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# Monograph of tribe Sipaneeae (Rubiaceae, Ixoroideae). A Neotropical group with its center of diversity on the Guiana Shield

Piero G. Delprete

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# Journal of Plant Taxonomy and Geography

**Piero G. Delprete**

Monograph of tribe Sipaneeae  
(Rubiaceae, Ixoroideae). A Neotropical  
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**Journal of Plant Taxonomy and Geography** (*Webbia*) is a peer-reviewed journal on Plant Taxonomy, Nomenclature, Phylogeny, Phytogeography and Palaeobotany of the Vascular Plants.

The journal aims to allow research in botanical topics such as taxonomy, systematics, nomenclature, molecular phylogeny, conservation, biogeography, and history of botany, and botanical collections.

It was founded in **1905** in Florence by **Ugolino Martelli** (1860-1934), a botanist well known for his studies of and contributions to the systematics of the tropical genus *Pandanus* and on the Flora of Sardinia.

In the 19th century Florence represented one of the most important European centres in Plant Taxonomy and Phytogeography with several notable Italian botanists worth mentioning such as Filippo Parlatore, Teodoro Caruel, Eugenio Baroni, Stefano Sommier, Odoardo Beccari and Ugolino Martelli himself. In 1842 **Filippo Parlatore** (1817-1877) founded in Florence the *Herbarium Centrale Italicum* (FI), which soon became one of the most important herbaria in the world. Most of the specimens described and/or cited in *Webbia* are still kept in it.

In 1905, and as a consequence of this multitude of activities in Plant Systematics and Phytogeography, Ugolino Martelli established the journal *Webbia-Raccolta di Scritti Botanici*, firstly published annually in a single issue, and later twice a year. *Webbia* also began to be a place of publication of contributions from Tropical Botany, especially after the Royal Colonial Herbarium founded in 1904 in Rome was moved to Florence in 1914, currently named Tropical Herbarium Study Center (Centro Studi Erbario Tropicale - Herbarium FT) belonging to the Department of Biology of the University of Florence.

*Webbia* had been created in honor of **Philip Barker Webb** (1793-1845), a close friend of Filippo Parlatore, who before passing away entrusted his personal herbarium and a library rich of old botanical books and publications to the then Botanical Museum in Florence.

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## Monograph of tribe Sipaneeae (Rubiaceae, Ixoroideae). A Neotropical group with its center of diversity on the Guiana Shield

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**Abstract.** The tribe Sipaneeae (subfamily Ixoroideae) includes the genera *Chalepophyllum* (3 spp.), *Dendrosipanea* (3 spp.), *Limnosipanea* (3 spp.), *Maguireothamnus* (3 spp.), *Neblinathamnus* (2 spp.), *Neobertiera* (5 spp.), *Pteridocalyx* (1 sp.), *Sipanea* (17 spp.), *Sipaneopsis* (8 spp.), and *Steyermarkia* (1 sp.), for a total of 44 species. This tribe has its center of diversity on the Guiana Shield (northern South America), where 9 of the 10 genera occur. Only *Sipanea* and *Limnosipanea* are also present on the Brazilian Shield and the Orinoquia Region with a total of 4 species, while *Steyermarkia*, *Sipanea* and *Limnosipanea* are present in Central America with one species each. The genera *Sipaneopsis*, *Chalepophyllum*, and *Dendrosipanea* are endemic to white sand areas of the Amazon Basin. The habit in the tribe Sipaneeae ranges from herbs (terrestrial, amphibian or rarely aquatic), subshrubs, shrubs to treelets. Within the tribe, *Chalepophyllum*, *Dendrosipanea*, *Neobertiera*, *Pteridocalyx* and *Sipanea* are heterostylous, while the other genera are homostylous. Several recent articles have been dedicated to the description of new species in this tribe, and only *Limnosipanea spruceana* var. *macrantha* is newly described here. In the present work 21 names are newly typified; a list of these names is present at the end of the taxonomic treatment. For all the taxa of this tribe, full synonymy, typification, description, ecological observations, geographic distribution, illustrations, IUCN conservation assessment, and cited specimens are provided.

**Keywords:** *Chalepophyllum*, *Dendrosipanea*, *Limnosipanea*, *Maguireothamnus*, *Neblinathamnus*, *Neobertiera*, *Pteridocalyx*, *Sipanea*, *Sipaneopsis*, *Steyermarkia*, Neotropics, Central America, South America, monographic treatment, heterostyly, homostyly.

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## INTRODUCTION

The tribe Sipaneeae is here delimited according to the molecular phylogenies published by Rova et al. (2002) and Delprete & Cortés-B. (2004). A key to all the genera Rondeletieae *sensu lato*, including the genera here included in the Sipaneeae, is available in Delprete (1999). To facilitate the identification of the members of the Sipaneeae as here delimited, a key to genera is provided. Keys to species are available under each genus.

## HISTORICAL SUMMARY

The present historical summary refers to the genera included in the tribe Sipaneeae as here delimited.

Aublet (1775: 147, tab. 56) published the first genus of this tribe, *Sipanea* Aubl. and positioned it in Pentandria Monogynia. He described this genus with the sole species *S. pratensis* Aubl., using specimens that he collected near Cayenne, French Guiana.

Rottbøll (1776: 7, tab. 2, fig. 2) published *Rondeletia biflora* Rottb. [= *Sipanea biflora* (Rottb.) Cham. & Schltld.] citing material collected by Rolander in Suriname (see discussion under *Sipanea biflora* for further information).

Linnaeus filius (1782 ["1781"]: 17) published the genus *Virecta* L.f. and placed it in Pentandria Monogynia. In *Virecta*, he described *V. biflora* L.f. [= *Sipanea biflora* (Rottb.) Cham. & Schltld.] without citing *Rondeletia biflora* Rottb. He certainly referred to the species described by Rottbøll, based on the habit, the floral characters, and the specific epithet. Therefore, the binomial *Virecta biflora* should be treated as a new combination. For a complete explanation regarding this taxon, see discussion under *Sipanea biflora* (Rottb.) Cham. & Schltld.

James Edward Smith (1818), in Abraham Rees' *Cyclopaedia* volume 4 part 2, described in great detail *Virecta* and the four species that he included in the genus: *V. biflora* [= *Sipanea biflora*], *V. procumbens* Sm. [= *Virectaria procumbens* (Sm.) Bremek.], *V. pratensis* [= *Sipanea pratensis*], and *V. multiflora* Sm. [= *Virectaria multiflora* (Sm.) Bremek.].

Kunth (1821 ["1820"]: 397–398) described two new species of *Sipanea* using material collected by Bonpland and Humboldt in Venezuela: *S. glomerata* Kunth and *S. dichotoma* Kunth [= *S. pratensis* var. *dichotoma* (Kunth) Steyerm.].

Chamisso and Schlechtendal (1829) proposed the new combination *Sipanea biflora* citing both *Rondeletia biflora* Rottb. and *Virecta biflora* L.f. as synonyms. Along

with this new combination, they cited the two species recently published by Kunth, *S. dichotoma* Kunth [= *S. pratensis* var. *dichotoma*] and *S. glomerata* Kunth. They also commented that *Sipanea* is similar to *Rondeletia* L., from which it can be distinguished by the corolla mouth pubescent and the herbaceous stems (vs. corolla mouth glabrous and woody stems in *Rondeletia*).

Achille Richard presented a new Rubiaceae classification of 11 tribes and 154 genera, with the descriptions of numerous new genera and new species, in an oral conference at the Royal Academy of Sciences in Paris on 7 July 1829. He submitted his *Mémoire sur la famille Rubiacées* for publication 1829, in Paris, but was published in December 1830 (and reprinted in 1834). In the preface of his *Mémoire* he published the following warning notes (“Avertissement”) (translated from French): “The *Mémoire* that I am publishing today was presented as an oral presentation at the Royal Academy of Sciences on 7 July 1829. Mister De Candolle at that time was studying the family Rubiaceae for the third volume of his *Prodromus*, and he had the kindness to ask me the presentation of my *Mémoire*, to avoid the double use [of names] that could result from the publication of the two works completed at the same time and on the same subject. I hastened to satisfy the request of this *savant*, and I gave him my manuscript and an atlas containing 45 plates in-4, all drawn by me, and representing the detailed analysis of 7/8 of the genera that compose the family Rubiaceae. From that atlas I extracted the 15 plates that accompany this *Mémoire*, as I was forced to reduce their number to avoid the considerable costs demanded for the impression of such high number of plates. Other circumstances independent of my will delayed until today the publication, and in this interval the fourth volume of the *Prodromus*, containing among other families, that of the Rubiaceae, was published. Meanwhile, I took advantage of the time that passed between the presentation of my *Mémoire* at the Academy and its publication, to make some improvements. It resulted from these circumstances, although my work was precedent of that of the Professor *Savant* of Geneva, that his work was published first, and seems to have priority over my work; and as both our works were published at the same time, numerous genera and species that I established, they are indicated in the *Prodromus* under other names. This inconvenient is not that serious; however, I thought that it is necessary to report it, so that I will not be accused of unnecessarily give new names to genera or species that already had a name. It was already too late, when the *Prodromus* was published, so that I could correspond my names of genera and species with those in the work by Mister De Candolle. Paris, 1 December 1830.”

Richard’s new taxa published in the *Prodromus* were inconsistently cited by Candolle, some of them followed by “Rich.” and others without the citation of A. Richard as original author. According to Stearn (1957), Delprete (1999) and Persson & Delprete (2017), the authority of the new taxa and new combinations of A. Richard published with Richard’s authority in Candolle’s *Prodromus* should be cited as: “A. Rich., in A.P. de Candolle” where “in A.P. de Candolle” is the bibliographic reference. However, Art. 46.8 of the current Code (Turland et al. 2018) states that “In determining the correct author citation, only internal evidence in the publication (as defined in Art. 35.4) where the name was validly published is to be accepted, including ascription of the name, statements in the introduction, title, or acknowledgements, and typographical or stylistic distinctions in the text.” Therefore, although there is overwhelming external evidence that Achille Richard is the rightful author of his new taxa published in the *Prodromus*, and that he was the author that studied the material at P, the use of the authority “A. Rich. in DC.” is incorrect according to the current Code, and “A. Rich. ex DC.” should be used instead. In addition, for Richard’s new taxa published in Candolle’s *Prodromus*, the original specimens are integrated in the Paris general herbarium (P), and highlighted by the note “Herb. Richard” that was handwritten in red ink by Albert Belhomme de Franqueville (1814–1891). While in G and G-DC are present only fragments of Richard’s original specimens that were extracted from the P specimens. All the above factors should be taken into account when the action of typification is undertaken for Richard’s new taxa published in Candolle’s *Prodromus*.

Achille Richard (December 1830) in his *Mémoire* described the tribe Cinchoneae to include the rubiaceous genera with bilocular, many-seeded capsules, and winged seeds, a group in which he included nine genera of the Rondeletieae s.l., with *Sipanea* among them. Within *Sipanea*, he included *S. pratensis*, and described the two African species that were already published in synonymy by A.P. de Candolle (September 1830) in *Virecta*: *Sipanea angustifolia* A. Rich. and *S. elatior* A. Rich., which are both illegitimate names (see below). Richard did not cite the two *Sipanea* species described by Kunth (1821 [“1820”]). He treated *Virecta* as a synonym of *Rondeletia* L., and published the new combination *Rondeletia biflora* (L.f.) A. Rich.; however, this binomial had been previously published by Rottbøll (1776), and Richard’s combination is an isonym. Richard explained the publication of this binomial by stating that Linnaeus filius described *Virecta* as a unilocular capsule, while in this species they are clearly bilocular.



August Pyramus de Candolle (September 1830) largely followed Achille Richard's classification (December 1830) in the manuscript that Richard gave to him to be published in the *Prodromus*. However, Candolle provided several modifications and innovations with respect to Richard's classification, presenting a system of 13 tribes and 223 genera. He divided the tribe Hedyotiadae (described as "Fructus capsularis bilocularis. Semina non alata") into two subtribes, and in the subtribe Rondeletieae (described as "Stipulae utriusque binae concreatæ aut distinctæ, nec vaginatae, nec multisetosae"), he positioned *Sipanea* and *Virecta* as closely related. He distinguished *Sipanea* from *Virecta* only by the included stamens and style, while he described the stamens and style of *Virecta* as exerted. Within *Sipanea*, Candolle included *S. pratensis*, *S. dichotoma* [= *S. pratensis* var. *dichotoma*], *S. glomerata*, and *S. biflora*. In *Virecta* he included *V. multiflora* Sm. [= *Virectaria multiflora* (Sm.) Bremek.], and *V. procumbens* Sm. [= *Virectaria procumbens* (Sm.) Bremek.], both names were originally published by J.E. Smith using material collected by Mr. Afzelius in Sierra Leone. Candolle (1830, p. 414) cited *Sipanea angustifolia* A. Rich. in synonymy under *V. multiflora*, and *Sipanea elatior* A. Rich. in synonymy under *V. procumbens*, making both Richard's names illegitimate and superfluous.

Joseph Dalton Hooker (1868: 38, tab. 1050) described the new genus *Limnosipanea* Hook.f., and positioned it in the Rondeletieae, to accommodate three species of semi-aquatic herbs: *L. spruceana* Hook.f., *L. schomburgkii* Hook.f. [= *L. palustris* (Seem.) Hook. f.], and *L. palustris* (Seem.) Hook.f.

Hooker (1873) proposed the first Rubiaceae classification influenced by the evolutionary concepts proposed by Darwin (1859). He was the first to introduce corolla aestivation as a significant character to be used for tribal definition within the Rubiaceae. He maintained *Sipanea* and *Limnosipanea* in the Rondeletieae, treating the herbaceous habit of these two taxa as a variable character within the tribe. In the same work, he published the new genus *Chalepophyllum* Hook.f., and positioned it in the Rondeletieae, indicating that it had only one species collected by Schomburgk in Guyana, but he did not publish the name of the species. Three years later, he published *Chalepophyllum guyanense* Hook.f., citing the same material collected by Schomburgk.

Baillon (1880, 1881), well-known for his excessive lumping of distinct genera, differed from Hooker (1873), and treated corolla aestivation as a trivial taxonomic character for tribal delimitation within the Rubiaceae. In addition, he treated *Limnosipanea* as a synonym of *Sipanea* and included the latter in the Portlandia Series or Portlandieae (Baillon 1881, pp. 331–337, 469–479). To

explain this decision, he wrote that (English version; Baillon 1881, p. 337) "The true *Sipanea* [or "*Eusipanea*"] has the flowers of *Rondeletia*, but with contorted corolla [lobes]. The calycinal divisions are lanceolate and subfoliaceous in those named *Limnosipanea* [sic!] in which stamens are exerted and the leaves are verticillate, whilst in *Sipanea* proper the sepals are subulate, the stamens enclosed and the leaves verticillate [sic! the leaves in *Sipanea* are opposite, and in *Limnosipanea* are opposite or whorled]. They are annual or perennial herbs of tropical America, with flowers in axillary and terminal, often corymbiform cymes."

Schumann (1889, 1891) followed Hooker's delimitation of the Rondeletieae, and positioned *Sipanea* and *Limnosipanea* in that tribe. In addition, Schumann (1889: 249; 1891: 38–39) divided *Sipanea* into two sections: 1) Sect. I. *Eusipanea* K.Schum. "inflorescencia terminalis multi-rarissime uniflora coarctata, demum in cincinnos plus minus elongates transiens; capsula crustaceo-sublignosa" [inflorescence terminal, multiflorous, or very rarely uniflorous, in more or less elongated cincinni; capsule crustaceous-sublignous] where he positioned *S. glomerata* and *S. pratensis*, and 2) Sect. II. *Panisea* K.Schum., "inflorescencia stricte axillaris 1–2 rarius 3-flora (rarius ob gemmam apicalem parvam spurie terminalis); capsula papyracea" [inflorescence strictly axillary, 1–2(–3)-flowered (rarely appearing terminal at the apical bud); capsule papyraceous], where he positioned *S. biflora*. However, the inflorescences of *S. biflora* are terminal, sometimes appearing subaxillary, due to the reiteration of the axillary bud subtending the terminal inflorescence. In addition, in *Flora Brasiliensis* he treated *S. pratensis* as widely delimited [incl. *S. dichotoma*, *S. trichantha*, *S. vinca*, *S. hispida* Benth. ex Wernham, *S. acinifolia* Spruce ex Sprague (= *S. veris* S. Moore)], and his description was produced with a mixture of characters derived from specimens of several species, which he cited in the material examined, and the figure of the supposed *S. pratensis* (Schumann 1889, tab. 122) is instead of *S. hispida* Benth. ex Wernham. Schumann's wide delimitation of *S. pratensis* gave rise to considerable confusion among specialists, and the identity of this species was eventually clarified by recent authors (e.g., Steyermark 1972a; Delprete & Steyermark 2004e; Delprete 2010c). An expanded discussion of Schumann's confusion about these two species is available under *S. pratensis* (see Taxonomic Treatment, below).

Spencer Moore (1895: 398) described *Sipanea veris* S. Moore from a collection that he made in the state of Mato Grosso, Brazil.

Nicholas Edward Brown (1901: 33, tab. 33, fig. 10–17) added a second species to *Chalepophyllum*, describing *C.*

*speciosum* N.E. Br., and cited three collections made by McConnell and Quelch on Mount Roraima, at the triple border of Venezuela, Guyana and Brazil.

Wernham (1911) described the new genus *Pteridocalyx* Wernham as monotypic, and included it in the Rondeletieae, stating that it “is distinct from the rest of the tribe in the basal insertion of the stamens, the bifid stipules, and the combination of contorted aestivation with petaloid development of one or more of the calyx-lobes. *Pallasia* [Klotzsch (1853: 498), *nom. illeg. hom.* = *Wittmackanthus* Kuntze (1891: 302)] seems to be the nearest ally, but in *Pallasia* the aestivation is imbricate, and the stipules entire.” The basal position of the stamens attributed to the *Pteridocalyx* was due to the fact that he studied a long-styled form of the taxon. Two years later, Wernham (1913) added a second species to the genus, *Pteridocalyx minor* Wernham, indicating that the “chief distinction from *P. appunii* lies in the undivided stipules, the much narrower foliaceous calyx-segments, and the wider corolla-tube.”

Wernham (1917) described the genus *Neobertiera* Wernham, with a single species, and positioned it in the Hamelieae. He stated that “This genus falls indisputably into the tribe Hamelieae on the score of its fruits, seed, and corolla-characters, but it cannot be included with any genus yet described. The nearest ally is, perhaps, *Pseudohamelia* [Wernham 1912: 242], from which the present plant is readily separated by its contorted corolla, appreciably long filaments, glabrous conspicuous disc, and comparatively few and large globose seeds.” He also stated that the inflorescence of *Neobertiera* is similar to those of a section of *Bertiera* Aubl., from which he derived the generic name. Wernham’s description and discussion of *Neobertiera* are erroneous because he stated that its fruits are berries with a few seeds; however, subsequent observations by various authors (e.g., Steyermark, Delprete) confirmed that this genus belongs to the Sipaneeae. In the same article, Wernham (1917) revised *Sipanea* and recognized the following species: *S. galioides* Wernham (1917: 172), *S. spraguei* Wernham [= *S. veris*], *S. veris*, *S. biflora*, *S. pratensis*, *S. glabrata* Wernham, *S. hispida* Benth. ex Wernham, *S. trianae* Wernham [= *S. hispida*], *S. brasiliensis* Wernham [= *S. hispida*], and *S. colombiana* Wernham [= *S. pratensis* var. *dichotoma* (Kunth) Steyermark.]. He also listed the following species of which he was unable to examine the type: *S. glomerata*, *S. trichantha* Miq. [= *S. pratensis* var. *dichotoma*], “*S. vinca* Mart. ex K. Sch. in Fl. Bras. VI. vi. 250 [*nom. illeg., pro syn.*], identified by Schumann with *S. pratensis*, may be *S. hispida*”, and “*S. carnea* Neumann in Rev. Hort. II. ii. 445 (cum tab.) has been referred to above” [= *Pentas lanceolata* (Forssk.) Deflers].

Sandwith (1928) described *Sipanea micrantha* Sandwith, the species with the smallest flowers in the genus, hence the specific epithet, and stated that it was most similar to *S. biflora*, and maintained the genus in the Rondeletieae.

Bremekamp (1934a) treated *Sipanea* in the *Flora of Surinam*, where he recognized *S. stahelii* Bremek., *S. pratensis*, *S. coppenamensis* Bremek. [= *S. pratensis* var. *pratensis*], *S. ovalifolia* Bremek., and *S. biflora*, without mentioning the tribal affiliation of the genus.

Bremekamp (1934b), focusing on the Rubiaceae of Surinam, founded the tribe Sipaneeae Bremek. (as “Sipaneeae”), stating that “The only Surinam genus of the Rondeletieae, *Sipanea*, ought to be excluded from that tribe on account of the contorted aestivation of its corolla lobes, and of its herbaceous growth. Together with the nearly related *Limnosipanea* it forms a separate tribe, for which I propose the name: *Sipaneeae*.”

