


Standard Paper

A taxonomic reassessment of the genus *Sticta* (lichenized Ascomycota: *Peltigeraceae*) in the Hawaiian archipelago

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Abstract

The taxonomy of the genus *Sticta* in Hawaii is reassessed, based on a separately published molecular phylogeny using the fungal barcoding marker ITS. Based on Magnusson and Zahlbruckner's treatment from 1943 and Magnusson's catalogue from 1955, seven species of *Sticta* and three infraspecific taxa had been reported from the archipelago, all widespread except the putative endemic *S. plumbicolor*. Here we provide a taxonomic treatment of 13 taxa, 12 species and one subspecies, distinguished in a previous phylogenetic analysis: *S. acyphellata*, *S. andina*, *S. antoniana*, *S. emmanueliana*, *S. flynnii*, *S. fuliginosa*, *S. hawaiiensis*, *S. limbata*, *S. plumbicolor*, *S. scabrosa* subsp. *hawaiiensis*, *S. smithii*, *S. tomentosa* and *S. waikamoi*. All taxa are described, discussed and illustrated and a dichotomous key is presented. The implications of revised species taxonomies for studies in other fields such as ecology, ecophysiology, biogeography, biochemistry, and applications such as environmental monitoring are discussed. We also propose a protocol to use *Sticta* lichens to monitor the environmental health of Hawaiian ecosystems.

Key words: environmental monitoring, Kauai, *Lobarioideae*, Maui, Molokai, Oahu

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Introduction

The Hawaiian lichen biota has generally been presumed to contain mostly widespread species, with a comparatively low degree of endemism at around 20–30% (Smith 1993, 2013; Eldredge & Miller 1995). In contrast, endemism in vascular plants is c. 80% (Wagner *et al.* 1999; Evenhuis & Eldredge 2002; Wagner & Herbst 2002). However, recent molecular phylogenetic approaches indicate that many of the presumably widespread taxa in Hawaii represent distinct, putatively endemic species. Thus, in *Lobariella* and *Pseudocyphellaria*, revised phylogenetic classifications suggest putative endemism to be around 75% (Moncada *et al.* 2014a; Lücking *et al.* 2017a).

The genus *Sticta* is the largest genus in *Peltigeraceae* subfamily *Lobarioideae*, with 200 species currently accepted and many more recognized on the basis of molecular phylogenetic studies (Moncada *et al.* 2014a, 2020; Lücking *et al.* 2017b; Simon *et al.* 2018). The most recent checklist of Hawaiian lichens (Smith 2013) listed 11 names under *Sticta*. One of these, *S. crocatoides* f. *sandwicensis* Zahlbr., belongs in the genus *Pseudocyphellaria* (Moncada *et al.* 2014b). The ten remaining names included seven at species level and three at the level of variety, viz. *S. ambavillaria* (Bory) Ach., *S. cyphellulata* (Müll. Arg.) Hue, *S. filix* (Sw.) Nyl., *S. fuliginosa* (Dicks.) Ach., *S. plumbicolor* (Zahlbr.) Zahlbr., *S. tomentosa* (Sw.) Ach., *S. weigeli* (Ach.) Vain., *S. weigeli* var. *beauvoisii* (Delise)

Hue, *S. weigeli* var. *lutescens* (Taylor) H. Magn. and *S. weigeli* var. *peruviana* (Delise) Vain. *Sticta beauvoisii* Delise was recently reinstated at species rank (McDonald *et al.* 2003; Galloway 2006), whereas the correct application of the names *S. weigeli* var. *lutescens* and *S. weigeli* var. *peruviana* is unclear (Moncada *et al.* 2020). Thus, prior to molecular studies, the genus *Sticta* was represented in Hawaii by eight species, with only one, *S. plumbicolor*, putatively endemic, resulting in an inferred endemism of 13%. However, a recent phylogenetic revision distinguished 13 species, including seven new to science and retaining only three previously reported taxa, *S. fuliginosa*, *S. plumbicolor* and *S. tomentosa*, thus raising the estimate of endemism to 69% (Moncada *et al.* 2020).

In the current study, we present an updated taxonomic treatment of the genus *Sticta* in the Hawaiian archipelago based on these results, including a revision of numerous collections, diagnostic descriptions and illustrations, notes on the distribution and ecology of the species, and an identification key.

Material and Methods

The underlying revised taxonomy of Hawaiian *Sticta* was based on a recent phylogenetic revision, which revealed recently collected Hawaiian material as belonging to 10 clades representing 13 species (Moncada *et al.* 2020). Based on these results, we also revised herbarium collections mostly at HAW but also at some other herbaria (DUKE, F, NY, US) and in the Lichen Portal of the Consortium of North American Lichen Herbaria (<https://lichenportal.org/cnalh>), to assign specimens to the newly recognized taxa.

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Morphological and anatomical details of the specimens were studied using a LEICA Zoom 2000 dissecting microscope and a ZEISS Axioskop compound microscope. We employed thin-layer chromatography (TLC) according to Orange *et al.* (2010).

Taxonomic Treatment

Key to species of *Sticta* in Hawaii

- 1 Vegetative propagules or marginal lobules absent; apothecia present; underside whitish, with thin tomentum and minute cyphellae; Kauai, Oahu, Molokai, Maui, Hawaii (Fig. 1A–D) ***Sticta tomentosa***
 Vegetative propagules or marginal lobules present; apothecia present or absent; underside variable 2
- 2(1) Vegetative propagules soredia, predominantly marginal, white-grey; lobes broadly rounded; Kauai, Maui (Fig. 1E–H) ***Sticta limbata***
 Vegetative propagules isidia or phyllidia, or marginal lobules present, concolorous with the thallus or darker; lobes variable 3
- 3(2) Vegetative propagules predominantly laminal isidia, regularly dispersed over the entire lobe surface; lobes more or less broadly rounded 4
 Vegetative propagules predominantly marginal isidia, phyllidia, or with marginal lobules, if also laminal then clustered and leaving larger surface areas free; lobes irregularly truncate to elongate 6
- 4(3) Thallus extremely small (often only to 0.5 cm), pedunculate; cyphellae absent; Oahu (Fig. 1I–L) ***Sticta acyphellata***
 Thallus small to robust (1–5 cm diam.), not pedunculate; cyphellae present 5
- 5(4) Thallus small (*c.* 1 cm diam.); lobes with conspicuous marginal, white cilia; cyphellae very small (to 0.2 mm diam.), rounded; Kauai, Oahu, Maui (Fig. 1M–P) ***Sticta hawaiiensis***
 Thallus robust (to 5 cm diam.); lobes lacking distinct cilia; cyphellae becoming large (1–3 mm diam.) and irregularly angulate; Kauai, Oahu, Maui, Hawaii (Fig. 1Q–T) ***Sticta fuliginosa***
- 6(3) Thallus with somewhat large, strictly marginal lobules; apothecia rather frequent; lower tomentum rather thick but abruptly ending and leaving bare lobe margins; Kauai, Maui (Fig. 1U–X) ***Sticta antoniana***
 Thallus with small, predominantly marginal but sometimes also laminal isidia or phyllidia; apothecia rare or absent 7
- 7(6) Thallus very small (*c.* 1 cm), distinctly pedunculate, consisting of sparsely branched lobes with a basal stipe ascending from the substratum 8
 Thallus small to robust (1–10 cm diam.), not pedunculate, with much branched lobes, overgrowing the substratum more or less horizontally 9
- 8(7) Cyphellae becoming rather large (1–3 mm diam.) and irregular; Kauai, Maui (Fig. 2A–D) ***Sticta flynnii***
 Cyphellae remaining small (0.2–0.5 mm diam.) and rounded; Oahu (Fig. 2E–H) ***Sticta smithii***
- 9(7) Thallus remaining small (1–3 cm diam.); lobes with distinct black, marginal cilia; Kauai, Maui (Fig. 2I–L) ***Sticta emmanueliana***
 Thallus becoming robust (3–10 cm diam.); lobes lacking or with indistinct or whitish cilia 10
- 10(9) Thallus bluish grey when fresh, bluish to yellowish grey when dry, with conspicuous phyllidia; underside whitish, with small, inconspicuous cyphellae; scattered apothecia usually present; Kauai, Oahu, Molokai, Maui, Hawaii (Fig. 2M–P) ***Sticta plumbicolor***
 Thallus olive green to grey-brown when fresh, brownish when dry, with cylindrical to flattened isidia or small phyllidia; underside light to dark brown, with conspicuous cyphellae contrasting with the darker tomentum 11
- 11(10) Lower tomentum marginally pale; vegetative propagules (phyllidia) marginal and laminal (then clustered), concolorous with thallus; lobe surface often thinly scabrous, particularly towards the tips, and also often shallowly scrobiculate-foveolate; Kauai, Oahu, Molokai, Maui, Hawaii (Fig. 2Q–T) ***Sticta scabrosa* subsp. *hawaiiensis***
 Lower tomentum uniformly dark; vegetative propagules (isidia or phyllidia) predominantly marginal, cylindrical, darker than the thallus; lobe surface glabrous, even to uneven 12
- 12(11) Usually on soil between bryophytes, rarely epiphytic over bryophyte mats; lobes 4–7 mm broad; with cylindrical to somewhat flattened isidia; rhizines conspicuous; Maui, Hawaii (Fig. 2U–V) ***Sticta waikamoi***
 Usually epiphytic on branches, stems or tree trunks; lobes 7–15 mm broad; mostly with flattened and dorsiventral phyllidia; rhizines short; Kauai, Oahu, Maui, Hawaii (Fig. 2W–X) ***Sticta andina***



Fig. 1. Habitus of Hawaiian *Sticta*. A–D, *S. tomentosa*. E–H, *S. limbata*. I–L, *S. acyphellata*. M–P, *S. hawaiiensis*. Q–T, *S. fuliginosa*. U–X, *S. antoniana*. Most of these images were taken in the field, therefore no scales are added. *Sticta antoniana*, *S. fuliginosa*, *S. limbata* and *S. tomentosa* are conspicuous species, whereas *S. acyphellata* and *S. hawaiiensis* are comparatively small, their individual thalli usually not exceeding 1 cm. In colour online.

The species

Sticta acyphellata Moncada & Lücking

Moncada *et al.*, *Pl. Fung. Syst.* **65**, 106 (2020); type: USA, Hawaii, Oahu, Koolau Range, Manoa Valley, 21°19'55"N, 157°48'43"W, 410–575 m, 2013, B. Moncada, R. Lücking & C. W. Smith 6923 (F—holotype!; B, HAW—isoatypes!).

(Fig. 1I–L)

Primary photobiont cyanobacterial (*Nostoc*). Stipe present, short. Thallus monophyllous, individual thalli irregularly arranged, delicate, irregularly branched and dissected; lobes to 5 mm broad, spatuliform to truncate, ascending, not usually overlapping,



Fig. 2. Habitus of Hawaiian *Sticta*. A–D, *S. flynnii*. E–H, *S. smithii*. I–L, *S. emmanueliana*. M–P, *S. plumbicolor*. Q–T, *S. scabra* subsp. *hawaiiensis*. U–V, *S. waikamoi*. W–X, *S. andina*. Most of these images were taken in the field, therefore no scales are added. *Sticta andina*, *S. fuliginosa*, *S. plumbicolor*, *S. scabra* subsp. *hawaiiensis* and *S. waikamoi* are conspicuous to large taxa, whereas *S. flynnii* and *S. smithii* are comparatively small, their individual thalli usually not exceeding 1 cm; *S. emmanueliana* is intermediate in size. In colour online.

plane to involute, their margins becoming dissected. *Upper surface* even, dark bluish grey when fresh, bluish grey when dry, glabrous, without papillae or pruina, with white maculae forming a reticulate pattern. *Isidia* frequent, marginal and laminal, 0.1–0.2 mm long and 0.05–0.1 mm broad, dark grey, shiny, flattened and somewhat imbricate, becoming somewhat arbuscular,

branched and coralloid; arbusculae to 0.2 mm long and broad, distinctly flattened, their base lacking cyphellae, concolorous with the thallus. *Lower surface* uneven, forming vein-like ridges, minutely scrobiculate-foveolate between the ridges, white to cream. *Primary tomentum* dense but short and inconspicuous, whitish; hairs 20–70 μm long, composed of single, mostly

unbranched, cylindrical, colourless hyphae. *Secondary tomentum* absent. *Cyphellae* absent.

