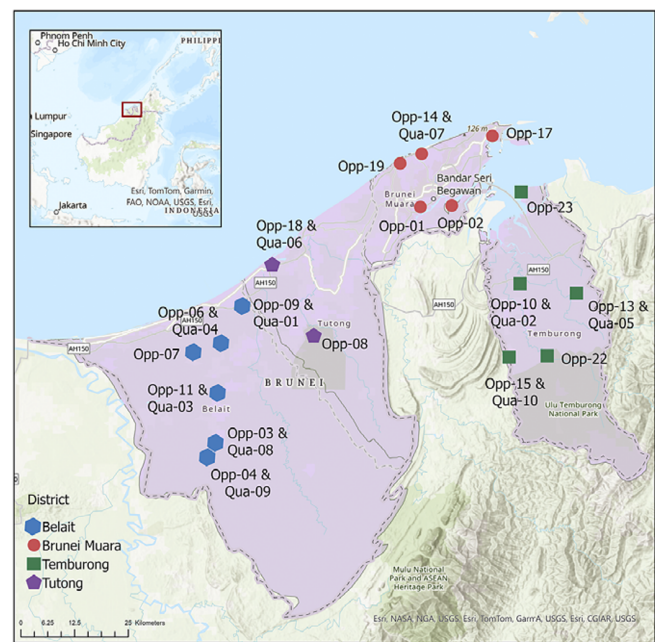


Figure 1. Map of the sampling sites within Brunei Darussalam. Each collection locality is indicated by a coloured shape corresponding to the four districts. The map was made using ArcGIS Pro 3.1. In colour online.

Table 2. List of species of foliicolous lichens found in the studied material from Brunei Darussalam. Taxa in bold are newly described in the present paper.

<i>Anisomeridium foliicola</i> R. Sant. & Tibell
<i>Arthonia concentrica</i> D. A. Ward, B. Moncada & Lücking sp. nov.
<i>Arthonia cyanea</i> Müll. Arg.
<i>Arthonia flavirugosa</i> D. A. Ward, B. Moncada & Lücking sp. nov.
<i>Arthonia flavoverrucosa</i> U. Becker & Lücking
<i>Arthonia lividula</i> Vain.
<i>Arthonia palmulacea</i> (Müll. Arg.) R. Sant.
<i>Arthonia ramosii</i> (Räsänen) R. Sant.
<i>Arthonia tenuilobata</i> D. A. Ward, B. Moncada & Lücking sp. nov.
<i>Arthonia trilocularis</i> Müll. Arg.
<i>Aspidothelium fugiens</i> (Müll. Arg.) R. Sant.
<i>Aspidothelium scutellarpum</i> Lücking
<i>Aulaxina minuta</i> R. Sant.
<i>Aulaxina opegraphina</i> Fée
<i>Badimia cateilea</i> (Vain.) Lücking, Lumbsch & Elix
<i>Badimia dimidiata</i> (Bab. ex Leight.) Vězda
<i>Badimia elegans</i> (Vain.) Vězda
<i>Badimia pallidula</i> (Kremp.) Vězda
<i>Badimia polillensis</i> (Vain.) Vězda
<i>Bapalmuia pallescens</i> Lücking
<i>Byssolecania fumosocaerulea</i> D. A. Ward, B. Moncada & Lücking sp. nov.
<i>Byssolecania fumosonigrans</i> (Müll. Arg.) R. Sant.
<i>Byssoloma annuum</i> (Vain.) G. Thor, Lücking & Tat. Matsumoto

(Continued)

Table 2. (Continued)

<i>Byssoloma chlorinum</i> (Vain.) Zahlbr.
<i>Byssoloma discordans</i> (Vain.) Zahlbr.
<i>Byssoloma inconspicuum</i> D. A. Ward, B. Moncada & Lücking sp. nov.
<i>Byssoloma incrustatimurinum</i> D. A. Ward, B. Moncada & Lücking sp. nov.
<i>Byssoloma leucoblepharum</i> (Nyl.) Vain.
<i>Byssoloma</i> aff. <i>multipunctatum</i> Lücking
<i>Byssoloma subaeruginosum</i> D. A. Ward, B. Moncada & Lücking sp. nov.
<i>Byssoloma subdiscordans</i> (Nyl.) P. James
<i>Byssoloma subundulatum</i> (Stirt.) Vězda
<i>Byssoloma tricholumum</i> (Mont.) Zahlbr.
<i>Byssoloma vanderystii</i> Sérus.
<i>Calenia bullatinoides</i> Lücking
<i>Calenia depressa</i> Müll. Arg.
<i>Calenia graphidea</i> Vain.
<i>Calenia phylogena</i> (Müll. Arg.) R. Sant.
<i>Calenia thelotremella</i> Vain.
<i>Calopadia fusca</i> (Müll. Arg.) Vězda
<i>Calopadia phylogena</i> (Müll. Arg.) Vězda
<i>Calopadia puiggarii</i> (Müll. Arg.) Vězda
<i>Calopadia subcoerulescens</i> (Zahlbr.) Vězda
<i>Caprettia amazonensis</i> Bat. & H. Maia
<i>Chroodiscus argillaceus</i> (Müll. Arg.) Lücking & Papong
<i>Chroodiscus defectus</i> Papong & Lücking
<i>Chroodiscus homchantarae</i> Papong & Lücking
<i>Chroodiscus lirellarpus</i> D. A. Ward, B. Moncada & Lücking sp. nov.
<i>Chroodiscus minutus</i> D. A. Ward & Lücking sp. nov.
<i>Chroodiscus verrucosus</i> R. Sant., Lücking & Vězda
<i>Coccocarpia epiphylla</i> (Fée) Kremp.
<i>Coenogonium disciforme</i> Papong, Boonpr. & Lücking
<i>Coenogonium epiphyllum</i> Vain.
<i>Coenogonium geralense</i> (Henn.) Lücking
<i>Coenogonium hypophyllum</i> (Vězda) Kalb & Lücking
<i>Coenogonium interplexum</i> Nyl.
<i>Coenogonium interpositum</i> Nyl.
<i>Coenogonium subluteum</i> (Rehm) Kalb & Lücking
<i>Cryphoncia albida</i> (Fée) Frisch & G. Thor
<i>Cryphoncia palaeotropica</i> Frisch & G. Thor
<i>Cryptothecia irregularis</i> Lücking, Aptroot, Kalb & Elix
<i>Echinoplaca diffluens</i> (Müll. Arg.) R. Sant.
<i>Echinoplaca epiphylla</i> Fée
<i>Echinoplaca hispida</i> Sipman
<i>Echinoplaca</i> aff. <i>hispida</i> Sipman
<i>Echinoplaca incrustaticiliata</i> Sérus.
<i>Echinoplaca leucotrichoides</i> (Vain.) R. Sant.

(Continued)

Table 2. (Continued)

<i>Echinoplaca pellicula</i> (Müll. Arg.) R. Sant.
<i>Echinoplaca septemseptata</i> D. A. Ward & Lücking sp. nov.
<i>Enterographa angustissima</i> (Vain.) R. Sant.
<i>Eremothecella cyaneoides</i> Lücking
<i>Eremothecella helicella</i> Aptroot & M. Cáceres
<i>Eremothecella macrocephala</i> (R. Sant.) G. Thor, Sérus., Lücking & Tat. Matsumoto
<i>Eremothecella macrosperma</i> (Zahlbr.) Sérus.
<i>Eremothecella rugosa</i> D. A. Ward, B. Moncada & Lücking sp. nov.
<i>Eremothecella variratae</i> (Aptroot & Sipman) Sérus.
<i>Eremothecella verrucispora</i> D. A. Ward & Lücking sp. nov.
<i>Eugeniella micrommata</i> (Kremp.) Lücking, Sérus. & Kalb
<i>Eugeniella psychotriae</i> (Müll. Arg.) Lücking, Sérus. & Kalb
<i>Fellhanera albidocincta</i> (Vain.) Lücking
<i>Fellhanera</i> aff. <i>bouteillei</i> (Desm.) Vězda
<i>Fellhanera dispersa</i> Lücking
<i>Fellhanera lambinonii</i> (Sérus.) Lücking & Sérus.
<i>Fellhanera mastothallina</i> (Vain.) Lücking & Sérus.
<i>Fellhanera parvula</i> (Vězda) Vězda
<i>Fellhanera punctata</i> Lücking
<i>Fellhanera semecarpi</i> (Vain.) Vězda
<i>Fellhanera tutongensis</i> D. A. Ward & Lücking sp. nov.
<i>Fouragea filicina</i> (Mont.) Trevis.
<i>Fouragea puiggarii</i> (Müll. Arg.) Zahlbr.
<i>Fouragea vegae</i> (R. Sant.) Ertz
<i>Gallaicolichen pacificus</i> Sérus. & Lücking
<i>Gyalectidium filicinum</i> Müll. Arg.
<i>Gyalectidium imperfectum</i> Vězda
<i>Gyalideopsis</i> sp.
<i>Heiomasia annamariae</i> Kalb
<i>Lasioloma arachnoideum</i> (Kremp.) R. Sant.
<i>Lasioloma phycophilum</i> (Vain.) R. Sant.
<i>Lasioloma phycophorum</i> (Vain.) R. Sant.
<i>Leptogium denticulatum</i> Tuck.
<i>Loflammia gabrielis</i> (Müll. Arg.) Vězda
<i>Loflammia intermedia</i> (R. Sant.) Vězda
<i>Lyromma palmae</i> (Cavalc. & A. A. Silva) Lücking & Sérus.
<i>Mazosia aptrootii</i> Sipman
<i>Mazosia bambusae</i> (Vain.) R. Sant.
<i>Mazosia bambusiradiata</i> D. A. Ward & Lücking sp. nov.
<i>Mazosia dispersa</i> (J. Hedrick) R. Sant.
<i>Mazosia melanophthalma</i> (Müll. Arg.) R. Sant.
<i>Mazosia paupercula</i> (Müll. Arg.) R. Sant.
<i>Mazosia phyllosema</i> (Nyl.) Zahlbr.

(Continued)

Table 2. (Continued)

<i>Mazosia pseudobambusae</i> Kalb & Vězda
<i>Mazosia rotula</i> (Mont.) A. Massal.
<i>Mazosia rugosa</i> D. A. Ward & Lücking sp. nov.
<i>Microtheliopsis uleana</i> Müll. Arg.
<i>Microxyphiomyces vainioi</i> (R. Sant.) Xavier-Leite, M. Cáceres & Lücking
<i>Musaespora coccinea</i> Aptroot & Sipman
<i>Musaespora epiphylla</i> (R. Sant.) R.C. Harris
<i>Musaespora kalbii</i> Lücking & Sérus.
<i>Myeloconis erumpens</i> P.M. McCarthy & Elix
<i>Myriostigma candidum</i> Kremp.
<i>Ocellularia andulaensis</i> D. A. Ward & Lücking sp. nov.
<i>Opegrapha albomarginata</i> D. A. Ward & Lücking sp. nov.
<i>Opegrapha dibbenii</i> Sérus.
<i>Opegrapha serusiauxii</i> Lücking
<i>Phyllobathelium nigrum</i> R. Sant. & Tibell
<i>Phylloblastia dolichospora</i> Vain.
<i>Phyllocraterina nuda</i> (Zahlbr.) Lücking & Sérus.
<i>Phylloporis phylogena</i> (Müll. Arg.) Clem.
<i>Phylloporis platypoda</i> (Müll. Arg.) Vězda
<i>Phylloporis verrucosula</i> D. A. Ward & Lücking sp. nov.
<i>Porina alba</i> (R. Sant.) Lücking
<i>Porina albicera</i> (Kremp.) Overeem & D. Overeem
<i>Porina applanata</i> Vain.
<i>Porina atriceps</i> (Vain.) Vain.
<i>Porina chrysophora</i> (Stirt.) R. Sant.
<i>Porina conica</i> R. Sant.
<i>Porina cupreola</i> (Müll. Arg.) F. Schill.
<i>Porina epiphylla</i> Fée
<i>Porina fusca</i> Lücking
<i>Porina imitatrix</i> Müll. Arg.
<i>Porina kamerunensis</i> F. Schill.
<i>Porina karnatakensis</i> Makhija, Adaw. & Patw.
<i>Porina leptosperma</i> Müll. Arg.
<i>Porina leptospermoides</i> Müll. Arg.
<i>Porina limbulata</i> (Kremp.) Vain.
<i>Porina monocarpa</i> (Kremp.) F. Schill.
<i>Porina multiloculata</i> Makhija, Adaw. & Patw.
<i>Porina perminuta</i> Vain.
<i>Porina riparia</i> D. A. Ward & Lücking sp. nov.
<i>Porina rubentior</i> (Stirt.) Müll. Arg.
<i>Porina rubrosphaera</i> R. Sant.
<i>Porina rufula</i> (Kremp.) Vain.
<i>Porina semecarpi</i> Vain.
<i>Porina similis</i> Kalb & Vězda

(Continued)

Table 2. (Continued)

<i>Porina tetramera</i> (Malme) R. Sant.
<i>Porina uluguruensis</i> (Krog) Vězda
<i>Porina vanuatuensis</i> Lücking
<i>Porina vezdae</i> Lücking
<i>Porina virescens</i> (Kremp.) Müll. Arg.
<i>Puiggariella nemathora</i> (Mont.) S.H. Jiang, Lücking & J.C. Wei
<i>Raciborskiella talaumae</i> (Racib.) Höhn.
<i>Racoplaca maculata</i> (Cooke & Massée) S.H. Jiang, Lücking & J.C. Wei
<i>Racoplaca melanobapha</i> (Kremp.) S.H. Jiang, Lücking & J.C. Wei
<i>Racoplaca subtilissima</i> Fée
<i>Rolueckia conspersa</i> (Stirt.) Papong, Thammath. & Boonpr.
<i>Rubrotricha helminthospora</i> (R. Sant.) Lücking, Sérus. & Vězda
<i>Semigyalecta paradoxa</i> Vain.
<i>Spinomyces rubrotrichoides</i> D. A. Ward, B. Moncada & Lücking sp. nov.
<i>Sporopodium antoninianum</i> Elix, Lumbsch & Lücking
<i>Sporopodium</i> aff. <i>antoninianum</i> Elix, Lumbsch & Lücking
<i>Sporopodium argillaceum</i> (Müll. Arg.) Zahlbr.
<i>Sporopodium cupuliferum</i> (Nyl.) Vain.
<i>Sporopodium leprieurii</i> Mont.
<i>Sporopodium phyllocharis</i> (Mont.) A. Massal.
<i>Sporopodium</i> aff. <i>podosphaera</i> Lücking & R. Sant.
<i>Sporopodium pycnoblustum</i> Vain.
<i>Sporopodium subflavescens</i> Lücking & Lumbsch
<i>Sporopodium</i> sp. 1
<i>Sporopodium</i> sp. 2
<i>Strigula concreta</i> (Fée) R. Sant.
<i>Strigula nigrocarpa</i> Lücking
<i>Strigula nitidula</i> Mont.
<i>Strigula schizospora</i> R. Sant.
<i>Strigula smaragdula</i> Fr.
<i>Tapellaria major</i> (Lücking) Lücking
<i>Tricharia novoguineensis</i> Sérus.
<i>Tricharia substipitata</i> Vězda
<i>Tricharia urceolata</i> (Müll. Arg.) R. Sant.
<i>Trichothelium alboatrum</i> Vain.
<i>Trichothelium annulatum</i> (P. Karst.) R. Sant.
<i>Trichothelium assurgens</i> (Cooke) Aptroot & Lücking
<i>Trichothelium epiphyllum</i> Müll. Arg.
<i>Trichothelium subrobinsonii</i> D. A. Ward & Lücking sp. nov.

value relative to absolute area, with over 34 species per km², four times higher than Costa Rica, and the sixth highest based on log(area) (Table 3).

The foliicolous lichen biota of Brunei has a strong affinity with other paleotropical regions, clustering within a group of countries representing insular South-East Asia and Australasia (Oceania),

specifically the Philippines, Indonesia, Papua New Guinea and Australia, with somewhat less affinity to continental South-East Asia (Figs 2 & 3). With the exception of Madagascar, the foliicolous lichen biota of selected tropical countries form three distinct clusters that represent the Neotropics, Afrotropics and eastern Palearctica (Asia and Oceania) (Fig. 3). Despite its geographical proximity to Africa, Madagascar clustered with Sri Lanka and Vietnam, which is a pattern that was similarly found in tropical tree genera and may be driven by shared climates (Slik *et al.* 2015). Vietnam did not cluster tightly with Indonesia, Malaysia and Thailand, despite being geographically close. This separation may be related to Vietnam's slightly differing climate and substrata, which are related to the geological history and location of the country. These differences can be summarized by Vietnam's mostly Indochinese floristic signature with temperate elements, in comparison to the Malesian-dominated affinities of Thailand, Malaysia, and Indonesia.

Taxa identified as characteristic elements of the Palearctica include, among others: *Arthonia ramosii*, *Badimia cateilea* and *B. elegans*, *Byssoloma annuum*, *Chroodiscus argillaceus*, *C. defectus*, *C. homchantarae* and *C. verrucosus*, *Echinoplaca incrustaticiliata*, *Eremothecella macrocephala*, *E. macrosperma* and *E. variratae*, *Eugeniella micrommata*, *Fellhanera albidocincta* and *F. mastothallina*, *Gallaicolichen pacificus*, *Lasioloma phycophilum* and *L. phycophorum*, *Mazosia aptrootii*, *Musaespora coccinea* and *M. epiphylla*, *Phyllobathelium nigrum*, *Phylloblastia dolichospora*, *Phyllocraterina nuda*, *Porina applanata*, *P. cupreola*, *P. monocarpa*, *P. multiloculata*, *P. vanuatuensis* and *P. virescens*, *Raciborskiella talaumae*, *Rubrotricha helminthospora*, *Semigyalecta paradoxa*, *Tricharia novoguineensis* and *Trichothelium assurgens*.

Selected individual leaves revealed between six and 30 species per leaf, with leaf sizes ranging from 60 to 459 cm² (Fig. 4, Table 4). While not as high as the current records of comparably sized leaves (125 and 98 cm²) from Costa Rica and Ecuador, with 49 and 46 species, respectively (Lücking & Matzer 2001), such high small-scale diversity is still remarkable. Our data also support the notion that closely related species (of the same genus) frequently grow side-by-side, demonstrating a high level of ecological equivalence. In the present material, this was observed particularly for species in the genera *Mazosia*, with up to seven species (out of a total of 24) on a single leaf (1278); in the case of the overall much more speciose genus *Porina*, only one leaf (1294) was found with a high number of species, namely eight out of 30 (Table 4).

Taxonomic Treatment

New or otherwise noteworthy taxa

Arthonia concentrica D. A. Ward, B. Moncada & Lücking sp. nov.

Index Fungorum No.: IF 905094

Differing from *Arthonia trilocularis* in the circular, slightly glossy thallus with concentrically arranged, thinly pruinose ascomata.

Type: Brunei Darussalam, Belait, Andulau Forest Reserve, 4° 39' 19.98"N, 114° 31' 20.244"E, 72 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 1 September 2021, D. A. Ward 274 (UBDH—holotype!; B—isotype!).

(Fig. 5A–E)

Thallus continuous, very regularly rounded, smooth, 7–15 mm across, very thin (15–20 µm), ecorticate, yellowish brown to olive-

Table 3. List of the 15 countries with the highest known richness of foliicolous lichens.

Country	Species	Area size (km ²)	Density/Area (1000 km ²)	Log(Area)	Density/Log(Area)
Brazil	455	8 510 000	0.05	6.93	65.7
Costa Rica	435	51 100	8.51	4.71	92.4
Ecuador	365	283 561	1.29	5.45	66.9
Mexico	340	1 973 000	0.17	6.30	54.0
Guyana	296	214 969	1.38	5.33	55.5
Australia	238	7 688 000	0.03	6.89	34.6
Bolivia	228	1 099 000	0.21	6.04	37.7
Colombia	228	1 142 000	0.20	6.06	37.6
Papua New Guinea	213	462 840	0.46	5.67	37.6
Brunei	199	5 765	34.52	3.76	52.9
Philippines	197	300 000	0.66	5.48	36.0
Peru	190	1 285 000	0.15	6.11	31.1
Tanzania	184	947 300	0.19	5.98	30.8
Ivory Coast	178	322 462	0.55	5.51	32.3
Democratic Republic of the Congo	171	2 345 000	0.07	6.37	26.8

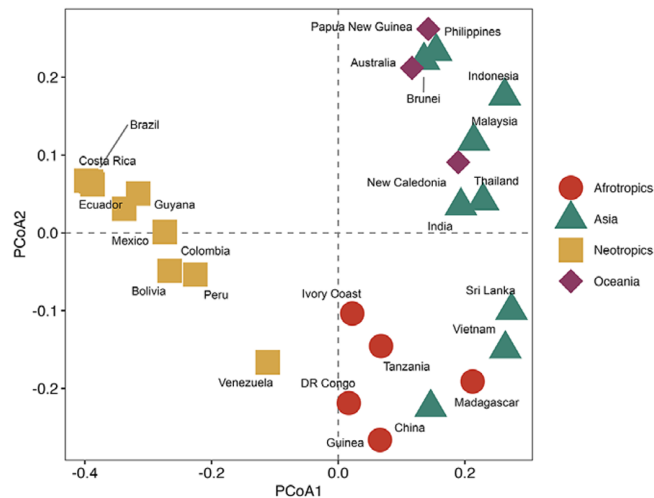


Figure 2. PCoA ordination of selected tropical countries based on similarities in their foliicolous lichen biota. In colour online.

brown, slightly glossy. *Photobiont cells* rectangular, 10–18 × 5–7 µm, in closed, regularly radiating plates.

Ascomata not or hardly raised above thallus level, conspicuously arranged in concentric fashion towards the periphery of the thallus, rounded to slightly irregular, 0.5–1.0 mm diam. and 30–40 µm high, greyish brown, appearing thinly purplish to brownish pruinose. *Hypothecium* inconspicuous. *Epithecium* formed by dense layer of parallel, periclinal hyphae, 3–5 µm high, colourless to pale brown, without any cover that would explain the pruinose appearance, K+ olive. *Hymenium* 30–40 µm high, colourless, I+ orange-red, KI+ pale bluish. *Paraphyses* branched and anastomosing. *Asci* broadly clavate to subglobose, 25–30 × 12–20 µm, I–, KI+ blue in inner parts of tholus. *Ascospores* 8 per ascus, drop-shaped, 2-septate, with the terminal cell enlarged, 12–15 × 4–5(–6) µm, grey-brown, I–.

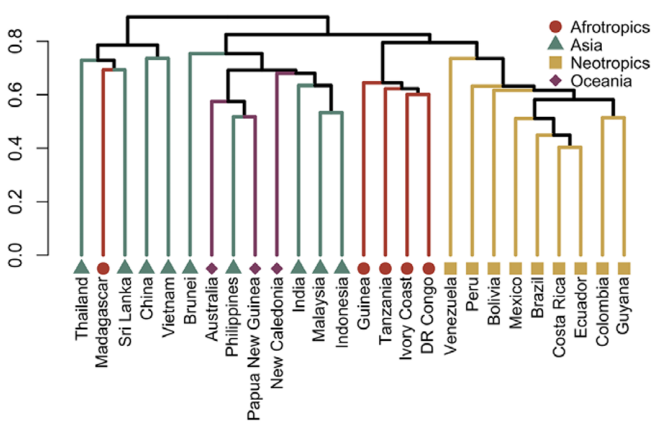


Figure 3. Cluster dendrogram of selected tropical countries based on similarities in their foliicolous lichen biota. The Neotropics, Afrotropics, and Eastern Paleotropics (Asia, Oceania) form three separate clusters, with the exception of Madagascar, clustering with Sri Lanka and Vietnam. Brunei forms part of a cluster including mostly insular South-East Asia and Oceania. In colour online.

Mature pycnidia not observed but one thallus had concentric rings of small, dark brown, hemispherical warts 0.05–0.07 mm diam., with a central pore visible under the microscope, that probably represent young pycnidia; the warts in section reacting K+ red.

Secondary chemistry. Not tested by TLC due to the very small thalli; standard spot tests on the thallus (C, K, P, UV) all negative; epithecium K+ olive, thallus warts (empty pycnidia?) K+ red.

Etymology. The epithet refers to the concentrically arranged ascomata.

Distribution and ecology. Known from a single locality of mixed dipterocarp forest in Brunei Darussalam.

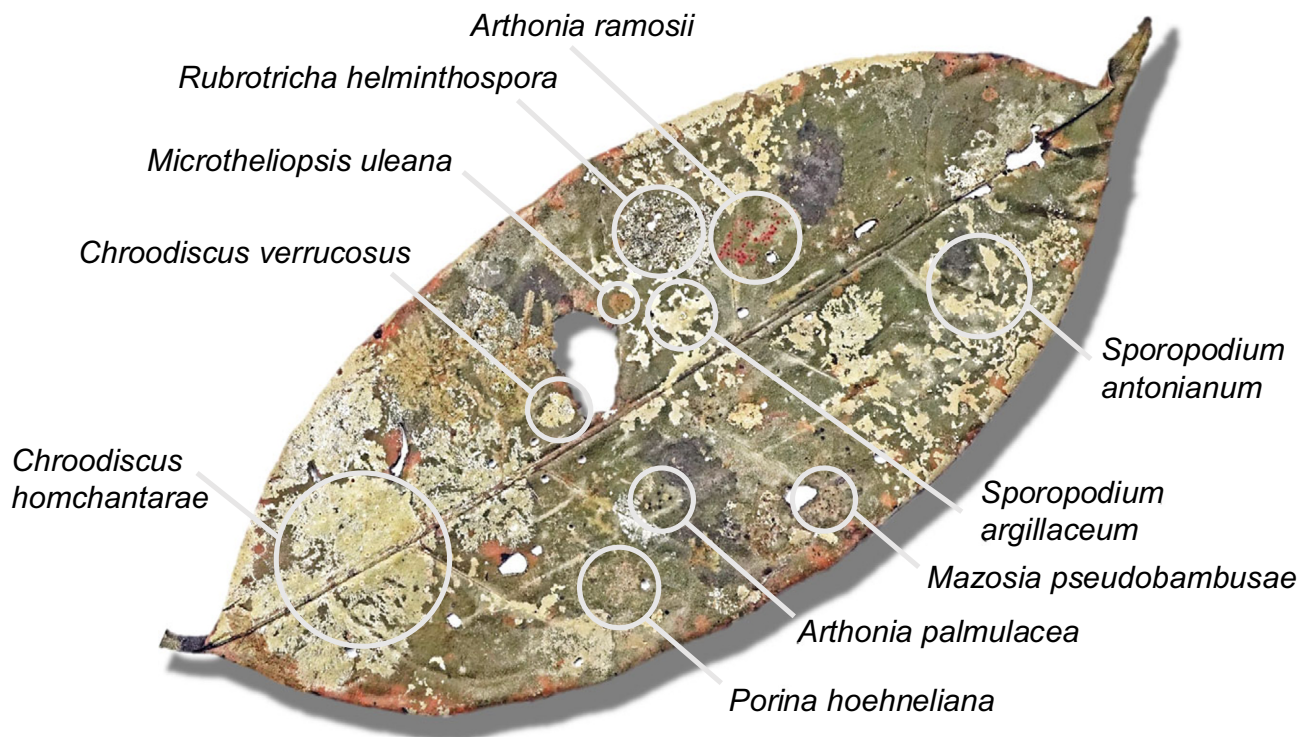


Figure 4. Selected entire leaf (1292; see Table 4) from the material studied from Brunei Darussalam with 15 different foliicolous lichen species, some of them mapped. In colour online.