Ducke (1935) described *Dendrosipanea* Ducke and positioned it in the Rondeletieae, commenting that it resembles *Ucristia* [certainly referring to *Ucristia longifolia* Spreng. = *Augusta longifolia* (Spreng.) Rehder, from central and southern Brazil], and *Sipanea*, in general aspect, although the latter is an herb and *Dendrosipanea* is a shrub or treelet. Ducke also stated that his new genus has loculicidal capsules, but, as Steyermark (1964: 195, 199) later corrected, its capsules are septicidal. *Dendrosipanea* differs from *Sipanea* by being a shrub or treelet with septicidal capsules, while species of *Sipanea* are prostrate, decumbent or erect herbs (a few species are somewhat woody at basal nodes) with loculicidal capsules. In addition, in the molecular phylogenetic analysis of Delprete and Cortés-B. (2004) *Dendrosipanea* was retrieved at a basal position within the tribe, indicating that the woody habit is ancestral within the tribe, while *Sipanea* was found on another clade.

Standley (1940) described *Steyermarkia* Standl. from material collected in Guatemala. He treated *Steyermarkia* as related to *Sipanea*, and placed these two genera in the widely circumscribed Rondeletieae (incl. Sipaneeae).

Verdcourt (1958) maintained *Sipanea*, *Limnosipanea* and *Steyermarkia* in the tribe Rondeletieae as widely delimited, treating the herbaceous habit as a trivial character for the separation of the Sipaneeae.

Bremekamp (1966: 20) proposed a new classification of the Rubiaceae, dividing the family into eight subfamilies. In this treatment, he characterized the Sipaneeae as “a small tribe containing but three genera; on account of their herbaceous growth they occupy a somewhat isolated position in the subfamily [Cinchonoideae]. These genera are *Sipanea* Aublet, *Virecta* Vahl [= *Sipanea*] and *Limnosipanea* Hook.f.”

Steyermark (1964) in the series *Botany of the Guayana Highlands* treated *Chalepophyllum*, and emended *Dendrosipanea*, separating them by numerous morphological characters. In the same work he described the new genera *Maguireothamnus* Steyermark and *Neblinathamnus* Steyermark, and positioned them in the Rondeletieae.

Steyermark (1967: 284–289) described the new genus *Sipaneopsis* Steyermark, where he included six species, stating that it is “similar to both *Sipanea* and *Rondeletia*. Because of the imbricate aestivation of the corolla lobes, it is more closely related to *Rondeletia*.” In the key to the Rondeletieae genera, Steyermark (1967: 234–235) characterized *Sipaneopsis* as having “Fruit indehiscent, endocarp hard, bony-crustaceous; seeds relatively few, turgid, 6–12 in a fruit; orifice of corolla with 5 thickened triangular projections covered with erect brushy white hairs.” In the same key to the Rondeletieae genera, he included: *Gleasonia* Standl., *Sipaneopsis*, *Cuatrecasasiodendron* Standl. & Steyermark. ex Steyermark. [= *Arachnothryx* Planch.], *Rondeletia* L., *Arachnothryx*, *Pteridocalyx*, *Neobertiera*, *Maguireothamnus*, *Neblinathamnus* [as “*Neblinanthus*”], *Sipanea*, *Limnosipanea*, *Chalepophyllum*, and *Dendrosipanea*.

Steyermark (1974), in the Rubiaceae of the *Flora de Venezuela* maintained the same delimitation of the Rondeletieae of 1967. Of the tribe Sipaneeae, as here delimited, he treated *Sipaneopsis*, *Maguireothamnus*, *Neblinathamnus*, *Sipanea*, *Limnosipanea*, *Chalepophyllum*, and *Dendrosipanea*, providing keys, full descriptions, geographic distributions, and specimens cited for the species occurring in Venezuela.

Robbrecht (1988) “provisionally maintained [the Sipaneeae as] Bremekamp’s segregate of Rondeletieae for these three genera with herbaceous habit and contorted aestivation” adding that “a revision of the Rondeletieae/Condamineae complex may well show that this is not justified”. In the Sipaneeae he included *Sipanea*, *Limnosipanea* and *Steyermarkia*, while he positioned the other genera of this tribe, as here delimited, in the tribe Rondeletieae, and treated *Neobertiera* as a dubious genus probably related to *Bertiera*.

Delprete (1999) followed Verdcourt (1958) and Steyermark (1964, 1967, 1974), and included the Sipaneeae and part of the Condamineae within a very widely circumscribed Rondeletieae, mostly due to general morphological similarities. In Delprete’s treatment, there is a key to all the genera of the broadly delimited Rondeletieae, including all the genera here included in the Sipaneeae.

Because of the standing uncertainty about the delimitation of the above cited tribes, Rova et al. (2002)

undertook a molecular phylogenetic study of the Condamineae-Rondeletieae-Sipaneeae complex using *trnL-F* sequence data, and arrived at several unexpected results. In that study, *Maguireothamnus*, *Sipanea*, *Sipaneopsis* and *Neobertiera* were found on a strongly supported clade, which corresponded to the tribe Sipaneeae as here delimited. The positioning of *Maguireothamnus* within this group was a surprise. Historically, it was placed within Rondeletieae s.str. due to its suffrutescent habit and many-seeded capsules, but was exceptional in either tribe because of its large, long-tubular corollas. To add morphological support for the position of *Maguireothamnus* in Sipaneeae, Rova et al. (2002) presented a convincing set of palynological characters. Also, Sipaneeae genera were retrieved, for the first time, within the subfamily Ixoroideae, along with a portion of Rondeletieae, sensu Delprete (1999). In addition, for the first time, the Sipaneeae clade was found to be sister to a small clade containing *Gleasonia* (tribe Henriquezieae), *Posoqueria* Aubl., and *Molopanthera* Turcz. The last two genera are unique in the family because of their peculiar pollen catapult mechanism (Schumann 1888; Delprete et al. 2005; Rova et al. 2002), and were later transferred by Delprete (2004, 2009) to the tribe Posoquerieae.

The results of Rova et al. (2002) stimulated Delprete and Cortés-B. (2004) to undertake a phylogenetic analysis of the Sipaneeae, using *trnL-F* and ITS sequences, where they included other genera believed to be related to Sipaneeae due to their overall morphological similarity with the core genera, and many representative members of the subfamily Ixoroideae. With these additional genera, the Sipaneeae group under study included *Chalepophyllum*, *Dendrosipanea*, *Limnosipanea*, *Maguireothamnus*, *Neblinathamnus*, *Neobertiera*, *Pteridocalyx*, *Sipanea*, *Sipaneopsis*, and *Steyermarkia*, for a total of about 50 species. In both combined *trnL-F* + ITS and *trnL-F* analyses, the tribe Sipaneeae was shown to be monophyletic, and positioned within the subfamily Ixoroideae. Within the Sipaneeae, the *Sipanea* clade was found to be sister to the *Neobertiera-Sipaneopsis* clade. Delprete and Cortés-B. (2004) also tested the two sections of *Sipanea* proposed by Steyermark (1967): 1) Sect. *Sipanea*, characterized by erect or ascending herbs with 3–20(–many)-flowered inflorescences and thick-walled capsules; 2) Sect. *Virectaria* (L.f.) Steyermark, characterized by prostrate or creeping herbs with 1–3(–5)-flowered inflorescences and thin-walled capsules. In the molecular phylogenies of Delprete and Cortés-B. (2004), the species of the two sections are intermixed, and therefore concluded that Steyermark’s sections are not monophyletic. In addition, it is interesting to note the alternation of erect and prostrate habit

of *Sipanea* species in the phylogenies obtained. However, because only 9 out of the 17 species were sampled, they refrained from suggesting any further evolutionary inferences within the genus. *Sipanea* and *Limnosipanea* have been traditionally treated as closely related genera (e.g., Bremekamp 1934b, 1966; Steyermark 1974; Delprete 1999), because of their herbaceous habit and morphological similarity, but the phylogenies of Delprete and Cortés-B. (2004) contrasted with this opinion. While their molecular analyses confirmed the monophyly of both genera, *Sipanea* and *Limnosipanea* are not sister taxa, and therefore the herbaceous habit originated at least twice within the tribe. The genera *Steyermarkia*, *Pteridocalyx* and *Neblinathamnus* were not included in Delprete and Cortés-B. (2004) analyses, due to unsuccessful attempts to extract DNA from relatively old herbarium specimens, and therefore, it was impossible to test their phylogenetic position within the tribe. However, because of their general morphological similarities (e.g., membranous corolla with left-contorted aestivation, capsular fruits, and stalked placenta with many seeds), they were tentatively maintained in the Sipaneeae, pending future molecular phylogenetic studies.

Delprete (2015a) emended the description of *Neobertiera*, reported for the first time that the genus is heterostylous, and described three additional species. The four species are restricted to the Guayana Shield, with two species probably restricted to Guyana, and two species probably restricted to French Guiana.

Delprete (2018) described two new species of *Dendrosipanea* and *Sipaneopsis*. The two new species, *D. prancei* Delprete and *S. duckei* Delprete, are endemic to white-sand areas from the Brazilian and Colombian Amazon. He demonstrated, for the first time, that *Dendrosipanea* is heterostylous and added a key to the three recognized species of this genus.

Delprete (2019a) revised *Pteridocalyx* and treated it as a monospecific, heterostylous genus. In addition, he described the placenta of *Pteridocalyx* as longitudinally adnate along the central septum; however, recent anatomical studies (Delprete, pers. obs., see below) revealed that the placenta has a minute stalk inserted at the distalmost portion of the septum, i.e., near the roof of the locule, and terminates with a pendulous, narrowly cylindrical extension almost as long as the locule. Following these studies, *Pteridocalyx* is here confirmed as unique within the Sipaneeae because of its calycophylls and placenta with a stalk inserted at the distalmost portion of the septum, with a pendulous cylindrical extension, on which the ovules are inserted.

Delprete (2019b) presented an additional study on *Neobertiera* in which a new species, *N. montedouraden-*

*sis* Delprete, was published based on a specimen from the town of Monte Dourado, near the Jari River, state of Pará, Brazil. It is unique within the genus because of hypanthia and fruits with basally tuberculate trichomes. Specimens recently analyzed showed that this species was collected in other localities in the states of Pará and Amapá. In the same study, the type specimen of *Bertiera palustris* A.Rich. (in A.P. de Candolle 1830: 392) was analyzed, and it was concluded that it is synonymous with *N. glomerata* Delprete, a name recently published for a species occurring in French Guiana; therefore, the new combination *N. palustris* (A.Rich.) Delprete was proposed.

In conclusion, according to the results and discussion presented by Delprete and Cortés (2004) and Delprete (2015a, 2018, 2019a, 2019b), the tribe Sipaneeae is here delimited to include the genera *Chalepophyllum* (1 spp.), *Dendrosipanea* (3 spp.), *Limnosipanea* (3 spp.), *Maguireothamnus* (3 spp.), *Neblinathamnus* (2 spp.), *Neobertiera* (5 spp.), *Pteridocalyx* (1 sp.), *Sipanea* (17 spp.), *Sipaneopsis* (8 spp.), and *Steyermarkia* (1 sp.), for a total of 44 species.

## MATERIAL AND METHODS

This study is based on examinations of herbarium specimens, material preserved in 60% ethanol, and field observations. Herbarium specimens were studied either on site or through loans from the B, B-W, BBS, BM, BR, BRB, C, CAY, CEN, COL, E, F, FI, G, G-DC, HEPH, HTO, IAN, IBGE, INPA, K, L, LINN-SM, MBM, MG, MO, MPU, NY, NX, P, P-AD, P-BONPL, P-JJR, P-JU, R, RB, U, UB, UFG, UFMT, UMP, US, and VEN herbaria. Digital images of herbarium specimens were analyzed through the following websites: Jstor Global Plants (<https://plants.jstor.org/>), Reflora – Brazilian Plants: Historic Rescue and Virtual Herbarium for Knowledge and Conservation of the Brazilian Flora (<http://reflora.jbrj.gov.br/reflora/PrincipalUC/PrincipalUC.do?lingua=en>), and INCT – Herbário Virtual da Flora e Fungos (<http://inct.splink.org.br/>).

Pollen observations were made on samples obtained from flower buds of specimens at CAY, F, S, U, and US herbaria. For pollen preparation, nearly mature flower buds, just before anthesis, were extracted from herbarium specimens and softened in 1:200 Agepon solution for 30 minutes. The anthers were then dissected and pollen was isolated by sieving with mesh of width 63  $\mu\text{m}$  after which they were dehydrated in glacial acetic acid and acetolysed in concentrated sulphuric acid and acetic acid 1:9 for 10 minutes in a heating block at

95°C. Grains destined for LM studies were mounted in Kaiser's glycerin jelly. Values of the length of polar and equatorial axes were based on LM measurements, using an Olympus BX 51 microscope, an Olympus ColorView Soft Imaging System camera and AnalySis software. Pollen images and measurements were made by Iris van der Beeten at the Meise Botanic Garden, Meise, Belgium.

Species descriptions are based on field observations, dried herbarium material, and spirit material. Measurements used in the descriptions were made from dry herbarium specimens. Barcode numbers of herbarium specimens, when available, are cited in square brackets after the herbarium acronym; when the barcode number is not available, the accession number, is cited preceded by "Acc. No." and in square brackets. All specimens cited have been examined, unless indicated by "n.v." (not seen) after the herbarium acronym.

Information about collection dates and localities of specimens gathered by Martius in Brazil were obtained from the text and the maps available in Spix and Martius (1976). Pohl's collection dates and localities in Brazil were obtained by Pohl's (1976) travel diary.

Coordinates from collecting sites in French Guiana, when not indicated on specimen labels, were obtained from Hoff and Cremers (1996).

A conservation status assessment of each taxon studied was made using the IUCN Red List Categories and Criteria (IUCN 2012, 2019).

#### SPECIES AND VARIETY CONCEPT

In this study, the taxonomic species concept of Davis and Heywood (1963) was used: "assemblages of individuals with morphological features in common and separable from other such assemblages by correlated morphological discontinuities in a number of features." I also tried to reevaluate with a critical approach many morphological characters that have been historically treated as significant for generic delimitation in the Rubiaceae (e.g., corolla aestivation, heterostyly, fruit dehiscence, placentation, vestiture, leaf shapes, stipules, etc.).

Steyermark's publications (1964, 1967, 1972a, 1972b, 1974) represent an important contribution towards the understanding of the members of the tribe Sipaneeae, as the group is mostly centered on the Guiana Shield. He expressed his concepts of infraspecific ranks in a note on *Sipanea pratensis* (Steyermark 1967: 271) in which he recognized numerous varieties and forms: "After a prolonged study of numerous specimens, it is believed in the best interests of taxonomy to render the great variation expressed by the assignment of varietal and for-

mal categories. No subspecies are given, since there does not appear to be any definite geographic range indicated within the variations, and the differences manifests appear to intergrade in various portions of the variable characters." In other words, Steyermark allowed varieties and forms to widely overlap throughout their geographic ranges (i.e., sympatric varieties). However, according to the concepts adopted in the present treatment, only one infraspecific rank is used, the variety, which is defined by a secondary variation with a morphological-geographical correlation, which largely corresponds to Steyermark's subspecies concept. In other words, geographically separated (allopatric) populations correlated with some morphological characters and that are not sufficiently distinct to be accepted as different species; therefore, I opted to use the rank of variety for such populations. This is in accordance with current practice in Neotropical Rubiaceae taxonomy (e.g., Delprete 1999, 2010a, 2010b, 2010c; Persson and Delprete 2017), and is used here to maintain nomenclatural stability.

#### GENERAL MORPHOLOGY

##### *Habit*

The habit in the tribe Sipaneeae ranges from annual or perennial herbs, subshrubs, shrubs to treelets. Plants that are basally woody and distally herbaceous are here called subshrubs, for lack of a better term. Therefore, species that are entirely herbaceous at early stage and with woody basal internodes at later stage are described as "herbs or subshrubs (woody at basal internodes)". However, plants that are up to 50 cm tall and entirely woody are also here called subshrubs. The degree of habit variation at the generic level within the Sipaneeae is discussed below.

For non-erect plants, three habits are found in the Sipaneeae for herbs, subshrubs and shrubs. The terminology adopted for these habits follows The American Heritage Dictionary of the English Language (2020) with the following definitions:

- 1) Decumbent: "Lying or growing on the ground but with erect or rising tips";
- 2) Prostrate: "Growing flat along the ground";
- 3) Ascending: "Growing or directing upward from a curved or slanted base".

A summary of the habits found in the genera of the Sipaneeae is presented below.

*Steyermarkia* is exceptional within the tribe by being a subsessile plant with a rosette of large leaves spreading near the ground, and a short, unbranched, woody stem, exceptionally to 18 cm long.

*Dendrosipanea* can be either a shrub or a treelet, 0.5–4 m tall; while *Chalepophyllum*, *Maguireothamnus* and *Neblinathamnus* are woody subshrubs or shrubs, 0.3–4 m tall, usually erect or rarely partially prostrate.

In *Neobertiera* the habit varies from perennial herbs, subshrubs (woody at basal internodes or entirely woody) to shrubs, 0.4–4 m tall, erect or basally decumbent, sparsely branched. *Neobertiera gracilis* Wernham and *N. palustris* range from perennial herbs to subshrubs (woody at basal internodes) to shrubs, 0.5–4 m tall; *N. micrantha* Delprete is a perennial herb, 0.5 m tall; while *N. montedouradensis* Delprete and *N. pakaraimensis* Delprete are shrubs (i.e., entirely woody), 1 m tall and 0.5–4 m tall, respectively.

*Pteridocalyx* is a single-stemmed woody plant, 1–2 m tall, with a central, thin stem, and sparsely branched at the top.

*Sipaneopsis* is a genus endemic to Amazonian white-sand areas, with most species ranging from subshrubs (partially or entirely woody) to shrubs, 0.3–1.6 m tall, erect, ascending, or rarely decumbent (basal portion sometimes prostrate), single-stemmed or with a few to many branches. Two species are exceptional within *Sipaneopsis* by having herbaceous habit: *S. pacimonien-sis*, which is a single-stemmed perennial herb 10–12 cm tall, and *S. cururuensis* J.H.Kirkb., which ranges from herb to subshrub (woody at basal internodes) 25–50 cm tall.

Most species of *Sipanea* are herbs, erect, trailing, procumbent or decumbent, often rooting at basal nodes, sometimes mat-forming, or rarely floating on water in inundated areas (*S. biflora*). Several species of *Sipanea* (*S. glomerata*, *S. hispida*, *S. pratensis* var. *dichotoma*, *S. prancei*, *S. wilson-brownei*) range from herbs to subshrubs, i.e., completely herbaceous or with stems woody at base and distally herbaceous, 0.3–1.5 m tall, and erect or decumbent. The degree of woodiness of the basal internodes in these species depends on the age of the plant.

The three species of *Limnosipanea* are herbs, either terrestrial, semi-aquatic (amphibious) or aquatic, erect, prostrate or decumbent; short-lived (2–4 months life span) when terrestrial or semi-aquatic, or perennial when growing in permanently flooded areas. *Limnosipanea erythraeoides* is a terrestrial or semi-aquatic (amphibious) herb, prostrate or decumbent, with main stems 8–20 cm long, single-stemmed or sparsely branched; with leaves opposite throughout the whole plant or 3–4 per node at basal nodes and opposite at distal nodes. *Limnosipanea palustris* is a terrestrial or semi-aquatic (amphibious) herb, ephemeral (2–4 months life span), erect, 5–40 cm tall, single-stemmed or sparsely

branched, with leaves commonly opposite, or sometimes ternate at basal nodes.

*Limnosipanea spruceana* is a polymorphic herb, adapted to terrestrial, seasonally flooded, or permanently flooded environments. Three main habits were detected in this species. In localities seasonally inundated, during full rainy season the water level might reach up to 4–5 m in depth, especially in Amazonian savannas; as the precipitations decrease, the water level gradually diminishes until the soil is still moist but no longer flooded; at this precise moment the terrestrial form of this species appears, sometimes forming large stands, easy to spot from a distance because of the dark red vegetative parts; this terrestrial form is erect, 3.5–25 cm tall, and particularly short-lived, as it can grow, disperse seeds and die within three months. A second form is found in permanently flooded areas, as in localities with natural springs; in this form, the submerged portion of the stem could be up to 40 cm long, not branched, green to whitish-green, with the basal portion leafless, adventitious roots at each node, and the distal submerged portion with 3–6(-8) linear to acicular leaves per node, and without adventitious roots. The aerial portion of these plants is 10–25 cm long (including inflorescences), branched, with stems and rachis red-vinaceous, with 2–5 leaves per node, and blades linear to lanceolate; this form is perennial. A third form is found in seasonally flooded areas, with water 20–30 cm deep during the rainy season; in this environment the plants are seasonally semi-aquatic (amphibious), with dimorphic leaves (i.e., submersed and aerial); at the end of the rainy season, when the water is completely dissipated, the plants become terrestrial and are decumbent, with the portion of stem that was submerged, 20–30 cm long and with 3–6(-8) linear to acicular leaves per node, leaning on the ground, and the distal portion erect, 10–20 cm long (including inflorescences), with 2–5 linear to lanceolate leaves per node; at this stage, the stem, leaves and the rachis are red to reddish, due to sun exposure; this latter form, has a life span of three to four months.