Apothecia not observed.

Secondary chemistry. No substances detected by TLC; medulla K–.

Distribution and ecology. This species is thus far known only from the island of Oahu, probably overlooked elsewhere. It is difficult to detect in the field due to its diminutive size. It is found in liverwort carpets, such as *Odontoschisma* spp., on the lower trunk and exposed roots, generally no higher than 1.5 m above ground, in open, non-native, mature rainforest understory at lower elevations (410–575 m). The only identified phorophytes to date are *Elaeocarpus bifidus* and *Cordyline fruticosa* (as *C. terminalis*).

Remarks. This species is unique within the genus due to its diminutive size and the complete lack of cyphellae. It provides a contrary example of what is seen in *Lobaria anomala* (Brodo & Ahti) T. Sprib. & McCune and *L. anthraspis* (Ach.) T. Sprib. & McCune. Although producing pseudocyphellae, these two species form part of *Lobaria* s. str., which otherwise lacks lower surface pores (McCune *et al.* 2014; Cornejo & Scheidegger 2015).

Additional specimens examined. USA: Hawaii: Oahu, Koolau Mountains, Tantalus, 467 m, 1977, G. Y. Daida 503 (HAW); Oahu, Koolau Range, Manoa Valley, Manoa Cliffs Trail, 21° 19'55"N, 157°48'43"W, 410–575 m, 2013, B. Moncada, R. Lücking & C. W. Smith 6918b (B), 6920 (B, F).

Sticta andina Moncada, Lücking & Sérusiaux

Moncada *et al.*, *Willdenowia* (in press); type: Colombia, Bogotá, D.C., Sendero Peña Blanca, 04°26'08" to 04°26'19"N, 74°08'36" to 74°08'37"W, 2840–2860 m, 2015, R. Lücking (with C. Vargas) 39464 (B—holotype!; JBB—isotype!).

(Fig. 2W & X)

Primary photobiont cyanobacterial (*Nostoc*). *Stipe* absent. *Thallus* monophyllous, forming suborbicular rosettes or becoming irregular, to 15 cm across, mostly anisotomously branched; lobes 7–15 mm broad, elongate to flabellate, ±horizontal, adjacent to imbricate, involute to slightly canaliculate, their margins entire to sinuose or shallowly crenate. *Upper surface* smooth to rugose or shallowly scrobiculate, olive when fresh, brownish when dry, glabrous, with or without scattered papillae, without pruina, with indistinct, cream maculae; marginal cilia not differentiated but lower tomentum sometimes projecting beyond the margins to resemble short, brown-black, agglutinate to fasciculate cilia. *Phyllidia* and flattened isidia present, predominantly marginal, to 1 mm long and broad, rather dark grey-brown, somewhat shiny, branched and becoming coralloid to palmate with a basal stipe with diminutive cyphellae. *Lower surface* uneven to undulate, dark brown to blackish. *Primary tomentum* thick and dense to the lobe margins, spongy, forming dark brown to blackish brown, arachnoid tufts of fasciculate hyphae; hairs 200–1000 µm long, in fascicles of 12–20, partly branched, agglutinate, apically intertwined, brown, cylindrical hyphae with free apices. *Secondary tomentum* discernible only in microscopic sections; hairs 10–35 µm long, composed of single, branched, moniliform hyphae with free apices. *Rhizines* present but short, scattered towards the thallus centre. *Cyphellae* rather dense, (20–)60–100

per cm², rounded, plane, erumpent to prominent, white, strongly contrasting with the dark tomentum; pore 0.3–1(–1.8) mm diam.; cells of basal membrane lacking papillae.

Apothecia not rare, often on thalli lacking phyllidia, mostly submarginal, dispersed, sessile to substipitate with a pronounced invagination on the underside, 2–4 mm diam., 0.5–0.6 mm high; disc orange-brown; proper margin verrucose to crenulate, sometimes thinly pilose when young, dark brown. *Excipulum* 100–150 µm broad. *Hymenium* 115–155 µm high; epithecium 2.5–5 µm thick, orange-brown. *Ascospores* fusiform, 1–3-septate, 27–38 × 5.5–7.5 µm.

Secondary chemistry. No substances detected by TLC; medulla and basal membrane of cyphellae K+ yellowish.

Distribution and ecology. *Sticta andina* is apparently native to the Neotropics and found most frequently in the northern Andes (Moncada *et al.* 2021). In Hawaii, this species is known from Hawaii, Kauai, Maui and Oahu, with many collections originating from introduced conifer forest on Maui. A lack of deviation in the ITS sequences compared to the main haplotype found in the northern Andes suggests the records from Hawaii to be the result of recent, perhaps anthropogenic long-distance dispersal (Moncada *et al.* 2020). In the northern Andes, *Sticta andina* is an upper montane to alpine taxon, typically confined to undisturbed forest and shrubby habitats, where it grows on trees and shrubs, rarely on rock. In Hawaii it was found in partially disturbed native rainforest and gulches of adjacent upland dry forest, between 1200 and 2400 m, with most collections originating from between 1500 and 2000 m. Reported phorophytes mostly include *Cheirodendron* and *Metrosideros*, but also *Coprosoma (montana)*, *Leptocophylla*, *Myrsine*, *Sophora (chrysophylla)* and *Vaccinium*.

Remarks. *Sticta andina* was described recently to accommodate a common taxon mostly occurring in the northern Andes. It corresponds to the *S. weigelii* morphodeme but is not related to *S. weigelii* s. str., differing in the thick lower tomentum and whitish cyphellae lacking yellow pigment (Moncada *et al.* 2021). *Sticta andina* is characterized by a rather robust thallus with an olive-brown colour when fresh (yellowish brown in the herbarium), with predominantly marginal, rather dark, mostly flattened isidia and phyllidia. It can be distinguished from *S. scabrosa* subsp. *hawaiiensis* by the glabrous, more or less shiny lobe surface, by the isidia and phyllidia being darker than the thallus, and by the uniformly dark lower tomentum. Its ecology is also different, being found mostly in higher elevation rainforest, whereas *S. scabrosa* subsp. *hawaiiensis* is a weedy taxon typically occurring in lower altitude rainforest or secondary and anthropogenic vegetation. *Sticta waikamoi* is quite similar to *S. andina* and co-occurs with it in the same habitats, but is a smaller lichen overall, with narrower lobes forming cylindrical to somewhat flattened isidia and conspicuous rhizines; in addition, it often also grows on the ground.

Specimens examined. USA: Hawaii: Hawaii, Mauna Loa, Pohakuloa training area, 1585 m, 1977, P. K. Higashino 327 (HAW); Kauai, West Kauai, Koke'e State Park, Pihea Trail, 22° 08'51"N, 159°37'53"W, 1250–1350 m, 2013, B. Moncada, R. Lücking & T. Flynn 7047 (B, PTBG); Maui, East Maui, Kipahulu Forest Reserve, 1385 m, 1976, P. K. Higashino & G. Mizuno 2034 (HAW); Maui, East Maui, Makawao Forest Reserve, 1800 m, 1975, C. W. Smith 1922 (HAW); Maui, East Maui, Haleakalā

Volcano, 1890–1950 m, 1981, *C. W. Smith* 5074 (HAW); Maui, East Maui, Haleakalā Volcano, Haleakalā National Park, 2100 m, 1975, *C. W. Smith* 2105, 2164, 2168 (HAW); Maui, East Maui, Haleakalā Volcano, Haleakalā National Park, Halemauu Trail, 2400 m, 1975, *C. W. Smith* 2075 (HAW); Maui, East Maui, Haleakalā Volcano, Lower Waikamoi Preserve, 20°48'23"N, 156°15'19"W, 1200–1300 m, 2013, *B. Moncada, R. Lücking & P. Bily* 6951 (F); Maui, East Maui, Haleakalā Volcano, Upper Waikamoi Preserve, 20°46'07"N, 156°14'17"W, 1800–2100 m, 2013, *B. Moncada, R. Lücking & P. Thomas* 6983 (B), 6984 (F), 6997 (B, F); Maui, Olinda, Koolau Forest Reserve North Haleakala, 910 m, 1992, *R. Rosentreter* 8108 (SRP); Maui, Kipahulu Valley, Haleakalā National Park, 2100 m, 1984, *A. C. Medeiros & D. Miranda* 322 (HAW); Maui, Paliku, 2130 m, 1976, *C. W. Smith* 3091 (HAW); Oahu, Waianae Mountain Range, Mt Kaala, 1212 m, 1980, *G. Y. Daida* 628 (HAW); Oahu, Gully *en route* from Kuiki to Paliku, 2130 m, 1975, *C. W. Smith* 2220 (HAW).

Sticta antoniana Moncada & Lücking

Moncada *et al.*, *Pl. Fung. Syst.* **65**, 108 (2020); type: USA, Hawaii, Kauai, West Kauai, Koke'e State Park, Pihea Trail, 22°08'51"N, 159°37'53"W, 1250–1350 m, 2013, *B. Moncada, R. Lücking & T. Flynn* 7053 (F—holotype!; B, HAW—isotypes!).

(Fig. 1U–X)

Primary photobiont cyanobacterial (*Nostoc*). *Stipe* absent. *Thallus* monophyllous, irregularly orbicular, to 10 cm across, frequently anisotomously branched; lobes to 7 mm broad, flabellate to truncate, ascending, not usually overlapping, their margins dissected into elongate lobules. *Upper surface* even, olive green when fresh, brownish grey when dry, glabrous, without papillae or pruina, with or without scattered, indistinct maculae. *Marginal lobules* abundant, much branched, 1–3(–5) mm long and 0.5–1 mm broad, concolorous with the thallus. *Lower surface* slightly uneven, whitish. *Primary tomentum* thick and dense, forming light grey-brown, arachnoid tufts of fasciculate hyphae except for a 2–5 mm broad marginal zone abruptly bare of tomentum; hairs 500–1500 µm long, formed of densely entangled, mostly unbranched, pale brown, cylindrical hyphae with free apices. *Secondary tomentum* inconspicuous; hairs scattered, 20–30 µm long, comprising single, unbranched, cylindrical, colourless hyphae. *Cyphellae* dense, 21–60 per cm², rounded, plane, immersed, white; pore 0.1–0.3 mm diam.; cells of basal membrane irregularly bulging but lacking distinct papillae.

Apothecia common, laminal, sessile, 0.7–1.5 mm diam., initially zeorine with hairy margins but mature apothecia biatorine, with remnants of thallus layer basally and with scattered marginal hairs; disc dark reddish brown; margin crenulate, cream to pale orange. *Ascospores* oblong-fusiform, 3-septate, 40–50 × 6–7 µm.

