

Six new apotheciate species of *Sticta* (lichenized Ascomycota: Lobariaceae) from the Colombian Andes

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Abstract: As part of a phylogenetic and taxonomic revision of the lichenized genus *Sticta* in Colombia, six new species with apotheciate thalli but lacking vegetative propagules are described: *Sticta atroandensis* Moncada & Lücking sp. nov., *S. brevior* Moncada & Lücking sp. nov., *S. lumbschiana* Moncada & Lücking sp. nov., *S. macrocyphellata* Moncada & Coca sp. nov., *S. parahumboldtii* Moncada & Lücking sp. nov., and *S. pseudohumboldtii* Moncada & Lücking sp. nov. The last two are related to *S. humboldtii* but phylogenetically distinct and differ in details of cyphellae morphology and spot reactions. *Sticta atroandensis* is similar to *S. andensis* but has a dark lower tomentum, whereas *S. brevior* belongs in the *S. kunthii* group, being characterized by mainly laminal apothecia with tomentose margins and a rather stout thallus. Both *S. lumbschiana* and *S. macrocyphellata* form part of the *S. dilatata* group and can be characterized by their lobe surface structure and cyphellae anatomy. Keys to species of the *S. dilatata* and *S. humboldtii* groups are presented.

Key words: ITS barcoding gene, lichens, montane rainforest, páramo vegetation, semi-cryptic species

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Introduction

The genus *Sticta* is defined by a unique trait: the cyphellae, well-differentiated ventral pores that facilitate gas exchange (Green *et al.* 1981; Moncada *et al.* 2013a). Its species are characteristic of humid, cool-temperate environments; in tropical latitudes of South America, where they grow luxuriously in easily accessible habitats such as andine páramos (Sipman 1999). Most species are associated with nitrogen-fixing cyanobacteria as primary photobiont and contribute substantially to local nitrogen input (Forman 1975; Green *et al.* 1980, 1993; Green & Lange 1991). Also important is their role in water

cycles, since these lichens are capable of storing up to over 500% of their dry weight as water and can release it over several hours into the neighbouring atmosphere (Green *et al.* 1985; Guzmán *et al.* 1990; Green & Lange 1991; Beckett 1995; Zotz *et al.* 1998; Lange *et al.* 2004). Certain species of *Sticta*, in particular green algal species characteristic of tropical montane rainforests, might be useful as indicators of ecological continuity and environmental health, similar to the *Lobariaceae*, in particular *Lobaria pulmonaria*, in Europe and North America (Scheidegger *et al.* 1995; Zoller *et al.* 2000; Radies *et al.* 2009). The species-rich communities at high altitudes that are mostly associated with cyanobacterial photobionts also appear to be affected by the ongoing destruction of páramo habitats (Luteyn 1999; Crespo *et al.* 2010; De Brieve & Calle 2011).

In his treatment of *Sticta weigeli* s. lat. in eastern North America, Harris (1984) anticipated that the systematics of this supposedly ‘easy’ genus would become more difficult. While Harris (1984) chiefly referred to extra-

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tropical taxa, his assessment also applies to tropical material, since names such as *S. fuliginosa* and *S. weigelii* are commonly applied to tropical montane species. Other groups of species are either restricted to, or are most diverse in, the tropics, such as green-algal species with scrobiculate-faveolate thalli, cyanobacterial forms with apothecia, in particular those with tomentum on the upper surface, and cyanobacterial taxa with isidia and a pale underside (Delise 1825; Nylander 1859, 1865; Joshi & Awasthi 1982; Swinscow & Krog 1988; Chen *et al.* 1994; Galloway 1998a). Yet recent discoveries of new species are rare (e.g., Aptroot 2008; Lumbsch *et al.* 2011). Currently, c. 120 species are accepted (Kirk *et al.* 2008). This is due to the fact that revisionary treatments have focused on extratropical regions (Galloway 1994, 1997, 1998b, 2001; Galloway *et al.* 1995; Galloway & Thomas 2004; Jørgensen & Tønsberg 2007; Makryi 2008), whereas only a few studies exist for tropical taxa (Joshi & Awasthi 1982; Swinscow & Krog 1988; Galloway 1998a; Büdel *et al.* 2000; Aptroot *et al.* 2002; Farkas 2003).

While several recent papers address the phylogeny and genus concepts in *Lobariaceae* (Miądlikowska *et al.* 2002; Thomas *et al.* 2002; Wiklund & Wedin 2003; Stenroos *et al.* 2003; Miądlikowska & Lutzoni 2004; Takahashi *et al.* 2006; Högnabba *et al.* 2009; Magain *et al.* 2012; Moncada *et al.* 2013a), only one study tested morphological species concepts in *Sticta*, focusing on the *S. weigelii* complex (McDonald *et al.* 2003). Reconstruction of phylogenetic affinities focusing on Colombian species, but within a global framework, suggested that phenotypes traditionally treated as within-species variants (Galloway 1994, 1997, 1998b) represent many distinct species (Moncada *et al.* 2013b). As a consequence, the actual number of species to be recognized in *Sticta* at a worldwide level should be revised from 120 up to possibly 500. Many of these are species new to science (Moncada & Lücking 2012; Suárez & Lücking 2013) and in the present paper six of these are described, comprising taxa forming apothecia, mainly in the *S. dilatata* and *S. humboldtii* groups.

Material and Methods

Fresh material for this study was collected during fieldwork in Colombia, Costa Rica and Ecuador, mostly within the framework of a systematic revision of the lichen genus *Sticta* in Colombia (Moncada 2012) and a neotropical workshop project (International Innovation 2012). In addition, we revised a large number of herbarium specimens housed at the Universidad Distrital Francisco José Caldas (UDBC), the National Herbarium of Colombia at the Universidad Nacional (COL), as well as other Colombian herbaria (ANDES, CUBC, FAUC, HUA, SINCHI), the collection at the Instituto Nacional de Biodiversidad in Costa Rica (INB), and collections from several parts of the Neotropics at the Field Museum of Natural History (F), the Botanical Garden & Botanical Museum Berlin-Dahlem (B), and the US National Herbarium at the Smithsonian Museum of Natural History (US). We also examined historical type material at or from BM, F, G, H, and PC. Most specimens were studied at the Universidad Distrital Francisco José Caldas and The Field Museum, using standard techniques of light microscopy and thin-layer chromatography (Orange *et al.* 2001; Lumbsch 2002). We used a standardized protocol of 163 morphological, anatomical, and chemical characters to describe each specimen (Moncada 2012; Moncada *et al.* 2013b). For definition of certain characters used in species delimitation, such as branching pattern, kind of vegetative propagules, tomentum, cyphellae morphology and anatomy, and upper cortex, see Moncada & Lücking (2012).

Results

Sticta atroandensis Moncada & Lücking sp. nov.

Mycobank No.: MB804394

GenBank ITS barcoding sequence:
KC732533

Differing from *Sticta andensis* in the dark, brown-black lower tomentum and the glabrous apothecial margin.

Type: Colombia, Boyacá, Mun. El Cocuy, Parque Nacional Natural El Cocuy, Valle de las Lagunillas, Cabaña Sisuma, 6°26'N, 72°22'O, 3800 m, 19 April 2011, D. Fonseca & F. Martínez 23 (UDBC—holotype; COL—isotype).

(Fig. 1)

Primary photobiont cyanobacterial (*Nostoc*). *Basal stipe* absent. *Thallus* orbicular, up to 10 cm diam., sparsely branched, with 0–2 branches for every 5 cm of radius, branching pattern polytomous. *Lobes* suborbicular, horizontal, imbricate, plane to slightly involute, with their tips rounded and plane to slightly involute and their margins entire, not thickened; lobe internodes (10–)20–30(–40) mm

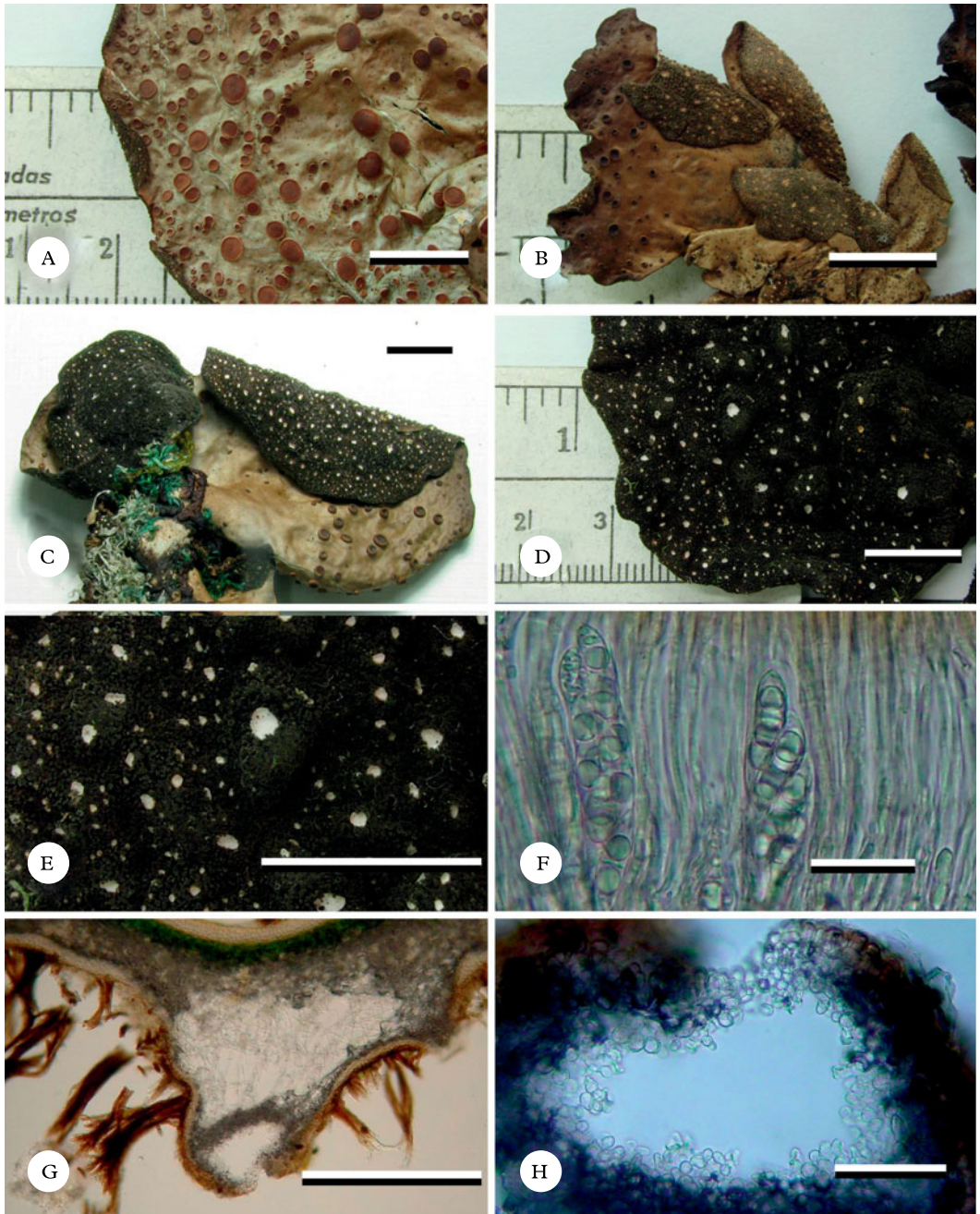


FIG. 1. *Sticta atroandensis* (holotype). A, dorsal view of lobe with numerous apothecia; B & C, thallus lobes with ventral and dorsal view; D & E, ventral view of undulate surface and dark tomentum with suprasessile cyphellae; F, hymenium and asci with ascospores; G, section through suprasessile cyphella; H, section through cyphella cavity showing details of cells of basal membrane. Scales: A–E = 10 mm; F = 20 μ m; G = 500 μ m; H = 100 μ m. In colour online.

