

# *Saxiloba*: a new genus of placodioid lichens from the Caribbean and Hawaii shakes up the *Porinaceae* tree (lichenized *Ascomycota*: *Gyalectales*)

Robert Lücking<sup>1\*</sup>, Bibiana Moncada<sup>2</sup>, Harrie J. M. Sipman<sup>1</sup>, Priscylla Nayara Bezerra Sobreira<sup>3</sup>, Carlos Viñas<sup>4</sup>, Jorge Gutiérrez<sup>4</sup> & Timothy W. Flynn<sup>5</sup>

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**Abstract.** The new genus *Saxiloba* is described with the two species *S. firmula* from the Caribbean and *S. hawaiiensis* from Hawaii. *Saxiloba* is characterized by a unique, placodioid thallus forming distinct lobes, growing on rock in shaded to exposed situations with a trentepohlioid photobiont and a fenestrate thallus anatomy with distinct surface lines. The material is often sterile, but *Porina*-like perithecia and ascospores had previously been described for the Caribbean taxon and were here confirmed for both species. Molecular sequence data also confirmed placement of this lineage in *Porinaceae*. Its position within that family supports the notion that *Porinaceae* should be subdivided into a larger number of genera than proposed in previous classification attempts. Compared to other *Porinaceae*, *Saxiloba* exhibits a unique morphology and anatomy that recalls taxa in the related family *Graphidaceae* and it substantially expands the known phenotypic variation within *Porinaceae*. The two recognized species are similar in overall morphology but, apart from their disjunct distribution and different substrate ecology, differ in lobe configuration, color and disposition of the crystal clusters and resulting surface patterns.

**Key words:** *Labyrinthina*, *Leucodecton*, *Poeltidea*, *Trichotheliaceae*, window lichens

## Introduction

Island ecosystems exhibit high levels of endemism, often harboring unique phenotypes (Magnusson & Zahlbruckner 1945; Johnson & Raven 1973; Wagner & Funk 1995; Pax et al. 1997; Morden et al. 2003). Archipelagos such as Hawaii and Galapagos, but also the Caribbean, are known for striking evolutionary radiations in vascular plants and vertebrates (Carlquist et al. 2003; O’Grady & DeSalle 2008; Parent & Crespi 2009; Givnish et al. 2009; Tye & Francisco-Ortega, J. 2011; Lerner et al. 2011; Knope et al. 2012). In contrast, island lichen biota are generally considered low in endemism with rates estimated between 10% and 30% (Weber 1986; Eldredge & Miller 1995; Aptroot & Bungartz 2007; Smith 2013). However, recent

molecular approaches and detailed morphological revisions suggest the opposite with endemism in lichen fungi often comparable to that of vascular plants (Moncada et al. 2014, 2017; Bungartz et al. 2016; Dal Forno et al. 2017; Lücking et al. 2017; Mercado-Díaz et al. 2020).

During a survey of three islands in Hawaii in 2013 to sample lichen material for molecular studies, RL and BM revised collections held at the National Tropical Botanical Garden herbarium (PTBG), including a strange lichen collected by TWF 24 years ago on shaded basalt on the island of Kauai. The taxonomic affinities of this lichen remained unresolved until similar material was found rather abundantly on shaded calcareous rock outcrops during an expedition to western Cuba (Pinar del Río) in April 2016, by RL, BM, CV and JG. While the overall morphology and anatomy of the two lichens suggested affinities with certain *Graphidaceae*, in particular the genera *Leucodecton* and *Sanguinotrema* (Frisch et al. 2006; Rivas Plata et al. 2010; Lücking et al. 2015), molecular sequence data unexpectedly placed the Cuban taxon within *Porinaceae*. Careful search for ascomata indeed revealed the presence of perithecia in a few specimens, producing 3–5-septate ascospores. Revision of taxa historically described from Cuba, as part of a checklist project

<sup>1</sup> Botanischer Garten und Botanisches Museum, Freie Universität Berlin, Königin-Luise-Straße 6–8, 14195 Berlin, Germany

<sup>2</sup> Licenciatura en Biología, Universidad Distrital Francisco José de Caldas, Cra. 4 No. 26D-54, Torre de Laboratorios, Herbario, Bogotá D.C., Colombia

<sup>3</sup> Departamento de Micología, Universidade Federal de Pernambuco, Av. Nelson Chaves s/n, Recife, PE 50670-420, Brasil

<sup>4</sup> Jardín Botánico Nacional, Carretera del Rocío km 3½, Calabazar, 19230 Habana, Cuba

<sup>5</sup> National Tropical Botanical Garden, 3530 Papalina Road, Kalaheo, HI 96741 USA

\* Corresponding author e-mail: [r.luecking@bgbm.org](mailto:r.luecking@bgbm.org)

together with CV and HJMS, turned up two names under which the lichen had been previously described, namely *Verrucaria firmula* Nyl. (Nylander 1892; nom. inval.) [= *Porina firmula* Nyl. ex Müll. Arg. (Müller 1885)] and *Endopyrenium incrassatum* Müll. Arg. (Müller 1885) [= *Dermatocarpon incrassatum* (Müll. Arg.) Zahlbr.].

