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Two new common, previously unrecognized species in the *Sticta weigelii* morphodeme (Ascomycota: Peltigeraceae)

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Abstract: *Sticta* is a subcosmopolitan genus most diverse in the tropics. Traditionally, many taxa were considered to be widespread and morphologically variable, following broadly circumscribed morphodemes. Among these is the *S. weigelii* morphodeme, characterized by a cyanobacterial photobiont and rather narrow, flabellate to truncate or tapering lobes producing predominantly marginal isidia. Molecular phylogenetic analyses focusing on the ITS fungal barcoding marker revealed that this morphodeme represents several species, some of which are only distantly related to each other. Here we describe two species and one subspecies of this morphodeme as new to science, based on analysis of 400 specimens, for 344 of which we generated ITS barcoding data. The two new species, *S. andina* and *S. scabrosa*, are broadly distributed in the Neotropics and also found in Hawaii, where the latter is represented by the new subspecies, *S. scabrosa* subsp. *hawaiiensis*; in the case of *S. andina*, the species is also found in the Azores. *Sticta andina* exhibits high phenotypic variation and reticulate genetic diversification, whereas the phenotypically rather uniform *S. scabrosa* contains two main haplotypes, one restricted to Hawaii. *Sticta andina* occurs in well-preserved montane to andine forests and paramos, whereas the two subspecies of *S. scabrosa* are found in tropical lowland to lower montane forests, tolerating disturbance and extending into anthropogenic habitats.

Key words: Ascomycota, Azores, Hawaii, Neotropics, Peltigeraceae, *Sticta*, *Sticta weigelii*

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Introduction

The genus *Sticta* is among the most conspicuous macrolichens, recognized by its usually large, leathery thalli with well-defined pores (cyphellae) on the lower side

(Galloway 1994, 2001, 2007; Brodo & al. 2001; Moncada & al. 2014). Prior to molecular phylogenetic studies, approximately 115 species had been distinguished in this genus (Kirk & al. 2008), many of them presumed to be widespread, and common taxa had been circum-

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scribed through broadly defined morphologies. For instance, cyanobacterial forms with broadly rounded lobes producing laminal isidia have been identified with the name *S. fuliginosa* (Dicks.) Ach. and those with narrow lobes producing predominantly marginal isidia as *S. weigelii* (Ach.) Vain. Other commonly employed names are *S. limbata* (Sm.) Ach. for cyanobacterial forms with marginal soredia, and *S. canariensis* (Bory) Delise, *S. damicornis* (Sw.) Ach. or *S. dichotoma* (Bory) Delise for species associating with green algae and forming dichotomously branched thalli (Joshi & Awasthi 1982; Swinscow & Krog 1988; Galloway & al. 1995; Büdel & al. 2000; Oliveira & al. 2002; Farkas 2003; Galloway & Thomas 2004; Jørgensen & Tønsberg 2007; Makryi 2008; Smith & al. 2009).

Molecular phylogenetic and revisionary studies showed that such broadly circumscribed taxa represent several to sometimes numerous, often only distantly related species (McDonald & al. 2013; Moncada & al. 2013, 2014, 2018; Magain & Sérusiaux 2015; Dal Forno & al. 2018; Simon & al. 2018; Ekman & al. 2019; Mercado-Díaz & al. 2020). The *Sticta weigelii* morphodeme evolved multiple times independently in various clades, resulting in the description of several new species, e.g. *S. borinquensis* Merc.-Díaz & Lücking and *S. rhizinata* B. Moncada & Lücking, and the reinstatement of some old names, such as *S. beauvoisii* Delise (Moncada & Lücking 2012; McDonald & al. 2003; Moncada & al. 2014; Mercado-Díaz & al. 2020). These more narrowly delimited species are not only phylogenetically supported but also exhibit diagnostic phenotypic characters that had previously been considered environmental or ontogenetical variation (Swinscow & Krog 1988; Galloway 1994, 1997).

As result of a broad sampling of mostly neotropical representatives of *Sticta*, we accumulated a large amount of data for two undescribed lineages corresponding to the *S. weigelii* morphodeme. Among all globally recognized clades corresponding to this morphodeme, the two newly recognized lineages were the most abundant. Yet, no names were found in the literature that could be applied to them and they are here formally described as new to science, under the names *S. andina* B. Moncada, Lücking & Sérus. and *S. scabrosa* B. Moncada, Merc.-Díaz & Bungartz, the latter with two subspecies, subsp. *scabrosa* from the Neotropics and subsp. *hawaiiensis* B. Moncada, Lücking & C. W. Sm. from Hawaii. Judging from pre-molecular treatments including specimens now assigned to these taxa, both had previously identified with the broadly delimited name *S. weigelii* and more recently also with the name *S. beauvoisii* (Benner & Vitousek 2012). However, the two species are not closely related to either *S. weigelii* s.str. or *S. beauvoisii* and both are also only distantly related to each other. The two lineages were first informally recognized using a broad ITS-based phylogeny (Moncada & al. 2014). In that study, what is now recognized as *S. andina* was believed to represent seven different species, labelled “*andina*”, “*colombiana*”, “*dioica*”, “*paramuna*”, “*phyl-*

lidiata”, “*aff. phyllidiata*” and “*squamifera*”. However, the data now available are more consistent with merging three of these (“*andina*”, “*colombiana*”, “*paramuna*”) into a single lineage, with apothecia and/or cylindric to mostly flattened isidia or phyllidia (Moncada & al. 2014: 220, fig. 4, 223, fig. 8; Moncada & al. 2020). In contrast, *S. scabrosa*, previously recognized as a single species (Moncada & al. 2014: 218, fig. 3), even with the now much expanded data set was found to be morphologically and genetically rather uniform, except for a unique surface morphodeme occurring solely in Hawaii.

