

First records of *Sticta weigelii* s.str. from Bolivia confirmed by molecular data

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Abstract: The first records of *Sticta weigelii* s.str. from Bolivia confirmed by molecular data are presented. The species is characterized by the presence of marginal isidia, which are darker than the thallus, usually cylindrical (not flattened), thin, dark brown to black lower tomentum and often partly yellow cyphellae. Previously, the presence of *S. weigelii* in Bolivia was based only on a morphological concept, encompassing various unrelated species, whereas the occurrence of *S. weigelii* s.str. was uncertain.

Keywords: Ascomycota, *Peltigeraceae*, *Lobarioideae*, ITSrDNA, morphodemes

INTRODUCTION

The subcosmopolitan genus *Sticta* (Schreb.) Ach. occurs in humid, cool to warm-temperature environments with high precipitation or humidity (Galloway, 1994, 1997, 2007; Moncada, 2012; Moncada et al., 2014a, 2020; Suárez & Lücking, 2013). It is characterized by foliose thalli with or without stipe, with different types of photobionts (green algae or/and cyanobacteria) and characteristic pores (cyphellae) on the lower surface. On the upper surface isidia, soredia, phyllidia or lobules may develop, with or without apothecia. Lobes are variously indented (Galloway, 1994, 1997, 2007; Moncada, 2012; Moncada & Lücking, 2012; Moncada et al., 2014b). Until now, more than 200 species of *Sticta* have been described (Moncada & Lücking, 2012; Moncada et al., 2013a, 2013b, 2020, 2021a, 2021b; Lücking et al., 2017; Mercado-Díaz et al., 2020), but according to Moncada et al. (2013b, 2021b) the number of species belonging to this genus is more than twice as high. The discrepancy between the described and the potential number of *Sticta* species is related to the fact that in many countries no detailed studies have been undertaken. For example, recent research conducted on *Sticta* in Puerto Rico revealed the presence of more than ten taxa potentially endemic to that island (Mercado-Díaz et al., 2020). Bolivia, conversely, is one of the relatively understudied countries in term of the presence of *Sticta* species.

The checklist of lichens from Bolivia (Rodríguez de Flakus et al., 2016) lists only 11 names under the genus *Sticta*, however, most of these reports are historical and require re-examination as in many cases very wide species delimitations were used: *S. damicornis* (Sw.) Ach. (a Caribbean endemic species), *S. fuliginosa* (Dicks.) Ach., *S. isidiokunthii* Moncada & Lücking, *S. kunthii* Hook, *S. laciniata* (Sw.) Ach., *S. sinuosa* Pers., *S. sinuosa* var. *macrophylla* (Bab.) Müll. Arg. [= *Sticta macrophylla* Bory ex Delise] (a paleotropical species), *S. tomentosa* (Sw.) Ach., *S. tomentosa* var. *dilatata* (Nyl.) Hue [= *S. dilatata* (Nyl.) Vain.], *S. umbilicariiformis* Hochst. ex Flot. (an African species) and *S. weigelii* (Ach.) Vain. (Nylander, 1859, 1861; Rusby, 1896; Herzog, 1922, 1923; Moncada & Lücking, 2012; Moncada et al., 2018; Simon et al., 2018; Lücking et al., 2021). Furthermore, intensive lichenological studies conducted in Bolivia indicate that the number of lichen taxa exceeds 1400 (Rodríguez de Flakus et al., 2016; Guzow-Krzemińska et al., 2019). Therefore, it can be assumed that the number of *Sticta* species might also be much higher than previously known in Bolivia. In Colombia, for example, a country with a similar high biodiversity as Bolivia, about 150 *Sticta* taxa have been described, of which 100 were recognized as new to science (Moncada et al., 2012–2014).

One of the *Sticta* species reported from Bolivia is *S. weigelii* s.lat. (Herzog, 1922, 1923; Feuerer et al., 1998). It associates with cyanobacteria as photobionts. The lobes are elongated with the

margins densely covered by dark, cylindrical isidia. The lower surface is dark reddish-brown with thin, dark tomentum and K⁺ intensive yellow medulla with white to yellow cyphellae (Galloway, 1994, 2006; Moncada, 2012, Moncada et al., 2021a). It occurs in tropical climate regions in well-preserved forest (Mercado-Díaz et al., 2020; Moncada et al., 2021a).