*Porinaceae* (syn.: *Trichotheliaceae*) is one of the dominant families of tropical crustose lichens, found mostly on bark and leaves in shady, wet forests, but also frequently on rocks (Aptroot & Sipman 1993; McCarthy 1993, 1995, 2001, 2003; Makhija et al. 1994; Lücking 1998; Lücking & Vězda 1998; Rivas Plata et al. 2008; Aptroot & Cáceres 2013; Harada 2015, 2016). Relatively few taxa occur in temperate regions. Species in this family are characterized by a thin, crustose, compact thallus with a trentepohlioid photobiont and by perithecioid ascomata with unbranched paraphyses, thin-walled, unitunicate asci, and hyaline ascospores with thin walls and septa (Aptroot & Sipman 1993; McCarthy 1993, 2001; Lücking 2008). Together with *Coenogoniaceae* and *Gyalectaceae*, *Porinaceae*, which also includes *Myeloconidaceae* (McCarthy & Elix 1996; Nelsen et al. 2014), is now placed in the resurrected order *Gyalectales*. The latter is sister to the also resurrected order *Graphidales* including *Graphidaceae* and *Gomphillaceae* (Grube et al. 2004; Baloch et al. 2010; Kraichak et al. 2018; Lücking 2019).

Whereas *Porinaceae* is well-delimited at family level, both phenotypically and phylogenetically, its internal classification has been the subject of much debate with proposals ranging from recognizing few genera only, including a single large genus, *Porina* (Lücking 1998, 2008; Lücking et al. 2017), to distinguish several smaller genera characterized by perithecial morphology and thallus characters (Hafellner & Kalb 1995; Harris 1995, 2005; McCarthy & Malcolm 1997). Molecular sequence data support the separation into smaller genera, but the phenotypes hitherto distinguished at genus level do not necessarily form monophyletic groups, and many taxa have not yet been sampled (Baloch & Grube 2006, 2009; Nelsen et al. 2014). Along with the recent recognition of a new genus, *Flabelloporina*, a possible future generic concept for *Porinaceae* was outlined (Sobreira et al. 2018). The placement of the newly discovered lineage further supports this solution. Also, the two lichens treated here add a new phenotype to the known morphological variation of this family. Since the phylogenetic analysis supports the uniqueness of this lineage, it is here described as a new genus, *Saxiloba*.

## Material and methods

The sequenced material was collected in the province of Pinar del Río in westernmost Cuba, during a field trip by RL, BM, CV, and JG; voucher specimens are deposited in B and HAJB. The new sequences for this study were generated using the Sigma REExtract-N-Amp Plant PCR Kit (St. Louis, Missouri, SA) for DNA isolation, following the manufacturer's instructions but with lower proportions for lower amounts of DNA. We targeted both the mitochondrial small subunit (mtSSU)

**Table 1.** GenBank accession numbers for the sequence data used in this study.

Genus	Species	mtSSU accession	Country or Territory
<i>Coenogonium</i>	<i>leprieurii</i>	AY584698	
<i>Coenogonium</i>	<i>luteum</i>	AY584699	
<i>Coenogonium</i>	<i>pineti</i>	AY300884	
<i>Myeloconis</i>	<i>erumpens</i>	KJ449328	New Caledonia
<i>Myeloconis</i>	<i>fecunda</i>	KJ449325	Brazil
<i>Myeloconis</i>	<i>guyanensis</i>	KJ449326	Puerto Rico
<i>Porina</i>	<i>aenea</i>	KR108906	Wales
<i>Porina</i>	<i>alba</i>	DQ168371	Costa Rica
<i>Porina</i>	<i>atrocoerulea</i>	DQ168390	Costa Rica
<i>Porina</i>	<i>austroatlantica</i>	KR108903	Falkland Islands
<i>Porina</i>	<i>byssophila</i>	KR108911	Wales
<i>Porina</i>	<i>chlorotica</i>	KR108908	Ireland
<i>Porina</i>	<i>cryptostoma</i>	KJ449308	Costa Rica
<i>Porina</i>	<i>dolichophora</i>	KJ449306	Costa Rica
<i>Porina</i>	<i>epiphylla</i>	DQ168374	Costa Rica
<i>Porina</i>	<i>exasperatula</i>	KJ449316	Panama
<i>Porina</i>	<i>exocha</i>	KF833333	Australia
<i>Porina</i>	<i>farinosa</i>	KJ449311	Panama
<i>Saxiloba</i>	<i>firmula</i>	MT371252	Cuba 41891 (piece 'd'); DB22547
<i>Saxiloba</i>	<i>firmula</i>	MT371253	Cuba 41891 (piece 'f'); DB22548
<i>Porina</i>	<i>guianensis</i>	DQ168384	Costa Rica
<i>Porina</i>	<i>heterospora</i>	KJ449318	Brazil
<i>Porina</i>	<i>imitatrix</i>	KJ449315	Panama
<i>Porina</i>	<i>karnatakensis</i>	DQ168376	Costa Rica
<i>Porina</i>	<i>lectissima</i>	DQ168414	Austria
<i>Porina</i>	<i>limbulata</i>	AY648893	Costa Rica
<i>Porina</i>	<i>lucida</i>	DQ168377	Costa Rica
<i>Porina</i>	<i>mastoidea</i>	DQ168382	Costa Rica
<i>Porina</i>	<i>nitidula</i>	DQ168392	Costa Rica
<i>Porina</i>	<i>nucula</i>	KJ449310	Costa Rica
<i>Porina</i>	<i>pacifica</i>	KT254300	Canada
<i>Porina</i>	<i>papillifera</i>	DQ168396	Costa Rica
<i>Porina</i>	<i>radiata</i>	DQ168386	Costa Rica
<i>Porina</i>	<i>repanda</i>	DQ168393	Costa Rica
<i>Porina</i>	<i>rubentior</i>	DQ168405	Costa Rica
<i>Porina</i>	<i>rufula</i>	DQ168407	Costa Rica
<i>Porina</i>	<i>subepiphylla</i>	DQ168380	Costa Rica
<i>Porina</i>	<i>subnitidula</i>	DQ168394	Mexico
<i>Porina</i>	<i>tetracerae</i>	KJ449314	Panama
<i>Trichothelium</i>	<i>annulatum</i>	DQ168415	Mexico
<i>Trichothelium</i>	<i>epiphyllum</i>	DQ168416	Costa Rica
<i>Trichothelium</i>	<i>pallidisetum</i>	AY648900	Costa Rica

