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A new corticolous species of *Mazosia* A.Massal.
(Roccellaceae, Arthoniales) from Guadeloupe,
remarkable by its byssoid thallus

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A new corticolous species of *Mazosia* A.Massal. (Roccellaceae, Arthoniales) from Guadeloupe, remarkable by its byssoid thallus

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ABSTRACT

An unknown species of Roccellaceae Chevall. was collected in 2022 and 2023 on the bark of trunks in a rainforest in Basse-Terre island (Guadeloupe, Lesser Antilles). Phylogenetic analyses using mtSSU, nuLSU and RPB2 sequences reveal the placement of the species in the genus *Mazosia* A.Massal. (Roccellaceae). The lichen is unusual for the genus by being the first species of *Mazosia* developing a byssoid thallus. It is described as *Mazosia byssoidea* Lebreton & Ertz, sp. nov. Besides its byssoid thallus, the new species is characterized by 1-septate ascospores, stipitate pycnidia and a chemistry with roccellic acid. Together, all these features make the new species a distinctive and important addition to the Arthoniales Henssen ex D.Hawksw. & O.E.Erikss. So far, it is only known from two large trees in a dense humid forest at low elevation, a locality that needs to be included in a protected area. A key to the corticolous species of *Mazosia* is provided.

KEY WORDS

Caribbean islands,
Lesser Antilles,
lichenized fungi,
phylogeny,
new species.

RÉSUMÉ

Une espèce nouvelle corticole de *Mazosia* A.Massal. (Roccellaceae, Arthoniales) de Guadeloupe, remarquable par son thalle byssôïde.

Une espèce inconnue de Roccellaceae Chevall. a été collectée en 2022 et 2023 sur écorce d'arbres dans une forêt tropicale dense et humide sur l'île de la Basse-Terre en Guadeloupe (Petites Antilles). Des analyses phylogénétiques utilisant les séquences mtSSU, nuLSU et RPB2 révèlent le placement de l'espèce dans le genre *Mazosia* A.Massal. (Roccellaceae). Ce lichen est inhabituel pour le genre car il s'agit de la première espèce de *Mazosia* développant un thalle byssôïde. Il est décrit comme *Mazosia byssoidea* Lebreton & Ertz, sp. nov. En plus de son thalle byssôïde, la nouvelle espèce est caractérisée par des ascospores à une cloison, des pycnides pédonculées et une chimie caractérisée par l'acide roccellic. L'ensemble de ces caractéristiques fait de cette nouvelle espèce un ajout singulier et important aux Arthoniales Henssen ex D.Hawksw. & O.E.Erikss. Jusqu'à présent, elle n'est connue que de deux grands arbres dans une forêt dense humide de basse altitude, une localité qui devrait être incluse dans une zone protégée. Une clé des espèces corticoles du genre *Mazosia* est fournie.

MOTS CLÉS
Caraïbes,
Petites Antilles,
champignons lichénisés,
phylogénie,
espèce nouvelle.

INTRODUCTION

As part of a contribution to the lichen checklist of Guadeloupe, an expedition aimed at collecting lichens in Guadeloupe was carried out in January 2022. Specimens challenging to determine by the second author were shown to Dr André Aptroot, which led to the conclusion that one of them was an undescribed species of Arthoniales Henssen ex D.Hawksw. & O.E.Erikss.

Since the specimen was insufficiently developed to be appropriately described, and in order to confirm the exceptional significance of this discovery through DNA analyses, additional fertile specimens were found and collected in the same rainforest during a second field trip in Guadeloupe (Fig. 1), conducted by the second author. The species has a distinct byssoid thallus, rounded apothecia, 1-septate ascospores, stipitate pycnidia and roccellic acid. This unusual combination of characters suggested that it might represent an undescribed genus. However, molecular data unequivocally revealed a surprising placement in *Mazosia* A.Massal., a genus for which all species known so far have a crustose compact thallus.

The genus *Mazosia* belongs to the family Roccellaceae Chevall., a diverse assemblage of taxa ranging from crustose to fruticose lichen-forming fungi (e.g. Tehler 1990; Follmann 2001; Tehler & Irestedt 2007; Aptroot & Sparrius 2008; Tehler *et al.* 2009, 2010; Ertz *et al.* 2015). Species of *Mazosia* are characterized by a crustose thallus; immersed-erumpent, rounded, apothecoid ascomata with a three-layered, zeorine margin composed of a proper excipulum formed by dark brown hyphae, a layer of crystals, and a thin, thallus layer dominated by the trentepohlioid photobiont; cylindrical-clavate to oblong asci; and transversely septate, hyaline ascospores (e.g. Lücking 2008). In some corticolous taxa, the characteristic apothecial margin is not visible (e.g. Sparrius 2004). All species are lichenized, with the exception of *M. adelphoparasitica* Matzer, lichenicolous on the foliicolous *M. rotula* (Mont.) A.Massal. (Matzer 1996). Species of *Mazosia* are found in (sub)tropical rainforests, more rarely in temperate forests, mainly growing on leaves of vascular plants, more rarely on the bark of trees.

