Rewriting the evolutionary history of the lichen genus *Sticta* (*Ascomycota*: *Peltigeraceae* subfam. *Lobarioideae*) in the Hawaiian islands

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Abstract. Hawaiian lichen species have been thought to be widespread, with low endemism. Nine species of the genus *Sticta* (*Peltigeraceae* subfamily *Lobarioideae*) have previously been reported for Hawaii, all supposedly cosmopolitan or Pantropical or widespread in the Paleotropics except for the putative endemic *S. plumbicolor*. This study is the first one employing a molecular phylogenetic approach to Hawaiian *Sticta*, elucidating the relationships of these conspicuous and ecologically important macrolichens. We sequenced the ITS fungal barcoding locus and used a maximum likelihood approach to reconstruct phylogenetic relationships of Hawaiian *Sticta* from a large dataset of more than 200 species. Thirteen species were identified among Hawaiian *Sticta*, four more than previously recorded. Of these, seven are new to science and putatively endemic to Hawaii. Only four previously reported species were confirmed: *S. fuliginosa*, *S. limbata*, *S. plumbicolor* and *S. tomentosa*. Together with *S. plumbicolor* and *S. scabrosa* subsp. *hawaiiensis* (described elsewhere), putative endemism in Hawaiian *Sticta* is estimated at 69%. The 13 species correspond to nine or ten colonization events, predominantly from the Australasian realm. Thus, the evolutionary history of *Sticta* lichens in the Hawaiian archipelago is very different from what has been assumed, and matches that of other organisms in many aspects. The seven new species, all with cyanobacterial photobionts, are *Sticta acyphellata*, a small, stipitate *Sticta* with isidia and lacking cyphellae; *S. antoniana*, a mid-sized *Sticta* with abundant marginal lobules, apothecia, and a thick, grey-brown lower tomentum ending abruptly to leave a bare marginal zone; *S. emmanueliana*, a small, shortly stipitate *Sticta* forming small lobes with marginal isidia and black cilia; *S. flynnii*, a small, shortly stipitate *Sticta* with largely unbranched thallus with marginal isidia and a veined underside producing large, irregular cyphellae; *S. hawaiiensis*, a small *Sticta* with a suborbicular thallus with laminal isidia, conspicuous white cilia, and papillae on the membrane of the cyphellae; *S. smithii*, a small, stipitate *Sticta* with marginal, flattened isidia and small cyphellae; and *S. waikamoi*, a small to mid-sized *Sticta* with a much-branched thallus with slightly canaliculate lobes and marginal, dark isidia, and a thick, dark brown lower tomentum with strongly contrasting whitish cyphellae.

Key words: Hawaiian archipelago, endemism, island biogeography

Introduction

Presumably the lichen biota of the Hawaiian islands is well-known, owing to the works of Magnusson & Zahlbruckner (1943, 1944, 1945), Magnusson (1955), Klement (1966, 1968) and more recently Smith and co-workers (Smith 1977, 1984, 1993, 1995, 2001, 2013; Stenroos & Smith 1993; Smith et al. 1997). The current checklist contains 880 species in 65 genera (Smith 2013), a comparatively high number considering that only 1386 native vascular plant species are recorded for the archipelago (Imada et al. 2012). However, while 80% of the vascular plants are endemic (Wagner et al. 1999; Wagner & Herbst 2002; Evenhuis & Eldredge 2002), only 20–30% of the lichen species may be unique to Hawaii (Eldredge & Miller 1995). This estimate is in line with the assumption that lichens are generally much more widespread than vascular plants (Jørgensen 1983, 1994; Ahti 1987;

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Stevens 1991; Galloway 1991, 1994a, 2008; Ahti & Aptroot 1992; Tibell 1994; Louwhoff 2001; Lücking & Kalb 2001; Lücking 2003; Sipman 2006; Seaward & Aptroot 2006; Feuerer & Hawksworth 2007; Werth 2011). Smith's (1993) treatment of the largest family of lichenized fungi, *Parmeliaceae*, set the stage for viewing Hawaiian lichens as generally widespread, with few endemics (Wirth 1997; Marbach 2000; Smith 2001; Inoue 2002; Sérusiaux & Lücking 2007). This is why the lichen biota of Hawaii has attracted considerably less interest than vascular plants have (Smith 1993). Few molecular studies have focused on Hawaiian lichens. Phylogenetic analysis showed that the presumably endemic genus *Ramalinopsis*, with the single species *R. mannii* (Follmann 1974), is nested within *Ramalina*, although it remains a distinctive, endemic species with a parmelioid habit (Lücking et al. 2017a; Kistenich et al. 2018). In a phylogenetic survey of the subcosmopolitan *Flavoplaca citrina* complex, the only available Hawaiian sample appeared on a very long branch (Vondrák et al. 2009), suggesting divergence over a long history of isolation.

Sticta is one of the best-known lichen taxa, due to its usually large, conspicuous thalli. It is easily recognized by its distinctive pores on the lower side, the cyphellae, which facilitate gas exchange (Green et al. 1981; Galloway 2007), although a small group of species centered around *S. wrightii* was shown to form a separate clade and was segregated as *Dendriscosticta* (Moncada et al. 2013a). Species of *Sticta* are characteristic of humid, cool- to warm-temperate environments with high precipitation or humidity. At tropical latitudes they are most diverse and abundant in wet montane forests and alpine grasslands (páramos in the Neotropics), but are also found occasionally in lowland rain forests. Given that under favorable conditions they can accumulate large biomass and that most species are associated with nitrogen-fixing cyanobacteria, species of *Sticta* are significant contributors to local nitrogen input as biological fertilizers (Kelly & Becker 1975; Becker 1980; Green et al. 1980; Green & Lange 1991; Antoine 2004; Benner et al. 2007; Benner & Vitousek 2012). Equally important is their role in the water cycle, since their thalli are capable of storing up to 800% of their dry weight in water and influence the microclimate of their immediate environment (Green et al. 1985; Guzmán et al. 1990; Green & Lange 1991; Beckett 1995; Zotz et al. 1998). Species of *Sticta* are highly sensitive to human-induced environmental changes and pollution, and have become extinct in many areas of North America and Europe (Wirth 1995; Brodo et al. 2001; Pišút 2005; Hodkinson et al. 2014; Magain & Sérusiaux 2015; Lendemer & Goffinet 2016; Simon et al. 2018a; Ekman et al. 2019). This sensitivity makes them excellent indicators of environmental health, including the effects of habitat disturbance and global climate change (Scheidegger et al. 1995; Zoller et al. 1999; Radies et al. 2009).

Checklists of Hawaiian lichens (Elix & McCarthy 1998, 2008; Smith 2013) list 11 names under *Sticta*, with one, *S. crocatoides* [sic] f. *sandwicensis*, an orthographic error for *S. crocata* f. *sandwicensis*, actually representing

Pseudocyphellaria sandwicensis (Moncada et al. 2014b; Lücking et al. 2017b). The remaining ten names correspond to seven species, viz. *Sticta ambavillaria, S. cyphellulata, S. filix, S. fuliginosa, S. plumbicolor, S. tomentosa* and *S. weigelii*, plus three varieties of the latter: *S. weigelii* var. *beauvoisii, S. weigelii* var. *lutescens* and *S. weigelii* var. *peruviana. Sticta weigelii* var. *beauvoisii* was recently accepted as a separate species (McDonald et al. 2003; Galloway 2006). The application of the name *S. lutescens* is unclear; Zahlbruckner (1925) gives *S. lutescens* as synonym of *S. xanthosticta*, which in turn is a synonym of *Pseudocyphellaria crocata* (Galloway 2001), but the lectotype of *S. lutescens*, described from Indonesia (Java), is a *Sticta* species. *Sticta weigelii* var. *peruviana* was described as *S. sylvatica* var. *peruviana* from Peru (Delise 1825) and subsequently considered a separate species (Nylander 1859). This taxon has been misunderstood, since the type material lacks isidia and bears abundant apothecia instead (Moncada 2012). One additional species, *S. limbata*, was identified in an ecological study (Benner & Vitousek 2012) but has not been included in the checklist (Smith 2013). Since identifications of Hawaiian material as *S. weigelii* var. *lutescens* and var. *peruviana* are likely incorrect and may refer to specimens of *S. weigelii* s.lat., we assume that the eleven names of *Sticta* reported for the archipelago (excluding *S. crocatoides* var. *sandwicensis*) represent nine species, with eight of them widespread and only *S. plumbicolor* (Zahlbruckner 1903, 1925) putatively endemic to Hawaii, resulting in an inferred endemism of 11%.

Of the nine species reported for Hawaii, one is a green algal taxon (*S. filix*). The others are cyanolichens, two exclusively apotheciate (*S. ambavillaria, S. tomentosa*), one sorediate (*S. limbata*), and five isidiate or phyllidiate (*S. beauvoisii, S. cyphellulata, S. fuliginosa, S. plumbicolor, S. weigelii*). Based on published records, the eight non-endemic species presumably represent six different distribution patterns: *S. filix* is a chiefly Australasian species (described from New Zealand; Galloway 2007; Ranft et al. 2018); *S. cyphellulata* is Australasian (described from Australia) but also occurs in India and the Mascarenes (Galloway 1998, 2008; Magain & Sérusiaux 2015; Simon et al. 2018b); *S. ambavillaria* (originally from Africa) has a Gondwanan distribution (Neotropics and African Paleotropics; Marcano et al. 1996; Bock et al. 2007; van den Boom et al. 2011; Eliasaro et al. 2012; Aptroot 2016; Simon et al. 2018b); *S. beauvoisii* (established from material from Cuba) is predominantly North American (Galloway 1995, 2006; McDonald et al. 2003); *S. tomentosa* (originally from Jamaica) has a Pantropical range (van den Boom et al. 2011; Moncada et al. 2014a); and *S. fuliginosa, S. limbata* (both described from Great Britain) and *S. weigelii* (described from Martinique) are subcosmopolitan (Galloway 2006; Moncada et al. 2014a; Magain & Sérusiaux 2015). This would paint an undifferentiated, diffuse picture of the assembly of Hawaiian *Sticta*, apparently with stochastic colonization events from both the Eastern (Australasia) and the Western Hemisphere (North America) and almost no separate evolutionary history on the archipelago.

A recent molecular phylogenetic revision of *Sticta* focusing on the northern Andes revealed that the morphological concept traditionally applied to delimit species in *Sticta* is ill-defined and that names such as *S. fuliginosa* and *S. weigelii*, assumed to represent cosmopolitan taxa, correspond to several distantly related lineages (Moncada et al. 2014a). Hence, we suspected that the names listed for Hawaii do not accurately reflect the diversity and taxonomic affinities of the species occurring there. This assumption is supported by two previous studies of Hawaiian lobarioid *Peltigeraceae*. Specifically, the seven presumably widespread species of *Pseudocyphellaria* s.lat. reported for Hawaii (Smith 2013) turned out to represent 12 species in three genera (*Crocodia*, *Podostictina*, *Pseudocyphellaria*), nine of them putatively endemic to the archipelago (Moncada et al. 2014b); for the genus *Lobariella*, Lücking et al. (2017c) found that instead of a single widespread species reported for Hawaii (Smith 2013), at least four taxa are present, three of them putatively endemic. In both cases, putative endemism had to be corrected from the previous 0% to 75%, close to the level characterizing vascular plants.

Since *Sticta* was the only genus in this subfamily with at least one presumably endemic species in Hawaii (*S. plumbicolor*), we expected that a molecular phylogenetic revision would reveal a degree of endemism even higher than for the other two groups. To test this hypothesis we collected fresh samples of *Sticta* from 14 sites on the four largest islands (Kauai, Oahu, Maui, the Big Island) and extracted DNA for molecular phylogenetic analysis. Based on the results, it is evident that the evolutionary history of *Sticta* in the Hawaiian archipelago must indeed be rewritten.

Materials and methods

Morphological study

Herbarium material of *Sticta* originating from Hawaii was revised at the US National Herbarium and at the herbarium of the University of Hawaii at Manoa (HAW). We performed thin-layer chromatography to determine the chemical constituents of selected samples, following the methods outlined in Orange et al. (2010). New fresh material was collected during field work in June 2013 on the islands of Oahu, Maui and Kauai (Fig. 1), in collaboration with Clifford Smith and Philip Thomas (University of Hawaii at Manoa), Pat Bily (The Nature Conservancy, Maui) and Daniel Kaniaupio-Crozier (West Maui Soil & Water Conservation District). In addition, we received some specimens collected by C. Smith on the Big Island (Hawaii). Specimens were initially identified using keys provided by Swinscow & Krog (1988), Joshi & Awasthi (1982) and Galloway (1994b, 2001, 2007) for southern South America, West Africa, India and Nepal, Australia and New Zealand. For alternative taxonomic scenarios, we then compared these identifications with the older concept provided by Magnusson and Zahlbruckner (1943) and the refined concept from Moncada et al. (2014a).

Molecular phylogeny

We obtained new sequences of the nuclear ITS barcoding locus for 149 samples, including 111 from Hawaii. Molecular work was performed at the Field Museum's Pritzker Laboratory for Molecular Systematics and Evolution. DNA was extracted using the QIAGEN DNeasy Plant Mini Kit. Dilutions of 10:1 up to 10:2 were used for PCR amplifications, with the primer pairs ITS1F

Figure 1. Hawaiian collection sites of *Sticta* material used for the molecular phylogenetic analysis. Based on map obtained from Wikimedia Commons [https://en.wikipedia.org/wiki/Kunia_Camp,_Hawaii#/media/File:USA_Hawaii_location_map.svg]

and ITS4 (Gardes & Bruns 1993; White et al. 1990). The 25 µl PCR reactions contained 2.5 µl buffer, 2.5 µl dNTP mix, 1 µl of each primer (10 µM), 5 µl BSA, 2 µl Taq, 2 µl genomic DNA extract and 9 µl distilled water. The thermal cycling parameters were set as follows: initial denaturation for 3 min at 95°C, followed by 30 cycles of 1 min at 95°C, 1 min at 52°C, 1 min at 73 °C, and final elongation for 7 min at 73°C. Amplification products were mounted on 1% agarose gels stained with ethidium bromide and, after cutting of the target bands, purified using the QIAGEN QIAquick PCR Purification Kit or Nucleo Spin DNA Purification Kit (Macherey-Nagel). Fragments were sequenced using the Big Dye Terminator reaction kit (ABI PRISM, Applied Biosystems). Sequencing and PCR amplifications were performed using the same sets of primers. Cycle sequencing was executed with the following setting: 25 cycles of 95°C for 30 sec, 48°C for 15 sec, 60°C for 4 min. Sequenced products were precipitated with 10 µl of sterile dH2O, 2 µl of 3 M Napa, and 50 µl of 95% EtOH, and subsequently loaded on an ABI 3100 (Applied Biosystems) automatic sequencer. Sequence fragments obtained were assembled with DNASTAR SeqMan 4.03, manually inspected and adjusted and, after quality control, submitted to GenBank (Table 1).