Material and methods

ITS barcoding sequences of the genus *Sticta* were assembled for a much expanded data set of ingroup 677 OTUs (Suppl. File S1; Moncada & al. 2020), as compared to 370 OTUs published previously (Moncada & al. 2014). The *S. andina* complex initially comprised 19 OTUs, all sampled in Colombia, as mentioned above corresponding to three OTUs informally labelled “*andina*”, “*colombiana*” and “*paramuna*” (Moncada & al. 2014). For an updated ITS-based phylogeny, we assembled a total of 164 OTUs from Central America, Colombia, Ecuador, Brazil, the Azores and Hawaii (Moncada & al. 2020). *Sticta scabrosa* was initially based on nine OTUs from Colombia and the Dominican Republic (Moncada & al. 2014), while the updated set included 180 OTUs from Mexico, Costa Rica, the Dominican Republic, Puerto Rico, Colombia, Brazil, Argentina, Galapagos and Hawaii (Moncada & al. 2020).

The updated alignment was assembled in BIOEDIT 7 (Hall 1999) and sequences were aligned with MAFFT 7 (Katoh & Standley 2013) using the [–auto] option. The alignment included 677 ingroup OTUs and was 626 bases long. We did not detect critical alignment ambiguity and so included all sites, in order to maximize terminal resolution. Phylogenetic analysis was performed using maximum likelihood in RAxML 8.2.12 on the CIPRES Science Gateway (Stamatakis 2015; Miller & al. 2010), applying the GTR-Gamma model and 98 bootstrap pseudoreplicates according to an automated saturation criterion. The resulting tree were visualized in FigTree 1.4.2 (Rambaut 2016).

Morphological characters of specimens of *Sticta andina* and *S. scabrosa* were assessed at the Universidad Distrital Francisco José de Caldas (Bogotá), the Field Museum (Chicago), the Université de Liège and the Botanischer Garten und Botanisches Museum, Freie Universität Berlin using standard microscopical techniques described in Moncada (2012) and Ranft & al. (2018).

Results and Discussion

Sticta andina and *S. scabrosa* form two large clades in the terminal portion of a global ITS-based *Sticta* phylog-

