Plant and Fungal Systematics 71(1): 42–63, 2026
DOI: https://doi.org/10.35535/pfsyst-2026-0006

ISSN 2544-7459 (print)
ISSN 2657-5000 (online)

Six new species of *Sporostigma* from Cuba and Colombia and confirmed placement of the genus in the *Arthothelium-Pachnolepia-Snippocia-Tylophoron* clade in *Arthoniaceae*

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Article info

Received: 16 Apr. 2026
Revision received: 26 May 2026
Accepted: 8 Jun. 2026
Published: 31 Jul. 2026

Associate Editor

Harrie Sipman

Abstract. Revision of recently collected material in Cuba and Colombia revealed a surprising diversity of *Sporostigma*, a hitherto monospecific genus with spot-like mazaedia and *Arthonia*-type, brown ascospores, previously only known from Florida. Newly generated molecular sequence data place the genus in the *Arthoniaceae*, specifically in the clade containing the genera *Arthothelium*, *Pachnolepia*, *Snippocia*, and *Tylophoron*. Quantitative analysis of morphological and anatomical characters led to the distinction of six new species, which are formally described in this work: from Cuba, *S. cubanum*, differing from *S. melasporum* in the compact thallus, the lirellate-stellate ascomata with black mazaedia and thickened, crenulate thalline margin, and the smooth ascospores; and from Colombia, *S. hieroglyphicum*, differing from *S. cubanum* in the immersed-erumpent mazaedia with even, flattened margin and often with a split between mazaedium and thallus margin; *S. immersellipsoideum*, differing from *S. melasporum* in the sharply delimited mazaedia and the compact and smooth thallus; *S. lobatum*, differing from *S. immersellipsoideum* in the clearly erumpent mazaedia which become elongate-lobate, the rough thallus, and the comparatively broader ascospores with a typically papilliform proximal cell; *S. pseudostromaticum*, differing from *S. cubanum* in the notably pseudostromatic ascomata with branched to dissected individual mazaedia and with an even thallus margin; and *S. stellatum*, differing from *S. pseudostromaticum* in the rough thallus, the lack of secondary divisions of the mazaedia, and the slightly larger ascospores. This contribution is dedicated to our esteemed colleague and friend, André Aptroot, for his numerous and invaluable contributions to tropical crustose lichen taxonomy.

Key words: environmental impact studies, levantamiento de veda, mitochondrial small subunit rDNA, morphometrics

Introduction

Arthoniaceae Rchb. is one of the most speciose families of lichenized fungi, encompassing over 700 species in about 25 genera (Grube 1998; Sundin 1999; Frisch et al. 2014; Lücking et al. 2017). It is morphologically and biologically diverse, possessing lichen formers, as well as containing lichenicolous and non-lichenized, saprotrophic lineages (Grube et al. 1995; Matzer 1996; Thiyagaraja et al. 2020; Diederich et al. 2025). The family is characterized by mostly spot-like, emarginate ascomata or asci scattered over the thallus, although other types of ascomata also occur. Ascospores are often asymmetric, with the terminal (and sometimes the proximal) cell enlarged, the result of macrocephalic formation of the septa in which no further septa are formed in the terminal (and proximal) cells (Willey 1890; Henssen & Jahns 1973; Eriksson 1982; Lücking 1995; Grube 1998, 2007).

Arthoniaceae is among several unrelated families across lichenized *Ascomycota* that includes lineages with mazaedia, in which the ascospores accumulate on the ascomata as dry, usually black masses, optimized for wind dispersal. Thus far, the family includes one mazaediate genus, *Tylophoron* Nyl. (cigarette lichens), forming prominent mazaedia with a thalline base in which the ascospore mass grows vertically, giving the mazaedia the appearance

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of miniature cigarettes; the ascospores are 1-septate and dark brown (Tibell 1996; Lumbsch et al. 2009; Ertz et al. 2011). In addition, several other genera in the family are known to produce sporodochia, reproductive structures that resemble mazaedia, but represent a type conidiomata with superficially produced asexual conidia; these include *Glomerulophoron* Frisch, Ertz & G. Thor, *Reichlingia* Diederich & Scheid., *Sporodophoron* Frisch, Y. Ohmura, Ertz & G. Thor, and the anamorph of *Tylophoron* (Diederich & Scheidegger 1996; Tibell 1996; Frisch et al. 2015; Ertz et al. 2020).

Arthonia Ach., the type genus of the family, is estimated to encompass about 500 species (Lücking et al. 2017; Sundin & Tehler 1998). However, many of these have not been critically revised and/or belong in other genera, such as *Arthothelium* A. Massal., *Coniarthonia* Grube, *Coniocarpon* DC., *Inoderma* (Ach.) Gray, *Naevia* Fr., or *Synarthonia* Müll. Arg. (Sundin & Tehler 1998; Sundin 1999; Grube 2001a; Aptroot et al. 2015; Frisch et al. 2015, 2020; van den Broeck et al. 2018; Thiyagaraja et al. 2020; Perlmutter et al. 2023). One peculiar species is *Arthonia melaspora* Tuck., described from Florida and thus far only known from that area (Tuckerman in Willey 1887). More than a century later, Grube (2001b) recognized the ascomata of this species as mazaediate and established the monospecific genus *Sporostigma* for it. *Sporostigma* agrees with many – especially tropical – species of *Arthonia* s.lat. in the flat, emarginate ascomata and the asymmetrical spores with large distal cell, but differs in the ascomata becoming mazaediate, with the asci disintegrating, and the ascospores becoming dark brown. Thus far, it has been classified as *incertae sedis* within the order *Arthoniales* (Grube 2001b; Lücking et al. 2017).

Taxonomic field and revisionary work in Cuba and Colombia revealed a surprising diversity of material corresponding to *Sporostigma*, with numerous specimens bearing mazaedia producing *Sporostigma*-type ascospores. As a result of thorough examination of this material, here we introduce six new species in this genus. In addition, the position of *Sporostigma* within *Arthoniales*, specifically within the *Arthoniaceae*, is confirmed by molecular sequence data from one of the new species.

Material and methods

Field work was undertaken in western Cuba, as part of the *Flora (y Funga) de la República de Cuba* project (Rankin-Rodríguez & Greuter 2016; Iturralde & Rankin-Rodríguez 2018; Falcón-Hidalgo et al. 2020; Lücking et al. 2020; González Gutiérrez et al. 2023), and in northeastern Colombia, as part of the environmental impact assessment studies for the projects "*Estudio de Impacto Ambiental para la Línea de Transmisión a 230 kV Chinú – Montería y Subestaciones Asociadas*" (Bastidas-Parrado 2022) and "*Biodiversidad asociada al Estudio de Impacto Ambiental del proyecto: Línea de transmisión Cerromatoso – Chinú – Copey 500 kV*" (ISA INTERCOLOMBIA E.S.P. S.A., Andina de Energía SAS 2025). These studies are required for any new infrastructural projects outside urban areas and in Colombia are called requests for "levantamiento de veda", i.e. lifting of environmental protection measures, as lichens are automatically protected by law in the country (Larrota-Estupiñan 2018). In addition, we revised material housed in the Herbario Forestal UDBC "*Gilberto Emilio Mahecha Vega*", Sección Criptógamas, of the Facultad del Medio Ambiente y Recursos Naturales, Universidad Distrital "Francisco José de Caldas", Bogotá, Colombia.

The material was examined morphologically, anatomically, and chemically, in the laboratories of the Herbario Forestal UDBC "*Gilberto Emilio Mahecha Vega*", Sección Criptógamas, and the Botanischer Garten und Botanisches Museum Berlin, Freie Universität Berlin (BGBM). For the morphological studies, we used a LEICA S6D and a LEICA Zoom 2000 stereomicroscope. Anatomy was assessed using a ZEISS Axiostar Plus and a ZEISS Axioskop compound microscope, with hand sections made in tap water. Macrophotography was done using a NIKON D5300 digital SLR camera with a NIKKOR AF-S DX Micro 40 mm macro lens, as well as a NIKON Z7 with a NIKKOR MC50/2.8 macro lens, in both cases with a RAYNOX Digital Camera Macroscopic Lens 4× attached to it, and a CULLMANN CUlight V 220DL LED light source. Microscopic images were taken under 400× and 1000× magnification with a SAMSUNG Galaxy A71 cell phone attached to the Pl 10×/20 ocular of the ZEISS Axioskop compound microscope. For spot tests, we used commercial bleach (C), 10% potassium hydroxid solution (K), and para-phenylen-diamin crystals dissolved in 96% ethanol (P). Thin-layer chromatography was performed following Orange et al. (2010), using Supelco TLC Silica Gel 60 F254 20 × 20 cm glass plates in solvents C (toluene:acetic acid = 170:30), B' (hexane:diethyl ether:-formic acid 140:72:18) and A (toluene:1,4-dioxan:acetic acid 180:45:5).

Sequence data for the mitochondrial small subunit rDNA (mtSSU) were generated from Cuban material of the newly described species, *Sporostigma cubanum*, and from Colombian material of the newly described species, *S. pseudostromaticum*, using the Sigma REDExtract-N-Amp Plant PCR Kit (St Louis, Missouri, USA) for DNA isolation, following the manufacturer's instructions, except that 40 µL of extraction buffer and 40 µL dilution buffer were used. The mtSSU was amplified using the SSU1R and SSU3R primers (Zoller et al. 1999). The 13-µL PCR reactions consisted of 6.0 µL of water, 0,1 µL of each PCR primer, 3.5 µL of REDExtract-n-AmpPCRReady Mix (Sigma–Aldrich) and 2µL DNA. The PCR cycling conditions were as follows: 95°C for 5 min, followed of 35 cycles of 94°C by 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. Attempts at also generating nuLSU (primers: AL2R, LR3; Vilgalys & Hester 1990; Mangold et al. 2008) and *rpb2* sequences (primers: GD1-*rpb2*-7cF, GD-*rpb2*_11aR; Kraichak et al. 2015) were unsuccessful. PCR reactions for the nuLSU contained 5.0 µL R4775 SIGMA REDExtract-N-Amp™ PCR ReadyMix, 0.5 µL of each primer (10 µM), 2 µL genomic DNA extract and 2 µL distilled water for a total of 10 µL. Thermal cycling parameters were: initial denaturation for 3 min at 94.5°C,

followed by 39 cycles of 35 s at 95°C, 30 s at 58°C, 45 s min at 72°C, and a final elongation for 10 min at 72°C; PCR reactions for the *rpb2* contained 5.0 µL R4775 SIGMA REDExtract-N-Amp™ PCR ReadyMix, 0.5 µL of each primer (10 µM), 2 µL genomic DNA extract and 2 µL distilled water for a total of 10 µL. Thermal cycling parameters were: initial denaturation for 3 min at 94.5°C, followed by 39 cycles of 45 s at 94°C, 60 s at 52°C, 90 s min at 72°C, and a final elongation for 10 min at 72°C.

PCR samples were visualized on a 1% ethidium bromide-stained agarose gel under UV light and PCR products were cleaned using Applied Biosystems™ ExoSAP-IT™ cleaning kit for PCR products. Samples were sequenced with the PCR primers at MacroGen Inc. (Korea), and sequences were manually assembled using BIOEDIT 7.09 (Hall 1999, 2011) and submitted to GenBank (Table 1).

After confirming that the mtSSU sequence of the target taxa fell within *Arthoniaceae*, the data were analyzed within a broader data set representing the diversity of genera within the family, selecting one (to three) terminals per species for a larger number of genera. We assembled a multiple sequence alignment including the newly generated sequence and sequences of 67 additional taxa downloaded from GenBank (Table 1) in BIOEDIT 7.2.5 (Hall 1999, 2011), comprising the arthonioid and cryptothecioid (sister) subclades according to Frisch et al. (2014) and using this topology for ingroup routing. The sequences were subjected to automated alignment with MAFFT 7 (Katoh & Standley 2013), with subsequent manual inspection (File S1). The phylogenetic tree was reconstructed by means of maximum likelihood, with 1,000 bootstrap pseudoreplicates and employing the universal GTRGamma model, using RAxML 8.2.0 (Stamatakis 2015). Tree visualization was done in FigTree 1.4.4 (https://tree.bio.ed.ac.uk/software/figtree; File S2).

For the quantitative assessment of the morphology and anatomy of the material, we assembled a character matrix for 24 specimens from six localities in Cuba and Colombia. The raw matrix contained 38 characters in binary or ordinal fashion, encompassing the morphology and anatomy of thallus and ascomata including ascospores (Table 2). Characters were assessed for each specimen (thallus) and for ten randomly selected ascomata of each specimen, resulting in a total of 240 units representing the 24 specimens (Files S3–S5). Prior to downstream analysis, the character matrix was normalized to values of a range between 0 and 1 for each character, using the formula $x_{Norm} = (x - x_{Min}) / (x_{Max} - x_{Min})$, where x_{Norm} = normalized value, x = raw value, x_{Min} = mininum value and x_{Max} = maximum value of the observed states for each character. The normalized matrix was subjected to Principal Component Analysis (PCA), using correlation as distance measure, and to two-way cluster analysis, using both correlation and relative Euklidean distance as

Table 1. GenBank accession numbers and voucher information for the mtSSU sequences used in this study. Newly generated sequences are in boldface.

Name of taxa	GB Accession	Extract	Country	Voucher
Arthonia albopulverea	OR490830	–	–	–
Arthonia apotheciorum	KJ850970	–	–	–
Arthonia atra	KY983978	–	–	–
Arthonia calcarea	EU704064	–	–	–
Arthonia physcidiicola	KF707646	–	–	–
Arthonia radiata	OQ646093	–	–	–
Arthonia ruana	OQ682856	–	–	–
Arthonia subfuscicola	KJ850972	–	–	–
Arthonia ulleungdoensis	MG495138	–	–	–
Arthonia vinosa	OQ646099	–	–	–
Arthothelium spectabile	OQ646105	–	–	–
Coniocarpon cinnabarinum	MN733981	–	–	–
Coniocarpon cuspidans	MN733973	–	–	–
Coniocarpon fallax	MN733961	–	–	–
Coniocarpon rubrocinctum	GU327684	–	–	–
Crypthonia palaeotropica	KJ850961	–	–	–
Cryptophaea phaeospora	KX077541	–	–	–
Cryptothecia bartlettii	PP051261	–	–	–
Cryptothecia inexspectata	PP051264	–	–	–
Cryptothecia punctosorediata	JX046450	–	–	–
Cryptothecia subnidulans	KJ850953	–	–	–
Herpothallon echinatum	OQ676537	–	–	–
Herpothallon inopinatum	KJ850964	–	–	–
Herpothallon kigeziense	KF707644	–	–	–
Herpothallon rubrocinctum	GU327693	–	–	–
Inoderma byssaceum	OQ646247	–	–	–
Inoderma nipponicum	KP870147	–	–	–
Inoderma sorediatum	MG207689	–	–	–
Inoderma subabietinum	KP870150	–	–	–

Table 1. Continued.

