SYSTEMATICS AND PHYLOGENY

Elucidating species richness in lichen fungi: The genus *Sticta* (Ascomycota: Peltigeraceae) in Puerto Rico

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Abstract Traditional taxonomic studies provide only a limited understanding of species richness within a group. Their usefulness for assessing species diversity could also be limited as many lack sufficient sampling and/or fail to integrate different data types for assessing species boundaries. To explore the challenges and limitations of estimating species richness in lichens, we employed an integrative taxonomic approach to elucidate diversification patterns of the genus *Sticta* (Peltigeraceae) in Puerto Rico. Specimens were collected throughout the island, and a six-locus dataset was generated to infer phylogenetic relationships among Puerto Rican *Sticta* and their continental counterparts. Phylogenetic analysis was combined with species delimitation methods and analysis of morpho-anatomical characters to assess diversity patterns and clarify species-level taxonomy. We found that *Sticta* is represented by 16 species in Puerto Rico and that at least 11 (69%) of them are potentially endemic to the island. We describe eight of these in this work: *S. borinquensis* sp. nov., *S. corymbosa* sp. nov., *S. densiphyllidiata* sp. nov., *S. guilartensis* sp. nov., *S. harrisii* sp. nov., *S. parvilobata* sp. nov., *S. riparia* sp. nov., and *S. tainorum* sp. nov. These species do not cluster in a monophyletic assemblage but are scattered over the broader *Sticta* phylogeny, indicating at least eight separate dispersal events. Putative endemic species were found to have close allies occurring in South America. Careful re-examination of material revealed phenotypical characters that separate most species, suggesting low levels of cryptic diversity. We highlight that integrating molecular methods and other sources of information in species discovery along with comprehensive sampling efforts can greatly enhance our knowledge about diversity patterns in poorly studied groups and regions. Furthermore, species and ecosystems in the Caribbean are being threatened by substantial human-driven changes (e.g., deforestation, climate change). Consequences of these impacts include reduction in already restricted habitats and potential extinction. We argue that studies analyzing species diversity within a phylogenetic framework could better inform conservation efforts aimed at addressing these challenges.

Keywords biodiversity; Caribbean; evolution; phylogenetics; species delimitation

Supporting Information may be found online in the Supporting Information section at the end of the article.

INTRODUCTION

A crucial task in biodiversity research, ecology and conservation is to quantify species richness—the number of different species in an ecological community. For example, when investigating how intra- and inter-specific interactions influence community assembly, community ecologists need a clear understanding of species occurrence and their abundance (Mittelbach, 2012). Similarly, the establishment of natural reserves depends on having realistic estimates of the number and identity of species present in those areas (Mace, 2004).

Intrinsic to obtaining accurate species richness estimates is the capacity of correctly identifying or delimiting species. Species delimitation is the process of identifying how individuals and populations fit into natural groups or species-level clusters (Carstens & al., 2013). Poor knowledge about a species' life history or other key taxonomic attributes can lead to incorrect delimitation of species which can bias diversity estimates and confound inferences of community structure. Efforts that incorporate species delimitation based on molecular approaches, particularly those using DNA barcodes, have been useful in this regard (Hebert & al., 2004; Bickford & al., 2007). Yet, a wider array of datasets are usually needed to meaningfully delimit, discover and identify species (Will & al., 2005). Integrative taxonomic approaches provide means for correctly delimiting species by combining various sources of information including phenotype and molecular data,

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distribution and ecology, phylogeography and population genetics, and life history traits (Dayrat, 2005; Will & al., 2005; Padial & De La Riva, 2010). These are therefore ideal for more accurately characterizing species richness.

Integrative taxonomic studies tend to sample the highest possible number of taxa within a clade throughout its entire range, making them valuable for assessing broad diversity and macroevolutionary patterns. These approaches have also helped clarify species boundaries in hard-to-resolve species complexes and have been useful for uncovering cryptic diversity in multiple groups (Meegaskumbura & al., 2002; Damm & al., 2010; Barrett & Freudenstein, 2011; Leavitt & al., 2011). Unfortunately, integrative studies seldom depict detailed species diversity patterns at local scales, hence are of less utility in conservation efforts. Studies focusing on small geographic regions could be help fill these gaps as they permit denser within-taxon sampling and facilitate consideration of fine-scaled environmental parameters (e.g., habitat type).

Islands are ideal systems to address this issue. They are usually much smaller in size compared to continental areas, which enables a much greater sampling density, likely to fully capture the species richness of a taxon under study. Communities can also be more readily defined, because island boundaries are discrete and area is fixed. Evolutionary processes in islands, such as radiations, may also lead to unique traits within a species, helping with species recognition. For example, in Hawaii, species with woody stems within the genus *Geranium* L. are only found in that archipelago (Pax & al., 1997; Kidd & Michaels, 2005); whereas endemic species of the mint family have lost their characteristic scent (Morden & Loeffler, 1999), a response usually linked to reduced herbivory.

Research on the biotas of the Caribbean islands, among the most biologically rich in the world (Myers & al., 2000), has increased our understanding of diversity patterns in insular regions. They have also provided unique insight into the processes of colonization, diversification and extinction (Ricklefs & Bermingham, 2008). This body of work has resulted in better diversity estimates for many groups, including amphibians (Hass & Hedges, 1991), rodents (Woods & al., 2001), shrubs (Judd, 2001) and lizards from the genus *Anolis*, the latter having undergone spectacular adaptive radiations in this region (Losos & al., 1998; Mahler & al., 2010). Unfortunately, there are comparatively less studies on some of the most diverse groups, such as lichens (Mercado-Díaz & Santiago-Valentín, 2010; Mercado-Díaz & al., 2014), organisms formed by a symbiotic relationship between a fungus and at least one photosynthetic partner (i.e., green algae and/or cyanobacteria). Lichens successfully colonize numerous habitats, including tropical forests where half of the estimated global number of species is predicted to occur (Lücking & al., 2009, 2011).

Although lichens have been collected extensively in the Caribbean region (Imshaug, 1957; Mercado-Díaz & Santiago-Valentín, 2010), knowledge of island-level species richness is poor. Previous work has suggested that the Greater Antilles are home to nearly 3500 species (Acevedo-Rodríguez, 1991), but estimates were not based on systematic inventories. In Cuba, an ongoing taxonomic inventory has identified nearly 1100 valid species names, but predictions suggest that about 2000 species could be present (Lücking & al., 2009). Although current documented richness for Puerto Rico (~1500 spp.) is comparable to estimated values (i.e., 1600 spp.; Lücking & al., 2009), the taxonomic status of names has not been revised, suggesting that documented diversity is perhaps overestimated and that a considerable proportion of the actual diversity is yet to be discovered. Harris (1989) studied the lichen biota of Puerto Rico, but the taxonomy has not been revised since then. Further work will likely increase the documented species in Puerto Rico and nearby islands.

Sticta (Schreb.) Ach. is a genus of conspicuous foliose macrolichens easily recognized by their large size, formation of photosymbiodemes, and the presence of characteristic pores (i.e., cyphellae) in the lower surface. It is as a monophyletic genus with unresolved affinities with *Pseudocyphellaria* Vain. s.l. (Moncada & al., 2013b; Widhelm & al., 2019), excluding taxa recently segregated to the genus *Lobaria* (Schreb.) Hoffm.—that is, *L. anomala* (Brodo & Ahti) T.Sprib. & McCune and *L. anthraspis* (Ach.) T.Sprib. & McCune (McCune & al., 2014). It is part of the recently circumscribed subfamily Lobarioideae in Peltigeraceae (Kraichak & al., 2018; Lumbsch & Leavitt, 2019). The group has a subcosmopolitan distribution with species largely restricted to humid tropical mountains and few extending to temperate zones (Moncada & Lücking, 2012; Moncada & al., 2013c; Magain & Sérusiaux, 2015). It has 200 species currently described (Lücking & al., 2017a), but more than 500 species are estimated to occur worldwide (Moncada & al., 2013c). Together with other Peltigeraceae, *Sticta* species are excellent indicators of ecosystem health, and in many areas their diversity is threatened by land use change (Kalwij & al., 2005; Werth & al., 2006; Ranft & al., 2018).

Harris (1989) recognized nine putative species of *Sticta* in Puerto Rico based on morphology alone (suppl. Fig. S1), but proper nomenclature for taxa was lacking. Limited geographic coverage of previous sampling efforts has also been an impediment for elucidating species richness patterns. Here, we used an integrative taxonomic approach to estimate species richness, understand species boundaries, determine levels of endemism and elucidate the evolutionary history of the group in Puerto Rico. We combined information from phylogenetic and species delimitation analyses with a comprehensive taxonomic re-evaluation of the group that included revision of historic material. Specifically, we sought answers to these questions: (1) How many species of *Sticta* occur in Puerto Rico? (2) What proportion of the biota is comprised of endemic species? (3) Does the morphology-based taxonomy proposed by Harris (1989) align with phylogeny? (4) Do *Sticta* species in Puerto Rico represent a monophyletic assemblage, suggesting radiation, or a polyphyletic group, suggesting multiple colonization events?

We include a species accumulation curve showing taxonomic knowledge of the genus as a function of collection efforts through time. This curve highlights the importance of taxonomic revisions and the value in integrating molecular methods with comprehensive sampling efforts to better characterize species richness in lichenized fungi. Formal taxonomic treatment for eight species and a key to identify taxa from Puerto Rico is provided. Conservation-related issues of *Sticta* in Puerto Rico and the Caribbean are discussed.

■ MATERIALS AND METHODS

Taxon sampling. — Collecting efforts focused on well-conserved, mid- (ca. 200 m) to high-elevation (ca. 1300 m) areas with vegetation classified as humid or rain forests (Fig. 1). These are preferred habitat conditions for *Sticta* in the tropics (Moncada, 2012). More than 80% of these areas are located inside protected forests that have been extensively surveyed in the past (e.g., El Yunque National Forest, Bosque Estatal de Carite, Bosque Estatal de Toro Negro). Sampling was carried out in these forests and in areas that have not been previously sampled but that contain suitable habitat for *Sticta* (i.e., Bosque Estatal Tres Picachos, Bosque Estatal de Maricao, Area Natural Protegida Cañon San Cristobal, and karstic forests associated with the Tanamá river). Altogether, these areas contain the majority of *Sticta* habitat present on the island. These sites are also considered centers of high species richness and endemism in plants and contain relict primary forests that survived intense agricultural activities in the island during the early 20th century (Figueroa-Colón, 1996). A total of 110 specimens were collected between October 2011 and July 2018 as part of these efforts. Most of this material was used to generate the molecular data presented in this work.

Taxonomic work. — In addition to the 110 specimens collected for molecular work, we also inspected 170 historic specimens that are housed in the four largest herbarium collections of *Sticta* from Puerto Rico (i.e., LSU, MSC, NY, US). Altogether, these comprise more than 95% of all existing *Sticta* specimens collected in the island and include material used by R.C. Harris for his key (Harris, 1989). Specimens in MICH are duplicates of material housed in NY and US. Recently collected material was brought to NY and side-by-side comparisons were made for determining correspondence with Harris's material. All specimens were inspected under dissecting microscopes, and photographs of each were taken for reference purposes. Thallus morphology of recently collected material was examined using a LEICA MS5 dissecting microscope. To assess microanatomy, sections of thalli and ascomata were cut by hand with a razor blade, mounted in wet slides and examined using ZEISS Axioskop 2 compound microscope. All measurements provided in taxonomic diagnoses below are given in water. High-performance thin-layer chromatography (HPTLC) was done using standard techniques with solvent C following Lumbsch (2002). Locality data for both historic and recently collected specimens was tabulated for assessing geographic distribution of species with respect to suitable *Sticta* habitats in the island. Coordinate data was georeferenced when available using ArcView 10 and overlaid with digital geographic layers (i.e., shapefiles) for ecological life zones (Ewel & Whitmore, 1973) (Fig. 1) and natural protected areas (downloaded from www.gis.pr.gov; not shown). Considering both historic collections and recent efforts, localities where *Sticta* has been collected have been sampled more than three times, the only exceptions being the Tanamá river area (sampled once), and the Cañon San

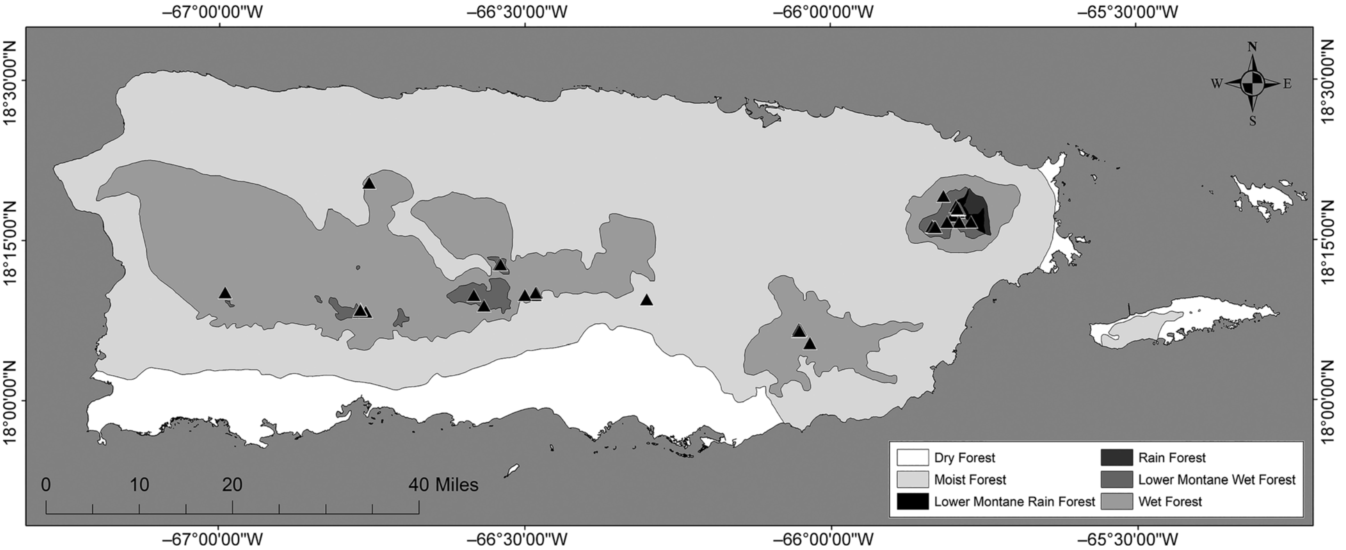

Fig. 1. Map showing main collecting sites (triangles) of recent sampling of *Sticta* in Puerto Rico. The ecological life zones of Puerto Rico (Ewel & Whitmore, 1973) are shown in shades of gray. High-humidity and high-elevation areas, which are preferred habitat for *Sticta* in the tropics, are represented by darker shades.

Cristobal Natural Protected Area and the Bosque Estatal de Guilarte, which were sampled twice.

Nomenclatural determinations were made based on all data available and analyses performed. Yet, we refrained from recognizing lineages as species when delimitation methods (described below) were in considerable conflict.

DNA extraction, amplification and sequencing. — We used the ZR Fungal/Bacterial DNA MiniPrep (Zymo Research, Irvine, California, U.S.A.) and the SIGMA RED Extract-N-Amp Plant PCR Kit (St. Louis, Missouri, U.S.A.) to extract DNA from a selection of specimens (92). Except for the use of 15 ml of extraction buffer and 15 ml dilution buffer with the SIGMA kit, extractions followed manufacturer's instructions.

Six loci were sequenced, including the internal transcribed spacer (ITS ~ 600 bp), which is the universal barcode for fungi (Schoch & al., 2012), the mitochondrial small subunit (mtSSU ~ 800 bp), the nuclear large subunit (nuLSU ~ 550 bp), the DNA replication licensing factor (*MCM7* ~ 600 bp), the RNA polymerase II largest subunit (*RPB1* ~ 900 bp), and RNA polymerase II second-largest subunit (*RPB2* ~ 700), the latter three being low-copy nuclear protein-coding genes. Except for *RPB2*, these loci were also used in Widhelm & al. (2018).

Primers and PCR conditions used in this study are described in table 2 of Widhelm & al. (2018). We designed new *Sticta*-specific primers for *RPB2* due to problems amplifying this locus with traditional primers. Primer sequences and PCR conditions were as follows: RPB2_*Sticta*_1F: AAGC CGGTGTCTCTCAAGTG, RPB2_*Sticta*_1R: GGCGCTTT GACTCGTTTGTT, 94°C for 3 min; 34 cycles: 94°C for 45 s, 50°C for 1 min, 72°C for 1.5 min; 72°C for 7 min. PCR amplification was carried out using 6.25 µl MyTaq Red DNA Polymerase (Bioline, Taunton, Massachusetts, U.S.A.), 0.25 µl of each primer (10 µm), 5.25 µl of nuclease-free water and 0.5 µl of diluted genomic DNA (10×) for a total of 12.5 µl per reaction. Amplification products were visualized on 1% agarose gels stained with ethidium bromide and subsequently purified with Exo SAP-IT (USB, Cleveland, Ohio, U.S.A.), following the manufacturer's instructions. Sequencing was performed using Big Dye Terminator v.3.1 (Applied Biosystems, Foster City, Calfiornia, U.S.A.) and the same primers used for amplification. The cycle sequencing conditions were as follows: 96°C for 1 min; 25 cycles: 96°C for 10 s, 50°C for 5 s and 60°C for 4 min. Sequenced products were precipitated with nuclease-free water, EDTA, and 70% EtOH before they were loaded on an ABI 3730 (Applied Biosystems) automatic sequencer. Molecular work was carried out at the Pritzker Laboratory for Molecular Systematics at the Field Museum, Chicago, Illinois, U.S.A.

Phylogenetic analysis. — Newly generated sequences are listed in Appendix 1. These sequences were assembled in Geneious v.8.1.7 (https://www.geneious.com) and queried in GenBank's BLASTn suite (Benson & al., 2018) to exclude potential contaminations. The "auto" mode threshold and default settings for MAFFT v.7.017 (Katoh & Standley, 2013) plugin in Geneious were used to generate both single-locus and multilocus concatenated alignments. Alignments were visually inspected and manually corrected if needed. Sequences used include those described in table 1 from Widhelm & al. (2018), which include the outgroups *Lobaria pulmonaria* (L.) Hoffm. and *Pseudocyphellaria crocata* (L.) Vain., and sequence data from two additional isolates in GenBank – *Sticta beauvoisii* Delise (Miadlikowska & al., 2006) and *Ricasolia amplissima* (Scop.) De Not. (Appendix 1). The latter was also used as an outgroup. A total 300 specimens of *Sticta* from Puerto Rico and other parts of the world are included in these alignments. The Gblocks web server (http://molevol.cmima.csic.es/castresana/Gblocks_server.html) was used to identify and remove ambiguously aligned sites in the ITS alignment, which showed lower levels of sequence conservation. Options for a less stringent selection (allowing for smaller final blocks, gap positions within the final blocks, and less strict flanking positions) were selected (Castresana, 2000; Talavera & Castresana, 2007; Tan & al., 2015).

We used both Bayesian and maximum likelihood approaches for phylogenetic reconstructions. The program RAxML v.8.1.16 (Stamatakis, 2014) was used for maximum likelihood analysis that employed a GTR+Γ substitution model. The bootstrap convergence test using the extended majority-rule consensus tree criterion (auto MRE) was used for *a posteriori* bootstrapping analysis. Topological conflict between individual gene trees was also assessed with RAxML. This analysis entailed searching for the best ML tree under the GTR+Γ model, using at least 100 bootstrap replicates and other default settings. No major conflicts were observed between trees obtained, therefore analysis proceeded with multilocus concatenated datasets. Sequence matrices were partitioned in RAxML using the -q option. For Bayesian analysis, we first evaluated models of DNA evolution for each locus with the program jModelTest v.2.1.10 (Guindon & Gascuel, 2003; Darriba & al., 2012). The models with the lowest Akaike information criterion (AIC) scores were considered best and were selected as follows: ITS: GTR+Γ, *MCM7*: K80+I+Γ, mtSSU: GTR+I+Γ, nuLSU: GTR+I+Γ, *RPB1*: GTR+Γ, *RPB2*: SYM+Γ. We used the Cipres Gateway server (http://www.phylo.org/portal2/login!input.action) to run MrBayes v.3.2.6 (MrBayes on XSEDE) (Miller & al., 2010; Ronquist & al., 2012). Two parallel runs with 30 million generations, starting with a random tree and employing four simultaneous chains, were used. Heating of chains was set to 0.2. Tree posterior probabilities were estimated by sampling trees using a variant of the Markov Chain Monte Carlo (MCMC) method. Every 1000th tree was sampled to avoid autocorrelation. Parameter values and trees were summarized using a 25% burn-in. The remaining 22,500 trees were pooled to calculate a 50% majority-rule consensus tree. The outputs of MrBayes were inspected in Tracer v.1.5 (Rambaut & Drummond, 2009) to assess convergence of different parameters, determine the approximate number of generations at which log likelihood values stabilized and identify the effective sample size (ESS) for each parameter. Additionally, the average standard deviation of split frequencies (Lakner & al., 2008) was monitored to ensure it dropped below 0.1, and the potential scale reduction factor (Gelman & Rubin, 1992) for all parameters was examined and found to approach 1.0. Only clades with bootstrap support equal or above 70% under ML and posterior probabilities equal or above 0.95 in Bayesian analysis were considered strongly supported. Phylogenetic trees were visualized using FigTree v.1.4.2 (Rambaut, 2012).

Species delimitation analyses. — We assessed species boundaries using three species delimitation methods (i.e., PTP, BPP, GMYC). Details about these methods are provided in the next sections, but in general, these programs perform delimitations by evaluating phylogenetic trees with branches representing either nucleotide substitutions (i.e., PTP) or time (i.e., GMYC). BPP, on the other hand, performs delimitations by simultaneously analyzing multilocus sequence alignments and population data.

Even though PTP and GMYC were designed for single-locus data, both methods are increasingly being applied to multilocus datasets (Luo & al., 2018); therefore, delimitations were done using both ITS and multilocus trees. RAxML trees were used for PTP, whereas two new ultrametric trees (using both ITS and multilocus alignments) were generated with BEAST v.1.10.4 (Suchard & al., 2018) for GMYC. At least two independent BEAST analyses were run on the CIPRES Science Gateway for the latter. Chain lengths for each of these analyses were of 1×10^8 with a sampling frequency of 10,000. Convergence and mixing of parameters were evaluated in Tracer v.1.6 (Rambaut & Drummond, 2009), and effective sample sizes (ESS) were confirmed to be >200. Trees from independent runs were combined in LogCombiner v.1.8.0 (Rambaut & Drummond, 2013a) after excluding the-first 25% of sampled trees as burn-in. A maximum clade credibility tree was generated in TreeAnnotator v.1.8.2 (Rambaut & Drummond, 2013b) from the combined posterior distribution of trees using a 0.5 posterior probability cutoff.

Removing identical haplotypes before running PTP and GMYC has been recommended because these methods could be affected by polytomies and zero-length terminal branches (Fujisawa & Barraclough, 2013; Talavera & al., 2013). In our case, analyses with trees including identical sequences did not result in major conflicts. Given that one goal of this work is to compare results between methods, and because removing identical haplotypes might lead to overestimates of parameters in BPP (Yang, 2015), species delimitation results highlighted in main figures are based on our complete dataset.

Poisson Tree Processes (PTP). — The Poisson Tree Processes (PTP) is a maximum likelihood point estimate of putative species boundaries on a rooted phylogenetic tree. It uses number of substitutions to model speciation rate or branching events based on the assumption that the number of substitutions between species is significantly higher than number of substitutions within species (Zhang & al., 2013). Because the method requires trees with branches equivalent to the number of substitutions, the delimitation schemes were based on both multilocus and ITS RAxML trees. Delimitation analysis was run using the bPTP web server (https://species.h-its.org/ptp/).

Our sampling includes many singleton species and generally well-sampled taxa from Puerto Rico. Because it has been suggested that the recent multi-rate implementation of PTP (i.e., mPTP) might underperform compared to PTP-ML when sufficient intraspecific sampling is lacking, (https://groups.google.com/forum/#!topic/ptp-species-delimitation/udcMEZF__P4) results reported here are based on the more general PTP-ML.

Generalized mixed Yule-coalescent (GMYC). — The Generalized mixed Yule-coalescent (GMYC) is a likelihood-based method for delimiting species by fitting within- and between-species branching models to reconstructed gene trees (Fujisawa & Barraclough, 2013). It assumes that species are independently evolving entities that accumulate mutations that result in distinctive genetic clusters. These clusters are separated from the rest by longer internal branches (Barraclough & al., 2003; Acinas & al., 2004). Genetic clusters are delimited by optimizing the set of nodes that define shifts between intraspecific and interspecific processes. Optimization consists in finding the maximum likelihood (ML) solution for a model that combines diversification between these processes (Fujisawa & Barraclough, 2013).

Ultrametric trees generated in BEAST were used for this analysis. We used the R statistical software package SPLITS v.1.0-19 (Ezard & al., 2009) to implement the GMYC species delimitation tool (Pons & al., 2006; Fontaneto & al., 2007). As recommended by Fujisawa & Barraclough (2013), only results from $\text{GMYC}_{\text{simple}}$ are presented.

Bayesian Phylogenetics Phylogeography (BPP). — BPP uses the multispecies coalescent model to compare different models of species delimitation and species phylogeny in a Bayesian framework. The method accounts for incomplete lineage sorting due to ancestral polymorphism and gene tree–species tree conflicts (Yang & Rannala, 2010, 2014; Rannala & Yang, 2013, 2017). BPP requires the use of a fully resolved "guide tree" and *a priori* assignment of samples to individual populations. We used the unguided species delimitation analysis ("A11"), which attempts to merge different populations into one species, while never attempting to split one population into multiple species (Yang, 2015). To take full advantage of this feature, populations within each Puerto Rican clade were defined as the least-inclusive subclades that showed high bootstrap support in our multilocus RAxML tree.

Following Leaché & Fujita (2010), we evaluated four different combinations of priors on population size parameters (θ_s) and divergence time at the root of the species tree (τ_0). These priors are assigned an inverse-gamma distribution IG (α, β) with a mean $m = \beta / (\alpha - 1)$ and variance $s^2 = \beta^2 / [(\alpha - 1)^2 \cdot (\alpha - 2)]$. The scenarios evaluated assume relatively small ancestral population sizes and shallow divergences ($\theta_s \sim$ IG [3, 0.002] and $\tau_0 \sim$ [3, 0.002]), small ancestral population sizes and deep divergences ($\theta_s \sim$ IG [3, 0.002] and $\tau_0 \sim$

[3, 0.2)]), large ancestral population sizes and shallow divergences (θ_s ~ IG [3, 0.2] and τ_0 ~ [3, 0.002]) and large ancestral population sizes and deep divergences (θ_s ~ IG [3, 0.2] and τ_0 ~ [3, 0.2]). The other divergence time parameters were specified by the uniform Dirichlet distribution (Yang & Rannala, 2010: equation 2). Each analysis was run at least twice to confirm consistency between runs. Both rjMCMC algorithms (0 and 1) were evaluated. The number of MCMC iterations was 220,000 (burnin = 10000, sample freq. = 2, num. samples = 100000). Sequence divergence in our full taxon sampling is higher than 10%, hence BPP analysis was carried out on clades from Puerto Rico and immediate sister taxa exclusively. Results presented are based on the second combination of priors (i.e., small ancestral population sizes and deep divergences) as they likely fit better the evolutionary history of the group (see Discussion). Results from other combinations are presented in supplementary Table S1 for comparative purposes. Analysis was carried out with BPP v.3.4 (Yang, 2015).

Species accumulation over time. — A species accumulation curve based on species sampled by different collectors throughout time was generated to illustrate the importance of increasing geographic coverage of sampling and integrating molecular methods for estimating species richness. Species names of historical collections were updated following the taxonomic revision presented here. Collection dates were obtained from specimen labels and used as sampling units. The function SPECACCUM (method = "collector") from the R package "vegan" v.2.5-6 (Oksanen & al., 2019) was used to generate the curve.

■ RESULTS

Phylogenetic analysis and species delimitation. — We obtained new sequence data for 83 specimens from Puerto Rico. These efforts resulted in 298 newly generated sequences for ITS (71, suppl. Appendix S1), *MCM7* (40, suppl. Appendix S2), mtSSU (16, suppl. Appendix S3), nuLSU (59, suppl. Appendix S4), *RPB1* (46, suppl. Appendix S5), and *RPB2* (66, suppl. Appendix S6). Removal of ambiguously aligned regions with Gblocks produced a reduced-sized ITS alignment of 444 bp (suppl. Appendix S7). Two multilocus concatenated alignments were consequently generated, one using the Gblocks output (4545 bp) and another using the complete ITS alignment (4710 bp). Even though coverage for mtSSU was low in our final alignments, we decided to keep data from this gene for downstream analyses given that previous work has found no evidence of biased phylogenetic inferences resulting from analyzing datasets with different levels of missing data (Wiens & Morrill, 2011). Phylogenetic reconstructions generated with these two concatenated alignments yielded similar topologies; therefore, trees presented are based on alignments using the complete ITS dataset. Results are highlighted using our MrBayes tree, which also include results from our multilocus species delimitation analyses (Fig. 2 [full version in suppl. Fig. S2]). Refer to supplementary Fig. S3 for the multilocus RAxML tree. The likelihood value for the two cold chains in our Bayesian trees was −33,953.99 and −33,972.26 whereas the final optimization likelihood for the ML tree was −35,919.15. Instances of conflict between inference methods are highlighted when needed.

Multilocus phylogenetic analysis shows that *Sticta* is a well-supported monophyletic clade with a strongly supported sister-group relationship with *Pseudocyphellaria* (Fig. 2). Within the ingroup, material from the island is distributed in 11 monophyletic clades, the exceptions being *S.* aff. *parvilobata* and *S. borinquensis* sp. nov., which are paraphyletic, and *S.* aff. *harrisii*, which is represented by a single specimen (Fig. 2, suppl. Figs. S2, S3). Concurrent morpho-anatomical analysis indicated that these clades correspond to distinct species (see Taxonomic treatment), most being closely related to species from South and Central America. *Sticta parvilobata* sp. nov. + *S.* aff. *parvilobata*, on the other hand, have close affinities with *S. ciliata* Tayl., which is widely distributed (Fig. 2).

Our specimens agree with four of the species delimited in Harris (1989) (Fig. 2). Six species (i.e., *S.* aff. *harrisii*, *S. weigelii* (Ach.) Vain. s.str., *S.* aff. *borinquensis*, *S. corymbosa* sp. nov., *S. guilartensis* sp. nov. and *S.* aff. *guilartensis*) were missed in collecting efforts associated with that work, whereas species "*Sticta* sp. 22678" and "*S. trichographis* Fée ined." contained material representative of two species each, *S. parvilobata* + *S.* aff. *parvilobata* and *S. densiphyllidiata* sp. nov. + *S. riparia* sp. nov., respectively.

Species delimitation analyses on our multilocus tree showed that PTP was the most conservative among methods used. It delimited 9 of the 14 species identified in our tree but failed at separating *Sticta parvilobata* from *S.* aff. *parvilobata*, *S. borinquensis* from *S.* aff. *borinquensis*, and "*S. scabrosa* ined." from several taxa from other regions (Fig. 2). BPP and GMYC estimated a slightly higher species diversity, both delimiting 10 of the recognized species. Both methods, however, similarly over split several species, namely *S. harrisii* sp. nov., *S.* aff. *parvilobata* and *S. scabrosa*. Delimitations on single-locus (ITS) trees, on the other hand, were similar to those from multilocus trees, but were generally more liberal. For instance, multilocus PTP analysis delimited *S. parvilobata* and *S.* aff. *parvilobata* as the same species, but single-locus delimitation regarded them as separate (suppl. Fig. S4). Similarly, single-locus GMYC analysis split *S.* aff. *parvilobata* into three species, whereas GMYC based on our multilocus tree delimited only two species (suppl. Fig. S5).

Results from species delimitation analysis with BPP under all combinations of priors are shown in supplementary Table S1. There were several instances of agreement, particularly between delimitations that assumed priors that modelled either shallow or deep divergences. Major differences were linked to priors that assumed large ancestral population sizes. That is, delimitations that assumed large ancestral population sizes tended to delimit less species compared to delimitations assuming small ancestral populations.

Species accumulation over time. — Patterns of species accumulation as a function of sampling efforts over time are shown in Fig. 3. Drastic increases in the number of species recorded in the island were first observed between 1900 and 1920 when collectors mainly from the United States, which included Elizabeth G. Britton and Nathaniel L. Britton from NY, visited the island (Mercado-Díaz & Santiago-Valentín, 2010). Species richness increased during a second period from 1960 to 1970 mostly due to efforts by Ismael Landrón-Concepción during his work on *Ramalina* Ach.

