

A new species of *Stylosanthes* (Leguminosae – Papilionoideae) from the Chapada das Mesas National Park in Maranhão, Brazil

DANILO SOARES GISSI¹, BENJAMIN M. TORKE², MARIO TOMAZELLO-FILHO³, AND ANA PAULA FORTUNA-PEREZ¹

¹Department of Biostatistics, Plant Biology, Parasitology and Zoology, São Paulo State University–UNESP, Institute of Biosciences–IBB, PO Box 510, Botucatu, SP 18618-970, Brazil; e-mail: dsgissi@gmail.com

²Institute of Systematic Botany, New York Botanical Garden, 2900 Southern Blvd, Bronx, NY 10458-5126, USA

³Department 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

Abstract. A new species of *Stylosanthes* (Leguminosae – Papilionoideae) from the Chapada das Mesas National Park in Maranhão, Brazil, is described. The new species, *S. acicularis*, was misidentified as *S. angustifolia* in the SLUI herbarium. It differs from *S. angustifolia* especially by inflorescence shape and rostrum length. The new species closely resembles *S. hippocampoides* by its small capitate inflorescences, absence of a rudimentary axis beneath the flower, only one inner bracteole, loments with only one fertile article and a very short rostrum, and the absence of a marginal vein and possession of up to five secondary veins in the leaflets. However, the two species differ by stem indumentum, bristle length, leaflet shape and venation, and shape of the outer bracteole margin. A morphological description, illustrations—including X-ray imaging of the leaflet venation—and notes on the geographical distribution, habitat, and conservation status of the new species are presented.

Keywords: Fabaceae, Dalbergieae, X-ray, venation, taxonomy, forage.

Stylosanthes Sw. comprises about 50 species and is distributed mainly in the Neotropics, with only two species in the Paleotropics (‘t Mannetje, 1984; Costa, 2006; Ferreira et al., 2020). It is characterized by subshrubby habit, trifoliolate leaves, amplexicaul fused stipules with two teeth, spiciform inflorescences, and papilionaceous, generally yellow flowers. Fruits are loments with one or two fertile articles and with a rostrum formed by the residual style (‘t Mannetje, 1984; Costa, 2006; Gissi, 2020). The genus was previously divided into two sections, sect. *Stylosanthes*, diagnosed by the presence of only one inner bracteole and the absence of a rudimentary axis in the inflorescence, and sect. *Styposanthes* Vogel, with two inner bracteoles and the presence of a rudimentary axis (i.e., an undeveloped, stiff structure that occurs beneath the flowers adjacent to the inner bracteoles) in the inflorescence (Vogel, 1838). This system was followed by other authors and is useful for

distinguishing species (Mohlenbrock, 1958; Kirkbride & Kirkbride, 1987; Costa, 2006). The sections, however, were found to be non-monophyletic in molecular phylogenetic studies (Vander Stappen et al., 2002, 2003; Oliveira et al., 2021).

Brazil harbors more species of *Stylosanthes* than any other country, with 32 species, 14 of which are endemic (Gissi, 2020). Within Brazil, 25 species of *Stylosanthes* are distributed mainly in the Cerrado domain, in open vegetation physiognomies (following Ribeiro & Walter, 2008), such as *cerrado típico*, *campo sujo*, *campo limpo*, *campo rupestre*, and *veredas* (Costa, 2006; Vanni, 2017; Gissi, 2020). Several species also occur in pastures, lawns, and roadsides (Gissi, 2020). They are sometimes considered to be agricultural weeds due to their invasive behavior in cultivated fields (Carvalho, 2013). Also, cultivars of *S. capitata* Vogel and *S. macrocephala* M.B. Ferreira & Sousa Costa are sold

commercially under the name of Estilosantes ‘Campo Grande’ and are planted for livestock forage (Embrapa Gado de Corte, 2007; Karia et al., 2010; Machado et al., 2010).

While examining herbarium specimens at SLUI, we encountered a specimen of *Stylosanthes* collected in Chapada das Mesas National Park in the state of Maranhão. Although previously identified as *S. angustifolia* Vogel, the specimen not only did not belong to that species but was new to science. Here, we provide a description and illustration of this new species.

Material and Methods

For this study, specimens of all South American *Stylosanthes* species deposited in the following herbaria were analyzed: ALCB, ASE, BOTU, CEN, EAC, ESA, HBRA, HUEFS, HVASF, IAN, INPA, L, MFS, NY, P, R, RB, SLUI, SP, UB, US, WAG (acronyms according to Thiers, 2021). The relevant taxonomic literature on *Stylosanthes* was also consulted (Vogel, 1838; Mohlenbrock, 1958; ‘t Mannetje, 1984; Costa, 2006; Vanni, 2017; Gissi, 2020). The use of morphological terms mainly follows Harris and Harris (2001) and Radford (1974). For a more complete terminology of leaves, Ellis et al. (2009) and Hickey (1973) were also consulted, especially regarding venation terms. Herborized leaflets were radiographed using a digital X-ray machine (Faxitron X-Ray, model MX-20 DC12), with an exposure time of 8 sec at a voltage of 26 kV (Schneider et al., 2018). Photographs of minute morphological traits were taken under a Leica M205C stereomicroscope (Leica, Germany) with an attached Leica DFC 425 camera. The radiographs were used to better characterize venation patterns. A distribution map was generated using QGIS 3.22, and a conservation status assessment was made employing the IUCN Red List categories and criteria (IUCN Standards and Petitions Committee, 2019).

Taxonomic Treatment

Stylosanthes acicularis Gissi & Fort.-Perez, sp. nov.—Type: Brazil. Maranhão, Carolina, Parque Nacional Chapada das Mesas, 337 m, 07°18'53.2"S, 47°02'28.0"W, 06 Apr 2017 (fl, fr), R. V. C. Saraiva s.n. (holotype: SLUI herb. no. 4987 [!]). (Figs. 1–3.)

Diagnosis.—*Stylosanthes acicularis* is similar to *S. hippocampoides* Mohlenbr. but differs by having leaflets linear, less than 1 mm wide, with the primary vein imperceptible, the secondary vein angles 5°–8° and uniform, the bristles on the stem up to 1 mm long and pilose-scabrous, and the outer bracteole bilobed (vs. leaflets elliptical, primary vein easily discernible, secondary vein angles 10°–15° and irregular, stem bristles 2–4 mm long and hispid-pubescent, and the outer bracteole unlobed in *S. hippocampoides*).

