

# Unravelling the diversity of the lichen genus *Porina* (Porinaceae) in Mauritius

Damien Ertz<sup>1,2,\*</sup> & Paul Diederich<sup>3</sup>

<sup>1</sup>Meise Botanic Garden, Research Department, Meise, Belgium

<sup>2</sup>Fédération Wallonie-Bruxelles, Service général de l'Enseignement supérieur et de la Recherche scientifique, Bruxelles, Belgium

<sup>3</sup>Musée national d'histoire naturelle, Luxembourg, Luxembourg

\*Corresponding author: [damien.ertz@jardinbotaniquemeise.be](mailto:damien.ertz@jardinbotaniquemeise.be)

---

**Background and aims** – Despite the publication of a recent checklist for Mauritius, a small archipelago in the south-western Indian Ocean, our knowledge of the lichen flora of this region remains incomplete. The present contribution is part of an ongoing study of lichen diversity of the islands of Mauritius and Rodrigues. It aims to unravel the diversity of the genus *Porina* s.l. on these islands and to improve the taxonomy and the phylogeny of the family Porinaceae following the morphological study and the sequencing of recently collected material.

**Material and methods** – Lichens were collected in 2016 and 2019 in a range of environments, from lowland dry habitats up to dense evergreen upland forests on the islands of Mauritius and Rodrigues. In total, 85 samples of *Porina* were examined using light microscopy. A molecular study using mtSSU sequences was performed in order to investigate the phylogenetic position of the species of *Porina* occurring in the study area.

**Key results** – The analyses revealed the presence of 23 species of *Porina* s.l. in Mauritius, while only four were previously accepted for this country. Five new species are described: *Porina covidii*, *P. griffithsii*, *P. mauritiana*, *P. nuculoides*, and *P. rupicola*, while two sterile species remain unidentified. The mtSSU phylogenetic tree includes 19 of the 23 species occurring in Mauritius. These species are dispersed throughout the phylogenetic tree, in at least eight main and strongly supported lineages, suggesting multiple colonizations of Mauritius. A new lineage only including Paleotropical and mainly foliicolous species (*P. epiphylloides*, *P. longispora*, *P. mauritiana*, and *P. mazosioides*) is revealed. *Pseudosagedia crocynioides*, a species that was previously known only from Florida, is newly reported from Mauritius, highlighting a remarkable disjunct distribution. Photos of each taxon are provided, along with an identification key to all species.

**Conclusion** – The study of the genus *Porina* in Mauritius highlights a rich flora. The true diversity of *Porina* species in the south-western Indian Ocean is certainly underestimated and in need of further investigation, while a taxonomic-phylogenetic revision of tropical *Porina* at a broader geographical scale is highly desirable. The identity of several Mauritian specimens remains uncertain despite the use of molecular data.

**Keywords** – Forest; Gyalectales; foliicolous; lichens; Mascarene Islands; phylogenetic analysis; *Pseudosagedia*; south-western Indian Ocean.

---

© 2022 Damien Ertz, Paul Diederich.

This article is published and distributed in Open Access under the terms of the [Creative Commons Attribution License \(CC BY 4.0\)](https://creativecommons.org/licenses/by/4.0/), which permits use, distribution, and reproduction in any medium, provided the original work (author and source) is properly cited.

*Plant Ecology and Evolution* is published by Meise Botanic Garden and Royal Botanical Society of Belgium

ISSN: 2032-3913 (print) – 2032-3921 (online)

## INTRODUCTION

*Porina* Ach. is a diverse and widespread genus with ca 75% of the species occurring in humid-subtropical and tropical latitudes, the remainder inhabiting mainly temperate regions. The genus forms one of the main elements of the epiphytic lichen communities in humid tropical forests. The taxa are usually substrate-specific, with nearly half of the species colonizing bark, one-third leaves, ca 20% rocks, and a few bryophytes or soil (McCarthy 1993, 2003). The genus is mainly recognized by the combination of the following characters: thallus crustose with a trentepohlioid photobiont, usually lacking secondary metabolites; ascomata perithecioid; paraphyses unbranched to sparingly branched; hymenium IKI–; asci unitunicate, 8-spored, IKI–; ascospores colourless, thin-walled, narrowly ellipsoid, fusiform to filiform, usually transversely septate, rarely muriform.

The family Porinaceae includes 359 accepted species (Lücking et al. 2017). Molecular phylogenies using mainly mitochondrial SSU rDNA (mtSSU) sequences recovered the genus *Porina* as paraphyletic, with the genera *Myeloconis* P.McCarthy & Elix and *Trichothelium* Müll.Arg. nested within *Porina* (Grube et al. 2004; Baloch & Grube 2006; Nelsen et al. 2014). Yet, these genera were maintained because they are well characterized: *Trichothelium* by perithecia with setae (Lücking 2008) and *Myeloconis* by yellow to orange medullary phenalenones (McCarthy & Elix 1996; Ernst-Russell et al. 2000). Attempts to define further smaller natural entities mainly used the thalline and perithecial morphology (e.g. presence of oxalate crystals in the thallus, pigmentation of the perithecial wall, degree of thallus cover of the perithecia, presence and type of setae on the perithecia, ascus and ascospores types), as well as environmental preferences and distributional trends (e.g. Hafellner & Kalb 1995; Harris 1995; Malcolm & Vězda 1995). Two new genera were even recently described, based mainly on the thallus type in combination with molecular data: flabelliform squamules for the genus *Flabelloporina* Sobreira, M.Cáceres & Lücking and placodioid thallus with a fenestrate anatomy for the genus *Saxiloba* Lücking, Moncada & Viñas (Sobreira et al. 2018; Lücking et al. 2020). However, a splitting of the Porinaceae in small generic entities has not been widely accepted because characters are often shared between genera and are highly variable (e.g. McCarthy & Malcolm 1997; Lücking 2008) so that a broader paraphyletic concept of *Porina* is currently in use. A generic rearrangement or at least a subgeneric arrangement of the Porinaceae could be possible but requires analyses supported by molecular data and a more complex combination of morphological characters instead of the previous rather schematic treatments (Lücking 2008: 271). A possible generic concept for Porinaceae was outlined using a molecular phylogeny, but the results were based on a single marker, the mtSSU (Sobreira et al. 2018; Lücking et al. 2020).

A first checklist of lichens and lichenicolous fungi in the Republic of Mauritius was recently published and includes 216 accepted species (Diederich & Ertz 2020). The genus *Porina* is represented only by four species, viz. *P. epiphylla* (Fée) Fée, *P. florensii* Diederich & Ertz (newly described

within the checklist), *P. nucula* Ach., and *P. tetracerae* (Ach.) Müll.Arg. var. *tetracerae*. Four additional taxa (*P. americana* Fée, *P. chlorotica* (Ach.) Müll.Arg., *P. innata* (Nyl.) Müll.Arg., *P. mastoidea* (Ach.) Müll.Arg. agg.) have been reported from Mauritius, but these were not accepted in the checklist, either because no relevant herbarium material has recently been examined, or because previous records are dubious or erroneous. With the aim of completing our knowledge of the lichens and lichenicolous fungi of the islands, about 2000 specimens were collected in Mauritius and Rodrigues during a field trip in August and September 2019. These include 79 specimens of *Porina*, a genus that obviously represents a species-rich group in the study area. The genus *Porina* has long been neglected, but important taxonomic works published in recent decades facilitate the identification of tropical specimens. A world-wide catalogue of the Porinaceae is available (McCarthy 2003, 2013) and important treatments have been published for the saxicolous species in the Southern Hemisphere (McCarthy 1993), the corticolous species in Australia (McCarthy 1994a, 1994b), the *Porina epiphylla* group (Lücking & Vězda 1998), and the foliicolous species in the Neotropics (Lücking 2008). Several regional identification keys are also available for northeastern Brazil (Cáceres 2007), Florida (Harris 1995), the Indian Subcontinent (Awasthi 1991), Japan (Harada 2015, 2016), and Macaronesia (Sérusiaux et al. 2007).

This paper aims to (1) unravel the diversity of the genus *Porina* in Mauritius by the identification of recently collected specimens, (2) update the phylogeny of the genus by sequencing all Mauritian species, and (3) describe new taxa resulting from our morphological and molecular investigations.

## MATERIAL AND METHODS

### Morphology and chemistry

Voucher specimens are deposited in the herbaria BR, MAU, and TAN. The external morphology was studied and measured using an Olympus SZX12 stereomicroscope. Macroscopic images were captured with a Keyence VHX-5000 digital microscope and a VH-Z20R/W/T lens. Hand-cut sections and squash preparations of ascomata and thalli were mounted in water, a 5% aqueous potassium hydroxide solution (K), or in Lugol's iodine solution (1% I<sub>2</sub>) without (I) or with K pretreatment (KI) and studied using an Olympus BX51 compound microscope. The K and I solutions were by default added to a water mount by running a drop under the edge of the coverslip. Calcium oxalate was identified by adding 25% H<sub>2</sub>SO<sub>4</sub> and the refractive ring structure of asci by using an ammoniacal Congo Red solution (1%). Measurements from ascomatal sections (e.g. hymenium, asci, ascospores) refer to dimensions in water. Measurements of asci are reported as minimum–maximum followed by the number of measurements (n), as only few were measured. Measurements of ascospores do not include the perispore (= gelatinous sheath) and are reported as (minimum–) SD – SD (–maximum), followed by the number of measurements (n), or as minimum–maximum when few ascospores were measured, and the values usually rounded to the nearest 0.5

µm. Micrographs were prepared using an Olympus BX51 compound microscope fitted with an Olympus SC50 digital camera. Colour reactions of the thallus were studied using K, household bleach (C), K followed by C (KC), crystals of paraphenylenediamine dissolved in ethanol (PD) and long-wave UV (366 nm). Lichen secondary metabolites were investigated using thin-layer chromatography (TLC) in solvent A (Orange et al. 2010), but only a few specimens were tested because *Porina* usually lacks acetone-soluble secondary metabolites detectable by TLC.

### Molecular techniques

Well-preserved specimens lacking any visible symptoms of fungal infection, either freshly collected (less than one month, except for *Porina borreii* Ertz 12130, *P. cf. malmei* Ertz 25249, and *P. perminuta* Diederich 18732 that were respectively a 12-year-old, a 14-month-old, and a one-year-old herbarium specimen) or kept in the freezer and frozen less than one month after collection, were used for DNA isolation. Hand-cut sections of the perithecia and the thallus, or a small number of soredia (*Porina* sp. B Ertz 23618) or isidia (*Porina florensii* Ertz 24283, *P. griffithsii* Ertz 23632, *P. sp. A* Ertz 23584) were used for direct PCR as described in Ertz et al. (2015). The material was placed directly in microtubes with 20 µl H<sub>2</sub>O. Amplification reactions were prepared for a 50 µl final volume, as detailed in Ertz et al. (2018). For all species, we tried to amplify a targeted fragment of ca 0.8 kb of the mtSSU rDNA using primers mrSSU1 and mrSSU3R (Zoller et al. 1999). For *Pseudosagedia crocynioides*, a fragment of about 0.6 kb of the nITS rDNA (ITS1 + 5.8S + ITS4) was amplified using primers ITS1F and ITS4 (White et al. 1990). Both strands were sequenced by Macrogen® using the amplification primers. Sequence fragments were assembled with Sequencher v.5.4.6 (Gene Codes Corporation, Ann Arbor, Michigan). Sequences were subjected to ‘megablast’ searches to verify their closest relatives and to detect potential contaminations.

### Taxon selection and phylogenetic analyses

A dataset of mtSSU sequences was assembled for placing the newly sequenced taxa in a phylogeny of the family Porinaceae (supplementary file 1). The closest relatives of the new sequences based on BLAST searches were retrieved from GenBank. Additional taxa were selected mainly from Baloch & Grube (2006, 2009), Nelsen et al. (2014), Orange (2015), Orange et al. (2020), an unpublished study (viz. the mtSSU sequences MT526252 to MT526259 from X. Zhao & F.-Y. Liu “Taxonomic study of the lichen genus *Porina* Ach. from Chinese mainland”), with others from Baloch et al. (2010), Diederich & Ertz (2020), Ertz et al. (2019), Grube et al. (2004), Lücking et al. (2020), Miadlikowska et al. (2014), and Sobreira et al. (2018) in order to include an exhaustive list of taxa belonging to the family Porinaceae and the genus *Porina* s.l. The sequences were aligned using MAFFT v.7.402 (Katoh et al. 2002) on the CIPRES Web Portal (Miller et al. 2010) and manually corrected for errors using Mesquite v.3.04 (Maddison & Maddison 2015). Terminal ends of sequences, ambiguously aligned regions, and introns were delimited manually following Lutzoni

et al. (2000) and excluded from the dataset. *Coenogonium lepreurii* (Mont.) Nyl., *C. luteum* (Dicks.) Kalb & Lücking, and *C. pineti* (Ach.) Lücking & Lumbsch were selected as outgroup taxa based on Sobreira et al. (2018). The GTR+I+G best-fit evolutionary model was selected based on the Akaike Information Criterion (AIC) as implemented in jModelTest v.2.1.6 (Darriba et al. 2012) on the CIPRES Web Portal (Miller et al. 2010). Maximum Likelihood (ML) analysis was performed using RAxML v.8.2.12 (Stamatakis 2014) on the CIPRES Web Portal (Miller et al. 2010) with 1000 ML bootstrap iterations (ML-BS) and the GTRGAMMA model. The ML tree is shown with the ML-BS values added above or near the internal branches (fig. 1). Internodes with ML-BS ≥ 70 were considered to be significant. Phylogenetic trees were visualized using FigTree v.1.4.2 (Rambaut 2012).

## RESULTS

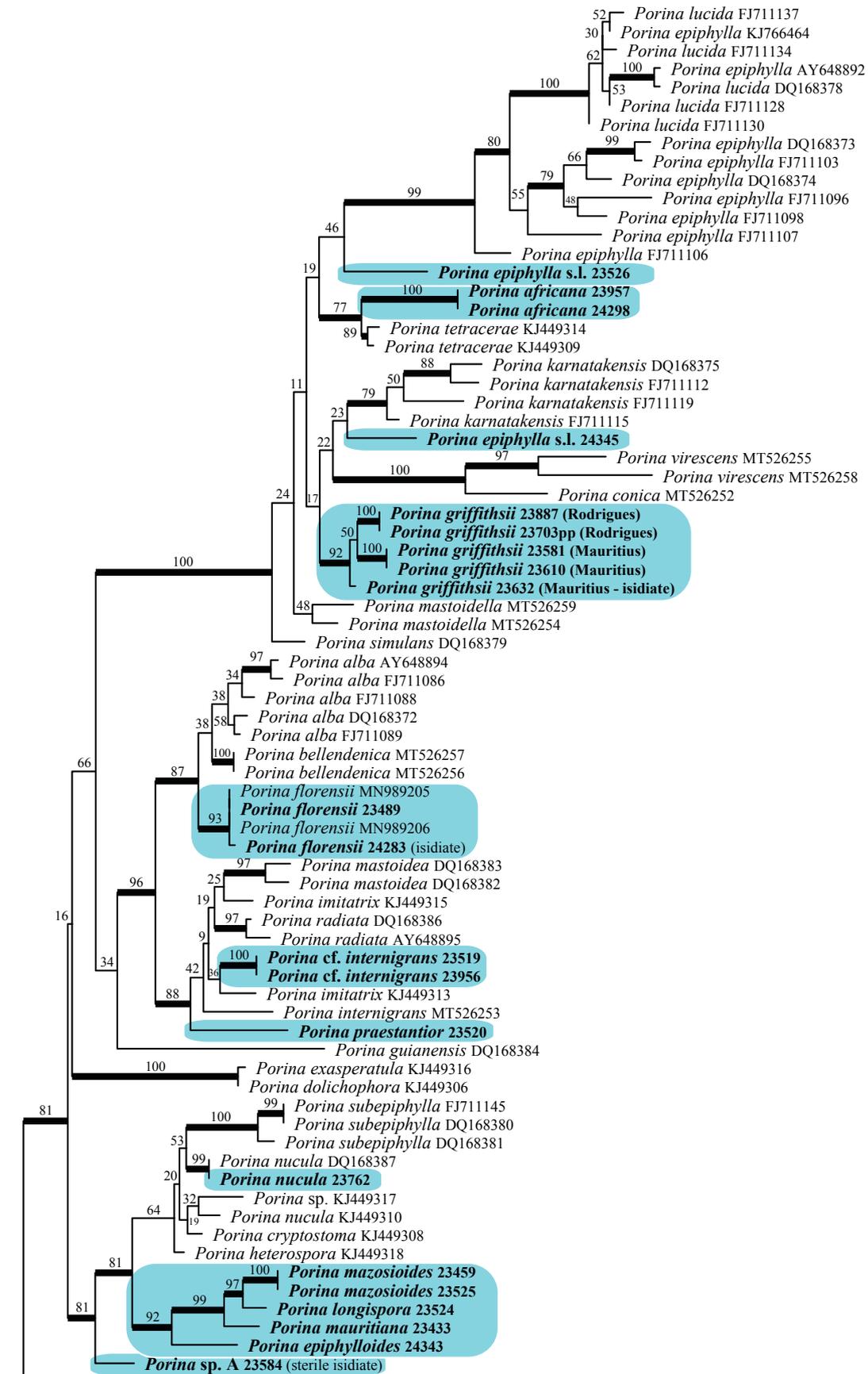
### Phylogenetic analysis

Partial mtSSU sequences were newly generated for 36 specimens of Porinaceae, belonging to 21 species. All were from Mauritius, except two that were sequenced for comparison with a newly described species (see under *P. covidii* in the taxonomy section below): *Porina borreii* (Trevis.) D.Hawksw. & P.James from Belgium and *P. cf. malmei* P.M.McCarthy from Madagascar (supplementary file 1). Eighty-nine additional sequences were retrieved from GenBank (fig. 1). The mtSSU matrix of Porinaceae consisted of 125 terminals and 594 unambiguously aligned sites. The RAxML tree obtained is shown in fig. 1. The main well-supported lineages are in accordance with the results obtained by Sobreira et al. (2018) and Orange et al. (2020). The nodes of the backbone of the tree are mainly poorly supported, not providing informative phylogenetic structure for the family. The genus *Porina* is recovered as paraphyletic, lineages being intermingled with those of the genera *Flabelloporina*, *Myeloconis*, *Saxiloba*, and *Trichothelium*. The newly prepared sequences are recovered in no less than eight main, strongly supported lineages.

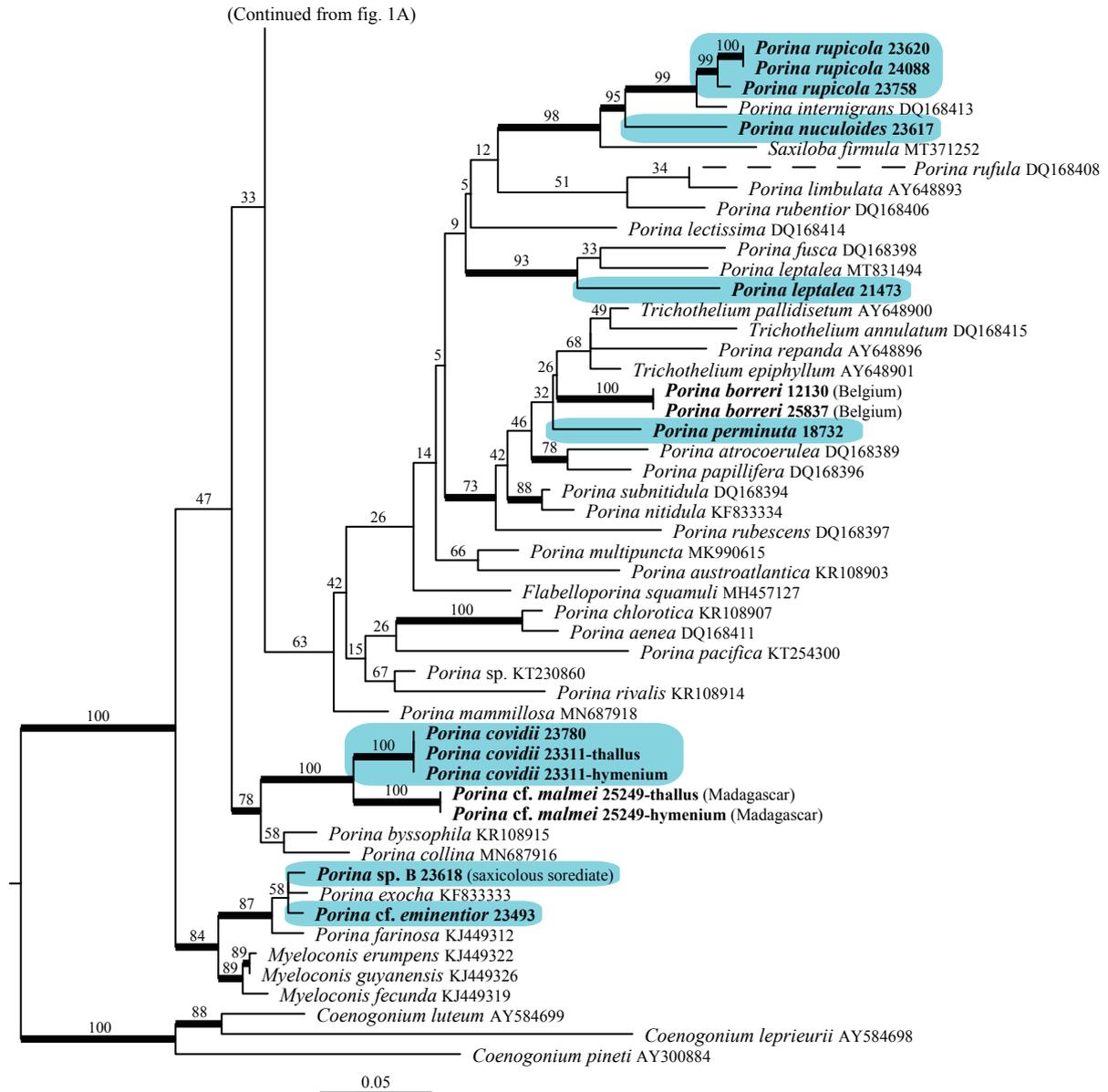
## TAXONOMIC TREATMENT

***Porina africana*** Müll.Arg. (Müller 1880: 41) (fig. 3A, C) – Type: ANGOLA • Quillu; *Pechuël-Lösche* 300; holotype: G[G00066036].