Only few species of *Mazosia* have been included in molecular phylogenies so far. The genus was placed phylogenetically in the Roccellaceae, as sister to a lineage formed by the genera *Dichosporidium* Pat., *Enterographa* Fée and *Erythrodictyon* G.Thor (Frisch *et al.* 2014; Ertz *et al.* 2015). Some species were recently newly described with the support of molecular data (Yao *et al.* 2021a, b). The generic type, *Mazosia rotula*, has not been included in phylogenies yet, but the genus is assumed to be monophyletic.

The aim of this study is to describe the new species and to elucidate its phylogenetic relationships.

MATERIAL AND METHODS

SAMPLING MATERIAL

This study is based on specimens collected by the second author during two field trips dedicated mainly to foliicolous lichen species in Guadeloupe, in January 2022 and in April 2023.

The specimens were carefully dried for weeks using absorbent paper with silica gel beads until DNA extraction. Collection of specimens was carried out under the collection permits no. 2022-03 and no. 2023-17 issued by the Guadeloupe National Park (request form: <https://www.guadeloupe-parcnational.fr/fr/le-parc-national-de-la-guadeloupe/reglementation/prelevements-vocation-scientifique>). Voucher specimens are deposited in the herbaria BR, PC, LG and GUAD.

MORPHOLOGICAL AND CHEMICAL CHARACTERIZATION

The external morphology was studied and measured using an Olympus SZX12 stereomicroscope. Macroscopic photographs were made with a Keyence VHX-5000 Digital Microscope and a VH-Z20R/W/T lens. Hand-cut sections and squash preparations of thallus were mounted in water, a 5% aqueous potassium hydroxide solution (K), or in Lugol's iodine solution (1% I₂) without (I) or with K pre-treatment (KI), and studied using an Olympus BX51 compound microscope. The K and I solutions were added to a water mount by running a drop under the edge of the coverslip. Calcium oxalate was identified by adding 25% H₂SO₄. Measurements from ascomatal sections (e.g. hymenium, asci, ascospores) refer to dimensions in water. Measurements of ascospores and pycnidia are reported as (minimum-) mean-standard deviation – mean+standard deviation (-maximum), followed by number of measurements (n). For other characters the range is given, with unusual values obtained only once shown in parentheses. Microscopic photographs were prepared using an Olympus BX51 compound microscope fitted with an Olympus SC50 digital camera. Colour reactions of the thallus were studied using K, common household bleach (C), K followed by common household bleach (KC), crystals of para-phenylenediamine 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).

MOLECULAR TECHNIQUES

Well-preserved and freshly collected specimens (less than five months) lacking any visible symptoms of fungal infection were used for DNA isolation in two different laboratories, at Meise Botanic Garden and at University of Liège. At Meise Botanic Garden, hand-made sections of the pycnidia (specimen *Lebreton 2310*), as well as thallus hyphae only (specimens *Lebreton 2310* and *2311*) were used for direct PCR as described in Ertz *et al.* (2015). The material was then added to a tube containing the PCR reaction mixture and amplified directly. Amplification reactions and PCR cycling conditions were the same as described in Ertz & Tehler (2023). A targeted fragment of about 1 kb of the RPB2 protein-coding gene was amplified using primers fRPB2-7cF and fRPB2-11aR (Liu *et al.* 1999), and a fragment of about 0.8 kb of the mtSSU rDNA was amplified using primers mrSSU1 and mrSSU3R (Zoller *et al.* 1999). At University of Liège (Botanical Institute), DNA from the thalli (*Lebreton 2310*) and from apothecia (*Lebreton 2311*) was extracted using the CTAB method (Cubero *et al.* 1999). A fragment of about 1.1 kb of the nuLSU rDNA was amplified using primers AL2R (Mangold *et al.* 2008) and LR6

(Vilgalys & Hester 1990). Both strands were sequenced by Macrogen® using 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 ANALYSIS

Two matrices were assembled: 1) a dataset of RPB2 sequences for placing the newly sequenced taxon in a phylogeny of the order Arthoniales; and 2) a three-locus dataset (nuLSU, mtSSU and RPB2 sequences) for providing a detailed phylogeny of the genus *Mazosia* with all sequences currently available for the genus. For the Arthoniales matrix, the new RPB2 sequences were included in the dataset published by Diederich & Ertz (2020). The dataset was slightly modified, notably by including additional sequences of *Mazosia* that were retrieved from GenBank. For the matrix of *Mazosia*, sequences published in Frisch *et al.* (2014), Ertz *et al.* (2015) and Yao *et al.* (2021a, b) were retrieved from GenBank (Table 1). The sequences were aligned using MAFFT v7.490 (Katoh & Standley 2013) on the CIPRES Web Portal (Miller *et al.* 2010) and manually corrected for errors using Mesquite 3.04 (Maddison & Maddison 2015). Terminal ends of sequences, ambiguously aligned regions and introns were delimited manually and excluded from the datasets. The resulting matrix of Arthoniales consisted of 73 terminals, while the matrix of *Mazosia* consisted of 18 terminals. *Arthothelium galapagoense* Huneck & Follmann was used as the rooting taxon in the Arthoniales dataset, while *Erythrodictyon granulatum* (Mont.) G.Thor was selected in the *Mazosia* dataset. The datasets of Arthoniales and *Mazosia* consisted of 921 and 2685 (1165 for nuLSU, 668 for mtSSU and 852 for RPB2) unambiguously aligned sites, respectively.