### Stipules

Delprete (1999: 25) proposed three degrees of stipule persistency in Rubiaceae: 1) readily caducous, present only at the vegetative bud, 2) caducous, present during leaf development, but caducous before the leaves fall off, and 3) persistent, present after the leaves of the same node fall off. According to these definitions, stipules are persistent in all Sipaneeae genera.

Stipules in the Sipaneeae are interpetiolar, and can be free or connate at the base or sometimes adnate to

the petioles of the same node. They are very variable and can provide important diagnostic characters for the identification of genera and species.

In *Chalepophyllum*, stipules are broadly triangular or sometimes becoming bifid at apex at older stages (Figure 1A–B). In *Dendrosipanea*, they are free or narrowly connate at the base, deltoid, and acuminate, bifid at apex, or with two small lobes on each side of the stem (Figure 1C–D). In *Limnosipanea*, they are minute to almost obsolete, reduced to a line between the petioles, sometimes with a small mucro or a seta at the center, often withering on the stem, and no abscission layer is formed (Fig. 1E). In *Maguireothamnus*, they are adnate to the petioles (Figure 1F), narrowly triangular or basally triangular and aristate (rarely linear), with a row of 3–7 colleters on each side, inserted just below the margin on the internal side or on the margin of the basal sheath. In *Neblinathamnus* they are adnate to the petioles, minute, broadly to shallowly triangular to truncate, and often bifid at apex, or divided into two lobes on each side of the stem (Figure 1K–L).

In *Neobertiera*, they are ovate to broadly ovate, acuminate or bifid at apex (Figure 1G–H), or narrowly triangular in *N. montedouradensis*. In *Pteridocalyx*, they are ovate to narrowly triangular, entire or bifid at apex (Figure 1I–J); this variation can be present on the same plant, as sometimes the stipules are entire at early stage and remain so at later stage, or they might become bifid at apex in later stages.

*Sipanea* is the largest genus in the tribe, and its stipules are quite variable in shape and size (Figure 2). They can be either free or basally adnate to petioles and vary from truncate to broadly transversally elliptic, broadly to narrowly triangular, suborbicular, subulate, linear, or rarely setaceous or reduced to a line between the petioles. Because of this variation, stipules provide a significant diagnostic characters that can be used to distinguish species within the genus.

In *Sipaneopsis* the stipules can be free or connate at base, broadly to narrowly triangular, acuminate and bilobed at apex, or bifid with narrowly triangular lobes (Figure 3), or topped by (1–)3–4 linear lobes (*S. morichensis*) or reduce to a line topped by several

lobes (*S. rupicola* (K.Schum.) Steyererm.). In certain species (e.g., *S. foldatsii* Steyererm.) they are triangular and consistently entire (i.e., not lobed). In *S. duckei* Delprete (Figure 3B), stipules are broadly triangular at base and linear at distal portion, or narrowly triangular to narrowly oblong-triangular; also, they can be entire at early stage and remain so at later stages, or they might rarely become bifid at apex on older nodes. In *S. rupicola* they are very variable (Figure 3F–H): they can be triangular, entire and caudate, or triangular at base topped by 2–3 acute lobes, or reduced to a line topped by 6–7 linear lobes or by two long lobes intercalated with shorter lobes.

In *Steyermarkia*, stipules are persistent, free at base, lanceolate to linear-lanceolate, and attenuate or bifid at apex.

#### Leaves

In most Sipaneae genera, the leaves are opposite and homophyllous, with two exceptions. In *Neblinathamnus*, the leaves might be opposite or ternate. In *Limnosipanea*, the leaves are opposite or whorled, and homophyllous or heterophyllous (see discussion below).

Leaf shape and size vary within and among genera, providing several diagnostic characters that can be used to distinguish genera and species.

In *Chalepophyllum*, the leaves are sessile to short-petiolate, with ovate, obovate, oblong or spatulate, subcoriaceous blades. In *Dendrosipanea*, they are sessile to short-petiolate, with oblong, spatulate or oblanceolate, subcoriaceous blades.

In *Limnosipanea*, the leaves are sessile, membranaceous or chartaceous, and can be opposite or whorled. They are homophyllous and opposite or ternate in terrestrial plants, or heterophyllous and with a different phyllotaxy in partially or seasonally submerged (semi-aquatic or amphibious) plants, and in permanently submerged (aquatic) plants. *Limnosipanea erythraeoides* is prostrate or decumbent herb, terrestrial or semi-aquatic, with homophyllous leaves, which can be opposite throughout the whole plant, or 3–4 leaves at basal nodes and

**Figure 1.** Stipules variation in selected genera of the tribe Sipaneae. A–B. *Chalepophyllum guyanense*, stipule variation on the same branch. A. Entire stipule. B. Bifid stipule. C–D. *Dendrosipanea revoluta*, stipule variation on the same branch. C. Entire stipule. D. Bifid stipule. E. *Limnosipanea erythraeoides*, node with base of two leaves, and extremely reduced stipule with three partially exerted colleters. F. *Maguireothamnus tatei*, nodes with permanent, overlapping stipules. G. *Neobertiera gracilis*, node with bifid stipule. H. *Neobertiera montedouradensis*, node with entire stipule. I–J. *Pteridocalyx appunii*, stipule shapes present on the same branch. I. Entire stipule. J. Bifid stipule. K–L. *Neblinathamnus argyreus*. K. Shallow, truncate stipule. L. Shallow, bilobed stipule. A–B: drawn from Delprete & Araujo 7429 (CAY); C–D: drawn from Wurdack & Adderley 42972 (US); E: drawn from Macedo 5537 (US); F: drawn from Maguire & Politi 28449 (US); G: drawn from Maguire & Fanshawe 22964 (F); H: drawn from Santos 414 (MG); I–J: drawn from Delprete & Benjamin 12813 (CAY). Illustration by Piero Delprete.

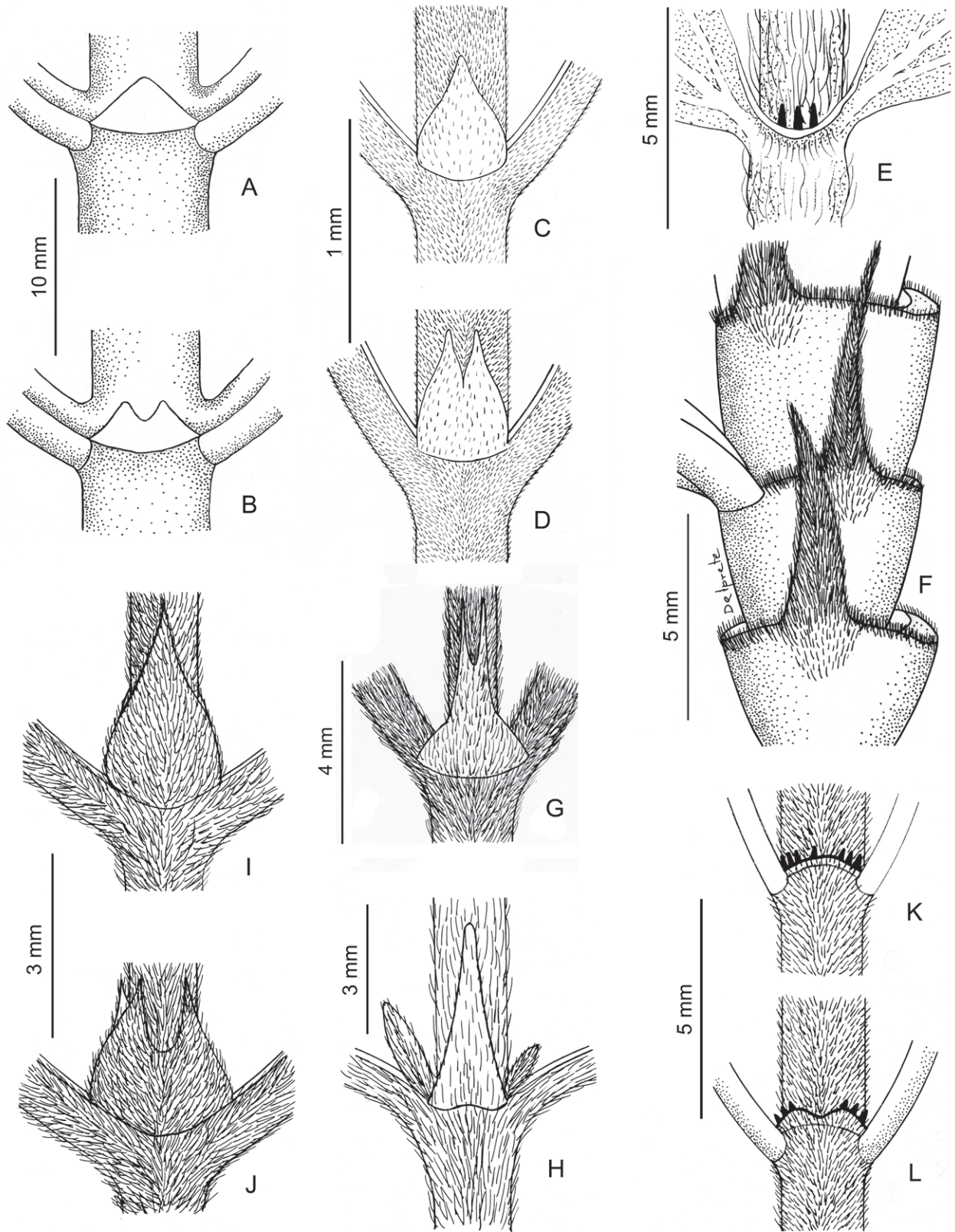


Figure 1.



opposite at distal nodes. *Limnosipanea palustris* is an erect, terrestrial or semi-aquatic (amphibious) herb, with homophyllous leaves, which are commonly opposite or sometimes ternate at basal nodes.

*Limnosipanea spruceana* is a polymorphic, erect or decumbent herb, adapted to terrestrial and to seasonally or permanently flooded environments. In this species, the leaves are homomorphic, opposite or whorled in terrestrial plants, or whorled and dimorphic in submerged plants. Three main forms were detected in this species. In the terrestrial, short-lived form, found in seasonally inundated localities, the leaves are homomorphic, opposite or 3–5 per node, with linear to lanceolate blades. The second form is perennial, and grows in permanently flooded areas, and has heteromorphic leaves; the basal portion of the submerged portion the stem is leafless and with adventitious roots at each node, while in the distal submerged portion the leaves are whorled, 3–6(-8) per node, linear to acicular blades; and the aerial portion has 2–5 leaves per node, with linear to lanceolate blades. The third form grows in seasonally flooded areas. During the rainy season, the plants are semi-aquatic (amphibious), with dimorphic submerged and aerial leaves, as described for the second form. At the end of the rainy season, when the water is completely dissipated, the portion of stem originally submerged, with whorled leaves (3–6(-8) per node), is laying on the ground, and the distal portion of the stem is erect, with 2–5 leaves per node, and linear to lanceolate blades.

In *Maguireothamnus*, the leaves are sessile, subsessile or short-petiolate, and the blades are ovate, obovate, oblong, oblanceolate to lanceolate, and thinly to thickly coriaceous. *Neblinathamnus* has short-petiolate or subsessile leaves, with elliptic, obovate or oblong, thinly coriaceous blades. In *Neobertiera* and *Pteridocalyx*, they are petiolate, and with elliptic, oblong-elliptic to oblanceolate, chartaceous blades.

In *Sipanea*, the leaves are sessile or subsessile to short-petiolate, rarely with axillary brachyblasts with numerous smaller leaves (e.g., *S. galioides* Wernham); and the blades are ovate, narrowly ovate, rhombic-ovate, elliptic, oblong-elliptic, oblong-lanceolate, or linear-

lanceolate to linear, and membranaceous, chartaceous or thinly subcoriaceous. *Sipaneopsis* has short-petiolate leaves, with ovate, elliptic, lanceolate or linear, and chartaceous or subcoriaceous blades.

*Steyermarkia* is a subsessile plant, with leaves in rosettes spreading near the ground. The leaves are short-petiolate, with large, narrowly obovate to oblanceolate, membranaceous to chartaceous blades.

#### Leaf domatia

Leaf domatia in Rubiaceae are commonly tufts of hairs, correlated or not with a pit or a crypt, and present on the abaxial side in the axils of the secondary veins, or rarely in the axils of the tertiary veins. Domatia are commonly associated with presence of mites. Leaf domatia are absent in all genera of the Sipaneeae, with the sole exception of the tuft-domatia present in the axils of secondary veins of *Chalepophyllum guyanense*.

#### Colleters

Colleters have been defined by Robbrecht (1988) as “pluricellular mucilage-secreting structures occurring inside stipules and on other organs.” He also reported that they have previously been called *drusen* (Solereder 1893), shaggy hairs (Solereder, 1908), glandular shaggy hairs (Metcalfé and Chalk 1950), *harzsecernierende drusen* (Krause 1909), *cérocystes* (Hallé 1967), *squamellae* (Ramaya and Bahadur 1968), and *annexes glanduleuses* (Boiteau and Allorge 1978). Steyermark (1964, 1967, 1974, 1984a, 1984b) called them “glándulas”, “glands” or “squamellae”. According to modern literature, these minute structures are called colleters (e.g., Esau 1965; Lersten 1974a, 1974b, 1975; Robbrecht 1988; Verdcourt 1976; Rogers 1984, 1987; Delprete 1999; Persson and Delprete 2017). Esau (1965) clarified that the term colleter is “derived from the Greek *Colla* [= glue], referring to the sticky excretion from this structure” and “they frequently produce a mixture of terpenes and mucilage.” In Spanish, they are called “coléter” (sing.) or

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**Figure 2.** Stipule variation in *Sipanea*. **A.** *Sipanea glaberrima* [Section *Sipanea*], node with stipule and petioles. **B.** *Sipanea glomerata* [Section *Sipanea*], node with sheathing stipule and leaf bases. **C.** *Sipanea pratensis* var. *pratensis* [Section *Sipanea*], node with sheathing stipule and leaf bases. **D.** *Sipanea veris* [Section *Sipanea*], node with sheathing stipule and partially exerted colleters, and leaf bases. **E.** *Sipanea micrantha* [Section *Virecta*], node with sheathing stipule with partially exerted colleters, and petioles. **F.** *Sipanea carrenoi* [Section *Virecta*], node with stipule and petioles. **G.** *Sipanea setacea* [Section *Virecta*], node with setaceous stipule and petioles. **H.** *Sipanea stahelii* [Section *Nudae*], node with stipule and basal portion of petioles. **I.** *Sipanea saxicola* [Section *Nudae*], node with stipule reduced to a line between petioles, exerted colleters, and basal portion of petioles (note long, erect trichomes). **A:** drawn from *Rombouts 223bis* (U, holotype); **B:** drawn from *Williams 13016* (US); **C:** drawn from *Delprete 12882* (CAY); **D:** drawn from *Molina & Barkley 18-V-161* (US); **E:** drawn from *McDowell 3779* (US); **F:** drawn from *Steyermark et al. 115598* (MO); **G:** drawn from *Huber et al. 8245* (NY, holotype); **H:** drawn from *Maguire 24314* (US); **I:** drawn from *Martinelli et al. 7074* (MG). Illustration by Piero Delprete.

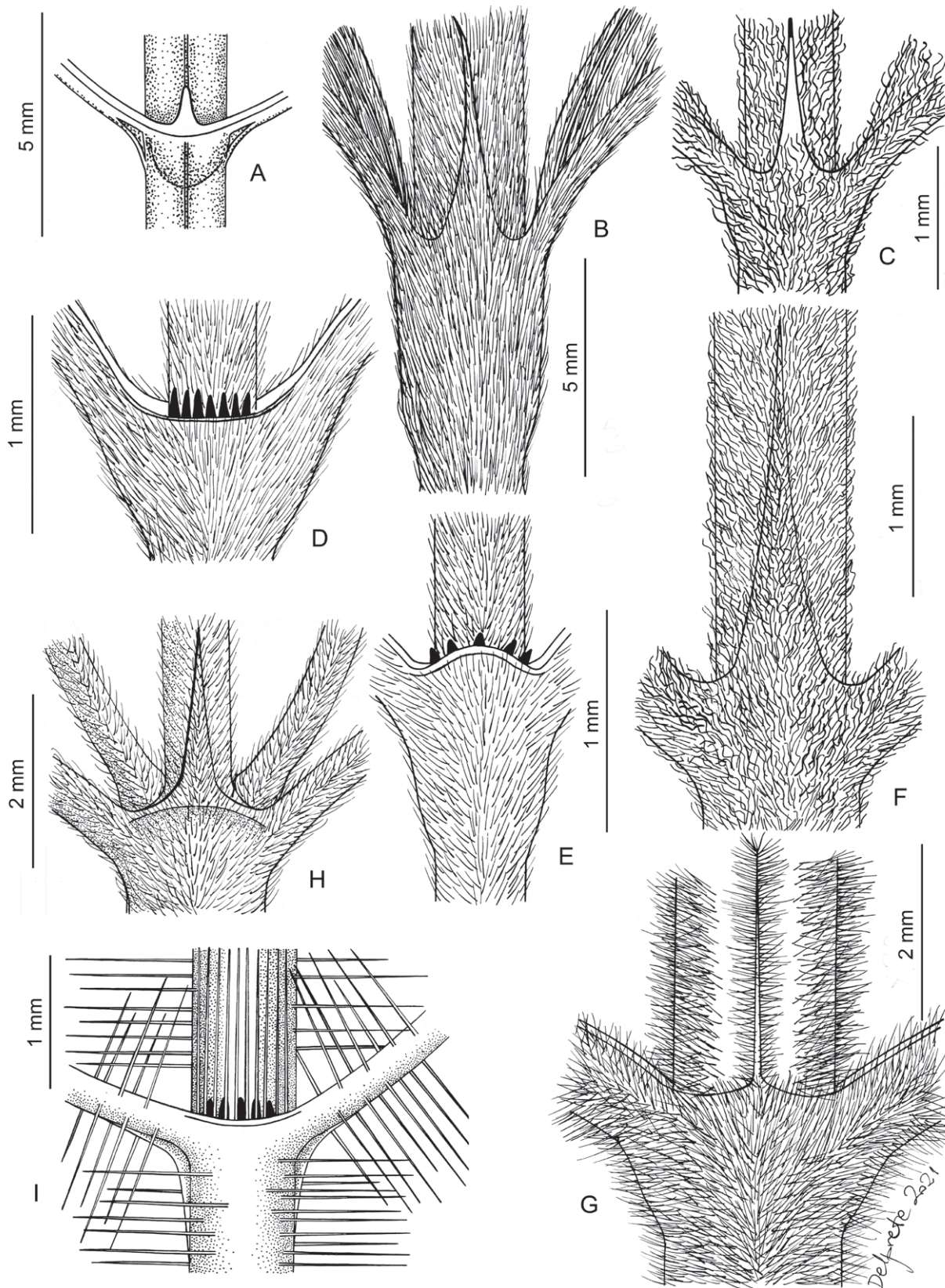
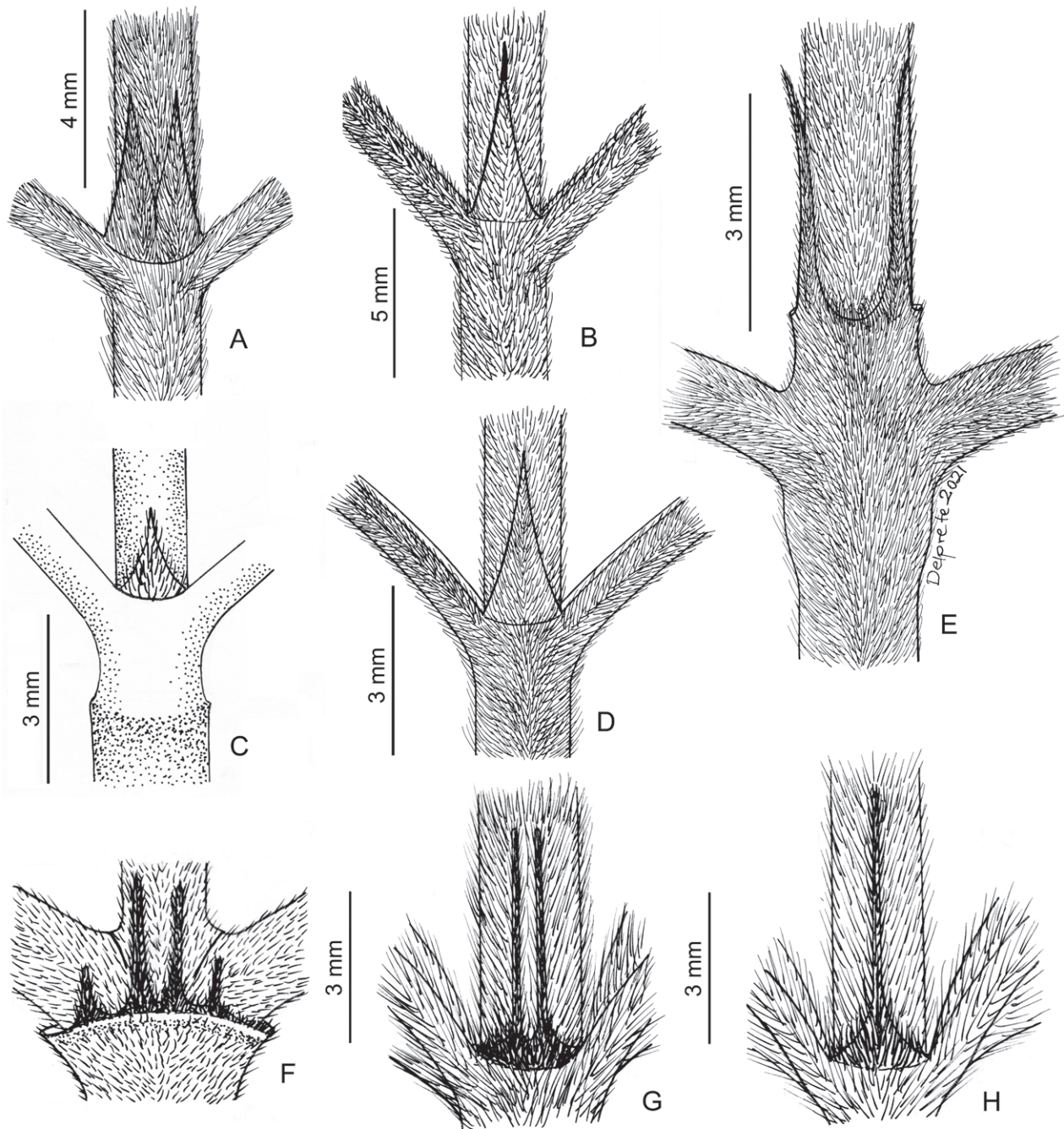


Figure 2.