and the nuclear large subunit rDNA (nuLSU), but only obtained sequences for the former; previous work suggests that nuLSU sequences are notoriously difficult to obtain for members of this family (Nelsen et al. 2014). The mtSSU was amplified using the primers SSU1R and SSU3R (Zoller et al. 1999). The 13- $\mu$ L PCR reactions consisted of 6.0  $\mu$ L of water, 0.1  $\mu$ L of each PCR primer, 3.5  $\mu$ L of REExtract-n-AmpPCRReady Mix (Sigma-Aldrich) and 2.0  $\mu$ L DNA. The PCR cycling conditions

were as follows: 95°C for 5 min, followed of 35 cycles at 94°C for 45 s, after 50°C for 1 min, 72°C for 1.5 min, followed by a single 72°C final extension for 10 min.

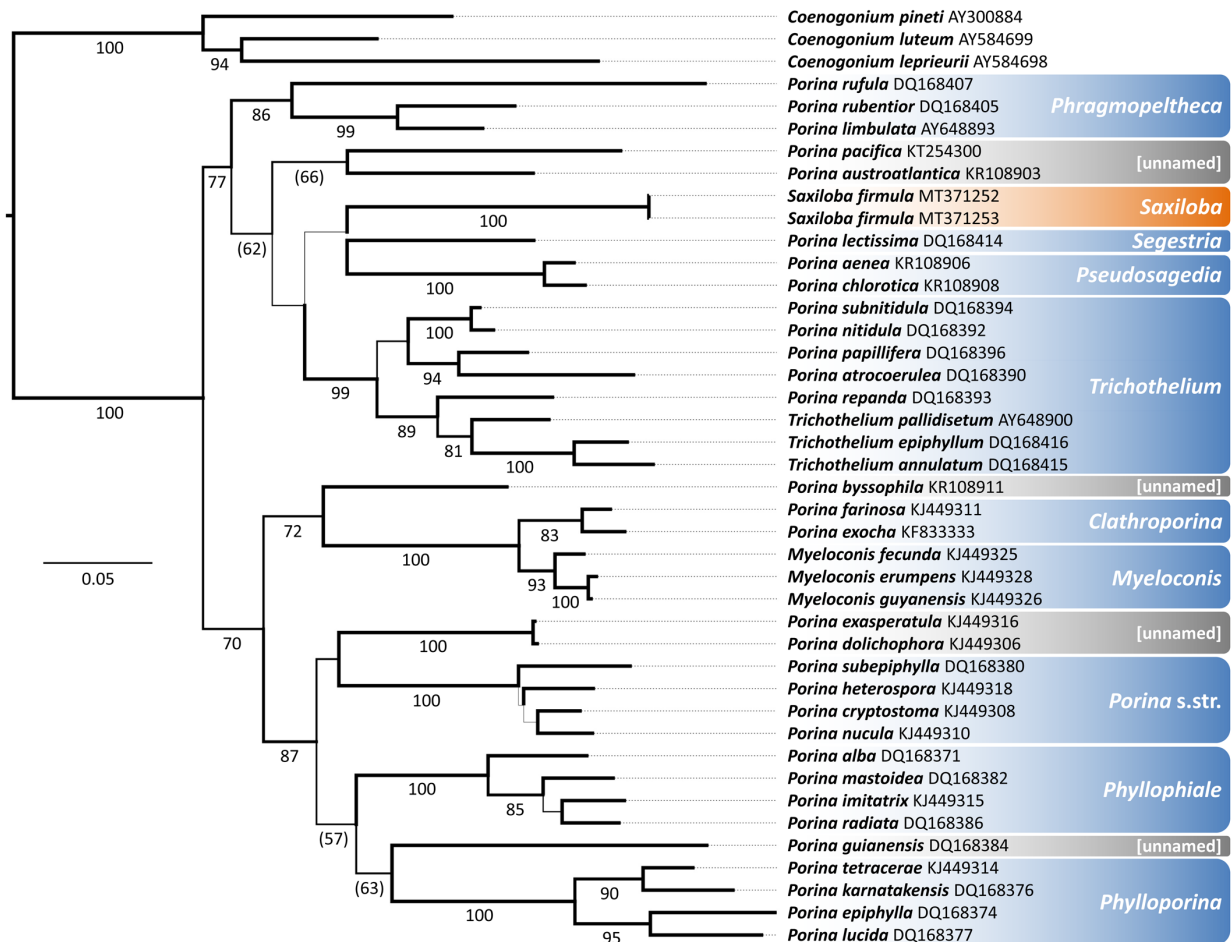
Prior to assembly, the obtained sequence reads were evaluated using BLASTn (Chen et al. 2015) and combined with selected sequences of *Porinaceae* from GenBank, using *Coenogonium* as outgroup (Table 1). All sequences were arranged in BIOEDIT 7 (Hall 1999) and aligned using MAFFT 7 (Kato & Standley 2013). The phylogenetic tree was built by means of maximum likelihood with 1000 bootstrap pseudoreplicates using RAxML 8 (Stamatakis 2014). The best-scoring tree was visualized in FigTree 1.4 (Rambaut & Drummond 2012).