**Notes** – New to Mauritius. Pantropical. Our material fits well with the concept of *P. africana* by perithecial verrucae ca 0.5–1 mm diam., a thallus with a black basal layer and 7–8(–10)-septate ascospores (33–)40–54.5(–63) × 5–6.5(–7) µm (n = 59). It deviates from the description of McCarthy (2001, “perispore not apparent”) by ascospores often having a thin gelatinous sheath ca 1 µm wide. The periostiolar area is often dark brown to black as in the holotype of *P. africana*, but perithecia in *Ertz* 24306 lack a dark pigmentation suggesting that this character state may be variable within the species. The mtSSU sequences of *Ertz* 23957 and *Ertz* 24298 are identical and form a sister clade to two sequences obtained from Neotropical specimens of *Porina tetracerae* (KJ449309 from Costa Rica, KJ449314 from Panama) but



(Continued in fig. 1B)



◀▲ **Figure 1– A–B.** Phylogeny of the Porinaceae based on a data set of mtSSU sequences that resulted from a RAxML analysis. Maximum Likelihood bootstrap values are shown above or near the internal branches. Internal branches considered strongly supported are represented by thicker lines. The newly sequenced samples are in bold and their names followed by collecting numbers of authors, which act as specimen and sequence identifiers. Lineages corresponding to sequences obtained from Mauritian specimens are highlighted. The length of the branch represented by dashed lines was reduced by 50% for layout reasons.

appear distinct from them because of the long branches. *Porina tetracerae* differs by somewhat smaller perithecial verrucae (0.36–0.8 mm diam.) and shorter ascospores (24–44 µm) (McCarthy 2001). When the black basal layer of the thallus is apparent, specimens recall *P. internigrans*, but the ascospores of the latter are longer and much broader. Unfortunately, no sequences of *P. africana* (originally described from Angola) are available on GenBank for comparison with our data.

**Specimens examined** – MAURITIUS – **Rivière Noire District** • Black River Gorges National Park, along trail from Plaine Champagne towards Piton de la Petite Rivière Noire; 20°24'52"S (± 1000 m), 57°24'43"E (± 500 m); 630–800 m; dense evergreen montane forest, on bark of a trunk ca 20 cm diam.; 7 Sep. 2019; *Ertz 23957*; BR, MAU (TLC, solvent A: nil) • *ibid.*, 5 km NW of Pétrin, Brise Fer Forest; 20°22'40"S, 57°26'25"E (± 200 m); 585 m; on bark; 10 Sep. 2019; *Ertz 24298, 24306, 24324 & Diederich*; BR, MAU.

*Porina covidii* Ertz & Diederich, **sp. nov.** (fig. 2) – Type: MAURITIUS – **Moka District** • Réduit, State House Park; 20°13'44"S, 57°29'13"E (± 200 m); 280 m; on bark; 30 Aug. 2019; *Ertz 23311 & Diederich*; holotype: MAU; isotypes: BR[BR5030105436478].

Mycobank no: MB 841119

**Diagnosis** – This species resembles *Porina borrieri* (Trevis.) D.Hawksw. & P.James by its black perithecia not immersed in distinct thallus verrucae and its mainly 7-septate ascospores but differs by having asci without an apical ring like structure and (5–)5.5–7.5(–8) µm broad ascospores that are at most 5.5 µm broad in *P. borrieri*.

**Description** – **Thallus** mostly epiphloeodal, continuous to rimose, smooth to slightly rugulose, matt, pale to dark greyish green to brownish green, thin ca 25–90(–125) µm thick, without crystals of calcium oxalate, without a black basal layer; prothallus non-apparent; isidia and soralia absent. Photobiont trentepohlioid; cells spherical ca 5–8 µm diam. or slightly elongated 8–10 × 5–7 µm. **Ascomata** perithecioid, solitary, rarely two or three contiguous, dispersed, subglobose, black, smooth, 150–260(–280) µm diam., the base to ca 2/3 of the perithecia immersed in the thallus, without forming distinct thallus verrucae; ostiole apical, inconspicuous; crystallostratum absent. **Proper excipulum** hyaline to pale brown, fused with the involucrellum in ± the upper half to 2/3, ca 15–20 µm below. **Involucrellum** dark reddish brown to carbonized, ca 30–40 µm thick, often extending down to the base of the perithecium, except in perithecia that are strongly immersed in the thallus where the involucrellum might extend only to 1/3 of the perithecia, K– or becoming darker (reddish brown pigment disappearing). **Hamathecium** hyaline, not interspersed, of thin, simple, 1–1.5 µm diam. paraphyses, 110–160 µm tall; subhymenium pale fawn, 7–13 µm thick. **Asci** cylindrical-clavate to ± fusiform, I–, ca 80–105 × 15–17 µm (n = 4), 8-spored; ascus apex rounded, without a ring structure. **Ascospores** hyaline, I–, transversely (5–)7-septate, elongate-fusiform to ± oblong, (20–)22.5–28.5(–32) × (5–)5.5–7.5(–8) µm, ratio L/B (3.5–)3.5–4(–4.5) (n = 25); gelatinous sheath usually poorly

visible, ca 2–3 µm thick. **Pycnidia** not observed. Chemistry: thallus K–, C–, KC–, PD–, UV–. TLC not performed.

**Distribution and ecology** – The species is known from two localities in Mauritius, where it inhabits the bark of trees in rather open forests including parklands, at low elevation (ca 280–360 m). It is probably also present in the Seychelles (Schumm & Aptroot 2010, sub. *P. borrieri* (Trevis.) D.Hawksw. & P.James).

**Etymology** – The epithet refers to the Coronavirus disease of 2019 (COVID-19). The new species was described during the COVID-19 pandemic.

**Notes** – Our material is similar to specimens identified as *Porina borrieri* from the Seychelles (Schumm & Aptroot 2010). However, *P. borrieri* differs from our Mauritian specimens in having asci with an apical ring structure and distinctly narrower ascospores: (3–)4.5–5(–5.5) µm for Great Britain and Ireland (Orange et al. 2009) and 3–5 µm for continental Europe (Sérusiaux et al. 2007). Moreover, *P. borrieri* and the new species are not related in our phylogenetic analyses (fig. 1), clearly supporting two different taxa. Among the saxicolous species keyed out by McCarthy (1993) for the Southern Hemisphere, *Porina malmei* P.M.McCarthy, described from Brazil, is similar in size to the perithecia and ascospores, but it differs in its saxicolous habit, a medium brownish grey thallus and a brown-black proper excipulum. We recently collected and sequenced a saxicolous specimen similar to *Porina malmei* in Madagascar, although our specimen differs in having a greenish thallus. In our phylogenetic tree, the latter is the sister species to *P. covidii*, but is phylogenetically distinct (long branches). *Porina subchlorotica* (Nyl.) Müll.Arg., known only from New Caledonia, is also similar but differs by larger (ca 300–400 µm diam.) perithecia and narrower ascospores (25–30 × 5–6 µm) (Nylander 1868). Among the similar Australian bryophilous or corticolous taxa reported by McCarthy (2001), only *Porina bryophila* P.M.McCarthy & Kantvilas is somewhat similar, but that species differs in having longer and narrower ascospores, 26–38 × 3–5.5 µm. Among the species reported by Harris (1995) for Florida and Cáceres (2007) for north-eastern Brazil, *Porina cestrensis* (Tuck.) Müll.Arg. (sub. *Trichothelium cestrense*) differs in having much longer ascospores, (32–)38–50 × 5.5–7.5 µm. Using the key of the corticolous and saxicolous species of *Porina* of Japan (Harada 2015, 2016), our material would be identified as *P. guentheri* (Flot.) Zahlbr., but that species differs by its saxicolous habit, larger perithecia (0.15–0.4 mm diam. in Harada 2016; 0.23–0.48 mm diam. in McCarthy 1993) and longer ascospores (27–42 µm in Harada 2016; 22.5–49 µm in McCarthy 1993), and is considered to be a predominantly antitropical species (McCarthy 1993).

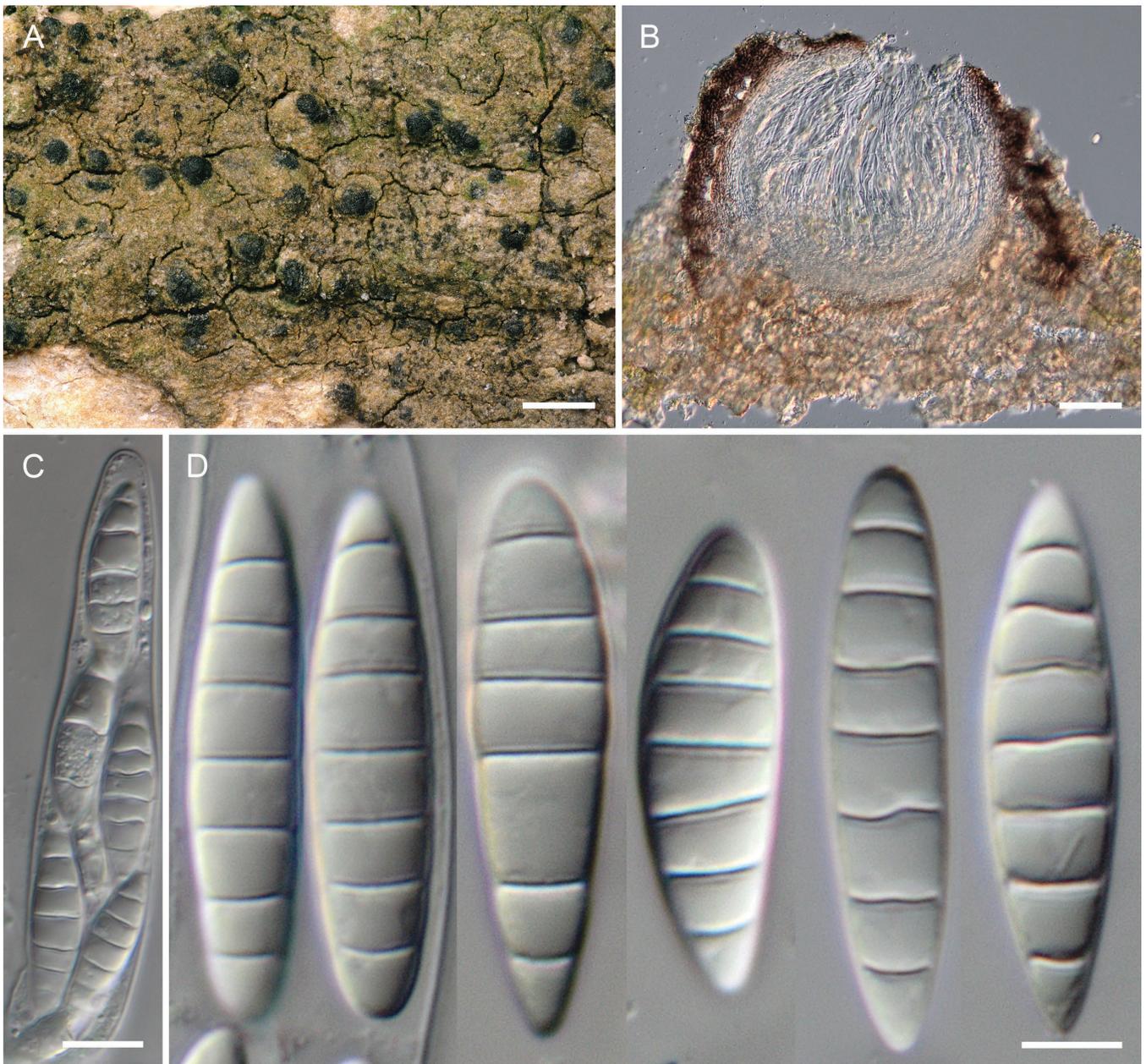
**Additional specimen examined** – MAURITIUS – **Rodrigues District** • Grande Montagne Nature Reserve; 19°42'22"S, 63°27'52"E (± 300 m); 330–360 m; on bark; 4 Sep. 2019; *Ertz 23780 & Diederich*; BR.

*Porina* cf. *eminentior* (Nyl.) P.M.McCarthy (Nylander 1861: 54) (fig. 3B, D) – Type: NEW CALEDONIA • ‘ad corticem

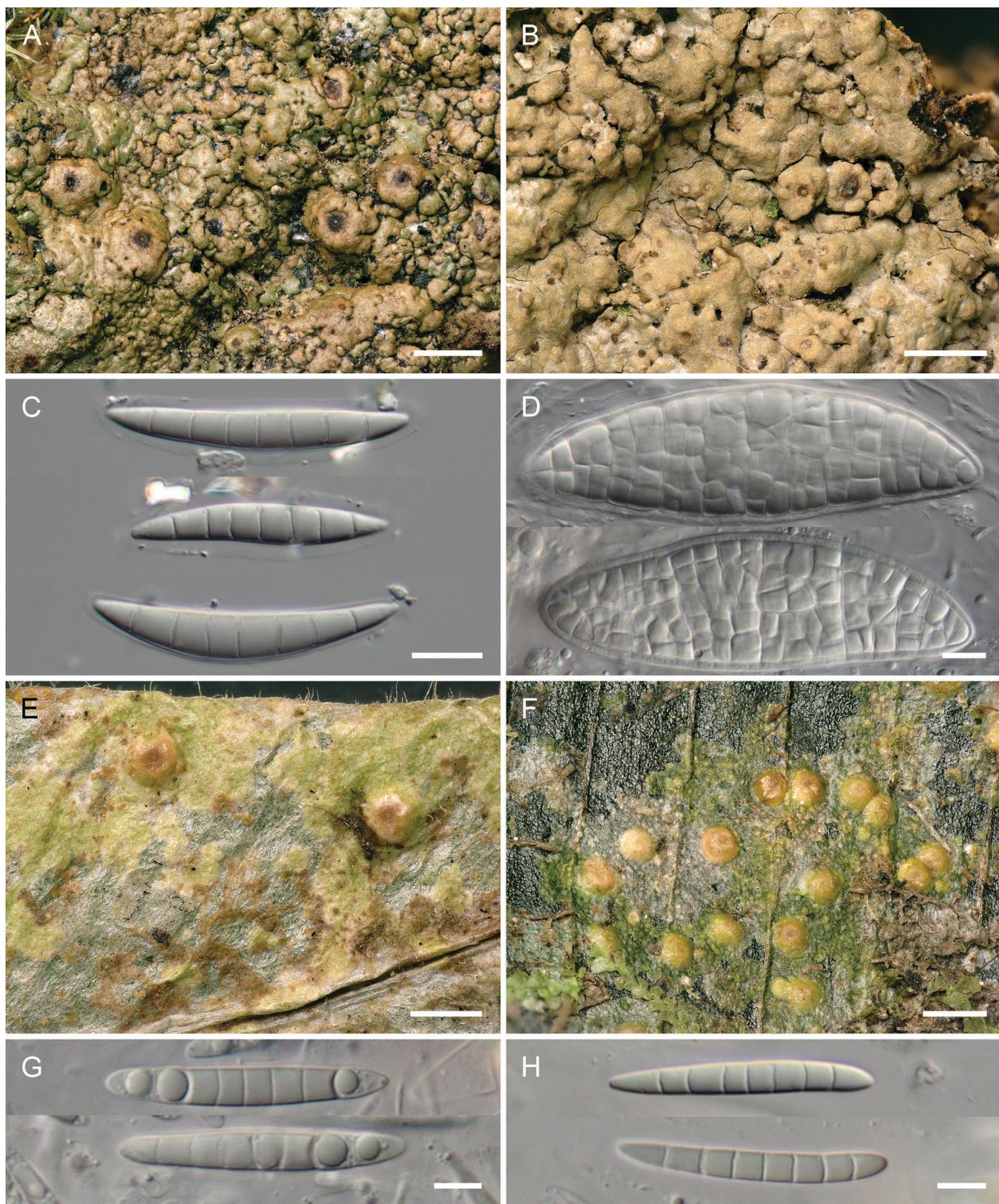
(*Baloghiae drupaceae?*); *Pancher s.n.*; holotype: H-NYL 1580 [H9505668].

**Notes** – New to Mauritius. Pantropical. The morphology of our specimens is somewhat intermediate between *Porina eminentior* and *P. farinosa* C.Knight. McCarthy (2001) already reported intermediate and often unidentifiable specimens, *P. farinosa* differing from *P. eminentior* only by its perithecia that tend to be more prominent and by its larger and more divided ascospores. In our material, the perithecia are weakly prominent, 0.65–0.8 mm diam., and better fit those of *P. eminentior*. The ascospores are ca 16–23 × 3–6 septate and 69–107 × 20–34 μm, and better fit those of *P. farinosa* by being slightly broader and having more

longitudinal septa according to the descriptions in McCarthy (2001): 12–22 × (1–)2–3(–4) septate, 42–109 × 13–29 μm in *P. eminentior*; 17–30 × (1–)2–4(–6) septate, 58–148 × 18–41 μm in *P. farinosa*. Therefore, we attribute our material to *P. eminentior* with some hesitation. In our phylogenetic tree, specimen 23493 groups with *P. exocha* (Nyl.) P.M.McCarthy and *P. farinosa*, but appears different from both. *Porina exocha* differs by having larger perithecial verrucae (0.7–1.5 mm) and larger ascospores (68–168 × 20–45 μm) with a perispore with persistent hyaline apical caps (McCarthy 2001). Unfortunately, no sequences of *P. eminentior* were available on GenBank.



**Figure 2** – *Porina covidii*. **A.** Thallus and perithecia. **B.** Section of a perithecium in water. **C.** Ascus in water. **D.** Ascospores in water. A–D from Ertz 23311 (BR). Scale bars: A = 0.5 mm, B = 50 μm, C = 10 μm, D = 5 μm.



**Figure 3** – Habit and ascospores (in water) of *Porina* species from Mauritius. **A, C.** *Porina africana*. **B, D.** *P. cf. eminentior*. **E, G.** *P. epiphylla* s.l. **F, H.** *P. epiphyloides*. **A, C** from Ertz 23957 (BR). **B** from Ertz 23493 (BR). **D** from Ertz 23703 (BR). **E** from Ertz 23526 (BR). **G** from Ertz 24345 (BR). **F, H** from Ertz 24343 (BR). Scale bars: A–B = 1 mm, E–F = 0.5 mm, C–D = 10 µm, G–H = 5 µm.

**Specimens examined** – MAURITIUS – **Rodrigues District** • Grande Montagne Nature Reserve; 19°42'22"S (± 300 m), 63°27'52"E (± 300 m); 330–360 m; over saxicolous mosses; 4 Sep. 2019; *Ertz 23703 pp & Diederich 19023*; BR, MAU. – **Savanne District** • Black River Gorges National Park, along trail to Mt Cocotte; 20°26'30"S (± 200 m), 57°28'16"E (± 500 m); 720–750 m; on bark; 1 Sep. 2019; *Ertz 23493 & Diederich*; BR, MAU (TLC, solvent A: nil).

*Porina epiphylla* (Fée) Fée s.l. (Fée 1825: 76) (fig. 3E, G) – Type: FRENCH GUIANA • ?*Leprieur s.n.*; lectotype: PC, designated by Santesson (1952: 234).

**Notes** – *Porina epiphylla* is a common and widely distributed species in the tropics. It has been reported from Mauritius on the fern *Acrostichum obductum* (S F74625) by Santesson (1952: 238). Our specimen 24345 is minute with perithecia having a ± dark brown periostiolar area. It probably does not belong to *P. epiphylla* s.s., but possibly to *P. atriceps* (Vain.) Vain. The latter taxon was regarded as a variety of *P. epiphylla* by Santesson (1952), but accepted as a distinct species by Lücking & Vězda (1998). In our specimen, the photobiont cells are angular-rounded, irregularly arranged, and the ascospores are 7-septate, 28–35(–38) × 3–4 µm. However, our specimen is too scanty, and more material is needed to resolve its identity and possibly confirm the presence of *P. atriceps* in Mauritius. The second specimen (23526) is more typical for *P. epiphylla* but has ascospores of 31–36 × 3.5–4 µm, thus slightly longer than those mentioned by Lücking & Vězda (1998; 26–32 µm long). It might better fit *P. karnatakensis* Makhija, Adawadkar & Patwardhan, but that species should have a black dot around the ostiole although becoming paler in old perithecia (Lücking 2008). In our phylogeny, the mtSSU sequences of our specimens do not group together, suggesting two different taxa, nor with those of the large clade of *P. epiphylla* from the Neotropics, indicating that our specimens belong to other taxa and that *P. epiphylla* s.s. might be absent from Mauritius. More material is needed to resolve the identity of the Mauritian taxa, as well as further molecular studies of the *Porina epiphylla*-group.