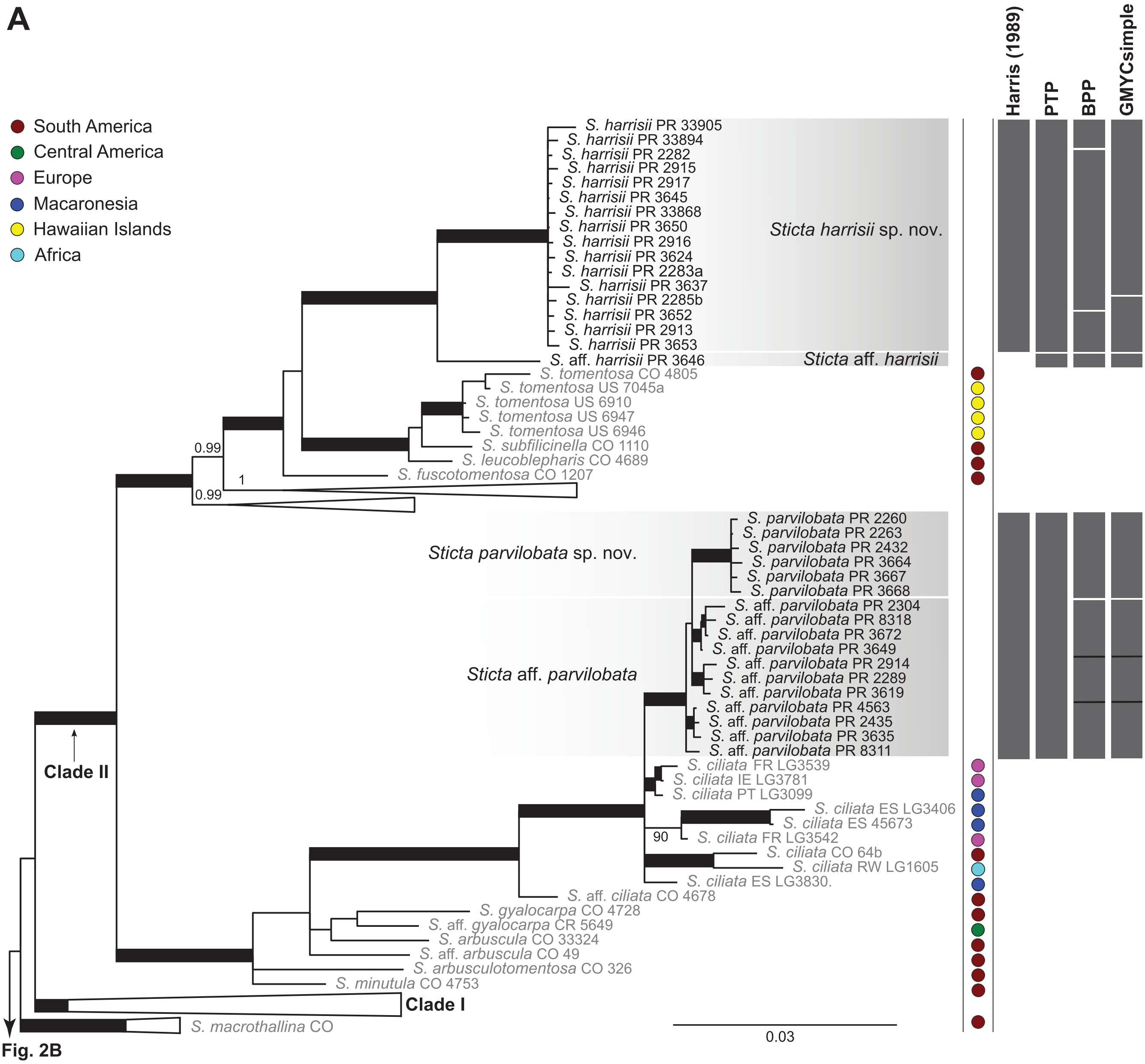

Fig. 2. Maximum clade credibility (MCC) tree obtained from MrBayes based on six nuclear and mitochondrial loci (ITS, *MCM7*, nuLSU, *RPB1*, *RPB2*, mtSSU). The tree shows species delimitations of Puerto Rican taxa that were used by Harris (1989) or obtained by analyzing the full taxon dataset with PTP, GMYC and BPP (gray boxes to the far right). Black lines separate species that were nested within other delimited species. That is, samples above the upper black line and below the lower black line were delimited as the same species. Missing boxes for Puerto Rican taxa in Harris (1989) indicate that specimens for the taxon in question were not obtained during that effort. Sequence data for 300 specimens of *Sticta* from Puerto Rico (83) and the rest of the world (217) (most in collapsed branches) were used to generate this tree. Clades I–V from Widhelm & al. (2018) are included for reference purposes (*S. macrothallina* is considered part of Clade II in that work). Geographic origin of samples from other regions is indicated by circles with different colors/patterns in the "Geography" column. Puerto Rican taxa are in black font and are highlighted using a gray gradient. Thickened branches indicate that the clade has both >0.95 posterior probabilities and >70 bootstrap statistical support. Clades supported only by Bayesian analysis show posterior probability values above branches, whereas those exclusively supported by maximum likelihood have bootstrap support below branches. Scale represents number of substitutions per site.

(Landrón-Concepción, 1972). Species richness remained at 11 species from 1975 to 2011 when efforts for the present work, which included increased sampling efforts and use of molecular data, started (dashed line, Fig. 3). As a result, a third increase in number of species recorded for the island was documented between 2011 and 2019.

DISCUSSION

Phylogenetic patterns, species richness and potential endemism. — Phylogenetic patterns recovered in this work are similar to those observed by others (Moncada & al., 2013b; Widhelm & al., 2018) and support the placement of

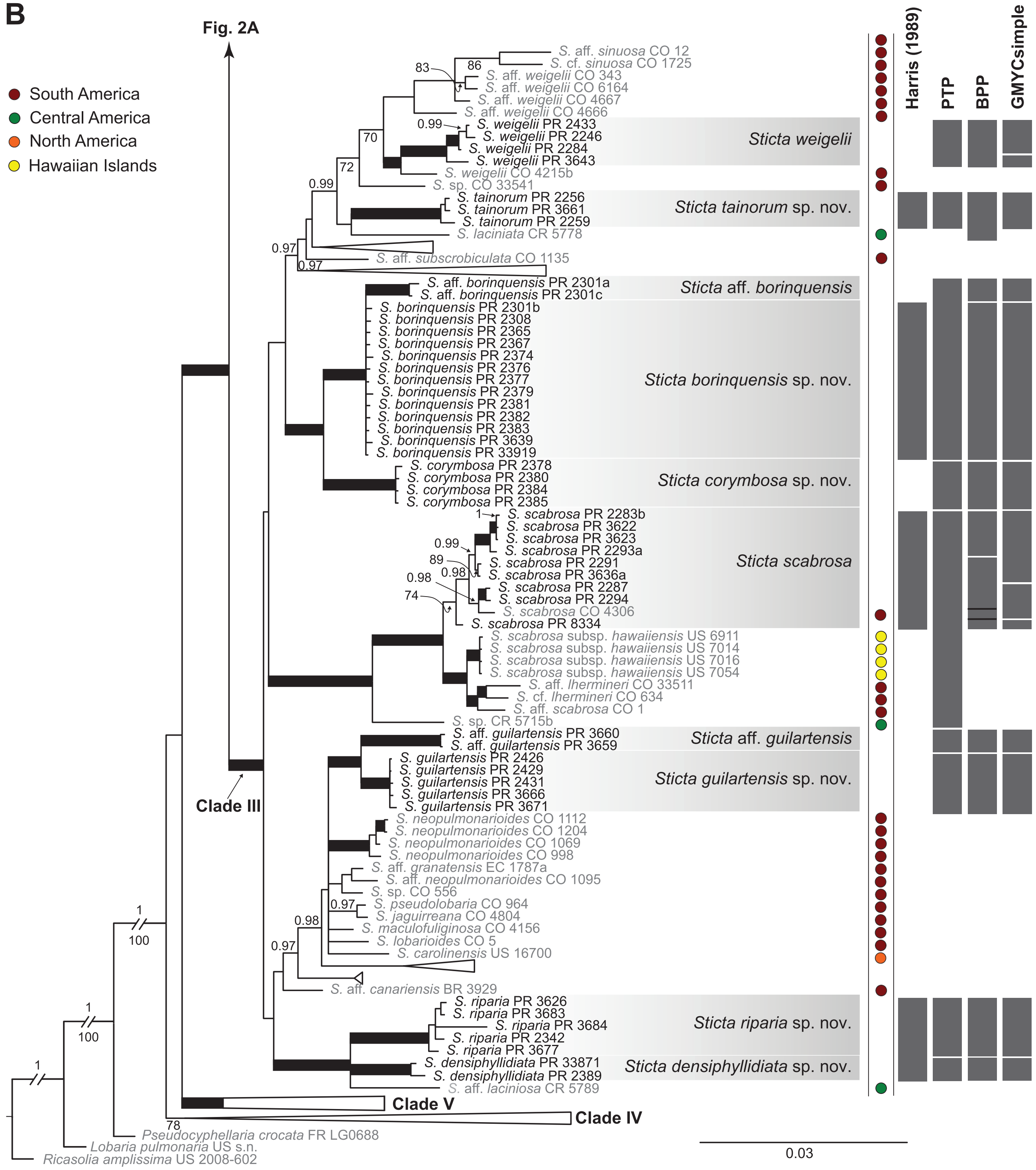

Fig. 2. Continued.

Sticta as a monophyletic group sister to *Pseudocyphellaria*. Moncada & al. (2013b), on the other hand, did not find strong support for this sister relationship. Phylogenetic relationships within this group were recently assessed by Widhelm & al. (2019) using a target enrichment approach of 400 single-copy nuclear genes. Although conflicting topological patterns among data types and phylogeny reconstruction methods used were observed, *Sticta* was most often recovered as sister to *Yarrumia* D.J.Galloway, a recently segregated genus from *Pseudocyphellaria* (Galloway, 2015) not included in Moncada & al. (2013b).

We recovered a topology highly similar to the one in Widhelm & al. (2018) and found strong support for the major clades highlighted in that work, except for Clade IV, which was strongly supported only in our maximum likelihood analysis (Fig. 2). Clade V was strongly supported but was recovered as sister to the clade containing Clades I, II, III as opposed of being sister to these clades and Clade IV, as was shown in Widhelm & al. (2018). Lack of support for Clade IV in our Bayesian phylogeny and conflicting placement of Clade V between both studies are likely due to slight differences in parameters used for phylogenetic reconstructions and in attributes of gene datasets analyzed (e.g., an additional marker [*RPB2*] was used in this study). Complex historical processes might also underlie some of these conflicts, as has been recently proposed by Widhelm & al. (2019). These could potentially confound phylogenetic reconstructions and result in clades with short branches and poor support, such as the one containing Clades I, II, III and V in Fig. 2. Interpretation of phylogenetic relationships among these clades should consequently be approached conservatively.

Most of the species represented in our main phylogeny (11) were recovered as monophyletic clades. Topological relationships between *S. parvilobata* + *S.* aff. *parvilobata* and *S. borinquensis* + *S.* aff. *borinquensis* were not fully resolved and/or had some degree of clade substructure and will require further study with additional data. Moreover, morpho-anatomical and chemical attributes of material representative of most of these species presented unique combinations of characters that are not known from other species within the genus, the exceptions being *S.* aff. *parvilobata*, which is morphologically cryptic with respect to *S. ciliata* (discussed below), and *S. scabrosa* and *S. weigelii*, which represent well-known, widely distributed species (Moncada, 2012; Moncada & al., in press).

Results from our analysis justify the formal taxonomic recognition of eight new species from Puerto Rico, whereas some of the lineages that are either not well resolved phylogenetically or represent few collections or singletons are labeled with only provisional designations at this moment. To this end, the following species are formally established: *S. borinquensis* sp. nov., *S. corymbosa* sp. nov., *S. densiphyllidiata* sp. nov., *S. guilartensis* sp. nov., *S. harrisii* sp. nov., *S. parvilobata* sp. nov., *S. riparia* sp. nov., and *S. tainorum* sp. nov. (refer to "New Taxa" section). Two phylogenetically recognized lineages (*S.* aff. *borinquensis*, *S.* aff. *guilartensis*) and *S.* aff. *harrisii* are considered distinct species but are not described here due to poor quality or insufficient amount of material to adequately assess morphological characters. We refrained from recognizing new species within *S.* aff. *parvilobata* because genetic variability and lack of distinctive morphological characters in material representative of this group prevented us from confidently separating it from *S. ciliata*. On the other hand, material from *Sticta* sp. 320 Harris (1989), a morphologically distinct species within the island (see below), was not collected during recent efforts. Given the general concordance between morphology and phylogeny that has been recently highlighted for this genus (Moncada & al., 2013c), there is little doubt that this lineage represents a phylogenetically distinct species-level clade. We refrained from providing

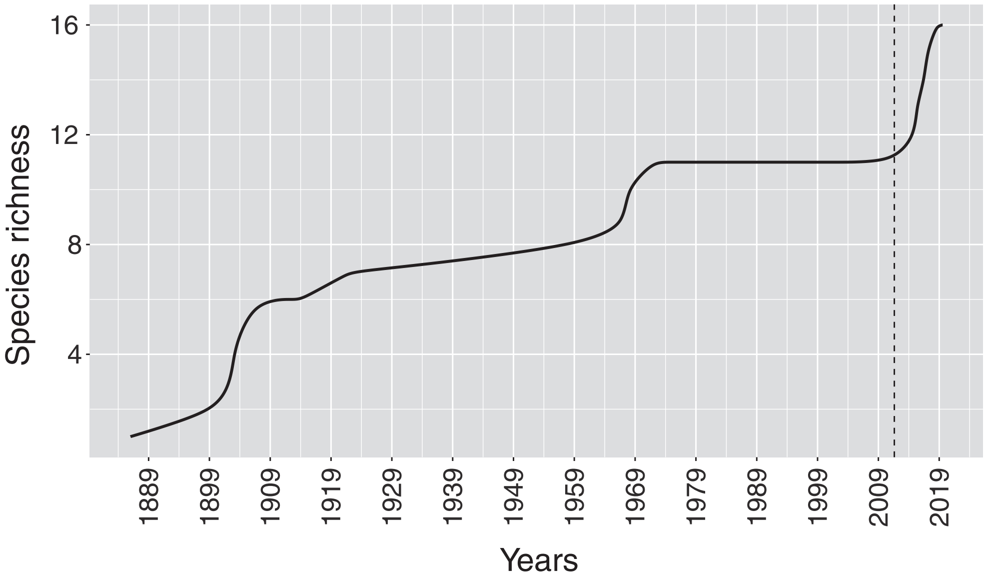

Fig. 3. Species accumulation curve showing species richness of *Sticta* in Puerto Rico as a function of sampling efforts over time. The black line represents species richness known at a specific sampling year in the horizontal axis. Dashed vertical line represents the year (2011) when we began expanding sampling efforts and incorporating molecular methods for studying *Sticta* species richness in Puerto Rico.

a formal description for it because historical material from this species is also scarce. The morphotype referred to as *Sticta* sp. 3725 in Harris (1989), on the other hand, is not considered different from *S. borinquensis* in spite of its K+ purple medullary reaction (refer to "Remarks" section in the *S. borinquensis* description below). It is therefore presumed to be represented in our phylogeny. Lastly, one specimen in US (*Hale 38304*) is similar to *Sticta* sp. 320 but considered a different species due to several morphological differences (see below). This species will remain undescribed and phylogenetically unresolved until additional material is obtained. Taken together, *Sticta* in Puerto Rico is represented by at least 16 species-level lineages, two solely recognized on morphological grounds (i.e., *Sticta* sp. 320 and *Sticta* sp. 38304). Further work should help determine if *S.* aff. *parvilobata* is comprised of one or several species-level lineages or if its conspecific with the widespread *S. ciliata*.

From a conservative standpoint, if we consider the two confirmed widespread species present on the island (*Sticta scabrosa*, *S. weigelii*) and assume that *S.* aff. *parvilobata* is eventually resolved as a geographic variant of *S. ciliata*, and that *Sticta* sp. 320 and *Sticta* sp. 38304 are found to represent widely distributed species, the minimum number of potentially endemic species level-lineages for Puerto Rico is 11 (i.e., the 8 newly described species + *S.* aff. *harrisii*, *S.* aff. *borinquensis* and *S.* aff. *guilartensis*). Putative endemism for this group in the island might therefore reach 69% (11 out of 16 species), a reasonable figure considering that islands are known to promote speciation and high levels of endemism in many types of organisms (Losos & Ricklefs, 2009). In the Caribbean, high endemism has been reported for many groups including reptiles (Scantlebury, 2014), amphibians (Hedges, 1989; Rodríguez & al., 2010), bats (Dávalos, 2007), and plants (Liogier & Martorell, 2000; Francisco-Ortega & al., 2007). For lichens, the scenario is less clear because diversity and distribution patterns have been less studied. Nevertheless, studies on *Sticta* and other Lobariaceae from other islands show levels of endemism similar to those reported for other groups and also to those reported here. For instance, previous phylogenetic studies revealed high endemism of 75% in the Hawaiian archipelago for the genera *Pseudocyphellaria* (Moncada & al., 2014) and *Lobariella* Yoshim. (Lücking & al., 2017b), whereas endemism based on morphological species concepts had been estimated at zero percent for these taxa. Recent phylogenetic work suggests that 9 out of the 13 species of *Sticta* found in Hawaii are endemic to this archipelago (i.e., 69% endemism; Moncada & al., 2020). Simon & al. (2018) showed that most *Sticta* species (31 out of 35 [89%]) found in Madagascar and the Indian Ocean Islands are restricted to either the Mascarene archipelago or a single region in Madagascar. Several other lichen genera from Puerto Rico, such as *Ocellularia* G.Mey. and *Cladestinotrema* Rivas Plata & al., are also believed to contain high number of endemics (Mercado-Díaz & al., 2014). Unfortunately, as stated before, the lichen biota in other islands of the Caribbean is still poorly known, particularly those of the larger islands of Cuba, Jamaica, and Hispaniola. For *Sticta*, only 4, 11 and 2 species have been formally recognized in each of these islands, respectively (Imshaug, 1957). This means that potential endemism within Puerto Rico reported here (69%) might be lower because further sampling efforts in these islands could show that some of these lineages are more widely distributed in the Caribbean. For instance, floristic similarities between Puerto Rico and the Lesser Antilles have been previously noted (Dewalt & al., 2016) and attributed to exposure to similar climatic regimes and presumed increased migration between these regions during the Pliocene (Beard, 1949). This hints that some of the putatively endemic species described here are likely to be found in high-elevation islands in the Lesser Antilles (e.g., Martinique, Guadeloupe, Dominica). Their presence in other islands of the Greater Antilles is also plausible, particularly if we consider the direction of hurricanes and their role as potential agents of long-distance dispersal (Andraca-Gómez & al., 2015). In paleogeographic terms, however, this latter scenario is less likely because *Sticta* was emerging as an independent evolutionary group (possibly from South America) between the Oligocene and the Miocene (Widhelm & al., 2018), which is the period when Puerto Rico separated from Hispaniola and the rest of the Greater Antilles (Graham, 2003). *Sticta* was therefore absent during a period that likely witnessed substantial biotic exchange between these areas. This is supported by our recent delimitation of *S. damicornis* (Sw.) Ach. as a Caribbean endemic occurring only in Cuba, Jamaica and Hispaniola, but not occurring in Puerto Rico (Moncada & al., 2018).

Evolution of *Sticta* in Puerto Rico. — Species from Puerto Rico do not form a single clade as would be expected in the scenario of a single origin and subsequent radiation, e.g., in the case of Madagascar and the Mascarenes (Simon & al., 2018). They form a polyphyletic assemblage of a few, widely distributed species that likely evolved elsewhere and colonized the island, and species that evolved *in situ* after multiple colonization events of ancestral lineages. These colonization events likely happened via long-distance dispersal because the origin of the group (30 million years ago [mya], Widhelm & al., 2018) postdates the Late Cretaceous (~76 mya), when the Proto-Antilles were at their closest distance to North and South America (Hedges, 2006). *Sticta* is also younger than the quasi-continuous land-bridge that allegedly connected South America to the Greater Antilles during the Eo-Oligocene boundary (~34 mya) (Iturralde-Vinent & MacPhee, 1999; but see Ali, 2012), supporting our hypothesis of long-distance dispersal origin for the group.

Although *Sticta* diversity on the island has not originated via major *in situ* radiations, the possibility of active micro-radiations in some clades cannot be ruled out. For example, while results from phylogenetic reconstructions, species delimitation analysis, and evaluation of morpho-anatomical characters did not yield unambiguous evidence for hidden cryptic diversity within *S.* aff. *parvilobata* and *S. scabrosa*, these analyses made clear that both lineages exhibit considerable haplotype variability at local scales. This hints at the presence of ongoing selective pressures that may lead to the evolution of new species (Levin, 2000; Givnish, 2010; Madriñán & al., 2013). In *S.* aff. *parvilobata*, observed short branching patterns and lack of monophyly suggest that this lineage might be undergoing a rapid radiation and/or contain recently diverged species (Shaw & al., 2003; Leavitt & al., 2016; Widhelm & al., 2019). This agrees with Magain & Sérusiaux's (2015) observations on *S. ciliata* as a clade that is in active divergence and dispersion and that may require recognition of additional species. Unique haplotypes of *S. scabrosa* from Puerto Rico were also recently recognized, although they were taxonomically resolved as geographic variants of this species (Moncada & al., in press). Our finding that a *S. scabrosa* sample from Colombia was, according to GMYC, conspecific with samples from Puerto Rico, partly supports this hypothesis.

The lack of evidence of major evolutionary radiations for this genus within the island was somewhat surprising. These events are known to be major factors shaping diversity patterns in this region. One example are the multiple radiation events of different *Anolis* ecomorphs in each island of the Greater Antilles (Losos & al., 1998; Mahler & al., 2010; Losos, 2011). Likewise, recent work suggests that many genera of endemic seed plants of the Caribbean originated via *in situ* radiations within islands (Nieto-Blázquez & al., 2017). Regional-scale radiations, on the other hand, have been amply documented in multiple groups apart from *Anolis* (e.g., frogs from the genus *Eleutherodactylus* [Hedges, 1989; Heinicke & al., 2007; Rodríguez & al., 2010], Phylostomid bats [Dávalos, 2007], extant and extinct non-volant mammals [MacPhee & Iturralde-Vinent, 1995; Van der Geer & al., 2010; Fabre & al., 2014; Brace & al., 2015], plants [Michelangeli & al., 2008; Perret & al., 2013], etc.), but additional sampling on other islands will be needed to determine if this type of process has contributed to present-day diversity patterns in this group.

Geographic affinities. — Phylogenetic analysis revealed that most taxa from Puerto Rico are associated with South American clades, which hints at stronger biogeographic links to that continent. For instance, many of the non-flying terrestrial vertebrate groups (Hedges, 2006; Marivaux & al., 2020) and even some invertebrates (e.g., McHugh & al., 2014) have their closest relatives in South America. Less evidence is available for plants, but recent work suggests that most West Indian *Adiantum* L. species originated from immigration events from that continent during the Miocene (Regalado & al., 2018).

These biogeographic affinities are reasonable considering that *Sticta* may have originated in the New World (Widhelm & al., 2018) and that South America is apparently a center of diversity for this group (Moncada & al., 2014); however, close links of several clades (e.g., *Sticta harrisii* + *S.* aff. *harrisii* and *S. parvilobata* + *S.* aff. *parvilobata*) to lineages from North and Central America or from extra-Neotropical areas (e.g., Hawaii, Macaronesia, Europe) hint at a more complex scenario. Active dispersers such as birds, bats or freshwater fishes, for example, are believed to have colonized the Caribbean islands from North and Central America (Hedges, 2006). In their recent study, Nieto-Blázquez & al. (2017) found that South America was the main ancestral area for only 5 of the 32 Caribbean endemic seed plant genera they analyzed, which is surprising considering floristic similarities that have been documented for many plant genera between both regions (Acevedo-Rodríguez & Strong, 2008). Furthermore, our dataset has a moderate overrepresentation of South American lineages, which might obscure underlying patterns. Molecular approaches of historical biogeography aimed at reconstructing the ancestral ranges of Caribbean taxa coupled with additional collecting activities in poorly studied regions will be needed to evaluate these patterns in more detail.

Species delimitation analyses. — Species delimitation analyses have been amply used for exploring diversity patterns in lichenized fungi, particularly for assessing boundaries within species complexes and/or uncover instances of cryptic speciation (Parnmen & al., 2012; Kraichak & al., 2015; Alors & al., 2016; Widhelm & al., 2016; Zhao & al., 2017). In this work, these methods provided additional means of evaluating species boundaries, particularly in complex clades such as those containing strongly supported subclades (e.g., *Sticta* aff. *parvilobata*) or those where morpho-anatomical differences between lineages were subtle (e.g., *Sticta borinquensis* + *S.* aff. *borinquensis*). For example, congruent with the analysis of morphological data, GMYC and BPP analyses on both multilocus and ITS datasets agreed in separating *S. parvilobata* from *S.* aff. *parvilobata* and *S.* aff. *borinquensis* from *S. borinquensis*. PTP on our multilocus tree, on the other hand, failed to separate these species. This latter analysis also delimited within *S. scabrosa* lineages now considered to represent separate species (Moncada & al., in press). Differences between GMYC and PTP were somewhat unexpected because when gene flow is presumed absent, both methods tend to produce similar estimates of species limits (e.g., Arrigoni & al., 2016; Del-Prado & al., 2016). These minor incongruences, however, are probably linked to the high number of species analyzed here since PTP has been found to outperform GMYC when fewer species are involved (Luo & al., 2018). Empirical work has also shown that GMYC delimitation could also result in over-splitting (Alors & al., 2016; Eberle & al., 2016; Guillemin & al., 2016), which might explain to some degree the disagreement between boundaries placed by these methods.

In general, species delimitation under the preferred combination of priors in BPP (i.e., θ_s [3, 0.002], τ_0 [3, 0.2]) showed low conflict with delimitations reached by other methods. Although this set of priors not always resulted in the highest posterior probabilities, we opted to favor delimitations based on them as they were thought to better represent the natural history of species in the island. This rationale was based on the relatively old geologic age of Puerto Rico (~100 million years; Mitchell, 1954), the estimated age of the group (~30 million years) and the idea that effective population sizes in island lineages should be small as they represent only a fraction of the individuals in mainland populations (Nei & al., 1975). Other prior combinations were less favored as they seemed to over- or underestimate the number of species. One example is *S. scabrosa*. As mentioned previously, recent work suggests that this species is widespread in the Neotropics and include local haplotypes in the island (Moncada & al., in press), yet, prior combination θ_s (3, 0.002) and τ_0 (3, 0.002) split our 10 specimens into 7 species. Conversely, large values of θ_s and small τ_0 apparently underestimated true diversity as it was seen with *S. guilartensis* and *S.* aff. *guilartensis*. These two strongly supported monophyletic lineages and morphologically divergent species were delimited as a single species under this prior combination. This agrees with previous work that suggests that large θ_s and small τ_0 tend to favor fewer delimited species (Leaché & Fujita, 2010; Yang & Rannala, 2010).

Incongruence between delimitation methods was not rampant although it was present in our analyses. Carstens & al. (2013) suggested that incongruence across results from different methods could be indicative of violation of assumptions or could be due to differences in the power to detect cryptic lineages in one or more of the approaches. Uneven sampling has also been linked to poor performance and conflict between delimitation methods (Lim & al., 2012; Rittmeyer & Austin, 2012) and likely explain some of the incongruences detected. In lichenized fungi, conflict between delimitation methods has also been attributed to limitations in placing boundaries in lineages with recent diversification histories (Wei & al., 2016). This might have affected delimitation within *S.* aff. *parvilobata*, which is most likely undergoing an active speciation process. Insufficient data for species delimitation may also explain oversplitting in some methods (e.g., GMYC; Lohse, 2009) and might underlie some of the conflict observed between them.

Our work reaffirms the value of species delimitation analyses for integrative studies but also illustrates the risks of using them in isolation. Previous work has suggested that some methods, such as BPP, cannot statistically distinguish genetic structure associated with population isolation vs. species boundaries, and thus might not be effective at diagnosing species (Sukumaran & Knowles, 2017; Huang, 2018). Other methods are relatively stable under different circumstances (i.e., GMYC) but might have a high incidence of wrongly delimited species and therefore could not be used as sufficient evidence for evaluating some clades (Talavera & al., 2013). These observations reiterate the importance of analyzing all available data (i.e., genetic, morphological and ecological) when interpreting species delimitations.

It should be noted that although PTP and GMYC have been increasingly applied to multilocus trees (Luo & al., 2018), their use and interpretation should preferably be based on the analysis of single-locus data (Fujisawa & Barraclough, 2013; Zhang & al., 2013). We are less concerned about presenting results obtained from analyzing multilocus trees because taxonomic determinations were mostly based on distinctive morphologies and strong branching patterns and clade support. In addition, delimitations produced with them were in general more conservative.

Molecular vs. morphological data. — Phylogenetic analysis and species delimitation methods were important for uncovering hidden diversity of this group in the island. These approaches showed that three of the species defined by Harris (1989) were representative of two lineages: *Sticta* sp. 22678 (*S.* aff. *parvilobata* + *S. parvilobata*), *Sticta* sp. 22494 (*S. borinquensis* + *S.* aff. *borinquensis*) and "*Sticta trichographis*" (*S. riparia* + *S. densiphyllidiata*). Interestingly, only *S.* aff. *parvilobata* should be considered cryptic in the sense of lacking unambiguous morphological characters to separate it confidently from *S. ciliata*. *Sticta* aff. *borinquensis* exhibit subtle morphological differences compared to *S. borinquensis* and is better described as a semi-cryptic species, whereas "*S. trichographis*" and *S. riparia* are not cryptic to each other because phenotypic characters useful for separating them were eventually found. Unaccounted diversity resulting from overlooked phenotypic characters is not a rare phenomenon in lichen studies. It is prevalent, particularly in otherwise cryptic lineages hiding within hitherto assumed widespread species (Lücking & al., 2014) including *Sticta* (Moncada & al., 2013c).

Morphological differences observed were usually sufficient for discriminating between species. Similarly, HPTLC analysis uncovered several unknown secondary compounds that are so far known from several species from the island (suppl. Table S2). The presence of these potentially informative substances reiterates the value of phenotypic characters in this group, which has traditionally been regarded as having a poor secondary chemistry (Moncada, 2012). While morphology-based species delimitation in lichenized fungi has been deemed inaccurate in many instances because of limited phenotypic variability between lineages and/or high degrees of homoplasy in morphological characters (Pino-Bodas & al., 2011; Parnmen & al., 2012; Zhao & al., 2017), our results add to the growing body of work challenging the notion of lichens as organisms with few taxonomically useful characters (Printzen, 2010). Conversely, they confirm that molecular-based species delimitations could be supported by previously overlooked phenotypic characters (Lumbsch & Leavitt, 2011). They also highlight that at least for island biotas, morphology is still relevant for characterizing species diversity. This is perfectly exemplified by endemic species of *Lobariella* in the Hawaiian archipelago, which bear unique morphologies compared to other species in the genus (Lücking & al., 2017b).

Implications for conservation. — Most species of *Sticta* from Puerto Rico discussed in this work (11) are potentially endemic to the island, which means they are likely found nowhere else on the planet. Because their unique genotypes are usually represented by a small number of individuals and because multiple factors threaten their survival, endemic species, especially those from biodiversity hotspots like the

Caribbean, are priorities for conservation (Myers & al., 2000). In Puerto Rico, an increasing urban footprint at the expense of forest cover is reducing the habitats available for many species (Lugo & al., 2004). Climate change may result in habitat shrinkage of high-elevation species, making them more susceptible to extinction (Dirnböck & al., 2011; Jennings & al., 2014). One species likely facing this fate is *S. corymbosa*, known from only a few individuals in peaks of El Yunque National Forest. Being more diverse in humid and shaded high-elevation environments of the island, species of *Sticta* are also threatened by increases in the frequency and magnitude of hurricanes in the Caribbean region (Mann & Emanuel, 2006). In fact, photographs of the thallus of the same *S. tainorum* individual that were taken both before and after Hurricane María (September 2017) show considerable browning (suppl. Fig. S6), suggesting damaging effects of increasing solar radiation due to reduced canopy foliage. Measures to further improve the protection of the habitats in which these species thrive will be essential for reducing potential risks of extinction linked to these changes.

Failing to collect *Sticta* sp. 320 and *Sticta* sp. 38304 suggests that these species are rare or potentially extinct, or perhaps that sampling efforts were inadequate, but this latter scenario is less likely because sampling included all areas surveyed in the past as well as other suitable habitats that were missed in previous efforts. Additionally, the observed increase in recorded species associated with our work (i.e., Fig. 3) demonstrates that our sampling was as exhaustive as those carried out by others in the past. This is supported by the discovery of several morphologically distinct species not documented in Harris (1989) (e.g., *S.* aff. *guilartensis*, *S.* aff. *harrisii*). The rarity or potential extinction of these species is therefore most likely linked to the negative effect of past disturbances and/or other current pressures (e.g., climate change).

Estimates of species richness are essential in conservation assessments and for the implementation of informed conservation policies. As evidenced in our species accumulation curve, accurate quantification of the species is most likely obtained when taxonomic revisions of target groups are coupled with molecular methods and comprehensive sampling within a region. Yet, as a metric to inform conservation efforts, species richness estimates should not be used in isolation (Fleishman & al., 2006). Phylogenetic approaches are valuable in this sense because they also provide insight on natural history aspects (e.g., genetic uniqueness) that are seldom available for species. Phylogeny-based metrics such as phylogenetic diversity and relative phylogenetic endemism are certainly promising in this regard (Rosauer & al., 2009; Thornhill & al., 2016).

■ TAXONOMY

Previous morphological taxonomy and herbarium revisions. — Previous to this work, only two species from Puerto Rico were known from the published literature: *Sticta sinuosa* and *S. weigelii* (Imshaug, 1957). Several specimens originally identified as *S. sinuosa* by Müller Argoviensis (1888) were examined in NY and US and found to correspond to *S. tainorum*. Excluding this taxon, nearly all species identified in this work would fall under the broad concept of *S. weigelii* (sensu Galloway, 1994). We were not able to revise specimens of *S. weigelii* in Müller Argoviensis (1888); therefore, it is unknown to which of the species described here this material corresponds to.

As mentioned before, nine species were recognized by Harris (1989) based on morphological characters. The valid name *Sticta weigelii* was used, but this material was found to correspond to *S. scabrosa*, a species within the *S. weigelii* morphodeme (Moncada & al., in press). None of the specimens evaluated by Harris (1989) correspond to *S. weigelii* sensu stricto. The two other species names in that work (i.e., "*S. trichographis*" and "*S. circumroda*") were never published and are therefore not valid. The taxonomy of *Sticta* sp. 320 in Harris (1989), on the other hand, is more complex. This species resembles *S.* aff. *guilartensis* in the linear-lingulate lobes that do not curl down (see Harris, 1989), but differs from it by the presence of scattered dark brown rhizines that project outward along lobe margins (not noted in Harris, 1989) and the considerable smaller length/width ratio of the lobes. We refrained from formally describing it here due to lack of molecular data and scarcity of specimens to assess morphology. *Sticta* sp. 3725 was found to be morphologically identical to *S. borinquensis* and is considered conspecific with this species; however, none of our specimens showed the KOH+ purple medullary reaction highlighted in Harris (1989) (refer to "Remarks" under the *S. borinquensis* description below). We re-examined the material in NY studied by Harris (1989) and confirmed the KOH+ reaction of the medulla in those specimens. *Sticta* sp. 22489, on the other hand, was found to be conspecific with *S. borinquensis*. Except for *Sticta* sp. 320, the taxonomy of the rest of the taxa in Harris (1989), which are also identified with collection numbers, is resolved in this work (see below).