Perennial subshrub, 0.6 m tall, branched from the base. Stems erect, ligneous near the base, upper branches green, striate, indumentum pilose-scabrous, viscid, with scattered bristles up to 1 mm long and more numerous non-glandular trichomes, the latter mostly restricted to one side of each internode (the side above the adjacent leaf, i.e., alternating between internodes). Stipules amplexicaul with a pilose-scabrous indumentum, sheath 3–6 mm long, the apex with two slightly spreading teeth on each side, the teeth 3–4 mm long. Leaves trifoliolate; pulvinus 0.5–0.75 mm long, petiole 5–7 mm long, adaxially channeled, sericeous with scattered bristles; rachis up to 1 mm long, pilose, rarely with bristles; pulvinules 0.5 mm long, pilose; leaflet blades 10–18 × 0.4–1 mm, linear, with the L:W ratio 12:1 to 25:1, mucronate at apex, narrowly acute-cuneate at base, chartaceous, V-shaped in cross-section; adaxial surface sparsely scabrous with scattered short bristles and appressed non-glandular trichomes; abaxial surface scabrous, with bristles concentrated mainly on the primary vein, primary vein imperceptible, secondary veins in 3–4 pairs, the angles with the primary vein 5°–8° and uniform, eucamptodromous with regular spacing and ex-current attachment to the midvein, immersed and inconspicuous above, prominent below, marginal vein lacking. Inflorescences terminal and axillary, formed by 1–2 congested spikes, more or less obovoid, 6–10 mm long, 2–4-flowered; outermost bract stipule-like, sheathed at base, with a 1–3-foliolate reduced leaf distally, the sheath 4–5 × 2–3 mm, with 3–5 pairs of veins, pilose-scabrous, rounded at base and more or less oblong, the apex with two slightly spreading teeth on each side, the teeth cuspidate-triangular, 2.8–4.2 mm long; other bracts similar to the outermost bract, but always 1-foliolate; bracteoles 2, hyaline, pilose externally, and margin ciliate; outer bracteole adaxially convex, truncate at base, somewhat dilated distally, apically bilobed, 2.6–3.6 × 1.1 mm, the lobes unequal, triangular-apiculate, the larger one 2 mm long, the smaller one ca. 1.5 mm long, inner



FIG. 1. *Stylosanthes acicularis*. A. Habit with inflorescences. B. Leaflet C. Outer bracteole. D. Inflorescence E. Loment. (Drawn from the holotype by Maira G. Mezzacappa).



FIG. 2. *Stylosanthes acicularis* (A–E). A. Stem with bristles with secretion drops (arrowheads) and non-glandular trichomes. B. Outer bracteole. C. Inflorescence highlighting the bract leaflets (arrowheads). D. Loment. E. Seed. F. *Stylosanthes angustifolia*, inflorescence bearing loment with exserted rostrum (arrowhead). *Stylosanthes hippocampoides* (G–I). G. Stem with bristles H. Outer bracteole I. Loment. [Scale bars: A–B; D–E, G–I = 1 mm; C = 5 mm; F = 1 mm.]

bracteole entire, ovate, abaxially convex, truncate at base, caudate at apex, ca. 3 mm long. Flowers exserted; calyx 3–4 mm long, 5-lobed, with the sepals united for ca. 2 mm, ciliate on the lobe margins, otherwise glabrous, dorsal lobes 1.5–1.6 mm long, obtuse, lateral lobes 1.4–1.6 mm, acute-triangular, ventral lobe 2–2.5 mm, acute-triangular, keeled; corolla yellow, glabrous, standard petal suborbicular, unguiculate, apically retuse, ca. 3.4 × 7.6 mm; wings elliptic, spurred at base, ca. 5.9

× 1.6 mm, keel petals apically fused, falcate, spurred at base, ca. 7.7 mm long; androecium monadelphous; anthers dimorphic, the shorter 5 basifixed, the longer 5 dorsifixed; ovary biovulated. Loment with one fertile article, orbicular, 3.2–3.5 × 2.3–2.4 mm, papillose at apex, reticulate; rostrum ca. 1 mm long, coiled, covered with long papillae. Seeds ca. 1.9 × 1.5 mm, reniform, brown with a lustrous testa and dark brown rim aril.

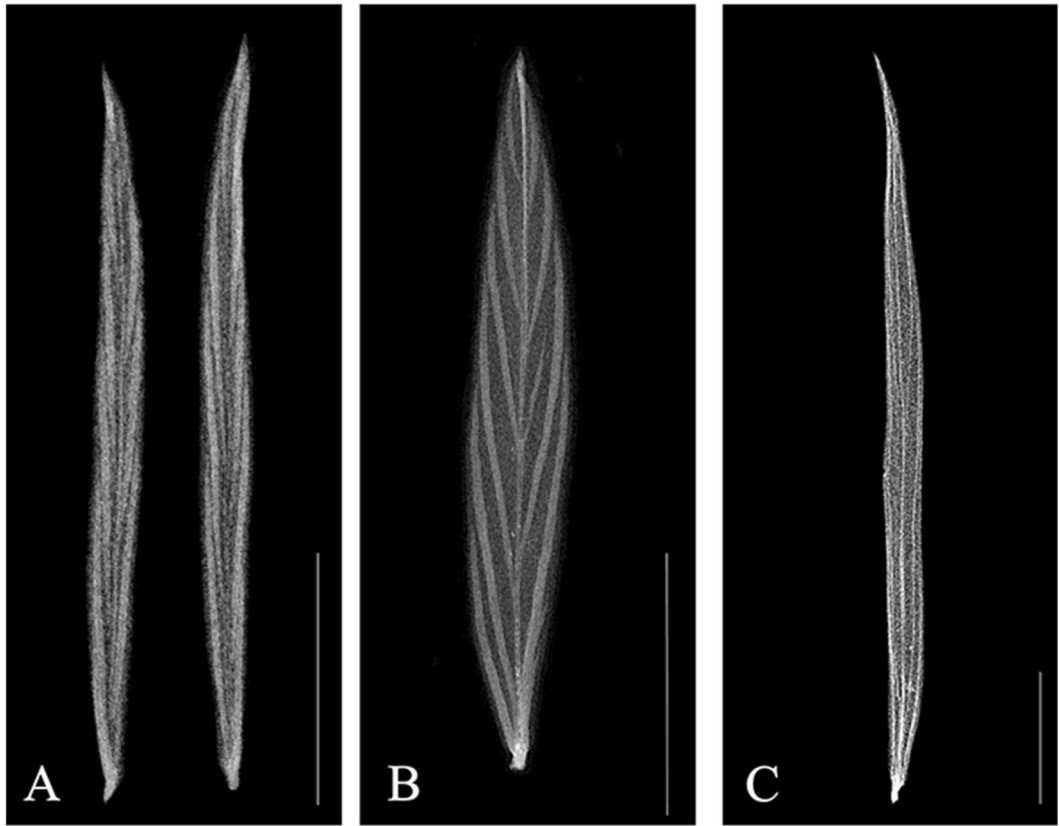


FIG. 3. Comparison of the leaflets of three species of *Stylosanthes* by X-ray method emphasizing venation. A. *S. acicularis*. B. *S. hippocampoides*. C. *S. angustifolia*. [Scale bars = 5 mm.]

