


Standard Paper

New species of *Arthoniales* from Cape Verde with an enlarged concept of the genus *Ingaderia*

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Abstract

Three new species of *Arthoniales* are described from Cape Verde: *Ingaderia dendritica*, with ascomata formed of richly branched-dendroid lirellae and containing erythrin; *Sparria caboverdensis*, with small stroma-like ascomata and ascospores with 3–7 transverse septa; and *Syncesia miesii*, with an I– thallus, a tomentose hymenial disc, and a chemistry with fatty acids only. Phylogenetic analyses using nuLSU and RPB2 sequences reveal the placement of *Fulvophyton sorediatum*, *Llimonaea occulta*, *L. sorediata* and *Sparria caboverdensis* in the family *Opegraphaceae*. The genus *Llimonaea* is recovered as paraphyletic, with *L. flexuosa* being placed as sister species to a lineage including the genera *Ingaderia* and *Paraingaderia*. In consequence, an enlarged concept of the genus *Ingaderia* is proposed, resulting in the transfer of *F. sorediatum*, *L. flexuosa*, *L. occulta*, *L. sorediata* and *Paraingaderia placodioides* to *Ingaderia*.

Key words: *Fulvophyton*, lichen, *Llimonaea*, *Opegraphaceae*, phylogeny, *Sparria*, *Syncesia*

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Introduction

Cape Verde is an Atlantic and volcanic archipelago that lies c. 570 km west of Senegal on the African coast. Since the publication of a critical checklist of lichens and allied fungi of the Cape Verde Islands by Mies (1993), considerable progress has been made in the study of its lichen flora. New species have been described from the archipelago in the genera *Amandinea*, *Buellia* (Elix & van den Boom 2022), *Caloplaca* (Arup & van den Boom 2011), *Cratiria* (Elix & van den Boom 2022), *Dirina* (Tehler *et al.* 2013), *Lecidella* (Knoph & Mies 1995), *Llimonaea* (Egea *et al.* 1995), *Plectocarpon* (Ertz & van den Boom 2012), *Rinodina* (Giralt & van den Boom 2008) and *Thelopsis* (van den Boom 2012). Many other additional species have been newly reported for the archipelago (e.g. Büdel & Mies 1993; Tehler *et al.* 2004; Llop & van den Boom 2009; van den Boom 2012; Ertz & van den Boom 2020; Zhurbenko *et al.* 2020).

The arid climate with salinic conditions through aerosol salts favours a diverse lichen vegetation dominated by *Arthoniales* (Fig. 1). Species of *Dirina*, *Lecanographa* and *Roccella* are abundant on coastal and mainly north-east exposed rocks when reached by maritime salt spray, blown in or uplifted by the trade winds, sometimes to rather high altitudes (c. 1000 m elev.) when the topography of the islands is without any high ascending interruption (Mies 1993). But the most peculiar *Arthoniales* is the Cape Verdean endemic *Gorgadesia mira* Tav., remarkable in its

fruticose thallus with lirelliform-dendroid ascomata (Tavares 1964; Follmann & Mies 1986) (Fig. 1).

A study of recent collections made by the authors in Cape Verde revealed several undescribed crustose *Arthoniales*. The aim of this study is to describe these new species. A phylogeny of the *Opegraphaceae* is provided, and the phylogenetic positions of the type species of the genus *Llimonaea* and of *Fulvophyton sorediatum* (Sparrius *et al.*) Tehler & van den Boom are revealed. The new molecular data result in an enlarged concept of the genus *Ingaderia*.

Materials and Methods

Voucher specimens are deposited in the herbaria BR, FR, M and S. The external morphology was studied and measured using an Olympus SZX12 stereomicroscope. Macroscopic images were captured with a Keyence VHX-5000 digital microscope and a VH-Z20R/W/T lens. Hand-cut sections and squash preparations of thalli were mounted in water, a 5% aqueous potassium hydroxide solution (K), or in Lugol's iodine solution (1% I₂) without (I) or with K pretreatment (KI), and studied using an Olympus BX51 compound microscope. Measurements of ascospores do not include the perispore (=gelatinous sheath) and are reported as (minimum–) (\bar{x} –SD) – (\bar{x} +SD) (–maximum), followed by number of measurements (n), and the values are rounded to the nearest 0.5 μ m. Measurements refer to dimensions in water. Microscopic images were captured 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

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Fig. 1. North-east coast of São Vicente between Baía das Gatas and Calhau, with large cliffs in arid and salinic conditions that favour a diverse lichen vegetation dominated by *Arthoniales*, including *Gorgadesia mira*, *Ingaderia dendritica*, *I. flexuosa* and *Sparria caboverdensis*. In colour online.

(PD) and long-wave UV (366 nm). Lichen secondary metabolites were investigated using thin-layer chromatography (TLC) in solvents EA and G (Orange *et al.* 2010).

Molecular techniques

Well-preserved and freshly collected specimens (less than two months) or specimens kept in a freezer and frozen less than two months after collection and lacking any visible symptoms of fungal infection were used for DNA isolation. Genomic DNA was isolated from lichen specimens using the CTAB extraction protocol (Doyle & Doyle 1990). For three specimens (*Llimonaea flexuosa* Ertz 17273, *L. occulta* Ertz 16919 and *L. sor-diata* Ertz 17030), hand-cut sections of the ascomata 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 were prepared for a 50 μ l final volume containing 5 μ l 10 \times DreamTaq buffer (Fermentas), 1.25 μ l of each of the 20 μ M primers, 5 μ l of 2.5 mg ml⁻¹ bovine serum albumin (Fermentas #B14), 4 μ l of 2.5 mM each dNTPs (Fermentas), 1.25 U DreamTaq DNA polymerase (Fermentas) and 1 μ l of template genomic DNA or tiny fragments of lichen material. A targeted fragment of *c.* 1 kb of the *RPB2* protein-coding gene was amplified using the primers fRPB2-7cF and fRPB2-11aR (Liu *et al.* 1999), and a fragment of *c.* 1.4 kb at the 5' end of the nuLSU rDNA was amplified using primers LIC15R (Miadlikowska *et al.* 2002) and LR7 (Vilgalys & Hester 1990). Cycling conditions for *RPB2* included initial denaturation at 95 °C for 3 min (genomic DNA) or for 10 min (direct PCR), 35 cycles of 95 °C for 45 s, 52 °C for 1 min and 72 °C for 1 min, with a final extension step at 72 °C for 10 min. Cycling conditions for nuLSU included initial denaturation at 95 °C for 3 min (genomic DNA) or for 10 min (direct PCR), 25 cycles of 95 °C for 45 s, 52 °C for 40 s and 72 °C for 2.5 min, 14 cycles of 95 °C for 45 s, 52 °C for 40 s and 72 °C for 2.5 min (+5 s per cycle), with a final extension step at 72 °C for 10 min. Both strands were sequenced by Macrogen[®] using amplification primers, and with the additional primers LR3R and LR3 (Vilgalys & Hester 1990) for nuLSU. Sequence fragments were

assembled with Sequencher v. 5.4.6 (Gene Codes Corporation, Ann Arbor, Michigan, USA). Sequences were subjected to MegaBLAST searches to verify their closest relatives and to detect potential contaminations.

Taxon selection and phylogenetic analyses

The newly generated sequences were subjected to NCBI BLAST searches (<https://www.ncbi.nlm.nih.gov>) in order to obtain a first approximation of phylogenetic affiliation. A two-locus dataset (nuLSU and *RPB2*) was assembled for placing the newly sequenced taxa in a phylogeny of the *Opoglyphaceae* as circumscribed by Ertz & Tehler (2011). Sequences published in Tehler & Irestedt (2007), Ertz *et al.* (2009), Ertz & Tehler (2011), Frisch *et al.* (2014), Ertz (2020), Diederich & Ertz (2020) and Perlmutter *et al.* (2020) were retrieved from GenBank. The sequences (Table 1) were aligned using MAFFT v. 7.490 (Katoh & Standley 2013) on the CIPRES Web Portal (Miller *et al.* 2010) and manually corrected for errors using Mesquite v. 3.04 (Maddison & Maddison 2015). Terminal ends of sequences, ambiguously aligned regions and introns were delimited manually and excluded from the datasets. The resulting matrix of *Opoglyphaceae* consisted of 63 terminals. Three species of *Roccellaceae*, viz. *Dichosporidium brunnthaleri* (Zahlbr.) G. Thor, *Enterographa crassa* (DC.) Fée and *Erythrodictyon granulatum* (Mont.) G. Thor, were selected as the rooting taxa from Frisch *et al.* (2014). The final concatenated alignment consisted of 1731 (828 for nuLSU and 903 for *RPB2*) unambiguously aligned sites.

Best-fit evolutionary models were estimated using the Akaike Information Criterion (AIC) as implemented in jModelTest v. 2.1.6 (Darriba *et al.* 2012). The TrN+I+G model was selected for the nuLSU dataset, the TIM1+G model was selected for the *RPB2*/1st position, the GTR+I+G model for the *RPB2*/2nd position and the TIM3+I+G model for the *RPB2*/3rd position datasets.

Analyses for topological incongruence among loci were carried out by analyzing 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 GTRGAMMA model was used and node support was assessed running 1000 bootstrap replicates. We analyzed the two single-locus datasets for topological incongruence by assuming a conflict to be significant when two different relationships (one being monophyletic and the other 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 and *RPB2* datasets were concatenated.

Bayesian analyses were carried out on the two-locus datasets under the selected models for four partitions (nuLSU, *RPB2*/1st, *RPB2*/2nd and *RPB2*/3rd positions) using the Metropolis-coupled Markov chain Monte Carlo method (MCMCMC) in MrBayes v. 3.2.7a (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003) on the CIPRES Web Portal (Miller *et al.* 2010). Two parallel MCMCMC runs were performed each using four independent chains and 40 million generations, sampling trees every 1000th generation. Posterior probabilities (PP) were determined by calculating a majority-rule consensus tree generated from the 60 002 post burn-in trees of the 80 002 trees sampled by the two MCMCMC runs using the sumt option of MrBayes. Tracer v. 1.7.1 (Rambaut *et al.* 2018) was used to ensure that stationarity was reached by plotting the log-likelihood values of the sample points against generation time, making sure that the ESS values were much higher than 200. Convergence between

Table 1. Specimens and DNA sequences used in this study, with their respective voucher information. GenBank Accession numbers in bold refer to sequences generated by this project. All other sequences were obtained directly from GenBank.