## Results and discussion

Although based on a single marker, the mitochondrial small subunit rDNA (mtSSU), the molecular phylogeny of *Porinaceae* was well-resolved and supported including in the backbone (Fig. 1). Overall the topology was congruent with that obtained by Sobreira et al. (2018). The family formed two large clades with 77% and 70% support, respectively. One contained taxa with exposed, black or red perithecia, the other those with perithecia covered by thallus, except for the black-fruited *Porina byssophila* lineage, which clustered with support with

*Clathroporina* and *Myeloconis*. Besides perithecial wall pigmentation, the lineages in the first large clade were largely distinguished by substrate (leaves vs. bark vs. rock) and biome ecology (tropical vs. temperate); most of these have generic names available. For instance, black-fruited tropical species on leaves clustered in the genus *Trichothelium*, whereas temperate-subtropical species on bark and rock, including aquatic taxa, formed separate lineages (*Pseudosagedia*, *P. pacifica* clade). Similarly, red-fruited, tropical, foliicolous species formed a lineage (*Phragmopelthea*) separate from temperate, corticolous taxa (*Segestria*). In the clade characterized by thallus-dominated perithecial verrucae, lineages were chiefly separated by ascospore septation (muriform in *Clathroporina* and *Myeloconis*) and shape (narrow filiform in the *P. dolichophora* clade), as well as habitat ecology, thallus morphology and substrate (*Porina* s.str., *Phyllophiale*, *P. guianensis* clade, *Phylloporina*).

The unique, placodioid taxon from Cuba, *Saxiloba firmula*, was placed in the first large clade, which is congruent with its red perithecia (present in few specimens) resembling those of *Phragmopelthea* and *Segestria*. However, it formed a strongly supported lineage on a long branch separate from the latter two, and monophyly of these three lineages was rejected with high significance (SH test employed in RAxML 8;  $p < 0.001$ ). Together



**Figure 1.** Best-scoring maximum-likelihood tree of *Porinaceae* based on the mtSSU marker, showing the position of the new genus *Saxiloba* within the context of newly recognized genus-level clades. Clade labels follow Sobreira et al. (2018). Some smaller clades partly consisting of singletons have no names available.



with the unique thallus morphology within the genus, we conclude that this lineage should be recognized at genus level, and introduce the genus *Saxiloba* for it.

## Taxonomy

*Saxiloba* Lücking, Moncada & Viñas, gen. nov. (Figs 2–3)

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Diagnosis: A new genus in the family *Porinaceae*, characterized by a placodioid thallus with clusters of columnar crystals visible from above areoles separated by a network of reticulate to meandering lines with reddish perithecia and with small, transversely septate ascospores, growing on rock.

Generic type: *Saxiloba firmula* (Nyl. ex Müller) Lücking, Moncada & Viñas.

**Description.** Thallus saxicolous, placodioid, convex with distinct marginal lobes, but densely appressed to the substrate; surface smooth, but with a distinct network of reticulate to meandering lines (best seen when hydrated). Photobiont *Trentepohlia*. Thallus in section with large, triangular to rhomboid crystal clusters embedded into the photobiont layer (somewhat appearing like teeth within gums), the photobiont layer developed horizontally beneath and vertically between the crystal clusters; above with a prosoplectenchymatous cortex and below with a medulla and a thick, dark brown hypothallus layer. Perithecia immersed to erumpent or somewhat prominent, largely covered by thallus, ostiolar area orange-red to cherry-red or dark reddish brown, lacking a thallus cover and slightly translucent; paraphyses and asci as in other genera of the family. Ascospores transversely 3–5-septate, small.

**Etymology.** Referring to the placodioid thallus with distinct marginal lobes, apparently growing exclusively on rock.

**Distribution and ecology.** Thus far only known from disjunct collections on islands in the Caribbean (Cuba, Isla de la Juventud, Puerto Rico) and the Hawaiian archipelago (Kauai); growing on calcareous or volcanic rock in shady to exposed situations.

**Notes.** Within *Porinaceae*, the new genus *Saxiloba* is readily distinguished by its placodioid thallus with columnar clusters of crystals embedded in a network of reticulate to meandering lines when seen from above. The unique thallus morphology and anatomy corresponds to its phylogenetic position on a separate, rather long branch. Notably, the largely thallus-covered perithecia of *Saxiloba firmula* resemble those of the larger second clade of the family, whereas those of *S. hawaiiensis* are more similar to those of red-fruited foliicolous species in the *Phragmopelthea* clade.

Except for the occasionally present perithecia, which immediately reveal its systematic affinities, the genus would not be considered a member of *Porinaceae*, but bears resemblance with lichens in some other related and unrelated families. Most similar are certain species in the genus *Leucodecton* in the related family *Graphidaceae*,

in particular *L. phaeosporum* (Rivas Plata et al. 2010; Rivas Plata & Lumbsch 2011), which are readily distinguished by the apothecioid, pore-like ascomata with apically thick-walled asci forming brown, muriform ascospores, and in the sterile state by the absence of distinct marginal lobes.

