

# Original article

# Redefinition of *Stachytarpheta sprucei* (Verbenaceae) reveals a remarkable geographic disjunction in tropical forests of South America

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#### **ABSTRACT**

Stachytarpheta is the second largest genus of Verbenaceae, mainly distributed in xeric habitats of South America. The morphological revision of South American specimens clarified the taxonomic identity of three previously accepted species from informal group Gesnerioides: S. sprucei (from the Amazon Forest domain), S. alata, and S. tomentosa (from the Atlantic Forest domain). A new taxonomic arrangement is proposed here, with the synonymization of S. alata and S. tomentosa under S. sprucei. Consequently, the newly circumscribed S. sprucei evidences a remarkable geographic disjunction, with populations separated by the Caatinga, Cerrado, and Chaco domains (the South American dry diagonal). It inhabits inselbergs, tepuis, and savannas in the Amazon Forest domain, and top of inselbergs surrounded by forest in the Atlantic Forest domain. A detailed species description, taxonomic comments, a geographic distribution map, photos of living specimens, and an identification key to the species from the Gesnerioides group are included.

Keywords: distribution, Duranteae, inselbergs, savannas, South American flora, tepuis.

## Introduction

Stachytarpheta species have fascinated naturalists for centuries due to the beauty of their flowers and attractive corolla colors, such as blue, bright red, and black (Atkins 2005). The genus comprises approximately 120 species and is an important component of the South American dry diagonal (Atkins 2005; Cardoso & Salimena 2020; Cardoso *et al.* 2021a), an open vegetation formation comprising the domains of the Caatinga, Cerrado, and Chaco (Ab'Saber

2003; Collevatti et al. 2020). In this region, Stachytarpheta is richest in the Brazilian Cerrado and Caatinga, where the majority of the species are endemic and restricted to a few localities or a single mountain range, occurring mainly in rocky fields, known as campos rupestres (Atkins 2005; Cardoso & Salimena 2020). Few species are distributed in tropical forests of South America, occurring mainly in open areas, such as restingas (vegetation complex occurring in the seaside lowlands of Brazil, establishing over sea deposits of sandy sediment), inselbergs, and savannas (Atkins 2005; Cardoso & Salimena 2020).

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Included in Duranteae, Stachytarpheta is a well-supported clade by molecular phylogenetic data (Marx et al. 2010) and has two functional stamens and two staminodes as a morphological synapomorphy (O'Leary et al. 2012). The inflorescence length and width are the main traits used by Walpers (1845) and Schauer (1847) to define two sections within the genus. In addition, the number of calyx teeth (two, four, or five) has traditionally been used as a diagnostic feature that helps to distinguish species (Atkins 2005). However, in some species this trait may vary and must be carefully observed to avoid confusion and misidentifications (Cardoso & Salimena 2020). Some species can have calyces with five teeth when immature, and at maturity the fifth tooth can be replaced by a sinus. In other species with 4-toothed calyces, the teeth may be almost fused in pairs, appearing 2-toothed.

In the review of *Stachytarpheta* in Brazil, Atkins (2005) established twelve informal groups based on the morphology and distribution of the species. The Gesnerioides group, according to Atkins (2005), comprised six species (Stachytarpheta alata, S. amplexicaulis, S. gesnerioides, S. reticulata, S. rupestris, and S. sprucei) characterized by the elongated inflorescences, calyx not embedded in the rachis excavations, 5-toothed, erect, corolla tubes between 1.5 and 2 cm long, blue, and fruits with a beaked apex. Recently, S. rupestris was considered a synonym of S. reticulata (Cardoso et al. 2022), and a new species, S. tomentosa, has been described and included within this group (Cardoso  $\it et$ al. 2019). In contrast with Atkins (2005), recent analysis has evidenced that calyces may be four or five toothed in this group (Cardoso et al. 2019; P.H. Cardoso, personal observation).