Current names	Voucher	<i>RPB2</i>	nucLSU
<i>Combea mollusca</i>	South Africa; A. Tehler 7725 (S)	DQ987626	EF081383
<i>Dichosporidium brunthaleri</i>	Réunion; D. Ertz 17968 (BR)	KJ524361	KJ524282
<i>Dictyographa arabica</i>	Galapagos Islands; D. Ertz 11678 (BR)	HQ454710	HQ454570
<i>D. varians</i>	Yemen, Socotra Island; A. Tehler 9346 (S)	HQ454716	HQ454576
<i>Dolichocarpus chilensis</i>	Chile; A. Tehler 8373 (S)	HQ454668	HQ454528
<i>Enterographa crassa</i>	France; D. Ertz 5041 (BR)	EU704020	EU704088
<i>Enterographa</i> sp.	Gabon; D. Ertz 9770 (BR)	EU704019	EU704087
<i>Erythrodictyon granulatum</i>	Gabon; D. Ertz 9908 (BR)	EU704022	EU704090
<i>Fouragea filicina</i>	Rwanda; D. Ertz 7994 (BR)	EU704031	EU704095
<i>F. vegae</i>	Comoros, Mayotte; D. Ertz 21823 (BR)	MT942599	MT944352
<i>F. viridistellata</i>	Réunion; D. Ertz 4795 (BR)	EU704040	EU704104
<i>Fulvophyton solediatum</i>	France, Corsica; D. Ertz 16412 (BR)	OP641889	OP630475
<i>F. solediatum</i>	Azores; D. Ertz 16690 (BR)	OP641890	OP630476
<i>F. solediatum</i>	Azores; D. Ertz 16878 (BR)	OP641891	OP630477
<i>F. solediatum</i>	Portugal; D. Ertz 16917 (BR)	OP641892	OP630478
<i>F. solediatum</i>	Portugal; D. Ertz 17049 (BR)	OP641893	NA
<i>F. solediatum</i>	France, Brittany; D. Ertz 17469 (BR)	OP641894	OP630479
<i>Ingaderia pulcherrima</i> 1	Chile; A. Tehler 8371 (S)	HQ454677	HQ454537
<i>I. pulcherrima</i> 2	Chile; A. Tehler 9886 (S)	HQ454679	HQ454539
<i>Llimonaea flexuosa</i>	Cape Verde; A. Tehler 10032 (S)	OP641895	NA
<i>L. flexuosa</i>	Canary Islands; D. Ertz 13880 (BR)	HQ454709	HQ454569
<i>L. flexuosa</i>	Cape Verde; D. Ertz 17243 (BR)	OP641896	NA
<i>L. flexuosa</i>	Cape Verde; D. Ertz 17273 (BR)	OP641897	OP630480
<i>L. occulta</i>	Portugal; D. Ertz 16908 (BR)	OP641898	OP630481
<i>L. occulta</i>	Portugal; D. Ertz 16919 (BR)	OP641899	OP630482
<i>L. occulta</i>	Portugal; D. Ertz 16935 (BR)	OP641900	OP630483
<i>L. occulta</i>	Portugal; D. Ertz 17079 (BR)	OP641901	OP630484
<i>L. solediatum</i>	Portugal; D. Ertz 17030 (BR)	OP641902	OP630485
<i>L. solediatum</i>	Portugal; D. Ertz 17076 (BR)	OP641903	OP630486
<i>Nyungwea pallida</i>	Uganda; A. Frisch 11/Ug24 (UPS)	KJ851145	KJ851066
<i>N. pyneei</i>	Mauritius; D. Ertz 21450 (BR)	MN989870	MT831070
<i>Opegrapha lithyriga</i>	Belgium; D. Ertz 8784 (BR)	EU704032	EU704096
<i>O. medusulina</i>	Gabon; D. Ertz 10024 (BR)	HQ454714	HQ454574
<i>O. niveoatra</i>	Belgium; D. Ertz 7529 (BR)	EU704034	EU704098
<i>O. vermicellifera</i>	Belgium; D. Ertz 7562 (BR)	EU704041	EU704105
<i>O. vulgata</i>	Belgium; D. Ertz 7564 (BR)	EU704044	EU704108
<i>Paraingaderia placodioidea</i> 1	Yemen, Socotra Island; A. Tehler 9315 (S)	HQ454772	HQ454632
<i>P. placodioidea</i> 2	Yemen, Socotra Island; A. Tehler 9344 (S)	HQ454773	HQ454633
<i>Paralecanographa grumulosa</i>	Great Britain, Gibraltar; A. Tehler 9809 (S)	HQ454682	HQ454542
<i>Paraschismatomma ochroleucum</i> 1	Mexico; A. Tehler 9090 (S)	HQ454757	HQ454617
<i>P. ochroleucum</i> 2	Mexico; A. Tehler 9111 (S)	HQ454758	HQ454618
<i>Pentagenella akompsa</i>	USA, California; D. Ertz 12406 (BR)	MT831981	MT831071

(Continued)

Table 1. (Continued)

Current names	Voucher	RPB2	nuLSU
<i>P. corallina</i> 1	Chile; A. Tehler 8416 (S)	DQ987637	EF081394
<i>P. corallina</i> 2	Peru; A. Tehler 8916 (S)	HQ454717	HQ454577
<i>P. fragillima</i> 1	Chile; A. Tehler 8381 (S)	DQ987638	EF081395
<i>P. gracillima</i> 1	Chile; A. Tehler 8366 (S)	HQ454674	HQ454534
<i>P. gracillima</i> 2	Chile; A. Tehler 8377 (S)	DQ987633	EF081390
<i>P. langei</i> 1	Chile; A. Tehler 8382 (S)	DQ987632	EF081389
<i>P. langei</i> 2	Chile; A. Tehler 9871 (S)	MT831983	MT831072
<i>P. ligulata</i> 1	Chile; A. Tehler 9870 (S)	MT831984	MT831073
<i>Pentagenella</i> sp. 1	Peru; A. Tehler 8882 (S)	MT831986	MT831074
<i>Pentagenella</i> sp. 2	Chile; A. Tehler 9932 (S)	MT831987	MT831075
<i>Schizopelte californica</i>	Mexico; A. Tehler 9082 (S)	HQ454760	HQ454620
<i>S. crustosa</i> 1	USA, California; A. Tehler 7844 (S)	DQ987636	EF081393
<i>S. crustosa</i> 2	Mexico; A. Tehler 9114 (S)	HQ454703	HQ454563
<i>S. parishii</i> 1	Mexico; A. Tehler 9099 (S)	HQ454672	HQ454532
<i>S. parishii</i> 2	Mexico; A. Tehler 9107 (S)	HQ454673	HQ454533
<i>Sparria caboverdensis</i>	Cape Verde; A. Tehler 10013 (S)	OP641904	OP630487
<i>S. caboverdensis</i>	Cape Verde; D. Ertz 17222 (BR)	OP641905	OP630488
<i>S. cerebriformis</i> 1	Mexico; A. Tehler 9097 (S)	HQ454705	HQ454565
<i>S. cerebriformis</i> 2	Mexico; A. Tehler 9144 (S)	HQ454707	HQ454567
<i>S. endlicheri</i> 1	Belgium; D. Ertz 14067 (BR)	HQ454653	HQ454512
<i>S. endlicheri</i> 2	Belgium; D. Ertz 14068 (BR)	HQ454654	HQ454513

runs was also verified using the PSRF (Potential Scale Reduction Factor), where values were all equal or close to 1.000.

In addition, a ML analysis was performed on the two-locus dataset 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 two-locus dataset was divided into four partitions (nuLSU, RPB2/1st, RPB2/2nd and RPB2/3rd positions) with the GTRGAMMA model. Phylogenetic trees were visualized using FigTree v. 1.4.2 (Rambaut 2012).

The ML tree did not contradict the Bayesian tree topology for the strongly supported branches. Therefore, only the ML tree is shown, with the ML-BS values added above the internal branches and the PP values added below the internal branches (Fig. 2). ML-BS ≥ 70 and PP ≥ 0.95 were considered to be significant.

Results

Phylogenetic analysis

Thirty-one new sequences (14 nuLSU, 17 RPB2) were obtained for this study and 92 additional sequences (46 nuLSU, 46 RPB2) were retrieved from GenBank, representing a total of 40 species and 63 specimens (Table 1). The RAxML tree obtained from the combined two-locus analysis of the *Opegraphaceae* dataset is shown in Fig. 2. Relationships within *Opegraphaceae* are generally well supported, except for the backbone of the tree. The main well-supported lineages are in accordance with the results obtained by Ertz (2020) and Perlmutter *et al.* (2020). The type of the genus *Llimonaea*, *L. occulta* Egea & Torrente, is sequenced for

the first time and forms with *L. solediatum* van den Boom *et al.* a well-supported lineage sister to the genus *Paraingaderia*. *Fulvophyton solediatum* is the sister species to *Llimonaea-Paraingaderia*, a relationship that is fully supported. Therefore, that species is well nested within the family *Opegraphaceae* and does not belong to *Fulvophyton* in the *Roccellographaceae*. The genus *Llimonaea* is recovered as paraphyletic because of the placement of *L. flexuosa* Egea *et al.* as sister to a clade including *Llimonaea* s. str. but also the genera *Ingaderia* and *Paraingaderia*, and *Fulvophyton solediatum*. *Sparria caboverdensis* Ertz & Tehler is the sister species to *Sparria cerebriformis* (Egea & Torrente) Ertz & Tehler and *S. endlicheri* (Garov.) Ertz & Tehler, a relationship that strongly supports its placement in the genus *Sparria*. We were unsuccessful with the sequencing of the other new species described from Cape Verde below, mainly because the DNA had not been extracted or the specimens kept in the freezer after collection became too old for sequencing.