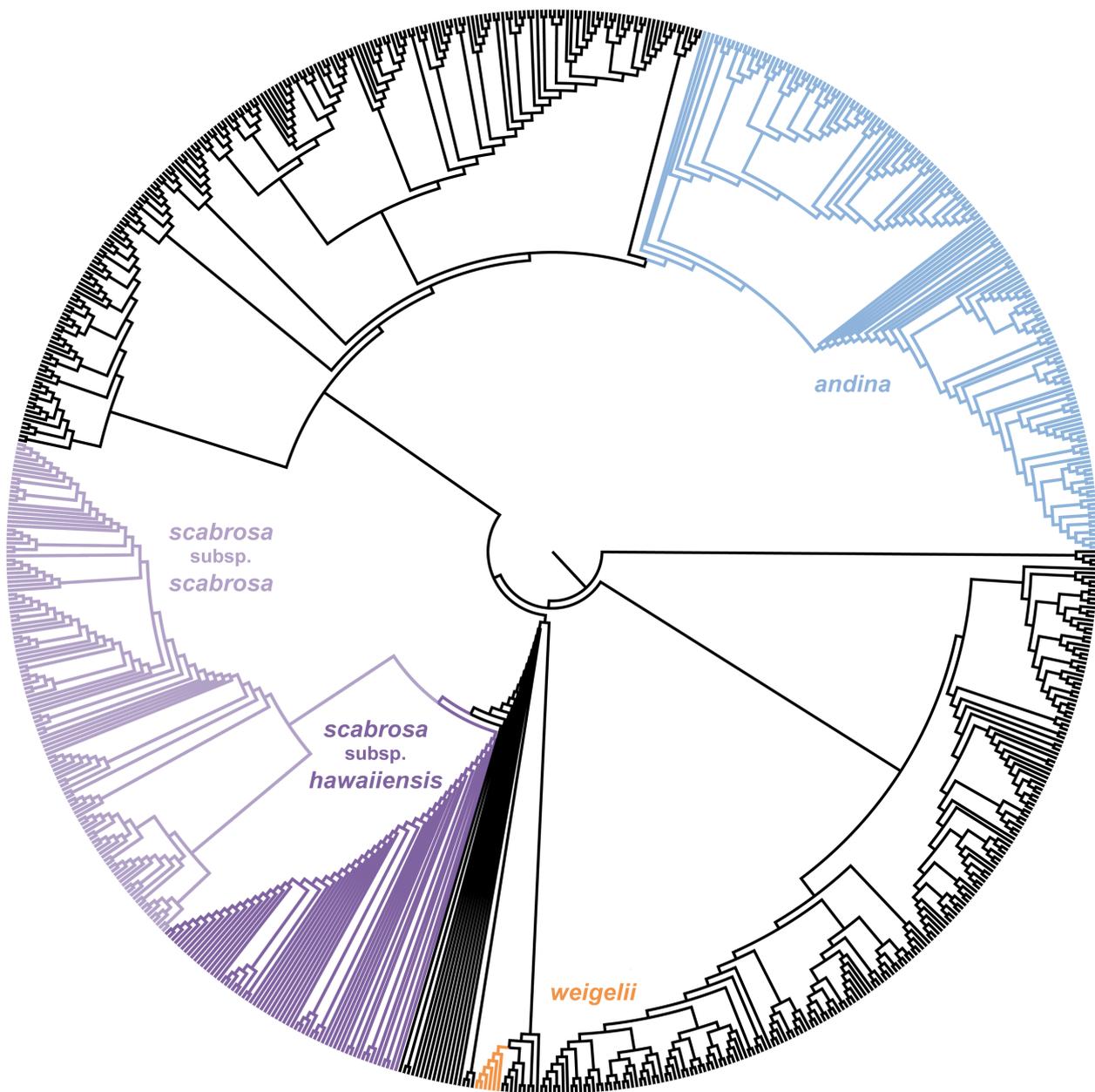


Fig. 1. Global phylogeny (circle cladogram) of the largest clade of the genus *Sticta* containing the target taxa, based on the ITS barcoding marker, showing the position of the newly recognized taxa with the *S. weigeli* morphodeme in relation to *S. weigeli* s.str. For full tree with bootstrap support values, see Suppl. File S2 (see also Moncada & al. 2020).

eny (Fig. 1; Suppl. File S2). Both species are geographically largely overlapping, exhibiting similar distribution ranges, predominantly across the Neotropics and Hawaii, with *S. scabrosa* also including the Caribbean (Dominican Republic and Puerto Rico) and the Galapagos Islands, whereas *S. andina* is further present in the Azores (Moncada & al. 2020). *Sticta andina* includes apotheciate and isidiate to phyllidiate specimens, as well as sun and shade forms (Fig. 2). *Sticta scabrosa* is uniformly phyllidiate but, besides most specimens having an uneven lobe surface, those from Hawaii may also present an unique surface with foveolate-pitted lobe tips (Fig. 3).

Until recently, representatives of *Sticta* with a cyanobacterial photobiont and predominantly marginal isidia

were considered a single species, *S. weigeli*, presumably with a subcosmopolitan distribution (Joshi & Awasthi 1982; Swinscow & Krog 1988; Galloway 1994, 2001, 2007; Galloway & al. 1995; Büdel & al. 2000; Brodo & al. 2001; Farkas 2003; Galloway & Thomas 2004). However, like other morphodemes in the genus (Moncada & al. 2014; Magain & Sérusiaux 2015; Simon & al. 2018), the *S. weigeli* morphodeme appears to have evolved multiple times within the genus, and most of the sequences previously deposited under this name do not represent this taxon (Moncada & al. 2014). *Sticta weigeli* s.str. is widely distributed in the Neotropics including the Caribbean (Fig. 1; Suppl. File S2). Material identified with this name from other regions does not represent this

taxon. For instance, the ITS accession identified as *S. weigelii* from Taiwan (AB245124) is an undescribed relative of the latter, whereas the sample from South Korea (KF730791) represents the cosmopolitan *S. fuliginosa* s.str. Another specimen from Guyana (AF524905) is an undescribed relative of *S. scabrosa* (see Suppl. File S2). *Sticta weigelii* s.str. is a species of tropical climates, similar in altitudinal zonation to *S. scabrosa*, but more affine to well-preserved forest, characterized by dark to blackened, marginal isidia, a rather thin and rather dark lower tomentum and partly yellow cyphellae (Galloway 2006; Moncada 2012; Mercado-Díaz & al. 2020). The two species newly recognized here, *S. andina* and *S. scabrosa*, represent the *S. weigelii* morphodeme in having a cyanobacterial photobiont and elongate lobes with marginal isidia and/or phyllidia, but are phylogenetically unrelated to each other and to *S. weigelii* (Fig. 1; Suppl. File S2). *Sticta andina* agrees with *S. weigelii* s.str. in the slightly shiny thallus surface and rather dark vegetative propagules, but it differs in the frequent formation of phyllidia; it also has a much thicker lower tomentum, persistently white cyphellae and frequently produces apothecia, and further differs in its preference for upper montane to andine habitats. *Sticta scabrosa* has a similar ecology as *S. weigelii*, although it is more commonly found in disturbed and anthropogenic habitats, but its thallus surface is opaque and thinly scabrose, especially toward the margins. The lower tomentum is grey-brown and much thicker, and its cyphellae are consistently white to at most cream-coloured but never yellow. The three species are therefore not only phylogenetically distinct but also morphologically and ecologically well distinguished.