Etymology.—The specific epithet refers to the linear leaflets of the species.

Distribution and habitat.—Known from a single collection from Chapada das Mesas National Park (CMNP) in the state of Maranhão, Brazil, where it was found in typical *cerrado* vegetation (Fig. 4) at 353 m. According to Saraiva et al. (2020), the relief in the CMNP ranges from 250 m in the valleys to 524 m in the hills, the local soil is mostly quartz sands, the local climate is classified as Tropical Aw in the Köppen (1884) classification, the average annual temperature is 26.1°C, and annual precipitation is 1250–1500 mm (IBAMA, 2013). The rainy season starts in November and extends through April. During the dry season (May to October) the local vegetation is especially vulnerable to fire outbreaks. (Saraiva et al., 2020).

Phenology.—The species was collected in April with flowers and mature seed-bearing fruits.

Conservation status.—Since the species is known from only a single collection, we assess it as Data Deficient (DD; see IUCN Standards and Petitions Committee, 2019). The species has been collected inside a protected area, but it may occur in other nearby Cerrado areas since other species of *Stylosanthes* are generally widely distributed. However, Cerrado areas are often threatened by the expansion of agriculture and fire in the region (Saraiva et al., 2020).

The combination of a single fertile article and very short rostrum in the loment, the absence of a rudimentary axis beneath the flowers in the inflorescence, and the presence of only a single inner bracteole suggest a close relationship between *Stylosanthes acicularis* and the ca. eight species of the *S. guianensis* complex (sensu ‘t Mannetje, 1977; Gissi et al., 2022). Species with these characteristics that have been sampled in molecular phylogenies form a well-supported clade (Vander

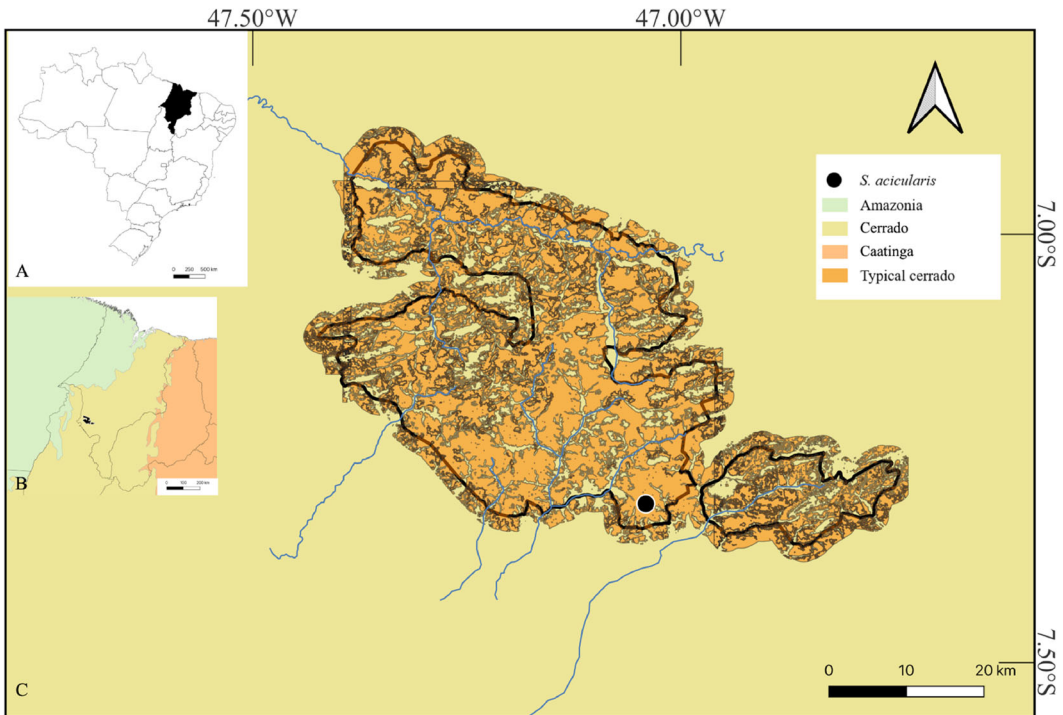


FIG. 4. Geographical distribution of *Stylosanthes acicularis* in the Chapada das Mesas National Park (CMNP). **A.** Map of Brazil highlighting the state of Maranhão. **B.** Location of the CMNP (black-shaded area) in Maranhão. The colors represent the phytogeographic domains present in the state. **C.** Cerrado vegetation in the CMNP; the black dot represents the type locality of *S. acicularis*.

Stappen et al., 2002; Vander Stappen et al., 2003; Oliveira et al., 2021).

Among species of the *Stylosanthes guianensis* complex, *S. acicularis* is most similar to *S. hippocampoides*, a wide-ranging species distributed from northeastern Brazil to central Bolivia, Paraguay, and northern Argentina. The two species can be distinguished from other species of the *S. guianensis* complex by the combination of small capitate inflorescences and the leaflets having up to five secondary veins and lacking a marginal vein. Although the new species is known from just a single specimen, and the type locality may lie within the geographical distribution of *S. hippocampoides*, we are confident of its distinction from *S. hippocampoides*. The latter species is relatively well characterized, being known from more than 50 analyzed collections, including type specimens, over its broad geographical range (Appendix 1). As enumerated in the diagnosis and Table 1, the type of *S. acicularis*

differs by multiple morphological characters, including indument, leaflet shape and venation, and lobing of the outer bracteole, from all collections of *S. hippocampoides*, including those from nearby localities in Northeast Brazil (Table 1).