Analyses for topological incongruence among loci were carried out for the *Mazosia* dataset by analysing the single locus datasets with a Maximum Likelihood (ML) approach using the program RAxML v.8.2.12 (Stamatakis 2014) on the CIPRES Web Portal (Miller *et al.* 2010). The GTR-GAMMA model was used and node support was assessed running 1000 bootstrap replicates. We analysed the three single locus datasets for topological incongruence by assuming a conflict significant when two different relationships (one being monophyletic and the other being non-monophyletic) for the same set of taxa were both supported with bootstrap values $\geq 70\%$ (Mason-Gamer & Kellogg 1996; Reeb *et al.* 2004). Based on this criterion, no conflict was detected and the nuLSU, mtSSU and RPB2 datasets were concatenated.

A ML analysis was performed on the two datasets using RAxML v.8.2.12 (Stamatakis 2014) on the CIPRES Web Portal (Miller *et al.* 2010) with 1000 ML bootstrap iterations (ML-BS). The *Mazosia* dataset was divided in three partitions, corresponding to the three loci, with the GTR-GAMMA model. Phylogenetic trees were visualised using FigTree v.1.4.2 (Rambaut 2012).

The ML trees are shown with the ML-BS values added above the internal branches when significant (Figs 2; 3). ML-BS ≥ 70 were considered to be significant.



FIG. 1. — Trunk with *Mazosia byssoidea* Lebreton & Ertz, sp. nov. in its type locality in Guadeloupe. Knife marks on bark correspond to paratypes sampling (Lebreton 1618, Lebreton 2310).

RESULTS

PHYLOGENETIC ANALYSIS

Eight new sequences (one nuLSU, five mtSSU and two RPB2) were obtained for this study, but since the mtSSU of both specimens of the new species obtained in Meise Botanic Garden and the University of Liège were identical, only three of the five are published (Table 1). The RAxML tree obtained from the Arthoniales dataset is shown in Figure 2, and the main well-supported lineages are in accordance with the results obtained by Diederich & Ertz (2020). The new species is nested within the genus *Mazosia* that form a well-supported lineage. It is the sister species to *M. carnea* (Eckfeldt) Aptroot & M.Cáceres, another corticolous species sequenced from Guadeloupe.

The RAxML tree obtained from the *Mazosia* dataset is shown in Figure 3. This tree is based on a three-locus dataset that has 35% of missing data (Table 1), so that the results must be taken with great care, but it has the advantage to include for the first time all data available on GenBank for the genus. The relationships are in accordance with those obtained by Yao *et al.* (2021a, b) for smaller single-locus datasets. The new species is sister to the foliicolous *Mazosia dispersa* (J.Hedrick) R.Sant., and both are sister to the corticolous *M. carnea*, but these relationships are poorly supported. As already pointed out previously, corticolous and foliicolous species do not

TABLE 1. — Species names, voucher specimens and GenBank accession numbers. The GenBank accession numbers of the sequences generated in this study are in **bold**.

Species	Voucher	RPB2	LSU	mtSSU
<i>Erythrodictyon granulatum</i>	Gabon, Ertz 9908 (BR)	EU704022	EU704090	EU704058
<i>Mazosia bambusae</i>	Guyana, Joensson 3C (UPS)	–	KJ851057	KJ851008
<i>Mazosia byssoidea</i> 2310	Guadeloupe, Lebreton 2310 (PC)	OR733353	–	OR725976
<i>Mazosia byssoidea</i> 2311	Guadeloupe, Lebreton 2311 (PC)	OR733354	OR725979	OR725977
<i>Mazosia carnea</i> 1	Guadeloupe, Ertz 15684 (BR)	KJ524394	KJ524308	–
<i>Mazosia carnea</i> 2	Guadeloupe, Ertz 15686 (BR)	KJ524395	KJ524309	–
<i>Mazosia dispersa</i>	Martinique, Ertz 18554 (BR)	KJ524396	–	OR725978
<i>Mazosia hainanensis</i> 1	China, Jiang HN20171277 (holo-, HMAS)	–	MT683119	–
<i>Mazosia hainanensis</i> 2	China, Jiang HN20171184 (HMAS)	–	MT683120	–
<i>Mazosia melanophthalma</i>	Guyana, Joensson 3b2 (UPS)	KJ851146	KJ851063	–
<i>Mazosia</i> aff. <i>melanophthalma</i> 1	Uganda, Frisch 11/Ug140b (UPS)	–	KJ851060	KJ851009
<i>Mazosia</i> aff. <i>melanophthalma</i> 2	Uganda, Frisch 11/Ug140c (UPS)	KJ851144	KJ851061	KJ851010
<i>Mazosia paupercula</i>	Gabon, Ertz 9264 (BR)	KJ524397	KJ524310	–
<i>Mazosia phyllosema</i> 1	China, HN20192543-1 (HMAS-L 0147112)	–	–	MW023084
<i>Mazosia phyllosema</i> 2	China, HN20192560-1 (HMAS-L 0147113)	–	–	MW023085
<i>Mazosia weii</i> 1	China, Wang 20190565 (holo-, HMAS-L 0146702)	–	MT899270	MT901037
<i>Mazosia weii</i> 2	China, Wang 20190437-4 (HMAS-L 0146703)	–	MT899271	MT901038
<i>Mazosia</i> sp.	Japan, Frisch 13Jp126 (TNS)	KJ524398	KJ524311	–

form separate clades (Yao *et al.* 2021b). Besides *M. carnea* and the new species, *Mazosia* sp. is also a corticolous species, but it is sister to the foliicolous *M. hainanensis* Z.T.Yao, S.H.Jiang & Z.F. Jia.