**Specimens examined** – MAURITIUS – **Rivière Noire District** • Black River Gorges National Park, 5 km NW of Pétrin, Brise Fer Forest; 20°22'40"S, 57°26'25"E (± 200 m); 585 m; on leaf of epiphytic fern; 10 Sep. 2019; *Ertz 24345 & Diederich*; BR, MAU. – **Savanne District** • Black River Gorges National Park, along trail to Mt Cocotte; 20°26'30"S (± 200 m), 57°28'16"E (± 500 m); 720–750 m; on leaves; 1 Sep. 2019; *Ertz 23526 & Diederich*; BR, MAU.

*Porina epiphyloides* Vězda (Vězda 1975: 393) (fig. 3F, H) – Type: TANZANIA • SW slope of Rwunge volcano; 1800–1900 m; Aug. 1972; *Pócs 6762*; holotype: PRA.

**Notes** – New to Mauritius. Palaeotropical, known notably from tropical East Africa and the Comoros (Lücking & Vězda 1998). Our specimen is typical for the species in having a verrucose thallus, small perithecia (0.2–0.35 mm diam.) and small 7-septate ascospores, ca 25–28 × 3–3.5 µm.

**Specimen examined** – MAURITIUS – **Rivière Noire District** • Black River Gorges National Park, 5 km NW of Pétrin, Brise Fer Forest; 20°22'40"S, 57°26'25"E (± 200 m);

585 m; on leaf of epiphytic fern; 10 Sep. 2019; *Ertz 24343 & Diederich*; BR, MAU.

*Porina florensii* Diederich & Ertz (Diederich & Ertz 2020: 53) (fig. 5A, C) – Type: MAURITIUS – **Rivière Noire District** • Black River Gorges National Park; trail from Plaine Champagne towards Piton de la Petite Rivière Noire; 20°25'17"S (± 200 m), 57°25'10"E (± 700 m); 630–700 m; on bark of trees; 5 Aug. 2016; *Diederich 18453*; holotype: MAU; isotype: BR.

**Notes** – Endemic to Mauritius. This species was recently described as fertile and non-isidiate (Diederich & Ertz 2020). Fertile specimens with isidia were collected by us in Brise Fer Forest, and our phylogeny supports their inclusion in *P. florensii*. The mitochondrial sequence of the isidiate specimen (*Ertz 24283*) differs from the non-isidiate ones by only three nucleotides. Our morphological and phylogenetic results suggest that isidia do not represent an important taxonomic character at the species level in the genus *Porina*.

*Porina* cf. *americana* was reported from Mauritius by Crittenden et al. (1995), and the same specimen was reported as *Porina mastoidea* agg. by David & Hawksworth (1995). The specimen (Plaines Wilhems, Vacoas, Macchabee Forest, on *Diospyros tesselaria*, 1990, Hawksworth (K-IMI 400613)) was revised and found to be *Porina florensii*. According to Lücking (2008), *P. americana*, first described from Cuba, resembles *P. nucula* in outward appearance, but it differs in having larger ascospores with more numerous septa. Moreover, it differs from *P. florensii* by a verrucose thallus, wart-shaped to subglobose, mature perithecia lacking a black periostiolar area and shorter and broader ascospores (65–80 × 15–20 µm in *P. americana*; 86–120 × 10.5–14 µm in *P. florensii*). None of our specimens match this species concept. *Porina mastoidea* differs from *P. florensii* by 7(–8)-septate and much smaller (32–66 × 6–13 µm) ascospores.

**Non-isidiate specimens examined** (see also Diederich & Ertz 2020 for 11 additional specimens including the type) – MAURITIUS – **Plaines Wilhems District** • Curepipe, Curepipe Botanic Gardens; 20°19'30"S, 57°30'50"E (± 200 m); 565 m; on bark; 9 Sep. 2019; *Ertz 24200 & Diederich*; BR, MAU. – **Rivière Noire District** • Black River Gorges National Park, along trail from Plaine Champagne towards Piton de la Petite Rivière Noire; 20°24'52"S (± 1000 m), 57°24'43"E (± 500 m); 630–800 m; dense evergreen montane forest; on bark; 7 Sep. 2019; *Ertz 23930, 24033*; BR, MAU • *ibid.*, 5 km NW of Pétrin, Brise Fer Forest; 20°22'40"S, 57°26'25"E (± 200 m); 585 m; on bark; 10 Sep. 2019; *Ertz 24292, 24305, 24307 & Diederich*; BR, MAU. – **Savanne District** • Black River Gorges National Park, along trail to Mt Cocotte; 20°26'30"S (± 200 m), 57°28'16"E (± 500 m); 720–750 m; on bark; 1 Sep. 2019; *Ertz 23489 & Diederich*; BR, MAU.

**Isidiate specimens examined** – MAURITIUS – **Rivière Noire District** • Black River Gorges National Park, 5 km NW of Pétrin, Brise Fer Forest; 20°22'40"S, 57°26'25"E (± 200 m); 585 m; on bark; 10 Sep. 2019; *Ertz 24283* (TLC nil, solvent A), *24297 p.p. & Diederich* (sub *P. griffithsii*); BR, MAU.

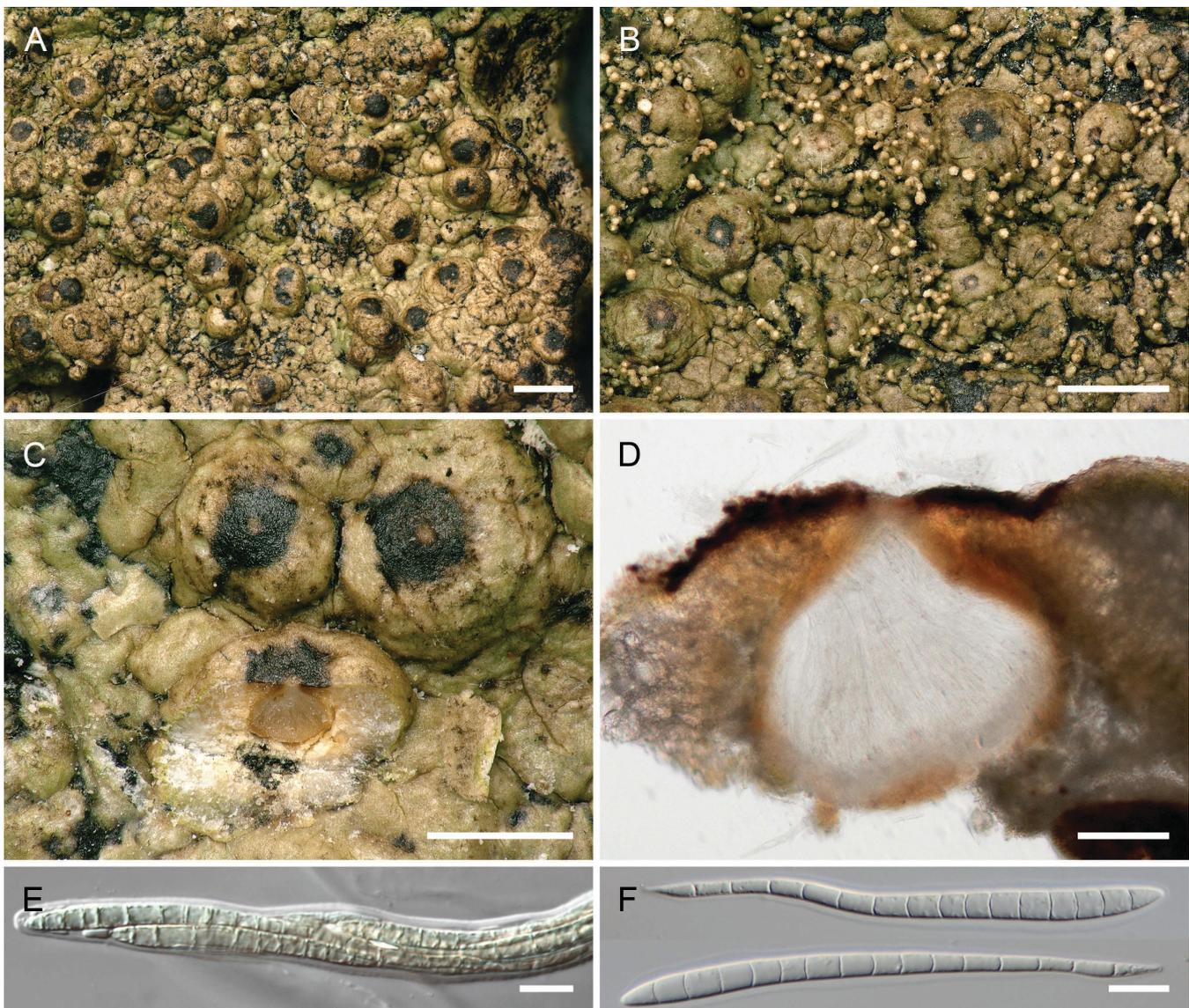
*Porina griffithsii* Ertz & Diederich, sp. nov. (fig. 4) – Type: MAURITIUS – Rivière Noire District • Chamarel, Ebony Forest, along the trail west of the viewpoint; 20°25'53"S (± 100 m), 57°22'21"E (± 300 m); 330–350 m; on the bark of *Diospyros*; 2 Sep. 2019; Ertz 23581 & Diederich; holotype: MAU; isotypes: BR[BR5030105681434], hb. Diederich.

**Mycobank no:** MB 841120

**Diagnosis** – This species resembles *Porina dolichophora* (Nyl.) Müll.Arg. by its perithecia immersed in hemispherical to subglobose, ± well-delimited thalline verrucae ca (0.5–)0.7–1 mm diam. and by its mainly 12–15-septate ascospores but differs by its dark brown to black periostiolar area, by having slightly narrower (3.5–)4–5.5(–6.5) µm ascospores and by having an isolated phylogenetic position.

**Description** – Thallus epiphloeodal, continuous to rimose, mostly verrucose, matt to slightly glossy, pale green,

creamish green to pale brownish, thin ca 100–160 µm, containing numerous large crystals of calcium oxalate ca 10–35 µm diam., with a thin black basal layer; rarely with few to many short, simple or shortly branched isidia, ca 200–250 × 80–120 µm concolorous with the thallus; soralia absent. Photobiont trentepohlioid. Ascomata perithecioid, solitary, rarely two contiguous, dispersed, immersed in hemispherical to subglobose, ± well-delimited verrucae ca (0.5–)0.7–1 mm diam., with a thick thallus layer; ostiole apical, rather inconspicuous; periostiolar area dark brown to black, ca 100–300(–400) µm diam., forming a superficial thin layer ca 12–18 µm thick; crystallostratum of calcium oxalate crystals (H<sub>2</sub>SO<sub>4</sub>!) well developed, ca 175–250 µm thick. Excipulum pale yellowish orange, ca 14–20 µm, K+ reddish. Hamathecium hyaline, not interspersed, of thin, simple, 1–1.5 µm diam. paraphyses. Asci narrowly obclavate to cylindrical-clavate, 1–, ca 138–174 × 11.5–16 µm (n = 7),



**Figure 4** – *Porina griffithsii*. A. Thallus and perithecia. B. Isidiate fertile thallus. C. Perithecia, including one sectioned perithecium. D. Section of a perithecium in water. E. Ascus in Lugol's iodine. F. Ascospores in water. A, C, D, F from Ertz 23581 (BR). B from Ertz 23632 (BR). E from Diederich 18936 (BR). Scale bars: A–B = 1 mm, C = 0.5 µm, D = 100 µm, E–F = 10 µm.

8-spored; ascus apex slightly truncate, with a ring structure. *Ascospores* hyaline, I-, transversely (9–)12–15(–17)-septate, elongate-fusiform to ± filiform, often tapering towards one end, (54–)64.5–87(–100) × (3.5–)4–5.5(–6.5) µm, ratio L/B (10–)13–20(–30) (n = 50); gelatinous sheath ca 1 µm thick. *Pycnidia* not observed. Chemistry: thallus K-, C-, KC-, PD-, UV-. No substances detected by TLC in specimens Ertz 23581, 23887 (solvent A).

**Distribution and ecology** – The species is known from three localities in Mauritius and two in Rodrigues, where it inhabits the bark of trees (e.g. *Diospyros*) in lowland and upland rainforests (ca 330–670 m).

**Etymology** – The new species is dedicated to Owen Griffiths, owner of Ebony Forest (type locality of the new species), for his efforts in the conservation of biodiversity of this tropical forest and other sites in the Indian Ocean.

**Notes** – *Porina dolichophora* (Nyl.) Müll.Arg. is very similar in the size of the perithecial thallus-dominated verrucae, (0.52–)0.83(–1.1) mm diam., and the 13–21-septate ascospores, (62–)84(–109) × (5–)6(–7) µm (McCarthy 1993: 48), but the ascospores are slightly wider than in the new species, and a large black periostiolar area is rarely observed in *P. dolichophora* (two type specimens from BR examined; photos of the lectotype of *P. dolichophora* on JSTOR: <https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.h9505781>). In our phylogenetic tree, the new species is part of a large clade from *Porina simulans* to *P. epiphylla*, while *P. dolichophora* forms a different and distantly related lineage with the very similar *P. exasperatula*, supporting the fact that it represents a different species. The saxicolous *P. exserta* Müll.Arg. has shorter ascospores (44–)57(–70) × (3.5–)4.5(–5.5) µm, (11–)15–17(–21)-septate, and the perithecial verrucae are devoid of a dark periostiolar area (McCarthy 1993). Amongst the similar Australian corticolous taxa keyed out by McCarthy (2001), two species have more than 7-septate ascospores: *Porina bellendenica* Müll.Arg. has much shorter, (9–)11–13(–15)-septate ascospores, 32–56 × 3–5 µm, and *P. internigrans* (Nyl.) Müll.Arg. has shorter and broader, (7–)9–11(–13)-septate ascospores, 51–92 × 9–17 µm with a 2–4 µm thick perispore. *Porina raphidiophora* (Nyl.) Müll.Arg., described from New Caledonia, differs by much smaller perithecia (0.26–0.48 mm diam.) not immersed in thallus verrucae, a thick greenish black involucrellum often extending to the exciple base level, and smaller, 9–11(–15)-septate ascospores, 41–72.5 × 2–4 µm (McCarthy 1994b). *Porina meridionalis* P.M.McCarthy from Tasmania differs in its much smaller perithecia (0.27–0.43 mm diam.), more septate (11–21-septate) and much broader (6–9.5 µm) ascospores (McCarthy 1994a). Among the non-foliicolous species keyed out by Awasthi (1991) for India, Nepal, and Sri Lanka, no species has more than 11-septate ascospores. Amongst the species keyed out by Harris (1995) for Florida, *Porina heterospora* (Fink) R.C.Harris has (9–)11–13-septate and much broader ascospores, 85–110 × 12–14 µm; it was considered to be a synonym of *P. guaranitica* Malme by McCarthy (1993), a species described from rocks, but the latter differs by 57–71 µm long ascospores with a mean number of 9.5 septa according to the revision of its lectotype by Harris (1995). *Porina raphidosperma* Müll.Arg. has rather similar but longer ascospores (13–20-septate, 100–140

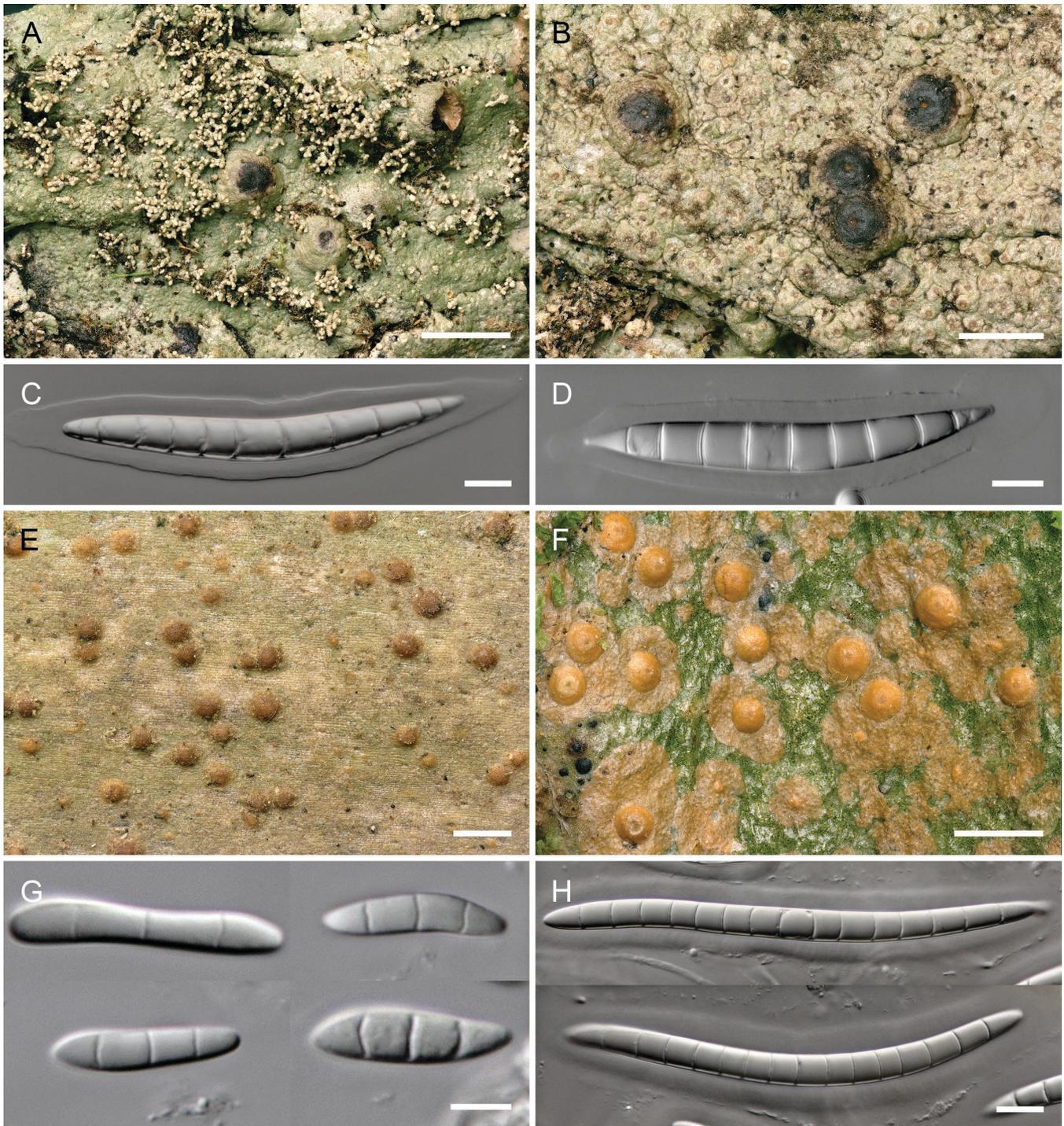
× 3–5 µm according to Harris 1995, under *Trichothelium raphidospermum* (Müll. Arg.) R.C.Harris), but differs from the new species notably by smaller (0.3 mm according to the original description by Müller 1895) and black perithecia not covered by a thallus layer. *Porina filispora* Lücking has similar ascospores but differs in having smaller (0.3–0.6 mm diam.) perithecia, a periostiolar area concolorous with the thallus and a foliicolous habit (Lücking 2008).

Our phylogenetic results show that the non-isidiate specimens from the islands of Mauritius and Rodrigues form distinct lineages suggesting an insular isolation of the populations. However, few specimens have been included in our analyses and the two specimens from Mauritius come from the same locality. Moreover, the isidiate specimen from the island of Mauritius does not cluster with these latter collections, having an early diverged position with low support. Therefore, we prefer to adopt a broad phylogenetic concept of the species despite the diverged haplotypes, and also to include the isidiate specimen in this species concept. A larger sampling from Mauritius and the Mascarenes would be interesting in order to investigate the genetic variability within our concept of *P. griffithsii*. Ascospores in the Mauritius material are (54–)62.9–85.3(–95) × (3.5–)3.8–4.6(–5) µm (n = 37), and in the Rodrigues material (60–)69.8–90.3(–100) × (3.3–)4.5–6.2(–6.6) µm (n = 13), thus slightly broader in the latter.

**Additional specimens examined** (non-isidiate, otherwise mentioned) – MAURITIUS – **Plaines Wilhems District** • Black River Gorges National Park, Le Pétrin, between Pétrin Information Centre and first viewpoint along trail to the west; 20°24'06"S (± 300 m), 57°27'43"E (± 1000 m); 640–670 m; on bark; 31 Aug. 2019; Ertz 23416 & Diederich; BR, MAU. – **Rivière Noire District** • Black River Gorges National Park, 5 km NW of Pétrin, Brise Fer Forest; 20°22'40"S, 57°26'25"E (± 200 m); 585 m; on bark; 10 Sep. 2019; Ertz 24297 pp. & Diederich 19425; BR, MAU • Ebony Forest (same locality as the type); on bark of *Diospyros*; 2 Sep. 2019; Ertz 23606, 23610 & Diederich 18936; BR, MAU • *ibid.*, SW part of forest; 20°26'13"S, 57°22'06"E (± 50 m); 345 m; on bark of *Diospyros*, 2 Sep. 2019; Ertz 23632 (fertile and isidiate), 23635 & Diederich; BR, MAU. – **Rodrigues District** • Grande Montagne Nature Reserve; 19°42'22"S, 63°27'52"E (± 300 m); 330–360 m; over saxicolous mosses; 4 Sep. 2019; Ertz 23703 p.p. & Diederich; BR, MAU • SE of Mont Lubin, Mont Limon, along the trail to the top; 19°42'25"S (± 200 m), 63°26'47"E (± 50 m); 360–390 m; 5 Sep. 2019; Ertz 23887 & Diederich 19031; BR, MAU.