The new species is also similar in some features to *Stylosanthes angustifolia*; indeed, the type specimen of *S. acicularis* was previously misidentified as *S. angustifolia*. Both species lack a rudimentary axis beneath the flower, and have only one inner bracteole, loment with only one fertile article, and linear leaflets lacking a marginal vein. *Stylosanthes angustifolia* is not considered a member of the *S. guianensis* complex because of the shape of the inflorescence and the rostrum length. With respect to its phylogenetic position, it is nested in the clade with other species with long rostrums (Vander Stappen et al., 2002). The geographical range of *S. acicularis* is also contained within that of *S. angustifolia*, which ranges from the Northeast Brazil to the Guianas. However, the new

TABLE 1. MORPHOLOGICAL COMPARISON OF THREE BRAZILIAN SPECIES OF *STYLOSANTHES*

Character	<i>S. acicularis</i>	<i>S. hippocampoides</i>	<i>S. angustifolia</i>
Stem indumentum	Pilose-scabrous, viscid	Hispid-pubescent, non-viscid	Hispid-pubescent, non-viscid
Bristle length	< 1 mm	2–4 mm	1–2 mm
Leaflet shape	Linear, 10–18 × 0.4–1 mm	Elliptical, 15–30 × 2–4 mm	Linear, 15–30 × 1–2 mm
L:W ratio of the lamina	12:1 to 25:1	10:1 to 5:1	10:1 to 20:1
Leaflet primary vein appearance	Imperceptible	Easily discernible	Imperceptible
Leaflet secondary vein angles	5°–8° and uniform	10°–15° and irregular	5°–8° and uniform
Inflorescence shape	Capitate	Capitate	Narrow, elongated
Inflorescence indumentum	Pilose-scabrous	Hispid-pubescent	Hispid-pubescent
Outer bracteole lobing	Bilobed	Unlobed	Unlobed
Fertile article number	1	1	2
Rostrum length	1 mm	1–1.5 mm	4–5 mm
Rostrum shape	Shortly coiled	Shortly coiled or uncinata	Uncinate

species consistently differs from *S. angustifolia* in its shorter rostrum and much less elongate inflorescence (Table 1).

Key to the species of *Stylosanthes* in Maranhão

1. Flowers and fruits subtended by a rudimentary axis; inner bracteoles 2.
 2. Bracts wider than long, more than 10 mm broad *S. capitata*
 2. Bracts longer than wide, up to 10 mm broad.
 3. Plants hispid; with long bristles, ca. 5 mm long; rostrum coiled.....*S. pilosa*
 3. Plants scabrous; with short bristles, ca. 2 mm long; rostrum uncinata.....*S. scabra*
1. Flowers and fruits not subtended by a rudimentary axis; inner bracteole 1.
 4. Leaflets linear, less than 2 mm broad.
 5. Inflorescences very narrow and elongated; rostrum longer than the upper article *S. angustifolia*
 5. Inflorescences short and capitate; rostrum shorter than the upper article *S. acicularis*
 4. Leaflets elliptical or obovate, more than 2 mm broad.
 6. Rostrum longer than the upper article..... *S. humilis*
 6. Rostrum shorter than the upper article.
 7. Loment with conspicuous oil glands at the base *S. guianensis*
 7. Loment without conspicuous oil glands at the base.
 8. Leaflets with marginal vein*S. gracilis*
 8. Leaflets without marginal vein.
 9. Loment with 1 article.
 10. Leaflets with more than 5 secondary veins *S. grandifolia*
 10. Leaflets with less than 5 secondary veins *S. hippocampoides*
 9. Loment with 2 articles.
 11. Rostrum coiled, loment straw-colored..... *S. viscosa*
 11. Rostrum uncinata, loment brown..... *S. nunoi*

Acknowledgments

The authors thank Dr. Katiane Reis Mendes for bringing the type specimen to our attention. We also thank the SLUI curator Francisca Helena Muniz for a loan of the material. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior–Brasil - CAPES–(Finance Code 001). DSG thanks CAPES (CAPES/Print, Process n° 88887.466909/2019-00). APFP thanks the

Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Process number 400567/2016-4; PQ 313945/2021-7), the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, Process number 2015/13386-0) and CAPES (CAPES/Print, Process n° 88887.373155/2019-00) for research funding. We also thank Máira Gonzalez Mezzacappa for the illustrations and the reviewers who contributed much to the quality of this paper.

Declarations

BMT was Editor-in-Chief of *Brittonia* during the review process, but was not involved in the peer review of this article or the decision to publish. The authors declare that they have no known competing interests that could have appeared to undermine the objectivity or integrity of the work reported in this paper.