Table 4. Number of foliicolous species found on selected leaves in the material studied from Brunei Darussalam.

Collection number	Size (cm ²)	Species	Species of <i>Mazosia</i>	Species of <i>Porina</i>
1294	170	30	0	8
1288	459	27	1	2
1278	201	24	7	2
1279	112	23	4	2
1289	251	23	0	2
1280	141	17	3	2
1286	127	16	1	2
1292	82	15	1	0
1290	247	15	5	1
1285	79	14	2	0
1277	173	13	6	0
1291	314	12	5	2
1287	134	11	3	2
1282	60	7	0	0
1276	82	7	3	0
1283	82	7	3	0
1284	71	6	1	0

Remarks. The genus *Arthonia* Ach. is a diverse element of foliicolous lichen communities, with 25 species currently accepted (Lücking 2008). Among these, there is a group of taxa with

predominantly 2-septate, grey-brown ascospores, including *A. flavoverrucosa*, *A. fuscocyanea* U. Becker & Lücking, and *A. trilocularis* (Becker & Lücking 1995; Lücking 2008).

Arthonia concentrica is a further species with 2-septate, grey-brown ascospores. It is overall most similar to *A. trilocularis* (Lücking 2008), with which it shares the same ascospore type (and size range), but it differs in the larger, regularly rounded, continuous, brownish yellow, slightly glossy thallus patches, with the ascomata and pycnidia formed in concentric fashion towards the thallus periphery and producing a thin pruina. *Arthonia trilocularis* is abundantly present in the material studied here (Fig. 5F) and the specimens come close to the type material from Madagascar. This taxon has an irregularly dispersed, rather opaque thallus, with the individual patches usually below 1 mm diam. and the entire thallus not exceeding 5(–10) mm. The ascomata and pycnidia are dispersed over the entire thallus. The ascomata are brownish black with an irregular outline and lacking a pruina, except sometimes for the margins of the ascomata, and the pycnidia are flattened and black and do not display a K+ red reaction (see also Lücking 2008). We also compared numerous specimens of *A. trilocularis* from different regions of the Neotropics, Madagascar (the type), the Seychelles (Fig. 5G), Thailand, Australia, and New Caledonia, and could not find a morphology similar to *A. concentrica*. *Arthonia trilocularis* itself is probably a collective species that requires further study (Lücking 2008). Externally more similar to the new species is *Arthonia accolens* Stirt. (Lücking 2008), which often has a slightly glossy thallus but which differs in the lighter brown, non-pruinose ascomata and the colourless ascospores.

***Arthonia flavirugosa* D. A. Ward, B. Moncada & Lücking sp. nov.**

Index Fungorum No.: IF 905095

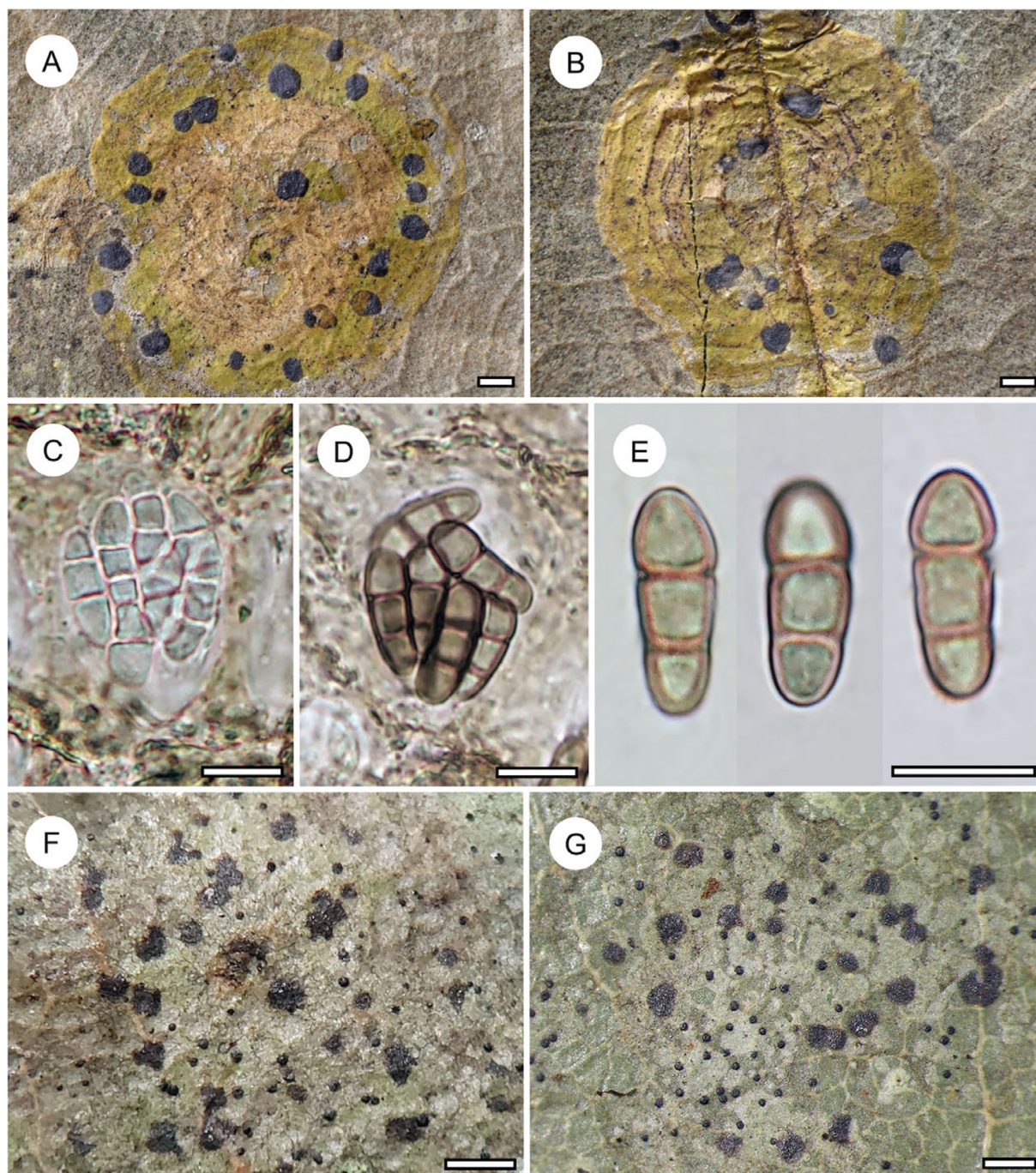


Figure 5. Habit and characteristics of newly described species. A–E, *Arthonia concentrica* (A & C–E, holotype; B, isotype). A & B, thalli with apothecia. C & D, asci with immature and mature ascospores. E, ascospores. F & G, *Arthonia trilocularis* for comparison (F, Brunei, Ward 620a; G, Seychelles, Norkett 17868A). Scales: A, B, F & G = 1 mm; C–E = 10 μ m. In colour online.

Differing from *Arthonia flavoverrucosa* in the delicate, light yellowish ridges and the smaller ascospores.

Type: Brunei Darussalam, Belait, Jalan Labi Heath Forest, 4° 28'32.4084"N, 114°28'2.7768"E, 51 m, tropical moist broadleaf forest ecoregion, heath forest, on palm leaves, 19 September 2021, D. A. Ward 765 (UBDH—holotype!; B—isotype!).

(Fig. 6A–C)

Thallus irregularly dispersed but individual patches connected by a translucent hypothallus delimited by a narrow, dark brown prothallus, finely rugose, 8–20 mm across, very thin (15–20 μ m),

ecorticate, light brown with a reddish tinge, opaque to slightly glossy; thallus patches furnished with delicate, irregular to radiating short ridges, often bordering the individual patches in concentric fashion, 0.1–0.3(–0.5) mm long and 50–80 μ m wide, light yellowish, UV+ orange, in microscopic view filled with small, brownish crystals that quickly dissolve in K producing a light yellow cloud and retaining an orange colour. *Photobiont cells* oblong to rounded, 7–12 $\times$ 4–6 μ m, in irregular plates leaving small interspaces.

Ascomata not raised above thallus level, rounded to elongate or irregularly angular, 0.4–0.6(–0.9) mm across and 40–45 μ m high, dark greyish brown to brownish black, epruinose or thinly greyish

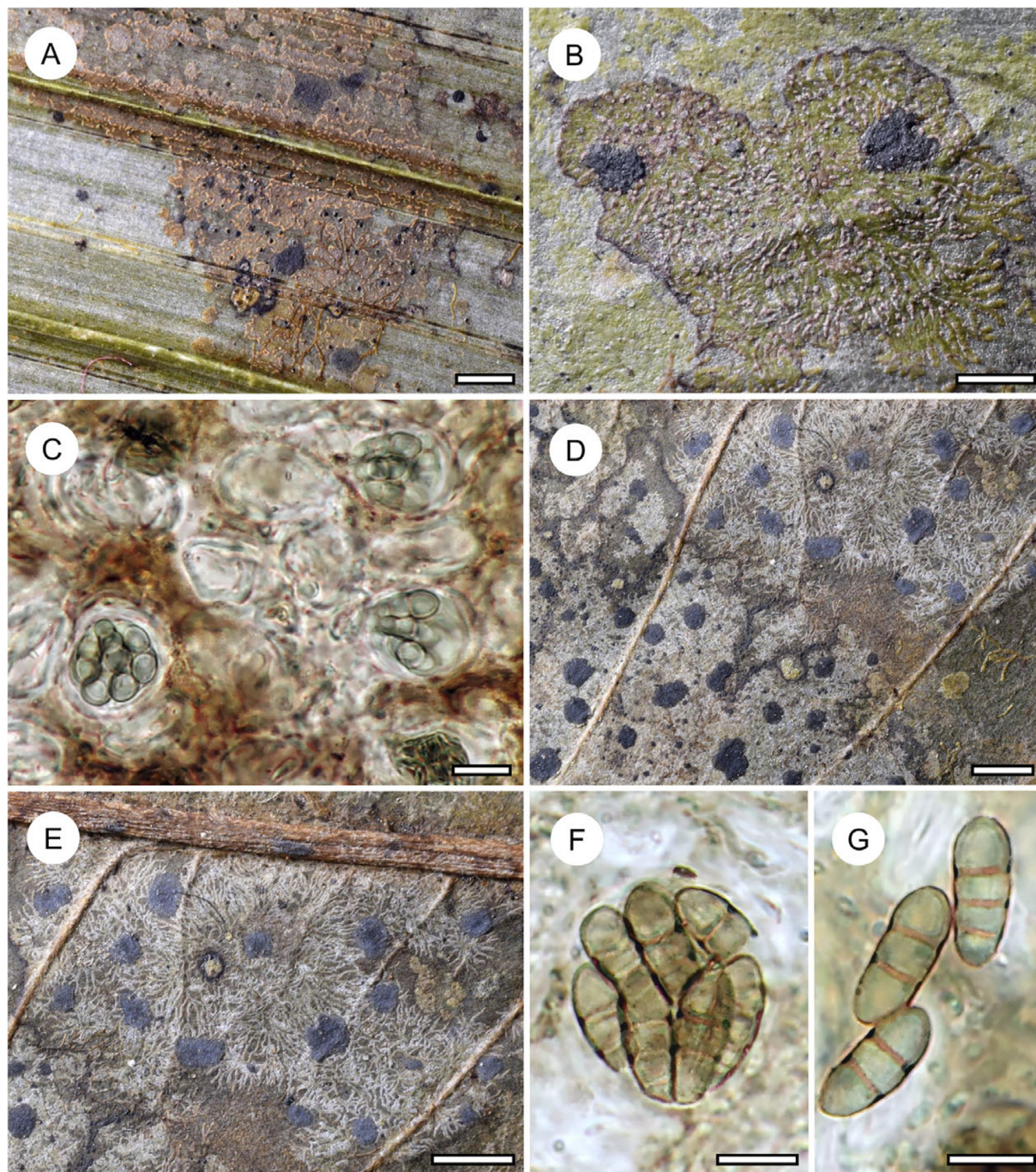


Figure 6. Habit and characteristics of newly described species. A–C, *Arthonia flavirugosa* (A & C, holotype; B, Ward 859). A & B, thalli with apothecia. C, asci with ascospores. D–G, *Arthonia tenuilobata* (holotype). D & E, thallus with apothecia. F, ascus with ascospores. G, ascospores. Scales: A, B, D & E = 1 mm; C, F & G = 10 μ m. In colour online.

pruinose. *Hypothecium* 5–7 μ m high, colourless to brownish, K+ olive. *Epithecium* formed by a thin layer of parallel, periclinal hyphae, 3–5 μ m high, brownish granulose, I–, the brownish granules dissolving in K forming a light yellow to greenish cloud, KI+ slightly olive. *Hymenium* 35–40 μ m high, colourless, I+ orange, KI–. *Paraphyses* branched and anastomosing. *Asci* obovate to subglobose, 20–25 $\times$ 12–15 μ m, I–, KI–. *Ascospores* 8 per ascus, drop-shaped, 2-septate, with the terminal cell enlarged, 10–12 $\times$ 3.5–4.5 μ m, initially colourless but soon becoming grey-brown, I–.

Pycnidia rather frequent, applanately hemispherical, 0.1–0.15 mm diam., black, wall composed of dark brown, radiating hyphae. *Conidia* not observed.

Secondary chemistry. Not tested by TLC due to the very small thalli; standard spot tests (C, K, P, UV) on the thallus negative, except for the ridges containing a brownish, crystalline pigment, with K+ light yellow efflux and retaining an orange colour, in surface view UV+ orange.

Etymology. The epithet refers to the light yellowish thallus ridges.

Distribution and ecology. Known from two localities of heath forest and mixed dipterocarp forest in Brunei Darussalam. The type collection on palm leaves is particularly plentiful.

Remarks. *Arthonia flavirugosa* is a second new species of foliicolous *Arthonia* with 2-septate, greyish brown ascospores discovered in material from Brunei, demonstrating a remarkable diversity of phenotypes in this group of species not recognized before. It differs from all other foliicolous species of *Arthonia* in the minutely rugose thallus with irregular to radiating or concentrically arranged, light yellowish ridges. This morphology is not entirely novel, as another species with thallus ornamentation, *Arthonia flavoverrucosa*, has previously been described from Côte d'Ivoire (Becker & Lücking 1995). Notably, that species was also found among the material from Brunei; it features pale yellow to orange-brown verrucae, much wider than the narrow ridges of *A. flavirugosa*. Its ascospores are also larger ($12\text{--}16 \times 4\text{--}6 \mu\text{m}$) than those of the new species. A morphologically similar species with thallus ornamentation is *Eremothecella rugosa*, described below, which differs in the yellow-green thallus and the much larger, multiseptate, colourless ascospores.

We carefully evaluated the possibility that these cases could represent lichenicolous species of *Arthonia* inhabiting other lichen thalli, as such ornamentation is not known from corticolous species. If that were the case, the only candidates for potential host thalli having ornamentation and a *Phycopeltis* photobiont are in the genera *Mazosia* and *Porina*. However, no known species in these two genera has thalli with an ornamentation comparable to the three species mentioned above, including the material from Brunei studied here, so one would have to assume unknown host lichens. Also, lichenicolous species tend to have much smaller ascomata. If harmful to the host, they are usually limited to certain parts of the thallus which show signs of damage; if non-harmful parasymbionts, they are regularly dispersed on the host thallus and intermingled with the ascomata of the host lichen (Matzer 1996; Grube & Lücking 2002). Since none of these criteria apply to the material of the ornamented species of *Arthonia* and *Eremothecella*, there is no reason to assume they could represent lichenicolous species.

Additional specimen examined. Brunei Darussalam: Belait: Jalan Labi Mixed Dipterocarp Forest, $4^{\circ}34'49''\text{N}$, $114^{\circ}28'35''\text{E}$, 81 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 10 ix 2021, D. A. Ward 859 (B).

***Arthonia tenuilobata* D. A. Ward, B. Moncada & Lücking sp. nov.**

Index Fungorum No.: IF 905096

Differing from *Arthonia lobulicarpa* in the more delicate lobes, pruinose ascomata and the brown ascospores.

Type: Brunei Darussalam, Belait, Andulau Forest Reserve, $4^{\circ}39'19.98''\text{N}$, $114^{\circ}31'20.244''\text{E}$, 72 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 1 September 2021, D. A. Ward 277a (UBDH—holotype!; B—isotype!).

(Fig. 6D–G)

Thallus continuous but finely dissected into thin lobes, smooth, 5–15 mm across, very thin ($15\text{--}20 \mu\text{m}$), ecorticate, yellowish brown,

opaque to slightly glossy; lobes irregularly branched to radiating, 0.05–0.08 mm wide, in microscopic view composed of radiating and proliferating plates of photobiont cells connected by hyaline fungal hyphae. *Photobiont cells* rectangular, $8\text{--}15 \times 3\text{--}5 \mu\text{m}$, in closed, regularly radiating plates.

Ascomata not or hardly raised above thallus level, rounded, 0.3–0.6 mm diam. and 40–45 μm high, greyish brown, thinly brownish to greyish pruinose, giving the ascomata a somewhat bluish to purplish tinge. *Hypothecium* 5–7 μm high, brownish, I–, KI+ olive. *Epithecium* formed by a thin layer of parallel, periclinal hyphae, 3–5 μm high, colourless, I–, KI+ slightly olive. *Hymenium* 35–40 μm high, colourless, I+ light orange, KI+ light blue. *Paraphyses* branched and anastomosing. *Asci* obovate to subglobose, $25\text{--}30 \times 12\text{--}15 \mu\text{m}$, I–, KI–. *Ascospores* 8 per ascus, drop-shaped, 2-septate, with the terminal cell enlarged, $12\text{--}15 \times 4\text{--}5 \mu\text{m}$, for some time colourless but becoming grey-brown when mature, I–.

Pycnidia applanately conical, 0.15–0.2 mm diam., greyish black, wall composed of dark brown, parallel to radiating hyphae. *Conidia* narrowly oblong to fusiform with acute ends, non-septate, $10\text{--}15 \times 2.5\text{--}3 \mu\text{m}$, colourless.

Secondary chemistry. Not tested by TLC due to the very small thalli, but standard spot tests (C, K, P, UV) all negative or at best darkening.

Etymology. The epithet refers to the thin thallus lobes.

Distribution and ecology. Known from several localities of mixed dipterocarp (and riparian) forest in Brunei Darussalam.

Remarks. *Arthonia tenuilobata* represents a third new species with 2-septate, grey-brown ascospores. All hitherto known species in this group, including *A. flavoverrucosa*, *A. fuscocyanea*, *A. trilocularis* and the two new species described above, have continuous to dispersed thalli with rounded patches not dissected into lobes, with the exception of some specimens of *A. trilocularis* in which the thallus is partly dissected into irregular lobes (Lücking 2008). However, the apothecia of *A. trilocularis* lack a pruina giving them a bluish tinge, and the type of conidia found in the new species is not known from the latter. *Arthonia fuscocyanea* features ascomata with a pruina giving them a bluish tinge, but they have an angular shape and the thallus morphology is different.

Lobate thalli are otherwise found in *Arthonia lobulicarpa* U. Becker & Lücking, as in *A. fuscocyanea* described from tropical Africa (Becker & Lücking 1995). However, in that species the ascospores are colourless, the ascomata are non-pruinose and the thallus lobes are wider and shorter. Rather thin and often radiating thallus lobes may also be formed in *Arthonia orbignyae* (H. B. P. Upadhyay) Matzer (Lücking 2008), but that species has distinctly lirellate ascomata and the ascospores are also colourless. The ascomata of *A. tenuilobata* resemble those of *A. cyanea* Müll. Arg. in the bluish tinge, but the latter species has a different thallus morphology and its ascospores are colourless.

The thin and radiating lobes of *Arthonia tenuilobata* may resemble those of narrowly lacinate forms of *Puigariella nemathora*. In close-up, however, there are fundamental differences. The thallus of the latter grows beneath the leaf cuticle, with *Cephaleuros* as photobiont, and has convex lobules bearing numerous small, white papillae, whereas the thallus of *Arthonia tenuilobata* grows above the cuticle, with a *Phycopeltis* photobiont and completely flattened, thin lobes.

Key to foliicolous species of *Arthonia* with 2(–3)-septate, grey-brown ascospores

- 1 Thallus ornamented with verrucae or delicate ridges filled with crystals 2
 Thallus smooth 3
- 2(1) Thallus with irregular, light yellow to orange-brown verrucae 0.03–0.05 mm diam.; ascospores 12–16 × 4–6 µm;
 pantropical ***Arthonia flavoverrucosa***
 Thallus with irregular to radiating or concentrically arranged, pale yellow, delicate ridges 0.1–0.3(–0.5) mm long and 50–80 µm
 wide; ascospores 10–12 × 3.5–4.5 µm; Eastern Paletropics (Brunei) ***Arthonia flavirugosa***
- 3(1) Thallus dissected into fine, radiating lobes; ascospores 12–15 × 4–5 µm; Eastern Paletropics (Brunei) ***Arthonia tenuilobata***
 Thallus continuous and circular to irregular or dispersed into rounded to irregular patches; ascospores 11–20 × 4–6 µm 4
- 4(3) Thallus forming large, circular patches; ascomata formed concentrically towards the thallus periphery; Eastern Paletropics
 (Brunei) ***Arthonia concentrica***
 Thallus irregular to dispersed; ascomata dispersed over the thallus 5
- 5(4) Ascomata with a rim of orange pruina, disc and pruina K+ purple; pantropical ***Arthonia mira***
 Ascomata non-pruinose or with a thin greyish to brownish pruina or a whitish pruinose rim not reacting K+ purple 6
- 6(5) Ascomata with a whitish pruinose rim, otherwise thinly whitish to greyish pruinose and with a distinctly purplish tinge;
 ascospores 13–19 × 2.7–4.5 µm, 4–5 times as long as wide; African Paletropics ***Arthonia fuscocyanea***
 Ascomata epruinose, brownish black to black; ascospores 11–20 × 4–6 µm, 2.5–3.5 times as long as wide; pantropical
 ***Arthonia trilocularis***

Additional specimen examined. Brunei Darussalam: *Belait*: Andulau Forest Reserve, 4°39'19.98"N, 114°31'20.244"E, 72 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 1 ix 2021, *D. A. Ward* 262 (UBDH); *Wasai Telingan*, Teraja, 4°22'19.2252"N, 114°27'58.3344"E, 149 m, tropical moist broadleaf forest ecoregion, riparian forest/mixed dipterocarp forest, on leaves, 30 x 2021, *D. A. Ward* (with *D. Cicuzza*) 1102 (B, UBDH). *Temburong*: Kampong Tamada, 4°32'55.0644"N, 115°4'47.406"E, 48 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 13 xi 2021, *D. A. Ward* 592a (B).

***Bysssolecania fumosocaerulea* D. A. Ward, B. Moncada & Lücking sp. nov.**

Index Fungorum No.: IF 905097

Differing from *Bysssolecania fumosonigricans* in greyish blue outer fringe of the apothecia.

Type: Brunei Darussalam, *Belait*, Andulau Forest Reserve, 4°39'19.98"N, 114°31'20.244"E, 72 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 1 September 2021, *D. A. Ward* 267 (UBDH—holotype!; B—isotype!).

(Fig. 7A–G)

Thallus continuous, irregular in outline, smooth, 10–30 mm across, very thin (15–25 µm), ecorticate, dark brown, opaque to slightly glossy. *Photobiont cells* bright green, rounded, 7–14 µm diam.

Ascomata not or hardly raised above thallus level, rounded to slightly irregular, 0.5–1.5 mm diam. and 30–40 µm high, light greyish brown in the centre but with a conspicuous, greyish blue rim around the centre, bordered by a thin, whitish margin, the entire ascoma UV+ bright blue. *Hypothecium* 5–10 µm high, dark aeruginous, I–, KI–. *Epithecium* indistinct. *Hymenium* 30–35 µm high, colourless, I+ blue, KI+ blue. *Paraphyses* unbranched, straight, rather thick (up to 3 µm) and densely arranged, embedded in a copious gelatinous matrix. *Asci* clavate, 28–33 × 8–10 µm, I+ blue, KI+ blue, with darker

blue tubular structure in the tholus. *Ascospores* 8 per ascus, oblong-ellipsoid (to almost fusiform), sometimes with the upper median cell somewhat enlarged, 3-septate, without constrictions at the septa, 10–13 × 3–4 µm, colourless, I–, with irregular hyphae.

Pycnidia not observed.

Secondary chemistry. Not tested by TLC due to the very small thalli, but standard spot tests on the thallus (C, K, P, UV) all negative. Apothecial disc UV+ bright blue.

Etymology. The epithet refers to the bluish hue of parts of the apothecial disc.

Distribution and ecology. Known from several localities of mixed dipterocarp forest in Brunei Darussalam.