Name of taxa	GB Accession	Extract	Country	Voucher
Myriostigma candidum	EU704052	–	–	–
Myriostigma flavescens	PP051268	–	–	–
Myriostigma hainana	PP051272	–	–	–
Myriostigma laxipunctata	PP051266	–	–	–
Myriostigma miniatum	KP843606	–	–	–
Naevia dispersa	OQ646089	–	–	–
Naevia punctiformis	KJ850973	–	–	–
Pachnolepia pruinata	KJ850967	–	–	–
Reichlingia anombrophila	MT141111	–	–	–
Reichlingia dendritica	MT141112	–	–	–
Reichlingia leopoldii	JF830773	–	–	–
Reichlingia syncesioides	KF707651	–	–	–
Reichlingia zwackhii	OQ646419	–	–	–
Snippocia nivea	MG207693	–	–	–
Sporodophoron cretaceum	KP870151	–	–	–
Sporodophoron gossypinum	KP870155	–	–	–
Sporodophoron primorskiense	LC086299	–	–	–
Sporostigma cubanum	**PZ452889**	MON5431	Cuba	Lücking & Moncada 43031a
Sporostigma cubanum	**PZ452890**	MON9114	Cuba	Lücking & Moncada 43031b
Sporostigma pseudostromaticum	**PZ452891**	MON9113a	Colombia	Torres s.n. (a)
Sporostigma pseudostromaticum	**PZ452892**	MON9113b	Colombia	Torres s.n. (a)
Stirtonia neotropica	KP843611	–	–	–
Synarthonia albopruinosa	MH251873	–	–	–
Synarthonia astroidestera	MT141113	–	–	–
Synarthonia aurantiacopruinosa	MH251874	–	–	–
Synarthonia fuscata	MH251875	–	–	–
Synarthonia inconspicua	MH251880	–	–	–
Synarthonia leproidica	MT141114	–	–	–
Synarthonia muriformis	MH251877	–	–	–
Synarthonia ochracea	MH251884	–	–	–
Synarthonia pilosella	MH251883	–	–	–
Tylophoron galapagoense	JF830776	–	–	–
Tylophoron hibernicum	JF830778	–	–	–

Table 2. Characters and their states used in the comparative morphometric analysis. In the matrix, characters were normalized to take a range between 0 and 1.

Character	State 1	State 2	State 3	State 4	State 5
Diameter [mm]	–	–	–	–	–
Diameter perpendicular [mm]	–	–	–	–	–
Dots	absent = 0	present = 1	–	–	–
Surface	smooth = 0	intermediate = 0.5	rough = 1	–	–
Ascoma density margin [per mm^2]	–	–	–	–	–
Ascoma density center [per mm^2]	–	–	–	–	–
Ascoma density center/margin ratio	–	–	–	–	–
Ascoma crowding	absent = 0	present = 1	–	–	–
Ascoma emergence	immersed = 0	erumpent = 0.5	prominent = 1	–	–
Ascoma shape	rounded = 0	elongate = 0.5	lirellate = 1	–	–
Ascoma branching	unbranched = 0	branched = 0.5	stellate = 1	–	–
Ascoma length [mm]	–	–	–	–	–
Ascoma width [mm]	–	–	–	–	–
Ascoma length/width ratio	–	–	–	–	–
Ascoma outline	diffuse = 0	sharp = 1	–	–	–
Ascoma slit vs. thallus	absent = 0	present = 1	–	–	–
Ascoma surface (mazaedium) color	grey = 0	dark grey = 0.5	black = 1	–	–
Ascoma divisions	absent = 0	present = 1	–	–	–
Ascoma margin	absent = 0	thin = 0.25	thickened = 0.5	thick = 0.75	broad = 1
Ascoma margin structure	effuse = 0	crenulate = 0.5	smooth = 1	–	–
Ascoma margin slope	flush = 0	gentle = 0.5	steep = 1	–	–

Table 2. Continued.

Character	State 1	State 2	State 3	State 4	State 5
Ascospore wall	thin = 0	thickened = 1	–	–	–
Ascospore septa constrictions	absent = 0	present = 1	–	–	–
Ascospore colour	brown = 0	dark brown = 1	–	–	–
Ascospore wall verrucae	absent = 0	present = 1	–	–	–
Ascospore septa MIN	–	–	–	–	–
Ascospore septa MAX	–	–	–	–	–
Ascospore cell papilliform	indistinct = 0	distinct = 1	–	–	–
Ascospore cell hyaline	indistinct = 0	distinct = 1	–	–	–
Ascospore length MIN [µm]	–	–	–	–	–
Ascospore length MAX [µm]	–	–	–	–	–
Ascospore width MIN [µm]	–	–	–	–	–
Ascospore length MAX [µm]	–	–	–	–	–
Ascospore length/width ratio MIN	–	–	–	–	–
Ascospore length/width ratio MAX	–	–	–	–	–

distance measure and Ward als clustering algorithm. All multivariate approaches were performed in PC-ORD 7 (McCune & Mefford 1999).

Results and discussion

The molecular phylogenetic analysis using the mtSSU marker placed *Sporostigma*, based on the newly described *S. cubanum* from Cuba, with absolute support in a large clade containing the genera *Snippocia* Ertz, Kukwa & N. Sand. (Ertz et al. 2018), *Tylophoron*, *Pachnolepia* A. Massal. (Frisch et al. 2014), and *Arthothelium* (*Arthothelium* subclade), as well as *Cryptophaea* Van den Broeck & Ertz (Van den Broeck & Ertz 2016), *Cryptothecia* Stirt., *Sporodophoron*, *Inoderma*, *Crypthonia* Frisch & G. Thor (Frisch & Thor 2010), *Herpothallon* Tobler, and *Myriostigma* Kremp. (*Cryptothecia* subclade) (Fig. 1). Within this large clade, *S. cubanum* clustered within the *Arthothelium* subclade with strong support (93%), sister to a clade formed by *Pachnolepia* and *Arthothelium* with strong support (95%), the entire clade sister to *Tylophoron* with good support (88%). *Sporostigma* is thus related to the other mazaediate genus in the family, *Tylophoron*, but the two genera do not form a monophyletic lineage, suggesting that their mazaediate ascomata may have evolved in parallel, which is supported by their different morphology and ascospore types (Tibell 1996; Grube 2001b).

The quantitative assessment of the morphological and anatomical characters allowed the distinction of eleven morphodemes (Fig. 2), defined by the outline and organization of the mazaedia (rounded to irregular vs. elongate-lirellate and even branched, sometimes forming pseudostromata; Fig. 3), the formation of a thalline rim (absent vs. well-developed), the disposition of the mazaedia over the thallus (scattered to dense, distant from vs. close to thallus margin), and whether the ascospores feature wall ornamentations and/or a differentiated, colorless, papilliform proximal cell. Based on careful assessment of this variation, the eleven morphodemes were assigned to seven species. Three morphodemes form non-overlapping clusters (Fig. 2), representing the type species, *S. melasporum*, as well as the newly described *S. cubanum* from Cuba and *S. lobatum* from Colombia. The remaining eight morphogroups form a large cluster of partly overlapping subclusters, particularly in the PCA axis combination 3–1 (Fig. 2). All are from the same region, seasonally dry tropical forest in the department of Córdoba in northeastern Colombia, representing four independent collection events. Based on the combination of the PCA results (all three axis combiations) and the two-way clustering, they are interpreted to represent four new species introduced below: *S. hieroglyphicum* (two morphogroups), *S. immersellipsoideum* (one morphogroup), *S. pseudostromaticum* (one morphogroup), and *S. stellatum* (four morphogroups; Fig. 2).

Analysis of chemical constituents revealed an unexpected diversity of secondary compounds, namely 2'-*O*-methylperlatolic acid, 2-*O*-methylperlatolic acid (minor), planaic acid, 2-*O*-methylconfluentic acid, 4-*O*-demethylplanaic acid, 2,2'-di-*O*-methylolivetoric acid, and an unidentified substance named "*Sporostigma* unknown" (Figs 4, 5). All six species (the type species, *Sporostigma melasporum* was not included) showed the same composition of substances, in only slightly varying concentrations. Therefore, the chemical makeup was not included in the quantitative analysis.

The seven species of *Sporostigma* distinguished here are rather uniform in their ascospore types, differing in the degree of ascospore pigmentation (very dark in *S. cubanum* and *S. melasporum*), the distinctiveness of a more or less colorless, papilliform proximal cell, and to some extent ascospore dimensions and particularly the length-to-width ratio. Most of the variation between the species is found in the morphology of the thallus (smooth to farinose) and the mazaedia, which range from immersed to prominent, from broadly rounded to lobate or narrowly lirellate to stellate, without or with a well-developed thalline margin and sometimes organized in pseudostromata (Fig. 3). These differences may appear subtle in some cases and need to be tested using molecular sequence data, but are supported by the quantitative multivariate approach using a matrix of 38 characters.

The description of six new species of the same genus and particularly of three new species from the same

collection may raise a red flag. However, the co-occurrence of closely related species in the same habitat and even growing side by side is not uncommon, especially in tropical crustose lichen communities. It has been documented for foliicolous lichens, e.g., in the genera *Mazosia* A. Massal. and *Porina* Müll. Arg., but also for corticolous species, for example of *Astrothelium* Eschw., *Graphis* Adans., and *Phaeographis* Müll. Arg. A striking case is the genus *Glyphis* Ach., where the three common species, *G. cicatricosa* Ach. (with pseudostromatic ascomata), *G. scyphulifera* (Ach.) Staiger (with rounded ascomata), and *G. substriatula* (Nyl.) Staiger (with lirellate ascomata) are not rarely found side by side. The differences in ascomata shape in this case are comparable to those of *Sporostigma pseudostromaticum*, *S. immersellipsoideum*, and *S. hieroglyphicum*, three of the six new species described below. In the rich collection Torres 298 from northeastern Colombia, three of the new species, *S. hieroglyphicum*, *S. lobatum*, and *S. stellatum*, grew side by side with numerous thalli, covering large areas of the

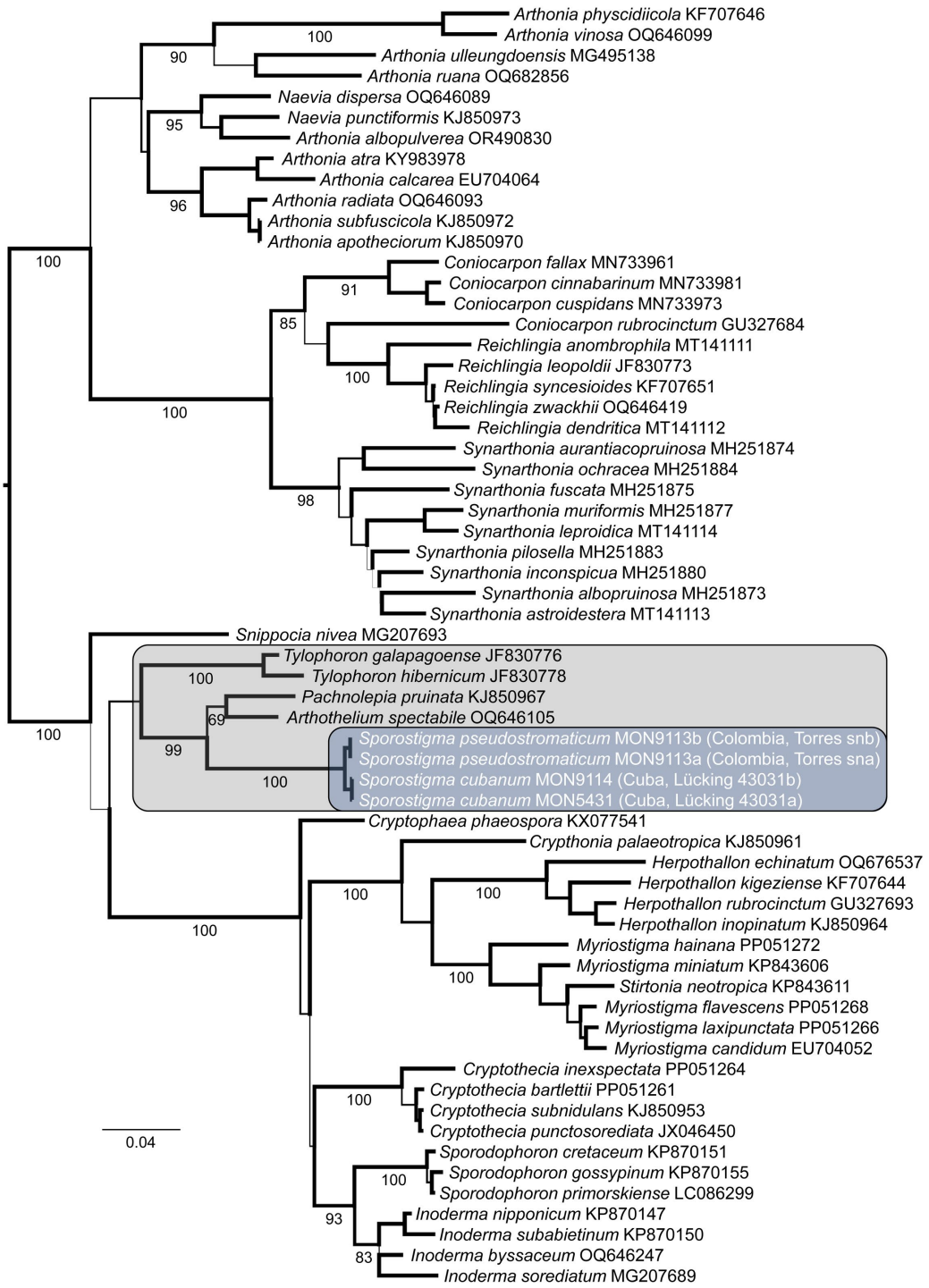

Figure 1. Best-scoring maximum-likelihood tree of the *Arthoniaceae* based on the mtSSU rDNA marker. Bootstrap support values of 70 and above are given below the branches. The tree represents the arthonioid and cryptotheciod subclades which form the *Arthoniales* crown, with a sister group relationship according to Frisch et al. (2014), suitable for ingroup routing.