The particular thallus anatomy found in *Saxiloba* can be compared to what has been coined ‘window lichens’ (‘Fensterflechten’; Vogel 1955; Follmann 1965), in analogy to the ‘stone plants’ (‘Fensterpflanzen’) in the former family *Mesembryanthemaceae* (now *Aizoaceae*). This anatomy was redescribed in much detail from a presumably monospecific genus, *Labyrinthia implexa* (Malcolm et al. 1995), recently recombined as *Poeltidea implexa* (Fryday & Hertel 2014), a rock-dwelling taxon in the unrelated family *Lecideaceae*. Malcolm et al. (1995) made no reference of the earlier treatments of ‘window lichens’ by Vogel (1995) and Follmann (1965), but Vondrák & Kubásek (2013) and Fryday & Hertel (2014) showed that this anatomy appears to have evolved in several unrelated lineages, although it is not frequent. Vertical stacks of algal cells separated by columnar crystal clusters or vertical stacks of fungal hyphae have been interpreted as adaptation to xeric habitats and/or high solar insolation (Vondrák & Kubásek 2013; Fryday & Hertel 2014). This hypothesis seems to fit the Hawaiian species, *Saxiloba hawaiiensis*, whereas *S. firmula* grows more frequently in shady conditions. Under such conditions, one could also imagine the vertical crystals to aid in light distribution across a thicker photobiont layer, thus enabling the accumulation of higher biomass under low light.

## Key to the known species of *Saxiloba*

- 1 Thallus regularly rosette-forming with radiating lobes with contiguous tips; lobes 0.5–1 mm wide; surface silvery grey-green; lines of crystal clusters forming a network of closed, isodiametric to elongate chambers; on calcareous rock in usually shady conditions; Caribbean . . . . . *Saxiloba firmula*  
Thallus irregular in outline with irregular lobes often leaving interspaces; lobes 1–0.15 mm wide; surface olive-yellow to yellowish grey-green; lines of crystal clusters forming a meandering, labyrinthine network of partially open, elongate to jigsaw-puzzle-shaped chambers; on basalt in more exposed conditions; Hawaii . . . . . *Saxiloba hawaiiensis*

*Saxiloba firmula* (Nyl. ex Müll. Arg.) Lücking, Moncada & Sipman, comb. nov. (Fig. 2)

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= *Porina firmula* Nyl. ex Müll. Arg., Bot. Jb. 6: 401. 1885; *Verrucaria firmula* Nyl., Flora 59: 365. 1876.

Type: Cuba. Unknown locality and date, C. Wright s.n. (G-G00293637, lectotype!, here designated; Lich. Cub. 7b; isolectotypes: G-G00293636, G-G00293638; Lich. Cub. 7).

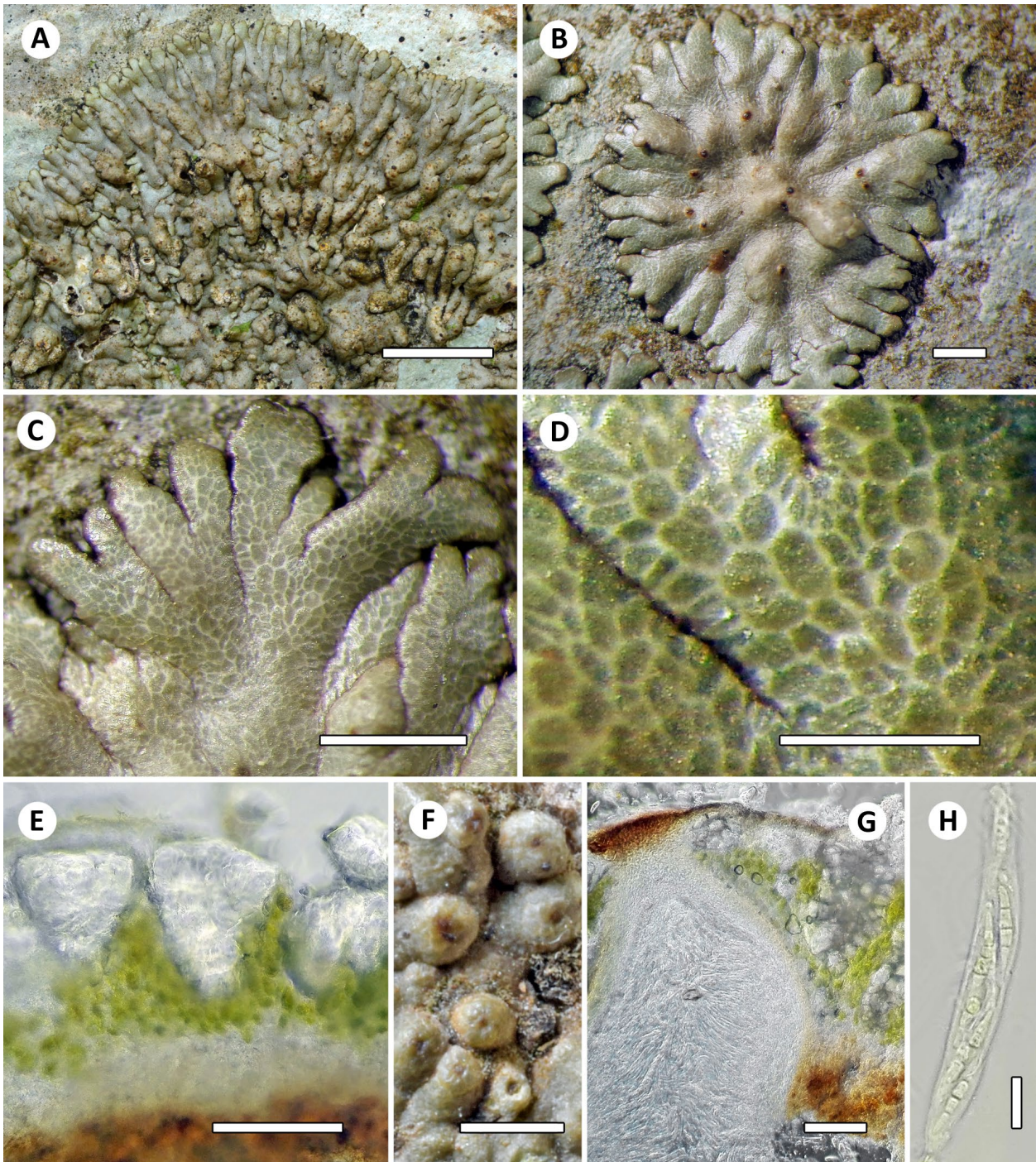
= *Endopyrenium incrassatum* Müll. Arg., Bot. Jb. 6: 377 (1885); *Dermatocarpon incrassatum* (Müll. Arg.) Zahlbr., Cat. Lich. Univers. 1: 218. 1921 [1922].