Taxonomy

New species

Ingaderia dendritica Ertz & Tehler sp. nov.

Mycobank No.: MB 846082

Differing from *Ingaderia flexuosa* (Egea *et al.*) Ertz & Tehler by the narrower (up to 0.4 mm wide), richly dichotomously branched lirellae remaining mostly immersed in the thallus, and by the production of erythrin as a major secondary metabolite.

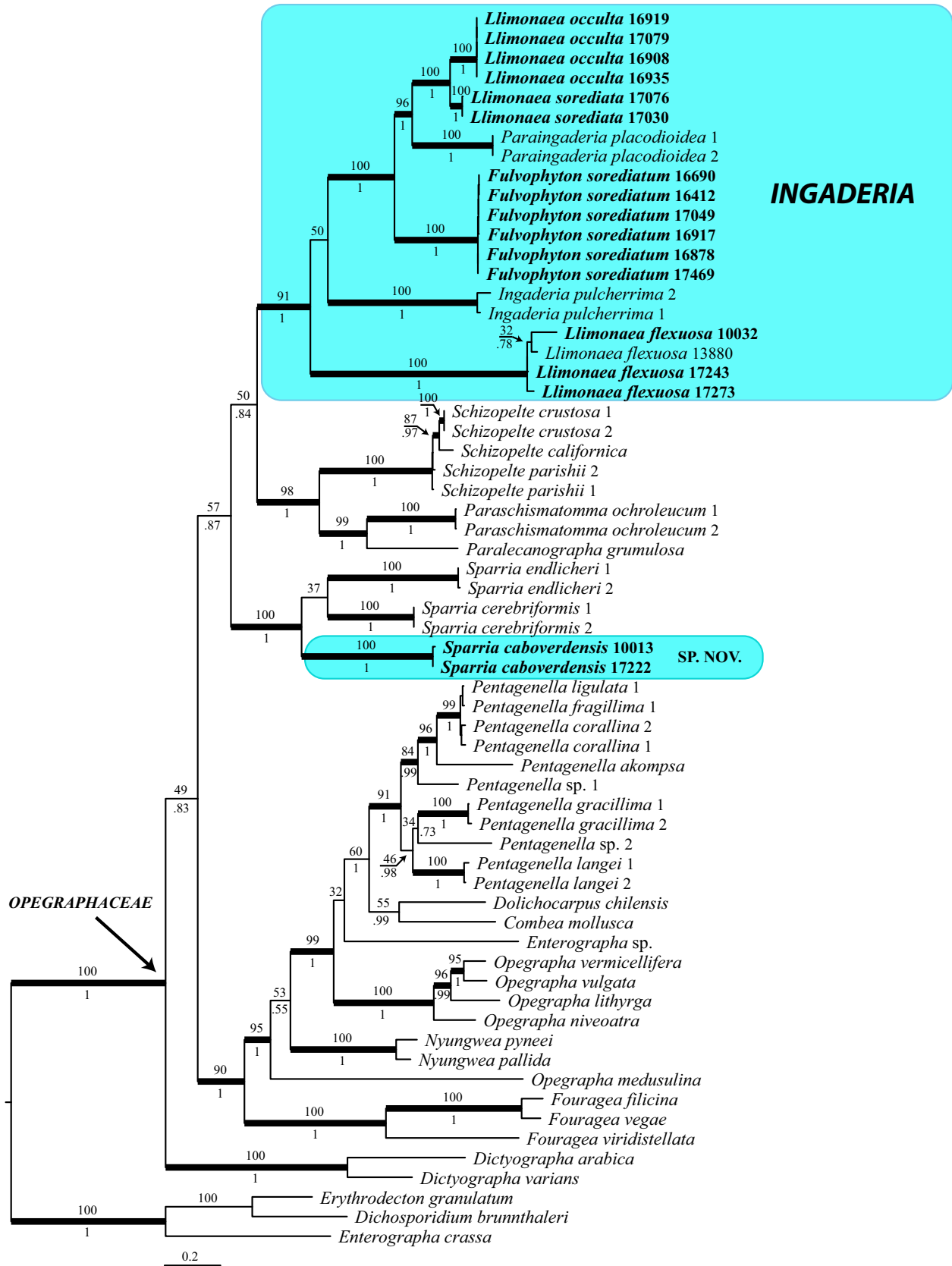


Fig. 2. Phylogeny of *Opegraphaceae* based on a dataset of nuLSU and *RPB2* sequences that resulted from the RAxML analysis. Maximum likelihood bootstrap values are shown above internal branches and posterior probabilities obtained from a Bayesian analysis are shown below. Internal branches, considered strongly supported by both analyses, are represented by thicker lines. The newly sequenced samples are in bold and their names are followed by collection numbers of authors, which act as specimen and sequence identifiers. The lineage corresponding to the enlarged concept of the genus *Ingaderia* is highlighted, as well as the new species *Sparria caboverdensis*. In colour online.

Type: Cape Verde, São Vicente, Praia Grande on NE-facing ridge above the beach, 16°51.549'N, 24°53.195'W, 100–200 m elev., on vertical N-facing cliffs, 1 January 2010, A. Tehler 10033 (S—holotype!).

(Fig. 3)

Thallus crustose, pale creamish, rimose-areolate, mostly flat, smooth to slightly rugulose, matt; areoles 0.3–0.8(–1) mm diam., in section *c.* 150–250 μ m thick; upper cortex inconspicuous

or poorly differentiated, *c.* 12–20 μ m thick, of ‘branched type’ (as defined by Aptroot & Schumm (2011: p. 7)); rich in crystals (polarized light), some dissolving in KOH and others of calcium oxalate ($H_2SO_4!$). *Photobiont* trentepohlioid; cells rounded to elongate, 7–20 \times 6–12 μ m.

Ascomata immersed in the thallus, becoming slightly elevated above the thallus surface, lirelliform, flexuose, richly dichotomously branched giving a dendritic appearance, remaining narrow, not forming stromatic aggregates, 1–8(–10) \times 0.15–0.3(–0.4) mm

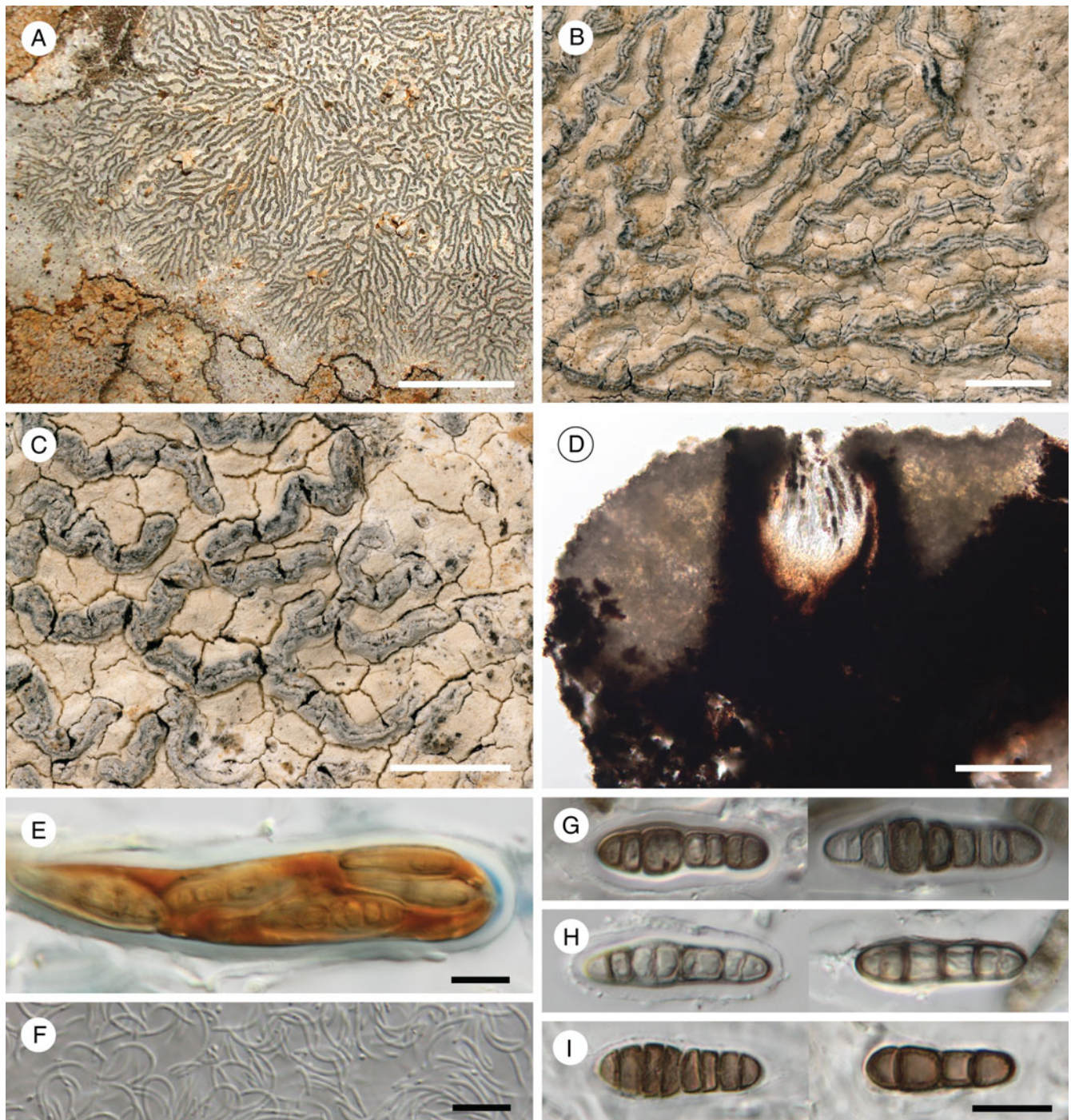


Fig. 3. *Ingaderia dendritica* (B, D, F & G, Tehler 10033; A, C, E & H, Ertz 17229; I, Ertz 17280). A–C, thallus and ascomata (A taken in the field). D, section through an ascoma in water. E, ascus in KI. F, conidia in K. G–I, ascospores in water, except the second G (right) in K. Scales: A = 1 cm; B & C = 1 mm; D = 100 μ m; E–I = 10 μ m (G, H and I, same magnification). In colour online.