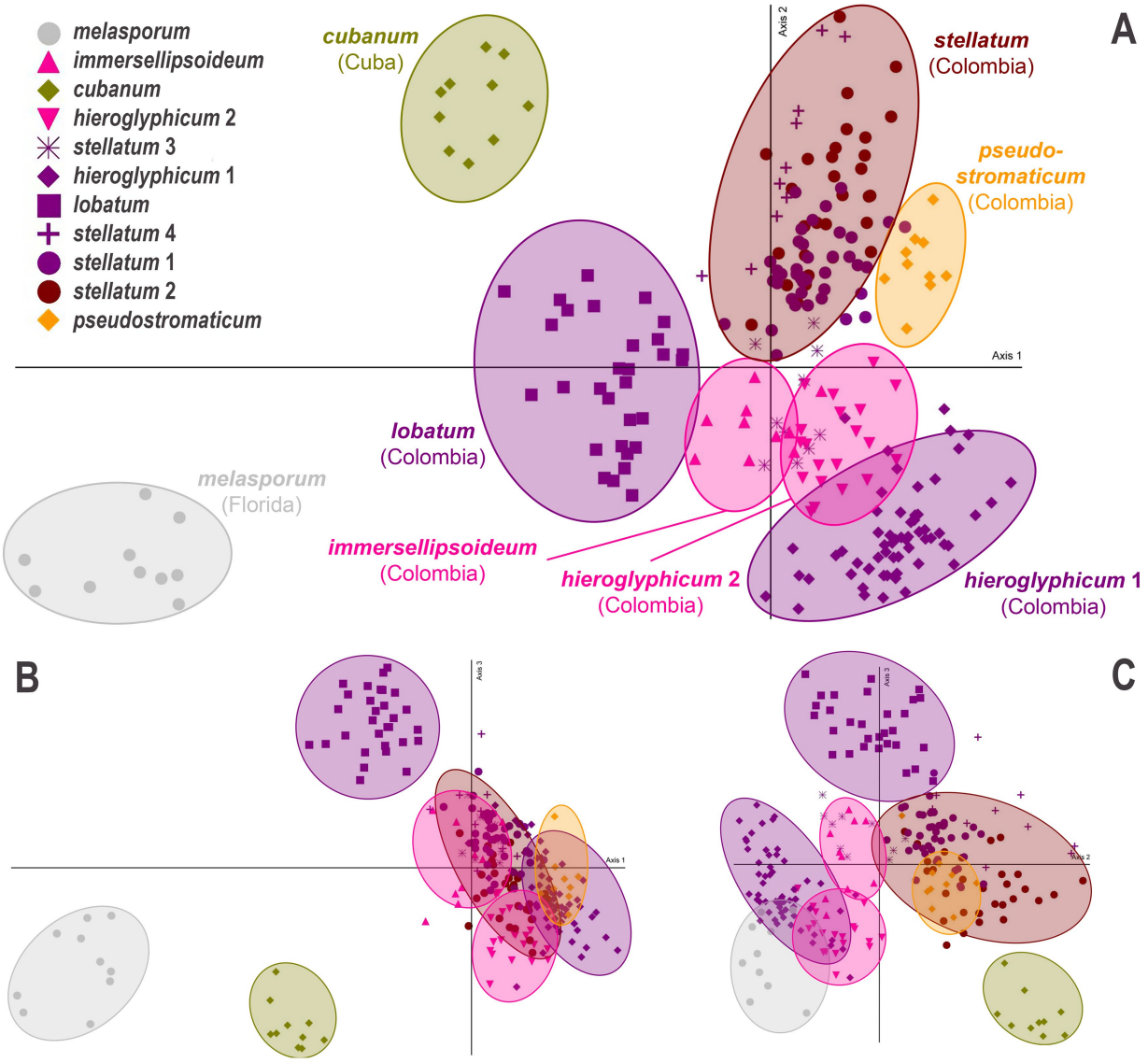

Figure 2. PCA ordination of the 240 analyzed units, representing 240 ascomata on 24 different thalli, based on the matrix of 38 normalized morpho-anatomical characters, with the axis combinations 2–1 (A), 3–1 (B), and 3–2 (C).

bark (Fig. 6). This helps to discern consistent morphological differences besides the different ascoma morphology, such as the always whiter thallus in *S. hieroglyphicum* or the broad marginal zone of the thallus bare of or with few, scattered ascomata in *S. lobatum*.

It is surprising that the species of this genus were not recognized before (Tibell 1996; Sipman & Aguirre-C. 2016; Moncada et al. 2022), although the genus was mentioned for Colombia in a biogeographic analysis (Soto-Medina et al. 2021). Given its local abundance in the places where it has been collected, the genus is certainly more widespread. It is possible that there are earlier collections, but they remained unidentified or were wrongly identified as, e.g., *Schistophoron* in herbaria (as in our case for samples held at UDBC). We also checked the synopsis of the genus *Arthonia* s.lat. by Willey (1890) to potentially discover names hidden in *Arthonia* that could represent *Sporostigma* species. Given the nature of the ascomata, ascospores, and substrate of *Sporostigma*, we would be looking for species described with black ascomata and 3–5-septate, (dark) brown ascospores growing on bark or wood. In Willey (1890), species with black ascomata and 3–5-septate ascospores growing on bark or wood are listed under the numbers 220–295. Among these, species with (dark) brown ascospores are:

[221] *Arthonia marmorata* Ach. ex. Nyl., based on *Spiloma marmoratum* Ach. [nom. inval.], with *Arthonia cinereopruinosa* var. *lobata* Nyl. as synonym; *A. marmorata* was established as a *nomen nudum* in a list of lichens of Finland but was validated by Willey (1890: 36); he lists the older names *Spiloma melaleucum* var. *leucopellaeum* Ach. and *Arthonia leucopellaea* (Ach.) Almq. as synonyms, which would make *A. marmorata* sensu Willey an illegitimate name and a synonym of *Felipes leucopellaeus* (Ach.) Frisch & G. Thor (Frisch et al. 2014), a non-mazediate taxon with ascospores becoming pale brown.

[229] *Arthonia melaspora* Tuck., i.e. *Sporostigma melasporum*, the ascospores of which Willey (1890: 37) describes as "…*the upper cell largest*, *very dark brown and almost black*…".

[240] *Arthonia turbatula* Nyl., from Argentina, with ascospores "… *brown or decolorate* …" (Willey 1890: 38);

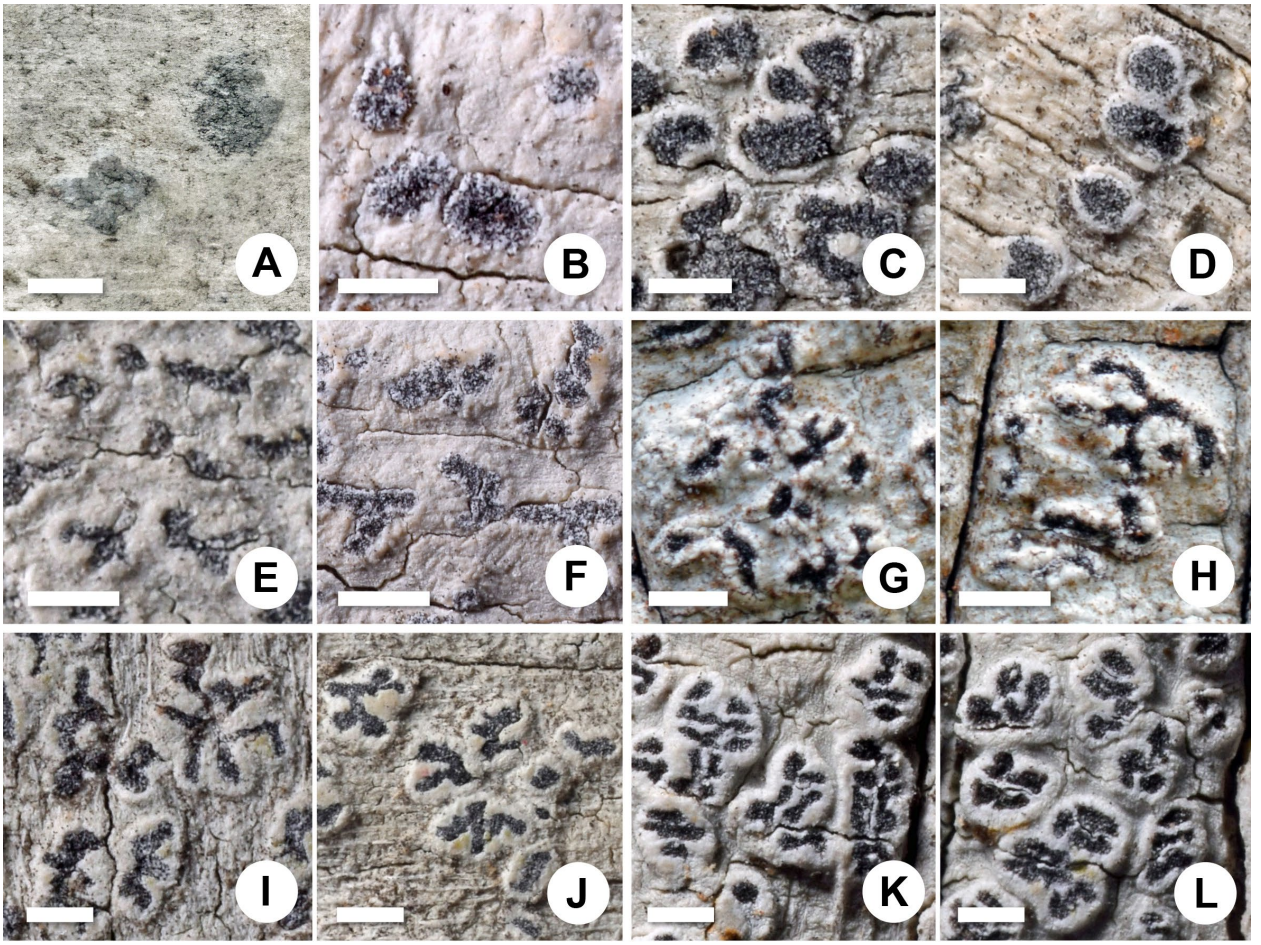

Figure 3. Morphology of the mazaedia in the different morphogroups and species of *Sporostigma*. A – *S. melasporum* (type); B – *S. immersellipsoideum* (type); C, D – *S. lobatum* (type); E, F – *S. hieroglyphicum* (type Cordero-Parada 2643-B); G, H – *S. cubanum* (type); I, J – *S. stellatum* (type; Torres 298-H); K, L – *S. pseudostromaticum* (type). Scale = 0.5 mm.

the type [https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.h9507479] is a non-mazaediate taxon with 3-septate, isodiametric ascospores.

[242] *Arthonia miserula* Nyl., from Colombia; likewise described as with brown or decolorate ascospores and likewise a non-mazaediate species.

[243] *Arthonia pruinosula* Nyl., also from Colombia, with non-mazaediate ascomata resembling those of *Coniocarpon* in shape but unpigmented.

[246] *Arthonia melanophthalma* Dufour ex Nyl., from South America, also non-mazaediate.

A few other taxa are described as having partly (pale) brown ascospores, but none revealed mazaedia after checking the types on JSTOR Global Plants and none with dark brown ascospores as described for *A. melaspora*. We are therefore confident that no further species of *Sporostigma* are hidden in historically established names under *Arthonia*. It would indeed be more likely to find such material under names described with mazaedia. However, the only fitting taxon would be *Schistophoron variabile* Tibell, described rather recently from Costa Rica (Tibell 1982). It is somewhat similar to *Sporostigma lobatum* and possibly is also a member of *Arthoniales*, but its ascospores are of a different shape and much smaller and so it is not a member of *Sporostigma*, let alone an available name for any of the species established herein (see also discussion below).

The placement of *Sporostigma* in *Arthoniaceae* is not surprising given especially the type of ascospores. In spite of the close relationship with *Pachnolepia* and *Arthothelium*, the latter two genera differ markedly in the compact, non-mazaediate ascomata and the usually colorless ascospores. A potentially related genus for which no sequence data are yet available is *Allophoron* Nádv., described from Colombia and so far, only known from the type material (Tibell 1996). Its mazaedia resemble those of *Sporostigma lobatum*, but are distinctly prominent to sessile. Its spores are small and muriform, but also asymmetric, although it is unclear whether they represent sexual ascospores or asexual conidia. Coincidentally, whereas sections of the mazaedia of *Sporostigma* generally reveal the presence of a hymenium with asci beneath the mazaedia, in some instances the same type of spores were clearly attached to hyaline hyphae, resembling conidia rather than ascospores.