Secondary chemistry. No substances detected by TLC; medulla K–, cyphellae K–.

Distribution and ecology. This species is thus far known only from the islands of Maui and Kauai where it is apparently restricted to more or less undisturbed or little disturbed montane rainforest at mid elevations (between 1200 and 1350 m). It grows on shaded bark of unidentified phorophyte trees.

Remarks. *Sticta antoniana* belongs to the *S. tomentosa* complex and cannot be phylogenetically separated from the latter on ITS sequences alone (Moncada *et al.* 2020). Due to its distinctive morphology, differing from typical *S. tomentosa* by the highly dissected lobe margins and the thick lower tomentum that leaves an abrupt bare margin, it is considered a separate species. Highly disparate, discrete morphologies in phylogenetically closely related lineages that may not be resolvable with standard barcoding markers are not rare in island biota, also being found in vascular plants (Baldwin *et al.* 1991; Baldwin & Sandersson 1998; Carlquist *et al.* 2003). In lichens, similar phenomena were also demonstrated for Hawaiian *Lobariella* and *Pseudocyphellaria* (Moncada *et al.* 2014b; Lücking *et al.* 2017a). The view that *S. antoniana* is a distinctive lineage not resolved by the ITS barcoding marker, and not a habitat-induced morph, is supported by the notion that the *S. antoniana* morphodeme is not known in populations of *S. tomentosa* outside Hawaii.

A recent example demonstrating a case where the ITS barcoding marker does not resolve two closely related species is the pair *Neuropogon antarcticus* (Du Rietz) I. M. Lamb versus *Neuropogon aurantiacoater* (Jacq.) I. M. Lamb, as shown by RADseq data (Grewe *et al.* 2018). The latter is a promising method to test cases where ITS exhibits limits of resolution, such as in *S. antoniana* versus *S. tomentosa*.

Additional specimens examined. USA: Hawaii: Maui, East Maui, Haleakalā Volcano, Lower Waikamoi Preserve, 20°48'23"N, 156°15'19"W, 1200–1300 m, 2013, *B. Moncada, R. Lücking & P. Bily* 6947 (B, F, HAW), 6948 (B, F); Kauai, West Kauai, Koke'e State Park, Pihea Trail, 22°08'51"N, 159°37'53"W, 1250–1350 m, 2013, *B. Moncada, R. Lücking & T. Flynn* 7045a (F), 7065 (F).

Sticta emmanueliana Moncada, Lücking & Lumbsch

Moncada *et al.*, *Pl. Fung. Syst.* **65**, 109 (2020); type: USA, Hawaii, Kauai, West Kauai, Koke'e State Park, Pihea Trail, 22°08'51"N, 159°37'53"W, 1250–1350 m, 2013, *B. Moncada, R. Lücking & T. Flynn* 7058 (F—holotype!; B, HAW—isotypes!).

(Fig. 2I–L)

Primary photobiont cyanobacterial (*Nostoc*). *Stipe* present, short and rather broad. *Thallus* mono- to polyphyllous, with individuals irregularly arranged, delicate, irregularly branched; lobes to 4 mm broad, irregularly elongate to tapering or truncate, horizontal to ascending, not usually overlapping, plane to slightly involute, their margins not thickened. *Upper surface* even, olive-brown to dark brown when fresh, brownish grey when dry, glabrous, without papillae or pruina, with scattered, white maculae; marginal cilia present, formed by submarginal tufts of primary tomentum that become visible beyond the margins, conspicuous particularly in younger lobes, evanescent in old lobes, brownish black, 0.1–0.4 mm long. *Isidia* present, predominantly marginal, 0.1–0.3 mm long and 0.05–0.1 mm broad, darker grey-brown, shiny, cylindrical, branched and becoming coralloid to arbuscular; arbusculae to 0.5 mm long and broad, their base lacking cyphellae. *Lower surface* uneven, mostly dark brown but marginally becoming white to cream. *Primary tomentum* becoming thin towards the margins, except for the cilia, otherwise forming loosely to densely arranged, brown tufts of fasciculate hyphae, much shorter and lighter than the cilia; hairs 100–200 µm long,

in fascicles of 10–20, mostly unbranched but loosely agglutinate, cylindrical hyphae with free apices, usually brownish. *Secondary tomentum* developed to the margins, thin, pubescent, whitish to light brownish; hairs 25–100 μm long, comprising single, mostly unbranched, cylindrical hyphae with free apices, somewhat pale brown. *Cyphellae* dense, 41–80 per cm^2 , rounded, immersed-erumpent, white, appearing pruinose, with cream to light brown margins bare of tomentum; pore 0.1–0.2 mm diam. towards the margins, 0.2–0.5 mm diam. towards the centre; cells of basal membrane irregularly bulging but without distinct papillae.

Apothecia not observed.

Secondary chemistry. No substances detected by TLC; medulla K– to K+ pale yellow.

Distribution and ecology. This species was found on the islands of Maui and Kauai, at altitudes between 1200 and 1800 m, chiefly at the same localities as *Sticta antoniana*. Like that species, it also occurred in rather undisturbed montane rainforest at mid to higher elevations, growing on shaded tree bark including branches, for example on *Myrsine*, usually associated with bryophyte mats.

Remarks. On account of its marginal isidia and black cilia, *Sticta emmanueliana* comes morphologically close to *Sticta cometiella* Vain., described from Mexico. The latter appears to be strictly neotropical and is only very distantly related, clustering in a different clade of the global *Sticta* phylogeny (Moncada *et al.* 2020). It also frequently produces laminal isidia. The Australasian *S. duplombata* (Hue) Vain. is also similar (Galloway 1998, 2001) but likewise only distantly related (Moncada *et al.* 2020). Within Hawaiian *Sticta*, the species is best recognized by its dark marginal cilia.

Additional specimens examined. USA: Hawaii: Maui, East Maui, Haleakalā Volcano, Lower Waikamoi Preserve, 20°48'23"N, 156°15'19"W, 1200–1300 m, 2013, B. Moncada, R. Lücking & P. Bily 6949 (F), 6954 (B, F, HAW), 6955 (F); Maui, East Maui, Makawao Forest Reserve, 1800 m, 1975, C. W. Smith 1922 (HAW); Kauai, West Kauai, Koke'e State Park, Pihea Trail, 22°08'51"N, 159°37'53"W, 1250–1350 m, 2013, B. Moncada, R. Lücking & T. Flynn 7045a (F), 7064 (F).

Sticta flynnii Moncada & Lücking

Moncada *et al.*, *Pl. Fung. Syst.* 65, 110 (2020); type: USA, Hawaii, Kauai, West Kauai, Koke'e State Park, Pihea Trail, 22°08'51"N, 159°37'53"W, 1250–1350 m, 2013, B. Moncada, R. Lücking & T. Flynn 7055 (F—holotype!).

(Fig. 2A–D)

Primary photobiont cyanobacterial (*Nostoc*). *Stipe* present, short and broad. *Thallus* mono- to polyphyllous, with one to few individuals that are irregularly arranged, delicate, unbranched to sparsely branched, becoming apically dissected; lobes to 7 mm broad, suborbicular to reniform or truncate, ascending, not usually overlapping, plane to involute, their margins becoming coarsely dissected. *Upper surface* even, olive green when fresh, bluish grey when dry, glabrous, with or without scattered papillae, without pruina, with scattered, white maculae. *Isidia* present,

abundant, mostly marginal but also laminal, isidia 0.1–0.2 mm long and 0.05–0.1 mm broad, darker brown, shiny, cylindrical to somewhat flattened, arbuscular, branched and becoming coral-loid; arbusculae to 2 mm long and broad, their base lacking cyphellae. *Lower surface* uneven, forming shallow, vein-like ridges, white to cream. *Primary tomentum* absent. *Secondary tomentum* developed to the margins, thin, pubescent, white; hairs 20–50 μm long, comprising single, mostly unbranched, cylindrical hyphae with free apices. *Cyphellae* scattered, 1–20 per cm^2 towards the thallus centre and 21–40 per cm^2 towards the margin, rounded to irregular or becoming angular, plane, immersed, white, appearing pruinose; pore 0.5–1 mm diam. towards the margins, 1–3 mm across towards the centre; cells of basal membrane irregularly bulging but without distinct papillae.

Apothecia not observed.

Secondary chemistry. No substances detected by TLC; medulla and membrane of cyphellae K–.

Distribution and ecology. This species has been found at the type locality on Kauai and one additional site on Maui. It was found in more or less undisturbed montane rainforest at mid to high elevations (between 1250 and 2300 m) on shaded tree bark associated with bryophytes. Given that it is a rather small species, it is likely to have been overlooked and might be more common.

Remarks. Together with *Sticta acyphellata* and *S. smithii*, *S. flynnii* is one of three Hawaiian species with small, caulescent, isidiate thalli. *Sticta acyphellata* is distinguished by the complete lack of cyphellae, whereas *S. smithii* differs in the small cyphellae and thicker tomentum. Several other, non-Hawaiian taxa share a caulescent, isidiate thallus, including *S. brevipes* (Müll. Arg.) Zahlbr., *S. cyphellulata* (Müll. Arg.) Hue, *S. hypochra* Vain., *S. longipes* (Müll. Arg.) Malme and *S. marginifera* Mont. (Galloway 1994a, 1998). These are all phylogenetically distinct (Moncada *et al.* 2020) and differ in their more robust thalli, as well as in other details. Notably, even the larger species do not appear to produce cyphellae as large as those found in *S. flynnii*.

Additional specimens examined. USA: Hawaii: Maui, East Maui, Haleakalā Volcano, Haleakalā National Park, 2233 m, 1975, C. W. Smith 1754 (HAW); Kauai, West Kauai, Koke'e State Park, Pihea Trail, 22°08'51"N, 159°37'53"W, 1250–1350 m, 2013, B. Moncada, R. Lücking & T. Flynn 7059 (HAW).

Sticta fuliginosa (Hoffm.) Ach.

Meth. Lichenum, 280 (1803).—*Lobaria fuliginosa* Hoffm., *Deutschl. Flora* 2, 109 (1796); type: United Kingdom, Wales, Cader Idris, Icon. in Dillenius, *Historia Muscorum*, tab. 26, fig. 100A (1742; lectotype *fide* Laundon (1984), 218–219); corresponding specimen from hb. Dillenius (OXF—epitype *fide* Jørgensen & Tønsberg (2007), 146).

(Fig. 1Q–T)

Primary photobiont cyanobacterial (*Nostoc*). *Stipe* absent. *Thallus* mono- to polyphyllous; individuals robust, unbranched to sparsely branched; lobes 5–8(–12) cm broad, suborbicular, ascending, imbricate, plane to slightly revolute, margins entire to irregular. *Upper surface* uneven to shallowly scrobiculate, dark brown-grey when fresh, greyish brown when dry, glabrous,

with or without scattered papillae, without pruina, with or without indistinct maculae. *Isidia* present, laminal, to 0.5 mm long and broad, dark grey to brownish grey, shiny, cylindrical to somewhat flattened, branched and becoming coralloid. *Lower surface* slightly uneven, white to cream. *Primary tomentum* rather thin and becoming thinner along the margins, whitish to pale brownish, forming somewhat scattered to more densely arranged tufts of fasciculate hyphae; hairs 100–200 µm long, in fascicles of 10–20, mostly unbranched but agglutinate, cylindrical hyphae with free apices. *Secondary tomentum* not discernible. *Cyphellae* numerous, 20–60 per cm², rounded to usually angular, plane, immersed, white to cream; pore 0.5–3(–5) mm diam.; cells of basal membrane without papillae.