**Figure 3.** Stipule variation in *Sipaneopsis*. **A.** *Sipaneopsis cururuensis*, node with stipule and basal portion of petioles. **B.** *Sipaneopsis duckei*, node with stipule and basal portion of petioles. **C.** *Sipaneopsis maguirei*, node with stipule and basal portion of petioles. **D.** *Sipaneopsis pacimoniensis*, node with stipule and basal portion of petioles. **E.** *Sipaneopsis huberi*, node with sheathing stipule and basal portion of petioles. **F–H.** *Sipaneopsis rupicola*, nodes with stipule variation. **A:** drawn from Egler & Raimundo 1265 (MG, isotype); **B:** drawn from Egler 273 (MG); **C:** drawn from Delprete et al. 7452 (CAY); **D:** drawn from Maguire et al. 37570 (NY, holotype); **E:** drawn from Huber & Medina 5786 (U, isotype); **F:** drawn from Williams 14897 (US); **G–H:** drawn from Gutierrez & Schultes 654 (US). Illustration by Piero Delprete.

“coléteres” (pl.), for which Font Quer (2000: 245) offers the following definition (translated from Spanish) “from Greek χόλλα, gum, and ουρητηρ, urethra. Hair secreting

mucilage.” Colleters in the Rubiaceae are most commonly present on the internal surface of the stipules, usually at the basal portion, and are also frequently found inside

the calyx, at the base of the calyx lobes or in the sinuses between them.

In most Rubiaceae genera, the colleters are commonly present on the internal side of the stipules and secrete a resinous substance in variable amounts. In certain genera the secretion could be abundant, and sometimes might form a globose unit above the apical stipules (e.g., *Elaeagia* Wedd., *Retiniphyllum* Bonpl.), and/or covering the distal portion of young braches. This exudate is believed to protect the vegetative buds and the young distal internodes against herbivory.

In the Sipaneeae, colleters have been observed on the internal surface of the stipules, sometimes at the axils of terminal branchlets of the inflorescences, at the side of bracteoles, and in the sinuses of calyx lobes. For the presence of colleters in the calyces of Sipaneeae genera, see the Section *Calyx* (below).

The present section deals with the colleters present on the internal (adaxial) side or at the margin, or rarely at the tip of the stipules. Within the Sipaneeae, Steyermark (1964: 195), distinguished *Chalepophyllum* from *Dendrosipanea* by having, among other characters, a “glutinous exudate abundant and obvious in uppermost parts of the branches at the base of the petioles, pedicels, or peduncles” while he wrote that in *Dendrosipanea* the “glutinous exudate of branches [is] lacking or inconspicuous.” However, he did not attempt to clarify the origin of the abundant exudate present in *Chalepophyllum* nor described the stipules of this genus.

Steyermark (1974: 384; translated from Spanish) reported that the stipules of *Limnosipanea* are “obsolete, interpetiolar, basal sheath adnate to the petioles and reduced to a seta or a solitary projection, with glands [i.e., colleters] inside.” While for *Dendrosipanea*, *Maguireothamnus*, *Neblinathamnus*, *Sipanea*, and *Sipaneopsis*, Steyermark (1974) described only the shape and the external side of the stipules and did not mention the presence of colleters.

In most genera of the Sipaneeae, the stipules are small or reduced to a line between the nodes (*Limnosipanea*), and, aside from *Chalepophyllum*, no resinous secretion has ever been reported. Nevertheless, this does not exclude the production of a resinous exudate by the stipular colleters of genera with minute stipules. A simple explanation could be that, if present, the amount of secretion of minute stipules with a few colleters might be so minor that it has not been observed.

Presence and characteristics of colleters inserted on the internal surface or at the margin or rarely at the tip of the stipules in Sipaneeae genera is presented below.

***Chalepophyllum*.** Stipules are free at base, broadly triangular to subtruncate (older stipules sometimes

becoming bifid at apex; Figure 1A–B), with the basal 2/3 covered by numerous dense colleters inside.

***Dendrosipanea*.** Stipules are free or basally adnate to petioles, deltoid, acuminate or bifid (Figure 1C–D), with basal 2/3 covered by numerous dense colleters intermixed with hairs inside.

***Limnosipanea*.** Stipules are reduced to a line between the petioles, sometimes obsolete, persistent, and withering on the stem with no abscission layer formed. They have 1–3 colleters inserted just below the margin, on the internal side, with the tips exerted beyond the stipule margin (Figure 1E). In stems with obsolete stipules, 1–2 colleters are inserted in the sinuses between the leaf bases. In submersed stems, stipules and colleters are absent.

***Maguireothamnus*.** Stipules have a basal sheath adnate to the petioles, with the free portion narrowly triangular to linear (Figure 1F), sometimes with an apical colleter. A row of 3–7 colleters is present on each side, either inserted just below the margin or on the margin of the basal sheath.

***Neblinathamnus*.** Stipules are basally adnate to the petioles, minute, broadly to shallowly triangular to truncate, sometimes shallowly bilobed, often bilobed at apex, or rarely constituted of two free lobes on each side of the stem (Figure 1K–L). A row of 7–9 sparse colleters is present at the margin of shallowly triangular to truncate stipules, or a row of 4–5 colleters is present at the margin of each lobe in bilobed stipules or in stipules constituted of two free lobes.

***Neobertiera*.** Stipules are basally adnate with the petioles, broadly ovate, ovate, oblong-ovate or narrowly triangular, acuminate or bifid at apex (Figure 1G–H). Their inner side is pubescent and with numerous colleters either in a row or as two groups on each side at medio-basal portion.

***Pteridocalyx*.** Stipules are basally adnate to the petioles, ovate to narrowly triangular, acuminate or bifid at apex (Figure 1I–J). The inner side has strigose hairs intermixed with colleters inserted at the medio-basal portion.

***Sipanea*.** Stipules are sheathing at base or basally adnate to the petioles, truncate to broadly transversally elliptic, broadly to narrowly triangular, suborbicular, subulate, linear, or rarely setaceous, or reduced to a line between the petioles (Figure 2). Colleters are inserted on the internal side or along the margin; a few to several colleters are inserted on each side or irregularly spread near the base or at the median portion or just below the margin, or inserted along the margin. The presence and position of colleters for each section is described below.

***Sipanea* section *Sipanea*** (corolla mouth with a ring of yellow hairs). In this section, the stipules are basally

adnate to the petioles, sheathing, with 2 colleters on each side of the central lobe in *S. galioides*, or with 3 colleters on each side of the central lobe in *S. glaberrima* (Figure 2A). In *S. glomerata*, 1–5 colleters are present on each side at the base of the central lobe, or sometimes 1–3 colleters are present near the apex of the linear lobe, either on the margins and/or at the tip. In *S. hispida*, the inner side of stipules has 5–6 colleters inserted just below the base of the central lobe, or 6–7 colleters are inserted just below the margin, often with exserted tips. In *S. pratensis*, 2–3 colleters are inserted at the margin on each side of the central lobe. In *S. veris*, 5–6 colleters are inserted along the stipular margin.

**Sipanea section Virecta** (corolla mouth with a ring of white hairs). In this section, stipules are adnate to the petioles, broadly triangular, shallowly obtuse to subacute (or very rarely bifid) at apex, or truncate, or with a central seta or two unequal setae in *S. setacea*, while the internal side and colleters have not been observed. In *S. biflora*, 2–6 colleters are inserted in a row near the base of the stipule. In *S. carrenoi*, 3–5 colleters are inserted on the median portion of the stipule. In *S. gleasonii*, 3–5 colleters are inserted at the median portion, or 7–10 colleters are irregularly distributed on the inner surface of the stipule. In both *S. micrantha* (Figure 2E) and *S. ovalifolia*, 3–5 colleters are inserted just below the margin, with the tips exserted beyond margin.

**Sipanea section Nudae** (corolla mouth glabrous or with sparse white hairs). In this section, stipules are also adnate to the petioles, and subulate, or broadly to narrowly triangular at base and narrowly triangular to linear distally, or very shallowly transversally ovate, or reduced to a line between the petioles. In *S. prancei*, 5–7 colleters are intermixed with a few hairs. In *S. saxicola*, 5–8 colleters are inserted in a row just below the margin (Figure 2I). In *S. stahelii*, 6–9 colleters are inserted in a row just below the margin or are concentrated just below the base of the central lobe. In *S. wilson-brownei*, 3–7 colleters are inserted at the base. In *S. ayangannensis*, the internal side of the stipules and the presence of colleters was not observed.

**Sipaneopsis.** Stipules in this genus are persistent, free or adnate to the petioles, or sometimes basally sheathing. The free portion is broadly to narrowly triangular, or broadly triangular at the base and linear or acuminate distally. They can also be bilobed or bifid at the apex, or topped by 2–4 linear lobes in *S. morichensis* and *S. rupicola* (Figure 3F–H). The colleters are inserted on the internal side at the medio-basal portion or just below the margin with their tips exserted, and range from 1 or 2 to 11. The stipules of *S. cururuensis* have just a few colleters at the base. In *S. duckei*, 4–7 colleters

inserted just below the margin with their tips exserted in the populations on Serra Aracá, or (1–)4–7 colleters inserted at the medio-basal portion in populations of Campos do Ariramba. In *S. maguirei*, 2–3 colleters are inserted just below the margin on each side of the central lobe. The stipules of *S. morichensis* have 6–7 colleters inserted just below the margin with their tips exserted; and those of *S. rupicola* have 10–11 colleters inserted just below the margin with their tips exserted. In *S. foldatsii* and *S. pacimoniensis*, the inner side of the stipules was not studied.

**Steyermarkia.** In this genus, the stipules are persistent, ovate or lanceolate to linear-lanceolate, attenuate or bifid at apex, densely white-hirsute outside. The inner side is covered with long, appressed hairs intermixed with numerous colleters; the colleters are linear, 2–2.3 mm long. In bilobed stipules, 1 colleter is present in the sinus between the lobes.

#### Inflorescences

In this treatment, the terminology of inflorescence position and architecture follows the concepts of Troll (1950) and Weberling (1992). In addition, Weberling (1977) published an overview on the typology of inflorescences in the Rubiaceae, which is here followed.

Numerous Rubiaceae genera have terminal inflorescences with secondary branches subtended by leaf-like bracts (i.e., pherophylls). These leaf-like bracts are similar to foliage leaves, and are gradually smaller toward the distal portion of the inflorescence. In several instances, the presence of leaf-like bracts in terminal inflorescences has led some workers to incorrectly describe the inflorescences as lateral and cymose, instead of terminal, paniculate, and frondose. This argument was convincingly made by Troll (1950) and Weberling (1977, 1992). Steyermark (1974) described the inflorescences of *Sipanea* as “axillary or terminal, once or twice dichasially branched...” (Steyermark 1974: 357; translated from Spanish). In this genus, some species have inflorescence with the secondary branches subtended by leaf-like bracts (i.e., pherophylls), which Steyermark interpreted as axillary inflorescences subtended by leaves. In the present treatment, according to the definitions proposed by Weberling (1977, 1992), the inflorescences with secondary branches subtended by leaf-like bracts are treated as terminal and frondose.

Inflorescences in Sipaneae may be terminal or truly axillary. Inflorescence position is consistent within each genus, and is an important diagnostic character that can be used to distinguish genera within the tribe. Within the Sipaneae, they are axillary in *Chalepophyllum*,

*Maguireothamnus*, *Neblinathamnus*, and *Steyermarkia*, while they are terminal in the remainder of the genera. A discussion about inflorescence position and architecture by genus is presented below.

In *Chalepophyllum*, the inflorescences are axillary, reduced-cymose, and 1–7 flowered. The flowers of *Maguireothamnus* are solitary, axillary on distal nodes, and subtended by two leaf-like bracts. In *Neblinathamnus*, the flowers are axillary, 1–2 per axil, and subtended by two setaceous bracts. In *Steyermarkia*, the inflorescences are axillary, long-pedunculate, capitate, congested-cymose, with 3 head-like cymules, and 10–12-flowered.

In *Dendrosipanea*, the inflorescences are terminal or terminal on distal axillary branches, cymose, often frondose, and few- to many-flowered.

In *Limnosipanea*, the flowers are terminal and solitary, or in terminal, cymose, 2–4-dichotomous, few- to many-flowered inflorescences.

In *Neobertiera*, the inflorescences are terminal, many-flowered, subcapitate (extremely reduced cymes), densely glomerulate, densely cymose, or laxly cymose; in glomerulate and in densely cymose inflorescences, the lateral branches terminate with flower glomerules, while in laxly cymose inflorescences, the ultimate branches are scorpioid (more evident when fully expanded).

In *Pteridocalyx*, the inflorescences are terminal, cymose, many-flowered, and with scorpioid ultimate branches (more evident when fully expanded).

In *Sipanea*, the inflorescences are terminal, sometimes appearing axillary as a result of a reiteration of the axillary bud subtending the inflorescence, and paniculate, simply or compoundly cymose, or corymbose, usually not frondose, or in a few species they are frondose, with leaf-like bracts (i.e., pherophylls) subtending secondary branches, pauci- to multi-florous, or rarely uniflorous. In several species (e.g., *S. carrenoi*, *S. ovalifolia*, *S. pratensis* var. *pratensis*) the inflorescences are congested-cymose (appearing fasciculate) at initial stages, and either they remain so or they might slightly expand in later stages until fruit maturity. Whereas, in several other species (e.g., *S. hispida*, *S. pratensis* var. *dichotoma*, *S. stahelii*, *S. wilson-brownii*), the inflorescences are initially condensed-cymose (extremely shortly-branched, appearing fasciculate), and during and after anthesis the rachis elongates and the secondary branches expand from subcapitate to scorpioid. Later expansion of the inflorescence is generally treated as a variation at specific level, correlated with different stages of development, therefore not deserving subspecific rank, with the exception of *S. pratensis* (see below). Additional details about the inflorescences in *Sipanea* are discussed below in the three sections recognized in the genus.

In *Sipanea* section *Sipanea* (corolla mouth with a ring of yellow hairs), the inflorescences are cymose, dichotomously or trichotomously branched, or either a single condensed head or trichotomous with three condensed heads in *S. glomerata*, or 1–2-flowered in *S. veris*. In this section, the inflorescences do not expand or expand only slightly after anthesis, with the exception of *S. pratensis*. In this latter species, two varieties with allopatric distribution, and with different infructescences and fruit shapes, are here recognized: var. *pratensis*, with inflorescences that are initially congested-cymose (appearing fasciculate), and secondary branches that do not elongate in later stages, infructescences congested-cymose (appearing fasciculate), and globose, subglobose, ovoid to obovoid capsules; and var. *dichotoma*, with inflorescence axes that are already elongated in early stages or congested in early stages and elongated during and after anthesis, producing a subsecund monochasial cyme of dichasial appearance, often with scorpioid secondary branches, and capsules that are longer than broad, cylindrical-oblong to oblong-narrowly ovoid (See *S. pratensis* for further information).

In *Sipanea* section *Virecta* (corolla mouth with a ring of white hairs), the inflorescences are 1–7-flowered, condensed dichotomous cymes, monochasial, or rarely dichotomous in *S. biflora*, and do not expand or expand only slightly after anthesis.

In *Sipanea* section *Nudae* (corolla mouth glabrous or with sparse white hairs), the inflorescences are 3–32-flowered, cymose, dichotomously branched, or modified dichasia, with 1–3 pairs of scorpioid lateral branches, and usually expanded after anthesis.

The inflorescences of *Sipaneopsis* are terminal, few- to many-flowered, congested-cymose in early stages (before anthesis), and slightly or much expanded and dichotomously branched during and after anthesis. In this genus, inflorescences range from reduced cymes of 2–3 flowers to compound dichasia, with scorpioid secondary branches, and from (12–)19–147-flowered. The smallest inflorescences in the genus are those of *S. pacimoniensis* Steyermark (1967: 289), which are 2–3-flowered cymes, and those of *S. maguirei* Steyermark (1967: 287), which are congested, 2–8(–13)-flowered cymes. The largest inflorescences are found in *S. huberi* Steyermark (1984c: 37, fig. 11), which has 31–147-flowered compound dichasia, with 5–9 pairs of secondary branches dichotomously branched.

### Flowers

In the Sipaneeae, flowers are commonly 5-merous. In the whole tribe, calyx lobes, corolla lobes, and sta-

mens are homomerous. In *Maguireothamnus*, flowers are exceptionally 6- or 7-merous. In *Limnosipanea*, a few flowers are exceptionally 4- or 6-merous. In *Sipanea*, flowers are commonly 5-merous, although in *S. galioides* they are exceptionally 6-merous, and in *S. pratensis* they might rarely be 4- or 6-merous. In some species of *Sipaneopsis*, a few flowers are exceptionally 6-merous. *Steyermarkia* is exceptional within the tribe by having flowers consistently 4-merous.

### Heterostyly

Schumann (1889, p. 247), in *Flora Brasiliensis*, was the first author to report heterostyly in a member of the Sipaneeae by describing *Sipanea* as having “flores actinomorphi pentameri heterostyli.” [flowers actinomorphic, pentamerous, heterostylous]. In the same publication, he also asserted that *Chalepophyllum* and *Limnosipanea* (Schumann 1889, pp. 245 and 252, respectively) are homostylous; however, the former is here shown to be heterostylous, while the latter is here confirmed to be homostylous.

Brown (1901) in the original description of *Chalepophyllum speciosum* N.E.Br. [= *Maguireothamnus speciosus* (N.E.Br.) Steyermark.], described the style as “about as long as the corolla tube, or shorter than the anthers or rarely exserted” and just below explained that “The variation in the length of the style would seem to imply that the flowers are heterostyled, but it may be due to a lengthening at various periods of development.” His explanation is correct, because he described the style at various stages of development, and this species, currently accepted as part of the genus *Maguireothamnus*, is homostylous, and with the style exserted well beyond the corolla mouth when fully expanded and receptive (i.e., with style branches separated from each other).

Verdcourt (1958) confirmed the presence of heterostyly in a genus of the Sipaneeae, by saying that “some species of *Sipanea* have the anthers at different heights in the corolla tube”.

Steyermark (1964: 192–193) in the emended description of *Chalepophyllum guyanense* var. *guyanense* wrote “tubo [corolla] 10–16 mm longo [...] stylis 5.5–13 mm longis; staminibus prope medium vel supra medium corolla insertis [...]” [corolla tube 10–16 mm long, [...] style 5.5–13 mm long; stamens inserted at the middle or above the middle of the corolla tube] and in that of *C. longilobum* Steyermark (1964: 193) wrote “tubo [corolla] 13–14 mm longo [...], filamentis liberis 2 mm longis paullo supra medium corollae tubi insertis ad basin adnatis; stylis 6–13 mm [...]” [corolla tube 13–14 mm long [...], filaments free, 2 mm long, inserted just above

the middle of the corolla tube, adnate at base; style 6–13 mm long, glabrous; [...].

Bremekamp (1966) described the tribe Sipaneeae, where he included *Sipanea*, *Virecta* Vahl [= *Sipanea*], and *Limnosipanea*; however, he did not mention the presence of heterostyly in the tribe. Bahadur (1968: 220) published an overview of heterostyly in the Rubiaceae in which he cited the flowers of *Sipanea* as “dimorphic, Verdcourt (1958).”