Remarks. The genus *Bysssolecania* is characterized by its flat (to slightly convex) apothecia resembling those of *Arthonia* but fundamentally differing from the latter in its internal anatomy, revealing it to be a member of the family *Ectolechiaceae* within the order *Lecanorales* (Lücking 2008). Santesson (1952) originally distinguished only two species, based on ascospore septation alone. However, discrete differences in apothecial shape and colour have led to the separation of additional taxa (Lücking & Kalb 2000; Herrera-Campos *et al.* 2004; Breuss & Neuwirth 2007; Lücking 2008). Thus far, seven species are recognized in this genus, differing mostly in the colour (and shape) of the apothecia and in ascospore septation. Among these, two species are characterized by completely flat apothecia and 3-septate ascospores, namely *B. fumosonigricans* (Müll. Arg.) R. Sant., with dark grey-brown apothecia and narrow whitish rim, and *B. hymenocarpa* (Vain.) Kalb *et al.*, with light brown apothecia and wide whitish rim, typically partly detached from the thallus (Lücking 2008).

The new taxon comes close to *B. fumosonigricans* in the rather dark apothecia with narrow whitish rim, which rarely become

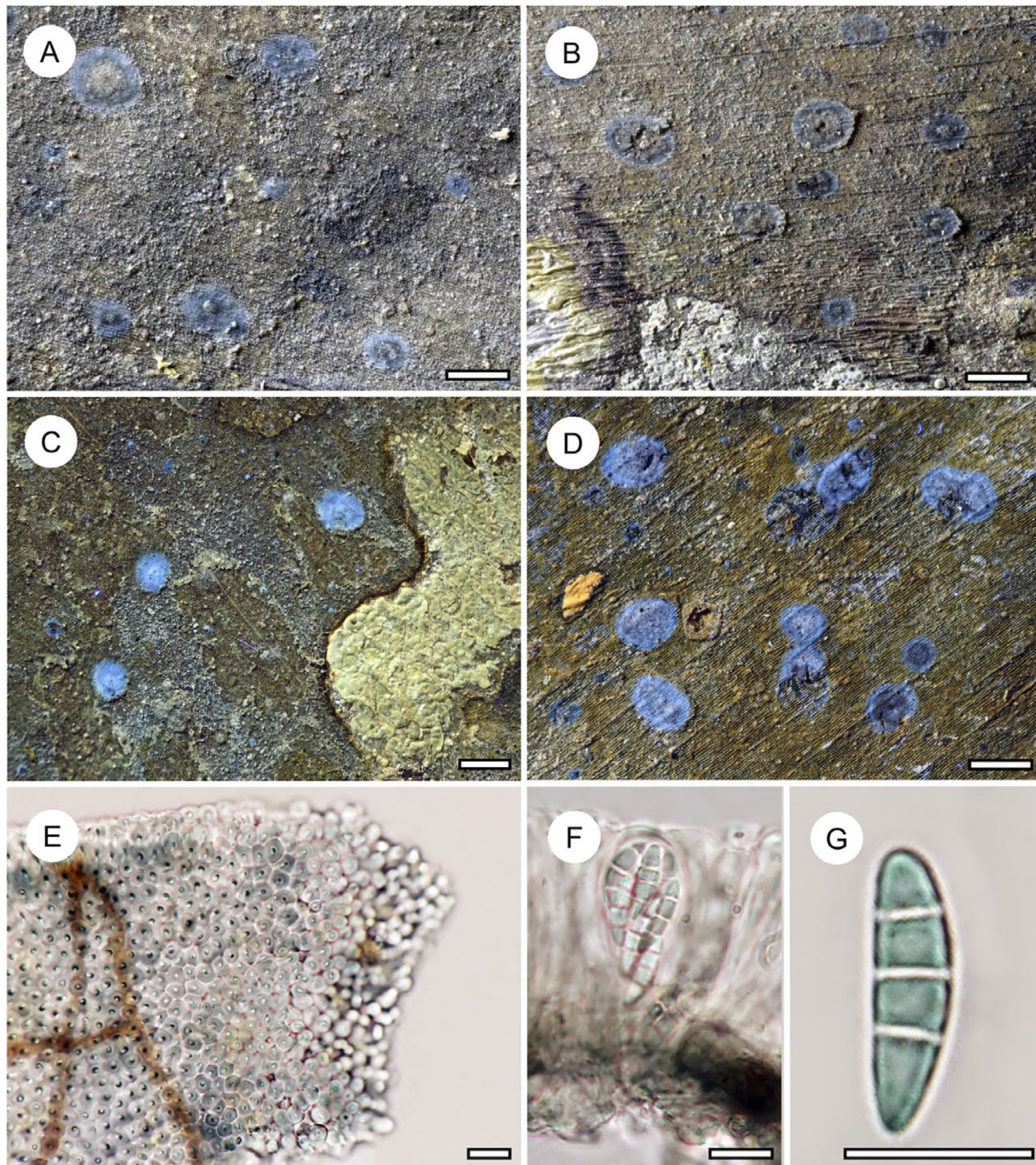


Figure 7. Habit and characteristics of newly described species. A–E, *Byssolecania fumosocaerulea* (holotype). A & B, thallus with apothecia. C & D, UV+ bright blue reaction of the apothecia. E, paraphyses seen from above. F, part of hymenium with ascus and ascospores. G, ascospore. Scales: A–D = 1 mm; E–G = 10 μ m. In colour online.

partly detached from the thallus. However, it differs in the presence of a rather wide, greyish blue outer fringe of the apothecia, between the inner, greyish brown centre and the thin whitish margin. The colour variation is caused by the development of the apothecia starting centripetally from the margin. The thin whitish margin is caused by a hyphal excipulum composed of rather thick hyphae with rounded tips. These hyphae then transition into vertical paraphyses which grow vertically towards the centre, after which the asci are formed. The central portion containing asci is then seen as a grey-brown, somewhat irregular spot

from above, whereas the fringe containing only paraphyses appears greyish blue, probably an effect of light reflection combined with the dark aeruginous hypothecium. We compared numerous specimens of *B. fumosonigricans* and never observed such a colour pattern.

The UV+ bright blue reaction of the apothecia came as a surprise. Upon checking, we found that other species of *Byssolecania* also display UV-fluorescence of the apothecia, usually bluish grey to greyish blue, but none as bright blue as in the new species.

Additional specimens examined. **Brunei Darussalam:** *Belait:* Andulau Forest Reserve, 4°39'19.98"N, 114°31'20.244"E, 72 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 1 ix 2021, *D. A. Ward* 466b (UBDH), *D. A. Ward* 470a (B); *Wasai Teraja*, 4°20'28.9536"N, 114°26'52.908"E, 173 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 5 ix 2021, *D. A. Ward* (with *D. Cicuzza* and *B. Zoletto*) 179a (UBDH). *Temburong:* Batu Apoi, 4°40'57.54"N, 115°13'14.538"E, 120 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 26 ix 2021, *D. A. Ward* 934 (B, UBDH).

***Byssoloma inconspicuum* D. A. Ward, B. Moncada & Lücking sp. nov.**

Index Fungorum No.: IF 905098

Differing from *Byssoloma microcarpum* in the dark brown apothecial disc and the excipulum lacking crystals.

Type: Brunei Darussalam, *Belait*, Andulau Forest Reserve, 4°39'19.98"N, 114°31'20.244"E, 72 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 1 September 2021, *D. A. Ward* 240a (UBDH—holotype!).

(Fig. 8A–H)

Thallus continuous, irregular in outline and overall inconspicuous or sometimes seemingly absent, in parts minutely farinose, 5–10 mm across, very thin (10–15 µm), ecorticate, light greyish to greyish brown, opaque, UV+ weakly light yellow; prothallus sometimes developed as thin, dark brown line. *Photobiont cells* green, rounded, 5–7 µm diam.

Ascomata biatorine with byssoid margin, sessile, rounded, 0.15–0.25 mm diam. and 120–150 µm high; disc dark brown to brownish black, UV+ bluish, margin cream-coloured to whitish, thin, not spreading laterally over the thallus surface; excipular hyphae hyaline, lacking crystals, 1.5–2 µm thick. *Hypothecium* 20–30 µm high, dark brown, K+ darker. *Epithecium* indistinct. *Hymenium* 50–60 µm high, colourless, I+ blue, KI+ blue. *Paraphyses* branched and somewhat anastomosing. *Asci* clavate, 40–50 × 8–12 µm, I+ blue, KI+ blue, with darker blue tubular structure in the tholus. *Ascospores* 8 per ascus, oblong, 3-septate, without constrictions at the septa, 10–13 × 2.5–3 µm, colourless, I–.

Pycnidia not observed.

Secondary chemistry. Not tested by TLC due to the very small thalli; most standard spot tests on the thallus (C, K, P) all negative except a weak UV+ yellow reaction; hypothecium K+ darkening and apothecial disc UV+ bluish.

Etymology. The epithet refers to the inconspicuous thallus and apothecia.

Distribution and ecology. Known from several localities of mixed dipterocarp forest and heath forest in Brunei Darussalam; most abundantly found and best developed on hairy leaves.

Remarks. *Byssoloma* is one of the most speciose genera in *Ectolechiaceae*, with close to 70 species currently recognized (Lücking 2008; Wang *et al.* 2020; Miyazawa & Ohmura 2023). Delimitation of species, particularly among taxa with 3-septate ascospores and otherwise lacking readily diagnostic features, remains a challenge, especially in the *B. leucoblepharum* complex, but the limited molecular

data available indicate that a high level of near-cryptic diversity may be present (Wang *et al.* 2020).

The new species is characterized by rather small apothecia with a thin, byssoid margin not spreading laterally over the thallus and lacking crystal inclusions. It could perhaps be considered a depauperate form of *B. leucoblepharum* or *B. chlorinum* s. lat. (Lücking 2008). However, the abundant material is very uniform and differs in several other characters from the latter two taxa: *B. leucoblepharum* has a smooth, dark green to bluish green thallus, whereas in *B. chlorinum*, the apothecial disc is typically almost black, creating a strong contrast with the whitish apothecial margin, and the thallus is well developed and light green. Other species that have small apothecia with a dark disc include *B. diderichii* Sérus., known from Macaronesia and western Europe (Sérusiaux 1998), and *B. microcarpum* Kalb & Vězda, known from Malaysia and Papua New Guinea (Kalb & Vězda 1994; Paukov *et al.* 2017). The first has even smaller apothecia with a bluish tinge and often produces bluish pycnidia with oval conidia, whereas the second has the byssoid excipulum encrusted with colourless crystals and the apothecial disc is blackish. It agrees with the new species in the bluish UV-reaction of the apothecial disc, but the thallus is much better developed and UV+ lemon yellow (see *B. incrustatimurinum* below for further discussion of UV-fluorescence in *Byssoloma*).

Additional specimens examined. **Brunei Darussalam:** *Belait:* Andulau Forest Reserve, 4°39'19.98"N, 114°31'20.244"E, 72 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 1 ix 2021, *D. A. Ward* 246 (B), 351 (B, UBDH); *Jalan Labi Heath Forest*, 4°28'32.4084"N, 114°28'2.7768"E, 51 m, tropical moist broadleaf forest ecoregion, heath forest, on leaves, 19 ix 2021, *D. A. Ward* 771 (UBDH), 1283e (B, filed under *Mazosia melanophthalma*); *Wasai Teraja*, 4°20'28.9536"N, 114°26'52.908"E, 173 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 6 xi 2021, *D. A. Ward* (with *D. Cicuzza*) 1189 (B).

***Byssoloma incrustatimurinum* D. A. Ward, B. Moncada & Lücking sp. nov.**

Index Fungorum No.: IF 905099

Differing from *Byssoloma murinum* in the shorter, non-tapering ascospores and the crystals in the excipulum.

Type: Brunei Darussalam, Tutong, Taman Kulimambang, Tasek Merimbun, 4°35'38.7384"N, 114°40'18.858"E, 31 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves (hypophyllous), 9 September 2021, *D. A. Ward* 221a (UBDH—holotype!; B—isotype!).

(Fig. 9A–D)

Thallus hypophyllous, continuous, irregular in outline and overall inconspicuous and difficult to delimit, 5–10 mm across, very thin (5–15 µm), ecorticate, not distinguishable in colour from the lower leaf surface, opaque; prothallus absent or inconspicuous. *Photobiont cells* bright green, rounded, 8–13 µm diam.

Ascomata biatorine with byssoid margin, sessile, rounded, 0.15–0.2 mm diam. and 60–70 µm high; disc grey-brown, thinly whitish pruinose, margin whitish, thin, not spreading laterally over the thallus surface; margin and pruina of the disc UV+ very brightly neon blue. *Hypothecium* 20–30 µm high, brown to dark brown, K+ darker (blackish) brown, without reddish tinge. *Epithecium* indistinct, with scattered, colourless crystal granules, not dissolving in

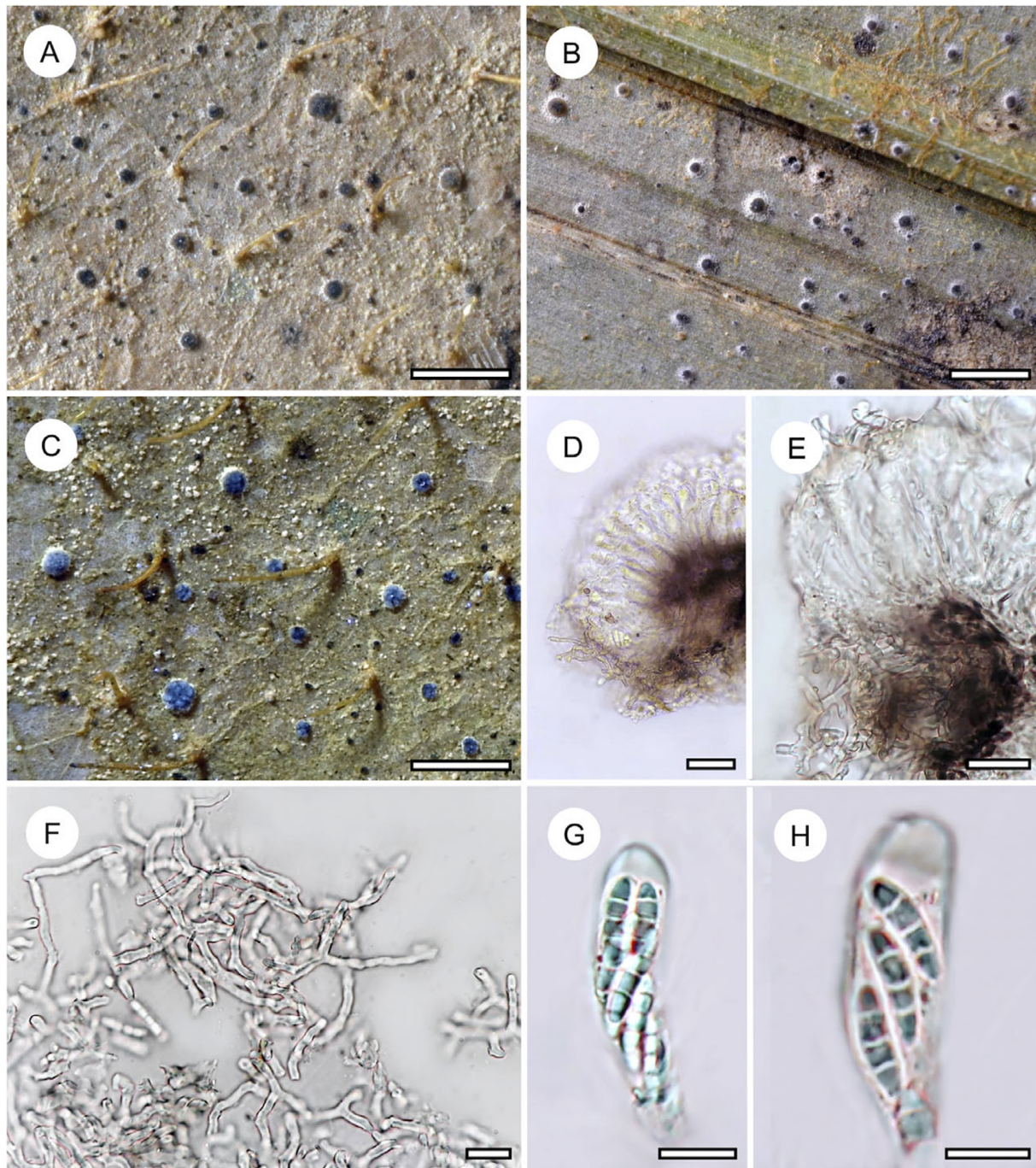


Figure 8. Habit and characteristics of newly described species. A–H, *Byssoloma inconspicuum* (A, C, D–H, holotype; B, Ward 771). A–C, thalli with apothecia, in C showing UV+ bluish reaction of the apothecial disc. D & E, section through apothecium. F, excipular hyphae. G & H, asci with ascospores. Scales: A–C = 1 mm; D & E = 20 μ m; F–H = 10 μ m. In colour online.

K. Hymenium 30–40 μ m high, colourless, I+ blue, KI+ blue. *Paraphyses* branched and somewhat anastomosing. *Asci* clavate, 25–30 $\times$ 8–10 μ m, I+ blue, KI+ blue, with darker blue tubular structure in the tholus. *Ascospores* 8 per ascus, oblong-ellipsoid, 3-septate, without constrictions at the septa, 9–12(–14) $\times$ 2–2.5 μ m, colourless, I–.

Pycnidia not observed.

Secondary chemistry. Not tested by TLC due to the very small thalli, but standard spot tests (C, K, P, UV) on the thallus all negative; apothecial margin and disc pruina with an unidentified, UV+ bright neon blue substance.

Etymology. The epithet refers to the excipulum encrusted with crystals, as compared to *Byssoloma murinum* Vězda.

Distribution and ecology. Growing hypophyllous on leaves of eudicots in the understorey of mixed dipterocarp forest; known from three localities in Brunei Darussalam.

Remarks. *Byssoloma incrustatimurinum* appears to be one of few genuinely hypophyllous species in this genus, together with *B. farkasiae* Sipman and *B. hypophyllum* Lücking & Kalb, both known from the Neotropics (Sipman 1992; Lücking & Kalb 2000; Lücking 2008), as well as *B. murinum* Vězda, described from

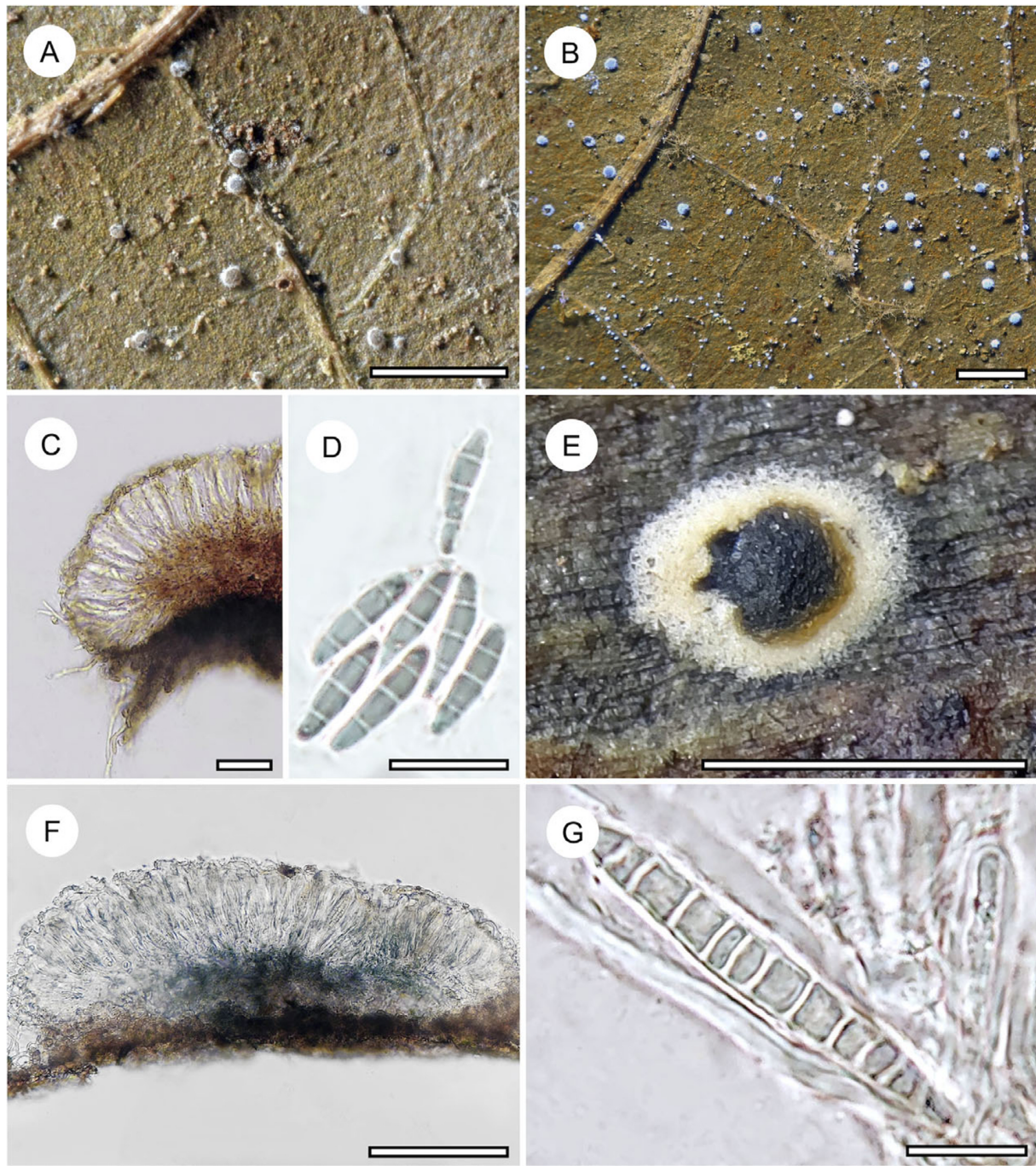


Figure 9. Habit and characteristics of newly described species. A–D, *Byssoloma incrustatimurinum* (holotype). A & B, thallus with apothecia, in B showing UV+ bright neon blue reaction of the apothecia. C, section through apothecium. D, ascospores. E–G, *Byssoloma subaeruginosum* (holotype). E, part of thallus with apothecium. F, section through apothecium showing aeruginous to smoky blue hypothecium. G, ascospore. Scales: A & B = 1 mm; C = 20 μ m; D & G = 10 μ m; E = 0.5 mm; F = 100 μ m. In colour online.

tropical Africa (Vězda 1987). The first two differ in the persistently 1-septate ascospores and the larger apothecia, which are distinctly pruinose in *B. farkasiae* and non-pruinose in *B. hypophyllum*. *Byssoloma murinum* is morphologically and anatomically very similar to the material studied here and at first we considered both conspecific. However, the ascospores of the new taxon are consistently shorter (9–11(–13) μ m vs (11–)13–16(–18) μ m) and not tapering (as illustrated for *B. murinum*; Vězda 1987: fig. 1.1a), and the small crystals encrusting the hyphae of the excipulum were not reported or illustrated for *B. murinum* (Vězda 1987: fig. 1.1a).

In the present taxon, the crystals are quite obvious under high magnification and it is unlikely that Vězda overlooked these in *B. murinum*, since he described other species in this genus containing excipular crystals. In addition, the reddish tinge of the hypothecium in *B. murinum*, becoming more distinctly reddish in K, was not observed in the new taxon.

The crystals of the excipulum and the pruina probably cause the UV+ bright neon blue fluorescence in *B. incrustatimurinum*. Specimens of *B. farkasiae* tested did not exhibit UV-fluorescence. In *B. hypophyllum*, the non-pruinose, orange-brown apothecia exhibit

a distinct, rather bright white UV-fluorescence. We also tested other species of *Byssoloma* for UV-fluorescence; most species did not react but typical specimens of *B. leucoblepharum* had the same bluish UV-fluorescence of the apothecial disc as found in *Byssolecania*. Specimens of *B. microcarpum* Kalb & Vězda show a combination of blue fluorescence of the apothecial disc and lemon yellow fluorescence of the farinose thallus, whereas in *B. subdiscordans* (Nyl.) P. James, the whitish thallus reacts UV+ light yellowish. The orange-brown apothecia of *B. minutissimum* Kalb & Vězda have the same UV+ white fluorescence as *B. hypophyllum*. Clearly, this character provides a very useful toolbox in the taxonomy of foliicolous lichens, which are often too small to perform TLC or HPLC, and we are grateful to one of the reviewers of this manuscript for pointing out this possibility.

Additional specimens examined. **Brunei Darussalam:** *Belait*: Andulau Forest Reserve, 4°39'19.98"N, 114°31'20.244"E, 72 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves (hypophyllous), 1 ix 2021, D. A. Ward 691 (B, UBDH). *Temburong*: Betayan, 4°42'9.99"N, 115°6'11.1204"E, 120 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves (hypophyllous), 17 ix 2021, D. A. Ward 737 (B).

Byssoloma aff. *multipunctatum* Lücking

Remarks. This material is characterized by a brownish thallus furnished with numerous dark, wart-shaped pycnidia and scattered apothecia with a dark brown disc, a blackish brown hypothecium and a cream-coloured to light brownish, rather thin but distinctly byssoid margin lacking crystals. The ascospores are 3-septate and c. $10 \times 3 \mu\text{m}$ in size. It comes close to *Byssoloma multipunctatum*, described from Costa Rica (Lücking 2008), but lacks the small black dots characteristic of the latter. Given that there is only a single specimen with few apothecia, we refrain from recognizing this material formally as a new species.

Specimen examined. **Brunei Darussalam:** *Temburong*: Batu Apoi, 4°40'57.54"N, 115°13'14.538"E, 120 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 26 ix 2021, D. A. Ward 521a (B).

Byssoloma subaeruginosum D. A. Ward, B. Moncada & Lücking sp. nov.

Index Fungorum No.: IF 905100

Differing from *Byssoloma usambarense* in the dark aeruginous hypothecium and the (olive-)brown thallus.

Type: Brunei Darussalam, *Belait*, Wasai Teraja, 4°20'28.9536"N, 114°26'52.908"E, 173 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 5 September 2021, D. A. Ward (with D. Ciccuzza and B. Zoletto) 183a (UBDH—holotype!).

