STRUCTURAL BOTANY - ORIGINAL ARTICLE



Morphological analyses support taxonomic updates in Brazilian species of *Stylosanthes* Sw. (Papilionoideae, Leguminosae)

Danilo Soares Gissi¹ • Benjamin M. Torke² • Marcelo Fragomeni Simon³ • Mario Tomazello-Filho⁴ • Ana Paula Fortuna-Perez¹

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Abstract

Stylosanthes Sw. is a pantropical genus primarily distributed throughout the Americas, with the Brazilian Cerrado serving as its principal center of diversity. Stylosanthes species have a subshrub habit, trifoliolate leaves, amplexicaul stipules, and loments with a rostrum derived from the remnant style. Many of its species hold significant economic potential and are widely used as cattle fodder. Systematic examinations involving morphology and nomenclature have highlighted the imperative need for taxonomic updates in select species. Given the observed morphological and ecological differences, a taxonomic reevaluation of Stylosanthes guianensis (Aubl.) Sw. was deemed necessary, leading to the elevation of its varieties to the species level. The taxonomic changes include the new combinations S. microcephala (M.B. Ferreira & Sousa Costa) Gissi, S. pauciflora (M.B. Ferreira & Sousa Costa) Gissi, and S. pubescens (Pilger) Gissi, as well as the reinstatement of Stylosanthes pohliana Taub. as an accepted species. X-ray imaging of leaflets emerges as a valuable tool for taxonomic discrimination. Additionally, a novel discovery is presented with the recognition of an elaiosome in the fruits of S. guianensis, constituting a noteworthy addition to the tribe Dalbergieae. A novel species within the genus is described, and a neotype for S. nunoi Brandão is designated due to the loss of the holotype. This study not only presents nomenclatural modifications but also provides illustrations, comments on diagnostic characteristics, distribution maps, and preliminary IUCN conservation assessments.

Keywords Dalbergieae · Elaiosome · Estilosantes · Fabaceae · Forage

1 Introduction

The genus *Stylosanthes* Sw. belongs to the Leguminosae Juss. family, subfamily Papilionoideae DC., and Dalbergieae Bronn ex DC. tribe. This tribe is divided into three informal clades: Adesmia, Dalbergia, and Pterocarpus. *Stylosanthes*

- □ Danilo Soares Gissi dsgissi@gmail.com
- ¹ Institute of Biosciences—IBB, Department of Biodiversity and Biostatistics, São Paulo State University—UNESP, PO Box 510, Botucatu, São Paulo 18618-970, Brazil
- ² Center for Biodiversity and Evolution, New York Botanical Garden, 2900 Southern Blvd., Bronx, NY 10458-5126, USA
- Embrapa Recursos Genéticos e Biotecnologia, PqEB, PO Box 02372, Brasília, Distrito Federal 70770–917, Brazil
- Department of Forest Resource, Escola Superior de Agricultura Luiz de Queiroz, University of São Paulo, Av. Pádua Dias N° 11, Piracicaba, São Paulo 13418-900, Brazil

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is nested in the last one (Lavin et al. 2001; Klitgaard and Lavin 2005). *Stylosanthes* species are easily distinguished from other Dalbergioids by their subshrub habit, trifoliolate leaves, amplexicaul and bidentate stipules, inflorescences composed of several spikes, and loment with one or two articles and a rostrum derived from the remnant style (Mohlenbrock 1957; Costa 2006). The genus has approximately 50 species mainly distributed throughout the Americas, with a few species native to Africa and Asia (Mohlenbrock 1957; Costa 2006). The Brazilian *Cerrado* represents the primary center of diversity for the genus, with 26 species (Mohlenbrock 1957; Costa 2006; Gissi 2020).

Many species of *Stylosanthes* are used as tropical forage. They stand out for their colonizing characteristics, prospering on low-fertility soils, high productivity of protein, and high seed production (Fernandes et al. 2005; Karia et al. 2010). Furthermore, like many legumes, plants of this genus are capable of fixing nitrogen (Taubert 1890; Miranda et al. 1999). N-fixing forage legumes may increase milk and meat production and even reduce greenhouse gas and enteric



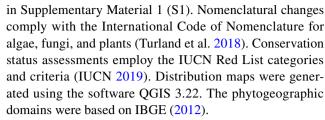
methane emissions (Boddey et al. 2020). Some studies have demonstrated a promising adaptive response of cultivated *Stylosanthes* species to elevated temperatures associated with climate change (Martinez et al. 2014; Alzate-Marin et al. 2021a). However, continued temperature increases could lead to a significant reduction in the distribution of wild species and disrupt pollination (Alzate-Marin et al. 2021b; Maluf et al. 2022; Bonifácio-Anacleto et al. 2024). Nevertheless, Brazil ranks among the foremost producers of *Stylosanthes* seeds, particularly the cultivar "Campo-Grande" of *Stylosanthes capitata* Vogel and *S. macrocephala* M.B. Ferreira & Sousa Costa, and the cultivar "Bela" of *Stylosanthes guianensis* (Aubl.) Sw. (Embrapa Gado de Corte 2007, 2019).

Several authors have extensively examined the taxonomy of this group (Burkart 1939; Mohlenbrock 1957, 1962; Ferreira and Costa 1979;'t Mannetje 1984; Costa 2006; Vanni 2017), but these studies often diverge in terms of recognition of some taxa, and the circumscription of species is still challenging. Despite Costa's (2006) revisional work, several species have been poorly studied in the genus, resulting in confusion about taxonomy and nomenclature, such as *Stylosanthes guianensis* infraspecific classification ('t Mannetje 1984; Vanni 2017).

During an extensive analysis of the morphology and nomenclature of *Stylosanthes* species from Brazil (Gissi 2022), it was clear that taxonomic updates were needed. In the present study, we reevaluated the complex infraspecific taxonomy of *Stylosanthes guianensis* by examination of herbarium specimens, including type collections, morphological analysis, and X-ray photographs of leaflets. Additionally, we recognize the presence of an elaiosome in the fruits for the first time within the genus. In addition, a new species of *Stylosanthes* is described, and a neotype for *Stylosanthes nunoi* Brandão is designated due to the loss of the holotype.