Steyermark (1974: 323) in *Flora de Venezuela*, described *Chalepophyllum guyanense* as having filaments inserted at the middle or at the distal  $\frac{3}{4}$  of the corolla tube. In the same publication, Steyermark (1974: 357) described *Sipanea* as having (translated from Spanish) “Stamens 5, included, inserted below or above the middle of the tube, rarely near the mouth” and reported only *S. pratensis* as a heterostylous species of the genus by having “Stamens included,  $\frac{2}{3}$  to  $\frac{3}{4}$  of the total length of the [corolla] tube from the base or at the distal part of the tube; anthers linear or linear-fusiform, 2.2–3 mm long; filaments 0.4–1.5 mm long, glabrous, inserted on tube at 3.5–8 mm below the [corolla] mouth. Style 5–19 mm long, glabrous.” (Steyermark 1974, p. 371, translated from Spanish). Therefore, although Steyermark (1964, 1974) reported for both *Chalepophyllum* and *Sipanea* that the stamens are inserted at different heights on the corolla tube and the style is either included or exserted, he did not explicitly state that these genera are heterostylous.

Robbrecht (1988, fig. 48) in the bubble diagram illustrating his Rubiaceae classification, indicated that heterodistyly is present in the Sipaneeae, probably referring to the distyly reported in *Sipanea* by previous authors (Verdcourt, 1958; Bahadur, 1968; Steyermark, 1974).

As a result of recent studies, Delprete (2015a, 2018, 2019a, 2019b) observed that in the Sipaneeae, heterostyly is present in several genera. In addition, presence or absence of heterostyly is consistent in all the genera, and can be used as a diagnostic character to distinguish them. Within the tribe, the genera *Limnosipanea*, *Maguireothamnus*, *Sipaneopsis*, and *Steyermarkia* are consistently homostylous, with exserted or partially exserted style when fully elongated and receptive (i.e., branches spread apart from each other).

Within the Sipaneeae, the genera *Chalepophyllum*, *Dendrosipanea*, *Neobertiera*, *Pteridocalyx* and *Sipanea* are heterostylous. In *Dendrosipanea*, *Neobertiera*, and *Sipanea*, most species were observed to be distylous, although in a few of them only the long-styled or the short-styled flowers were examined, due to lack of available material. However, it was assumed that the five above-cited genera are entirely heterostylous. The heterostylous genera of the Sipaneeae are discussed below.

In *Chalepophyllum*, the short-styled flowers have stamens inserted at the upper portion of the corolla throat and are included, and the style is short and included. While in long-styled flowers, the stamens are inserted at medio-basal portion of corolla throat and are included, and the style is exerted well beyond corolla mouth.

The distylous condition of *Dendrosipanea* was first observed by Delprete (2018) in both *D. revoluta* and *D. spigelioides*. In short-styled flowers of these two species, the stamens are included, with filaments inserted at the distal portion of corolla throat and linear anthers, while the style is much shorter than the corolla tube. In long-styled flowers, the stamens are also included, although the filaments are inserted at the distal portion of the corolla throat and the anthers are also linear, while the style is barely exerted, with only the branch tips exerted beyond the corolla mouth. Ducke (1935) in the original description of *Dendrosipanea* wrote that the filaments are inserted at the middle of the corolla tube and the style is as long as the corolla tube; therefore, he based the original genus description on long-style flowers of the type specimen of *D. spigelioides*.

Steyermark (1964: 198, fig. 72a–g) described *Dendrosipanea wurdackii* Steyermark as having the style 3–3.5 mm long with branches 2–2.5 mm long. He distinguished it from *D. spigelioides* by other characters, a “much shorter style not reaching the height of the anthers.” Therefore, Steyermark’s description of *D. wurdackii* is based on the short-styled flowers of the type gathering (Maguire & Wurdack 35558), and, in agreement with Delprete and Steyermark (2004a), these two taxa are conspecific.

Delprete (2018) recently described *Dendrosipanea prancei* Delprete from three collections. In all of them the style is barely exerted beyond the corolla mouth, and the stamens are inserted the basal portion of the corolla tube, with the anthers presented at the medio-distal portion of the corolla tube. As the other two species of the genus are distylous, the three collections of *D. prancei* were interpreted as long-styled, and this species is also distylous.

Wernham (1917) described *Neobertiera* with a sole species, *N. gracilis* Wernham, using a single specimen (Jenman 2388, BM). He assumed that its flowers are homostylous and wrote “Stamina 4 [sic, 5], infra corollae fauces inserta; anthereae in tergo prope basin tamen in filamentum latum longiusculum fixae, lanceolato-oblongae” [Stamens 4 [sic, 5], inserted at corolla mouth; anthers dorsally attached on long filaments, oblong-lanceolate]. The flowers of the holotype specimen correspond with Wernham’s description in having stamens inserted at the medio-distal portion of the

corolla, with rather long filaments and anthers presented near the corolla mouth. Following Wernham’s original description, *Neobertiera* has been reported by Sandwith (1931) and Steyermark (1967) as monospecific and homostylous. However, Delprete (2015a, 2019b) recently described four additional species in *Neobertiera*, and stated that out of the five species in the genus, four are distylous and one is tristylous. The heterostyly in each species of this genus is discussed below.

The distyly of *Neobertiera gracilis* has been observed in numerous herbarium specimens. In long-styled flowers, the filaments are short and inserted at the medio-basal portion of the corolla tube and, and the style is about the same length or slightly longer than the corolla tube (Delprete, 2015a, fig. 6E). In short-styled flowers, the filaments are long and inserted at the medio-distal portion of corolla tube, and the style is much shorter than the corolla tube (Delprete, 2015a, fig. 6D). Therefore, Wernham’s original description of this species was made studying the short-styled flowers of the holotype specimen.

*Neobertiera palustris* is the only species observed by Delprete (2015a, as *N. glomerata* Delprete) to be tristylous in the Sipaneeae. One form of long-styled flowers has stamens inserted at about the middle of corolla tube, with narrowly sagittate anthers, and the style is slightly shorter than the corolla tube (Delprete 2015a, fig. 3C). In the other form of long-styled flowers, the stamens are inserted near the base of corolla tube, also with narrowly sagittate anthers, and the style is about as long as the corolla tube, with the branch tips barely exerted (Delprete 2015a, fig. 3D). In short-styled flowers, the stamens are inserted above the middle of the corolla tube, with linear anthers, and the style is much shorter than the corolla tube (Delprete 2015a, fig. 3E).

In *Neobertiera micrantha* Delprete, *N. pakaraimensis* Delprete, and *N. montedouradensis* Delprete, only the long-styled flowers were observed (Delprete 2015a, 2019a), as these species are only known by the type specimens (Cremers & Granville 14097, Henkel et al. 1449, and Santos 414, respectively). In these specimens, the stamens are inserted at about the middle of the corolla tube, and the anthers are narrowly sagittate in *N. micrantha* and *N. pakaraimensis* or linear in *N. montedouradensis*, while the style is about as long as the corolla tube in the former two species, or slightly longer, with the branch tips barely exerted, in *N. montedouradensis*. Because the stamen insertions and the proportion of the style with the corolla tube of these three species resemble the long-styled flowers of *N. palustris* and *N. gracilis* and are assumed to be distylous, although the short-styled flowers have not yet been observed.



Delprete (2019a, fig. 1), as a result of field observations of natural populations and the study of numerous herbarium specimens, concluded that *Pteridocalyx* is distylous. In long-styled flowers the stamens are included and inserted near the base of corolla tube, with anthers 1.8–2 mm long, and the style is about the same length as the corolla tube (with the tip of branches barely exerted) or exerted just beyond corolla mouth. In short-styled flowers, the stamens are inserted at the distal portion of corolla tube, included, and with anthers 2.5–2.7 mm long, and the style is about half the length of the corolla tube.

*Sipanea* is the most diverse and most widely distributed genus of the tribe, and displays the widest variation in corolla shape and dimensions. In *Sipanea*, most species were observed to be distylous, although in a few species only the long-styled or only the short-styled flowers were examined, due to the lack of available material. Generally, in long-styled flowers the stamens are inserted near the base or at the middle of the corolla tube, and the style is as long as the corolla tube or exerted. In short-styled flowers the stamens are inserted at the middle or at the medio-distal portion of the corolla tube, and the style is shorter than the point of insertion of the stamens. The term medium-styled flowers is here introduced, observed in *S. hispida*, for flowers that have the stamens inserted in lower-median portion of the corolla tube, just below the tips of the style branches, and the style is about half the length of the corolla tube, equal in height with the middle or upper tip of the anthers. Three sections are here recognized within *Sipanea*, and the various aspects of distyly are discussed below under each section.

*Sipanea* section *Sipanea* is characterized by flowers with a ring of yellow hairs at the corolla mouth. Within this section, *S. galioides*, *S. glomerata*, *S. pratensis* and *S. veris* were observed to be distylous. In the long-styled flowers of these species, the stamens are inserted about the middle of the corolla tube, and the style is exerted beyond the corolla mouth. While in short-styled flowers the stamens are inserted at the distal portion of the corolla tube, and the style is much shorter than the point of insertion of the stamens.

In *Sipanea hispida*, a member of section *Sipanea*, in short-styled flowers, the stamens are inserted at medio-distal portion of the corolla tube, just above or at the same height as the tips of the style branches, and the style is shorter than the stamen insertions on the corolla tube. Whereas, in medium-styled flowers the stamens are inserted below the tips of the style branches, at about the middle of the tube, and the fully elongated style equal in height to the middle or upper tips of the

anthers, which are inserted at the median portion of the tube.

For five species of *Sipanea* section *Sipanea*, distyly remains to be confirmed, due to the lack of available material. In *S. glaberrima* (Bremek.) Steyerl., known only from the type, only short-styled flowers were observed, with stamens inserted just below the corolla mouth, and a short, included style. In *S. micrantha* Sandwith (1928: 378), known from three collections, only long-styled flowers were observed, with stamens inserted near the base of corolla tube, and the style about as long as the corolla tube. In *S. setacea* Steyerl., also known only from the type, only long-styled flowers were examined, with stamens inserted at medio-distal portion of tube, and style slightly exerted beyond the corolla mouth.

Species of *Sipanea* section *Virecta* are characterized by a ring of white hairs at the corolla mouth. Within this section, only *S. biflora* and *S. ovalifolia* are here confirmed to be distylous, following the observations of numerous specimens from throughout their distribution range. In both species, the long-styled flowers have stamens inserted at the lower portion of the corolla tube, and style about as long as corolla tube (tip of branches exerted) or exerted beyond corolla mouth. In short-styled flowers the stamens are inserted at the distal portion of the corolla tube, and the style is much shorter than the corolla tube.

Within *Sipanea* section *Virecta*, only the long-styled flowers of *S. carrenoi* Steyerl., known only from the type, *S. micrantha*, known from three collections, and *S. setacea*, known only from the type, were observed, due to the paucity of material available. In these three species, the flowers observed have the stamens inserted at the basal (*S. micrantha*) or medio-distal (*S. carrenoi* and *S. setacea*) portion of the corolla tube, and the style is about the same length as corolla tube or exerted beyond the corolla mouth. In *Sipanea gleasonii* Steyerl., also known only from the type, only short-styled flowers were observed, with stamens inserted just below the corolla mouth, and the style much shorter than the corolla tube.

Species of *Sipanea* section *Nudae* are characterized by the corolla mouth glabrous or with a few sparse white hairs. Within this section, only *S. stahelii* Bremek. and *S. wilson-brownei* Cowan were observed to be distylous, based on analyses of numerous herbarium specimens. In both species the long-styled flowers have stamens inserted at the basal portion of corolla tube, and the style is about the same length or slightly longer than the corolla tube. While in short-styled flowers the stamens are inserted at distal portion of corolla tube, and the style is much shorter than the corolla tube. Within this sec-

tion, for *S. ayangannensis* Steyererm., only known from the type, and *S. saxicola* J.H.Kirkbr., known from a few collections, only short-styled flowers are known, which have stamens inserted at medio-distal portion of the corolla tube, and the style much shorter than the corolla tube.

In *Sipanea prancei* Steyererm., also of *Sipanea* section *Nudae*, only the flowers of three collections were analyzed, due to the paucity of material available. In these flowers, the stamens are inserted at about the middle (1/2 or 3/5 from the base) of the corolla tube, and the style is slightly longer than the point of insertion of the stamens. However, in all of them the style is not completely elongated and the branches are still appressed against each other (i.e., not opened). Therefore, additional specimens with styles completely elongated are needed, to confirm the distyly of this species.

#### Flowering modality

In all genera of the Sipaneeae, except for *Sipaneopsis* (see below), the corolla lobes open after the corolla tube is completely elongated, and the reproductive parts are subsequently available to pollinators. In all genera of the tribe, the flowers are protandrous, with the anthers maturing, dehiscing, and releasing pollen before the style is completely elongated. After the pollen has been released, the style expands to full length and the branches spread apart from each other, exposing the stigmatic surfaces on the adaxial side.

The flowering modality of *Sipaneopsis* is unique within the Rubiaceae and was described in detail by Delprete (2015a, 2017). In Figures 80B–C is an inflorescence of *S. maguirei* with flowers at different developmental stages. During the initial stage of anthesis the flowers are very small but the corolla lobes are already open and erect, although not fully expanded, before tube elongation (Figure 82A–B). At this stage, the triangular appendages present at the base of the corolla lobes are appressed against each other, forming a convex structure at the corolla mouth (Figure 82A–B), obstructing the entrance of any visitors or pollinators. During successive stages of anthesis, the corolla tube and lobes elongate, and the corolla lobes remain erect and the corolla lobe appendages are still appressed against each other (Figure 82C–F), continuing to obstruct the entrance of any visitors or pollinators. At the final stage of anthesis, the corolla lobes reflex and become perpendicular to the tube, corolla hypocrateriform, and the corolla lobe basal appendages become erect, not touching each other (Figure 82G–H), allowing visitors and pollinators to access the corolla tube and nectar disk. More details about the

flowers modality of this genus are discussed and illustrated in *Sipaneopsis* (see below).

#### Hypanthia

All genera of the Sipaneeae, as in most Rubiaceae genera, have an inferior ovary. Following Radford et al. (1974: 99), the hypanthium is “the fused or coalesced basal portion of floral parts (sepals, petals, stamens) around the ovary.” Therefore the external portion surrounding the ovary (i.e., below the calyx) should be called the hypanthium, although some specialists erroneously call this external portion the “ovary”.

In the Sipaneeae, hypanthia vary in shape from globose, obovoid, narrowly obovoid, obconical, turbinate or rarely subcampanulate-urceolate (in one species of *Sipaneopsis*), and are considerably variable in dimensions (see below).

Vestiture of hypanthia in this tribe is also quite variable, as they can be glabrous, or minutely puberulent, densely pubescent, strigillose, strigose, hispidulous, hispid, or sericeous. Trichomes are most commonly simple (i.e., not basally tuberculate) in most species of the tribe. Exceptionally, hairs are basally tuberculate in several species of *Sipanea* (e.g., *S. hispida*, *S. gleasonii*, *S. ovalifolia*, *S. stahelii*, and *S. wilson-brownei*), and in *Neobertiera montedouradensis*. In these species, the tubercle is multicellular, and surrounds the base of the central hair.

In *Chalepophyllum*, the hypanthia are obconical or turbinate, 1–1.5 × 1–1.3 mm, and glabrous or minutely puberulent. In *Dendrosipanea*, the hypanthia are obconical, turbinate to narrowly obovoid, 1.5–3 × 1.2–2.5 mm, and glabrous or strigillose. In *Limnosipanea*, the hypanthia are narrowly ellipsoid to narrowly obovoid, 0.3–1 × 0.2–1.3 mm, and densely hispid. In *Maguireothamnus*, the hypanthia are oblong-obconical, obconical, narrowly obconical to narrowly obovoid, 2–6 × 1.5–5 mm, and glabrous, minutely puberulent, densely pubescent, antrorse-hispidulous, antrorse-hispid to densely spreading strigose. In *Neblinathamnus*, the hypanthia are obovoid, oblong-ovoid, turbinate or narrowly obovoid, 1.8–2.5 × 1.4–2 mm, and sparsely to densely hirtellous.

In *Neobertiera*, the hypanthia are globose, broadly obovoid to obovoid, 0.5–1.5 × 0.5–1.5 mm, with appressed-strigose, simple trichomes (i.e., not basally tuberculate) in most species. *Neobertiera montedouradensis* is unique within the genus by having hypanthia and fruits with trichomes basally tuberculate.

In *Pteridocalyx*, the hypanthia are oblong-obovoid, 1.5–2 × 1.1–1.3 mm, and appressed strigose-pubescent.

In *Sipanea*, the hypanthia display a wide range of size, shape and vestiture. In most species the trichomes

on the hypanthia are simple (i.e., not basally tuberculate). In a few species, in each of the three sections, the hypanthia have trichomes with basal multi-cellular tubercles. Hence, size, shape, vestiture and kind of trichomes of the hypanthia offer an important set of diagnostic characters, and these features are discussed below within each of the three sections recognized in the genus.

In *Sipanea* section *Sipanea* (corolla mouth with a ring of yellow hairs), the hypanthia are obconical, obovoid, turbinate to narrowly obovoid, 0.7–5 × 0.5–2.5 mm, glabrous or sparsely to densely antrorse setose-strigulose, appressed pubescent, densely antrorse hispid sericeous or densely appressed-strigillose; the hairs are simple (i.e., not basally tuberculate).

In *Sipanea* section *Virecta* (corolla mouth with a ring of white hairs), the hypanthia are subglobose, broadly to narrowly obovoid or obconical, 0.7–2.5 × 0.7–1.5 mm, glabrous or with a few appressed hairs, sparsely appressed-strigillose on the distal half and glabrous below, appressed-strigillose throughout or densely antrorse hispid-strigose. In most species of this section, the trichomes on the hypanthia are simple (i.e., not basally tuberculate), with the exception of *S. gleasonii* and *S. ovalifolia*, which have hypanthia with basally tuberculate trichomes.

In *Sipanea* section *Nudae* (corolla mouth glabrous or with sparse white hairs), the hypanthia are globose, subglobose, broadly turbinate, narrowly obconical, narrowly ovoid to obovoid, 0.7–2 × 0.5–2 mm, densely antrorse-strigose, densely antrorse-pubescent, densely erect-sericeous, densely antrorse-pubescent, or appressed strigose-pubescent. Within this section, *S. stahelii* and *S. wilson-brownei* are exceptional in having hypanthia with basally tuberculate trichomes.

In *Sipaneopsis*, the hypanthia are subglobose, globose, broadly turbinate, turbinate, subcampanulate-urceolate, broadly-obovoid, obovoid-turbinate, obconical or oblong-obovoid, 1–2 × 0.8–1.7 mm, scabrous, densely hispid, densely hispidulous strigillose, densely to sparsely strigose, sericeous-strigose or sericeous.

In *Steyermarkia*, the hypanthia are turbinate, 1.5–2 × 1–1.5 mm, and densely antrorse-hispid. The hairs are long, white, and simple (i.e., not basally tuberculate).

### *Calyces*

In the Sipaneeae, the calyx lobes are commonly free, with an extremely reduced the calyx tube, or sometimes shallowly connate at the base, and persistent on the fruit or sometimes breaking off in old fruits.

Regarding calycine colleters in Rubiaceae, Robbrecht (1988) wrote that “The inside of the calyx is beset

with colleters of the same type of those of the stipules. Colleter number and position is diverse. They may cover the entire inside or only a part of it, occur in a ring all around the inside of the calyx-base, or be limited to small groups (sometimes isolated colleters) on the inside between or at the margin of the lobes.” Additional information about colleters is available in the section *Colleters*.

In all genera of the Sipaneeae, one to several colleters are inserted at the calyx lobe sinuses, either on both sides of the lobe bases or at the middle of the sinuses, usually just below the margin of each sinus, on the internal side. Hooker (1868) was probably the first specialist to report calycine colleters in members of the Sipaneeae, as he described the calyx lobes of *Limnosipanea* as “lanceolate, subfoliaceis, intus basi glandulose, persistentes” and in figure 4 of plate 1050, of the same publication, is depicted a dissected flower with colleters at the base of the calyx lobes.

Schumann (1889), in *Flora Brasiliensis*, also reported calycine colleters in several members of the Sipaneeae. He wrote that the calyx of *Sipanea* is “fere ad basin in laciniis elongates basi denticulo glandulose solitario interpositas divisus persistens, tubo intus eglandulosus” [with a solitary small glandular tooth inserted approximately near the base at sinus of calyx lobe, tube non glandular inside], and that the calyx of *S. pratensis* and *S. biflora* have a “denticulo solitario glanduloso interjectas divis.” [a solitary small glandular tooth at sinus between calyx lobes] (Schumann, 1889, pp. 247–251). For *Limnosipanea*, he stated that the calyx lobes have a “denticulo solitario glanduloso interposita, inferne breviter coadunate persistentia intus eglandulosa.” [a solitary small glandular tooth at lobe sinus, lobes basally connate, inner side non glandular] (Schumann 1889, p. 252). He also reported calycine colleters in *Sipaneopsis rupicola* (K.Schum.) Steyermark. (as *Rondeletia rupicola* K.Schum.) by describing its calyx as “fere ad basin in laciniis ovarium paulo superantes subulatas inaequilongas denticulis solitaris vel binis interpositas extus ad nervam medianum pilosulas ciliolatas divisa” [calyx lobes connate at base, slightly longer than the “ovary” [hypanthium], unequal, with one or two small teeth at sinus, with a pilose-ciliolate middle vein ] (Schumann 1889: 222 [incorrectly numbered “224”]).