(Fig. 9E–G)

Thallus continuous, irregular in outline, smooth, 10–20 mm across, very thin (10–15 μm), ecorticate, dark brown to dark olive, opaque, sometimes hypophyllous; prothallus sometimes developed as thin, dark brown line. **Photobiont cells** bright green, rounded, 5–8 μm diam.

Ascomata biatorine with byssoid margin, adnate to prominent, round, 0.3–0.5 mm diam. and 90–110 μm high; disc dark brown to

blackish brown (or greyish when hypophyllous), slightly convex, UV+ bluish, margin cream-coloured to whitish, thin but more or less spreading laterally over the thallus surface. **Hypothecium** 40–50 μm high, very intensely dark aeruginous to smoky blue, in thicker sections appearing blackish, I–, KI–; apothecial base blackish brown. **Epithecium** indistinct. **Hymenium** 45–55 μm high, colourless, I+ blue, KI+ blue. **Paraphyses** branched and somewhat anastomosing. **Asci** clavate, 45–50 $\times$ 10–13 μm , I+ blue, KI+ blue, with I+ darker blue tubular structure in the tholus. **Ascospores** 8 per ascus, arranged in a bundle, oblong-fusiform, (5–)7(–11)-septate, without constrictions at the septa, 27–35(–40) $\times$ 3–4 μm , colourless, I–.

Pycnidia wart-shaped, 0.04–0.07 mm diam., black in surface view, dark aeruginous under the microscope, wall composed of aeruginous, irregular hyphae. **Conidia** not observed.

Secondary chemistry. Not tested by TLC due to the very small thalli, but standard spot tests (C, K, P) all negative; apothecia with a UV+ bluish reaction.

Etymology. The epithet refers to the aeruginous hypothecium.

Distribution and ecology. Known from several localities of mixed dipterocarp forest in Brunei Darussalam.

Remarks. Species with multiseptate ascospores are comparatively rare in the genus *Byssoloma*. Closest in septation and size of the ascospores are *B. vanderystii* and *B. usambarense* Vězda, both described from Africa (Sérusiaux 1979; Vězda 1987), with predominantly 7-septate ascospores c. $25\text{--}30 \times 2.5\text{--}3.5 \mu\text{m}$ in size. However, *B. vanderystii* has strongly convex, reddish brown apothecia with a brown hypothecium, whereas *B. usambarense* differs in the (light) brown apothecia with reddish brown hypothecium, both lacking an aeruginous to smoky blue tinge in the subhymenial layers. Both also differ in the lighter greenish thallus.

The UV+ bluish reaction of the apothecial disc appears to be the same as observed in several *Byssolecania* species and in *Byssoloma leucoblepharum* (see above under *Byssolecania fumosocaerulea* and *Byssoloma incrustatimurinum*), although it is much less intense than in *Byssolecania fumosocaerulea*.

Additional specimens examined. **Brunei Darussalam:** *Belait*: Andulau Forest Reserve, 4°39'19.98"N, 114°31'20.244"E, 72 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 1 ix 2021, D. A. Ward 245 (B), 701a (B); Wasai Teraja, 4°20'28.9536"N, 114°26'52.908"E, 173 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 5 ix 2021, D. A. Ward (with D. Ciccuzza and B. Zoletto) 185 (UBDH), 196b (B, filed under *Phylloporis verrucosula*); *ibid.*, 6 xi 2021, D. A. Ward (with D. Ciccuzza) 1183b (UBDH). *Temburong*: Batu Apoi, 4°40'57.54"N, 115°13'14.538"E, 120 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 26 ix 2021, D. A. Ward 935 (B, UBDH), 936a (UBDH); *ibid.*, on dicot leaves, 26 ix 2021, D. A. Ward 1291a (B).

Chroodiscus lirellicarpus D. A. Ward, B. Moncada & Lücking sp. nov.

Index Fungorum No.: IF 905101

Differing from *Chroodiscus argillaceus* in the lirellate apothecia.

Type: Brunei Darussalam, *Temburong*, Kampong Tamada, 4°32'55.0644"N, 115°4'47.406"E, 48 m, tropical moist broadleaf

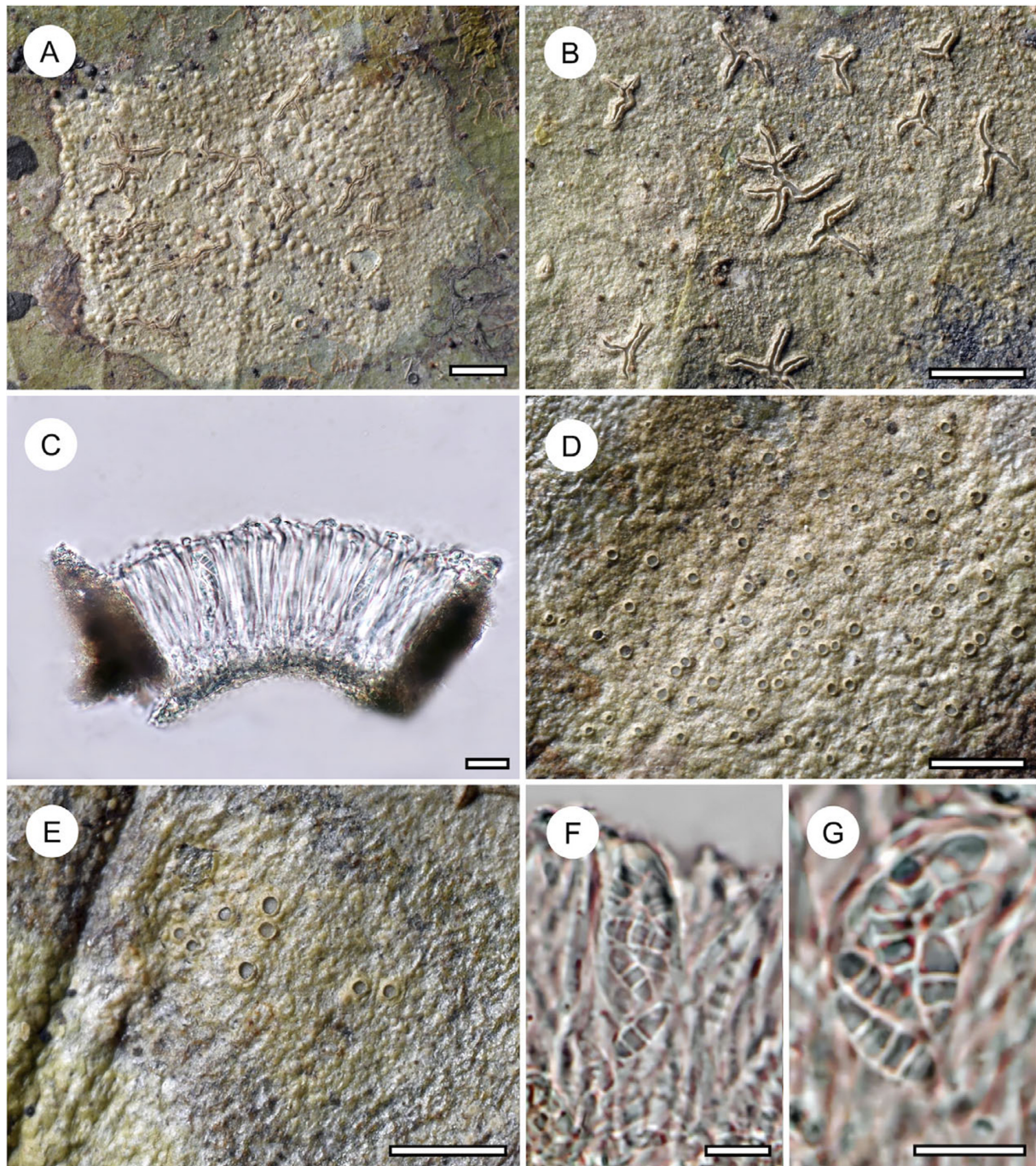


Figure 10. Habit and characteristics of newly described species. A–C, *Chroodiscus lirelllicarpus* (A & C, holotype; B, Ward 1262). A & B, thalli with apothecia. C, section through apothecium. D–G, *Chroodiscus minutus* (D, F & G, holotype; E, Ward 316). D & E, thallus with apothecia. F & G, asci with ascospores. Scales: A, B, D & E = 1 mm; C, F & G = 10 µm. In colour online.

forest ecoregion, mixed dipterocarp forest, on leaves, 13 November 2021, D. A. Ward 1224 (UBDH—holotype!; B—isotype!).

(Fig. 10A–C)

Thallus continuous, rounded to irregular in outline, uneven to irregularly verrucose, 5–10 mm across, thin (20–30 µm), with a cartilaginous corticiform layer, pale (yellowish) grey, slightly nitidous; verrucae 0.05–0.15(–0.2) mm diam., pale (yellowish) grey, in section filled with large clusters of calcium oxalate crystals.

Photobiont cells oblong to almost rounded, 7–14 × 4–7 µm, in irregular plates leaving small to larger interspaces.

Apothecia immersed-erumpent, distinctly lirelliform, unbranched to branched or sometimes stellate, (0.3–)0.5–1(–1.5) mm long, 0.15–0.2 mm wide, and 50–60 µm high; disc slit-like, barely visible, plane, light greyish brown, K+ yellow then orange; thalline margin prominent, pale (yellowish) grey, K+ yellow then orange. *Excipulum* 5–8 µm wide, colourless to dirty yellowish or appearing brownish in thicker sections, K+ orange. *Hypothecium* 10–20 µm high, colourless to pale yellowish. *Epithecium* indistinct. *Hymenium* 35–40 µm high,

colourless. *Paraphyses* unbranched. *Asci* clavate, $35\text{--}40 \times 7\text{--}8\ \mu\text{m}$, I–, KI–. *Ascospores* ellipsoid-fusiform, (1–)3-septate, without constrictions at septum, $8\text{--}12 \times 2.5\text{--}3\ \mu\text{m}$, colourless.

Pycnidia not observed.

Secondary chemistry. Stictic acid; not tested by TLC due to the very small thalli, but thallus and apothecial sections with K+ persistently light yellow efflux and apothecia P+ orange; other spot tests (C, UV) negative.

Etymology. The epithet refers to the lirellate apothecia.

Distribution and ecology. Known from a single locality of mixed dipterocarp forest in Brunei Darussalam.

Remarks. *Chroodiscus* (Müll. Arg.) Müll. Arg. is a small genus of exclusively foliicolous lichens in the *Graphidaceae*. Species either have an orange-red, K+ purple disc or lack pigment (but then invariably produce stictic acid). Within that latter group, all known species have rounded, rather conspicuous apothecia, which sets the new species apart rather easily. In ascospore type, it is most similar to *C. argillaceus* (Müll. Arg.) Lücking & Papong (Papong *et al.* 2009) and the newly described *C. minutus* (see below). The only other species with lobate-lirellate apothecia in *Chroodiscus* is *C. graphideus* Lücking & Kalb (Lücking 2008), which has larger apothecia representing the group with bright orange-red discs; in *C. graphideus*, the apothecia are more irregularly branched and wider.

The larger verrucae on the thallus of the new species are reminiscent of perithecia in the genus *Porina*, which initially led us to think that this species grows initially on thalli of that genus, as has been reported for several other species of *Chroodiscus* (Lücking & Grube 2002). However, all verrucae checked contained crystals only.

Chroodiscus lirellicarpus is yet another example of species with disparate ascoma morphology being closely related within a single genus. Similar cases among foliicolous taxa include the aforementioned, lirellate *Arthonia orbignyae* and the lirellate *Aulaxina opegraphina* versus the mostly rounded to angular ascomata in other foliicolous species of these genera. Another prominent example is the corticolous genus *Glyphis* in *Graphidaceae*. The new species somewhat resembles a species of *Platythecium* in *Graphidaceae*, but the latter genus differs fundamentally in thallus structure, including a distinct, true cortex, and in ascospore type, featuring graphidean ascospores with thickened, amyloid walls and lens-shaped to rounded lumina.

Additional specimen examined. Brunei Darussalam: Temburong: Kampong Tamada, $4^{\circ}32'55.0644''\text{N}$, $115^{\circ}4'47.406''\text{E}$, 48 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 13 xi 2021, D. A. Ward 1262 (B).

Chroodiscus minutus D. A. Ward & Lücking sp. nov.

Index Fungorum No.: IF 905102

Differing from *Chroodiscus argillaceus* in the very small apothecia.

Type: Brunei Darussalam, Belait, Andulau Forest Reserve, $4^{\circ}39'19.98''\text{N}$, $114^{\circ}31'20.244''\text{E}$, 72 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 1 September 2021, D. A. Ward 693 (UBDH—holotype!; B—isotype!).

(Fig. 10D–G)

Thallus continuous, rounded to irregular in outline, uneven to irregularly verrucose, 4–6 mm across, thin ($20\text{--}30\ \mu\text{m}$), with a cartilaginous corticiform layer, (yellowish) grey, slightly nitidous; verrucae $0.03\text{--}0.1\text{--}(0.15)\ \text{mm}$ diam., (yellowish) grey, in section filled with large clusters of calcium oxalate crystals. *Photobiont cells* oblong to almost rounded, $6\text{--}15 \times 4\text{--}7\ \mu\text{m}$, in irregular plates leaving small to larger interspaces.

Apothecia immersed-erumpent, regularly rounded, $0.15\text{--}0.2\text{--}(0.25)\ \text{mm}$ diam., $50\text{--}60\ \mu\text{m}$ high; disc largely exposed, plane, light greyish brown, K+ yellow then orange; thalline margin prominent, (yellowish) grey, K+ yellow then orange. *Excipulum* $3\text{--}6\ \mu\text{m}$ wide, colourless to pale yellowish. *Hypothecium* $5\text{--}10\ \mu\text{m}$ high, colourless to pale yellowish. *Epithecium* indistinct. *Hymenium* $35\text{--}40\ \mu\text{m}$ high, colourless. *Paraphyses* unbranched. *Asci* clavate, $35\text{--}40 \times 7\text{--}8\ \mu\text{m}$, I–, KI–. *Ascospores* ellipsoid-fusiform, (1–)3-septate, without constrictions at septa, $7\text{--}10 \times 2.5\text{--}3\ \mu\text{m}$, colourless.

Pycnidia not observed.

Secondary chemistry. Stictic acid; not tested by TLC due to the very small thalli, but thallus and apothecial sections with K+ persistently light yellow efflux and apothecia P+ orange; other spot tests (C, UV) negative.

Etymology. The epithet refers to the small thallus and apothecia.

Distribution and ecology. Known from two areas of mixed dipterocarp forest in Brunei Darussalam.

Remarks. *Chroodiscus minutus* is another new species in the *C. argillaceus* group, characterized by a non-pigmented apothecial disc, an uneven-verrucose thallus with irregular photobiont, and stictic acid as secondary compound. The round apothecia and small, 3-septate ascospores, together with the absence of (disc-shaped) isidia, place it in the vicinity of *C. argillaceus* (Papong *et al.* 2009). The latter differs in the much larger apothecia (up to 0.5 mm diam.) and the overall lighter thallus and light grey to yellowish apothecial disc. *Chroodiscus argillaceus* was found frequently in the present material and the morphological differences are constant and quite obvious.

Additional specimens examined. Brunei Darussalam: Belait: Andulau Forest Reserve, $4^{\circ}39'19.98''\text{N}$, $114^{\circ}31'20.244''\text{E}$, 72 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 1 ix 2021, D. A. Ward 316a (B), 317a (UBDH). Temburong: Kampong Tamada, $4^{\circ}32'55.0644''\text{N}$, $115^{\circ}4'47.406''\text{E}$, 48 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 13 xi 2021, D. A. Ward 1204 (UBDH), 1209 (B, UBDH).

Echinoplaca aff. *hispida* Sipman

(Fig. 11A)

Remarks. This unidentified taxon was represented only by a single, small specimen, characterized by a densely verrucose-bullate thallus furnished with whitish setae. This thallus type is rare among *Gomphillaceae* and not yet known in combination with sterile setae. *Echinoplaca hispida* Sipman, which was also found in the material, is somewhat similar, but the thallus verrucae are more irregular and separated by thinner thallus parts (Aptroot & Sipman 1993). Another similar species is *Gyalectidium microcarpum* (Vězda) Lücking *et al.* (Ferraro *et al.* 2001), which produces

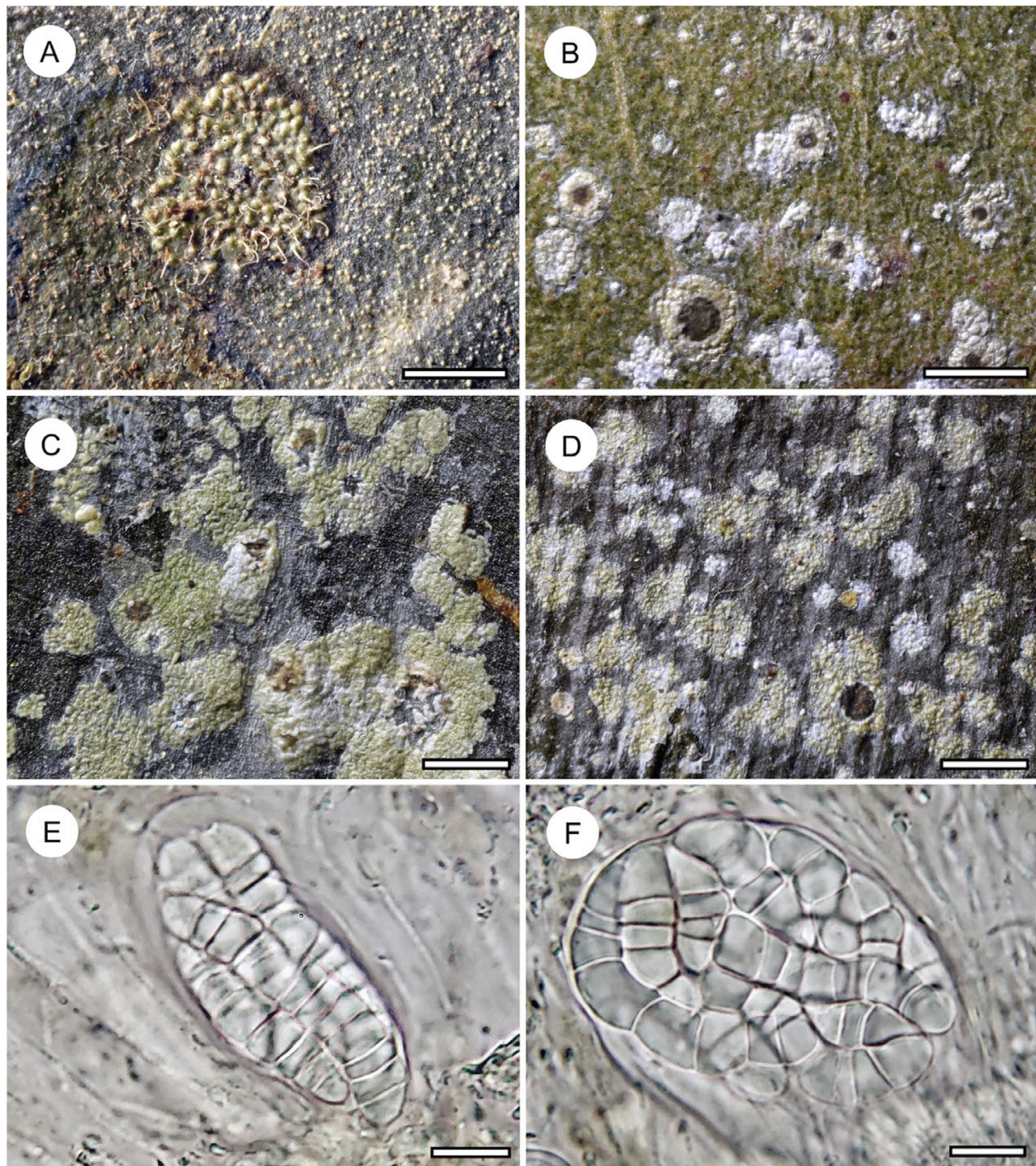


Figure 11. Habit and characteristics of newly described or otherwise interesting species. A, *Echinoplaca* aff. *hispida* (Ward 169a), thallus with sterile setae. B–F, *Echinoplaca septemseptata* (holotype). B–D, thallus with apothecia. E & F, asci with ascospores. Scales: A–D = 1 mm; E & F = 10 μ m. In colour online.

rather large, regular verrucae, but in that species the sterile setae are more robust.

Specimen examined. **Brunei Darussalam:** *Belait*: Wasai Telingan, Teraja, 4°22'19.2252"N, 114°27'58.3344"E, 149 m, tropical moist broadleaf forest ecoregion, riparian forest/mixed dipterocarp forest, on leaves, 5 ix 2021, D. A. Ward (with D. Cicuzza and B. Zoletto) 169a (B).

***Echinoplaca septemseptata* D. A. Ward & Lücking sp. nov.**

Index Fungorum No.: IF 905103

Differing from *Echinoplaca tetrapla* in the 7-septate ascospores.

Type: Brunei Darussalam, Temburong, Betayan, 4°42'9.99"N, 115°6'11.1204"E, 120 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 17 September 2021, D. A. Ward 494a (UBDH—holotype!).

(Fig. 11B–F)

Thallus dispersed, with individual patches becoming confluent, up to 10 mm across, irregular in outline but individual patches rounded, up to 1 mm diam., connected through a translucent hypothallus,

15–25 µm thick, with a cartilaginous corticiform layer, their surface finely verrucose, pale greenish grey to whitish, slightly nitidous; verrucae 0.05–0.1 mm diam., whitish, in section filled with clusters of calcium oxalate crystals. *Photobiont cells* rounded to somewhat angular, 4–5 µm diam.

Apothecia adnate and spot-like, emarginate, rounded, 0.2–0.5 mm diam., 50–60 µm high; disc plane, greyish brown. *Excipulum* composed of branched, radiating hyphae embedded in gelatinous matrix, reduced and spreading over thallus surface, 30–50 µm wide, colourless. *Hypothecium* 5–10 µm high, pale yellowish. *Epithecium* 3–5 µm high, yellowish granulate. *Hymenium* 45–50 µm high, colourless. *Paraphyses* branched and anastomosing. *Asci* clavate to ellipsoid, 40–45 × 12–16 µm, I–, KI–. *Ascospores* oblong, 5–7-septate, with slight constrictions at the septa, 20–25 × 5–6 µm, colourless.

Pycnidia not observed.

Secondary chemistry. Not tested by TLC due to the very small thalli, but standard spot tests (C, K, P, UV) all negative.

Etymology. The epithet refers to the 7-septate ascospores.

Distribution and ecology. Known from several localities of mixed dipterocarp (and riparian) forest in Brunei Darussalam.

Remarks. This new species belongs to a group of species with dark, brownish apothecia and small, transversely septate ascospores. Previously included in a broadly defined *Echinoplaca pellicula* (Santesson 1952), forms with dark apothecia were later separated under the name *E. tetrapla* (Zahlbr.) Lücking (Lücking 2001, 2008). However, this still appears to represent a species complex. Genuine *E. tetrapla*, described from China (Zahlbruckner 1930), is characterized by a dispersed to confluent thallus and rather small (12–14 × 5–6 µm), 3-septate ascospores. Neotropical material identified with this name has a more or less continuous, marginally somewhat diffuse thallus, the apothecia are quite dark, and the ascospores are predominantly 5-septate and 18–26 × 5–7 µm in size (Lücking 2008). The present material combines the external morphology of authentic material of *E. tetrapla* with the much larger ascospore size of the neotropical material; however, it differs from both in the mostly 7-septate ascospores, thus justifying its consideration as a separate taxon. As a consequence, the neotropical material will also have to be recognized as a separate taxon.

Additional specimens examined. **Brunei Darussalam:** *Belait:* Andulau Forest Reserve, 4°39'19.98"N, 114°31'20.244"E, 72 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 1 ix 2021, D. A. Ward 340 (UBDH); Wasai Telingan, Teraja, 4°22'19.2252"N, 114°27'58.3344"E, 149 m, tropical moist broadleaf forest ecoregion, riparian forest/mixed dipterocarp forest, on leaves, 5 ix 2021, D. A. Ward (with D. Cicuzza and B. Zoletto) 170 (B).

Eremothecella cyaneoides Lücking

(Fig. 12A–D)

Distribution and ecology. Follicolous in the understorey of tropical rainforests. A new record for tropical Asia.

Remarks. This species was so far known only from Australia, based on rather limited material (Lücking *et al.* 2001). The material from Brunei has mostly 5(–7)-septate ascospores, whereas in the type

collection from Australia they are (3–)5-septate, but since the size is about the same (30–35 × 7–9 µm vs 25–35 × 8–10 µm) we consider the material from Brunei conspecific. Pycnidia with conidia were not found in the present material. The species resembles *Arthonia cyanea* Müll. Arg. (Lücking 2008), *Eremothecella ajaysinghii* Jagad. Ram & G. P. Sinha (Jagadeesh Ram & Sinha 2019) and *E. macrocephala* (Thor *et al.* 2000) in the pruinose ascomata with a bluish tinge, but is intermediate in ascospore dimensions and septation between the *Arthonia* and the other two *Eremothecella* species.

Specimens examined. **Brunei Darussalam:** *Belait:* Andulau Forest Reserve, 4°39'19.98"N, 114°31'20.244"E, 72 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on dicot leaves, 1 ix 2021, D. A. Ward 257 (B, UBDH), 304 (B), 1280m (B; filed under *Raciborskiella talaumae*); *ibid.*, on fern leaves, 1 ix 2021, D. A. Ward 710a (UBDH).

Eremothecella helicella Aptroot & M. Cáceres

(Fig. 12E & F)

Distribution and ecology. Corticolous and follicolous in the understorey of tropical rainforests. A new record for tropical Asia.

Remarks. *Eremothecella helicella* was described as a species based on pycnidia only, with the conidia having the shape of a spiral (Cáceres *et al.* 2014). Two follicolous specimens with pycnidia only, producing spirally twisted conidia, were found in the present material and are identified with this name, although we suspect that possibly more than one species, including still undescribed taxa, might produce such conidia.

Specimens examined. **Brunei Darussalam:** *Belait:* Andulau Forest Reserve, 4°39'19.98"N, 114°31'20.244"E, 72 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 1 ix 2021, D. A. Ward 260 (B, UBDH), 266 (UBDH).

Eremothecella rugosa D. A. Ward, B. Moncada & Lücking sp. nov.