2 Materials and methods

Field expeditions were conducted in the state of São Paulo (in the municipalities of Botucatu, Pardinho, and Buri) and in the Distrito Federal (Brasília), where numerous taxa addressed in this study were observed and collected. The collected samples were deposited in the herbarium BOTU. Exsiccates from the herbaria B, BHCB, BLA, BM, BOTU, CEN, CEPEC, ESA, F, FURB, GH, HVAT, HUEFS, K, M, MBM, NY, P, PACA, PAMG, RB, UB, UFMT, UPCB, US, W, and WAG were examined personally or using virtual herbaria such as Reflora—https://floradobrasil.jbrj.gov.br/reflora/herbarioVirtual/(BFG 2022) and SpeciesLink—https://specieslink.net (CRIA 2023). All the cited acronyms follow the Index Herbariorum (Thiers, updated continuously). The complete list of the examined specimens is presented



The morphological terminology adopted in this study was based on Font-Quer (1993), Harris and Harris (2001), and Beentje (2010) for general morphological descriptions. For 2-D and 3-D shape descriptions, the framework provided by Radford et al. (1974) was followed. Inflorescence morphology was characterized following Weberling (1989), while leaf venation patterns were described according to Ellis et al. (2009). Morphological characters were photographed under a stereomicroscope (Leica M205C, Germany) with an attached camera (Leica DFC 425).

We employed the morphological species concept to assess and delineate species boundaries (Cronquist 1978; Bisby and Coddington 1995). This concept defines species as "the smallest natural populations permanently separated from each other by a distinct discontinuity in the series of biotypes" (Cronquist 1978; Bisby and Coddington 1995). In alignment with this approach, we conducted a detailed analysis of the characteristics currently used to distinguish taxa within the genus, focusing particularly on traits such as indumentum, leaf venation, and fruit rostrum size.

Fruits of *Stylosanthes guianensis* were chosen for study due to the presence of visible glands on their bases (Figs. 1a, d, g, j, 2e). They were transverse-sectioned by hand and treated with Sudan IV reagent to detect total lipids (Johansen 1940). One non-sectioned fruit was fully immersed in the reagent. The slides were examined using a BX 41 photomicroscope (Olympus, Japan) and the relevant results were documented using a coupled C-7070 digital camera (Olympus, Japan).

X-ray images of the leaflets were obtained using a digital X-ray machine (Faxitron X-ray, MX-20 DC12), with an exposure time of 8 s at a voltage of 26 kV (Schneider et al. 2018). Dried terminal leaflets were chosen and photographed abaxially. Measurements were made using the ImageJ software (Schneider et al. 2012).

3 Results

Taxonomic updates in Brazilian *Stylosanthes* – The morphological analysis, particularly of leaflet venation, as well as ecological differences, support the distinction of the varieties of *S. guianensis* sensu Costa (2006, Table 1) and justifies their elevation to species level. The examination of the type of *Stylosanthes pohliana* Taub., a name that has been treated as a synonym of *S. guianensis* (Mohlenbrock 1957;



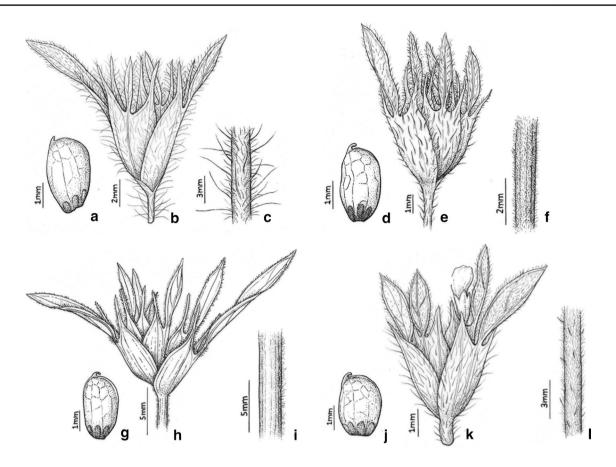


Fig. 1 Inflorescences, articles, and stems of the new combinations of *Stylosanthes*. S. guianensis: a Article; b Inflorescence; c Stem. S. microcephala: d Article; e Inflorescence; f Stem. S. pubescens: g Article; h Inflorescence; i Stem. S. pauciflora: j Article; k Inflorescence; l Stem. a, b, c Coradin 8425 d, e, f Coradin 8397 g, h, i Coradin 8152 j, k, l Coradin 8105

Costa 2006), allowed us to conclude that it corresponds to a completely different taxon, which is re-established here as an accepted species. During our herbarium survey, we encountered specimens representing a new species of *Stylosanthes*, which is described herein. These nomenclatural changes and taxonomic updates are elaborated in greater detail in the taxonomic treatment provided below.

Typification of Stylosanthes nunoi — Given the apparent loss of all original material of S. nunoi, a neotype is designated from materials of the species deposited in the PAMG herbarium. While, as indicated by personal communication with curators at PAMG who collaborated with Professor Mitzi Brandão, it seems likely that errors were made in the citation of material in the protologue, we have no way of resolving the details of those errors and were unable to locate any material that was definitely associated with S. nunoi by Brandão prior to or at the time of its publication; nor did we find any duplicates of the type gathering.

Fruit histochemistry – The pericarp of *S. guianensis*, in its basal portion, exhibits glands containing lipophilic

compounds that reacted positively with Sudan IV (Fig. 2e-g). The cross-section of the fruit in that portion shows that the pericarp has a one-layered exocarp with papillose cells and a multilayered parenchymatous mesocarp, with cells of irregular shapes and varying in size. The endocarp is also one-layered, with thin-walled cells. All of the pericarp cells exhibit a lipophilic content.

X-ray images of the leaflets – X-ray images of leaflets revealed distinctive characteristics crucial for species differentiation within the genus (Fig. 3, Table 2). The venation type is eucamptodromous with an excurrent attachment of the secondaries to the midvein. Higher-order ramification was not observed in the studied species. The secondaries are alternate and may or may not form a thick marginal vein. Differences between the studied species include the presence or absence of a marginal vein, the number of secondary veins, the extent to which they reach the leaflet margin, and their spacing (Fig. 3, Table 2).