but regularly divided into shorter fragments corresponding to the thallus areoles, black, mostly covered by a thin layer of thallus *c.* 5–25 µm thick, often appearing slightly whitish pruinose along the slit-like opening; hymenial disc remaining slit-like. *Excipulum* dark brown to black, *c.* 45–95 µm thick, fused with the hypothecium below, K+ becoming slightly darker. *Hymenium* clear, hyaline to pale fawn, 80–115 µm tall, I+ red, KI+ pale blue; *epihymenium* hyaline, I+ red, KI+ pale blue. *Paraphysoids* richly branched-anastomosing, 2–2.5 µm thick, not or slightly enlarged to 3.5 µm in epihymenium. *Hypothecium* dark brown, thick, extending to the substratum, 125–250 µm thick, I–, K+ becoming slightly darker. *Asci* (4–)8-spored, narrowly clavate, 80–105 × 17–22 µm, with a distinct ocular chamber; wall not distinctly thicker at apex; endoascus KI+ blue with a KI+ blue apical ring. *Ascospores* fusiform with the upper half often wider, 3–7(–8)-septate, dark brown from an early stage, with a distinct dark brown verruculose ornamentation on the wall, K+ becoming slightly darker, (17–)20–26.5(–31) × (5–)5–7(–9) µm (*n* = 35); gelatinous sheath *c.* 0.5–1.5 µm sometimes present.

Pycnidia immersed in the thallus, visible as dark brown dots, sometimes slightly whitish pruinose, surrounded by a thin whitish to creamish margin, level with the thallus surface and separated from it by a crack, *c.* 90–190 µm diam.; spherical in cross-section; wall dark brown; *conidia* hyaline, filiform, slightly curved to sickle-shaped, 13–18 × 1 µm.

Chemistry. Thallus C+ red, K–, UV–. TLC (solvent EA): erythrin (major) (specimens tested: Ertz 17229, 17280 and Tehler 10033).

Etymology. The epithet is named after the dendritic appearance of the ascomata.

Distribution and ecology. So far known only from the island of São Vicente in Cape Verde, where it inhabits volcanic rock of vertical N-facing cliffs in arid and open conditions near the sea.

Discussion. The new species differs from *Ingaderia flexuosa* (see emended description below) by its narrower (up to 0.4 mm wide vs up to 0.6 mm in *I. flexuosa*) richly branched-dendroid lirellae remaining immersed in the thallus, becoming only slightly elevated above the thallus surface, and by the production of erythrin. *Ingaderia occulta* (Egea & Torrente) Ertz also has a thick black excipulum and hypothecium, similar ascospores and produces erythrin. It differs from *I. dendritica* by the ascomata that are shortly lirellate to roundish, that become elevated, with a slit-like opening which gets wider at maturity (Torrente & Egea 1991; Egea *et al.* 1995).

Additional specimens examined. **Cape Verde:** São Vicente: S of the road between Baía das Gates and Calhau, NE of Monte Verde, 16°52'29"N, 24°54'46"W, *c.* 200 m elev., on vertical NE-facing coastal volcanic outcrops, on rock, 2011, D. Ertz 17229 (BR); *ibid.*, NW of Calhau, northern slope of Goa Baixo, 16°51'27"N, 24°52'42"W, *c.* 120 m elev., strongly sloping and vertical coastal volcanic outcrops, on rock, 2011, D. Ertz 17280 (BR).

Sparria caboverdensis Ertz & Tehler sp. nov.

MycoBank No.: MB 846083

Differing from *Sparria cerebriformis* (Egea & Torrente) Ertz & Tehler by having smaller stroma-like ascomata 0.5–1.5(–2) mm

diam., a narrower hymenium (95–190 µm) and non-muriform ascospores with 3–7 transverse septa.

Type: Cape Verde, São Vicente, Praia da Ceilada do Calhau, 2–3 km NW of Calhau on NE-facing ridge above the beach, 16°51.552'N, 24°52.741'W, *c.* 150 m elev., on vertical N-facing cliffs, 30 December 2009, A. Tehler 10013 (S—holotype!).

(Fig. 4)

Thallus crustose, pale creamish, rimose-areolate, flat or bullate, smooth to slightly rugulose, matt; areoles 0.3–2 mm diam., in section up to 0.7 mm thick; upper cortex *c.* 50–90 µm thick, of 'branched type' (as defined by Aptroot & Schumm (2011: p. 7)); rich in crystals (polarized light), some dissolving in KOH and others of calcium oxalate (H₂SO₄). *Photobiont* trentepohlioid; cells rounded to elongate, 11–20 × 8–14 µm.

Ascomata immersed, first lirelliform with short branches or rarely irregularly rounded, becoming ±cerebriform or aggregated into rounded to slightly elongated and elevated stroma-like structures 0.5–1.5(–2) mm diam., surrounded by a thin white thalline margin *c.* 25–60 µm thick; hymenial disc plane, level with the thallus margin, black, often covered with a thin layer of whitish pruina. *Excipulum* thin, brownish, *c.* 10–20 µm, sometimes inconspicuous, K+ becoming slightly darker. *Hymenium* clear, hyaline to pale fawn, 95–190 µm tall, I+ red, KI+ pale blue, sometimes with strands of hyphae richly covered by hyaline crystals; *epihymenium* dark brown, *c.* 13–25 µm thick, I+ red, KI+ pale blue. *Paraphysoids* richly branched-anastomosing, 2–3 µm thick, slightly enlarged to 4 µm and often pale brownish in the epihymenium. *Hypothecium* dark brown, extending to medulla or substratum, (40–)150–350 µm thick, I–, K+ becoming slightly darker. *Asci* (6–)8-spored, clavate, 90–125 × 22–30 µm, with a distinct ocular chamber; wall KI–. *Ascospores* fusiform with the upper half often wider, 3–7-septate, dark brown from an early stage, with a distinct dark brown verruculose ornamentation on the wall, K+ becoming slightly darker, (23–)26–32(–35) × (7–)7.5–10(–11) µm (*n* = 26); gelatinous sheath *c.* 0.5–1 µm sometimes present.

Pycnidia immersed in the thallus, visible as dark brown dots, surrounded by a thin whitish to cream margin, level with the thallus surface and separated from it by a crack, 80–115 µm diam.; spherical in cross-section; wall dark brown; *conidia* hyaline, filiform, slightly curved to sickle-shaped, 17–22 × 1–1.4 µm.

Chemistry. Thallus C+ red, K–, UV–. TLC (solvents EA and G): erythrin.

Etymology. The epithet is named after the archipelago of Cape Verde, where the new species was collected.

Distribution and ecology. So far known only from the island of São Vicente in Cape Verde, where it inhabits volcanic rock of vertical N- and NE-facing cliffs in arid and open conditions near the sea.

Discussion. The species belongs to the genus *Sparria* according to our phylogenetic tree (Fig. 2). This generic position is also supported by morphological and chemical data since the new species shares the following with the generic type, *S. cerebriformis*: a crustose, epilithic, corticate thallus; lirellate and immersed ascomata surrounded by a white rim and forming stroma-like structures; a black hymenial disc with whitish pruina; a thin, dark brown proper exciple; a thick dark brown hypothecium;