Index Fungorum No.: IF 905104

Differing from *Eremothecella calamicola* in the ridged thallus and the much longer conidia.

Type: Brunei Darussalam, *Belait*, Andulau Forest Reserve, 4°39'19.98"N, 114°31'20.244"E, 72 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 1 September 2021, D. A. Ward 255 (UBDH—holotype!; B—isotype!).

(Fig. 13A–F)

Thallus dispersed into irregular patches, rugose, 5–15 mm across, very thin (7–10 µm), ecorticate, yellowish green, slightly glossy, with flattened irregular to elongate warts and ridges, up to 30 µm thick, filled with colourless crystals that dissolve in K. *Photobiont cells* angular-elongate, 5–10 × 4–6 µm, in irregular to partly radiating plates.

Ascomata hardly raised above thallus level, rounded, 0.4–0.8 mm diam. and 50–60 µm high, brownish black. *Hypothecium* 3–5 µm high, colourless, I–, KI–. *Epithecium* formed by dense layer of parallel, periclinal hyphae, 5–8 µm high, reddish brown with purplish tinge, K+ olive to military green, I+ brownish, KI+

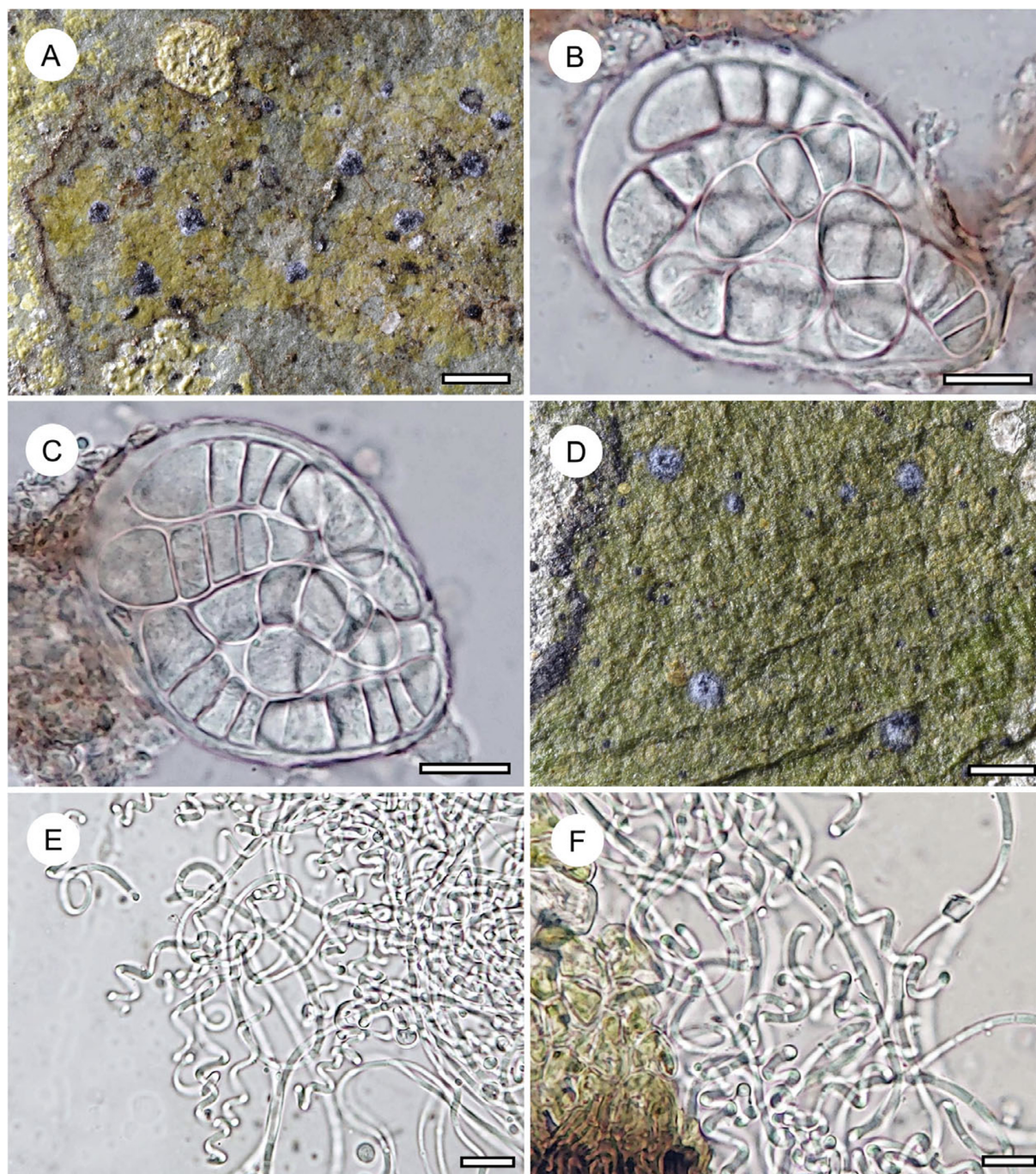


Figure 12. Habit and characteristics of newly described or otherwise interesting species. A–D, *Eremothecella cyaneoides* (A–C, Ward 257; D, Ward 204). A & D, thalli with apothecia. B & C, asci with ascospores. E & F, *Eremothecella helicella* (Ward 260), conidia. Scales: A & D = 1 mm; B, C, E & F = 10 μ m. In colour online.

greenish grey. *Hymenium* 45–50 μ m high, colourless, I–, KI–. *Paraphyses* branched and anastomosing. *Asci* obovate to globose, 35–40 $\times$ 30–35 μ m, I–, KI–. *Ascospores* 8 per ascus, clavate, 5–6-septate, with the terminal cell enlarged, 30–35 $\times$ 7–8 μ m, colourless, I–.

Pycnidia applanate, elongate, 0.5–0.6 mm long and 0.15–0.2 mm wide, brownish black in surface view, dark brown under the microscope, wall composed of dark brown, parallel to radiating hyphae. *Conidia* long filiform with tapering ends, 50–60-septate, 300–400 $\times$ 2–2.5 μ m, colourless.

Secondary chemistry. Not tested by TLC due to the very small thalli, but standard spot tests (C, K, P, UV) all negative except for the crystals in the warts and ridges dissolving in K.

Etymology. The epithet refers to the rugose thallus.

Distribution and ecology. Known from several localities of mixed dipterocarp forest in Brunei Darussalam; particularly abundant in Andulau Forest Reserve.

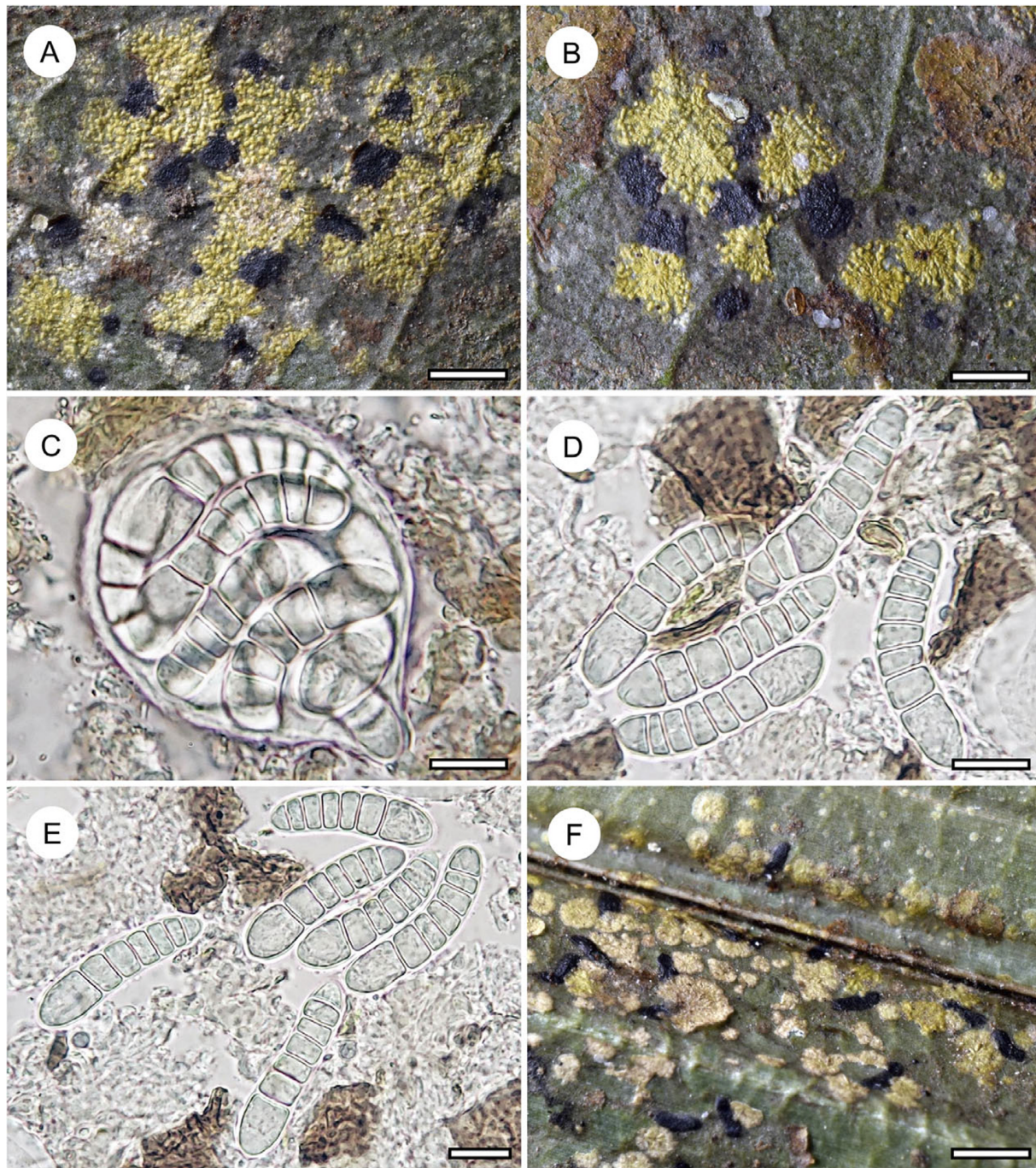


Figure 13. Habit and characteristics of newly described species. A–F, *Eremothecella rugosa* (A–E, holotype; F, Ward 272). A & B, thallus with apothecia. C, ascus with ascospores. D & E, ascospores. F, thallus with pycnidia. Scales: A, B & F = 1 mm; C–E = 10 μ m. In colour online.

Remarks. *Eremothecella* is a comparatively small genus of foliicolous lichens comprising ten species, separated from *Arthonia* by the long-filiform conidia and from foliicolous species of *Arthonia* by the longer, multiseptate ascospores (Lücking 2008; Jagadeesh Ram & Sinha 2019). Within this genus, species are distinguished by ascospore septation and size, as well as the presence or absence of a variously coloured pruina on the ascomata. *Eremothecella rugosa* is the first species in the genus producing a thallus ornamented with warts and ridges. Its non-pruinose ascomata, with comparatively small ascospores, place it otherwise near *E. calamicola*, which differs in the entirely smooth thallus (Lücking 2008). In its thallus

morphology, the new species resembles *Arthonia flavoverrucosa* and *A. flavirugosa* (see above), but both differ clearly in the small, 2-septate, grey-brown ascospores. The conidia of the new species appear to be by far the longest known in the genus.

Additional specimens examined. **Brunei Darussalam:** *Belait:* Andulau Forest Reserve, 4°39'19.98"N, 114°31'20.244"E, 72 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 1 ix 2021, D. A. Ward 252 (UBDH), 253 (B, UBDH), 272a (B), 275 (B, UBDH), 338 (B), 408 (B), 460a (UBDH), 690a (B, UBDH); *Jalan Labi Heath Forest*, 4°28'32.4084"N, 114°

28°2.7768"E, 51 m, tropical moist broadleaf forest ecoregion, heath forest, on leaves, 19 ix 2021, D. A. Ward 1283f (B, filed under *Mazosia melanophthalma*); Jalan Labi Mixed Dipterocarp Forest, 4°34'49"N, 114°28'35"E, 81 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 10 ix 2021, D. A. Ward 1285g (B, filed under *Semigyalecta paradoxa*); Wasai Teraja, 4°20'28.9536"N, 114°26'52.908"E, 173 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 6 xi 2021, D. A. Ward (with D. Cicuzza) 1186 (UBDH); *ibid.*, on dicot leaves, 6 xi 2021, D. A. Ward (with D. Cicuzza) 1290h (B; filed under *Mazosia melanophthalma*). Temburong: Batu Apoi, 4°40'57.54"N, 115°13'14.538"E, 120 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 26 ix 2021, D. A. Ward 1292l (B, filed under *Microtheliopsis uleana*); Kampong Tamada, 4°32'55.0644"N, 115°4'47.406"E, 48 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 13 xi 2021, D. A. Ward 1196 (B).

Eremothecella verrucispora D. A. Ward & Lücking sp. nov.

Index Fungorum No.: IF 905105

Differing from *Eremothecella calamicola* in the brown, ornamented ascospores with more numerous septa.

Type: Brunei Darussalam, Belait, Wasai Teraja; 4°20'28.9536"N, 114°26'52.908"E, 173 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 5 September 2021, D. A. Ward (with D. Cicuzza and B. Zoletto) 175 (UBDH—holotype!).

(Fig. 14A–D)

Thallus dispersed into irregular patches, smooth, 5–10 mm across, very thin (7–10 µm), ecorticate, greenish, opaque. *Photobiont cells* angular-elongate, 5–10 × 4–6 µm, in irregular to partly radiating plates.

Ascomata hardly raised above thallus level, rounded to somewhat irregular in outline, 0.4–0.7 mm diam. and 50–60 µm high, dark brown to blackish brown. *Hypothecium* 3–5 µm high, colourless, I–, KI–. *Epithecium* formed by dense layer of parallel, periclinial hyphae, 5–8 µm high, brownish, K– to K+ sordid olive green, KI+ sordid olive green. *Hymenium* 45–50 µm high, colourless, I–, KI–. *Paraphyses* branched and anastomosing. *Asci* obovate to globose, 45–50 × 35–40 µm, I–, KI–. *Ascospores* 8 per ascus, clavate, (7–)9-septate, with the terminal cell enlarged, 35–40 × 9–10 µm, at first colourless and with smooth walls but soon walls developing minute verrucae and ascospores finally becoming brown, I–.

Pycnidia not observed.

Secondary chemistry. Not tested by TLC due to the very small thalli, but standard spot tests (C, K, P, UV) all negative.

Etymology. The epithet refers to the minutely verrucose ascospores.

Distribution and ecology. Known only from the type collection from a mixed dipterocarp forest in Brunei Darussalam.

Remarks. Although pycnidia with filiform conidia, characteristic of the genus *Eremothecella*, were not observed in the material, the new species is placed in this genus given the multiseptate, worm-like ascospores (Lücking 2008; Jagadeesh Ram & Sinha 2019). *Eremothecella verrucispora* is the first species in this genus known to produce brown, verruculose ascospores, such ascospores otherwise

being found in some corticolous species of *Arthonia* and *Opegrapha* s. lat. Within *Eremothecella*, *E. ajaysinghii* and *E. microcephalica* Sipman have been described with ascospores becoming brown and wrinkled (Sipman 2008; Jagadeesh Ram & Sinha 2019), but this appears to be an effect of overaging, and no verrucae are produced. In external appearance and ascospore size, the new species comes close to *E. calamicola* Syd., but in the number of septa it is intermediate between *E. calamicola* and *E. macrosperma* (Jagadeesh Ram & Sinha 2019).

Fellhanera aff. *bouteillei* (Desm.) Vězda

(Fig. 14E & F)

Distribution and ecology. A presumably subcosmopolitan species with a wide ecological amplitude, ranging from tropical to temperate climates and found on leaves, needles and bark.

Remarks. *Fellhanera bouteillei*, though not usually abundant, is presumed to be the most widespread species commonly found on leaves, and also known from bark and rock (Fig. 15). Its wide ecological amplitude challenges its status as a single taxon, but so far attempts to apply a more detailed species concept have failed, although molecular data support a multispecies complex (Santesson 1952; Lücking 2008; Wang *et al.* 2020). The only species thus far described as a separate taxon within this complex is *F. parvula* (Vězda) Vězda (Vězda 1986), also identified in the present material, differing in the lack of secondary compounds, the somewhat translucent apothecia, and the smaller ascospores. In the present material, we found several well-developed individuals that could be identified as *F. bouteillei* s. lat., due to the 1-septate ascospores and the yellowish apothecia. However, they consistently differ from typical *F. bouteillei* in the light yellowish green (vs pale bluish grey), UV+ bright yellow thallus and the small (0.1–0.2 mm diam.), light yellow (vs larger, orange-yellow) apothecia, as well as the smaller ascospores (10–12 × 3–4 µm vs 13–17 × 4–6 µm). In the size of the apothecia and the ascospores, the material comes close to *F. parvula*, but the apothecia are not translucent and the distinctive thallus colour and UV-reaction suggests the presence of various secondary compounds. Unfortunately, due to the small thalli, we have not yet been able to assess the secondary chemistry of this taxon. We did check all synonyms listed under *Fellhanera bouteillei*, including three from the Philippines and one from Tanzania (see Santesson 1952), but none fits this material. The fact that all specimens with this morphology were found in a single locality supports the notion of a potentially undescribed, recently evolved species.

Specimens examined. **Brunei Darussalam:** Brunei Muara: Bukit Tempayan Pisang, 5°0'43.9236"N, 115°2'42.8028"E, 56 m, tropical moist broadleaf forest ecoregion, secondary forest, on leaves, 6 xii 2021, D. A. Ward (with J. Wong) 605 (B), 606b (B; filed under *Coenogonium subluteum*), 610b (UBDH; filed under *Mazosia melanophthalma*), 612b (UBDH).

Fellhanera tutongensis D. A. Ward & Lücking sp. nov.

Index Fungorum No.: IF 905106

Differing from *Fellhanera microdiscus* in the irregularly 3–7-septate, more elongate and narrower ascospores.

Type: Brunei Darussalam, Tutong, Tutong Kerangas, 4°44'34.4004"N, 114°35'8.6172"E, 25 m, tropical moist broadleaf

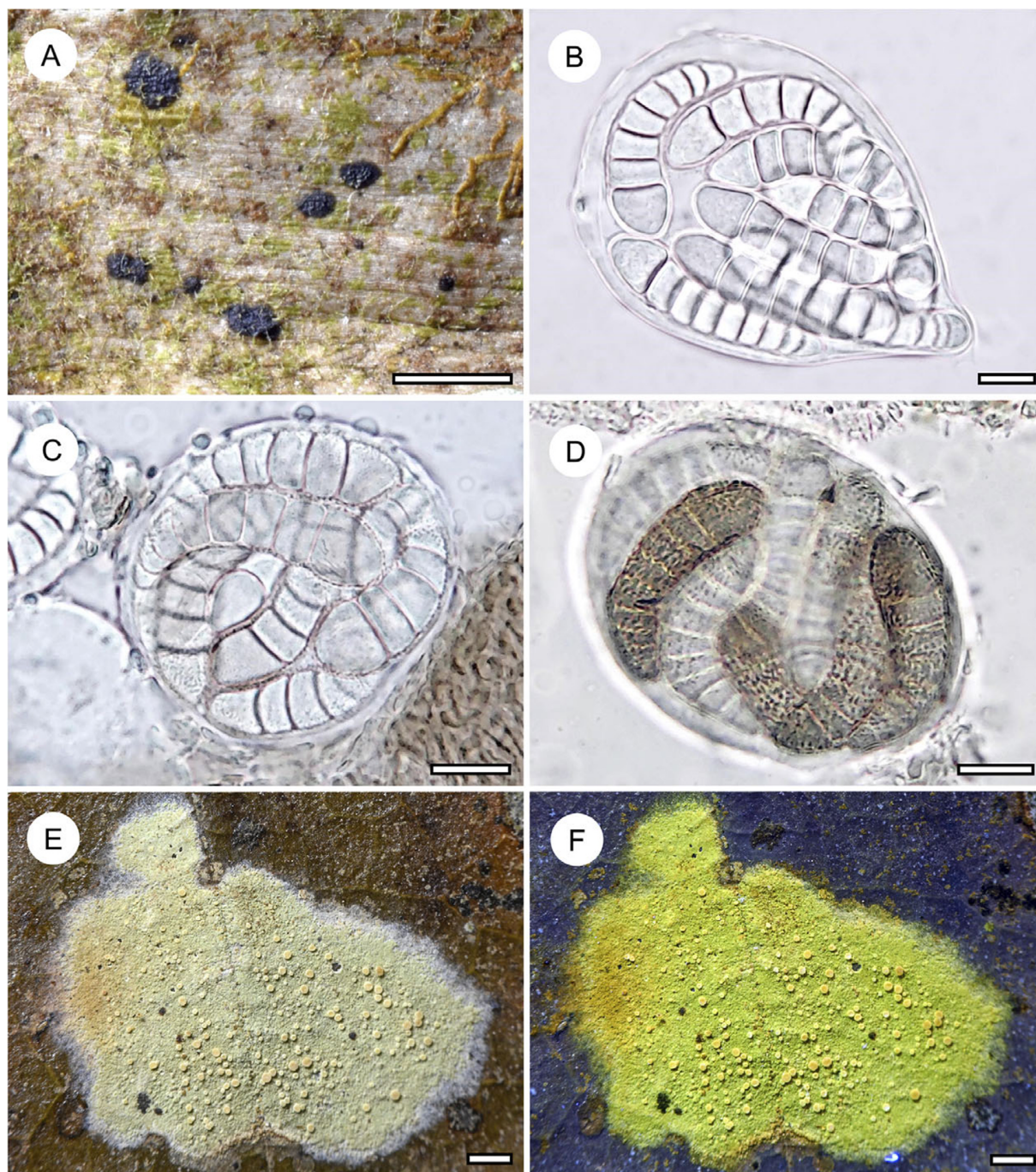


Figure 14. Habit and characteristics of newly described or otherwise interesting species. A–D, *Eremothecella verrucispora* (holotype). A, thallus with apothecia. B–D, asci with immature and mature ascospores. E & F, *Fellhanera* aff. *bouteillei* (Ward 605), thallus with apothecia, in F showing UV+ yellow fluorescence. Scales: A, E & F = 1 mm; B–D = 10 μ m. In colour online.

forest ecoregion, heath forest, on leaves, 18 October 2021, D. A. Ward 986 (UBDH—holotype!).

(Fig. 16A–E)

Thallus continuous, 5–10 mm across and 8–15 μ m thick, very minutely farinose, light brown with an orange tinge, UV+ faintly orange.

Apothecia round, 0.2–0.3 mm diam. and 80–100 μ m high; disc plane, dark brown; margin thin but distinct, chamois-coloured.

Excipulum paraplectenchymatous, 15–25 μ m wide, partly brownish, encrusted with ochraceous crystals dissolving in K forming a spurious, yellowish cloud. *Hypothecium* 10–15 μ m high, orange-brown, K+ blackish brown; apothecial base blackish, K+ black. *Epithecium* indistinct, 3–5 μ m high, pale yellowish. *Hymenium* 35–40 μ m high, colourless. *Asci* 30–35 $\times$ 7–8 μ m. *Ascospores* 8 per ascus, cylindrical with the distal end slightly tapering, irregularly 3–7-septate, without constrictions at the septa, 18–25 $\times$ 2–2.5 μ m, 9–10 times as long as wide.

Pycnidia not observed.

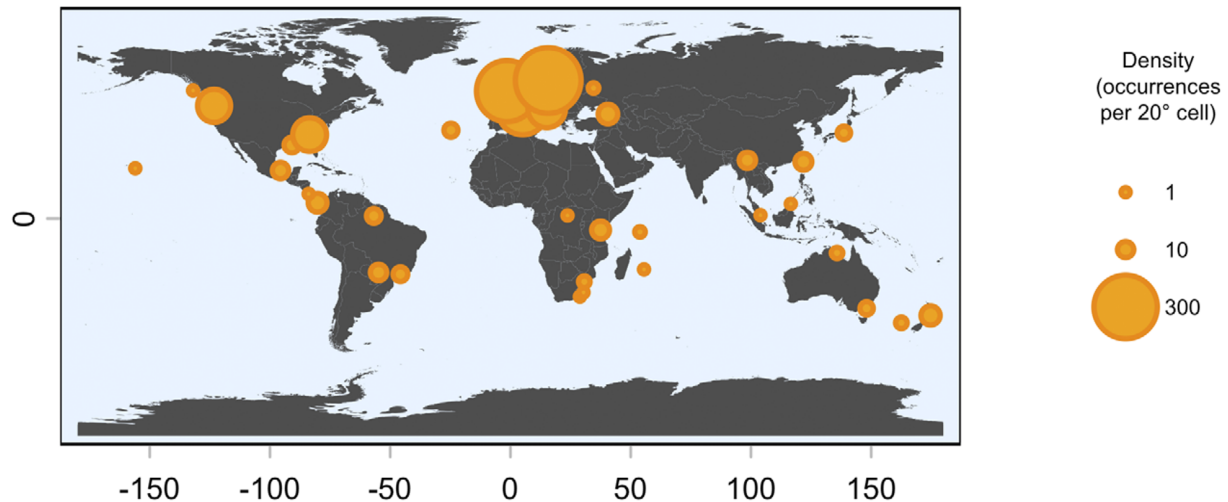


Figure 15. Presumed world distribution of *Fellhanera bouteillei* as documented by occurrence records in the GBIF platform (GBIF.org (09 February 2026); GBIF Occurrence Download <https://doi.org/10.15468/dl.ktzap8>). In colour online.

Secondary chemistry. Not tested by TLC due to the very small thalli, but most standard spot tests (C, K, P) negative except for the ochraceous, K+ dissolving crystals in the excipulum and the faint UV+ orange reaction of the thallus, suggesting the presence of xanthones.

Etymology. The epithet refers to the type region.

Distribution and ecology. Known from two localities of heath forest and mixed dipterocarp forest in Brunei Darussalam.