long, (20–)25–70(–100) mm wide, coriaceous. *Upper surface* scrobiculate to strongly scrobiculate, olive-green when fresh, brown-grey to dark brown in the herbarium, glossy, the marginal line concolourous to slightly paler; surface glabrous, without papillae, without pruina, with irregular, sparse, cream-coloured maculae. *True marginal cilia* absent but projections of lower tomentum resembling cilia usually present. *Vegetative propagules* absent. *Medulla* compact, white, K–, C–, KC–, P–. *Lower surface* undulate, beige to dark brown to almost black towards the centre. *Primary lower tomentum* dense and thick, sparse and thinner towards the margin, spongy, soft, brown-black. *Secondary lower tomentum* pubescent to arachnoid, pale. *Rhizines* absent. *Cyphellae* abundant, 1–20 per cm² towards the thallus centre and 41–60 per cm² towards the margin, dispersed, rounded, urceolate, sessile to suprasessile, below the level of the primary tomentum, with the margin raised and involute to revolute, brown to brown-black, without tomentum; pore (0.2–)0.7–1.0(–1.5) mm diam. towards the thallus centre; basal membrane pubescent, white to cream-coloured or yellowish, K–, C–, KC–, P–.

Upper cortex paraplectenchymatous, 30–40 µm thick, uniform, formed of 4–5 cell layers, 5–10 µm diam., cell walls 1.25–2.50 µm thick and cell lumina rounded to isodiametric, 4.0–7.5 µm diam. *Photobiont layer* 45–75 µm thick, cells 10–15 µm diam. *Medulla* 40–150 µm thick, medullary hyphae 2.5 µm wide, without crystals. *Lower cortex* paraplectenchymatous, 20–35 µm thick, formed of 3–4 cell layers; cells 4–12 µm diam., cell walls 1.25–2.50 µm thick. *Lower primary tomentum* 240–550 µm long, composed of fascicles formed of 12–20 hyphae, hyphae branched, septate with their tips interwoven. *Lower secondary tomentum* 17–25 µm long, composed of simple, septate hyphae with their tips free. *Cavity of the cyphellae* 40–220 µm high; cells of basal membrane without papillae.

Apothecia abundant, laminal, dispersed, subpedicellate, basal invagination pronounced, up to 3 mm diam., biatorine, up to 370 µm high, with indistinct stipe; *excipulum* up to

115 µm thick; *disc* orange-red to red-brown, glossy, K–; margin entire to slightly verrucose, cream-coloured to beige. *Hymenium* up to 105 µm high; *epihymenium* up to 2.5 µm high, orange, K–. *Ascospores* hyaline, 30–35 × 7–8 µm, fusiform, with 1–3 septa.

Pycnidia immersed.

Chemistry. No substances detected by TLC.

Etymology. The epithet of this new species refers to the similarity with *Sticta andensis*, from which it differs chiefly in the dark lower tomentum, as well as the glabrous apothecial margins.

Ecology and distribution. Colombian Andes. *Sticta atroandensis* appears to be restricted to the páramo and superpáramo life zones and was found on the western slopes of the Cordillera Central and in the Cordillera Oriental, between 3600 and 4800 m (Rangel-Ch. 1995, 2000; Rodríguez *et al.* 2006; Moncada *et al.* 2013c). It is epiphytic in semi-exposed to exposed microsites and is generally associated with liverworts of the genus *Metzgeria* and the family *Lejeuneaceae*.

Notes. *Sticta atroandensis* is a broad-lobed, cyanobacterial species with scrobiculate, otherwise glabrous, upper surface lacking true marginal cilia, conspicuous cyphellae, abundant apothecia, lacking vegetative propagules, and is best characterized by its dark underside. No other species in Colombia has this combination of characters. Most similar are *S. andensis* Nyl. and *S. ambavillaria* (Bory) Ach. (Acharius 1810; Galloway 1995). *Sticta andensis*, also described from Colombia (Nylander in Stizenberger 1895), is mainly distinguished by the pale lower tomentum and the pubescent apothecial margins, whereas the African *S. ambavillaria* (Swinscow & Krog 1988; Galloway 1995) has a generally thinner, fragile thallus (when dry) with pale lower tomentum and marginally ciliate apothecia (at least when young). Other cyanobacterial species with apothecia and a dark brown lower side, such as *S. paramuna* Moncada & Lüicking and relatives, can be distinguished by their narrower, irregular lobes with mostly smooth surfaces, corresponding

to apotheciate forms of the *S. weigelii* morphodeme (B. Moncada, A. Suárez, A. & R. Lücking, unpublished data). The difference in the colour of the lower tomentum between *S. andensis* and *S. atroandensis* is consistent in the material studied and is supported as a diagnostic character by the phylogenetic placement of both species, as well as by the fact that larger clades within *Sticta* are often uniformly characterized by an either pale or dark lower tomentum (Moncada et al. 2013b).

Additional specimens examined. **Colombia:** Boyacá: Mun. El Cocuy, Parque Nacional Natural El Cocuy, Valle de las Lagunillas, Cabaña Sisuma, 06°26'24"N, 72°22'18.16"W, 3800 m, 2 vii 2010, F. Martínez s. n. (UDBC); *ibid.*, 3800 m, 2011, D. Fonseca & F. Martínez 21, 23, 29a, 29b, 30, 32, 35, 40, 42, 45, 59, 61, 79, 85 (UDBC); sendero Cabaña Sisuma to Pico Pan de Azúcar, 3800–4800 m, 2011, D. Fonseca & F. Martínez 97, 99, 112 (UDBC); Alto de la Cueva, 3800 m, 2011, D. Fonseca & F. Martínez 135, 179, 183, 188b, 238 (UDBC). **Cundinamarca:** Mun. Bogotá D.C., Parque Nacional Natural Sumapaz, Corregimiento Nazareth, sector Andabobos, 3610 m, 2004, B. Moncada & R. Dávila 2266 (UDBC); *ibid.*, 3610 m, 2005, B. Moncada & R. Dávila 2353 (UDBC). **Risaralda:** Mun. Pereira, Parque Nacional Natural Los Nevados, Laguna de Otún, 3975 m, 1980, T. Boekhout 10 (B, COL); *ibid.*, 3930 m, 1980, T. Boekhout 175 (COL); Mun. Santa Rosa de Cabal, Volcán de Santa Rosa, 3975 m, 1980, T. Boekhout 26 (COL).

***Sticta brevior* Moncada & Lücking sp. nov.**

MycoBank No.: MB804395

Differing from *Sticta impressula* in the tomentose-pubescent rather than hirsute apothecial margins with a beige to pale brown colour.

Type: Colombia, Huila, Mun. La Plata, Vereda La Candelaria, cascada del Río La Candelaria, 2300 m, 6 October 1984, J. Aguirre & H. Sipman 6134 (B—holotype; COL—isotype).

(Fig. 2)

Primary photobiont cyanobacterial (*Nostoc*). *Basal stipe* absent. *Thallus* irregular to palmate, up to 5 cm diam., moderately branched, with 3–5 branches per 5 cm of radius, branching pattern polytomous to pleurotomous. *Lobes* flabellate, horizontal to slightly ascendent, imbricate, undulate to involute, with their tips rounded and plane to undulate and their margins entire to sinuous and slightly thickened; lobe internodes (6–)10–13(–15) mm

long, (2–)10–25(–30) mm wide, coriaceous. *Upper surface* pitted (foveolate) to centrally rugose, dark olive when fresh, pale brown to reddish brown and darker towards the tips in the herbarium, glossy, the marginal line darker; surface glabrous, without or with sparse papillae and sometimes with papillotrichomes towards the tips, without pruina, with irregular, abundant, cream-coloured maculae. *True marginal cilia* abundant, sometimes resembling projections of the lower tomentum, fasciculate, golden beige-brown, up to 0.5 mm long. *Vegetative propagules* absent. *Medulla* slightly compacted, white to cream-coloured, K+ pale yellow, C–, KC–, P–. *Lower surface* undulate, white to cream-coloured to pale brown. *Primary lower tomentum* dense up to the margin, thick but thinner towards the margin, spongy, soft, greyish beige to chocolate brown towards the centre. *Secondary lower tomentum* absent. *Rhizines* absent. *Cyphellae* abundant, 21–40 per cm² towards the thallus centre and 61–100 per cm² towards the margin, dispersed, rounded to angular, urceolate with wide pore, erumpent to suprasessile, below the level of the primary tomentum, with the margin raised and involute to erect, white to cream-coloured to dark brown, without tomentum; pore (0–3–)0.5–0.8(–1.25) mm diam. towards the thallus centre; basal membrane pubescent, white, K+ pale yellow, C–, KC–, P–.

Upper cortex paraplectenchymatous, 20–28 µm thick, uniform, formed of 2–3 cell layers, cells 4–14 µm diam., cell walls 1.25 µm thick and cell lumina rounded to isodiametric, 2.5–12.0 µm diam. *Photobiont layer* 45–65 µm thick, cells 10–18 µm diam. *Medulla* 35–125 µm thick, medullary hyphae 2.5 µm wide, without crystals. *Lower cortex* paraplectenchymatous, 17–30 µm thick, with 2–3 cell layers; cells 5–14 µm diam., cell walls 0.6–2.5 µm thick. *Lower primary tomentum* 80–600 µm long, formed of fascicles of more than 20 hyphae, hyphae branched, septate with their tips interwoven. *Cavity of the cyphellae* 100–180 µm high; cells of basal membrane with one papilla each.