The six currently accepted species of the informal group Gesnerioides inhabit different phytogeographic domains in South America: Stachytarpheta gesnerioides and S. reticulata are endemic to the Cerrado domain; S. amplexicaulis, S. alata, and S. tomentosa occur in the Atlantic Forest domain; and S. sprucei is distributed in the Amazon Forest domain (Atkins 2005; Cardoso & Salimena 2020). Morphologically, S. amplexicaulis, S. gesnerioides, and S. reticulata are well-circumscribed species, while the boundaries between S. alata, S. sprucei, and S. tomentosa are not clear, and require further taxonomic studies. Therefore, the main objective of this work is to explore the morphological variation of these three species in order to verify whether they are different entities or the same taxon, and discuss their geographic distribution.

### **Materials and methods**

This study was carried out based on specimens deposited at BHCB, CESJ, R, and RB herbaria (acronyms follow Thiers, 2022), personally analyzed, as well as images of specimens available in the GBIF (https://www.gbif.org/), REFLORA

(https://reflora.jbrj.gov.br/) and speciesLink (https://www.splink.org.br/) databases. Type specimens were analyzed from images on the JSTOR Global Plants (https://plants.jstor.org/) and through digital images obtained by personal communication with herbarium curators. Due to the high number of *Stachytarpheta* species in the South American dry diagonal, plants of the Amazon and Atlantic Forests are often neglected and poorly collected, so there are not many specimens from these domains.

After the examination of specimens with the help of a stereomicroscope and the key literature (Moldenke 1940; 1949; Atkins 2005; Cardoso et al. 2019; 2021b), we aimed to recognize as conspecific those sets of specimens morphologically similar following the taxonomic species concept (Stuessy 1990). Morphological terms are based on Harris & Harris (2003), Atkins (2005), and Gonçalves & Lorenzi (2007). Data on habitat, elevations, and fertile period were obtained from exsiccate labels. The geographic distribution map was based on the specimen occurrence spreadsheets using the software QGIS ver. 3.8. The delimitation of the Atlantic Forest followed Ramos et al. (2019), and of the Amazonian Forest it followed IBGE (2021) for Brazil, and Eva & Huber (2005) for other South American countries. For those specimens lacking coordinates, the estimated georeferencing was done using the geoLoc tool (http://splink.cria.org.br/geoloc) from the information available on the labels.

### **Results and discussion**

Stachytarpheta alata and S. tomentosa (from the Atlantic Forest domain) are proposed here as new heterotypic synonyms of S. sprucei (from the Amazon Forest domain) after the study of ca. 30 specimens from these three taxa. Consequently, a remarkable disjunction is reported for the newly circumscribed S. sprucei, occurring in rock outcrops of the inselbergs and tepuis surrounded by forest or savannas, within the major rain forests of South America. Its populations are geographically isolated by the South American dry diagonal, since the species is not found in other inselbergs of the Caatinga domain or in open vegetation from the Cerrado domain.

Mori *et al.* (1981) and Fiaschi & Pirani (2009) listed several other angiosperms disjunctly distributed in the Amazon and Atlantic Forests domains, but occurring mainly along forest areas. Barbosa-Silva *et al.* (2022), when investigating floristic and phylogenetic connections among Neotropical inselbergs, found little overlap between lineages of the Amazonian Forest and Atlantic Forest, and no example of disjunction was reported. In this sense, *S. sprucei* represents a rare example of a species with disjunction occurring in open areas of these two domains.

Other *Stachytarpheta* species known to have a disjunct distribution are *S. crassifolia* and *S. mexiae*, however,



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occurring mainly in areas of Caatinga and/or Cerrado, with isolated populations in the Atlantic Forest domain. The first inhabits *campos rupestres* with sandy soils of the Espinhaço Range (Caatinga and Cerrado domains), states of Bahia and Minas Gerais, and *restingas* of the state of Rio de Janeiro (Atlantic Forest domain) (Cardoso & Salimena 2020). This disjunction pattern, *campos rupestres – restingas*, has also been well documented for several species by Alves *et al.* (2007). The second species is endemic to the state of Minas Gerais, growing in *campos rupestres* of the Espinhaço Range (Cerrado domain), and found in *campos rupestres* of Serra Negra, Mantiqueira Range (Atlantic Forest domain) (Cardoso *et al.* 2018).