Mazosia byssoidea Lebreton & Ertz, sp. nov.
(Fig. 4)

Differing from all species of *Mazosia* by the combination of a distinct byssoid thallus, 1-septate ascospores, stipitate pycnidia and by the production of roccelic acid as a major secondary metabolite.

HOLOTYPE. — **Guadeloupe**. Sainte-Rose municipality, forest managed by the Office national des forêts, hiking trail from Sofaïa to Saut des Trois Cornes, on the banks of the moustique river, 16°17'9.179"N, 61°43'34.374"W, 200-300 m elevation, riparian tropical rainforest, on tree, 03.IV.2023, *Elise Lebreton 2311* (holo-, PC[PC0779827]; GenBank [OR733354, OR725979, OR725977]).

ISOTYPE. — **Guadeloupe**. Sainte-Rose municipality, forest managed by the Office national des forêts, hiking trail from Sofaïa to Saut des Trois Cornes, on the banks of the moustique river, 16°17'9.179"N, 61°43'34.374"W, 200-300 m elevation, riparian tropical rainforest, on tree, 03.IV.2023, *Elise Lebreton 2311* (iso-, BR[BR5030170788830]).

PARATYPE. — **Guadeloupe**. Sainte-Rose municipality, forest managed by the Office national des forêts, hiking trail from Sofaïa to Saut des Trois Cornes, 16°17'13.463"N, 61°43'33.146"W, 200-300 m elevation, dense tropical rainforest, on tree, 03.IV.2023, *Elise Lebreton 2310* (para-, GUAD, LG[PSA10A-18060]; GenBank [OR733353, OR725976]); *ibid.*, 29.I.2022, *Elise Lebreton 1618* (para-, GUAD, LG[IMV00A-14517]).

ETYMOLOGY. — The epithet is derived from the structure of the thallus that is distinctly byssoid.

CHEMISTRY. — Thallus surface, medulla and lower side of thallus and pycnidia K–, C–, KC–, PD–, UV–. TLC (solvent A): roccelic acid (major) (specimens *Lebreton 2310* and *Lebreton 2311* tested).

DISTRIBUTION AND ECOLOGY. — So far known only from Guadeloupe (Basse-Terre island) in the Lesser Antilles, where it inhabits a dense humid forest or riparian forest managed by the Office national des

forêts. It is only known from two large trees. The holotype (*Lebreton 2311*) was found on the riverbank, on a tree that was sparsely colonized by the lichen. The paratypes (*Lebreton 1618*, *Lebreton 2310*) were collected on the second tree, in 2022 and 2023 respectively (Fig. 1). This tree was on the hiking trail and the trunk was abundantly covered with *M. byssoidea* Lebreton & Ertz, sp. nov. but only a few thalli had apothecia. *Mazosia byssoidea* Lebreton & Ertz, sp. nov. is clearly rare and the current populations should be protected and monitored in the future. The locality is not included in the National Park and should therefore be included in a natural reserve. The species should be searched for elsewhere in Guadeloupe and the Caribbean islands to better access its conservation status.

MYCOBANK. — MB850668.

DESCRIPTION

Thallus up to *c.* 5 cm in diam., loosely attached to the substrate, byssoid, smooth, rarely sparsely squamulose, effuse, pale olive-grey, matt, ecorticate, esorediate, heteromerous, *c.* 150 µm thick. Prothallus poorly differentiated, byssoid, white to dark brownish, sometimes white with a dark brownish margin. Photobiont layer forming the upper part of the thallus; photobiont trentepohlioid, in chains, formed of rounded to elongate, 9–22 × 8–15 µm cells. Medulla thick, white, I+ pale orange, KI+ pale orange, formed of 2–3 µm wide hyphae, with numerous crystals of calcium oxalate (H₂SO₄), 1–7 (–10) µm diam. Hypothallus loosely byssoid, thin and discontinuous, dark brown to blackish, formed of (2.5–)3–4 µm wide dark brown hyphae; hypothallus free areas on the lower thallus surface whitish, rarely pale cream. Ascomata apothecoid, sessile, often distinctly constricted at the base, rounded, single, not forming stromatic aggregates, sparsely distributed on the thallus, 0.33–0.85 mm diam. (n = 24); margin prominent, of the same colour of the thallus, smooth, (90–)150–210 µm thick, epruinose; hymenial disc black, covered by a very thin layer of whitish hairs; hairs straight, vertical, *c.* 10–13 × 2–3 µm. Excipulum inconspicuous. Hymenium clear, hyaline to pale fawn, 60–90 µm tall, I+ pale reddish brown, KI+ pale blue; epihymenium pale brown to orange, K–, I+ pale reddish brown, KI+ pale blue. Paraphysoids branched-anastomosing, *c.* 2 µm