Apothecia abundant, principally laminal, dispersed, pedicellate, basal invagination pronounced, up to 3 mm diam.; biatorine, up to

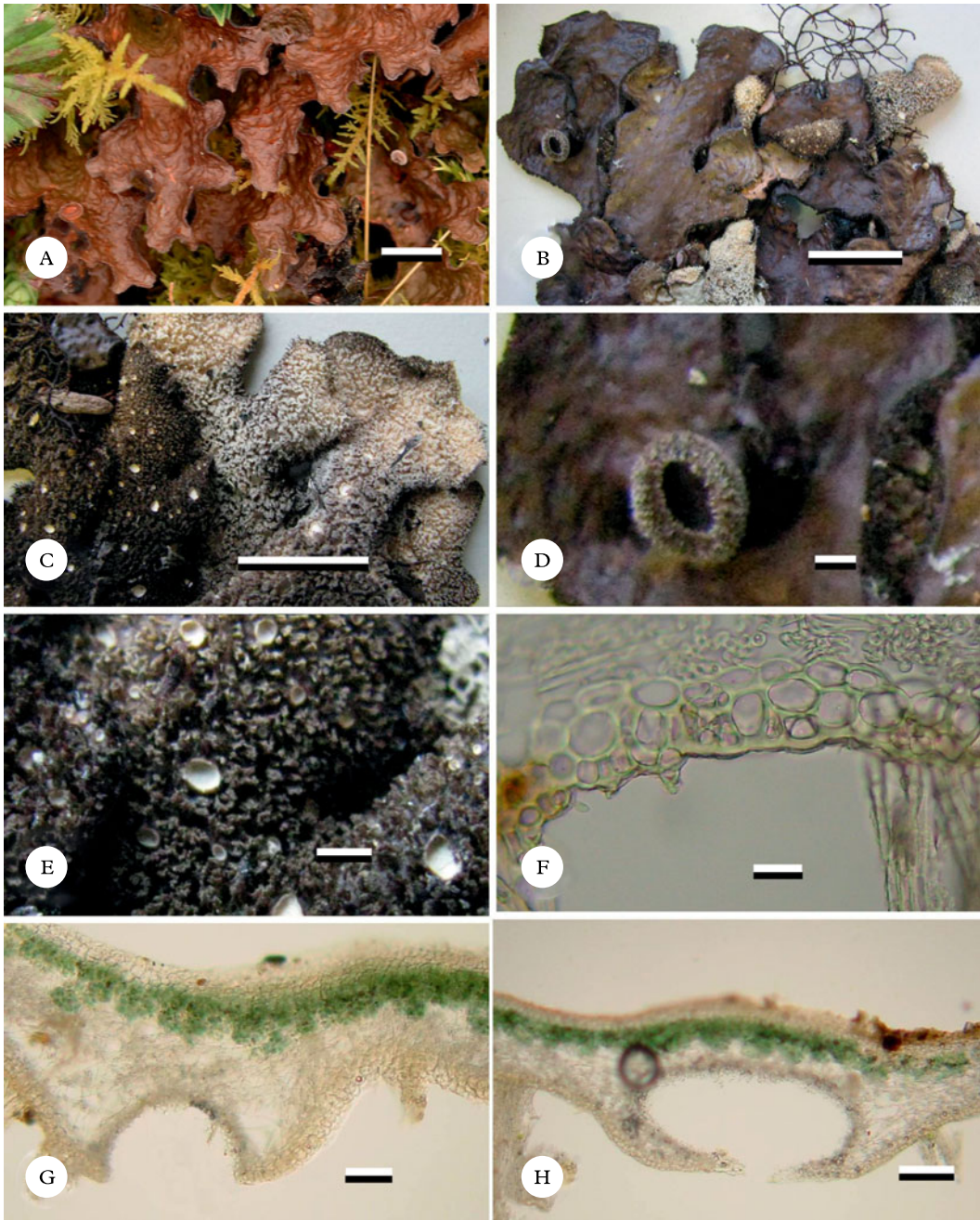


FIG. 2. *Sticta brevior* (holotype except A). A, thallus *in situ* (Lücking 34041); B, dorsal view of thallus in the herbarium; C, ventral view of thallus with tomentum; D, detail of apothecium with tomentose margin; E, detail of ventral tomentum and cyphellae; F, section through lower cortex and tomentum; G & H, sections through cyphellae.

Scales: A–C = 10 mm; D & E = 1 mm; F = 10 μ m; G = 50 μ m; H = 100 μ m. In colour online.

600 µm high, with distinct stipe; *disc* reddish orange to reddish brown, glossy, K–; margin tomentose, pubescent to shortly hirsute, with abundant, cream-coloured trichomes that remain in mature apothecia except for the upper margin bordering the disc which appears crenulate and glabrous. *Excipulum* up to 125 µm wide, with tomentum. *Hymenium* up to 125 µm high; *epihymenium* up to 2.5 µm high, orange-brown, K–. *Ascospores* hyaline, 30–40 × 7–8 µm, fusiform, with 1–3 septa.

Pycnidia immersed.

Etymology. This new species includes a specimen (*Lindig* 2548) previously studied by Nylander (1863) and compared to *S. lenormandii* as follows: “*Forma brevior, thallo brevior, datur and Choachi, altit. 2600 metr., in coll. Lindig. 2548*”. We took the adjective ‘brevior’ up as epithet. One could possibly interpret Nylander’s (1863: 18) text as a formal description of a new taxon, in which case the epithet ‘brevior’ could be elevated to species level, with Nylander as basionym author. However, on the same page, Nylander (1863: 18) establishes *f. laevis* of *S. lenormandii*, with a very different formatting style (including setting the epithet *laevis* in italics), suggesting that “*Forma brevior...*” denotes an informal description of a deviating specimen and not a formal taxon. A different interpretation of Nylander’s statement does not affect the validity of the new species name introduced here.

Ecology and distribution. Colombian Andes. The species was found between 2300 and 3600 m in (sub-)andine forests bordering páramo vegetation in usually semi-exposed microsites. It is known from the Cordillera Central and the Cordillera Occidental in sub-andine, andine and páramo regions (Rangel-Ch. 1995, 2000; Rodríguez *et al.* 2006; Moncada *et al.* 2013c), and grows mostly as an epiphyte, more rarely on the ground; it is often associated with liverworts of the family *Lejeuneaceae* and the genera *Frullania* and *Jubula*, as well as *Sphagnum* mosses. It may also grow close to the ground on *Blechnum* ferns.

Notes. *Sticta brevior* belongs to the *S. kunthii* group, which includes a number of closely related, cyanobacterial, mostly apotheciate species with rather broad lobes with pitted upper surface and pale underside, forming one papilla per cell on basal membranes of the cyphellae (Moncada 2012; Moncada *et al.* 2013b). The species in this group are mostly separated by the position of the apothecia and the nature of the tomentum on the apothecial margins. *Sticta brevior* has generally laminal apothecia with irregular marginal tomentum and a coriaceous, rather stout thallus, whereas *S. lenormandii* (Nyl.) Zahlbr., a Peruvian species (Nylander 1858, 1859, 1860), has a distinctly hirsute marginal tomentum and a less robust, more spreading thallus.

Additional specimens examined. **Colombia:** *Cauca:* Mun. Puracé, Carretera La Plata to Puracé, 3300 m, 1984, *J. Aguirre & H. Sipman* 6017 (B, COL). *Cundinamarca:* Mun. Choachi, 2600 m, 1860, *Lindig* 2548 (PC); Mun. Choachi, El Verjón, Parque Ecológico Matarredonda, 04°33′08.0″N, 73°59′55.0″W, 3220 m, 2011, *B. Moncada* 4590b (UDBC); without locality, *Lindig* 2584 (BM); Mun. La Calera, Zona de amortiguación Parque Nacional Natural Chingaza, Via del Ángulo al Rincón del Oso, 3600 m, 2011, *B. Moncada* 4971, 4988, 4990 (UDBC); Mun. San Bernardo, La Soledad, costado occidental del filo de Paquiló, 2900 m, 1981, *J. Aguirre* 2388 (COL); Mun. Villapinzón, Páramo de Villapinzón, 3300 m, 2002, *M. Pinzón* 1375 (COL). *Huila:* Mun. La Plata, Vereda La Candelaria, cascada del Río La Candelaria, 2300 m, 1984, *J. Aguirre & H. Sipman* 6134 (B, COL).

***Sticta lumbschiana* Moncada & Lüicking sp. nov.**

Mycobank No.: MB804396

GenBank ITS barcoding sequence:
KC732575

Differing from *Sticta dilatata* in the shorter stipe, the tomentose apothecial margin and the cells in the basal membrane of the cyphellae forming only one papilla per cell.

Type: Colombia, Cundinamarca, Mun. Guasca, Páramo de Guasca, 3200 m, 18 August 2011, *R. Lüicking* 33370 (UDBD—holotype; F—isotype).

(Fig. 3)

Primary photobiont cyanobacterial (*Nostoc*). *Basal stipe* indistinct, up to 5 mm long. *Thallus* palmate to irregular, up to 15 cm diam.,