Apothecia not observed.

Secondary chemistry. No substances detected by TLC; medulla K–, membrane of cyphellae K–.

Distribution and ecology. *Sticta fuliginosa* in the strict sense is a subcosmopolitan species, with specimens confirmed through sequence data known from most regions of the world, including Hawaii (Magain & Sérusiaux 2015; Moncada et al. 2020). Although exhibiting little genetic variation, there is some subtle geographical structure in the ITS sequence data, suggesting a very recent, rapid, yet natural expansion of this taxon. In Hawaii, it is usually epiphytic in more or less undisturbed rainforest habitats and gulches in adjacent dry forest. It tolerates a certain degree of disturbance and may also be found in secondary or anthropogenic vegetation, as records from introduced trees in botanical gardens demonstrate. Together with *S. tomentosa*, *S. fuliginosa* is the most common and widespread *Sticta* species in Hawaii, with a well-documented, broad altitudinal range between under 500 to over 2300 m. Identified phorophytes include indigenous species of *Cordyline (fruticosa)*, *Dodonaea (viscosa)*, *Leptecophylla*, *Metrosideros (collina)*, *Rubus (hawaiiensis)*, and *Sophora (chrysophylla)*.

Remarks. The name *Sticta fuliginosa* has traditionally been applied to all forms with more or less broad, rounded lobes with laminal isidia (Joshi & Awasthi 1982; Swinscow & Krog 1988; Galloway 1994a, 2001, 2007; Galloway et al. 1995; Büdel et al. 2000; Brodo et al. 2001; Farkas 2003; Galloway & Thomas 2004; Jørgensen & Tønsberg 2007; Makryi 2008; Smith et al. 2009). Molecular phylogenetic data, however, have demonstrated that this morphodeme corresponds to more than a dozen, mostly unrelated species (Moncada et al. 2014a, 2015, 2020; Magain & Sérusiaux 2015). Surprisingly, even in a narrow sense supported by molecular data, *S. fuliginosa* s. str. remains the most widespread species of the genus. Morphologically, it is best characterized (and separated from similar species) by the rather robust thalli, the glabrous lobe surface, the cylindrical isidia, the whitish underside with rather large, plane cyphellae that often become angular in outline, and the lack of papillae on the cells of the membrane of the cyphellae. The only similar species in Hawaii is *S. hawaiiensis*, which differs in the much smaller thalli and lobes, the distinct, white, marginal cilia, and the numerous papillae on the membrane of the cyphellae.

Specimens examined. USA: Hawaii: Hawaii, Mauna Loa, Pohakuloa training area, 1585 m, 1977, P. K. Higashino 525 (HAW); Hawaii, Puu Huluhulu Saddle Road, 19°51'20"N, 155°08'56"W, 2365 m, 1992, W. L. Culbertson 22164 (DUKE); Kauai,

Koke'e State Park, Kalua Puhi Trail, 1070 m, 1985, W. A. Weber & D. Randolph L-77946 (US); Kauai, West Kauai, Koke'e State Park, Mohihi Trail, 467 m, 1979, G. Y. Daida 267 (HAW); Kauai, West Kauai, Koke'e State Park, Pihea Trail, 22°08'51"N, 159°37'53"W, 1250–1350 m, 2013, B. Moncada, R. Lücking & T. Flynn 7043 (B), 7052 (F); Kauai, West Kauai, Waimea Canyon, Iliau Nature Loop & Kukui Trail at Kokee Road, 22°03'04"N, 159°39'36"W, 900 m, 2013, B. Moncada, R. Lücking & T. Flynn 7023 (B, F), 7026 (B, F, HAW); Kauai, Alakai Swamp, C. W. Smith 6179 (HAW); Maui, East Maui, Haleakalā National Park, 2070 m, 1977, C. W. Smith 3343 (HAW); Maui, Auahi Forest Reserve, 760 m, 1992, P. DePriest 8213 (US); Maui, East Maui, Haleakalā Volcano, 1890–1950 m, 1981, C. W. Smith 5072 (HAW); Maui, East Maui, Haleakalā Volcano, Haleakalā National Park, 2233 m, 1975, C. W. Smith 1762 (HAW); Maui, East Maui, Haleakalā Volcano, Lower Waikamoi Preserve, 20°48'23"N, 156°15'19"W, 1200–1300 m, 2013, B. Moncada, R. Lücking & P. Bily 6945 (F); Maui, East Maui, Haleakalā Volcano, Upper Waikamoi Preserve, 20°46'07"N, 156°14'17"W, 1800–2100 m, 2013, B. Moncada, R. Lücking & P. Thomas 6978 (B, F, HAW), 6979 (F), 6982 (HAW), 6988 (B, F), 6990 (F), 6994 (F), 6998 (HAW); Maui, East Maui, Kipahulu Forest Reserve, 1160 m, 1976, P. K. Higashino & G. Mizuno 2551 (HAW); Maui, Olinda, Koolau Forest Reserve, 20°49'23"N, 156°16'12"W, 910 m, 1992, R. Rosentreter 8085, 8087, 8101 (SRP); Oahu, Honolulu, Ho'omaluhia Botanical Garden, 21°23'08"N, 157°48'16"W, 1991, S. C. Tucker 30518 (LSU); Oahu, Honolulu, Wahiawa Botanical Garden, 21°25'N, 158°00'W, 1991, S. C. Tucker 30485 (LSU); Oahu, Waahila Ridge, 275 m, 1979, G. Y. Daida 251 (HAW); Oahu, Waianae Mountains, Honouliuli Forest Reserve, 945 m, 1978, C. W. Smith 4112 (HAW); Oahu, Waianae Mountains, Kaua Trail, 945 m, 1978, G. Y. Daida 203 (HAW).

Sticta hawaiiensis Moncada & Lücking

Moncada et al., *Pl. Fung. Syst.* 65, 111 (2020); type: USA, Hawaii, Kauai, West Kauai, Koke'e State Park, Pihea Trail, 22°08'51"N, 159°37'53"W, 1250–1350 m, 2013, B. Moncada, R. Lücking & T. Flynn 7048 (F—holotype!; HAW—isotype!).

(Fig. 1M–P)

Primary photobiont cyanobacterial (*Nostoc*). *Stipe* indistinct or absent. *Thallus* mono- to polyphyllous, with one to few individuals that are irregularly arranged, delicate, unbranched; lobes 0.5–1 cm broad, suborbicular, ascending, not usually overlapping, plane to revolute, margins entire to irregular. *Upper surface* irregularly verruculose-rugose, dark grey when fresh, dark bluish grey when dry, thinly whitish tomentose, with or without scattered papillae, without pruina, without distinct maculae; marginal cilia abundant and distinct, particularly in younger thalli, white, 0.2–0.7 mm long; hairs of upper tomentum 10–20 µm long, of single, branched, moniliform hyphae with free apices. *Isidia* present, laminal, to 0.2 mm long and broad, dark grey to brownish grey, shiny, cylindrical, branched and becoming somewhat coralloid. *Lower surface* slightly uneven, white to cream. *Primary tomentum* developed except along the margins, forming somewhat scattered to more densely arranged, mottled brown tufts of fasciculate hyphae; hairs 100–150 µm long, in fascicles of 10–20, mostly unbranched but agglutinate, cylindrical hyphae with free apices. *Secondary tomentum* developed to the margins,

thin, pubescent, white; hairs 10–15 μm long, comprising single, branched, strongly moniliform hyphae with globose cells and free apices. *Cyphellae* scattered, 1–20 per cm^2 , rounded, plane, immersed to becoming erumpent, white; pore 0.1–0.2 mm diam.; cells of basal membrane irregularly bulging, with numerous tiny papillae per cell.

Apothecia not observed.

Secondary chemistry. No substances detected by TLC; medulla K–, membrane of cyphellae K–.

Distribution and ecology. The ecology of this putatively endemic species is rather similar to that of *Sticta antoniana* and *S. emmanueliana*, as it was found chiefly at the same localities on the islands of Maui and Kauai, between 1200 and 1300 m. It occurs in rather undisturbed montane forest at mid elevations, on shaded tree bark over and between bryophyte mats. However, an older collection was identified from Oahu, in non-indigenous rainforest at lower altitude.

Remarks. This species belongs to the apparently pantropical *Sticta ciliata* complex which appears to contain several recently-diverged, phenotypically cryptic lineages (Magain & Sérusiaux 2015; Mercado-Díaz *et al.* 2020; Moncada *et al.* 2020). Species of this clade resemble *S. fuliginosa* with respect to their rounded lobes with laminal isidia but are much smaller overall and are consistently set apart by the conspicuous, white marginal cilia.

Additional specimens examined. USA: Hawaii: Oahu, Koolau Mountains, Tantalus, 467 m, 1977, G. Y. Daida 520 (HAW); Maui, East Maui, Haleakalā Volcano, Lower Waikamoi Preserve, 20°48'23"N, 156°15'19"W, 1200–1300 m, 2013, B. Moncada, R. Lücking & P. Bily 6953 (B, F, HAW).

Sticta limbata (Sm.) Ach.

Meth. Lichenum, 280 (1803).—*Lichen limbatus* Sm. in Smith & Sowerby, *Engl. Bot.*, 16, tab. 1104 (1803); type: United Kingdom, Wales, Cardiganshire, Haford, J. E. Smith s. n. (BM-BM000763531—lectotype!).

(Fig. 1E–H)

Primary photobiont cyanobacterial (*Nostoc*). *Stipe* absent. *Thallus* mono- to more rarely polyphyllous; individuals small, unbranched to sparsely branched; lobes 1–3 cm broad, suborbicular, ascending, imbricate, plane, their margins entire to irregular. *Upper surface* uneven, brown-grey when fresh, greyish brown when dry, glabrous, with or without scattered papillae, without pruina, with or without indistinct maculae. *Soredia* present, marginal, forming labriform soralia, white-grey. *Lower surface* slightly uneven, white to cream. *Primary tomentum* rather thin and becoming thinner along the margins, whitish to pale brownish, forming somewhat scattered to more densely arranged tufts of fasciculate hyphae; hairs 100–150 μm long, in fascicles of 10–20, mostly unbranched, agglutinate, cylindrical hyphae with free apices. *Secondary tomentum* not discernible. *Cyphellae* numerous, 20–60 per cm^2 , rounded to usually angular, plane, immersed, white to cream; pore 0.5–3 mm diam.; cells of basal membrane without papillae.

Apothecia not observed.

Secondary chemistry. No substances detected by TLC; medulla K–, membrane of cyphellae K–.

Distribution and ecology. Similar to *Sticta fuliginosa*, *S. limbata* is a subcosmopolitan species with specimens confirmed through sequence data, known from many regions of the world including Hawaii (Moncada *et al.* 2020). *Sticta limbata* usually grows epiphytically on trunks and branches in undisturbed habitats. It is generally much rarer than *S. fuliginosa*, although the known collections indicate a similarly broad altitudinal range between 900 and 2100 m.

Remarks. The formation of soredia is remarkably rare in the genus *Sticta*. Even so, sorediate forms traditionally identified with the name *S. limbata* represent several unrelated species (Moncada *et al.* 2014a). *Sticta limbata* s. str. is characterized by suborbicular lobes with a whitish underside and cyphellae that become rather large and angular, similar to those of the closely related *S. fuliginosa*. In Hawaii, the species is unmistakable.