In view of the new taxonomic arrangement for *Stachytarpheta sprucei*, the Gesnerioides group of Atkins (2005) comprises now four species. Future population genetic studies, species distribution modeling, as well as morphometric and phylogeographic analysis should be done in *S. sprucei*, since taxa with geographic disjunctions can serve as models to elucidate possible geological connections among regions (Wiens & Donoghue 2004), and because the possibility of having cryptic species not differentiated by morphology cannot be ruled out (cryptic species are unusual in *Stachytarpheta*). This highlights the need for more detailed studies in highly diverse and poorly understood groups, as is the case of *Stachytapheta* and *Lippia* in Verbenaceae, and other plant genera and families in general.

#### Taxonomic treatment

Stachytarpheta sprucei Moldenke, Phytologia 1: 474. 1940. Type: Venezuela: Rio Orinoco, near Maypures, Jun. 1854, R. Spruce 3631 (holotype, NY [barcode NY00138113 image!]; isotypes, BM [barcode BM000992676 image!], BR [barcode BR0000005503872 image!], E [barcode E00414365 image!], G [barcode G00366602 image!], K [barcode K000487017 image!]). (Fig. 1).

- = Stachytarpheta roraimensis Moldenke, Phytologia 1: 458. 1940. Type: Guiana: Mount Roraima, 1843, M.R. Schomburgk 499 (holotype, K [K000648695, pro parte, image!]; isotypes, BM [barcodes BM000992674 and BM000992675 images!], F [barcode F0074463F image!], G [barcode G00366589 image!], LL [barcode LL00375201 image!], US [barcode US00118937 image!]).
- = Stachytarpheta roraimensis var. pubescens Moldenke, Phytologia 3: 117. 1949. Type: Venezuela: Bolívar, Gran Sabana, near Santa Elena, 13 February 1946, F. Tamayo 2765 (holotype, VEN [barcode VEN27069 image!]).
- = Stachytarpheta alata (Moldenke) S.Atkins, Kew Bull. 60(2): 206. 2005. Basionym: Stachytarpheta gesnerioides var. alata Moldenke, Phytologia 54(5): 399. 1983. Type: Brazil: Minas Gerais, Medina, paredões rochosos, 13 May 1983, G. Hatschbach 46323 (holotype, LL [barcode LL00373701 image!]; isotypes, G [barcode G00366586 image!], HBG [barcode HBG513508 image!], K [barcode K000065514 image!], MBM [barcode MBM081690 image!]). syn. nov.

= Stachytarpheta tomentosa P.H.Cardoso & Salimena, Phytotaxa 400(5): 274. 2019. Type: Brazil: Espírito Santo, Itarana, Alto Várzea Alegre, Pedra da Onça, 19 April 2013, R.C. Forzza et al. 7530 (holotype, CESJ [no 69104!]; isotypes, RB [barcode RB00810044!], VIES [barcode VIES023550 image!]). **syn. nov.** 