Steyermark (1967, 1974, 1984a, 1984b, etc.) reported the presence of colleters at the calyx lobe sinuses in the species descriptions of *Neobertiera*, *Sipanea*, and *Sipaneopsis*, and called them “glándulas”, “glands”, “glandulae”, “squamellae” or “esquamelas”. The latter two terms are rather awkward for describing colleters, as the proper Spanish term for these secretory structures is “coléteres”

(Font Quer 2000), whereas squamellae are small scales without secretory function (Stearn 1995).

Steyermark (1967: 284–289), along with the emended description of *Neobertiera*, distinguished this genus from *Sipanea* by, among other characters, “The calycine squamellae [i.e., colleters] do not arise at the sinus [in *Sipanea*] but at the base on either side of the calyx-lobe, thus two squamellae are evident between the calyx-lobes.”

The variation in calyx lobe size and shape, as well as number, point of insertion, and characteristics of the colleters at lobe sinuses, provide a significant set of diagnostic characters that can be used to distinguish genera and species in the Sipaneeae. These characters are discussed below for each genus.

In *Chalepophyllum*, the calyx lobes are subequal to unequal, oblong-triangular, ovate-lanceolate, oblong-lanceolate, lanceolate, or elliptic to oblong-spathulate, 2–17 × 1–3.5 mm; just below each lobe sinus, on the internal side, is inserted a fascicle of 3–5, oblong to linear, 0.25–0.5 mm long colleters.

Ducke (1935: 69; liberal translation from Latin) described the calyx of his new genus *Dendrosipanea* as “persistent, short, divided to the base into erect-patent lobes, with fascicles of minute glands [i.e., colleters] alternate to the lobes.” In fact, in *D. spigelioides* Ducke, the calyx lobes are deltoid to narrowly triangular, with fascicles of 2–4 colleters at each lobe sinus. In *Dendrosipanea*, currently recognized as a genus of three species (Delprete 2018), the calyx lobes are subequal to unequal, deltoid, narrowly triangular, oblong, narrowly oblong, lanceolate, or spatulate, 1–9 × 0.7–3.5 mm, and at each lobe sinus there are 1–4 colleters, linear, 0.3–0.5 mm long.

In *Limnosipanea*, the calyx lobes are subequal, oblong, lanceolate to linear, 1.5–5.5 × 0.3–0.6 mm, aristate at apex (arista caducous) or not. On the internal side, in each calycine sinus, there is one colleter broadly conical to conical, 0.05–0.1 mm long.

In *Maguireothamnus*, the calyx lobes are subequal or unequal, large, elliptic, narrowly-elliptic, oblong, narrowly lanceolate to linear, 8–23 × 1.5–7 mm, attenuate, acute or acuminate at apex; in each calycine sinus, there is a fascicle of 5–7 colleters, narrowly-lanceolate to oblong-lanceolate, 0.4–0.7 mm long.

In *Neblinathamnus*, the calyx lobes are equal to subequal, spatulate, lanceolate, linear-acuminate, or linear-spathulate, 4–7 × 0.3–1 mm, acuminate, subacute to obtuse at apex; at each lobe sinus, there are 2 or 3 colleters, linear, 0.2–0.3 mm long.

Wernham (1917) in the original description of *Neobertiera* did not mention the presence of calycine

colleters. Steyermark (1967: 289) emended the description of the genus, and, among other characters, added “inter lobos basi intus utriusque lateris glandulis duabus interpostis.” In *Neobertiera*, the calyx lobes are commonly unequal, narrowly-lanceolate, linear-lanceolate to narrowly lanceolate, 1.5–5 × 0.2–1.1 mm, acute at apex. In each calycine sinus, there are 1 or 2 colleters, oblong, 0.1–0.25 mm long.

In *Pteridocalyx*, one or two calyx lobes per flower are expanded, petaloid (i.e., calycophylls), stalked, with blades ovate to narrowly ovate, white, and palmately-veined (see Section Calycophylls, below); while the not-enlarged calyx lobes are subequal, small, linear to linear-lanceolate, 2–4.5 × 0.4–0.7 mm long, and acute at apex. Wernham (1911, 1913) did not mention the presence of calycine colleters in his descriptions of the two species of *Pteridocalyx*. This genus is currently treated as monospecific (Delprete 2019a), and on the calyx there are 1 or 2, oblong, 0.15–0.2 mm long colleters at each lobe sinus.

*Sipanea* is the most diverse and geographically most widespread genus of the Sipaneeae. Accordingly, calyx lobes in *Sipanea* display a wide variation in shape and size. They can be equal, subequal or unequal, and sometimes they vary within the same species from oblong-lanceolate, lanceolate, subulate, linear to setiform, 1.3–13 × 0.1–1.2 mm, and are acute or acuminate at the apex. The smallest calyx lobes in the genus are found in *S. micrantha*, 1.3–1.7 × 0.2–0.3 mm, and the largest ones are those of *S. glomerata*, 7–13 × 0.7–1.2 mm, expanding to 15–17 mm long on the fruits. The shape and size of calyx lobes provide some useful diagnostic characters to identify several species within the genus.

Steyermark (1967) indicated the presence of a solitary colleter in calycine sinuses, using the term “glandula” in the Latin descriptions of several *Sipanea* species: in *S. cowanii* Steyermark. [= *S. biflora* (Rottb.) Cham. & Schltld.] as “inter lobos in sinus glandula solitaria subovoidea obtusa 0.05–0.1 mm longa disco breviori interposita” (Steyermark 1967: 265), in *S. gleasonii* Steyermark. as “inter lobos in sinus glandula solitaria ca. 0.1 mm longo interposita” (Steyermark 1967: 266), in *S. stahelii* Bremek. as “inter lobos in sinus glandula solitaria subulata 0.1–0.2 mm longa disco breviori interposita” (Steyermark 1967: 269), in *S. glaberrima* (Bremek.) Steyermark. as “inter lobos glandula solitaria subulata 0.4–0.5 mm longa apicem disci aequanti interposita” (Steyermark 1967: 270), and in *S. pubinoda* Steyermark. [= *S. pratensis* var. *dichotoma*] as “inter lobos in sinu glandula solitaria 0.2 mm longa interposita” (Steyermark 1967: 278). Steyermark (1974) also cited the presence of calycine colleters in the descriptions of several species of *Sipanea* in the *Flora de Venezuela*, where he called them, in Spanish,

“esquamelas” (see comments about the use of this term in section *Colleters*, above). In all species of *Sipanea*, in each calycine sinus there are 1 or 2 colleters 0.1 to 0.5 mm long, which vary in shape from conical (obtuse at apex), narrowly conical (acute at apex), linear to setiform.

In *Sipaneopsis*, the calyx lobes are equal or subequal, and vary from ovate, narrowly ovate, narrowly lanceolate to linear-lanceolate, 1.5–3 × 0.2–0.7 mm, acute at the apex. Calyx lobes in *Sipaneopsis* do not have an ample range of shape and dimensions, and, aside from their vestiture, do not provide any useful characters for the identification of the species.

Steyermark (1967) reported the presence of calycine colleters (as “glandula” or glandulae”; see comments about the use of this term in section *Colleters*, above) in all the species of *Sipaneopsis* known to him, as follows (translated from Latin): 1 colleter, lanceolate, acute, 1/5 of calyx lobes length in each calycine sinus of *S. rupicola*; 1 or 2 colleters, lanceolate, ca. 1/10 calyx lobes length in each calycine sinus in *S. morichensis*; 1 colleter, 0.1 mm long, in each calycine sinus of *S. maguirei*; 1 colleter, 0.1 mm long, on each side of each calyx lobe of *S. wurdackii*; 1 colleter on each side of the calyx lobes of *S. foldatsii*; and 1 colleter, 0.1–0.2 mm long, in each calycine sinus of *S. pacimoniensis*.

Following recent detailed observations, in all species of *Sipaneopsis*, in each calycine sinus, there are 1 or 2 colleters, 0.2–0.3 mm long, which vary in shape from narrowly conical, ellipsoid, narrowly ellipsoid, narrowly oblong to narrowly cylindro-conical, and acute at apex.

In *Steyermarkia*, the calyx tube is extremely reduced, 0.5–1 mm long, and the lobes are erect, narrowly ovate-lanceolate to linear-lanceolate, 10–15 × 1–1.5 mm. In each calycine sinus there is one linear colleter, 0.7 mm long.

### *Calycophylls*

Calycophylls are enlarged calyx lobes that serve to attract pollinators and/or function as an aid for seed dispersal (Delprete 1996a, 1996b, 1996c, 1997, 1998a, 1998b, 2019a). A succinct overview of Rubiaceae genera with calycophylls was presented by Delprete (2019a). In flowers with semaphyllous calycophylls, calyx lobes are fully expanded during anthesis and have the function of attracting pollinators, and can be of various colors, ranging from white to greenish-white, yellow, pink, orange, red to purplish-red. They commonly lose their pigmentation when still present after anthesis, or change or rarely maintain their pigmentation after anthesis, and they may fall off before seed dispersal. Semaphyllous cal-

ycophylls, when persistent after anthesis and associated with dehiscent capsules, might have a secondary function of helping to shake the capsules, therefore contributing to the dissemination of wind-dispersed seeds.

In flowers with pterophyllous calycophylls, one, several or all calyx lobes are small or slightly larger during anthesis (sometimes functioning as semaphylls) and expand during fruit ripening, and are associated with indehiscent fruits, e.g., *Cosmocalyx* Standl., *Jackiopsis* Ridsdale, *Nematostylis* Hook.f., and some species of *Alberta* E.Mey. At fruit maturity they are fully expanded and form a wind-dispersed unit with the indehiscent fruit, and therefore they are not analogous to semaphyllous calycophylls.

*Pteridocalyx* is the only genus with calycophylls in the Sipaneeae. A detailed account on the calycophylls of this genus was presented by Delprete (2019a). In *Pteridocalyx*, 1 or 2 calyx lobes per flower are expanded, petaloid, and palmately veined (i.e., calycophylls). Regular small calyx lobes, as well as the calycophylls, are pure white when fresh, and turn cream-white to beige on dried specimens. Calycophylls in *Pteridocalyx* can vary in size and shape on the same inflorescence or even on the same calyx (Figures 36, 37, 39). The smaller calycophylls (Figure 39C–E) do not have a distinguishable stalk, and are linear, narrowly oblanceolate to narrowly oblong-oblanceolate, 4.5–9.5 × 0.8–1.5 mm, and are 1–3-veined, including the midrib. The larger calycophylls (Figure 39A–B) have stalks 2–5 mm long and blades narrowly elliptic elliptic to ovate, 4–13 × 5–9 mm, which can be acute, obtuse to round at base, and acute to obtuse at apex, and are palmately-veined, with 5–7 veins (including midrib). During anthesis, they are pure white and act as an aid for pollinator attraction, hence, they are semaphyllous calycophylls. After anthesis and during fruit development, they turn cream-white to yellowish-white. As they dry on the fruit, they commonly break off before capsule dehiscence, or might persist on the capsule, hence helping in seed dispersal by shaking the capsules.

### *Corollas*

Corollas in the Sipaneeae display a wide range of dimensions. Corolla shape and dimension supply an important set of diagnostic characters to differentiate genera in the tribe. Also, as corolla size, shape and proportions between corolla tube and lobes are variable among species of the same genus, they are a helpful set of characters that can be used to differentiate species.

Corollas in the Sipaneeae are actinomorphic. The most common corolla shape in the tribe is hypocrateri-

form, except several species of *Sipanea* section *Virecta*, and *Chalepophyllum* (see below). Corolla lobes are left-contorted in all genera, except for a few species of *Sipaneopsis*, which might have imbricate aestivation (see below).

In *Chalepophyllum* (1 sp.), the corollas are infundibuliform, 17–31 mm long, white to cream-white, sometimes with tube reddish or greenish at base. The tubes are obconical, 10–16 mm long, much wider at the mouth, externally strigose, internally pubescent throughout or only at the mouth, densely yellow-pubescent at the mouth inside. The lobes are ovate, narrowly ovate to oblong-elliptic, 7–15 × 4–5.5 cm, round, obtuse, acute or short-acuminate at apex.

Corollas in *Dendrosipanea* (3 spp.) are hypocrateriform, 17–30 mm long, white to cream-white, sometimes with the tube green. The tubes are narrowly infundibuliform, 11–20 mm long, glabrous, sparsely appressed-strigulose or hirtellous outside, basal portion glabrous and medio-distal portion villous inside, with a dense ring of yellow hairs at mouth inside. The lobes are subequal, sometimes slightly asymmetrical and of slightly different width on the same corolla, ovate, narrowly ovate, oblong to ovate-oblong, 7.5–16 × 4–7.5 mm, and obtuse to acute at apex.

In *Limnosipanea* (3 spp.), the corollas are hypocrateriform, 3–16(–18) mm long, white, cream-white, pinkish-white, pink to lilac. The tubes are narrowly cylindrical, 2–9 mm long, externally glabrous or strigose, internally villous, with a pubescent ring at the orifice; and the lobes are left-contorted, ovate or oblong-ovate, 1–8 × 0.5–4 mm, obtuse to round at apex. The shape and dimensions of the corollas are important diagnostic characters to distinguish the three species of the genus. The largest flowers in the genus are those of *Limnosipanea erythraeoides* K.Schum., which has corollas 11.5–16(–18) mm long (tubes 7–9 mm long, lobes 4.5–8 × 2–4 mm). Whereas, the corollas of *L. palustris* are 5.7–10 mm long, with the tubes 3.5–6.5 mm long and lobes 2.2–3.5 × 0.7–0.9 mm, and in *L. spruceana* Hook.f., the corollas are 3–5.5 mm long, with the tubes 2–2.5 mm long and lobes 1–3 × 0.5–0.7 mm.

*Maguireothamnus* (3 spp.) has the largest flowers in the tribe. The corollas are hypocrateriform, 8–17 cm long, with the tube pale green, greenish-yellow, cream-white to pale yellowish-green, sometimes reddish at base and white lobes. The tubes are long-cylindrical and slightly wider at mouth, 6.5–13 cm long, externally glabrous, internally puberulent, with a pubescent ring at orifice inside, and the lobes are ovate, lanceolate, oblong, oblong-ovate to obovate, 0.7–5 × 0.3–1.5(–2) cm, and round, obtuse, acute or acuminate at apex. The largest

flowers in the genus (and in the tribe) are found in *M. speciosus*, which has corollas 9–17 cm long, with tubes (6.5–)8–13 cm long and lobes 2.3–5 cm long.

In *Neblinathamnus* (2 spp.), the corollas are hypocrateriform, 15–22 mm long, green to yellowish-green, or with a red tube and yellowish or greenish lobes. The tubes are narrowly cylindrical and slightly wider at mouth, 9–16 mm long, externally glabrous or hirtellous, internally puberulent throughout or pubescent at mouth, the portion corresponding with the anthers with vermiform/multicellular hairs, and a pubescent ring at orifice inside. The lobes vary from ovate, narrowly ovate, elliptic to oblong, 5–6 × 2.5–5 cm, and are obtuse or round at the apex.

Corollas in *Neobertiera* (5 spp.) are hypocrateriform, 3.9–15.5 mm long, white. The tubes are narrowly cylindrical and slightly wider at mouth, 3–9 mm long, appressed strigose-sericeous outside, puberulent inside, with a narrow line of sparse yellow moniliform hairs at mouth. Corolla lobes are thickened at base, narrowly oblong or oblong-ovate, 0.9–6 × 0.5–2.7 mm, and round or acute at apex. The smallest corolla in the genus are those of *N. micrantha*, which has corollas 3.9–4.2 mm long, and the largest are those of *N. gracilis*, which has corollas 9.5–15.5 mm long.

In *Pteridocalyx* (1 sp.), the corollas are hypocrateriform, 14–19 mm long, with the corolla tube pale brown or white and brownish at medial portion, and pink lobes with a basal white triangle of glandular hairs inside. The tubes are narrowly cylindrical, slightly wider at mouth, 10.5–13.5 mm long, and the lobes are oblong-ovate to ovate, 3.5–5.5 × 1.7–3 mm, and obtuse to acute at apex.

*Sipanea* (17 spp.) is the largest and most widespread genus in the tribe, and has a wide variation in corolla shape, size, and color. The corollas vary from hypocrateriform, narrowly infundibuliform, narrowly campanulate to campanulate, and can be white, pinkish-white, cream-white, pink, or pale purple, or sometimes the lobes are pink and with a white basal triangular area forming a star shape at mouth, with the five lobes. The tubes can be glabrous, puberulent, short-pubescent or hirsute, or with the lower half glabrous and the distal portion pubescent outside, and glabrous, puberulent or pubescent at the stamen insertion and the rest glabrous, or puberulent or pubescent throughout inside. In the present treatment three sections are recognized within *Sipanea*, which are characterized by the internal vestiture of the corolla mouth: 1) Section *Sipanea*, with a ring of yellow hairs; 2) Section *Virecta*, with a ring of white hairs; 3) Section *Nudae*, glabrous or with sparse white hairs. The variation of corolla shape and size for each section is discussed below.

In *Sipanea* section *Sipanea*, the corollas are consistently hypocrateriform and with a dense ring of yellow hairs exerted beyond the mouth. The corollas range from (8–)8.5 to 27.5(–28) mm in length, with tubes narrowly cylindrical and slightly wider towards the mouth, 6–18 mm long, and with (4)5(6) lobes varying from round, broadly obovate, broadly elliptic, elliptic, oblong-elliptic, obovate to oblanceolate, and 2.5–10.5 × 1.5–8 mm. Corolla color in this section varies from pink, pale pink, whitish-pink, or with tube pink and lobes white, while in *S. glomerata* is consistently white, and in *S. veris* is pale to intense pink, turning paler after anthesis, with lobes basally white (non-glandular), forming a white ring at mouth. The smallest corollas in this section are found in *S. hispida*, which has corollas 8.5–15(–16.5) mm long, with the tubes 6–10(–12.5) mm long and lobes 2.5–5 × 1.5–3 mm, and in *S. pratensis*, which has corollas 14–28 mm long, with the tubes (8–)10–17 mm long and lobes (2.5–)4–11 × (2–)2.5–7 mm. The largest corollas are found in *S. galioides*, which has corollas (18.5–)22.5–27.5(–28) mm long, with the tubes (13–)15–18 mm long and lobes (5.5–)7.5–10.5 × 3–6(–7.5 mm), and also in *S. pratensis*, which has corollas 14–28 mm long, with the tubes (8–)10–17 mm long and lobes (2.5–)4–11 × (2–)2.5–7 mm. In *S. galioides*, *S. pratensis* and *S. veris*, the corollas are very variable in size throughout their geographic range, sometimes varying in size within the same population or even on the same individual, and with lobes sometimes unequal or of slightly different shapes within the same corolla. Corolla lobes in *Sipanea galioides* vary from broadly ovate or obovate to elliptic-ovate, (5.5–)7.5–10.5 × 3–6(–7.5 mm), and subobtusate to acute at the apex. In *Sipanea pratensis*, lobes vary from round, broadly elliptic, elliptic, obovate, oblong-elliptic to oblanceolate, and can vary in shape and size within the same population, or sometimes they may be unequal or of slightly different shape on the same corolla, (2.5–)4–11 × (2–)2.5–7 mm, and round, obtuse to acute, rarely apiculate when subobtusate or acute, or indented when obtuse or round at the apex. In *S. veris*, the lobes vary from obovate to round, 6–10 × 4.5–8 mm, and are obtuse to subacute at the apex.

*Sipanea* section *Virecta* is characterized by a ring of white hairs at the corolla mouth. Contrary to the other two sections, the corolla shape in this section is quite variable, being hypocrateriform in *S. biflora* and *S. carrenoi*, narrowly infundibuliform in *S. gleasonii* and *S. setacea*, and campanulate or narrowly campanulate in *S. micrantha* and *S. ovalifolia*. The corolla color is also more variable in this section. In *S. gleasonii*, the corollas vary from pale pink to white, at the end of anthesis, and in *S. micrantha* and *S. ovalifolia* is consistently white. In

*S. biflora* the corollas vary from pink, deep pink to pale purple, and the lobes have a narrowly triangular basal area with white glandular hairs, forming a star-like pattern with the five lobes. In *S. carrenoi*, a species only known by the type specimen, the corollas are pink, and in *S. setacea*, also known only by the type, the corolla is reported to be purple (fide specimen label of *Huber et al.* 8246). Corollas in this section are also more variable in size, ranging from 4 to 21(–29) mm long, with tubes 2.5–13(–15) mm long and lobes varying from round, broadly ovate, ovate, oblong-obovate, obovate to narrowly oblong, and 1.5–8.5(–14) × 1–5.5(–7) mm. The smallest corollas in this section are those of *S. micrantha*, which are campanulate, 4–6.5 mm long, with the tubes 2.5–3.5 mm long and lobes 1.5–3 × 1–1.5 mm. The largest corollas in section *Virecta* are found in *S. biflora*, which has corollas very variable in size throughout the geographic range, often varying in size within the same population or even within the same individual; they are hypocrateriform, and ranging from (8–)15 to 21(–29) mm long, with the tubes 5–13(–15) mm long and lobes 3–8.5(–14) × 2–5.5(–7) mm.