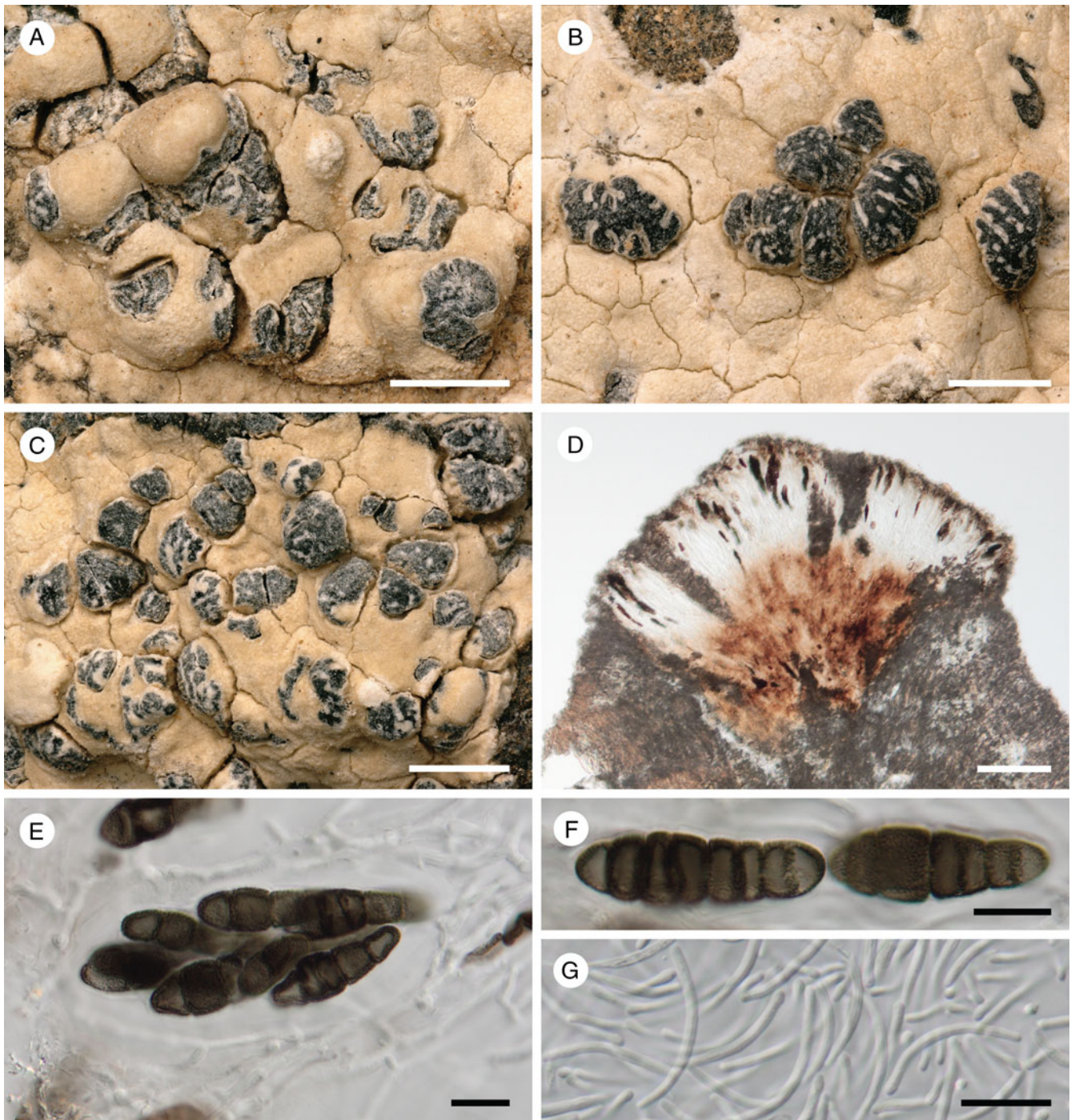


Fig. 4. *Sparria caboverdensis* (A & B, D–G, Tehler 10013; C, Ertz 17277). A–C, thallus and ascomata. D, section through an ascoma. E, ascus and paraphysoids in K. F, ascospores in K. G, conidia in water. Scales: A–C = 1 mm; D = 100 μ m; E–G = 10 μ m. In colour online.

brown ascospores; the production of erythrin. *Sparria cerebriformis* differs from the new species by the larger stroma-like structures (1–3 mm diam.), a taller hymenium (300–350 μ m) and muriform ascospores. Furthermore, it is known only from the coastal areas of California and Baja California (Egea & Torrente 1995). The only other species known in the genus *Sparria*, the European *S. endlicheri*, differs by having a sorediate thallus and a chemistry with lecanoric acid only (Cannon *et al.* 2021). The ascomata were very rarely observed in *S. endlicheri*, with ascospores described as 3–5-septate,

14–20 \times 5–7 μ m (Cannon *et al.* 2021), thus smaller than in the new species. *Sparria caboverdensis* differs from *Ingaderia flexuosa* (Egea *et al.* 1995; sub. *Llimonaea flexuosa*, description emended in this study, see below) by the different ascomata type (long lirelliform and never forming stroma-like structures in *I. flexuosa*), a much thinner excipulum (60–100(–150) μ m in *I. flexuosa*), much wider ascospores (4–6 μ m in *I. flexuosa*) and the production of erythrin as secondary thallus metabolite (gyrophoric acid often with a trace of lecanoric acid in *I. flexuosa*).

Additional specimens examined. **Cape Verde:** São Vicente: NW of Calhau, northern slope of Goa Baixo, 16°51'27"N, 24°52'42"W, c. 120 m elev., on vertical cliffs, on rock, 2011, Ertz 17277 (BR); *ibid.*, S of the road between Baia das Gates and Calhau, NE of Monte Verde, 16°52'29"N, 24°54'46"W, c. 200 m elev., on vertical NE-facing cliffs, on rock, 2011, Ertz 17221, 17222 (BR).

***Syncesia miesii* Tehler & Ertz sp. nov.**

MycoBank No.: MB 846084

Differing from *Syncesia sulphurea* (Vainio) Tehler by an I– thallus, a tomentose hymenial disc, a taller hymenium (85–115 µm) and a different chemistry with fatty acids only (including cf. roccellic acid).

Type: Cape Verde, São Vicente, E of Mindelo, Monte Verde, 16°52'22"N, 24°55'58"W, c. 670 m elev., sheltered volcanic rocks, 3 December 2011, D. Ertz 17188 (BR—holotype!).

(Fig. 5)

Thallus crustose to somewhat placodioid, creamy white to white brownish, continuous to rimose-areolate, mostly flat, ecorticate, smooth to rugulose, matt, pruinose; areoles 0.2–1 mm diam., in section c. 0.2–0.5(–0.8) mm thick, with a white to white-greyish medulla often becoming dirty brown below; rich in crystals (polarized light), some dissolving in KOH and others of calcium oxalate (H₂SO₄!). *Prothallus* ±byssoid, dark brown, 1–2 mm wide. *Photobiont* trentepohlioid; cells rounded to elongate, (8–)11–23 × 7–13 µm.

Ascomata pluricarpocentral, apothecioid, synascoma absent or poorly developed, circular in outline, first flat and level with the thallus surface, becoming elevated and often strongly convex, usually without constricted base, 0.8–2(–2.5) mm diam.; thalline margin poorly developed, non-prominent, entire to slightly undulating, white to creamish white; hymenial disc dark brown, covered with a thin layer of whitish pruina giving a white-grey tinge to the apothecial disc, sometimes with cracks. *Excipulum* thin, almost inconspicuous, brownish, c. 6–10 µm. *Hymenium* clear, hyaline to pale fawn, 85–115 µm tall, I+ blue turning orange-reddish in parts, KI+ pale blue turning orange in parts; *epihymenium* pale brown, c. 22–27 µm thick, I+ blue turning orange-reddish in parts, KI+ pale blue. *Paraphysoids* sparsely branched-anastomosing but richly branched in the epihymenium, 2.5–3 µm thick, not or slightly enlarged to 4 µm and often pale brownish in the epihymenium. *Hypothecium* dark brown to black, extending to the substratum, up to 1 mm thick, I–, K– or slightly olivaceous. *Asci* (4–)8-spored, clavate, 65–95 × 15–18 µm, with a tiny ocular chamber; endoascus KI+ blue with a KI+ blue apical ring. *Ascospores* fusiform, straight to slightly curved, 3-septate, hyaline, (19–)22.5–27(–29) × (4–)4.5–5.5(–6) µm (*n* = 34); gelatinous sheath not seen.

Pycnidia immersed in the thallus, visible as dark brown dots, surrounded by a thin whitish to cream margin, level with the thallus surface, c. 90–180 µm diam.; spherical in cross-section; wall dark brown; *conidia* hyaline, filiform, slightly curved to sickle-shaped, 10–16 × 1–1.4 µm.

Chemistry. Thallus C–, I–, K–, PD–, UV–. TLC (solvent G): cf. roccellic acid and an unidentified fatty acid of R_f 27 (all specimens tested).

Etymology. The epithet is named after Bruno Mies for his important contribution to the lichen flora of Cape Verde, where the new species was collected, and for having collected the new species first.

Distribution and ecology. So far known only from the islands of São Nicolau and São Vicente in Cape Verde, where it inhabits sheltered volcanic rocks in rather open conditions at relatively high elevations (e.g. near the summit of Monte Verde on São Vicente).

Discussion. The new species is most similar to *Syncesia sulphurea* (Vainio) Tehler, which differs by having a thallus I+ dark blue in patches, a non-tomentose hymenial disc, a shorter hymenium (55–80 µm) and a chemistry notably with protocetraric acid (Tehler 1997). *Syncesia leprobola* Tehler differs by the verrucose, nearly isidiate thallus, synascomata and the production of gyrophoric and protocetraric acids in addition to roccellic acid. *Syncesia myrticola* (Fée) Tehler, widespread in Europe and Macaronesia, can grow both on bark and rocks. It differs from the new species notably by the much longer ascospores (35–44 µm) and the production of protocetraric acid.

Additional specimens examined. **Cape Verde:** São Vicente: E of Mindelo, Monte Verde, 16°52'22"N, 24°55'58"W, c. 670 m elev., sheltered volcanic rocks, 2011, D. Ertz 17192 (BR); *ibid.*, Monte Verde along road on the E side of the mountain, 16°52.570'N 24°55.680'W, 550 m elev., 2010, A. Tehler 10039 (S-F206151). São Nicolau: Punta Espechim, W Ribeira Funda, N-Küste, 16°40'N, 24°20'W, 280 m elev., N. expos., 1988, B. Mies CV-4296 [divided into five envelopes: 940,2; 940,3; 940,4; 940,5; 940,6] (S-F160224, S-F160225, S-F160226, S-F160227, S-F160228).

New combinations, a new name and emended description of *Ingaderia*

***Ingaderia* Darb. emend.**

Berichte der Deutschen Botanischen Gesellschaft 15, 6 (1897); type: *Ingaderia pulcherrima* Darb.

Syn. nov.: *Llimonaea* Egea & Torrente, in Torrente & Egea, *Nova Hedwigia* 52, 239 (1991); type: *Llimonaea occulta* Egea & Torrente.

Syn. nov.: *Paraingaderia* Ertz & Tehler, *Fungal Diversity* 49, 56 (2011); type: *Paraingaderia placodioides* Ertz & Tehler.

Thallus saxicolous, rarely corticolous, lichenized, crustose, placodioid with subfruticose outgrowths or fruticose, pale creamish or white, sometimes pinkish when fresh or greyish brown, matt, sometimes sorediate, usually rich in crystals notably of calcium oxalate, ecorticate or corticate; cortex when present of 'branched type' or of 'periclinial plectenchyma' (as defined by Aptroot & Schumm (2011: p. 7)). *Photobiont* trentepohlioid.