Shrubs 1-4 m tall, erect, strongly branched, branches tetragonal, slightly or conspicuously winged, wings usually more developed towards the apex, densely strigose, pubescent or tomentose, often with two opposite sides more hairy than the other two, becoming glabrescent at maturity. Leaves opposite, patent, rarely with smaller leaves in the axil of adult leaves, petiole 0.4-0.9 cm long, blade  $3.4-12 \times 1.3-6$ cm, elliptical or ovate, chartaceous, slightly discolorous, nectaries present abaxially, apex acute, obtuse or rounded, base cuneate or attenuate, decurrent into petiole, margin entire near the base, crenate-serrate towards the apex, ciliate, adaxial surface strigose or puberulent, abaxial surface densely pubescent or tomentose, veins prominent abaxially. *Inflorescences*  $14-40 \times 1.2-1.8$  cm, densely flowered, rachis visible or not, sparsely strigose or pubescent; bracts 0.8–1.6 cm long, often surpassing the calyx, narrow triangular or triangular, green, apex conspicuously caudate, abaxial surface sparsely strigose, puberulent, minutely pubescent or tomentose, with nectaries, ciliate at margin. Flowers sessile; calyx 0.9–1.6 cm long, not embedded in excavations of the rachis, erect, green, 4-toothed with 2 sinuses, tips acute, adaxial sinus deeper, hirsute along the ribs, puberulent or tomentose between the ribs, nectaries present apically; corolla blue or blue-lilac, throat yellow, green, or rarely white, densely strigose, tube 1.6–2.3 cm long, infundibular, curved, lobes ca. 0.4 cm in diam, style 2–2.6 cm long, longexerted, white. Fruits ca. 0.5 cm long, beaked at apex, with long stylopodium, base with prominent attachment scar, external surface reticulate.

**Notes:** Stachytarpheta sprucei and S. roraimensis were described by Moldenke (1940) from the Amazon Forest, South America. Stachytarpheta sprucei was originally collected in Rio Orinoco, near Maipures, Venezuela, and characterized by the tetragonal and pubescent branches, petiolate leaves, ovate-elliptic leaf blades, chartaceous, adaxially puberulent, abaxially pubescent or velutinous, and inflorescences with bracts ca. 1 cm long, narrowly lanceolate, very elongated at apex, abaxially densely puberulent, and corolla tube ca. 1.5 cm long (Moldenke 1940). Stachytarpheta roraimensis was originally collected in Mount Roraima, Guyana, and characterized by the lanceolate leaves, chartaceous, adaxially sparsely puberulent, abaxially with denser indument, and inflorescences with bracts ca. 1 cm long, lanceolate, caudate at apex, abaxially minutely pubescent or glabrescent (Moldenke 1940). Later, Moldenke (1949) described S. roraimensis var. pubescens based on a specimen originally collected in Bolívar, Gran Sabana, Amazon Forest of Venezuela. It was distinguished by the densely pubescent branches, leaves, bracts, and





**Figure 1.** Stachytarpheta sprucei. **A**- habit. **B**- Leaf, abaxial surface. **C, D**- Details of the inflorescences showing flowers and buds. A, B and C from inselbergs of Minas Gerais, Brazil. D. from an inselberg of Guyana. Photo A by Suzana Martins; B and C by Marcelo Brotto; D by Whaldener Endo.

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calyces (Moldenke 1949). However, both *S. roraimensis* and *S. roraimensis* var. *pubescens* were merged under the name *S. sprucei* by Aymard & Jansen-Jacobs (2007), and they are clearly the same taxon.

Stachytarpheta sprucei shares the winged branches with S. gesnerioides, S. alata, and S. tomentosa, a peculiar feature within the genus. However, leaf and flower morphology in S. sprucei promptly evidenced similarity only with S. alata and S. tomentosa. First described as S. gesnerioides var. alata (Moldenke 1983), later raised to species level by Atkins (2005), S. alata remained known only by the type specimen from the municipality of Medina, state of Minas Gerais (Atkins 2005; Cardoso & Salimena 2020). It was characterized by the conspicuously winged branches, chartaceous leaves, and loosely-flowered inflorescence with rachis visible (Atkins 2005). Stachytarpheta tomentosa was originally described from an inselberg from the municipality of Itarana, state of Espírito Santo (Cardoso et al. 2019). However, its distribution was extended to other inselbergs of the states of Espírito Santo and Minas Gerais (Cardoso et al. 2021b). This species was characterized by the winged branches, elliptical or ovate leaf blades, adaxially puberulent or strigose, abaxially tomentose, and inflorescences with bracts caudate at apex, tomentose abaxially, calyx with four teeth, and blue corolla with white or yellow throat (Cardoso et al. 2019; 2021b).