This narrow circumscription corresponding to a phylogenetically redefined species (Mercado-Díaz et al., 2020) is in contrary to a previous broad application of *S. weigelii* that included any material with cyanobacteria and marginal isidia. However, molecular results indicate that this broad morphological species concept is inappropriate, because it includes several phylogenetically distant taxa, which are overall similar but differ in various morphological details (McDonald et al., 2003; Moncada et al. 2014b, 2020, 2021a). Consequently, records of *S. weigelii* complex may refer to various species, including e.g., *S. andina* B. Moncada, Lücking & Sérus., *S. beauvoisii* Del., *S. carolinensis* McDonald, *S. scabrosa* B. Moncada, Merc.-Díaz & Bungartz, or *S. tatamana* Moncada & Coca (McDonald et al., 2003; Moncada, 2012, Moncada et al., 2013b, 2014b; 2021a). Therefore, proper identification of *S. weigelii* s.str. should be supported by molecular analyses. In addition, the wide geographical distribution of this taxa should be treated as „possible” until confirmed by phylogenetic results (Moncada, 2012; Moncada et al., 2021a).

The main aim of study was to revise specimens belonging to *Sticta weigelii* complex from Bolivia. In this paper the first molecular evidence for the presence of *S. weigelii* s.str. in Bolivia is presented, based on the results of phylogenetic studies, supplemented by morphological and anatomical description of the taxon, its geographical distribution and ecological requirements together with the discussion on taxa belonging to the *S. weigelii* complex.

MATERIALS AND METHODS

Taxon sampling

Fresh material (in total ca. 200 specimens of *Sticta*) for this study was collected during fieldwork in Bolivia in 2010–2017 and is deposited in LPB and UGDA. In addition, ca. 100 specimens

deposited in KRAM and LPB were reviewed. The morphology and anatomy were studied under the stereomicroscope and diagnostic features reported in previous literature references were examined. In addition, a spot test reaction in K (10–20% potassium hydroxide solution) was performed (Orange et al., 2001).

A total of 60 isidiate *Sticta* specimens were used for morphological and chemical studies (data not shown), and only nine of these were consistent with the present circumscription of *S. weigelii* s.str.. Two fresh specimens were used for DNA extraction and phylogenetic analyses.

DNA extraction, amplification and sequencing

DNA was extracted using the Plant & Fungi DNA Purification Kit (Eurx, Poland) according to the manufacturer’s protocol. DNA extracts were amplified using the primers ITS1F and ITS 4A (White et al., 1990; Gardes & Bruns, 1993). PCR reactions were performed with the following program: initial denaturation 94°C for 3 min and 33 cycles of 94°C for 30 sec; annealing at 52°C for 45 sec; extension at 72°C for 1 min and final extension at 72°C for 10 min. The PCR products were cleaned using Wizard SV Gel and PCR Clean Up System (Promega, US) following the instructions of the manufacturer and sequenced using the MacroGen sequencing service (<http://www.macrogen.com>).

Phylogenetic analyses

The newly obtained sequences were compared with *Sticta* sequences deposited in GenBank using BLAST search (Altschul et al., 1997). The new sequences were automatically aligned together with selected representatives of the *S. weigelii* morphodeme in Seaview (Galtier et al., 1996; Gouy et al., 2010) using the algorithm Muscle (Edgar, 2004). The final alignment consisted of 31 ITSrDNA sequences and 568 characters. Twenty-nine sequences of *Sticta* were downloaded from GenBank. Sequence of *Lobaria pulmonaria* (L.) Hoffm. (AF129284) was used as outgroup.