*Porina* cf. *internigrans* (Nyl.) Müll.Arg. (Nylander 1868: 128) (fig. 5B, D) – Type: NEW CALEDONIA • Loyalty Island [Lifu]; 1864; *Déplanche s.n.*; holotype: H-NYL 1911 [H9505755].

**Notes** – According to McCarthy (2001), *P. internigrans* has (7–)9–11(–13)-septate ascospores (mainly 9-septate according to the identification key), 51–92 × 9–17 µm, with a 2–4 µm thick perispore. Our specimens fit rather well the concept of *P. internigrans* by the (7–)9-septate ascospores 72–83 × (8–)9–10 µm. In our phylogenetic tree, they group with a specimen of *P. internigrans* from China with low support. Another specimen of *P. internigrans* from Costa



**Figure 5** – Habit and ascospores (in water) of *Porina* species from Mauritius. **A.** Isidiate thallus of *Porina florensii*. **C.** Ascospore of *Porina florensii*. **B., D.** *P. cf. internigrans*. **E., G.** *P. leptalea*. **F., H.** *P. longispora*. **A., C** from Ertz 24283 (BR). **B** from Ertz 23956 (BR). **D** from Ertz 23519 (BR). **E., G** from Ertz 21473 (BR). **F., H** from Ertz 23967 (BR). Scale bars: **A** = 2 mm, **B, F** = 1 mm, **E** = 0.5 mm, **C–D, H** = 10  $\mu\text{m}$ ; **G** = 5  $\mu\text{m}$ .

Rica (DQ168413) is part of another clade where it is sister to *P. rupicola*, leaving doubts about the correct phylogenetic position of the species.

**Specimens examined** – MAURITIUS – **Rivière Noire District** • Black River Gorges National Park, along trail from Plaine Champagne towards Piton de la Petite Rivière Noire; 20°24'52"S (± 1000 m), 57°24'43"E (± 500 m); 630–800 m; dense evergreen montane forest; on bark; 7 Sep. 2019; *Ertz 23956*; BR, MAU. – **Savanne District** • Black River Gorges National Park, along trail to Mt Cocotte; 20°26'30"S (± 200 m), 57°28'16"E (± 500 m); 720–750 m; on bark; 1 Sep. 2019; *Ertz 23519 & Diederich*; BR, MAU.

*Porina leptalea* (Durieu & Mont.) A.L.Sm. (Durieu & Montagne 1848: 268) (fig. 5E, G) – Type: ALGERIA • ‘in caulibus siccis semiputridisque *Rusci hypoglossi*’; *s.col. s.n.*; holotype: PC.

**Notes** – New to Mauritius. A widespread species in temperate regions of both hemispheres, occasional in the tropics (McCarthy 2001). Only few ascospores were observed in five examined perithecia of our specimen, but they fit well with the species concept, although being on the lower end of the range for width: 3-septate, 13–20 × 3–3.5 µm (3.5–5 µm broad according to Orange et al. (2009) for Great Britain and Ireland, but 2–4(–5) µm broad according to McCarthy (2001) for Australia). In our phylogenetic tree, the Mauritian specimen clusters with a sample of *P. leptalea* from Belgium and *P. fusca* Lücking, but it appears to be distinct, suggesting a pronounced genetic diversity within the *P. leptalea* species concept. This deserves further study using a larger sample size from tropical and temperate regions.

**Specimen examined** – MAURITIUS – **Pamplemousses District** • Jardin Botanique Sir Seewoosagur Ramgoolam; 20°06'21"S, 57°34'49"E; 80 m; on bark of *Dypsis lutescens*; 29 Dec. 2016; *Ertz 21473*; BR, MAU.

*Porina longispora* Vězda (Vězda 1975: 394) (fig. 5F, H) – Type: TANZANIA • Tanga, East Usambara Mountains, near Amani; 1000 m; submontane rain forest; 29 Dec. 1969; *Pócs 6097*; holotype: PRA! [PRA-V-13586].

**Notes** – New to Mauritius, where it was collected on epiphytic ferns and leaves of shrubs in two montane forests at 630–800 m elev. The species was described from Tanzania (Vězda 1975) and reported from Australia (Sipman 1991 as “cf.”; Lücking et al. 2001; McCarthy 2001). Our specimens fit well *P. longispora* in having a delicately verrucose thallus, the photobiont with rectangular cells in distinctly radiate rows, the size of ascomata, ca 0.5–0.8 mm diam. (vs 0.5–0.6 mm), and the (10–)12–15(–16)-septate ascospores 79–110 × (6–)7 µm (n = 10) (vs 15-septate, 80–100 × 6–9 µm). Our specimens deviate slightly from the holotype of *P. longispora* (*Pócs 6097*, PRA-V-13586) by having immature ascomata more lens-shaped rather than hemispherical and by being less wart-shaped when mature. Ascospores in our specimens have a thick, gelatinous sheath 6–10 µm in water. A pronounced halo was also reported by Sipman (1991), while this character was not described in the original description (Vězda 1975; Lücking & Vězda 1998). In our phylogenetic tree, *P. longispora* is sister to *P. mazosioides*. Lücking &

Vězda (1998: 208) suggested that *P. longispora* was most closely related to that species based on morphological grounds, differing from it only in the much longer, 15-septate ascospores.

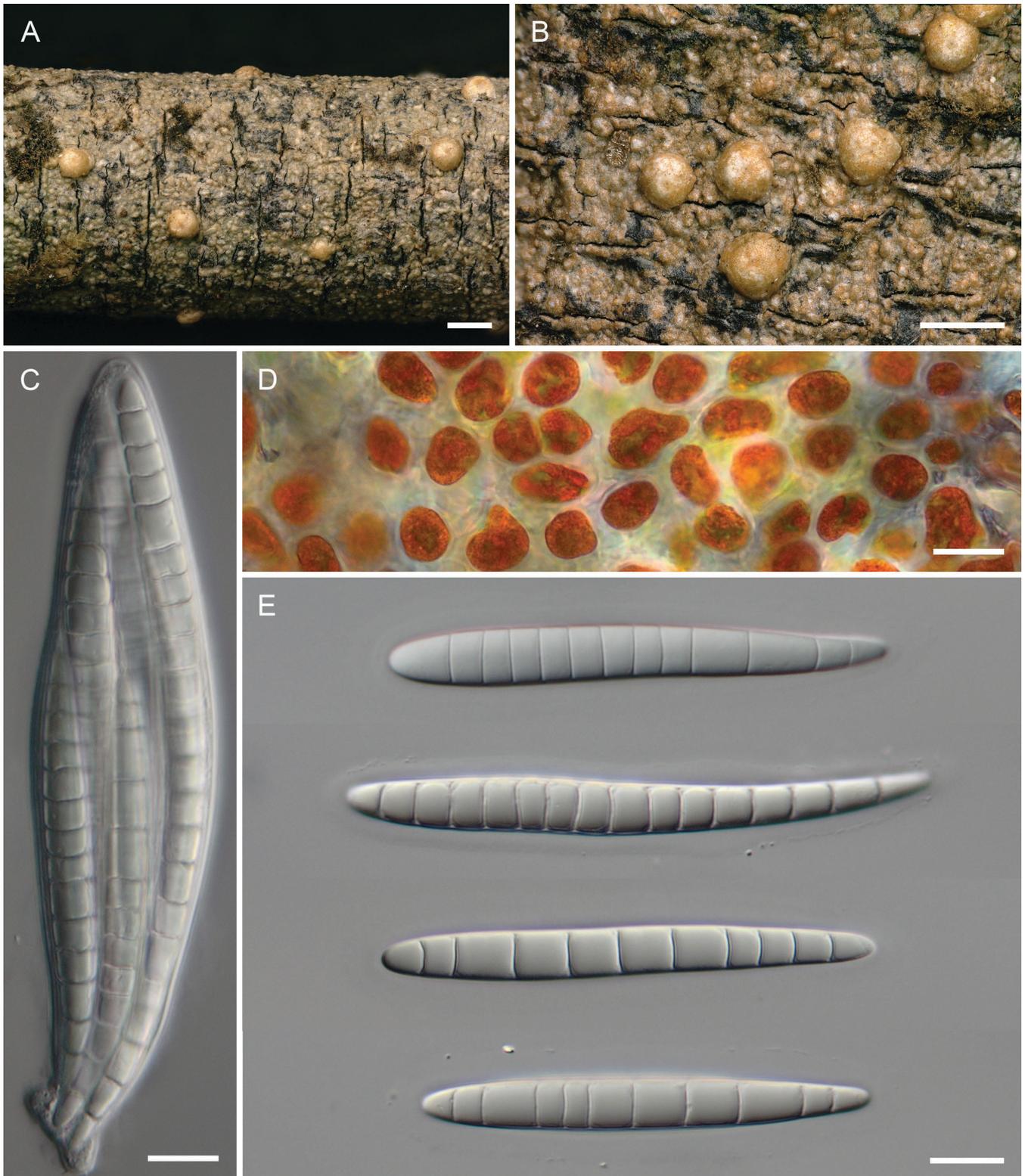
**Specimens examined** – MAURITIUS – **Rivière Noire District** • Black River Gorges National Park, along trail from Plaine Champagne towards Piton de la Petite Rivière Noire; 20°24'52"S (± 1000 m), 57°24'43"E (± 500 m); 630–800 m; dense evergreen montane forest; on leaves of a shrub; 7 Sep. 2019; *Ertz 23967*; BR, MAU. – **Savanne District** • Black River Gorges National Park, along trail to Mt Cocotte; 20°26'30"S (± 200 m), 57°28'16"E (± 500 m); 720–750 m; on epiphytic fern; 1 Sep. 2019; *Ertz 23524, 23530 & Diederich*; BR, MAU.

*Porina mauritiana* Ertz & Diederich, **sp. nov.** (fig. 6) – Type: MAURITIUS – **Plaines Wilhems District** • Black River Gorges National Park, Le Pétrin, along trail W of Pétrin Information Centre, up to 600 m W of first viewpoint; 20°24'01"S (± 200 m), 57°27'30"E (± 400 m); 620–660 m; on bark of twigs of a shrub; 31 Aug. 2019; *Ertz 23433 & Diederich*; holotype: MAU; isotype: BR [BR5030105558583].

**Mycobank no:** MB 841121

**Diagnosis** – This species resembles *Porina longispora* Vězda by its finely verrucose thallus, its convex, hemispherical to subglobose, pale cream to pale orange thalline verrucae ca (0.35–)0.45–0.65 mm diam. lacking a black periostolar area and by its mainly 15-septate ascospores but differs by having a corticolous habit (vs foliicolous in *P. longispora*), a trentepohlioid photobiont with angular-rounded cells arranged in irregular plates (vs rectangular and arranged in distinctly radiate rows in *P. longispora*), and by having slightly shorter (58–)62–84.5(–90) µm ascospores (vs 80–108 µm long in *P. longispora*).

**Description** – **Thallus** epiphloeodal, continuous to rimose, finely verrucose, slightly glossy, orange-brownish when fresh, becoming pale greenish grey in the herbarium, thin ca 20–50 µm, containing large crystals of calcium oxalate in the verrucae of ca 40–80 µm diam., without a black basal layer, sometimes with a narrow, blackish, inconspicuous prothallus; isidia and soralia absent. Photobiont trentepohlioid with angular-rounded cells arranged in irregular plates; cells ca 5–11 µm diam. or 9–12 × 5–8 µm. **Ascomata** perithecioid, solitary, rarely two contiguous, dispersed, entirely immersed in well-delimited, hemispherical to subglobose, pale orange cream (when fresh) or pale cream (in herbarium) thalline verrucae ca (0.35–)0.45–0.65 mm diam.; ostiole apical, rather inconspicuous; periostolar area lacking dark pigmentation; crystallostratum of calcium oxalate crystals (H<sub>2</sub>SO<sub>4</sub>!) well developed, ca 50–70 µm thick. **Excipulum** pale yellowish all around, laterally ca 7–10 µm thick. **Hamathecium** hyaline, not interspersed, of thin, simple, 1.5–2 µm diam. paraphyses. **Asci** narrowly ellipsoid, I–, ca 105–110 × 18–25 µm (n = 3), 8-spored. **Ascospores** hyaline, I–, transversely (8–)9–15-septate, narrowly fusiform or oblong, often tapering towards one end, (58–)62–84.5(–90) × (6–)7–8.5(–9) µm, ratio L/B (7.5–)8.5–10.5(–11) (n = 19); surrounded by a gelatinous sheath that is very variable



**Figure 6** – *Porina maurittiana*. **A–B**. Thallus and perithecia. **C**. Ascus in water. **D**. Photobiont in water. **E**. Ascospores in water. A–E from Ertz 23433 (BR). Scale bars: A–B = 0.5 mm, C–E = 10  $\mu$ m.

in thickness, ca 1–7 µm (in water). *Pycnidia* not observed. Chemistry: thallus K–, C–, KC–, PD–, UV–.

**Distribution and ecology** – The species is known only from the type locality in Mauritius, where it grows on the twigs of shrubs in upland rainforest (ca 620–660 m).

**Etymology** – The specific epithet refers to the occurrence of the new species in Mauritius.

**Notes** – *Porina longispora* is the most similar species in the size and shape of the perithecial thallus-dominated verrucae and the 15-septate ascospores, but that species differs from *P. mauritiana* by its foliicolous habit, a photobiont with rectangular cells arranged in distinctly radiate rows and slightly longer ascospores (80–100 µm according to Vězda 1975 and Lücking & Vězda 1998; 84–108 µm according to McCarthy 2001). In our phylogenetic tree, the new species is sister to the clade of the foliicolous *Porina longispora*+*P. mazosioides*, suggesting that it represents a distinct species and not a corticolous morph of *P. longispora*. *Porina mazosioides* Lücking & Vězda differs in having 7-septate ascospores and a foliicolous habit (Lücking & Vězda 1998). Among the species keyed out by Santesson (1952), *P. multiseptata* Müll.Arg. also has 15-septate ascospores, but differs from the new species by a foliicolous habit and pilose perithecia and thallus. Among the foliicolous species keyed out by Lücking (2008), *P. americana* Fée has 9–13-septate and much broader (15–20 µm) ascospores; *P. filispora* Lücking differs notably by its much narrower (3.5–4 µm) 15–19-septate ascospores. Australian corticolous taxa keyed out by McCarthy (2001) with similar septation have either much shorter ascospores (viz. *P. bellendenica*, 32–56 µm), or perithecia that are not immersed in thallus-dominated verrucae (viz. *P. raphidiophora*, *P. meridionalis*).

***Porina mazosioides*** Lücking & Vězda (Lücking & Vězda 1998: 210) (fig. 7A, C) – Type: TANZANIA • N-Uluguru Mountains; 1700–1850 m; mossy forest; Dec. 1972; *Pócs et al.* 6851; holotype: PRA.

**Notes** – New to Mauritius. *Porina mazosioides* was previously known from Africa and Madagascar (Lücking & Vězda 1998; Farkas 2004). Our specimens are a good match for *P. mazosioides* due to the foliicolous habit, the finely verrucose thallus, the rectangular photobiont cells in distinctly radiate rows, the lens-shaped to hemispherical perithecia mainly of 0.4–0.6 mm diam., and the large 7-septate ascospores of (38–)42–51(–55) × (5–)5–6.5(–7) µm (n = 31) (Lücking & Vězda 1998). In our phylogenetic tree, the species is sister to *P. longispora*, a close relationship already suggested by Lücking & Vězda (1998) based on morphological similarities.

**Specimens examined** – MAURITIUS – **Plaines Wilhems District** • Black River Gorges National Park, Le Pétrin, along trail W of Pétrin Information Centre, up to 600 m W of first viewpoint; 20°24'01"S (± 200 m), 57°27'30"E (± 400 m); 620–660 m; on leaves; 31 Aug. 2019; *Ertz 23459 & Diederich 18784*; BR, MAU. – **Rivière Noire District** • Black River Gorges National Park, 5 km NW of Pétrin, Brise Fer Forest; 20°22'40"S, 57°26'25"E (± 200 m); 585 m; on leaf of epiphytic fern; 10 Sep. 2019; *Ertz 24342 & Diederich 19248, 19249*; BR, MAU • *ibid.*, along trail from

Plaine Champagne towards Piton de la Petite Rivière Noire; 20°24'52"S (± 1000 m), 57°24'43"E (± 500 m); 630–800 m; dense evergreen montane forest; on leaves; 6 Aug. 2016; *Diederich 18457*; BR, MAU • *ibid.*, 7 Sep. 2019, *Ertz 23925, 23966, 23968, 24006* (TLC, solvent A: nil); BR, MAU. – **Savanne District** • Black River Gorges National Park, along trail to Mt Cocotte; 20°26'30"S (± 200 m), 57°28'16"E (± 500 m); 720–750 m; on leaves; 1 Sep. 2019; *Ertz 23525, 23529 & Diederich 18893*; BR, MAU.

***Porina nitidula*** Müll.Arg. (Müller 1883: 336) (fig. 7B, D) – Type: BRAZIL • São Paulo, Apiahy; *Puiggari s.n.*; lectotype: G[G00293663], designated by Santesson (1952: 225).

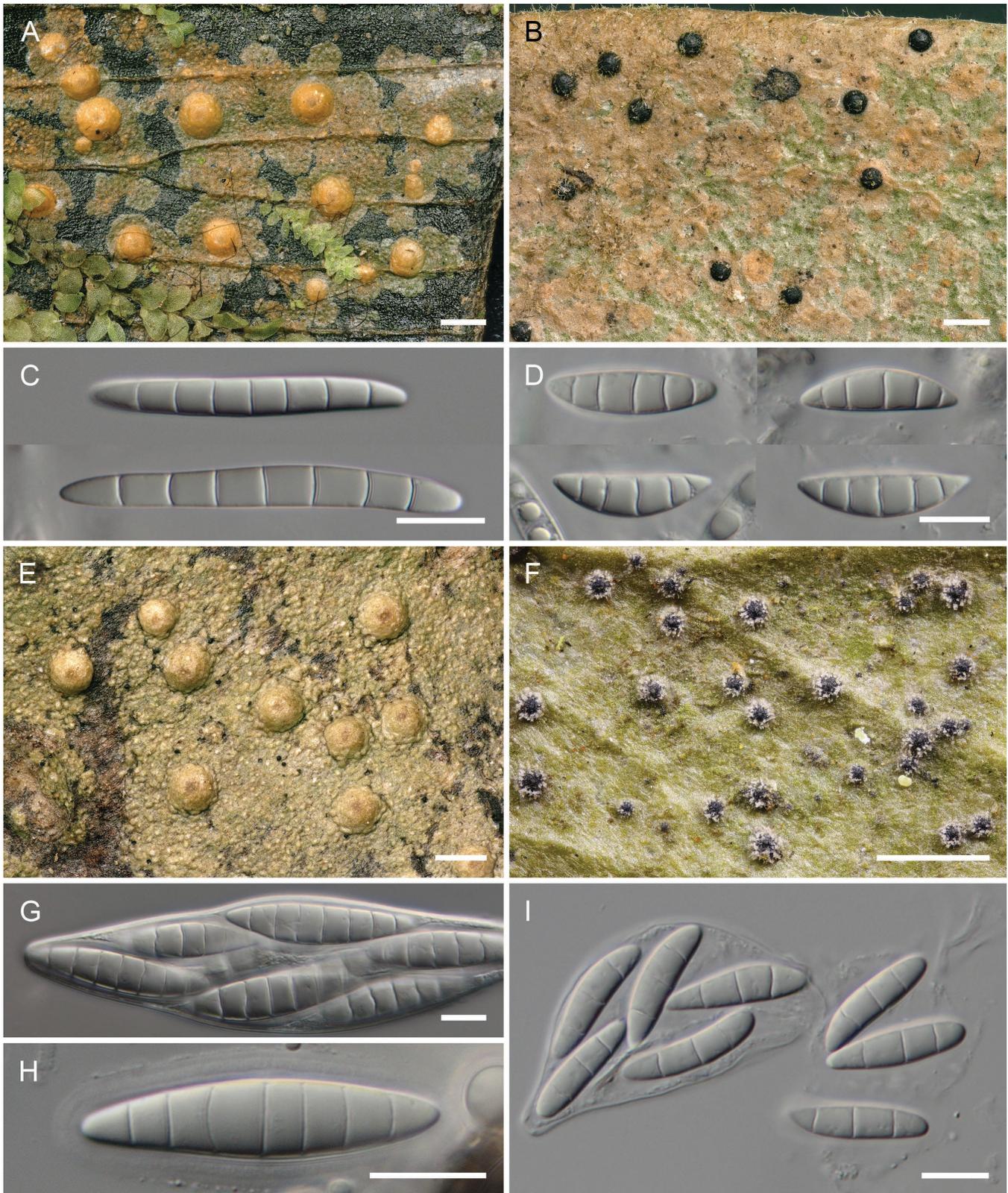
**Notes** – New to Mauritius. Pantropical. Our specimen can be accommodated in *P. nitidula* by virtue of its black perithecia 250–270 µm diam. and its 5-septate ascospores, 20–25 × 5–6 µm (Santesson 1952; McCarthy 2001; Farkas 2004; Lücking 2004, 2008). However, unlike our specimen, which has glabrous perithecia, *P. nitidula* has perithecia that are usually thinly whitish pilose, but the species is considered quite variable with respect to its perithecial morphology (Lücking 2008). Our attempts to sequence the Mauritian specimen failed.