Sporostigma is thus far known exclusively from the Neotropics, with *S. melasporum* present in subtropical Florida, *S. cubanum* in the Caribbean, and the remaining species in the northeastern portion of the Colombian Caribbean. There is also one collection cited from São Paulo state in Brazil [https://www.gbif.org/occurrence/1585207479], but it is unclear whether this identification is correct. Our revision of material in the UDBC herbarium revealed one collection tentatively identified as

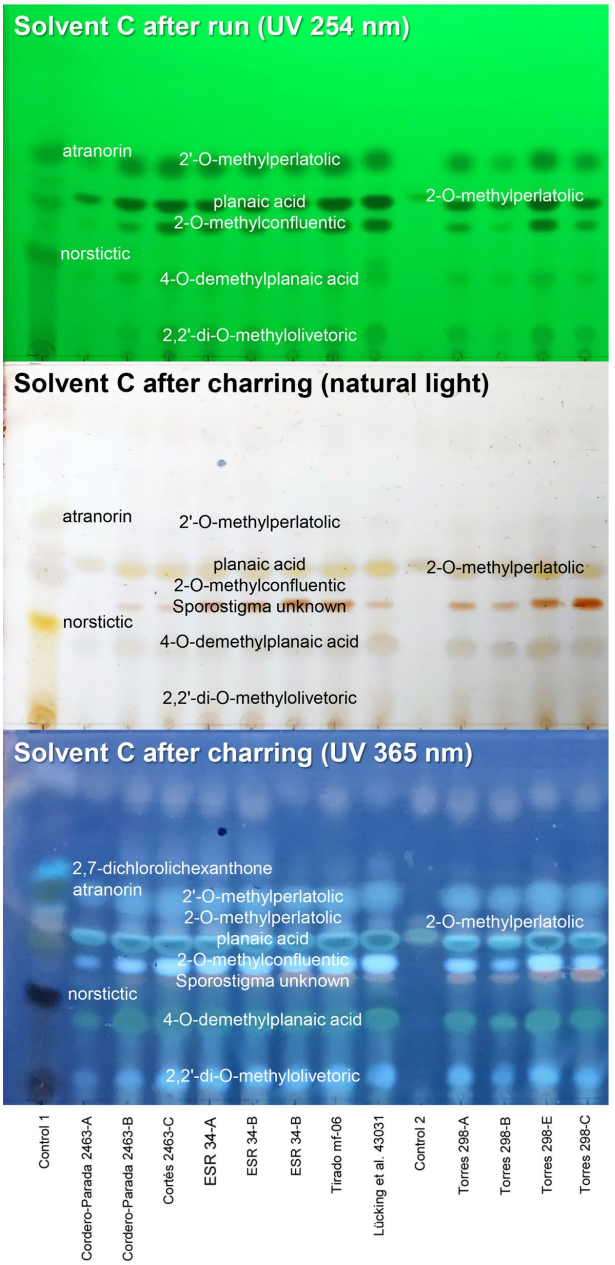

Figure 4. Chemical constituents of species of *Sporostigma*, visualized after TLC in solvent C (above: plate after run, UV 254 nm; middle; plate after charring, visible light; below: same, UV 365 nm). 1 – control 1 (atranorin, norstictic acid, 2,7-dichlorolichexanthone); 2 – *S. immersellipsoideum* (Cordero-Parada 2463-A); 3–4 – *S. hieroglyphicum* (Cordero-Parada 2463-B, 2463-C); 5–7 – *S. stellatum* (ESR 34-A, 34-B, 34-C); 8 – *S. pseudostromaticum* (Tirado mf-06); 9 – *S. cubanum* (Lücking & Moncada 43031); 10 – control 2 (2-*O*-methylperlatolic acid, plus unknown above in UV); 11 – *S. lobatum* (Torres 298-A); 12 – *S. hieroglyphicum* (Torres 298-B); 13–14 – *S. stellatum* (Torres 298-E, 298-C).

Tylophoron. It is quite possible that unidentified material of *Sporostigma* is housed in herbarium and fungarium collections, especially under the name *Schistophoron* Stirt. and *S. variabile* Tibell which, according to the monographic treatment by Tibell (1996), which does not include the later described genus *Sporostigma*, would be the closest match for *Sporostigma* species.

The hitherto available material suggests that species of *Sporostigma* prefer seasonally dry to subtropical forests and woodlands, preferably occurring on dead wood or the hard bark of palm trunks in somewhat exposed situations that facilitate wind dispersal. We expect that *Sporostigma* will turn out to be an important element of crustose lichen communities in seasonally dry tropical forests.

Taxonomic treatment

Sporostigma Grube, The Lichenologist 33: 388. 2001.

MycoBank MB 28544

Type: *Sporostigma melasporum* (Tuck.) Grube.

Description. Thallus usually growing on dead wood or the hard bark of palm trees, crustose, white, ecorticate, usually with black prothallus line. Photobiont trentepohlioid. Ascomata mazaedia, immersed to prominent, rounded to elongate to lobate or lirellate to stellate, sometimes organized in pseudostromata, grey to black; thalline margin absent or mostly present and then usually thickened, with gently to steeply sloping sides. Hymenium containing asci and anastomosing paraphyses usually present beneath the mazaedium, the mazaedium K+ blackening to smoke-grey or olive; asci broadly clavate, 8-spored, lacking an apical tholus structure, eventually disintegrating for passive ascospore dispersal. Ascospores obovate with the distal cell enlarged (macrocephalic) or very rarely divided into two (to three) cells, then uppermost cell smaller, or very rarely two-celled and isodiametric, (1–)3–4(–5)-septate, at first hyaline, but soon becoming medium to dark brown even within the asci, K+ blackening to smoke-grey or olive, with thin to mostly thickened walls and thickened, in part blackish brown septa, lacking constrictions or rarely slightly constricted at the septa; proximal cell paler to colorless, often thin-walled and papilliform.

Secondary chemistry. (Not known for the type species, *Sporostigma melasporum*) 2'-*O*-methylperlatolic acid, 2-*O*-methylperlatolic acid (minor), planaic acid, 2-*O*-methylconfluentic acid, 4-*O*-demethylplanaic acid, 2,2'-di-*O*-methylolivetoric acid, and an unknown substance with Rf values 43 in solvent A, 16 in solvent B', and 35 in solvent C, forming a narrow red-brown spot with pink UV fluorescence after charring under 365 nm; thallus surface and medulla C+ pale yellowish, K–, P–, UV–, in section nubilous with small, grey crystals dissolving in K without color reaction.

Remarks. The original description of *Sporostigma* is here emended to account for the variation in the morphology of the thallus and mazaedia. Apart from the abundant crystals in the medulla and the secondary chemistry, one feature not mentioned in the original description of the genus is the fenestrate thallus organization, with vertically arranged clusters of photobiont cells.

Among the known mazaediate genera with crustose thallus and sessile to adnate ascomata, the diagnostic characters of the genus are the obovate, (dark) brown ascospores with enlarged upper cell, their shape and septation resembling those of many tropical *Arthonia* s.lat. species. Among other crustose lichens with mazaedia, *Sporostigma* comes closest to *Schistophoron*, in particular *S. variabile* (Fig. 7E, F), which is actually not a genuine *Schistophoron*, but belongs in an

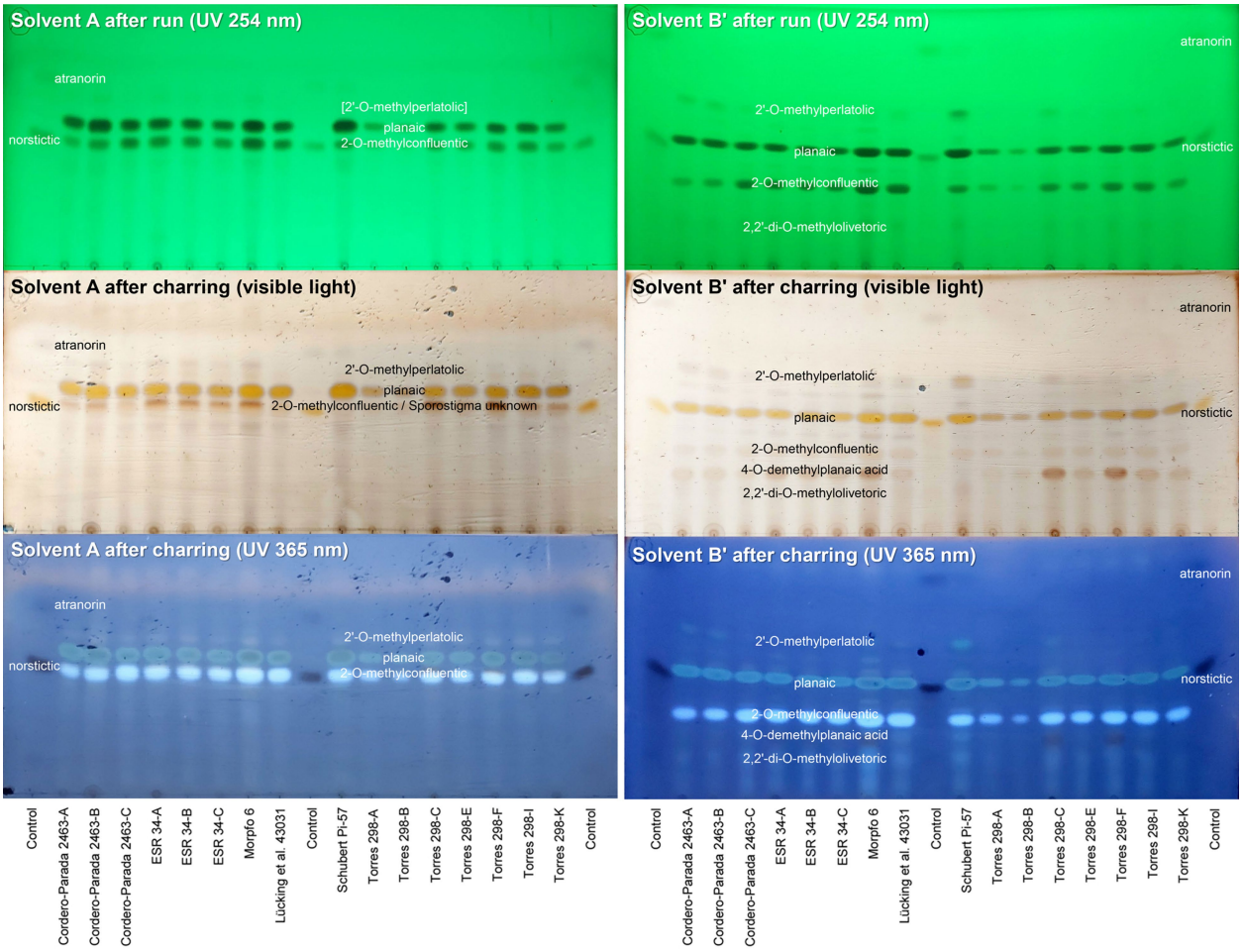

Figure 5. Chemical constituents of species of *Sporostigma*, visualized after TLC in solvents A and B' (above: plate after run, UV 254 nm; middle; plate after charring, visible light; below: same, UV 365 nm). 1, 10, 19 – control (atranorin, norstictic acid); 2 – *S. immersellipsoideum* (Cordero-Parada 2463-A); 3–4 – *S. hieroglyphicum* (Cordero-Parada 2463-B, 2463-C); 5–7 – *S. stellatum* (ESR 34-A, 34-B, 34-C); 8 – *S. pseudostromaticum* (Tirado mf-06); 9 – *S. cubanum* (Lücking & Moncada 43031); 11 – *S. cubanum* (Schubert Pi-57); 12, 16 – *S. lobatum* (Torres 298-A, 298-F); 13 – *S. hieroglyphicum* (Torres 298-B); 14–15, 17, 18 – *S. stellatum* (Torres 298-C, 298-E, 298-I, 298-K).

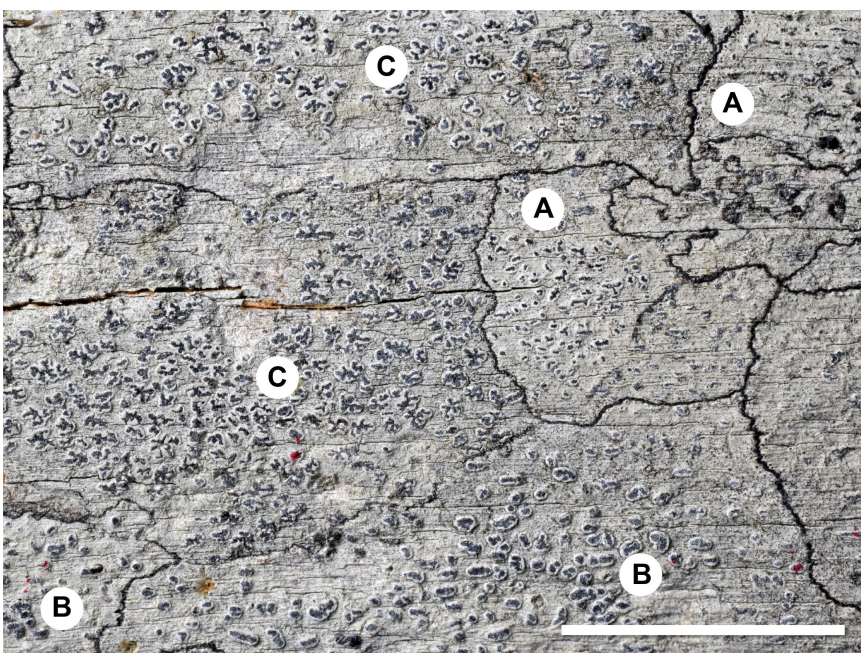

Figure 6. Three species of *Sporostigma* growing side-by-side on the bark of a palm tree (Colombia, Torres 298). A – *S. hieroglyphicum*, note the white, smooth thallus and the smaller immersed to erumpent, lirellate mazaedia; B – *S. lobatum*, with white-grey, rough thallus and larger, distinctly erumpent, rather broad, ellipsoid to lobate mazaedia; C – *S. stellatum*, with white-grey, rough thallus and narrower, branched to stellate, almost pseudostromatic mazaedia. Large areas of the palm trunk were covered in similar fashion. Scale = 10 mm.

unknown genus. It agrees with *Sporostigma* in overall appearance, but its ascospores are ellipsoid in shape and much smaller in size (11–15 × 6–7 µm). *Schistophoron variabile* has not yet been sequenced, but may also belong in *Arthoniales*.

Another similar and potentially related taxon is *Allophoron farinosum* (Fig. 7A–D), characterized by small muriform spores (Tibell 1996). It agrees with some species of *Sporostigma*, particularly *S. lobatum*, in external morphology, but differs in the peculiar ascospore type. This genus is also predicted to belong in *Arthoniales*.

Several samples labeled with the genus name *Sporostigma* were listed in the environmental impact assessment study "*Biodiversidad asociada al Estudio de Impacto Ambiental del proyecto: Interconexión Cuestecitas – Copey – Fundación 500/220 mil voltios*" (ANLA 2021; SIB 2023; ISA INTERCOLOMBIA E.S.P. S.A., Andina de Energía SAS 2024). However, it is unclear where this material has been deposited, so it was unavailable for further study.