The optimal DNA substitution model was determined using AIC (Akaike Information Criterion) within MrModeltest 2.0 (Nylander, 2004) for MrBayes settings. The GTR+I model was selected. Bayesian analyses (BI) were performed using MrBayes v. 3.2.2 (Huelsenbeck & Ronquist,

2001; Ronquist & Huelsenbeck, 2003) on the CIPRES Science Gateway (Miller et al., 2010). Metropolis-coupled Markov chain Monte Carlo (MCMCMC) was used. Two parallel MCMCMC runs were performed, using four independent chains and 1 million generations, sampling every 1000th tree. The initial 250 trees (25%) were discarded as burn-in, and posterior probabilities were estimated by constructing a 50% majority rule consensus tree of all sampled post burn-in

trees. The Bayesian tree is presented in Fig. 1 with added posterior probabilities.

RESULTS & DISCUSSION

Sequences of two specimens of *S. weigeli* s.str. (MZ292976 and MZ292977), as defined by Mercado-Diaz et al. (2020), were obtained from material collected in Bolivia. In the phylogenetic tree (Fig. 1), they clustered within the clade



Fig. 1. Phylogenetic relationships of *Sticta weigeli* morphodem based on Bayesian analysis of nucITS rDNA dataset. Posterior probabilities values are shown near the internal branches. GenBank accession numbers of sequences downloaded from GenBank are listed on the tree with species names. Clade of *S. weigeli* is highlighted. Specimens newly sequenced for this study of *S. weigeli* are in bold. KC732471 *Sticta* sp. * undescribed species provincially called *Sticta lobulata* in Moncada (2012) and Moncada et al. (2014, 2020).

corresponding to *S. weigelii* s.str. with sequences obtained by Moncada et al. (2014b), Widhelm et al. (2018) and Mercado-Díaz et al. (2020). These specimens are characterized by the presence of marginal, cylindrical isidia darker than the thallus, a thin, dark tomentum, white to yellow cyphellae, and K+ intensive yellow medulla. Additional material was compared with these two specimens and it allowed determining further seven specimens of this taxon from the collection of *Sticta* specimens from Bolivia.

According to Moncada et al. (2014b, 2020, 2021a) the morphotype *S. weigelii* comprises species from the following clades (species with quotation marks – not yet formally described): *S. weigelii* (*S. weigelii* s.str., *S. "luteocyphellata"*, *S. tatamana*), *S. scabrosa* (*S. "laselvae"*, *S. "pseudobeaivosii"*, *S. scabrosa* B. Moncada, Merc.-Díaz & Bungartz), *S. kunthii* (*S. phyllidiokunthii* B. Moncada & Lücking, *S. isidiokunthii*); *S. canariensis* (*S. carolinensis*, *S. fragilinata* McDonald), *S. fuliginosa* (*S. tunjensis* Moncada & Lücking, *S. harrisii* Merc.-Díaz, Moncada & Lücking), *S. andina* (*S. andina*, *S. "phyllidata"*, *S. "squamifera"*), *S. beaivosii*, *S. "hypoglabra"*,

Sticta sp. [an undescribed species provincially called *Sticta "lobulata"* in Moncada (2012) and Moncada et al. (2014b, 2020)], *S. rhizinata* B. Moncada & Lücking and *S. waikamoi* B. Moncada & Lücking. The colour and thickness of the lower tomentum, the type and morphology of vegetative propagules, and the colour of the cyphellae, are features that distinguish these taxa from *S. weigelii* s.str. (Table 1), in addition to their ecology (McDonald et al., 2003; Moncada et al., 2014b, 2021a,b; Widhelm et al., 2018; Mercado-Díaz et al., 2020). *Sticta andina*, *S. fragilinata*, *S. lasalvae*, *S. phyllidiokunthii*, *S. "pseudobeaivosii"* and *S. scabrosa* produce dorsiventral phyllidia (Moncada et al., 2013, 2014b, 2020, 2021a). *Sticta "phyllidata"* and *S. "squamifera"* produce lobules instead of isidia (Moncada, 2012). Other taxa have isidia that are morphologically different from those present in *S. weigelii* s.str., e.g., in *S. "hypoglabra"* they are paler than the thallus (Moncada, 2012). The colour of the tomentum is also a distinguishing feature, e.g. in *S. isidiokunthii* it is beige vs. dark brown in *S. weigelii* s.str. (Moncada & Lücking, 2012).