In *Stylosanthes guianensis*, there is no marginal vein present, and some of the secondary veins fail to reach the margin of the leaflet (Fig. 3a). The number of secondaries varies



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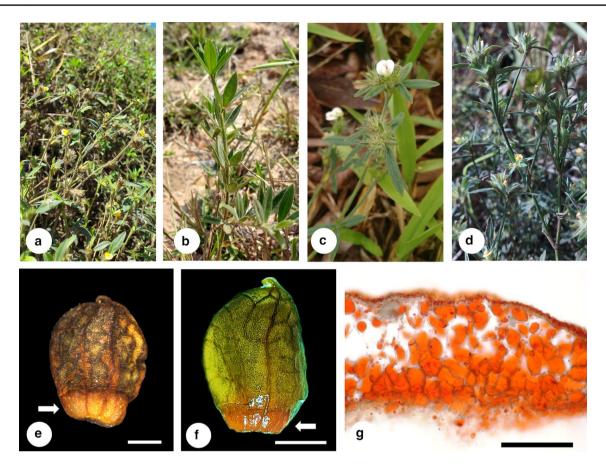


Fig. 2 Morphological aspects of *Stylosanthes*. **a** *S. guianensis* in the field; **b** *S. pauciflora* in the field; **c** *S. microcephala* in the field; **d** *S. pubescens* in the field; **e** *S. guianensis* loment with glandular tissue indicated by the white arrow; **f** Loment of *S. guianensis* with the oil glands stained with Sudan IV (arrow); **g** Photomicrograph of a transverse section of the oil glands at the loment base of *S. guianensis*, stained with Sudan IV, displaying cells impregnated with lipophilic material

Table 1 Taxonomic changes in the *Stylosanthes guianensis* complex

t' Mannetje (1977, 1984), Mohlenbrock (1957)	Ferreira and Costa (1979)	Costa (2006)	Vanni (2017)	This study
S. guianensis var. guianensis	S. guianensis var. vulgaris	S. guianensis var. guianensis	S. guianensis var. guianensis	S. guianensis
_	S. guianensis var. canescens	S. guianensis var. canescens	S. guianensis var. gracilis	S. pubescens
_	S. guianensis var. microcephala	S. guianensis var. microcephala	S. guianensis var. guianensis	S. microcephala
_	_	S. guianensis var. pauciflora	Nomen nudum	S. pauciflora
_	_	S. guianensis var. guianensis	_	S. pohliana
_	_	S. nunoi	S. guianensis var. guianensis	S. nunoi

from 6 to 9 pairs, and their spacing from 2.5 to 3.7 mm. In *S. pauciflora* (M.B. Ferreira & Sousa Costa) Gissi, all the secondaries reach the margin, where their thick terminal portions form a distinct marginal vein (Fig. 3b). The number of secondaries varies from 7 to 9 pairs, and their spacing from 1.7 to 2.5 mm. In *S. microcephala* (M.B. Ferreira & Sousa Costa) Gissi, no marginal vein is present, although all the secondaries reach the margin (Fig. 3c). The number of secondaries varies from 4 to 5 pairs, and their spacing from

2.0 to 3.0 mm. In *S. pubescens* (Pilger) Gissi, there is also no marginal vein present, and all secondary veins reach the margin (Fig. 3d). The number of secondaries varies from 7 to 9 pairs, and their spacing varies from 2.5 to 3.2 mm. In *S. arundinella* Gissi, a marginal vein is not apparent, and all secondaries reach the margin (Fig. 3e). The number of secondaries varies from 6 to 10 pairs, and their spacing from 2.0 to 3.0 mm. In *S. nunoi*, there is no marginal vein present and all secondaries reach the margin (Fig. 3f). The number



Fig. 3 Leaflets' x-ray photographs. a S. guianensis; b S. pauciflora; c S. microcephala; d S. pubescens; e S. arundinella; f S. nunoi; g S. pohliana; h S. campestris. Scale: 10 mm. a Gissi 425 b Coradin 8077 c Gissi 421 d Gissi 384 e Labiak 5989 f Onishi 980 g Pereira-Silva 5309 h Viana 3483

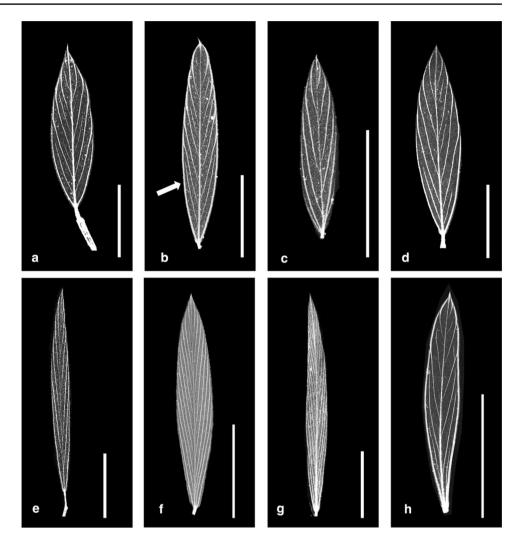


Table 2 Morphological characteristics of secondary veins in different *Stylosanthes* species

Species	Marginal vein presence	Secondary veins reaching margin	Number of sec- ondary veins	Spacing between secondary veins (mm)
S. guianensis	No	Not all	6–9	2.5–3.7
S. pauciflora	Yes	All	7–9	1.7-2.5
S. microcephala	No	All	4–5	2.0-3.0
S. pubescens	No	All	7–9	2.5-3.2
S. arundinella	No	All	6–10	2.0-3.0
S. nunoi	No	All	7–12	0.8-1.0
S. pohliana	No	All	7–12	1.1-1.7
S. campestris	Yes	Not all	6–8	2.3-2.7

of secondaries varies from 7 to 12 pairs, and their spacing from 0.8 to 1.0 mm. In *S. pohliana*, there is no marginal vein present and all secondary veins reach the margin of the leaflet (Fig. 3g). The number of secondaries varies from 7 to 12 pairs and their spacing is from 1.1 to 1.7 mm. In *S. campestris* M.B. Ferreira & Sousa Costa, a marginal vein is formed by the thick basalmost veins that extend through

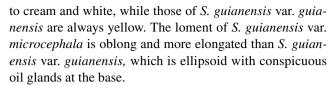
two-thirds of the blade length and continue through the distal portions of subsequent secondary veins (Fig. 3h). Not all secondary veins reach the margin of the leaflet. The number of secondaries varies from 6 to 8 and their spacing is from 2.3 to 2.7 mm.