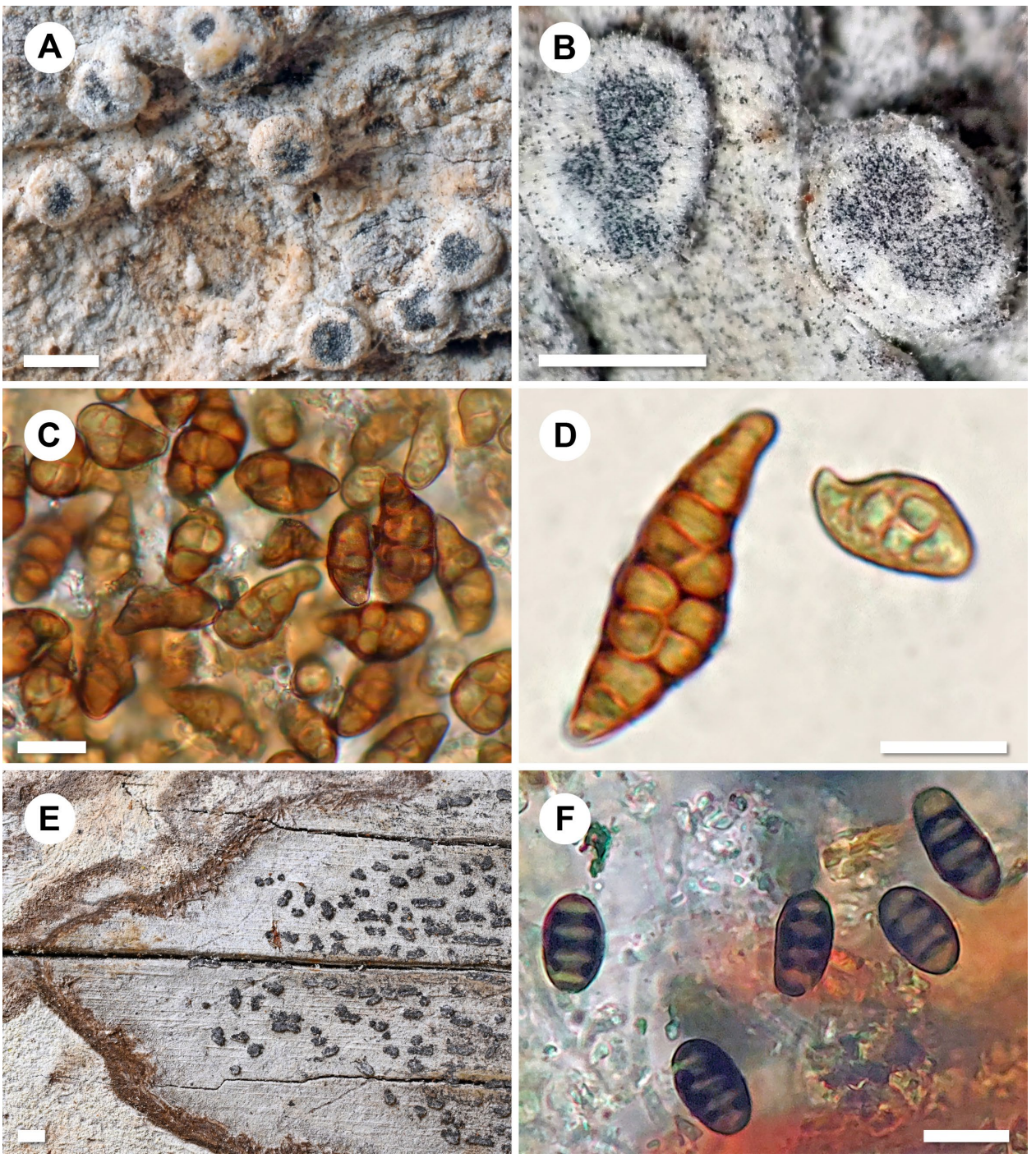

Figure 7. Two mazaediate taxa with some similarities with *Sporostigma* and possibly belonging in *Arthoniales*. A–D – *Allophoron farinosum* (Colombia, holotype in M), thallus with mazaedia and ascospores. E, F – *Schistophoron variabile* (Costa Rica, Sipman 51709 in B), thallus with mazaedia and ascospores. Scales: A, B, E = 1 mm; C, D, F = 10 µm.

Sporostigma cubanum Lücking, Viñas & B. Moncada, sp. nov. (Fig. 8)

MycoBank MB 863857

Diagnosis: Differing from *Sporostigma melasporum* in the compact thallus, the lirellate-stellate ascomata with black mazaedia and thickened, crenulate thalline margin, and the smooth ascospores, and from *S. stellatum* in the narrower mazaedia with crenulate thalline margin, not becoming pseudostromatic, and the darker ascospores with often distinctly papilliform proximal cell.

Type: Cuba, La Habana: Jardín Botánico Nacional, 12 km S of La Habana, area near headquarters; 23°00′N, 82°20′W, 90 m; planted trees and woodland, on wooden leaf bases of palm, 23 Mar. 2017, R. Lücking & B. Moncada 43031 (HAJB – holotype!; B – isotype!).

Etymology. The epithet refers to the discovery of this new species in Cuba.

Description. Thallus white-grey, uneven, rough, thin (following the contours of the bark), ecorticate, with black prothallus line; in section 80–130 µm thick, strongly nubilous with small, grey crystals that slowly dissolve in K without any color reaction, except for a thick layer of grey crystals remaining near the surface, showing a structure of densely packed, irregularly perpendicular hyphae alternating with large, vertical pockets of groups of 3–7 µm large algal cells in between, giving the thallus a fenestrate structure. Ascomata abundant, about equally dense up to the thallus margin, erumpent to prominent; mazaedium (elongate to) lirellate, becoming irregularly to stellately branched, 1–2 mm long, 0.15–0.2(–0.25) mm broad, black, with mostly diffuse marginal zone; thalline margin thickened, irregularly crenulate, with steeply sloping sides. Hymenium bowl-shaped, 80–100 µm high, consisting of densely arranged interascal hyphae and irregularly distributed asci, covered by a 50–80 µm thick, blackish brown mazaedium layer, the latter K+ blackening; asci broadly clavate, 45–60 × 20–30 µm, 8-spored. Ascospores obovate with distal cell enlarged (macrocephalic) or rarely divided into two cells, then uppermost cell smaller, 3–4(–5)-septate, 22–33 × 9–13 µm, 2.3–2.6 times as long as broad, at first hyaline but soon becoming dark brown even within the asci, K+ blackening to smoke-grey with a greenish hue, with thickened walls and blackish brown, thickened septal bands, slightly constricted at the septa; proximal cell paler to colorless, often thin-walled and papilliform, in 4–5-septate ascospores second cell from below also often paler to colorless and thin-walled.

Secondary chemistry. 2'-*O*-methylperlatolic acid, 2-*O*-methylperlatolic acid (minor), planaic acid, 2-*O*-methylconfluentic acid, 4-*O*-demethylplanaic acid, 2,2'-di-*O*-methylolivetoric acid, and an unknown substance with Rf values 43 in solvent A, 16 in solvent B', and 35 in solvent C, forming a narrow red-brown spot with pink UV fluorescence after charring under 365 nm; thallus surface and medulla C+ pale yellowish, K–, P–,

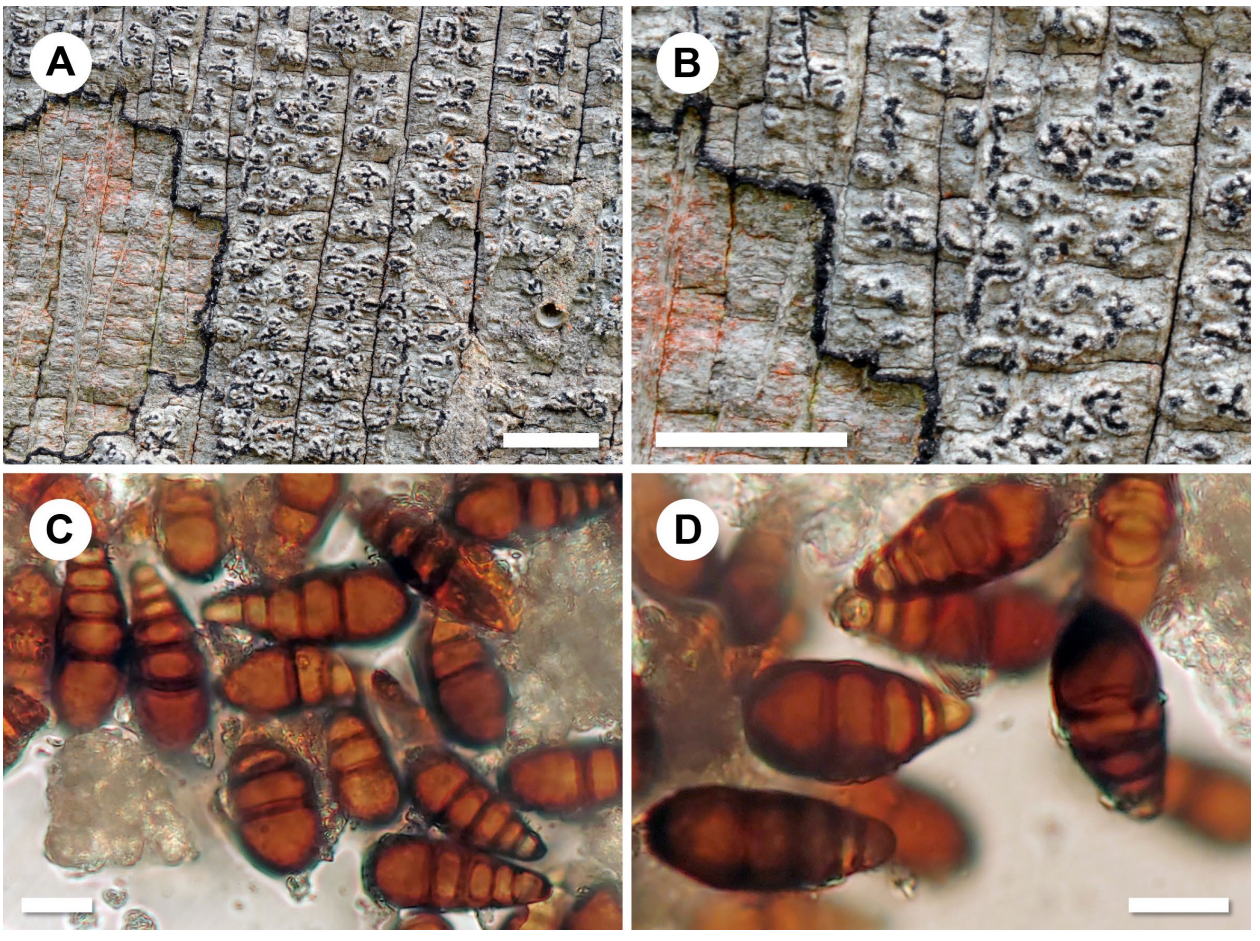

Figure 8. *Sporostigma cubanum* (holotype). A, B – thallus with mazaedia; C, D – ascospores. Scales: A, B = 2 mm; C, D = 10 µm.

UV–, in section nubilous with small, grey crystals dissolving in K without color reaction.

Ecology and distribution. Thus far known from the bark and the woody leaf bases of free-standing palms in the National Botanical Garden near Havana, Cuba.

Remarks. *Sporostigma cubanum* shares with *S. melasporum* the very dark brown ascospores with slight constrictions at the septa; the other newly described species from Colombia have lighter brown ascospores lacking constrictions. *Sporostigma melasporum* differs from *S. cubanum* in the farinose thallus, the effuse ascomata with rounded to somewhat irregular, light grey mazaedium lacking a thalline margin, and the minutely verrucose ornamentation of the ascospores. Morphologically most similar to *S. cubanum* is *S. stellatum*, which agrees in the lirellate-stellate ascomata with thickened thalline margin. However, its mazaedia are broader [(0.15–)0.2–0.3 mm], their thalline margin not appearing crenulate, and they are often stellately arranged in somewhat diffuse pseudostromata. Also, the ascospores are lighter brown and without distinct constrictions, and the proximal cell is only slightly paler and usually not distinctly papilliform. The thallus structure of *S. cubanum*, best visible after applying K, is distinctly fenestrate, whereas in the other species the algal packages are more irregularly arranged.

Additional specimens examined. CUBA. Isla de la Juventud: Mogote de Bibijagua; 21°54.5′N, 82°46.7′W, sea level; April–May 1975, R. Schubert Pi 57 (B 60 0198921).

Sporostigma hieroglyphicum J.-M. Torres, Lücking & B. Moncada, sp. nov. (Fig. 9)

MycoBank MB 863858

Diagnosis: Differing from *Sporostigma cubanum* in the immersed-erumpent mazaedia with even, flattened margin and often with a split between mazaedium and thallus margin.

Type: Colombia, Córdoba: Chinu, Flechas Sevilla; 75.5199029°W, 9.0150542°N, 35 m; on bark of palm; 28 Mar. 2015, J.-M. Torres 298-B (UDBC – holotype!).

Etymology. The epithet refers to the script-like mazaedia and the superficial similarity in some aspects with the lirellae of the unrelated species *Diorygma hieroglyphicum* (Pers.) Staiger & Kalb (*Graphidaceae*), in which the lirellae are also immersed, with a thin split towards the surrounding, white thallus.

Description. Thallus white, plane to uneven, smooth, thin (following the contours of the bark), ecorticate, with thin black prothallus line; in section 150–220 µm thick, with some crystals especially towards the surface that slowly dissolve in K without any color reaction, except for a layer of grey crystals remaining near the surface, showing a structure of densely packed, irregularly perpendicular hyphae with large pockets of groups of 3–7 µm large algal cells in between. Ascomata abundant, almost equally dense across the thallus, immersed (to erumpent); mazaedium lirellate, becoming irregularly to sometimes stellately branched, 0.5–1(–2.5) mm long, 0.15–0.2(–0.25) mm broad, dark grey to black, with rather sharply delimited marginal zone and often with a narrow slit towards the thalline margin; thalline margin narrow to broad, even, flattened, flush with the thallus (then sometimes hard to discern) or with gently sloping sides. Hymenium bowl-shaped, 80–120 µm high, consisting of densely arranged interascal hyphae and irregularly distributed asci, covered by a 70–100 µm thick, blackish brown mazaedium layer, the latter K+ blackening; asci broadly clavate, 50–70 × 20–30 µm, 8-spored. Ascospores obovate with distal cell enlarged (macrocephalic) or rarely divided into two or three cells, then uppermost cell smaller, (2–)3–4(–5)-septate, 18–28(–32) × 9–13(–14) µm, 1.8–2.3(–2.5) times as long as broad, at first hyaline but soon becoming medium to dark brown, K+ blackening to smoke-grey, with equally thickened walls and septa, the septa laterally with blackish, triangular pigmentation, not constricted at the septa; proximal cell distinctly paler to colorless and then often with a thin wall and papilliform.

Secondary chemistry. 2'-*O*-methylperlatolic acid, 2-*O*-methylperlatolic acid (minor), planaic acid, 2-*O*-methylconfluentic acid, 4-*O*-demethylplanaic acid, 2,2'-di-*O*-methylolivetoric acid, and an unknown substance with Rf values 43 in solvent A, 16 in solvent B', and 35 in solvent C, forming a narrow red-brown spot with pink UV fluorescence after charring under 365 nm; thallus surface and medulla C+ pale yellowish, K–, P–, UV–, in section nubilous with small, grey crystals dissolving in K without color reaction.

Ecology and distribution. Thus far known from the bark of free-standing palms in the northeastern department of Córdoba in Colombia, co-occurring with several other species of the genus.