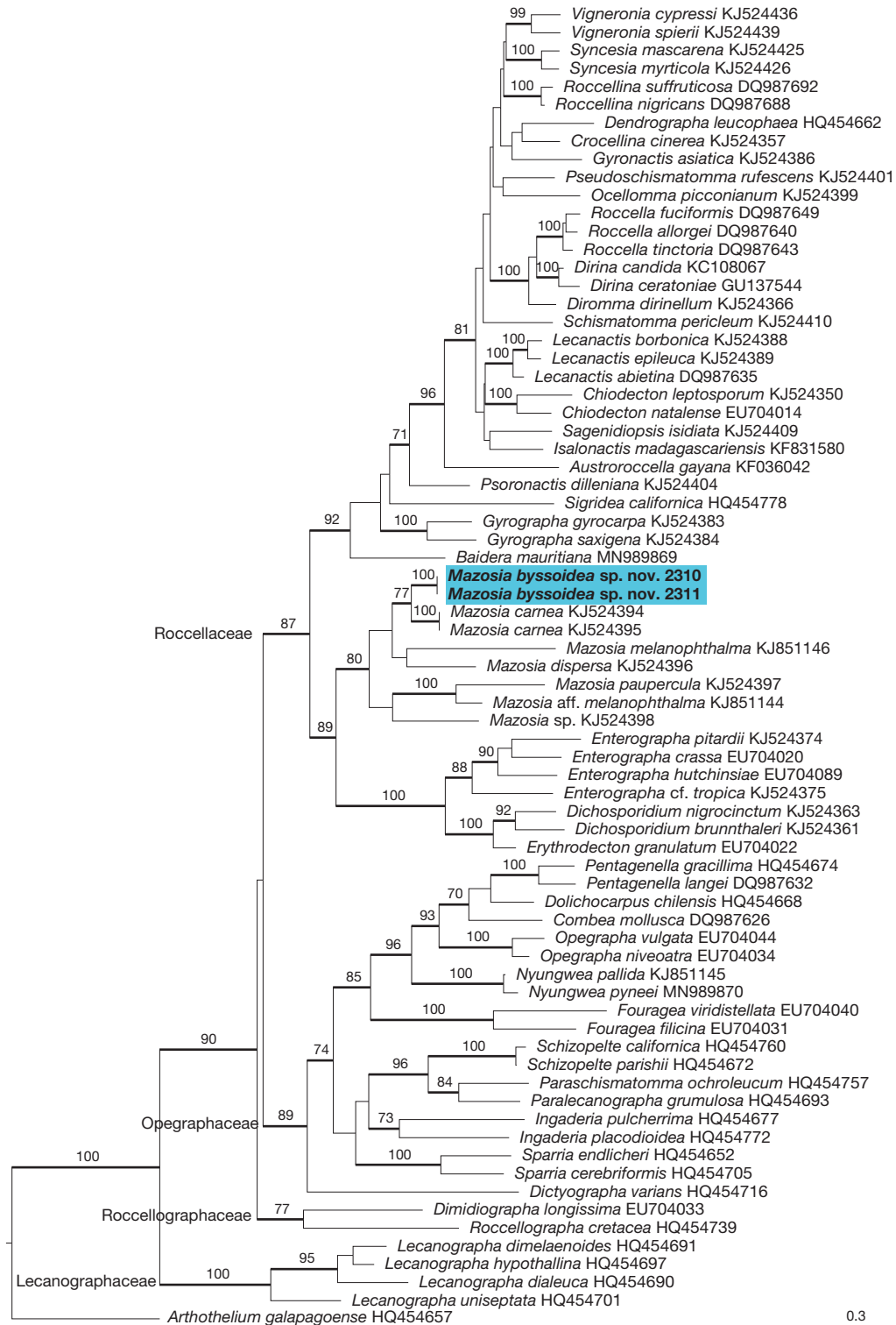


Fig. 2. — Phylogeny of Roccellaceae Chevall. based on a dataset of RPB2 sequences that resulted from a RAxML analysis. Maximum likelihood bootstrap values, when significant (≥ 70), are shown near internal branches. Internal branches considered as strongly supported are represented by **thicker lines**. The newly sequenced samples are in **bold** and their names are followed by collection numbers, which act as specimen and sequence identifiers. The lineage corresponding to the new species is in a **blue rectangle**.

thick, often slightly enlarged in epihyemium (*c.* 3 μm) and forming straight hyaline hairs on the surface of the hymenial disc. Hypothecium dark brown, thick, not extending to the substrate, 75–100 μm thick, I–, K+ olivaceous. Ascus 8-spored,

narrowly clavate, 54–65 \times 12–15 μm ($n = 5$), with a tiny but often poorly developed ocular chamber; endoascus I+ reddish, KI+ pale blue with a KI+ dark blue apical ring. Ascospores hyaline, \pm fusiform or narrowly ovoid, with the upper half