**Specimen examined** – MAURITIUS – **Moka District** • along the trail from Moka to Le Pouce; 20°12'09"S, 57°31'31"E (± 200 m); ca 500 m; on leaves; 8 Sep. 2019; *Ertz 24110*; BR, MAU.

***Porina nucula*** Ach. (Acharius 1814: 112) (fig. 7E, G–H) – Type: GUINEA • *s.col. s.n.*; lectotype: H-ACH 731-A [H9501493], designated by Harris (1995: 174).

**Notes** – New to the island of Rodrigues. The species was already reported from Mauritius (Jardin Botanique Pamplemousse, *Ertz 21461*) by Diederich & Ertz (2020). In our phylogeny, specimen *Ertz 23762* groups with *Porina nucula* from Costa Rica (DQ168387, identical mtSSU sequence), confirming the wide distribution of the species. A second specimen from Costa Rica (KJ449310) has a slightly different phylogenetic position as sister to *P. cryptostoma*, but this relationship is poorly supported. Our material has 7-septate ascospores, 45–60 × 10–12 µm, that fit well the description in McCarthy (2001; ascospores 35–65(–83) × 10–18 µm), although the width of the ascospores is on the lower range. Specimen *Diederich 19512* has more applanate perithecial verrucae and is tentatively included here.

**Specimens examined** – MAURITIUS – **Moka District** • Réduit, State House Park; 20°13'44"S, 57°29'13"E (± 200 m); 280 m; on bark of a big trunk; 30 Aug. 2019; *Ertz 23310 & Diederich*; BR, MAU. – **Rivière Noire District** • Black River Gorges National Park, along trail from Plaine Champagne towards Piton de la Petite Rivière Noire; 20°24'52"S (± 1000 m), 57°24'43"E (± 500 m); 630–800 m; dense evergreen montane forest; on bark; 7 Sep. 2019; *Ertz 23909*; BR, MAU • *ibid.*, 5 km NW of Pétrin, Brise Fer Forest; 20°22'40"S, 57°26'25"E (± 200 m); 585 m; on bark; 10 Sep. 2019; *Ertz 24285 & Diederich*; BR, MAU. – **Rodrigues District** • Grande Montagne Nature Reserve; 19°42'22"S, 63°27'52"E (± 300 m); 330–360 m; on bark of *Pandanus*; 4 Sep. 2019; *Diederich 19512 & Ertz*; BR, MAU •



**Figure 7** – Habit, ascus, and ascospores (in water) of *Porina* species from Mauritius. **A, C.** *Porina mazosioides*. **B, D.** *P. nitidula*. **E, G–H.** *P. nucula*. **F, I.** *P. perminuta*. A, C from Ertz 24342 (BR). B, D from Ertz 24110 (BR). E, G from Ertz 23709 (BR). H from Ertz 23717 (BR). F, I from Diederich 18732 (BR). Scale bars: A–B, E–F = 0.5 mm, C–D, G–I = 10  $\mu$ m.

ibid., on bark of *Olea*, 4 Sep. 2019, Ertz 23700 & Diederich; BR, MAU • ibid., on bark, 4 Sep. 2019, Ertz 23709, 23717, 23762 & Diederich; BR, MAU.

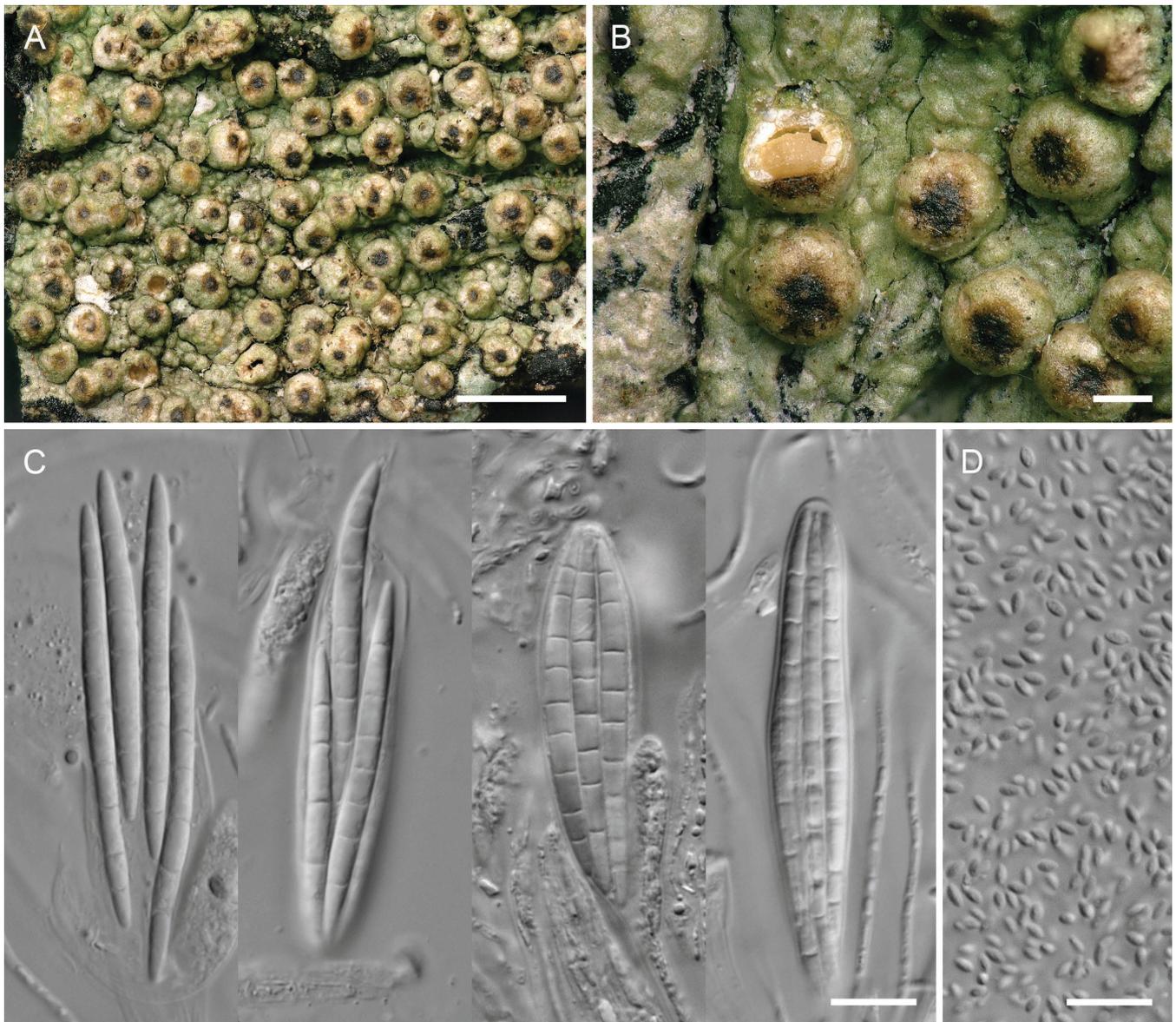
***Porina nuculoides*** Ertz & Diederich, **sp. nov.** (fig. 8) – Type: MAURITIUS – Rivière Noire District • Chamarel, Ebony Forest, along the trail west of the viewpoint; 20°25'53"S (± 100 m), 57°22'21"E (± 300 m); 330–350 m; on the bark of *Diospyros*; 2 Sep. 2019; Ertz 23617 & Diederich; holotype: MAU; isotype: BR[BR5030105717577].

**Mycobank no:** MB 841122

**Diagnosis** – This species resembles *Porina tetracerae* (Ach.) Müll. Arg. by its pale green, faintly verrucose thallus and by the perithecia immersed in subglobose thalline verrucae ca 0.3–0.4 mm diam. but differs by having (5–)7–9(–10)-septate

ascospores (vs consistently 7-septate in *P. tetracerae*) that are narrower (2.5–)3–3.5(–4) µm (vs 3.5–7 µm in *P. tetracerae*).

**Description** – Thallus epiphloeodal, pale green, faintly verrucose, epruinose, matt to slightly glossy, continuous to faintly rimose, homoiomerous, without a black basal layer, ca 15–90 µm thick, large crystals of calcium oxalate ca 5–35 µm (H<sub>2</sub>SO<sub>4</sub>!) at least near the perithecia, ecorticate; prothallus not apparent; isidia and soralia absent. Photobiont trentepohlioid; cells ca 5–10 × 5–8 µm. Ascomata perithecioid, solitary, sometimes 2–6 contiguous, numerous, ± densely distributed, entirely immersed in ca 0.3–0.4 mm diam., well-delimited, subglobose thalline verrucae; ostiole apical, visible as a pale dot; periostiole area pale to dark brown or black, ca 115–175 µm diam.; crystallostratum of calcium oxalate crystals (H<sub>2</sub>SO<sub>4</sub>!) well developed, with crystal clusters ca 35–60 µm diam.; thalline margin ca 50–85



**Figure 8** – *Porina nuculoides*. A–B. Thallus and perithecia, with a sectioned perithecium shown in B. C. Asci and ascospores in water. D. Conidia in water. A–D from Ertz 23617 (BR). Scale bars: A = 1 mm, B = 200 µm, C–D = 10 µm.

$\mu\text{m}$  thick; wall not carbonized. Excipulum hyaline to pale yellowish all around, laterally ca 10–15  $\mu\text{m}$  thick, basally ca 8–10  $\mu\text{m}$ , K+ orange. Centrum globose, ca 150–210  $\mu\text{m}$  diam. Hamathecium hyaline, not interspersed, of thin, simple, 1.5–2  $\mu\text{m}$  diam. paraphyses. Asci cylindrical-clavate, ca 55–70  $\times$  10–14  $\mu\text{m}$  (n = 6), 8-spored; ascus apex rounded, without a ring structure. Ascospores hyaline, I–, transversely (5–)7–9(–10)-septate, fusiform to filiform, (38–)40.5–51.5(–60)  $\times$  (2.5–)3–3.5(–4)  $\mu\text{m}$ , ratio L/B (3.75–)4–5(–5.5) (n = 17); perispore absent or ca 1–1.5  $\mu\text{m}$  thick. Pycnidia not observed. Chemistry: thallus K $\pm$  brownish, C–, KC–, PD–, UV–. TLC not performed.

**Distribution and ecology** – The species is known only from the Ebony Forest in Mauritius, where it inhabits the bark of trunks of *Diospyros*, at low elevation (ca 330–350 m).

**Etymology** – The specific epithet refers to the external similarity with *Porina nucula*.

**Notes** – Among the similar Australian corticolous taxa documented by McCarthy (2001), *P. internigrans* has much larger (51–92  $\times$  9–17  $\mu\text{m}$ ) and usually more septate (7–13 septa) ascospores, usually with a 2–4  $\mu\text{m}$  thick perispore; *P. africana* has broader and less prominent perithecial verrucae, 0.58–1 mm, and broader ascospores, 4–6.5  $\mu\text{m}$  wide; *P. tetracerae* differs by its consistently 7-septate ascospores that are usually wider (3.5–7  $\mu\text{m}$ ), except in var. *persimilis* (Müll.Arg.) P.M.McCarthy (2–3.5  $\mu\text{m}$ ) which differs by its larger perithecial verrucae (0.42–0.7 mm diam.) and shorter ascospores (26–43.5  $\mu\text{m}$ ) (McCarthy 1994a). Moreover, in our phylogeny, the new species is part of a different lineage

including the genus *Saxiloba*, *P. rupicola* and a specimen of *P. internigrans*. Among the similar corticolous taxa from India, Nepal and Sri Lanka keyed out by Awasthi (1991), *P. desquamescens* Fée has broader reddish brown perithecia (0.4–1 mm diam.) and usually shorter ascospores, 34–38(–55)  $\times$  4–5  $\mu\text{m}$ . The small, prominent perithecial verrucae of the new species resemble those of *Porina nucula* Ach., which is abundant in Mauritius, but the latter has much broader ascospores (10–18  $\mu\text{m}$  wide).

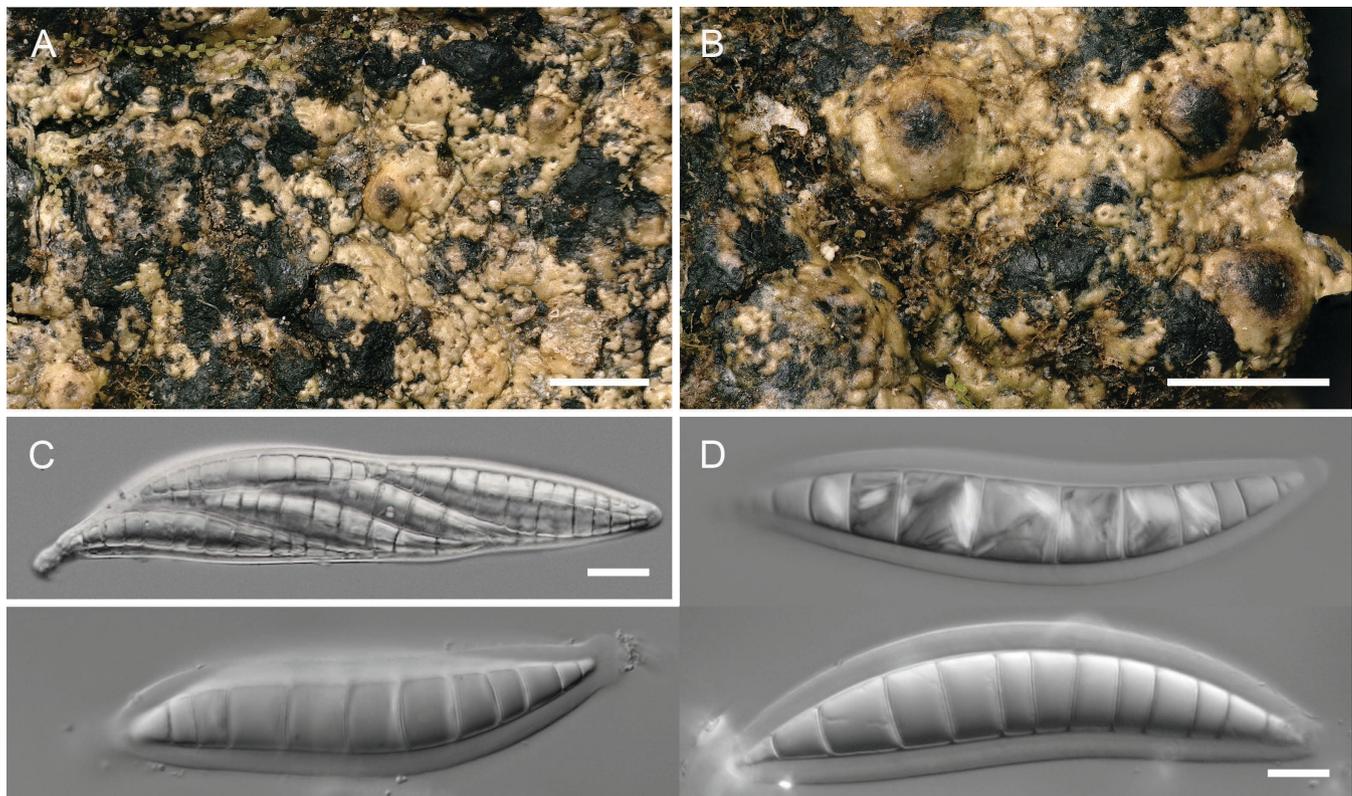
***Porina perminuta*** Vain. (Vainio 1924: 14) (fig. 7F, I) – Type: FRENCH POLYNESIA • Tahiti; Faaa District; on leaves of Mango trees; 1 Jun. 1922; *Setchell & Parks 5085*; isotypes: NY[NY01219349], M[M0023848].

**Notes** – New to Mauritius. A widespread, Palaeotropical species for which the closest locality is the Seychelles archipelago (Vězda 2000; Schumm & Aptroot 2010). Our specimen is characterized by its black perithecia 70–120  $\mu\text{m}$  diam., with ca 30 short white hairs per perithecium and 3-septate ascospores 16–23  $\times$  3.5–5  $\mu\text{m}$ .

**Specimen examined** – MAURITIUS – Moka District • Réduit, State House Park; 20°13'44"S, 57°29'13"E ( $\pm$  200 m); 280 m; on leaves; 30 Aug. 2019; *Diederich 18732 & Ertz*; BR, MAU.

***Porina praestantior*** Müll.Arg. (Müller 1882: 400) (fig. 9) – Type: INDONESIA • Java; (on bark); *s.col. s.n.* [‘ex. hb. Hampe 1877’]; holotype: G[G00295587].

**Description** – Thallus epiphloeodal, glossy,  $\pm$  verruculose, thin, creamish-green, ca 75–130  $\mu\text{m}$ , containing numerous



**Figure 9** – *Porina praestantior*. **A–B.** Thallus and perithecia. **C.** Ascus in water. **D.** Ascospores in water. A–D from *Ertz 23520* (BR). Scale bars: A–B = 1 mm, C = 20  $\mu\text{m}$ , D = 10  $\mu\text{m}$ .

large crystals of calcium oxalate ca 10–25  $\mu\text{m}$  diam., often discontinuous on a black basal layer ca 50–100  $\mu\text{m}$ ; prothallus not observed; isidia or soralia absent. Photobiont trentepohlioid; cells ca 7–12  $\times$  5–8  $\mu\text{m}$ . Ascomata perithecioid, solitary, dispersed, immersed in lens-shaped to hemispherical thalline verrucae ca (0.5–)0.6–0.9 mm diam., with a thick thallus layer; ostiole apical, black; periostiolar area dark brown to black, ca (130–)200–450  $\mu\text{m}$  diam., forming a superficial thin layer ca 10–20  $\mu\text{m}$  thick; crystallostratum of calcium oxalate crystals ( $\text{H}_2\text{SO}_4$ !) well developed, ca 35–150  $\mu\text{m}$  thick. Excipulum pale yellowish to pale orange all around, ca 30–40  $\mu\text{m}$  thick, K+ dark orange to red. Hamathecium hyaline, not interspersed, of thin, simple, ca 2  $\mu\text{m}$  diam. paraphyses. Asci narrowly obclavate, I–, ca 220  $\times$  35  $\mu\text{m}$  (n = 1), 8-spored. Ascospores hyaline, I–, transversely (9–)10–14(–18)-septate, elongate-fusiform, 80–118  $\times$  12–15  $\mu\text{m}$  (n = 12); gelatinous sheath 2–5  $\mu\text{m}$  thick. Pycnidia not observed. Chemistry: thallus K+ brownish, C–, KC–, PD–, UV–. TLC not performed.

**Distribution and ecology** – The species is known from Java and Mauritius. In the latter, it inhabits the bark of trees in a humid upland forest (elev. 720–750 m).

**Notes** – Although our specimen is somewhat similar to *Porina internigrans*, it differs from it (see also under *P. cf. internigrans*) by having longer (ca 80–118  $\mu\text{m}$ ) and usually more septate ascospores (mainly 9-septate ascospores, 51–92  $\mu\text{m}$  long for *P. internigrans*, McCarthy 2001). Among the names that are nowadays considered to be synonyms of *Porina internigrans* (e.g. Index Fungorum 2021), *P. praestantior* Müll.Arg. (photo of the type on JSTOR: <https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00295587>), described from Java, is very similar to our specimen by having a creamish thallus with a black basal layer, hemispherical to subglobose,  $\pm$  well-delimited perithecial verrucae ca 0.5–0.9 mm diam., a dark brown to black periostiolar area, and elongate-fusiform, large, 9–15-septate ascospores. Although the ascospores were described as being broader, 15–20  $\mu\text{m}$  without perispore (Müller 1882), our specimen is a good match for *P. praestantior*. In our phylogenetic tree, several other taxa are part of the same clade as *P. praestantior* and all are phylogenetically and morphologically distinct: *P. mastoidea* differs notably by the 7(–8)-septate ascospores, 32–66  $\times$  6–13  $\mu\text{m}$  (McCarthy 2001); *P. imitatrix* Müll.Arg. is mainly foliicolous but also found on bark and is characterized by a purplish black prothallus, mainly lens-shaped perithecia 0.6–1 mm diam, 7(–9)-septate ascospores, 38–64  $\times$  6.5–10  $\mu\text{m}$ , with a gelatinous sheath (Lücking & Vězda 1998); *P. radiata* Kalb, Lücking & Vězda is a very different species distinguished by a thallus with regular radiate ridges and lacking a visible prothallus, a species of *Phycopeltis* as photobiont with rectangular cells in radiate plates, small lens-shaped perithecia 0.3–0.45 mm diam., and small 7-septate ascospores, 28–35(–43)  $\times$  3.5–4.5  $\mu\text{m}$  (Lücking & Vězda 1998); and *P. internigrans* (see above).

**Specimen examined** – MAURITIUS – Savanne District • Black River Gorges National Park, along trail to Mt Cocotte; 20°26'30"S ( $\pm$  200 m), 57°28'16"E ( $\pm$  500 m); 720–750 m; on bark; 1 Sep. 2019; Ertz 23520 & Diederich; BR.