It is worth noting that material from Puerto Rico have also been identified under the names *S. xanthotropa* (Kremp.) D.J.Galloway, *S. mexicana* D.J.Galloway, *S. beauvoisii*, *S. tomentosa* (Sw.) Ach., *S. wrightii* Tuck. and *S. duforii* Delise (http://lichenportal.org/portal/index.php). These determinations apparently followed broad species concepts from other works (e.g., Galloway & Thomas, 2004). After revising this material, we determined that none of these species occurred on the island.

Several specimens evaluated during our revision of herbarium material deserve special mention due to their peculiar morphology. Hale's specimen *38304* (US) keys out as *Sticta* sp. 320 in Harris (1989), but several differences in its morphology suggest that its most likely a different species. It shares with *Sticta* sp. 320 the presence of lingulate lobes, branched isidia and a short tomentum, but differs from that species in the absence of dark brown rhizines projecting outwards along lobe margins and presence of a distinctly yellow tinge that is so far absent from any of the Puerto Rican material studied to date. Hale's specimen also resembles *S.* aff. *guilartensis*, in its large thallus with linear-lingulate lobes and a very short tomentum throughout but contrasting to it by its wider lobes and shorter internode distances. On the other hand, B. Fink's specimen *1892* (NY, US), which was identified in Harris (1989) as "*Sticta weigelii* auct.", is regarded here as conspecific with *S. scabrosa*. Its smaller thallus size and lobe widths and relatively smooth upper surface, however, make this material worth of further study.

Lastly, chemical analysis by HPTLC revealed the presence of several unidentified secondary compounds in some species of the island. A general description of chromatographic properties of these substances is provided in supplementary Table S2.

Key to the species of *Sticta* in Puerto Rico

1. Photobiont green .... ***S. tainorum***
1. Photobiont blue-green 2
2. Vegetative propagules present and usually abundant 3
2. Thallus without vegetative propagules or with small marginal lobules. White, reticulated maculae throughout. Known only from Bosque Estatal de Guilarte .... ***S. guilartensis***
3. Phyllidia present 4
3. Isidia present 11
3. Corymbose, sorediiform isidia along margins present .... ***S. corymbosa***
4. Tomentum short to pubescent 5
4. Tomentum rather thick 8
5. Lobes rounded to suborbicular. Without marginal rhizines projecting outwards 6
5. Lobes lingulate. With or without marginal rhizines projecting outwards 7
6. Lobes broad (3.5–7 mm), tomentum tan to brown, lower surface cream-colored to light brown, primary tomentum hairs not branching, specimens usually turning reddish with age .... ***S. densiphyllidiata***
6. Lobes narrower (2–4 mm), tomentum brown to dark brown, lower surface greyish-brown to dark brown, primary tomentum hairs sometimes branching, specimens dark brown to gray in herbarium .... ***S. riparia***
7. Lobes with marginal rhizines projecting outwards........... .... ***Sticta* sp. 320**
7. Marginal rhizines absent, lower surface turning yellowish in herbarium .... ***Sticta* sp. 38304**
8. Tomentum towards margins whitish to greyish-brown 9
8. Tomentum towards margins brown to black 10
9. Margins distinctly ciliate and highly dissected due to abundance of branched phyllidia. Lobe internode short (0.4–4 mm). Tomentum becoming sparse towards margins. Upper surface smooth. Apothecia frequent. Cells of basal membrane with numerous papillae. Upper surface never maculate .... ***S. harrisii***
9. Margins rarely ciliate although tomentum hairs frequently extend outwards resembling cilia. Phyllidia mostly marginal and occasionally laminal, less dense. Lobe internode long (5–7 mm). Tomentum remaining more or less dense towards margins. Upper surface becoming scrobiculate to slightly faveolate, particularly towards center. Apothecia absent to sparse. Cells of basal membrane without papillae. Upper surface occasionally maculate ... . ***S. scabrosa***
10. Tomentum brown. Thallus mostly horizontal. Apothecia and pycnidia absent or infrequent. Known only from high-elevation forests to the west of the island................ .... ***S.* aff. *borinquensis***
10. Tomentum darker brown to blackish, particularly towards the center. Thallus usually ascending. Apothecia and pycnidia frequent. Abundant in high-elevation forests to the east of the island.................................... ***S. borinquensis***
11. Isidia laminal 12
11. Isidia marginal 14
12. Lobes lingulate to spathulate, regularly branching. Known only from El Yunque National Forest .... ***S.* aff. *harrisii***
12. Lobes rounded, unbranched to rarely branching 13
13. Lobes usually broad (10–25 mm), frequently overlapping other lobes, stacked in appearance. Mature lobe apices distinctly revolute. Isidia becoming arbuscular with distinct stipe, forming distinct rounded clusters scattered throughout the thallus. Minutely dotted appearance under high magnification due to small, whitish granules. Distributed throughout the island .... ***S.* aff. *parvilobata***
13. Lobes rarely exceeding 12 mm in width, with individual thalli usually scattered throughout the substrate. Mature lobe apices levelled to weakly revolute. Isidia granular to coralloid, with more homogeneous distribution throughout the thallus. Thallus with white microfibrils visible under high magnification. Known from high-elevation forests to the west of the island .... ***S. parvilobata***
14. Lobes long, linear, length > 3–4 times larger than width .... ***S.* aff. *guilartensis***
14. Lobes rounded to lingulate, length < 3–4 times larger than width 15
15. Tomentum thick, spongy towards center. Lobes rounded. Isidia truly cylindrical, dense .... ***S. weigelii***
15. Tomentum thin, pubescent or strigose throughout. Lobes lingulate. Isidia slightly flattened, elongated and branching or simple, scattered and sometimes clustered............... 16
16. Marginal rhizines projecting outwards along lobe margins, tomentum strigose, lower surface not turning yellowish in herbarium.................................. ***Sticta* sp. 320**
16. Marginal rhizines absent, tomentum pubescent, lower surface turning yellowish in herbarium .... ***Sticta* sp. 38304**

New taxa

Sticta borinquensis Merc.-Díaz & Lücking, **sp. nov.** [MycoBank # 834856] – Holotype: PUERTO RICO. Mun. Río Grande, Barrio Guzmán Arriba, along El Toro Trail, near Pico El Toro, El Yunque National Forest; 18°16′22″N, 65°50′02″W; 982 m; 28 Dec 2015, *Mercado-Díaz 2381* (F barcode C0243203F; isotype: UPR).

Species is illustrated in Fig. 4.

Diagnosis. – Differing from *Sticta scabrosa* in the smooth upper surface, darker brown tomentum and frequent occurrence of apothecia.

Description. – Primary photobiont cyanobacterial (*Nostoc* Vaucher ex Bornet & Flahault). Basal stipe absent. Thallus irregular to orbicular in outline, up to 15 cm diam., densely branched, with 6–10 branches per 5 cm radius, branching polytomous; lobes suborbicular to lingulate, horizontal to ascending, imbricate, involute to undulate, with rounded to irregular, plane to revolute apices; margins entire to crenate, not thickened; lobe internodes 1–5 mm long, (2–)2.5–5(–6) mm broad; thallus resistant, coriaceous. Upper surface smooth, slate grey to olive-grey when fresh and brown-grey to light brown and darkening towards the apices in the herbarium, glossy; surface glabrous, marginal line color brown, without papillae, pruina, or cilia. Maculae sparse to absent, white and irregular. Apothecia sparse, marginal to submarginal, subaggregated, pedicillated, base invagination pronounced, 1–4 mm diam., disc color reddish-brown to brown and slightly glossy to opaque both when fresh and in herbarium, margin dark brown, with lighter inner rim, verrucose and tomentose (particularly when young) to smooth and weakly crenulate when old. Tomentum on apothecial margin denser towards base. Phyllidia abundant, marginal (only laminal when injured), dispersed, mostly linear, simple to branched, becoming coralloid to palmate, with irregular orientation, to 1 mm long and 0.1–0.5 mm broad, same color as thallus, becoming darker with age, glossy, flattened to dorsiventral in section, lingulate to weakly spathulate, basal stalk applanate, with cyphellae initials. Lower surface smooth to uneven, glossy, cream-colored to dark brown becoming blackish towards center; primary tomentum dense, absent towards margin, thick, becoming thinner towards margins, spongy, soft, brown, hairs occasionally whitish toward apices. Rhizines absent. Cyphellae abundant, 21–40 per cm^2 towards the thallus center and 61–100 per cm^2 towards the margin, dispersed, rounded to irregular, urceolate with wide pore, erumpent to prominent, margin remaining below the level of the primary tomentum, elevated and involute, cream-colored to brown, without tomentum; pore 0.5–2 mm diam.; basal membrane weakly pruinose (more evident in younger cyphellae), white, K+ yellow–ochre, C–, KC–, P–. Medulla compact, white to cream-colored, K+ yellow–ochre, C–, KC–, P–. Borinquensis unknown (major), Harrisii unknown (minor), Unknown 2 (minor). Pycnidia immersed, black. No cephalodia observed.

Upper cortex paraplectenchymatous, 35–45 μm thick, with two differentiated layers, the upper layer sometimes darkened, consisting of 3–4 cell layers with cells 5–20 μm diam., their walls 1–2.5 μm thick and their lumina rounded to isodiametric, 3.5–19 μm diam. Photobiont layer 25–62 μm thick, its cells 8–14 μm diam. Medulla 50–100 μm thick, its hyphae 2.5–3.5 μm broad, without crystals. Lower cortex paraplectenchymatous, 25–35 μm thick, with 2–3 cell layers; cells 5–20 μm diam., their walls 1–2.5 μm thick. Hairs of lower primary tomentum 200–1100 μm long, in fascicles of 12–20 hyphae, unbranched, cylindrical, septate with intertwined apices. Cyphellae internal pore cavity 100–225 μm deep; cells of basal membrane without papillae. Apothecia biatorine, 700–1200 μm high, with stipe; excipulum 75–150 μm broad. Hymenium 80–125 μm high; epihymenium 2.5–5 μm high, dirty orange to light brown, without gelatinous layer above. Ascospores 1–3 septate, 32–43 × 5–9 μm, fusiform, hyaline.

Distribution and ecology. – Although populations of *Sticta borinquensis* have been found in scattered locations in forests to the west of the island, the distribution of this species seems to be centered around high-elevation forests to the east, particularly in El Yunque National Forest. It seems to be mostly epiphytic and individuals have been found on several tree species including *Prestoea acuminata* var. *montana* (Graham) A.J.Hend. & Galeano, *Cecropia schreberiana* Miq. subsp. *schreberiana* and *Clusia* L. spp. It is often found growing in partly shaded conditions in very humid environments.

Etymology. – The epithet refers to “Borinquen”, the Taíno name for the island of Puerto Rico.

Remarks. – *Sticta borinquensis* is identified in Harris (1989) as *Sticta* sp. 22494 and is one of the largest species to be found among the cyanobacterial representatives of this genus in the island. Phylogenetic analysis shows that this species is most closely related to *S.* aff. *borinquensis*, which is known only from mountain summits within the Bosque Estatal Tres Picachos to the west of the island and is sympatric with *S. borinquensis* in that forest. Both are morphologically very similar and difficult to separate; however, phylogenetic patterns, nearly consistent species delimitation analyses results and subtle morphological differences convince us of treating *S.* aff. *borinquensis* as a separate species. Unfortunately, more material from *S.* aff. *borinquensis* will be needed before a formal taxonomic description of this species is made. It is worth noting, on the other hand, that maculae are sparsely seen in *S. borinquensis*. Yet, these seem to be more evident in larger, older thalli.

Our revision of historical material revealed that the type specimen for *S. weigelii* f. *schizophylliza* (Nyl.) Hue collected in Guadeloupe (i.e., *Husnot #436*; Nylander, 1869) may be conspecific with *S. borinquensis*. This observation was unexpected because Hue (1901) indicated that this material was similar to a specimen identified by Fée as “*S. circumroda*”, an unpublished name covering the taxon now named *S. harrisii* (Harris, 1989; see below). Diagnostic characters that place the Guadeloupean specimen closer to *S. borinquensis* are the abundance of linear marginal phyllidia, the brown to black lower cortex and the dense brown tomentum. Yet, given the high endemism that has been recently documented for this

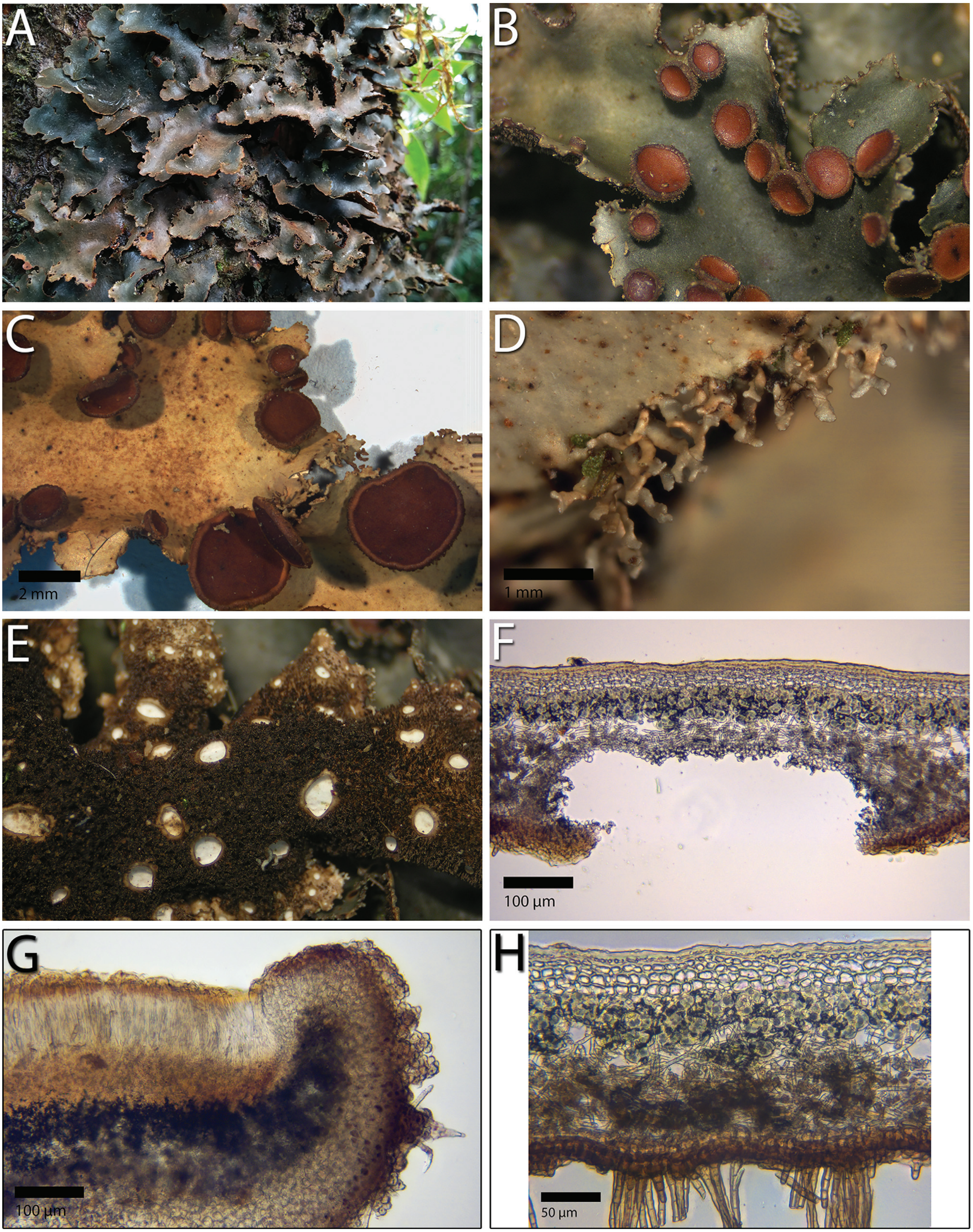

Fig. 4. *Sticta borinquensis* Merc.-Díaz & Lücking. **A**, View of thallus in the field; **B**, Lobes with apothecia when fresh; **C**, Lobes with apothecia and phyllidia when dry; **D**, Detail of marginal branched phyllidia; **E**, Lower surface with dark brown tomentum and cyphellae; **F**, Section of cyphellae; **G**, Section of apothecia; **H**, Section through thallus. Photographs by J.A. Mercado-Díaz (A, C, D, F–H) and R. Lücking (B, E).

group in other tropical island systems (Moncada & al., 2014; Dal Forno & al., 2017; Lücking & al., 2017b; Simon & al., 2018) and the lack of additional molecular and morphological data to assess if this specimen corresponds to *S. borinquensis*, we decided not to take up the infraspecific epithet for the Puerto Rican taxon. Should in the future *S. weigelii* f. *schizophylliza* indeed be shown to be conspecific with *S. borinquensis*, the latter name retains priority at the species level.

Sticta sp. 3725 was separated from *S. borinquensis* (identified in Harris, 1989 as *Sticta* sp. 22494) for its medullary K+ purple reaction but is otherwise identical in morphology to *S. borinquensis* and is treated here as the same taxon. This reaction has not been documented in any of the recently collected material from this species, and the reasons for this remain unclear. Considering that some of the old material show signs of poor drying after collecting, it is possible that this reaction is explained by decomposition of otherwise undetectable secondary substances or even by intrathalline fungi that could have grown because of prolonged duration of moisture within medulla.

Additional specimens examined. – PUERTO RICO. Mun. Humacao, El Yunque National Forest, recreation area, trail up to Mt. Britton; 850–950 m; 9 Jun 1988, *Harris 22497A* (NY). Mun. Jayuya, Bosque Estatal Tres Picachos, trail to Tres Picachos peaks; 18°12′52″N, 66°32′23″W; 1153 m; 18 Aug 2013, *Mercado-Díaz 1958* (UPR). Mun. Luquillo, El Yunque National Forest, near G. González (USFS) "Britton Palm" plot; 18°18′16″N, 65°47′43″; 917 m; 27 Sep 2011, *Mercado-Díaz 957* (UPR). Mun. Río Grande, El Yunque National Forest, along El Toro trail; 18°16′18″N, 65°49′52″W; 1006 m; 28 Dec 2015, *Mercado-Díaz 2365* (UPR). Mun. Orocovis, Bosque Estatal de Toro Negro, along Hwy 143, 3.5 mi. E. of Hwy 139; 27 Feb 1981, *Buck 3725* (NY). Refer to Appendix 2 for additional specimens revised.

Sticta corymbosa Merc.-Díaz & Moncada, **sp. nov.** [MycoBank # 834857] – Holotype: PUERTO RICO. Mun. Las Piedras, Barrio El Río, at summit of Pico El Toro, El Yunque National Forest; 18°16′20″N, 65°49′44″W; 1048 m; 28 Dec 2015, *Mercado-Díaz 2385* (F barcode C0172453F; isotype: UPR).

Species is illustrated in Fig. 5.

Diagnosis. – Differing from *Sticta sublimbata* (J.Steiner) Swinscow & Krog in the suborbicular lobes with black marginal cilia and the marginal and laminal corymbose isidia that erode into sorediiform propagules.

Description. – Primary photobiont cyanobacterial (*Nostoc*). Basal stipe absent. Thallus irregular in outline, up to 10 cm diam., moderately branched, with 6–10 branches per 5 cm radius, branching pleurotomous to polytomous; lobes suborbicular, horizontal to ascending, adjacent to imbricate, involute, with rounded, plane to undulate apices; margins entire to sinuose and eroding, not thickened; lobe internodes 3–6 mm long, 2–5(–6) mm broad; thallus resistant, coriaceous. Upper surface smooth, grey when fresh and grey to dark brown in herbarium, moderately glossy; surface glabrous, without papillae, pruina or maculae. Cilia sparse, simple, hyaline when young and dark brown to black when old, to 0.5 mm, more evident in younger lobes. Apothecia not observed. Isidia abundant, eroding and becoming sorediiform, both marginal and laminal, aggregated and continuous along margins, branched, corymbose, vertically oriented, to 1.5 mm long and 0.4–1.3 mm broad, darker than thallus (especially near tips), glossy, rounded, granular to cylindrical, basal stalk cylindrical. Lower surface weakly scrobiculate-rugose, grey to brown, becoming darker in older portions of thallus; primary tomentum dense, sparse towards margins, thin throughout, becoming absent in old portions of the thallus, arachnoid, soft, white. Rhizines abundant, thallus centered to dispersed, dark brown to black with white tips, barbulate, to 2 mm. Cyphellae abundant, 40–60 per cm^2 towards the thallus center and 61–100 per cm^2 towards the margin, dispersed, rounded, urceolate with wide pore to cupuliform, prominent, at or above level of primary tomentum; margin elevated and involute to erect, cream-colored to brown, with tomentum near base; pore 0.3–1.5 mm diam.; basal membrane smooth, cream-colored, K+ yellow–orange, C–, KC–, P–. Medulla compact, white to cream-colored, K+ yellow–orange, C–, KC–, P–. Tainorum unknown (major). No pycnidia or cephalodia observed.

Upper cortex paraplectenchymatous, 35–50 μm thick, with two differentiated layers, consisting of 4–5 cell layers with cells 7–20 μm diam., their walls 2–3.5 μm thick and their lumina rounded to isodiametric, 4–18 μm diam. Photobiont layer 85–125 μm thick, its cells 5–12 μm diam. Medulla 100–200 μm thick, its hyphae 2.5–5 μm broad, without crystals. Lower cortex paraplectenchymatous, 25–45 μm thick, with 2–3 cell layers; cells 4–20 μm diam., their walls 2.5–5 μm thick. Hairs of lower primary tomentum 25–75 μm long, dispersed, branched, apically moniliform, septate with free apices. Cyphellae internal pore cavity 100–300 μm deep; basal membrane cell papillae absent.

Distribution and ecology. – *Sticta corymbosa* is an epiphytic species known only from the summit of Pico El Toro in El Yunque National Forest. Highly humid and open to partly shaded environments are therefore the assumed preferred habitat for this species. Because collecting activities in other mountain summits in this forest have failed to detect it, we suspect this is the only locality where this species is to be found. If true, *S. corymbosa* would be the species with the smallest geographical range in the island.

Etymology. – This name alludes to the shape (i.e., corymbose) of the isidia that are abundant along the lobe margins of this species.

Remarks. – *Sticta corymbosa* is a morphologically distinct species within the *S. limbata* (Sm.) Ach. morphodeme (sensu Moncada & al., 2013c). Although it resembles *S. sublimbata* in many aspects, the presence of tightly packed sorediiform and corymbose isidia both along the margins and in the surface, as well as the presence of black marginal cilia makes it easy to distinguish from that species. It also has very distinctive barbulate rhizines and a thin, arachnoid primary

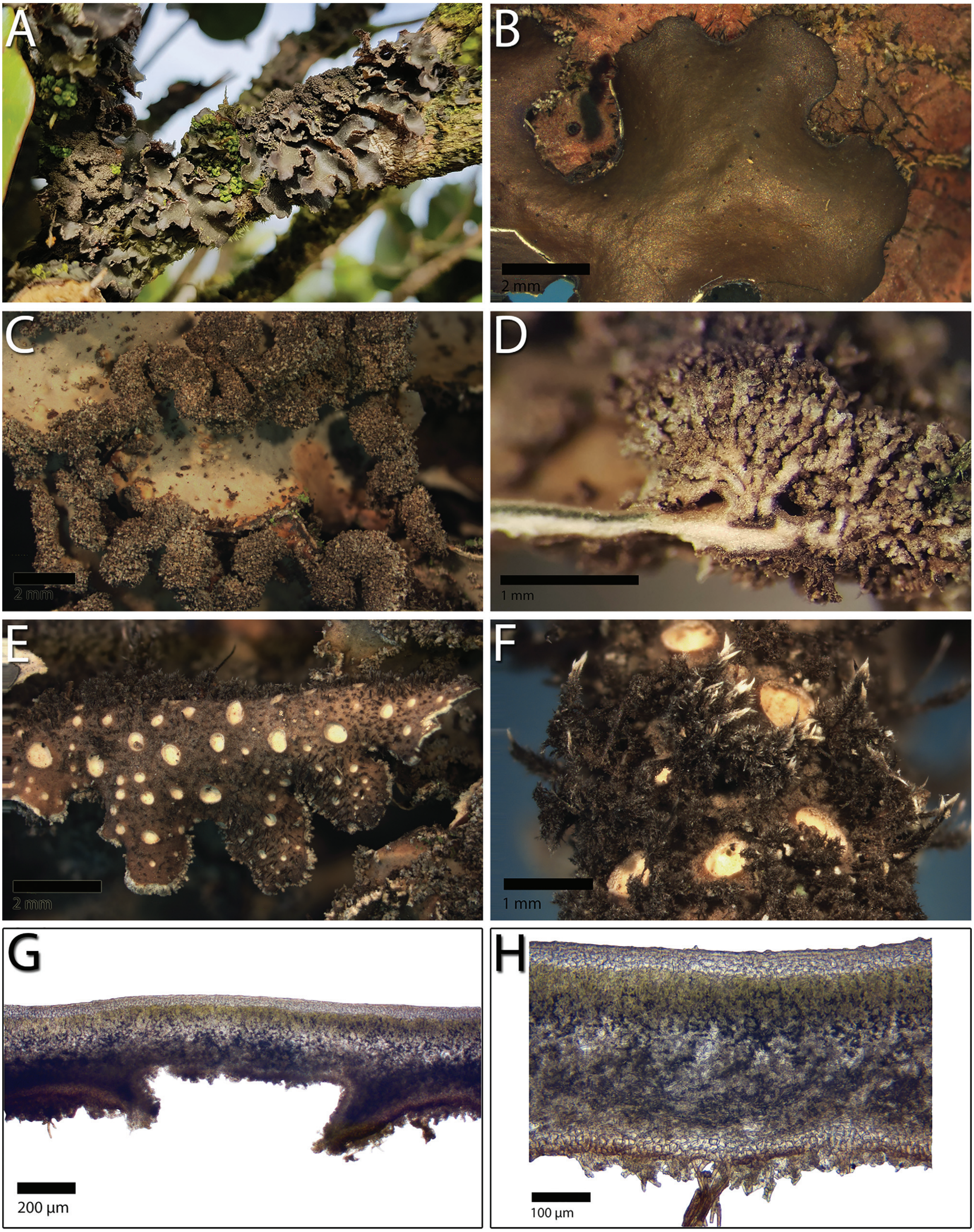

Fig. 5. *Sticta corymbosa* Merc.-Díaz & Moncada. **A**, Thallus in the field; **B**, Detail of a young lobe with black marginal cilia; **C**, Tightly packed clusters of marginal corymbose sorediiform isidia; **D**, Section of corymbose isidia; **E**, Lower surface with short arachnoid tomentum, rounded cyphellae and rhizines; **F**, Detail of barbulate rhizines; **G**, Section of cyphellae; **H**, Section through thallus. Photographs by J.A. Mercado-Díaz.

tomentum. Within Puerto Rico, it is most closely related to *S. borinquensis*.

Because it thrives at a mountain summit, *S. corymbosa* was thought to have been most affected by Hurricane María in September 2017. Fortunately, several healthy individuals were observed during a recent survey in July 2018. Given the locality it was found, we believe that *S. corymbosa* is one of the most susceptible species to climate change in the island. This is because it has been proposed that climate change may reduce the habitat size of high elevation species (Dirnböck & al., 2011; Jennings & al., 2014). Because of its unique habitat preferences and apparently small population size, we suspect that *S. corymbosa* is perhaps the most threatened species of *Sticta* in Puerto Rico. Additional population-level studies will be required to further determine the degree of threat that this species might currently be facing.

Additional specimens examined. – PUERTO RICO. Mun. Las Piedras, Barrio El Río, El Yunque National Forest, at summit of Pico El Toro; 18°16′20″N, 65°49′44″W; 1048 m; 28 Dec 2015, *Mercado-Díaz 2378* (UPR). Refer to Appendix 2 for additional specimens revised.

Sticta densiphyllidiata Merc.-Díaz & Lücking, **sp. nov.** [MycoBank # 834859] – Holotype: PUERTO RICO: Mun. Río Grande, Barrio Mameyes II, along Mt. Britton Trail near Mt Britton Tower, El Yunque National Forest; 18°18′05″N, 65°47′34″W; 909 m; 4 Oct 2011, *Lücking & Mercado-Díaz 33871* (F barcode C0172458F; isotype: UPR).

Species is illustrated in Fig. 6.

Diagnosis. – Differing from *Sticta beauvoisii* in the suborbicular lobes, shorter tomentum, presence of phyllidia and frequent reddish tinge of thalli in herbarium.

Description. – Primary photobiont cyanobacterial (*Nostoc*). Basal stipe absent. Thallus orbicular to irregular in outline, up to 20 cm diam., moderately branched, with 4–6 branches per 5 cm radius, branching polytomous; lobes suborbicular, horizontal, imbricate, involute to canaliculate, with rounded, plane to weakly revolute apices; margins entire, not thickened; lobe internodes 3–8 mm long, (2–)3.5–7(–11) mm broad; thallus resistant, coriaceous. Upper surface smooth, grey to dark olive-grey when fresh and grey to light brown, occasionally turning reddish in herbarium, opaque; surface glabrous, without papillae, pruina, maculae or cilia. Apothecia not observed. Phyllidia abundant, marginal (only laminal when injured), dispersed but occasionally clustered and imbricated, branched, coralloid to palmate, with oblique to vertical orientation, to 0.8 mm long and 0.1–0.8 mm broad, darker than thallus, slightly glossy, flattened, cylindrical to spathulate, basal stalk subcylindrical. Lobules sparse, marginal, dispersed, unbranched, horizontal, to 3 mm long, 1–3 mm broad, usually associated with injured areas. Gall-like structures protruding from margins frequent, dispersed, unbranched, irregularly oriented, and without photobiont cells (type material only). Lower surface smooth to weakly rugose, cream-colored (fresh) becoming light brown to reddish in herbarium; primary tomentum thin and dense throughout, but becoming naked in old portions of the thallus, pubescent to hirsute, soft, tan to brown, hairs occasionally whitish toward apices. Rhizines sparse, toward thallus center, penicillated. Cyphellae abundant, 41–60 per cm^2 towards the thallus center and 100–200 per cm^2 towards the margin, dispersed, rounded, urceolate with wide pore, prominent, margin at or above level of primary tomentum, elevated and involute, cream-colored, without tomentum; pore 0.4–1.8 mm diam.; basal membrane pruinose, cream-colored, K– or K+ weak pink, C–, KC–, P–. Medulla compact, white to cream-colored, K– or K+ weak pink, C–, KC–, P–. Riparia unknown (major). No pycnidia or cephalodia observed.

Upper cortex paraplectenchymatous, 32–50 µm thick, with two differentiated layers, the upper layer darkened, consisting of 4–5 cell layers with cells 5–15 µm diam., their walls 1.2–2.5 µm thick and their lumina rounded to isodiametric, 3.75–12.5 µm diam. Photobiont layer 35–75 µm thick, its cells 10–15 µm diam., upper margin in line with cortex. Medulla 75–130 µm thick, its hyphae 2–3 µm broad, without crystals. Lower cortex paraplectenchymatous, 20–30 µm thick, with 2–3 cell layers; cells 5–15 µm diam., their walls 2–3.5 µm thick. Hairs of lower primary tomentum 75–250 µm long, in fascicles of 6–12 hyphae, unbranched, cylindrical, septate with free or intertwined apices. Cyphellae internal pore cavity 50–150 µm deep; basal membrane cell papillae absent.

Distribution and ecology. – *Sticta densiphyllidiata* is one of the most commonly encountered species in well-preserved rainforests to the east of the island, particularly in El Yunque National Forest. Highly humid and shaded environments seem to be the preferred habitat for this species. It is most commonly found growing on rocks but could also grow epiphytically.

Etymology. – This name refers to the high density of branched phyllidia that are usually found along the lobe margins of this species.