Type: Cuba. Unknown locality and date, C. Wright s.n. (G-G00291774, lectotype!, here designated; Lich. Cub., Ser. II: 535; isolectotype: G-G00291775; Lich. Cub., Ser. II: 535).



**Description.** Thallus saxicolous on calcareous rocks, up to 5–10(–20) mm diam. with regularly radiating lobes with closely contiguous tips; lobes 0.5–0.1 mm wide; surface silvery grey-green with a network of reticulate lines around isodiametric to elongate chambers (best seen when hydrated). Thallus in section 200–300  $\mu\text{m}$  thick with large, up to 100  $\mu\text{m}$  high and broad, triangular to rhomboid crystal clusters embedded into the photobiont layer, the latter developed horizontally beneath and

vertically between the crystal clusters; above with a 20–30  $\mu\text{m}$  thick, prosoplectenchymatous cortex and below with a 30–50  $\mu\text{m}$  thick medulla and a 40–70  $\mu\text{m}$  thick, dark brown hypothallus layer. Perithecia erumpent from the thallus and almost up to the ostiolar area covered with a thick thallus layer, up to 0.5 mm diam.; excipulum 25–35  $\mu\text{m}$  thick, outer parts paraplectenchymatous, pale yellowish, K<sup>+</sup> deep orange-red, inner parts prosoplectenchymatous, colourless; involucrellum only



**Figure 2.** Habit of *Saxiloba firmula*. A – thallus on calcareous rock; B – young thallus with immature perithecia; C–D – thallus lobes hydrated (in D enlarged) to show crystal clusters embedded in a network of hyphae with the photobiont layer beneath; the crystals reflect the greenish color of the photobiont, whereas the pale color of the reticulate lines is caused by the upper cortex; E – thallus section showing disposition of crystal clusters, photobiont layer, upper cortex, medulla and hypothallus; F – perithecia; G – section through perithecium showing laterally covering thallus layer with details of crystal clusters; H, ascus with ascospores. (A – Lücking et al. 41865; B–D – Lücking et al. 41891; E–G – Lücking & Moncada 45298; H – lectotype). Scales: A = 5 mm; B–C, F = 1 mm; D = 0.5 mm; E, G = 100  $\mu\text{m}$ ; H = 10  $\mu\text{m}$ .



developed around the ostiolar area, 30–60 µm thick, paraplectenchymatous, reddish brown with a distinct reddish tinge when seen from the outside. Ascospores 8 per ascus, oblong-fusiform, transversely 3–5(–7)-septate, 15–20(–25) × 3–4(–6) µm, hyaline. Pycnidia rare, up to 0.1 mm diam., appearing as brownish red warts. Conidia oblong-bacillar, non-septate, 3–4 × 1 µm, hyaline.

**Distribution and ecology.** Thus far known from Cuba, including Isla de la Juventud (also known as Isle of Pines or Isla de Pinos) and further reported from the Bahamas and Puerto Rico (Müller 1885; Riddle 1923; Gannutz 1970; Mercado-Díaz 2009). Possibly a Caribbean endemic, in Cuba quite common on calcareous rocks in mostly shaded microhabitats in the dry forests of western and central Cuba. In Puerto Rico, it would be expected in similar habitats, but has not been found in recent surveys. According to Gannutz (1970), the Puerto Rican material was collected at El Yunque National Forest, a rather wet forest with a geology dominated by volcanic rock. This would broaden the ecological range for *Saxiloba firmula*, but since we have not been able to obtain the material corresponding to this record, we are considering these data with care.

**Notes.** *Saxiloba firmula* was first introduced as nomen nudum by Nylander (1876) in the genus *Verrucaria* and shortly after validated by Müller (1885) in the genus *Porina*. Müller (1885: 401) did not properly describe the unique thallus morphology of the species, likely because the type material had originally been scraped off the substrate and is fragmented into numerous, small pieces in the lectotype and isolectotypes. Müller (1885: 377) described the same species also as *Endopyrenium incrassatum*, possibly because of the few, young ascomata ('*apothecia pauca valde juvenilia offerunt*') with small (18–20 × 4–6 µm), 1-septate ascospores, not realizing the identity of the material. McCarthy (1993) did not mention the name in his treatment of saxicolous *Porina* species; he annotated the type material in 1992 as 'probably not *Porina*'.

Riddle (1923) reported the species from Isla de la Juventud (Isle of Pines). One of the two cited collections was reported as '... Cerro San Juan del Mar, Columbia ...' (Riddle 1923: 71), which may cause confusion, as there is indeed such a location in Colombia. However, the material refers to Cerros de San Juan in the Columbia community on Isla de la Juventud (Kallunki 1980; Boom 1996; Sastre de Jesús & Santiago-Valentín 1996). In the same paper, Riddle (1923) described *P. subfirmula* Riddle, also from Isla de la Juventud. That species has, however, a very different, crustose thallus morphology (isotype in NY, NY01219352, Britton & Wilson 15741 checked).