Remarks. *Fellhanera* is one of the most diverse genera segregated from the collective genus *Bacidia* (Vězda 1986), with well over 100 species known (Sérusiaux 1996; Lücking 2008; Farkas 2015b; van den Boom 2021). This new species belongs in a diverse morphogroup of species characterized by 3–7-septate ascospores and brownish apothecia. Within this group, it is characterized by the K+ blackening hypothecium, in combination with rather narrow ascospores, and the orange-brown thallus. Most similar are *F. endopurpurea* Hafellner & Vězda, *F. rhipidophylli* (Rehm) Vězda, and *F. wirthii* (Vězda) Vězda (Vězda 1986; Vězda & Hafellner 1991; Lücking 2008), all with regularly 3-septate ascospores and a greyish to greenish thallus. *Fellhanera endopurpurea* and *F. wirthii* also differ in the larger apothecia with a reddish tinge and K+ purplish hypothecium; *F. endopurpurea* has wider ascospores ($18\text{--}25 \times 3.5\text{--}4 \mu\text{m}$, 5–7 times as long as wide), whereas those of *F. wirthii* are much shorter ($8\text{--}13 \times 2\text{--}2.5 \mu\text{m}$, 4–5 times as long as wide). *Fellhanera rhipidophylli* differs in the aeruginous apothecial base and in the shorter and wider ascospores ($12\text{--}16 \times 3\text{--}5 \mu\text{m}$, 3–5 times as long as wide). *Fellhanera microdiscus* (Vain.) Vězda (Santesson 1952; Vězda 1986) is morphologically similar to the new species in the often somewhat brownish thallus and the small apothecia, as well as the irregularly 3–5-septate ascospores, but in that species the ascospores are shorter and wider ($14\text{--}21 \times 3.5\text{--}5 \mu\text{m}$, 5–7 times as long as wide) and the thallus lacks an orange tinge.

The orange-brown colour of the thallus of the new species is not an artifact of preservation, since the entire material was carefully collected and preserved and the leaves harbouring the new species also have many other species present, with typically developed thalli.

Additional specimens examined. **Brunei Darussalam:** *Belait:* Jalan Labi Mixed Dipterocarp Forest, $4^{\circ}34'49''\text{N}$, $114^{\circ}28'35''\text{E}$, 81 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 10 ix 2021, D. A. Ward 813b (B). *Temburong:* Kampong Tamada, $4^{\circ}32'55.0644''\text{N}$, $115^{\circ}4'47.406''\text{E}$, 48 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 13 xi 2021, D. A. Ward 594a (B).

Graphis pinicola Zahlbr.

(Fig. 16F)

Remarks. Species of *Graphis* are only accidentally found on leaves and then almost invariably on thick, often sclerophyllous leaves, where they penetrate the cuticle. We checked several specimens from the Neotropics and they all seem to represent the same species.

Specimen examined. **Brunei Darussalam:** *Tutong:* Tutong Kerangas, $4^{\circ}44'34.4004''\text{N}$, $114^{\circ}35'8.6172''\text{E}$, 25 m, tropical moist broadleaf forest ecoregion, heath forest, on dicot leaves, 18 x 2021, D. A. Ward 953a (B).

Gyalideopsis sp.

(Fig. 17A–F)

Remarks. This material is represented by two thalli lacking apothecia but bearing hyphophores, with a short, whitish stipe, c. $100 \times 15 \mu\text{m}$, and an apical, subglobose to bell-shaped, dark grey hyphal bunch projecting laterally from the bent tip of the stipe. The diahyphae are densely packed and moniliform with spermatozoid end cells. No species is currently known with this combination of characters, but in the absence of apothecia we refrain from recognizing this taxon formally. The spermatozoid end cells of the diahyphae are reminiscent of the genera *Actinoplaca* and *Vezdaemyces* (Xavier-Leite et al. 2022, 2023; Lebreton et al. 2025).

Specimen examined. **Brunei Darussalam:** *Tutong:* Tutong Kerangas, $4^{\circ}44'34.4004''\text{N}$, $114^{\circ}35'8.6172''\text{E}$, 25 m, tropical moist broadleaf forest ecoregion, heath forest, on dicot leaves, 18 x 2021, D. A. Ward 995a (B).

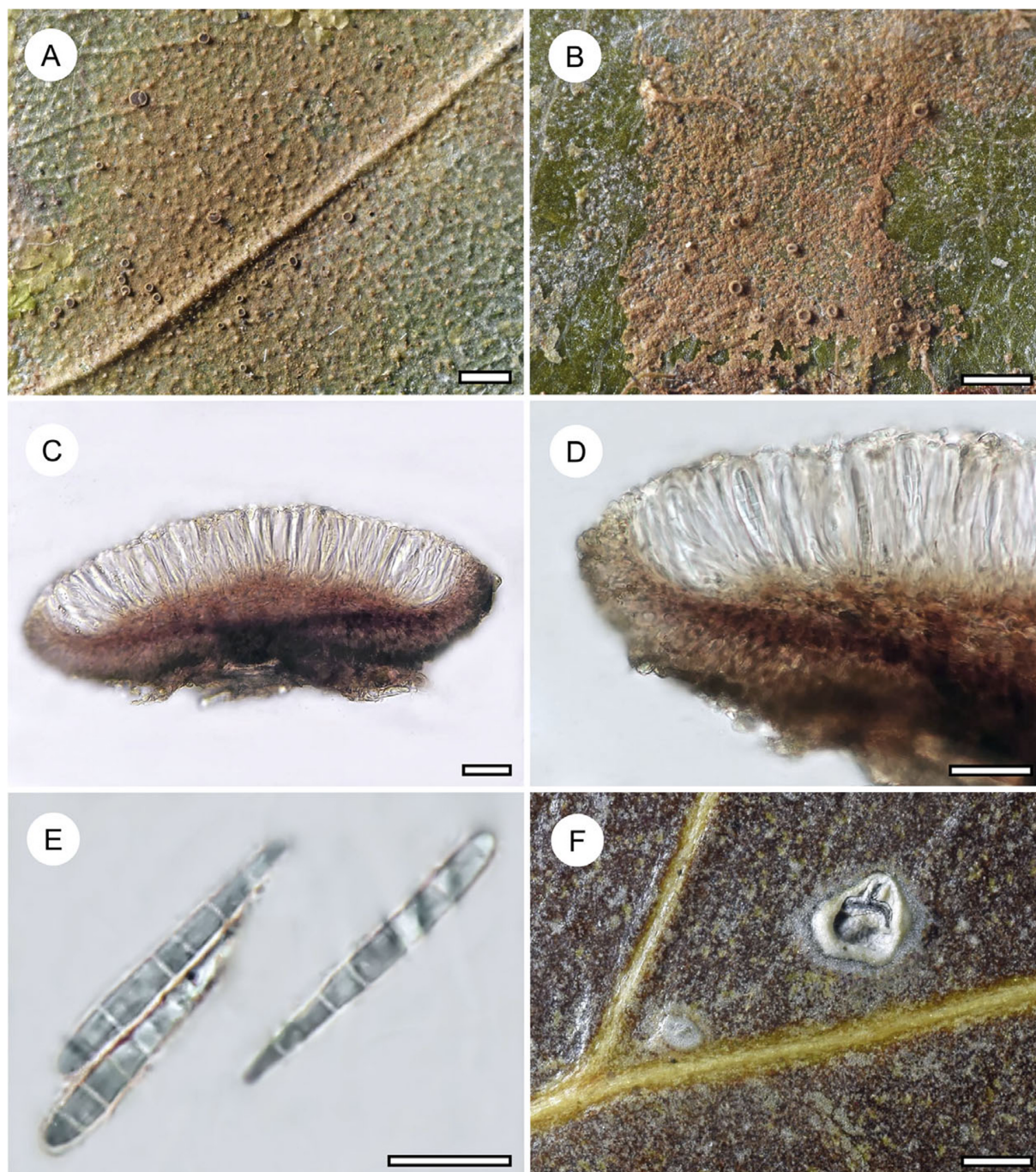


Figure 16. Habit and characteristics of newly described or otherwise interesting species. A–E, *Fellhanera tutongensis* (holotype). A & B, thallus with apothecia. C & D, section through apothecium. E, ascospores. F, *Graphis pinicola* (Ward 953a), thallus with lirellae. Scales: A, B & F = 1 mm; C & D = 20 μ m; E = 10 μ m. In colour online.

***Mazosia bambusiradiata* D. A. Ward & Lücking sp. nov.**

Index Fungorum No.: IF 905107

Differing from *Mazosia bambusae* in the radiately arranged thallus verrucae.

Type: Brunei Darussalam, Temburong, Batu Apoi, 4° 40' 57.54"N, 115° 13' 14.538"E, 120 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 26 September 2021, D. A. Ward 908a (UBDH—holotype!; B—isotype!).

(Fig. 18A–D)

Thallus continuous to marginally dispersed, finely verrucose, 5–25 mm across, thin (10–15 μ m), brownish grey to olive green, matt to slightly shiny, usually with dark brown prothallus (sometimes fuzzy or only partially developed); verrucae 0.02–0.03 mm diam., dark brown to blackish brown, arranged in distinct (to sometimes diffuse), often radiating lines, especially near the apothecia. *Photobiont* cells rectangular, 10–15 $\times$ 4–5 μ m, in regularly radiating plates.

Ascomata round, 0.4–0.6 mm diam. and 70–80 μ m high; disc dark grey to black, translucent when moistened; margin gently sloping outwards, usually darker than the thallus. *Excipulum* 20–35 μ m thick, formed by a layer of blackish brown hyphae, externally

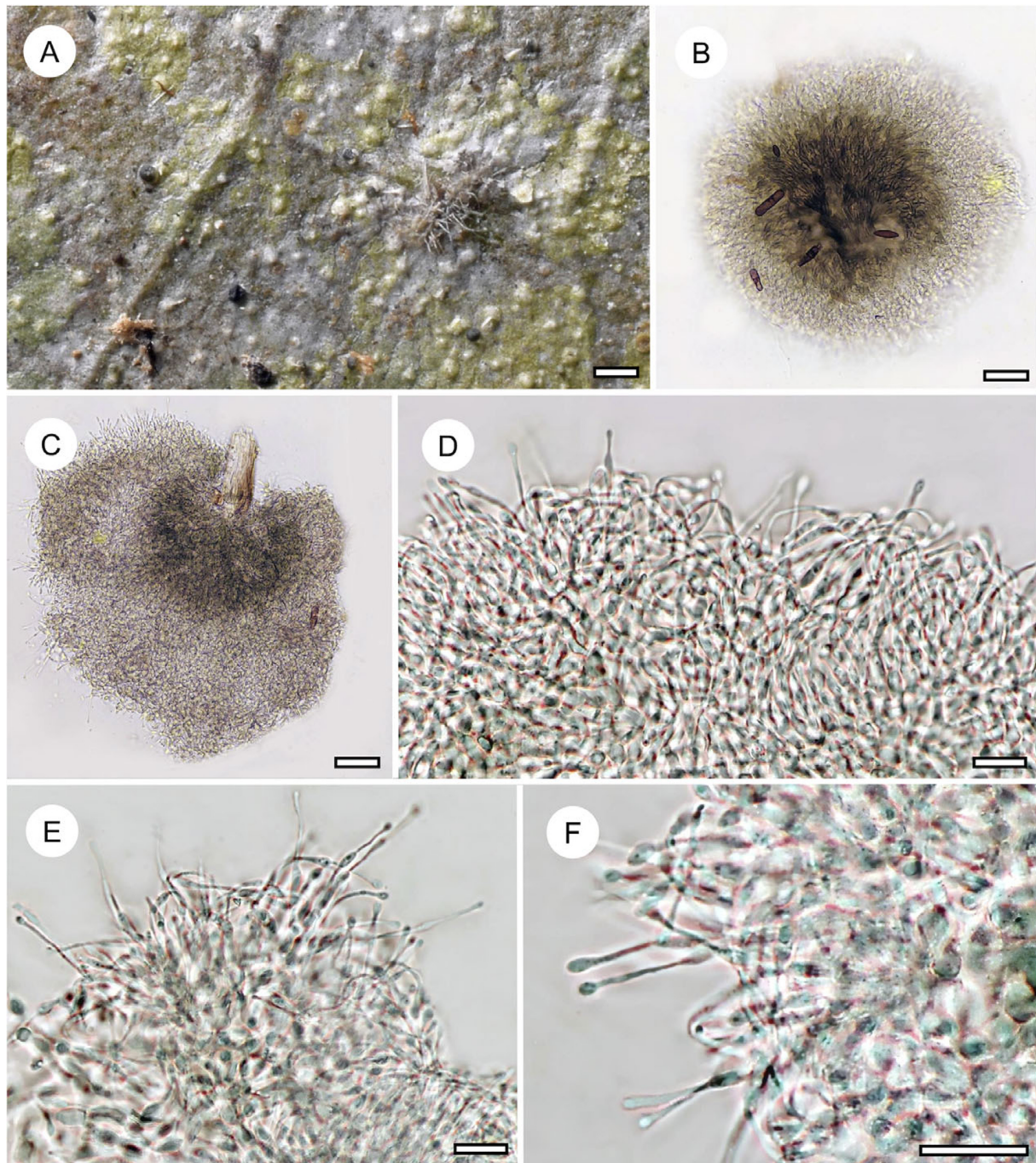


Figure 17. Habit and characteristics of newly described or otherwise interesting species. A–F, *Gyalideopsis* sp. (Ward 995a). A, thallus with hyphophores. B & C, diahyphal ball. D–F, diahyphae. Scales: A = 1 mm; B & C = 20 μ m; D–F = 10 μ m. In colour online.

covered by a thin layer of greyish crystals, a single photobiont layer and a thin layer of colourless hyphae. *Hypothecium* 10–15 μ m high, pale yellowish brown. *Hymenium* 60–70 μ m high. *Asci* 50–60 $\times$ 10–14 μ m. *Ascospores* fusiform, 3-septate, 18–25 $\times$ 4–5 μ m, upper median cell slightly enlarged, colourless.

Pycnidia low conical, 0.1–0.15 mm diam. *Macroconidia* not observed. *Microconidia* ellipsoid, non-septate, 2.5–3.5 $\times$ 1–1.3 μ m.

Secondary chemistry. Not tested by TLC due to the very small thalli, but standard spot tests (C, K, P, UV) on the thallus all negative.

Etymology. The epithet refers to the similarity with *Mazosia bambusae* (Vain.) R. Sant. and the radiately arranged thallus verrucae.

Distribution and ecology. Known from several localities of mixed dipterocarp and heath forest in Brunei Darussalam; particularly abundant in Andulau Forest Reserve.

Remarks. This new species is similar to *Mazosia bambusae* (Santesson 1952; Lücking 2008; see Fig. 18E & F) in most aspects, in particular the thin, brownish olive thalli with dark prothallus and

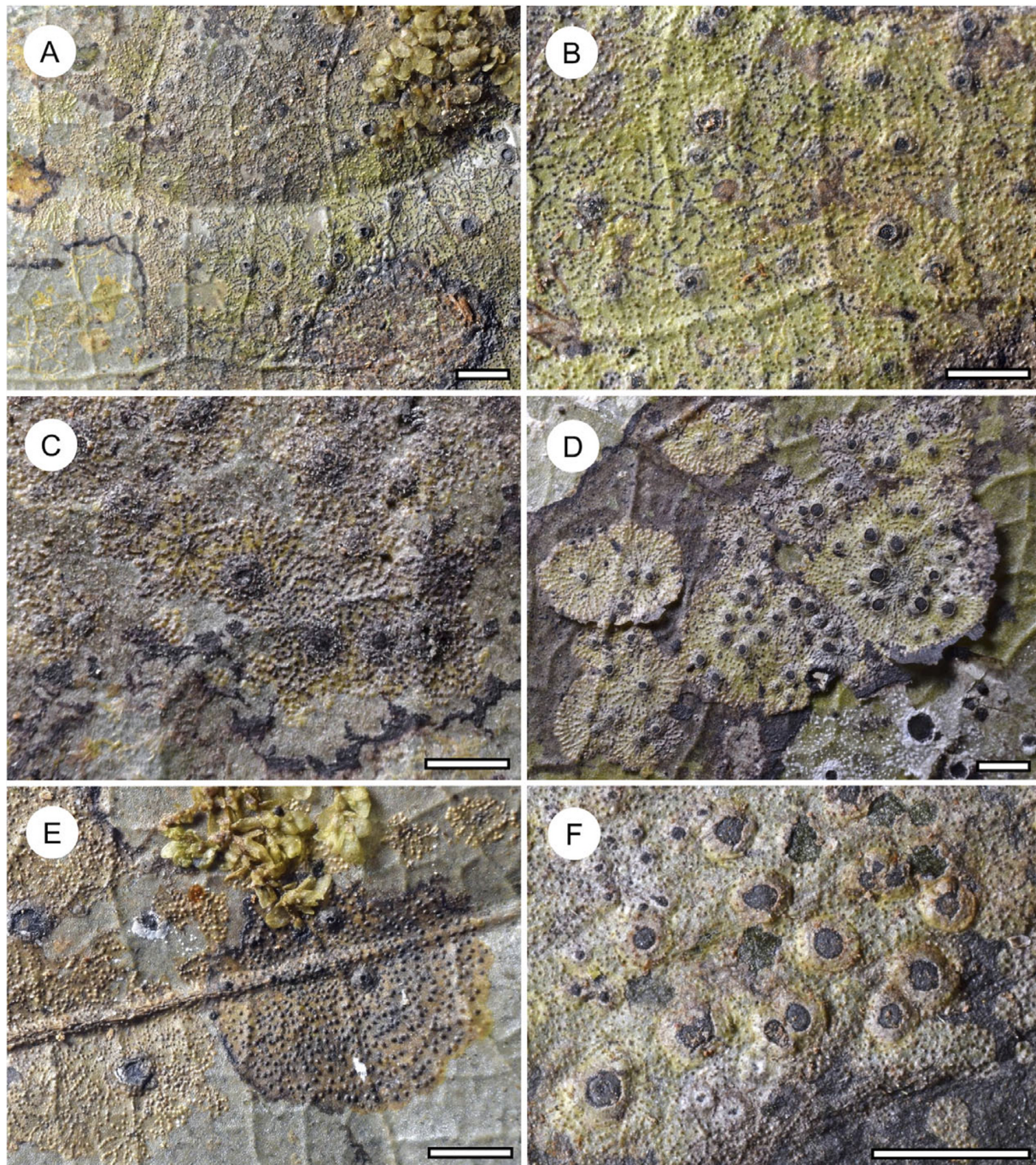


Figure 18. Habit and characteristics of newly described or otherwise interesting species. A–D, *Mazosia bambusiradiata* (A & B, holotype; C, Ward 430; D, Ward 505a). A–D, thalli with apothecia, in part showing the somewhat fuzzy, dark prothallus; in D a rather wide, dark prothallus. E & F, *Mazosia bambusae* (E, Ward 908c; F, Ward 463), thallus with apothecia. Scales = 1 mm. In colour online.

very small, dark verrucae. However, in the latter species, which often occurs sympatrically in the present material, the verrucae are always dispersed over the thallus and not arranged in (radiating) lines. Indeed, the arrangement of the verrucae gives the new species a characteristic appearance. It also provides a morphology that is intermediate between the mostly verrucose species of *Mazosia* and *M. rotula* (Mont.) A. Massal., which feature radiating ridges (Santesson 1952; Lücking 2008).

Additional specimens examined. **Brunei Darussalam:** *Belait:* Andulau Forest Reserve, 4°39'19.98"N, 114°31'20.244"E, 72 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 1 ix 2021, D. A. Ward 374 (B, UBDH), 378 (B), 381 (UBDH), 430 (B), 435b (UBDH; filed under *Porina rufula*), 467 (B), 699b (B; filed under *Badimia elegans*), 1277d (B; filed under *Coenogonium interplexum*), Ward 1278c (B; filed under *Bapalmuia pallescens*); *Jalan Labi Heath Forest*, 4°28'32.4084"N, 114°28'2.7768"E, 51 m, tropical

moist broadleaf forest ecoregion, heath forest, on leaves, 19 ix 2021, *D. A. Ward* 505a (B); Jalan Labi Mixed Dipterocarp Forest, 4°34'49"N, 114°28'35"E, 81 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 10 ix 2021, *D. A. Ward* 861a (B); Wasai Teraja, 4°20'28.9536"N, 114°26'52.908"E, 173 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 5 September 2021, *D. A. Ward* (with *D. Cicuzza* and *B. Zoletto*) 191 (UBDH). *Temburong*: Betayan, 4°42'9.99"N, 115°6'11.1204"E, 120 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 17 ix 2021, *D. A. Ward* 739a (B, UBDH); Kampong Tamada, 4°32'55.0644"N, 115°4'47.406"E, 48 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 13 xi 2021, *D. A. Ward* 1217b (B, UBDH), 1236b (UBDH; filed under *Mazosia bambusae*). *Tutong*: Tutong Kerangas, 4°44'34.4004"N, 114°35'8.6172"E, 25 m, tropical moist broadleaf forest ecoregion, heath forest, on leaves, 18 x 2021, *D. A. Ward* 964 (UBDH), 979a (UBDH).

***Mazosia melanophthalma* (Müll. Arg.) R. Sant.**

(Fig. 19A–D)

Distribution and ecology. A presumably pantropical species, usually growing in the shaded forest understorey.

Remarks. *Mazosia melanophthalma* is a presumably widespread species, found in all tropical regions (Santesson 1952; Lücking 2008; Aptroot *et al.* 2014). However, molecular data suggest some degree

of hidden diversity in this taxon (Yao *et al.* 2021). To some extent, there are also distinct morphodemes mixed into this species. In the present material, two morphodemes could be distinguished, one with fine, distinct verrucae corresponding to what is typically understood as *M. melanophthalma*, and one with wider, shallower, confluent verrucae. For the latter, the name *Metasphaeria incompleta* Rehm is theoretically available, described from the Philippines (Santesson 1952) and agreeing in the shallow, confluent verrucae. However, a more thorough study is needed on ample material of this complex from all tropical regions before applying a more refined species concept.

***Mazosia rugosa* D. A. Ward & Lücking sp. nov.**

Index Fungorum No.: IF 905108

Differing from *Mazosia pseudobambusae* in the rugose instead of verrucose thallus surface.

Type: Brunei Darussalam, Belait, Jalan Labi Mixed Dipterocarp Forest, 4°34'49"N, 114°28'35"E, 81 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 10 September 2021, *D. A. Ward* 853 (UBDH—holotype!; B—isotype!).

(Fig. 20A–F)

Thallus continuous but algiferous patches irregularly dispersed over a darkened hypothallus, finely rugose, 10–30 mm across, thin

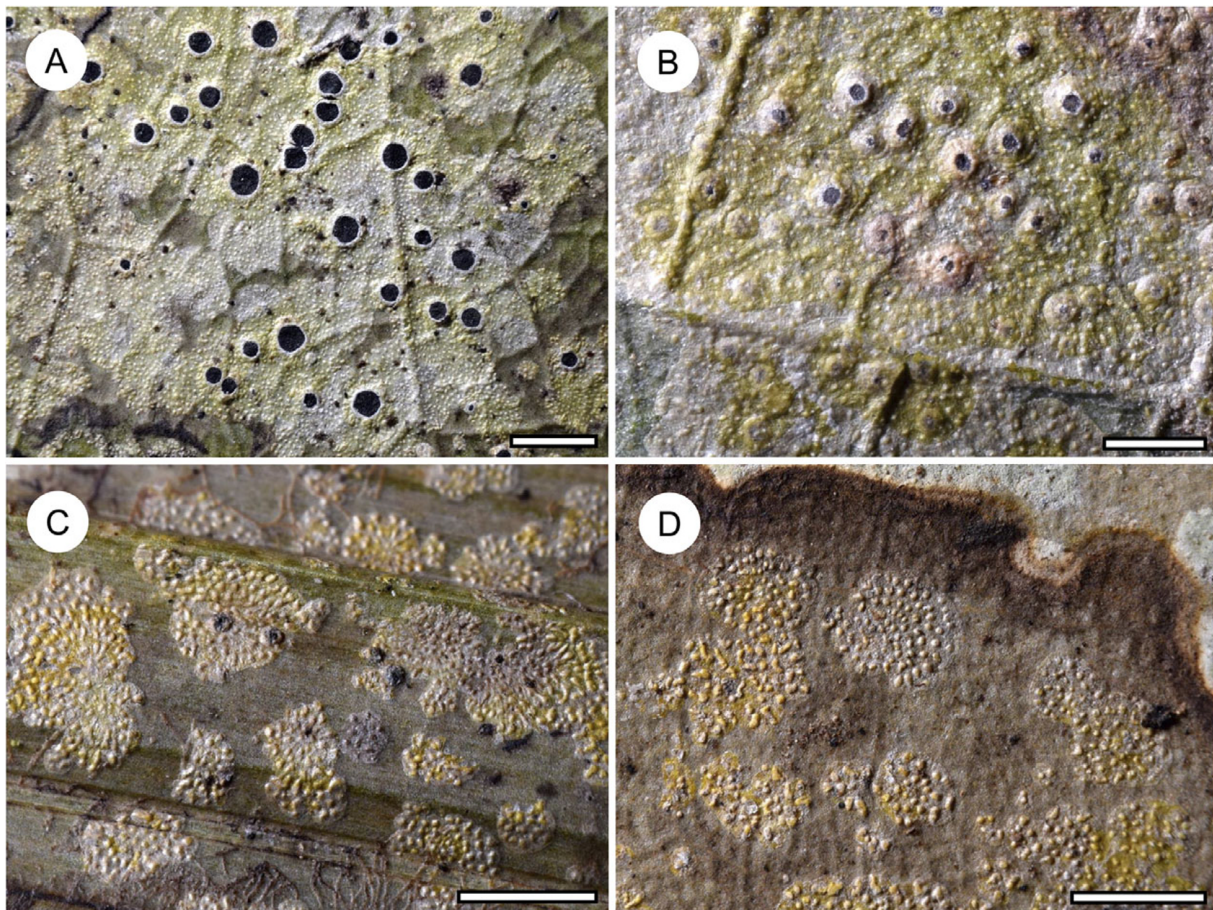


Figure 19. Habit and characteristics of newly described or otherwise interesting species. A–D, *Mazosia melanophthalma* (A, *Ward* 506; B, *Ward* 743; C, *Ward* 774; D, *Ward* 796), thalli with apothecia. Scales = 1 mm. In colour online.