Remarks. – Within Puerto Rico, *Sticta densiphyllidiata* is most closely related to the morphologically similar *S. riparia*. It can be distinguished from that species by the generally larger lobes and lighter lower cortex color. Specimens of *S. densiphyllidiata* also tend to turn reddish when in herbarium. Material belonging to this species was identified by Harris (1989) as "*S. trichographis*", a name attributed to Fée and not validly published in Hue (1901), referring to Husnot's specimen n. 437 collected in Guadeloupe (Nylander, 1869). Hue regarded this specimen conspecific with *S. weigelii* but noted that that material from Guadaloupe was saxicolous and had a reddish tinge in herbarium, which agrees with *S. densiphylllidiata*. Although this hints that *S. densiphyllidiata* might be more widely distributed in the Lesser Antilles, additional collecting efforts and molecular work will be needed to confirm its presence in those islands. On the other hand, several individuals of *S. densiphyllidiata* were encountered during collecting efforts in El Yunque after Hurricane María hit Puerto Rico in September, 2017. Thalli from these individuals had white spots and necrotic areas, which suggests

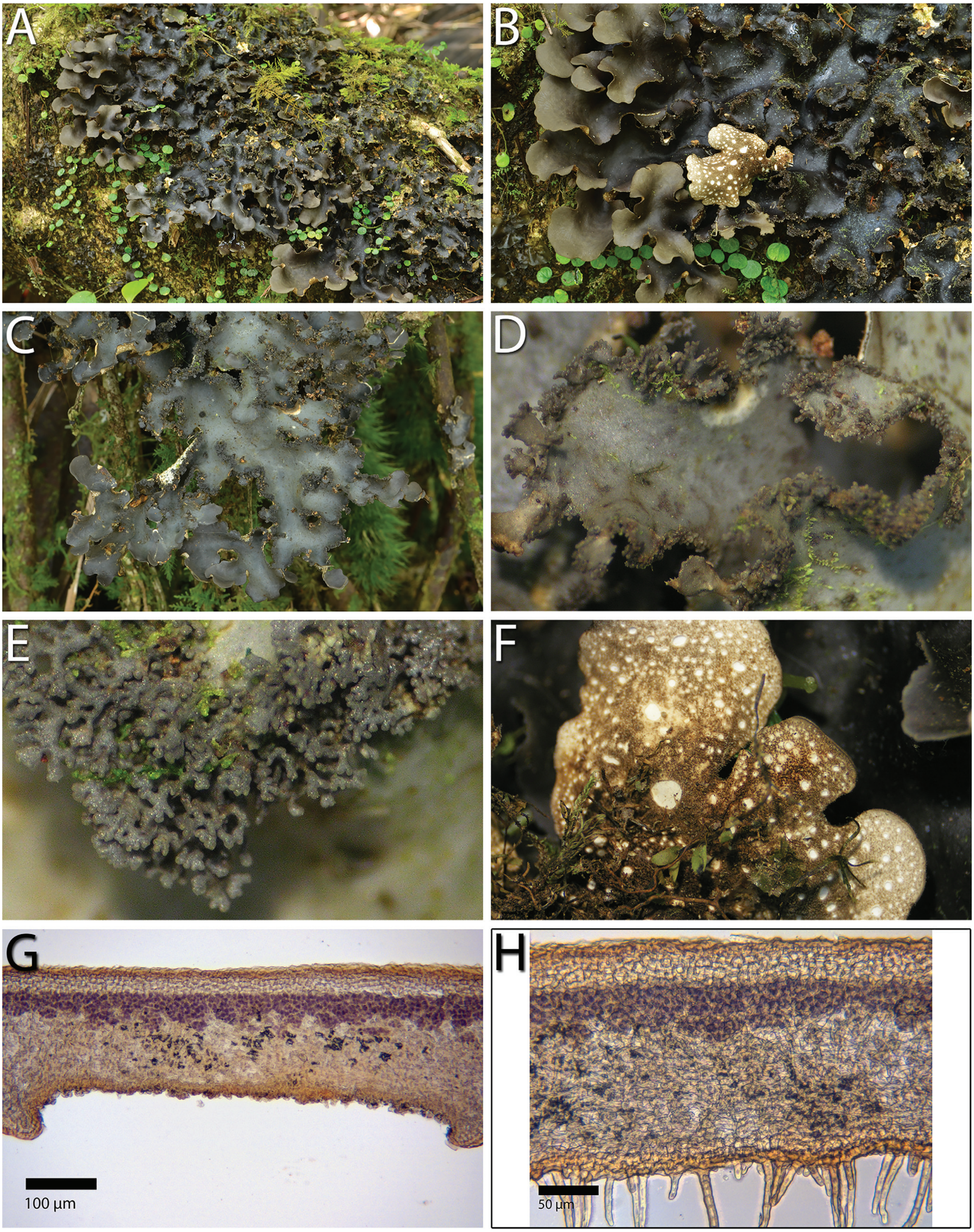

Fig. 6. *Sticta densiphyllidiata* Merc.-Díaz & Lücking. **A**, Thallus in the field; **B**, Close-up of thallus in the field showing upper and lower surface; **C**, Upper surface of branched lobes; **D**, Detail of lobes with marginal phyllidia; **E**, Detail branched coralloid to palmate phyllidia; **F**, Detail of lower surface with short brown tomentum and cyphellae; **G**, Section of cyphellae; **H**, Section through thallus. Photographs by R. Lücking (A–F) and J.A. Mercado-Díaz (G–H).

that this species is susceptible to increased solar radiation due to reduced canopy foliage.

Additional specimens examined. – PUERTO RICO. Mun. Humacao, El Yunque National Forest, Luquillo Experimental Forest, on moist rocky slopes near the base of a waterfall; Jul 1969, *Rundel s.n.* (US). Mun. Luquillo, El Yunque National Forest, near G. González (USFS) "Britton Palm" plot; 18° 18′16″N, 65°47′43″W; 917 m; 27 Sep 2011, *Mercado-Díaz 958* (UPR). Mun. Naguabo, El Yunque National Forest, Sierra de Naguabo, Barrio de Maizales, on rock in ravine; 8 Mar 1914; 600 m; *Britton & Cowell 2195* (NY). Mun. Río Grande, El Yunque National Forest, trail to LFDP, El Verde Field Station; 18°19′13″N, 65°48′56″W; 415 m; 12 Dec 2015, *Mercado-Díaz 2389* (UPR). Refer to Appendix 2 for additional specimens revised.

Sticta guilartensis Merc.-Díaz, **sp. nov.** [MycoBank # 834860] – Holotype: PUERTO RICO. Mun. Adjuntas, Barrio Guilarte, Bosque Estatal Guilarte, along trail to Pico Guilarte; 18°08′37″N, 66°46′08″W; 1100 m; 30 Jul 2018, *Mercado-Díaz 3666* (F barcode C0172455F; isotype: UPR).

Species is illustrated in Fig. 7.

Diagnosis. – Differing from the cyanomorph of *Sticta lobarioides* Moncada & Coca in the glossy, gray to brown upper surface, absence of fasciculate cilia and the presence of marginal lobules.

Description. – Primary photobiont cyanobacterial (*Nostoc*). Basal stipe absent. Thalli irregular in outline, up to 10 cm diam. but frequently aggregating and forming patches >30 cm diam., densely branched, with more than 10 branches per 5 cm radius, branching pleurotomous to polytomous; lobes flabellate to suborbicular, adnate to horizontal, imbricate, involute to undulate, with rounded to undulate apices; margins irregular to crenate, not thickened; internodes 0.5–3 mm long, 1–3 mm broad; thallus fragile, papyraceous. Upper surface smooth but becoming somewhat faveolate with age, grey to brown, moderately glossy; surface glabrous, without papillae, pruina or cilia, although minute marginal hyaline projections of up to 0.05 mm are sometimes observed. Maculae abundant, white, reticulated. Apothecia not observed. Lobules abundant, marginal, sometimes appearing to emerge from the lower surface, dispersed, simple or branched, coralloid to palmate, imbricated, horizontal to oblique, to 1 mm long and 0.1–0.8 mm broad, darker than thallus, glossy, applanate to dorsiventral in section, spathulate to lobuliform, basal stalk applanate. Lower surface irregular, becoming scrobiculate to costillate near margins, white to cream-colored. Primary tomentum sparse, absent towards margin, thick, becoming thinner towards margin, hirsute to weakly spongy, soft, tan to brown. Secondary tomentum pubescent, white to cream-colored. Rhizines not observed. Cyphellae abundant, 21–40 per cm^2 towards the thallus center and 41–60 per cm^2 towards the margin, dispersed, irregular to angular, cupuliform to pseudocyphelloid, erumpent to prominent, at or below level of the primary tomentum; margin erect to elevated and weakly involute, white to cream-colored, without tomentum; pore 0.1–0.6 mm diam.; basal membrane smooth with pruinose appearance, white, K+ light yellow, C–, KC–, P–. Medulla lax, white, K+ light yellow, C–, KC–, P–. No substances detected by HPTLC. No pycnidia or cephalodia observed.

Upper cortex paraplectenchymatous, 12.5–22 μm thick, homogeneous, sometimes with darkened outer cortex, consisting of (1–)2–3(–4) cell layers with cells 5–17 μm diam., their walls 1–2.5 μm thick and their lumina rounded to isodiametric, 4–15.5 μm diam. Photobiont layer 25–90 μm thick, its cells 12–20 μm diam. Medulla 15–112 μm thick, its hyphae 2.5–3.5 μm broad, without crystals. Lower cortex paraplectenchymatous, 20–30 μm thick, with 2–3 cell layers; cells 6–20 μm diam., their walls 1.5–3 μm thick. Hairs of lower primary tomentum 100–300 μm long, dispersed, unbranched, cylindrical, septate with intertwined apices. Hairs of lower secondary tomentum 12–50 μm long, dispersed, unbranched, cylindrical, septate with free apices. Cyphellae internal pore cavity 80–150 μm deep; basal membrane cell papillae absent.

Distribution and ecology. – *Sticta guilartensis* is known from a single locality in Bosque Estatal de Guilarte in the central-west region of the island. It has been found growing on rocks as well as in roots and trunks of several trees including *Prestoea acuminata* var. *montana*. It seems to prefer shaded, very humid conditions and is commonly found growing among bryophytes.

Etymology. – This species is named after the forest where this species was found: Bosque Estatal de Guilarte.

Remarks. – *Sticta guilartensis* is morphologically similar to the cyanomorph of species that form photosymbiodemes, particularly to *S. lobarioides*, a recently described species from Colombia that is found in well-preserved forests (Moncada & al., 2013a). For *S. lobarioides*, it is the chloromorph counterpart that is most commonly found in those forests, suggesting that pristine ecological conditions are most likely a pre-requisite for the chloromorphs to occur. Because Puerto Rico underwent substantial land degradation at the beginning of the 20th century (Grau & al., 2003), the likelihood for a chloromorph of *S. guilartensis* to be found is low, but it may have been present before that period. Within Puerto Rico, it is most closely related to the morphologically dissimilar *S.* aff. *guilartensis*, an undescribed species from the western mountains of the island.

Even though lichen collecting efforts have occurred in the past, to our knowledge, no species of *Sticta* have been collected in Bosque Estatal de Guilarte previous to our efforts. This species may have escaped detection because of its broad resemblance to other genera of cyanolichens like *Leptogium* (Ach.) Gray, with whom it shares the foliose growth habit, dark color when wet, and occurrence in humid microhabitats. On the other hand, during our examination of the *S. guilartensis* material, we noted the frequent presence of clusters of free living *Nostoc* on the upper thallus surface. An interesting avenue of research would be to determine if the presence of these

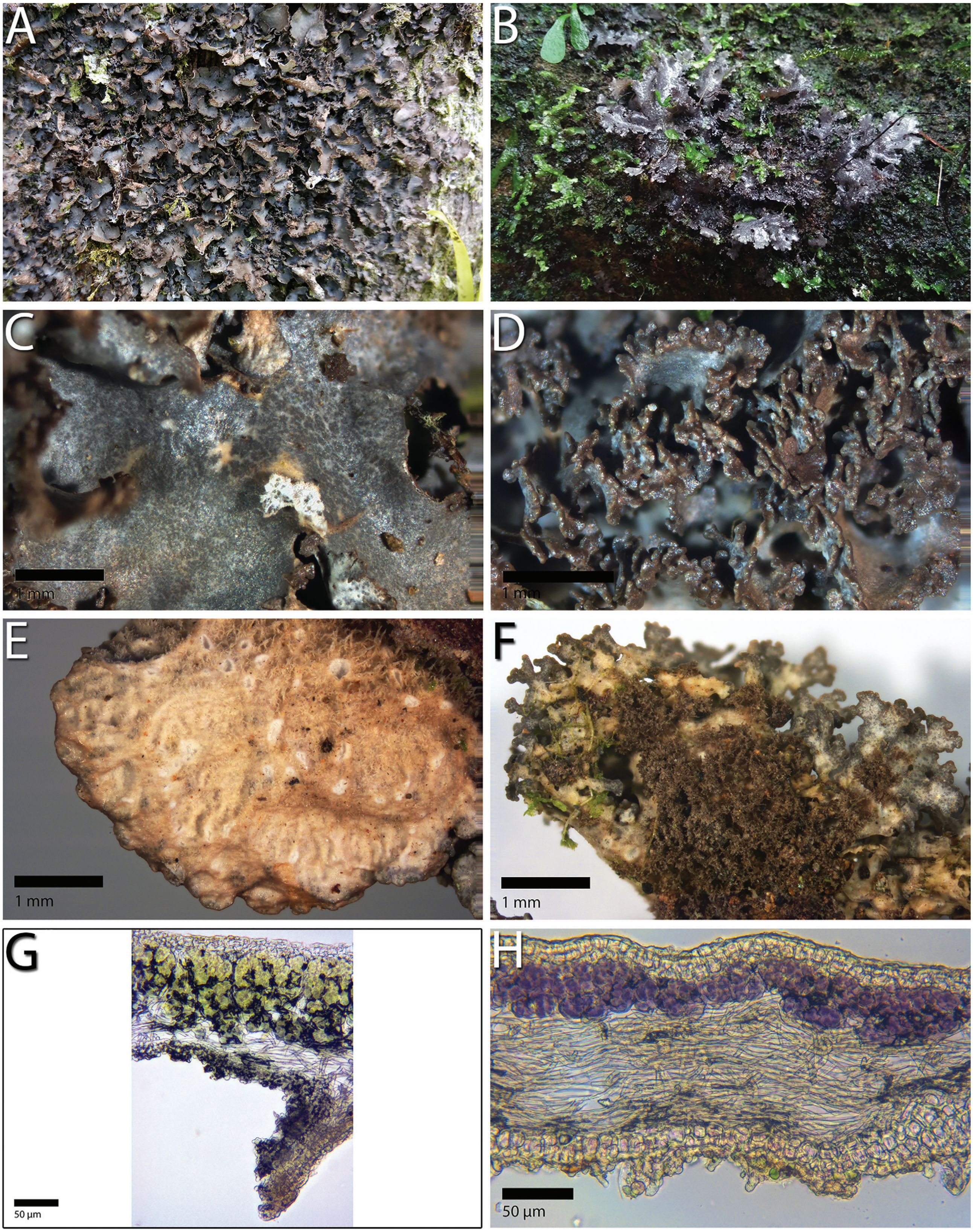

Fig. 7. *Sticta guilartensis* Merc.-Díaz. **A**, View of dry thallus in the field; **B**, View of moistened thallus in the field; **C**, Reticulated maculae on thallus upper surface; **D**, Detail of marginal lobules; **E**, Rugose lower surface near lobe margins and cyphellae; **F**, Lower primary tomentum and underside of marginal lobules; **G**, Section through cyphellae; **H**, Section through thallus. Photographs by J.A. Mercado-Díaz.

clusters is due to random growth of foreign *Nostoc* on the surface or if it resulted from the growth of previously lichenized *Nostoc* that escaped lichenization.

Additional specimens examined. – PUERTO RICO: Mun. Adjuntas, Bosque Estatal Guilarte, Along trail to Pico Guilarte; 18°08′24″N, 66°46′12″W; 1100 m; 27 Dec 2016, *Mercado-Díaz 2426* (UPR). Refer to Appendix 2 for additional specimens revised.

Sticta harrisii Merc.-Díaz, Moncada & Lücking, **sp. nov.** [MycoBank # 834861] – Holotype: PUERTO RICO. Mun. Naguabo, Barrio Río Blanco, at the beginning of Trailwinds trail, El Yunque National Forest; 18°16′48″N, 65°47′24″W; 667 m; 26 Jul 2016, *Mercado-Díaz 2913* (F barcode C0172454F; isotype: UPR).

Species is illustrated in Fig. 8.

Diagnosis. – Differing from *Sticta tomentosa* in the absence of a basal stipe and the presence of a thick tomentum and branched phyllidia.

Description. – Primary photobiont cyanobacterial (*Nostoc*). Basal stipe absent. Thallus irregular in outline, sometimes rosette-shaped, up to 15 cm diam., densely branched, with 6–10 branches per 5 cm radius, branching pleurotomous to polytomous; lobes flabellate to lingulate, horizontal to ascending, adjacent to imbricate, involute becoming undulate, with irregular, plane or weakly revolute apices, margins crenate to dissected, not thickened; lobe internodes 0.2–4 mm long, (1–)1.5–4(–5) mm broad; thallus resistant, subcoriaceous. Upper surface smooth, brownish grey to olive-grey both when fresh and in the herbarium, marginal line color same as lobe surface, moderately glossy; surface glabrous, without papillae, pruina, and maculae; Cilia marginal, abundant, simple and tapering, white, to 0.5 mm. Apothecia sparse to abundant, submarginal to marginal, dispersed to subaggregated, subpedicillated, base invagination pronounced, 0.4–1.5 mm diam., disc color dirty orange to brown and glossy when fresh to dark brown and opaque in herbarium, margin entire to minutely verrucose, rarely ciliate (mostly when young), cream-colored. Phyllidia abundant, marginal, dispersed, branched, simple to coralloid and becoming isidioid toward apices, irregularly oriented, up to 2 mm long and 0.1–2 mm broad, same color as thallus but becoming darker with age, slightly glossy, weakly flattened to dorsiventral in section, subcylindrical to squamiform, basal stalk flattened with cyphellae initials. Lower surface smooth to sinuose, pale white to cream-colored; primary tomentum dense, sparse or absent towards margin, thick, becoming thinner toward margins, spongy, soft, tan to dark brown, becoming yellowish when old, hairs occasionally whitish toward apices; secondary tomentum pubescent, pale white to cream-colored. Rhizines absent. Cyphellae abundant, 21–40 per cm^2 towards the thallus center and 41–60 per cm^2 towards the margin, dispersed, rounded to irregular (especially near margins), urceolate with wide pore to cupuliform, prominent, margin remaining below the level of the primary tomentum, elevated and involute to erect, pale white to cream-colored, without tomentum; pore 0.2–1.5 mm diam.; basal membrane smooth to weakly pruinose, white, K+ yellow to dirty orange, C–, KC–, P–. Lower cortex K+ yellow, C–, KC+ yellow-orange, P–. Medulla compact, white, K+ yellow to dirty orange, C–, KC–, P–. Harrisii unknown (major). Pycnidia and cephalodia not seen.

Upper cortex paraplectenchymatous, 20–50 µm thick, homogeneous, consisting of 2–3(–4) cell layers with cells 5–23 µm diam., their walls 2–6 µm thick and their lumina rounded to isodiametric, 3.5–22 µm diam. Photobiont layer 50–75 µm thick, its cells 12.5–17.5 µm diam. Medulla 50–125 µm thick, its hyphae 2.5–3.5 µm broad, without crystals, becoming moniliform in apices. Lower cortex paraplectenchymatous, 20–35 µm thick, with 1–2 cell layers; cells 10–22 µm diam., their walls 2–5 µm thick. Hairs of lower primary tomentum 150–1750 µm long, in fascicles of more than 12 hyphae, unbranched, cylindrical, septate with intertwined apices. Hairs of lower secondary tomentum 20–50 µm long, dispersed, unbranched, cylindrical, with free apices. Cyphellae internal pore cavity 75–350 µm deep; cells of basal membrane with numerous papillae. Apothecia biatorine, 300–800 µm high, with stipe; excipulum 70–150 µm broad, minutely papillose. Hymenium 80–120 µm high; epihymenium 2.5–5 µm high, dirty orange to dark brown, without gelatinous layer above. Ascospores 1–septate, 25–42 × 5–7.5 µm, fusiform, hyaline.

Distribution and ecology. – *Sticta harrisii* is restricted to high-elevation rain forests to the east of the island, specifically in El Yunque National Forest and Bosque Estatal de Carite. It is mostly epiphytic and has been found growing on individuals of *Heterotrichum cymosum* (Wendl.) Urban and *Cecropia schreberiana* var. *schreberiana*, as well as on vines, ferns and less frequently on rocks. It seems to prefer shaded environments with high humidity.

Etymology. – This species is named after lichenologist Richard C. Harris, who prepared the first formal taxonomic treatment of lichens for the island and the first key to species of *Sticta* in Puerto Rico.

Remarks. – *Sticta harrisii* has a somewhat variable morphology that is apparently determined by age and/or microhabitat. Under shaded and humid conditions, mature individuals of this species usually feature moderately sized thalli that spread more horizontally on the substrate (Fig. 8A). Other individuals, however, exhibit smaller, rosette-shaped thalli that have a higher density of imbricately arranged lobes (Fig. 8B). It is most similar to *S. tomentosa* with respect to its greyish color, smooth surface, marginal cilia, rather light-colored tomentum and presence of apothecia, but its easily separated from that species by the presence of phyllidia. It is also remotely reminiscent of species within the *S. weigelii* morphodeme, most similar perhaps to "*S. pseudobeauvoisii* ined." (see Moncada, 2012), with which it shares the presence of applanate, dorsiventral phyllidia, but from which differs in the distinctly lighter tomentum towards the margins and the highly dissected lobes. Within Puerto Rico, it is most closely related to *S.* aff. *harrisii*, a

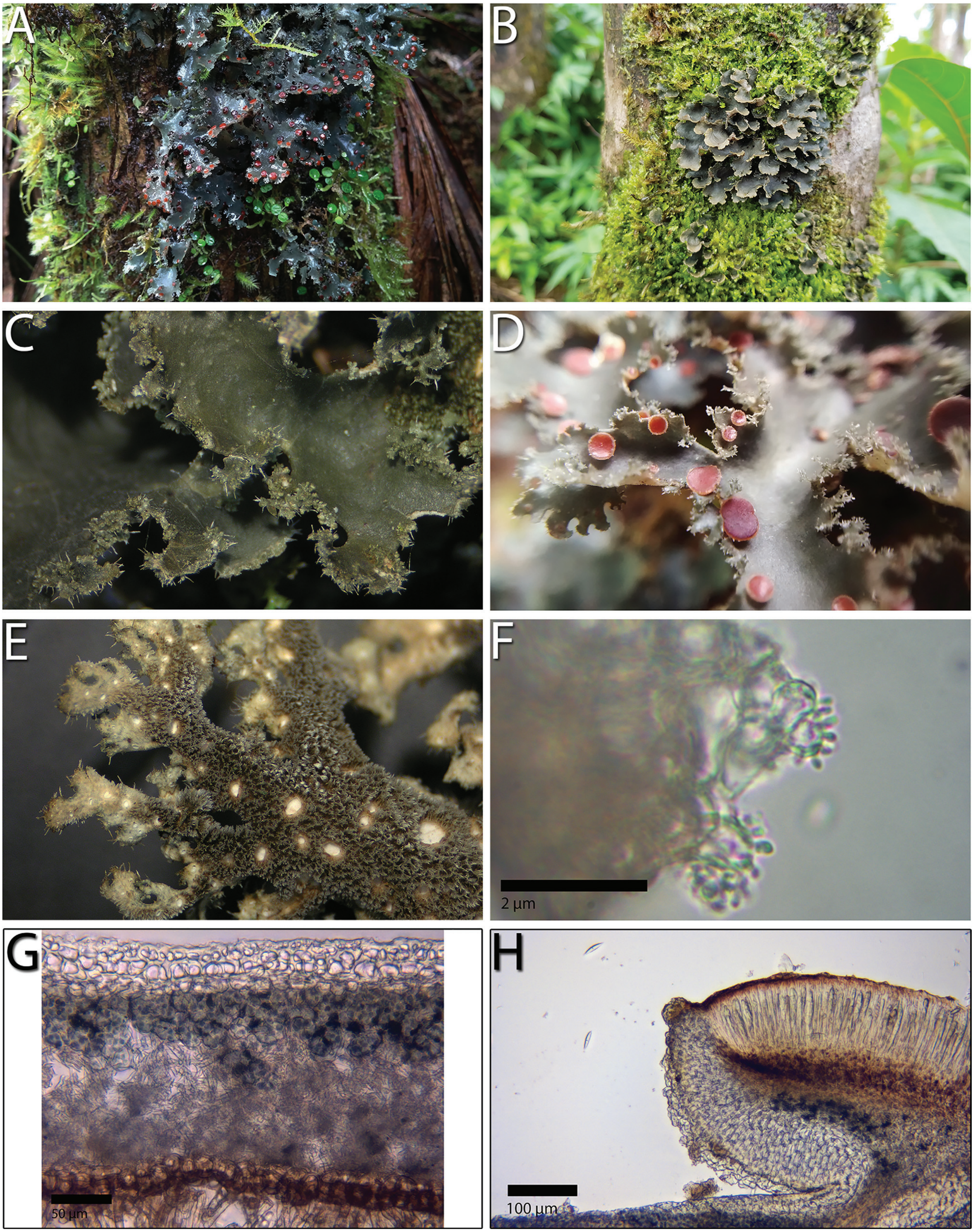

Fig. 8. *Sticta harrisii* Merc.-Díaz, Moncada & Lücking. **A**, View of mature thallus in the field; **B**, View of rosette-shaped thallus in the field; **C**, Lobes with white marginal cilia; **D**, Lobes with submarginal and marginal apothecia and scattered marginal phyllidia; **E**, Lower surface with brown-gray primary tomentum and cyphellae; **F**, Detail of cyphellae basal membrane cells with numerous papillae; **G**, Section through thallus; **H**, Section of apothecia. Photographs by J.A. Mercado-Díaz (A, B, D, F–H) and R. Lücking (C, E).

new, but still undescribed species from El Yunque National Forest.

Material in NY corresponding to *Sticta harrisii* was identified by Harris (1989) as "*S. circumroda*", a name attributed to Fée that was not validly published in Hue (1901). According to Hue (1901), material originally identified by Fée as "*S. circumroda*" was similar to a specimen collected by Husnot in Guadeloupe (i.e., *Husnot #436*; Nylander, 1869) that corresponded to *S. weigelii* f. *schizophylliza* (Nyl.) Hue. Curiously, high-resolution images showed that this material is more similar to *S. borinquensis*, a new species from Puerto Rico described here (see above). The characteristic marginal cilia and paler lower cortex and tomentum toward margins that characterize *S. harrisii* are in fact absent in this material. Specimens referred to as "*Sticta schizophylliza* ined." in Moncada & al. (2013c; i.e., *Lücking 33894*, *Lücking 33905*, *Lücking 33868*), on the other hand, correspond to this species.

Several individuals of *Sticta harrisii* were encountered by the first author during recent collecting efforts in El Yunque National Forest after Hurricane María hit Puerto Rico in September 2017. Different to other species discussed here (i.e., *S. densiphyllidiata* and *S. tainorum*), thalli from these individuals did not have necrotic areas and showed no signs of browning, which would be indicative of damage due to increase solar radiation after defoliation caused by the hurricane. On the contrary, *S. harrisii* individuals were more conspicuous and appeared to be abundant than before the hurricane. This suggests that *S. harrisii* might be better at taking advantage of newly available resources (i.e., opened substrate space) after this type of disturbances when compared to other sympatric species.

Additional specimens examined. – PUERTO RICO. Mun. Humacao, El Yunque National Forest, recreation area, trail up to Mt. Britton; 850–950 m; 9 Jun 1988, *Harris 22497* (NY). Mun. Luquillo, El Yunque National Forest, near G. González (USFS) "Britton Palm" plot; 18°18′16″N, 65°47′43″W; 917 m; 27 Sep 2011, *Mercado-Díaz 960* (UPR). Mun. Río Grande, El Yunque National Forest, along trail to El Toro Peak from El Verde; 18°16′18″N, 65°49′53″W; 1006 m; 28 Dec 2015, *Mercado-Díaz 2375* (UPR). Mun. San Lorenzo, Bosque Estatal de Carite, along road that access TV network's antennas; 18°06′42″N, 66°03′00″W; 865 m; 29 Jan 2015, *Mercado-Díaz 2282* (UPR). Refer to Appendix 2 for additional specimens revised.

Sticta parvilobata Merc.-Díaz, **sp. nov.** [MycoBank # 834862] – Holotype: PUERTO RICO. Mun. Adjuntas, Barrio Guilarte, Bosque Estatal de Guilarte, along trail to Pico Guilarte; 18°08′37″N, 66°46′08″W; 1100 m; 30 Jul 2018, *Mercado-Díaz 3668* (F barcode C0172456F; isotype: UPR).

Species is illustrated in Fig. 9.

Diagnosis. – Differing from *Sticta ciliata* in the smaller lobes, presence of microfibrils in upper surface, branched isidia that are rarely strongly arbuscular, and frequent occurrence of maculae in central portion of young lobes.

Description. – Primary photobiont cyanobacterial (*Nostoc*). Thallus flabellate when young, eventually orbicular in outline, up to 2 cm diam., sparsely branched, with 0–2 branches per 5 cm radius, branching pleurotomous to polytomous, occasionally in clusters of overlapping lobes; lobes suborbicular, ascending, interspaced to imbricate, plane to involute, with plane to weakly revolute apices, margins entire to weakly crenate, not thickened; lobe internodes 0.05–1 mm long, 4–12 mm broad; thallus fragile, papyraceous. Upper surface smooth to scrobiculate-faveolated when old and pitted with scars of broken isidia, grey to brownish grey, both when fresh and in herbarium, marginal line color same as lobe surface, opaque; surface glabrous but with pubescent appearance under high magnification due to small, whitish microfibrils; without papillae or pruina. Cilia scarce, but sometimes abundant in young lobes, nearly absent with age, simple, white or pale, to 0.5 mm. Minute maculae frequent in young lobes, reticulated, white, more evident toward central portions of thallus. Apothecia not observed. Isidia abundant, laminal extending towards margins, dispersed to subaggregated, branched, simple to coralloid, vertically oriented, up to 0.5 mm long and 0.02–0.06 mm broad, same color as thallus, opaque to weakly glossy, rounded in section, granular to globular, basal stalk cylindrical. Lobules rare, marginal, dispersed, unbranched, horizontal, to 1 mm and 0.6–1.4 mm broad, same color as thallus, opaque, dorsiventral in section, lobuliform, basal stalk cylindrical. Lower surface costillate to scrobiculate, cream-colored; primary tomentum sparse but sometimes dense in points of attachment to substrate, becoming sparser towards margins, thin throughout, hirsute to fasciculated, soft, white to cream-colored; secondary tomentum pubescent, pale white to cream-colored. Rhizines absent. Cyphellae sparse, 1–20 per cm^2 towards the thallus center and 21–40 per cm^2 towards the margin, dispersed, irregular to angular, cupuliform to pseudocyphelloid, prominent to suprasessile, levelled or above the level of the primary tomentum, margin erect to weakly revolute, white, tomentum occasionally present; pore 0.1–1.8 mm diam.; basal membrane smooth, white, K+ yellow to weak orange, C–, KC–, P–. Medulla lax, white, K+ yellow to weak orange, C–, KC–, P–. No substances detected by HPTLC. Pycnidia and cephalodia not seen.

Upper cortex paraplectenchymatous, 10–15 µm thick, homogeneous, consisting of 1(2) cell layers with cells 7–15 µm diam., their walls 1.5–2.5 µm thick and their lumina rounded to isodiametric, 5–14 µm diam. Photobiont layer 25–70 µm thick, its cells 10–20 µm diam. Medulla 25–65 µm thick, its hyphae 2–3 µm broad, without crystals. Lower cortex paraplectenchymatous, 10–14 µm thick, with 1(2) cell layers; cells 8–17 µm diam., their walls 1.5–2.5 µm thick. Hairs of lower primary tomentum 100–400 µm long, in fascicles of more than 6–12 hyphae, mostly unbranched, septate but septa less evident in older hairs, with free to intertwined, cylindrical apices. Hairs of lower secondary tomentum 12–25 µm long, dispersed, occasionally branching, septate, moniliform, with free apices. Cyphellae internal pore cavity

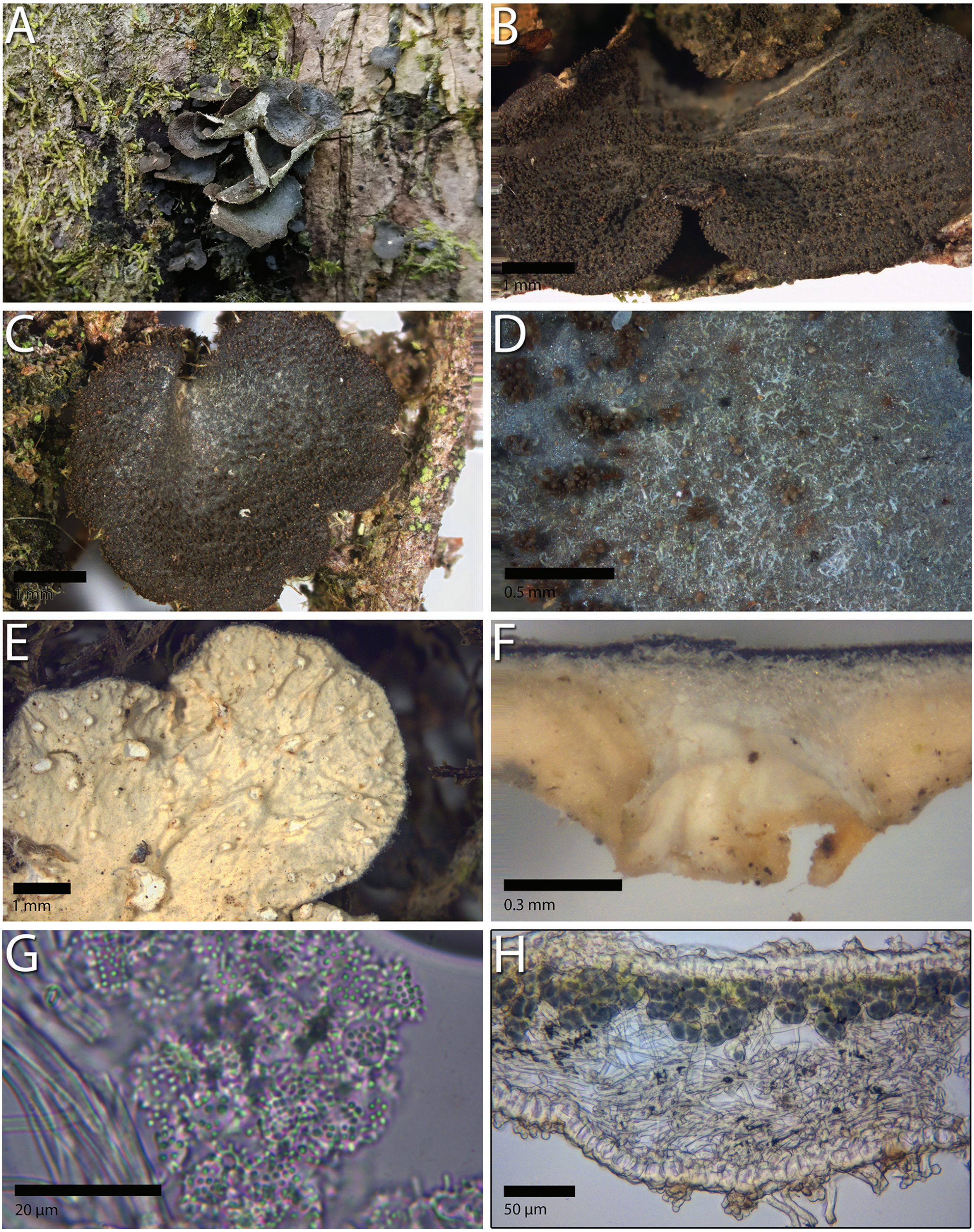

Fig. 9. *Sticta parvilobata* Merc.-Díaz. **A**, Thallus in the field; **B**, Lobes upper surface with laminal isidia; **C**, Young lobe with maculae in the center; **D**, Microfibrils in the upper surface; **E**, Lower surface with cyphellae; **F**, Section of cyphellae; **G**, Detail of cyphellae basal membrane cell papillae; **H**, Section through thallus. Photographs by J.A. Mercado-Díaz.