Müller (1885) described (and illustrated the ascospores on the type material as predominantly 5-septate and 20–30 µm long. In our recently collected material, we found only few thalli with perithecia with the ascospores mostly 3-septate and 15–20 µm long. Annotations on NY specimens by R.C. Harris also indicate 3-septate ascospores and a discrepancy with Müller's description (J. Lendemer, pers. comm. 2020). Revision of the

lectotype showed the ascospores to be mostly 3-septate, more rarely 4–5-septate, and 15–20(–25) µm long. It is therefore unclear how Müller (1885) derived his observations, although based on annotations by R. C. Harris, the material from the Bahamas apparently also features ascospores with more numerous septa (J. Lendemer, pers. comm. 2020).

**Specimens examined.** BAHAMAS. Andros, Mastic Point and Vicinity; 25°03'N, 77°57'W; 19–28 March 1907, L. J. K. Brace 7048a (FH). Cockburn Town, Watling's Island; 12–13 March 1907, N. L. Britton & C. F. Millsbaugh 6126 (FH). CUBA. The type material of *P. firmula* and *E. incrassatum*. Artemisa: Candelaria, Jardín Botánico Orquideario Soroa; 22°47'N, 83°01'W, 210 m; on shaded calcareous rock face; 24 March 2017, R. Lücking & B. Moncada 43034 (B, HAJB). Cienfuegos: Cumanayagua, Las Vegas del Matagua, trail from Lucia's house to Las Lagunas; 21°59'14"N, 80°11'54"W, 665 m; evergreen lower montane (mesophyllous) rain forest, on calcareous rock; 21 March 2018; R. Lücking & B. Moncada 45155 (B, HAJB), 45157 (B). Caletón de Don Bruno, trail from town towards coastal mangrove; 22°04'16"N, 80°27'44"W, 0–25 m; matorral costero, on calcareous rock; 22 March 2018, R. Lücking & B. Moncada 45298 (B). Pinar del Río: Rio Guao; 27 February 1911; N. L. Britton et al. 9668 (FH). Viñales, Pinar del Río National Park, Sierra de Quemado, Moncada, 20 km WSW of Viñales, 'mogote' behind Malagones monument; 22°33'N, 83°51'W, 180 m; mesophyllous semideciduous forest on karst, on calcareous rock face; 9 April 2016, R. Lücking et al. 41865, 41891 (B, HAJB). Sancti Spiritus: Trinidad, Parque Natural Protejido Topes de Collantes, trail to Pico de Potrerillo; 21°53'17"N to 21°54'19"N, 80°00'11"W to 80°00'31"W; 650–860 m; on calcareous rock; 19 March 2018, R. Lücking & B. Moncada 44918 (B). Isla de la Juventud: SW of Nueva Gerona, Sierra de Casas, Mogote El Abra; 21°85'N, 82°82'W; April–May 1975, R. Schubert (B, HAL). Cerro San Juan del Mar; 20 February 1916, N.L. Britton & P. Wilson 14683 (FH, NY). Cerros de Bibijagua; 28 February 1916, N.L. Britton & P. Wilson 15047 (FH, NY).

*Saxiloba hawaiiensis* Lücking, Moncada & Flynn, sp. nov. (Fig. 3)