Although *Sticta andina* and *S. scabrosa* have broadly overlapping geographic ranges, they exhibit different evolutionary histories, which may be explained by their autecology. As a species largely confined to undisturbed andine forests and paramos, *S. andina* underwent fragmentation and partial isolation in the recent past, due to the insular nature of these habitats both in space and time (Moncada & al. 2020). Similar effects on genetic diversification have been shown for andine orchids, bromeliads and paramo plants (Küper & al. 2004; Givnish 2010; Madriñan & al. 2013; Givnish & al. 2014, 2015). The level of genetic and morphological diversification in *S. andina* is indeed much higher than in other widespread species of the genus, particularly *S. fuliginosa* s.str. and *S. limbata* s.str. (Moncada 2012; Moncada & al. 2014; Magain & Sérusiaux 2015). Based on an earlier ITS-based phylogeny of *Sticta* (Moncada & al. 2014), the clade now recognized as *S. andina*, at that time with 19 accessions from Colombia, had been tentatively divided into three taxa (“*andina*”, “*colombiana*”, “*paramuna*”). In our much-expanded dataset, with more than eight times as many accessions, the original “*andina*” corresponds to a small group in one of the subclades, whereas “*colombiana*” and “*paramuna*” largely represent two

other subclades. Despite the observed phylogenetic structure and morphological variation, separating these subclades at species level is not warranted, because the internal topology is not supported and there is no clear-cut correlation between the subclades and the observed morphological variation.

In contrast, *Sticta scabrosa* was found to be phylogenetically less complex, with a distinctive haplotype present only in Hawaii, and morphologically more uniform, except for a deviating morphodeme with foveolate surface in part of the Hawaiian material. Because this species is frequent in tropical settings and tolerates disturbances, it may retain more effective genetic interchange between populations (Moncada & al. 2020). *Sticta scabrosa* is thus rather well-defined as a taxon and the Hawaiian metapopulation is formally best classified as a subspecies.

Taxonomic treatment

Sticta andina B. Moncada, Lücking & Sérus., **sp. nov.** – MycoBank 836871. – Fig. 2.

Holotype: Colombia, Cundinamarca, Mun. Chipaque, Vereda Marilandia, vía Santuario, 04°26'N, 74°01'W, 2400 m, 8 Sep 2011, B. Moncada 4802 (UDBC).

- “*Sticta andina*” B. Moncada & Lücking in Moncada, El Género *Sticta* (Schreb.) Ach. en Colombia: Taxonomía, Ecogeografía e Importancia: 44. 2012, nom. inval. (Turland & al. 2018: Art. 29.1, F.5).
- “*Sticta colombiana*” B. Moncada & Lücking in Moncada, El Género *Sticta* (Schreb.) Ach. en Colombia: Taxonomía, Ecogeografía e Importancia: 61. 2012, nom. inval. (Art. 29.1, F.5).
- “*Sticta paramuna*” B. Moncada & Lücking in Moncada, El Género *Sticta* (Schreb.) Ach. en Colombia: Taxonomía, Ecogeografía e Importancia: 147. 2012, nom. inval. (Art. 29.1, F.5).

Diagnosis — Differing from *Sticta weigelii* in the formation of mostly flattened or dorsiventral isidia and phyllidia instead of cylindrical isidia, a thicker lower tomentum, consistently white cyphellae, and the upper montane versus lower montane-tropical habitat preferences.

ITS barcoding marker accession — KC732688 (holotype).

Description — Thallus forming suborbicular rosettes or becoming irregular, up to 15 cm in diam., moderately branched, with 3–5 branches per 5 cm radius; ramification anisotomous to pleurotomous or rarely appearing polytomous. Lobes leathery, flabellate to ligulate with rounded tips, adnate to horizontal or slightly ascending, adjacent to imbricate, undulate to slightly canalliculate; margins entire to sinuose or shallowly crenate, not thickened; lobe internodes (5–)7–12(–15) mm long,