50–400 μm deep; cells of basal membrane with numerous papillae.

Distribution and ecology. – *Sticta parvilobata* has only been found in high-elevation forests of the Bosque Estatal de Toro Negro and Bosque Estatal de Guilarte, two natural protected areas in the central-west region of the Cordillera Central. It is therefore considered to have a western distribution within the island. It is epiphytic and is commonly found growing among bryophytes.

Etymology. – This name refers to the generally smaller lobes (compared to *S. ciliata*) of mature individuals of this species.

Remarks. – *Sticta parvilobata* is closely related to *S. ciliata*, a lineage characterized by thalli formed by single, suborbicular to palmate lobes that frequently overlap each other, simple laminal isidia, papillose cyphellae basal membrane cells and marginal white cilia (Magain & Sérusiaux, 2015). It is very similar to *S.* aff. *parvilobata* from Puerto Rico, but distinguishable from it by its generally smaller-sized mature lobes, shorter branched isidia that are usually more evenly distributed in the surface, occasional presence of microfibrils in the upper surface and minutely maculate young lobes. Also, mature lobe margins in *S.* aff. *parvilobata* are usually more sharply revolute than in *S. parvilobata*. Harris (1989) referred to both *S. parvilobata* and *S.* aff. *parvilobata* as *Sticta* sp. 22678. Both lineages form a monophyletic Puerto Rican clade with unresolved affinities to *S. ciliata*. While more work will be needed to clarify phylogenetic relationships, results from phylogenetic and morphoanatomical analyses, in combination with molecular species delimitation approaches and geographical patterns convinced us of treating *S. parvilobata* as a separate species. Conversely, while *S.* aff. *parvilobata* exhibited some degree of genetic structure within the island, genetic signal was not sufficiently robust to resolve relationships between subclades. Additionally, this lineage is nearly morphologically indistinguishable from *S. ciliata*, which made resolving boundaries within this clade more challenging.

Sticta parvilobata is distributed in the western region of the island; therefore, material that resembles this species but is collected closer to the east most likely belong to *S.* aff. *parvilobata*. Specimens collected to the west, however, would need to be carefully inspected for proper identification given that both species are sympatric in this region. Lastly, even though apothecia are known to occur in *S. ciliata* (Magain & Sérusiaux, 2015), these reproductive structures have not been observed in *S. parvilobata* and *S.* aff. *parvilobata*. More specimens will be needed to corroborate their presence in material from the island.

Additional specimens examined. – PUERTO RICO. Mun. Adjuntas, Barrio Guilarte, Bosque Estatal de Guilarte, along trail to Pico Guilarte; 18°08′24″N, 66°45′36″W; 927 m; 27 Dec 2016, *Mercado-Díaz 2432* (UPR). Mun. Orocovis, Barrío Bauta Abajo, Along El Bolo trail, Bosque Estatal de Toro Negro; 18°10′19″N, 66°29′07″W; 927 m; 22 Jan 2015, *Mercado-Díaz 2260* (UPR). Refer to Appendix 2 for additional specimens revised.

Sticta riparia Merc.-Díaz, **sp. nov.** [MycoBank # 834863] – Holotype: PUERTO RICO. Mun. Aibonito, Barrio Asomante, San Cristobal Canyon, on rock face by the river; 18°09′34″N, 65°18′05″W; 465 m; 31 Jul 2018, *Mercado-Díaz 3677* (F barcode C0172457F; isotype: UPR).

Species is illustrated in Fig. 10.

Diagnosis. – Differing from *Sticta densiphyllidiata* in the darker lower surface, smaller lobes, presence of pycnidia and occasionally branched primary tomentum hairs.

Description. – Primary photobiont cyanobacterial (*Nostoc*). Basal stipe absent. Thalli mostly orbicular in outline, up to 10 cm diam. but frequently aggregating and forming patches >50 cm diam., densely branched, with 6–10 branches per 5 cm radius, branching pleurotomous to polytomous; lobes suborbicular, adnate to horizontal, imbricate, undulate, with rounded, undulate to weakly revolute apices, margins entire, not thickened; lobe internodes 1–3 mm long, (1.5–) 2–4(–5.5) mm broad; thallus resistant, subcoriaceous. Upper surface smooth, grey to brown both when fresh and in herbarium, becoming darker brown towards lobes, especially in exposed conditions, marginal line color slightly darker to same as lobe surface, opaque to weakly glossy; surface glabrous, without papillae, pruina, maculae or cilia. Apothecia not observed. Phyllidia abundant, marginal, aggregated, branched, palmate and sometimes isidiate in appearance due to strong imbrication of phyllidia, oblique, up to 0.5 mm long and 0.1–0.5 mm broad, dark brown, glossy, flattened in section, spathulate, basal stalk applanate. Lower surface smooth to weakly scrobiculate toward margins, light greyish-brown to dark brown, becoming darker towards center; primary tomentum dense, absent towards margin, thin, becoming thinner towards margin, pubescent to hirsute, soft, brown. Rhizines sparse, dispersed or towards thallus center, simple becoming penicillate, whitish to cream-colored, up to 3 mm. Cyphellae abundant, 41–60 per cm^2 towards the thallus center and 101–200 per cm^2 towards the margin, dispersed, rounded to irregular, urceolate with wide pore, erumpent to prominent, at or above level of primary tomentum; margin levelled to elevated and involute, cream-colored to light brown, without tomentum; pore 0.1–0.8 mm diam.; basal membrane smooth, white, K+ weak yellow, C–, KC–, P–. Medulla compact, white, K+ weak yellow, C–, KC–, P–. Riparia unknown (major). Pycnidia erumpent, brown, protruding to the lower surface when mature (resembling a tubercle). Cephalodia not seen.

Upper cortex paraplectenchymatous, 25–40 μm thick, homogeneous, darkening towards outer cortex, consisting of (2–)3–4 cell layers with cells 5–15 μm diam., their walls 1.25–3 μm thick and their lumina rounded to isodiametric, 3.5–14 μm diam. Photobiont layer 40–75 μm thick, its cells 12–18 μm diam. Medulla 50–90 μm thick, its hyphae 2.5 μm broad, without crystals. Lower cortex paraplectenchymatous, 12.5–25 μm thick, with 1–2(–3) cell layers; cells 5–15 μm diam., their walls 1–2.5 μm thick. Hairs of lower primary tomentum 50–150 μm long, dispersed, occasionally branching, cylindrical, highly septate with free moniliform apices.

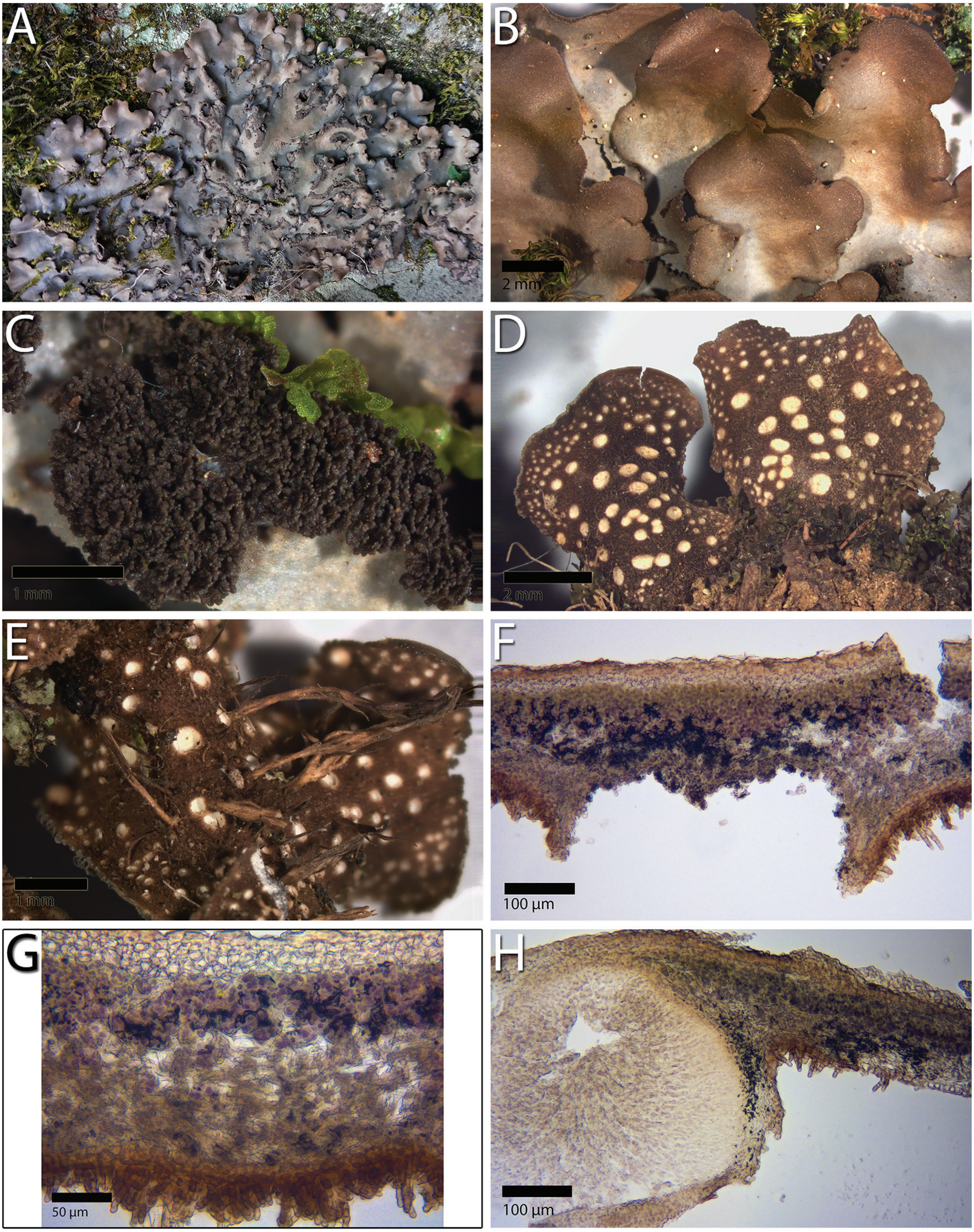

Fig. 10. *Sticta riparia* Merc.-Díaz. **A**, Thallus in the field; **B**, Close-up of upper surface and lobes configuration; **C**, Detail of marginal, agglutinated phyllidia; **D**, Lower surface with short brown tomentum and cyphellae; **E**, Detail of long, whitish to cream-colored penicillated rhizines; **F**, Section of cyphellae; **G**, Section through thallus; **H**, Section through thallus with internal pycnidia in initial stages of development. Photographs by J.A. Mercado-Díaz.

Cyphellae internal pore cavity 80–150 µm deep; cells of basal membrane without papillae.

Distribution and ecology. – *Sticta riparia* has been collected mostly along riverbanks or areas not far from rivers along the Cordillera Central, at elevations not higher than 800 m. It seems to prefer well-conserved areas, but it has also been collected in secondary forests in both semi-open and shaded conditions. Although this species has been found growing on tree branches, rocks seem to be its preferred substrate. *Sticta riparia* has been collected at 270 m (Tanamá river, near entrance to Radio Telescopio cave), which is lowest recorded elevation for any of the species that occur on the island.

Etymology. – The name alludes to the common occurrence of this species near rivers or riverbanks.

Remarks. – Together with *Sticta densiphyllidiata*, *S. riparia* is referred to in Harris (1989) as "*S. trichographis* Fée ined.". It is similar to that species in many respects, such as the presence of small, branched to palmate phyllidia along the margins and the very short tomentum which becomes absent towards lobe margins. However, *S. riparia* differs from *S. densiphyllidiata* by its lobes of smaller average size, presence of pycnidia and generally darker lower cortex. Based on our molecular data, *S. riparia* and *S. densiphylllidiata* are closely related to each other and also to *S. laciniosa* D.J.Galloway, a species with a green algal photobiont that apparently lacks a cyanomorph counterpart. It is worth noting that although specimen *Mercado-Díaz 3684* is well nested within the *Sticta riparia* clade and is considered representative of that species, this material exhibits a pale-beige lower cortex and lighter grey upper surface which is not typical for this species. Its longer branch length also suggests some degree of incipient divergence within the clade. More material and additional sequences from this variant will be needed to further clarify these issues.

Additional specimens examined. – PUERTO RICO: Mun. Aibonito, San Cristobal Canyon, on rock face by the river; 18°09′34″N, 65°18′05″W; 465 m; 31 Jul 2018, *Mercado-Díaz 3678* (UPR). Mun. Arecibo, Barrio Esperanza, Surroundings of Río Tanamá, near to entrance of the Radiotelescopio cave; 18°20′30″N, 66°45′19″W; 185 m; 13 Apr 2015, *Mercado-Díaz 2342* (UPR). Mun. Orocovis, Distr. Ponce: Cordillera Central, above Villalba, Doña Juana recreation area; 800–1000 m; 2 Jun 1988, *Harris 22034* (NY). Mun. Patillas, Carite State Forest, Charco Azul Recreation Area, in camping area by the river; 18°05′28″N, 66°02′04″W; 599 m; 15 Jul 2018, *Mercado-Díaz 3626* (UPR). Refer to Appendix 2 for additional specimens revised.

Sticta tainorum Merc.-Díaz, **sp. nov.** [MycoBank # 834864] – Holotype: PUERTO RICO. Mun. Orocovis, Barrio Bauta Abajo, along trail to observation tower, Toro Negro State Forest; 18°10′15″N, 66°28′52″W; 1036 m; 22 Jan 2015, *Mercado-Díaz 2259* (F barcode C0172450F; isotype: UPR).

Species is illustrated in Fig. 11.

Diagnosis. – Differing from *Sticta damicornis* f. *rudiuscula* Vain. in the lighter thallus color, narrower lobes and presence of sparse, simple papillae.

Description. – Primary photobiont a green alga. Basal stipe absent. Thallus irregular to orbicular in outline, up to 30 cm diam., densely branched, with 6–10 branches per 5 cm radius, branching anisotomic to pleurotomous; lobes lingulate to flabellate, horizontal to ascending, interspaced to adjacent, plane to involute, with rounded to truncate, plane to revolute apices; margins entire, slightly thickened; lobe internodes 2–7 mm long, 2–5(–9) mm broad; thallus resistant, coriaceous. Upper surface smooth, green when fresh and greenish grey to tan and darkening toward margins in the herbarium, glossy; surface glabrous, sometimes with submarginal, simple papillae. No pruina, cilia or maculae observed. Apothecia sparse, marginal, dispersed to subaggregated, pedicillated, base invagination pronounced, 1–3 mm diam., disc color reddish-brown both when fresh and in herbarium, darkening with age, opaque, margin cream-colored to brown, verrucose, becoming weakly crenulate and occasionally tomentose. Lobules absent to sparse, marginal, dispersed, unbranched, simple, with horizontal orientation, to 3 mm long and 1–2 mm broad, same color as thallus, moderately glossy, dorsiventral in section, lobuliform, basal stalk applanate. Lower surface smooth, cream-colored to light brown; primary tomentum dense, sparse towards margin, thin throughout, hirsute to strigose towards margins becoming spongy towards center, soft, brown. Rhizines sparse, submarginally aggregated, fasciculated, dark brown, to 2 mm. Cyphellae abundant, 40–60 per cm^2 towards the thallus center and 61–100 per cm^2 towards the margin, dispersed, rounded, urceolate with wide pore, erumpent to prominent, margin remaining below the level of the primary tomentum, elevated and involute, cream-colored, without tomentum; pore 0.2–1 mm diam.; basal membrane pruinose, white, K+ yellow–orange, C–, KC–, P–. Medulla compact, cream colored, K+ yellow–orange, C–, KC–, P–. Tainorum unknown (major) Harrisii unknown (minor), Unknown 1 (minor). Pycnidia immersed, brown. Cephalodia internal.

Upper cortex paraplectenchymatous, 25–35 µm thick, homogeneous, consisting of 3–4 cell layers with cells 5–17 µm diam., their walls 1.5–2.5 µm thick and their lumina rounded to isodiametric, 4–14 µm diam. Photobiont layer 15–30 µm thick, its cells 2.5–5 µm diam. Medulla 75–150 µm thick, its hyphae 2.5–3.5 µm broad, without crystals. Lower cortex paraplectenchymatous, 20–30 µm thick, with 2–3 cell layers; cells 5–18 µm diam., their walls 2–3 µm thick. Hairs of lower primary tomentum 200–700 µm long, in fascicles of 6–12 hyphae, unbranched, cylindrical, septate with free apices. Cyphellae internal pore cavity 100–200 µm deep; basal membrane cell papillae absent. Apothecia biatorine, 800–1100 µm high, with stipe; excipulum 100–130 µm broad, rarely with tomentum. Hymenium 100–120 µm high; epihymenium 2.5–5 µm high, dirty orange without gelatinous layer above. Ascospores 3-septate, 25–35 × 5–8.5 µm, fusiform, hyaline.

Distribution and ecology. – *Sticta tainorum* is the only green *Sticta* found in Puerto Rico. It is restricted to high-

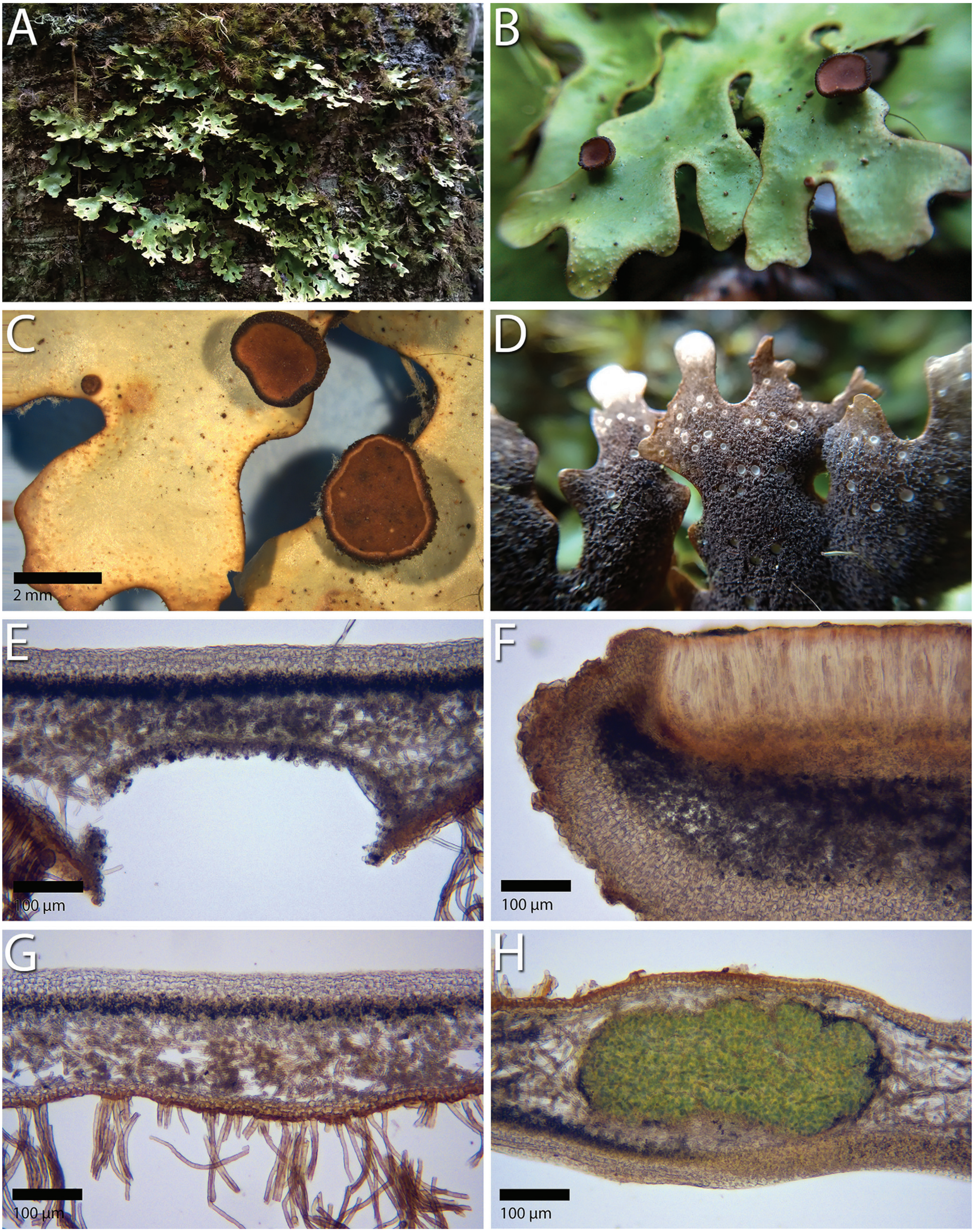

Fig. 11. *Sticta tainorum* Merc.-Díaz. **A**, Thallus in the field; **B**, Lobes upper surface with apothecia when fresh **C**, Detail of lobes and apothecia when dry; **D**, Lower surface with short brown tomentum and small cyphellae; **E**, Section of cyphellae; **F**, Section of apothecia; **G**, Section through thallus; **H**, Section of internal cephalodia. Photographs by J.A. Mercado-Díaz.

elevation, well-conserved forests to the west of the island, specifically near Pico Doña Juana in the Bosque Estatal de Toro Negro. *S. tainorum* is a rather rare species known only from a few trees in that mountain. Individuals of this species may cover large areas of the trunks in this forest.

Etymology. – This species is dedicated to the Taíno people, the indigenous people that inhabited Puerto Rico before the Spanish invasion.

Remarks. – *Sticta tainorum* is identified in Harris (1989) as *Sticta* sp. 1155. Delimitation analysis with BPP suggested that this species and a specimen of *S. laciniata* Ach. from Costa Rica were the same species. Considering the poor support for their sister relationship in our multilocus tree and the fact that other species delimitation methods considered them separate, we argue they should be treated as different species. In terms of morphology, *S. tainorum* it is most similar to the type material of *S. sinuosa* Pers. collected in Brazil and *S. sinuosa* var. *flavicans* Müll.Arg. collected in Jamaica. Because of their geographic proximity it is possible that the material from Puerto Rico and Jamaica belong to the same species. Yet, we have generally observed differences between the lichen biota of Cuba and Jamaica on one hand and Puerto Rico on the other, the latter showing stronger affinities with the Lesser Antilles. Therefore, we are not taking up the infraspecific epithet "flavicans" for the present taxon. It easily distinguished from the recently established *S. aongstroemii* Dal-Forno & al. (Dal Forno & al., 2018) and the Caribbean endemic *S. damicornis* (Moncada & al., 2018) by the shape of the lobes, being lingulate-flabellate in *S. tainorum* vs. linear in *S. aongstroemii* and *S. damicornis*. This species also resembles *Sticta damicornis* f. *rudiuscula*, a putative endemic species from Colombia that is known only from the type specimen (Moncada, 2012).

As highlighted above, living individuals of *S. tainorum* were examined in the field after Hurricane María (Sept. 2017). These thalli showed considerable browning, possibly resulting from prolonged exposure to sunlight resulting from canopy defoliation (suppl. Fig. S6). High resistance of desiccated thalli due to extreme climatic conditions (such as increased irradiation) is a general feature in lichens (Kranner & al., 2008); however, experimental increases in temperature and light simulating the effects of logging on other members within Peltigerales (i.e., *Lobaria pulmonaria*) showed that increased solar irradiation can have lethal consequences on natural populations (Gauslaa & Solhaug, 1999). We, therefore, suggest that increased irradiation currently threaten the long-term persistence of *S. tainorum* populations within the island. Because this species is also known from just few tree individuals in the Toro Negro State Forest, studies to assess the conservation status of this species are urgently needed.

Additional specimens examined. – PUERTO RICO. Mun. Adjuntas, unk. elev., 6 Jan 1886, *Sintenis L.123* (NY, US). Mun. Orocovis, Toro Negro State Forest, along trail to observation tower; 18°10′15″N, 66°28′52″W; 1036 m; 22 Jan 2015, *Mercado-Díaz 2256* (UPR). Mun. Ponce, San Narciso; 900 m; 6–8 Feb 1923, *N.L. & E.G. Britton 7313* (NY, US). Mun. Utuado, upper slopes of Mount Morales; approx. 900 m; 19 Mar 1906, *Howe 1155* (NY). Refer to Appendix 2 for additional specimens revised.

■ CONCLUSIONS

The Caribbean islands have long been recognized as an important region for global biodiversity. Although past studies using a variety of molecular and taxonomic approaches advanced our knowledge on biotic richness for many groups in this region, none until this study focused on lichens. We showed that species richness of *Sticta* in Puerto Rico is higher than previously assumed and that most species (~69%) are potentially endemic to the island. Furthermore, phylogenetic analyses showed that species from Puerto Rico do not form a monophyletic clade. This suggests that the current species assemblages resulted from multiple colonization events and that evolutionary radiations did not play a major role in the diversification of *Sticta* within the island. Evolutionary relationships inferred from our phylogenies also suggested stronger biogeographic links to South America, but ancestral area reconstruction studies will be needed to properly assess geographic affinities.

One interesting finding was observing that similar to Harris (1989), most species delimited in this work could still be separated using morpho-anatomical characters, reiterating the validity of morphology-based species delimitations in some groups of lichens. Although this observation has been previously made for *Sticta* and other members within Lobarioideae, its significance for biodiversity research and conservation in the Caribbean cannot be overstated. The capability of separating species based on morphology provides a straightforward way of documenting species richness, an important metric used by community ecologists to describe the unique biodiversity in these islands. It also opens the door to more frequent integration of lichens in biodiversity inventories and conservation initiatives and more participation of non-experts in this type of efforts. This is particularly important in areas where local biotas are under threat, such as the Caribbean islands which have been severely affected by past agricultural activities and are affected by anthropogenically driven factors such as urban sprawl and climate change.

Our study adds to numerous studies highlighting the importance of integrating molecular methods for obtaining more accurate estimates of lichen species richness in a region. It also shows that inferences of species diversity should be made preferentially after repeated sampling of areas with suitable habitat for the target taxa. To conclude, it is worth noting that patterns uncovered for *Sticta* in this study could also exist for other groups and other islands in the region. Unfortunately, most aspects about the diversity, distribution and conservation status of the lichen biota of the Caribbean remain poorly known. More studies applying methods similar to those used here will be critical for filling these knowledge gaps. They should also demonstrate that Caribbean biodiversity hotspot still have much to contribute towards the study of ecological and evolutionary processes, as well as conservation of biodiversity in island ecosystems.

■ AUTHOR CONTRIBUTIONS

JAMD conceived the study, carried out fieldwork, generated molecular data, prepared taxonomic treatment, conducted analyses and co-wrote the manuscript. RL carried out fieldwork, provided voucher specimens and molecular data, assisted in analyses and taxonomic treatment and co-wrote the manuscript. BM carried out fieldwork, provided voucher specimens and molecular data, assisted in taxonomic treatment and reviewed the manuscript. TJW provided molecular data and reviewed the manuscript. HTL assisted in analyses and co-wrote the manuscript. — JAMD, https://orcid.org/0000-0003-2193-0023; RL, https://orcid.org/0000-0002-3431-4636; BM, https://orcid.org/0000-0001-9984-2918; TJW, https://orcid.org/0000-0001-6453-3429; HTL, https://orcid.org/0000-0003-1512-835X

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■ LITERATURE CITED

Acevedo-Rodríguez, P. 1991. Angiosperms in the Greater Antilles. *Fl. Gr. Antilles Newslett.* 1. Retrieved from https://www.nybg.org/bsci/fga/Newsletter/FGANno1.htm

Acevedo-Rodríguez, P. & Strong, M.T. 2008. Floristic richness and affinities in the West Indies. *Bot. Rev. (Lancaster)* 74: 5–36. https://doi.org/10.1007/s12229-008-9000-1

Acinas, S.G., Klepac-Ceraj, V., Hunt, D.E., Pharino, C., Ceraj, I., Distel, D.L. & Polz, M.F. 2004. Fine-scale phylogenetic architecture of a complex bacterial community. *Nature* 430: 551. https://doi.org/10.1038/nature02649

Ali, J.R. 2012. Colonizing the Caribbean: Is the GAARlandia land-bridge hypothesis gaining a foothold? *J. Biogeogr.* 39: 431–433. https://doi.org/10.1111/j.1365-2699.2011.02674.x

Alors, D., Lumbsch, H.T., Divakar, P.K., Leavitt, S.D. & Crespo, A. 2016. An integrative approach for understanding diversity in the *Punctelia rudecta* species complex (Parmeliaceae, Ascomycota). *PLoS ONE* 11: 1–17. https://doi.org/10.1371/journal.pone.0146537

Andraca-Gómez, G., Ordano, M., Boege, K., Domínguez, C.A., Piñero, D., Pérez-Ishiwara, R., Pérez-Camacho, J., Cañizares, M. & Fornoni, J. 2015. A potential invasion route of *Cactoblastis cactorum* within the Caribbean region matches historical hurricane trajectories. *Biol. Invas.* 17: 1397–1406. https://doi.org/10.1007/s10530-014-0802-2

Arrigoni, R., Berumen, M.L., Chen, C.A., Terraneo, T.I., Baird, A.H., Payri, C. & Benzoni, F. 2016. Species delimitation in the reef coral genera *Echinophyllia* and *Oxypora* (Scleractinia, Lobophylliidae) with a description of two new species. *Molec. Phylogen. Evol.* 105: 146–159. https://doi.org/10.1016/j.ympev.2016.08.023

Barraclough, T.G., Birky, C.W. & Burt, A. 2003. Diversification in sexual and asexual organisms. *Evolution* 57: 2166–2172. https://doi.org/10.1111/j.0014-3820.2003.tb00394.x

Barrett, C.F. & Freudenstein, J.V. 2011. An integrative approach to delimiting species in a rare but widespread mycoheterotrophic orchid. *Molec. Ecol.* 20: 2771–2786. https://doi.org/10.1111/j.1365-294X.2011.05124.x

Beard, J. 1949. *The natural vegetation of the Windward and Leeward Islands*, 1st ed. Oxford: Clarendon Press.

Benson, D.A., Cavanaugh, M., Clark, K., Karsch-Mizrachi, I., Ostell, J., Pruitt, K.D. & Sayers, E.W. 2018. GenBank. *Nucl. Acids Res.* 46: D41–D47. https://doi.org/10.1093/nar/gkx1094

Bickford, D., Lohman, D.J., Sodhi, N.S., Ng, P.K.L., Meier, R., Winker, K., Ingram, K.K. & Das, I. 2007. Cryptic species as a window on diversity and conservation. *Trends Ecol. Evol.* 22: 148–155. https://doi.org/10.1016/j.tree.2006.11.004

Brace, S., Turvey, S.T., Weksler, M., Hoogland, M.L.P. & Barnes, I. 2015. Unexpected evolutionary diversity in a recently extinct Caribbean mammal radiation. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 282: 20142371. https://doi.org/10.1098/rspb.2014.2371

Carstens, B.C., Pelletier, T.A., Reid, N.M. & Satler, J.D. 2013. How to fail at species delimitation. *Molec. Ecol.* 22: 4369–4383. https://doi.org/10.1111/mec.12413

Castresana, J. 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molec. Biol. Evol.* 17: 540–552. https://doi.org/10.1093/oxfordjournals.molbev.a026334

Dal Forno, M., Bungartz, F., Yánez-Ayabaca, A., Lücking, R. & Lawrey, J.D. 2017. High levels of endemism among Galapagos basidiolichens. *Fungal Diversity* 85: 45–73. https://doi.org/10.1007/s13225-017-0380-6

Dal Forno, M., Moncada, B. & Lücking, R. 2018. *Sticta aongstroemii*, a newly recognized species in the *S. damicornis* morphodeme (Lobariaceae) potentially endemic to the Atlantic Forest in Brazil. *Lichenologist* 50: 691–696. https://doi.org/10.1017/S0024282918000403

Damm, S., Schierwater, B. & Hadrys, H. 2010. An integrative approach to species discovery in odonates: From character-based DNA barcoding to ecology. *Molec. Ecol.* 19: 3881–3893. https://doi.org/10.1111/j.1365-294X.2010.04720.x

Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. 2012. jModelTest 2: More models, new heuristics and parallel computing. *Nature, Meth.* 9: 772. https://doi.org/10.1038/nmeth.2109

Dávalos, L.M. 2007. Short-faced bats (Phyllostomidae: Stenodermatina): A Caribbean radiation of strict frugivores. *J. Biogeogr.* 34: 364–375. https://doi.org/10.1111/j.1365-2699.2006.01610.x

Dayrat, B. 2005. Towards integrative taxonomy. *Biol. J. Linn. Soc.* 85: 407–415. https://doi.org/10.1111/j.1095-8312.2005.00503.x

Del-Prado, R., Divakar, P.K., Lumbsch, H.T. & Crespo, A.M. 2016. Hidden genetic diversity in an asexually reproducing lichen forming fungal group. *PLoS ONE* 111(8): e0161031. https://doi.org/10.1371/journal.pone.0161031

Dewalt, S.J., Ickes, K. & James, A. 2016. Forest and community structure of tropical sub-montane rain forests on the island of Dominica, Lesser Antilles. *Caribbean Naturalist*, Spec. Iss. 1: 116–137. https://data.fs.usda.gov/research/pubs/iitf/ja_iitf_2016_DeWalt001.pdf

Dirnböck, T., Essl, F. & Rabitsch, W. 2011. Disproportional risk for habitat loss of high-altitude endemic species under climate change.

Global Change Biol. 17: 990–996. https://doi.org/10.1111/j.1365-2486.2010.02266.x

Eberle, J., Warnock, R.C.M. & Ahrens, D. 2016. Bayesian species delimitation in *Pleophylla chafers* (Coleoptera) – The importance of prior choice and morphology. *B. M. C. Evol. Biol.* 16: 94. https://doi.org/10.1186/s12862-016-0659-3

Ewel, J.J. & Whitmore, J.L. 1973. *The ecological life zones of Puerto Rico and the U.S. Virgin Islands*. Forest Service Research Paper ITF 18. Río Piedras, PR: Institute of Tropical Forestry.