Table 1. Differences in type of vegetative propagules and their morphology as well as the colour of the tomentum between species of *S. weigelii* morphodeme

Species	Vegetative propagules	Morphology of propagules	Tomentum
<i>S. harrisii</i>	phyllidia in all species	narrow at the base and easily detachable from the thalli	dark brown
<i>S. fragilinata</i>			grey to brown
<i>S. lasalvae</i>			grey to brown
<i>S. phyllidiokunthii</i>			grey to golden brown
<i>S. pseudobeaivosii</i>			pale grey to dark brown
<i>S. scabrosa</i>			pale grey to dark grey
<i>S. phyllidata</i>	lobules in all species	small lobes	brown to black
<i>S. squamifera</i>			dark brown
<i>S. tatamana</i>	absent	-	golden-brown
<i>S. andina</i>	isidia and phyllidia	flattened	dark brown to black
<i>S. beaivosii</i>		cylindrical to flattened	brown gold
<i>S. carolinensis</i>		phyllidate	cream
<i>S. hypoglabra</i>		cylindrical	grey to brown
<i>S. isidiokunthii</i>		branched to coralloid	beige
<i>S. luteocyphellata</i>	isidia in all species	simple to branched	grey to brown
<i>S. rhizinata</i>		branched to coralloid	brown to black
<i>S. tunjensis</i>		branched to coralloid	white to cream
<i>S. waikamoi</i>		cylindrical to flattened	dark brown
<i>S. weigelii</i>		coralloid	brown to black

* *Sticta* sp. undescribed species provincially called *Sticta lobulata* in Moncada (2012) and Moncada et al. (2014, 2020) is characterized by the presence of lobules.

Taxa closely related to *S. weigelii* s.str. are *S. "luteocyphellata"* and *S. tatamana* (Fig. 1). However, in *S. tatamana* the tomentum is pale golden-brown and in *S. "luteocyphellata"* brown-grey with paler apices. Additionally, in *S. tatamana* no vegetative propagules were observed (Moncada, 2012; Moncada et al., 2013a).

Recently, new taxa morphologically similar to *S. weigelii* s.str. have been described: *S. waikamoi* from Hawaii and *S. harrisii* from Puerto Rico (Mercado-Díaz et al., 2020; Moncada et al., 2020, 2021b). *Sticta harrisii* is characterised by the presence of phyllidia and tomentum is paler than in *S. weigelii* s.str. and becomes yellowish in herbarium specimens (Mercado-Díaz et al., 2020). In *S. waikamoi*, the marginal isidia are cylindrical to somewhat flattened (Moncada et al., 2020, 2021b). Both species are unrelated phylogenetically to *S. weigelii* s.str. (Mercado-Díaz et al., 2020; Moncada et al., 2020, 2021b).

THE SPECIES

STICTA WEIGELII (Ach.) Vain. (Fig. 2)

Description. Photobiont: cyanobacteria. Stipe absent. Thallus closely to loosely adnate, up to 8 cm wide, irregular to suborbicular, moderately branched. Lobes 7–10 mm wide and 2–18 mm long, lacinate, elongate with rounded apices, margins sinuous, not thickened, densely isidiate. Upper surface reddish-brown to dark brown with black marginal line, smooth to slightly scrobiculate, shiny, without papillae. Apothecia and cilia absent. Isidia numerous, mainly marginal, aggregated, branched-coralloid, darker than the thallus, blackish-brown. Medulla white to cream-white, K⁺ intensive yellow. Lower surface beige to red-brown toward the centrum. Tomentum rather thin, dense but shorter on margins, spongy, dark brown. Rhizines often present, irregularly scattered, black, up to 2 mm long. Cyphellae abundant, 0.5–1 mm diam, with white to beige or partly yellow basal membrane, margins raised and involute, brown to black, rounded to irregular; K⁺ yellow-orange.