When analyzing the *Stachytarpheta* collection of the largest Brazilian herbarium (RB), we found two specimens (A.P. Duarte 8786 and 10409) collected in the municipality of Medina, the original locality of *S. alata*. These two specimens share all characteristics described in the protologue of *S. alata*, but in contrast with the type specimen, they have branches with less conspicuous wings, similarly to *S. tomentosa*. In addition, they present flowers with 4-toothed calyces. Consequently, it was possible to verify a gradient of morphological variation between the specimens of *S. alata* and *S. tomentosa*, and conclude that they should belong to the same taxon.

Cardoso et al. (2019) differentiated S. tomentosa from S. sprucei mainly by the winged branches of the first, vs. not winged branches of the later, following the poorly detailed description of *S. sprucei* provided by Atkins (2005), which unfortunately has some inconsistencies and led to taxonomic misinterpretations. However, although more conspicuous in the type specimen of *S. alata*, the wings are always present in S. sprucei and S. tomentosa specimens. The careful morphological analyses of the specimens of these three taxa showed that their diagnostic features are the same: tetragonal branches, winged, petiolate leaves, chartaceous, densely hairy abaxially, inflorescences with bracts caudate at apex, calyx hirsute along the ribs, 4-toothed with 2 sinuses, and corolla blue or blue-lilac, the throat yellow, green or white, and with infundibular, and curved tube. Thus, despite the extensive geographical distance between populations of previously recognized S. sprucei, S. atala and S. tomentosa, no additional morphological feature was found that could allow the differentiation between them.

Even when these plants occur in two different phytogeographic domains isolated by a dry corridor of Caatinga to the north, Cerrado in the central portion, and Chaco to the south (Ab'Sáber 2003), we conclude, through the morphological concept, that *S. sprucei*, *S. alata*, and *S. tomentosa* are conspecific. Therefore, we propose *S. alata* and *S. tomentosa* as new heterotypic synonyms of *S. sprucei*, the first published name (Moldenke 1940; Atkins 2005; Cardoso *et al.* 2019).

**Distribution and Habitat:** Stachytarpheta sprucei is endemic to South America, occurring in northern and eastern Brazil, Colombia, Guyana, and Venezuela (Fig. 2). It inhabits inselbergs, tepuis, and savannas in the Amazon Forest domain, and tops of inselbergs surrounded by forest in the Atlantic Forest domain. Collected at altitudes between 150 and 1000 m.

It is the unique species of *Stachytarpheta* that grows in islands of montane vegetation (inselbergs and tepuis) of South America. The influence of past climatic fluctuations in tropical rainforests during the Pleistocene, especially in South America, has been widely debated, showing that species distributions have been strongly affected (e.g.: Cerling et al. 1997; Jackson & Overpeck 2000; Colinvaux et al. 2000; Kukla et al. 2002; Auler et al. 2004; Mayewski et al. 2004; Ledru et al. 2005; Pessenda et al. 2005; Santos et al. 2007; Lawing & Polly 2011; Dutton & Lambeck 2012; Maciel et al. 2017; Masa-Iranzo et al. 2021). During these fluctuations between wet and dry periods, inselbergs and tepuis of the rain forest zone formed xeric islands as refuges for several species, which became extinct elsewhere (Duellman 1979; Prance 1982; Porembski et al. 1994; Prance 1996). Thus, the current distribution of S. sprucei in distant islands of montane vegetation of the Amazon and Atlantic Forests may be a relict. This hypothesis is of course something that should be further investigated.