Literature cited

- Carvalho, L. B. de.** 2013. Plantas daninhas. Lages, Santa Catarina.
- Corte, E. G. de.** 2007. Cultivo e uso do estilosantes-campo-grande. Embrapa Gado de Corte, Campo Grande, Mato Grosso do Sul.
- Costa, N. M. S.** 2006. Revisão do género *Stylosanthes* Sw. Doctoral thesis. Universidade Técnica de Lisboa, Lisboa.
- Ellis, B., D. C. Daly, L. Hickey, K. Johnson, J. Mitchell, P. Wilf & S. Wing.** 2009. Manual of Leaf Architecture. Cornell University Press, Ithaca, New York.
- Ferreira, J. J. D. S., D. S. Gissi, A. P. F. Perez & J. S. Silva.** 2020. Two new species of *Stylosanthes* Sw. (Leguminosae—Papilionoideae) endemic to Bahia State, Brazil. *Phytotaxa* 456: 157–165.
- Gissi, D. S.** 2020. *Stylosanthes in: Flora e Funga do Brasil, Jardim Botânico do Rio de Janeiro.* Downloadable from: <http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB29854>. Accessed 5 Feb 2022
- Gissi, D. S., D. P. Seixas, A. P. Fortuna-Pereza, B. M. Torke, M. F. Simon, G. Souza, G. P. Lewis & T. M. Rodrigues.** 2022. Leaf and stem anatomy of the *Stylosanthes guianensis* complex (Aubl.) Sw. (Leguminosae, Papilionoideae, Dalbergiaceae) and its systematic significance. *Flora* 287: 151992, 9 pp.
- Harris, J. G. & M. W. Harris.** 2001. Plant Identification Terminology: An Illustrated Glossary. Ed. 2. Spring Lake Publishing, Spring Lake, Utah.
- Hickey, L. J.** 1973. Classification of the architecture of dicotyledonous leaves. *American Journal of Botany* 60: 17–33. <https://doi.org/10.1002/J.1537-2197.1973.TB10192.X>.
- IBAMA.** 2013. Plano operativo de prevenção e combate aos incêndios florestais do Parque Nacional da Chapada das Mesas. Downloadable from: http://www.ibama.gov.br/phocadownload/prevfogo/planos_operativos/plano_operativo_pama_da_chapada_das_mesas.pdf. Accessed 25 Feb 2022
- IUCN Standards and Petitions Committee.** 2019. Guidelines for Using the IUCN Red List Categories and Criteria, Version 14. Downloadable from: <http://www.iucnredlist.org/documents/RedListGuidelines.pdf>. Accessed 25 Feb 2022
- Karia, C. T., R. P. de Andrade, C. D. Fernandes & R. M. Schunke.** 2010. O género *Stylosanthes*. Pp. 366–401 in: D. M. da Fonseca & J. A. Martuscello (eds.), Plantas Forrageiras. UFV, Viçosa, Minas Gerais.
- Kirkbride, J. H. J. & M. C. G. Kirkbride.** 1987. Typification of *Stylosanthes* (Leguminosae) and its sections. *Taxon* 36: 455–458. <https://doi.org/10.2307/1221449>
- Köppen, W.** 1884. Die Wärmezonen der Erde, nach der Dauer der heissen, gemässigten und kalten Zeit und nach der Wirkung der Wärme auf die organische Welt betrachtet. *Meteorologische Zeitschrift* 1: 5–226.
- Machado, L. A. Z., B. Lempp, C. Borges do Valle, L. Jank, L. Rocha, S. Postiglioni, R. Simeao, C. Dornelas, J. Rosemeire, J. Ferreira, G. Lessa de Assis & C. Soares.** 2010. Principais espécies forrageiras utilizadas em pastagens para gado de corte. Pp. 375–417 in: A. V. Pires (ed.), Bovinocultura de Corte. FEALQ, Piracicaba, São Paulo.
- Mohlenbrock, R. H.** 1958. A revision of the genus *Stylosanthes*. *Annals of the Missouri Botanical Garden* 44: 299–355. <https://doi.org/10.2307/2394648>.
- Oliveira, M. A. S., T. Nunes, M. A. Dos Santos, D. Ferreira Gomes, I. Costa, B. Van-Lume, S. S. Marques Da Silva, R. S. Oliveira, M. F. Simon, G. S. A. Lima, D. S. Gissi, C. C. de S. Almeida, G. Souza & A. Marques.** 2021. High-Throughput Genomic Data Reveal Complex Phylogenetic Relationships in *Stylosanthes* Sw. (Leguminosae). *Frontiers in Genetics* 12: Article 727314, 18 pp. <https://doi.org/10.3389/FGENE.2021.727314>
- Radford, A., W. C. Dickison, J. R. Massey & C. R. Bell.** 1974. *Vascular Plant Systematics*. Harper and Row, New York.
- Ribeiro, J. F. & B. M. T. Walter.** 2008. As principais fitofisionomias do bioma Cerrado. Pp.153–212 in: S. M. Sano, S. P. Almeida & J. F. Ribeiro (eds.), Cerrado: Ecologia e Flora, 1st ed., Embrapa Informação Tecnológica, Brasília.
- Saraiva, R. V. C., L. V. Leonel, F. F. Reis, F. A. M. M. A. Figueiredo, F. O. Reis, J. R. P. Sousa, F. H. Muniz & T. M. Ferraz.** 2020. Cerrado physiognomies in Chapada das Mesas National Park (Maranhão, Brazil) revealed by patterns of floristic similarity and relationships in a transition zone. *Anais da Academia Brasileira de Ciências* 92: 1–16. <https://doi.org/10.1590/0001-3765202020181109>.
- Schneider, J. V., R. Rabenstein, J. Wesenberg, K. Wesche, G. Zizka & J. Habersetzer.** 2018. Improved non-destructive 2D and 3D X-ray imaging of leaf venation. *Plant Methods* 14: 1–15. <https://doi.org/10.1186/S13007-018-0274-Y>.
- ‘t Mannetje, L.** 1977. A revision of varieties of *Stylosanthes guianensis* (Aubl.) Sw. *Australian Journal of Botany* 25: 347–362. <https://doi.org/10.1071/BT9770347>.
- ‘t Mannetje, L.** 1984. Considerations on the taxonomy of the genus *Stylosanthes*. Pp. 1–21 in: H. M. Stace & L. A. Edye (eds.), *The Biology and Agronomy of Stylosanthes*. Academic Press, Sydney.
- Thiers, B.** 2021. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden’s Virtual Herbarium. <http://sweetgum.nybg.org/ih/> (accessed 4 Feb 2022).
- Vander Stappen, J., J. De Laet, S. Gama-Lopez, S. Van Campenhout & G. Volckaert.** 2002. Phylogenetic analysis of *Stylosanthes* (Fabaceae) based on the internal transcribed spacer region (ITS) of nuclear ribosomal DNA. *Plant Systematics and Evolution* 234: 27–51. <https://doi.org/10.1007/s00606-002-0193-1>.

Vander Stappen, J., S. Marant & G. Volckaert. 2003.

Molecular characterization and phylogenetic utility of the rDNA external transcribed spacer region in *Stylosanthes* (Fabaceae). Theoretical and Applied Genetics 107: 291–298. <https://doi.org/10.1007/s00122-003-1245-9>.

Vanni, R. O. 2017. The genus *Stylosanthes* (Fabaceae, Papilionoideae, Dalbergiaceae) in South America. Boletín de La Sociedad Argentina de Botánica 52: 549–585. <https://doi.org/10.31055/1851.2372.v52.n3.18033>.

Vogel, J. R. T. 1838. *Stylosanthes*. Linnaea 12: 63–71.

Springer Nature or its licensor holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.

Appendix 1

SELECTED EXAMINED MATERIAL

Stylosanthes hippocampoides Mohlenbr.