Upper cortex 40–50 µm thick, differentiated into two cell layer; upper layer 3.5–5 µm diam, 1 cell layer; lower layer 6–12 µm diam, 4–5 cells. Photobiont layer 40–50 µm thick, cells 12–20 µm diam, with orange-yellow crystals. Lower cortex 27–33 µm thick, cells 6–12 µm diam with wall

1–2.5 µm thick. Tomentum 170–320 µm long, in dense fascicles. Cyphellae por 210–740 µm diam, basal membrane 240–950 µm diam (based on own observations and Moncada 2012).

Notes. The diagnostic features of *S. weigelii* s.str. are the cylindrical isidia darker than the thallus, the dark brown, rather thin lower tomentum, and the white to partly yellow cyphellae (Moncada, 2012; Moncada et al., 2021a). For differences from other similar taxa see Table 1.

Distribution and habitat. The records of *S. weigelii* s.str. presented here are the first from Bolivia supported by molecular data. So far, it was reported only by Herzog (1922, 1923) and Feuerer et al. (1998), but these records were not confirmed using molecular markers and may represent other species. In Bolivia the species occurs in the departments Cochabamba, La Paz, Tarija and Santa Cruz, where it grows on bark of trees and rocks, at 750–3950 m above sea level. *Sticta weigelii* s.str. was reported also from Colombia, Martinique (type locality), and Puerto Rico (Galloway, 2006; Moncada, 2012; Moncada et al., 2014a, 2021a; Mercado-Díaz et al. 2021). Previously, *S. weigelii* s.lat. was considered as a widespread species, reported from many localities in Asia, East Africa, Central and South America, Australia and several Pacific islands (Swinscow & Krog, 1988; Galloway, 1994, 1997, 2006 and literature cited therein). However, according to Moncada et al. (2021a) records outside the Neotropical region should be considered doubtful until confirmed by phylogenetic results.

Specimens examined: BOLIVIA. Dept. Cochabamba, Prov. Chapare, Parque Nacional Carrasco, 148 km of the old road from Cochabamba to Villa Tunari, 17°07'S, 65°34'W, alt. 1050 m, fallen tree in humid forest, corticolous, 10 Oct. 1997, leg. K. Bach 657 & M. Kessler, E. Rapp (LPB); Dept. La Paz, Prov. Nor Yungas, near Paccallo village, 16°12'10"S, 67°50'39"W, alt. 1360 m, montane forest, on stone, 03 Aug. 2008, leg. M. Kukwa 7152 (LPB, UGDA; GenBank accession no MZ292977); Dept. La Paz, Prov. Nor Yungas, near Pongo village, near the road Coroico-Laz Paz, 16°19'28"S, 67°57'21"W, alt. 3822 m, Páramo Yungueño, 26 Nov. 2011, leg. M. Kukwa 10456 (LPB, UGDA); Dept. La Paz, Prov. Sud Yungas, Alto Beni Sapecho, Colonia Tupiza, Parcela Permanente III, on Pousenia