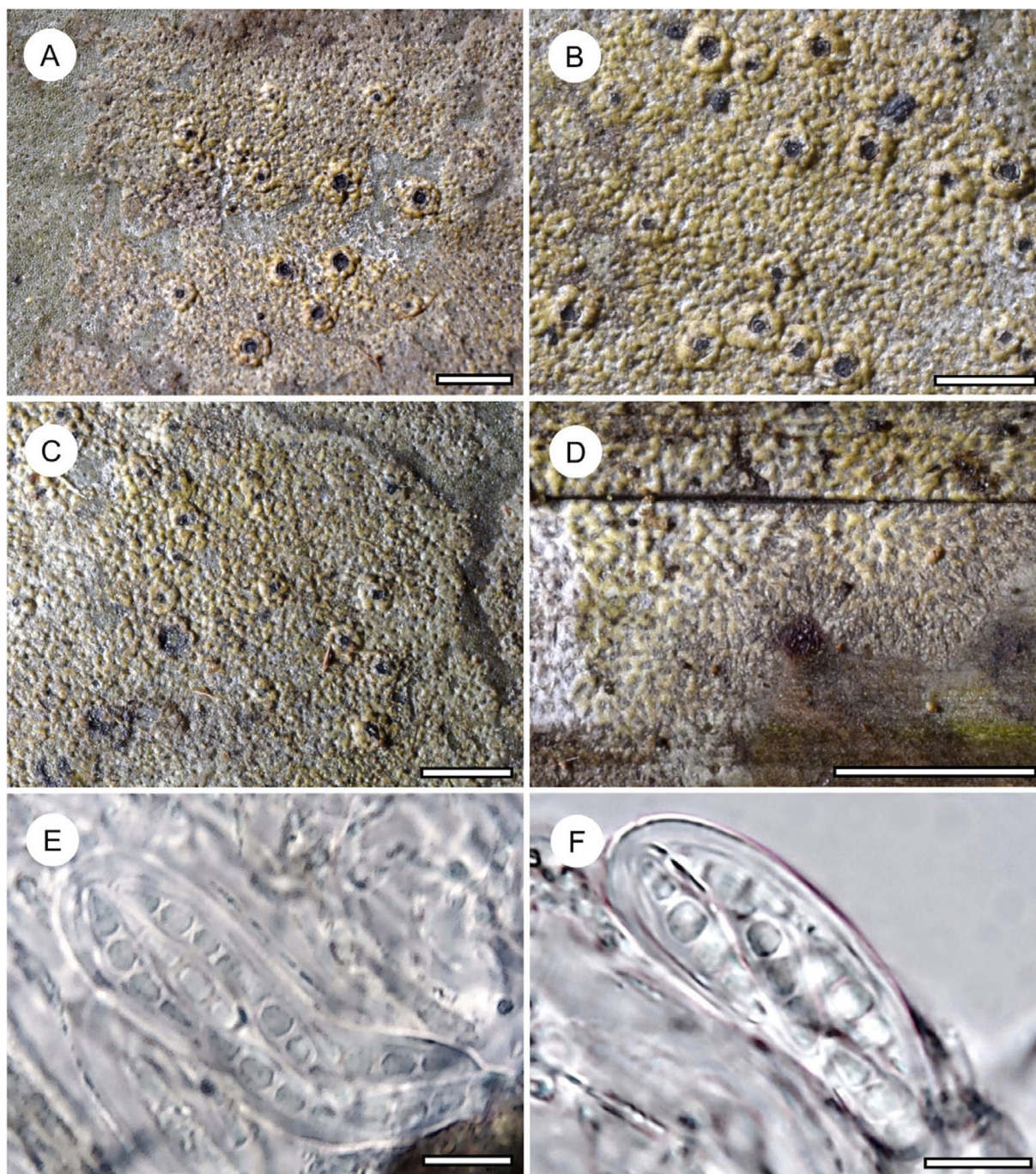


Figure 20. Habit and characteristics of newly described or otherwise interesting species. A–F, *Mazosia rugosa* (A, B, E & F, holotype; C, Ward 852; D, Ward 778). A–D, thalli with apothecia. E & F, asci with ascospores. Scales: A–D = 1 mm; E & F = 10 μ m. In colour online.

(10–20 μ m), algiferous patches light brownish grey to cream-coloured and slightly shiny, UV+ patchily bluish white, hypothallus brown to dark brown, opaque; thallus delimited by a dark brown prothallus; ridges formed by confluent verrucae, covering the algiferous patches, 0.03–0.05 mm thick, cream-coloured, forming a minutely reticulate pattern leaving tiny depressions. *Photobiont cells* rectangular to oblong, 9–15 $\times$ 4–5 μ m, in irregular plates leaving small interspaces.

Ascomata round, 0.3–0.4 mm diam. and 70–80 μ m high; disc black, translucent when moistened; margin irregular, gently to

sometimes steeply sloping outwards, the light grey to cream-coloured thalline cover often disrupted to expose the blackish excipulum. *Excipulum* 10–25 μ m thick, formed by a layer of blackish brown hyphae, externally partly covered by a thin layer of greyish crystals, a single photobiont layer and a thin layer of colourless hyphae. *Hypothecium* 10–15 μ m high, pale yellowish brown to brown. *Hymenium* 60–70 μ m high. *Asci* 50–60 $\times$ 12–15 μ m. *Ascospores* fusiform, 3-septate, 15–20 $\times$ 4–6 μ m, upper median cell very slightly enlarged, colourless.

Pycnidia not observed.

Secondary chemistry. Not tested by TLC due to the very small thalli, but standard spot tests (C, K, P, UV) on the thallus all negative.

Etymology. The epithet refers to the rugose thallus.

Distribution and ecology. Known from several localities of mixed dipterocarp and heath forest in Brunei Darussalam; particularly abundant in Andulau Forest Reserve.

Remarks. *Mazosia rugosa* at first glance resembles *M. pseudobambusae* Kalb & Vězda (see Lücking 2008), due to its rather light thallus bordered by a dark prothallus and the apparently pale verrucae. However, on closer inspection, the thallus does not produce discrete verrucae; instead, these are strongly confluent to form irregular, reticulate ridges, giving the thallus a rugose appearance. Such a morphology is thus far unique within the genus *Mazosia*. All other species with a verrucose thallus have discrete verrucae, including *M. tumidula* (Müll. Arg.) Zahlbr. and the corticolous *M. ocellata* (Nyl.) R. C. Harris, in which the verrucae are quite large (Lücking 2008), hence identification with any of these species is not possible. The apothecia are also smaller than in most other species and the thalline cover of the excipulum is usually incomplete or in patches, another unique feature of this new species. The algiferous thallus patches are irregular in outline and are dispersed over a dark hypothallus, and they feature a non-radiating photobiont, a combination of characters likewise unknown in other species of the genus.

Mazosia rugosa was found quite abundantly at various localities, with very little variation in its morphology, supporting its interpretation as a new and possibly regionally endemic species.

Additional specimens examined. **Brunei Darussalam:** *Belait:* Andulau Forest Reserve, 4°39'19.98"N, 114°31'20.244"E, 72 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 1 ix 2021, *D. A. Ward* 356 (UBDH), 358 (B, UBDH), 376 (B, UBDH), 382 (B, UBDH); *Jalan Labi Heath Forest*, 4°28'32.4084"N, 114°28'2.7768"E, 51 m, tropical moist broadleaf forest ecoregion, heath forest, on leaves, 19 ix 2021, *D. A. Ward* 778a (UBDH); *Jalan Labi Mixed Dipterocarp Forest*, 4°34'49"N, 114°28'35"E, 81 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 10 ix 2021, *D. A. Ward* 852b (B; filed under *Mazosia dispersa*). *Temburong:* *Batu Apoi*, 4°40'57.54"N, 115°13'14.538"E, 120 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 26 ix 2021, *D. A. Ward* 868a (UBDH).

***Ocellularia andulauensis* D. A. Ward & Lücking sp. nov.**

Index Fungorum No.: IF 905109

Differing from *Ocellularia daniana* in the more delicate, foliicolous thallus and the much smaller ascospores.

Type: Brunei Darussalam, Belait, Andulau Forest Reserve, 4°39'19.98"N, 114°31'20.244"E, 72 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 1 September 2021, *D. A. Ward* 434 (UBDH—holotype!).

(Fig. 21A–D)

Thallus continuous, coarsely verrucose, up to 30 mm across, moderately thick (50–150 µm), light greenish yellow to light green,

opaque to slightly shiny, prothallus absent; verrucae prominent, 0.1–0.2 mm diam. *Photobiont cells* oblong to irregular, 7–12 × 5–7 µm, in irregular groups or short threads. Thallus in section with dense, prosoplectenchymatous cortex, irregular photobiont layer, and irregular, white medulla; verrucae strongly encrusted with clusters of calcium oxalate crystals and medulla nubilous with numerous small, grey crystals.

Ascomata round, erumpent to prominent, with complete thalline margin, 0.25–0.4 mm diam., 0.15–0.2 mm high; disc covered by 0.05–0.1 mm wide pore, filled by black-tipped columella; proper margin indistinct, sometimes visible as thin whitish rim around the pore; thalline margin entire, smooth, light greenish yellow to light green. *Excipulum* entire, light orange-brown, 20–30 µm wide, laterally fused with thalline margin; laterally covered by algiferous, corticate thallus layer with thick medulla containing numerous small, grey crystals; columella present, finger-like, up to 50 µm wide and up to 100 µm high, carbonized. *Hypothecium* prosoplectenchymatous, 10–15 µm high, yellowish. *Hymenium* 70–80 µm high, hyaline, clear. *Epithecium* indistinct. *Paraphyses* unbranched, apically smooth; periphysoids absent. *Asci* cylindrical to clavate, 70–75 × 12–13 µm. *Ascospores* 8 per ascus, irregularly arranged, oblong-ellipsoid, 5-septate, 13–15 × 4.5–5 µm, c. 3 times as long as wide, hyaline, distoseptate with lens-shaped lumina, I+ violet-blue.

Secondary chemistry. Probably protocetraric acid and satellite substances; medulla C–, K– to K+ faintly yellowish, P+ deep orange (–red); thallus, apothecia and medulla UV–.

Etymology. The epithet refers to the type locality.

Distribution and ecology. Growing epiphyllous in the understorey of tropical rainforests; thus far known only from the type collection.

Remarks. While *Graphidaceae* is the most diverse and abundant family of tropical lichens (Lücking *et al.* 2014), its members very rarely grow on living leaves, with the exception of the genus *Chroodiscus* (Santesson 1952; Papong *et al.* 2009). Typically corticolous species may grow opportunistically foliicolous, although mostly at higher elevations on leathery, long-lived leaves. The material described above is apparently the first species of *Ocellularia* G. Mey. and related taxa reported from living leaves, *Myriotrema foliicola* (Hale) Hale not actually being a foliicolous species (Hale 1975, 1980; Lücking *et al.* 2016). Due to its chemistry and the presence of a columella, the material belongs in the *O. perforata* (Leight.) Müll. Arg. morphodeme, which was traditionally circumscribed as a single, variable taxon but represents many, often not directly related species differing in various phenotypic characters (Lücking 2014). *Ocellularia andulauensis* is in most aspects closest to the recently described *O. daniana* Lücking from Cuba (Lücking 2015), including the coarsely verrucose thallus, the non-carbonized, orange excipulum combined with a carbonized, finger-like columella and the 5-septate ascospores, in addition to the identical chemistry. However, overall it is much more delicate and the ascospores are distinctly smaller (20–25 × 7–8 µm). Given that the ascospores are mature, with a well-developed, amyloid endospore, the possibility that this foliicolous material is a juvenile form of *O. daniana* can be rejected. The genus *Ocellularia* is otherwise quite diverse in Brunei, with numerous species detected on bark (D. H. Ward *et al.*, unpublished data), but none of these exhibit characters in agreement with this foliicolous collection. We therefore consider it justified to formally describe this taxon.

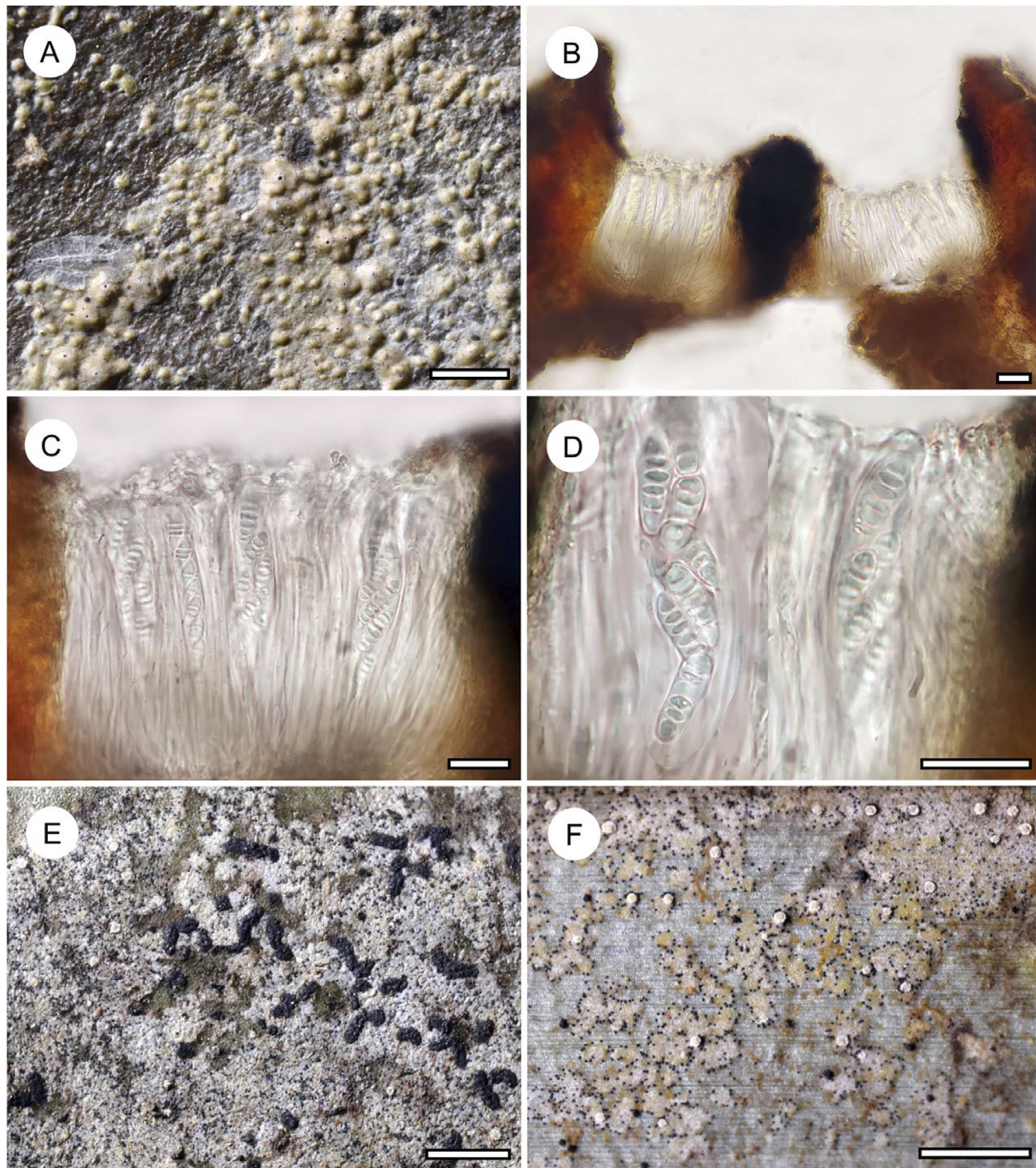


Figure 21. Habit and characteristics of newly described species. A–D, *Ocellularia andulauensis* (holotype). A, thallus with apothecia. B, section through apothecium. C, section through hymenium enlarged. D, asci with ascospores. E & F, *Opegapha albomarginata* (E, holotype; F, Ward 414). E, thallus with ascomata. F, thallus with goniocystangia. Scales: A, E & F = 1 mm; B–D = 20 μ m. In colour online.

Opegapha albomarginata D. A. Ward & Lücking sp. nov.

Index Fungorum No.: IF 905110

Differing from all other species of *Opegapha* with goniocystangia, in the white margin of the goniocystangia.

Type: Brunei Darussalam, Belait, Andulau Forest Reserve, 4° 39' 19.98"N, 114° 31' 20.244"E, 72 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 1 September 2021, D. A. Ward 411 (UBDH—holotype!).

(Fig. 21E & F)

Thallus dispersed into minute, irregular patches becoming confluent and leaving irregular interspaces, entire thallus bordered by a dark brown prothallus, 5–10 mm across, smooth, thin (8–12 μ m), whitish to very pale greenish grey, UV+ faintly pale yellow, with numerous scattered, minute (20–35 μ m diam.) black dots originally bordering each patch but eventually irregularly dispersed, opaque. *Photobiont* cells oblong to irregular, 8–13 $\times$ 4–6 μ m, in irregular plates. *Goniocystangia* abundant, rounded, 0.08–0.1 mm diam.,

with white margins, contents (goniocyts) pale greenish, UV+ pale yellow.

Ascomata adnate, shortly elongate to lirellate, unbranched, 0.2–0.5 mm long and 0.1–0.15 mm wide, 70–90 μm high; disc slit-like; margin thick, black. Excipuloid tissue 20–30 μm thick, basally up to 40 μm wide, absent below hypothecium. *Hypothecium* 7–15 μm high, colourless. *Hymenium* in all sectioned ascomata degenerated, without asci and ascospores.

Pycnidia not observed.

Secondary chemistry. Not tested by TLC due to the very small thalli, but most standard spot tests (C, K, P) on the thallus negative except for the faint, pale yellow UV-reaction of the thallus and goniocyts.

Etymology. The epithet refers to the white margin around the goniocystangia.

Distribution and ecology. Known from several locations in mixed dipterocarp forest in the Belait area.

Remarks. *Opegrapha* is one of the largest genera of lichenized fungi, considered to contain c. 300 species (Lücking *et al.* 2017); however, molecular studies have shown it to be a collective genus, with several smaller groups already segregated (Ertz & Tehler 2011; Ertz *et al.* 2015; Ertz 2018). Around a dozen species are foliicolous, some of them now recognized in the genus *Fouragea* (Frisch *et al.* 2014; Ertz 2020). A small group of five species is known to produce so-called goniocystangia, soralia-like structures with a defined border, namely *O. dibbenii*, *O. lambinonii* Sérus., *O. luzonensis* Sérus., *O. santessonii* Sérus. and *O. serusiauxii* Lücking (Sérusiaux 1978, 1985; Lücking 2008). All produce goniocystangia with black margins and, with the exception of *O. luzonensis*, have a photobiont with rectangular cells in radiating rows, resulting in a continuous, rounded thallus with a characteristic appearance. The goniocystangia with white margins differentiates the new species from all others with those structures; it agrees with *O. luzonensis* in the irregular photobiont but, apart from the black margins of the goniocystangia, this species has a brown thallus with scattered or indistinct black dots. Sorediate species are otherwise rare in *Opegrapha*; one paleotropical taxon is *Zwackhia sorediifera* (P. James) Ertz (Ertz 2009), but here the soralia are diffuse and not delimited in regularly circular, well-delimited structures. The degenerated hymenia suggest that the species is mainly dispersed by its goniocyts.

Additional specimens examined. **Brunei Darussalam:** Belait: Andulau Forest Reserve, 4°39'19.98"N, 114°31'20.244"E, 72 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 1 ix 2021, D. A. Ward 414 (B), 686b (B; filed under *Badimia polillensis*); Jalan Labi Mixed Dipterocarp Forest, 4°34'49"N, 114°28'35"E, 81 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 10 ix 2021, D. A. Ward 1286e (B; filed under *Musaespora epiphylla*); Wasai Teraja, 4°20'28.9536"N, 114°26'52.908"E, 173 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on dicot leaves, 6 xi 2021, D. A. Ward (with D. Cicuzza) 1290f (B; filed under *Mazosia melanophthalma*).

Phylloporis verrucosula D. A. Ward & Lücking sp. nov.

Index Fungorum No.: IF 905111

Differing from *Phylloporis palmae* in the small perithecia and comparatively narrow ascospores.

Type: Brunei Darussalam, Belait, Wasai Telingan, Teraja, 4°22'19.2252"N, 114°27'58.3344"E, 149 m, tropical moist broadleaf forest ecoregion, riparian forest/mixed dipterocarp forest, on leaves, 30 October 2021, D. A. Ward (with D. Cicuzza) 1061 (UBDH—holotype!; B—isotype!).

(Fig. 22A–G)

Thallus supracuticular, continuous, 5–15 mm across and 5–10 μm thick, very minutely verrucose, grey, slightly shiny, often bordered by a narrow, dark brown prothallus; verrucae wart-shaped, 0.02–0.03 mm diam., blackish. *Photobiont* a species of *Phycopeltis*, cells rectangular to oblong, 8–13 $\times$ 3–5 μm , forming nets with distinct interspaces.

Perithecia covered by a thin thallus layer up to ostiole, wart-shaped to almost conical, 0.15–0.25 mm diam. and 70–100 μm high, greyish black. *Excipulum* prosoplectenchymatous, 7–10 μm thick, colourless to brownish. *Involucrellum* carbonized, 15–25 μm thick, black. *Paraphyses* unbranched. *Asci* obclavate (widest near the base), 25–30 $\times$ 6–7 μm . *Ascospores* irregularly biserial, oblong, 1-septate, not constricted at the septum, 10–12 $\times$ 1.8–2.3 μm , 5–6 times as long as wide.

Pycnidia not observed.

Secondary chemistry. Not tested by TLC due to the very small thalli, but standard spot tests (C, K, P, UV) on the thallus all negative.

Etymology. The epithet refers to the minutely verrucose thallus.

Distribution and ecology. Known from several localities of mixed dipterocarp (and riparian) forest in Brunei Darussalam; particularly abundant in Andulau Forest Reserve and in Teraja.

Remarks. *Phylloporis* is a small genus of ten species, recently resurrected to accommodate species with a supracuticular thallus, all closely related and with little variation in perithecial anatomy and ascospore size (Jiang *et al.* 2020). So far two species are known with a minutely verrucose thallus, *P. cinefaciens* (Nyl.) S. H. Jiang *et al.* [= *P. multipunctata* (G. Merr. ex R. Sant.) Vězda] and *P. palmae* (Cavalc. & A. A. Silva) S. H. Jiang *et al.* Both differ in ascospore size (12–16 $\times$ 3.5–4.5 vs 8.5–10 $\times$ 2–3 μm ; Jiang *et al.* 2020). The new species described here is distinguished by its very small perithecia, not exceeding 0.3 mm in size, whereas in the other two species they are 0.4–0.7 mm in diameter. The ascospores are intermediate in length between the other two species but much narrower, with a length-to-width ratio of c. 5–6 vs 3.5–4.5 in *P. cinefaciens* and *P. palmae*. *Phylloporis verrucosula* may be more widespread in tropical Asia but might have been confused with *P. cinefaciens* (= *P. multipunctata*).

Additional specimens examined. **Brunei Darussalam:** Belait: Andulau Forest Reserve, 4°39'19.98"N, 114°31'20.244"E, 72 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 1 ix 2021, D. A. Ward 416 (UBDH), 419 (UBDH), 421b (UBDH; filed under *Phylloblastia dolichospora*), 424 (B, UBDH), 425 (B, UBDH); Wasai Telingan, Teraja, 4°22'19.2252"N, 114°27'58.3344"E, 149 m, tropical moist broadleaf forest ecoregion, riparian forest/mixed dipterocarp forest, on leaves, 5 ix 2021, D. A. Ward (with D. Cicuzza and B. Zoletto) 160a (B, UBDH), 196a (B); *ibid.*, 30 x 2021, D. A. Ward (with D. Cicuzza) 1052b (B; filed under *Calenia phyllogena*), 1103a (B), 1113b (UBDH; filed under *Sporopodium argillaceum*). Temburong: Batu Apoi, 4°

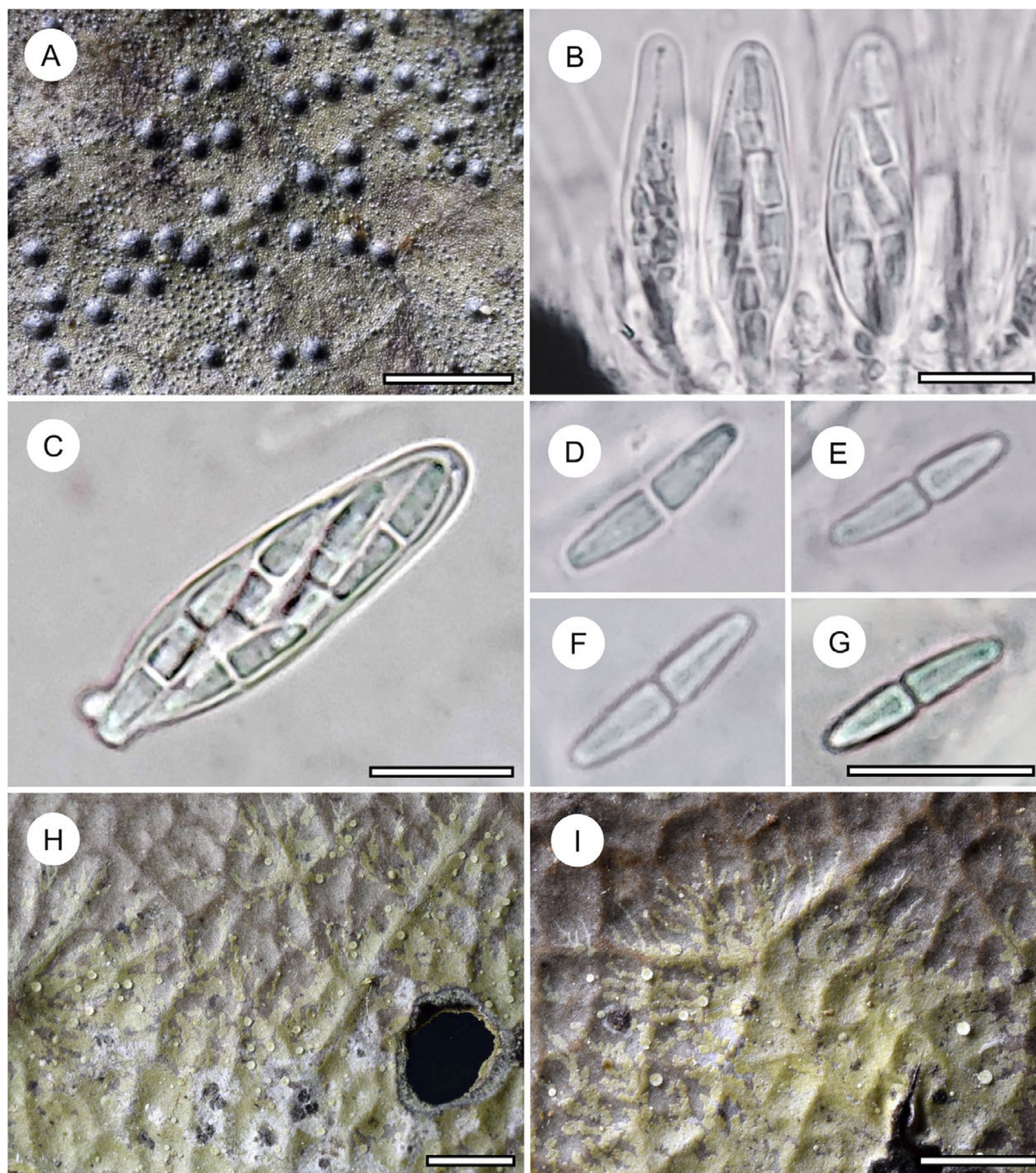


Figure 22. Habit and characteristics of newly described species. A–G, *Phylloporis verrucosula* (holotype). A, thallus with perithecia. B & C, asci with ascospores. D–G, ascospores. H & I, *Porina riparia* (holotype), thallus with disc-shaped isidia. Scales: A, H & I = 1 mm; B–G = 10 μ m. In colour online.