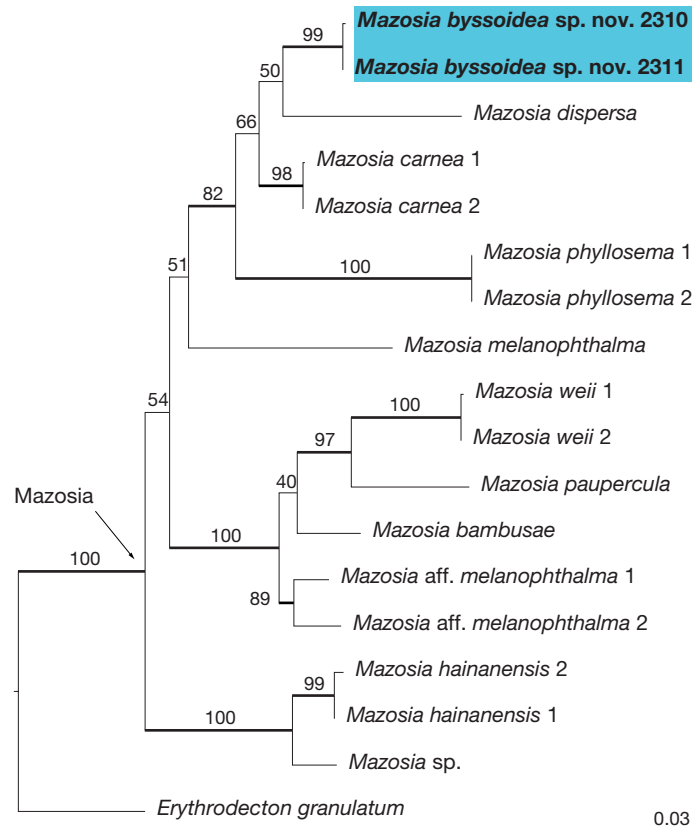


FIG. 3. — Phylogeny of the genus *Mazosia* A. Massal. (with *Erythrodecton granulatum* (Mont.) G. Thor as outgroup) based on a dataset of nuLSU, mtSSU and RPB2 sequences that resulted from a RAxML analysis. Maximum likelihood bootstrap values are shown above or near internal branches. Internal branches considered as strongly supported (bootstrap value ≥ 70) are represented by **thicker lines**. The newly sequenced samples are in **bold** and their names followed by collection numbers, which act as specimen and sequence identifiers. The lineage corresponding to the new species is in a **blue rectangle**.

often slightly wider, 1-septate, not constricted at the septum, with the cells equal or one slightly longer, I+ pale yellowish, (13-)13.6-16.6(-19) \times (4-)4.2-5(-5) μm (n = 25); gelatinous sheath sometimes visible, c. 0.5-0.8 μm thick. Pycnidia single, very rarely grouped by two, sparsely distributed on the thallus, straight, stipitate, cylindrical or slightly wider at the base or at the half upper part, not or slightly constricted at the base, unbranched, whitish or of the same colour as the thallus except for the top that is pale greyish and with the ostiole visible as a tiny black dot, epruinose, (0.39-)0.45-0.75(-0.89) \times (0.19-)0.23-0.3(-0.33) mm (n = 24); wall in section pale brown to orange, K+ olivaceous, surrounded by a thick white medulla layer with trentepohlioid photobiont present near the surface; conidiogenous cells unbranched, straight, hyaline, 6-8 \times 2-2.5 μm ; conidia hyaline, non-septate, fusiform-ellipsoid, 5.5-7 \times 2.5-3 μm (n = 20).

NOTES

The new species is unique within the genus *Mazosia* by its byssoid thallus. All other species in the genus have a compact thallus. Some species produce a pilose thallus such as *Mazosia pilosa* Kalb & Vězda and *M. weii* Z.T. Yao, S.H. Jiang & Z.F. Jia, or a tomentum such as *M. tomentifera* Vězda & Lumbsch (see Yao *et al.* 2021b for a key to species of *Mazosia* with pilose thalli). These hairs like structures are developed from compact

thalli, which are very different from the loosely arranged filamentous structure of a byssoid thallus. All these pilose species also differ notably by their foliicolous habit and usually more septate ascospores (Kalb & Vězda 1988; Lumbsch & Vězda 1990; Lücking 2006; Yao *et al.* 2021b). Besides *M. byssoidea* Lebreton & Ertz, sp. nov., only two other species of *Mazosia* produce 1-septate mature ascospores: the lichenized *M. uniseptata* Lücking and the lichenicolous *M. adelphoparasitica*, which both are species confined to leaves of vascular plants (Matzer 1996; Lücking 2006).

Mazosia byssoidea Lebreton & Ertz, sp. nov. differs from other taxa of Roccellaceae having a byssoid thalli by the combination of apothecoidal ascomata not forming stromatic structures, 1-septate ascospores, stipitate pycnidia and a chemistry with roccellic acid. Among the byssoid Roccellaceae, the new species is most similar to the genus *Tania* Egea, Torrente & Sipman, but species of this genus differ by a chemistry with schizopeltic acid and by 3-5-septate ascospores (Egea *et al.* 1995; Harada & Yamamoto 2006). Species of the genus *Sagenidiopsis* R.W. Rogers & Hafellner differ by 3-septate ascospores, different secondary metabolites (e.g. Rogers & Hafellner 1987; Egea *et al.* 1995) and only a distantly phylogenetic position (Fig. 2). Species of the genera *Dichosporidium* and *Streimannia* G. Thor differ by perithecioid ascomata aggregated in stroma-like structures (Thor 1990; Egea *et al.* 1995).