4 Discussion

Stylosanthes guianensis nomenclature changes - Stylosanthes guianensis was first described in the genus Trifolium L. by Aublet (1775) and later transferred to Stylosanthes by Swartz (1789). Since then, several taxonomic changes have been proposed related to S. guianensis (Chodat 1898; Hassler 1919;'t Mannetje 1977, 1984; Vanni 2017), see Table 1. Mohlenbrok (1957) recognized two subspecies and considered more than 20 synonyms under them, considering that the morphological variation within the species forms a gradient, and that synonymized taxa do not display geographical disjunctions. Subsequently, 't Mannetje (1977) recognized six infraspecific names within the species. Focusing on the Brazilian material, studies led by Mitzi Brandão Ferreira and Nuno M. S. Costa described several new species of the genus from Minas Gerais and identified four varieties within S. guianensis (Ferreira and Costa 1979; Brandão et al. 1990). More recently, Vanni (2017) retained only two varieties and subsumed within S. guianensis several additional names as synonyms.

The four varieties recognized by Ferreira and Costa (1979) and by Brandão et al. (1990) were Stylosanthes guianensis var. vulgaris M.B. Ferreira & Sousa Costa, S. guianensis var. canescens M.B. Ferreira & Sousa Costa, S. guianensis var. microcephala M.B. Ferreira & Sousa Costa, and S. guianensis var. pauciflora M.B. Ferreira & Sousa Costa. These varieties were united under the same species mainly because of the loment with visible glands at the base and a very short (less than 1 mm), generally rudimentary rostrum. However, other attributes, particularly anatomic features (Gissi et al. 2022), distinguish these varieties consistently and support their recognition as distinct species. For example, S. guianensis var. canescens is unique in the combination of lacking secretory emergences on the stem and leaves and having non-glandular trichomes alternately distributed along the stem, and whitish, non-glandular trichomes covering the inflorescences. S guianensis var. pauciflora can be recognized by its large fiber caps at the margins of the leaflets and an eccentric midrib. Although S. guianensis var. guianensis and S. guianensis var. microcephala were indistinguishable from each other in terms of anatomical features of the leaflets and stem (Gissi et al. 2022), they can be distinguished by macromorphological characters. Stylosanthes guianensis var. microcephala differs from S. guianensis var. guianensis in the stems glabrescent or covered with short bristles (< 1 mm vs. 1-3 mm) and nonglandular trichomes. The leaflets are smaller (10–15 mm vs. 20–40 mm). The inflorescence is formed by one, rarely two, spikes, in cupuliform shape, 6-10 mm long, in opposition to capitate or globose in S. guianensis var. guianensis, formed by more than 2 spikes. The flowers vary from yellow



The nomenclature adopted by Ferreira and Costa 1979; Brandão et al. 1990 had some inconsistencies. For example, *Stylosanthes guianensis* var. *vulgaris* cannot be used as a type variety and needs to be treated as a synonym of *Stylosanthes guianensis* var. *guianensis*. Furthermore, *S. guianensis* var. *canescens* was found to be a synonym of *S. guianensis* var. *pubescens* Pilger after the examination of the holotypes of these taxa.

Our analysis of herbarium specimens from Brazil and abroad, as well as the study of living specimens in the field, leads us to adopt a strict definition of S. guianensis, corresponding with the formely recognized typical variety. The other taxa treated as varieties of S. guianensis by Ferreira and Costa (1979) and by Brandão et al. (1990) are individually distinct in morphology and are therefore treated here as distinct species, necessitating three new combinations: S. microcephala (M.B. Ferreira & Sousa Costa) Gissi, S. pauciflora (M.B. Ferreira & Sousa Costa) Gissi, and S. pubescens (Pilger) Gissi. We propose this nomenclatural solution as a more accurate reflection of the taxonomic diversity within the S. guianensis complex. Furthermore, assigning species rank rather than varietal rank may enhance conservation focus on the group, as species-level classifications typically garner greater attention in conservation initiatives. Anatomical and molecular studies corroborate our decision to treat the recognized taxa as distinct species (Karia 2008; Santos-Garcia et al. 2012; Gissi et al. 2022).

Additionally, while S. pohliana was historically treated as a synonym of S. guianensis (Mohlenbrock 1957; Costa 2006), re-examination of the type specimen at NY herbarium revealed sufficient morphological characteristics to warrant its recognition as a distinct species. Stylosanthes pohliana can be separated from S. guianensis mainly by having an erect habit (vs. prostate), leaflets narrowly elliptic (vs. elliptic), terminal inflorescence formed by 1 spike (vs. inflorescence capitate formed by 2-6 spikes), loment with one or sometimes two fertile articles, oblong, weakly reticulate, without elaiosome (vs. only one article, ellipsoid, markedly reticulate, with distinct elaiosomes at the base). Some specimens were also identified as S. campestris, which can be distinguished by its stems lacking bristles, discolorous leaflets that are predominantly obovate to elliptical with a conspicuous marginal vein extending up to three-quarters of the leaflet length, and an acuminate apex (Fig. 3h). In S. campestris, bristles are confined to the leaflet margins and midvein, giving the leaflets a serrate appearance, and the inflorescence is capitate.



Typification of Stylosanthes nunoi – Stylosanthes nunoi was initially described by Prof. Mitzi Brandão (1991) based solely on material collected by N.M.S. Costa (#15) in Urucuia, Minas Gerais, which was reportedly deposited in the RB and PAMG herbaria. However, these materials could not be located, and consultations with specialists familiar with Prof. Brandão suggested the possibility of their loss. Furthermore, Vanni (2017) cited J. Ramos & R. Sousa 66 (holotype RB, isotype P) as types of S. nunoi, but this material does not correspond to the one designated by Brandão (1991), and no official neotypification was carried out in accordance with the Code (Turland et al. 2018). During a visit to the PAMG herbarium, where Prof. Brandão had worked, several materials identified by her were found, matching the original description and illustration. Consequently, we have designated a new specimen as the neotype. We selected V. C. Souza 14,245 (PAMG44619) as the neotype, as no other materials from the type locality were found. This neotype closely aligns with the original description and was identified by the author of the species. Additionally, duplicates of this specimen are held in other herbaria (ESA, MBM, HUEFS, UFMT).

Loment elaiosome – The loments of *S. guianensis*, *S. microcephala*, *S. pauciflora*, and *S. pubescens* (exhibit noticeable glandular tissue at the basis of the article (Figs. 1a, d, g, j, 2e). Nevertheless, the nature of the secretory content was not clear. Histochemical tests using Sudan IV reagent revealed that these glands secrete oils (Fig. 2f–g). Therefore, this tissue could be classified as an elaiosome, implying a potential association with ant dispersal, with the whole article forming a diaspore.