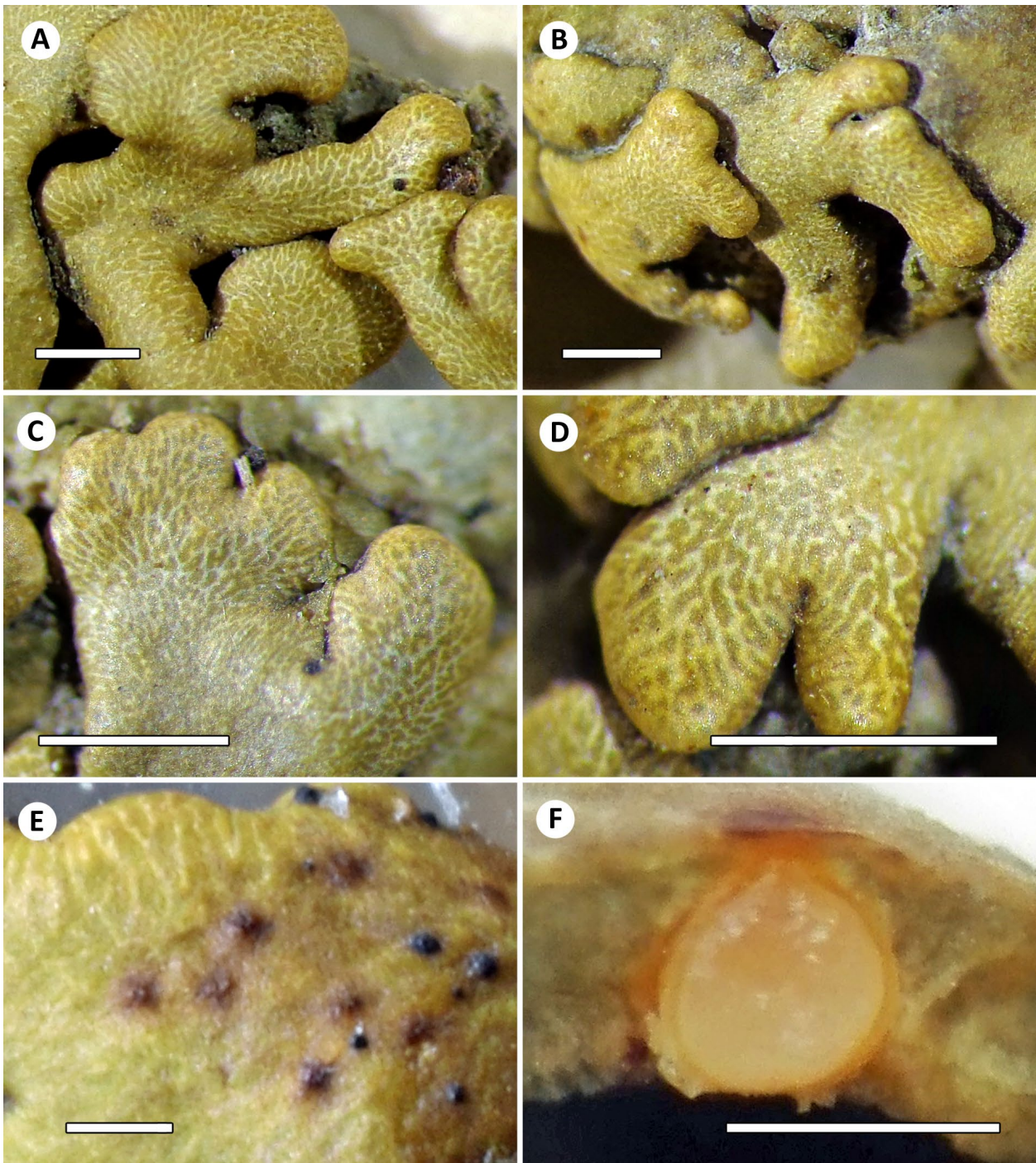
MycoBank MB 835480

Diagnosis: Differing from *Saxiloba firmula* in the irregular thallus outline with the lobes often leaving interspaces, and the surface lines forming a meandering, labyrinthine network with partially open, elongate to jigsaw-puzzle-shaped chambers.

Type: USA. Hawaii, Kauai, Waimea District, Na Pali-Kona Forest Reserve, Mahanaloa Valley; 410 m (1340 ft); disturbed forest dominated by *Aleurites* with *Kokia*, *Pisonia*, *Hibiscus*, *Nototrichium*, *Psidium*, *Rubus*, *Microlepidia*, and *Christella*, on shaded basalt face, locally common; 24 August 1992, T. Flynn et al. 5095 (PTBG 1000024450 – holotype; B, WIS – isotypes).

**Description.** Thallus saxicolous on basalt, up to 10 mm diam. with irregularly branched lobes usually leaving interspaces; lobes 1.0–1.5 mm wide; surface yellowish olive with meandering, labyrinthine lines forming a network of partially open, elongate to jigsaw-puzzle-shaped chambers. Thallus in section 400–800 µm thick with large, up to 300 µm high and up to 150 µm high broad, narrowly rhomboid crystal clusters embedded into the photobiont layer, the latter developed horizontally beneath and vertically between the crystal clusters; above with a 20–30 µm





**Figure 3.** Habit of *Saxiloba hawaiiensis* (isotype). A–C – thallus fragments removed from basalt; D–E – thallus lobes enlarged to show meandering crystal clusters embedded in a network of hyphae with the photobiont layer beneath; the crystals reflect the greenish color of the photobiont, whereas the pale color of the reticulate lines is caused by the upper cortex; F – young thalli developing atop an old, decaying thallus portion. Scales: A–D = 1 mm; E–F = 0.5 mm.

thick, prosoplectenchymatous cortex and below with an up to 300  $\mu\text{m}$  thick medulla and a 30–50  $\mu\text{m}$  thick, brownish black hypothallus layer. Perithecia immersed in the thallus and almost up to the ostiolar area covered with a thick thallus layer, up to 0.6 mm diam.; excipulum 25–35  $\mu\text{m}$  thick, outer parts paraplectenchymatous, yellowish, K+ deep orange-red, inner parts prosoplectenchymatous, colourless; involucrellum only developed around the ostiolar area, 30–50  $\mu\text{m}$  thick, paraplectenchymatous, reddish brown with a distinct reddish tinge when seen from the outside. Ascospores 8 per ascus, oblong-fusiform,

transversely 3-septate, 15–20  $\times$  3.5–4.5  $\mu\text{m}$ , hyaline. Pycnidia not observed.

**Distribution and ecology.** Thus far known only from the type locality on the island of Kauai in Hawaii, like the type species growing on shaded rocks, but on volcanic basalt.

**Notes.** The material here described as *Saxiloba hawaiiensis* was collected by TWF and colleagues more than 25 years ago, but left unidentified. During a visit by RL and BM to the National Tropical Botanic Garden on Kauai, the material drew our attention. With the

subsequent discovery of a similar lichen in Cuba, we were able to finally put a name on the Hawaiian lichen as well, especially as upon close inspection, we discovered the presence of perithecia producing asci and ascospores typical of *Porinaceae*. *Saxiloba hawaiiensis* shares with *S. firmula* the placodioid thallus with the striking surface pattern formed by the columnar thallus crystals. Although we do not have sequence data for this taxon, the irregular lobe configuration, the more robust lobes, the differences in the patterns of the surface lines surrounding the crystalline clusters, and the different substrate and disjunct distribution leave no doubt that this species is distinct from the Caribbean taxon.

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