The obtained sequences were aligned with previously published sequences of the genus *Sticta* (Moncada et al. 2014a; Magain & Sérusiaux 2015; Simon et al. 2018b; Widhelm et al. 2018; Mercado-Díaz et al. 2020; Table S1). Sequences were assembled in BIOEDIT 7.0.9 (Hall 2011) and aligned with MAFFT 7.164 using the '--add' option (Katoh & Frith 2012; Katoh & Standley 2013), using the '--auto' option and with subsequent manual inspection. The alignment was subjected to analysis of ambiguously aligned regions using the GUIDANCE webserver (Penn et al. 2010a, 2010b), but based on the results, no columns were removed, resulting in an alignment length of 684 bases (File S1). Phylogenetic analysis was performed using maximum likelihood in RAxML 8.2.0 (Stamatakis 2014) on the CIPRES Science Gateway (Miller et al. 2010), with non-parametric bootstrapping using 402 pseudoreplicates (based on an automated saturation criterion) under the GTRGAMMA model. Trees were visualized in FIGTREE 1.4.2 (Drummond & Rambaut 2007).

Time-calibrated tree

Using a subset of 190 ingroup sequences representing different species each, a relaxed, uncorrelated lognormal molecular clock model was employed to date the evolutionary origin of the Hawaiian colonizations by *Sticta lineages*. BEAST 1.7.5 and 1.8.4 (Drummond & Rambaut 2007; Drummond et al. 2012) were used for this purpose, locally and on the CIPRES Science Gateway (Miller et al. 2010), with the GTR substitution model with base frequencies estimated and Gamma and invariant sites with four Gamma categories. Speciation was estimated through a Yule process with the 'yule.birthRate' prior set to an exponential distribution with 0.7 as mean. Based on Simon et al. (2018b) and Widhelm et al. (2018), we set treeModel.rootHeight (*Lobaria-Sticta* split) to 45 Mya and

the *Sticta* crown node to 25 Mya, both with a normal distribution and 5 and 3 my standard deviation, respectively. The final analysis was run for 10 million generations and every 1,000th tree was sampled, for a total of 10,001 trees and a burn-in of 2,500 trees. The resulting log file was analysed in TRACER 1.5 and the maximum clade credibility tree was compiled using TREE ANNOTATOR 1.7.5 (Drummond & Rambaut 2007).

Results and discussion

Phylogenetic relationships

The ITS-based phylogeny binned the Hawaiian *Sticta* samples into ten clades, of which two were closely related and eight were not closely related and were dispersed across the tree (Fig. 2; Fig. S1). The ten clades exhibited three different topological patterns: (1) six clades corresponded to distinct lineages representing exclusively Hawaiian specimens; (2) two clades were more widely distributed in the tropics but the Hawaiian material formed (near-)exclusive shallow subclades; and (3) two clades were more widely distributed or even subcosmopolitan and the Hawaiian specimens were dispersed within these clades, with no phylogenetic distinction from non-Hawaiian samples.

Clade-based taxonomic assessment

Morphological analysis revealed that the ten clades corresponded to 13 distinct phenotypes. The six distinct, exclusively Hawaiian lineages were each morphologically homogeneous; none of these correspond to known species and they are therefore considered undescribed taxa new to science. All are marginally isidiate and most are caulescent, but they differ in thallus size and particularly in the development and color of the lower tomentum. The early-diverging lineages 1 to 4, below described as *S. acyphellata*, *S. emmanueliana*, *S. flynnii* and *S. smithii*, represent diminutive species which in most cases do not correspond to previously reported names (e.g., Magnusson & Zahlbruckner 1943; Magnusson 1955), except for lineage 4, which has been reported as *S. cyphellulata* (Elix & McCarthy 1998, 2008). These taxa have apparently been overlooked in previous surveys or were mistaken for young forms of other species. For instance, of 175 specimens of *Sticta* in HAW, only two corresponded to taxa representing these lineages; previously these had been identified as *S. plumbicolor* and *S. weigelii*, respectively. The other two lineages would correspond morphologically to either *S. fuliginosa* s.lat. (lineage 5) or *S. weigelii* s.lat. (lineage 6); in HAW, two specimens of lineage 5 had been identified as *S. fuliginosa* and three specimens of lineage 6 as *S. weigelii*. However, lineage 5 belongs in a complex centered around the recently reinstated *S. ciliata* and within that complex is most closely related to the recently described *S. parvilobata* from Puerto Rico.

The two clades containing shallow, nested subclades correspond to two more widely distributed taxa, *S. scabrosa* and *S. tomentosa*. *Sticta scabrosa* is one of the few species of the genus typically found at lower elevations

Table 1. Genbank accession numbers of newly generated ITS sequences for Hawaiian and other representatives of *Sticta* used in this study.

Genus	Species	Accession	Extract 1	Extract 2	Country	Collector	Number
Sticta	*acyphellata*	MT132648	DNA8055	MON1186	Hawaii Oahu	Moncada	6923
Sticta	*andina*	MT132671	DNA8083	MON1214	Hawaii Maui	Moncada	6951
Sticta	*andina*	MT132681	DNA8119	MON1250	Hawaii Maui	Moncada	6983
Sticta	*andina*	MT132682	DNA8120	MON1251	Hawaii Maui	Moncada	6984
Sticta	*andina*	MT132693	DNA8133	MON1264	Hawaii Maui	Moncada	6997
Sticta	*andina*	MT132715	DNA8186	MON1317	Hawaii Kauai	Moncada	7047
Sticta	*antoniana*	MT132720	DNA8192	MON1323	Hawaii Kauai	Moncada	7053a
Sticta	*antoniana*	MT132721	DNA8193	MON1324	Hawaii Kauai	Moncada	7053b
Sticta	*antoniana*	MT132722	DNA8194	MON1325	Hawaii Kauai	Moncada	7053c
Sticta	*antoniana*	MT132733	DNA8210	MON1341	Hawaii Kauai	Moncada	7065
Sticta	aff. *ciliata* 2	MT132628	DNA7356	MON0817	Colombia	Moncada	6135
Sticta	aff. *ciliata* 2	MT132633	DNA7635	MON1011	Colombia	Moncada	6134
Sticta	aff. *ciliata* 2	MT132747	DNA12542	MON2542	Colombia	Moncada	8587
Sticta	aff. *ciliata* 3	MT132621	DNA7258	MON0719	Costa Rica	Moncada	5713
Sticta	aff. *ciliata* 3	MT132622	DNA7263	MON0724	Costa Rica	Moncada	5702
Sticta	aff. *ciliata* 3	MT132623	DNA7265	MON0726	Costa Rica	Moncada	5740
Sticta	aff. *ciliata* 3	MT132624	DNA7268	MON0729	Costa Rica	Moncada	5659
Sticta	aff. *ciliata* 3	MT132625	DNA7272	MON0733	Costa Rica	Moncada	5775
Sticta	aff. *ciliata* 3	MT132626	DNA7275	MON0736	Costa Rica	Moncada	5782
Sticta	aff. *ciliata* 3	MT132634	DNA7740	MON1116	Colombia	Lücking	35839
Sticta	aff. *ciliata* 3	MT132744	DNA12145	MON2145	Colombia	Moncada	8022
Sticta	*cyphellulata*	MT152342	UCONN4313	–	China	Wang	1547066
Sticta	*cyphellulata*	MT152343	UCONN4315	–	China	Wang	1547096
Sticta	*cyphellulata*	MT152344	UCONN4317	–	China	Wang	1547106
Sticta	*emmanueliana*	MT132673	DNA8087	MON1218	Hawaii Maui	Moncada	6954a
Sticta	*emmanueliana*	MT132674	DNA8088	MON1219	Hawaii Maui	Moncada	6954b
Sticta	*emmanueliana*	MT132675	DNA8089	MON1220	Hawaii Maui	Moncada	6955
Sticta	*emmanueliana*	MT132726	DNA8202	MON1333	Hawaii Kauai	Moncada	7058b
Sticta	*emmanueliana*	MT132732	DNA8209	MON1340	Hawaii Kauai	Moncada	7064
Sticta	*flynnii*	MT132723	DNA8196	MON1327	Hawaii Kauai	Moncada	7055a
Sticta	*flynnii*	MT132728	DNA8205	MON1336	Hawaii Kauai	Moncada	7059
Sticta	*fuliginosa*	MT132666	DNA8077	MON1208	Hawaii Maui	Moncada	6945
Sticta	*fuliginosa*	MT132677	DNA8115	MON1246	Hawaii Maui	Moncada	6979b
Sticta	*fuliginosa*	MT132680	DNA8118	MON1249	Hawaii Maui	Moncada	6982
Sticta	*fuliginosa*	MT132685	DNA8124	MON1255	Hawaii Maui	Moncada	6988
Sticta	*fuliginosa*	MT132687	DNA8126	MON1257	Hawaii Maui	Moncada	6990
Sticta	*fuliginosa*	MT132691	DNA8130	MON1261	Hawaii Maui	Moncada	6994
Sticta	*fuliginosa*	MT132694	DNA8134	MON1265	Hawaii Maui	Moncada	6998
Sticta	*fuliginosa*	MT132710	DNA8159	MON1290	Hawaii Kauai	Moncada	7023
Sticta	*fuliginosa*	MT132713	DNA8182	MON1313	Hawaii Kauai	Moncada	7043
Sticta	*fuliginosa*	MT132719	DNA8191	MON1322	Hawaii Kauai	Moncada	7052
Sticta	*fuliginosa*	MT132748	DNA13512	MON3512	New Zealand	Lücking	39122
Sticta	*fuliginosa*	MT132749	DNA13514	MON3514	New Zealand	Lücking	38570
Sticta	*fuliginosa*	MT132750	DNA13518	MON3518	New Zealand	Lücking	38537
Sticta	*fuliginosa*	MT132751	DNA13519	MON3519	New Zealand	Lücking	39100
Sticta	*fuliginosa*	MT132756	DNA13793	MON3793	New Zealand	Lücking	38256
Sticta	*fuliginosa*	MT132757	DNA13800	MON3800	New Zealand	Lücking	38418
Sticta	*fuliginosa*	MT132758	DNA13802	MON3802	New Zealand	Lücking	38433
Sticta	*fuliginosa*	MT132759	DNA13803	MON3803	New Zealand	Lücking	38454
Sticta	*fuliginosa*	MT132760	DNA13806	MON3806	New Zealand	Lücking	38913
Sticta	*fuliginosa*	MT132766	MON5191	–	Hawaii Big Island	Smith	s.n.
Sticta	*hawaiiensis*	MT132672	DNA8086	MON1217	Hawaii Maui	Moncada	6953
Sticta	*hawaiiensis*	MT132716	DNA8187	MON1318	Hawaii Kauai	Moncada	7048
Sticta	*limbata*	MT132695	DNA8135	MON1266	Hawaii Maui	Moncada	6999
Sticta	*limbata*	MT132711	DNA8160	MON1291	Hawaii Kauai	Moncada	7024
Sticta	*limbata*	MT132752	DNA13523	MON3523	New Zealand	Lücking	39101
Sticta	*limbata*	MT132753	DNA13525	MON3525	New Zealand	Lücking	38533a
Sticta	*limbata*	MT132754	DNA13531	MON3531	New Zealand	Lücking	38549
Sticta	*limbata*	MT132755	DNA13636b	MON3636b	New Zealand	Lücking	38585
Sticta	*limbata*	MT132761	DNA13840	MON3840	New Zealand	Lücking	38424

Table 1. Continued.

Genus	Species	Accession	Extract 1	Extract 2	Country	Collector	Number
Sticta	*limbata*	MT132762	DNA13845	MON3845	New Zealand	Lücking	38820
Sticta	*marginifera*	MT132630	DNA7863	MON0947	India	Schumm	18900
Sticta	*marginifera*	MT132631	DNA7875	MON0959	Reunion	Schumm	18783
Sticta	*peltigerella*	MT132627	DNA7353	MON0814	Colombia	Moncada	6359
Sticta	*peltigerella*	MT132629	DNA7803	MON0887	Colombia	Lücking	35239
Sticta	*peltigerella*	MT132763	DNA14410	MON4410	Colombia	Lücking	39523
Sticta	*plumbicolor*	MT132635	DNA8041a	MON1172a	Hawaii Oahu	Moncada	6910a
Sticta	*plumbicolor*	MT132641	DNA8049	MON1180	Hawaii Oahu	Moncada	6918
Sticta	*plumbicolor*	MT132651	DNA8057	MON1188	Hawaii Oahu	Moncada	6925
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132636	DNA8041b	MON1172b	Hawaii Oahu	Moncada	6910b
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132637	DNA8043	MON1174	Hawaii Oahu	Moncada	6912
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132638	DNA8045	MON1176	Hawaii Oahu	Moncada	6914
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132639	DNA8046	MON1177	Hawaii Oahu	Moncada	6915
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132640	DNA8048	MON1179	Hawaii Oahu	Moncada	6917
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132642	DNA8050	MON1181	Hawaii Oahu	Moncada	6919
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132643	DNA8051	MON1182	Hawaii Oahu	Moncada	6919a
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132644	DNA8053a	MON1184a	Hawaii Oahu	Moncada	6921
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132645	DNA8053b	MON1184b	Hawaii Oahu	Moncada	6921
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132646	DNA8054a	MON1185a	Hawaii Oahu	Moncada	6922
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132647	DNA8054b	MON1185b	Hawaii Oahu	Moncada	6922
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132649	DNA8056a	MON1187a	Hawaii Oahu	Moncada	6924
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132650	DNA8056b	MON1187b	Hawaii Oahu	Moncada	6924
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132652	DNA8058	MON1189	Hawaii Oahu	Moncada	6926
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132653	DNA8059	MON1190	Hawaii Oahu	Moncada	6927
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132654	DNA8060a	MON1191a	Hawaii Oahu	Moncada	6928
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132655	DNA8060b	MON1191b	Hawaii Oahu	Moncada	6928
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132656	DNA8061	MON1192	Hawaii Oahu	Moncada	6929
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132657	DNA8063a	MON1194a	Hawaii Maui	Moncada	6934
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132658	DNA8063b	MON1194b	Hawaii Maui	Moncada	6934
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132659	DNA8064	MON1195	Hawaii Maui	Moncada	6935
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132660	DNA8065	MON1196	Hawaii Maui	Moncada	6938
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132661	DNA8066	MON1197	Hawaii Maui	Moncada	6939
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132662	DNA8070a	MON1201a	Hawaii Maui	Moncada	6936
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132663	DNA8070b	MON1201b	Hawaii Maui	Moncada	6936
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132664	DNA8071a	MON1202a	Hawaii Maui	Moncada	6937
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132665	DNA8071b	MON1202b	Hawaii Maui	Moncada	6937
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132698	DNA8144	MON1275	Hawaii Maui	Moncada	7008
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132699	DNA8145	MON1276	Hawaii Maui	Moncada	7009
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132700	DNA8146	MON1277	Hawaii Maui	Moncada	7010
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132701	DNA8147	MON1278	Hawaii Maui	Moncada	7011
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132702	DNA8148	MON1279	Hawaii Maui	Moncada	7012
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132703	DNA8149	MON1280	Hawaii Maui	Moncada	7013
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132704	DNA8151	MON1282	Hawaii Maui	Moncada	7015
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132705	DNA8153	MON1284	Hawaii Maui	Moncada	7017
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132706	DNA8154	MON1285	Hawaii Kauai	Moncada	7018
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132707	DNA8155	MON1286	Hawaii Kauai	Moncada	7019
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132708	DNA8156	MON1287	Hawaii Kauai	Moncada	7020
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132709	DNA8158	MON1289	Hawaii Kauai	Moncada	7022
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132712	DNA8161	MON1292	Hawaii Kauai	Moncada	7025
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132718	DNA8190	MON1321	Hawaii Kauai	Moncada	7051
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132724	DNA8198	MON1329	Hawaii Kauai	Moncada	7056
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132725	DNA8199	MON1330	Hawaii Kauai	Moncada	7057
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132729	DNA8206	MON1337	Hawaii Kauai	Moncada	7060
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132731	DNA8208	MON1339	Hawaii Kauai	Moncada	7063
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132735	DNA8214	MON1345	Hawaii Kauai	Moncada	7069
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132736	DNA8215	MON1346	Hawaii Kauai	Moncada	7070
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132737	DNA8216	MON1347	Hawaii Kauai	Moncada	7071
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132738	DNA8217	MON1348	Hawaii Kauai	Moncada	7072
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132739	DNA8219	MON1350	Hawaii Kauai	Moncada	7074
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132740	DNA8220	MON1351	Hawaii Kauai	Moncada	7075