Argentina. Córdoba: Sierra Achala: La Cuesta de La Ensenada, 4 Jan 1885 (fl., fr.), *F. Kurtz 8303* (NY). Sierra Chica: Potrero de Loza, 30 Dec 1979 (fl., fr.), *C. Galander s.n.* (NY). Sierra Chica: Santa Catalina, 28 Feb 1891 (fl., fr.), *F. Kurtz 6983* (NY). Sierra Chica: March 1891 (fl., fr.), *F. Kurtz s.n.* (NY). Unquillo: Mar 1926 (fl., fr.), *C. Bruch s.n.* (NY). Bella Vista: 19 km S de Bella Vista, Est. Cuevas, 24 May 1973 (fl., fr.), *A. Schinini 6552* (NY). Capital: Santa Catalina, 31 Oct 1944 (fl., fr.), *T. S. Ibarrola 928* (NY). Concepción: Estancia Tranquera de Hierro, 66 km al NE de Chavarría, camino a Concepción, 3 Dec 1996 (fl., fr.), *M. M. Arbo 6938* (NY). Empedrado: Arroyo Gonzales, 6 Mar 1974 (fl., fr.), *G. J. Schwarz 10,011* (NY). Empedrado: EE INTA, s.d. (fl., fr.), *A. Schinini 16,227* (NY). Itatí: Ramada Paso, 11 Feb 1972 (fl., fr.), *A. Krapovickas 16,478* (NY). Ituzaingó: Ruta 12, Bajo Vedoya, ca 1 km al E del peaje, 14 Jan 2001 (fl., fr.), *M. M. Arbo 8771* (NY). Ituzaingó: Villa Olivari, ruta 12M, 24 km W de Ituzaingó, 21 Dec 1983 (fl., fr.), *R. Vanni 428* (NY). Lavalle: Estancia “La Pastoril”, 24 Nov 1971 (fl., fr.), *T. M. Pedersen 10,007* (NY). Monte Caseras: Juan Pujol, 8 Feb 1945 (fl., fr.), *T. S. Ibarrola 2331* (NY). Paso de los Libres: Bonpland costa rio Uruguay, 19 Jan 1945 (fl., fr.), *T. S. Ibarrola 2142* (NY). Paso de los Libres: Ea. “El Recreo”, 21 km E de Bonpland, 19 Feb 1979 (fl., fr.), *A. Schinini 17,345* (NY). San Martín: 14 Jul 1944 (fl., fr.), *T. S. Ibarrola 1683* (NY). San Martín: Yapeyú, Costa del río Uruguay, 12 Feb 1979 (fl., fr.), *A. Schinini 16,995* (NY). San Martín: Yopeyú, 31 Dec 1944 (fl., fr.), *T. S. Ibarrola 1918* (NY). Santa Teresa: 25 Dec 1947 (fl., fr.), *T. M. Pedersen 79* (NY). Santo Tomé: Cuay Grande, 8 Jul 1944 (fl., fr.), *T. S. Ibarrola 1607* (NY). Santo Tomé: Pueblo al NE 2 leguas, s.d. (fl., fr.), *T. S. Ibarrola 1514* (NY). Between San Cosme and Ramada Paso, 9 Dec 1947 (fl., fr.), *J. L. Stephens 15* (NY). **Misiones:**

Candelaria: Puerto Santa Ana, 31 Jan 1945 (fl., fr.), *G. J. Schwarz 608* (NY). Posadas, Bompland, in Campina trans Martines Chico: 20 Jan 1908 (fl., fr.), *E. L. Ekman 1742* (NY). **Sarà:** Santa Cruz: Lomas secas, campos de Buena Vista, 6 Feb 1925 (fl., fr.), *J. Steinbach 6916* (NY).

Bolivia. Santa Cruz: Wames Province: Pampa de Viru-Viru, a 17 km al N de ciudad de Sta. Cruz., 13 Feb 1994 (fl., fr.), *M. Menacho 450* (NY).

Brasil. Bahia: Correntina: 7 km SW de Correntina., 2 Feb 1963 (fl., fr.), *A. Krapovickas 30,162* (NY). **Goiás:** Alto Paraíso de Goiás: 5–6 km N of Alto Paraíso, peat of E & NE aspect by highway, 30 Nov 1988 (fl., fr.), *R. Kral 75,742* (NY). Guará: ca. 9 km S of Guará, 20 Mar 1968 (fl., fr.), *H. S. Irwin 21,515* (NY). **Maranhão:** Carolina: Transamazonian Highway, BR-230 and BR-010, Pedra Caida, 35 km N of Carolina, ponto turístico W towards Serra de Baleia, 14 Apr 1983 (fl., fr.), *E. L. Taylor E1235* (NY). **Pará:** Bragança: Desvio da estrada PA-242, no km 15 - Viseu km 7, 25 Nov 1988 (fl., fr.), *N. M. de Sousa Costa 2420* (BOTU, CEN). **Pará:** São Graldo do Araguaia: Fazenda Andorinhas, retiro Santa Cruz, margem esquerda do rio Araguaia, 21 Apr 2004 (fl., fr.), *G.-Silva-Pereira 8903* (BOTU, CEN). **Paraná:** Jaguaruaíva: above Rio das Mortes on road to Senges., 18 Jan 1965 (fl., fr.), *L. B. Smith 14,771* (NY). Lapa: Rio Passa 2, 2 Mar 1970 (fl., fr.), *C. Koczicki 253* (NY). Tibagi: along the river southeast of Tibagi., 10 Nov 1935 (fl., fr.), *R. Reiss 75a* (NY); at foot of Pico de Cajurú, 15 km SE of Jaguaruaíva., 4 Mar 1966 (fl., fr.), *J. C. Lindeman 1455* (NY). Piraí do Sul: Fazenda Nova Era, 15 Feb 2013 (fl., fr.), *M. L. Brotto et al. 931* (ESA). **Rio Grande do Sul:** Santa Maria: Estação Experimental de Silvicultura, 28 Feb 1956 (fl., fr.), *O. R. Camargo 5* (BLA). Tupanciretã: Estação Experimental, 7 Feb 1969 (fl., fr.), *A. Pott 74* (BLA). Quaraí: Cerro do Jarau, 12 Nov 1987 (fl., fr.), *F. R. Galvani & M. R. Freitas s.n.* (HUCS). 55 km W de Rosário do Sul, 8 Dec 1978 (fl., fr.), *A. Krapovickas 34,236* (NY). **Santa Catarina:** Mafra: 7 km NW of Mafra on the road to Barracas (20 km), 13 Mar 1957 (fl., fr.), *L. B. Smith 12,090* (NY). **São Paulo:** Botucatu: Distrito de Rubião Júnior, em frente ao Haras Apache WO, 29 Sep 2018 (fl., fr.), *D. S. Gissi 403* (BOTU); 7 Feb 2019 (fl., fr.), *D. S. Gissi 426* (BOTU). Botucatu: Distrito Rubião Júnior, 8 Feb 2017 (fl., fr.), *T. P. Tunes 11* (BOTU).

Paraguay. Boqueron: Colonias Mennonitas, 2 May 1995 (fl., fr.), *R. Vanni 3492* (NY). **Guairá:** Independencia: Arroyo Guazú, camino a San Gervasio, 27 Mar 1993 (fl., fr.), *A. Schinini 28,079* (NY). Central: near Ituagua, 14 Feb 1948 (fl., fr.), *J. L. Stevens 94* (NY). San Pedro: 10 km W de San Estanislao, bañado del río Tapiracuí, 19 Feb 1994 (fl., fr.), *A. Krapovickas 44,879* (NY).