Remarks. *Sporostigma hieroglyphicum* differs from *S. cubanum* in the immersed-erumpent mazaedia with flattened, often flush margin with an even surface, not crenulate as in *S. cubanum*. It agrees in many aspects with *S. stellatum*, described below. It differs in the thicker, more or less smooth, white thallus (lacking a greyish tinge), the flush to hardly erumpent ascomata with narrower mazaedia, not appearing pseudostromatic, but often with a slit between the mazaedium and the thalline margin, and the rather distinctly papilliform proximal cell of the ascospores. Overall, the differences are gradual in nature, but the co-occurrence of both species side-by-side in the same collections demonstrates the consistency of the diagnostic characters and excludes microhabitat parameters as a potential explanation for this discrete variation. This is also reflected by the rather well separated cluster in the quantitative analysis, supporting the interpretation of *S. hieroglyphicum* and *S. stellatum* as separate species.

Additional specimens examined. CÓRDOBA: Chinu, Flechas Sevilla; 75.5199029°W, 9.0150542°N, 35 m; on bark of palm; 28 Mar. 2015, J.-M. Torres 298-D, 298-L, 298-M, 298-N, 298-O (UDBC). Chinu, Cañahuate; 75.323954°W, 9.0617949°N, 88 m; gallery forest, on bark of *Sabal mauritiformis* palm; 21 Mar. 2025, A.F. Blanco Narvaez 301 (UDBC). Buenavista, Vereda Mejor Esquina; 08°13′34″N, 75°32′34″W, 78 m; on bark of palm [Environmental impact assessment study "Linea de transmisión Cerromatoso-Chinú-Copey 500 kV"], 18 May 2017, Z. Cordero-Parada 2463-B, 2463-C (UDBC C-0022365).

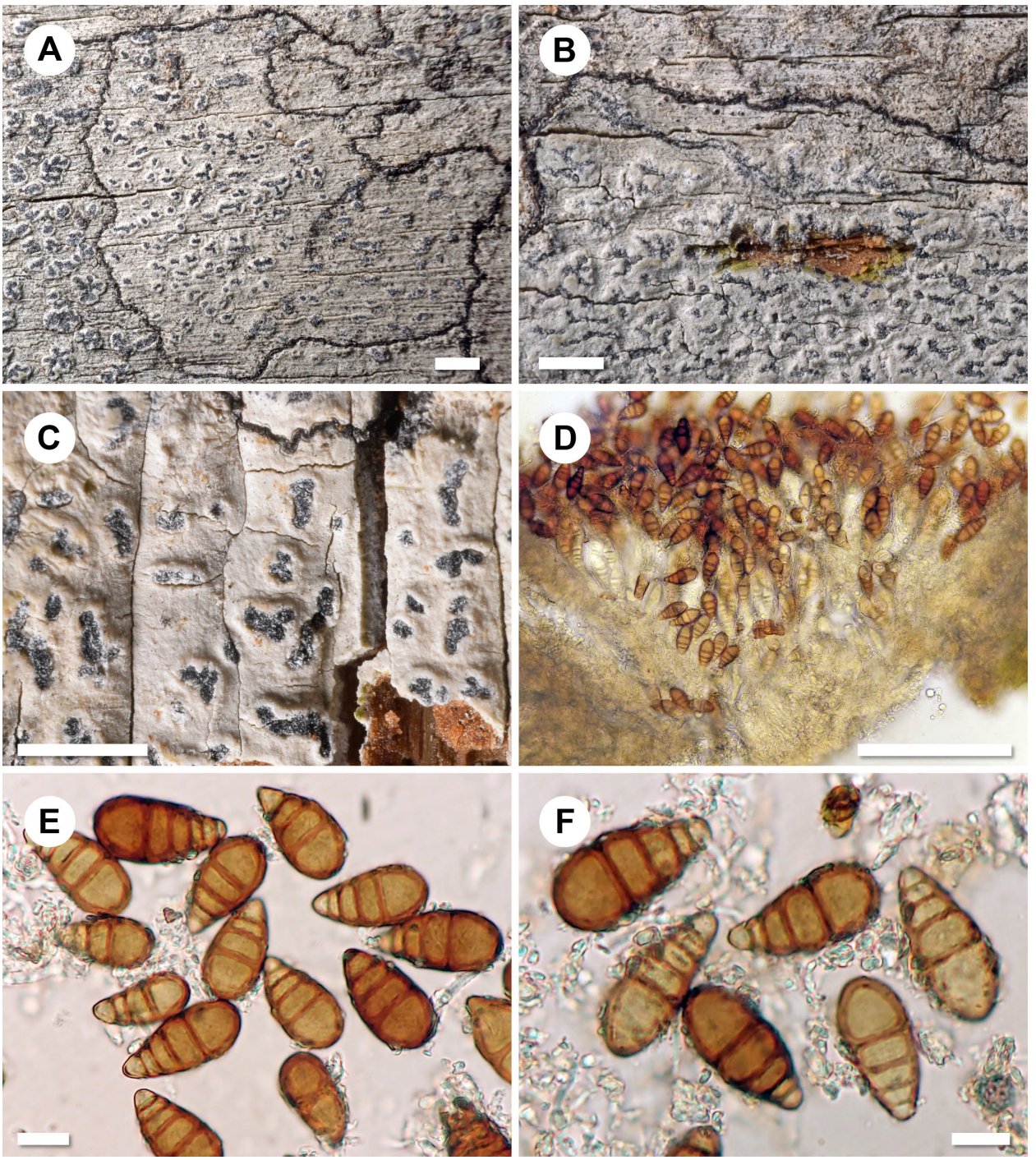

Figure 9. *Sporostigma hieroglyphicum* (A, B, D–F: holotype; C: Cordero-Parada 2463-C); A–C – thallus with mazaedia; D – section through mazaedium showing lower layer with asci; E, F – ascospores. Scales: A–C = 1 mm; D = 100 µm; E, F = 10 µm.

Sporostigma immersellipsoideum Lücking & B. Moncada, sp. nov. (Fig. 10)

MycoBank MB 863860

Diagnosis: Differing from *Sporostigma lobatum* in the immersed (to slightly erumpent) ascomata and the comparatively narrower ascospores, with the proximal cell rarely papilliform; differing from *S. melasporum* in the sharply delimited mazaedia and the compact and smooth thallus.

Type: Colombia, Córdoba: Buenavista, Vereda Mejor Esquina; 08°13′34″N, 75°32′34″W, 78 m; on bark of palm [Environmental impact assessment study "Linea de transmisión Cerromatoso-Chinú-Copey 500 kV"], 18 May 2017, Z. Cordero-Parada 2463-A (UDBC C-0022365 – holotype!).

Etymology. The epithet refers to the typically immersed, ellipsoid mazaedia.

Description. Thallus white, uneven, smooth, thin (following the contours of the bark), ecorticate, with thin black prothallus line; in section 100–150 µm thick, strongly nubilous with small, grey crystals that quickly and completely dissolve in K without any color reaction, then showing a structure of densely packed, irregularly perpendicular hyphae with large pockets of groups of 3–7 µm large algal cells in between. Ascomata abundant, becoming sparser towards the thallus margin, immersed (to slightly erumpent); mazaedium rounded to ellipsoid or elongate,

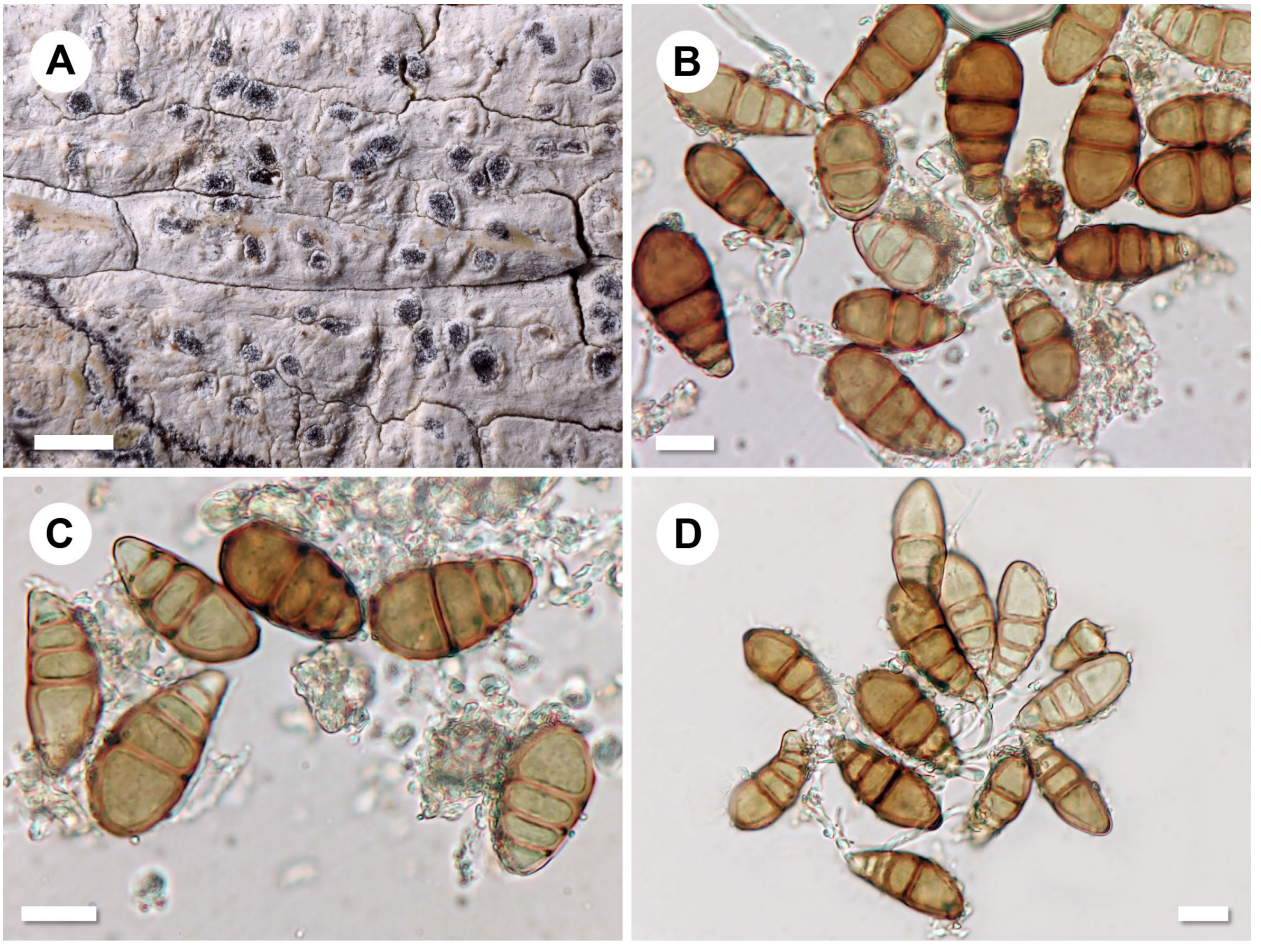

Figure 10. *Sporostigma immersellipsoideum* (holotype). A – thallus with mazaedia; B–D – ascospores. Scales: A = 1 mm; B–D = 10 µm.

mostly unbranched, 0.4–0.6 mm long, 0.3–0.5 mm broad, more or less black, with rather sharply delimited marginal zone; thalline margin rather thin, even, flush or with gently sloping sides. Hymenium bowl-shaped, 70–100 µm high, consisting of densely arranged interascal hyphae and irregularly distributed asci, covered by a 50–70 µm thick, blackish brown mazaedium layer, the latter K+ olive-green; asci broadly clavate, 45–55 × 20–25 µm, 8-spored. Ascospores obovate with distal cell enlarged (macrocephalic) or rarely divided into two or three cells, then uppermost cell smaller, (2–)3–4(–5)-septate, 19–32 × 9–13 µm, 1.9–2.5(–2.7) times as long as broad, at first hyaline, but soon becoming medium to dark brown, K+ olive-green, with equally thickened walls and septa, the septa laterally with blackish, triangular pigmentation, not constricted at the septa; proximal cell paler, with a somewhat thinner wall but usually not distinctly papilliform.

Secondary chemistry. 2'-*O*-methylperlatolic acid, 2-*O*-methylperlatolic acid (minor), planaic acid, 2-*O*-methylconfluentic acid, 4-*O*-demethylplanaic acid, 2,2'-di-*O*-methylolivetoric acid, and an unknown substance with Rf values 43 in solvent A, 16 in solvent B', and 35 in solvent C, forming a narrow red-brown spot with pink UV fluorescence after charring under 365 nm; thallus surface and medulla C+ pale yellowish, K–, P–, UV–, in section nubilous with small, grey crystals dissolving in K without color reaction.

Ecology and distribution. So far only known from the type locality in northeastern Colombia, on bark of palm in a seasonally dry forest region.

Remarks. *Sporostigma immersellipsoideum* is similar in the shape of the mazaedia to *S. lobatum*, described below, although they tend to remain shorter and mostly unbranched, but differs in the immersed (to slightly erumpent) ascomata and the narrower ascospores (9–13 µm vs. 10–15 µm in the latter) in which the proximal cell is rarely papilliform. The new species agrees with *S. melasporum* in the flush mazaedia, but they have a more distinct margin and are much darker and more sharply delimited; Also, the thallus is compact and smooth vs. farinose in *S. melasporum*.

Sporostigma lobatum J.-M. Torres, Lücking & B. Moncada, sp. nov. (Fig. 11)

MycoBank MB 863861

Diagnosis: Differing from *Sporostigma immersellipsoideum* in the clearly erumpent mazaedia which become elongate-lobate, the rough thallus, and the comparatively broader ascospores with a typically papilliform proximal cell.

Type: Colombia, Córdoba: Chinu, Flechas Sevilla; 75.5199029°W, 9.0150542°N, 35 m; on bark of palm; 28 Mar. 2015, J.-M. Torres 298-F (UDBC – holotype!).

Etymology. The epithet refers to the mazaedia becoming (broadly) lobate when older.