Table 1. Continued.

Genus	Species	Accession	Extract 1	Extract 2	Country	Collector	Number
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132741	DNA8221	MON1352	Hawaii Kauai	Moncada	7076
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132742	DNA8223a	MON1354a	Hawaii Kauai	Moncada	7078
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132743	DNA8223b	MON1354b	Hawaii Kauai	Moncada	7078
Sticta	*scabrosa* subsp. *hawaiiensis*	MT132765	MON5190	–	Hawaii Big Island	Smith	s.n.
Sticta	*tomentosa*	MT132632	DNA7623	MON0999	Colombia	Lücking	35339b
Sticta	*tomentosa*	MT132667	DNA8079a	MON1210a	Hawaii Maui	Moncada	6947
Sticta	*tomentosa*	MT132668	DNA8079b	MON1210b	Hawaii Maui	Moncada	6947
Sticta	*tomentosa*	MT132669	DNA8080	MON1211	Hawaii Maui	Moncada	6948
Sticta	*tomentosa*	MT132670	DNA8082	MON1213	Hawaii Maui	Moncada	6950
Sticta	*tomentosa*	MT132676	DNA8111	MON1242	Hawaii Maui	Moncada	6977
Sticta	*tomentosa*	MT132678	DNA8116	MON1247	Hawaii Maui	Moncada	6980
Sticta	*tomentosa*	MT132679	DNA8117	MON1248	Hawaii Maui	Moncada	6981
Sticta	*tomentosa*	MT132683	DNA8121	MON1252	Hawaii Maui	Moncada	6985
Sticta	*tomentosa*	MT132684	DNA8122	MON1253	Hawaii Maui	Moncada	6986
Sticta	*tomentosa*	MT132686	DNA8125	MON1256	Hawaii Maui	Moncada	6989
Sticta	*tomentosa*	MT132688	DNA8127	MON1258	Hawaii Maui	Moncada	6991
Sticta	*tomentosa*	MT132689	DNA8128	MON1259	Hawaii Maui	Moncada	6992
Sticta	*tomentosa*	MT132690	DNA8129	MON1260	Hawaii Maui	Moncada	6993
Sticta	*tomentosa*	MT132692	DNA8132	MON1263	Hawaii Maui	Moncada	6996
Sticta	*tomentosa*	MT132697	DNA8137	MON1268	Hawaii Maui	Moncada	7001
Sticta	*tomentosa*	MT132714	DNA8183	MON1314	Hawaii Kauai	Moncada	7044
Sticta	*tomentosa*	MT132717	DNA8189	MON1320	Hawaii Kauai	Moncada	7050
Sticta	*tomentosa*	MT132727	DNA8204	MON1335	Hawaii Kauai	Moncada	7062
Sticta	*tomentosa*	MT132730	DNA8207	MON1338	Hawaii Kauai	Moncada	7061
Sticta	*tomentosa*	MT132734	DNA8211	MON1342	Hawaii Kauai	Moncada	7066
Sticta	*tomentosa*	MT132745	DNA12175	MON2175	Colombia	Moncada	8060
Sticta	*tomentosa*	MT132746	DNA12477	MON2477	Colombia	Silano	P11
Sticta	*tomentosa*	MT132764	MON4891	–	Ecuador	Lücking	40214
Sticta	*waikamoi*	MT132696	DNA8136	MON1267	Hawaii Maui	Moncada	7000

and in more exposed situations, tolerant to disturbances, and sometimes even with a weedy aspect. The Hawaiian specimens differ consistently in two distant positions of the ITS and exhibit a tendency towards scrobiculate to foveolate (pitted) lobe tips; these are considered a subspecies (subsp. *hawaiiensis*; Moncada et al., unpublished). In their ecology they are similar to the nominal subspecies, which is widely distributed in the Neotropics. In Hawaii, this is by far the most frequent and widespread *Sticta*: 59 of the 127 sequenced specimens (46%) and one third of the collections in HAW correspond to this taxon. By contrast, the Hawaiian material of *S. tomentosa* differs consistently from Neotropical and Paleotropical specimens only in one ITS position, with one specimen from Ecuador even corresponding to the Hawaiian haplotype; therefore, given the absence of any morphological differences, we consider this material to represent *S. tomentosa* s.str.

However, the Hawaiian material clustering phylogenetically with *S. tomentosa* contains two additional, very distinct morphotypes. One agrees with *S. tomentosa* in overall morphology, including the characteristic bluish hue, the whitish underside with thin tomentum, and the apothecia soon becoming biatorine, but features abundant laminal and marginal phyllidia and also differs in the branching pattern of the lobes, which are narrower than in typical *S. tomentosa* and often show shallow constrictions. This material matches the type of *S. plumbicolor*, which had been considered the only Hawaiian endemic species in this genus. The second morphotype strongly deviates from *S. tomentosa* in the strongly ascending, distinctly brownish (no bluish hue) lobes with rather thick and darker lower tomentum, with only the lobe tips abruptly bare of tomentum, the strongly dissected, lacinulate-lobulate lobe tips, and the apothecia remaining zeorine. This morphology corresponds perfectly to what Zahlbruckner (in Magnusson & Zahlbruckner 1943) had identified with the name *S. ambavillaria* and is here described as *S. antoniana* (see below).

Finally, the two widespread clades with Hawaiian material nested or dispersed within correspond to three distinct morphotypes. One clade is currently being described as *S. andina*, with an *S. weigelii* morphology but unrelated to the latter (Moncada et al., unpublished). *Sticta andina* differs from *S. weigelii* in the much thicker lower tomentum, It is more common in high-altitude forest and shrubland, and is the most frequently encountered species in the Andean páramos. The Hawaiian material represents a single haplotype that is identical to specimens from the Northern Andes and from the Azores. The second clade represents the widespread taxa *S. fuliginosa* and *S. limbata*. Both are morphologically quite distinct, producing laminal isidia vs. marginal soredia, but based on ITS data cannot be resolved, a phenomenon that has not yet been clarified (Moncada et al. 2014a; Magain & Sérusiaux 2015). Both taxa are present in Hawaii and correspond morphologically to specimens from other regions.
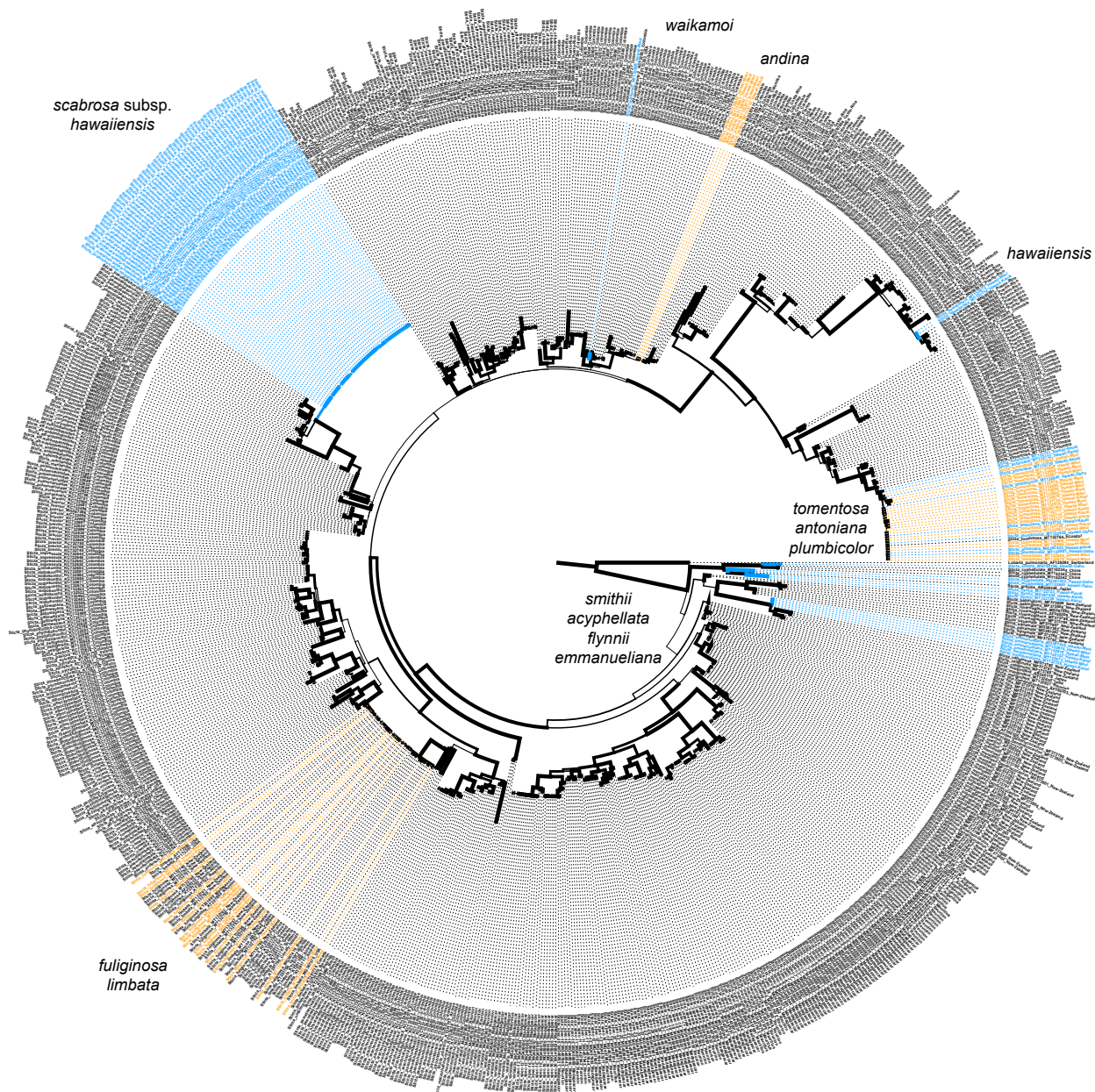
Figure 2. Best-scoring ML circle tree of *Sticta* based on the ITS barcoding marker. Hawaiian specimens are marked in blue (exclusive Hawaiian clades) and orange (Hawaiian specimens nested within more widely distributed taxa), and taxon names are indicated. For detailed tree with bootstrap values, see Fig. S1.

No green algal *Sticta* species was collected despite intensive searching. The report of *S. filix* by Tuckerman (1866) is likely erroneous, as already suggested by Magnusson & Zahlbruckner (1943).

As against the nine species previously reported from Hawaii, with one presumably endemic (11%), we found 13 taxa in the studied material, corresponding to ten phylogenetic lineages and three additional, distinct morphotypes that are not resolved with ITS. While the case of *S. fuliginosa* vs. *S. limbata* is a well-known phenomenon of two subcosmopolitan species (Moncada et al. 2014a; Magain & Sérusiaux 2015), the other two cases are putative endemics in the *S. tomentosa* clade and are similar to the case reported for the putative Hawaiian endemics *Pseudocyphellaria philipiana* and *P. pomaikaiana*, each exhibiting distinct phenotypes but sharing identical ITS

sequences (Moncada et al. 2014b). Since there is no phylogenetic support in the ITS fungal barcoding for these phenotypes to be recognized as species, two alternative scenarios are possible: (1) the phenotypes represent habitat-induced morphological plasticity of identical genotypes, as known for instance from photosymbiodemes; (2) the phenotypes represent distinct lineages but the ITS is not resolved to reflect this. The first scenario is not likely, since the taxa in question co-occur in the same habitats and often even side-by-side and the variation is discrete, not gradual. Support for the second scenario comes from the well-documented case of *S. fuliginosa* vs. *S. limbata*, which cannot be separated based on ITS but cannot be considered morphodemes of the same species, as they represent highly distinctive forms of vegetative reproduction (laminal isidia vs. marginal soredia). High

morphological divergence going along with very similar genotypes has also been found in Hawaiian vascular plants, such as the Silversword alliance in the *Asteraceae* (Baldwin et al. 1991; Baldwin & Sandersson 1998; Carlquist et al. 2003).