This study provides the first documentation of an elaiosome in a Dalbergioid legume. It may also represent the first record of an elaiosome associated with the fruit in the family Leguminosae. While elaiosomes have been previously reported in various legume genera, including *Acacia* Mill., *Cytisus* Desf., *Eriosema* (DC.) G. Don., and *Ulex* L., these structures were consistently derived from the seed funicle (Berg 1975; Grear and Dengler 1976; Lengyel et al. 2010; Ortega-Olivencia et al. 2021). Notably, none of these previously studied genera belong to the Dalbergieae tribe.

Further studies on *Stylosanthes* ecology may investigate the possibility of myrmecochory occurring within this genus.

Leaflet X-ray images — Our analysis of leaflet venation in *Stylosanthes* species revealed significant variability in patterns, particularly regarding the number and spacing of secondary veins and the presence or absence of a marginal vein. We observed consistent differences between *S. pauciflora* and the typical variety of *S. guianensis*, which can serve as a distinguishing feature. Additionally, venation patterns help

distinguish *S. pohliana* from *S. campestris*, which is currently misidentified as this species. Secondary vein spacing also provides diagnostic value; in species like *S. nunoi* and *S. pohliana*, the spacing is narrow (no more than 2 mm wide), while in others, such as *S. guianensis* and *S. arundinella*, the broader spacing exposes larger areas of the leaflet blade.

These results add to a growing body of literature showing the taxonomic utility of X-ray imaging of leaflet venation in various taxa of Leguminosae (Lima et al. 2021; Silva et al. 2022; Gissi et al. 2023). Extending the application of this technique to additional species of *Stylosanthes* has the potential to further clarify the taxonomy of the genus, and may even contribute to the discovery of new species.

Taxonomic treatment – In this section, we provide a new circumscription for the *S. guianensis* species complex, which now comprises five species. We also designate a neotype for *S. nunoi* in light of the holotype's loss and describe a new species based on our herbarium examination.

Stylosanthes guianensis (Aubl.) Sw., Kongl. Vetensk. Acad. Handl. 1789: 291. 1789. Trifolium guianense Aubl., Hist. Pl. Guiane: 776. 1775. Astyposanthes guianensis (Aubl.) Herter, Revista Sudamer. Bot. 7: 209. 1943. Stylosanthes biflora var. guianensis (Aubl.) Kuntze, Revis. Gen. Pl. 1: 209. 1891.—Lectotype (designated by t'Mannetje 1977: 351): French Guiana, Macouria, F. Aublet s.n. (BM! [BM00611204]).

Trifolium fluminense Vell. Fl. Flumin.: 316 .1829.—Lectotype: [illustration] published in Vellozo, Fl. Flumin. Icones 7: t. 143. 1831.

Trifolium mediterraneum Vell. Fl. Fumin.: 317. 1829.—Lectotype: [illustration] published in Vellozo, Fl. Flumin. Icones 7: t. 144. 1831.

Stylosanthes guyanensis var. subviscosa Benth., Fl. Bras. 15 (1A): 92. 1859.—Lectotype (designated by Calles 2010: 313): Brazil, Minas Gerais, Córrego do Jaraguá et Rio Jequitinhonha, 1836, J.E. Pohl s.n. (K! [K205133]). syn. nov.

Stylosanthes guianensis var. subviscosa f. viscosissima Hassl., Repert. Spec. Nov. Regni Veg. 16: 221. 1919.—Lectotype (designated here): Paraguay. In campo Nandurucay Sierra de Maracayu, E. Hassler 6454 (NY! [NY3924], isolectotype: GH! [GH26778]). Stylosanthes guianensis var. vulgaris M.B. Ferreira & Sousa Costa, Gen. Stylosanthes: 45. 1979.—Holotype: Brazil. Minas Gerais. Betim. M.B. Ferreira & N.M. de Sousa Costa 310 (RB! [RB00540423], isotype: PAMG! [PAMG5572]).

Figures 1a-c, 2a, 3a.



Distribution and habitat—Stylosanthes guianensis is widely distributed from Mexico to Argentina in savanna environments, grasslands, pastures, swamps, roadsides, and even anthropic and disturbed areas (Fig. 7a).

IUCN conservation assessment (preliminary)—Least Concern (LC). Due to its wide distribution and ruderal characteristics.

Notes—Stylosanthes guianensis comprises plants with prostrate to decumbent habit, highly branched herbaceous stems, covered by viscid, long bristles (1–3 mm) and whitish non-glandular trichomes, elliptical leaflets with inconspicuous secondary veins, and lacking a marginal vein, globose inflorescences with multiple spikes, but lacking a rudimentary axis, only one inner bracteole, yellow flowers, only one fertile article which is ellipsoid in shape and bears a vestigial rostrum, and evident oil glands at the article base forming an elaiosome.

Uses—Several cultivars of S. guianensis are used as fodder in South America, Africa, Asia, and Australia for beef cattle and other animals (Chakraborty 2004; Karia et al. 2010). In Brazil, the most common cultivars are 'Mineirão', 'Cook', 'Pucallpa', and 'Bela' (Karia et al. 2010; Embrapa Gado de Corte 2019). These plants stand out for their high capacity for nitrogen fixation and their ability to incorporate organic matter into the soil, which contributes to soil recovery. The cultivar 'Estilosantes Bela' is more adaptable for argillic soils than other cultivars and may even be useful for nematode control (Embrapa Gado de Corte 2019). Owing to its invasive behavior, S. guianensis can also be considered a weed in cultivated areas and anthropic environments (Lorenzi 2008; Carvalho 2013). Nonetheless, studies have indicated that S. guianensis has potential as a viable cover crop for rehabilitating soils degraded by mining activities or environmental disasters (Silva and Correa 2010; Starr et al. 2013; Velásquez Ramírez et al. 2021).

 Stylosanthes microcephala (M.B. Ferreira & Sousa Costa) Gissi, comb. & stat. nov. Stylosanthes guianensis var. microcephala M.B. Ferreira & Sousa Costa, Gen. Stylosanthes: 46. 1979.—Holotype: Brazil, Minas Gerais, Caeté, 4 Mar 1976, M.B. Ferreira & N.M. de Sousa Costa 306 (RB! [RB00200930], isotype: PAMG! [PAMG5548]).

Stylosanthes guianensis var. gracilis f. esetosa Hassl. Repert. Spec. Nov. Regni Veg. 16: 221. 1919.—Lectotype (designated by Calles 2010: 313): Paraguay. Gran Chaco, Santa Elisa, 23°10′S, 5 Oct. 1903. E. Hassler 2834 (K! [K264199]; isolectotypes: BM! [BM538202], W! [W1906-1175], NY!), syn. nov.