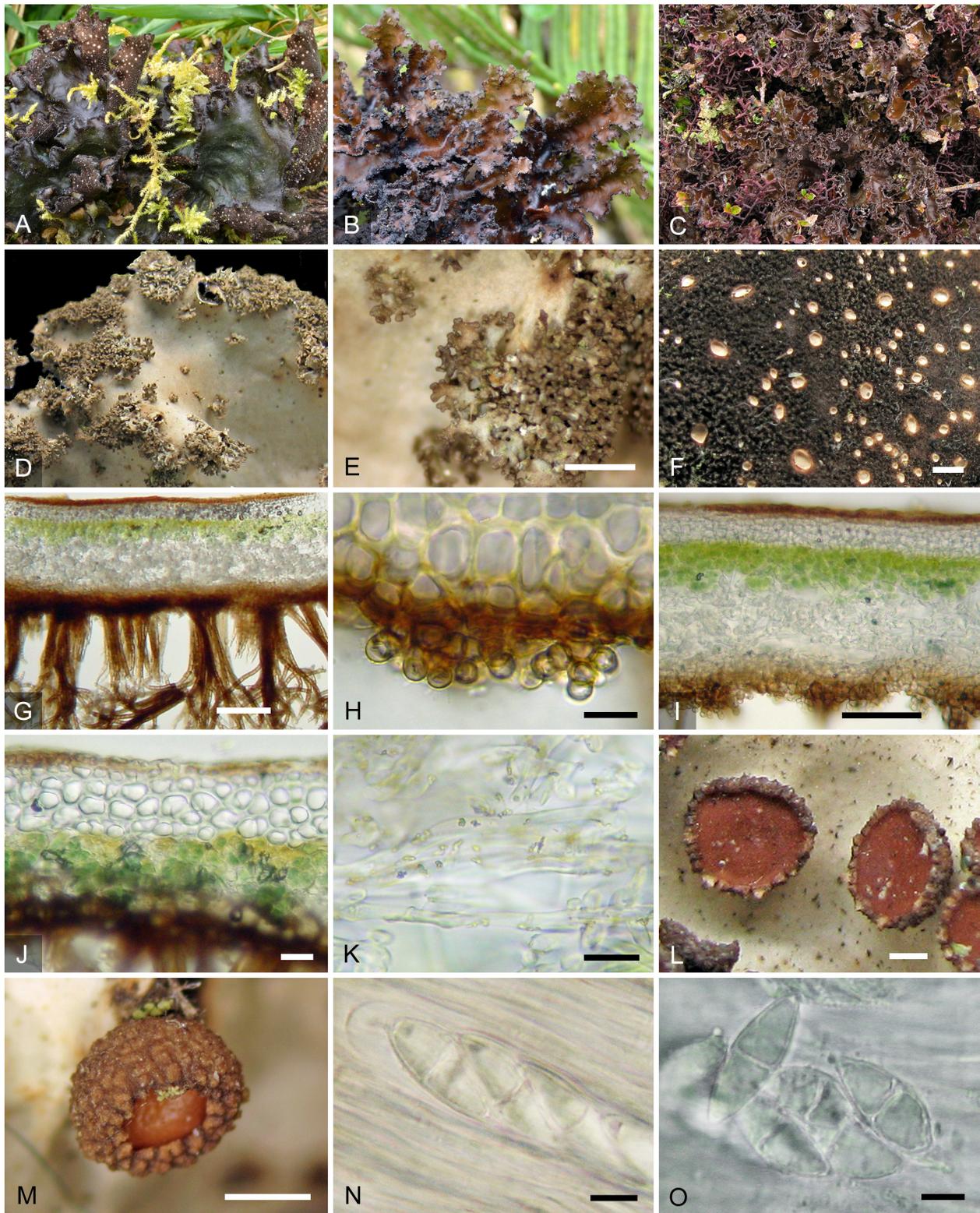


Fig. 2. *Sticta andina*, morphology and anatomy. – A–C: specimens in situ (A: Colombia, *Moncada* 7452; B: Colombia, *Moncada* 7948; C: Colombia, *Moncada* 4802, holotype); D, E: lobe tip and phyllidia enlarged (Colombia, *Moncada* 4802, holotype); F: lower surface tomentum and cyphellae (Colombia, *Moncada* 4936); G: section showing lower primary tomentum (Colombia, *Moncada* 4936); H: section showing lower secondary tomentum (Colombia, *Moncada* 4592); I: thallus section showing upper and lower cortex, photobiont layer and medulla (Colombia, *Moncada* 4936); J: close-up of section showing upper cortex (Colombia, *Moncada* 4592); K: close-up of medulla showing crystals (Colombia, *Moncada* 4592); L: mature apothecia (Colombia, *Moncada* 4592); M: immature apothecium (Colombia, *Moncada* 4936); N: ascus with ascospores (Colombia, *Moncada* 4592); O: ascospores (Colombia, *Moncada* 4936). – Scale bars: E, F = 1 mm; L, M = 0.1 mm; G, I = 100 μ m; H, J, K, N, O = 10 μ m.

(3–)7–15(–20) mm broad. Upper surface smooth to rugose or shallowly scrobiculate, glabrous, without or with scattered papillae, olive when fresh, with various shades of brown when dry, shiny, with lobe margins of same colour and with abundant but usually indistinct, irregular, cream-coloured maculae. Medulla compact, white to cream-coloured, sometimes with yellowish patches, K+ yellow, C–, KC–, P–. Marginal cilia rare, up to 0.5 mm long, agglutinate to fasciculate, dark brown to blackish; tomentum sometimes projecting laterally beyond lobe margins to resemble cilia. Lower surface usually uneven to undulate, dark brown to blackish. Lower tomentum composed of two types; primary tomentum dense up to lobe margins, rather thick and spongy, becoming thinner toward lobe margins, dark brown to blackish brown, composed of fascicles of 12–20 agglutinate, branched and apically intertwined hyphae, 0.2–1 mm long; secondary tomentum appressed to surface, arachnoid, pale, composed of individual, branched, moniliform hyphae 10–35 µm long. Rhizines abundant, developed centrally to submarginally along lobe undersides, fasciculate to squarrose or anziform to hapteriform, dark brown, up to 4 mm long. Cyphellae abundant, about (40–)60–100 per cm² toward periphery and 1–20 per cm² toward centre of thallus, erumpent to prominent or becoming sessile, below level of tomentum, rounded, broadly urceolate, (0.1–)0.3–1(–1.8) mm in diam., with inner, basal membrane somewhat wider and cavity 60–150(–300) µm high; margin light to dark brown or blackish, glabrous; basal membrane white, pubescent, K+ yellow, C–, KC–, P–; cells of basal membrane lacking papillae on outer side.