Ascomata often numerous, elongate to lirellate, rarely punctiform or roundish, immersed or elevated above the thallus, often with a thallus cover, unbranched to densely branched, straight or flexuose; hymenial disc remaining slit-like or exposed, epruinose or pruinose. *Excipulum* thick, black, c. 10–100(–150) µm thick laterally, K+ becoming slightly darker or olivaceous, merged with the hypothecium below. *Hymenium* clear, colourless to pale fawn, 75–140 µm tall, usually hemiamyloid; *epihymenium* hyaline or brown, rarely with an olivaceous tinge. *Paraphysoids* branched and anastomosing, 1–2.5 µm thick, often slightly enlarged at the apices. *Hypothecium* dark brown to black, extending to medulla or substratum, 25–400 µm thick. *Asci* (4–)8-spored, narrowly clavate, not thickened near apex, 50–110 × 10–22 µm, with a tiny ocular

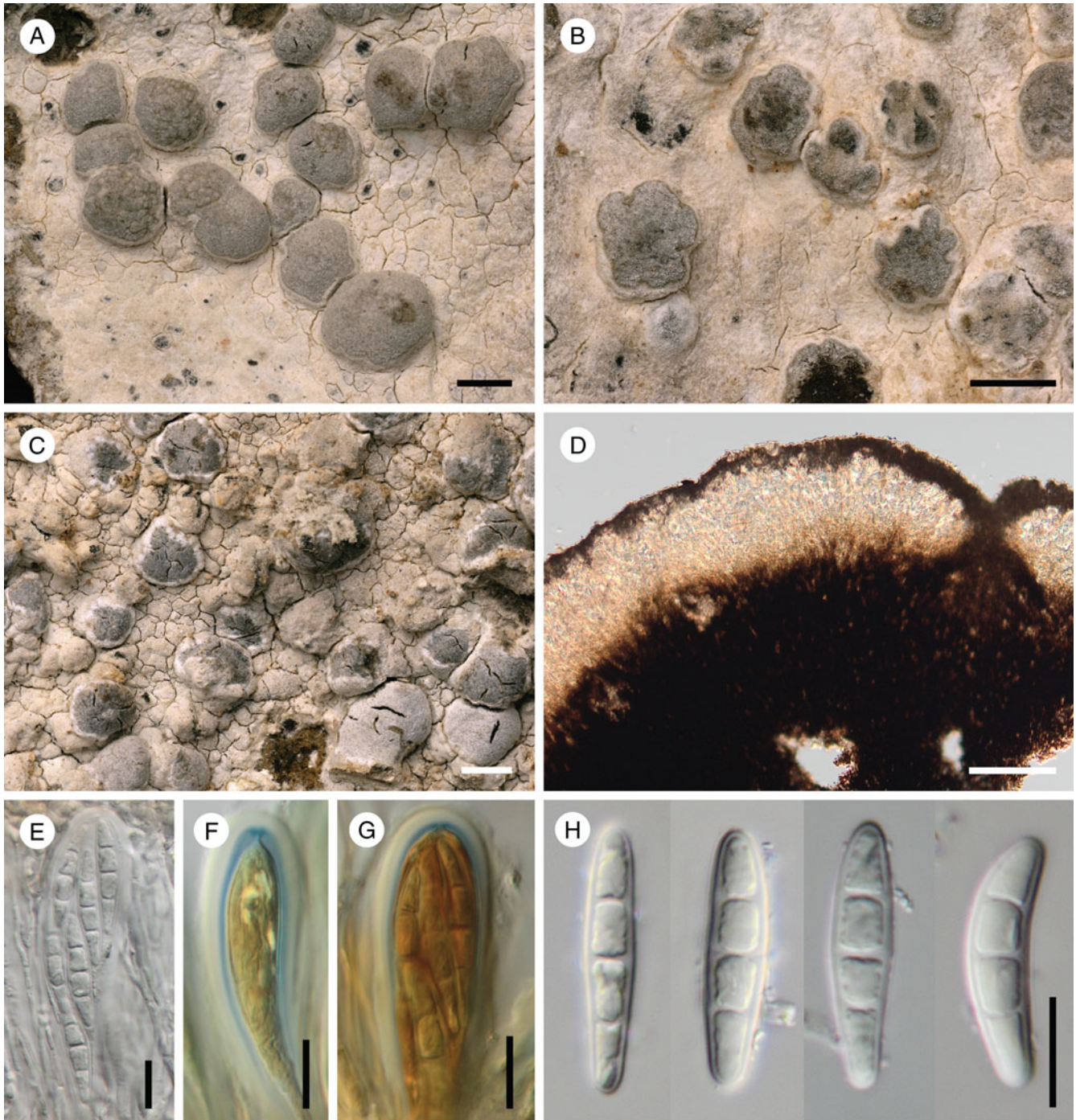


Fig. 5. *Synnesia miesii* (A, B, D, E & H, Ertz 17188; C, F & G, Ertz 17192). A–C, thallus and ascomata. D, section through an ascoma in water. E, ascus in water. F & G, asci in KI. H, ascospores in water. Scales: A–C = 1 mm; D = 100 μ m; E–H = 10 μ m. In colour online.

chamber; endoascus KI+ blue usually with an apical KI+ blue ring. *Ascospores* obtusely fusiform or fusiform, sometimes with the upper half wider, (1–)3–7(–14)-septate, thick-walled, often becoming dark brown at an early stage or when old, 15–50 \times 4–8(–9) μ m, often with a gelatinous sheath c. 0.5–2 μ m.

Pycnidia immersed in the thallus, visible as dark brown to black dots, level with or slightly elevated above the thallus surface, c. 90–190 μ m diam.; \pm spherical in cross-section; wall dark brown; *conidia* hyaline, filiform, slightly curved to sickle-shaped, 12–24 \times 0.7–1 μ m.

Chemistry. Often with erythrin, gyrophoric acid and/or lecanoric acid, rarely with psoromic acid, as major secondary metabolites.

Ingaderia flexuosa (Egea, Torrente & Mies) Ertz & Tehler comb. nov. & emend.

Mycobank No.: MB 846085

Llimonaea flexuosa Egea et al., *Mycotaxon* 53, 63 (1995) [Basionym]; type: Cape Verde Islands, Boa Vista, Mt Gude/

Passarao, ombrophobous, shady overhangs, above tuffets and soil, 250 m, N. expos., 9 November 1987, B. Mies 616c, CV-3520 (MUB or BCN—holotype, lost?; FR—former isotype designated here as lectotype! MBT 10010350; F—isotype lost?).

(Fig. 6)

Thallus crustose, pale creamish or whitish, continuous to rimose-areolate, flat or bullate, smooth to slightly farinose-rugulose, matt; areoles 0.3–0.6(–1) mm diam., in section c. 0.1–0.7 mm thick; ecorticate or with a poorly developed upper cortex c. 25–30 µm thick, of ‘branched type’ (as defined by Aptroot & Schumm (2011: p. 7)); rich in crystals (polarized light!), some dissolving in KOH and others of calcium oxalate (H₂SO₄). *Photobiont* trentepohlioid; cells rounded to elongate, 10–20 (–25) × 8–15 µm.

Ascomata lirelliform, black, first immersed in the thallus, becoming quickly elevated to sessile, often with a thallus cover c. 55–65 µm thick in the lower third to half part, rarely up to the slit-like opening, simple or rarely with 1(–2) short branch(es), straight or flexuose, (0.3–)0.4–4 × 0.2–0.6 mm; hymenial disc remaining slit-like, epruinose. *Excipulum* thick, black, 60–100(–150) µm thick laterally, K+ becoming slightly darker-olivaceous, merged with the hypothecium below. *Hymenium* clear, hyaline, 100–140 µm tall, I+ red, KI+ pale blue; *epihymenium* hyaline, I+ red, KI+ pale blue. *Paraphysoids* richly branched-anastomosing, 2 µm thick, not or slightly enlarged to 3 µm at the hyaline apex. *Hypothecium* dark brown to black, extending to medulla or substratum, 200–400 µm thick. *Asci* (6–)8-spored, narrowly clavate, not thickened near apex, 85–110 × 15–17 µm, with a tiny ocular chamber; endoascus KI+ blue with an apical KI+ blue ring. *Ascospores* fusiform, sometimes with the upper half wider, 3–7(–8)-septate, dark brown from an early stage, with a distinct dark brown verruculose ornamentation on the wall, K+ becoming slightly darker, (22–)23.5–29(–32) × (4–)4.5–5.5(–6) µm (*n* = 40), with a gelatinous sheath c. 1–2 µm.

Pycnidia immersed in the thallus, visible as dark brown to black dots, level with or slightly elevated above the thallus surface, 100–150 µm diam.; ±spherical in cross-section; wall dark brown; *conidia* hyaline, filiform, slightly curved to sickle-shaped, 12–15(–20) × 1 µm.

Chemistry. Thallus C+ red, K–, UV–. TLC (solvents EA and G): gyrophoric acid (major), often with a trace of lecanoric acid (specimens tested: Ertz 13880, 17228, 17239, 17243, 17273, Mies 835d and lectotype (FR)).

Distribution and ecology. So far known from the islands of Boa Vista, Santiago and São Vicente in Cape Verde and from the island of El Hierro in the Canary Islands, where it inhabits volcanic rock in arid and open conditions near the sea.

Discussion. The holotype of *Ingaderia* (*Llimonaea*) *flexuosa* is missing in MUB and BCN. No specimen could be found by the curator under the name *Llimonaea flexuosa*, nor under the names ‘*Opegrapha undulata* Stirton’ (a name under which the specimen Mies 616c (CV-3520) was listed in the thesis of Mies (1989: p. 162), before it was selected as the holotype for the description of *Llimonaea flexuosa*) or ‘*Opegrapha* 3’ (an older working name; B. Mies, personal communication). In the original description of *L. flexuosa*, two isotypes (‘herb. Mies, herb. Lumbsch’) were listed, as well as a paratype (‘Mies 835/836e,

CV-4004 (M)’). Fortunately, the isotype from ‘herb. Mies’ was found in FR and the paratype in M, but no isotype could be found in F where hb. Lumbsch is now hosted. The information on the label of the paratype specimen in M slightly differs from the original publication: ‘W of Mt Graciosa’ and ‘Mies 835/836e’ are indicated in the original publication, while ‘N des Mt Graciosa’ and ‘Mies 835d1’ are written on the printed label of the specimen (and ‘835/836d1’ is also written with a pencil on the envelope). However, both have the second collecting number (CV-4004).