Usefulness of the ITS barcoding marker for species delimitation

The available data from Hawaiian *Sticta* allow further assessment of the usefulness of the fungal ITS barcoding marker for species delimitation in this genus. Multi-marker studies have previously shown that ITS phylogenies are highly congruent with those of other markers in this genus (Magain & Sérusiaux 2015; Simon et al. 2018b; Widhelm et al. 2018), with no evidence of artifacts. This is also supported by the strong correlation between ITS-delimited species-level clades and their phenotypes (Moncada et al. 2013b, c, 2015; Magain & Sérusiaux 2015). Thus, given the large amount of data available, there is little evidence for potential type I errors when using ITS for species delimitation in this genus. On the other hand, a few well-documented cases suggest the possibility of type II errors, that is, species not resolved by ITS alone, for example *S. fuliginosa* vs. *S. limbata*, *S. filix* vs. *S. lacera*, or in the present case also the three discrete morphodemes found in Hawaiian *S. tomentosa* s.lat. (Magain & Sérusiaux 2015; Ranft et al. 2018; this paper).

This underlines the point that the use of ITS in revising species taxonomy in the genus *Sticta* can considerably improve previous treatments based on morphology alone. It should also be noted that due to the broad coverage of the current ITS phylogeny of the genus, branches appeared relatively compressed even if corresponding to substantial differences (Fig. S1). For the species recognized below, with the exception of the *S. ciliata* and *S. tomentosa* complexes, similarity (based on ITS substitutions and indels combined) to the most closely related taxa oscillated between 94.0% and 96.1% (Table 2), distinctly below the lowest fixed threshold level of 98.5% applied as default

for species hypotheses (Nilsson et al. 2019). Given the critical situation of conservation of native biodiversity in island biota such as Hawaii, it also seems prudent to be more discriminant in recognizing lineages as taxa, following the concept of recognizing evolutionarily significant units (Casacci et al. 2014; Cornejo et al. 2017).

Biogeography and evolutionary history

Among the 13 taxa of *Sticta* now known from Hawaii, four are demonstrably widespread: *S. andina*, *S. fuliginosa*, *S. limbata* and *S. tomentosa*. The other nine are putative endemics, representing eight species and one subspecies. Notably, the only previously considered endemic species, *S. plumbicolor*, is phylogenetically unresolved from *S. tomentosa* based on ITS, although it displays a distinctive morphology not known from collections of *S. tomentosa* found elsewhere. Overall, this results in a degree of 69% putative endemism, comparable to the 75% found in *Lobariella* and in *Pseudocyphellaria* s.lat. but overall slightly lower (Moncada et al. 2014b; Lücking et al. 2017c). Of the nine names previously recorded for Hawaii, only four could be confirmed: *S. fuliginosa*, *S. limbata*, *S. plumbicolor* and *S. tomentosa*. Thus, between the prior taxonomy and the taxonomy to be implemented based on the results, the Sørensen overlap is only 36%, which is higher than for *Pseudocyphellaria* s.lat. (11%; Moncada et al. 2014b) but slightly lower than for *Lobariella* (40%; Lücking et al. 2017c). Our findings thus challenge the assumption that Hawaiian lichens are widespread. In addition, lichen diversity in Hawaii appears to be substantially underestimated; if the results from the studies of lobarioid *Peltigeraceae* are any indication, the current number of 880 listed species represents only around 50% of the real diversity, according to which Hawaiian lichen diversity would surpass that of vascular plants (Imada et al. 2012). Overall, given the significantly increased degree of putative endemism and the substantial changes in the taxonomy of Hawaiian *Sticta*, the evolutionary history of this genus in the archipelago

Table 2. Quantitative analysis of ITS differences and similarity between newly recognized Hawaiian species of *Sticta* and their closest relatives. Length = alignment length (alignment reduced to corresponding target clade); % = similarity based on number of substitutions or indels (and total) relative to alignment length. Total similarity values below 98.5% are bolded and underlined.

Species	Species compared	Length	Substitutions	Indels	Total	% Substitutions	% Indels	% Total
Acyphellata	*flynnii* + *gracilis*	579	19	7	26	96.7	98.8	**95.5**
Emmanueliana	*Caliginosa*	596	10	13	23	98.3	97.8	**96.1**
Emmanueliana	*Marginifera*	596	7	18	25	98.8	97.0	**95.8**
Flynniana	*Gracilis*	579	12	23	35	97.9	96.0	**94.0**
Hawaiiensis	*ciliata* s.str.	544	6	0	6	98.9	100.0	98.9
Hawaiiensis	aff. *ciliata* 1	544	3	0	3	99.4	100.0	99.4
Hawaiiensis	aff. *ciliata* 2	544	5	0	5	99.1	100.0	99.1
Hawaiiensis	aff. *ciliata* 3	544	6	0	6	98.9	100.0	98.9
Hawaiiensis	aff. *ciliata* 4	544	4	2	6	99.3	99.6	98.9
Hawaiiensis	*Parvilobata*	544	10	0	10	98.2	100.0	98.2
Hawaiiensis	aff. *parvilobata*	544	2	0	2	99.6	100.0	99.6
Smithii	*cyphellulata*	579	15	11	26	97.4	98.1	**95.5**
Waikamoi	aff. *cordillerana*	540	7	0	7	98.7	100.0	98.7
Waikamoi	aff. *rhizinata*	540	6	1	7	98.9	99.8	98.7
Waikamoi	*Rhizinata*	540	4	0	4	99.3	100.0	99.3

is very different from what had previously been assumed (Magnusson & Zahlbruckner 1943; Magnusson 1955; Smith 2013).

Thus far, the lichen biota on islands has been investigated using molecular approaches in only a few cases. For the genus *Sticta*, the most important studies are those of Simon et al. (2018b) for Madagascar and the Mascarenes and Mercado-Díaz et al. (2020) for Puerto Rico. Particularly the first offers some basis for comparison, given that the evolutionary history of the genus *Sticta* in the Hawaiian archipelagos is strikingly different. The diversity of Hawaiian *Sticta* is the result of multiple independent colonization events, with almost no evidence of radiation or post-colonization speciation except perhaps for the closely related *S. flynnii* and *S. smithii* and the three phylogenetically unresolved species in the *S. tomentosa* complex. In contrast, in Madagascar and the Mascarenes a subclade of *Sticta* underwent a radiation giving rise to at least 31 species following a single colonization event (Simon et al. 2018b). Regarding other lobarioid taxa in Hawaii, the patterns in *Pseudocyphellaria* (Moncada et al. 2014b) are comparable to that of Hawaiian *Sticta*, whereas that of *Lobariella* reflects a potential microradiation, which, however, yielded only four species (Lücking et al. 2017c).

Under the assumption of a molecular clock, our inferences for Hawaiian *Sticta* suggest recent, multiple independent colonization events, mostly between 1 Mya and 2.5 Mya, and in one case (*S. acyphellata*) 6 Mya (Fig. 3). For comparison, the *Lobariella* microradiation in Hawaii was estimated, also based on ITS, at (1–)8 Mya (Lücking et al. (2017c). In contrast, the substantial Madagascar–Masquarenes radiation was dated in our analysis to between 13 Mya (crown node) and 17 Mya (stem node), between three and 15 times older than any of the inferred Hawaiian colonizations. Given that lichen fungi clearly do have a potential for insular radiations comparable to that of vascular plants (Simon et al. 2018b), the absence of such radiation in Hawaiian *Sticta* is therefore attributable to recent colonization of the archipelago by this genus.

While molecular clock approaches have to be considered with caution, particularly when using the length-variable ITS marker, a comparison with other time trees of the genus *Sticta* supports our results showing a substantial relative difference between the colonization of Hawaii and that of Madagascar and the Masquarenes. With three markers (mtSSU, nuLSU, *RPB1*) but with reduced ingroup sampling, Simon et al. (2018b) computed the *Sticta* stem node at 42 Mya, the crown node at 16 Mya, and the stem node of the Madagascar–Masquarenes radiation at 12 Mya, about 30% younger than our ITS-based analysis. Hawaiian lineages were not included. With the *Lobaria-Sticta* split recovered at 46 Mya and the *Sticta* crown node at 27 Mya, Widhelm et al. (2018), adding two further markers (MCM7, ITS), estimated the stem and crown nodes of the Madagascar–Masquarenes radiation at 27 Mya and 15 Mya, respectively. Their crown age estimate was close to ours, whereas their stem age suggested a much older divergence of this clade. The latter is explained by a deviating underlying topology, different from other published phylogenies, with the

Madagascar–Masquarenes radiation sister to the remainder of *Sticta*. In the same analysis, the divergences of the included Hawaiian lineages were estimated at 5–10 Mya, about 1.5–2 times (crown node) and 2.7–5.5 times (stem node) younger than the Madagascar–Masquarenes radiation. Thus, independent of the markers employed and the underlying topology, the finding that Hawaiian colonization by the genus *Sticta* was much more recent than in the case of Madagascar and the Masquarenes remains.

Besides an obvious correlation between time of colonization and the potential for subsequent radiation, even in lineages that did not radiate, the phylogenetic distinctiveness of putative endemics among Hawaiian *Sticta* appears to be a function of time. The nine putative endemic taxa can be divided into two groups: *S. acyphellata*, *S. emmanueliana*, *S. flynnii* and *S. smithii* are taxonomically well-distinguished, whereas the other five taxa are either morphologically cryptic (*S. hawaiiensis*, *S. scabrosa* subsp. *hawaiiensis*, *S. waikamoi*) or cannot be resolved based on the ITS (*S. antoniana*, *S. plumbicolor*). The first four species exhibit inferred mean divergence times of 2–6 Mya, the other five only 1–2 Mya (Fig. 3). Thus, the degree of phylogenetic and phenotypic distinctiveness of the putative endemics clearly correlates with time of isolation. In addition, the first four species all emerged from basally diverging clades in the genus *Sticta*, with Australasian affinities, whereas the other five taxa are placed in a large clade corresponding to a later-diverging subclade and exhibit affinities with Neotropical lineages (Fig. 2). This indicates two distinct periods of Hawaiian colonization by the genus *Sticta*: according to our timetree, one chiefly from Australasia in the Pliocene and another chiefly from South America in the Pleistocene. By contrast, the Madagascan–Masquarene radiation goes back to the Miocene (Simon et al. 2018b; this paper).

The notion that the absence of radiation in Hawaiian *Sticta* may be due to colonization events more recent than for Madagascar and the Masquarenes is consistent with findings for vascular plants. For instance, Hawaiian lobeliads in the family *Campanulaceae* radiated into six genera comprising 126 species, following a single colonization event about 13 Mya in the Miocene (Givnish et al. 2009), comparable to the Madagascan–Masquarene radiation in *Sticta*. While Madagascar is a continental island and Mauritius and Réunion are comparatively close (less than 900 km apart), the Hawaiian archipelago is nearly 4,000 km distant from North America and over 6,000 km from eastern Asia and Australasia (Wagner & Funk 1995; Fleischer et al. 1998). Why were vascular plants able to colonize Hawaii much earlier than lichens in the genus *Sticta*? Besides the stochastic nature of dispersal history, one reason could be that epiphytic macrolichens in *Peltigeraceae* subfam. *Lobarioidaeae* thrive in more or less undisturbed forest, so their successful establishment depends on the prior formation of such ecosystems after initial colonization by vascular plants. By contrast, forest ecosystems on a continental island such as Madagascar were present long before the geological events that led to its isolation, so initial colonization by macrolichen lineages could have led to rapid radiation.

Figure 3. Chronogram of the genus *Sticta* based on the ITS barcoding marker, showing time of Hawaiian colonization events (in blue and orange). For comparison, the Madagascan–Masquarene radiation is highlighted in olive-green.

The multiple colonization of the genus *Sticta* in Hawaii offers some statistical basis to assess the biogeographic affinities of Hawaiian lineages, as briefly outlined above. In the present case, five of the ten lineages and 13 species have Australasian affinities, including Hawaiian specimens of *S. fuliginosa*, which appear to be closest to those studied from New Zealand (Fig. S1). On the other hand, Hawaiian *Sticta limbata* matches specimens from Western Europe rather than from New Zealand. Three lineages and taxa appear to have New World affinities (*S. andina*, *S. scabrosa*, *S. waikamoi*), whereas two additional lineages corresponding to four species (*S. hawaiiensis* and the *S. tomentosa* complex) remain unresolved based on the geography of their closest relatives, but in our taxon sampling are also closely related to Neotropical taxa. Thus, the Hawaiian *Sticta* biota exhibits a slight prevalence of Australasian elements. This is comparable to the genus *Pseudocyphellaria* (Moncada et al. 2014b) and also agrees with the origin of the majority of vascular plant lineages. For instance, dominant forest trees of the genera *Acacia* (*Fabaceae*), *Cheirodendron* (*Araliaceae*) and *Metrosideros* (*Myrtaceae*) have Indopacific–Australasian relationships (Mueller-Dombois 1987; Wright et al. 2001; Percy et al. 2008; Brown et al. 2012; Mitchell et al. 2012), presumably due to the northern subtropical jet stream as predominant dispersal agent (Geiger et al. 2007). Biogeographic relationships with North, Central and South America have been detected in some plant groups, such as the Hawaiian Silverswords, whose closest relatives are the North American Tarweeds (Baldwin et al. 1991; Barrier et al. 2001; Carlquist et al. 2003). The only available biogeographical study of Hawaiian lichens found that most *Cladoniaceae* have Australasian relationships (Stenroos & Smith 1993), whereas Neotropical affinities are apparent in the genus *Lobariella* (Yoshimura 1984, 1998; Yoshimura & Arvidsson 1994; Lücking et al. 2017c). Thus, our results in the genus *Sticta* fit findings for other organisms and also support the notion of a complex evolutionary history of the Hawaiian biota.

Sticta offers another example of how an island biota can evolve unique phenotypes, with the first species known in the genus to entirely lack cyphellae, *S. acyphellata*. A comparable situation was found in the Hawaiian *Phaeophyscia laciniata* (Esslinger 1978), and in the presumably endemic genus *Ramalinopsis* (Follmann 1974) which represents a foliose species nested within the fruticose genus *Ramalina* (Kistenich et al. 2018). Hawaiian *Lobariella* revealed a novel, unique, near-fruticose phenotype in *L. flynniana* (Lücking et al. 2017c). The phenomenon of developing novel morphotypes on islands has been well documented for vascular plants (Fosberg 1936; Pax et al. 1997; Kidd 2005). Thus, in general it appears that *Sticta* and other lichen-forming fungi do not behave differently from vascular plants or other organisms in terms of their evolutionary history but match them in aspects such as endemism, diversification (related to age of origin), and the evolution of peculiar phenotypes. This has also been found for other groups of organisms such as bryophytes, which traditionally have been thought to exhibit evolutionary stasis (Medina et al. 2018).