Specimens examined. USA: Hawaii: Kauai, West Kauai, Waimea Canyon, Iliau Nature Loop & Kukui Trail at Kokee Road, 22° 03'04"N, 159°39'36"W, 900 m, 2013, B. Moncada, R. Lücking & T. Flynn 7024 (B, F); Maui, East Maui, Haleakalā Volcano, Upper Waikamoi Preserve, 20°46'07"N, 156°14'17"W, 1800–2100 m, 2013, B. Moncada, R. Lücking & P. Thomas 6995 (HAW), 6999 (F).

Sticta plumbicolor (Zahlbr.) Zahlbr.

Cat. Lich. Univers. 3, 398 (1925).—*Stictina plumbicolor* Zahlbr., *Annls Mycol.* 1, 356 (1903); type: USA, Hawaii, Molokai, 760 m, on shrubs, D. D. Baldwin 17 (W—holotype!).

(Fig. 2M–P)

Primary photobiont cyanobacterial (*Nostoc*). *Stipe* absent or indistinct (in young thalli). *Thallus* monophyllous, irregularly orbicular to palmate, to 5 cm across, anisotomously to polytomously branched; lobes 3–6 mm broad, flabellate to truncate, horizontal, not usually overlapping, their margins entire to slightly crenate. *Upper surface* even, bluish grey when fresh, bluish to yellowish grey when dry, glabrous, without papillae or pruina, with scattered, whitish maculae, with marginal, fasciculate, white cilia. *Phyllidia* present, predominantly marginal but frequently also extending onto the lamina, to 0.7 mm long and broad, dark bluish grey, darker than the thallus, branched and forming coralloid to palmate clusters with a basal, flattened stipe lacking cyphellae. *Lower surface* uneven to ridged-scribulate, white to pale cream (becoming yellow-orange in the herbarium). *Primary tomentum* thin, sparse towards the margins, fasciculate, whitish to pale yellowish grey; hairs 70–250 μm long, in fascicles of 10–20, mostly unbranched but agglutinate, colourless, cylindrical hyphae with free apices. *Secondary tomentum* thinly arachnoid, whitish; hairs scattered, 10–20 μm long, comprising single, unbranched, moniliform, colourless hyphae. *Cyphellae* scattered, 20–40(–60) per cm^2 , rounded to somewhat irregular in outline, plane, immersed-erumpent, white; pore 0.1–0.3 mm diam.; cells of basal membrane with 2–4 papillae per cell.

Apothecia present, submarginal, sessile, 0.8–1.5 mm diam., biatorine, glabrous or rarely with scattered marginal hairs; disc reddish brown; margin smooth to minutely crenulate, cream to

pale orange. Ascospores oblong-fusiform, (1–)3-septate, 30–40 × 7–8 µm.

Secondary chemistry. No substances detected by TLC; medulla K–, cyphellae K–.

Distribution and ecology. *Sticta plumbicolor* is known with certainty only from Hawaii. Reports from other regions, such as Jamaica (Minter et al. 2001; three collections housed at DUKE: 1967, *C. Racine* s. n.; 1968, *W. L. Culberson* & *C. F. Culberson* 13860, 13884), are misidentifications probably pertaining to *S. filicinella* (Nyl.) Zahlbr. In Hawaii, the species is found on all major islands (Kauai, Oahu, Molokai, Maui, Hawaii), generally in more or less undisturbed rainforests at low to mid elevation (between 75 and 640 m; a single outlier is from 2100 m). Notably, the closely related *S. tomentosa*, which cannot be separated using the ITS barcoding marker, is mostly found between 1000 and 2200 m (see below). *Sticta plumbicolor* grows mainly on tree trunks and branches, rarely on other substrata, often associated with bryophytes; identified phorophytes include *Cordyline (fruticosa)*, *Metrosideros*, *Myrsine* and *Psidium (cattleianum)*.

Remarks. Prior to our molecular phylogenetic revision of Hawaiian *Sticta* (Moncada et al. 2020), *S. plumbicolor* was considered to be the only potentially endemic taxon, bearing in mind that reports from Jamaica were erroneous (see above). To our surprise, *S. plumbicolor* proved to be phylogenetically indistinguishable from *S. tomentosa* based on the ITS barcoding marker. However, for the time being it is retained as a separate taxon, given the discrete morphological differences, providing a similar case to that of *S. antoniana* (see discussion above). *Sticta plumbicolor* is smaller and more delicate than *S. tomentosa* and forms abundant marginal and partly laminal clusters of conspicuous phyllidia. This morphology is not known from any collection outside Hawaii, while *S. tomentosa* in its typical form is a pantropical taxon. The most similar species appears to be the neotropical *S. filicinella* which produces delicate, cylindrical isidia instead of robust phyllidia.

Specimens examined. USA: Hawaii: Hawaii, east coast, Honolii area, 1977, *P. K. Higashino* & *J. Green* 324 (HAW); Maui, East Maui, Haleakalā National Park, Paliku cabin, 2100 m, 1975, *C. W. Smith* 2131 (HAW); Molokai, Wailau Valley, 150 m, 1977, *L. Stemmermann* 2062 (HAW); Oahu, Ewa District, Ewa Forest Reserve, 1975, *D. Vitt* 14519 (MIN); Oahu, Honolulu, Manoa Valley, Manoa Falls Trail, 75 m, 1992, *B. D. Ryan* 29039 (ASU); Oahu, Koolau Mountains, ridge from Tantalus to Puu Konahuanui, 1970, *C. W. Smith* 130c (HAW); Oahu, Koolau Mountains, Tantalus, Manoa Cliffs Trail, 467 m, 1977, *G. Y. Daida* 463 (HAW); Oahu, Koolau Range, Manoa Valley, Manoa Cliffs, 21°19'55"N, 157°48'43"W, 410–575 m, 2013, *B. Moncada*, *R. Lücking* & *C. W. Smith* 6910 (B, F, HAW), 6918a (F), 6925 (B); Oahu, Waianae Mountains, Makaleha Valley, Mokuleia Forest Reserve, 400 m, 1975, *C. W. Smith* 1717 (HAW).

***Sticta scabrosa* subsp. *hawaiiensis* Moncada, Lücking & C.W. Sm.**

Moncada et al., *Willdenowia* (in press); type: USA, Hawaii, Oahu, Koolau Range, Manoa Valley, Manoa Cliffs Trail, 21°19'55"N, 157°48'43"W, 410–575 m, 2013, *B. Moncada* et al. 6915 (BISH—holotype!; B, F—isotypes!).

(Fig. 2Q–T)

Primary photobiont cyanobacterial (*Nostoc*). *Stipe* absent. *Thallus* monophyllous, forming suborbicular rosettes or becoming irregular, to 20 cm across, anisotomously to polytomously branched; lobes 5–10 mm broad, flabellate, more or less horizontal, imbricate, undulate to slightly canaliculate, their margins entire to shallowly crenate. *Upper surface* uneven to foveolate-pitted, olive when fresh, greyish brown when dry, glabrous, with or without scattered papillae bearing tiny trichomes, without pruina but especially towards the margins thinly scabrous, with indistinct, cream maculae; rarely with marginal, pale to golden brown cilia. *Phyllidia* present, predominantly marginal but frequently also extending onto the lamina, to 0.5 mm long and broad, grey-brown, branched and becoming coralloid to palmate with a basal, flattened stipe lacking cyphellae. *Lower surface* uneven to undulate, dark brown to blackish. *Primary tomentum* dense but becoming sparse towards the lobe margins, spongy, forming pale to dark grey-brown, arachnoid tufts of fasciculate hyphae; hairs 200–1000 µm long, in fascicles of 6–12, partly branched, agglutinate, apically intertwined, pale to light brown, cylindrical hyphae with free apices. *Secondary tomentum* appressed, arachnoid; hairs 15–25 µm long, composed of single, branched, moniliform hyphae with free apices. *Rhizines* sparse. *Cyphellae* rather dense, 20–60 per cm², rounded, plane, erumpent to prominent, cream; pore 0.5–1.2(–1.8) mm diam.; cells of basal membrane lacking papillae.

Apothecia not observed.

Secondary chemistry. No substances detected by TLC; medulla and basal membrane of cyphellae K+ (pale) ochraceous(-yellow).

Distribution and ecology. The typical subspecies, *Sticta scabrosa* Moncada et al. subsp. *scabrosa*, is widely distributed in the Neotropics, whereas subsp. *hawaiiensis* is known only from Hawaii (Moncada et al. 2020, 2021). Both subspecies share the same ecology, being found in more tropical climates than most other *Sticta* species and often in somewhat exposed microsites in disturbed or secondary and anthropogenic habitats, sometimes with a weedy character. The taxon typically grows on tree trunks but is also found occasionally on rocks and other substrata. Most specimens were collected below 1000 m altitude, more rarely up to 1350 m and exceptionally (two collections) between 1800 and 2130 m. The broad range of reported phorophytes includes various native and introduced taxa: *Araucaria*, *Casuarina*, *Cocos (nucifera)*, *Cordyline (fruticosa)*, *Eucalyptus*, *Eugenia (cumini)*, *Leptecophylla (tameiameiae)*, *Litchi (chinensis)*, *Metrosideros (collina, tremuloides)*, *Myrsine*, *Osteomeles (anthyllidifolia)*, *Pisonia*, *Sapindus*, *Schinus (terebinthifolius)*, *Stachytarpheta (jamaicensis)* and *Trema (micrantha)*.

Remarks. *Sticta scabrosa* is another recently established species of the *S. weigeli* morphodeme (Moncada et al. 2021). It is only distantly related to *S. weigeli* and differs in several important features: the opaque, apically thinly scabrous lobe surface, the flattened phyllidia that are concolorous with the thallus, the rather thick, paler lower tomentum, and the lack of a yellow pigment in the cyphellae. The Hawaiian material differs consistently from neotropical populations in two substitutions in the ITS region and was formally recognized as a subspecies (Moncada et al. 2021). The only similar taxa in Hawaii are *S. andina* and *S. wai-kamoi*, from which *S. scabrosa* subsp. *hawaiiensis* can be

distinguished by the paler lower tomentum, the phyllidia being frequently laminal and concolorous with the thallus, the opaque lobe surface that becomes thinly scabrous towards the apices, and the sometimes scrobiculate-foveolate lobe tips. It also differs ecologically in its weedy character, being found mostly in somewhat exposed situations at lower altitudes. Specimens previously identified under the name *S. beauvoisii* (Elix & McCarthy 1998, 2008; Benner & Vitousek 2012; Smith 2013) largely correspond to this taxon.