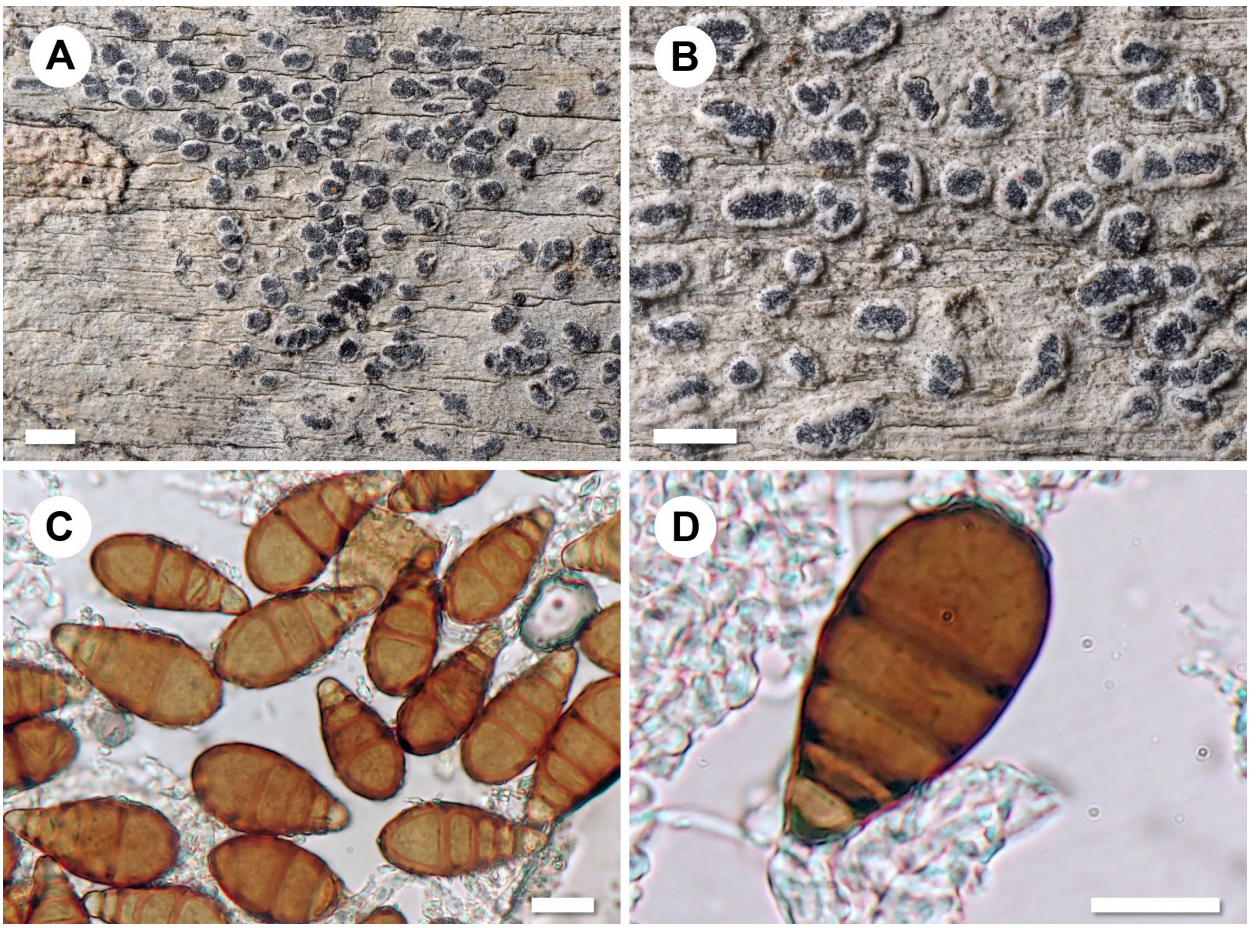

Figure 11. *Sporostigma lobatum* (holotype). A, B – thallus with mazaedia; C, D – ascospores. Scales: A, B = 1 mm; C, D = 10 µm.

Description. Thallus white, uneven, rough, thin (following the contours of the bark), ecorticate, with thin black prothallus line; in section 90–120 µm thick, strongly nubilous with small, grey crystals that dissolve in K without any color reaction, then showing a structure of densely packed, irregularly perpendicular hyphae with large, more or less vertically oriented pockets of groups of 3–7 µm large algal cells in between. Ascomata abundant, becoming sparse towards the thallus margin, erumpent; mazaedium rounded to elongate, unbranched to rarely sparsely branched, appearing lobate, 0.4–1.2 mm long, 0.3–0.5 mm broad, dark grey to almost black, with rather diffuse marginal zone; thalline margin thickened, even to somewhat irregular, with steeply sloping sides. Hymenium bowl-shaped, 100–150 µm high, consisting of densely arranged interascal hyphae and irregularly distributed asci, covered by a 50–100 µm thick, dark brown mazaedium layer, the latter K+ blackening to smoke-grey; asci broadly clavate, 50–70 × 20–30 µm, 8-spored. Ascospores obovate with distal cell enlarged (macrocephalic) or rarely divided into two or three cells, then uppermost cell smaller, (2–)3–4(–5)-septate, 19–32 × 10–15 µm, 1.8–2.2(–2.4) times as long as broad, at first hyaline but soon becoming medium to dark brown, K+ blackening to smoke-grey with a greenish tinge, with thickened walls and septa, the septa laterally with blackish, triangular pigmentation, not constricted at the septa; proximal cell distinctly paler to colorless and then often with a thin wall and papilliform.

Secondary chemistry. 2'-*O*-methylperlatolic acid, 2-*O*-methylperlatolic acid (minor), planaic acid, 2-*O*-methylconfluentic acid, 4-*O*-demethylplanaic acid, 2,2'-di-*O*-methylolivetoric acid, and an unknown substance with Rf values 43 in solvent A, 16 in solvent B', and 35 in solvent C, forming a narrow red-brown spot with pink UV fluorescence after charring under 365 nm; thallus surface and medulla C+ pale yellowish, K–, P–, UV–, in section nubilous with small, grey crystals dissolving in K without color reaction.

Ecology and distribution. Thus far known from the bark of free-standing palms in the northeastern department of Córdoba in Colombia, co-occurring with several other species of the genus.

Remarks. *Sporostigma lobatum* differs from most of the other species of the genus in the comparatively short and broad, unbranched to somewhat lobate mazaedia. In contrast to *S. melasporum*, the mazaedia are more elongate, distinctly erumpent from the thallus, and feature a thalline margin, and they are darker in appearance. Sporostigma inspersellipsoideum can be distinguished by the typically immersed mazaedia that do not become lobate, the smooth thallus, and the somewhat narrower ascospores (9–13 µm vs. 10–15 µm in *S. lobatum*).

Additional specimens examined. COLOMBIA. Córdoba: Chinu, Flechas Sevilla; 75.5199029°W, 9.0150542°N, 35 m; on bark of palm; 28 Mar. 2015, J.-M. Torres 298-G (UDBC).

Sporostigma melasporum (Tuck.) Grube (Fig. 12)

Sporostigma melasporum [as "*melaspora*"] (Tuck.) Grube, The Lichenologist 33: 388. 2001.

MycoBank MB 580615

≡ *Arthonia melaspora* Tuck. in Willey, Suppl. Introd. Stud. Lich.: 54. 1887.

MycoBank MB 376641

Type: USA, Florida: Unknown locality, Miss Wilson s.n. (ex herb. Tuckerman; H 9507681!, UPS! – isotypes).

Etymology. The epithet refers to the dark brown ascospores, a feature not usually seen in the genus *Arthonia*, in which the species was originally described.

Description. Thallus whitish, farinose-leprose, ecorticate, lacking a distinct prothallus line; in section 100–200 µm thick. Ascomata scattered, denser in some parts of the thallus, adnate and spot-like; mazaedium angular-rounded to irregular in outline, 0.3–0.6 mm diam., grey, marginally somewhat diffuse, lacking a proper margin (excipulum); thalline margin absent. Hymenium 60–85 µm high, consisting of branched and anastomosing interascal hyphae and irregularly distributed asci; asci broadly clavate, with uniformly thickened walls lacking a tholus, 60–80 × 25–35 µm, 8-spored, eventually disintegrating and releasing the ascospores passively to accumulate as a 50–100 µm thick mazaediate layer above the hymenium. Ascospores obovate, with the distal cell enlarged (macrocephalic), 3–5-septate, 22–36 × 9–15 µm, about 2–2.5 times as long as broad, at first hyaline, but soon becoming dark brown even within the asci, with rather thin walls and blackish brown, somewhat thickened septal bands, their walls minutely verruculose, slightly constricted at the septa; proximal cell paler to colorless, thin-walled, papilliform.

Secondary substances. Not tested.

Ecology and distribution. Known from the Florida peninsula, with one unverified record from Massachusetts; usually on the leaf bases of *Sabal palmetto* in *Sabal palmetto-Quercus virginiana* hammock and mixed, palm-rich hardwoods. Reports from northeastern Colombia [e.g., https://www.gbif.org/occurrence/4538303704] are not that species, but one of the newly described taxa in this study.

Figure 12. *Sporostigma melasporum* (isotype in H). Thallus with mazaedia. Scale = 1 mm.

Remarks. The species is treated in detail by Grube (2001b). Its distinguishing features include the leprose-farinose thallus, not as compact as in the other species treated here, and the diffuse, grey rather than black mazaedia.

Sporostigma pseudostromaticum J.-M. Torres, Lücking & B. Moncada, sp. nov. (Fig. 13)

MycoBank MB 863862

Diagnosis: Differing from *Sporostigma cubanum* in the notably pseudostromatic ascomata with branched to dissected individual mazaedia and with an even thallus margin; and from *S. stellatum* also in the pseudostromatic ascomata and the compacted, smooth thallus.

Type: Colombia, Córdoba: Pueblo Nuevo, La Gloria; 75.5227377°N, 8.5323641°W, 125 m; trees in pasture, on bark of *Sabal mauritiformis* palm; 16 Mar. 2024, *C. Tirado mf-06* (UDBC – holotype!).

Etymology. The epithet refers to the pseudostromatic ascomata with branched to dissected mazaedia.

Description. Thallus white, uneven, smooth, thin (following the contours of the bark), ecorticate, with thin black prothallus line; in section 100–130 µm thick, strongly nubilous with small, grey crystals that slowly dissolve in K without any color reaction, except for a layer of grey crystals remaining near the surface, showing a structure of densely packed, irregularly perpendicular hyphae with large pockets of groups of 3–7 µm large algal cells in between. Ascomata abundant, about equally dense across the thallus, (erumpent to) prominent; mazaedium angular-rounded to elongate-lirellate, unbranched to irregularly or rarely stellately branched, 0.2–1 mm long, 0.15–0.2 mm broad, black, with rather sharply delimited marginal zone, often becoming secondarily divided by thalline bridges; thalline margin thick, even, flattened above, with steeply sloping sides, giving the mazaedia a distinct pseudostromatic appearance, the pseudostromata rounded to irregular in outline, up to 1 mm broad. Hymenium bowl-shaped, 80–120 µm high, consisting of densely arranged interascal hyphae and irregularly distributed asci, covered by a 30–70 µm thick, blackish brown mazaedium layer, the latter K+ blackening; asci broadly clavate, 50–60 × 25–30 µm, 8-spored. Ascospores obovate with distal cell enlarged (macrocephalic) or rarely divided into two or three cells, then uppermost cell smaller, 3–4(–5)-septate, 17–26 × 9–12 µm, 1.8–2.2 times as long as broad, at first hyaline, but soon becoming medium to dark brown, K+ blackening, with equally thickened walls and septa, the septa laterally with blackish, triangular pigmentation, not constricted at the septa; proximal cell paler, rarely colorless, with a somewhat thinner wall, rarely appearing papilliform.

Secondary chemistry. 2'-*O*-methylperlatolic acid, 2-*O*-methylperlatolic acid (minor), planaic acid,

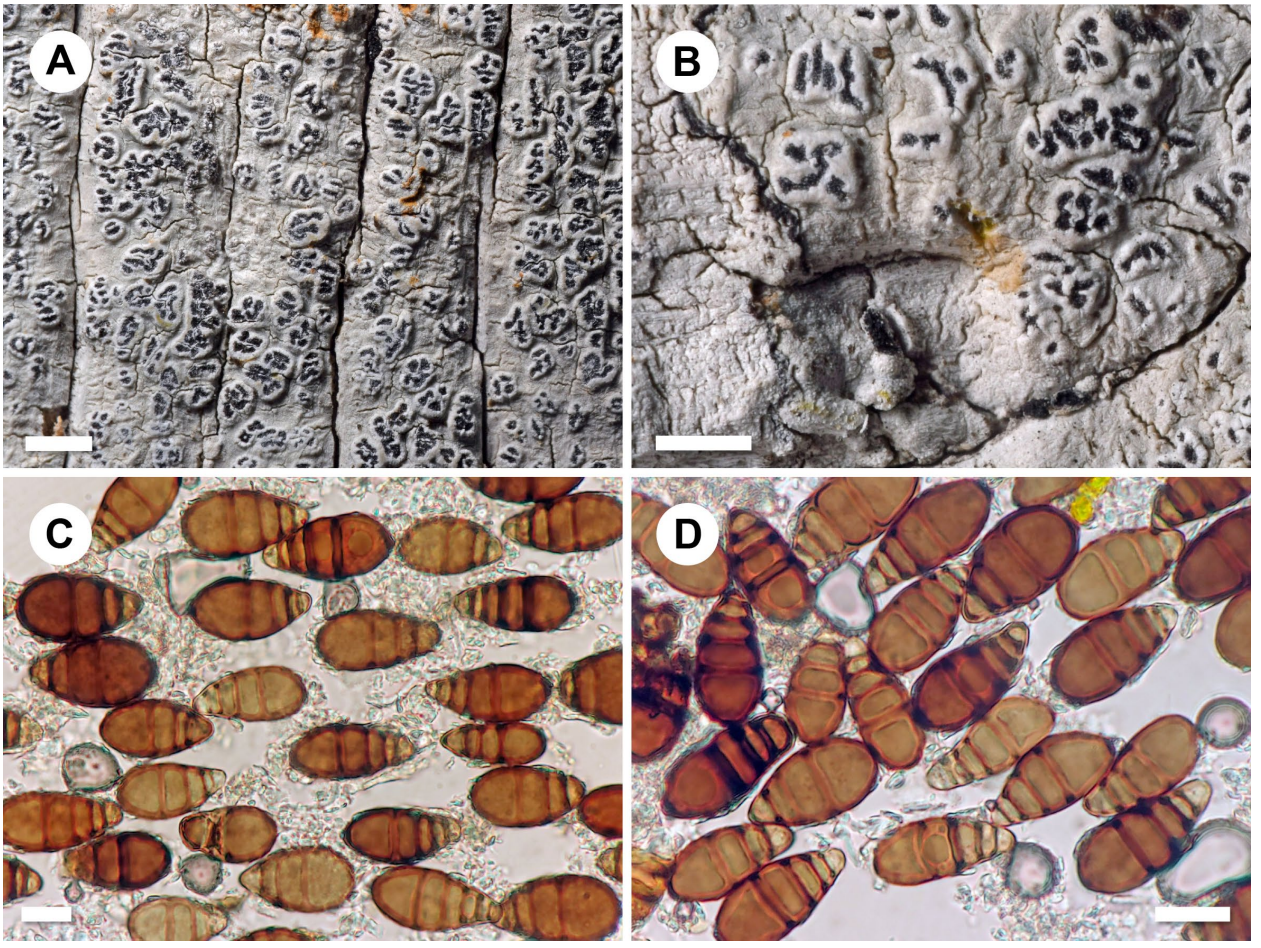

Figure 13. *Sporostigma pseudostromaticum* (holotype). A, B – thallus with mazaedia; C, D – ascospores. Scales: A, B = 1 mm; C, D = 10 µm.