The new species

Sticta acyphellata Moncada & Lücking, sp. nov.

(Fig. 4A–E)

MycoBank MB 835286

Diagnosis: A diminutive, epiphytic, stipitate *Sticta* with a cyanobacterial photobiont, laminal to marginal isidia, and a pale underside lacking cyphellae.

Type: USA. Hawaii: Oahu, Koolau Range, Manoa Valley, 6 km ENE of Honolulu and 8 km WSW of Kaneohe, Manoa Cliffs Trail, Moleka Trailhead to Forestry Exclosure: 21°19′55″N, 157°48′43″E, 410–575 m; partially disturbed secondary forest with some exposed vegetation and some planted trees, on tree root between bryophytes; 9 June 2013, B. Moncada, R. Lücking & C. Smith 6923 (F – holotype!; B, HAW – isotypes!).

ITS barcoding sequences: MT132648 (holotype), MG367423 (paratype).

= *Sticta* 'maculohyposcrobiculata' in Widhelm et al., Molec. Phylogenet. Evol. 126: 61. 2018, nom. inval.

Description. Epiphytic on bark covered with bryophyte mats; primary photobiont cyanobacterial (*Nostoc*). Stipe present, short. Thallus monophyllous, with several individual thalli arranged irregularly, groups of individual thalli up to 3 cm across; individual thalli very delicate, irregularly branched and dissected, with 7–10 branches per 5 cm radius; lobes spathuliform to truncate, ascending, not usually overlapping, plane to involute, margins becoming dissected, not thickened; lobe internodes 0.2–0.5 cm long, 0.2–0.5 cm broad. Upper surface even, dark bluish grey when fresh, remaining bluish grey in the herbarium, matte; surface glabrous, without papillae, without pruina, with distinct white maculae forming a reticulate pattern; marginal cilia absent. Lower surface uneven, forming distinct vein-like ridges in longitudinal direction, to finely scrobiculate-faveolate, white to cream-colored; primary tomentum present, dense but very short and inconspicuous, whitish; secondary tomentum absent. Rhizines absent. Cyphellae absent. Medulla lax, white. Upper cortex paraplectenchymatous, 20–30 μm thick, uniform, consisting of 2–3 cell layers with cells 4–8 μm diam., their walls 1–2 μm thick and their lumina rounded to isodiametric, 3–6 μm diam., the innermost layer having larger cells. Photobiont layer 40–60 μm thick, its cells 5–10 μm diam. Medulla 40–60 μm thick, its hyphae 2–2.5 μm broad, nubilous due to enclosed air. Lower cortex paraplectenchymatous, 20–30 μm thick, with 1–2 cell layers; cells 5–10 μm diam., their walls 1 μm thick. Hairs of lower primary tomentum 20–70 μm long, of single, mostly unbranched, cylindrical, colorless hyphae. Apothecia not observed. Isidia present, abundant, marginal and laminal, becoming arbuscular, much-branched and coralloid; arbusculae up to 0.2 mm long and broad, distinctly flattened, with the base of thallus color and lacking cyphellae, individual isidia 0.1–0.2 mm long and 0.05–0.1 broad, dark grey, shiny, flattened and slightly imbricate. Secondary chemistry: no substances detected by TLC; medulla and cyphellae K–.

Etymology. The epithet refers to the lack of cyphellae, a unique feature within the genus.
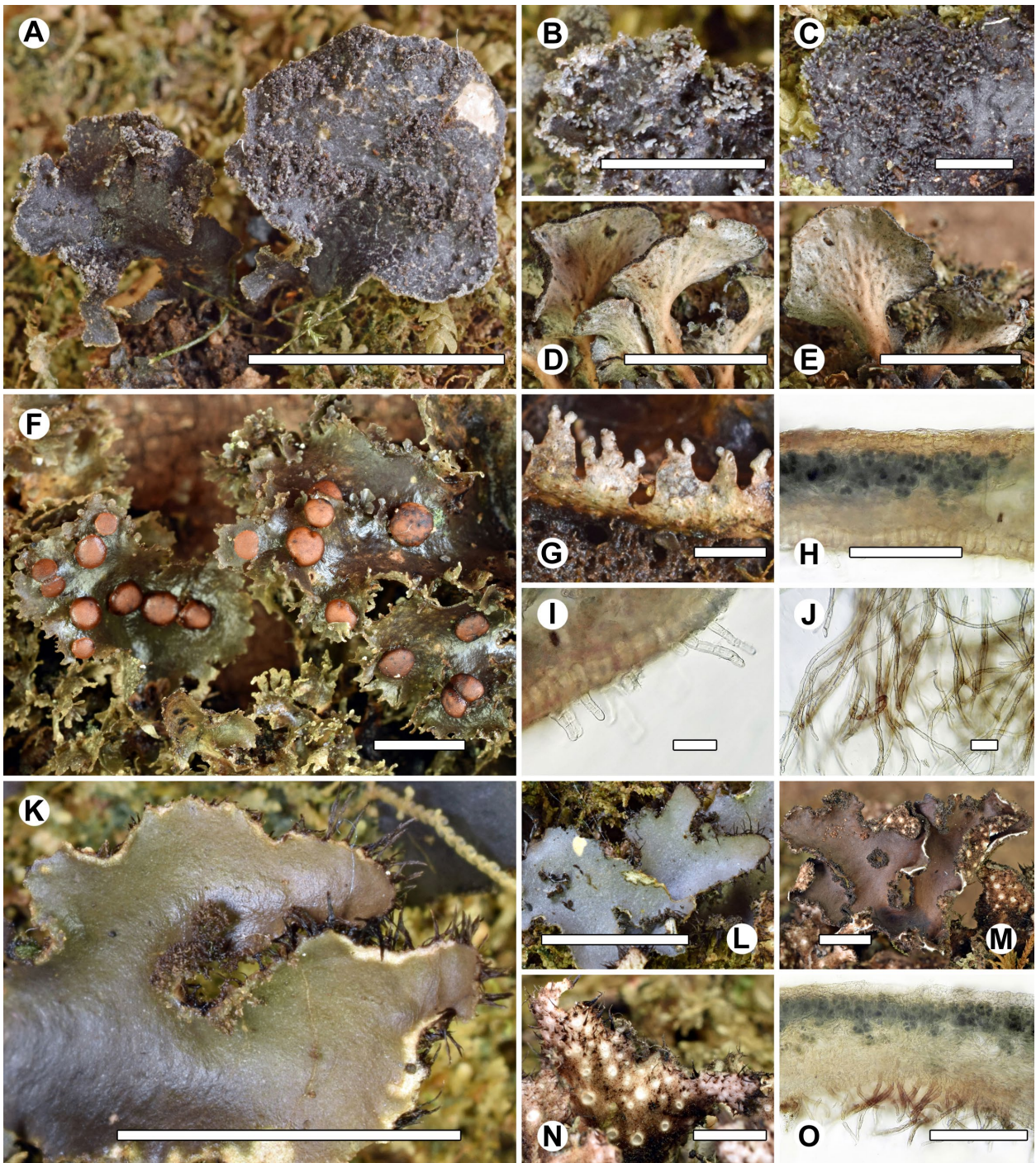
Figure 4. Morphology and anatomy of new Hawaiian *Sticta* species. A–E – *S. acyphellata* (A, thallus; B–C, upper lobe surface showing largely laminal isidia; D–E, lobe underside showing absence of cyphellae); F–J – *S. antoniana* (F, thallus with apothecia and marginal lobules; G, marginal lobules enlarged; H, section through thallus showing differentiated upper and lower cortex; I, section through lobe underside showing secondary tomentum hairs; J, primary tomentum hairs); K–O – *S. emmanueliana* (K–M, thallus lobes with isidia and marginal black cilia; N, lobe underside showing dark tomentum contrasting with whitish cyphellae and black cilia; O, section through thallus showing primary tomentum). Scales: A, D–F, K–L = 5 mm; B–C, G, M–N = 1 mm; H, O = 100 μm; I–J = 10 μm.

Distribution and ecology. Notably, this unique species was only found in a partially disturbed secondary forest on the densely populated and strongly altered island of Oahu, where it grew epiphytic in the shaded understory near the base and on the roots of tree trunks, between bryophytes.

Notes. *Sticta acyphellata* is a unique species, given its diminutive size and the complete lack of cyphellae. It

is the first species in the genus known with this feature. In a strictly morphological sense it would have to be classified as *Lobaria* s.lat., but the molecular data place it clearly within *Sticta* s.str. It falls near the base of the tree (Fig. 2; Fig. S1) near other cyanobacterial, stipitate species such as *S. caulescens*, *S. gaudichaudii*, *S. hypochra*, *S. gracilis* and *S. cyphellulata*, all from the Southern Hemisphere and/or Australasia (Galloway 1994b, 1998, 2001, 2007). Two other putative Hawaiian endemics,

S. flynnii and *S. smithii* (see below), also belong in this clade, suggesting a previously unrecognized level of diversification in this group of species and also indicating the Southern Hemisphere and Australasia as major sources of colonization of the Hawaiian archipelago.

Phylogenetically, *Sticta acyphellata* is unsupported sister to a clade formed by *S. gracilis* (Japan) and *S. flynnii* (Hawaii). The two clades differ substantially in 19 substitutions and seven indels in the ITS (Table 2; Fig. S1).

Additional specimen examined. USA. Hawaii: Oahu, Koolau Range, Manoa Valley, 6 km ENE of Honolulu and 8 km WSW of Kaneohe, Manoa Cliffs Trail, Moleka Trailhead to Forestry Exclosure: 21°19′55″N, 157°48′43″E, 410–575 m; partially disturbed secondary forest with some exposed vegetation and some planted trees, on tree base between bryophytes; 9 June 2013, B. Moncada, R. Lücking & C. Smith 6920 (B, F – paratypes!).

Sticta antoniana Moncada & Lücking, sp. nov.

(Fig. 4F–J)

MycoBank MB 835287

Diagnosis: A mid-sized, epiphytic *Sticta* with a cyanobacterial photobiont, with much-branched, brownish grey thallus forming ascending lobes featuring abundant marginal lobules, frequent apothecia, and a thick, grey-brown lower tomentum ending abruptly to leave a bare, marginal, whitish zone; closely related to *S. tomentosa* but differing from the latter in color, the marginally lobulate lobes and the thick, abruptly ending lower tomentum.

Type: USA, Hawaii: Kauai, West Kauai, western slopes of Mount Wai'ale'ale, Koke'e State Park, 20 km ENE of Waimea and 35 km NW of Lihue, at end of Kokee Road, Pihea Trail; 22°08′51″N, 159°37′53″E, 1250–1350 m; mostly undisturbed montane mesic forest, on tree bark; 15 June 2013, B. Moncada, R. Lücking & T. Flynn 7053 (F – holotype!; B, HAW – isotypes!).

ITS barcoding sequences: MT132720, MT132721, MT132722 (holo- and isotypes), MG367433, MT132733 (paratypes).

= *Sticta* 'tomentosa/hawaiiensis 3' in Widhelm et al., Molec. Phylogenet. Evol. 126: 62. 2018, nom. inval.

Description. Epiphytic on bark; primary photobiont cyanobacterial (*Nostoc*). Stipe absent. Thallus monophyllous, irregularly orbicular, up to 10 cm across, frequently anisotomously branched, with 7–15 branches per 5 cm radius; lobes flabellate to truncate, ascending, not usually overlapping, margins much dissected into elongate lobules, not thickened; lobe internodes 0.2–0.5 cm long, 0.2–0.5 cm broad. Upper surface even, olive-green when fresh, brownish grey in the herbarium, slightly shiny; surface glabrous, without papillae, without pruina, without or with scattered, indistinct maculae; cilia absent. Lower surface slightly uneven, whitish; primary tomentum thick and dense, forming light grey-brown, arachnoid tufts of fasciculate hyphae except for 2–5 mm broad marginal zone abruptly bare of tomentum; secondary tomentum absent. Rhizines absent. Cyphellae rather dense, 21–60 per cm^2, rounded, plane, immersed, white; pore 0.1–0.3 mm diam. Medulla lax, white. Upper cortex paraplectenchymatous, 20–30 μm thick, uniform, consisting

of 2–3 layers, cells 5–8 μm diam., their walls 1–2 μm thick and their lumina rounded to isodiametric, 3–6 μm diam., yellowish. Photobiont layer 30–50 μm thick, its cells 5–10 μm diam. Medulla 30–50 μm thick, its hyphae 2–2.5 μm broad, nubilous due to enclosed air. Lower cortex paraplectenchymatous, 20–30 μm thick, with single cell layer; cells 7–12 μm diam., more or less palisadic (higher than broad), their walls 1–1.5 μm thick, yellowish. Hairs of lower primary tomentum 500–1500 μm long, formed by densely entangled, mostly unbranched, pale brown, cylindrical hyphae with free apices; hairs of lower secondary tomentum scattered, 20–30 μm long, of single, unbranched, cylindrical, colorless hyphae. Cells of basal membrane of cyphellae irregularly bulging but lacking distinct papillae. Apothecia common, laminal, sessile, at first zeorine with hairy margins but mature apothecia biatorine, with remnants of thallus layer basally and with scattered marginal hairs; disc rather dark reddish brown; margin crenulate, cream-colored to pale orange. Ascospores oblong-fusiform, 3-septate, 40–50 × 6–7 μm. Marginal lobules abundant, much-branched, 1–3(–5) mm long and 0.5–1 mm broad, of the same color as thallus. Secondary chemistry: no substances detected by TLC; medulla and cyphellae K–.

Etymology. The species name honors the legacy of Anton Zahlbruckner, for his invaluable contributions to lichenology, including Hawaiian lichens, a work he did not see completed before his death (Magnusson & Zahlbruckner 1943), and who first noted the distinctiveness of this species.

Distribution and ecology. *Sticta antoniana* was found on the islands of Maui and Kauai, in both cases in more or less undisturbed montane forest at mid elevations (between 1000 and 1500 m), on shaded tree bark.