Ezard, T., Fujisawa, T. & Barraclough, T.G. 2009. SPLITS: SPecies' LImits by Threshold Statistics. R Package, version 1.0-19. https://rdrr.io/rforge/splits/

Fabre, P.H., Vilstrup, J.T., Raghavan, M., Der Sarkissian, C., Willerslev, E., Douzery, E.J.P. & Orlando, L. 2014. Rodents of the Caribbean: Origin and diversification of hutias unravelled by next-generation museomics. *Biol. Lett.* 10: 20140266. https://doi.org/10.1098/rsbl.2014.0266

Figueroa-Colón, J.C. 1996. Phytogeographical trends, centers of high species richness and endemism, and the question of extinctions in the native flora of Puerto Rico. *Ann. New York Acad. Sci.* 776: 89–102. https://doi.org/10.1111/j.1749-6632.1996.tb17414.x

Fleishman, E., Noss, R.F. & Noon, B.R. 2006. Utility and limitations of species richness metrics for conservation planning. *Ecol. Indicators* 6: 543–553. https://doi.org/10.1016/j.ecolind.2005.07.005

Fontaneto, D., Herniou, E.A., Boschetti, C., Caprioli, M., Melone, G., Ricci, C. & Barraclough, T.G. 2007. Independently evolving species in asexual bdelloid rotifers. *PLoS Biol.* 5: e87. https://doi.org/10.1371/journal.pbio.0050087

Francisco-Ortega, J., Santiago-Valentín, E., Acevedo-Rodríguez, P., Lewis, C., Pipoly, J., Meerow, A.W. & Maunder, M. 2007. Seed plant genera endemic to the Caribbean Island Biodiversity Hotspot: A review and a molecular phylogenetic perspective. *Bot. Rev. (Lancaster)* 73: 183–234. https://doi.org/10.1663/0006-8101(2007)73[183:SPGETT]2.0.CO;2

Fujisawa, T. & Barraclough, T.G. 2013. Delimiting species using single-locus data and the generalized mixed Yule-coalescent approach: A revised method and evaluation on simulated data sets. *Syst. Biol.* 62: 707–724. https://doi.org/10.1093/sysbio/syt033

Galloway, D.J. 1994. Studies on the lichen genus *Sticta* (Schreber) Ach.: I. Southern South American Species. *Lichenologist* 26: 223–282. https://doi.org/10.1006/lich.1994.1019

Galloway, D.J. 2015. Contributions to a history of New Zealand lichenology 5*. James Murray (1923–1961). *Phytotaxa* 198: 1–67. https://doi.org/10.11646/phytotaxa.198.1.1

Galloway, D.J. & Thomas, M.A. 2004. *Sticta*. Pp. 513–524 in: Nash, T.H., III, Ryan, B.D., Diederich, P., Gries, C. & Bungartz, F. (eds.), *Lichen flora of the Greater Sonoran Desert Region*, vol. 2. Tempe: Lichens Unlimited, Arizona State University.

Gauslaa, Y. & Solhaug, K.A. 1999. High-light damage in air-dry thalli of the old forest lichen *Lobaria pulmonaria*—Interactions of irradiance, exposure duration and high temperature. *J. Exp. Bot.* 50: 697–705. https://doi.org/10.1093/jxb/50.334.697

Gelman, A. & Rubin, D.B. 1992. Inference from iterative simulation using multiple sequences. *Statist. Sci.* 7: 457–472. https://doi.org/10.1214/ss/1177011136

Givnish, T.J. 2010. Ecology of plant speciation. *Taxon* 59: 1329–1366. https://doi.org/10.2307/20774033

Graham, A. 2003. Geohistory models and Cenozoic paleoenvironments of the Caribbean region. *Syst. Bot.* 28: 378–386.

Grau, H.R., Aide, T.M., Zimmerman, J.K., Helmer, E.H. & Zou, X. 2003. The ecological consequences of socioeconomic and land-use changes in postagriculture Puerto Rico. *BioScience* 53: 1159–1168. https://doi.org/10.1641/0006-3568(2003)053[1159:TECOSA]2.0.CO;2

Guillemin, M.L., Contreras-Porcia, L., Ramírez, M.E., Macaya, E.C., Contador, C.B., Woods, H., Wyatt, C. & Brodie, J. 2016. The bladed Bangiales (Rhodophyta) of the South Eastern Pacific: Molecular species delimitation reveals extensive diversity. *Molec. Phylogen. Evol.* 94: 814–826. https://doi.org/10.1016/j.ympev.2015.09.027

Guindon, S. & Gascuel, O. 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by Maximum Likelihood. *Syst. Biol.* 52: 696–704. https://doi.org/10.1080/10635150390235520

Harris, R. 1989. *Working keys to the lichen-forming fungi of Puerto Rico*. Bronx: published by the author.

Hass, C.A. & Hedges, S.B. 1991. Albumin evolution in West Indian frogs of the genus *Eleutherodactylus* (Leptodactylidae): Caribbean biogeography and a calibration of the albumin immunological clock. *J. Zool.* 225: 413–426. https://doi.org/10.1111/j.1469-7998.1991.tb03825.x

Hebert, P.D., Penton, E.H., Burns, J.M., Janzen, D.H. & Hallwachs, W. 2004. Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator*. *Proc. Natl. Acad. Sci. U.S.A.* 101: 14812–14817. https://doi.org/10.1073/pnas.0406166101

Hedges, S.B. 1989. An island radiation: Allozyme evolution in Jamaican frogs of the genus *Eleutherodactylus* (Leptodactylidae). *Caribbean J. Sci.* 25: 123–147.

Hedges, S.B. 2006. Paleogeography of the Antilles and origin of West Indian terrestrial vertebrates. *Ann. Missouri Bot. Gard.* 93: 231–244. https://doi.org/10.1007/s00586-014-3395-7

Heinicke, M.P., Duellman, W.E. & Hedges, S.B. 2007. Major Caribbean and Central American frog faunas originated by ancient oceanic dispersal. *Proc. Natl. Acad. Sci. U.S.A.* 104: 10092–10097. https://doi.org/10.1073/pnas.0611051104

Huang, J.-P. 2018. What have been and what can be delimited as species using molecular data under the multi-species coalescent model? A case study using Hercules beetles (Dynastes; Dynastidae). *Insect Syst. Divers.* 2(2): 3. https://doi.org/10.1093/isd/ixy003

Hue, A.M. 1901. Lichenes Extra-Europaei. *Nouv. Arch. Mus. Hist. Nat.*, sér. 4, 3: 21–146.

Imshaug, H.A. 1957. *Catalogue of West Indian Lichens*, 1st ed. Bulletin of the Institute of Jamaica, Science Series 6. Kingston: Institute of Jamaica.

Iturralde-Vinent, M.A. & MacPhee, R.D.E. 1999. Paleogeography of the Caribbean Region: Implications for the Cenozoic biogeography. *Bull. Amer. Mus. Nat. Hist.* 238: 1–95.

Jennings, L.N., Douglas, J., Treasure, E. & González, G. 2014. *Climate change effects in El Yunque National Forest, Puerto Rico, and the Caribbean region*. General Technical Report SRS-GTR-193. Asheville, NC: USDA-Forest Service, Southern Research Station.

Judd, W. 2001. Phylogeny and biogeography of *Lyonia* sect. *Lyonia* (Ericaceae). Pp. 63–75 in: Woods, C. & Sergile, F. (eds.), *Biogeography of the West Indies: Patterns and perspectives*, 2nd ed. Boca Raton: CRC Press.

Kalwij, J.M., Wagner, H.H. & Scheidegger, C. 2005. Effects of stand-level disturbances on the spatial distribution of a lichen indicator. *Ecol. Applic.* 15: 2015–2024. https://doi.org/10.1890/04-1912

Katoh, K. & Standley, D.M. 2013. MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molec. Biol. Evol.* 30: 772–780. https://doi.org/10.1093/molbev/mst010

Kidd, S.A. & Michaels, H.J. 2005. *Molecular phylogenetics of the Hawaiian geraniums*. M.S. Thesis. Bowling Green State University, Bowling Green, Ohio, U.S.A.

Kraichak, E., Lücking, R., Aptroot, A., Beck, A., Dornes, P., John, V., Lendemer, J.C., Nelsen, M.P., Neuwirth, G., Nutakki, A., Parnmen, S., Sohrabi, M., Tønsberg, T. & Lumbsch, H.T. 2015. Hidden diversity in the morphologically variable script lichen (*Graphis scripta*) complex (Ascomycota, Ostropales, Graphidaceae). *Organisms Diversity Evol.* 15: 447–458. https://doi.org/10.1007/s13127-015-0219-5

Kraichak, E., Huang, J.P., Nelsen, M., Leavitt, S.D. & Lumbsch, H.T. 2018. A revised classification of orders and families in the two major subclasses of Lecanoromycetes (Ascomycota) based on a temporal approach. *Bot. J. Linn. Soc.* 188: 233–249. https://doi.org/10.1093/botlinnean/boy060

Kranner, I., Beckett, R., Hochman, A. & Nash, T.H. 2008. Desiccation-tolerance in lichens: A review. *Bryologist* 111: 576–593. https://doi.org/10.1639/0007-2745-111.4.576

Lakner, C., Van Der Mark, P., Huelsenbeck, J.P., Larget, B. & Ronquist, F. 2008. Efficiency of Markov Chain Monte Carlo tree proposals in Bayesian phylogenetics. *Syst. Biol.* 57: 86–103. https://doi.org/10.1080/10635150801886156

Landrón-Concepción, I. 1972. *The lichen genus Ramalina Ach. in the West Indies with notes on its role in the vegetation of Puerto Rico*. Michigan State University, East Lansing, Michigan, U.S.A. http://agris.fao.org/agris-search/search.do?recordID=US201300325718

Leaché, A.D. & Fujita, M.K. 2010. Bayesian species delimitation in West African forest geckos (*Hemidactylus fasciatus*). *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 277: 3071–3077. https://doi.org/10.1098/rspb.2010.0662

Leavitt, S.D., Fankhauser, J.D., Leavitt, D.H., Porter, L.D., Johnson, L.A. & St. Clair, L.L. 2011. Complex patterns of speciation in cosmopolitan 'rock posy' lichens – Discovering and delimiting cryptic fungal species in the lichen-forming *Rhizoplaca melanophthalma* species-complex (Lecanoraceae, Ascomycota). *Molec. Phylogen. Evol.* 59: 587–602. https://doi.org/10.1016/j.ympev.2011.03.020

Leavitt, S.D., Grewe, F., Widhelm, T., Muggia, L., Wray, B. & Lumbsch, H.T. 2016. Resolving evolutionary relationships in lichen-forming fungi using diverse phylogenomic datasets and analytical approaches. *Sci. Rep.* 6: 1–11. https://doi.org/10.1038/srep22262

Levin, D.A. 2000. *The origin, expansion, and demise of plant species*. New York: Oxford University Press. https://books.google.at/books?id=bI83LxrWKAcC

Lim, G.S., Balke, M. & Meier, R. 2012. Determining species boundaries in a world full of rarity: Singletons, species delimitation methods. *Syst. Biol.* 61: 165–169. https://doi.org/10.1093/sysbio/syr030

Liogier, H.A. & Martorell, L.F. 2000. *Flora of Puerto Rico and adjacent islands: A systematic synopsis*, 2nd ed. San Juan: Editorial de la Universidad de Puerto Rico.

Lohse, K. 2009. Can mtDNA barcodes be used to delimit species? A response to Pons et al. (2006). *Syst. Biol.* 58: 439–442. https://doi.org/10.1093/sysbio/syp039

Losos, J.B. 2011. *Lizards in an evolutionary tree: Ecology and adaptive radiation of Anoles*, 1st ed. Berkeley: University of California Press. Retrieved from https://books.google.at/books?id=SakwDwAAQBAJ

Losos, J.B. & Ricklefs, R.E. 2009. Adaptation and diversification on islands. *Nature* 457: 830–836. https://doi.org/10.1038/nature07893

Losos, J.B., Jackman, T.R., Larson, A., De Queiroz, K. & Rodríguez-Schettino, L. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. *Science* 279: 2115–2118. https://doi.org/10.1126/science.279.5359.2115

Lücking, R., Rivas-Plata, E., Chaves, J.L., Umaña, L. & Sipman, H.J.M. 2009. How many tropical lichens are there … really? Pp. 399–418 in: Thell, A., Seaward, M.R.D. & Feuerer, T. (eds.), *Diversity of lichenology.* Bibliotheca Lichenologica 100. Berlin & Stuttgart: J. Cramer.

Lücking, R., Seavey, F., Common, R.S., Beeching, S.Q., Breuss, O., Buck, W.R., Crane, L., Hodges, M., Hodkinson, P., Lay, E., Lendemer, J.C., McMullin, R.T., Mercado-Díaz, J.A., Nelsen, M.P., Rivas Plata, E., Sanders, W.B., Schaefer, H.P. & Seavey, J. 2011. The lichens of the Fakahatchee Strand Preserve State Park, Florida: Proceedings from the 18th Tuckerman Workshop. *Bull. Florida Mus. Nat. Hist.* 49: 127–186.

Lücking, R., Dal-Forno, M., Sikaroodi, M., Gillevet, P.M., Bungartz, F., Moncada, B., Yanez-Ayabaca, A., Chaves, J.L., Coca, L.F. & Lawrey, J.D. 2014. A single macrolichen constitutes hundreds of unrecognized species. *Proc. Natl. Acad. Sci. U.S.A.* 111: 11091–11096. https://doi.org/10.1073/pnas.1403517111

Lücking, R., Hodkinson, B.P. & Leavitt, S.D. 2017a. The 2016 classification of lichenized fungi in the Ascomycota and Basidiomycota. *Bryologist* 119: 361–416. https://doi.org/10.1639/0007-2745-120.1.058

Lücking, R., Moncada, B. & Smith, C.W. 2017b. The genus *Lobariella* (Ascomycota: Lobariaceae) in Hawaii: Late colonization, high inferred endemism and three new species resulting from micro-radiation. *Lichenologist* 49: 673–691. https://doi.org/10.1017/S0024282917000470

Lugo, A.E., López, T. del M. & Ramos-González, O. 2004. *Urbanización de los terrenos en la periferia de El Yunque*. General Technical Report WO-66. Washington, D.C.: U.S. Department of Agriculture, Forest Service.

Lumbsch, H.T. 2002. Analysis of phenolic products in lichens for identification and taxonomy. Pp. 281–295 in: Kraner, I, Beckett, R.P. & Varma, A.K. (eds.), *Protocols in lichenology*, 1st ed. Berlin: Springer. https://doi.org/10.1007/978-3-642-56359-1

Lumbsch, H.T. & Leavitt, S.D. 2011. Goodbye morphology? A paradigm shift in the delimitation of species in lichenized fungi. *Fungal Diversity* 50: 59–72. https://doi.org/10.1007/s13225-011-0123-z

Lumbsch, H.T. & Leavitt, S.D. 2019. Introduction of subfamily names for four clades in Cladoniaceae and Peltigeraceae (Lecanoromycetes). *Mycotaxon* 134: 271–273. https://doi.org/10.5248/134.271

Luo, A., Ling, C., Ho, S.Y.W. & Zhu, C.D. 2018. Comparison of methods for molecular species delimitation across a range of speciation scenarios. *Syst. Biol.* 67: 830–846. https://doi.org/10.1093/sysbio/syy011

Mace, G.M. 2004. The role of taxonomy in species conservation. *Philos. Trans., Ser. B* 359: 711–719. https://doi.org/10.1098/rstb.2003.1454

MacPhee, R.D.E. & Iturralde-Vinent, M.A. 1995. Origin of the Greater Antillean land mammal fauna, 1: New tertiary fossils from Cuba and Puerto Rico. *Amer. Mus. Novit.* 3141: 1–31.

Madriñán, S., Cortés, A.J. & Richardson, J.E. 2013. Páramo is the world's fastest evolving and coolest biodiversity hotspot. *Frontiers Genet.* 4: 192. https://doi.org/10.3389/fgene.2013.00192

Magain, N. & Sérusiaux, E. 2015. Dismantling the treasured flagship lichen *Sticta fuliginosa* (Peltigerales) into four species in Western Europe. *Mycol. Progr.* 14: 97. https://doi.org/10.1007/s11557-015-1109-0

Mahler, D.L., Revell, L.J., Glor, R.E. & Losos, J.B. 2010. Ecological opportunity and the rate of morphological evolution in the diversification of greater Antillean anoles. *Evolution* 64: 2731–2745. https://doi.org/10.1111/j.1558-5646.2010.01026.x

Mann, M.E. & Emanuel, K.A. 2006. Atlantic Hurricane trends linked to climate change. *Eos, Trans. Amer. Geophys. Union* 87: 233–241. https://doi.org/10.1029/2006EO240001

Marivaux, L., Vélez-Juarbe, J., Merzeraud, G., Pujos, F., López, L.W. V., Boivin, M., Santos-Mercado, H., Cruz, E.J., Grajales, A., Padilla, J., Vélez-Rosado, K.I., Philippon, M., Léticée, J., Münch, P. & Antoine, P. 2020. Early Oligocene chinchilloid caviomorphs from Puerto Rico and the initial rodent colonization of the West Indies. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 287: 20192806. https://doi.org/10.1098/rspb.2019.2806

McCune, B., Rosentreter, R., Spribille, T., Breuss, O. & Wheeler, T. 2014. *Montana lichens: An annotated list*. Monographs in North American Lichenology 2. Corvallis: Northwest Lichenologists.

McHugh, A., Yablonsky, C., Binford, G. & Agnarsson, I. 2014. Molecular phylogenetics of Caribbean *Micrathena* (Araneae: Araneidae) suggests multiple colonisation events and single island endemism. *Invertebr. Syst.* 28: 337–349. https://doi.org/10.1071/IS13051

Meegaskumbura, H., Bossuyt, F., Pethiyagoda, R., Manamendra-Arachchi, K., Bahir, M., Milinkovitch, M.C. & Schneider, C.J. 2002. Sri Lanka: An amphibian hot spot. *Science* 298: 379. https://doi.org/10.1126/science.298.5592.379

Mercado-Díaz, J.A. & Santiago-Valentín, E. 2010. Lichenological studies in Puerto Rico: History and current status. *Harvard Pap. Bot.* 15: 93–101. https://doi.org/10.3100/025.015.0124

Mercado-Díaz, J.A., Lücking, R. & Parnmen, S. 2014. Two new genera and twelve new species of Graphidaceae from Puerto Rico: A case for higher endemism of lichenized fungi in islands of the Caribbean? *Phytotaxa* 189: 186–203. https://doi.org/10.11646/phytotaxa.189.1.14

Miadlikowska, J., Kauff, F., Hofstetter, V., Fraker, E., Grube, M., Hafellner, J., Reeb, V., Hodkinson, B.P., Kukwa, M., Lücking, R., Hestmark, G., Otalora, M.G., Rauhut, A., Büdel, B., Scheidegger, C., Timdal, E., Stenroos, S., Brodo, I., Perlmutter, G.B., Ertz, D., Diederich, P., Lendemer, J.C., May, P., Schoch, C.L., Arnold, A.E., Gueidan, C., Tripp, E., Yahr, R., Robertson, C. & Lutzoni, F. 2006. New insights into classification and evolution of the Lecanoromycetes (Pezizomycotina, Ascomycota) from phylogenetic analyses of three ribosomal RNA- and two protein-coding genes. *Mycologia* 98: 1088–1103. https://doi.org/10.1080/15572536.2006.11832636

Michelangeli, F.A., Judd, W.S., Penneys, D.S., Skean, J.D., Bécquer-Granados, E.R., Goldenberg, R. & Martin, C.V. 2008. Multiple events of dispersal and radiation of the tribe Miconieae (Melastomataceae) in the Caribbean. *Bot. Rev. (Lancaster)* 74: 53–77. https://doi.org/10.1007/s12229-008-9004-x

Miller, M.A., Pfeiffer, W. & Schwartz, T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Pp. 45–52 in: *Proceedings of the Gateway Computing Environments Workshop (GCE)*, New Orleans, Louisiana, 14 Nov 2010. Piscataway: IEEE. https://doi.org/10.1109/GCE.2010.5676129

Mitchell, R.C. 1954. *A survey of the geology of Puerto Rico*. Technical Paper 13. Río Piedras: University of Puerto Rico Agricultural Experiment Station.

Mittelbach, G. 2012. *Community ecology.* Sunderland, MA: Sinauer.

Moncada, B. 2012. *El género Sticta (Schreb.) Ach. en Colombia: Taxonomía, ecogeografía e importancia*. Doctoral thesis. Universidad Nacional de Colombia, Bogotá, Colombia. http://www.bdigital.unal.edu.co/11296/1/190844.2012.pdf

Moncada, B. & Lücking, R. 2012. Ten new species of *Sticta* and counting: Colombia as a hot spot for unrecognized diversification in a conspicuous macrolichen genus. *Phytotaxa* 74: 1–29. https://doi.org/10.11646/phytotaxa.74.1.1

Moncada, B., Coca, L.F. & Lücking, R. 2013a. Neotropical members of *Sticta* (lichenized Ascomycota: Lobariaceae) forming photosymbiodemes, with the description of seven new species. *Bryologist* 116: 169–200. https://doi.org/10.1639/0007-2745-116.2.169

Moncada, B., Lücking, R. & Betancourt-Macuase, L. 2013b. Phylogeny of the Lobariaceae (lichenized Ascomycota: Peltigerales), with a reappraisal of the genus *Lobariella*. *Lichenologist* 45: 203–263. https://doi.org/10.1017/S0024282912000825

Moncada, B., Lücking, R. & Suárez, A. 2013c. Molecular phylogeny of the genus *Sticta* (lichenized Ascomycota: Lobariaceae) in Colombia. *Fungal Diversity* 64: 205–231. https://doi.org/10.1007/s13225-013-0230-0

Moncada, B., Reidy, B. & Lücking, R. 2014. A phylogenetic revision of Hawaiian *Pseudocyphellaria* sensu lato (lichenized Ascomycota: Lobariaceae) reveals eight new species and a high degree of inferred endemism. *Bryologist* 117: 119–160. https://doi.org/10.1639/0007-2745-117.2.119

Moncada, B., Mercado-Díaz, J.A. & Lücking, R. 2018. The identity of *Sticta damicornis* (Ascomycota: Lobariaceae): A presumably widespread taxon is a Caribbean endemic. *Lichenologist* 50: 591–597. https://doi.org/10.1017/S0024282918000373

Moncada, B., Lücking, R. & Lumbsch, H.T. 2020. Rewriting the evolutionary history of the lichen genus *Sticta* (Ascomycota: Peltigeraceae subfam. Lobarioideae) in the Hawaiian islands. *Pl. Fungal Syst.* 65: 95–119. https://doi.org/10.35535/pfsyst-2020-0005

Moncada, B., Mercado-Díaz, J.A., Smith, C.W., Bungartz, F., Sérusiaux, E., Lumbsch, H.T. & Lücking, R. In press. Two new common, previously unrecognized species in the *Sticta weigelii* morphodeme (Ascomycota: Peltigeraceae). *Willdenowia* 50.

Morden, C.W. & Loeffler, W. 1999. Fragmentation and genetic differentiation among subpopulations of the endangered Hawaiian mint *Haplostachys haplostachya* (Lamiaceae). *Molec. Ecol.* 8: 617–625. https://doi.org/10.1046/j.1365-294X.1999.00601.x

Müller Argoviensis, J. 1888. Lichenes Portoricenses ab egregio Sintenis lectis, in hujus collect. exs. sub citatis numeris editi, et a cl. Dr. Urban communicati, adjunctis nonnullis a Barone Egger in St. Domingo lectis, quos determinavit Dr. J. Müller. *Flora* 71: 490–496.

Myers, N., Mittermeler, R.A., Mittermeler, C.G., Da Fonseca, G.A.B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858. https://doi.org/10.1038/35002501

Nei, M., Maruyama, T. & Chakraborty, R. 1975. The bottleneck effect and genetic variability in populations. *Evolution* 29: 1–10. https://doi.org/10.2307/2407137

Nieto-Blázquez, M.E., Antonelli, A. & Roncal, J. 2017. Historical biogeography of endemic seed plant genera in the Caribbean: Did GAARlandia play a role? *Ecol. Evol.* 7: 10158–10174. https://doi.org/10.1002/ece3.3521

Nylander, W. 1869. Énumération des lichens récoltés par H. Husnot aux Antilles Françaises. *Bull. Soc. Linn. Normandie*, sér. 2, 3: 259–280.

Oksanen, A.J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, R.B., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E. & Wagner, H. 2019. vegan: Community Ecology Package, version 2.5-6. https://CRAN.R-project.org/package=vegan

Padial, J.M. & De La Riva, I. 2010. A response to recent proposals for integrative taxonomy. *Biol. J. Linn. Soc.* 101: 747–756. https://doi.org/10.1111/j.1095-8312.2010.01528.x

Parnmen, S., Rangsiruji, A., Mongkolsuk, P., Boonpragob, K., Nutakki, A. & Lumbsch, H.T. 2012. Using phylogenetic and coalescent methods to understand the species diversity in the *Cladia aggregata* complex (Ascomycota, Lecanorales). *PLoS ONE* 7(12): e52245. https://doi.org/10.1371/journal.pone.0052245

Pax, D.L., Price, R.A. & Michaels, H.J. 1997. Phylogenetic position of the Hawaiian geraniums based on *rbcL* sequences. *Amer. J. Bot.* 84: 72–78. https://doi.org/10.2307/2445884

Perret, M., Chautems, A., De Araujo, A.O. & Salamin, N. 2013. Temporal and spatial origin of Gesneriaceae in the New World inferred from plastid DNA sequences. *Bot. J. Linn. Soc.* 171: 61–79. https://doi.org/10.1111/j.1095-8339.2012.01303.x

Pino-Bodas, R., Burgaz, A.R., Martín, M.P. & Lumbsch, H.T. 2011. Phenotypical plasticity and homoplasy complicate species delimitation in the *Cladonia gracilis* group (Cladoniaceae, Ascomycota). *Organisms Diversity Evol.* 11: 343–355. https://doi.org/10.1007/s13127-011-0062-2

Pons, J., Barraclough, T.G., Gomez-Zurita, J., Cardoso, A., Duran, D.P., Hazell, S., Kamoun, S., Sumlin, W.D. & Vogler, A.P. 2006. Sequence-based species delimitation for the DNA taxonomy of undescribed insects. *Syst. Biol.* 55: 595–609. https://doi.org/10.1080/10635150600852011

Printzen, C. 2010. Lichen systematics: The role of morphological and molecular data to reconstruct phylogenetic relationships. *Progr. Bot.* 71: 233–275. https://doi.org/10.1007/978-3-642-02167-1_10

Rambaut, A. 2012. FigTree, version 1.4.0. Edingburgh: University of Edinburgh, Institute of Evolutionary Biology. http://tree.bio.ed.ac.uk/software/figtree/

Rambaut, A. & Drummond, A.J. 2009. Tracer, version 1.5. http://beast.bio.ed.ac.uk/Tracer

Rambaut, A. & Drummond, A. 2013a. LogCombiner, version 1.8.2. https://beast.community/logcombiner

Rambaut, A. & Drummond, A. 2013b. TreeAnnotator, version 1.8.0. https://beast.community/treeannotator

Ranft, H., Moncada, B., De Lange, P.J., Lumbsch, H.T. & Lücking, R. 2018. The *Sticta filix* morphodeme (Ascomycota: Lobariaceae) in New Zealand with the newly recognized species *S. dendroides* and *S. menziesii*: Indicators of forest health in a threatened island biota? *Lichenologist* 50: 185–210. https://doi.org/10.1017/S0024282917000706

Rannala, B. & Yang, Z. 2013. Improved reversible jump algorithms for Bayesian species delimitation. *Genetics* 194: 245–253. https://doi.org/10.1534/genetics.112.149039

Rannala, B. & Yang, Z. 2017. Efficient Bayesian species tree inference under the multispecies coalescent. *Syst. Biol.* 66: 823–842. https://doi.org/10.1093/sysbio/syw119

Regalado, L., Lóriga, J., Bechteler, J., Beck, A., Schneider, H. & Heinrichs, J. 2018. Phylogenetic biogeography reveals the timing and source areas of the *Adiantum* species (Pteridaceae) in the West Indies, with a special focus on Cuba. *J. Biogeogr.* 45: 541–551. https://doi.org/10.1111/jbi.13119

Ricklefs, R. & Bermingham, E. 2008. The West Indies as a laboratory of biogeography and evolution. *Philos. Trans., Ser. B* 363: 2393–2413. https://doi.org/10.1098/rstb.2007.2068

Rittmeyer, E.N. & Austin, C.C. 2012. The effects of sampling on delimiting species from multi-locus sequence data. *Molec. Phylogen. Evol.* 65: 451–463. https://doi.org/10.1016/j.ympev.2012.06.031

Rodríguez, A., Vences, M., Nevado, B., Machordom, A. & Verheyen, E. 2010. Biogeographic origin and radiation of Cuban *Eleutherodactylus* frogs of the *auriculatus* species group, inferred from mitochondrial and nuclear gene sequences. *Molec. Phylogen. Evol.* 54: 179–186. https://doi.org/10.1016/j.ympev.2009.08.023

Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. 2012. MrBayes 3.2: Efficient bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Rosauer, D., Laffan, S.W., Crisp, M.D., Donnellan, S.C. & Cook, L.G. 2009. Phylogenetic endemism: A new approach for identifying geographical concentrations of evolutionary history. *Molec. Ecol.* 18: 4061–4072. https://doi.org/10.1111/j.1365-294X.2009.04311.x

Scantlebury, D.P. 2014. *Patterns of adaptive radiation in insular reptiles and amphibians*. Thesis. University of Rochester, Rochester, New York, U.S.A.

Schoch, C.L., Seifert, K.A., Huhndorf, S., Robert, V., Spouge, J.L., Levesque, C.A., Chen, W. & Fungal Barcoding Consortium 2012. Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for Fungi. *Proc. Natl. Acad. Sci. U.S.A.* 109: 6241–6246. https://doi.org/10.1073/pnas.1117018109

Shaw, A.J., Cox, C.J., Goffinet, B., Buck, W.R. & Boles, S. B. 2003. Phylogenetic evidence of a rapid radiation of pleurocarpous mosses (Bryophyta). *Evolution* 57: 2226–2241. https://doi.org/10.1554/03-284

Simon, A., Goffinet, B., Magain, N. & Sérusiaux, E. 2018. High diversity, high insular endemism and recent origin in the lichen genus *Sticta* (lichenized Ascomycota, Peltigerales) in Madagascar and the Mascarenes. *Molec. Phylogen. Evol.* 122: 15–28. https://doi.org/10.1016/j.ympev.2018.01.012

Stamatakis, A. 2014. RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Suchard, M.A., Lemey, P., Baele, G., Ayres, D.L., Drummond, A.J. & Rambaut, A. 2018. Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. *Virus Evol.* 4: vey016. https://doi.org/10.1093/ve/vey016

Sukumaran, J. & Knowles, L.L. 2017. Multispecies coalescent delimits structure, not species. *Proc. Natl. Acad. Sci. U.S.A.* 114: 1607–1612. https://doi.org/10.1073/pnas.1607921114

Talavera, G. & Castresana, J. 2007. Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. *Syst. Biol.* 56: 564–577. https://doi.org/10.1080/10635150701472164

Talavera, G., Dincă, V. & Vila, R. 2013. Factors affecting species delimitations with the GMYC model: Insights from a butterfly survey. *Meth. Ecol. Evol.* 4: 1101–1110. https://doi.org/10.1111/2041-210X.12107

Tan, G., Muffato, M., Ledergerber, C., Herrero, J., Goldman, N., Gil, M. & Dessimoz, C. 2015. Current methods for automated filtering of multiple sequence alignments frequently worsen single-gene phylogenetic inference. *Syst. Biol.* 64: 778–791. https://doi.org/10.1093/sysbio/syv033

Thornhill, A.H., Mishler, B.D., Knerr, N.J., González-Orozco, C.E., Costion, C.M., Crayn, D.M., Laffan, S.W. & Miller, J.T. 2016. Continental-scale spatial phylogenetics of Australian angiosperms provides insights into ecology, evolution and conservation. *J. Biogeogr.* 43: 2085–2098. https://doi.org/10.1111/jbi.12797

Van der Geer, A., Lyras, G., De Vos, J. & Dermitzakis, M. 2010. *Evolution of island mammals: Adaptation and extinction of placental mammals on islands*. Chichester: Wiley-Blackwell. https://doi.org/10.1002/9781444323986

Wei, X., McCune, B., Lumbsch, H.T., Li, H., Leavitt, S., Yamamoto, Y., Tchabanenko, S. & Wei, J. 2016. Limitations of species delimitation based on phylogenetic analyses: A case study in the *Hypogymnia hypotrypa* group (Parmeliaceae, Ascomycota). *PLoS ONE* 11: e0163664. https://doi.org/10.1371/journal.pone.0163664

Werth, S., Wagner, H.H., Holderegger, R., Kalwij, J.M. & Scheidegger, C. 2006. Effect of disturbances on the genetic diversity of an old-forest associated lichen. *Molec. Ecol.* 15: 911–921. https://doi.org/10.1111/j.1365-294X.2006.02838.x

Widhelm, T.J., Egan, R.S., Bertoletti, F.R., Asztalos, M.J., Kraichak, E., Leavitt, S.D. & Lumbsch, H.T. 2016. Picking holes in traditional species delimitations: an integrative taxonomic reassessment of the *Parmotrema perforatum* group (Parmeliaceae, Ascomycota). *Bot. J. Linn. Soc.* 182: 868–884. https://doi.org/10.1111/boj.12483

Widhelm, T.J., Bertoletti, F.R., Asztalos, M.J., Mercado-Díaz, J.A., Huang, J.P., Moncada, B., Lücking, R., Magain, N., Sérusiaux, E., Goffinet, B., Crouch, N., Mason-Gamer, R. & Lumbsch, H.T. 2018. Oligocene origin and drivers of diversification in the genus *Sticta* (Lobariaceae, Ascomycota). *Molec. Phylogen. Evol.* 126: 58–73. https://doi.org/10.1016/j.ympev.2018.04.006

Widhelm, T.J., Grewe, F., Huang, J.P., Mercado-Díaz, J.A., Goffinet, B., Lücking, R., Moncada, B., Mason-Gamer, R. & Lumbsch, H.T. 2019. Multiple historical processes obscure phylogenetic relationships in a taxonomically difficult group

(Lobariaceae, Ascomycota). *Sci. Rep.* 9: 8968. https://doi.org/10.1038/s41598-019-45455-x

Wiens, J.J. & Morrill, M.C. 2011. Missing data in phylogenetic analysis: Reconciling results from simulations and empirical data. *Syst. Biol.* 60: 719–731. https://doi.org/10.1093/sysbio/syr025

Will, K.W., Mishler, B.D. & Wheeler, Q.D. 2005. The perils of DNA barcoding and the need for integrative taxonomy. *Syst. Biol.* 54: 844–851. https://doi.org/10.1080/10635150500354878

Woods, C., Borroto-Paéz, R. & Kilpatrick, C. 2001. Insular patterns and radiations of West Indian rodents. Pp. 335–353 in: Woods, C. & Sergile, F. (eds.), *Biogeography of the West Indies: Patterns and perspectives*, 2nd ed. Boca Raton: CRC Press.