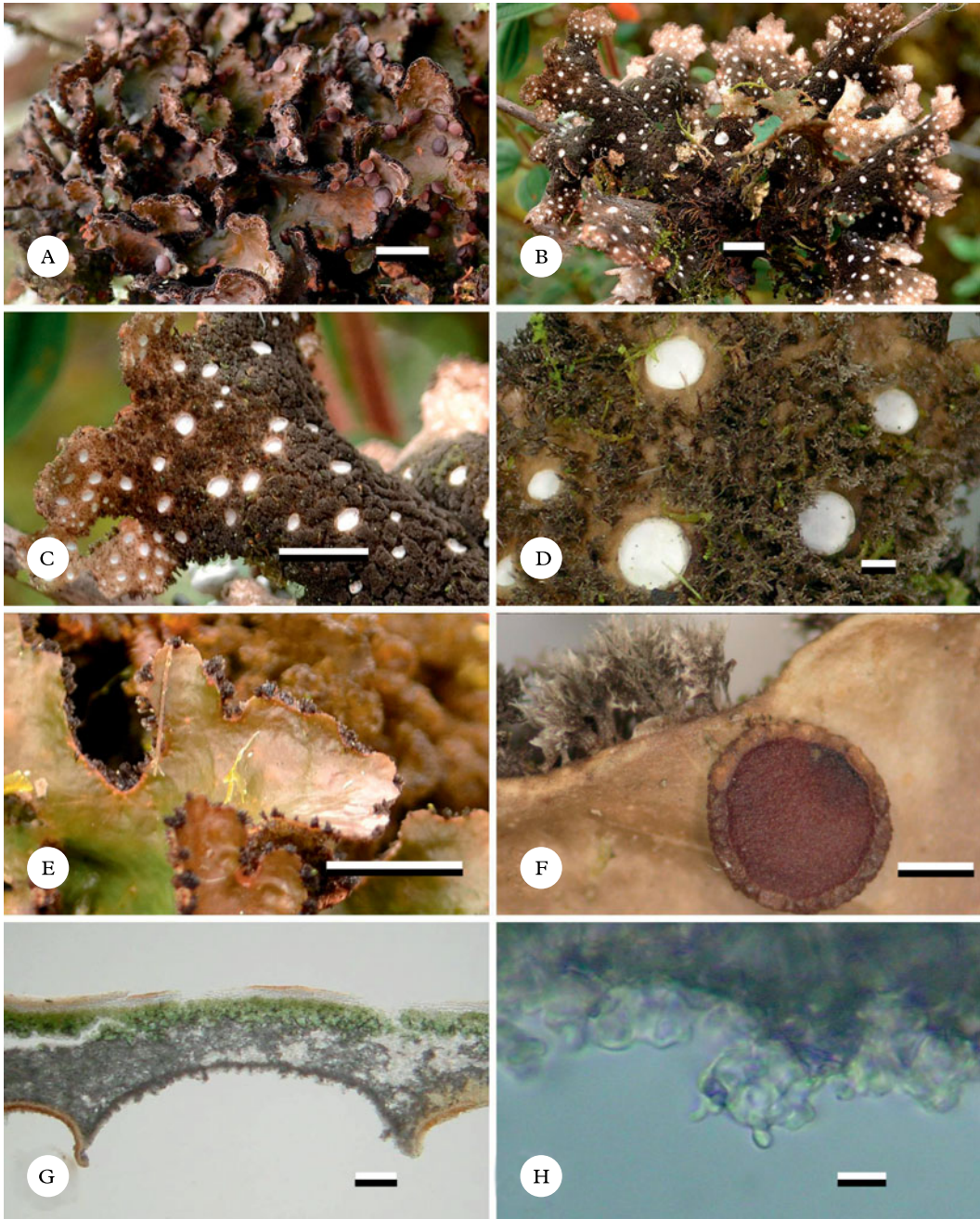


FIG. 3. *Sticta lumbschiana* (A–E, Lücking 34051; F–H, Lücking 33364). A, thallus *in situ*; B–D, ventral view of thallus *in situ* showing detail of tomentum and cyphellae; E, lobe detail showing penicillate cilia; F, lobe in the herbarium, enlarged showing apothecium and marginal, penicillate cilia; G, section through cyphella; H, papillate cells of basal membrane showing single papilla per cell. Scales: A–C & E = 10 mm; D & F = 1 mm; G = 100 μm ; H = 10 μm .
In colour online.

moderately branched, with 3–5 branches for every 5 cm of radius, branching pattern polytomous to anisotomous. *Lobes* lacinate to flabellate, ascendant to erect, adjacent to imbricate, involute to slightly canaliculate, with their tips rounded and involute and their margins entire to crenate, not thickened; lobe internodes (6–)8–13(–15) mm long, (5–)7–20(–25) mm wide, coriaceous, fragile. *Upper surface* smooth to scrobiculate towards the tips, dark olive when fresh, reddish brown and darker towards the tips in the herbarium, glossy, the marginal line concolourous to brown-black; surface glabrous, without papillae, without pruina, with irregular, abundant, cream-coloured maculae. *True marginal cilia* abundant, penicillate to agglutinate, dark greyish brown, up to 1.5 mm long. *Vegetative propagules* absent. *Medulla* compact, white to cream-coloured, K+ ochraceous-yellow, C–, KC–, P–. *Lower surface* smooth to slightly undulate, beige to brown-black towards the centre. *Primary lower tomentum* dense and thick but sparse and thinner towards the margin, spongy to penicillate, soft, greyish to reddish brown with their tips white. *Secondary lower tomentum* arachnoid, pale, sometimes indistinct. *Rhizines* absent. *Cyphellae* abundant, 1–10 per cm² towards the thallus centre and 21–40 per cm² towards the margin, dispersed, rounded, cupuliform to urceolate with wide pore, erumpent to sessile, below the level of the primary tomentum, with the margin raised to slightly involute, white to cream-coloured, without tomentum; pore (1.0–)1.25–2.50(–3.0) mm diam. towards the thallus centre; basal membrane pubescent, white, K+ yellow, C–, KC–, P–.

Upper cortex paraplectenchymatous, 35–45 µm thick, differentiated into two layers: upper layer formed of 1–2 cell layers, of 3–5 µm diam., cell walls 2.5 µm thick and cell lumina rounded to isodiametric, 1.25–2.50 µm diam.; lower layer formed of 3–4 cell layers; cells 5–11 µm diam., cell walls 0.60–1.25 µm thick and cell lumina rounded to isodiametric, 5–10 µm diam. *Photobiont layer* 75–100 µm thick, cells 10–25 µm diam. *Medulla* 110–200 µm thick, medullary hyphae 2.5 µm wide, without crystals. *Lower cortex* paraplectenchymatous, 20–25 µm thick, with 2–3 cell

layers; cells 5–11 µm diam., cell walls 0.6–2.5 µm thick. *Lower primary tomentum* 160–650 µm long, formed of fascicles of more than 20 hyphae, hyphae simple, septate with their tips interwoven. *Lower secondary tomentum* 12–25 µm long, of single hyphae, hyphae branched, moniliform with their tips free. *Cavity of the cyphellae* 90–280 µm high; cells of basal membrane with one papilla per cell. *Apothecia* abundant, biatorine, up to 380 µm high, with indistinct stipe; principally submarginal, dispersed, subpedicellate, basal invagination pronounced, up to 3 mm diam.; *disc* reddish brown, glossy, K–; margin entire to tomentose, tomentum short-pubescent, with sparse larger trichomes, dark brown, evanescent in mature apothecia. *Excipulum* up to 120 µm thick. *Hymenium* up to 125 µm high; *epihymenium* up to 2.5 µm high, orange-brown, K–. *Ascospores* hyaline, 30–40 × 6–8 µm, fusiform, with 1–3 septa.

Pycnidia absent.

Etymology. It is an honour for us to name this new species after our colleague Thorsten Lumbsch, outstanding lichenologist and mycologist, for his invaluable contributions to lichenology and his support of this project on the genus *Sticta*.

Ecology and distribution. Colombian Andes. The species is known from 2100 to 3750 m altitude in (sub-)andine forests and páramo vegetation, in (semi-)exposed microsites. It was found in the Cordillera Central and the eastern slopes of the Cordillera Oriental (Rangel-Ch. 1995, 2000; Rodríguez *et al.* 2006; Moncada *et al.* 2013c). *Sticta lumb-schiana* grows on bark, fallen trunks and occasionally on soil, generally associated with liverworts of the genera *Metzgeria*, *Bazzania*, *Plagiochila* and *Radula*.

Notes. This species, as well as the following one, belongs to the *S. dilatata* group, characterized by pedunculate, much branched thalli having rather narrow, distinctly ciliate lobes that produce very large and conspicuous cyphellae with papillae on the basal membranes (Moncada 2012). The latter character is very consistent and characterizes entire clades within *Sticta* (Moncada *et al.* 2013b).

The name *S. dilatata* (Nyl.) Vain. is misapplied in the literature. Zahlbruckner (1925) indicated that Vainio (1913) based his combination on *S. laciniata* var. *dilatata* Nyl., a taxon described from Colombia that was later renamed *S. granatensis* Nyl. (Nylander 1874). However, Vainio (1913) based his combination on a different, morphologically and phylogenetically unrelated lichen, *S. tomentosa* var. *dilatata* Nyl., also described from Colombia (Nylander 1860).

The most distinctive feature of *S. lumbschii* is the presence of one papilla per cell of the basal membrane of the cyphellae, whereas other species in this group have more than one papilla. It also has a shorter stipe and narrower lobes than *S. dilatata*, and the lobes are slightly scrobiculate; furthermore, its apothecia have a tomentose margin, at least when young (see also key below).

Additional specimens examined. Colombia: Antioquia: Mun. Medellín, Estación Forestal Piedras Blancas, 2100 m, 8 viii 1980, R. Bernal & G. Galeano s. n. (COL). *Cundinamarca:* Mun. Choachí, El Verjón. P. E. Matarredonda, 04°33'08.0"N, 73°59'55.0"W, 3220 m, 2011, B. Moncada 4587c (UDBC); Mun. Guasca, Páramo de Guasca, 3200 m, 2011, R. Lücking 33364b, 33364, 34038, 34051 (F, UDBC); Mun. La Calera, Zona de Amortiguación Parque Nacional Natural Chingaza, Vía del Ángulo al Rincón del Oso, 3600 m, 2011, B. Moncada 4994, 4995 (UDBC); *ibid.*, R. Lücking 34038, 34051 (F, UDBC). *Nariño:* Mun. La Cruz, La Estancia, sector Loma larga, 3310 m, 2001, S. L. Díaz 1980b (CAUP, COL). *Risaralda:* Mun. Santa Rosa de Cabal, Costado Occidental, Cordillera Central, 1 km NE de la Finca la Sierra, 3750 m, 1984, J. Aguirre & H. Sipman 5518, 5522 (B, COL).

***Sticta macrocyphellata* Moncada & Coca sp. nov.**

Mycobank No.: MB804397

GenBank ITS barcoding sequence:
KC732662

Differing from *Sticta silverstonii* in the smooth upper surface and the cells of the membrane of the cyphellae having 2–4 papillae per cell.

Type: Colombia, Risaralda, Mun. Santuario, Parque Nacional Natural Tatamá, Planes de San Rafael, towards Monte Zancudo, 2800 m, 14 January 2011, L. F. Coca et al. 1267 (FAUC—holotype).

(Fig. 4)

Primary photobiont cyanobacterial (*Nostoc*). *Basal stipe* absent. Thallus irregular, up to 10 cm diam., much branched, with 6–10

branches for every 5 cm of radius, branching pleurotomous. *Lobes* lacinate to ligulate, horizontal to slightly ascendent, adjacent to slightly imbricate, plane to slightly canaliculate, with their tips rounded to truncate and plane to revolute and their margins entire to sinuose, not thickened; lobe internodes (3–)4–8(–12) mm long, (3–)5–9(–10) mm wide, subcoriaceous, fragile. *Upper surface* smooth to shallowly scrobiculate, dark olive when fresh, pale cinnamon brown and darker towards the tips in the herbarium, glossy, the marginal line brown; surface glabrous, without papillae, without pruina, with punctiform, abundant, cream-coloured maculae. *True marginal cilia* abundant, penicillate, golden brown to brown-black with their tips free, up to 2 mm long. *Vegetative propagules* absent. *Medulla* lax, cream-coloured, K+ ochraceous-yellow, C–, KC–, P–. *Lower surface* smooth, beige to dark brown, glossy. *Primary lower tomentum* sparse, thick, spongy to arachnoid, soft, dark brown with paler tips. *Secondary lower tomentum* absent. *Rhizines* absent. *Cyphellae* abundant, 1–10 per cm² towards the thallus centre and 21–40 per cm² towards the margin, dense, rounded, urceolate with wide pore to cupuliform, immersed to prominent, below the level of the primary tomentum, with the margin raised and involute to erect, cream-coloured to black, without tomentum; pore (0.7–)1.0–1.5(–2.5) mm diam. towards the thallus centre; basal membrane pruinose, cream-coloured to yellow, K– to K+ vine red in cyphellae with yellow colour, C–, KC–, P–.