Figures 1d-f, 2c, 3c.



Distribution and habitat—Stylosanthes microcephala is found in Paraguay and Brazil, specifically in the states of Bahia, Distrito Federal, Goiás, Maranhão, Mato Grosso do Sul, Minas Gerais, Pará, Rio de Janeiro, São Paulo, and Tocantins, thriving in habitats such as the *Cerrado*, grasslands, and pastures (Fig. 7b).

IUCN conservation assessment (preliminary)—Least Concern (LC). *S. microcephala* is common throughout the Brazilian and Paraguayan savanna areas.

Notes—This species can be distinguished by its prostrate habit, stems that are either glabrescent or covered with short bristles (<1 mm), and non-glandular trichomes. It generally has smaller leaflets compared to *S. guianensis* (10–15 mm in *S. microcephala* versus 20–40 mm in *S. guianensis*). The inflorescence is cupuliform, 6–10 mm long, and formed by one, or rarely two, spikes, in shape (vs. capitate or globose, in *S. guianensis*). The loment is oblong and more elongated than in *S. guianensis*, with conspicuous oil glands at the base. The flowers vary from yellow to cream and white. It resembles *S. hippocampoides* Mohlenbr., but that species differs in having an indumentum adorned with lengthy golden bristles, capitate inflorescences, and an orbicular upper article.

 Stylosanthes pauciflora (M.B. Ferreira & Sousa Costa) Gissi, comb. & stat. nov. Stylosanthes guianensis var. pauciflora M.B. Ferreira & Sousa Costa, An. Cong. Nac. Bot. 36: 236. 1985. – Lectotype (designated here): Brazil, Minas Gerais, João Pinheiro, 29 May 1976, N.M. de Sousa Costa 628, (PAMG! [PAMG5548], isolectotype: OUPR [OUPR19931]).

Stylosanthes viscosa var. acutifolia Benth. Fl. Bras. 15(1A): 91. 1859.—Lectotype (designated by Calles 2010: 313): Brazil. Pernambuco. Olinda. Sep 1837. G. Gardner 972 (K! [K205132], isolectotypes: P! [P00204807, P00204808], K! [K000205131]). syn. nov.

Figures 1j-1, 2b, 3d.

Distribution and habitat—Stylosanthes pauciflora occurs in Brazil, Venezuela, Peru, and Paraguay, especially in savanna environments such as the *Cerrado*, but also in *Chaco*, highland rocky fields, grassland pastures, and anthropic areas. The main distribution center is in Central Brazil (Fig. 7a).

IUCN conservation assessment (preliminary)—Least Concern (LC). *Stylosanthes pauciflora* is widely distributed in South America.

Notes—Stylosanthes pauciflora presents an erect shrubby habit, a viscid indument with abundant secretory bristles, only one fertile article with conspicuous oil glands at the base, and generally yellow seeds. It can be differentiated from *S. guianensis* by the presence of leaflets with

conspicuous marginal veins and cupuliform inflorescences with only one or two spikes, whereas *S. guianensis* has capitate, globose inflorescences with multiple spikes. Molecular studies corroborate the separation of this species from other species (treated as varieties in those studies) of the *S. guianensis* complex (Karia 2008; Matida et al. 2012; Santos-Garcia et al. 2012).

Nomenclature—In the protologue of *S. guianensis* var. pauciflora (Brandão et al. 1990), a specimen at RB was designated the holotype. However, the material was not found, and we believe the authors have never sent the material to RB. Therefore, we designate the PAMG material, previously the isotype, as the lectotype.

Uses—The cultivars 'Bandeirante' and 'Tardio' refer to this species, which is acknowledged for its high tolerance to anthracnose (Karia et al. 2010).

4. Stylosanthes pubescens (Pilger) Gissi, comb. & stat. nov. Stylosanthes guianensis var. pubescens Pilger, in Engl. Bot. Jahrb. 30: 160. 1901.—Holotype: Brazil, Mato Grosso. Rio Ronuro, May 1899, R. Pilger 625 (B! [B10024417]).

Stylosanthes guianensis var. canescens M.B. Ferreira & Sousa Costa, Gen. Stylosanthes: 44. 1979.—Holotype: Brazil, Minas Gerais, Caeté, 4 Feb 1976, N.M. Sousa Costa & M.B. Ferreira 308, (RB! [RB00200920], isotype: PAMG! [PAMG5561]), syn. nov.

Figures 1g-i, 2d, 3d.

Distribution and habitat—In Brazil, *S. pubescens* occurs in the *Cerrado*, grassland, pasture, and roadside areas. It is also recorded for Bolivia in urban environments (Fig. 7b).

IUCN conservation assessment (preliminary)—Least Concern (LC). *Stylosanthes pubescens* is widely distributed in Brazil and is frequently collected in disturbed areas.

Notes—This species can be recognized by the absence of bristles in the whole plant body. The stems and inflorescences are covered only by whitish non-glandular trichomes, especially in the bracts conferring a canescent aspect. In the stem, non-glandular trichomes are present only on the side adjacent to the axillary buds, and alternate in distribution along the stem.

Taxonomy—Stylosanthes guianensis var. pubescens was previously regarded as a synonym of S. guianensis by Calles and Schultze-Kraft (2010) and by Vanni (2017). When S. guianensis var. canescens was described, the authors did not examine Pilger's material. Vanni (2017) considered all these names to be synonyms of S. guianensis var. guianensis. Upon comparing the type specimens of S. guianensis var. canescens and S. guianensis var. pubescens, we determined that they refer to the same taxon, with Pilger's epithet taking precedence. We chose to recognize this taxon as

a distinct species based on study of additional herbarium material from throughout the range of this taxon, as well as examination of populations in the field, both of which indicated that the taxon is consistently diagnoseable.

Furthermore, *Stylosanthes pubescens* is anatomically distinct from *S. guianensis* by the absence of secretory emergences (Gissi et al. 2022). Secretory structures are valuable for distinguishing species and other taxonomic levels (Lersten and Curtis 1996; Jiang et al. 2010; Bombo et al. 2012; Fortuna-Perez et al. 2012). Molecular studies also support recognizing this variety as a distinct species (Karia 2008; Santos-Garcia et al. 2012).