***Porina rufula*** (Kremp.) Vain. (Krempelhuber 1874: 20) (fig. 10A, C) – Type: MALAYSIA • Sarawak [Borneo]; 1866; *Beccari s.n.*; holotype: M[M0023867]; isotype: G[G00293679].

**Notes** – New to Mauritius. Pantropical. Ascospores in our specimens are 3-septate, 23.5–27  $\times$  4–5  $\mu\text{m}$  and fit well the descriptions in Lücking (1996, 2008).

**Specimen examined** – MAURITIUS – Savanne District • Black River Gorges National Park, along trail to Mt Cocotte; 20°26'30"S ( $\pm$  200 m), 57°28'16"E ( $\pm$  500 m); 720–750 m; on leaves; 1 Sep. 2019; Ertz 23528 & Diederich 18897; BR, MAU.

***Porina rupicola*** Ertz & Diederich, **sp. nov.** (fig. 11) – Type: MAURITIUS – Rodrigues District • Grande Montagne Nature Reserve; 19°42'22"S, 63°27'52"E ( $\pm$  300 m); 330–360 m; on shaded rock; 4 Sep. 2019; Ertz 23758 & Diederich; holotype: MAU; isotypes: BR[BR5030105842484], hb. Diederich.

**Mycobank no:** MB 841123

**Diagnosis** – This species resembles *Porina crassa* P.M.McCarthy by its perithecia almost entirely immersed in the thallus and its 5–7-septate ascospores but differs by having a thinner thallus (200–350  $\mu\text{m}$  vs 150–600  $\mu\text{m}$  in *P. crassa*) and by having much larger ascospores ((27–)31–37(–40)  $\times$  (6–)7–8(–9)  $\mu\text{m}$  vs 18–29  $\times$  4–6  $\mu\text{m}$  in *P. crassa*).

**Description** – Thallus epilithic, pale greyish green to dark olivaceous brown, smooth, epruinose, matt or slightly glossy, faintly rimose, ca 200–350  $\mu\text{m}$  thick, heavily impregnated with large crystals of calcium oxalate ca 5–38  $\mu\text{m}$  diam. ( $\text{H}_2\text{SO}_4$ !), sometimes appearing as white dots on the thallus surface, corticate, with a hyaline 8–15  $\mu\text{m}$  thick upper paraplectenchymatous layer of rounded cells, 3–5  $\mu\text{m}$ ; prothallus not apparent or a very thin black borderline when contiguous with other thalli; isidia and soralia absent. Photobiont trentepohlioid; cells ca 7–12  $\times$  6–8  $\mu\text{m}$ . Ascomata perithecioid, solitary, sometimes two or three contiguous, dispersed, subglobose, either entirely immersed in the thallus, rarely with the top slightly protruding above the thallus surface, or immersed in distinct, hemispherical thallus-dominated verrucae ca (0.5–)0.6–0.9 mm diam.; apex plane to slightly convex, smooth; ostiole apical, pale yellowish, surrounded by a dark reddish brown to black periostiolar area ca 0.2–0.5 mm diam. and ca 5–15  $\mu\text{m}$  thick; crystallostratum present in the thalline margin, with large crystals ca 5–25  $\mu\text{m}$ . Excipulum pale yellowish orange all around, ca 10–15  $\mu\text{m}$  thick, K+ reddish. Hamathecium hyaline, not interspersed, of thin, simple, 1.5–2  $\mu\text{m}$  diam. paraphyses. Asci cylindrical-clavate, I–, KI–, ca 150–170  $\times$  15–18  $\mu\text{m}$  (n = 5), 8-spored; ascus apex slightly truncate, with a ring structure. Ascospores hyaline, I–, transversely 5–7-septate, fusiform, (27–)31–37(–40)  $\times$  (6–)7–8(–9)  $\mu\text{m}$ , ratio L/B (3.5–)4–5(–6) (n = 54), with a perispore ca 2.5–5  $\mu\text{m}$  thick. Pycnidia immersed, brown-black above, colourless to pale brown below, 150–260  $\mu\text{m}$  diam., with a richly convoluted conidiogenous layer; conidia hyaline, simple, fusiform, 3–3.5  $\times$  1–1.2  $\mu\text{m}$ . Chemistry: thallus K+ reddish brown, C–, KC+ reddish brown, PD–, UV–. TLC not performed.

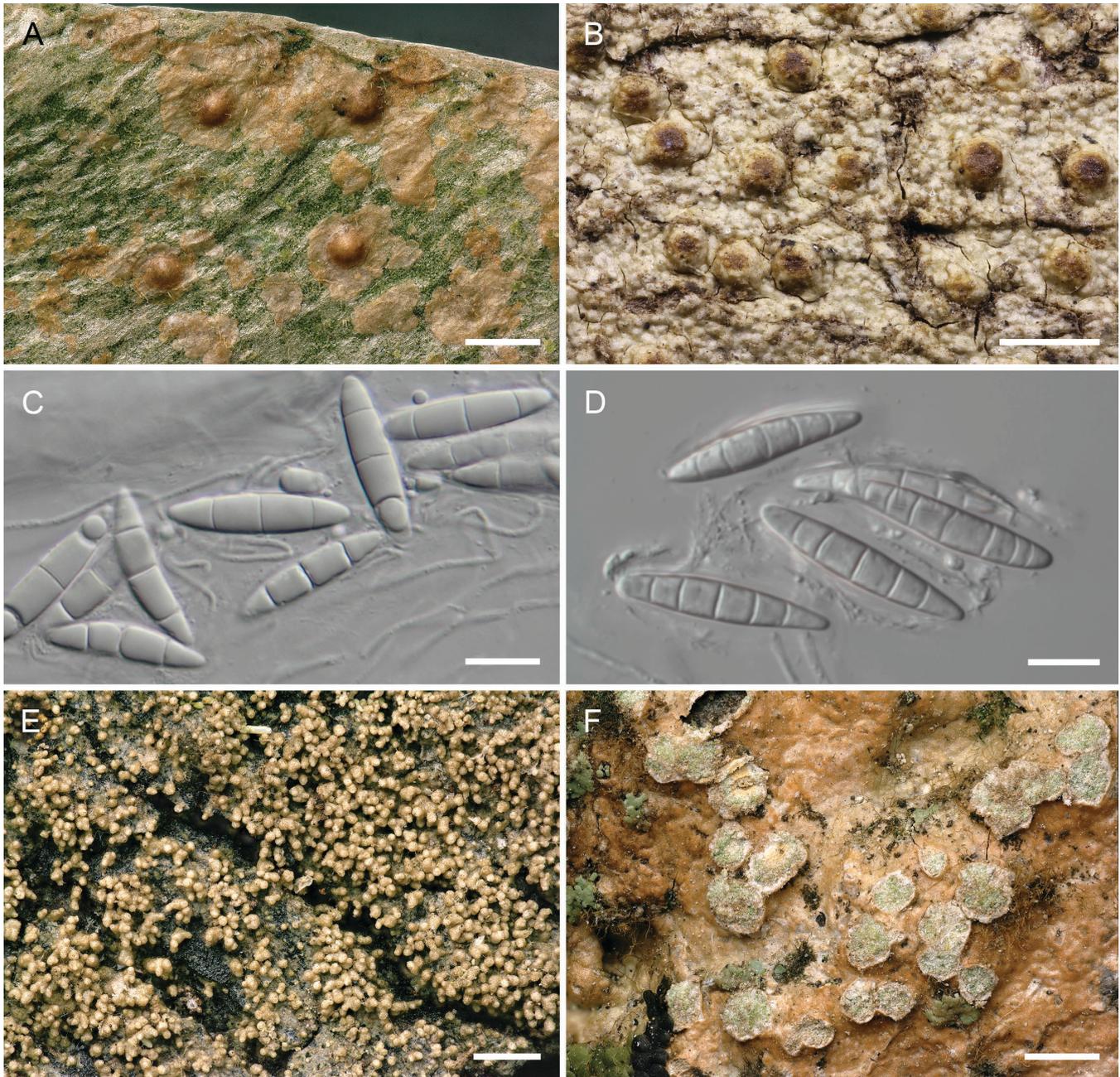
**Distribution and ecology** – The species is known from the type locality in Rodrigues and from two localities in Mauritius, where it inhabits rocks in rather dense forests, at low elevation (ca 330–490 m).

**Etymology** – The specific epithet refers to the saxicolous habit of the species.

**Notes** – *Porina rupicola* is accepted here as a rather variable taxon in terms of perithecial morphology: the perithecia can be almost entirely immersed in the thallus, not in thallus-dominated verrucae (holotype from Rodrigues island), or they are immersed in thallus-dominated verrucae that

protrude above the thallus surface (specimens from Mauritius island). These two morphotypes are phylogenetically close but slightly distinct (fig. 1A). Further material and studies are needed to investigate whether the material included under *P. rupicola* represents more than one species.

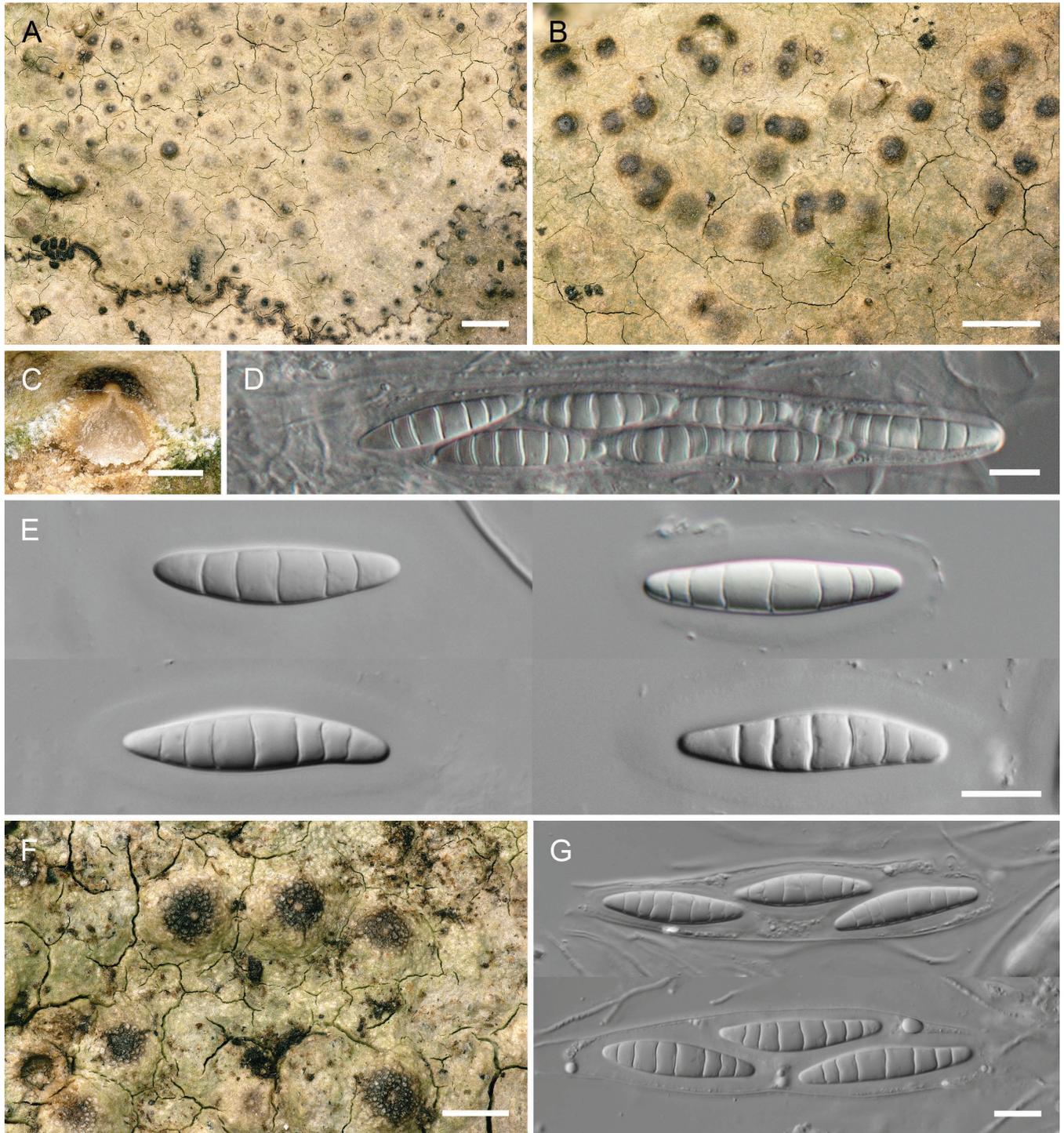
Among the saxicolous species of the Southern Hemisphere keyed out by McCarthy (1993), the new species would key out near the pantropical *P. mastoidea* and *P. tetracerae*. *Porina mastoidea* differs by a mainly corticolous habit (including the type specimen from Manila, Philippines), a thallus usually with a brown-black basal layer, and larger



**Figure 10** – Habit and ascospores (in water) of *Porina* species from Mauritius. **A, C.** *Porina rufula*. **B, D.** *P. aff. tetracerae*. **E.** *Porina* sp. **A, F.** *Porina* sp. **B, A, C** from Ertz 23528 (BR). **B, D** from Diederich 18542 (BR). **E** from Ertz 23584 (BR). **F** from Ertz 23618 (BR). Scale bars: **A, E** = 0.5 mm, **B, F** = 1 mm, **C–D** = 10  $\mu$ m.

ascospores  $(32-49(-66) \times (6-9(-13)) \mu\text{m}$  (McCarthy 1993, 2001). In our phylogenetic tree, two terminals of *P. mastoidea* from Costa Rica (Baloch & Grube 2006) are part of a different and distantly related lineage (fig. 1B). *Porina tetracerae* differs by having a thinner thallus (up to  $150 \mu\text{m}$ ), narrower ascospores,  $(3.5-5(-7)) \mu\text{m}$  broad, usually lacking a gelatinous sheath (McCarthy 1993). In our phylogenetic

tree, *P. tetracerae* is part of a different and distantly related lineage (fig. 1B). *Porina crassa* P.M. McCarthy and *P. pelochroa* Müll. Arg. are similar by having perithecia almost entirely immersed in the thallus and by their 7-septate ascospores. However, *P. crassa* has an exceptionally thick thallus ( $0.15-0.6 \text{ mm}$  thick) and much smaller ascospores,  $18-29 \times 4-6 \mu\text{m}$ , while *P. pelochroa* differs in having much



**Figure 11** – *Porina rupicola*. A–B, F. Thallus and perithecia. C. Sectioned perithecium. D. Ascus in water. E, G. Ascospores in water. A–E from Ertz 23758 (BR). F–G from Ertz 23620 (BR). Scale bars: A–B = 1 mm, C = 0.2 mm, D–E, G = 10  $\mu\text{m}$ , F = 0.5 mm.

longer and narrower ascospores,  $29.5\text{--}59.5 \times 4.5\text{--}6 \mu\text{m}$  (McCarthy 1993).

**Specimens examined** – MAURITIUS – Same locality as holotype, *Diederich 19020 & Ertz*; BR, MAU. – **Rivière Noire District** • Chamarel, Ebony Forest, along the trail west of the viewpoint;  $20^{\circ}25'53''\text{S}$  ( $\pm 100 \text{ m}$ ),  $57^{\circ}22'21''\text{E}$  ( $\pm 300 \text{ m}$ ); 330–350 m; on shaded rock; 2 Sep. 2019; *Ertz 23620 & Diederich* (TLC nil!); BR, MAU. – **Moka District** • along the trail from Moka to Le Pouce;  $20^{\circ}12'09''\text{S}$ ,  $57^{\circ}31'31''\text{E}$  ( $\pm 200 \text{ m}$ ); 490 m; on shaded rock; 8 Sep. 2019, *Ertz 24088*; BR, MAU.

*Porina* aff. *tetracerae* (Ach.) Müll.Arg. (Acharius 1803: 121) (fig. 10B, D) – Type: SIERRA LEONE • *Afzelius s.n.*; lectotype: H-ACH 838-C [H9501638], designated by Harris (1995: 172); isolectotypes: LD, S, UPS.

**Notes** – The species is known from a single specimen reported from Mauritius by Diederich & Ertz (2020). It agrees well with *Porina tetracerae* var. *tetracerae* by having small perithecial verrucae 0.4–0.55 mm diam. and ascospores of  $28\text{--}34 \times 4\text{--}6 \mu\text{m}$ , but it differs in its 4–6(–7)-septate ascospores with a gelatinous sheath, while McCarthy (1993, 2001) reported consistently 7-septate ascospores, usually lacking a gelatinous sheath. Therefore, the Mauritian specimen probably represents a different species, but our attempts to sequence it were unsuccessful. It is probable that the pantropical *P. tetracerae* as currently accepted represents a species-rich complex in the need of a revision.

**Specimen examined** – MAURITIUS – **Rivière Noire District** • Chamarel, Ebony Forest, close to park buildings;  $20^{\circ}26'10''\text{S}$ ,  $57^{\circ}22'15''\text{E}$  ( $\pm 100 \text{ m}$ ); 300 m; on bark; 8 Aug. 2016; *Diederich 18542*; BR, MAU.

*Porina* sp. A (sterile and isidiate) (fig. 10E)

**Notes** – The specimen of *Porina* sp. A is sterile and characterized by numerous, short, brownish green isidia. We first believed that it could be a sterile isidiate morph of *P. griffithsii*, a species that is abundant in the same locality (Ebony Forest) and for which one fertile specimen (*Ertz 23632*) has similar isidia. However, the phylogenetic results suggest that *Porina* sp. A represents a different species because it clusters far away from the *P. griffithsii* clade, as sister to the large clade from *P. epiphyllodes* to *P. subepiphylla* (fig. 1). It is surprising that *Porina* sp. A has no close relative among our sequenced species from Mauritius. Further sampling is needed.

**Specimen examined** – MAURITIUS – **Rivière Noire District** • Chamarel, Ebony Forest, along trail W of the viewpoint;  $20^{\circ}25'53''\text{S}$  ( $\pm 100 \text{ m}$ ),  $57^{\circ}22'21''\text{E}$  ( $\pm 300 \text{ m}$ ); 330–350 m; on bark of *Diospyros*; 2 Sep. 2019; *Ertz 23584 & Diederich*; BR, MAU.

*Porina* sp. B (sterile and sorediate) (fig. 10F)

**Notes** – The specimen of *Porina* sp. B is sterile and sorediate. In the Porinaceae, some taxa reproduce vegetatively by means of isidia, rarely soredia. The latter are known in the small genus *Myeloconis* (McCarthy & Elix 1996), but also in *Porina*, e.g. *Porina eminentior* f. *sorediifera* (Müll.Arg.) P.M.McCarthy (McCarthy 2001, 2003), *P. multipuncta*

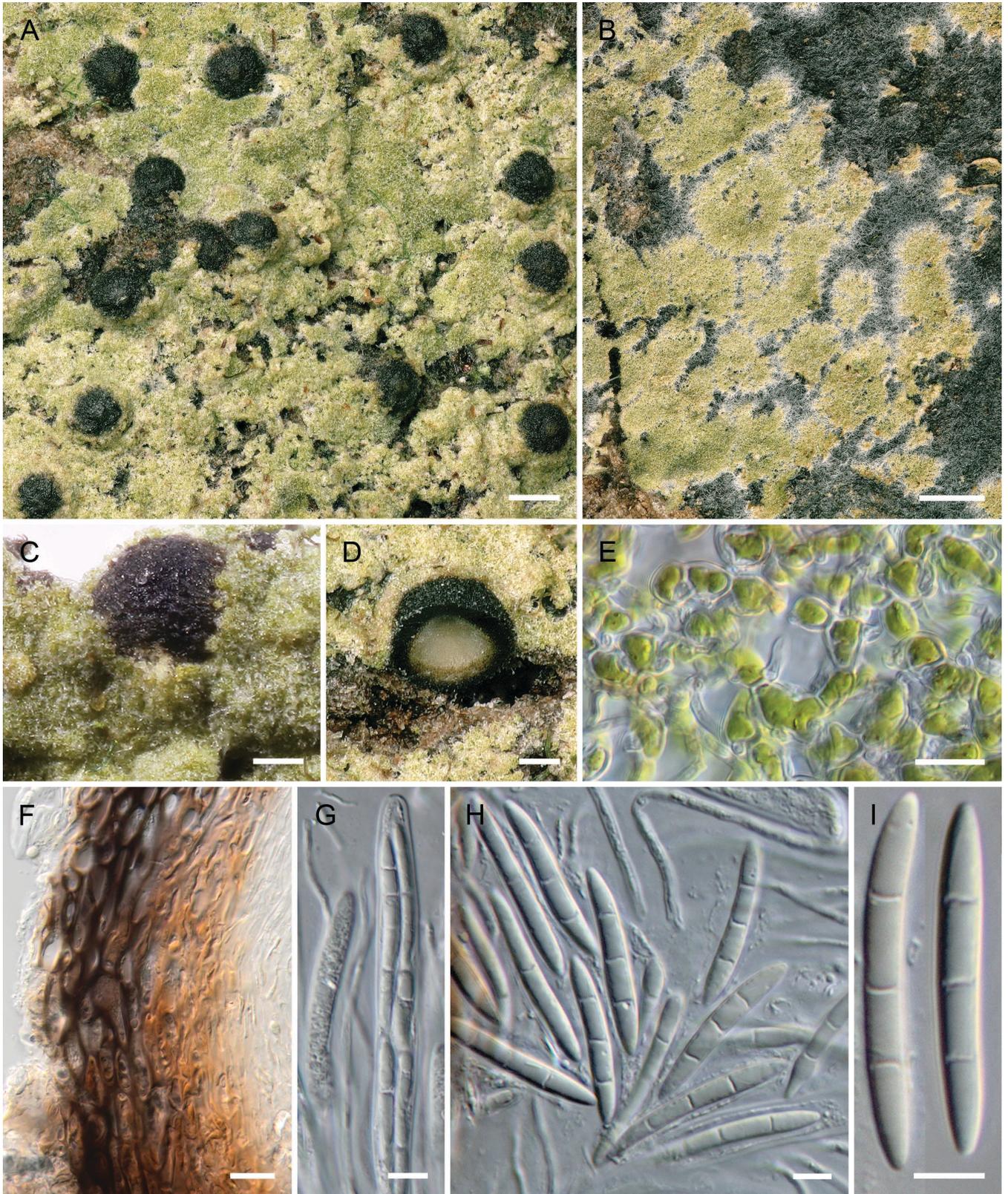
(Coppins & P.James) Ertz, Coppins & Frisch (Ertz et al. 2019), and *P. sorediata* Aptroot, Lücking & M.Cáceres (Hyde et al. 2019). In our phylogenetic tree (fig. 1), it is closely related to *Porina* cf. *eminentior*; however, it is genetically slightly distinct and we prefer to keep it as a separate taxon for the time being.