Upper cortex paraplectenchymatous, 25–45 µm thick, composed of two differentiated strata; upper stratum brownish, composed of a single cell layer, with small, pachydermatous cells 3–5 µm in diam., with their walls 1.3–2.5 µm thick; lower stratum composed of 3–5 cell layers, with larger, leptodermatous cells 6–12 µm in diam., with their walls 0.7–1.3 µm thick. Photobiont a species of *Nostoc* Vaucher ex Bornet & Flahault; photobiont layer 35–75 µm thick, with individual photobiont cells 10–17 µm in diam. Medulla 50–100(–170) µm thick, with individual hyphae 2–2.5 µm broad, interspersed with yellow-orange crystals. Lower cortex paraplectenchymatous, 17–35 µm thick, composed of 2 or 3 cell layers; cells 5–14 µm in diam., with their walls 0.7–2.5 µm thick.

Vegetative propagules (flattened) isidia to phyllidia, formed densely along lobe margins and extending onto lamina, richly branched and becoming palmate to coralloid, up to 1 mm long and 0.5 mm broad, with terminal parts dorsiventrally flattened to squamiform and basal part forming a short, cylindrical stipe, often with cyphellae primordia; phyllidia of same colour as thallus or often somewhat darker on upper side, somewhat paler on underside, nitidous.

Apothecia common, often on thalli lacking vegetative propagules, rarely both developed on same thallus;

apothecia biatorine, mostly submarginal, sometimes laminal or marginal, usually dispersed, sessile to substipitate with pronounced invagination on underside, 2–4 mm in diam. and 0.5–0.6 mm high; disc orange-brown, opaque to slightly shiny; 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 broadly fusiform, 1(–3)-septate, 27–38 × 9–13 µm. Pycnidia immersed.

Etymology — The epithet was selected among the names originally considered for this complex (Moncada & al. 2014), because it best fits the centre of distribution and the ecology of this species.

Distribution and ecology — Naturally distributed across the Neotropics, with its centre in the northern Andes. Given that the records from Hawaii and the Azores represent the same haplotype as one of the common haplotypes present in the Andes, these disjunct records may be the result of recent, perhaps anthropogenic long-distance dispersal. Biogeographic connections between the Neotropics, Hawaii and the Azores have been reported for other lichens and bryophytes, e.g. the *Sticta ciliata* Taylor complex (Magain & Sérusiaux 2015; Mercado-Díaz & al. 2020; Moncada & al. 2021) and the liverworts *Leptoscyphus azoricus* Grolle (Vanderpoorten & Long 2006; Devos & Vanderpoorten 2009) and *Syzygiella rubricaulis* (Nees) Steph. (Maciel-Silva & al. 2016). However, in these cases, the material found in different regions represents distinct lineages and not identical haplotypes as in *S. andina*.

In South America, *Sticta andina* is an upper montane to andine species mostly found above 2500 m elevation and usually confined to well-preserved forest and paramo habitats, typically growing epiphytically on trunks and branches of trees and shrubs. In Hawaii and in the Azores, the species is also found in humid montane forests, although generally at lower altitudes due to a mass elevation effect.

Remarks — *Sticta andina* is one of a number of partially unrelated species that share the *S. weigeli* morphodeme, i.e. associated with a cyanobacterial photobiont and forming marginally isidiate-phyllidiate lobes. From *S. weigeli* s.str. (Galloway 2006; Moncada 2012; Mercado-Díaz & al. 2020), *S. andina* can be differentiated by the often flattened to dorsiventral isidia and phyllidia (vs. consistently cylindrical isidia in *S. weigeli*), the much thicker lower tomentum, the uniformly white cyphellae (vs. partially yellow in *S. weigeli*) and the upper montane versus lower montane-tropical habitat. *Sticta rhizinata* is also similar but can be distinguished by the narrower lobes, the more or less cylindrical, rather dark isidia, the formation of conspicuous, large rhizines on the underside, and the predominant growth on the ground between bryophytes (Moncada

& Lücking 2012). *Sticta scabrosa* (see below) differs by the marginally thinly scabrose lobe surface, the lighter brown phyllidia that are concolorous with the thallus, and the light grey-brown lower tomentum, together with a preferred growth in tropical, often disturbed or anthropogenic habitats.

Additional specimens examined — See Suppl. File S1.