Notes. This new species is here formally introduced, although the molecular data of the ITS fungal barcoding locus do not provide sufficient resolution to distinguish it phylogenetically from *Sticta tomentosa* (Fig. 2; Fig. S1). Yet, morphologically, it is set apart from the latter by the brownish (not bluish) grey thallus with numerous marginal lobules and by the thick, abruptly ending lower tomentum; *S. tomentosa* only rarely produces adventive lobules and the lower tomentum is uniformly pale and becomes gradually thinner towards margins. Zahlbruckner (in Magnusson & Zahlbruckner 1943: 90) was the first to notice the features of this taxon, the material at that time being included under the name *S. ambavillaria*: 'Die Exemplare aus Kauai zeichnen sich durch stark gegliederte Lappen des Lagers aus und stimmen darum weniger wit der Figur in Delise, Hist. Lich. ...'. *Sticta ambavillaria* does not seem to occur in Hawaii; at least we have not found any authentic material. That species produces rather broad, uneven lobes lacking marginal lobules.

Additional specimen examined: U.S.A. Hawaii: Maui, East Maui, Haleakalā Volcano, Lower Waikamoi Preserve (The Nature Conservancy), 5 km SE of Pulakani and 18 km SE of Kahului, lower access trail to preserve off Olinda Road; 20°48′23″N, 156°15′19″E, 1200–1300 m;

disturbed primary forest dominated by *Acacia koa* and *Campanulaceae*, with invasive *Hedychium gardnerianum* in lower portions; on tree bark at base in shaded conditions, 11 June 2013, B. Moncada, R. Lücking & P. Bily 6947 (B, F, HAW – paratypes!), 6948 (B, F – paratypes!). Kauai, West Kauai, western slopes of Mount Wai'ale'ale, Koke'e State Park, 20 km ENE of Waimea and 35 km NW of Lihue, at end of Kokee Road, Pihea Trail; 22°08′51″N, 159°37′53″E, 1250–1350 m; mostly undisturbed montane mesic forest, on tree bark; 15 June 2013, B. Moncada, R. Lücking & T. Flynn 7045a (F – paratype!); ibid., on tree bark of *Cheirodendron* sp., 15 June 2013, B. Moncada, R. Lücking & T. Flynn 7065 (F – paratype!).

Sticta emmanueliana Moncada, Lücking & Lumbsch, sp. nov.   (Fig. 4K–O)

MycoBank MB 835288

Diagnosis: A small, epiphytic, shortly stipitate *Sticta* with a cyanobacterial photobiont, with branched, olive-brown to brownish grey thallus forming small lobes with marginal, arbuscular-coralloid isidia and black cilia.

Type: USA, Hawaii: Kauai, West Kauai, western slopes of Mount Wai'ale'ale, Koke'e State Park, 20 km ENE of Waimea and 35 km NW of Lihue, at end of Kokee Road, Pihea Trail; 22°08′51″N, 159°37′53″E, 1250–1350 m; mostly undisturbed montane mesic forest, on tree bark; 15 June 2013, B. Moncada, R. Lücking & T. Flynn 7058 (F – holotype!; B, HAW – isotypes!).

ITS barcoding sequences: MT132726 (holotype), MG367425, MT132673, MT132674, MT132675, MT132732 (paratypes).

= *Sticta* 'isidiopedunculata' in Widhelm et al., Molec. Phylogenet. Evol. 126: 61. 2018, nom. inval.

Description. Epiphytic on bark covered with bryophyte mats or more rarely on branches; primary photobiont cyanobacterial (*Nostoc*). Stipe present, short and broad. Thallus mono- to polyphyllous, with one to few individual thalli arranged irregularly, groups of individual thalli up to 5 cm across; individual thalli delicate, irregularly branched, with 2–4 branches per 5 cm radius; lobes irregularly elongate to tapering or truncate, horizontal to ascending, not usually overlapping, plane to slightly involute, margins not thickened; lobe internodes 3–5 mm long, 1–3 mm broad. Upper surface even, olive-brown to dark brown when fresh, brownish grey in the herbarium, matte; surface glabrous, without papillae, without pruina, with scattered white maculae; marginal cilia present, formed by isolated, submarginal tufts of primary tomentum that become visible beyond margins, conspicuous particularly in younger lobes, becoming evanescent in old lobes, (brown-)black, 0.1–0.4 mm long. Lower surface uneven, mostly dark brown (particularly towards center) but marginally becoming white to cream-colored, either in streaks or entirely so; primary tomentum present but becoming thin towards margins except for the (sub-marginal) cilia, otherwise forming loosely to densely arranged brown tufts of fasciculate hyphae, much shorter and lighter than the (sub-)marginal cilia; secondary tomentum developed up to margins, thin, pubescent, whitish to light brownish. Rhizines absent. Cyphellae dense, 41–80 per cm^2, rounded, immersed-erumpent, white, appearing pruinose, with cream-colored to light brown margin bare of tomentum; pore 0.1–0.2 mm diam. towards margins, 0.2–0.5 mm diam. towards center. Medulla lax, white. Upper cortex paraplectenchymatous, 10–15 μm thick, uniform, consisting of 2–3 cell layers with cells 4–8 μm diam., their walls 1–2 μm thick and their lumina rounded to isodiametric, 3–6 μm diam. Photobiont layer 20–30 μm thick, its cells 5–10 μm diam. Medulla 30–50 μm thick, its hyphae 2–2.5 μm broad, nubilous due to enclosed air. Lower cortex paraplectenchymatous, 15–25 μm thick, with 2–3 cell layers; cells 5–10 μm diam., their walls 1–2 μm thick. Hairs of lower primary tomentum 100–200 μm long, in fascicles of 10–20, mostly unbranched but loosely agglutinate, cylindrical hyphae with free apices, usually brownish; hairs of lower secondary tomentum 25–100 μm long, of single, mostly unbranched, cylindrical hyphae with free apices, pale brown. Cells of basal membrane of cyphellae irregularly bulging but without distinct papillae. Apothecia not observed. Isidia present, abundant, predominantly marginal, arbuscular, much-branched and becoming coralloid; arbusculae up to 0.5 mm long and broad, with the base of thallus color and lacking cyphellae, individual isidia 0.1–0.3 mm long and 0.05–0.1 mm broad; grey-brown, shiny, cylindrical. Secondary chemistry: no substances detected by TLC; medulla and cyphellae K– to K+ pale yellow.

Etymology. We are delighted to dedicate this new species to our colleague and friend, Emmanuël Sérusiaux, on the occasion of his official retirement from formal duties but certainly not from lichenology. Emmanuël has made numerous invaluable contributions to lichenology in almost all taxonomic groups and geographic areas, but especially in tropical lichenology. We congratulate him on his great achievements!

Distribution and ecology. *Sticta emmanueliana* appears to be similar in ecology to *S. antoniana*, having been found at exactly the same localities on the islands of Maui and Kauai, in both cases in more or less undisturbed montane forest at mid elevations (between 1000 and 1500 m), on shaded tree bark. An older collection is also from Maui, at higher elevation (1800 m).

Notes. Based on the marginal isidia and black cilia, this new species would perhaps be identified with the name *Sticta cometiella*, originally described from Mexico. However, the latter, apparently a strictly Neotropical taxon, is entirely unrelated, clustering in a different clade in another portion of the tree, and differs also in the frequently laminal isidia (Moncada 2012; Moncada et al. 2014a). Another similar stipitate species with marginal isidia and cilia is *S. duplolimbata*, which has an Australasian distribution (Galloway 1998). However, the latter is also unrelated to *S. emmanueliana* but in turn sister to *S. cometiella* (Fig. S1). This is another example of superficially similar phenotypes that evolved independently in different lineages of the genus, as already shown for *S. fuliginosa* and *S. limbata* (Moncada et al. 2014a; Magain & Sérusiaux 2015).

Phylogenetically close to *S. emmanueliana* are the Paleotropical *S. marginifera* and *S. caliginosa* from New Zealand; both are stipitate and marginally isidiate but lack cilia (Galloway 1998, 2007). *Sticta emmanueliana* is strongly supported sister to a clade formed by the latter two species (Fig. 2; Fig. S1), forming a basal, paraphyletic grade. It differs from *S. caliginosa* (New Zealand) substantially in ten substitutions and 13 indels and from *S. marginifera* (Paleotropics) in seven substitutions and 18 indels in the ITS (Table 2).

Additional specimen examined. USA. Hawaii: Maui, East Maui, Haleakalā Volcano, Lower Waikamoi Preserve (The Nature Conservancy), 5 km SE of Pulakani and 18 km SE of Kahului, lower access trail to preserve off Olinda Road; 20°48′23″N, 156°15′19″E, 1200–1300 m; disturbed primary forest dominated by *Acacia koa* and *Campanulaceae*, with invasive *Hedychium gardnerianum* in lower portions; on tree bark, 11 June 2013, B. Moncada, R. Lücking & P. Bily 6949 (F – paratype!), 6954 (B, F, HAW – paratypes!), 6955 (F – paratype!). Maui, East Maui, Makawao Forest Reserve, below Pu'u Nianiau; 1800 m; over moss on *Myrsine* trunk, 15 June 1975, C. W. Smith 1922 (HAW). Kauai, West Kauai, western slopes of Mount Wai'ale'ale, Koke'e State Park, 20 km ENE of Waimea and 35 km NW of Lihue, at end of Kokee Road, Pihea Trail; 22°08′51″N, 159°37′53″E, 1250–1350 m; mostly undisturbed montane mesic forest, on tree bark; 15 June 2013, B. Moncada, R. Lücking & T. Flynn 7045a (F – paratype!); ibid., on tree bark, 15 June 2013, B. Moncada, R. Lücking & T. Flynn 7064 (F – paratype!).

Sticta flynnii Moncada & Lücking, sp. nov. (Fig. 5A–E)

MycoBank MB 835289

Diagnosis: A small, epiphytic, shortly stipitate *Sticta* with a cyanobacterial photobiont, with largely unbranched, olive-green to bluish grey thallus with marginal, arbuscular-coralloid isidia, with pale, shallowly veined underside producing rather large, irregular cyphellae.

Type: USA, Hawaii: Kauai, West Kauai, western slopes of Mount Wai'ale'ale, Koke'e State Park, 20 km ENE of Waimea and 35 km NW of Lihue, at end of Kokee Road, Pihea Trail; 22°08′51″N, 159°37′53″E, 1250–1350 m; mostly undisturbed montane mesic forest, on tree bark; 15 June 2013, B. Moncada, R. Lücking & T. Flynn 7055 (F – holotype!).

ITS barcoding sequences: MT132723–MG367434 (holotype), MT132728 (paratype).

= *Sticta* 'albohypoarbuscula' in Widhelm et al., Molec. Phylogenet. Evol. 126: 60. 2018, nom. inval.

Description. Epiphytic on bark covered with bryophyte mats; primary photobiont cyanobacterial (*Nostoc*). Stipe present, short and broad. Thallus mono- to polyphyllous, with one to few individual thalli arranged irregularly, groups of individual thalli up to 5 cm across; individual thalli delicate, unbranched to sparsely branched, with 0–1 branches per 5 cm radius but becoming apically dissected; lobes suborbicular to reniform or truncate, ascending, not usually overlapping, plane to involute, margins becoming coarsely dissected, not thickened; lobe internodes 0.5–1 cm long, 1–3 cm broad. Upper surface even, olive-green when fresh, bluish grey in the herbarium, matte; surface glabrous, without or with scattered papillae,

without pruina, with scattered white maculae; marginal cilia absent. Lower surface uneven, forming shallow, vein-like ridges. in longitudinal direction, white to cream-colored; primary tomentum absent; secondary tomentum developed up to margins, thin, pubescent, white. Rhizines absent. Cyphellae scattered, 1–20 per cm^2 towards thallus center and 21–40 per cm^2 towards margin, rounded to irregular or becoming angular, plane, immersed, white, appearing pruinose; pore 0.5–1 mm diam. towards margins, 1–3 mm across towards center. Medulla lax, white. Upper cortex paraplectenchymatous, 20–30 μm thick, uniform, consisting of 2–3 cell layers with cells 5–10 μm diam., their walls ~1 μm thick and their lumina isodiametric, 4–9 μm diam. Photobiont layer 30–70 μm thick, its cells 5–10 μm diam. Medulla 30–50 μm thick, its hyphae 2–2.5 μm broad, nubilous. Lower cortex paraplectenchymatous, 20–25 μm thick, with 1–2 cell layers; cells 5–10 μm diam., their walls 1–2 μm thick. Hairs of lower secondary tomentum 20–50 μm long, of single, mostly unbranched, cylindrical hyphae with free apices. Cells of basal membrane of cyphellae irregularly bulging but without distinct papillae. Apothecia not observed. Isidia present, abundant, mostly marginal but in part also laminal, arbuscular, much-branched and becoming coralloid; arbusculae up to 2 mm long and broad, with the base of thallus color and lacking cyphellae, 0.1–0.2 mm long and 0.05–0.1 broad; brown, shiny, cylindrical to flattened. Secondary chemistry: no substances detected by TLC; medulla and cyphellae K–.

Etymology. This new species is dedicated to Timothy Flynn, Curator at the herbarium (PTBG) of the National Tropical Botanical Garden and co-collector of the type material.

Distribution and ecology. *Sticta flynnii* has only been found twice at the type locality, growing in undisturbed montane forest at mid elevations (between 1000 and 1500 m) on shaded tree bark. An older collection comes from Haleakalā National Park on Maui, indicating a distribution and ecology similar to those of *S. antoniana*, *S. emmanueliana* and *S. hawaiiensis*. Like several other new species described here, due to its small size this taxon likely has been overlooked and might be more common.

Notes. *Sticta flynnii* is one of three new Hawaiian species, and putative endemics, clustering in an early diverging clade close to *S. gracilis* and *S. cyphellulata* (Fig. 2; Fig. S1). Quite a number of cyanobacterial species in the genus share the caulescent morphology with marginal isidia, beside *S. cyphellulata* also *S. brevipes*, *S. hypochra*, *S. longipes* and *S. marginifera* (Galloway 1994b, 1998). All differ in morphological details such as size, the robustness and degree of branching of the thallus and the nature of the isidia. *Sticta flynnii* is a smaller species compared to the others mentioned here but it produces among the largest cyphellae, reaching up to 3 mm in diam. (usually up to 1 mm in the other species). This feature also distinguishes it from the closely related *S. smithii*.