2-*O*-methylconfluentic acid, 4-*O*-demethylplanaic acid, 2,2'-di-*O*-methylolivetoric acid, and an unknown substance with Rf values 43 in solvent A, 16 in solvent B', and 35 in solvent C, forming a narrow red-brown spot with pink UV fluorescence after charring under 365 nm; thallus surface and medulla C+ pale yellowish, K–, P–, UV–, in section nubilous with small, grey crystals dissolving in K without color reaction.

Ecology and distribution. Known from the type locality, growing on the bark of palms in a seasonally dry forest.

Remarks. *Sporostigma pseudostromaticum* is characterized by the prominent, distinctly pseudostromatic mazaedia which become secondarily divided within the pseudostroma, a feature not or very rarely observed in the other species. At first, we interpreted them as a late stage in the development of the mazaediae in *S. stellatum*, described below, but this is contradicted by the smaller size of the mazedia and the overall smallest ascospore size in *S. pseudostromaticum*, the ascospores also appearing stouter as in the other species, although this difference is gradual.

Sporostigma stellatum J.-M. Torres, Lücking & B. Moncada, sp. nov. (Fig. 14)

MycoBank MB 863863

Diagnosis: Differing from *Sporostigma pseudostromaticum* in the rough thallus, the lack of secondary divisions of the mazaedia, and the slightly larger ascospores.

Type: Colombia, Córdoba: Chinu, Flechas Sevilla; 75.5199029°W, 9.0150542°N, 35 m; on bark of palm; 28 Mar. 2015, J.-M. Torres 298-E (UDBC – holotype!).

Etymology. The epithet refers to the mazaedia becoming in part stellately branched.

Description. Thallus white, uneven to rough, thin (following the contours of the bark), ecorticate, with thin black prothallus line; in section 100–150 µm thick, nubilous with small, grey crystals that quickly dissolve in K without any color reaction, showing a structure of densely packed, irregularly perpendicular hyphae with large pockets of groups of 3–7 µm large algal cells in between. Ascomata abundant, becoming less dense towards the thallus margin, erumpent (to prominent); mazaedium elongate to lirellate, becoming irregularly to stellately branched, 0.6–1.5(–2.5) mm long, 0.15–0.3 mm broad, dark grey to black, with somewhat diffuse to mostly sharply delimited marginal zone; thalline margin thick, even, somewhat flattened above, with steeply sloping sides, giving the mazaedia a pseudostromatic appearance, the pseudostromata rounded to irregular in outline, up to 1.5 mm broad. Hymenium bowl-shaped, 80–130 µm high, consisting of densely arranged interascal hyphae and irregularly distributed asci, covered by a 50–100 µm thick, dark brown mazaedium layer, the latter K+ blackening, with an olive tinge; asci broadly clavate, 50–60 × 20–25 µm, 8-spored. Ascospores obovate with distal cell

enlarged (macrocephalic) or rarely divided into two or three cells, then uppermost cell smaller, (1–)3–4(–5)-septate, 20–30(–32) × 10–13(–15) µm, 1.9–2.5 times as long as broad, at first hyaline, but soon becoming medium to dark brown, K+ blackening with an olive tinge, with equally thickened walls and septa, the septa laterally with blackish, triangular pigmentation, not constricted at the septa; proximal cell paler, but usually not colorless, with a somewhat thinner wall.

Secondary chemistry. 2'-*O*-methylperlatolic acid, 2-*O*-methylperlatolic acid (minor), planaic acid, 2-*O*-methylconfluentic acid, 4-*O*-demethylplanaic acid, 2,2'-di-*O*-methylolivetoric acid, and an unknown substance with Rf values 43 in solvent A, 16 in solvent B', and 35 in solvent C, forming a narrow red-brown spot with pink UV fluorescence after charring under 365 nm; thallus surface and medulla C+ pale yellowish, K–, P–, UV–, in section nubilous with small, grey crystals dissolving in K without color reaction.

Ecology and distribution. Known from several collections in north-eastern Colombian seasonally dry forest, growing on the bark of palms.

Remarks. *Sporostigma stellatum* is somewhat intermediate between *S. cubanum* and *S. pseudostromaticum*. *Sporostigma cubanum* differs in the narrower mazaedia with

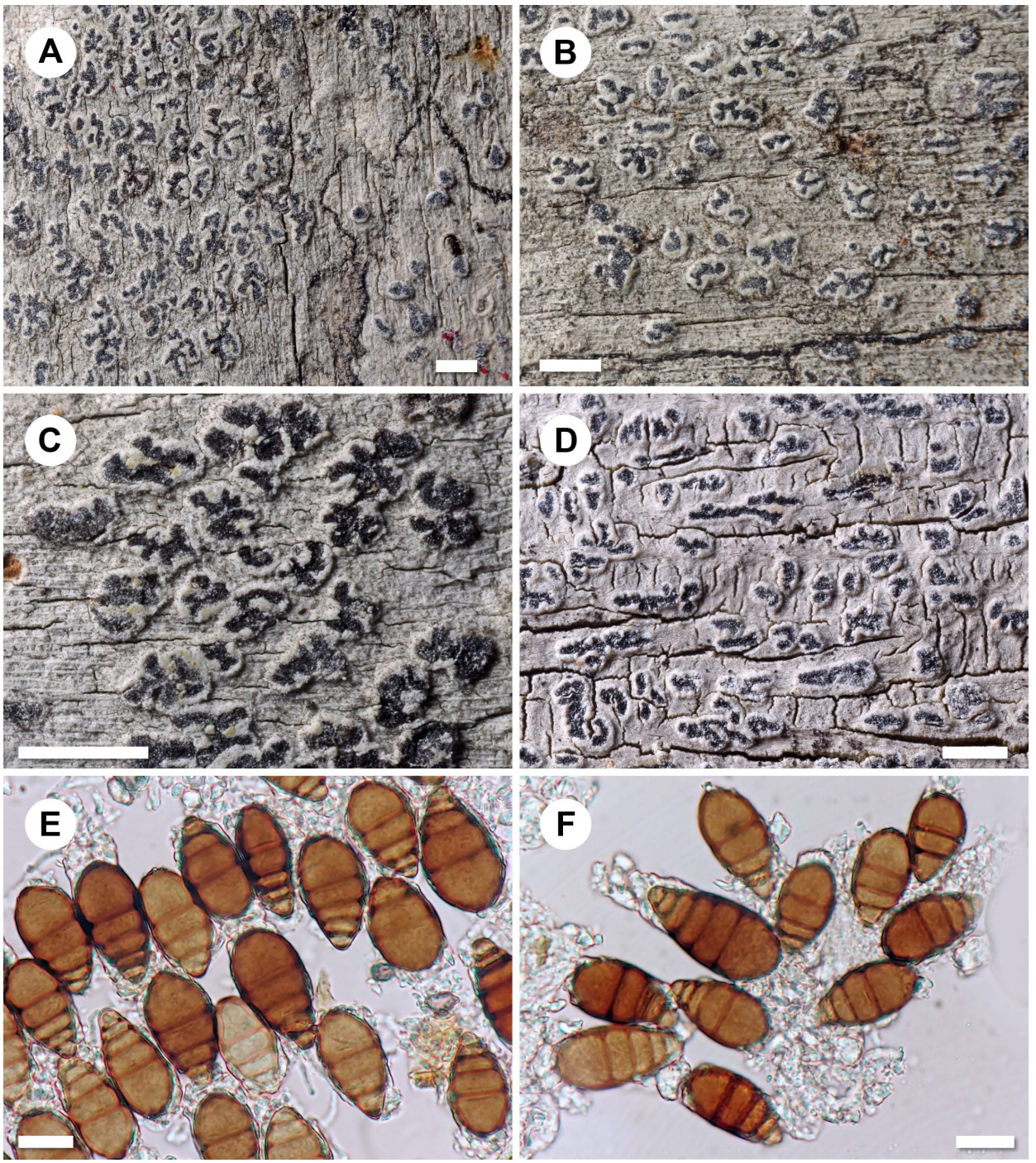

Figure 14. *Sporostigma stellatum* (A, E, F, holotype; B, Torres 289-H, C, Torres 298-K, D, ESR-34). A–D – thallus with mazaedia; E, F – ascospores. Scales: A–D = 1 mm; E, F = 10 µm.

a crenulate thalline rim. The ascospores of *S. stellatum* are not as dark as those of *S. cubanum*, lack constrictions, and the proximal cell is not as distinctly differentiated and papilliform as in *S. cubanum*. *Sporostigma pseudostromaticum* has more distinctly differentiated pseudostromata, with the mazaedia secondarily divided, and the thallus is smooth and white rather than rough and white-grey. Its ascospores are also slightly smaller and stouter than those of *S. stellatum*.

Additional specimens examined. COLOMBIA. Córdoba: Chinu, Flechas Sevilla; 75.5199029°W, 9.0150542°N, 35 m; on bark of palm; 28 Mar. 2015, J.-M. Torres 298-C, 298-H, 298-I, 298-J, 298-K (UDBC). Picolo; on bark of palm; ESR 34 (UDBC C-0027829).

Key to the species of *Sporostigma*

1 Thallus farinose; mazaedia (pale) grey, flush with the thallus, rounded to irregular in outline, with effuse marginal zone and lacking a thalline margin; ascospores minutely verruculose, rather thin-walled, with slight constrictions at the septa and the proximal cell pale and papilliform; SE USA (Florida) . . . . . ***S. melasporum***

Thallus compact; mazaedia dark grey to black, flush to prominent, rounded to mostly lirellate or becoming stellate, with diffuse to sharply delimited marginal zone and usually with a thalline margin; ascospores smooth, else variable 2

2(1) Mazaedia rounded to elongate, mostly unbranched or sparsely branched and becoming lobate, 0.3–0.6 mm broad 3

Ascomata (elongate to) lirellate, sparsely to irregularly branched or becoming stellate, sometimes secondarily divided, 0.15–0.3 mm broad 4

3(2) Mazaedia immersed to very slightly erumpent, the thin thalline margin more or less flush with the thallus surface; mazaedia rather sharply delimited, less than 1 mm long and up to 2 times as long as broad; ascospores 9–13 µm broad, with proximal cell only slightly paler and not distinctly papilliform; Colombia . . . . . ***S. immersellipsoideum***

Mazaedia distinctly erumpent, with thickened thalline margin with steeply sloping margin; mazaedia rather diffusely delimited, up to 2 mm long and up to 6 times as long as broad; ascospores 10–15 µm broad, with proximal cell paler to colorless and often distinctly papilliform; Colombia . . . . . ***S. lobatum***

4(2) Mazaedia in erumpent to prominent, pseudostromatic groups, pseudostromata up to 1 mm broad 5

Mazaedia not in pseudostromatic groups, immersed to erumpent, less than 0.5 mm broad including the thalline margin 6

5(4) Pseudostromata distinct, prominent, the individual mazaedia often secondarily divided within the pseudostromata and hence short and more or less isodiametric; ascospores up to 26 × 12 µm; thallus smooth, white; Colombia . . . . . ***S. pseudostromaticum***

Pseudostromata indistinct, erumpent, the individual mazaedia rarely secondarily divided and usually lirelliform; ascospores up to 32 × 15 µm; thallus rough, white-grey; Colombia . . . . . ***S. stellatum***

6(4) Mazaedia immersed to slightly erumpent, with broad, even, gently sloping thalline margin; mazaedia often separated from the thalline margin by a thin slit; ascospores medium to dark brown, with equally thickened walls and septa and septa mostly lacking constrictions, with proximal cell only slightly paler and not distinctly papilliform; thallus smooth, white; Colombia . . . ***S. hieroglyphicum***

Mazaedia erumpent to prominent, with thickened, irregularly crenulate, steeply sloping thalline margin; ascospores very dark brown, with rather thin walls and thickened septa and often with slight constrictions at the septa, with proximal cell pale to colorless and papilliform; thallus rough, white-grey; Cuba . . . . . ***S. cubanum***

Acknowledgements

The authors thank Z. Cordero-Parada for donating and depositing in the UDBC herbarium the material collected during the field phase of the Environmental impact assessment study "Linea de transmisión Cerromatoso-Chinú-Copey 500 kV", carried out in the departments of Córdoba, Sucre, Bolívar, and Magdalena. The workshop at the UDBC herbarium during which the material was taxonomically assessed was supported by the DRYLICH project "Establishing a Network of Expertise for the Lichen Biota of the Tropical Dry Forest", a bilateral project between the Botanical Garden and Botanical Museum of Berlin and the Universidad del Norte, Barranquilla, funded by the Federal Ministry of Education and Research (Bundesministerium für Bildung und Forschung – BMBF; Förderkennzeichen 01DN23013) and the Ministry of Science, Technology and Innovation (MinCiencias; Contract Number 80740-032-2023), within the program "Promoting Scientific and Technological Cooperation Projects with Colombia" (Förderung von Projekten der wissenschaftlich-technologischen Zusammenarbeit mit Kolumbien).

Author contributions

RL, JMT and BM conceived the study. All authors contributed to the collection and analysis of the data. RL wrote the initial manuscript draft and all authors revised the manuscript and approved the final version.

Data availability

Sequence data used in this study were submitted to GenBank. The underlying mtSSU alignment and tree file ae available as Supplementary Files S1 and S2. The morphometric data matrices are available as Supplementary Files S3–S5.

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Supplementary electronic materials

File S1. *Sporostigma* Alignment (mtSSU). Download file
File S2. *Sporostigma* Best-scoring tree (mtSSU). Download file
File S3. *Sporostigma* Data matrix (raw). Download file
File S4. *Sporostigma* Data matrix (second). Download file
File S5. *Sporostigma* Data matrix (main normalized). Download file

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