Sticta scabrosa B. Moncada, Merc.-Díaz & Bungartz, **sp. nov.** – MycoBank 836872. – Fig. 3A–O.

Holotype: Colombia, Cesar, Mun. Río de Oro, 08°16'51"N, 73°25'01"W, 1714 m, 15 Oct 2010, B. Moncada 4403 (UDBC; isotype: COL).

– “*Sticta scabrosa*” B. Moncada & Lücking in Moncada, El Género *Sticta* (Schreb.) Ach. en Colombia: Taxonomía, Ecogeografía e Importancia: 172. 2012, nom. inval. (Turland & al. 2018: Art. 29.1, F.5).

Diagnosis — Differing from *Sticta beauvoisii* in the thinly scabrose versus glabrous lobe surface, the formation of dorsiventrally flattened phyllidia instead of cylindrical isidia, and the more greyish lower tomentum.

Description — Thallus forming suborbicular rosettes or becoming irregular, up to 20 cm in diam., frequently branched, with 6–10 branches per 5 cm radius; ramification anisotomous to polytomous. Lobes leathery, flabellate to ligulate with rounded tips, adnate to horizontal, imbricate, undulate to slightly canaliculate; margins entire to shallowly crenate, not thickened; lobe internodes 5–7(–10) mm long, 3–10(–15) mm broad. Upper surface uneven to weakly scrobiculate toward older portions of thallus (subsp. *scabrosa* and subsp. *hawaiiensis* p.p.) to rarely foveolate-pitted toward lobe tips (subsp. *hawaiiensis* p.p.), often sparsely scabrous toward margins, without or rarely with scattered papillae featuring trichomes (subsp. *hawaiiensis* p.p.), olive when fresh, with various shades of brown when dry, usually opaque, with lobe margins of same colour and with usually indistinct, irregular, cream-coloured maculae. Medulla compact, light cream-coloured, K– to K+ pale ochraceous-yellow, C–, KC–, P–. Marginal cilia rare, when present up to 0.5 mm long, fasciculate, pale to golden brown; lower tomentum often protruding beyond margins and then resembling short cilia. Lower surface undulate, pale brown to brownish yellow. Lower tomentum composed of two types; primary tomentum dense but sparser toward lobe margins, rather thick and spongy, becoming thin toward lobe margins, pale to dark grey-brown, composed of fascicles of 6–12 agglutinate, branched and apically intertwined hyphae, 0.2–1 mm long; secondary tomentum appressed to surface, arachnoid, pale, composed of individual, branched, moniliform hyphae 15–25 µm long. Rhizines sparse, dispersed, fasciculate to fibrillose, grey-brown with pale tips, up to 2 mm long. Cyphellae abundant, about 40–60 per cm² toward

periphery and 20–40 per cm² toward centre of thallus, erumpent to prominent, below level of tomentum, rounded, broadly urceolate, (0.3–)0.5–1.2(–1.8) mm in diam., with inner, basal membrane somewhat wider and cavity 90–150(–250) µm high; margin cream-coloured to light brown sometimes with a yellowish tinge, usually tomentose; basal membrane cream-coloured to pale yellowish, pubescent, K+ ochraceous, C–, KC–, P–; cells of basal membrane lacking papillae on outer side.

Upper cortex paraplectenchymatous, 25–30 µm thick, homogeneous, composed of 3 or 4 cell layers, cells 4–12 µm in diam., with their walls 0.7–2.5 µm thick. Photobiont a species of *Nostoc*; photobiont layer 50–70 µm thick, with individual photobiont cells 10–15 µm in diam. Medulla 80–170 µm thick, with individual hyphae 2–2.5 broad, lacking crystals. Lower cortex paraplectenchymatous, 20–30 µm thick, composed of 2 or 3 cell layers; cells 4–12 µm in diam., with their walls 0.7–2.5 µm thick.

Vegetative propagules phyllidia, formed densely along lobe margins but sometimes extending onto lamina, richly branched and becoming palmate to coralloid, up to 0.5 mm long and 0.3 mm broad, with terminal parts dorsiventrally flattened to squamiform and basal part forming a short, flattened stipe, without cyphellae primordia; phyllidia of same colour as thallus or somewhat darker on upper side, somewhat paler on underside, slightly nitidous.

Apothecia not observed. Pycnidia immersed.

Etymology — The epithet refers to the often thinly scabrose lobe surface toward the tips.

Distribution and ecology — *Sticta scabrosa* is widely distributed in the Neotropics, including the Caribbean and the Galapagos Islands (subsp. *scabrosa*) and also found in Hawaii (subsp. *hawaiiensis*, see below). In contrast to *S. andina*, it is a lowland to lower montane, tropical species found both in forest habitats and in disturbed or anthropogenic situations, e.g. on planted trees along roads, sometimes with a weedy character. Both subspecies have a similar ecology (Moncada & al. 2021).