Additional specimens examined. USA: Hawaii: Hawaii, Black Sand Beach, 1980, G. Y. Daida 594 (HAW); Hawaii, Hilo, Rainbow Falls, 70 m, 1976, C. W. Smith 2460 (HAW); Hawaii, North Kohala District, Hawi, 305 m, 1978, C. W. Smith 4366 (HAW); Kauai, South Kauai, Hawaii Agro Forestry Products Agro Forestry Demonstration plot, 21°57'49"N, 159°24'56"W, 140 m, 2013, B. Moncada, R. Lücking & T. Flynn 7076 (F, PTBG), 7078 (F); Kauai, South Kauai, Kahili Adventist School near Kahili Mountain Park, 21°57'49"N, 159°29'03"W, 275 m, 2013, B. Moncada, R. Lücking & T. Flynn 7069 (B, PTBG), 7070 (B, F), 7071 (PTBG), 7075 (B); Kauai, South Kauai, Kahili Ridge Trail, 21°57'52"N, 159°29'29"W, 300–450 m, 2013, B. Moncada, R. Lücking & T. Flynn 7072 (F), 7074 (F); Kauai, West Kauai, Koke'e State Park, Pihea Trail, 22°08'51"N, 159°37'53"W, 1250–1350 m, 2013, B. Moncada, R. Lücking & T. Flynn 7051 (F, HAW), 7054 (B, F, PTBG), 7056 (PTBG), 7057 (F), 7060 (B), 7063 (F); Kauai, West Kauai, Waimea Canyon, Iliu Nature Loop & Kukui Trail at Kokee Road, 22°03'04"N, 159°39'36"W, 900 m, 2013, B. Moncada, R. Lücking & T. Flynn 7025 (B, F, PTBG); Kauai, Koke'e State Park, Mohihi Trail, 1220 m, 1979, G. Y. Daida 287 (HAW); Kauai, Lawai Cemetery, 1978, G. Y. Daida 126 (HAW); Kauai, Na Pali, Kona Forest Reserve, 1035 m, 1975, P. K. Higashino 1018 (HAW); Kauai, Wahiawa Bog, 707 m, 1979, G. Y. Daida 293, 295 (HAW); Maui, East Maui, Makawao Forest Reserve, 1800 m, 1975, C. W. Smith 1924 (HAW); Maui, East Maui, Haleakalā Volcano, Haleakalā National Park, 2130 m, 1977, C. W. Smith 3256 (HAW); Maui, East Maui, Manawainui Valley, 1976, P. K. Higashino & G. Mizuno 2304 (HAW); Maui, East Maui, East Maui Irrigation (EMI), 20°53'06"N, 156°12'29"W, 225 m, 2013, B. Moncada & R. Lücking 6934 (B, F, HAW), 6935 (B, F), 6938 (F, HAW); Maui, East Maui, Hana Highway, Nua'ailua Bay scenic lookout, 20°51'33"N, 156°09'13"W, 100 m, 2013, B. Moncada & R. Lücking 6937 (B, F, HAW); Maui, East Maui, Kipahulu Forest Reserve, 1160 m, 1976, P. K. Higashino & G. Mizuno 2588 (HAW); Maui, Kipahulu Valley, 520 m, 1980, G. Y. Daida 759 (HAW); Maui, West Maui Mountains, Maunalei Arboretum, 20°58'46"N, 156°37'14"W, 400 m, 2013, B. Moncada, R. Lücking & P. Thomas 7013 (F), 7014 (F), 7015 (B, F, HAW), 7018 (F), 7019 (HAW), 7020 (B, F, HAW); Molokai, Pakuwoaku Ridge, 150 m, 1977, L. Stemmermann 2048 (HAW); Molokai, Wailau Valley, 1975, P. K. Higashino 315 (HAW); Molokai, Kalaupapa Cliff Trail, 21°10'40"N, 157°00'13"W, 30–470 m, 1993, C. W. Smith s. n. (HAW); Oahu, Koolau Mountains, Kahuku Forest Reserve, 275 m, 1975, C. W. Smith 1648 (HAW); Oahu, Koolau Mountains, Likeke Trail, 300 m, 1975, C. W. Smith 1448 (HAW); Oahu, Koolau Mountains, Manoa Valley, Manoa Falls Trail, 1975, P. K. Higashino 160 (HAW); Oahu, Koolau Range, Manoa Valley, Manoa Cliffs Trail, 21°19'55"N, 157°48'43"W, 410–575 m, 2013, B. Moncada, R. Lücking & C. W. Smith 6911 (F, HAW), 6912 (F), 6914 (F), 6917 (F, HAW), 6919 (B, F, HAW),

6922 (B, F, HAW), 6924 (B, F), 6919b (B, F); Oahu, Niu Ridge, 290 m, 1980, G. Y. Daida 428 (HAW); Oahu, Upper Manoa Valley, 1978, S. Conant 304 (HAW); Oahu, Waahila Ridge, 275 m, 1979, G. Y. Daida 250 (HAW); Oahu, Waialae Iki Ridge, 1983, W. Char 312 (HAW); Oahu, Waianae Mountains, Honouliuli Forest Reserve, 945 m, 1978, C. W. Smith 4129 (HAW); Oahu, Waianae Mountains, Makua Keaau Forest Reserve, 250 m, 1975, E. Funk 302 (HAW); Oahu, Waianae Mountains, Mokuleia Forest Reserve, 550–670 m, 1977, L. Stemmermann 319 (HAW); Oahu, Waianae Range, Land of 10 000 Snails, 730 m, 2011, C. W. Smith s. n. (HAW); Oahu, Waianae Range, Makahela Valley, 1975, L. Yoshida 318 (HAW); Oahu, Kahuku, 275 m, 1979, E. Funk 311 (HAW); Oahu, summit of Waikane Trail, 395 m, 1977, G. Y. Daida 115 (HAW); Oahu, Tantalus, 460 m, 1979, K. Clark 4 (HAW); Oahu, Waahila Ridge Trail, 1979, C. S. Futa 47 (HAW).

Sticta smithii Moncada & Lücking

Moncada *et al.*, *Pl. Fung. Syst.* **65**, 113 (2020); type: USA, Hawaii, Oahu, Koolau Range, Manoa Valley, Manoa Cliffs Trail, 21°19'55"N, 157°48'43"W, 410–575 m, 2013, B. Moncada, R. Lücking & C. W. Smith 6916 (F—holotype!; B, HAW—isotypes!).

(Fig. 2E–H)

Primary photobiont cyanobacterial (*Nostoc*). *Stipe* present, short. *Thallus* mono- to polyphyllous, with one to few individuals that are irregularly arranged, delicate, irregularly branched and dissected; lobes to 0.5 mm broad, spatuliform to truncate, ascending, not usually overlapping, plane to involute, their margins becoming strongly dissected. *Upper surface* even, olive-grey when fresh, bluish grey when dry, glabrous, without papillae or pruina, with scattered, white maculae. *Isidia* present, predominantly marginal, 0.1–0.2 mm long and 0.05–0.1 mm broad, darker grey-brown, shiny, somewhat flattened, arbuscular, much branched and becoming coralloid; arbusculae to 1 mm long and broad, distinctly flattened, base lacking cyphellae. *Lower surface* uneven, forming shallow, vein-like ridges, white to cream, with pale orange streaks towards the centre. *Primary tomentum* dense but short, becoming even shorter towards the margins, whitish; hairs 50–100 µm long, of single to somewhat agglutinate, mostly unbranched, cylindrical, colourless hyphae with free apices. *Secondary tomentum* absent. *Cyphellae* rather dense, 21–40 per cm², rounded to somewhat irregular, plane, immersed, white; pore 0.2–0.5 mm diam.; cells of basal membrane irregularly bulging, each cell with 1–3 elongated papillae, therefore appearing thorny. *Apothecia* not observed.

Secondary chemistry. No substances detected by TLC; medulla K–, membrane of cyphellae K–.

Distribution and ecology. *Sticta smithii* is known from a partially disturbed secondary rainforest on the densely populated and strongly altered island of Oahu, growing in shaded conditions on tree trunks between bryophytes, at c. 500 m altitude. It was previously also collected on Maui, on Haleakalā Volcano, at an altitude of nearly 2000 m. This suggests that this small species has been overlooked and might be more common.

Remarks. *Sticta smithii* is similar to *S. flynnii* in that both have small, caulescent, isidiate thalli. The main difference between

these two species is the size of the cyphellae: they remain small and rounded in *S. smithii* but become rather large and irregular in *S. flynnii*.

Additional specimen examined. USA: Hawaii: Maui, East Maui, Haleakalā Volcano, 1890–1950 m, 1981, C. W. Smith 5073 (HAW).

***Sticta tomentosa* (Sw.) Ach.**

Meth. Lichenum, 279 (1803).—*Lichen tomentosus* Sw., *Prodr.*, 147 (1788).—*Lobaria tomentosa* (Sw.) Räscher, *Nomenclat. Bot.* 3, 330 (1797).—*Stictina tomentosa* (Sw.) Nyl., *Syn. Meth. Lich.* 1 (2), 343 (1860).—*Dystictina tomentosa* (Sw.) Clem., *Gen. Fung.*, 175 (1909); type: Jamaica, unknown locality, Swartz s. n. (STB sheet 44, lectotype! *vide* Galloway (1994b), 47).

(Fig. 1A–D)

Primary photobiont cyanobacterial (*Nostoc*). *Stipe* absent. *Thallus* monophyllous, irregularly orbicular to palmate, to 5 cm across, anisotomously to polytomously branched; lobes 7–15 mm broad, flabellate to truncate, horizontal to ascending, not usually overlapping, their margins entire to slightly crenate. *Upper surface* even, bluish grey when fresh, bluish to yellowish grey when dry, glabrous, without papillae or pruina, with scattered, whitish maculae, with marginal, fasciculate, white cilia. *Isidia* and *soralia* not observed. *Lower surface* uneven to ridged-scrobiculate, white to pale cream. *Primary tomentum* thin, sparse towards the margins, fasciculate to somewhat spongy towards the centre, whitish to pale grey; hairs 70–300(–500) μm long, in fascicles of 10–20, mostly unbranched but agglutinate, colourless, cylindrical hyphae with free apices. *Secondary tomentum* thinly arachnoid, whitish; hairs scattered, 10–25 μm long, composed of single, unbranched, moniliform, colourless hyphae. *Cyphellae* dense, (20–)40–60(–100) per cm^2 , rounded, plane, immersed-erumpent, white; pore 0.1–0.3(–0.5) mm diam.; cells of basal membrane with 2–4 papillae per cell.

Apothecia common, submarginal, sessile, 1–2 mm diam., biatorine, glabrous or with scattered marginal hairs; disc reddish brown; margin crenulate, cream. *Ascospores* oblong-fusiform, 1–3-septate, 30–45 \times 6–10 μm .

Secondary chemistry. No substances detected by TLC; medulla K–, cyphellae K–.

Distribution and ecology. On the basis of molecular data, *Sticta tomentosa* is demonstrably a pantropical species (Moncada *et al.* 2020). It is found in more or less undisturbed, mid- to high-elevation rainforest habitats. In Hawaii it has been collected in numerous localities on all major islands, at altitudes between 500 and 2200 m but mostly above 1000 m. It typically grows on bark and is often associated with bryophytes, with the following identified phorophyte species: *Broussasia (arguta)*, *Dodonaea*, *Geranium (multiflorum)*, *Metrosideros (collina, tremuloides)*, *Myrsine* and *Pinus*.

Remarks. *Sticta tomentosa* is characterized by the typically bluish grey thallus with ciliate margins, the numerous apothecia, and the white underside with a very thin tomentum and tiny, often barely discernible cyphellae (Galloway 1994b; Galloway & Thomas 2004; Moncada 2012). In Hawaii, it is the only species that reproduces via apothecia and ascospores only and that does not form

vegetative propagules or marginal lobules. Most similar is *S. antoniana*, but in that taxon, the lobe margins are deeply dissected into narrow lobules and the underside features a thick, grey-brown tomentum abruptly ending short of the margins and leaving the margins entirely bare.