Stylosanthes angustifolia Vogel.

Brazil. Amapá: Amapá: BR-156, km 38 do trevo de Amapá para Tartarugalzinho, 2 Sep 1988 (fl., fr.), *N. M. de Sousa Costa 2245* (BOTU, CEN). BR-156, 48 km do trevo de Amapá para

Tartarugalzinho, 2 Sep 1988 (fl., fr.), *N. M. de Sousa Costa 2247* (BOTU, CEN). Ferreira Gomes: a 1 km do entroncamento da BR-156 para Porto Grande, 28 Jan 1988 (fl., fr.), *N. M. de Sousa Costa 2172* (BOTU, CEN). Macapá: Km 92 da BR-156, 27 Aug 1988 (fl., fr.), *N. M. de Sousa Costa 2122* (BOTU, CEN). Tartarugalzinho: BR-156, 13 km S de Tartarugalzinho, 2 Sep 1988 (fl., fr.), *N. M. de Sousa Costa 2252* (BOTU, CEN); BR-156, 17 km de Tartarugalzinho para Ferreira Gomes, 3 Sep 1988 (fl., fr.), *N. M. de Sousa Costa 2262* (BOTU, CEN). **Bahia**: ca. 25km W of Barreiras, 3 mar 1971 (fl., fr.), *H. S. Irwin et al. 31349* (UB). Barreiras: BR-242, km 938, Rodovia Brasília-Fortaleza, beira de estrada, 29 Sep 1978 (fl., fr.), *L. Coradin 1175* (BOTU, CEN). São Desidério: Fazenda Estiva, Córrego Galheirão., 9 Apr 1989 (fl., fr.), *R. C. Mendonça 1457* (RB). **Ceará**: Juazeiro do Norte: Rodovia Juazeiro do Norte - Crato, km 2, (pista dupla), 24 Jun 1987 (fl., fr.), *L. Coradin 7766* (BOTU, CEN). São Luis do Curu: BR-222, km 70, Fortaleza - Sobral, beira da estrada, 13 Jun 1979 (fl., fr.), *L. Coradin 1896* (BOTU, CEN). Tianguá: rodovia Tianguá-Teresina (BR-22), km 27, 1 Jul 1987 (fl., fr.), *L. Coradin 7898* (BOTU, CEN); rodovia Tianguá-Teresina (BR-222), km 4, chapada da Serra de Ibiapaba, 1 Jul 1987 (fl., fr.), *L. Coradin 7889* (BOTU, CEN); rodovia Tianguá-Teresina (BR-222), km 4, chapada da Serra de Ibiapaba, 1 Jul 1987 (fl., fr.), *L. Coradin 7892* (BOTU, CEN). **Maranhão**: Alto Parnaíba: entrada de Alto Parnaíba desde Balsas na área da caixa d'água municipal, 21 May 1991 (fl., fr.), *J. F. M. Valls 13,046* (BOTU, CEN). **Maranhão**: Balsas: borda de ampla lagoa 12 km ao sul de Balsas na saída para Alto Parnaíba, fazenda Brejo da Lagoa, 20 May 1991 (fl., fr.), *J. F. M. Valls 13,031* (BOTU, CEN). Carolina: Laje de Arenito ao longo do rio Farinha, 7 Apr 2016 (fl., fr.), *A. C. Sevilha 5664* (BOTU, CEN); margem esquerda do rio Farinha, próximo à ponte na BR-010, 25 Apr 2008 (fl., fr.), *G. Silva-Pereira 13,321* (BOTU, CEN); Parque Nacional Chapada das Mesas, acesso E no km 612 da BR-230, 20 km em estrada vicinal em direção à localidade Buenos Aires, próximo ao rio Farinha, 7 Apr 2016 (fl., fr.), *M. F. Simon 2746* (BOTU, CEN); Rodovia BR-010, Carolina-Estreito, km 26, entrada para a cachoeira do Dodô, 24 Apr 2008 (fl., fr.), *G. Silva-Pereira 13,265* (BOTU, CEN). Peritoró: Rodovia Caxias-Peritoró (BR-316), km 48, 2 Jul 1987 (fl., fr.), *L. Coradin 7946* (BOTU, CEN). **Pará**: Monte Alegre: 26 Mar 1924 (fl., fr.), *J. G. Kuhlmann 1770* (RB). Augusto Correa: estrada PA-242 Augusto Correia km 2,2, 25 Jan 1988 (fl., fr.), *N. M. de Sousa Costa 2423* (BOTU, CEN). Bragança: Bragança-Ajuruteua, a 300 m da praia, 24 Nov 1988 (fl., fr.), *N. M. de Sousa Costa 2414* (BOTU, CEN); Bragança-Ajuruteua, km 30,5, 24 Nov 1988 (fl., fr.), *N. M. de Sousa Costa 2408* (BOTU, CEN); Bragança-Ajuruteua, km 4,7, 24 Nov 1988 (fl., fr.), *N. M. de Sousa Costa 2404* (BOTU, CEN); entroncamento Bragança, Mirasselas, 23 Nov 1988 (fl., fr.), *N. M. de Sousa Costa 2391* (BOTU, CEN); trevo Bragança-Mirasselas, km 1,3, 23 Nov 1988 (fl., fr.), *N. M. de Sousa Costa 2393* (BOTU, CEN). Capanema: Capanema-Bragança, km 5, 22 Nov 1988 (fl., fr.), *N. M. de Sousa Costa 2371* (BOTU, CEN). Castanhal: rodovia PA-136, Castanhal-Curuçá, km 23, 19 Nov 1988 (fl., fr.), *N. M. de Sousa Costa 2325* (BOTU, CEN). Curuca: rodovia Curuçá-Marudá km 1,4, 19 Nov 1988 (fl., fr.), *N. M. de Sousa Costa 2329* (BOTU, CEN). Irituia: Capitão Poço-Irituia, km 34, 28 Nov 1988 (fl., fr.), *N. M. de Sousa Costa 2460* (BOTU, CEN); Capitão Poço-Irituia, km 39,4, 28 Nov 1988 (fl., fr.), *N. M. de Sousa Costa 2464* (BOTU, CEN). Nova Timboteua: Nova Timboteua-Salinópolis, km 10, 20 Nov 1988 (fl., fr.), *N. M. de Sousa Costa 2340* (BOTU, CEN). Ourém: Ourém-Capitão Poço, km 3,7, 27 Nov 1988 (fl., fr.), *N. M. de Sousa Costa 2445* (BOTU, CEN). Salinópolis: alto da praia do Atalaia, 20 Nov 1988 (fl., fr.), *N. M. de Sousa Costa 2347* (BOTU, CEN). Santa Isabel do Pará: trevo da BR-010-Vigia, ca. 700 m, 17 Nov 1988 (fl., fr.), *N. M. de Sousa Costa 2275* (BOTU, CEN). São João de Pirabas: entroncamento PA-124, Capanema km 2, 21 Nov 1988 (fl., fr.), *N. M. de Sousa Costa 2361* (BOTU, CEN). Vigia: estrada de Santa Isabel do Pará-Vigia km 48, 17 Nov 1988 (fl., fr.), *N. M. de Sousa Costa 2292* (BOTU, CEN); saída para Santa Isabel do Pará, 18 Nov 1988 (fl., fr.), *N. M. de Sousa Costa 2296* (BOTU, CEN). Viseu: estrada PA-242 Viseu-Bragança km 41, desvio para a rodovia Pará-Maranhão, 26 Nov 1988 (fl., fr.), *N. M. de Sousa Costa 2434* (BOTU, CEN). **Paraíba**: Baía da Traição: dunas fixas, utilizadas como pasto, 27 Jul 2001 (fl., fr.), *V. C. Souza & J. P. Souza 26626* (ESA). **Pernambuco**: Petrolina: entre Caboclo e Dormente, 22 Apr 1971 (fl., fr.), *E. P. Heringer et al. 275* (UB); rodovia Petrolina-Santa Maria da Boa Vista, km 87, 5 Apr 1979 (fl., fr.), *L. Coradin 1293* (BOTU, CEN). **Piauí**: Piracuruca: Divisa CE/ PI-Teresina (BR-222), km 52, 1 Jul 1987 (fl., fr.), *L. Coradin 7914* (BOTU, CEN). Piracuruca: Parque Nacional de Sete Cidades, área A1 do levantamento fitossociológico, 12 May 2007 (fl., fr.), *M. R. A. Mendes 11* (UB); Parque Nacional de Sete Cidades, área A1 do levantamento fitossociológico., 7 Jul 2007 (fl., fr.), *M. R. A. - Mendes 66* (UB); Parque Nacional de Sete Cidades., 21 Jul 2007 (fl., fr.), *M. R. A. Mendes 162* (UB). **Roraima**: Caracará: Parque Nacional Viruá, Piçarra na beira da estrada vicinal, área aberta., 16 Sep 2010 (fl., fr.), *C. M. Siniscalchi 76* (RB). **Tocantins**: Babaculândia: margem do rio Taboca, 26 Nov 2009 (fl., fr.), *G. Silva-Pereira 14,797* (BOTU, CEN). Darcinópolis: margem direita do rio Curicaca, cachoeira da fazenda do Sr. Marcelo, 17 Apr 2008 (fl., fr.), *G. Silva-Pereira 13,005* (BOTU, CEN).