40°57.54'N, 115°13'14.538"E, 120 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 26 ix 2021, D. A. Ward 531c (UBDH; filed under *Calenia phyllogena*), 556 (B, UBDH), 880 (B), 893a (UBDH), 900a (B, UBDH), 947a (B, UBDH), 948a (UBDH).

***Porina riparia* D. A. Ward & Lücking sp. nov.**

Index Fungorum No.: IF 905112

Differing from *Porina pseudoapplanata* [= *Phyllophiale viridis*] in the finely lacinate thallus with non-radiating photobiont.

Type: Brunei Darussalam, Temburong, Batu Apoi, 4°40'57.54"N, 115°13'14.538"E, 120 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 26 September 2021, D. A. Ward 943a (UBDH—holotype!; B—isotype!).

(Fig. 22H & I)

Thallus continuous but starting out as radiating laciniae and remaining irregularly lacinate towards the margins, often leaving irregular interspaces, smooth, 5–15 mm across and 8–10 μ m thick, pale greenish grey, opaque to slightly shiny. *Isidia* of the *Phyllophiale*-type always present, usually scattered, disc-shaped, flattened

to slightly concave, 0.1–0.15 mm diam., lighter than the thallus to whitish, under the microscope composed of a plate of regularly radiating, colourless hyphae with a cluster of algal cells in the central part. *Photobiont cells* angular-rounded to oblong, $8\text{--}12 \times 4\text{--}6\ \mu\text{m}$, in irregular plates.

Perithecia not observed.

Pycnidia not observed.

Secondary chemistry. Not tested by TLC due to the very small thalli, but standard spot tests (C, K, P, UV) on the thallus all negative.

Etymology. The epithet refers to the occurrence in a riverine forest.

Distribution and ecology. Known from various localities on leaves in mixed dipterocarp forest, partly near streams.

Remarks. The genus *Phyllophiale* was originally established by Santesson (1952) for a single, sterile species producing regularly disc-shaped isidia. Much later, Santesson (in Lücking 1991) described a second species, *P. fusca* R. Sant., and a third species, *P. viridis* Lücking & M. Cáceres, was subsequently discovered (Lücking & Cáceres 1999). It was eventually found that *Phyllophiale*-type isidia were associated with *Porina*-type perithecia (Aptroot & Sipman 1993; Lücking & Vězda 1998), and the original species was recombined into *Porina*, as *P. alba* (R. Sant.) Lücking, whereas *Phyllophiale fusca* and *P. viridis* were established as synonyms of *Porina fusca* Lücking and *P. pseudoapplanata* Lücking & M. Cáceres, respectively (Lücking 2004).

The new species is most similar to *P. pseudoapplanata* and *P. weghiana* Van den Broeck *et al.* in having a smooth, pale greenish

grey thallus lacking crystals, but differs from both species in the finely lacinate thallus and from *P. pseudoapplanata* also in the non-radiating photobiont; from *P. alba* it differs in the absence of calcium oxalate crystals in the thallus (see key below). In his description of *Phyllophiale alba*, Santesson (1952) gave the thallus as rough to smooth and the photobiont with radiating or irregular plates, so in the material he cited from across the tropics, he probably mixed specimens now separated as *P. pseudoapplanata*, *P. weghiana* and *P. riparia* within a broadly defined *Phyllophiale alba*. Despite a careful search, we have not seen any *Porina* with a similar thallus that could be the fertile counterpart to the isidiate specimens in the material.

Additional specimens examined. **Brunei Darussalam:** Belait: Andulau Forest Reserve, $4^{\circ}39'19.98''\text{N}$, $114^{\circ}31'20.244''\text{E}$, 72 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 1 ix 2021, D. A. Ward 666a (B), 671a (B), 706a (B, UBDH), 1278b (B; filed under *Bapalmuia pallescens*), 1279u (B; filed under *Aspidothelium fugiens*); Jalan Labi Mixed Dipterocarp Forest, $4^{\circ}34'49''\text{N}$, $114^{\circ}28'35''\text{E}$, 81 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 10 ix 2021, D. A. Ward 863 (UBDH), 1286k (B; filed under *Musaespora epiphylla*). Temburong: Batu Apoi, $4^{\circ}40'57.54''\text{N}$, $115^{\circ}13'14.538''\text{E}$, 120 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 26 ix 2021, D. A. Ward 569 (B), 1294g (B; filed under *Bapalmuia pallescens*); *ibid.*, on dicot leaves, 26 ix 2021, D. A. Ward 1291b (B; filed under *Byssoloma subaeruginosum*); Kampong Tamada, $4^{\circ}32'55.0644''\text{N}$, $115^{\circ}4'47.406''\text{E}$, 48 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 13 xi 2021, D. A. Ward 1200 (UBDH), 1266 (UBDH).

Key to foliicolous species of *Porina* with *Phyllophiale*-type isidia

- 1 Thallus minutely rough, under the microscope containing clusters of calcium oxalate crystals; isidia whitish; perithecia appanately lens-shaped with spreading base, in section with a crystallostratum covering the perithecial wall; ascospores 7-septate; pantropical ***Porina alba*** [= *Phyllophiale alba*]
Thallus smooth, lacking clusters of calcium oxalate crystals; isidia, perithecia and ascospores variable 2
- 2(1) Thallus brown, more or less finely lacinate; isidia brownish; perithecia subglobose, orange-brown; ascospores 3-septate; pantropical ***Porina fusca*** [= *Phyllophiale fusca*]
Thallus pale greenish grey, finely lacinate or formed by dispersed, confluent patches; isidia lighter than thallus or whitish; perithecia where known appanately lens-shaped with spreading base, orange; ascospores where known 7–9-septate 3
- 3(2) Photobiont forming rectangular cells in radiating plates; thallus composed of dispersed, soon confluent patches; perithecia appanately lens-shaped with spreading base, orange; ascospores 7-septate; neotropical ***Porina pseudoapplanata*** [= *Phyllophiale viridis*]
Photobiont forming angular-rounded to oblong cells in irregular plates; thallus dispersed to lacinate; perithecia hemispherical to subglobose, light yellowish; ascospores (7–) 9-septate; or perithecia and ascospores unknown; paleotropical 4
- 4(3) Thallus dispersed into rounded to irregular patches; perithecia hemispherical to subglobose, light yellowish; ascospores (7–) 9-septate; tropical Africa ***Porina weghiana***
Thallus finely lacinate, at least towards the margin; perithecia and ascospores not known; paleotropical ***Porina riparia***

Spinomyces rubrotrichoides D. A. Ward, B. Moncada & Lücking
sp. nov.

Index Fungorum No.: IF 905113

Differing from *Rubrotricha helminthospora*, with which it agrees in ascospore type, in the entirely whitish, more delicate sterile thallus setae.

Type: Brunei Darussalam, Temburong, Batu Apoi, 4°40'57.54"N, 115°13'14.538"E, 120 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 26 September 2021, D. A. Ward 513a (UBDH—holotype!).

(Fig. 23A & B)

Thallus continuous, smooth, 5–10 mm across, very thin (8–15 µm), with a cartilaginous corticiform layer, light greenish grey, slightly glossy, furnished with whitish, apically somewhat bent, 0.5–0.7 mm long and 30–40 µm wide, sterile setae, concentrated around the apothecia; no conspicuous prothallus. *Photobiont cells* bright green, rounded, 5–9 µm diam.

Apothecia biatorine, sessile, regularly rounded, 0.15–0.2 mm diam. and 0.15–0.2 µm high; disc deeply immersed, beige, slightly translucent; proper margin strongly prominent, entire, thin, pale beige to almost white, slightly translucent. *Hypothecium* 20–30 µm high, colourless, I–, KI–. *Epithecium* inconspicuous. *Hymenium* 120–150 µm high, colourless, I–, KI–. *Paraphyses* unbranched,

embedded in a gelatinous matrix. *Asci* clavate to oblong, 75–110 × 25–45 µm, I–, KI–. *Ascospores* (1–)2(–4) per ascus, cylindrical to worm-shaped, (7–)9–11-septate, (50–)60–80 × 10–13(–15) µm, with constrictions at the septa, colourless, I–.

Hyphophores not observed.

Secondary chemistry. Not tested by TLC due to the very small thalli, but standard spot tests (C, K, P, UV) all negative.

Etymology. The epithet refers to the similarity of the ascospores to those of *Rubrotricha helminthospora*.

Distribution and ecology. Known from several localities of mixed dipterocarp (and riparian) forest in Brunei Darussalam.

Remarks. On account of its smooth thallus with white setae and its sessile apothecia with thin but distinct, prominent margin, this new species is placed in the recently reinstated genus *Spinomyces* Bat. & Peres ex Xavier-Leite *et al.* (Xavier-Leite *et al.* 2023). It somewhat resembles *Spinomyces aggregatus* (Lücking) Xavier-Leite *et al.*, in particular in the white sterile setae clustered around the apothecia, but the latter is overall larger, with yellow apothecia, and the ascospores are muriform. Indeed, no species of *Spinomyces* with long, multiseptate ascospores is so far known, and such spores are generally rare in *Gomphillaceae*. Among those with sterile setae formerly classified in *Tricharia* s. lat., only two feature such

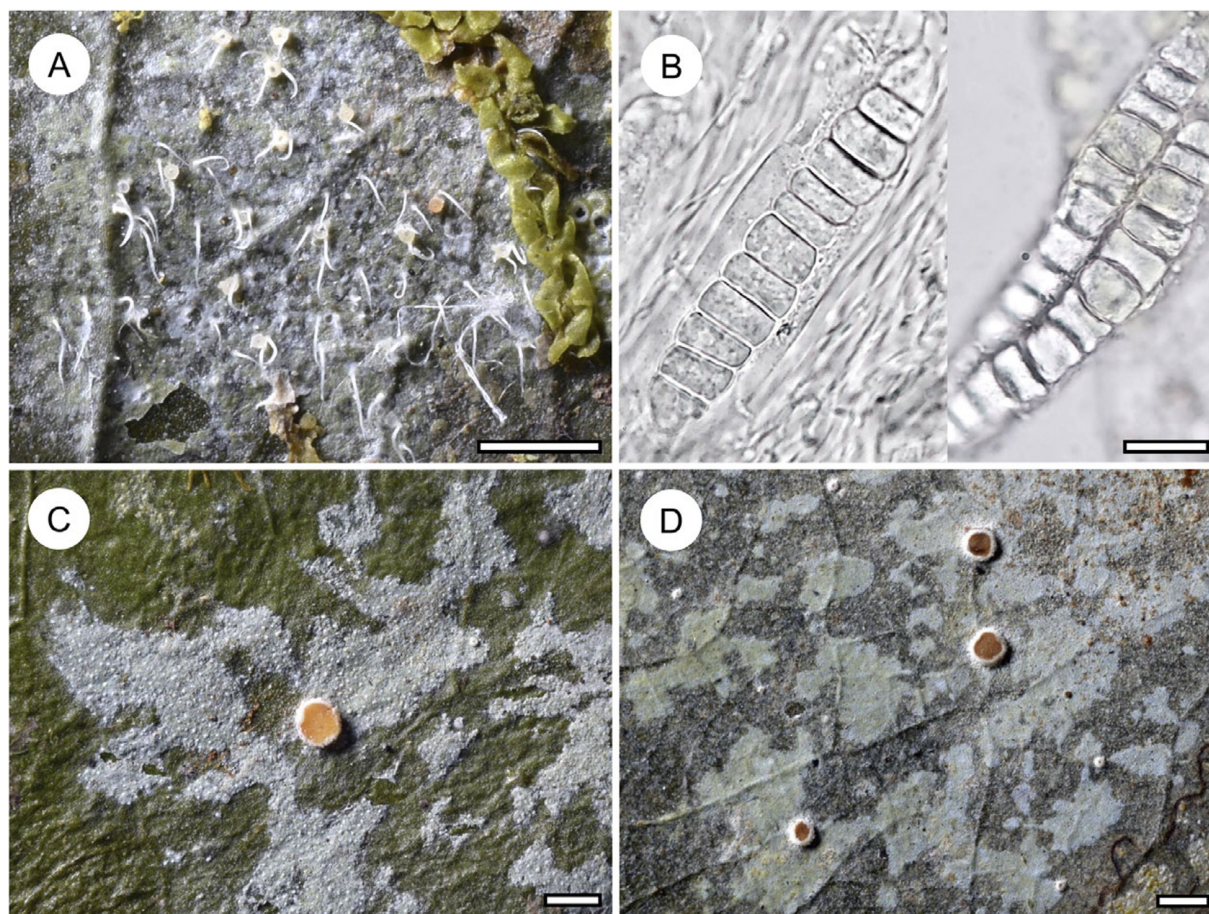


Figure 23. Habit and characteristics of newly described species. A & B, *Spinomyces rubrotrichoides* (holotype). A, thallus with setae and apothecia. B, ascospores. C, *Sporopodium* sp. 1 (Ward 680), thallus with apothecia. D, *Sporopodium* sp. 2 (Ward 810), thallus with apothecia. Scales: A, C & D = 1 mm; B = 10 µm. In colour online.

ascospores, namely *Rubrotricha helminthospora* and *R. subhelminthospora* Lücking (Santesson 1952; Lücking *et al.* 2005; Lücking 2008). In both species, the ascospores and apothecia are similar to the new taxon described here but the sterile setae are longer (up to 2 mm) and more robust, and for most of their length reddish brown, with only the apical portion pale.

Additional specimens examined. **Brunei Darussalam:** *Belait*: Wasai Telingan, Teraja, 4°22'19.2252"N, 114°27'58.3344"E, 149 m, tropical moist broadleaf forest ecoregion, riparian forest/mixed dipterocarp forest, on leaves, 30 x 2021, *D. A. Ward* (with *D. Cicuzza*) 1024 (UBDH); Wasai Teraja, 4°20'28.9536"N, 114°26'52.908"E, 173 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 6 xi 2021, *D. A. Ward* (with *D. Cicuzza*) 1149 (B), 1164 (B), 1289p (B; filed under *Raciborskiella talaumae*).

Sporopodium aff. *antoninianum* Elix, Lumbsch & Lücking

Remarks. The present material is characterized by a pale greenish, finely verrucose thallus with the central portions furnished with densely arranged, pale hairs. It resembles *Sporopodium antoninianum*, which differs in producing the hairs on an algal-free prothallus (Elix *et al.* 1995; Lücking 2008). Due to the sparse material, the taxonomic status of this form cannot be assessed further.

Specimen examined. **Brunei Darussalam:** *Belait*: Wasai Teraja, 4°20'28.9536"N, 114°26'52.908"E, 173 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 5 ix 2021, *D. A. Ward* (with *D. Cicuzza* and *B. Zoletto*) 202 (B).

Sporopodium cupuliferum (Nyl.) Vain.

Remarks. This name is reinstated here for material similar to *Sporopodium lepreurii* Mont. but featuring apothecia with a dark brown apothecial margin.

Specimen examined. **Brunei Darussalam:** *Belait*: Wasai Teraja, 4°20'28.9536"N, 114°26'52.908"E, 173 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 5 ix 2021, *D. A. Ward* (with *D. Cicuzza* and *B. Zoletto*) 205 (UBDH).

Sporopodium aff. *podosphaera* Lücking & R. Sant.

Remarks. This material consists of two well-developed specimens with a pale yellowish grey, smooth thallus and grey, pruinose campylidia lacking a distinct socle. It differs from other species of the genus in the UV+ yellow (not orange) reaction, indicating the presence of lichexanthone instead of, or in addition to, chlorinated xanthones (Elix *et al.* 1995).

Specimen examined. **Brunei Darussalam:** *Brunei Muara*: Bukit Tempayan Pisang, 5°0'43.9236"N, 115°2'42.8028"E, 56 m, tropical moist broadleaf forest ecoregion, secondary forest, on leaves, 6 xii 2021, *D. A. Ward* (with *J. Wong*) 611 (B, UBDH).

Sporopodium sp. 1

(Fig. 23C)

Remarks. The two collections feature a taxon with an irregularly lacinate thallus leaving large interspaces, with a pale bluish grey colour and minute, whitish verrucae, and a single apothecium with

vividly orange disc and cream-coloured, hairy margin. There is no known species of *Sporopodium* that corresponds with this material (Sérusiaux *et al.* 2008), but unfortunately it is too scanty to describe formally as a new taxon.

Specimens examined. **Brunei Darussalam:** *Belait*: Andulau Forest Reserve, 4°39'19.98"N, 114°31'20.244"E, 72 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 1 ix 2021, *D. A. Ward* 680a (B, UBDH). *Tutong*: Tutong Kerangas, 4°44'34.4004"N, 114°35'8.6172"E, 25 m, tropical moist broadleaf forest ecoregion, heath forest, on leaves, 26 xii 2021, *D. A. Ward* 616 (B, UBDH).

Sporopodium sp. 2

(Fig. 23D)

Remarks. This material is similar to *Sporopodium* sp. 1, but the thallus is smooth, lacking verrucae, and the apothecial disc is brown rather than orange. Here also, no corresponding species is known (Sérusiaux *et al.* 2008).

Specimen examined. **Brunei Darussalam:** *Belait*: Jalan Labi Mixed Dipterocarp Forest, 4°34'49"N, 114°28'35"E, 81 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 10 ix 2021, *D. A. Ward* 810 (B).

Trichothelium subrobinsonii D. A. Ward & Lücking sp. nov.

Index Fungorum No.: IF 905114

Differing from *Trichothelium robinsonii* in the consistently 7-septate ascospores.

Type: Brunei Darussalam, Temburong, Batu Apoi, 4°40'57.54"N, 115°13'14.538"E, 120 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 26 September 2021, *D. A. Ward* 514 (UBDH—holotype!; B—isotype!).

(Fig. 24A–F)

Thallus continuous but finely lacerate-reticulate, leaving small interspaces, smooth, 5–10 mm across and 5–10 µm thick, light grey, slightly shiny. **Photobiont cells** angular-rounded to oblong, 6–10 × 3–6 µm, in irregular plates leaving small interspaces.

Perithecia sessile, subglobose, 0.2–0.3 mm diam. and 250–300 µm high, apically setose, brownish orange, matt; setae 7–10, acute to bristle-like, projecting horizontally, 0.3–0.5 mm long and 30–80 µm wide at base, pale orange to beige. **Excipulum** prosoplectenchymatous, 5–15 µm thick, pale yellowish, K+ orange. **Involucrellum** not distinctly separated from the excipulum, paraplectenchymatous, 25–35 µm thick, yellowish to orange, K+ orange-red, externally covered by 5–10 µm thick, yet indistinct, algiferous thallus layer. **Paraphyses** unbranched, flexuose. **Asci** narrowly fusiform, 130–150 × 10–12 µm. **Ascospores** oblong-bacillar to narrowly fusiform, with the distal end somewhat tapering and sometimes slightly bent, 7-septate, without or with very slight constrictions at septa, 50–65(–80) × 4–5(–6) µm, 9–12(–15) times as long as wide, colourless.

Pycnidia not observed.

Secondary chemistry. Not tested by TLC due to the very small thalli, but standard spot tests (C, K, P, UV) on the thallus all negative; perithecial wall containing *Porina* yellow, K+ orange-red.

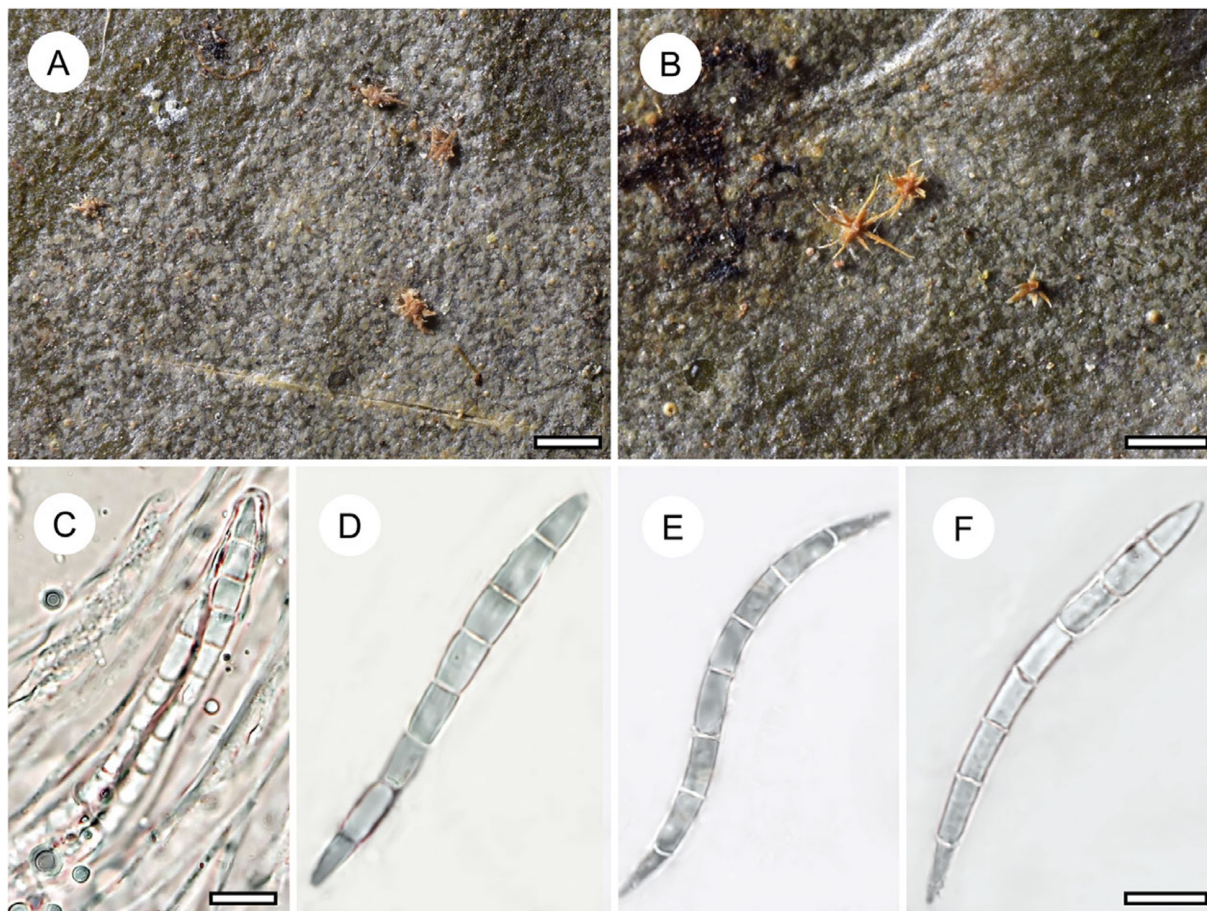


Figure 24. Habit and characteristics of newly described species. A–F, *Trichothelium subrobinsonii* (holotype). A & B, thallus with perithecia. C, ascus with ascospores. D–F, ascospores. Scales: A & B = 1 mm; C–F = 10 μ m. In colour online.

Etymology. The epithet refers to the similarity with *Trichothelium robinsonii* Vain.

Distribution and ecology. Known only from the type locality but represented by several collections; growing foliicolous in mixed dipterocarp forest.

Remarks. This new species is externally indistinguishable from *Trichothelium robinsonii*, described from the Philippines (Vainio 1921). Both share the continuous, yet finely lacerate, light greyish thallus and the orange perithecia with distinct setae containing *Porina* yellow in their walls. Vainio (1921: 322) gave no ascospore details for his new species, describing *T. robinsonii* with the remark: ‘*Tantum unum apothecium lectum et eam ob causam microscopio haud examinatum.*’ However, Lücking (2008) examined the type material and found the ascospores to be 9–13(–15)-septate, similar to those of *T. croceum* Sérus., another species described from Papua New Guinea. Lücking (2008) considered the two taxa potentially conspecific, but *T. croceum* differs in the rounded thallus patches with the photobiont forming rectangular, regularly radiating cells, and in the white setae contrasting with the orange perithecial wall; the ascospores are also somewhat wider. *Trichothelium subrobinsonii* agrees with *T. robinsonii* in external morphology and ascospore type, but the ascospores are always only 7-septate and hence have very elongate cells.

Additional specimens examined. **Brunei Darussalam:** Temburong: Batu Apoi, 4°40'57.54"N, 115°13'14.538"E, 120 m, tropical moist broadleaf forest ecoregion, mixed dipterocarp forest, on leaves, 26 ix 2021, D. A. Ward 517a (UBDH), 1294z (B; filed under *Bapalmua pallescens*).

Supplementary Material. The Supplementary Material for this article can be found at <http://doi.org/10.1017/S0024282926101406>.

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Competing Interests. The authors declare none.

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