Specimens examined. USA: Hawaii: Hawaii, Olaa Forest Tract, 1150 m, 1979, P. J. Burton 428 (HAW); Kauai, West Kauai, Koke'e State Park, Pihea Trail, 22°08'51"N, 159°37'53"W, 1250–1350 m, 2013, B. Moncada, R. Lücking & T. Flynn 7044 (F), 7050 (HAW), 7061 (B), 7062 (F), 7066 (F); Kauai, Kalalau Lookout area, 1220 m, 1979, G. Y. Daida 297, 304 (HAW); Kauai, Wahiawa Bog, 707 m, 1979, G. Y. Daida 293 (HAW); Maui, East Maui, Haleakalā National Park, 1920 m, 1977, L. Stemmermann 2224 (HAW); Maui, East Maui, Haleakalā National Park, 1982, A. Medeiros 313 (HAW); Maui, East Maui, Haleakalā National Park, Kipahulu Valley, 2100 m, 1984, A. Medeiros & D. Miranda 314 (HAW); Maui, East Maui, Haleakalā National Park, Paliku, C. W. Smith 2163, 3098 (HAW); Maui, East Maui, Kipahulu Forest Reserve, 1995 m, 1976, P. K. Higashino & G. Mizuno 326, 1719 (HAW); Maui, East Maui, Wainapanapa, 2060 m, 1977, L. Stemmermann 2450 (HAW); Maui, East Maui, Haleakalā Volcano, Haleakalā National Park, Paliku, 1950 m, 1975, W. J. Hoe 3761 (HAW); Maui, East Maui, Haleakalā Volcano, Lower Waikamoi Preserve, 20°48'23"N, 156°15'19"W, 1200–1300 m, 2013, B. Moncada, R. Lücking & P. Bily 6946 (F), 6950 (B, F); Maui, East Maui, Haleakalā Volcano, Upper Waikamoi Preserve, 20°46'07"N, 156°14'17"W, 1800–2100 m, 2013, B. Moncada, R. Lücking & P. Thomas 6977 (F, HAW), 6980 (B), 6981 (F), 6989 (F), 6991 (B, F, HAW), 6992 (B), 6993 (F), 6996 (B, F, HAW), 7001 (HAW); Maui, Kipahulu Valley, 520 m, 1980, G. Y. Daida 756 (HAW); Maui, Olinda, Koolau Forest Reserve, 20°49'23"N, 156°16'12"W, 910 m, 1992, R. Rosentreter 8086b, 8094, 8107 (SRP); Maui, Olinda Koolan Forest Reserve, 20°49'40"N, 156°14'10"W, 1280 m, 1992, T. H. Nash III 42205 (ASU, MIN, WIS); Maui, Waikamoi Nature Conservancy Reserve, 20°46'12"N, 156°14'48"W, 2073 m, 1992, R. Rosentreter 8129b (F, SRP); Molokai, Molokai Forest Reserve, 1975, P. K. Higashino 460 (HAW); Oahu, Koolau Mountains, 1970, C. W. Smith 130f (HAW); Oahu, Waianae Mountains, 1220 m, on scrub *Metrosideros*, 1985, C. W. Smith 8421 (HAW); Oahu, Waianae Mountain Range, Kaua Trail, 945 m, 1978, G. Y. Daida 201 (HAW); Oahu, Kaala, C. W. Smith 1742 (HAW); Oahu, Waahila Ridge Trail, 1979, C. S. Futa 12 (HAW).

***Sticta waikamoi* Moncada & Lücking**

Moncada *et al.*, *Pl. Fung. Syst.* 65, 114 (2020); type: USA, Hawaii, Maui, East Maui, Haleakalā Volcano, Upper Waikamoi Preserve, 20°46'07"N, 156°14'17"W, 1800–2100 m, 2013, B. Moncada, R. Lücking & P. Thomas 7000 (F—holotype!; B, HAW—isoatypes!).

(Fig. 2U & V)

Primary photobiont cyanobacterial (*Nostoc*). *Stipe* absent. *Thallus* monophyllous, irregularly orbicular, to 7 cm across, anisotomously branched; lobes 4–7 mm broad, elongate to narrowly flabellate, more or less horizontal, not usually overlapping, involute to shallowly canaliculate, their margins entire to broadly crenulate. *Upper surface* even, olive-grey to grey-brown when fresh, light yellowish to greyish brown when dry, glabrous, without

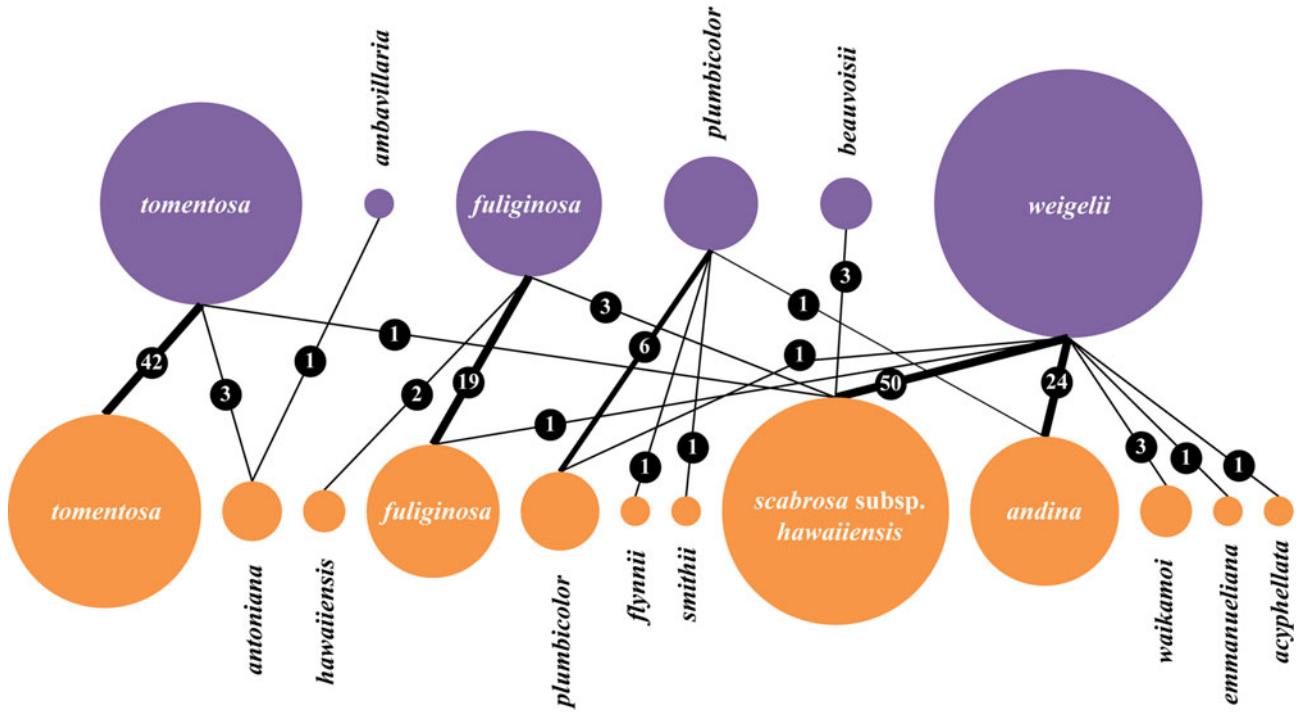


Fig. 3. Correspondence of identifications of *Sticta* lichens in HAW under the previous (above, purple) and the revised taxonomic concept (below, orange). The size of the circles is proportional to the number of specimens corresponding to a given name. The number of specimens corresponding to a particular ‘pair’ of identifications ‘before’ vs. ‘after’ is also indicated. In colour online.

papillae or pruina, without distinct maculae; marginal cilia not differentiated but lower tomentum often projecting beyond the margins to resemble short, brown-black cilia. *Isidia* present, predominantly marginal, to 0.5 mm long and broad, grey-brown, somewhat shiny, usually somewhat flattened, branched and becoming coralloid. *Lower surface* slightly uneven, dark brown. *Primary tomentum* thick and dense, forming dark brown, arachnoid tufts of fasciculate hyphae; hairs 100–300 µm long, in fascicles of 10–20, mostly unbranched but strongly agglutinate, dark brown, cylindrical hyphae with free apices. *Secondary tomentum* not discernible except in microscopic sections; hairs 20–30 µm long, comprising single, branched, weakly moniliform hyphae with somewhat inflated cells and free apices. *Rhizines* present, scattered towards the thallus centre. *Cyphellae* rather dense, 21–60 per cm², rounded, plane, immersed to becoming erumpent, white to cream, strongly contrasting with the dark tomentum; pore 0.3–1(–1.5) mm diam.; cells of basal membrane irregularly bulging but lacking papillae. *Apothecia* not observed.

Secondary chemistry. No substances detected by TLC; medulla K– to slowly K+ faintly yellowish, cyphellae K+ slowly ochraceous.

Distribution and ecology. *Sticta waikamoii* is so far known only from a small number of collections, at mid to high altitudes between 1585 and 2195 m, including mixed conifer forest on the island of Maui. While this type of forest conveys the impression of being rather undisturbed, it is not native to Hawaii, since all conifers have been introduced to the archipelago. While the type was growing on the ground over bryophytes, the species may occasionally also be epiphytic, then usually over bryophyte mats.

Remarks. Together with *Sticta andina*, *S. waikamoii* corresponds best to what has been traditionally identified with the name *S. weigelia*. However, the latter is a neotropical taxon and not directly related (Moncada *et al.* 2020). *Sticta weigelia* s. str. also deviates in its thinner lower tomentum and the often yellow cyphellae (Galloway 2006; Moncada 2012). *Sticta andina* differs in the generally narrower lobes and lack of rhizines and typically grows epiphytically. *Sticta waikamoii* is closely related to *S. rhizinata* but differs in several substitutions in the ITS barcoding marker and is much smaller overall, with less conspicuous rhizines (Moncada & Lücking 2012; Moncada *et al.* 2020).

Additional specimens examined. USA: Hawaii: Hawaii, Mauna Loa, Pohakuloa training area, 1585 m, 1977, P. K. Higashino 323 (HAW); Maui, East Maui, Makawao Forest Reserve, 1800 m, 1975, C. W. Smith 1950a (HAW); Maui, Haleakalā, N slope, Frisbee meadow above Pouli Flats, 2195 m, 1987, C. W. Smith 8455 (HAW).

Revised taxonomic concept and excluded names

Several names previously reported in the genus *Sticta* for Hawaii must be excluded from the Hawaiian lichen biota, including at least one name from digital online repositories. We also performed an analysis of the specimens housed in HAW to see how previously applied names correspond to the revised taxonomy (Fig. 3). Thus, the two common species confirmed to be present in Hawaii, *S. fuliginosa* and *S. tomentosa*, were largely identified correctly but some specimens also corresponded to other taxa, including *S. antoniana* and *S. scabrosa* var. *hawaiiensis* in the case of *S. tomentosa* and *S. hawaiiensis* and *S. scabrosa* var. *hawaiiensis* in the case of *S. fuliginosa*. Specimens previously

identified as *S. weigelii* represented no less than seven different taxa, mostly *S. andina* and *S. scabrosa* subsp. *hawaiiensis*. *Sticta plumbicolor* was mostly correctly identified but some specimens corresponded to *S. andina* and to the newly recognized *S. flynnii* and *S. smithii* (Fig. 3).

Sticta ambavillaria (Bory) Ach. — Not present in Hawaii; specimens identified with this name represent *S. antoniana* (Moncada et al. 2020).

Sticta babingtonii D. J. Galloway — The name of this green-algal species was applied to an unpublished herbarium collection from Maui (Olinda, Koolau Forest Reserve North Haleakala, 910 m, 1992, R. Rosentreter 8108 (SRP)), reported in the Lichen Portal of the Consortium of North American Lichen Herbaria (CNALH): [<https://lichenportal.org/cnalh/collections/individual/index.php?occid=1577932&clid=0>]. Revision of a digital image of the specimen revealed it to be *S. andina*.