Phylogenetically, *Sticta flynnii* is supported sister to *S. gracilis* (Japan). The two clades differ substantially
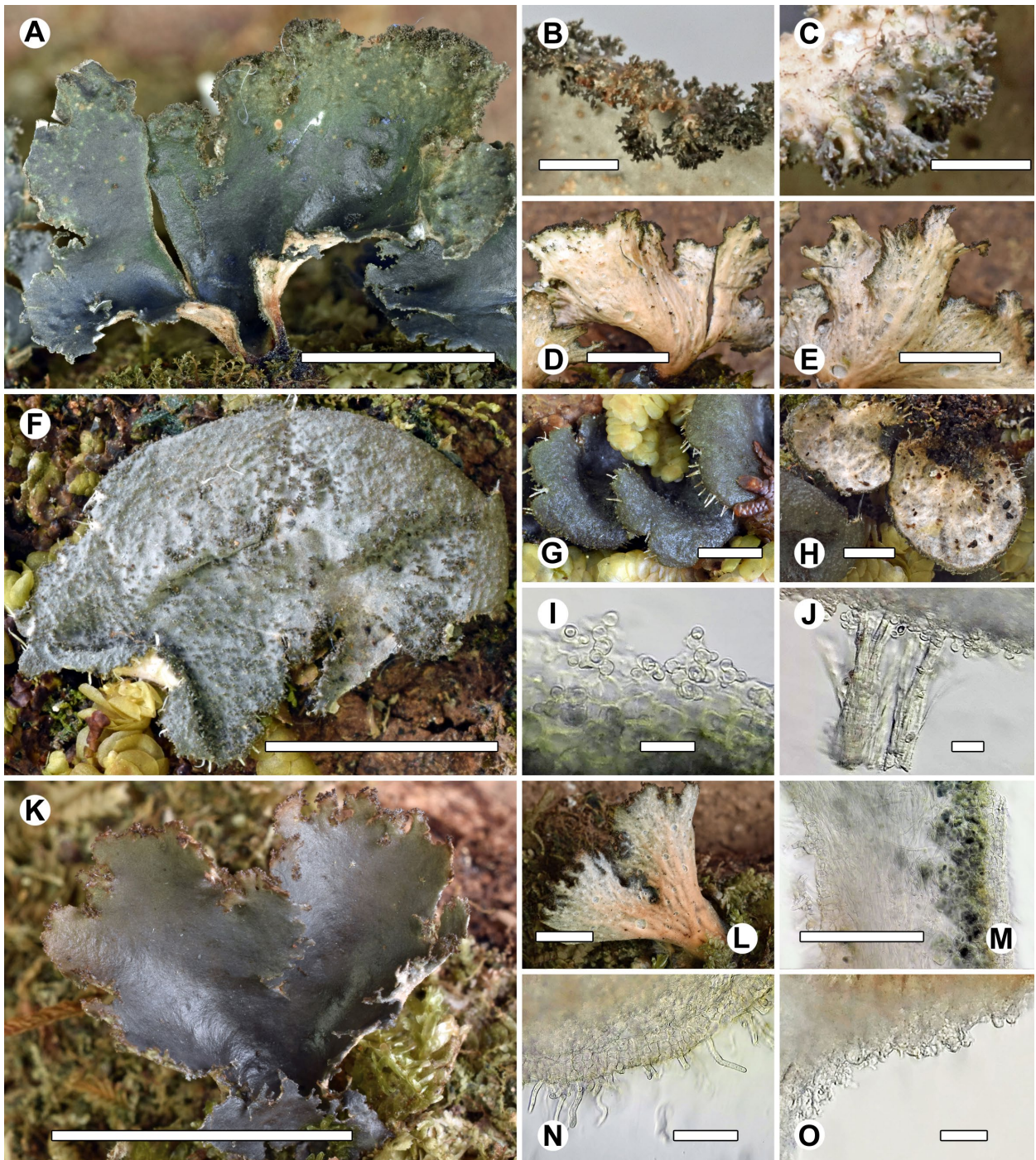
Figure 5. Morphology and anatomy of new Hawaiian *Sticta* species. A–E – *S. flynnii* (A, thallus; B–C, marginal arbuscular isidia seen from above and below; D–E, lobe underside showing large cyphellae); F–J – *S. hawaiiensis* (F, mature thallus lobe showing laminal isidia; G, young lobes with conspicuous white cilia; H, lobe underside showing minute cyphellae; I, section through lobe showing upper surface tomentum; J, section through lobe showing fascicle of lower surface primary tomentum); K–O – *S. smithii* (K, thallus with marginal isidia; L, lobe underside showing minute cyphellae; M, section through lobe; N, section through lobe showing secondary tomentum; O, section through membrane of cyphella showing papillae). Scales: A, D–F, K = 5 mm; G–H, L = 1 mm; B–C = 0.5 mm; M = 100 μm; N = 50 μm; I–J, O = 10 μm.

in 12 substitutions and 23 indels in the ITS (Table 2; Fig. S1).

Additional specimen examined. USA. Hawaii: Maui, East Maui, Haleakalā Volcano, Haleakalā National Park, 1/8 mile E of Hosmer's Grove campsite; 2233 m; deep gully with steep sides, on dead twigs of *Dodonea* 1 m above ground in open position; 12 June 1975, C. W. Smith 1754 (HAW). Kauai, West Kauai, western slopes of Mount Wai'ale'ale, Koke'e State Park, 20 km ENE of Waimea and 35 km NW of Lihue, at end of Kokee Road,

Pihea Trail; 22°08′51″N, 159°37′53″E, 1250–1350 m; mostly undisturbed montane mesic forest, on tree bark; 15 June 2013, B. Moncada, R. Lücking & T. Flynn 7059 (HAW – paratype!).

Sticta hawaiiensis Moncada & Lücking, sp. nov.

(Fig. 5F–J)

MycoBank MB 835290

Diagnosis: A small, epiphytic *Sticta* with cyanobacterial photo-biont, with largely unbranched, suborbicular, bluish to brownish

grey thallus with laminal, coralloid isidia, with conspicuous white cilia, and with pale underside producing small cyphellae.

Type: USA, Hawaii: Kauai, West Kauai, western slopes of Mount Wai'ale'ale, Koke'e State Park, 20 km ENE of Waimea and 35 km NW of Lihue, at end of Kokee Road, Pihea Trail; 22°08′51″N, 159°37′53″E, 1250–1350 m; mostly undisturbed montane mesic forest, on tree bark; 15 June 2013, B. Moncada, R. Lücking & T. Flynn 7048 (F – holotype!; HAW – isotype!).

ITS barcoding sequences: MT132716 (holotype), MT132672 (paratype).

Description. Epiphytic on bark covered with bryophyte mats; primary photobiont cyanobacterial (*Nostoc*). Stipe indistinct (in young thalli) to absent. Thallus mono- to polyphyllous, with one to few individual thalli arranged irregularly, groups of individual thalli up to 5 cm across; individual thalli delicate, unbranched; lobes suborbicular, ascending, not usually overlapping, plane to revolute, margins entire to irregular, not thickened; lobes 0.2–0.5 cm long, 0.5–1 cm broad. Upper surface irregularly verruculose-rugose in concentric patterns, dark grey when fresh, rather dark bluish grey in the herbarium, matte; surface very thinly whitish tomentose, without or with scattered papillae, without pruina, without distinct maculae; marginal cilia abundant and distinct, particularly in younger thalli, white, 0.2–0.7 nm long, usually curved slightly downwards and often flattened. Lower surface slightly uneven, white to cream-colored; primary tomentum present (except for margins), forming scattered (towards center more densely arranged), mottled brown tufts of fasciculate hyphae; secondary tomentum developed up to margins, thin, pubescent, white. Rhizines absent. Cyphellae scattered, 1–20 per cm², rounded, plane, immersed to becoming erumpent (best seen when thallus hydrated), white; pore 0.1–0.2 mm diam. Medulla lax, white. Upper cortex paraplectenchymatous, 15–20 μm thick, uniform, consisting of 1–2 cell layers with cells 5–10 μm diam., their walls 1–2 μm thick and their lumina rounded to isodiametric, 3–8 μm diam. Photobiont layer 20–30 μm thick, its cells 5–10 μm diam. Medulla 30–50 μm thick, its hyphae 2–2.5 μm broad, nubilous due to enclosed air. Lower cortex paraplectenchymatous, 10–20 μm thick, with single cell layer; cells 7–12 μm diam., their walls 1–1.5 μm thick. Hairs of upper tomentum 10–20 μm long, of single, branched, moniliform hyphae with free apices. Hairs of lower primary tomentum 100–150 μm long, in fascicles of 10–20, mostly unbranched but agglutinate, cylindrical hyphae with free apices; hairs of lower secondary tomentum 10–15 μm long, of single, branched, strongly moniliform hyphae with globose cells and free apices. Cells of basal membrane of cyphellae irregularly bulging, with numerous tiny papillae per cell. Apothecia not observed. Isidia present, abundant, laminal, branched and becoming coralloid; clusters of isidia up to 0.2 mm long and broad, rather dark grey to brownish grey, shiny, cylindrical. Secondary chemistry: no substances detected by TLC; medulla and cyphellae K–.

Etymology. The epithet refers to the archipelago of Hawaii, as this new species is a putative endemic in a highly derived, apparently subcosmopolitan species complex.

Distribution and ecology. Besides *Sticta antoniana* and *S. emmanueliana*, this is a third species with a similar ecology, having been found at the same two localities on the islands of Maui and Kauai, in both cases in more or less undisturbed montane forest at mid elevations (between 1000 and 1500 m), on shaded tree bark. Another, older collection stems from Oahu, in a more disturbed habitat.

Notes. The *Sticta ciliata* complex is one of more than a dozen mostly unrelated lineages that exhibit *S. fuliginosa* morphology, with broadly rounded lobes featuring laminal isidia and generally a pale underside. This distinctive lineage was first recognized in a broad phylogenetic analysis by Moncada et al. (2014a), based on material from Colombia, but Magain & Sérusiaux (2015) eventually established that *S. ciliata*, described from Ireland, is a representative of this clade. The data now available characterize this clade as a species complex, with uniform morphology and anatomy (small size; broad, laminally isidiate lobes; marginal whitish cilia; cells of the cyphella membrane with numerous tiny papillae).

The complex has been shown to be present in Western Europe, the Neotropics, and now Hawaii. It forms several distinct lineages (Fig. 2; Fig. S1): two chiefly in South America, two in Western Europe (one including the type), two in the Caribbean (Puerto Rico; recently described as *S. parvilobata*; Mercado-Díaz et al. 2020) and one in Hawaii. The Hawaiian taxon *S. hawaiiensis* appears to be most closely related to *S.* aff. *parvilobata* from Puerto Rico, from which it differs in only one substitution, whereas *S. parvilobata* s.str. (also Puerto Rico) differs in ten substitutions. *Sticta ciliata* s.str. deviates in six substitutions, whereas the other, unnamed clades exhibit differences between three and six substitutions and between zero and two indels in the ITS (Table 2; Fig. 6). It therefore seems prudent to formally recognize the Hawaiian material as a distinct taxon, as the two named species in this complex show substantial differences, whereas the more similar lineages have not yet been named. Given the difference of only one substitution between *S. hawaiiensis* and the Puerto Rican *S.* aff. *parvilobata*, the latter could be considered to represent the same species, which would be a remarkable disjunction in this clade. However, the substitution present in *S.* aff. *parvilobata* is unique among all lineages in the entire clade (Fig. 6) and therefore we consider it unlikely that this lineage is conspecific with *S. hawaiiensis*. Overall, *S. ciliata* s.lat. appears to represent a relatively recent radiation in active, phenotypically cryptic speciation but with a distinct geographic signal (Magain & Sérusiaux 2015; Mercado-Díaz et al. 2020).

Additional specimen examined. USA. Hawaii: Oahu, Koolau Mountains, Tantalus; 467 m; exposed ridge, on *Cordyline terminalis*; 26 July 1977, G. Y. Daida 520 (HAW). Maui, East Maui, Haleakalā Volcano, Lower Waikamoi Preserve (The Nature Conservancy), 5 km SE of Pulakani and 18 km SE of Kahului, lower access trail to preserve off Olinda Road; 20°48′23″N, 156°15′19″E, 1200–1300 m; disturbed primary forest dominated by *Acacia koa* and *Campanulaceae*, with invasive *Hedychium gardnerianum* in lower portions; on tree
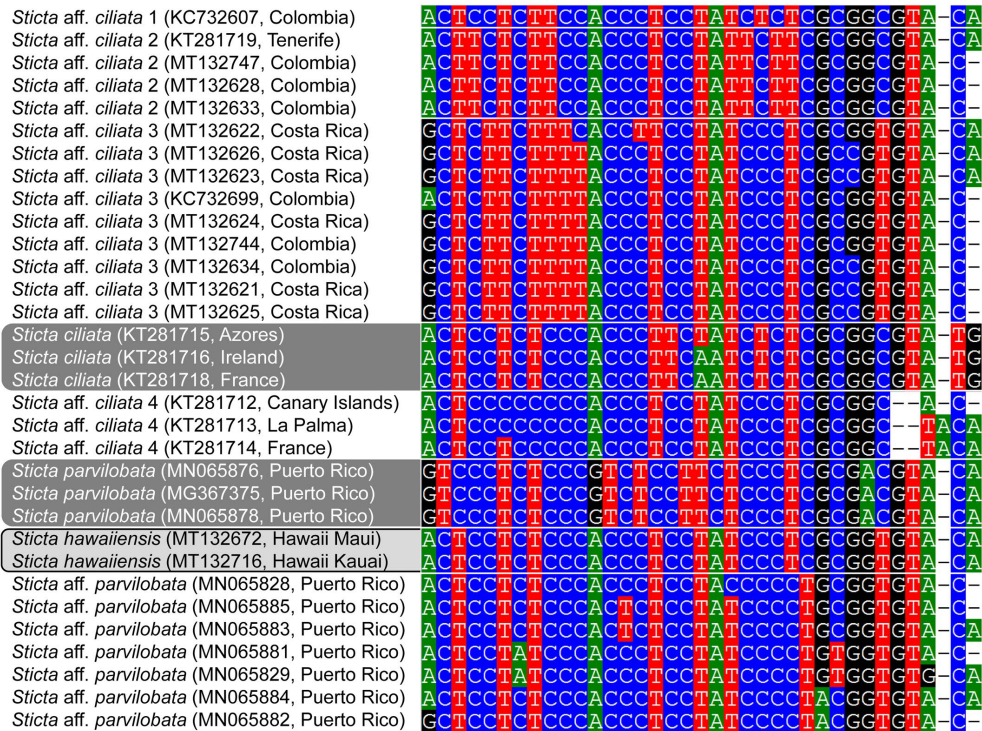
Figure 6. Comparison of variable sites in the fungal ITS barcoding marker in the *Sticta ciliata* complex (screenshot from BIOEDIT). All constant columns and the few autapomorphic, parsimony-uninformative singleton sites were deleted. Formally named taxa are highlighted. Note that the variation is structured in blocks that largely correlate with geography. The Hawaiian lineage is most similar to two unnamed lineages, namely *S.* aff. *ciliata* 4 (four substitutions) and *S.* aff. *parvilobata* (one substitution). While the difference towards *S. parvilobata* appears minor, it corresponds to two unique substitutions in the latter not present in any of the other lineages.

bark, 11 June 2013, B. Moncada, R. Lücking & P. Bily 6953 (B, F, HAW – paratypes!).