Yang, Z. 2015. The BPP program for species tree estimation and species delimitation. *Curr. Zool.* 61: 854–865. https://doi.org/10.1093/czoolo/61.5.854

Yang, Z. & Rannala, B. 2010. Bayesian species delimitation using multilocus sequence data. *Proc. Natl. Acad. Sci. U.S.A.* 107: 9264–9269. https://doi.org/10.1073/pnas.0913022107

Yang, Z. & Rannala, B. 2014. Unguided species delimitation using DNA sequence data from multiple loci. *Molec. Biol. Evol.* 31: 3125–3135. https://doi.org/10.1093/molbev/msu279

Zhang, J., Kapli, P., Pavlidis, P. & Stamatakis, A. 2013. A general species delimitation method with applications to phylogenetic placements. *Bioinformatics* 29: 2869–2876. https://doi.org/10.1093/bioinformatics/btt499

Zhao, X., Fernández-Brime, S., Wedin, M., Locke, M., Leavitt, S.D. & Lumbsch, H.T. 2017. Using multi-locus sequence data for addressing species boundaries in commonly accepted lichen-forming fungal species. *Organisms Diversity Evol.* 17: 351–363. https://doi.org/10.1007/s13127-016-0320-4

Appendix 1. Voucher information and GenBank accession numbers for taxa used in phylogenetic analyses in this study.

Information presented in the following order: Species, authority, country, large political subunit, collector, collector number, herbarium and GenBank accession numbers for ITS, MCM7, mtSSU, nuLSU, *RPB1*, *RPB2*, respectively. Newly generated sequences are highlighted in bold. Missing sequences are indicated by a dash (–).

Lobaria pulmonaria (L.) Hoffm.: U.S.A., Michigan, *Widhelm s.n.* (F), MG367435, MF984336, MG754091, MG063078, MG754080, –. ***Pseudocyphellaria crocata*** (L.) Vain.: France, Réunion, *Magain & Sérusiaux LG0688* (LG), JQ735976, –, JQ736009, JQ735993, KT281770, –. ***Ricasolia amplissima*** (Scop.) De Not.: U.S.A., Alaska, *Dillman 2008-602* (WSL), KX385118, –, KC494188, –, –, KX385158. ***Sticta ambavillaria*** (Bory) Ach.: France, Réunion, *Magain & Sérusiaux LG0992* (LG), JQ735978, –, JQ736011, JQ735995, –, –. ***Sticta andensis*** (Nyl.) Trevis.: Colombia, Cundinamarca, *Lücking & Moncada 35422* (B, F, UDBC), KC732548, MF984317, MG754134, MG062956, –, –. ***Sticta*** aff. ***andensis*** (Nyl.) Trevis.: Colombia, Cundinamarca, *Moncada 4009* (B, F, UDBC), KC732467, MF984316, MG754142, MG062955, –, –. ***Sticta andina*** Moncada, Lücking & Sérus.: Colombia, Boyacá, *Suárez 212* (B, F, UDBC), MG367388, MF984249, MG754100, MG062970, MG754086, –; Colombia, Cundinamarca, *Alfonso 4* (B, F, UDBC), KC732537, MF984248, MG754099, MG062967, MG754084, –; Colombia, Cundinamarca, *Moncada 4592* (B, F, UDBC), KC732548, MF984247, MG754101, MG062966, –, –; Colombia, Cundinamarca, *Moncada 4802* (B, F, UDBC), KC732688, MF984321, MG754161, MG062969, –, –; Colombia, Cundinamarca, *Moncada 4814* (B, F, UDBC), KC732753, MF984250, MG754159, MG062972, MG754085, –; Colombia, Cundinamarca, *Moncada 4944* (B, F, UDBC), MG367394, MF984245, MG754163, MG062968, –, –; Colombia, Cundinamarca, *Moncada & Lücking 4594* (B, F, UDBC), KC732712, –, –, MG062975, –, –; Ecuador, –, *Dal Forno 1773* (B, F), MG367415, MF984251, MG754160, MG062971, –, –. ***Sticta*** aff. ***andina*** Moncada, Lücking & Sérus.: Colombia, Boyacá, *Simijaca 1698* (B, F, UDBC), KC732546, MF984246, MG754105, MG062974, MG754083, –; Colombia, Cundinamarca, *Moncada 3119* (B, F, UDBC), KC732486, –, –, MG062973, –, –. ***Sticta*** aff. ***andreana*** (Müll. Arg.) Zahlbr.: Costa Rica, San José, *Moncada 5620* (B, F, CR), MG367402, MF984284, –, MG063062, –, –. ***Sticta arachnofuliginosa*** Moncada & Lücking: Colombia, Cundinamarca, *Moncada 4007* (B, F, UDBC), KC732524, MF984306, –, MG062946, –, –. ***Sticta arbuscula*** Moncada & Lücking: Colombia, Cundinamarca, *Lücking & Moncada 33324* (B, F, UDBC), KC732682, –, –, MG063046, –, –. ***Sticta*** aff. ***arbuscula*** Moncada & Lücking: Colombia, Boyacá, *Fonseca 49* (B, F, UDBC), KC732619, –, MG754092, MG063045, MG754090, –. ***Sticta arbusculotomentosa*** Moncada & Betanc.: Colombia, Cundinamarca, *Betancourt 326* (B, F, UDBC), KC732572, MF984220, –, MG063041, –, –. ***Sticta atlantica*** Magain & Sérus.: Ireland, Munster, *Sérusiaux LG3747* (LG), KT281734, –, KT281690, KT281645, –, –; Portugal, Azores, *Sérusiaux LG3858* (LG), KT281737, –, KT281693, KT281648, KT281784, –. ***Sticta atroandensis*** Moncada & Lücking: Colombia, Boyacá, *Fonseca 23* (B, F, UDBC), KC732533, MF984310, –, MG062952, MG754082, –. ***Sticta babingtonii*** D.J.Galloway: New Zealand, Northland, *De Lange 12640* (AK, B, F), MF373808, MF984256, MG754167, MG063012, –, –. ***Sticta beauvoisii*** Delise: Colombia, Boyacá, *Suárez 318* (B, F, UDBC), KC732707, MF984328, –, MG062958, –, –; U.S.A, North Carolina, *Quedensley 16699* (F), MG754194, MF984244, –, MG062957, –, –; U.S.A., Georgia, *Fraker & al. 872* (DUKE), –, –, DQ986867, DQ986769, –, DQ992456; U.S.A., North Carolina, *Goffinet 11137* (LG), KT281725, –, KT281681, KT281636, KT281787, –; U.S.A., North Carolina, *Goffinet 11141* (LG), KT281724, –, KT281680, KT281635, KT281786, –. ***Sticta borinquensis*** Merc.-Díaz & Lücking: Puerto Rico, Jayuya, *Mercado-Díaz 2308* (F, UPR), **MN065850**, –, –, –, –, –; Puerto Rico, Jayuya, *Mercado-Díaz 2301b* (F, UPR), **MN065849**, –, –, **MN065965**, **MN066014**, **MN066067**; Puerto Rico, Rio Grande, *Lücking 33919* (F, UPR), MG367397, MF984263, –, MG062976, **MN066016**, –; Puerto Rico, Rio Grande, *Mercado-Díaz 2365* (F, UPR), **MN065851**, –, –, –, –, –; Puerto Rico, Rio Grande, *Mercado-Díaz 2367* (F, UPR), **MN065852**, –, –, –, –, –; Puerto Rico, Rio Grande, *Mercado-Díaz 2374* (F, UPR), **MN065853**, –, –, –, –, **MN066068**; Puerto Rico, Rio Grande, *Mercado-Díaz 2376* (F, UPR), **MN065854**, –, –, –, –, –; Puerto Rico, Rio Grande, *Mercado-Díaz 2377* (F, UPR), **MN065855**, –, –, –, –, **MN066069**; Puerto Rico, Rio Grande, *Mercado-Díaz 2379* (F, UPR), **MN065856**, –, –, –, –, **MN066070**; Puerto Rico, Rio Grande, *Mercado-Díaz 2381* (F, UPR), **MN065857**, –, –, –, –, –; Puerto Rico, Rio Grande, *Mercado-Díaz 2382* (F, UPR), **MN065858**, –, –, –, –, –; Puerto Rico, Rio Grande, *Mercado-Díaz 2383* (F, UPR), **MN065859**, –, –, –, –, **MN066071**; Puerto Rico, Rio Grande, *Mercado-Díaz 3639* (F, UPR), **MN065860**, –, –, **MN065966**, **MN066017**, **MN066122**. ***Sticta*** aff. ***borinquensis*** Merc.-Díaz & Lücking: Puerto Rico, Jayuya, *Mercado-Díaz 2301a* (F, UPR), **MN065847**, –, –, **MN065963**, **MN066015**, **MN066065**; Puerto Rico, Jayuya, *Mercado-Díaz 2301c* (F, UPR), **MN065848**, –, –, **MN065964**, –, **MN066066**. ***Sticta brevior*** Moncada & Lücking: Colombia, Cundinamarca, *Moncada 4590b* (B, F, UDBC), MG367386, –, MG754108, MG062929, –, –. ***Sticta caliginosa*** D.J.Galloway: New Zealand, Manawatu-Manganui, *Lücking & al. 39038* (AK, B, F), MF373767, –, MG754136, MG063036, –, –; New Zealand, Waikato, *Lücking & al. 39060a* (AK, B, F), MF373760, MF984229, MG754135, MG063035, –, –. ***Sticta*** aff. ***caliginosa*** D.J.Galloway: U.S.A., Hawaii, *Moncada 6949* (F), MG367425, MF984211, MG754137, MG063037, –, –. ***Sticta canariensis*** (Bory) Bory ex Delise: Ireland, Munster, *Sérusiaux LG3741* (LG), KT281733, –, KT281689, KT281644, KT281779, –; Spain, Canary Islands, *Sérusiaux LG1333* (LG), KT281700, –, KT281658, KT281612, KT281752, –. ***Sticta*** aff. ***canariensis*** (Bory) Bory ex Delise: Brazil, Santa Catarina, *Gumboski 3929* (B, F, JOI), MG367417, –, –, MG063000, –, –. ***Sticta caperata*** (Nyl.) Nyl.: France, Réunion, *Magain & Sérusiaux LG0962* (LG), JQ735979, –, JQ736012, JQ735996, KT281745, –. ***Sticta carolinensis*** T.McDonald: U.S.A, North Carolina, *Quedensley 16700* (F), –, MF984234, MG754116, MG063074, –, –. ***Sticta*** cf. ***lhermineri*** (Nyl. ex Stizenb.) Vain.: Colombia, Casanare, *Vargas & Herrera 634* (B, F, UDBC), MG367393, MF984331, –, MG063009, –, –. ***Sticta*** cf. ***sinuosa*** Pers.: Colombia, Boyacá, *Simijaca 1725* (B, F, UDBC), KC732554, MF984296, –, MG062977, –, –. ***Sticta ciliata*** Taylor: Colombia, Casanare, *Vargas & Herrera 64b* (B, F, UDBC), KC732699, MF984325, –, MG063040, –, –; France, Brittany, *Gérault LG3539* (LG), KT281718, –, KT281674, KT281630, KT281774, –; France, Brittany, *Gérault LG3542* (LG), KT281714, –, KT281670, KT281626, KT281772, –; Ireland, Munster, *Sérusiaux LG3781* (LG), KT281716, –, KT281672, KT281628, KT281773, –; Portugal, Azores, *Divakar LG 3099* (LG), KT281715, –, KT281671, KT281627, KT281762, –; Rwanda, –, *Sérusiaux LG1605* (LG), KT281717, –, KT281673, KT281629, KT281763, –; Spain, Canary Islands, *Sérusiaux LG3406* (LG), KT281713, –, KT281669, KT281625, KT281780, –; Spain, Canary Islands, *Sérusiaux LG3830* (LG), KT281719, –,

Appendix 1. Continued.

KT281675, KT281631, KT281775, –; Spain, Canary Islands, *Van den Boom 45673* (LG), KT281712, –, KT281668, KT281624, –, –. ***Sticta*** aff. ***ciliata*** Taylor: Colombia, Valle del Cauca, *Moncada 4678* (B, F, UDBC), KC732607, MF984324, MG754144, MG063039, –, –. ***Sticta cinereoglauca*** Hook.f. & Taylor: New Zealand, Chatham Islands, *De Lange CH2449* (AK, B, F), MG367380, MF984224, –, MG063027, –, –; New Zealand, Hawke's Bay, *Lücking & al. 38646* (AK, B, F), MF373798, MF984241, MG754140, MG063029, –, –; New Zealand, Hawke's Bay, *Lücking & al. 38776* (AK, B, F), MF373794, MF984242, MG754139, MG063028, –, –. ***Sticta cometia*** Ach.: Colombia, Riseralda, *Coca 1067* (B, F, UDBC), KC732626, MF984222, MG754178, MG062927, –, –. ***Sticta cometiella*** Vain.: Colombia, Cesar, *Moncada 4209* (B, F, UDBC), KC732517, MF984221, MG754177, MG062926, –, –. ***Sticta*** aff. ***cordillerana*** Gyeln.: Colombia, Boyacá, *Simijaca 1731* (B, F, UDBC), KC732553, MF984252, MG754120, MG062963, –, –. ***Sticta corymbosa*** Merc.-Díaz & Moncada: Puerto Rico, Rio Grande, *Mercado-Díaz 2378* (F, UPR), **MN065843**, –, –, **MN066002**, –, **MN066097**; Puerto Rico, Rio Grande, *Mercado-Díaz 2380* (F, UPR), **MN065844**, –, –, **MN066003**, **MN066054**, **MN066098**; Puerto Rico, Rio Grande, *Mercado-Díaz 2384* (F, UPR), **MN065845**, –, –, **MN066004**, –, **MN066099**; Puerto Rico, Rio Grande, *Mercado-Díaz 2385* (F, UPR), **MN065846**, –, –, **MN066005**, –, **MN066100**. ***Sticta dendroides*** (Nyl.) Moncada, Lücking & De Lange: New Zealand, Hawke's Bay, *Lücking & al. 38734* (AK, B, F), MF373799, MF984272, MG754188, MG063025, –, –; New Zealand, Manawatu-Manganui, *Lücking & al. 39007* (AK, B, F), MF373805, MF984253, –, MG063026, –, –; New Zealand, Waikato, *Lücking & al. 39060b* (AK, B, F), –, MF984233, –, MG063073, –, –. ***Sticta densiphyllidiata*** Merc.-Díaz & Lücking: Puerto Rico, Rio Grande, *Lücking 33871* (F, UPR), MG367398, MF984239, –, MG062987, –, **MN066081**; Puerto Rico, Rio Grande, *Mercado-Díaz 2389* (F, UPR), **MN065890**, **MN065905**, –, **MN065980**, –, **MN066080**. ***Sticta dichotoma*** Bory ex Delise: France, Réunion, *Magain & Sérusiaux LG0945* (LG), JQ735981, –, JQ736014, JQ735998, KT281743, –; France, Réunion, *Magain & Sérusiaux LG0984* (LG), JQ735982, –, JQ736015, JQ735999, KT281746, –. ***Sticta dilatata*** (Nyl.) Vain.: Colombia, Risaralda, *Coca 1077a* (B, F, UDBC), KC732647, –, MG754125, MG063057, –, –. ***Sticta*** aff. ***dilatata*** (Nyl.) Vain.: Costa Rica, San José, *Moncada 5675* (B, F, CR), MG367405, MF984214, MG754127, MG063058, –, –. ***Sticta duplolimbata*** (Hue) Vain.: France, Réunion, *Magain & Sérusiaux LG1040* (LG), JQ735984, –, JQ736001, JQ736017, KT281751, –; Rwanda, –, *Sérusiaux LG0919* (LG), KT281696, –, KT281654, KT281651, KT281741, –. ***Sticta filix*** (Sw.) Nyl.: New Zealand, Manawatu-Manganui, *Lücking & al. 39034* (AK, B, F), MF373766, –, –, MG063011, –, –; New Zealand, North Island, *De Lange 12284* (AK, B, F), MG367379, MF984228, –, MG063010, –, –. ***Sticta fuliginoides*** Magain & Sérus.: France, Brittany, *Séité LG3551* (LG), KT281729, –, KT281685, KT281640, KT281777, –; France, Grand Est, *Sérusiaux LG1421* (LG), KT281701, –, KT281659, KT281613, KT281753, –; Ireland, Munster, *Sérusiaux LG3733* (LG), KT281732, –, KT281688, KT281643, KT281781, –; Spain, Canary Islands, *Sérusiaux LG3012* (LG), KT281722, –, KT281678, KT281634, KT281765, –; United Kingdom, England, *Magain LGS4* (LG), KT281738, –, KT281694, KT281649, KT281785, –; United Kingdom, Wales, – *SN739972* (B, F), KC732454, MF984215, –, MG063047, –, –. ***Sticta*** aff. ***fuliginoides*** Magain & Sérus.: Colombia, Cundinamarca, *Moncada & Lücking 4786* (B, F, UDBC), KC732709, MF984304, –, MG063048, –, –. ***Sticta fuliginosa*** (Dicks.) Ach.: Australia, Tasmania, *Lumbsch & al. 2376* (F, UPR), MG754192, MF984305, MG754180, MG062943, –, –; Brazil, Rio Grande do Sul, *Gumboski 3536* (B, F, JOI), MG367419, MF984303, MG754184, MG062939, –, –; France, Brittany, *Bouffinier LG3537* (LG), KT281727, –, KT281683, KT281638, KT281766, –; France, Réunion, *Magain & Sérusiaux LG0989* (LG), KT281698, –, KT281656, KT281610, KT281747, –; Ireland, Munster, *Sérusiaux LG3729* (LG), KT281731, –, KT281687, KT281642, KT281768, –; Madagasgar, Fianarantosa, *Sérusiaux LG0795* (LG), KT281695, –, KT281653, KT281609, KT281740, –; Portugal, Azores, *Divakar LG3100* (LG), KT281704, –, KT281662, KT281616, KT281756, –; Rwanda, –, *Sérusiaux LG1611* (LG), KT281702, –, KT281660, KT281614, KT281754, –; South Africa, –, *Goffinet 10242* (LG), KT281703, –, KT281661, KT281615, KT281755, –; Spain, Canary Islands, *Sérusiaux LG3010* (LG), KT281721, –, KT281677, KT281633, KT281776, –; U.S.A., Hawaii, *Moncada 6978* (F), MG367426, –, MG754185, MG062941, –, –; U.S.A., Hawaii, *Moncada 6979* (F), MG367427, MF984300, MG754186, MG062944, –, –; U.S.A., Hawaii, *Moncada 7026* (F), MG367432, MF984301, MG754182, MG062942, –, –; United Kingdom, England, *Magain LGS9* (LG), KT281739, –, –, KT281650, KT281769, –. ***Sticta*** aff. ***fuliginosa*** (Dicks.) Ach.: Canada, British Columbia, *Goward 09_246b* (LG), KT281723, –, KT281679, –, –, –; Spain, Canary Islands, *Sérusiaux LG2229* (LG), KT281705, –, KT281663, KT281617, KT281757, –; Spain, Canary Islands, *Van den Boom 46379* (LG), KT281720, –, KT281676, KT281632, KT281764, –; U.S.A., Oregon, *McCune s.n.* (F, hb. McCune), MG367377, MF984203, –, –, MG754081, –. ***Sticta fuscotomentosa*** Moncada, Coca & Lücking: Colombia, Risaralda, *Coca 1207* (B, F, UDBC), KC732661, MF984280, MG754126, MG063070, –, –. ***Sticta gallowayana*** Moncada, A.Suárez & Lücking: Colombia, Cundinamarca, *Moncada 4637* (B, F, UDBC), KC732496, MF984285, –, MG062934, MG754087, –. ***Sticta globulifuliginosa*** Moncada, A.Suárez & Lücking: Colombia, Cundinamarca, *Moncada 4757* (B, F, UDBC), KC732608, –, –, MG062924, –, –. ***Sticta*** aff. ***granatensis*** Nyl.: Ecuador, –, *Dal Forno 1787a* (B, F), MG367416, –, MG754117, MG062990, –, –. ***Sticta guilartensis*** Merc.-Díaz: Puerto Rico, Adjuntas, *Mercado-Díaz 2426* (F, UPR), **MN065863**, **MN065908**, –, **MN065955**, –, **MN066060**; Puerto Rico, Adjuntas, *Mercado-Díaz 2429* (F, UPR), **MN065861**, **MN065909**, –, **MN065956**, **MN066032**, **MN066061**; Puerto Rico, Adjuntas, *Mercado-Díaz 2431* (F, UPR), –, **MN065910**, –, **MN065957**, –, **MN066062**; Puerto Rico, Adjuntas, *Mercado-Díaz 3666* (F, UPR), **MN065862**, **MN065907**, –, **MN065958**, **MN066030**, **MN066114**; Puerto Rico, Adjuntas, *Mercado-Díaz 3671* (F, UPR), **MN065864**, **MN065906**, **MN065954**, **MN065959**, **MN066031**, **MN066120**. ***Sticta*** aff. ***guilartensis*** Merc.-Díaz: Puerto Rico, Orocovis, *Mercado-Díaz 3659* (F, UPR), **MN065866**, –, –, **MN066013**, **MN066033**, **MN066104**; Puerto Rico, Orocovis, *Mercado-Díaz 3660* (F, UPR), **MN065865**, –, **MN065941**, **MN066012**, **MN066034**, **MN066103**. ***Sticta gyalocarpa*** (Nyl.) Trevis.: Colombia, Cundinamarca, *Moncada 4728* (B, F, UDBC), KC732594, MF984327, MG754111, MG063043, MG754089, –. ***Sticta*** aff. ***gyalocarpa*** (Nyl.) Trevis.: Costa Rica, San José, *Moncada 5649* (B, F, CR), MG367403, MF984326, –, MG063044, –, –. ***Sticta harrisii*** Merc.-Díaz, Moncada & Lücking: Puerto Rico, Patillas, *Mercado-Díaz 3624* (F, UPR), **MN065836**, **MN065916**, –, **MN065996**, **MN066041**, **MN066112**; Puerto Rico, Rio Grande, *Lücking 33868* (F, UPR), **MN065835**, –, –, **MN065995**, **MN066048**, **MN066095**; Puerto Rico, Rio Grande, *Lücking 33894* (F, UPR), **MN065834**, –, –, **MN065994**, **MN066046**, **MN066093**; Puerto Rico, Rio Grande, *Lücking 33905* (F, UPR), KC732774, MF984282, MG754190, MG063072, **MN066047**, **MN066094**; Puerto Rico, Rio Grande, *Mercado-Díaz 2913* (F, UPR), **MN065830**, **MN065918**, –, **MN065991**, –, **MN066091**; Puerto Rico, Rio Grande, *Mercado-Díaz 2915* (F, UPR), **MN065831**, **MN065919**, –, **MN065992**, –, **MN066092**; Puerto Rico, Rio Grande, *Mercado-Díaz 2916* (F, UPR), **MN065832**, –, –, –, –, –; Puerto Rico, Rio Grande, *Mercado-Díaz 2917* (F, UPR), **MN065833**, –, –, **MN065993**, –, –; Puerto Rico, Rio Grande, *Mercado-Díaz 3637* (F, UPR), –, **MN065915**, –, –, **MN066040**, **MN066123**; Puerto Rico, Rio Grande, *Mercado-Díaz 3645* (F, UPR), **MN065838**, **MN065914**, **MN065947**, **MN066000**, **MN066039**, **MN066111**; Puerto Rico, Rio Grande, *Mercado-Díaz 3650* (F, UPR), **MN065839**, **MN065913**, **MN065948**, **MN065999**, **MN066044**, **MN066113**; Puerto Rico, Rio Grande, *Mercado-Díaz 3652* (F, UPR), **MN065840**, **MN065912**, **MN065946**, **MN065998**, **MN066043**, **MN066110**; Puerto Rico, Rio Grande, *Mercado-Díaz 3653* (F, UPR), **MN065841**, **MN065911**, **MN065945**, **MN065997**, **MN066042**, **MN066109**; Puerto Rico, San Lorenzo, *Mercado-Díaz 2282* (UPR), MG367376, MF984281, –, MG063071, **MN066045**, **MN066089**; Puerto Rico, San Lorenzo, *Mercado-Díaz 2283a* (F, UPR), –, **MN065917**, –, **MN065989**, –, **MN066090**; Puerto Rico, San Lorenzo, *Mercado-Díaz 2285b* (F, UPR), **MN065837**, –, –, **MN065990**, –, **MN066096**. ***Sticta*** aff. ***harrisii*** Merc.-Díaz, Moncada & Lücking: Puerto Rico, Rio Grande, *Mercado-Díaz 3646* (F, UPR), **MN065842**, **MN065898**, **MN065949**, **MN066001**, **MN066038**, **MN066108**. ***Sticta hirsutofuliginosa*** Moncada, A.Suárez & Lücking: Colombia, Cundinamarca, *Moncada 4731* (B, F, UDBC), KC732610, MF984311, MG754152, MG062950, –, –. ***Sticta humboldtii*** Hook.: Colombia, Valle del Cauca, *Diaz-Escandón L2* (B, F, UDBC), KC732702, MF984312, MG754118, MG062951, –, –. ***Sticta*** aff. ***humboldtii*** Hook.: Colombia, Cundinamarca, *Moncada 4733* (B, F, UDBC), KC732580, MF984309, MG754154, MG062948, –, –. ***Sticta impressula*** (Nyl.) Zahlbr.: Colombia, Risaralda, *Coca 1014* (B, F, UDBC), KC732646, MF984287, MG754110, MG062931, –, –. ***Sticta isidiokunthii*** Moncada & Lücking: Colombia, Cundinamarca, *Moncada 4630* (B, F, UDBC), KC732522, MF984288, MG754189, MG062930, MG754088, –. ***Sticta jaguirreana*** Moncada, A.Suárez & Lücking: Colombia, Cundinamarca, *Moncada 4804* (B, F, UDBC), MG754195, –, MG754162, MG062999, –, –. ***Sticta laciniata*** Ach.: Costa Rica, San José, *Moncada 5778* (B, F, CR), MG367399, –, MG754179, MG062984, –, –. ***Sticta*** aff. ***laciniosa*** D.J.Galloway: Costa Rica, San José, *Moncada 5789* (B, F, CR), MG367401, MF984240, –, MG062988, –, –. ***Sticta laevis*** (Nyl.) Vain.: Colombia, Boyacá, *Fonseca 259* (B, F, UDBC), MG367409, MF984206, –, MG063052, –, –. ***Sticta latifrons*** A.Rich.: New Zealand, Chatham Islands, *De Lange CH2517* (AK, B, F), MF373763, MF984230, MG754173, MG063015, –, –;

Appendix 1. Continued.