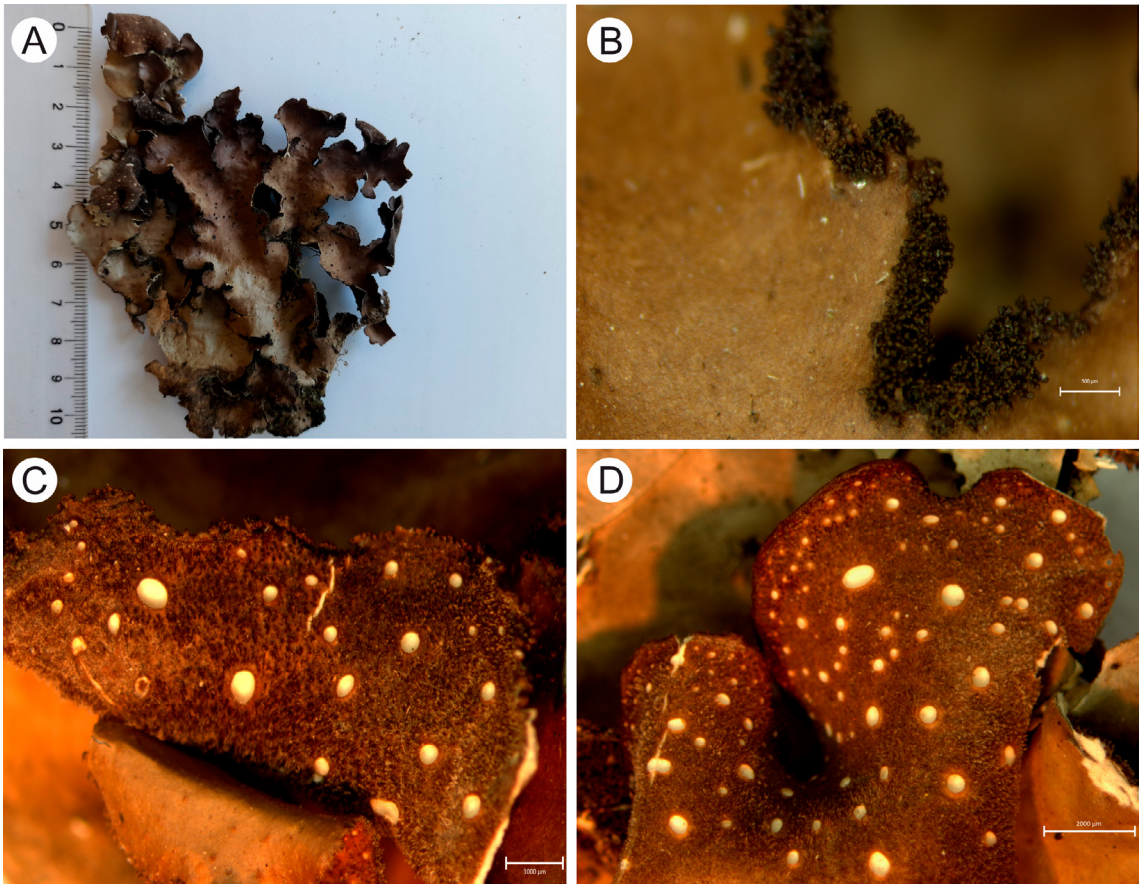


Fig. 2. Morphology of *Sticta weigelii* (Ach.) Vain. A – thallus; B – upper surface with dark marginal isidia; C – lower surface with black tomentum, cyphellae and marginal isidia; D – lower surface with black tomentum and cyphellae. All from *Flakus 18429* (LPB, KRAM). Scale bars: 1000 µm.

armata, 15°31'S, 67°17'W, alt. 750 m, Evergreen to semi-deciduous forest, on branches, 02 July 1999, leg. A. Acebey (LPB); Dept. La Paz, Prov. B. Saavedra, 15 km from Charazani to Apollo, 15°11'S, 68°52'W, alt. 3500 m, humid forest, corticolous, 04 July 1997, leg. K. Bach 346 & M. Kessler, J. Gonzales, A. Acebey, V. Rapp (LPB); Dept. La Paz, Prov. B. Saavedra, 3 km de Pauji-Tuyo hacia Charazani, 15°02'S, 68°29'W, alt. 1300 m, evergreen virgin forest, corticolous, 05 June 1997, leg. K. Bach 144 & M. Kessler, A. Acebey, E. Rapp (LPB); Dept. La Paz, Prov. Umrillo, arriba Chururagni, alt. 1900 m, 28 Aug. 1988, leg. S. Stab 264 (LPB); Dept. Santa Cruz, Prov. Manuel Caballero, near Siberia, 17°49'38"S, 64°44'45"W, alt. 3950 m, open Yungas cloud forest, corticolous 16 Aug. 2012,

leg. M. Kukwa 11422 (LPB, UGDA); Dept. Tarija, Prov. Aniceto Arce, Filo de Sidras, 22°14'50"S, 64°33'28"W, alt. 1064 m, Tucumano-Boliviano submontane forest, corticolous 22 Nov. 2010, leg. A. Flakus 18429 (LPB, KRAM; GenBank accession no MZ292976).

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