Sticta cyphellulata (Müll. Arg.) Hue — Not present in Hawaii; specimens identified with this name represent *S. smithii* and probably also *S. flynnii* (Moncada et al. 2020).

Sticta filix (Sw.) Nyl. — Not present in Hawaii; an erroneous report of uncertain origin (Moncada et al. 2020).

Sticta weigelii (Ach.) Vain. — Not present in Hawaii; specimens identified with this name represent *S. andina*, *S. scabrosa* subsp. *hawaiiensis* and *S. waikamoi* (Moncada et al. 2020).

Sticta beauvoisii Delise; *S. weigelii* var. *beauvoisii* (Delise) Hue — Not present in Hawaii; specimens identified with this name represent *S. scabrosa* subsp. *hawaiiensis* (Moncada et al. 2020).

Sticta weigelii var. *lutescens* (Taylor) H. Magn. — Not present in Hawaii; specimens identified with this name probably represent *S. scabrosa* subsp. *hawaiiensis* (Moncada et al. 2020).

Sticta weigelii var. *peruviana* (Delise) Vain. — Not present in Hawaii; specimens identified with this name probably represent *S. scabrosa* subsp. *hawaiiensis* (Moncada et al. 2020).

Discussion

As outlined above and by Moncada et al. (2021), eight species of *Sticta* had previously been listed for Hawaii: *S. ambavillaria*, *S. beauvoisii*, *S. cyphellulata*, *S. filix*, *S. fuliginosa*, *S. plumbicolor*, *S. tomentosa* and *S. weigelii* (Elix & McCarthy 1998, 2008; Smith 2013). One additional species, *S. limbata*, was listed in an ecophysiological study (Benner & Vitousek 2012). Of these, only three widespread taxa (*S. fuliginosa*, *S. limbata*, *S. tomentosa*) and one putatively endemic species (*S. plumbicolor*) could be confirmed as a result of a molecular phylogenetic revision (Moncada et al. 2021). Of the 13 species now recognized, one was a new record (*S. andina*) and eight were taxa new to science (seven species and one subspecies). Thus, the overlap in names recorded for Hawaii before and after this revision is only 38%. This substantial change in the taxonomic delimitation of Hawaiian *Sticta* has implications for other studies of these lichens, including their potential applications, for example as environmental monitors.

For example, Czacuga et al. (1997) analyzed carotenoid content in various lichens including *S. weigelii* from Hawaii. No voucher information was given but the locality data (Oahu, *Melaleuca*) indicate that the studied material probably represented *S. scabrosa* subsp. *hawaiiensis*, which is common in that area. Hagiwara (2016) and Hagiwara et al. (2016) analyzed antioxidant and antitumoral properties in a range of lichens collected in Hawaii and Iceland, including *Pseudocyphellaria hawaiiensis*

H. Magn., *P. xanthosticta* (Pers.) Moncada & Lücking, and *Sticta weigelii*. While the taxonomy of *Pseudocyphellaria* followed the earlier revision by Moncada et al. (2014a), the material identified as *S. weigelii* is likely to correspond to *S. scabrosa* subsp. *hawaiiensis*, because the Hawaiian lichens in that study had been collected at low altitudes (0–500 m).

Benner et al. (2007), Benner (2011) and Benner & Vitousek (2012) investigated the correlation between phosphorus, nitrogen and cyanolichens in Hawaiian forests, including experimental P fertilization. Lobaroid species included in these studies were *Crocodia aurata* (Ach.) Link (as *Pseudocyphellaria*), *Lobariella crenulata* (Hook.) Yoshim., *P. crocata* (L.) Vain., *Sticta beauvoisii*, *S. fuliginosa*, *S. limbata*, *S. tomentosa* and *S. weigelii*. The presence of *L. crenulata* in Hawaii has not been confirmed by molecular data and the studied material may represent the newly recognized *L. sandwicensis* Lücking et al. (Lücking et al. 2017a). *Crocodia aurata* indeed occurs in Hawaii (Moncada et al. 2014a). However, *Lobariella* and *Crocodia* are chlorolichens and it is unclear why they were classified as cyanolichens, with rather high rates of N-fixation (Benner & Vitousek 2012), raising doubt about the underlying species identifications. *Pseudocyphellaria crocata* s. str. is absent from the Hawaiian archipelago and the material studied by Benner et al. (2007) and Benner & Vitousek (2012) refers to one or several newly distinguished taxa (Moncada et al. 2014a). In the absence of voucher material, it is impossible to ascertain which species were studied. In the case of the five representatives of *Sticta*, the material identified as *S. beauvoisii* is likely to represent *S. scabrosa* subsp. *hawaiiensis*, whereas *S. weigelii* could well refer to *S. andina*. The identifications of the other three taxa (*S. fuliginosa*, *S. limbata*, *S. tomentosa*) appear to be correct. Notably, Benner & Vitousek (2012) found that the forest plot fertilized with P showed an increased abundance of lobaroid macrolichens, including species of *Sticta*. Between the two species of *Sticta* specifically tested for N-fixation, *S. tomentosa* showed higher N-fixation in the non-fertilized control plot, whereas for *S. beauvoisii* (= *S. scabrosa* subsp. *hawaiiensis*) it was higher in the P-fertilized plot. This result can be viewed in a new light, given the finding that among Hawaiian *Sticta*, *S. tomentosa* is largely confined to undisturbed forests (see also Smith 1991), whereas *S. scabrosa* subsp. *hawaiiensis* is frequent in disturbed and anthropogenic vegetation.

These examples show that revised species taxonomies also challenge the results of studies in ecology, ecophysiology, biogeography, biochemistry and other fields of research, a largely overlooked problem. Due to the frequent lack of voucher citations, correct identification of taxa used in such studies can often not be ascertained. It is therefore of the utmost importance that such studies deposit voucher material in public herbaria in the same way as taxonomic works, preferably with accessible digital information including specimen imagery. Collaboration with experts or DNA barcoding may improve the taxonomic component of such studies (e.g. Paudel et al. 2008; Plaza et al. 2014; Bajpai et al. 2015; Xu et al. 2016), but this does not replace proper deposition and citation of voucher material. DNA barcoding in particular is also often misinterpreted. In a study on physiological and genetic effects of chromium on thalli of *Pyxine cocolos* in India (Bajpai et al. 2015), the authors used ITS barcodes to support the identification of their material. However, our own revision of ITS sequences available for *P. cocolos* revealed that it forms three distinct clades: one neotropical clade (KX512936), sister to a clade including a subclade formed by two specimens from Singapore

Table 1. Proposed environmental scores (1=least disturbed, 5=most disturbed) for currently distinguished species of Hawaiian *Sticta* to be used in a simple monitoring protocol to assess ecosystem health.

Species	Preferred vegetation and disturbance level	Score
<i>S. andina</i>	undisturbed rainforest	1
<i>S. antoniana</i>	undisturbed rainforest	1
<i>S. emmanueliana</i>	undisturbed rainforest	1
<i>S. flynnii</i>	undisturbed rainforest	1
<i>S. hawaiiensis</i>	undisturbed rainforest	1
<i>S. limbata</i>	undisturbed rainforest	1
<i>S. plumbicolor</i>	undisturbed rainforest	1
<i>S. tomentosa</i>	undisturbed rainforest	1
<i>S. waikamoi</i>	undisturbed rainforest	1
<i>S. acyphellata</i>	partly disturbed or secondary old-growth rainforest	2
<i>S. smithii</i>	partly disturbed or secondary old-growth rainforest	2
<i>S. fuliginosa</i>	closed rainforest to partially disturbed and exposed vegetation	3
<i>S. scabrosa</i> subsp. <i>hawaiiensis</i>	disturbed and anthropogenic, more or less exposed sites	5

and China (AF540540, KY611874), and another subclade formed by the Indian specimens from the above study (KF691782, KF691783, KF691784, KF691785, KF691786, KF691787). Based on the underlying topology and the large number of substitutions in the ITS barcoding marker, these clades represent three different species. Yet, even with these data to hand, the authors did not provide an adjusted taxonomy and identified their material uncritically with the name *P. cocoes*.

Another important aspect of revised and refined species taxonomies is the use of lichens in environmental monitoring. In a study of the *Sticta filix* group in New Zealand, Ranft *et al.* (2018) showed that two previously unrecognized species in this group had a higher fidelity for undisturbed forest vegetation than the two species previously distinguished based on a broader approach to species delimitation. Given the particular situation in Hawaii as a threatened island biota (Kirch 1982; Stone & Scott 1985; Stone *et al.* 1992; Sakai *et al.* 2002; Department of Land and Natural Resources 2007; US Fish and Wildlife Service 2010; Wood 2012), the disparate ecology of Hawaiian *Sticta* enables the use of these lichens to monitor ecosystem health. This approach is further facilitated by the possibility of identifying the currently recognized taxa in the field. Nine of the species now recognized appear to be confined to closed or more or less undisturbed forest (Table 1). As 'undisturbed' one may thereby also classify non-native old-growth forest such as the introduced conifer forest on Maui. On the other side of the spectrum is the widespread and somewhat weedy *S. scabrosa* subsp. *hawaiiensis*. *Sticta fuliginosa* is somewhat intermediate in its ecological requirements, being found in undisturbed forest but also disturbed sites. These observations would allow the establishment of a protocol using *Sticta* species along a disturbance gradient (Table 1) (1 = least disturbed, 5 = most disturbed), using an abundance-weighted environmental monitoring score *E* based

on relative species abundance at a given monitoring site:


$$E = \sum E_i \times A_i$$

where E_i = individual species score (see Table 1) and A_i = individual relative species abundance (e.g. using a grid system or other sampling design). For example, a site with *S. scabrosa* subsp. *hawaiiensis* (90% abundance) and *S. fuliginosa* (10%) would give a weighted score of $E = 5 \times 0.9 + 3 \times 0.1 = 4.8$ (highly disturbed). In contrast, a site with *S. andina* (30%), *S. flynnii* (5%), *S. fuliginosa* (10%), *S. smithii* (5%) and *S. tomentosa* (50%) would result in a weighted score of $E = 1 \times 0.3 + 1 \times 0.05 + 3 \times 0.1 + 2 \times 0.05 + 1 \times 0.5 = 1.25$ (less disturbed).

Traditional taxonomy of the genus *Sticta* in Hawaii would not have allowed such an approach, as for instance the ecologically disparate *S. andina* and *S. scabrosa* subsp. *hawaiiensis* or *S. hawaiiensis* and *S. fuliginosa* had been subsumed under the names *S. weigelii* and *S. fuliginosa*, respectively. This impact of accurate taxonomy on the use of lichens as biomonitors was also discussed in a study of the *S. filix* group in New Zealand (Ranft *et al.* 2018).

Conceivably, a next step following these results would be a conservation assessment of *Sticta* lichens in Hawaii. However, since this is the first study that offers an accurate taxonomic treatment of the species, we consider it premature to carry out such an assessment with the current data. Instead, we hope this treatment encourages researchers to study the genus in more detail and with quantitative approaches, including the protocol proposed above. The small species especially need to be looked for more extensively, since these are likely to have been overlooked in the past or misinterpreted as young specimens not worth collection. It is therefore difficult to state whether these species are genuinely rare. Among the conspicuous taxa, *S. fuliginosa* and *S. scabrosa* subsp. *hawaiiensis* are certainly of the least concern, as they seem to tolerate various degrees of disturbance. Also *S. tomentosa*, although mostly found in undisturbed forest, appears to be abundant where forest vegetation is properly protected.

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