**Specimen examined** – MAURITIUS – **Rivière Noire District** • Chamarel, Ebony Forest, along the trail west of the viewpoint;  $20^{\circ}25'53''\text{S}$  ( $\pm 100 \text{ m}$ ),  $57^{\circ}22'21''\text{E}$  ( $\pm 300 \text{ m}$ ); 330–350 m; on shaded rock; 2 Sep. 2019; *Ertz 23618 & Diederich*; BR, MAU.

*Pseudosagedia crocynioides* (R.C.Harris) R.C.Harris (Harris 1995: 179) (fig. 12). – Type: UNITED STATES • Florida; Highlands County, Highlands Hammock State Park; swampy area near stream, on cypress; 22 Dec. 1965; *Wetmore 13907*; holotype: NY[NY01219895]; isotypes: FLAS, MIN.

**Description** – **Thallus** epiphloeodal, sometimes overgrowing corticolous mosses, up to ca 10 cm diam., loosely attached to the substrate, byssoid, effuse, smooth, epruinose, entire, pale olivaceous greenish, homoiomerous except the lowermost black part, thin ca 50–100  $\mu\text{m}$  thick, lacking calcium oxalate; hyphae with smooth walls not covered by crystals, 1.5–2  $\mu\text{m}$  diam.; prothallus often present, black, very thin; isidia and soralia absent. Photobiont trentepohlioid, in branched chains; cells ca 6–10(–13)  $\times$  5–7  $\mu\text{m}$ . **Ascomata** perithecioid, solitary, rarely two or three contiguous, dispersed, subglobose, black, smooth, strongly convex, 170–300  $\mu\text{m}$  diam., the base usually immersed in the thallus, but sometimes covering up to ca 2/3 of the perithecia; ostiole apical, inconspicuous; crystallostratum absent. **Excipulum** carbonized all around, dark brown-black in the outer 2/3, pale orange in the inner 1/3, laterally ca 40–45  $\mu\text{m}$  thick, basally slightly thinner, ca 30  $\mu\text{m}$ , K–. **Hamathecium** hyaline, not interspersed, of thin, simple, 1.5–2  $\mu\text{m}$  diam. paraphyses. **Asci** cylindrical-clavate, I–, ca 70–90  $\times$  7–8  $\mu\text{m}$  ( $n = 5$ ), 8-spored; ascus apex slightly truncate, with a ring structure. **Ascospores** hyaline, I–, transversely 3-septate, elongate-fusiform, (18–)21.5–25.5(–26)  $\times$  (2.5–)2.5–3(–3)  $\mu\text{m}$ , ratio L/B (6–)7–9(–10) ( $n = 27$ ); gelatinous sheath absent or poorly visible as a halo of ca 1–1.5  $\mu\text{m}$ , becoming more distinct in K. **Pycnidia** not observed. Chemistry: thallus K–, C–, KC–, PD–, UV–. No substances detected by TLC in specimen *Ertz 24301* (solvent A).

**Notes** – *Pseudosagedia crocynioides* is characterized by a distinctly byssoid thallus with a black hypothallus, smooth black perithecia 170–300  $\mu\text{m}$  diam., and 3-septate ascospores, (18–)21.5–25.5(–26)  $\times$  (2.5–)2.5–3(–3)  $\mu\text{m}$ . It is unique within the genus and the family Porinaceae by having a byssoid thallus. The ascomatal characters, the hamathecium, ascus and ascospore types are, however, typical for *Porina* as currently accepted by most authors. *Flabelloporina squamulifera* (Breuss, Lücking & Navarro) Sobreira, M.Cáceres & Lücking is similar, due to its minute brown-black perithecia with 3-septate ascospores. However, the thallus is very different, being composed of non-byssoid squamules (Sobreira et al. 2018). This monospecific genus has a rather isolated position and is nested in *Porina* s.l. in phylogenetic studies using mtSSU sequences (e.g. Sobreira et al. 2018; Diederich & Ertz 2020). We failed to



**Figure 12** – *Pseudosagedia crocynioides*. A, C. Thallus and perithecia. B. Thallus showing the black prothallus. D. Sectioned perithecium. E. Photobiont. F. Section of the excipulum in water. G. Asci in water. H–I. Ascospores in water. A–B, D–I from Ertz 24301 (BR). C from Diederich 19247. Scale bars: A = 0.2 mm, B = 0.5 mm, C–D = 0.1 mm, E–F = 10  $\mu$ m, G–I = 5  $\mu$ m.

Key to the species of *Porinaceae* in Mauritius (sterile taxa not included)

1. Thallus foliicolous ..... 2
- 1'. Thallus corticolous or saxicolous..... 8
2. Perithecia black..... 3
- 2'. Perithecia yellowish to reddish brown or with a greenish thallus cover..... 4
3. Ascospores 3-septate; perithecia 70–120 µm diam. .... *P. perminuta* Vain.
- 3'. Ascospores 5-septate; perithecia 140–270 µm diam. .... *P. nitidula* Müll.Arg.
4. Ascospores 3-septate; perithecia reddish brown, without an algiferous thalline cover.....  
..... *P. rufula* (Kremp.) Vain.
- 4'. Ascospores 7–15-septate; perithecia yellowish to orange, with an algiferous thalline cover..... 5
5. Ascospores (10–)12–15(–16)-septate, ca 79–110 × 7 µm ..... *P. longispora* Vězda
- 5'. Ascospores 7-septate, < 60 µm long ..... 6
6. Photobiont cells angular-rounded, irregularly arranged; thallus rough; ascospores ca 28–35 × 3–4 µm ..... *P. epiphylla* (Fée) Fée s.l.
- 6'. Photobiont cells rectangular, in distinctly radiate rows; thallus with distinct verrucae..... 7
7. Ascospores ca 25–28 × 3–3.5 µm; perithecia 0.2–0.35 mm diam. .... *P. epiphyloides* Vězda
- 7'. Ascospores ca 38–55 × 5–7 µm; perithecia 0.4–0.6 mm diam. .... *P. mazosioides* Lücking & Vězda
8. Ascospores 3-septate; perithecia not immersed in thallus-dominated verrucae ..... 9
- 8'. Ascospores with more than 3 septa; perithecia immersed in the thallus or in thallus-dominated verrucae (if not then ascospores < 29 µm long) ..... 10
9. Thallus byssoid; perithecia black ..... *Pseudosagedia crocynioides* (R.C.Harris) R.C.Harris
- 9'. Thallus compact; perithecia brownish orange ..... *P. leptalea* (Durieu & Mont.) A.L.Sm.
10. Ascospores muriform..... *P. cf. eminentior* (Nyl.) P.M.McCarthy
- 10'. Ascospores transversely septate..... 11
11. Ascospores < 60 µm long, 4–9(–10)-septate ..... 12
- 11'. Ascospores > 60 µm long, (8–)10–15(–18)-septate..... 17
12. Perithecia black, not immersed in thallus-dominated verrucae, 150–280 µm diam.; ascospores (20–) 22.5–28.5(–32) × (5–)5.5–7.5(–8) µm ..... *P. covidii* Ertz & Diederich
- 12'. Perithecia with a yellowish to reddish brown wall but sometimes black in the upper third, immersed in the thallus or in thallus-dominated verrucae usually larger than 300 µm diam..... 13
13. Ascospores 45–60 × 10–12 µm; on bark ..... *P. nucula* Ach.
- 13'. Ascospores < 10 µm wide; on bark or rock ..... 14
14. Ascospores 2.5–4 µm wide; on bark ..... *P. nuculoides* Ertz & Diederich
- 14'. Ascospores 4.5–8(–9) µm wide; on bark or rock..... 15
15. On rock; ascospores (6–)7–8(–9) µm wide..... *P. rupicola* Ertz & Diederich
- 15'. On bark; ascospores 4.5–6.5(–7) µm wide ..... 16
16. Perithecial verrucae 0.5–1 mm diam.; ascospores (33–)40–55(–63) µm long, 7–8(–10)-septate .....  
..... *P. africana* Müll.Arg.
- 16'. Perithecial verrucae 0.4–0.55 mm diam.; ascospores 28–34 µm long, 4–7-septate .....  
..... *P. aff. tetracerae* (Ach.) Müll.Arg.

- 
17. Ascospores (54–)64.5–87(–100) × (3.5–)4–5.5(–6.5) μm.....*P. griffithsii* Ertz & Diederich  
17'. Ascospores > 6 μm wide.....18
18. Periostiolar area lacking a dark pigmentation; perithecial verrucae (0.35–)0.45–0.65 mm diam.;  
ascospores 6–9 μm wide ..... *P. mauritiana* Ertz & Diederich
- 18'. Periostiolar area dark brown to black; perithecial verrucae 0.6–2 mm diam.; ascospores 8–15 μm  
wide.....19
19. Thallus matt, smooth to rough, with a homogenous pale olivaceous grey or green colour; ascospores  
ca (86–)93–111(–120) × (10.5–)11.5–13.5(–14) μm ..... *P. florensii* Diederich & Ertz
- 19'. Thallus glossy, smooth to strongly rugulose-verruculose, with black patches .....20
20. Ascospores (7–)9-septate, 72–83 × (8–)9–10 μm..... *P. cf. internigrans* (Nyl.) Müll.Arg.
- 20'. Ascospores (9–)10–14(–18)-septate, ca 80–118 × 12–15 μm .....*P. praestantior* Müll.Arg.
- 

obtain a mtSSU sequence from *P. crocynioides* despite two attempts from both the thallus and the hymenium. However, we succeeded in obtaining an nITS sequence, a locus unfortunately available for a more limited number of species of *Porina*. Therefore, a phylogenetic tree is not presented here, mainly because the ITS region in the available sequences of *Porina* is very variable resulting in large ambiguous parts, but the sequence is deposited on GenBank (GB number OK058473) for further studies. It is likely to be part of the *Trichothelium* subclade of *Porina* as delimited by Sobreira et al. (2018).

*Pseudosagedia crocynioides* was previously known only from Florida where it inhabits trunks of *Taxodium* in swampy forests. No significant morphological differences between our specimens and the original description of *P. crocynioides* were found. In the latter, ascospores were described as being slightly longer than in our specimens, “20–30 × 3–4 μm” in the Latin diagnosis but “20–35 × 2.5–3.5 μm” in the English description, and 3(–6)-septate. Asci were also slightly larger, 95–110 × 8–9 μm. As the original description is rather short and as the disjunct distribution is surprising, a detailed description of the Mauritian material is provided above. In the absence of molecular data from the populations of Florida, we cannot exclude the possibility of having two distinct species despite the similar morphology.

**Specimen examined** – MAURITIUS – **Rivière Noire District** • Black River Gorges National Park, 5 km NW of Pétrin, Brise Fer Forest; 20°22'40"S, 57°26'25"E (± 200 m); 585 m; on bark of a big trunk; 10 Sep. 2019; Ertz 24301 & Diederich 19247; BR, MAU.

## DISCUSSION

The genus *Porina* is diverse on the islands of the south-western Indian Ocean, with 46 species currently known from the region (Seaward & Aptroot 2009; Schumm & Aptroot 2010; van den Boom et al. 2011; Aptroot 2016; Diederich et al. 2017; this study). Our revision of Mauritian material has highlighted a rich flora, with 23 species, five of which are described as new. The five *Porina* species found in the island of Rodrigues (*P. covidii*, *P. cf. eminentior*, *P. griffithsii*, *P.*

*nucula*, and *P. rupicola*) are also present in Mauritius. This might be explained by the fact that these islands are close to each other (ca 574 km apart) and that Rodrigues is the smaller island (109 km<sup>2</sup> of land area vs 1865 km<sup>2</sup> for Mauritius) with the highest point (Mt Limon) reaching only 398 m in altitude (vs 828 m at Piton de la Petite Rivière Noire in Mauritius). Moreover, all pristine forests in Rodrigues have been destroyed by past human activity, unlike Mauritius that retains ca 2% of its native forest vegetation (Thébaud et al. 2009; Baider et al. 2010).

The genus *Porina* s.l. is well-represented on the other islands of the south-western Indian Ocean. Thus, 16 species have been reported from Réunion (van den Boom et al. 2011), seven of which are shared with Mauritius; 15 species are known from Madagascar (Aptroot 2016, and *P. cf. malmei* newly reported here), of which one-third are shared with Mauritius and the same proportion with Réunion; only one species (*P. epiphyllodes* Vězda) was reported from the Comoro Islands (Lücking & Vězda 1998) but no checklist is available for this archipelago; 24 species are known from the Seychelles (Seaward & Aptroot 2009; Schumm & Aptroot 2010; Diederich et al. 2017), of which nine are shared with Mauritius. Only three species (*P. epiphylla* s.l., *P. internigrans*, and *P. nitidula*) are shared between Mauritius, Réunion, Madagascar, and the Seychelles. Two species (*P. atrocoerulea* Müll.Arg. and *P. lucida* R.Sant.) are present in the three latter, but are absent from Mauritius. These numbers do not include *Trichothelium* species, none of which have been collected in Mauritius.

The real species diversity of the genus in this region of the Indian Ocean is certainly underestimated. The lichen flora of the Comoros archipelago is largely unknown, and the checklist of Madagascar is only preliminary. In Mauritius, several sites known for their rich and original biodiversity were not visited by us for our revision of the genus, such as the Bambou Mountain Range, the Corps de Garde, and several offshore islets (e.g. Île aux Aigrettes and Round Island), and some of those visited were only partly explored. A morphologically well-characterized species of *Porina* (*P. morelii* Aptroot & Diederich) was even recently described

from the Seychelles even though this archipelago can be considered as the best-explored in the south-western Indian Ocean (Diederich et al. 2017). The only species of *Porina* described from Réunion in the past (*P. innata* (Nyl.) Müll. Arg.) was not listed by van den Boom et al. (2011); indeed, it has never been reported since its description in 1858.

Future field work and subsequent taxonomic investigations are almost certain to uncover additional species of *Porina* on the islands of the south-western Indian Ocean. Conversely, it is likely that some epithets have been misapplied, as much of the available data is the result of using identification keys by different authors who simply chose the most similar species. Ideally, a taxonomic-phylogenetic revision of *Porina* from these islands and of the genus *Porina* on a much broader geographical scale is needed to confirm those identifications. This would almost certainly change the total number of species known from the region, and, at the same time, the degree of overlap in the composition of *Porina* taxa between the various islands and island groups.

While species of Porinaceae are sometimes found on more than one substratum type (bark, leaves, and rock; e.g. McCarthy 2001; Lücking 2008), most Mauritian species appear to be confined to one. Among the 23 species of *Porina* s.l. present in Mauritius, 12 are strictly corticolous, seven strictly foliicolous, and two species occur only on rock. Two species, *P. griffithsii* and *P. cf. eminentior*, occur on bark and also on mossy rock. However, they do not appear to grow directly on the rock surface. Foliicolous species were found mainly in upland humid forests above 500 metres, except *P. perminuta*, which was collected in a park at 280 metres. No species were found in coastal habitats.

Apart from the new species, the most surprising discovery of the present study is *Pseudosagedia crocynioides*, which was previously known only from Florida (Harris 1995, 2005). In the absence of molecular data from the American populations, we cannot exclude the possibility of there being two distinct species, but, for the moment, the similar and distinctive morphology leaves little doubt of their conspecificity. This disjunct distribution is difficult to explain and might be the result of long-distance dispersal, although a direct colonization from Florida to Mauritius (or the reverse) is hardly imaginable, in particular as the species is confined to a pristine forest in Mauritius. The species might have had a wider distribution in the tropics. However, it is also possible that the current distribution is the result of the disappearance of the species over parts of its original range due to the destruction of primary forests by human activity, and we cannot exclude the discovery of other populations in the future, as the lichen flora of the tropics is still poorly known. It is probable that long-term vicariance of these forests will promote allopatric speciation between these very isolated populations.

*Pseudosagedia crocynioides* is most unusual within the family Porinaceae by having a byssoid thallus, a rare type that has evolved in several unrelated lineages of lichenized fungi. The species is a further prime example of parallel evolution of byssoid thalli within genera known otherwise to have a more compact thallus, besides e.g. species formerly

placed in the genus *Crocynia* but now subsumed within *Phyllopsora* (Kistenich et al. 2018), *Lecanactis mollis* (Stirt.) Frisch & Ertz in the Roccellaceae (Ertz et al. 2015), and *Thelopsis byssoidea* Diederich in the Gyalectaceae (Aptroot et al. 1997; Ertz et al. 2021). A byssoid thallus is considered to be an adaptation to constantly humid climatic conditions characteristic of a tropical forest understory (Lakatos et al. 2006; Nelsen et al. 2010). It favours gas exchange because a byssoid thallus is a more ventilated structure compared to the denser organisation of most crustose lichen thalli. In many tropical *Porina* species, the thallus contains large amounts of calcium oxalate crystals often forming punctiform or elongate agglomerations, that render the thallus warted or ridged. The content of these structures is hydrophobic and prevents the thallus from getting completely soaked (Hafellner & Kalb 1995). *Pseudosagedia crocynioides* grows on large trunks in the famous pristine relict forest of Brise Fer. It is a dense humid forest inhabited by many other corticolous lichens that have developed thalli with strategies to enhance gas exchange. These include taxa having an effuse, leproid or byssoid thallus, sometimes with hydrophobic characteristics (*Crocynia*, *Crypthonia*, *Herpothallon*, *Lepraria finkii*, *Phyllopsora mauritiana*) or *Porina* species containing large amounts of oxalate crystals, e.g. *Porina africana*, *P. florensii*, and *P. griffithsii*.

The mtSSU phylogenetic tree includes 19 of the 23 species occurring in Mauritius. These species are dispersed throughout the phylogenetic tree, in at least eight main and strongly supported lineages, suggesting multiple colonizations of Mauritius. A new lineage strictly including Paleotropical and mainly foliicolous species (*P. epiphyllodes*, *P. longispora*, *P. mauritiana*, and *P. mazosioides*) is revealed as sister to *Porina* s.s. (= clade from *P. heterospora* to *P. subepiphylla*, including the type of the genus, *P. nucula*). Our phylogenetic results bring new insights but also challenge the recent attempts to define smaller (sub)generic entities in the family. *Porina griffithsii* does not cluster with the other similar species having long multiseptate ascospores tapering at one end, viz. *P. dolichophora* and *P. exasperatula* (= *P. dolichophora* clade sensu Sobreira et al. (2018)), but it belongs to the *P. simulans*-*P. epiphylla* clade (= *Phylloporina* clade sensu Sobreira et al. (2018)). Moreover, the genus *Saxiloba* is represented by the single species sequenced so far, but instead of forming its own rather distinct lineage as shown in the original description of this genus (Lücking et al. 2020), it is part of a strongly supported lineage with saxicolous and corticolous *Porina* species having crustose and non-lobate thalli (e.g. *P. nuculoides* and *P. rupicola*). This raises some doubts about the use of the ascospores and thallus type alone for defining genera in the Porinaceae. Interestingly, newly sequenced species with black perithecia cluster in two lineages of species also having black perithecia: *Porina borreri* and *P. perminuta* are part of the *Trichothelium* clade sensu Sobreira et al. (2018), while *P. covidii* and *P. cf. malmeyi* form a distantly more basal lineage sister to *P. byssophila*+*collina* (*P. byssophila* clade sensu Sobreira et al. (2018)). The internal generic classification of the family currently suffers from the lack of a broader sampling, but more importantly also from the lack of multigene analyses that would allow a better refinement of the generic concepts.

Much remains to be done to improve the phylogeny of the Porinaceae, a highly diverse group as highlighted by our new sequences.