Remarks — Like *Sticta andina*, *S. scabrosa* also corresponds to the *S. weigeli* morphodeme, but is more similar to *S. beauvoisii* than to *S. weigeli* s.str., a species only recently removed from synonymy under *S. weigeli* (McDonald & al. 2003). *Sticta scabrosa* is not closely related to either *S. weigeli* s.str. or *S. beauvoisii* (Moncada & al. 2014; this paper) and differs from the latter in the thinly scabrose versus glabrous lobe surface, the formation of dorsiventrally flattened phyllidia instead of mostly cylindrical isidia, and the more greyish lower tomentum. The two subspecies, subsp. *scabrosa* and subsp. *hawaiiensis*, are morphologically mostly identical, but the latter includes a distinctive lobe surface morphodeme (see below).



Fig. 3. *Sticta scabrosa*, morphology and anatomy. – A–L: *S. scabrosa* subsp. *scabrosa*; M–O: *S. scabrosa* subsp. *hawaiiensis*; A: thallus lobes (Colombia, *Moncada* 4310); B: lobes with phyllidia (Colombia, *Moncada* 4403, holotype); C: phyllidia enlarged (Colombia, *Moncada* 4403, holotype); D: lower tomentum with cyphellae (Colombia, *Moncada* 4403, holotype); E: section showing lower tomentum (Colombia, *Moncada* 4403, holotype); F–O: specimens in situ, in part showing lower tomentum with cyphellae (F: Colombia, Cauca, *Moncada* 7357; G: Costa Rica, *Lücking* 34607; H: Colombia, Cauca, *Moncada* 7366; I–K: Brazil, *Lücking* 40042; L: Brazil, *Lücking* 40087; M–O: Hawaii, *Moncada & al.* 6937, 7011, 7015). – Scale bars: C, D = 1 mm; E = 10 μ m.

Sticta scabrosa subsp. *scabrosa* – Fig. 3A–L.

Diagnosis — Differing from subsp. *hawaiiensis* in two positions in the ITS (see Suppl. File S3), namely position 143 (T > C) and position 401 (T > C). Upper lobe surface smooth to uneven, never pitted.

ITS barcoding marker accession — MT936608, MT936611 (both holotype).

Description — See above.

Distribution and ecology — Widely distributed in the Neotropics, lowlands to lower montane zones, often in exposed situations (Moncada & al. 2021).

Remarks — See above.

Additional specimens examined — See Suppl. File S1.

Sticta scabrosa subsp. *hawaiiensis* B. Moncada, Lücking & C. W. Sm., **subsp. nov.** – MycoBank 836873. – Fig. 3M–O.

Holotype: U.S.A., Hawaii, Oahu, Koolau Range, Manoa Valley, 6 km ENE of Honolulu and 8 km WSW of Kaneohe, Manoa Cliffs Trail, Moleka trailhead to forestry enclosure, 21°19'55"N, 157°48'43"W, 410–575 m, partially disturbed secondary forest with some exposed vegetation and some planted trees, 9 Jun 2013, B. Moncada & al. 6915 (BISH; isotypes: B, F).

Diagnosis — Differing from subsp. *scabrosa* in two positions in the ITS (see Suppl. File S3), namely position 143 (C > T) and position 401 (C > T). Upper lobe surface variable, smooth to uneven but in some forms distinctly foveolate-pitted.

ITS barcoding marker accession — MT132639 (holotype).

Description — See above.

Etymology — The subspecific epithet refers to the geographic distribution of this subspecies.

Distribution and ecology — Restricted to the Hawaiian archipelago, where it has been found on all five major islands (Hawaii or Big Island, Oahu, Molokai, Maui and Kauai). In lowlands to lower montane zones, often in exposed microhabitats (Moncada & al. 2021). Its ecology is the same as in the species as a whole. It is the only taxon of the genus present in Hawaii consistently found in disturbed habitats.

Remarks — *Sticta scabrosa* subsp. *hawaiiensis* is here separated as a formal taxon due to its consistent phylogenetic differences with subsp. *scabrosa*, with a clear geographic

correlation. Because both subspecies cannot be separated morphologically (with exception of the additional lobe surface morphodeme present in Hawaii) and the phylogenetic differences are small (two substitutions out of 550 in a pairwise ITS alignment, i.e. 99.6% similarity; see Suppl. File S3), we consider the rank of subspecies appropriate, to reflect the phylogenetic distinctiveness of this lineage and its geographic distribution in an isolated archipelago distant from the geographic range of subsp. *scabrosa*.

Additional specimens examined — See Suppl. File S1.

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Supplemental content online

See <https://doi.org/10.3372/wi.51.51103>

Suppl. File S1. Voucher table for the specimens of the newly described taxa used in this study. For GenBank accessions of additional species used in the global phylogeny, see Suppl. File S2.

Suppl. File S2. Best-scoring maximum likelihood tree of the largest clade of the genus *Sticta* containing the target taxa, based on the ITS barcoding marker, showing the position of the newly recognized taxa with the *S. weigeli* morphodeme in relation to *S. weigeli* s.str. Branches are thickened relative to support and bootstrap support values are indicated.

Suppl. File S3. Alignment of ITS sequences of *Sticta scabrosa* subsp. *scabrosa* and subsp. *hawaiiensis* (in FASTA format), showing diagnostic differences in positions 143 and 401.

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