In *Sipanea* section *Nudae*, all species have hypocrateriform corollas, glabrous or with a few sparse white hairs at mouth. Corollas of this section are entirely pink, or with a pale green to greenish-white or red tube, and the lobes are pinkish-white, pink or lavender. *Sipanea wilson-brownei* differs from the other species of this section by having corolla lobes pink often with a median linear white area, microscopically glandular, at the base, forming a white star-like pattern with the five lobes. In this section the corollas vary from 8.5 to 27.5 mm in length, with tubes narrowly cylindrical and slightly wider towards the mouth, or slightly wider at median portion in *S. prancei*, and from 5.7 to 18 mm long. Corolla lobes in this section vary from elliptic, narrowly elliptic, oblong-obovate, narrowly obovate, obovate to ligulate, 2.7–9.5 × 1.4–4.7 mm, and are round, obtuse or acute at apex. The smaller corollas in this section are those of *S. prancei*, which are 8.5–11 mm long, with the tubes 5.7–7.5 mm long and lobes 2.7–3.5 long). The largest corollas in this section are found in *S. ayangannensis*, which has corollas 25–27.5 mm long, with the tubes 17–18 mm long and lobes 8–9.5 long, and in *S. wilson-brownei*, which has corollas 13–28 mm long, with the tubes (7–)10–15 mm long and lobes 4–8.5(–14) long.

*Sipaneopsis*, a genus endemic to Amazonian white-sand areas, has a unique flowering modality within the Rubiaceae, which was discussed and illustrated by Delprete (2015a, 2018; see discussion in *Flowering Modality*). In this genus, the corollas change shape and size as they go through subsequent flowering stages (Fig-

ures 80, 82). At the initial and intermediate stages, the corollas are small, campanulate, with a short tube, with lobes already opened and erect, with basal appendages appressed against each other and obstructing the corolla mouth. At the final stage of anthesis, the corollas expand becoming much larger and hypocrateriform, with the tube narrowly cylindrical, the lobes reflexed and perpendicular to the tube, and the appendages become erect, allowing access to visitors and pollinators into the corolla. The corollas in *Sipaneopsis* are pink during anthesis and turn pinkish-white to white at final stage. The corolla lobes in *Sipaneopsis* are commonly left-contorted, or they might exceptionally be irregularly imbricate, with 1–3 interior lobes, in *S. cururuensis* and *S. rupicola*.

Because in *Sipaneopsis* the corollas change shape and size during the flowering process, and because the corolla lobes are already open before anthesis, corolla dimensions have sometimes been reported from flowers not yet fully expanded (e.g., Steyermark, 1967, 1974, 1984). In the present treatment, shapes and sizes are reported only from fully expanded corollas, i.e., when the lobes are perpendicular to the tube. In *Sipaneopsis*, the fully expanded corollas are hypocrateriform and range from 13 to 30 mm long, with tubes cylindrical and slightly wider at mouth, 9.5 to 22 mm long. Fully expanded corollas lobes vary in shape from round, ovate, oblong-ovate elliptic to obovate,  $4.2\text{--}9 \times 1.8\text{--}4$  mm, and are round, obtuse or acute at the apex. In addition, fully expanded corolla lobes are often slightly unequal, and may vary in shape and size on the same plant or the same corolla. The smallest corollas in the genus are those of *S. huberi*, which are 13–14 mm long, with the tubes 9.5–10 mm long, and lobes  $4\text{--}4.5 \times 2.5\text{--}3$  mm, when fully expanded. The largest corollas are found in *S. pacimoniensis*, only known from a single fully expanded corolla on the type specimen, 27.5–28.5 mm long, tube 19 mm long, lobes  $8.5\text{--}9.5 \times 4.5\text{--}5.5$  mm, and in *S. maguirei* Steyer., which is the most widespread species in the genus, with corollas 21–30 mm long, corolla tubes 15–22 mm long, and lobes  $4.5\text{--}9 \times 3\text{--}4.2$  mm, when fully expanded.

*Steyermarkia* is exceptional within the tribe by having consistently 4-merous flowers. Its corollas are pink, hypocrateriform, with a cylindrical tube 3.5–4.5 cm long, and broadly ovate lobes,  $1.4\text{--}2 \times 0.9\text{--}1.3$  cm.

### Stamens

In the genera of this tribe the filaments are free at the base, and equal or subequal. The anthers are dorsifixed near the base or at the middle of the corolla, and dehisce by longitudinal slits.

Within the Sipaneeae, the genera *Limnosipanea*, *Maguireothamnus*, *Sipaneopsis*, and *Steyermarkia* are homostylous. The stamens of these genera are discussed below.

*Limnosipanea* is only genus of the tribe with well-exserted stamens. In this genus, the filaments are glabrous and inserted near the mouth of the corolla tube, and the anthers are narrowly elliptic or oblong, dorsifixed near the middle. In all other genera of the tribe the stamens are included, except for those of the short-styled flowers of *Dendrosipanea*, which may have partially exserted anthers.

In *Maguireothamnus* the filaments are inserted near or just below the corolla mouth and short. The anthers are subsessile, elongate and dorsifixed near the base.

In *Sipaneopsis* the filaments are extremely short, inserted at the middle of the corolla tube. The anthers are subsessile, linear and dorsifixed near the base.

In *Steyermarkia* the filaments are inserted on the upper part of the corolla tube, short, and glabrous. The anthers are subsessile, elongate and dorsifixed near the base.

The genera *Chalepophyllum*, *Dendrosipanea*, *Nebelinathamnus*, *Neobertiera*, *Pteridocalyx* and *Sipanea* are heterostylous. Aside from the stamens inserted at different heights on the corolla tube, the anthers may also differ in shape and size in the long-styled and the short-styled flowers of the same species.

In *Chalepophyllum*, the filaments of short-styled flowers are inserted at the upper portion of corolla throat, and the anthers are narrowly oblong. In long-styled flowers, they are inserted at the medio-basal portion of the corolla throat, and the anthers are also narrowly oblong.

In *Dendrosipanea*, the stamens of short-styled flowers are included or partially exserted, with filaments inserted at distal portion of corolla throat, and the anthers are linear, and the style is included. In long-styled flowers, the stamens are included, with filaments also inserted at basal portion of corolla throat, and anthers are also linear, while the style is barely exserted, with the branch tips presented just beyond corolla mouth.

In *Nebelinathamnus*, the stamens of short-styled flowers are included, with extremely short filaments (anthers subsessile) inserted on the distal most portion of the corolla throat with the anther tips at corolla mouth or barely exserted, and the anthers are linear. The stamens of long-styled flowers are included, with extremely short filaments (anthers subsessile) inserted at upper portion of corolla throat with the anther tips much below the corolla mouth, and the anthers are nar-



rowly elliptic, much shorter than those of short-styled flowers.

In *Neobertiera*, the filaments of short-styled flowers are inserted at about the middle or at the distal portion of the corolla tube and anthers are linear. Those of long-styled flowers are inserted near the base or at the middle of corolla tube, and the anthers are linear or narrowly sagittate.

In *Pteridocalyx*, the filaments of short-styled flowers are inserted at the distal portion of corolla tube, and the anthers are linear. The filaments of long-styled flowers are inserted near the base of the corolla tube, and the anthers are also linear.

*Sipanea* is the most diverse genus of the tribe, and is here subdivided into three sections. The characteristics and points of insertion of the stamens are discussed by section. In section *Sipanea*, the filaments of long-styled flowers are inserted near the base, at about the middle, or at medio-distal portion of the corolla tube, and the anthers are narrowly oblong-elliptic to linear. The filaments of short-styled flowers are inserted at the distal portion of the corolla tube, and the anthers are narrowly oblong-elliptic, very narrowly lanceolate or linear. In the medium-styled flowers of *Sipanea hispida* the filaments are inserted at 3/10 to 1/2 from the base of the corolla tube, just below the tips of the style branches, and the anthers are linear.

In *Sipanea* section *Virecta* and section *Nudae*, the filaments of long-styled flowers are inserted near the base or at medio-distal portion of the corolla tube, and the anthers are narrowly oblong to linear; while the filaments of short-styled flowers are inserted at the distal portion of the corolla tube, and the anthers are linear.

### Pollen

In all the genera of the Sipaneeae, pollen grains are released in monads and are colpate. The number of colpi are either 3 or 4. In most genera the number of colpi are consistently 3 or 4, which represent a good diagnostic character for the identification of genera. In a few genera, the colpi are commonly 3 or exceptionally 4, or vice versa. Dimensions and descriptions of pollen grains in the Sipaneeae are presented below, organized by genus.

***Chalepophyllum*.** (Figure 4AB). Pollen grains are  $32.37\text{--}33.83 \times 26.50\text{--}29.52 \mu\text{m}$ , and are the second largest in the tribe, after those of *Maguireothamnus*, which corresponds with the corolla tubes 1.7–3.1 cm long, which are also the second largest in the tribe. The number of colpi is commonly 4 or exceptionally 3. The external surface (sexine) is foveolate-reticulate.

***Dendrosipanea*.** (Figure 4C–D). Pollen grains are  $18.68\text{--}29.53 \times 18.50\text{--}25.42 \mu\text{m}$ , which are average dimensions for most genera of the tribe. They are consistently 4-colporate in all the species. External ornamentation is either foveolate or foveolate-reticulate.

***Limnosipanea*.** (Figure 4E–F). Pollen grains are  $20.27\text{--}30.38 \times 20.45\text{--}27.06 \mu\text{m}$ , which are average dimensions for most genera of the tribe. They are 3-colporate in all the species, although they could exceptionally be 4-colporate in *L. palustris*. Their external ornamentation is shallowly foveolate, without perforations in *L. erythraeoides* and *L. spruceana* var. *spruceana*, or either without perforations or finely perforate in *L. palustris*.

***Maguireothamnus*.** (Figure 4G–H). Pollen grains are the largest of the tribe, by being  $69.11\text{--}75.38 \times 54.60\text{--}67.84 \mu\text{m}$ . The large size of the pollen corresponds with the long-tubular corollas, with corolla tubes 6.5–13 cm long, which are also the largest in the Sipaneeae. Grains are commonly 3-colporate, although they may be 3- or 4-colporate in *M. speciosus*. The external wall in this genus is either smooth or finely foveolate.

***Neblinathamnus*.** (Figure 4I). Pollen grains are  $17.28\text{--}23.17 \times 18.14\text{--}25.12 \mu\text{m}$ , consistently 3-colporate, and foveolate-reticulate. There is a difference in size between the 2 species recognized in the genus:  $20.52\text{--}23.17 \times 21.61\text{--}25.12 \mu\text{m}$  in *N. argyreus*, and  $17.28\text{--}19.58 \times 18.14\text{--}20.42 \mu\text{m}$  in *N. brasiliensis*. Pollen size corresponds with the length of the corolla tubes, which are 10.5–14.5(-16) mm long in *N. argyreus*, and 9–12 mm long in *N. brasiliensis*.

***Neobertiera*.** (Figure 4K). A genus of 5 species of perennial herbs, subshrubs or shrubs endemic to the Guiana Shield. One these species, *N. micrantha* Delprete, is only known from the type specimens, and the other two are only known by three collections, *N. montedouradensis* Delprete, *N. pakaraimensis* Delprete. The only species of *Neobertiera* studied, *N. gracilis*, has pollen

**Figure 4.** SEM images of pollen grains of Sipaneeae genera. **A–B.** *Chalepophyllum guyanense* **A.** side view. **B.** polar view. **C.** *Dendrosipanea prancei*, side view. **D.** *Dendrosipanea prancei*, polar view. **E–F.** *Limnosipanea spruceana* var. *spruceana* **E.** side view. **F.** detail of exine cerebriform sculpturing. **G–H.** *Maguireothamnus speciosus*. **G.** side view, with smooth exine. **H.** polar view. **I.** *Neblinathamnus brasiliensis*, side view. **J.** *Neobertiera gracilis*, side view. **K.** *Neobertiera palustris*, polar view. **L.** *Pteridocalyx appunii*, side view. **A–B:** from Delprete & Benjamin 12860 (CAY); **C–D:** from Prance et al. 16199 (F); **E–F:** from Delprete et al. 7433 (CAY); **G–H:** from Steyermark 59801 (F); **I:** from Silva & Brazão 60907 (F); **J:** from Grenwald & Persaud 110 (U); **K:** from Delprete 11860 (CAY); **L:** from Delprete & Benjamin 12860 (CAY). All scale bars are 1  $\mu\text{m}$ , except G–H that are 10  $\mu\text{m}$ . Images made by Iris van der Beeten.

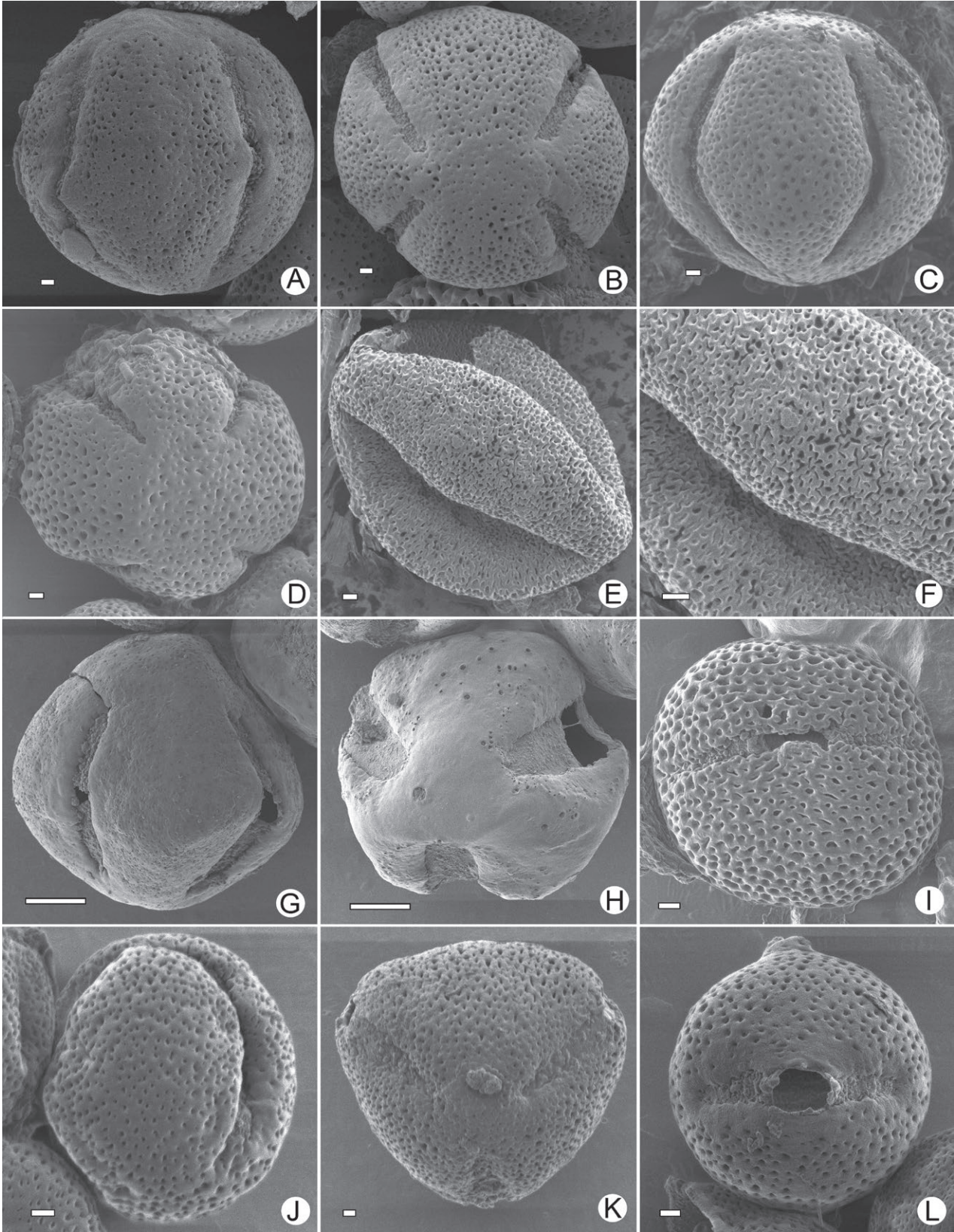


Figure 4.

grains  $13.14\text{--}15.43 \times 14.15\text{--}17.58 \mu\text{m}$ , 3-colporate, and foveolate.

***Pteridocalyx***. (Figures 4L, 5A–B). A monospecific genus endemic to central Guyana, in the Potaro River Basin. Pollen grains are  $13.13\text{--}15.06 \times 13.55\text{--}16.85 \mu\text{m}$ , 3-colporate. The exine is foveolate-reticulate and with a rugulate surface.

***Sipanea***. (Figure 5C–H). A genus of 17 species, with the widest geographic distribution and the highest diversity in the Sipaneeae. The five species studied in this genus have 3-colporate pollen grains,  $15.75\text{--}23.77 \times 14.49\text{--}22.25 \mu\text{m}$ , and with foveolate-reticulate or finely foveolate external ornamentation. Three sections are here recognized in the genus: 1) section *Sipanea*, with a ring of yellow hairs at corolla mouth, 2) section *Virecta*, with a ring of white hairs at corolla mouth, and 3) section *Nudae*, with a corolla mouth glabrous or a few sparse hairs. Pollen grains dimensions and external ornamentation are amply overlapping and do not offer any diagnostic characters for these sections. The possible pollen dimorphism in distylous species was observed only in *S. pratensis* var. *pratensis*. In both forms pollen grain dimensions and external ornamentation, foveolate-reticulate, are similar, and it seems that at least in this species there is no pollen dimorphism.

***Sipaneopsis***. (Figure 5I–J). *Sipaneopsis* is a genus of 8 species endemic to white-sand savannas of the Amazon Basin. Two species are known only from the type specimens and 3 from a few collections, and flower buds of these specimens could not be extracted for palynological studies. Two species, *S. duckei* and *S. maguirei*, known from numerous collections, were studied. They have 4-colporate,  $18.85\text{--}25.85 \times 17.70\text{--}25.40 \mu\text{m}$ , shallowly foveolate pollen grains.

***Steyermarkia***. (Figure 5K–L). One collection with several duplicates (*Hammel et al.* 15637), with several flowers on each specimen, allowed the extraction of one flower bud. Pollen grains are  $27.98\text{--}35.48 \times 26.72\text{--}31.34 \mu\text{m}$ , 3-colporate, and externally foveolate.

An article dedicated to the pollen morphology of this tribe, with LM and SEM images, discussions, and vouchers cited, is being prepared and will soon be submitted for publication (Delprete, van der Beeten and De Block, in progress).

## Styles

The styles in the Sipaneeae are included or exerted, and have two style branches. On the adaxial side of each style branch there is a minutely papillose stigmatic surface, which becomes receptive after the style branches have spread apart from each other. The genera *Limnosipanea*, *Maguireothamnus*, *Sipaneopsis*, and *Steyermarkia* are homostylous. In *Limnosipanea*, the style is exerted, glabrous, and with oblong or ovate branches. In *Maguireothamnus*, the style is exerted well beyond the corolla mouth, antrorse-papillose at distal portion, and with elliptic branches. In *Sipaneopsis*, the style is included or barely exerted, with the branch tips exerted, glabrous, and with lanceolate to narrowly lanceolate branches. In *Steyermarkia*, the style is included, and has oblong branches.

The genera *Chalepophyllum*, *Dendrosipanea*, *Neblinathamnus*, *Neobertiera*, *Pteridocalyx* and *Sipanea* are heterostylous. Aside from the variation in length of the style, the style branches may also be of different shape and size in the long-styled and short-styled flowers of the same species.

In *Chalepophyllum* and *Dendrosipanea*, the style is much shorter than the corolla tube in short-styled flowers, or is exerted well beyond corolla mouth in long-styled flowers. The style branches are oblong in both forms.

In *Neblinathamnus*, the stamens are included, with short filaments inserted at distal portion of corolla throat, and the anthers are linear. In short-styled flowers, the style is included and with linear branches. In long-styled flowers, the stamens are also included with short filaments, but they are inserted at medio-basal or median portion of corolla throat; the anthers are narrowly oblong or linear; the style is as long as corolla tube with the style branches barely exerted beyond corolla mouth or exerted, with narrowly ovate, narrowly lanceolate or linear branches.

In *Neobertiera*, the style is much shorter than the corolla tube, with narrowly oblong or elliptic branches, in short-styled flowers; or is about the same length of the corolla tube with the tips of the branches barely exerted or exerted beyond the corolla mouth, with narrowly

**Figure 5.** SEM images of pollen grains of Sipaneeae genera. **A–B.** *Pteridocalyx appunii*. **A.** Polar view. **B.** Detail of exine sculpturing (note rugulate surface). **C.** *Sipanea galiodes*, side view. **D.** *Sipanea glomerata*, polar view. **E–F.** *Sipanea pratensis* var. *pratensis*. **E.** Side view. **F.** Polar view. **G.** *Sipanea biflora*, lateral view. **H.** *Sipanea wilson-brownei*, lateral view. **I–J.** *Sipaneopsis duckei*. **I.** lateral view. **J.** polar view. **K–L.** *Steyermarkia guatemalensis*. **K.** Lateral view. **L.** Polar view. **A–B:** from Delprete & Benjamin 12860 (CAY); **C:** from Delprete & Araujo 7414 (CAY); **D:** from Delprete et al. 7438 (CAY); **E–F:** from Delprete 12633 (CAY); **G:** from Feuillet 735 (CAY); **H:** from Granville et al. 5953 (CAY); **I–J:** from Farney & Batista 2057 (US); **K–L:** from Hammel et al. 15637 (F). All scale bars are 1  $\mu\text{m}$ . Images made by Iris van der Beeten.