 Stylosanthes pohliana Taub., Verh. Bot. Vereins Prov. Brandenburg 32: 29. 1890.—Holotype: Brazil. Hab. in Brasiliae provincia Bahiensis et provincia ignota ad Corgodo ("Córrego do") Padre, 1836, J.B.E. Pohl 1997 (W! [W10014]; isotypes: M! [M0110711], NY! [NY3928], K! [K00328045]).

Figures 3g, 6g-h.

Distribution and habitat—Stylosanthes pohliana is restricted to the Brazilian states of Goiás and Bahia, where it occurs in the *Cerrado*, in rock outcrop vegetation (Fig. 7c).

IUCN conservation assessment (preliminary)—Endangered (EN). B2ab(iii,iv,v); S. pohliana is known from only a few collections, none of which were made in protected areas. It occurs in Cerrado vegetation threatened by the expansion of agriculture, deforestation, and out-of-control fires (Klink and Machado 2005).

Notes—Stylosanthes pohliana can be recognized by its erect subshrub habit, setose-sericeous, viscid indumentum characterized by long secretory bristles (1–3 mm long) as well as non-glandular trichomes, indistinguishable or very short (0.5 mm) leaf rachis, concolorous, narrowly elliptic or linear to narrowly oblanceolate, papyraceous leaflets, setose-sericeous lower leaflet surface, with bristles widespread throughout the blade, eccentric midvein, 10–14 pairs of conspicuous, alternate, secondary veins, lack of a marginal vein, terminal inflorescence formed by a single obovate spike, loment with one or sometimes two oblong, weakly reticulate fertile articles, which are glabrous or with scattered trichomes at the base, and with the beak 0.5 mm long, coiled, and glabrous.

6. Stylosanthes nunoi Brandão, Daphne 2 (1): 5. 1991.— Holotype: Brazil. Minas Gerais, Urucuia, solo arenoso, relevo suave ondulado, 500 msm, N.M. de Sousa Costa 15 (RB, not found; isotype: PAMG, not found).—Neotype (designtated here): Brazil. Mato Grosso, São Felix do Araguaia, Beira do Rio Araguaia, entre São Félix



do Araguaia e o encontro com o Rio das Mortes, Praia do Gado, 16 Mar 1997, *V. C. Souza 14,245* (PAMG! [PAMG44619], isoneotypes: ESA! [ESA38368], MBM! [MBM244492], HUEFS! [HUEFS46633], UFMT [UFMT 38712]).

Figures 3f, 4g-i.

Distribution and habitat—Stylosanthes nunoi is restricted to Brazil, where it occurs in the *Cerrado* phytogeographic domain in *Cerrado* vegetation and grasslands (Fig. 7c).

IUCN conservation assessment (preliminary)—Vulnerable (VU). B2ab(iii,iv,v); S. nunoi is restricted to Central Brazil in the Cerrado areas. Deforestation, fire, and agricultural expansion highly threaten these areas (Klink and Machado 2005).

Notes—Stylosanthes nunoi closely resembles Stylosanthes hippocampoides Mohlenbr., but the two species can be differentiated by several morphological characteristics. Stylosanthes hippocampoides typically exhibits up to six secondary veins in the leaflets, whereas S. nunoi presents more than seven. Additionally, the spacing between the secondary veins is larger in S. hippocampoides (1.0–1.3 mm) compared

to *S. nunoi* (0.4–0.6 mm). Another key distinguishing feature is the seed color, with *S. hippocampoides* producing brown seeds, while *S. nunoi* yields black seeds.

7. Stylosanthes arundinella Gissi, sp. nov.—Holotype: Brazil, Tocantins, Arraias. Estrada Vicinal no trevo de Arraias para Campos Belos (TO-050). 8 Mar 2015, *P. H. Labiak*, 5989 (RB! [RB01053500]; isotypes: BOTU!; CEPEC! [CEPEC149991]; UPCB! [UPCB87493]).

Figures 3e, 4a-f, 5, 6a-f.

Diagnosis—Stylosanthes arundinella is similar to S. nunoi Brandão but differs by having pilose-scabrous stems, with very short bristles (0.2–0.3 mm), leaflets narrowly-elliptic (L:W>8), widely spaced secondary veins (>1 mm), allowing the blade to be abaxially visible, inflorescence obovoid to oblong, while S. nunoi has pilose-hispid stems, with longer bristles (0.5–1.0 mm), leaflets elliptic (L:W < 6), narrowly spaced secondary veins (<1 mm), almost covering the entire blade abaxially, and inflorescence globose, capitate.

Fig. 4 Stylosanthes arundinella: a Stems; b Leaf; c Leaf detail with the end of the petiole with a tuft of trichomes and the rachis; d Inflorescence with flower; e Calyx; f Loment with a single article. S. nunoi: g leaflet; h loment; i inflorescence. a-f Labiak 5989 g-i Onishi 980





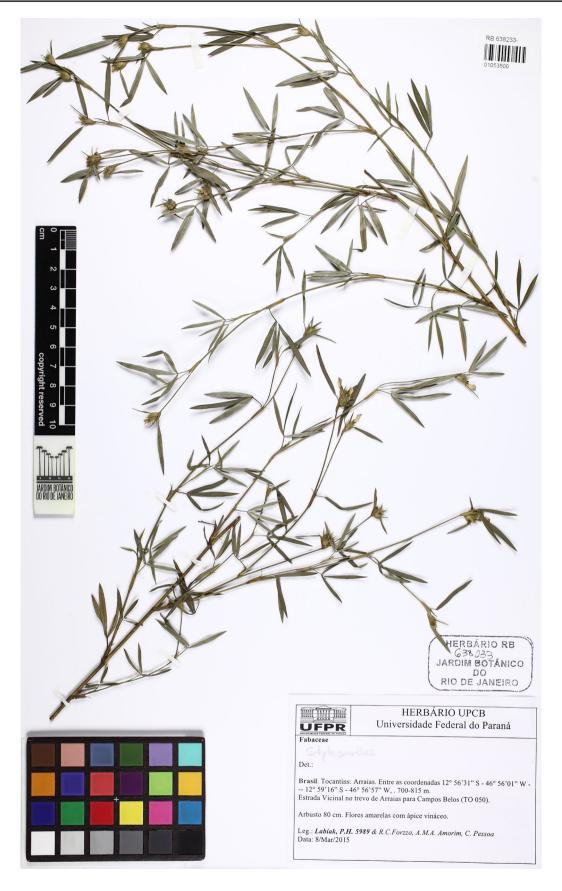
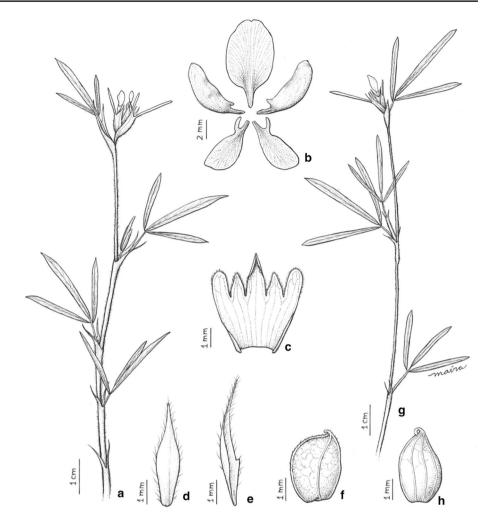