New Zealand, Waikato, *Lücking & al. 38815* (AK, B, F), MF373800, –, –, MG063016, –, –. ***Sticta leucoblepharis*** Mont.: Colombia, Valle del Cauca, *Moncada 4689* (B, F, UDBC), KC732597, MF984276, –, MG063063, –, –. ***Sticta*** aff. ***lherminieri*** (Nyl. ex Stizenb.) Vain.: Colombia, Valle del Cauca, *Lücking & Moncada 33511* (B, F, UDBC), KC732673, MF984269, MG754145, MG063008, –, –. ***Sticta limbata*** (Sm.) Ach.: Canada, British Columbia, *Goward 09-246a* (LG), KT281710, –, –, KT281622, –, –; France, Brittany, *Gérault LG3544* (LG), KT281728, –, KT281684, KT281639, KT281767, –; Portugal, Azores, *Divakar LG3105* (LG), KT281709, –, KT281667, KT281621, –, –; Portugal, Azores, *Sérusiaux LG3868* (LG), KT281711, –, –, KT281623, KT281761, –; Spain, Canary Islands, *Sérusiaux LG2230* (LG), KT281706, –, KT281664, KT281618, KT281758, –; Spain, Canary Islands, *Van den Boom 46085* (LG), KT281708, –, KT281666, KT281620, KT281760, –; United Kingdom, Scotland, *Coppins LG2690* (LG), KT281707, –, KT281665, KT281619, KT281759, –. ***Sticta*** aff. ***limbata*** (Sm.) Ach.: Brazil, Rio Grande do Sul, *Gumboski 3560* (B, F, JOI), MG367418, MF984294, MG754183, MG062945, –, –; U.S.A., Hawaii, *Moncada 6995* (F), MG367428, MF984298, MG754181, MG062940, –, –; U.S.A., Oregon, *McCune s.n.* (F, hb. McCune), MG367378, MF984292, –, –, –, –. ***Sticta lobarioides*** Moncada & Coca: Colombia, Cundinamarca, *Alfonso 5* (B, F, UDBC), KC732555, MF984238, MG754113, MG062992, –, –. ***Sticta lumbschiana*** Moncada & Lücking: Colombia, Cundinamarca, *Lücking & Moncada 33370* (B, F, UDBC), KC732575, MF984212, MG754124, MG063055, –, –. ***Sticta macrocyphellata*** Moncada & Coca: Colombia, Risaralda, *Coca 1267* (B, F, UDBC), KC732662, MF984313, –, MG063056, –, –. ***Sticta macrophylla*** Bory ex Delise: France, Réunion, *Magain & Sérusiaux LG0946* (LG), JQ735985, –, JQ736018, JQ736002, KT281744, –. ***Sticta macrothallina*** Moncada & Coca: Colombia, Risaralda, *Coca 1115* (B, F, UDBC), KC732629, MF984208, MG754122, MG063034, –, –; Colombia, Risaralda, *Coca 1210* (B, F, UDBC), KC732655, MF984314, MG754106, MG063032, –, –; Colombia, Risaralda, *Coca 1376* (B, F, UDBC), KC732637, –, MG754107, MG063033, –, –. ***Sticta maculofuliginosa*** Moncada & Lücking: Colombia, Cundinamarca, *Moncada 4156* (B, F, UDBC), KC732514, MF984235, –, –, –, –. ***Sticta marginalis*** Bory: France, Réunion, *Magain & Sérusiaux LG1023* (LG), JQ735980, –, JQ736013, JQ735997, KT281748, –. ***Sticta*** aff. ***marginalis*** Bory: U.S.A., Hawaii, *Moncada 6916* (F), MG754196, –, MG754095, MG062921, –, –. ***Sticta menziesii*** Hook.f. & Taylor: New Zealand, Manawatu-Manganui, *Lücking & al. 39001* (AK, B, F), MF373788, MF984254, –, MG063014, –, –; New Zealand, Manawatu-Manganui, *Lücking & al. 39011* (AK, B, F), –, MF984257, –, MG063076, –, –; New Zealand, Waikato, *Lücking & al. 39050* (AK, B, F), MF373761, MF984225, MG754191, MG063013, –, –; New Zealand, Waikato, *Lücking & al. 39062a* (AK, B, F), –, MF984255, –, MG063075, –, –. ***Sticta minutula*** Moncada, A.Suárez & Lücking: Colombia, Cundinamarca, *Moncada 4753* (B, F, UDBC), KC732583, MF984297, –, MG063042, –, –. ***Sticta neopulmonarioides*** Moncada & Coca: Colombia, Risaralda, *Coca 949* (B, F, UDBC), KC732625, MF984204, MG754115, –, –, –; Colombia, Risaralda, *Coca 998* (B, F, UDBC), KC732652, –, –, MG062995, –, –; Colombia, Risaralda, *Coca 1069* (B, F, UDBC), KC732651, –, –, MG062994, –, –; Colombia, Risaralda, *Coca 1112* (B, F, UDBC), KC732628, –, –, MG062989, –, –; Colombia, Risaralda, *Coca 1204* (B, F, UDBC), KC732636, MF984236, –, MG062993, –, –. ***Sticta*** aff. ***neopulmonarioides*** Moncada & Coca: Colombia, Risaralda, *Coca 1095* (B, F, UDBC), KC732654, –, –, MG062997, –, –. ***Sticta papillata*** Moncada & Lücking: Colombia, Cundinamarca, *Alfonso 3* (B, F, UDBC), KC732552, MF984232, MG754123, MG063053, –, –; Colombia, Cundinamarca, *Lücking & Moncada 35400* (B, F, UDBC), MG367414, MF984283, MG754133, MG063054, –, –. ***Sticta parahumboldtii*** Moncada & Lücking: Colombia, Cundinamarca, *Moncada 4016* (B, F, UDBC), KC732550, MF984308, MG754151, MG062949, –, –. ***Sticta parvilobata*** Merc.-Díaz: Puerto Rico, Adjuntas, *Mercado-Díaz 2432* (F, UPR), **MN065878**, –, –, **MN065968**, –, **MN066074**; Puerto Rico, Adjuntas, *Mercado-Díaz 3664* (F, UPR), **MN065877**, **MN065923**, –, **MN065978**, **MN066020**, **MN066119**; Puerto Rico, Adjuntas, *Mercado-Díaz 3667* (F, UPR), **MN065879**, **MN065922**, –, **MN065975**, **MN066019**, **MN066117**; Puerto Rico, Adjuntas, *Mercado-Díaz 3668* (F, UPR), **MN065880**, **MN065921**, –, **MN065974**, **MN066018**, **MN066118**; Puerto Rico, Orocovis, *Mercado-Díaz 2260* (UPR), MG367375, MF984323, **MN065939**, MG063038, **MN066024**, **MN066072**; Puerto Rico, Orocovis, *Mercado-Díaz 2263* (F, UPR), **MN065876**, **MN065924**, –, **MN065967**, **MN066025**, **MN066073**. ***Sticta*** aff. ***parvilobata*** Merc.-Díaz: Puerto Rico, Adjuntas, *Mercado-Díaz 2435* (F, UPR), **MN065884**, –, –, –, –, –; Puerto Rico, Adjuntas, *Mercado-Díaz 3672* (F, UPR), **MN065889**, **MN065902**, –, **MN065973**, –, **MN066078**; Puerto Rico, Cayey, *Mercado-Díaz 2289* (F, UPR), **MN065885**, –, –, **MN065972**, **MN066023**, **MN066079**; Puerto Rico, Jayuya, *Coca 4563* (F, UPR), **MN065882**, –, –, –, **MN066029**, **MN066076**; Puerto Rico, Jayuya, *Mercado-Díaz 2304* (F, UPR), **MN065829**, **MN065904**, –, **MN065971**, **MN066028**, **MN066077**; Puerto Rico, Jayuya, *Moncada 8311* (F, UPR), **MN065828**, **MN065903**, –, **MN065969**, **MN066026**, –; Puerto Rico, Jayuya, *Moncada 8318* (F, UPR), **MN065881**, –, –, **MN065970**, **MN066027**, **MN066075**; Puerto Rico, Patillas, *Mercado-Díaz 3619* (F, UPR), **MN065886**, **MN065901**, –, **MN065976**, –, –; Puerto Rico, Rio Grande, *Mercado-Díaz 2914* (F, UPR), **MN065883**, –, –, –, –, –; Puerto Rico, Rio Grande, *Mercado-Díaz 3635* (F, UPR), **MN065887**, **MN065900**, –, **MN065979**, **MN066022**, **MN066124**; Puerto Rico, Rio Grande, *Mercado-Díaz 3649* (F, UPR), **MN065888**, **MN065899**, **MN065950**, **MN065977**, **MN066021**, **MN066115**. ***Sticta*** aff. ***peltigerella*** (Nyl.) Trevis.: Colombia, Cundinamarca, *Buitrago 24* (B, F, UDBC), MG367410, MF984216, MG754158, MG063049, –, –. ***Sticta phyllidiofuliginosa*** Moncada, A.Suárez & Lücking: Colombia, Cundinamarca, *Moncada 4051* (B, F, UDBC), KC732495, MF984329, –, –, –, –. ***Sticta phyllidiokunthii*** Moncada & Lücking: Colombia, Cundinamarca, *Moncada 4758* (B, F, UDBC), KC732593, MF984291, MG754112, MG062932, –, –; Colombia, Risaralda, *Coca 1206* (B, F, UDBC), KC732638, MF984286, MG754109, MG062933, –, –. ***Sticta plumbeociliata*** Moncada, A.Suárez & Lücking: Colombia, Cundinamarca, *Moncada 4820* (B, F, UDBC), KC732767, MF984290, –, MG062935, –, –. ***Sticta pseudohumboldtii*** Moncada & Lücking: Colombia, Cundinamarca, *Moncada 4928* (B, F, UDBC), KC732736, MF984307, –, MG062947, –, –. ***Sticta pseudolobaria*** Moncada & Coca: Colombia, Risaralda, *Coca 964* (B, F, UDBC), KC732650, –, –, MG062996, –, –. ***Sticta rhizinata*** Moncada & Lücking: Colombia, Cundinamarca, *Moncada 4638* (B, F, UDBC), KC732491, –, MG754097, MG062962, –, –. ***Sticta riparia*** Merc.-Díaz: Puerto Rico, Aibonito, *Mercado-Díaz 3677* (F, UPR), **MN065892**, **MN065926**, –, **MN066007**, **MN066036**, **MN066107**; Puerto Rico, Aibonito, *Mercado-Díaz 3683* (F, UPR), **MN065894**, **MN065925**, –, **MN066006**, –, **MN066106**; Puerto Rico, Aibonito, *Mercado-Díaz 3684* (F, UPR), **MN065893**, **MN065928**, **MN065942**, **MN066008**, **MN066035**, **MN066105**; Puerto Rico, Arecibo, *Mercado-Díaz 2342* (UPR), MG367373, MF984275, –, MG062986, **MN066037**, **MN066082**; Puerto Rico, Patillas, *Mercado-Díaz 3626* (F, UPR), **MN065891**, **MN065927**, **MN065951**, –, –, **MN066125**. ***Sticta scabrosa*** Moncada, Mercado-Díaz & Bungartz: Colombia, Cesar, *Moncada 4306* (B, F, UDBC), MG367387, MF984258, –, –, –, –; Puerto Rico, Cayey, *Mercado-Díaz 2287* (F, UPR), **MN065871**, **MN065933**, –, **MN065983**, **MN066051**, **MN066085**; Puerto Rico, Cayey, *Mercado-Díaz 2291* (UPR), MG367374, MF984334, –, MG063002, **MN066052**, **MN066086**; Puerto Rico, Cayey, *Mercado-Díaz 2294* (F, UPR), **MN065872**, **MN065935**, –, **MN065985**, –, **MN066088**; Puerto Rico, Cayey, *Mercado-Díaz 2293a* (F, UPR), **MN065827**, **MN065934**, –, **MN065984**, **MN066053**, **MN066087**; Puerto Rico, Patillas, *Mercado-Díaz 3622* (F, UPR), **MN065873**, **MN065931**, **MN065953**, **MN065988**, –, –; Puerto Rico, Patillas, *Mercado-Díaz 3623* (F, UPR), **MN065874**, **MN065930**, **MN065952**, **MN065987**, **MN066049**, –; Puerto Rico, Rio Grande, *Mercado-Díaz 3636a* (F, UPR), **MN065875**, **MN065929**, –, **MN065986**, –, –; Puerto Rico, San Lorenzo, *Mercado-Díaz 2283b* (F, UPR), **MN065870**, **MN065932**, –, **MN065982**, **MN066050**, **MN066084**; Puerto Rico, Villalba, *Moncada 8334* (F, UPR), **MN065869**, –, –, **MN065981**, –, **MN066083**. ***Sticta*** aff. ***scabrosa*** Moncada, Mercado-Díaz & Bungartz: Colombia, Boyacá, *Ardila 1* (B, F, UDBC), KC732478, MF984265, MG754143, MG063007, –, –. ***Sticta scabrosa*** subsp. ***hawaiiensis*** Moncada, Lücking & C.W.Sm.: U.S.A., Hawaii, *Moncada 6911* (F), MG367422, –, MG754148, MG063003, –, –; U.S.A., Hawaii, *Moncada 7014* (F), MG367429, MF984266, MG754147, MG063004, –, –; U.S.A., Hawaii, *Moncada 7016* (F), MG367431, MF984267, MG754149, MG063005, –, –; U.S.A., Hawaii, *Moncada 7054* (F), MG367430, MF984268, MG754146, MG063006, –, –. ***Sticta*** aff. ***sinuosa*** Pers.: Colombia, Boyacá, *Barragán 12* (B, F, UDBC), KC732476, MF984295, –, –, –, –. ***Sticta* sp.** –: Brazil, São Paulo, *Lücking 30122* (B, F, SP), KC732568, MF984319, –, MG062954, –, –; Colombia, Boyacá, *Fonseca 65* (B, F, UDBC), MG367407, MF984213, –, –, –, –; Colombia, Boyacá, *Fonseca 255* (B, F, UDBC), MG367408, MF984209, MG754174, MG063061, –, –; Colombia, Boyacá, *Álvaro 41218a* (B, F, UDBC), KC732482, MF984271, MG754098, MG062960, –, –; Colombia, Boyacá, *Álvaro 41218b* (B, F, UDBC), KC732727, –, –, MG062961, –, –; Colombia, Casanare, *Vargas & Herrera 556* (B, F, UDBC), MG367391, MF984237, MG754119, MG062998, –, –; Colombia, Cauca, *Diaz-Escandón L1* (B, F, UDBC), KC732701, MF984243, MG754175, –, –, –; Colombia, Cundinamarca, *Moncada 4026* (B, F, UDBC), KC732470, MF984217, –, MG062965, –, –; Colombia, Cundinamarca, *Moncada 4588* (B, F, UDBC), KC732557, –, MG754114, MG062937, –, –; Colombia, Cundinamarca, *Moncada 4746* (B, F, UDBC), KC732581, MF984289, MG754150, MG062928, –, –; Colombia,

Appendix 1. Continued.

Cundinamarca, *Moncada 4870* (B, F, UDBC), MG367395, MF984205, –, MG063060, –, –; Colombia, Cundinamarca, *Moncada 4987* (B, F, UDBC), KC732732, MF984333, –, MG062964, –, –; Colombia, Cundinamarca, *Moncada 4992* (B, F, UDBC), KC732761, MF984219, –, MG062936, –, –; Colombia, Cundinamarca, *Moncada 6131* (B, F, UDBC), MG367412, MF984207, MG754176, MG062938, –, –; Colombia, Cundinamarca, *Pérez Perez 1* (B, F, UDBC), MG367411, –, MG754153, –, –, –; Colombia, Valle del Cauca, *Lücking & Moncada 33541* (B, F, UDBC), KC732667, MF984322, MG754104, MG063001, –, –; Costa Rica, San José, *Moncada 5715b* (B, F, CR), –, MF984264, MG754121, MG063077, –, –; U.S.A., Hawaii, *Moncada 6920* (F), MG367423, MF984302, MG754093, MG062922, –, –; U.S.A., Hawaii, *Moncada 7056* (F), MG367434, MF984210, MG754094, MG062923, –, –. ***Sticta squamata*** D.J.Galloway: New Zealand, Auckland, *Lücking & al. 39200* (AK, B, F), MG367382, MF984226, MG754168, MG063031, –, –; New Zealand, Gisborne, *Lücking & al. 38562* (AK, B, F), MG367381, MF984260, MG754138, MG063030, –, –. ***Sticta stipitata*** C.Knight: Australia, Tasmania, *Lumbsch & al. 2210* (F, UPR), MG754197, MF984274, MG754141, MG063024, –, –. ***Sticta subcaperata*** (Nyl.) Nyl.: New Zealand, Auckland, *Knight s.n.* (B, F), MG754193, MF984223, MG754187, MG063021, –, –; New Zealand, Bay of Plenty, *Lücking & al. 38436* (AK, B, F), MG367383, MF984270, MG754172, MG063018, –, –; New Zealand, Hawke's Bay, *Lücking & al. 38656* (AK, B, F), MG367384, MF984227, MG754171, MG063019, –, –; New Zealand, Manawatu-Manganui, *Lücking & al. 38949* (AK, B, F), MG754200, MF984273, –, MG063022, –, –; New Zealand, Manawatu-Manganui, *Lücking & al. s.n.* (AK, B, F), MG367385, MF984261, –, MG063020, –, –; New Zealand, Waikato, *Lücking & al. 38819* (AK, B, F), MG754199, –, MG754170, MG063023, –, –; New Zealand, Waikato, *Lücking & al. 39061* (AK, B, F), MG754198, MF984231, MG754169, MG063017, –, –. ***Sticta subfilicinella*** Moncada, Coca & Lücking: Colombia, Risaralda, *Coca 1110* (B, F, UDBC), KT354937, –, –, MG063064, –, –. ***Sticta sublimbata*** (J.Steiner) Swinscow & Krog: Democratic Republic of the Congo, –, *Sérusiaux LG0885* (LG), JQ735986, –, JQ736019, JQ736003, KT281771, –; France, Réunion, *Magain & Sérusiaux LG1038* (LG), KT281699, –, KT281657, KT281611, KT281750, –. ***Sticta*** aff. ***sublimbata*** (J.Steiner) Swinscow & Krog: Colombia, Cundinamarca, *Valbuena 126* (B, F, UDBC), KC732466, –, –, MG062959, –, –. ***Sticta*** aff. ***subscrobiculata*** (Nyl.) Gyeln.: Colombia, Risaralda, *Coca 1135* (B, F, UDBC), KC732639, –, MG754096, MG062985, –, –. ***Sticta*** aff. ***subtomentella*** (C.Knight ex Shirley) Zahlbr.: Colombia, Risaralda, *Coca 1363* (B, F, UDBC), KC732730, MF984259, –, MG063059, –, –. ***Sticta sylvatica*** (Huds.) Ach.: France, Brittany, *Gérault LG3536* (LG), KT281726, –, KT281682, KT281637, KT281788, –; France, Grand Est, *Sérusiaux LG3837* (LG), KT281736, –, KT281692, KT281647, KT281783, –; Ireland, Munster, *Sérusiaux LG3780* (LG), KT281735, –, KT281691, KT281646, KT281782, –; United Kingdom, England, *Wolseley LG3723* (LG), KT281730, –, KT281686, KT281641, KT281778, –. ***Sticta*** aff. ***sylvatica*** (Huds.) Ach.: Colombia, Boyacá, *Suárez 306* (B, F, UDBC), KC732724, MF984335, –, MG062953, –, –. ***Sticta tainorum*** Merc.-Díaz: Puerto Rico, Orocovis, *Mercado-Díaz 2256* (UPR), MG367371, MF984330, **MN065944**, **MN065960**, –, **MN066063**; Puerto Rico, Orocovis, *Mercado-Díaz 2259* (F, UPR), **MN065867**, **MN065936**, –, **MN065961**, –, **MN066064**; Puerto Rico, Orocovis, *Mercado-Díaz 3661* (F, UPR), **MN065868**, **MN065937**, **MN065940**, **MN065962**, **MN066055**, **MN066121**. ***Sticta tomentosa*** (Sw.) Ach.: Colombia, Cundinamarca, *Moncada 4805* (B, F, UDBC), KC732690, MF984279, MG754128, MG063065, –, –; U.S.A., Hawaii, *Moncada 6910* (F), MG367420, –, MG754130, MG063066, –, –; U.S.A., Hawaii, *Moncada 6946* (F), MG367424, MF984278, MG754131, MG063069, –, –; U.S.A., Hawaii, *Moncada 6947* (F), MG367421, MF984277, MG754132, MG063067, –, –; U.S.A., Hawaii, *Moncada 7045a* (F), MG367433, –, MG754129, MG063068, –, –. ***Sticta*** aff. ***tomentosa*** (Sw.) Ach.: Costa Rica, San José, *Moncada 5653* (B, F, CR), MG367404, MF984218, MG754156, MG063050, –, –; Costa Rica, San José, *Moncada 5694* (B, F, CR), MG367406, MF984315, MG754157, MG063051, –, –. ***Sticta umbilicariiformis*** Hochst. ex Flot.: Rwanda, –, *Sérusiaux LG0925* (LG), KT281697, –, KT281655, KT281652, KT281742, –. ***Sticta variabilis*** Ach.: France, Réunion, *Magain & Sérusiaux LG1037* (LG), JQ735987, –, JQ736020, JQ736004, KT281749, –. ***Sticta viviana*** Alej.Suárez & Lücking: Colombia, Cundinamarca, *Lücking & Moncada 33311* (B, F, UDBC), KC732680, –, MG754155, MG062925, –, –. ***Sticta weigelii*** (Isert.) Ach.: Colombia, Cesar, *Moncada 4215b* (B, F, UDBC), KC732483, MF984262, MG754102, MG062982, –, –; Puerto Rico, Adjuntas, *Mercado-Díaz 2433* (F, UPR), **MN065896**, –, –, **MN066009**, **MN066059**, –; Puerto Rico, Maricao, *Mercado-Díaz 2246* (UPR), MG367370, MF984332, **MN065943**, MG062978, **MN066056**, **MN066101**; Puerto Rico, Rio Grande, *Mercado-Díaz 3643* (F, UPR), **MN065895**, **MN065938**, –, **MN066011**, **MN066057**, **MN066116**; Puerto Rico, San Lorenzo, *Mercado-Díaz 2284* (F, UPR), **MN065897**, –, –, **MN066010**, **MN066058**, **MN066102**. ***Sticta*** aff. ***weigelii*** (Isert.) Ach.: Colombia, Casanare, *Vargas & Herrera 343* (B, F, UDBC), MG367392, MF984293, MG754166, MG062979, –, –; Colombia, Cundinamarca, *Moncada 6164* (B, F, UDBC), MG367413, –, MG754164, MG062981, –, –; Colombia, Valle del Cauca, *Moncada & Lücking 4666* (B, F, UDBC), KC732710, MF984320, MG754165, MG062980, –, –; Colombia, Valle del Cauca, *Moncada & Lücking 4667* (B, F, UDBC), MG367390, MF984299, MG754103, MG062983, –, –. ***Sticta*** aff. ***zahlbruckneri*** B.de Lesd.: Costa Rica, San José, *Moncada 5785* (B, F, CR), MG367400, MF984318, –, MG062991, –, –.

Appendix 2. Additional specimens examined for eight new species of *Sticta* from Puerto Rico. The specimens are sorted alphabetically based on municipality ("Mun.").

Sticta borinquensis Merc.-Díaz & Lücking

Additional specimens examined: PUERTO RICO. Mun. Humacao, El Yunque National Forest, recreation area, trail up to Mt. Britton; 850–950 m; 9 Jun 1988, *Harris 22494, 22503* (NY). Mun. Jayuya, Bosque Estatal Tres Picachos, trail to Tres Picachos peaks; 18°12′52″N, 66°32′23″W; 1153 m; 29 Mar 2015, *Mercado-Díaz 2308* (UPR). Mun. Luquillo, El Yunque National Forest, Mt. Britton; 27 Jun 1963, *Imshaug 29503A, 29514* (MSC). Mun. Luquillo, El Yunque National Forest, The Pinnacles; 28 Jun 1963, *Imshaug 29551* (MSC). Mun. Luquillo, El Yunque National Forest, South of Mt. Britton on route PR-191; 29 Jun 1963, *Imshaug 29573* (MSC). Mun. Luquillo, El Yunque National Forest, PR-191 Km 11.0; 27 Jun 1967, *Landrón-Concepción 10, 12, 17, 27, 33, 39, 41, 61, 96* (MSC); ibid., 28 Jun 1967, *Landrón-Concepción 72* (MSC). Mun. Luquillo, El Yunque National Forest, PR-930 Km 1.5; 28 Jun 1967, *Landrón-Concepción 108, 122, 124, 175, 179, 183* (MSC). Mun. Luquillo, El Yunque National Forest, PR-191 Km. 13.7; 29 Jun 1967, *Landrón-Concepción 232* (MSC). Mun. Luquillo, El Yunque National Forest, Espíritu Santo River, PR-186 El Verde; Jun 23 & 30, 1967, *Landrón-Concepción 288* (MSC). Mun. Luquillo, El Yunque National Forest, East Peak, PR-186 Km. 7.7; 10–11 Jul 1967, *Landrón-Concepción 963* (MSC). Mun. Luquillo, El Yunque National Forest, Palo Colorado Association; 11 Jul 1967, *Landrón-Concepción 1008, 1016, 1020, 1024, 1032, 1044* (MSC). Mun. Luquillo, El Yunque National Forest, Palm Brake, Route to El Toro, PR-191 Km 14; 14 Jul 1967, *Landrón-Concepción 1108* (MSC). Mun. Luquillo, El Yunque National Forest, trail to El Yunque; 850 m; Mar 1985, *McCune 14773* (NY). Mun. Luquillo, El Yunque National Forest, Dwarf ridgetop forest, Mt. Britton; 1000 m; Mar 1985, *McCune 14785, 14787* (NY). Mun. Río Grande, El Yunque National Forest, Elfin forest; 18°18′04″N, 65°47′35″W; 909 m; 4 Oct 2011, *Lücking & Mercado-Díaz 33919* (F). Mun. Río Grande, El Yunque National Forest, along El Toro trail; 18°16′22″N, 65°50′02″W; 982 m; 28 Dec 2015, *Mercado-Díaz 2367* (UPR). Mun. Río Grande, El Yunque National Forest, along El Toro trail; 18°16′18″N, 65°49′52″W; 1006 m; 28 Dec 2015, *Mercado-Díaz 2374* (UPR). Mun. Río Grande, El Yunque National Forest, along El Toro trail; 18°16′22″N, 65°50′02″W; 982 m; 28 Dec 2015, *Mercado-Díaz 2376* (UPR). Mun. Río Grande, El Yunque National Forest, along El Toro trail; 18°16′18″N, 65°49′22″W; 1006 m; 28 Dec 2015, *Mercado-Díaz 2377* (UPR). Mun. Río Grande, El Yunque National Forest, along El Toro trail; 18°16′20″N, 65°49′44″W; 1049 m; 28 Dec 2015, *Mercado-Díaz 2379* (UPR). Mun. Río Grande, El Yunque National Forest, along El Toro trail; 18°16′22″N, 65°50′02″W; 982 m; 28 Dec 2015, *Mercado-Díaz 2381* (UPR). Mun. Río Grande, El Yunque National Forest, along El Toro trail; 18°16′22″N, 65°50′02″W; 982 m; 28 Dec 2015, *Mercado-Díaz 2382* (UPR). Mun. Río Grande, El Yunque National Forest, along El Toro trail; 18°16′18″N, 65°49′52″W; 1006 m; 28 Dec 2015, *Mercado-Díaz 2383* (UPR). Mun. Río Grande, El Yunque National Forest, trail to Pico El Toro from Cubuy; 18°16′24″N, 65°50′02″W; 976 m; 19 Jul 2018, *Mercado-Díaz 3638* (UPR). Mun. Río Grande, El Yunque National Forest, trail to Pico El Toro from Cubuy; 18°16′24″N, 65°50′04″W; 980 m; 26 Jul 2018, *Mercado-Díaz 3639* (UPR).

Appendix 2. Continued.

Sticta corymbosa Merc.-Díaz & Moncada

Additional specimens examined: PUERTO RICO. Mun. Las Piedras, Barrio El Río, El Yunque National Forest, at summit of Pico El Toro; 18°16′20″N, 65°49′44″W; 1048 m; 28 Dec 2015, *Mercado-Díaz 2380, 2384* (UPR). Mun. Las Piedras, Barrio El Río, El Yunque National Forest, at summit of Pico El Toro; 18°16′19″N, 65°49′45″W; 1048 m; 26 Jul 2018, *Mercado-Díaz 3654* (UPR).

Sticta densiphyllidiata Merc.-Díaz & Lücking

Additional specimens examined: PUERTO RICO. Mun. Humacao, El Yunque National Forest, about 9 mi. south of Mameyes; 16 Jun 1970, *Tucker 8645* (LSU). Mun. Luquillo, El Yunque National Forest, Catalina-Yunque trail, Luquillo Mountains, on rock; 23–26 Feb 1923, *EG Britton 7765* (NY, US). Mun. Luquillo, El Yunque National Forest, El Verde, vicinity of El Verde Biological Station; 23–24 Feb 1981, *Buck 3419* (NY). Mun. Luquillo, El Yunque National Forest; 7 Jul 1968, *Griffin III s.n.* (LSU). Mun. Luquillo, El Yunque National Forest, Valley of La Mina river; 30 Jun 1963, *Imshaug 29606, 29616* (MSC). Mun. Luquillo, El Yunque National Forest, El Verde, PR-186 Km 7.7; 2 Jun & 14 Jun 1967, *Landrón-Concepción 385* (MSC). Mun. Luquillo, El Yunque National Forest, La Mina; 29 Jun & 11 Jul 1967, *Landrón-Concepción 992, 993, 995* (MSC). Mun. Luquillo, El Yunque National Forest, foothills of El Yunque, Luquillo Mountains; 17 Jul 1902, *Wilson 316* (NY). Mun. Naguabo, El Yunque National Forest, Sierra de Naguabo, Barrio de Maizales, on rock in ravine; 600 m; 8 Mar 1914, *N.L. Britton & Cowell 3091, 3094* (NY). Mun. Naguabo, El Yunque National Forest, Río Prieto and adjacent hills, on rock; 690–1035 m; 10–15 Aug 1914, *Schafer 3696* (NY, US). Mun. Río Grande, El Yunque National Forest, trail to LFDP, El Verde Field Station; 18°19′13″N, 65°48′56″W; 415 m; 19 Jun 2013, *Mercado-Díaz 2004* (UPR). Mun. Río Grande, El Yunque National Forest, northwest slopes of low mountains, ca. one km northwest of El Yunque; 500 m; 9 Dec 1963, *Merrill-King s.n.* (US). Mun. Río Grande, El Yunque National Forest, El Verde Experimental Station, off Rt. 186 at Km. 19.1, on rock in rain forest; 2000 ft.; 22 Jan 1974, *Schmitt 1693* (US).

Sticta guilartensis Merc.-Díaz

Additional specimens examined: PUERTO RICO. Mun. Adjuntas, Bosque Estatal Guilarte, along trail to Pico Guilarte; 18°08′24″N, 66°46′12″W; 1100 m; 27 Dec 2016, *Mercado-Díaz 2429* (UPR). Mun. Adjuntas, Barrio Guilarte, along trail to Pico Guilarte, Bosque Estatal de Guilarte; 18°08′35″N, 66°46′11″W; 1095 m; 12 Dec 2016, *Mercado-Díaz 2431* (UPR). Mun. Adjuntas, Bosque Estatal Guilarte, along trail to Pico Guilarte; 18°08′37″N, 66°46′08″W; 1100 m; 30 Jul 2018, *Mercado-Díaz 3669* (UPR). Mun. Adjuntas, Bosque Estatal Guilarte, along trail to Pico Guilarte; 18°08′34″N, 66°46′09″W; 1133 m; 30 Jul 2018, *Mercado-Díaz 3670, 3671* (UPR).

Sticta harrisii Merc.-Díaz, Moncada & Lücking

Additional specimens examined: PUERTO RICO. Mun. Humacao, El Yunque National Forest, Mt. El Toro, trail from El Verde, side on Hwy 186; 1000–1074 m; 4 Jun 1988, *Buck 16041* (NY). Mun. Humacao, El Yunque National Forest, recreation area, trail up to Mt. Britton; 850–950 m; 9 Jun 1988, *Buck 16166* (NY). Mun. Humacao, El Yunque National Forest, recreation area, trail up to Mt. Britton; 850–950 m; 9 Jun 1988, *Harris 22477, 22479, 22490* (NY). Mun. Luquillo, El Yunque National Forest, Catalina-Yunque trail; 23–26 Feb 1923, *Britton E.G. 7757 (NY), 7762* (NY, US). Mun. Luquillo, El Yunque National Forest, along trail up to Mt. Britton; 941 m; 24 Feb 1981, *Buck 3527* (NY). Mun. Luquillo, El Yunque National Forest, Summit and upper slopes of Pico del Este, roadside and cloud forest; 1051 m; 5 Mar 1981, *Buck 4149* (NY). Mun. Luquillo, El Yunque National Forest; 7 Jul 1968, *Griffin III s.n.* (LSU). Mun. Luquillo, El Yunque National Forest, Mt. Britton; 27 Jun 1963, *Imshaug 29509* (MSC). Mun. Luquillo, El Yunque National Forest, PR-191 Km 11.0; 27 Jun 1967, *Landrón-Concepción 43, 95* (MSC). Mun. Luquillo, El Yunque National Forest, PR-930 Km 1.5; 28 Jun 1967, *Landrón-Concepción 104* (MSC). Mun. Luquillo, El Yunque National Forest, La Mina; 29 Jun 1967, *Landrón-Concepción 269* (MSC); ibid., 29 Jun & 11 Jul 1967, *Landrón-Concepción 270, 271, 277, 278, 279, 280, 281* (MSC). Mun. Luquillo, El Yunque National Forest, El Verde, PR-186 Km 7.7; 2 Jun & 4 Jun 1967, *Landrón-Concepción 339* (MSC). Mun. Luquillo, El Yunque National Forest, East Peak; 10 Jul 1967, *Landrón-Concepción 926, 925* (MSC). Mun. Luquillo, El Yunque National Forest, East Peak, PR-186 Km 7.7; 10–11 Jul 1967, *Landrón-Concepción 982* (MSC). Mun. Luquillo, El Yunque National Forest, La Mina; 29 Jul & 11 Jul 1967, *Landrón-Concepción 987* (MSC). Mun. Luquillo, El Yunque National Forest, Mt. Britton; 11 Jul 1967, *Landrón-Concepción 1003, 1010, 1014, 1019, 1045, 1046, 1048* (MSC). Mun. Luquillo, El Yunque National Forest, Route to El Toro, PR-191 Km 14; 14 Jul 1967, *Landrón-Concepción 1101* (MSC). Mun. Luquillo, El Yunque National Forest, Ridge from Mt. Britton to the Pinnacles; 14 Jul 1967, *Landrón-Concepción 1115, 1123, 1124, 1125* (MSC). Mun. Luquillo, El Yunque National Forest; 27 Jun 1968, *Lowy s.n., s.n.* (LSU); ibid., 21 Jun 1968, *Lowy 5316* (LSU). Mun. Luquillo, El Yunque National Forest, Dwarf ridgetop forest, Mt. Britton; 1000 m; Mar 1985, *McCune 14786* (NY). Mun. Luquillo, El Yunque National Forest, near G. González (USFS) "Britton Palm" plot; 18°18′16″N, 65°47′43″W; 917 m; 27 Sep 2011, *Mercado-Díaz 956* (UPR). Mun. Luquillo, El Yunque National Forest; 3700 ft.; 12 Jul 1902, *Wilson 165* (NY). Mun. Río Grande, El Yunque National Forest, along Mt. Britton trail; 18°18′03.6″N, 65°47′35″W; 909 m; 4 Oct 2011, *Lücking & Mercado-Díaz 33864* (UPR). Mun. Río Grande, El Yunque National Forest, along Mt. Britton trail; 18°18′05″N, 65°47′34″W; 760–940 m; 4 Oct 2011, *Lücking & Mercado-Díaz 33866* (UPR). Mun. Río Grande, El Yunque National Forest, along Mt. Britton trail; 18°18′00″N, 65°47′31″W; 812 m; 4 Oct 2011, *Lücking & Mercado-Díaz 33868* (UPR). Mun. Río Grande, El Yunque National Forest, at Mt. Britton; 18°18′03.6″N, 65°47′35″W; 909 m; 4 Oct 2011, *Lücking & Mercado-Díaz 33905, 33894* (UPR). Mun. Río Grande, El Yunque National Forest, along road PR-9338, in front of entrance to Mt. Britton trail; 18°17′55″N, 65°47′28″W; 755 m; 26 Jul 2016, *Mercado-Díaz 2915* (UPR). Mun. Río Grande, El Yunque National Forest, along Tradewinds trail; 18°16′48″N, 65°47′24″W; 667 m; 26 Jul 2016, *Mercado-Díaz 2916* (UPR). Mun. Río Grande, El Yunque National Forest, along Tradewinds trail; 18°16′48″N, 65°48′36″W; 823 m; 26 Jul 2016, *Mercado-Díaz 2917* (UPR). Mun. Río Grande, El Yunque National Forest, trail to Pico El Toro from Cubuy; 18°16′18″N, 65°49′53″W; 1006 m; 19 Jul 2018, *Mercado-Díaz 3637* (UPR). Mun. Río Grande, El Yunque National Forest, trail to Pico El Toro from Cubuy; 18°16′19″N, 65°49′50″W; 900 m; 26 Jul 2018, *Mercado-Díaz 3645, 3647, 3648* (UPR). Mun. Río Grande, El Yunque National Forest, near Pico El Toro summit; 18°16′20″N, 65°49′45″W; 1040 m; 26 Jul 2018, *Mercado-Díaz 3650, 3651* (UPR). Mun. Río Grande, El Yunque National Forest, along trail to Pico El Toro; 18°16′20″N, 65°49′50″W; 980 m; 26 Jul 2018, *Mercado-Díaz 3652* (UPR). Mun. Río Grande, El Yunque National Forest, along trail to Pico El Toro; 18°16′19″N, 65°49′50″W; 980 m; 26 Jul 2018, *Mercado-Díaz 3653* (UPR). Mun. San Lorenzo, Bosque Estatal de Carite, along road that access TV network's antennas; 18°06′36″N, 66°03′05″W; 885 m; 29 Jan 2015, *Mercado-Díaz 2283a* (UPR). Mun. San Lorenzo, Bosque Estatal de Carite, along road that access TV network's antennas; 18°06′36″N, 66°03′05″W; 885 m; 29 Jan 2015, *Mercado-Díaz 2283a, 2285, 2285b* (UPR). Mun. San Lorenzo, Bosque Estatal de Carite, along road that access TV network's antennas; 18°06′36″N, 66°03′00″W; 885 m; 29 Jan 2015, *Mercado-Díaz 2288, 2290* (UPR). Mun. San Lorenzo, Bosque Estatal de Carite, along road that access TV network's antennas; 18°06′36″N, 66°03′05″W; 885 m; 16 Jul 2018, *Mercado-Díaz 3624* (UPR).

Sticta parvilobata Merc.-Díaz

Additional specimens examined: PUERTO RICO. Mun. Adjuntas, Barrio Guilarte, Bosque Estatal de Guilarte, along trail to Pico Guilarte; 18°08′41″N, 66°46′08″W; 1058 m; 30 Jul 2018, *Mercado-Díaz 3664* (UPR). Mun. Adjuntas, Barrio Guilarte, Bosque Estatal de Guilarte, along trail to Pico Guilarte; 18°08′37″N, 66°46′08″W; 1100 m; 30 Jul 2018, *Mercado-Díaz 3667* (UPR). Mun. Adjuntas, Barrio Guilarte, Bosque Estatal de Guilarte, along trail to Pico Guilarte; 18°08′34″N, 66°46′08″W; 1138 m; 30 Jul 2018, *Mercado-Díaz 3672* (UPR). Mun. Orocovis, Barrio Bauta Abajo, Toro Negro State Forest, along El Bolo trail; 18°10′19″N, 66°29′07″W; 927 m; 22 Jan 2015, *Mercado-Díaz 2263* (UPR).

Sticta riparia Merc.-Díaz

Additional specimens examined: PUERTO RICO. Mun. Aibonito, San Cristobal Canyon, rock inside riparian forest; 18°09′35″N, 65°18′04″W; 465 m; 31 Jul 2018, *Mercado-Díaz 3683* (UPR). Mun. Orocovis, Valleys near Dona Juana Waterfall, Toro Negro. Among rocks; 700 m; 3 Mar 1922, *N.L. Britton, EG Britton, MS Brown 6395* (NY, US).

Sticta tainorum Merc.-Díaz

Additional specimens examined: PUERTO RICO. Mun. Orocovis, Toro Negro State Forest, along trail to observation tower; 18°10′14″N, 66°28′52″W; 1037 m; 27 Jul 2018, *Mercado-Díaz 3661* (UPR).