Sticta smithii Moncada & Lücking, sp. nov. (Fig. 5K–O)

MycoBank MB 835291

Diagnosis: A diminutive, epiphytic, stipitate *Sticta* with a cyanobacterial photobiont, marginal, arbuscular, typically flattened isidia, and a pale underside with small cyphellae.

Type: USA, Hawaii: Oahu, Koolau Range, Manoa Valley, 6 km ENE of Honolulu and 8 km WSW of Kaneohe, Manoa Cliffs Trail, Moleka Trailhead to Forestry Exclosure: 21°19′55″N, 157°48′43″E, 410–575 m; partially disturbed secondary forest with some exposed vegetation and some planted trees, on tree root between bryophytes; 9 June 2013, B. Moncada, R. Lücking & C. Smith 6916 (F – holotype!; B, HAW – isotypes!).

ITS barcoding sequences: MG754196 (holotype).

Description. Epiphytic on bark covered with bryophyte mats; primary photobiont cyanobacterial (*Nostoc*). Stipe present, short. Thallus monophyllous, with few individual thalli arranged irregularly, groups of individual thalli up to 3 cm across; individual thalli delicate, irregularly branched and dissected, with 2–4 branches per 5 cm radius; lobes spathuliform to truncate, ascending, not usually overlapping, plane to involute, margins becoming strongly dissected, not thickened; lobe internodes 0.3–0.6 cm long, 0.2–0.5 cm broad. Upper surface even, olive-grey when fresh, bluish grey in the herbarium, matte; surface glabrous, without papillae, without pruina, with scattered white maculae; marginal cilia absent. Lower surface uneven, forming shallow, vein-like ridges

in longitudinal direction, white to cream-colored, with pale orange streaks towards center; primary tomentum present, dense but very short, becoming shorter towards margins, whitish; secondary tomentum absent. Rhizines absent. Cyphellae rather dense, 21–40 per cm^2, rounded to irregular, plane, immersed, white; pore 0.2–0.5 mm diam. Medulla lax, white. Upper cortex paraplectenchymatous, 20–30 μm thick, uniform, consisting of 2–3 cell layers with cells 4–8 μm diam., their walls 1–2 μm thick and their lumina rounded to isodiametric, 3–6 μm diam., the innermost layer having larger cells. Photobiont layer 40–60 μm thick, its cells 5–10 μm diam. Medulla 100–150 μm thick, its hyphae 2–2.5 μm broad, nubilous due to enclosed air and grey crystals. Lower cortex paraplectenchymatous, 20–30 μm thick, with 1–2 cell layers; cells 5–10 μm diam., their walls 1–2 μm thick. Hairs of lower primary tomentum 50–100 μm long, of single to agglutinate, mostly unbranched, cylindrical, colorless hyphae with free apices. Cells of basal membrane of cyphellae irregularly bulging, each cell with 1–3 elongated papillae, therefore appearing thorny. Apothecia not observed. Isidia present, abundant, predominantly marginal, arbuscular, much-branched and becoming coralloid; arbusculae up to 1 mm long and broad, distinctly flattened, with the base of thallus color and lacking cyphellae, individual isidia 0.1–0.2 mm long and 0.05–0.1 broad; grey-brown, shiny, typically flattened. Secondary chemistry: no substances detected by TLC; medulla and cyphellae K–.

Etymology. The epithet honors Clifford Smith for his invaluable contributions to our knowledge of Hawaiian

lichens and for his tireless conservation efforts to preserve native Hawaiian ecosystems, including its lichens (Smith 1991; Tunison et al. 1992; Ellshoff et al. 1995; Smith 2002; Rohrer et al. 2006).

Distribution and ecology. Like *Sticta acyphellata*, this new species was only found in a partially disturbed secondary forest on the densely populated and strongly altered island of Oahu, where it grew epiphytic in shaded conditions on tree trunks between bryophytes.

Notes. *Sticta smithii* is overall most similar to *S. flynnii*, sharing the small, stipitate, cyanobacterial thallus with marginal isidia and the cyphellate underside. A major difference is the size of the cyphellae, becoming large and irregular in *S. flynnii* but remaining diminutive in *S. smithii*. Also, the distribution and ecology of the two species appear to differ, as judged from the limited data.

Phylogenetically, *Sticta flynnii* is not directly related to *S. flynnii* but is supported sister to *S. cyphellulata* (China). The two clades differ substantially in 15 substitutions and 11 indels in the ITS (Table 2; Fig. S1).

Sticta waikamoi Moncada & Lücking, sp. nov.

(Fig. 7A–F)

MycoBank MB 835292

Diagnosis: A small to mid-sized epiphytic *Sticta* with a cyanobacterial photobiont, a brownish, much-branched thallus with sligly canaliculate lobes and marginal, coralloid isidia, and a thick, dark brown lower tomentum with strongly contrasting, conspicuous, whitish cyphellae.

Type: USA, Hawaii: Maui, East Maui, Haleakalā Volcano, Upper Waikamoi Preserve (The Nature Conservancy), 12 km SE of Pulakani and 25 km SE of Kahului, upper access trail to preserve bordering Haleakalā National Park; 20°46′07″N, 156°14′17″E, 1800–2100 m; introduced mixed conifer forest intermingled with *Acacia koa* and other native trees; 12 June 2013, B. Moncada, R. Lücking & P. Thomas 7000 (F – holotype!; B, HAW – isotypes!).

ITS barcoding sequences: MT132696 (holotype).

Description. Epiphytic over bryophytes; primary photobiont cyanobacterial (*Nostoc*). Stipe absent. Thallus monophyllous, irregularly orbicular, up to 7 cm across, anisotomously branched, with 3–5 branches per 5 cm radius; lobes elongate to narrowly flabellate, more or less horizontal, not usually overlapping, involute to shallowly canaliculate, margins entire to broadly crenulate, not thickened; lobe internodes 0.5–1.5 cm long, 0.3–0.5 cm broad. Upper surface even, olive-grey to grey-brown when fresh, light yellowish to greyish brown in the herbarium, matte; surface glabrous, without papillae, without pruina, without distinct maculae; marginal cilia not differentiated but lower tomentum often projecting beyond margins to resemble short, brown-black cilia. Lower surface slightly uneven, dark brown; primary tomentum thick and dense, forming dark brown, arachnoid tufts of fasciculate hyphae; secondary tomentum not discernable. Rhizines scattered towards thallus center. Cyphellae rather dense, 21–60 per cm², rounded, plane, immersed to becoming erumpent, white to cream-colored, strongly contrasting with the

dark tomentum; pore 0.3–1(–1.5) mm diam. Medulla lax, white. Upper cortex paraplectenchymatous, 30–50 μm thick, differentiated, consisting of 3–5 cell layers, the upper 1–2 layers with cells 3–5 μm diam., their walls 1–2 μm thick and their lumina rounded to isodiametric, 2–3 μm diam., yellowish, the lower 2–3 layers with cells 5–10 μm diam., their walls 1–1.5 μm thick and their lumina isodiametric, 4–9 μm diam., colorless. Photobiont layer 50–70 μm thick, forming vertical (perpendicular) clusters, its cells 5–10 μm diam. Medulla 30–50 μm thick, its hyphae 2–2.5 μm broad, nubilous due to enclosed air. Lower cortex paraplectenchymatous, 20–30 μm thick, with 2–3 cell layers; cells 7–12 μm diam., their walls 1–2 μm thick, becoming brown towards margin. Hairs of lower primary tomentum 100–300 μm long, in fascicles of 10–20, mostly unbranched but strongly agglutinate, dark brown, cylindrical hyphae with free apices; hairs of lower secondary tomentum 20–30 μm long, of single, branched, weakly moniliform hyphae with slightly inflated cells and free apices. Cells of basal membrane of cyphellae irregularly bulging but lacking papillae. Apothecia not observed. Isidia present, abundant, predominantly marginal, branched and becoming coralloid; clusters of isidia up to 0.5 mm long and broad, grey-brown, shiny, individual isidia usually flattened. Secondary chemistry: no substances detected by TLC; medulla K– to slowly K+ faintly yellowish, cyphellae K+ slowly ochraceous.

Etymology. The epithet is a noun in apposition referring to the Waikamoi Preserve (The Nature Conservancy), the largest private nature reserve in the state of Hawaii.

Distribution and ecology. This new species is so far only known from a single collection, found at high altitude in mixed conifer forest. In spite of the well-preserved appearance of this forest, no conifer is native to Hawaii and all have been introduced. It is therefore difficult to speculate about the ecology of this species. Its closest relatives, *S.* aff. *cordillerana*, *S. rhizinata* and *S.* aff. *rhizinata*, are from North and South America (McDonald et al. 2003; Moncada & Lücking 2012; Moncada et al. 2014a).

Notes. *Sticta waikamoi* is one of two species in Hawaii (the other being *S. andina*) best corresponding to the morphology of what has been called *S. weigelii*. The latter species in a strict sense appears to be a Neotropical taxon and is not directly related (Fig. S1); it differs in the thinner lower tomentum and the often yellow cyphellae. In Hawaii, *S. waikamoi* can be confused with *S. andina*, which is found in the same habitat, but differs in the generally narrower lobes and is also not directly related (Fig. 2; Fig. S1). Although *S. waikamoi* is closely related to *S. rhizinata*, it appears to be a much smaller species, and rhizines, a characteristic feature of the latter (Moncada & Lücking 2012), are sparse and not conspicuous.

Phylogenetically, the new species forms part of a complex of four lineages, including *Sticta rhizinata* from Colombia and two as yet undescribed taxa from Colombia and North America (Fig. S1). Overall, *S. waikamoi* differs from *S. rhizinata* in four substitutions, and from the other two taxa in six to seven substitutions and up to
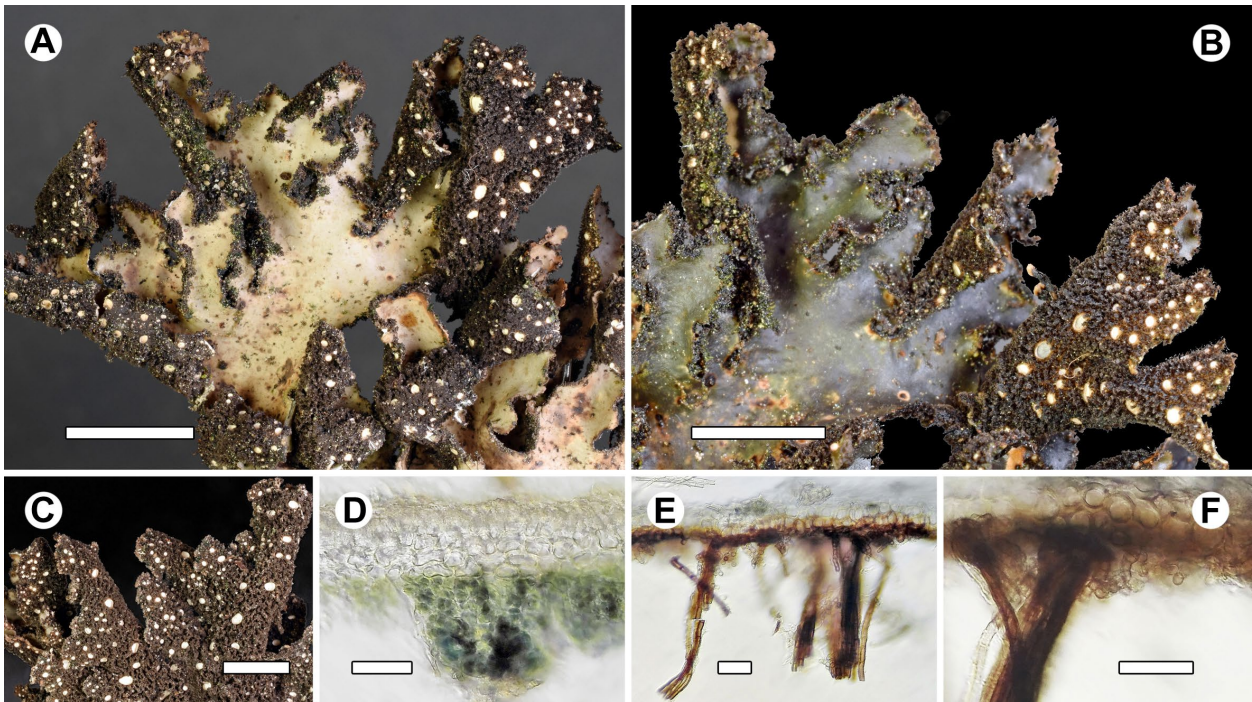
Figure 7. Morphology and anatomy of new Hawaiian *Sticta* species. A–F – *S. waikamoi* (A–C, dry and wet lobes showing marginal isidia and dark lower tomentum contrasting with whitish cyphellae; D, section through thallus showing vertically organized groups of photobiont cells; E–F; section through thallus showing lower primary and secondary tomentum). Scales: A–C = 1 mm; D–F = 20 μm.

one indel. Given these limited differences, one may also consider the alternative of applying subspecies level to the Hawaiian material. However, compared to the case of *S. scabrosa* subsp. *hawaiiensis* (Moncada et al., unpublished), there are twice as many differences in the ITS between *S. waikamoi* and *S. rhizinata* (Table 2) and these correlate with the deviating morphology. We therefore consider species level to be more appropriate, and we apply it also to raise awareness of this apparently very rare taxon until it can be studied from more material.

Acknowledgements

Supplementary electronic material

Figure S1. Best-scoring ML circle tree of *Sticta* based on the ITS barcoding marker. Hawaiian specimens are marked in blue (exclusive Hawaiian clades) and orange (Hawaiian specimens nested within more widely distributed taxa). Bootstrap values are indicated above branches. Download file

Table S1. Genbank accession numbers of ITS sequences of non-Hawaiian (or previously accessioned) representatives of *Sticta* (and outgroup) used in this study. Download file

File S1. Alignment of the fungal ITS barcoding marker for 859 OTUs of Sticta used in this study (Fasta format). Download file

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