The loss of the holotype of *Ingaderia flexuosa* is problematic because the original description appears to be based on material from two different species. Indeed, the chemistry is described as ‘erythrin and lecanoric/gyrophoric acids detected by TLC’, while we could detect only gyrophoric and lecanoric acids in our specimens. Moreover, the ascomata are described as ‘at first dendroid and immersed, later lirelliform and elevated. Lirellae 1–5 × 0.2–0.7 mm, flexuose, simple or slightly branched’, while we have not observed dendroid lirellae in our specimens. Among the figures of the holotype (Egea *et al.* 1995), fig. 1 shows lirellae that are mostly unbranched-flexuose, elevated and black. These lirellae are similar to those of the isotype in FR (designated here as lectotype) and to our specimens of *I. flexuosa*, but fig. 4 ‘detail of young ascomata’, though of poor quality, shows lirellae that are richly branched-dendroid, narrow and mostly immersed in the thallus. These latter, dendroid lirellae are somewhat reminiscent of the species described here under the name *Ingaderia dendritica*, a species that produces erythrin but not lecanoric/gyrophoric acids. Therefore, it is highly probable that the original description of *I. flexuosa* is based on material of two different species, *I. flexuosa* s. str. (as accepted here) and *I. dendritica*, and that the holotype is a mix of these two species. This might explain why the chemistry was described as including erythrin and lecanoric/gyrophoric acids. We decided to consider the isotype in FR as the reference for *I. flexuosa* (therefore designate that specimen as lectotype) and to describe the second species as *I. dendritica*. The species of the lectotype (FR) is also the one that appears to constitute most of the holotype of *I. flexuosa* (see fig. 1 in Egea *et al.* (1995)) and that better fits the original description in the mature lirellae that are prominent, mostly simple and more robust (0.2–0.7 mm wide, while those of *I. dendritica* never become wider than 0.4 mm). Since the holotype probably represents a mix of two different species, an emended description of *L. flexuosa* is provided above using the lectotype (FR) and our recent material.

The lirellae of *I. flexuosa* as accepted here are quite variable regarding the thallus margin, being sometimes almost devoid of, or almost entirely covered laterally by, a thallus cover. This variability can sometimes be observed within the same thallus (e.g. in the paratype).

The specimen Ertz 13880 was already reported as *Llimonaea flexuosa* from the Canary Islands (island of El Hierro) by van den Boom & Ertz (2012).

Additional specimens examined. **Cape Verde:** Santiago: N des Mt Graciosa, N von Tarrafal, auf Felsblöcken, 200 m elev., N. expos., 1988, Mies 835d1, CV-4004 (M—paratype). São Vicente: S of the road between Baía das Gates and Calhau, NE of Monte Verde, 16°52′29″N, 24°54′46″W, 200 m elev., on vertical NE-facing coastal volcanic outcrops, on rock, 2011, Ertz 17228, 17239, 17243 (BR); *ibid.*, NW of Calhau, northern slope of Goa Baixo, 16°51′27″N, 24°52′42″W, c. 120 m elev., strongly sloping and vertical coastal volcanic outcrop, on rock, 2011, Ertz 17273

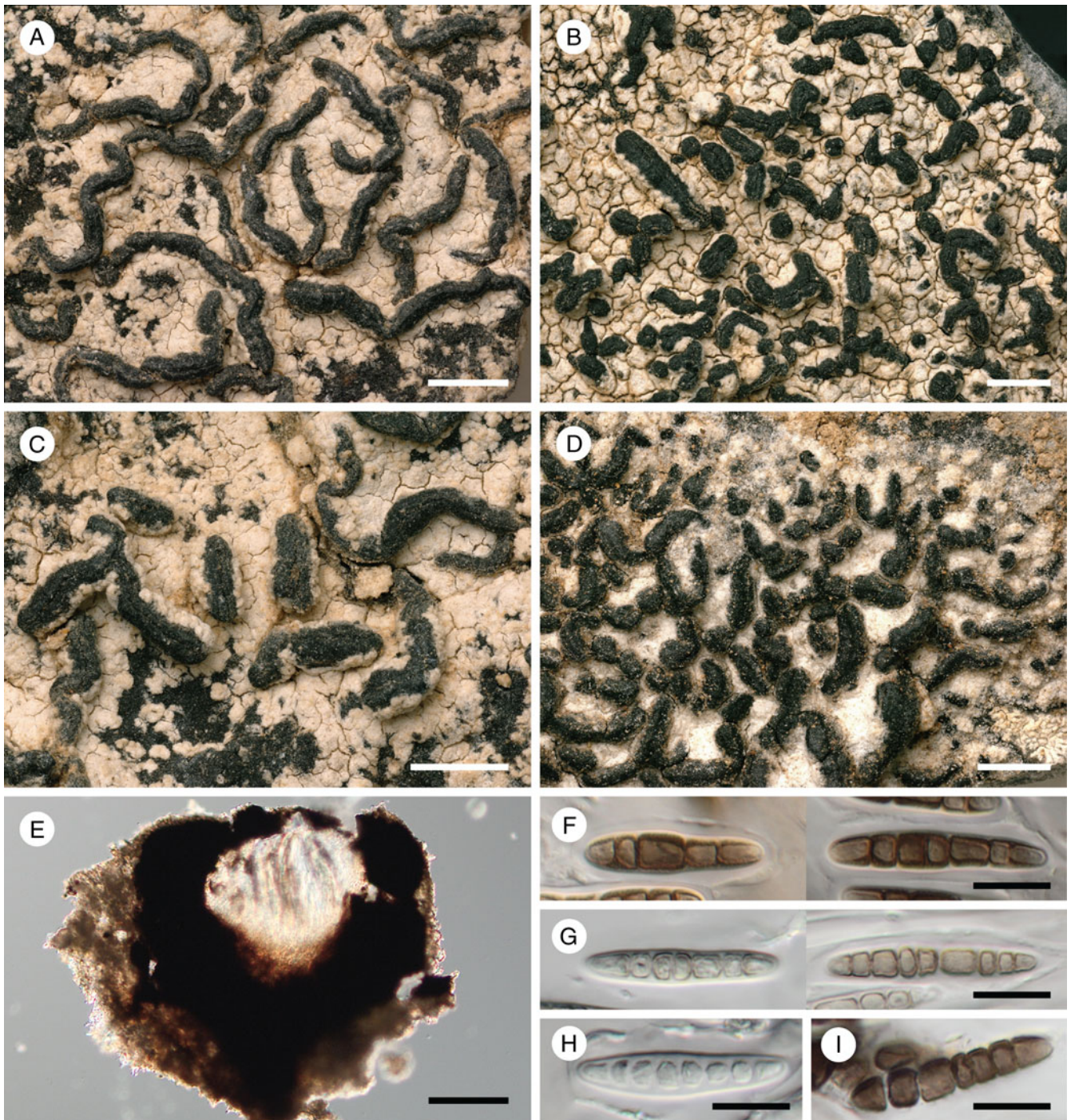


Fig. 6. *Ingaderia flexuosa* (A, C & G, Mies 616c (isotype FR); B & H, Ertz 17243; D–F, Ertz 13880; I, Mies 835d1). A–D, thallus and ascomata. E, section through an ascoma in water. F–I, ascospores in water. Scales: A–D = 1 mm; E = 100 μ m; F–I = 10 μ m. In colour online.

(BR).—**Spain:** *Canary Islands:* El Hierro, Guarazoca, c. 500 m NE of mirador de la Peña, NE-facing rocky outcrop, 27°48'29"N, 17°58'46"W, 630 m elev., overhang of a small rocky outcrop, 2009, Ertz 13880 (BR).

Ingaderia occulta (Egea & Torrente) Ertz comb. nov.

Mycobank No.: MB 846086

Llimonaea occulta Egea & Torrente, in Torrente & Egea, *Nova Hedwigia* **52**, 239 (1991) [Basionym]; type: Portugal,

Estremadura, Sintra, Cabo Roca, 20–140 m elev., 19 February 1987, J. M. Egea (MUB 13619—holotype).

Ingaderia placodioidea (Ertz & Tehler) Ertz & Tehler comb. nov.

Mycobank No.: MB 846087

Paraingaderia placodioidea Ertz & Tehler, *Fungal Diversity* **49**, 56 (2011) [Basionym]; type: Yemen, Socotra Island, Sefflah, the ridge just S of the village on S coast at the E most part of the island,

400–600 m elev., 12°30'43.4"N, 54°26'02.2"E, on limestone, 24 March 2008, A. Tehler 9344 (S—holotype!; BR—isotype!).

Ingaderia sorediata (Sparrius, P. James & M. A. Allen) Ertz comb. nov.

Mycobank No.: MB 846088

Sclerophytonomyces circumscriptus var. *sorediatus* Sparrius *et al.* [as 'Sclerophytomyces'], *Lichenologist* 37, 285 (2005) [Basionym].—*Peterjamesia sorediata* (Sparrius *et al.*) D. Hawksw., *Lichenologist* 38, 189 (2006).—*Roccellographa sore-diata* (Sparrius *et al.*) Coppins & Fryday, in Fryday & Coppins, *Lichenologist* 44, 734 (2012).—*Fulvophyton sorediatum* (Sparrius *et al.*) van den Boom [as 'sorediata'], in van den Boom & Giralt, *Sydowia* 64, 152 (2012) nom. inval. (Art. 41.5).—*Fulvophyton sorediatum* (Sparrius *et al.*) Tehler & van den Boom, in Tehler, *Lichenologist* 49, 173 (2017); type: Spain, Canary Islands, La Palma, Lomo Machín, Barlovento, 250 m elev., 21 September 1979, C. Hernández Padron (E 197301—holotype; TFC 849, BM—isotypes).