Fig. 5 Stylosanthes arundinella holotype deposited at RB herbarium: Labiak 5989. Reflora-Herbário Virtual (2024)



Fig. 6 S. arundinella: a Habit; b Corolla; c Calyx; d Outer bracteole; e Inner bracteole; f Loment. S. pohliana: g habit; h loment. a-f Labiak 5989 g-h Pereira-Silva 5309



Description—Perennial subshrub 0.8-1 m tall, branched from the base. Stems erect, ligneous near the base, upper branches green with spaced internodes, striate, indumentum pilose-scabrous, viscid, with non-glandular trichomes and short bristles (0.2–0.3 mm). Stipules amplexical with a pilose-scabrous indumentum, sheath 7–12 mm long, teeth needle-like, 3-5 mm long. Leaves trifoliolate. Petiole densely scabrous, adaxially channeled with a tuft of long (ca. 1 mm), non-glandular trichomes and bristles at the apex, 7-11 mm long. Rachis 1.5–2.5 mm long, pilose, rarely with bristles, pulvinule, 0.5 mm long, pilose. Leaflets narrowly elliptic, linear to narrowly oblanceolate, 17-45×2-6 mm, mucronate, rounded at the base, papyraceous, upper surface V-shaped in cross-section, sparsely scabrous with scattered short bristles on the blade and margins, also with appressed non-glandular trichomes, secondary veins inconspicuous, lower surface scabrous, with bristles concentrated mainly above the midvein, midvein slightly eccentric, secondary veins apparent, 6–10 pairs, alternate, marginal vein lacking. Inflorescences terminal and axillary, formed by 1-2(3)spikes, obovoid to oblong, 6-10 mm long, peduncles 1-11 mm long. External bract 1–3-foliolate, sheath $5-6\times3-4$ mm, with golden bristles, teeth of bracts triangular, acute, aristate in the tip; inner bracts unifoliate or without leaflets. Bracteoles 2, hyaline, margins ciliate, outer bracteole entire or with a small lobe at the side, 5 mm long, inner bracteole entire, 4 mm long, rudimentary axis absent. Flowers exserted with a pedicel 1.5 mm long; calyx 3–5 mm long, 5-lobed, margin ciliate, internal and external surfaces glabrous, upper lobes 2-3.5 mm long, obtuse, slightly truncate, lateral lobes 2–3 mm long, acute, lower lobe 3–4 mm, the longest, acute, keel-like. Corolla yellow, glabrous, standard petal with red stripes, suborbicular, unguiculate, retuse at apex, $9.5-11\times10-11$ mm; wings elliptic, spurred at the base, 7×2 mm, keel petals fused at the apex, falcate, spurred at the base, 7×4 mm long; androecium monadelphous; anthers dimorphic, the shorter 5 basifixed, the longer 5 dorsifixed, ovary biovulate. Loment with one fertile article, sometimes also with one aborted article, widely oblong, $2.5-3\times2-2.2$ mm, papillose, strongly reticulate, beak 1 mm long, short hooked, covered with long papillae. Seed purplish-black.

Distribution and habitat—This species is known only from southern Tocantins and northern Goiás, in *Cerrado* vegetation (Fig. 7c).

IUCN conservation assessment (preliminary)—Endangered (EN). B2ab(iii,iv,v); Stylosanthes arundinella is



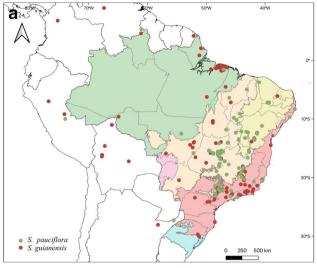






Fig. 7 Distribution maps. **a** *S. pauciflora* (green dots) and *S. guianensis* (red dots); **b** *S. microcephala* (black dots) and *S. pubescens* (purple dots); **c** *S. nunoi* (yellow dots), *S. pohliana* (green dots) and *S. arundinella* (pink dots)

known only from a few collections made outside of protected areas. The *Cerrado* vegetation in these areas is threatened by the expansion of agriculture, deforestation, and poorly controlled fires (Klink and Machado 2005).

Notes—Stylosanthes arundinella is characterized by viscid, pilose-scabrous stems with very short bristles (0.2 mm), an elongate leaf rachis (1.5–2.5 mm long), narrowly-elliptic leaflets with 6–10 pairs of alternate, secondary veins spaced > 1 mm apart but lacking a marginal vein, widely oblong, reticulate-surfaced loments with only one fertile article covered with papillae and short trichomes and a reduced or short-hooked rostrum, and the seeds black and reniform. This species is similar to *S. nunoi*, but the latter has leaves with more than 10, more closely spaced (<1 mm apart) secondary veins, and capitate, golden-hispid inflorescences.

Etymology—L. *arundo*, reed + -*ella*, in reference to the plant habit resembling a small reed or bamboo (Fig. 5).

Paratypes—BRAZIL. **Goiás**, Monte Alegre de Goiás, ca. 25 km by road SW of Monte Alegre de Goiás. 12/III/1973. *W.R. Anderson 6933* (NY! [NY2481785], UB! [UB41854], WAG! [WAG1044515], MO [MO3215649]).

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Author contributions DSG performed the taxonomic and nomenclatural analysis, described the new species, performed the anatomical studies, analyzed the slides, and prepared the images. MTF helped with the x-ray images, not only providing the equipment, but also discussing the results. All authors contributed to the conception and design of the study and the writing of the manuscript.

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Declarations

Conflict of interests The authors assert that the manuscript is free from any conflicts of interest. The objectives and content of the work are original and have not been published previously.



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