Upper cortex paraplectenchymatous, 50–60 µm thick, differentiated into two layers: upper layer formed of 1–2 cell layers, 3–5 µm diam., cell walls 2.5 µm thick and cell lumina rounded to isodiametric, 1.25–2.50 µm diam.; lower layer formed of 2–3 cell layers; cells 6–16 µm diam., cell walls 1.25 µm thick and cell lumina rounded to isodiametric, 5–15 µm diam. *Photobiont layer* 25–37 µm thick, cells 10–15 µm diam. *Medulla* 65–140 µm thick, medullary hyphae 2.5 µm wide, with yellow crystals. *Lower cortex* paraplectenchymatous, 20–25 µm thick, with 2–3 cell layers; cells 6–13 µm diam., cell walls 1.25–2.50 µm thick. *Lower primary tomentum* 25–550 µm long, composed of

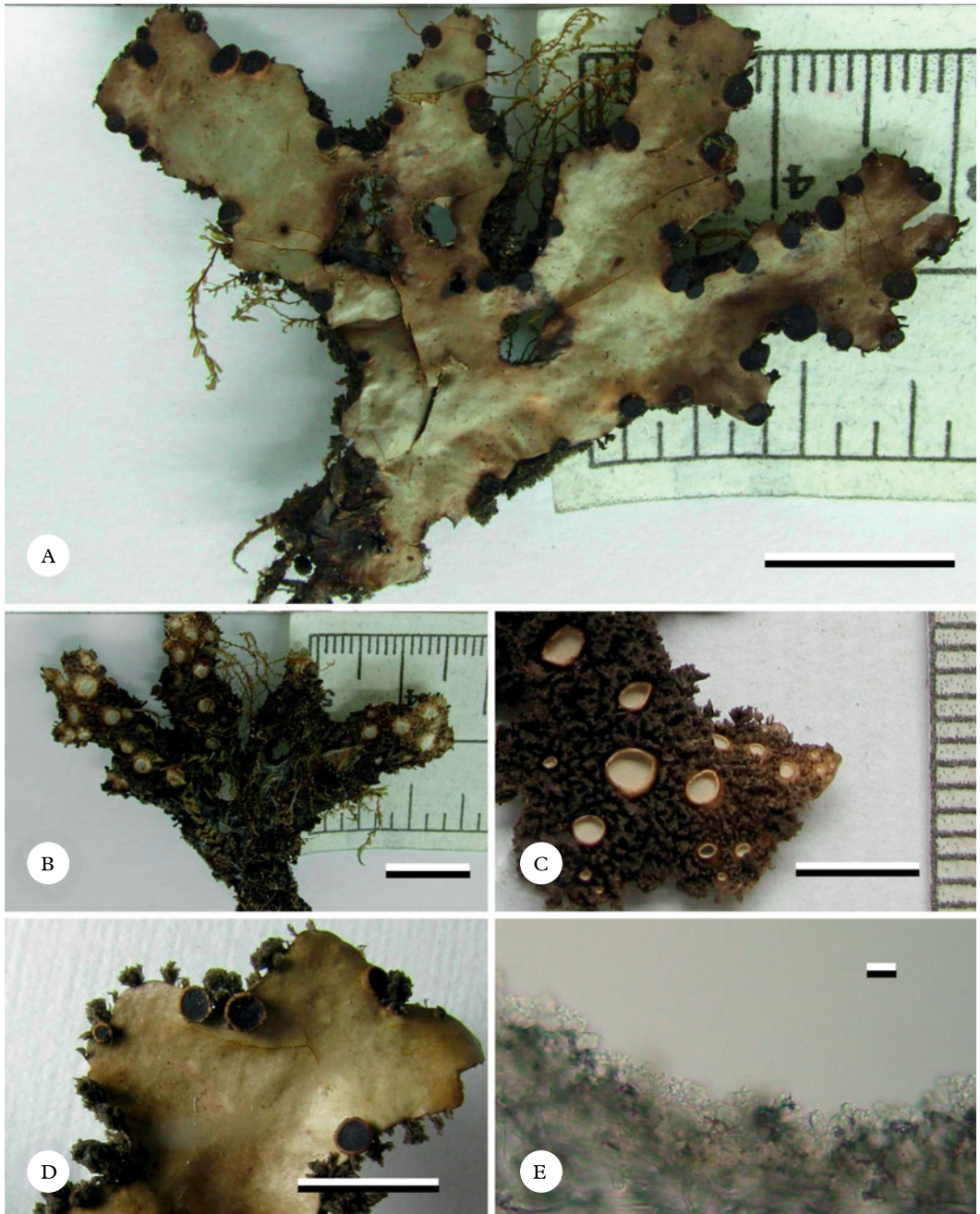


FIG. 4. *Sticta macrocyphellata* (holotype). A, dorsal view of thallus; B, ventral view of thallus; C, detail showing lower tomentum and cyphellae; D, lobe detail showing apothecia and penicillate marginal cilia; E, papillate cells of basal membrane showing several papillae per cell. Scales: A & B = 10 mm; C & D = 5 mm; E = 10 μ m. In colour online.

fascicles formed of 12–20 hyphae, hyphae branched, septate with their tips interwoven. *Cavity of the cyphellae* 40–270 µm high; cells of basal membrane with 4–6 papillae each.

Apothecia abundant, principally laminal, dispersed, biatorine, up to 380 µm high, with indistinct stipe; subpedicellate, basal invagination pronounced, up to 2 mm diam.; *disc* reddish brown to brown-black when mature, glossy, K–; margin entire to ciliate, cream-coloured to dark brown when mature. *Excipulum* up to 130 µm thick. *Hymenium* up to 135 µm high; *epihymenium* up to 2.5 µm high, orange-brown, K–. *Ascospores* hyaline, 30–40 × 7–9 µm, fusiform, with 1–3 septa.

Pycnidia immersed.

Etymology. The epithet refers to the dense, large cyphellae prominent over much of the underside.

Ecology and distribution. Colombian Andes. *Sticta macrocyphellata* was found between 2200 and 3400 m in subandine to andine forests in semi-exposed microsites. It is known from the Cordillera Oriental, the eastern slopes of the Cordillera Occidental and the western slopes of the Cordillera Central (Rangel-Ch. 1995, 2000; Rodríguez *et al.*

2006; Moncada *et al.* 2013c). The species grows on bark and rocks, often associated with bryophytes of the genera *Plagiochila*, *Lophocolea*, *Bazzania*, *Omphalanthus* and *Macromitrium*.

Notes. Like the preceding species, *Sticta macrocyphellata* belongs to the *S. dilatata* group, being characterized by rather narrow, distinctly ciliate lobes, large cyphellae, and cells of basal membrane of the cyphellae forming papillae (Moncada 2012; Moncada *et al.* 2013b). It is most similar to *S. silverstonii* Moncada & Lücking, which differs in the distinctly ampullate upper surface (Moncada & Lücking 2012). The five species currently known in the *S. dilatata* group are separated in the key below.

Additional specimens examined. **Colombia:** *Cundinamarca:* Mun. San Bernardo, La Soledad, W slope of Filo de Paquiló, 2900 m, 1981, *J. Aguirre* 2385 (COL). *Magdalena:* Mun. Santa Marta, Sierra Nevada de Santa Marta, Transecto Buritaca, 2700 m, 1977, *G. van Reenen & O. Rangel* 294 (B, COL, U). *Meta:* Mun. Cubarral, Parque Nacional Natural Sumapáz, Cerro Nevado del Sumapaz, Quebrada El Buque, 3400 m, 1973, *A. M. Cleef* 7788 (B, COL, U). *Risaralda:* Mun. Santa Rosa de Cabal, Vereda El Cedral, vía El Cedral, Laguna del Otún, 2200 m, 2003, *B. Moncada & R. Dávila* 1976 (UDBC).

Key to species of the *Sticta dilatata* group

- 1 Upper surface ampullate (caused by ‘imprint’ of cyphellae from lower surface); marginal cilia simple to fasciculate; cyphellae covering almost entire lower surface; apothecia principally marginal ***Sticta silverstonii***
- Upper surface plane; marginal cilia always penicillate to fasciculate; cyphellae separated by narrow areas of tomentum; apothecia laminal to submarginal 2
- 2(1) Basal membrane of cyphellae with only 1 papilla per cell; lobe surface scrobiculate towards the tips; cyphellae up to 3 mm wide ***Sticta lumbschiana***
- Basal membrane of cyphellae with 4–6 papillae per cell; lobe surface plane to shallowly scrobiculate towards the tips; cyphellae up to 1.5 mm wide, if wider (up to 2.5 mm), then lobe surface plane 3
- 3(2) Lobes up to 25(–50) mm wide, usually shallowly scrobiculate towards the tips; cyphellae up to 1.5 mm wide; apothecial margins verrucose to crenulate
- ***Sticta dilatata***
- Lobes up to 10(–15) mm wide, plane; cyphellae up to 2.5 mm wide; apothecial margin entire or ciliate 4
- 4(3) Cyphellae plane, up to 1.8 mm wide; apothecial margin entire . . . ***Sticta papillata***
- Cyphellae urceolate with wide pore, up to 2.5 mm wide; apothecial margin often ciliate. ***Sticta macrocyphellata***

***Sticta parahumboldtii* Moncada & Lücking sp. nov.**

Mycobank No.: MB804398

GenBank ITS barcoding sequence:
KC732550

Differing from *Sticta humboldtii* in the more fragile thallus, the K+ pale ochraceous medulla, and the K+ pale salmon reaction of the cyphellae membrane.

Type: Colombia, Cundinamarca, Mun. Bogotá D.C., Alrededores Laguna de Chisacá, 04°17'21.7"N, 74°12'26.9"O, 3724 m, 15 August 2010, B. Moncada et al. 4016 (UDBD—holotype; COL—sotype).

(Fig. 5)

Primary photobiont cyanobacterial (*Nostoc*). *Basal stipe* absent. *Thallus* orbicular to sub-orbicular, up to 10 cm diam., sparsely branched, with 0–2 branches for every 5 cm of radius, branching pattern polytomous to anisotomous. *Lobes* suborbicular, horizontal to subpendulous, imbricate, undulate, with their tips rounded and undulate, involute and their margins entire, not thickened; lobe internodes (5–)16–35(–45) mm long, (17–)18–50(–60) mm wide, subcoriaceous to coriaceous, fragile. *Upper surface* scrobiculate to rugose or undulate, emerald green when fresh, beige to pale yellow-brown or whitish in the herbarium, opaque, the marginal line concolourous; surface arachnoid to spongy, without papillae, without pruina, with irregular, sparse, cream-coloured maculae. *True marginal cilia* abundant, mingled with projections of the upper and lower tomentum, fasciculate to agglutinate, white to cream-coloured, up to 0.2 mm long. *Vegetative propagules* absent. *Medulla* compact, white to cream-coloured, K+ pale yellow-ochraceous, C–, KC–, P–. *Lower surface* undulate, cream-coloured. *Primary lower tomentum* dense up to the margin, thick but thinner towards the margin, spongy, soft, cream-coloured. *Secondary lower tomentum* arachnoid, pale. *Rhizines* absent. *Cyphellae* abundant, 21–40 per cm² towards the thallus centre and 100–200 per cm² towards the margin, dispersed, rounded to irregular, plane to urceolate with wide pore, immersed to erumpent, below the level of the primary tomentum, with the margin levelled to slightly

involute to erect, cream-coloured, with tomentum; pore (0.1–)1.0–2.5(–5.0) mm diam. towards the thallus centre; basal membrane pubescent, white to cream-coloured, K+ yellow to pale salmon-coloured, C–, KC+ yellow-ochraceous, P–.