There is no information on the dispersion mechanism of *Stachytarpheta* species. Fruits are dry, schizocarpic, divided at maturity into two cluses, the outer surface is brown to black, reticulate or smooth (Atkins 2005; O'Leary *et al.* 2012). The commissure is often hardly discernible as a fine line between the cluses, and many species have a long apical stylopodium (Atkins 2005; Cardoso & Salimena 2020). According to Atkins (2004), in most Verbenaceae genera, the fruits remain within the persistent calyx, which closes completely, and presumably are dispersed from the mother plant as a single unit. Presumably, after dispersion, perhaps by rain-wash (soil and water movement), the calyx would eventually rot away, leaving the fruits ready to germinate under favorable conditions (Atkins 2004).

**Morphological affinities:** *Stachytarpheta sprucei* is similar to *S. gesnerioides*, sharing with this species the winged branches, blue or blue-purplish corollas, yellow, green or white at throat, with infundibular, and curved tube.



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They can be distinguished by the degree of ramification of the plant, insertion and consistency of the leaves, and number of calyx teeth. The main differences between *S. sprucei* and the similar *Stachytarpheta* species from Gesnerioides group are resumed in the Table 1. All of them are endemic to South America, occurring mainly in Brazil (Atkins 2005), but are not sympatric. Illustrations of the species can be found in Atkins (2005) and Cardoso *et al.* (2019).

Specimens examined: Brazil. Espírito Santo: Água Doce do Norte, 28 April 2008, A.P. Fontana et al. 5094 (MBML); Águia Branca, Rochedo, 7 June 2006, V. Demuner et al. 2457 (CESJ, MBML); Itarana, Pedra da Onça, 16 January 2013, L. Kollmann et al. 12593 (MBML); Itarana, Pedra da Onça, 1 June 2000, L. Kollmann et al. 2938 (CESJ, MBML), Itarana, Pedra da Onça, 20 April 2020, P.M. Gonella et al. 1156 (MBML); Mantenópolis, 25 September 2012, A.P. Fontana et al. 7462 (MBML); Nova Venécia, APA da Pedra do Elefante, 15 December 2016, L. Kollmann et al. 13244 (CESJ, MBML). Minas Gerais: Mantena, 14 December 1995, G.E. Valente & A. Azevedo 152 (VIC, CESJ); Medina, 25 February 1967, A.P. Duarte 10409 (RB, RFA); Medina, entre Itaobim e Medina, 3 February 1965, A.P. Duarte 8786 (RB); Mucury, [Teófilo Otoni], 1874, C. Schreiner s.n. (R 32300); Monte Formoso, Fazenda Boa Vista, 2 January 2005, D.R. Silva 12 (HUEM); Teófilo Otoni, Mg-418, 8 January 2011, L.F.A. de Paula et al. 166 (BHCB); Teófilo Otoni, Fazenda de Dr. Vitor Caminhas, ilha de vegetação sobre inselbergue, 20 December 2015, L.F.A. de Paula 1016 (RB); Teófilo Otoni, Mg-418, 27 Dec. 2011, L.F.A. de Paula et al. 604 (BHCB). Roraima: Cantá, Serra Grande, 13 November 2014, R.C. Forzza et al. 8387 (CESJ, RB); estrada Boa Vista-Pacaraima (BR-174), Vila Pacaraima, 19 October 1991, S. Almeida & M. Cordeiro 595 (HUEFS); Rio Branco, frontier between territorio do Rio Branco, Brazil and Estado Bolivar, Venezuela, 31 December 1954, B. Maguire & C.K. Maguire 40460 (NY); Rio Branco - Rio Surumu, February 1909, E. Ule 7975 (K); Serra do Sol, 11 October 1995, I.S. Miranda 1162 (INPA); Urucuá, contraforte da Serra do Maturuca, 19 November 1954, W.A. Rodrigues 102 (INPA). Colombia. Casanare: 4 kms. al norte de Tauramena, en Cañoseco, 1 July 1961, L. Uribe 3769 (US). Guyana. Potaro-Siparuni: Pakaraima Mts, near base of Malakwalai-Tipu, 9 July 1994, T.W. Henkel & M. Chin 5483 (U, US); U. Takutu-U. Essequibo: Kanuku Mts., Moco Moco Mt., 10 November 1987, M.J. Jansen-Jacobs 830 (U, US), 10 Km E of Dadanawa Ranch Compound, 4 June 1997, D. Clarke 5161 (U, US); Rupununi savannas, Baboon Hill (Sabrina Tau) 1.5 km S of Sand Creek Village, 24 June 1989, L.J. Gillespieet al. 1775 (U, US). Venezuela. Bolívar: Agua Amena, 265 km SW of Caicara del Orinoco, 6 September 1985, J.A. Stevermark et al. s.n. (USF 131433); Río Parguaza, Cerro Negro Parado, 27 December 1955, J.J. Wurdack & J.V. Monachino 40980 (P, US).