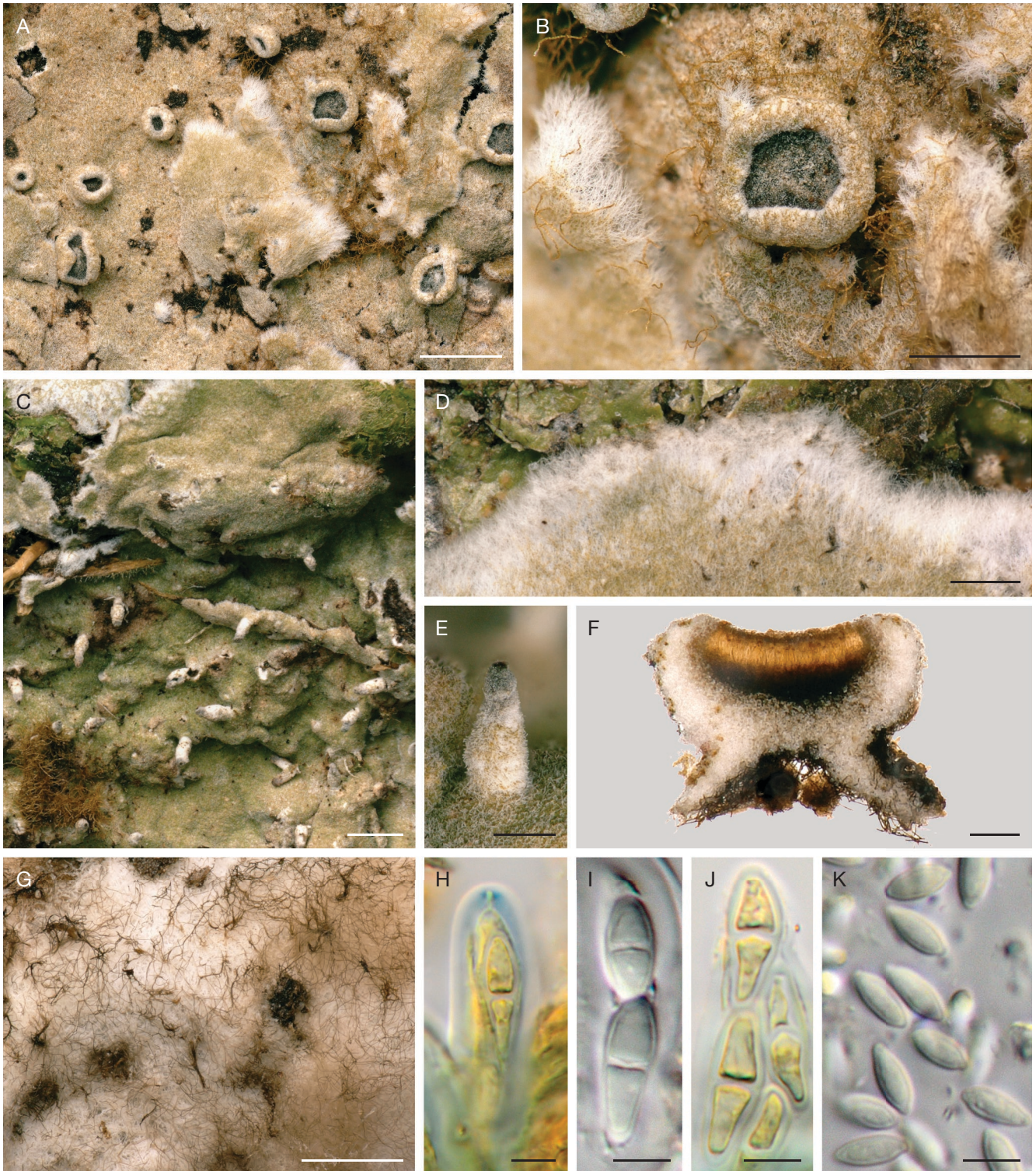


FIG. 4. — *Mazosia byssoidea* Lebreton & Ertz, sp. nov. (A, B, F, H–J, *Lebreton 2311*; C–E, G, K, *Lebreton 2310*): A, B, thallus and apothecia; C, thallus with pycnidia; D, prothallus; E, one pycnidium; F, section of one apothecium in water; G, lower side of the thallus; H, ascus in KI; I, ascospores in water; J, ascospores in KI; K, conidia in water. Scale bars: A, C, 1 mm; B, D, G, 500 μ m; E, 250 μ m; F, 100 μ m; H–K, 5 μ m.

The new species is also reminiscent of the monotypic genus *Catarraphia* A.Massal. that also has a thallus loosely adherent to the substrate and apothecioid ascomata. However, *Catarraphia* differs from the new species by a corticate

thallus; ascomata entirely (including margins) covered by a whitish or bluish pruina; an excipulum made of hyaline hyphae that are densely aggregated, arranged in an anticlinal manner and completely masked by brown granules that

dissolve in K; paraphysoids that are gelatinized in the lower half; 3(-4)-septate ascospores having mucilaginous attenuated appendages at both ends; and a more complex chemistry with cyclographin (Elix *et al.* 1995) and several unidentified substances that are visible under UV light on the TLC plates and show a light yellow color after developing with sulfuric acid (Egea & Torrente 1993; Egea *et al.* 1996). Moreover, its single species, *C. dictyoplaca* (Mont. & Bosch) A.Massal., is only known from the eastern Paleotropics and Melanesia (Egea *et al.* 1996).