Upper cortex paraplectenchymatous, 25–35 µm thick, uniform, formed of 3–4 cell layers, cells 4–10 µm diam., cell walls 1.25–2.50 µm thick and cell lumina rounded to isodiametric, 2.5–7.5 µm diam. *Photobiont layer* 50–60 µm thick, cells 10–15 µm diam. *Medulla* 60–140 µm thick, medullary hyphae 2.5 µm wide, without crystals. *Lower cortex* paraplectenchymatous, 20–30 µm thick, with 1–2 cell layers; cells 4–12 µm diam., cell walls 1.25–2.50 µm thick. *Primary upper tomentum* 110–370 µm long, composed of fascicles formed of 6–12 hyphae, hyphae branched, apically moniliform with their tips free. *Secondary upper tomentum* 15–25 µm long, of single hairs, hyphae branched, moniliform with their tips free. *Lower primary tomentum* 120–400 µm long, composed of fascicles formed of 12–20 hyphae, hyphae branched, apically moniliform with their tips interwoven. *Lower secondary tomentum* 15–35 µm long, of single hairs, hyphae branched, moniliform with their tips free. *Cavity of the cyphellae* 80–100 µm high; cells of basal membrane without papillae.

Apothecia abundant, principally laminal, dispersed, pedicellate, biatorine, up to 400 µm high, with distinct stipe; basal invagination pronounced, up to 3 mm diam.; *disc* orange to reddish orange, becoming reddish brown in the herbarium, opaque, K–; margin tomentose to hirsute, tomentum white but proper margin cream-coloured. *Excipulum* up to 105 µm wide, with tomentum. *Hymenium* up to 95 µm high; *epihymenium* up to 2.5 µm high, orange, K–. *Ascospores* hyaline, 27–35 × 7.5–10.0 µm, fusiform, with 1–3 septa.

Pycnidia immersed.

Etymology. The epithet of this new species (Greek: 'para' = next to, near) reflects the similarity to, and close relationship with, *Sticta humboldtii*.

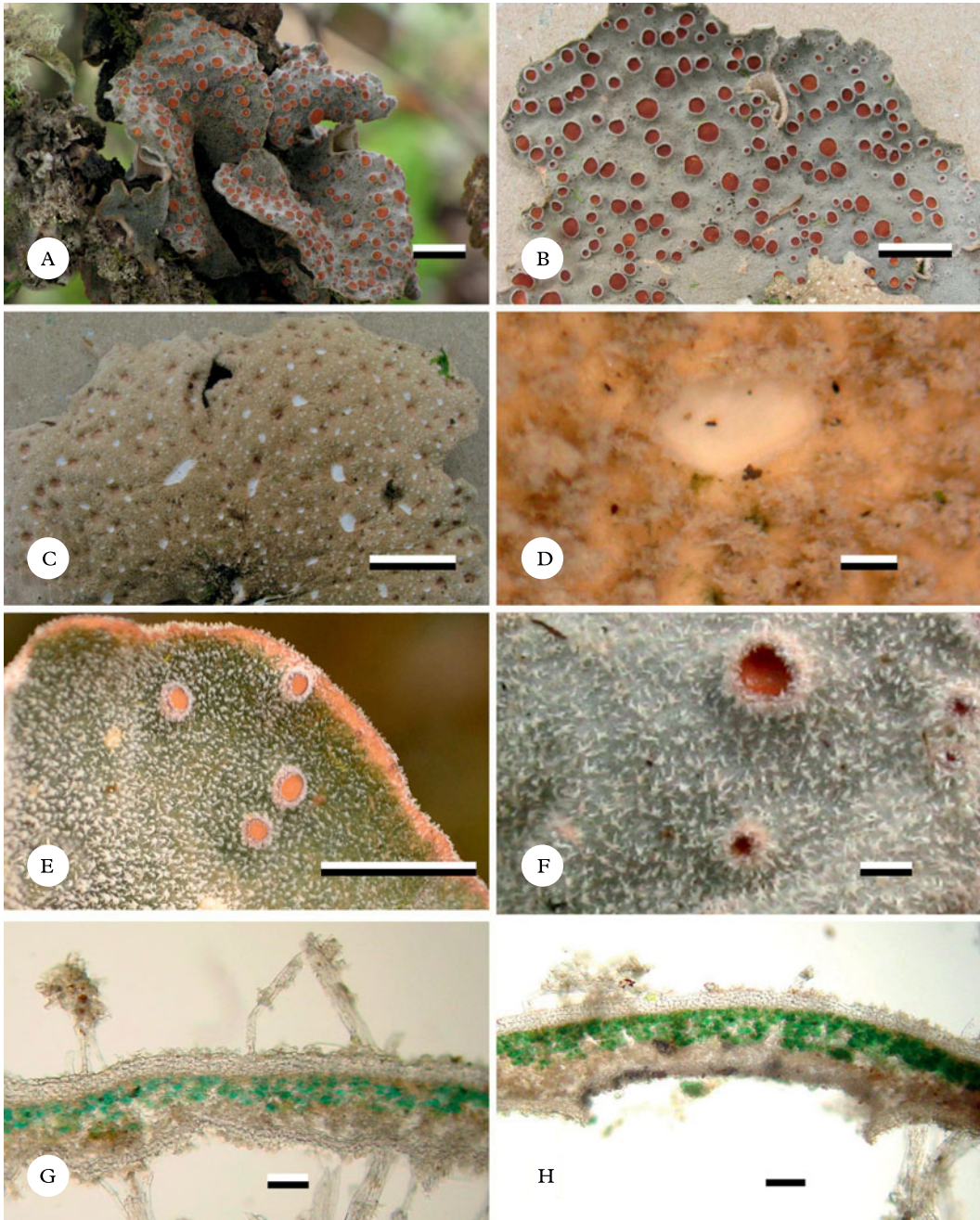


FIG. 5. *Sticta parahumboldtii* (A & B, Lücking s.n., holotype; E & F, Lücking 34043; C, D, G & H, Betancourt 144f). A, thallus *in situ*; B, dorsal view of lobe in the herbarium; C, ventral view of thallus showing tomentum and immersed cyphellae; D, detail of lower tomentum and cyphella; E & F, detail of dorsal tomentum and apothecia; G, section through thallus showing upper and lower tomentum; H, section through cyphella. Scales: A–C & E = 10 mm; D & F = 1 mm; G & H = 100 μ m. In colour online.

Ecology and distribution. Colombian Andes. The species was found between 3000 and 4000 m in high-andine forests and páramo vegetation, in shaded to semi-exposed microsites. It is known from the Cordillera Central and Cordillera Occidental, and the western slopes of the Cordillera Oriental (Rangel-Ch. 1995, 2000; Rodríguez *et al.* 2006; Moncada *et al.* 2013c), growing epiphytically and on mossy soil, generally associated with species of *Metzgeria*, *Frullania* and *Leptogium*.

Notes. *Sticta parahumboldtii* is one of only a few species in the genus with an upper tomentum, cyanobacterial photobiont, and lack of vegetative propagules. Two other species in Colombia have a very similar morphology: *S. humboldtii* Hook. (Hooker 1822, 1829; Galloway 1995) and *S. pseudohumboldtii* (see below). Their taxonomy and phylogenetic relationships are discussed under the latter species.

Additional specimens examined. **Colombia:** *Cauca:* Mun. Puracé, Sur del Volcán del Puracé, Filo de la Cordillera San Francisco, 3400 m, 1943, *J. Cuatrecasas* 14585, 14597 (COL); Volcán del Puracé, cabeceras Río Vinagre, El Alfombrado, 3800 m, 1972, *A. M. Cleef* 637a (COL); Volcán del Puracé, 1–2 km W of Alto de San Rafael, 3300 m, 1972, *A. M. Cleef* 2644 (COL, U); Mun. Santa Rosa, Macizo Colombiano, páramo de las Papas, alrededores de Valencia, 3150 m, 1958, *H. G. Barclay* & *P. Juajibioy* 5881 (COL). *Cundinamarca:* Mun. Bogotá D.C., Parque Nacional Natural Sumapaz, Páramo de Chisacá, 3600 m, 22 iii 1983, *M. Castro* s. n. (UPTC); Corregimiento Nazareth, sector Andabobos, 3610 m, 2004, *B. Moncada* & *R. Dávila* 2278, 2304 (UDBC); Alrededores Laguna de Chisacá, 04°17'21.7"N, 74°12'26.9"W, 3730 m, 2008, *B. Moncada* & *A. López* 2647 (UDBC); *ibid.*, *I. Ardila* & *B. Gómez* 191 (UDBC); *ibid.*, 3724 m, 2010, *B. Moncada et al.* 4016, 4119 (UDBC); *ibid.*, 3600 m, 2010, *L. Bétantcourt* 144f, 144g (UDBC); Mun. Choachí, Páramo del Verjón, 3500 m, 1940, *J. Cuatrecasas* 10450 (COL); *ibid.*, 3050–3350 m, 2001, *E. Duarte et al.* 93 (UPTC); *ibid.*, 3220 m, 2007, *D. Hernández et al.* 21 (UDBC); *ibid.*, *L. Castro et al.* 16 (UDBC); Mun. Cogua, Páramo entre Cógua and San Cayetano, cercanías Laguna Seca, 3685 m, 1972, *A. M. Cleef* 6139b (COL); Mun. Fómeque, Parque Nacional Natural Chingaza, Sendero La Arboleda, quebrada Babilonia, 3020 m, 2003, *B. Moncada* & *R. Dávila* 1584 (UDBC); Mun. Guasca, Piedras Gordas, 3200 m, 1988, *H. Sipman* & *J. Aguirre* 27378, 27380 (B, COL); Mun. La Calera, Páramo de Palacio, Hacienda la Siberia, 3500 m, 1953, *L. E. Mora* 638 (COL); Páramo de Siberia, 3470 m, 1971, *G. Guzmán* 9110 (COL); Páramo de Palacio, Hacienda la Siberia, km 17.5 camino La Calera to La Mina, 3000 m, 1971,

G. Guzmán 9117, 9122 (COL); *ibid.*, 3450 m, 1971, *G. Guzmán* 9780 (COL); Mun. Villapinzón, Páramo de Villapinzón, 3300 m, 2002, *M. Pinzón* 1396 (COL). *Meta:* Mun. Cubarral, Parque Nacional Natural Sumapaz, Cerro Nevado del Sumapaz, Quebrada El Buque, 3450 m, 1973, *A. M. Cleef* 7882 (COL, U). *Risaralda:* Mun. Pereira, Parque Nacional Natural Los Nevados, Laguna de Otún, 3930 m, 1980, *T. Boekhout* 174 (COL). *Tolima:* Mun. Ibagué, Las Juntas, vía Nieves, 3500 m, 2002, *D. Moreno* & *P. Hincapié* 153 (COL); Las Juntas, Vía la Cueva, 4000 m, 2002, *D. Moreno* & *P. Hincapié* 183 (COL); Mun. Santa Isabel, Valle del Río Totarito, 3650 m, 1980, *H. Valencia* & *T. Boekhout* 131, 154b (COL). *Valle del Cauca:* Mun. Tuluá, Corregimiento de Barragán, hoya del Río Bugalagrande, Páramo de Bavaya, 3520 m, 1946, *J. Cuatrecasas* 20196 (COL).