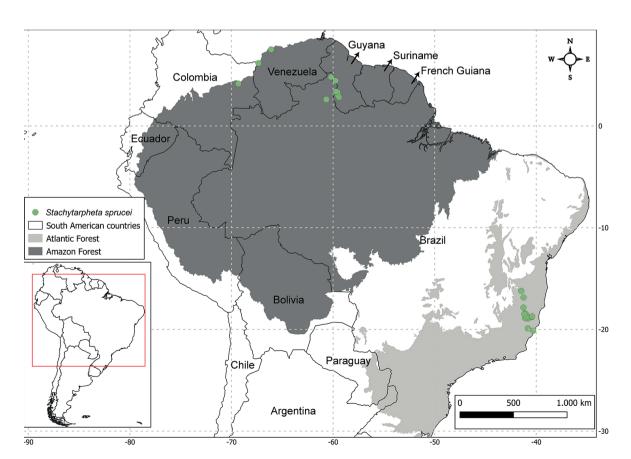


Figure 2. Distribution map of Stachytarpheta sprucei.

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**Table 1.** Morphological comparison between Stachytarpheta sprucei and the species from the informal group Gesnerioides.

Caracter	S. amplexicaulis	S. gesnerioides	S. reticulata	S. sprucei
Ramification	much branched	little branched	much branched, rarely little branched	much branched
Wings of the branches	absent	present	absent	present
Leaves insertion	sessile	sessile or subsessile	sessile or petiolate	petiolate
Leaf blade consistency	chartaceous	subcoriaceous or coriaceous	strongly coriaceous	chartaceous
Leaf blade base	auriculate	cuneate or attenuate	cuneate, truncate, or cordate	cuneate or attenuate
Leaf blade abaxial surface	not foveolate	often foveolate	foveolate	not foveolate
Bracts length	0.7–1.1 cm	1–1.2 cm	0.6–1 cm	0.8-1.6
Calyx teeth	four	five	five	four
Corolla tube in relation to rachis	straight or curved	curved	straight or curved	curved
Color of the corolla throat	blue	yellow, green, or rarely white	white	yellow, green, or rarely white

### Identification key to species in the Gesnerioides group of Stachytarpheta

1. Leaf base auriculate, auricles overlapping those of the opposite leaf	S. amplexicaulis
1'. Leaf base attenuate, cuneate, truncate or cordate	2
2. Leaves chartaceous; calyx 4-toothed (plants from the Amazon and Atlantic Forests)	S. sprucei
2'. Leaves subcoriaceous to strongly coriaceous; calyx 5-toothed (plants from the South American d	ry diagonal) 3
3. Branches winged; bracts $1\!-\!1.2$ cm long; calyx externally hirsute along the ribs, puberulent or pube corolla throat often yellow or green, rarely white	
3'. Branches not winged; bracts 0.6–1 cm long; calyx externally puberulent or pubescent; corolla the	

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