Discussion. *Sclerophytonomyces circumscriptus* var. *sorediatus* (Sparrius *et al.* 2005) was erected to species level by Hawksworth (2006) as *Peterjamesia sorediata*, because he considered it to be genotypically distinct from the non-sorediate taxon (= *P. circumscripta* (Taylor) D. Hawksw.) since it grows with it and does not intergrade with it. In a publication on the phylogeny of the *Arthoniales*, Ertz & Tehler (2011) sequenced *P. circumscripta* and found that the genus *Peterjamesia* D. Hawksw. should be included under the earlier generic name *Roccellographa* J. Steiner. As a consequence, the type species of the former genus (*P. circumscripta*) was transferred into *Roccellographa*. Subsequently, *P. sorediata* was transferred to *Roccellographa* by Fryday & Coppins (2012), despite the species not being sequenced. However, van den Boom & Giralt (2012) simultaneously transferred it to *Fulvophyton* because they found a fertile specimen having notably roundish to shortly lirellate ascomata immersed in the thallus, a brownish excipulum, a hyaline hypothecium and (4–)6–8-septate, hyaline ascospores, 20–35 × 5–7 µm, with a distinct gelatinous sheath. This latter combination was invalid and was eventually validated in Tehler (2017). The sequencing of several specimens during the present study revealed that the species was related to neither *Roccellographa circumscripta* nor even to the family *Roccellographaceae* (where the genera *Roccellographa* and *Fulvophyton* belong) but to the family *Opegraphaceae*. Following the phylogenetic results (Fig. 2), *F. sorediatum* is transferred to the genus *Ingaderia*. The generic concept of *Ingaderia* is enlarged by the inclusion of a species producing psoromic acid. Specimen Ertz 16878 has many lirellae, but only a small number of ascospores were observed that fit the description of van den Boom & Giralt (2012): hyaline, 7-septate, 25–26 × 5 µm. However, in our specimen, the wall of the ascospores becomes brown when overmature and a thick dark brown hypothecium is present.

Sequenced specimens (all sterile, except Ertz 16878 with many lirellae). **France:** Brittany: Finistère Dept., Camaret-sur-Mer, Pointe de Pen Hir, 35 m elev., affleurement rocheux siliceux de bord de mer, entouré de landes, sur rocher abrité, 2012, D. Ertz 17469 (BR). **Corsica:** Marchese (Cargèse), Punta d'Omigna, entre le Golfe de Chiuni et le Golfe de Peru, c. 30 m elev., sur

rocher, 2011, D. Ertz 16412 (BR).—**Portugal:** Azores: Pico, between Sao Miguel Arcanjo (Sao Roque do Pico) and Prainha de Cima, c. 90 m elev., on rock, 2011, D. Ertz 16690 (BR); Terceira, NE of Serreta, Ponta do Queimado, c. 30 m elev., volcanic rock near the sea, 2011, D. Ertz 16878 (BR). **Algarve Prov.:** SW of Aljezur, c. 40 m elev., on rock, 2011, D. Ertz 16917 (BR). **Estremadura Prov.:** Sintra, Cabo da Roca, c. 50 m elev., siliceous outcrops, 2011, D. Ertz 17049 (BR).

Ingaderia vandenboomii Ertz nom. nov.

Mycobank No.: MB 846089

Llimonaea sorediata van den Boom *et al.*, in van den Boom & Brand, *Lichenologist* 39, 310 (2007) [replaced synonym] non *Ingaderia sore-diata* (Sparrius *et al.*) Ertz, in Ertz & Tehler, *Lichenologist*: this publication; type: Portugal, Estremadura, E of Nazaré, São Bartolomeu, on top of small rocky hill, on E-exposed overhanging outcrops, 9°03.7'W, 39°35.5'N, 150 m elev., 15 July 2001, P. & B. van den Boom 27645 (LG—holotype; hb. v.d. Boom—isotype).

Discussion. Since *Fulvophyton sorediatum* and *Llimonaea sore-diata* need to be combined in *Ingaderia* (see Discussion below), and since both species have the same epithet, a new name has to be introduced for one of the two species. We decided to introduce a new name for the most recently described epithet (thus for *L. sorediata*) and to dedicate the new name to Pieter van den Boom for his important contribution to lichenology and the discovery and description of this species.

Discussion

Ingaderia is a genus described by Darbishire in 1897 for *I. pulcherrima* Darb., a fruticose lichen endemic to the coasts of Chile (Darbishire 1897). The ascomata were described (and illustrated) as simple to ramified and elongate lirellae lacking a thal-line margin, with a brownish black excipulum and hypothecium, thus similar to species of *Opegrapha*. Tehler (1990) provided a detailed description of *I. pulcherrima*, characterizing the thallus as fruticose, pendent, corticate, with complanate or roundish branches, often with apically black papillae from which pycnidia often develop, with filiform and curved conidia and producing erythrin, lecanoric acid and an unidentified blue fluorescent substance. However, as *I. pulcherrima* is often infected by parasites, Tehler (1990) concluded that the ascomata originally described as the mycobiont by Darbishire (1897) refer to those of a lichenicolous species, and as a consequence the ascomata of *I. pulcherrima* were considered as unknown. Nevertheless, *I. pulcherrima* has been placed in the family *Opegraphaceae* in a molecular phylogenetic study (Ertz & Tehler 2011) and our new phylogenetic data (Fig. 2) place *Ingaderia* close to taxa producing similar ascomata (i.e. lirellate with a thick black excipulum and hypothecium). Therefore, the ascomata described originally by Darbishire (1897) for *Ingaderia* are very likely to be those of the mycobiont. Moreover, Tehler (1990: p. 2477) provided a detailed description of this type of ascomata in *I. pulcherrima* and described the ascospores as '7-septate, thick-walled, not constricted at septa, narrowly ellipsoidal, straight, hyaline, 20–25 × 4–5 µm'. The ascospores are thus also similar to those observed in most of the taxa belonging to the same lineage as *Ingaderia pulcherrima* (e.g. *Llimonaea flexuosa*, *L. occulta*, *Fulvophyton sorediatum*), though the ascospores often become dark brown.

Ascospores that are dark brown at maturity in the inner part of the cell walls are a rare feature in the *Arthoniales*, but not uncommon in the *Opegraphaceae*. In the lineage *Sparria caboverdensis* to *Llimonaea occulta* (Fig. 2), it is shared by species of *Llimonaea*, *Paraingaderia placodioidea*, *Sparria caboverdensis*, *S. cerebriformis*, *Schizopelte californica* Th. Fr. and *S. crustosa* Ertz & Tehler. However, the colour of the ascospores might vary with maturity even within a species. In *L. flexuosa*, ascospores are dark brown in an early stage or at maturity in most specimens, but we mainly observed hyaline mature ascospores in specimen Ertz 17243 (Fig. 6H). In our sequenced specimens of *Llimonaea occulta*, ascospores are still hyaline at maturity and become brown only when old.


With the phylogenetic placement of *Llimonaea flexuosa* outside the strongly supported lineage *Fulvophyton sorediatum*-*Llimonaea occulta* (Fig. 2), generic delimitation becomes problematic. Based on the phylogeny, there are four possibilities for the generic delimitation of the lineage *Llimonaea flexuosa*-*L. occulta*.

- 1) Five genera: the genus *Llimonaea* (including *L. occulta* and *L. sorediata*) / the monotypic genus *Ingaderia* / the monotypic genus *Paraingaderia* / a new genus for *Fulvophyton sorediatum* / a new genus for *Llimonaea flexuosa*.
- 2) Four genera: same as for the five genera, but with *Paraingaderia* included in *Llimonaea*.
- 3) Three genera: *Fulvophyton sorediatum* and *Paraingaderia* are included in *Llimonaea* together with *L. occulta* and *L. sorediata* / the monotypic genus *Ingaderia* / a new genus for *Llimonaea flexuosa*.
- 4) One genus: all the taxa are included in the genus *Ingaderia*, the oldest generic name available.

There are few morphological characters that can be used to give generic rank to subgroups within the lineage *Llimonaea flexuosa*-*L. occulta*. All taxa share a developed dark brown to black excipulum and hypothecium, ascospores that are elongate-fusiform, thick-walled, transversally septate and medium-sized (c. 15–50 × 4–8 µm) and conidia that are filiform-curved (not seen in *L. sorediata* and *F. sorediatum*). The genera *Ingaderia* and *Paraingaderia* have fruticose and subfruticose thallus growth forms, respectively, contrasting with the crustose thallus of the other lichens. However, genera with a diversity in thallus growth form, ranging from crustose to fruticose thalli, are already known in the *Arthoniales*, viz. the genera *Dendrographa*, *Pentagenella* and *Roccellina* (Tehler & Irestedt 2007; Ertz & Tehler 2011; Perlmutter *et al.* 2020). A thalline margin laterally covering the black excipulum is absent in *Ingaderia* but characterizes the genus *Llimonaea*, while *Fulvophyton sorediatum* and *Paraingaderia placodioidea* have ascomata immersed in the thallus (and thus can be considered as having a lateral thalline margin). However, in *Llimonaea flexuosa* this character is highly variable even within a specimen, with a thalline margin absent or almost entirely covering the excipulum. In the *Graphidaceae*, a high diversity in thallus cover is observed within the lirellate genus *Graphis*, with species lacking a thalline margin to species having a complete and thick thalline margin (Lücking *et al.* 2009). Erythrin and lecanoric acid are produced by all taxa of the lineage *Llimonaea flexuosa*-*L. occulta*, except *L. flexuosa* (gyrophoric acid) and *Fulvophyton sorediatum* (psoromic acid), but the chemistry is often variable within genera. As a consequence, a split into five, four or three genera would lead to poorly

characterized, potentially mainly monotypic genera. Accepting *Llimonaea*, even by including *Paraingaderia* and possibly also *Fulvophyton sorediatum*, would make *Llimonaea* paraphyletic, while a new genus for *L. flexuosa* is difficult to justify. We instead suggest including all taxa of the lineage *Llimonaea flexuosa*-*L. occulta* in *Ingaderia*. This results in a phylogenetically distinct and enlarged concept of *Ingaderia* that, however, is rather difficult to characterize morphologically. The sequencing of more crustose lirellate *Arthoniales*, in particular from South America, will be essential to make further progress in our understanding of the evolution in this subgroup of the *Opegraphaceae*.

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