***Sticta pseudohumboldtii* Moncada & Lücking sp. nov.**

MycoBank No.: MB804399

GenBank ITS barcoding sequence:
KC011071

Differing from *Sticta humboldtii* in the coriaceous thallus, the K- to K+ pale yellow medulla, and the urceolate, prominent to sessile cyphellae with K+ dark yellow reaction.

Type: Colombia, Cundinamarca, El Verjón, Parque Ecológico Matarredonda, 04°33'37.7"N, 74°00'02.2"O, 3220 m, 23 January 2011, *B. Moncada* 4614 (UDBC—holotype).

(Fig. 6)

Primary photobiont cyanobacterial (*Nostoc*). **Basal stipe** absent. **Thallus** orbicular to irregular, up to 10 cm diam., moderately branched, with 3–5 branches for every 5 cm of radius, branching pattern anisotomous to polytomous. **Lobes** flabellate to suborbicular, horizontal to subpendulous, imbricate, undulate, with their tips rounded to truncate, involute and their margins entire to crenate, not thickened; lobe internodes (8–)10–20(–25) mm long, (3–)10–45(–55) mm wide, coriaceous. **Upper surface** undulate to scrobiculate, emerald green to green-brown when fresh, greenish grey to pale brown or whitish in the herbarium, opaque, the marginal line concolourous or brownish; surface arachnoid to spongy, with papillae towards the margin, without pruina, with irregular, sparse, cream-coloured maculae. **True marginal cilia** abundant, mingled with projections of the upper and lower tomentum, fasciculate to agglutinate, white to cream-coloured, up to 0.2

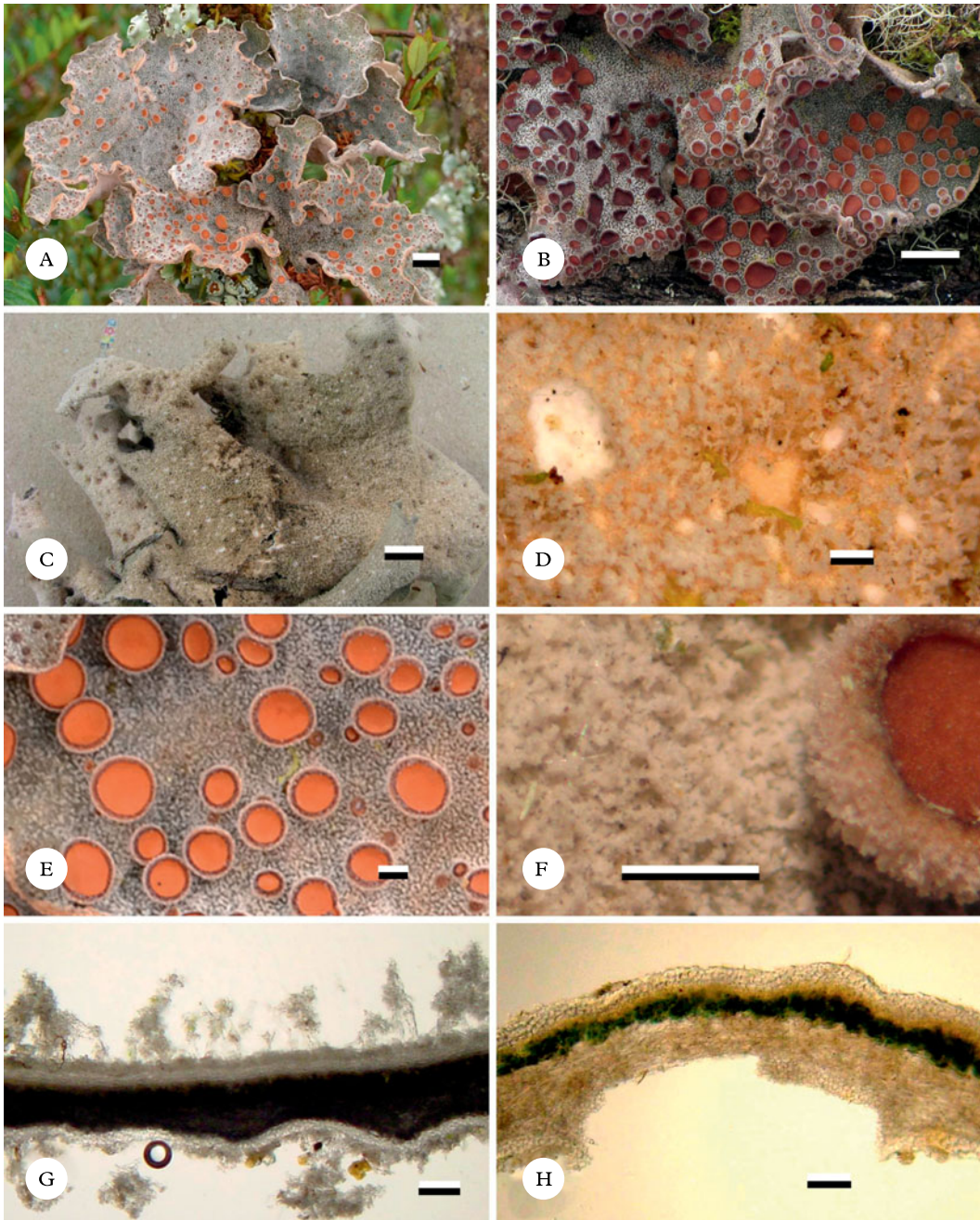


FIG. 6. *Sticta pseudohumboldtii* (Moncada 4586). A & B, thallus *in situ*; C, ventral view of thallus; D, detail of lower tomentum and cyphellae; E & F, detail of upper tomentum and apothecia; G, section through thallus showing upper and lower tomentum; H, section through cyphella. Scales: A–C = 10 mm; D–F = 1 mm; G & H = 100 μ m. In colour online.

mm long. *Vegetative propagules* absent. *Medulla* compact, white to cream-coloured, K- or K+ pale yellow, C-, KC-, P-. *Lower surface* undulate, cream-coloured. *Primary lower tomentum* dense up to the margin, thick but thinner towards the margin, spongy to intertwined, soft to rough, cream-coloured to greyish brown. *Secondary lower tomentum* arachnoid, pale. *Rhizines* absent. *Cyphellae* abundant, 21–40 per cm² towards the thallus centre and 100–200 per cm² towards the margin, dispersed, rounded to angular, urceolate with wide pore, prominent to sessile, below the level of the primary tomentum, with the margin elevated and involute to erect, cream-coloured, with tomentum; pore (0.7–)1.2–2.5(–3.5) mm diam. towards the thallus centre; basal membrane pubescent, white to cream-coloured, K+ dark yellow, C-, KC+ pale yellow, P-.

Upper cortex paraplectenchymatous, 20–25 µm thick, uniform, formed of 3–4 cell layers, cells 4–10 µm diam., cell walls 1.25–2.50 µm thick and cell lumina rounded to isodiametric, 5–8 µm diam. *Photobiont layer* 25–40 µm thick, cells 10–15 µm diam. *Medulla* 55–75 µm thick, medullary hyphae 2.5 µm wide, without crystals. *Lower cortex* paraplectenchymatous, 12–18 µm thick, with 1–2 cell layers; cells 4–10 µm diam., cell walls 1.25–2.50 µm thick. *Primary upper tomentum* 110–370 µm long, composed of fascicles formed of 4–6 hyphae, hyphae branched, apically moniliform with their tips free. *Secondary upper tomentum* 20–25 µm long, of single hairs, hyphae branched, moniliform with their tips free. *Lower primary tomentum* 130–500 µm long, composed of fascicles formed of 12–20 hyphae, hyphae branched, apically moniliform with their tips interwoven. *Lower secondary tomentum* 20–25 µm long, of single hairs, hyphae branched, moniliform with their tips free. *Cavity of the cyphellae* 110–230 µm high; cells of basal membrane without papillae.

Apothecia abundant, principally laminal, dispersed, pedicellate, biatorine, up to 400 µm high, with distinct stipe, basal invagination pronounced, up to 5 mm diam.; disc orange to reddish brown, opaque, K-; margin tomentose to hirsute, tomentum white

to brown. *Excipulum* up to 100 µm wide, with tomentum. *Hymenium* up to 130 µm high; *epihymenium* up to 2.5 µm high, orange, K-. *Ascospores* hyaline, 25–38 × 7.5–8.5 µm, fusiform, with 1–3 septa.

Pycnidia immersed.

Etymology. The epithet of this new species [Greek: 'pseudo' = false] was chosen since the species resembles *Sticta humboldtii* but, contrary to *S. parahumboldtii* (see above), is not the closest relative of *S. humboldtii* but sister to the morphologically different *S. arachnofuliginosa*.

Ecology and distribution. Colombian Andes. The species was found between 1900 and 3975 m in subandine forests and páramo vegetation. It is known from all three major Cordilleras (Rangel-Ch. 1995, 2000; Rodríguez *et al.* 2006; Moncada *et al.* 2013c), growing epiphytically, generally associated with *Metzgeria* spp., *Heterodermia circinalis*, *Leptogium* spp., and *Oropogon bicolor*.

Notes. Based on study of the type material of *Sticta humboldtii* (Hooker 1822, 1829; Galloway 1995) and our field experience with the species in Costa Rica and the northern Andes, we initially considered this to be a rather well-defined species, characterized by large thalli with a dense tomentum on the upper surface and densely tomentose apothecial margins. Molecular phylogeny, however, demonstrated that three species were involved (Fig. 7), forming a clade with other dorsally tomentose species that produce isidia (Moncada *et al.* 2013b). The isidiate species are rather well distinguished by their unique lobe morphologies, such as the deeply faveolate *S. arachnofuliginosa* Moncada & Lücking (Moncada & Lücking 2012), which is sister to *S. pseudohumboldtii* (Fig. 7). The three non-isidiate species, *S. humboldtii*, *S. parahumboldtii*, and *S. pseudohumboldtii*, can be separated using the key below.

Additional specimens examined. **Colombia:** *Antioquia:* Mun. Medellín, Estación Forestal Piedras Blancas, 2100 m, 1974, K. Dumont *et al.* 1592 (COL). *Boyacá:* Mun. Socha, Carretera Socha-Sácama, pasando el páramo de Pisba, 3050 m, 1982, J. Aguirre *et al.* 2854 (COL). *Caldas:* Mun. Manizales, Río Blanco, 2000 m, 18 iii 2008, F. Sarria & S. Valdes s.n. (CUVC); Mun.