*Porina nucula* is the only species for which a mtSSU sequence was identical to a sequence available on GenBank, while other previously published species had very divergent haplotypes as shown by the long branches in our phylogenetic tree (e.g. *P. internigrans*, *P. leptalea*). Baloch & Grube (2009) demonstrated that *P. epiphylla* and four other species of the *P. epiphylla*-group (sensu Baloch & Grube 2006) include a surprisingly large number of sympatric and highly diverged haplotypes in tropical rainforests of Costa Rica. This high diversity of cryptic genetic lineages within each species is surprising, in particular as a narrow morphological concept is already in use within this group of leaf-colonizing lichens and as it was based on the mtSSU locus known to have a low intraspecific variation (Baloch & Grube 2009 and references therein). This also calls into question the use of branch length for the distinction between taxa. The highly diverged haplotypes found in the foliicolous Mauritian material first referred to the *Porina epiphylla*-group based on morphology strengthen the results of Baloch & Grube (2009) and call for further molecular studies of this group in the Paleotropics.

Specimens of *Porina griffithsii* and *P. florensii* are usually devoid of isidia, but a few fertile specimens were also found with isidia. Their identification was confirmed by our molecular results, although the mtSSU sequence of the isidiate specimen of the first is quite divergent (fig. 1) and deserves further studies using a larger sampling and a more variable locus. These results suggest that the use of the presence or absence of vegetative reproductive structures such as isidia might sometimes be misleading to distinguish taxa that are otherwise morphologically similar as shown for other groups (e.g. Otálora et al. 2017).

The rich diversity of *Porina* s.l. found in Mauritius highlights the importance of the fragments of original forest cover that remain after four centuries of human occupation of the islands. It should encourage the considerable efforts deployed for their conservation management work to fight alien species and for the restoration of these primary forests. The real species diversity of the genus in the region of the south-western Indian Ocean is certainly underestimated and in need of further studies. The identity of several specimens remains uncertain despite the use of molecular data that are still too limited for tropical taxa. Indeed, a taxonomic-phylogenetic revision of tropical *Porina* at a broader geographical scale is highly desirable.

#### SUPPLEMENTARY FILE

**Supplementary file 1** – Species names, voucher specimens, and GenBank accession numbers of mtSSU sequences used in this study. Newly generated sequences are in bold. is. = island.

<https://doi.org/10.5091/plecevo.84545.suppl>

#### ACKNOWLEDGEMENTS

We wish to warmly thank all those who supported our collecting trips to Mauritius and Rodrigues, who kindly

provided us with the necessary permits, and who guided us during our excursions, especially Cláudia Baider and Kersley Pynee (The Mauritius Herbarium, Réduit) and Vincent Florens (University of Mauritius, Réduit), Kevin Ruhomaun, Parmananda Ragen and Mario Allet (National Parks and Conservation Service, Réduit), Zayd Jhumka (Forestry Service, Curepipe), Owen Griffiths (owner of Ebony Forest, Chamarel), and François Leguat (Giant Tortoises Reserve and Cave, Rodrigues), Nicolas Zuel, Christabelle Duhamel and Christine Griffiths (Ebony Forest, Chamarel), Richard Payendee (Commissioner for Environment, Rodrigues), Stephen Kirsakye (Mauritian Wildlife Foundation, Rodrigues) and Laurent Schley (Administration de la nature et des forêts, Luxembourg). We are indebted to the staff of the Parc Botanique et Zoologique de Tsimbazaza in Antananarivo (Madagascar) for logistical support of our research and to the Ministère des Eaux et Forêts for collection and export permits. Timothée Le Péchon (Meise Botanic Garden) and Tahina Razafindrahaja (Parc Botanique et Zoologique de Tsimbazaza, Antananarivo) are thanked for help for the joint collecting trip in Madagascar where *Porina* cf. *malmei* was collected. We warmly thank the curators of PRA for the loan of the holotype of *P. longispora*, and Lynn Delgat and Wim Baert (Meise Botanic Garden) for their help with the molecular work. We also wish to warmly thank Patrick McCarthy, Robert Lücking, and an anonymous referee who helped us to improve the manuscript. The specimens were collected and transported under permits FD No. 971/A/III (Forestry Service, Curepipe, 25 July 2016), NP57/1 V5 (National Parks and Conservation Service, Réduit, 28 July 2016), and 93999 AW/gp (Ministère de l'environnement, du climat et du développement durable, Luxembourg, 10 Sept. 2019).

#### REFERENCES

- Acharius E. 1803. *Methodus Lichenum*. Stockholm.
- Acharius E. 1814. *Synopsis Methodica Lichenum*. Lund.
- Aptroot A. 2016. Preliminary checklist of the lichens of Madagascar, with two new thelotremoid Graphidaceae and 131 new records. *Willdenowia* 46(3): 349–365. <https://doi.org/10.3372/wi.46.46304>
- Aptroot A., Diederich P., Sérusiaux E. & Sipman H.J.M. 1997. Lichens and lichenicolous fungi from New Guinea. *Bibliotheca Lichenologica* 64: 1–220.
- Awasthi D.D. 1991. A key to the microlichens of India, Nepal and Sri Lanka. *Bibliotheca Lichenologica* 40: 1–340.
- Baider C., Florens F.B.V., Baret S., et al. 2010. Status of plant conservation in oceanic islands of the Western Indian Ocean. Proceedings of the 4<sup>th</sup> Global Botanic Gardens Congress, June 2010: 1–9.
- Baloch E. & Grube M. 2006. Evolution and phylogenetic relationships within Porinaceae (Ostropomycetidae), focusing on foliicolous species. *Mycological Research* 110(2): 125–136. <https://doi.org/10.1016/j.mycres.2005.09.009>
- Baloch E. & Grube M. 2009. Pronounced genetic diversity in tropical epiphyllous lichen fungi. *Molecular Ecology* 18(10): 2185–2197. <https://doi.org/10.1111/j.1365-294X.2009.04183.x>
- Baloch E., Lücking R., Lumbsch H.T. & Wedin M. 2010. Major clades and phylogenetic relationships between lichenized

- and non-lichenized lineages in Ostropales (Ascomycota: Lecanoromycetes). *Taxon* 59(5): 1483–1494. <https://doi.org/10.1002/tax.595013>
- Cáceres M.E.S. 2007. Corticolous crustose and microfoliose lichens of northeastern Brazil. *Libri Botanici* vol. 22. IHW Verlag.
- Crittenden P.D., David J.C., Hawksworth D.L. & Campbell F.S. 1995. Attempted isolation and success in the culturing of a broad spectrum of lichen-forming and lichenicolous fungi. *New Phytologist* 130(2): 267–297. <https://doi.org/10.1111/j.1469-8137.1995.tb03048.x>
- Darriba D., Taboada G.L., Doallo R. & Posada D. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9: 772. <https://doi.org/10.1038/nmeth.2109>
- David J.C. & Hawksworth D.L. 1995. Lichens of Mauritius I: some new species and records. *Bibliotheca Lichenologica* 57: 93–111.
- Diederich P. & Ertz D. 2020. First checklist of lichens and lichenicolous fungi from Mauritius, with phylogenetic analyses and descriptions of new taxa. *Plant and Fungal Systematics* 65(1): 13–75. <https://doi.org/10.35535/pfsyst-2020-0003>
- Diederich P., Lücking R., Aptroot A., et al. 2017. New species and new records of lichens and lichenicolous fungi from the Seychelles. *Herzogia* 30(1): 182–236. <https://doi.org/10.13158/hea.30.1.2017.182>
- Durieu de Maisonneuve M.C. & Montagne J.P. 1848 [1846–1949]. Exploration scientifique de l'Algérie pendant les années 1840, 1841, 1842. *Sciences Naturelles, Botanique Lichens: I Cryptogamie*. vol. 1: 198–295.
- Ernst-Russell M.A., Chai C.L.L., Elix J.A. & McCarthy P.M. 2000. Myeloconone A2, a new phenalenone from the lichen *Myeloconis erumpens*. *Australian Journal of Chemistry* 53: 1011–1013.
- Ertz D., Tehler A., Irestedt M., Frisch A., Thor G. & van den Boom P. 2015. A large-scale phylogenetic revision of Roccellaceae (Arthoniales) reveals eight new genera. *Fungal Diversity* 70(1): 31–53. <https://doi.org/10.1007/s13225-014-0286-5>
- Ertz D., Sanderson N., Lúbek A. & Kukwa M. 2018. Two new species of Arthoniaceae from old-growth European forests, *Arthonia thoriana* and *Inoderma soreliatum*, and a new genus for *Schismatomma niveum*. *Lichenologist* 50(2): 161–172. <https://doi.org/10.1017/S0024282917000688>
- Ertz D., Sanderson N., Coppins B.J., Klepsland J.T. & Frisch A. 2019. *Opegrapha multipuncta* and *Schismatomma quercicola* (Arthoniomycetes) belong to the Lecanoromycetes. *Lichenologist* 51(5): 395–405. <https://doi.org/10.1017/S002428291900029X>
- Ertz D., Sanderson N. & Lebouvier M. 2021. *Thelopsis* challenges the generic circumscription in the Gyalectaceae and brings new insights on the taxonomy of *Ramonia*. *Lichenologist* 53(1): 45–61.
- Farkas E. 2004. Recent additions to the knowledge of the foliicolous lichen flora of South Africa. *Bibliotheca Lichenologica* 88: 111–125.
- Fée A.L.A. 1825 [1824] *Essai sur les cryptogames des écorces exotiques officinales*. D. Didot, Paris.
- Grube M., Baloch E. & Lumbsch H.T. 2004. The phylogeny of Porinaceae (Ostropomycetidae) suggests a neotenic origin of perithecia in Lecanoromycetes. *Mycological Research* 108(10): 1111–1118. <https://doi.org/10.1017/S0953756204000826>
- Hafellner J. & Kalb K. 1995. Studies in Trichotheliales ordo novus. *Bibliotheca Lichenologica* 57: 161–186.
- Harada H. 2015. Saxicolous and corticolous species of *Porina* (lichenized Ascomycota, Porinaceae) of Japan (part 1). *Lichenology* 14: 1–26.
- Harada H. 2016. Saxicolous and corticolous species of *Porina* (Lichenized Ascomycota, Porinaceae) of Japan (Part 2). *Lichenology* 14: 91–118.
- Harris R.C. 1995. More Florida Lichens. Including the 10¢ Tour of the Pyrenolichens. Published by the Author, Bronx, New York.
- Harris R.C. 2005. Some name changes in *Porina* s. lat. *Opuscula Philolichenum* 2: 15–16.
- Hyde K.D., Tennakoon D.S., Jeewon R., et al. 2019. Fungal diversity notes 1036–1150: taxonomic and phylogenetic contributions on genera and species of fungal taxa. *Fungal Diversity* 96(1): 1–242. <https://doi.org/10.1007/s13225-019-00429-2>
- Index Fungorum 2021. Available from <http://www.indexfungorum.org/names/names.asp> [accessed 3 Sep. 2021].
- Katoh K., Misawa K., Kuma K. & Miyata T. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* 30(14): 3059–3066. <https://doi.org/10.1093/nar/gkf436>
- Krempelhuber A. 1874. Lichenes foliicolae quos legit O. Beccari annis 1866 et 1867 in insula Borneo. Privately published, München.
- Kistenich S., Timdal E., Bendiksby M. & Ekman S. 2018. Molecular systematics and character evolution in the lichen family Ramalinaceae (Ascomata: Lecanorales). *Taxon* 67(5): 871–904. <https://doi.org/10.12705/675.1>
- Lakatos M., Rascher U. & Büdel B. 2006. Functional characteristics of corticolous lichens in the understory of a tropical lowland rain forest. *New Phytologist* 172(4): 679–695. <https://doi.org/10.1111/j.1469-8137.2006.01871.x>
- Lücking R. 1996. Taxonomic studies in foliicolous species of the genus *Porina*. I. The *Porina rufula* aggregate. *Botanica Acta* 109(3): 248–260. <https://doi.org/10.1111/j.1438-8677.1996.tb00570.x>
- Lücking R. 2004. A revised key to foliicolous Porinaceae (Ascomycota: Trichotheliales). *Bibliotheca Lichenologica* 88: 409–426.
- Lücking R. 2008. Foliicolous lichenized fungi. *Flora Neotropica Monograph* 103: 1–866.
- Lücking R. & Vězda A. 1998. Taxonomic studies in foliicolous species of the genus *Porina* (lichenized Ascomycotina: Trichotheliaceae) - II. The *Porina epiphylla* group. *Willdenowia* 28(1/2): 181–225. <https://doi.org/10.3372/wi.28.2818>
- Lücking R., Streimann H. & Elix J.A. 2001. Further records of foliicolous lichens and lichenicolous fungi from Australasia, with an updated checklist for continental Australia. *Lichenologist* 33(3): 195–210. <https://doi.org/10.1006/lich.2000.0316>
- Lücking R., Hodkinson B.P. & Leavitt S.D. 2017. (“2016”). The 2016 classification of lichenized fungi in the Ascomycota and Basidiomycota – Approaching one thousand genera. *The Bryologist* 119(4): 361–416. <https://doi.org/10.1639/0007-2745-119.4.361>
- Lücking R., Moncada B., Sipman H.J.M., et al. 2020. *Saxiloba*: a new genus of placodioid lichens from the Caribbean and Hawaii shakes up the Porinaceae tree (lichenized Ascomycota: Gyalectales). *Plant and Fungal Systematics* 65(2): 577–585. <https://doi.org/10.35535/pfsyst-2020-0031>

- Lutzoni F., Wagner P., Reeb V. & Zoller S. 2000. Integrating ambiguously aligned regions of DNA sequences in phylogenetic analyses without violating positional homology. *Systematic Biology* 49(4): 628–651. <https://doi.org/10.1080/106351500750049743>
- Maddison W.P. & Maddison D.R. 2015. Mesquite: a modular system for evolutionary analysis. Version 3.04. Available from <http://mesquiteproject.org> [accessed 9 Feb. 2016].
- Malcolm W.M. & Vězda A. 1995. New foliicolous lichens from New Zealand I. *Folia Geobotanica et Phytotaxonomica* 30: 91–96.
- McCarthy P.M. 1993. Saxicolous species of *Porina* Müll.Arg. (Trichotheliaceae) in the Southern Hemisphere. *Bibliotheca Lichenologica* 52: 1–134.
- McCarthy P.M. 1994a. Corticolous species of *Porina* (lichenized Ascomycotina, Trichotheliaceae) in Australia. I. *Nova Hedwigia* 58: 391–403.
- McCarthy P.M. 1994b. Corticolous species of *Porina* (lichenized Ascomycotina, Trichotheliaceae) in Australia. II. *Nova Hedwigia* 59: 509–516.
- McCarthy P.M. 2001. Trichotheliaceae. In: McCarthy P.M. (ed.) *Flora of Australia*, Vol. 58A, Lichens 3: 105–157. ABR/CSIRO Australia, Melbourne.
- McCarthy P.M. 2003. Catalogue of the lichen family Porinaceae. *Bibliotheca Lichenologica* 87: 1–164.
- McCarthy P.M. 2013. Catalogue of Porinaceae. Australian Biological Resources Study, Canberra. Version 4 December 2013. Available from <https://www.anbg.gov.au/abrs/lichenlist/PORINACEAE.html> [accessed 1 May 2021].
- McCarthy P.M. & Elix J.A. 1996. *Myeloconis*, a new genus of pyrenocarpous lichens from the tropics. *Lichenologist* 28(5): 401–414. <https://doi.org/10.1006/lich.1996.0038>
- McCarthy P.M. & Malcolm W.M. 1997. The genera of Trichotheliaceae. *Lichenologist* 29(1): 1–8.
- Miadlikowska J., Kauff F., Högnabba F., et al. 2014. A multigene phylogenetic synthesis for the class Lecanoromycetes (Ascomycota): 1307 fungi representing 1139 infrageneric taxa, 317 genera and 66 families. *Molecular Phylogenetics and Evolution* 79: 132–168. <https://doi.org/10.1016/j.ympev.2014.04.003>
- Miller M.A., Pfeiffer W. & Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 Nov. 2010: 1–8. New Orleans, LA.
- Müller J. 1880. Lichenes Africae occidentalis a cll. Dr. Pechuel-Loesche et Soyaux e regione fluminis Quillu et ex Angola missi, in Mus. bot. reg. berlinensi servati. *Linnaea* 43: 31–48.
- Müller J. 1882. Lichenologische Beiträge. XV. *Flora* 65: 397–402.
- Müller J. 1883. Lichenologische Beiträge. XVIII. *Flora* 66: 330–338.
- Müller J. 1895. Lichenes exotici III. *Hedwigia* 34: 27–38.
- Nelsen M.P., Lücking R., Rivas Plata E. & Mbatchou J.S. 2010. *Heiomasia*, a new genus in the lichen-forming family Graphidaceae (Ascomycota: Lecanoromycetes: Ostropales) with disjunct distribution in Southeastern North America and Southeast Asia. *The Bryologist* 113(4): 742–751. <https://doi.org/10.1639/0007-2745-113.4.742>
- Nelsen M.P., Lücking R., Andrew C.J., et al. 2014. Molecular phylogeny reveals the true colours of Myeloconidaceae (Ascomycota: Ostropales). *Australian Systematic Botany* 27(1): 38–47. <https://doi.org/10.1071/SB13040>
- Nylander W. 1861. Expositio lichenum Novae Caledoniae. *Annales des Sciences Naturelles, Botanique*, sér. 4, 15: 37–54.
- Nylander W. 1868. Synopsis lichenum Novae Caledoniae. *Bulletin de la Société Linnéenne de Normandie* 2: 39–140.
- Otálora M.A.G., Martínez I., Aragón G. & Wedin M. 2017. Species delimitation and phylogeography of the *Pectenia* species-complex: A misunderstood case of species-pairs in lichenized fungi, where reproduction mode does not delimit lineages. *Fungal Biology* 121: 222–233. <https://doi.org/10.1016/j.funbio.2016.12.001>
- Orange A. 2015. A new freshwater *Porina* (Porinaceae, Ostropales) from Great Britain. *Lichenologist* 47(6): 351–358. <https://doi.org/10.1017/S0024282915000365>
- Orange A., Purvis O.W. & James P.W. 2009. *Porina* Ach. (1809). In: Smith C.W., Aptroot A., Coppins B.J., et al. (eds) *The Lichens of Great Britain and Ireland: 729–737*. British Lichen Society, London.
- Orange A., James P.W. & White F.J. 2010. *Microchemical methods for the identification of lichens*. Second edition. British Lichen Society, London.
- Orange A., Palice Z. & Klepsland J. 2020. A new isidiate saxicolous species of *Porina* (Ascomycota, Ostropales, Porinaceae). *Lichenologist* 52(4): 267–277. <https://doi.org/10.1017/S0024282920000183>
- Rambaut A. 2012. FigTree. Version 1.4.2. Available from <http://tree.bio.ed.ac.uk/software/figtree/> [accessed 8 Apr. 2016].
- Santesson R. 1952. Foliicolous lichens I. A revision of the taxonomy of the obligately foliicolous, lichenized fungi. *Symbolae Botanicae Upsalienses* 12(1): 1–590.
- Schumm F. & Aptroot A. 2010. *Seychelles Lichen Guide*. Beck OHG, Süssen, Germany.
- Seaward M.R.D. & Aptroot A. 2009. Checklist of lichens for the Seychelles group. *Bibliotheca Lichenologica* 99: 335–366.
- Sérusiaux E., Berger F., Brand M. & van den Boom P. 2007. The lichen genus *Porina* in Macaronesia, with descriptions of two new species. *Lichenologist* 39(1): 15–33. <https://doi.org/10.1017/S0024282907005993>
- Sipman H.J.M. 1991. More foliicolous lichens from Australia. *Nova Hedwigia* 53: 255–264.
- Sobreira P.N.B., Cáceres M.E.S., Maia L.C. & Lücking R. 2018. *Flabelloporina*, a new genus in the Porinaceae (Ascomycota, Ostropales), with the first record of *F. squamulifera* from Brazil. *Phytotaxa* 358(1): 67–75. <https://doi.org/10.11646/phytotaxa.358.1.4>
- Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30(9): 1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>
- Thébaud C., Warren B.H., Cheke A.C. & Strasberg D. 2009. *Mascarene Islands, Biology*. In: Gillespie R.G. & Clague D. (eds) *Encyclopedia of Islands: 612–619*. California University Press, Berkeley, U.S.A.
- Vainio E.A. 1924. Lichenes a W. A. Setchell et H. E. Parks in insula Tahiti a 1922 collecti. *University of California Publications in Botany* 12(1): 1–16.
- van den Boom P.P.G., Brand M., Ertz D., et al. 2011. Discovering the lichen diversity of a remote tropical island: working list of species collected on Reunion (Mascarene archipelago, Indian Ocean). *Herzogia* 24: 325–349.

Vězda A. 1975. Foliicole Flechten aus Tanzania (Ost-Africa). *Folia Geobotanica et Phytotaxonomica* 10: 383–432.

Vězda A. 2000. Lichenes Rariores Exsiccati, Fasciculi 43, (numeris 421). Brno, Julius 2000. 4 pp.

White T.J., Bruns T.D., Lee S.B. & Taylor J.W. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis M.A., Gelfand D.H., Sninsky J.J. & White T.J. (eds) *PCR protocols—a guide to methods and applications*: 315–322. Academic Press, New York.

Zoller S., Scheidegger C. & Sperisen C. 1999. PCR primers for the amplification of mitochondrial small subunit ribosomal DNA

of lichen-forming ascomycetes. *Lichenologist* 31(5): 511–516.

<https://doi.org/10.1006/lich.1999.0220>

Communicating editor: Jérôme Degreef.

Submission date: 31 May 2021

Acceptance date: 20 Sep. 2021

Publication date: 30 Mar. 2022