French Guiana. Cayenne: Jan 1845 (fl., fr.), *H. C. Rothery* (NY). **Kourou**: Centre Spatial Guyanais, white sand savanna, 30 Aug 2005 (fl., fr.), *P. J. M. Mass 9692* (NY). **Laussat**: Bassin de la Basse Mana: 15 Apr 1989 (fl., fr.), *G. Cremers 10,628* (NY); route de Sinnamary, entreé de Marosi, 1 Jun 1957 (fl., fr.), *Hooek s.n.* (NY).

Guyana. Rupunini: Dadanawa: between Dadanawa and Mountainpoint, 3 Oct 1992 (fl., fr.), *M. J. Jansen-Jacobs 2721* (NY). Manari: 12 Jul 1995 (fl., fr.), *M. J. Jansen-Jacobs 4402* (NY); 20 Oct 1979 (fl., fr.), *P. J. M. Mass 3659* (NY). Mountain Point: 13 Jun 1995 (fl., fr.), *M. J. Jansen-Jacobs 4054* (NY). St. Ignatius: 12 Jul 1958 (fl., fr.), *S. G. Harrison 1257* (NY). Lethem: Moka Creek flood plain, Stand 18., 5 Sep 1963 (fl., fr.), *R. Goodland 607* (NY); Rupununi Savanna, Lethem., 28 Oct 1987 (fl., fr.), *M. J. Jansen-Jacobs 567* (NY). **U. Takutu-U. Essequibo:** Essequibo, South Rupununi Savanna, Dadanawa., 17 Jun 1989 (fl., fr.), *L. J. Gillespie 1638* (NY); Sand Creek, Sand Creek to Shea Village, 1996 May 1996 (fl., fr.), *D. Clarke 1774* (NY). Karanambo, savanna near airstrip, sandy clay with an overlay of lateritic gravel, 4 Sep 1988 (fl., fr.), *P. J. M. Mass 7228* (NY); Waranama Ranch, intermediate savanna, Berbice River, 10 Jun 1958 (fl., fr.), *S. G. Harrison 1083* (NY).

Suriname. Coebiti: Saramacca: 28 Dec 1982 (fl., fr.), *A. P. Everaarts 729* (NY). **Paramaribo:** Zanderij: vicinity of Zanderij, 50 km S of Paramaribo. Zanderij Savanna on white sand, near Matta., 19 Sep 1976 (fl., fr.), *S. Mori 8357* (NY); Wayambo River, 15 Nov 1923 (fl., fr.), *D. H. Linder 97* (NY); Jan (fl., fr.), *Hostmam 1018* (NY); May 1846 (fl., fr.), *H.A.H. Kegel 1113* (NY).

Venezuela. Apure: Pedro Camejo: P.N. Santos Luzardo. Río Cinaruco, 30 min abajo del paso Cinaruco, camino al Orinoco., 2 Nov 1989 (fl., fr.), *A. Castillo 3110* (NY). **Bolivar:** Cedeño: Caicara del Orinoco, Jan 1989 (fl., fr.), *S. Elcoro 210* (NY); entre los km 12–120 de la carretera Caicara del Orinoco–Pto. Ayacucho, al sur de Caicara del Orinoco., 18 Nov 1984 (fl., fr.), *G. Aymard & B. Stergios 3142* (NY). Cerro San Borja: Middle Orinoco, 12 Dec 1955 (fl., fr.), *J. J. Murdack 39,850* (NY).