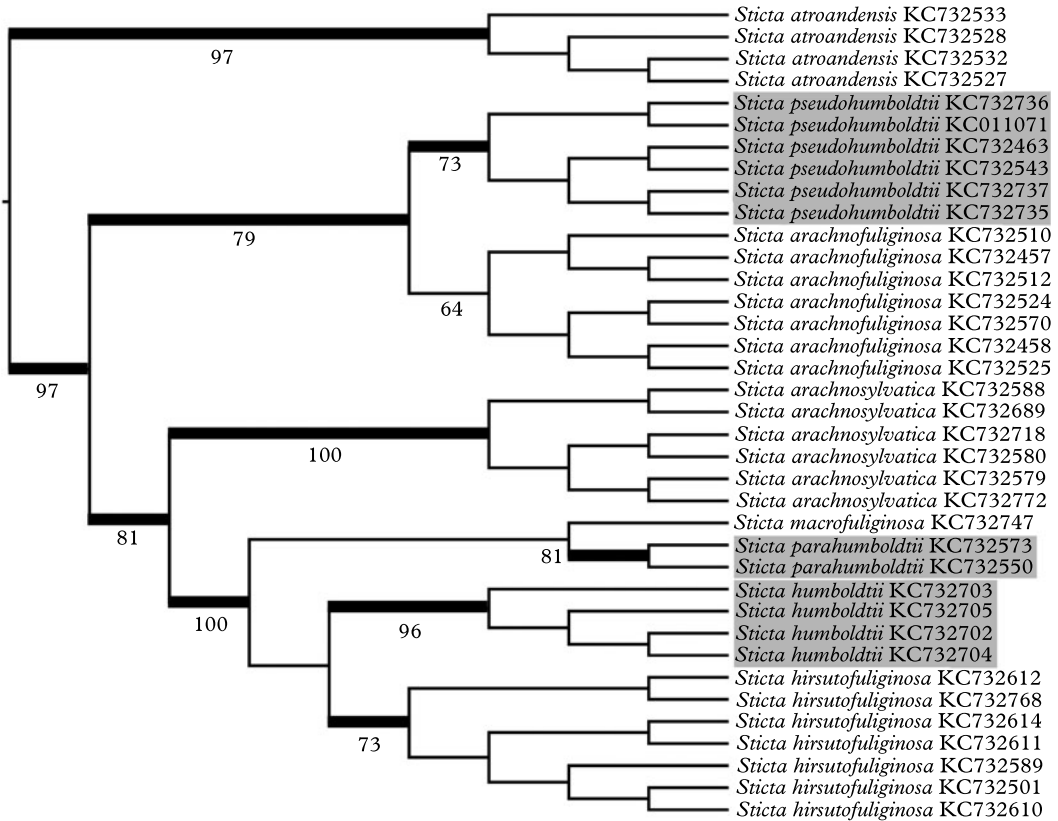


FIG. 7. Partial ITS phylogeny of the *Stictia humboldtii* clade, highlighting the apotheciate species corresponding to the *S. humboldtii* morphodeme (adapted from Moncada *et al.* 2013b). Thick branches indicate bootstrap support >70% and support values given.

Villa María, Nevado del Ruiz, costado noroccidental, a 500 m de la estación de Televisión, 3900 m, 1979, *H. Sipman* & *H. Valencia* 10476 (B, COL). *Cauca*: Mun. Puracé, Páramo de San Rafael, cerca de la cascada del río San José, 3200–3350 m, 1961, *J. Cuatrecasas* & *L. Willard* 26289, 26290 (COL); Bosque en los alrededores de Pilimbalá, 3470 m, 1972, *A. M. Cleef* & *A. Fernández-P.* 493b (COL, U); Parque Nacional Natural Puracé, Pilimbalá-Laguna de San Rafael, 3300 m, 1984, *J. Aguirre* & *H. Sipman* 5978 (B, COL); Carretera La Plata-Puracé, cerca a la cabaña del Inderena, 3300 m, 1984, *J. Aguirre* & *H. Sipman* 6018 (B, COL); Termales de San Juan, 3000 m, 1985, *J. Aguirre* & *H. Sipman* 5919 (B, COL); Parque Nacional Natural Puracé, Pilimbalá-Laguna de San Rafael, 3280 m, 2000, *B. Moncada* & *R. Dávila* 523 (UDBC); Pilimbalá-Volcán Puracé, 3710 m, 2000, *B. Moncada* & *R. Dávila* 623 (UDBC); Mun. Santa Rosa, Macizo Colombiano, páramo de las Papas, entre El Boquerón y La Hoyola, 3200–3510 m, 1958, *H. Bischler* 711 (COL). Cundinamarca: Mun. Bogotá D.C., Parque Nacional Natural Sumapaz, Páramo de Chisacá, Santa Rosa, Bodegas de Sumapaz, Valle del río Colorados (o Santa Rosita), 3460 m, 1976, *T. v. d. Hammen* &

R. Jaramillo-M. 4325 (COL); Alrededores de Laguna Grande, 3700 m, 1984, *J. Aguirre* & *H. Sipman* 5003 (B, COL); *ibid.*, 3500 m, 1986, *H. Sipman et al.* 34499 (B, COL); Carretera a la Laguna Larga, 3500 m, 1986, *N. Cardona de Hollaender et al.* 38 (CUVC); Corregimiento Nazareth, Cerro al costado oriental de la Caseta Los Pinos, 3460 m, 2004, *B. Moncada* & *R. Dávila* 2208, 2243 (UDBC); Alrededores Laguna de Chisacá, 04°17'21.7"N, 74°12'26.9"W, 3730 m, 2008, *B. Moncada* & *A. López* 2658 (UDBC); *ibid.*, 3734 m, 2008, *D. Beltrán et al.* 26 (UDBC); *ibid.*, *I. Ardila* & *B. Gómez* 186, 188, 209 (UDBC); *ibid.*, 3724 m, 2010, *B. Moncada et al.* 4022b, 4104, 4114, 4116, 4117, 4120, 4122, 4123 (UDBC); Mun. Choachí, Páramo de Cruz Verde, 3150 m, 1938, *J. Cuatrecasas* 450b, 450d (US); Páramo de Cruz Verde, Vertiente hacia Choachí, 3200 m, 1961, *J. Idrobo* & *Dumont* 4536 (COL); Páramo del Verjón, 3220 m, 2007, *D. Hernández et al.* 19 (UDBC); *ibid.*, *K. Malaver et al.* 70 (UDBC); *ibid.*, *L. Castro et al.* 40 (UDBC); *ibid.*, *Y. Carreño et al.* 21, 28 (UDBC); Sendero el Silencio, 3220 m, 2007, *A. López et al.* 28 (UDBC); El Verjón, Parque Ecológico Matarredonda, 04°33'37.7"N, 74°00'02.2"W, 2900–3220 m, 2010,

B. Moncada 3276, 3285 (UDBC); *ibid.*, 3220 m, 2011, *B. Moncada* 4586 (UDBC); Mun. Fômeque, Parque Nacional Natural Chingaza, Río La Playa-Chuza, 3183 m, 1999, *C. Cuellar et al.* 94 (UDBC); *ibid.*, 3154 m, 1999, *C. Gaitán et al.* 99 (UDBC); Río la Playa, Valle de los Frailejones, 3154 m, 1999, *B. Moncada & R. Dávila* 277, 308 (UDBC); Sendero La Arboleda, quebrada Babilonia, 3060 m, 2003, *B. Moncada & R. Dávila* 1491b, 1513, 1529, 1591b (UDBC); Parque Nacional Natural Chingaza, 04°44'19"N, 73°50'36"W, 3460 m, 2011, *D. Fonseca & F. Martínez* 31 (UDBC); Mun. Guasca, Páramo de Guasca, carretera Guasca-Gachetá, 3300 m, 1979, *H. Sipman et al.* 10611 (B, COL); *ibid.*, 3100 m, 1983, *L. B. Cruz* 499 (COL); Carretera a Bogotá, 3380 m, 2001, *D. Ros* 178 (COL); Páramo de Guasca, 3350 m, 2011, *B. Moncada* 4768b, 4769a (UDBC); *ibid.*, *R. Lücking* 33385, 34024, 34036, 34042 (UDBC, F); Mun. La Calera, Páramo de Palacio, Hacienda la Siberia, 3500 m, 1960, *L. E. Mora* 909 (COL); Bosque Alto Andino, abajo del páramo de Palacio, 3100 m, 1960, *L. E. Mora* 974 (COL); Hacienda La Siberia, km 17.5 camino La Calera a la Mina, 3400 m, 1971, *G. Guzmán* 9114, 9773 (COL); *ibid.*, 3450 m, 1983, *L. B. Cruz* 329a (COL); Parque Nacional Natural Chingaza, Monterrendondo, 04°44'11.6"N, 73°50'31.3"W, 3430 m, 2011, *B. Moncada* 4620, 4635a (UDBC); Laguna de Siecha, 04°44'18.8"N, 73°50'36"W, 3456 m, 2011, *Y. Orozco & R. Soto* 83 (UDBC); *ibid.*, 2011, *Y. Orozco & R. Soto* 104 (UDBC); Zona de Amortiguación Parque Nacional Natural Chingaza, Vía del ángulo al Rincón del Oso, 3600 m, 2011, *B. Moncada* 4921, 4928, 4964, 4980 (UDBC); Mun. Villapinzón, Páramo de Villapinzón, 3300 m, 2002, *M. Pinzón* 1409, 1472, 1483, 1507, 1522, 3001 (COL). *Huila*: Mun. La Plata, Vereda La Candelaria, cascada del Río La Candelaria, 2300 m, 1984, *J. Aguirre & H. Sipman* 6143, 6145c (COL). *Risaralda*: Mun. Pereira, Parque Nacional Natural Los Nevados, Laguna de Otún, margen occidental, 3975 m, 1980, *T. Boekhout* 8b (COL); Mun. Santa Rosa de Cabal, Alrededores Finca La Sierra, 3740 m, 1980, *J. Aguirre* 1371 (COL); Costado Occidental, Cordillera Central, Finca La Sierra, 3750 m, 1984, *J. Aguirre & H. Sipman* 5458 (B, COL).

Key to species of the *Sticta humboldtii* group

- 1 Cyphellae urceolate (with their margin distinctly raised and involute and the cavity more than 100 µm high), prominent to sessile (basal membrane at or above lower cortex level), mostly rounded to slightly angular; upper tomentum dense, hiding the surface beneath ***Sticta pseudohumboldtii***
- Cyphellae plane (with their margin levelled or slightly raised and erect and the cavity less than 100 µm high), immersed to erumpent (basal membrane below lower cortex level), usually angular; upper tomentum not dense, at least partially exposing the surface beneath 2
- 2(1) Lobes with pale marginal line; medulla K+ ochraceous; cyphellae K+ pale yellow to pale salmon ***Sticta parahumboldtii***
- Lobes with dark marginal line; medulla K+ pale yellow; cyphellae K+ yellow ***Sticta humboldtii***

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