Because the thallus is unusual for a species of *Mazosia* and reminiscent of the thalli of some Arthoniales growing in Guadeloupe such as *Dichosporidium nigrocinctum* (Ehrenb.) G.Thor, we wondered whether the ascomata of the new species might represent a lichenicolous fungus growing on the thallus of a second sterile species, in particular as a lichenicolous species (*M. adelphoparasitica*) is already known in the genus. In order to test this hypothesis, some of the sequences used in this study were produced by direct PCRs using a few thallus hyphae only taken far from the ascomata (see Methods). These sequences supported a placement in *Mazosia*. Moreover, no necrotic areas were observed around the ascomata and the chemistry of the thallus is different from *D. nigrocinctum* that always produces protocetraric acid and pycnidia that are not stipitate (Thor 1990). For these reasons, we are convinced that the new species is a lichenized *Mazosia*.

DISCUSSION

Mazosia was considered as a strictly foliicolous genus until Harris (1990) transferred *Platygrapha ocellata* Nyl. to the genus. Since then, no less than seven corticolous species are now accepted in the genus, all differing from the foliicolous taxa and all having a compact crustose thallus and 3-septate ascospores: *M. bruguierae* A.Sakata & H.Harada, *M. carnea*, *M. corticola* Kantvilas, *M. endonigra* (Nyl.) Sparrius, *M. japonica* A.Sakata & H.Harada, *M. leptosticta* (Nyl.) Sparrius and *M. viridescens* (Fée) Aptroot & M.Cáceres (Sparrius 2004; Aptroot *et al.* 2014; Sakata *et al.* 2017; Kantvilas 2020). *Mazosia byssoidea* Lebreton & Ertz, sp. nov. is a new addition to this list of corticolous *Mazosia* and is easily recognizable by its byssoid thallus with stipitate pycnidia and 1-septate ascospores.

Lichens with a byssoid thallus are rare and are known in several only distantly related lineages of lichenized fungi, like in the orders Arthoniales (e.g. Thor 1990; Egea *et al.* 1995; Aptroot *et al.* 2009; Frisch & Thor 2010), Lecanorales (e.g. Hafellner & Vězda 1992; Harris 1995; Kistenich *et al.* 2018; Ertz & Diederich 2022) and Gyalectales (e.g. Aptroot *et al.* 1997; Ertz *et al.* 2021). Within the Arthoniales, parallel evolution of byssoid thalli occurred in the families Arthoniaceae and the Roccellaceae and is usually considered as a synapomorphy of some generic level lineages like *Crypthonia* Frisch & G.Thor, *Dichosporidium*, *Herpothallon* Tobler and *Sagenidiopsis*. More rarely, species of Arthoniales with a distinct byssoid thallus also occur in genera otherwise known

to have a more compact thallus, as proven by molecular data for *Lecanactis mollis* (Stirt.) Frisch & Ertz, a species originally placed in the genus *Sagenidium* Stirt. (Ertz *et al.* 2015). *Mazosia byssoidea* Lebreton & Ertz, sp. nov. is a further prime example of a species having a byssoid thallus and placed in a lineage of species having a compact thallus.

The byssoid thallus is an example of how lichens have diversified and adapted to specific environmental conditions. It is a specialized type of thallus that enables better gas exchange due to its loosely arranged filamentous structure, as compared to the denser thallus structure of most crustose lichens. This adaptation enables lichens to inhabit ecological niches with high moisture levels or frequent rainfall (Lakatos *et al.* 2006; Nelsen *et al.* 2010), as in the dense tropical forest where *Mazosia byssoidea* Lebreton & Ertz, sp. nov. was discovered.

The new species *M. byssoidea* Lebreton & Ertz, sp. nov. is notable for several distinguishing features. Besides its most prominent characteristic, the byssoid thallus, it is also recognized by 1-septate ascospores and stipitate pycnidia, which are rare character states within the family Roccellaceae. Together, these features make the new species a distinctive addition to the Arthoniales.

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WORLDWIDE KEY TO CORTICOLOUS SPECIES OF THE GENUS *MAZOSIA* A.MASSAL. (UPDATED FROM Sakata *et al.* 2017)

1. Thallus byssoid; ascospores 1-septate; pycnidia stipitate *M. byssoidea* Lebreton & Ertz, sp. nov.
— Thallus compact; ascospores 3-septate; pycnidia not stipitate 2
2. Apothecia prominently elevated above the thallus, sharply to slightly delimited in outline 3
— Apothecia slightly elevated above the thallus, semi-immersed to immersed, not sharply delimited in outline ..
..... 6
3. Thallus with irregular and partly confluent verrucae; apothecial margin warty and irregular
..... *M. viridescens* (Fée) Aptroot & M.Cáceres
— Thallus slightly verrucose or almost smooth; apothecial margin crenulate 4
4. Epihymenium with crystals 5
— Epihymenium lacking crystals *M. bruguierae* A.Sakata & H.Harada
5. Thallus slightly verrucose; apothecia prominently elevated above the thallus, slightly delimited in outline
..... *M. carnea* (Eckfeldt) Aptroot & M.Cáceres
— Thallus smooth; apothecia prominently elevated above the thallus, sharply delimited in outline
..... *M. endonigra* (Nyl.) Sparrius
6. Ascospores (15-)18-20 × 3-4 µm *M. japonica* A.Sakata & H.Harada
— Ascospores larger 7
7. Ascospores (17-)19-25(-27) × 4-5.5(-6.5) µm; thallus with psoromic acid *M. corticola* Kantvilas
— Ascospores (22-)28-35 × 4-7 µm; thallus lacking psoromic acid *M. leptosticta* (Nyl.) Sparrius

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