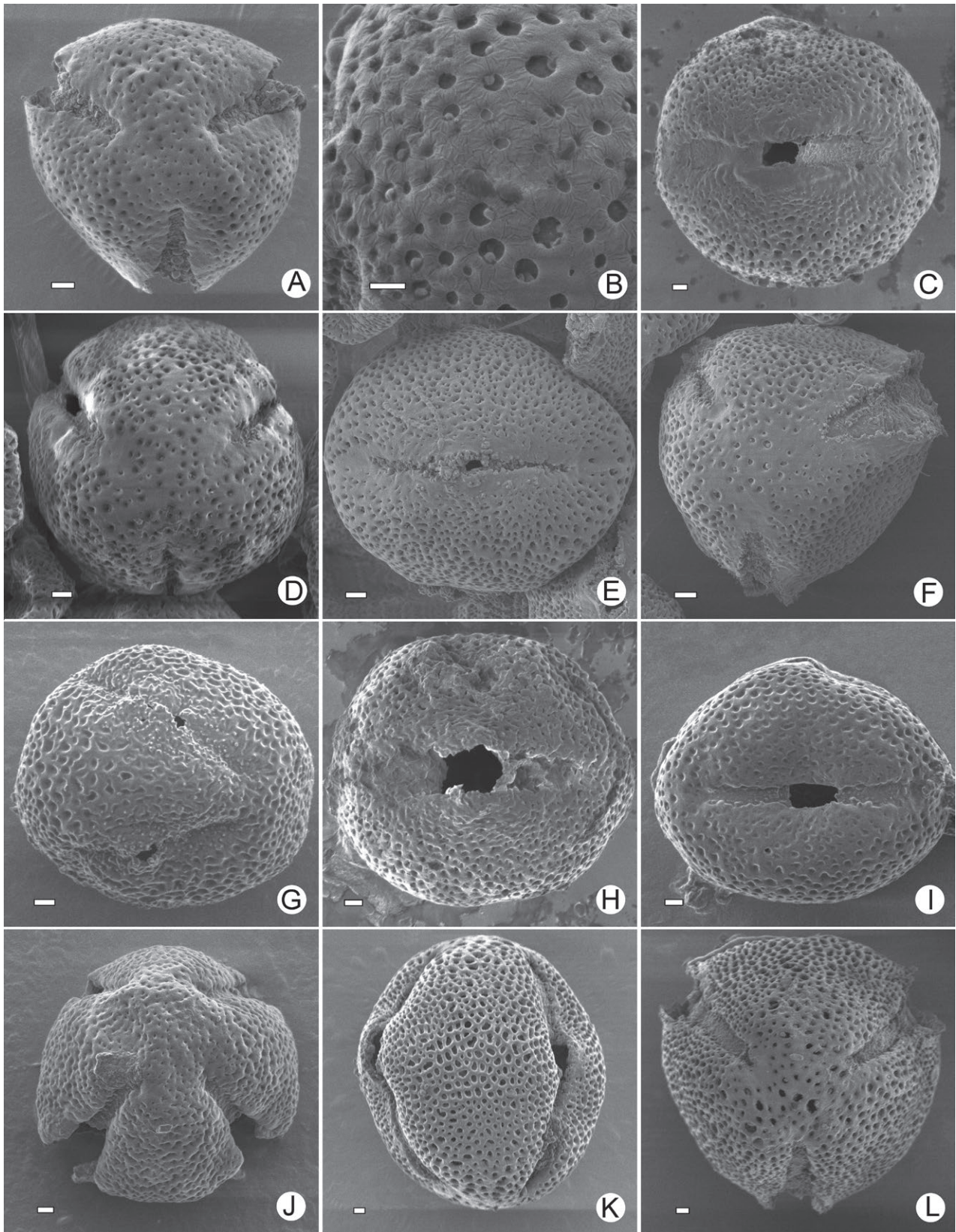


Figure 5.

oblong, narrowly lanceolate to linear branches in long-styled flowers. In *Pteridocalyx*, the style is much shorter than the corolla tube and with narrowly lanceolate branches in short-styled flowers; while it is as long as the corolla tube with the tips of the branches barely exerted or exerted just beyond the corolla mouth and with linear branches in long-styled flowers.

*Sipanea* is the most diverse genus of the tribe, and is here subdivided into three sections. In section *Sipanea* (corolla mouth with a ring of yellow hairs), the style of long-styled flowers is as long as the corolla tube with the tips of branches exerted or exerted beyond the corolla mouth, with oblong or obovate branches (0.6–)1–1.3 mm long. In short-styled flowers, it is much shorter than the corolla tube, and with linear branches 2–3 mm long. In the medium-styled flowers of *Sipanea hispida*, the style is about half the length of the corolla tube and corresponds with the middle or the upper tips of the anthers (stamens inserted at 3/10 to 1/2 from the base of the corolla tube, and has linear branches, 1–3 mm long. In section *Virecta* (corolla mouth with a ring of white hairs), the style of long-styled flowers is as long as the corolla tube with the tips of the branches exerted or exerted beyond the corolla mouth and has obovate, very narrowly lanceolate or linear branches 0.6–2 mm long. In short-styled flowers, it is much shorter than the corolla tube, with linear branches 1–1.6 mm long. In section *Nudae* (corolla mouth glabrous or with sparse white hairs), the style of long-styled flowers is as long as corolla tube with the branches obovate, very narrowly lanceolate or linear to filiform, 0.6–2.5 mm long, branch tips exerted. In short-styled flowers, the style is much shorter than the corolla tube and with the branches narrowly ovate, narrowly lanceolate or linear, 1–3.5 mm long.

#### Ovaries

In the Sipaneeae, the ovaries are inferior, bilocular, with axile placentation, and with many ovules per locule. In most genera, the placenta has a stalked extension inserted at the middle, medio-basal, or distalmost portion of the septum near the roof of the locule. *Dendrosipanea* is exceptional in the tribe by having a fleshy placental extension adnate along the entire length of the septum. In *Chalepophyllum*, *Limnosipanea*, *Maguireothamnus*, *Neblinathamnus*, *Neobertiera*, *Sipaneopsis* and *Steyermarkia*, the placental stalk is inserted at the middle of the septum, and terminates with a hemi-ellipsoid, oblong-ellipsoid, or hemi-elliptic extension, or with a globose extension in *Sipaneopsis*.

In *Sipanea*, the placental stalk is inserted at the middle or medio-basal portion of the septum, and termi-

nates with an oblong or hemi-elliptic extension, with the ovules inserted on the placental extension. In some species of this genus, the stalk of the young ovaries is very short, giving the impression that the ovules are inserted directly on the central septum.

*Dendrosipanea* is unique within the tribe in having a fleshy placental extension adnate along the entire length of the septum, with the ovules irregularly peltate on the longitudinal placental extension.

Delprete (2019) described the placenta of *Pteridocalyx* as longitudinally adnate along the central septum. However, additional anatomical studies revealed that this genus is unique within the tribe by having a placental stalk inserted at the distalmost portion of the septum, near the roof of the locule, with a pendulous, narrowly cylindrical extension almost as long as the locule, and the ovules are inserted on the cylindrical extension.

#### Fruits

Most genera of the Sipaneeae have persistent, bilocular, multi-seeded, basipetally dehiscent capsules with a central placenta in each locule, which dehisce and release the wind-dispersed seeds. *Neobertiera* and *Sipaneopsis* are exceptional within the tribe, by having indehiscent, crustaceous fruits that fall off as dispersal units, leaving a tiny round scar and subtending bracts on the infructescence branches.

Shape and dimensions of capsules are rather consistent within each genus, with the exception of *Sipanea*, the most diverse genus in the tribe, with fruits varying in size and shape. They vary among genera, offering a good practical aid for generic distinction. In *Chalepophyllum*, capsules are ovoid to ellipsoid, 7–17 × 5–7 mm; in *Dendrosipanea*, turbinate to oblong-turbinate, (5–)7–11.5 × 3–5.7 mm; in *Limnosipanea*, are globose or ovoid to subglobose, 2.5–4 × 1.5–3 mm; in *Maguireothamnus* are obovoid, ovoid to ellipsoid, 10–27 × 8–15 mm; in *Neblinathamnus* are subturbinate, obovoid-subglobose to broadly obconical, 4–5 × 3–4 mm; in *Pteridocalyx* are oblong-ellipsoid to narrowly oblong, 6–14 × 2–3 mm; in *Sipanea* are globose, subglobose, broadly ovoid, ovoid to narrowly ovoid, obovoid, ellipsoid, oblong-ovoid, oblong, narrowly oblong-elliptic, oblong-turbinate or cylindrical-oblong, 2.5–11 × 1.5–5.5 mm; and in *Steyermarkia* are subglobose, 6.5–8 mm in diam.

The indehiscent fruits of *Sipaneopsis* and *Neobertiera* are quite similar in shape and size, being globose or subglobose, rarely urceolate in *Sipaneopsis*, 3–5 in diam. in the former, and globose, 1.2–4 mm in diam. in the latter.

Capsular dehiscence is a valuable diagnostic character to identify genera within the Sipaneeae. They are sep-

ticidal in *Chalepophyllum*, *Dendrosipanea* and *Pteridocalyx*, and loculicidal in *Limnosipanea*, *Maguireothamnus*, *Neblinathamnus*, *Sipanea*, and *Steyermarkia*.

The term secondary dehiscence (Delprete 1999) refers to the distal splitting of the valves that occur in advanced stages of capsule maturity, usually after and perpendicular to the primary dehiscence. In the Sipaneeae, secondary dehiscence was observed only in the old capsules of *Chalepophyllum*.

## SYSTEMATIC TREATMENT

### *Description of the tribe Sipaneeae*

Tribe **Sipaneeae** Bremek. (as "Sipanea"). Rec. Trav. Bot. Neerl. 31: 253. 1934

Type: *Sipanea* Aubl.

**Herbs**, subshrubs or shrubs, rarely treelets; generally terrestrial, or semi-aquatic (amphibious) or free-floating herbs in *Limnosipanea* and a few species of *Sipanea*; wood, when present, whitish, yellowish or reddish. **Raphides** absent. **Stipules** interpetiolar, entire or bifid, or entire when young and becoming bifid when older, rarely with several linear lobes in *Sipaneopsis*, with colleters on the adaxial side secreting a resinous substance, persistent or caducous. **Leaves** opposite and decussate, ternate, or rarely in whorls of 3–6(–8) leaves per node in *Limnosipanea*, sessile, subsessile or petiolate; blades chartaceous, papyraceous, subcoriaceous to coriaceous; domatia commonly absent, or tuft-domatia on leaves of *Chalepophyllum*. **Inflorescences** terminal (*Dendrosipanea*, *Limnosipanea*, *Neobertiera*, *Pteridocalyx*, *Sipanea*, and *Sipaneopsis*) or axillary (*Chalepophyllum*, *Maguireothamnus*, *Neblinathamnus*, and *Steyermarkia*), simple, capitate, condensed, or cymose, congested or short- to long-branched, with 2–8 orders of branching, pauci- to multi-florous or uniflorous. **Flowers** actinomorphic or subzygomorphic in *Maguireothamnus*, bisexual, 4–5(–6)-merous, protandrous, homostylous (*Limnosipanea*, *Maguireothamnus*, *Sipaneopsis*, and *Steyermarkia*) or heterostylous (*Chalepophyllum*, *Dendrosipanea*, *Neblinathamnus*, *Neobertiera*, *Pteridocalyx*, and *Sipanea*). **Calyx** persistent (crowning the fruit); tube extremely reduced or absent, with lobes free; lobes often minute, equal or subequal, rarely foliose, or with 1 or 2 lobes per flower expanded into white to cream-white calycophylls in *Pteridocalyx*. **Corolla** commonly hypocrateriform, or narrowly infundibuliform, infundibuliform, narrowly campanulate to campanulate, white (sometimes

tube pale green), cream-white, pinkish-white, pink, rarely lilac (*Limnosipanea*), or corolla tube red with yellowish or greenish lobes in *Neblinathamnus*; aestivation contorted or rarely irregularly imbricate (1–3 lobes internal in two species of *Sipaneopsis*). **Stamens** as many as corolla lobes, inserted near the base, or at the medial zone, or near the corolla mouth, sometimes all positions present in di- or tri-stylous species; anthers included or exerted, oblong to narrowly elliptic to button-shaped, 2-locular, dehiscing by longitudinal slits, dorsifixed near the base or around the middle, introrse. **Pollen** released in monads, 3–4 colpi, exine reticulate or foveolate. **Style** included or exerted; style branches 2, with stigmatic surface smooth or glandular. **Ovary** inferior, 2-locular, placentation axile, with a stalked placental extension; the stalk commonly inserted at the middle or medio-basal portion of the septum, terminating in a hemi-ellipsoid, oblong-ellipsoid or hemi-elliptic extension, or with a globose extension in *Sipaneopsis*; or the stalk inserted at the distalmost portion of the septum (i.e., near the roof of the locule) with a pendulous, narrowly cylindrical extension in *Pteridocalyx*; or with a fleshy placental extension adnate along the entire length of the septum in *Dendrosipanea*. **Fruits** capsular, loculicidal (*Limnosipanea*, *Maguireothamnus*, *Neblinathamnus*, *Sipanea*, *Steyermarkia*) or septicidal (*Chalepophyllum*, *Dendrosipanea*, *Pteridocalyx*), persistent, opening basipetally, woody or crustaceous, or indehiscent, crustaceous, falling off as dispersal units (*Neobertiera* and *Sipaneopsis*), with persistent calyx. **Seeds** globose, ovoid or irregularly tetrahedral; wings absent or extremely reduced and concentric in *Maguireothamnus*.

The tribe Sipaneeae, as here delimited, includes the genera *Chalepophyllum* (1 sp.), *Dendrosipanea* (3 spp.), *Limnosipanea* (3 spp.), *Maguireothamnus* (3 spp.), *Neblinathamnus* (2 spp.), *Neobertiera* (5 spp.), *Pteridocalyx* (1 sp.), *Sipanea* (17 spp.), *Sipaneopsis* (8 spp.), and *Steyermarkia* (1 sp.), for a total of 44 species.

## KEY TO THE SIPANEEAE GENERA

Some of the genera of this tribe have variable habit (i.e., herb, subshrub or shrub) and/or phyllotaxy (i.e., leaves opposite, ternate or whorled, e.g., *Limnosipanea*); these genera are found in multiple entries in this key.

1. Plant acaulescent or nearly so, sometimes with a woody stem to 18 cm long; leaves in basal rosettes, crowded at the apex of a short stem; flowers 4-merous (southern Mexico (Chiapas) and Guatemala; on rock walls, in rain forest understory) ..... 10. *Steyermarkia*

1. Plants with a well-developed stem; cauline leaves regularly spaced along the stem, not in basal rosettes; flowers (4)5(6)-merous ..... 2
2. Prostrate, decumbent or erect herbs..... 3
2. Subshrubs (plant basally woody and distally herbaceous, or shrubs less than 50 cm tall), shrubs or small trees..... 7
3. Leaves whorled, 3–6(–8) per node (Panama, Colombia, Venezuela, Guyana, Brazil and Bolivia; ephemeral herb, terrestrial or semi-aquatic; periodically inundated open fields, margins of small water courses, and swamps) ..... 3. *Limnosipanea*
3. Leaves opposite (opposite or ternate in *Neblinathamnus*).... 4
4. Plant semi-aquatic, amphibious or terrestrial; flowers homostylous; stamens exerted well beyond the corolla mouth ..... 3. *Limnosipanea*
4. Plant terrestrial; flowers homostylous or heterostylous; stamens included, or exerted just beyond the corolla mouth in short-styled flowers of some species of *Sipanea* ..... 5
5. Fruit a loculicidal capsule, persistent (flowers distylous; corolla lobes without a glandular area at base) (Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Guianas, Peru, Brazil, Bolivia and Paraguay; open savannas, forest undercanopy, and rocky outcrops)..... 8. *Sipanea*
5. Fruit indehiscent, falling off as dispersal unit; plant erect. 6
6. Flowers homostylous; corolla mouth with 5 thickened triangular projections at base of each corolla lobe, covered with erect brushy white hairs at base of corolla lobes; corolla lobes glabrous on adaxial side, opening before complete elongation of the corolla tube (Guayana Shield: Colombia, southern Venezuela, northern Brazil, N of the Amazon River, except for *S. cururuensis* and *S. maguirei*, found S or the Amazon River; white-sand savannas, mostly lowlands or moderate elevations) ..... 9. *Sipaneopsis*
6. Flowers distylous or exceptionally tristylous; corolla mouth without thickened triangular projections at base of each corolla lobe; corolla lobes opening after complete elongation of the corolla tube, with glandular triangular area at base (Guyana, Suriname, French Guiana, northern Brazil (Pará); forest undercanopy, usually near creeks) ..... 6. *Neobertiera*
- 7(2). Some flowers of the inflorescence with 1 or 2 calyx lobes expanded and petaloid (calycophylls), white (Guyana: Upper Potaro River)..... 7. *Pteridocalyx*
7. Flowers without expanded, petaloid, calyx lobes..... 8
8. Corolla 9–17 cm long, tube 5–13 cm long (Endemic to the tepuis of the Guayana Shield: Venezuela, Guyana and northern Brazil; on exposed sandstone outcrops, open scrub formations, *Bonnetia roraimae* forests, shrubby savannas, and open wet savannas, in sandy soils, at 1300–2600 m altitude) ..... 4. *Maguireothamnus*
8. Corolla < 5 cm long, tube < 3.5 cm long ..... 9
9. Inflorescence axillary, 1–7-flowered (Endemic to Guayana Shield, at 300–1900 m altitude)..... 10
9. Inflorescence terminal, many-flowered ..... 11
10. Leaves opposite; inflorescence 1–7-flowered; corolla infundibuliform, white to cream-white (sometimes the tube reddish or greenish at base outside), lobes 7–15 × 4–5.5 mm; capsules septicidal, ovoid to ellipsoid, 7–17 × 5–7 mm, the valves secondarily splitting at apex (Guiana Shield: Venezuela, Guyana and northern Brazil, at 300–1430 m altitude)..... 1. *Chalepophyllum*
10. Leaves opposite or ternate; inflorescence 1–2-flowered or cymose, (2–)3–5-flowered; corolla hypocrateriform, green to yellowish-green, or tube red and lobes yellowish- or whitish-green, lobes 4.5–6 × 2.5–3 mm; capsules loculicidal, subturbinate to obovoid-subglobose, 4–5 × 3–4 mm, the valves not secondarily splitting at apex (Sierra de la Neblina Massif, Venezuelan and Brazilian sides, at 1300–1900 m altitude) ..... 5. *Neblinathamnus*
11. Fruit indehiscent, falling off as dispersal unit; flowers homostylous; corolla mouth with 5 thickened triangular projections at base of each corolla lobe, covered with erect brushy white hairs at base of corolla lobes; corolla lobes glabrous on adaxial side, opening before complete corolla elongation (Guayana Shield: Colombia, southern Venezuela, northern Brazil, N of the Amazon River, except for *S. cururuensis* and *S. maguirei*, found S or the Amazon River; white-sand savannas, mostly lowlands or moderate elevations) ..... 9. *Sipaneopsis*
11. Fruit capsular, or indehiscent in *Neobertiera*; flowers distylous or tristylous; corolla mouth without triangular projections; corolla lobes with or without a basal triangular area with glandular hairs on adaxial side, opening after corolla tube complete elongation ..... 12
12. Shrubs or small trees; placenta with a fleshy extension adnate along the entire length of the septum (i.e., not stalked), with the ovules irregularly peltate on the longitudinal placental extension (Amazonian Colombia (Guianía), Venezuela (Amazonas), and Brazil (Amazonas); white-sand savannas)..... 2. *Dendrosipanea*
12. Subshrubs (plant basally woody and distally herbaceous, or shrubs less than 50 cm tall), or shrubs; placenta stalked, with the stalk inserted at the middle or medio-basal portion of the septum and an oblong hemi-elliptic or hemi-elliptic extension, with the ovules inserted on the placental extension ..... 13
13. Fruit indehiscent, falling off as dispersal unit; plant erect; flowers distylous or tristylous; corolla lobes linear-oblong to narrowly lanceolate, or ovate and with a white-glandular triangular area at base in *N. montedouradensis* (Guyana, French Guiana, Brazil (Pará); forest undercanopy, usually near creeks)..... 6. *Neobertiera*

13. Fruit a loculicidal capsule, persistent; plant erect, trailing or decumbent; flowers distylous; corolla lobes round, broadly ovate, obovate, elliptic-ovate or lanceolate, commonly without a white-glandular area at base, or sometimes with a median linear white area microscopically glandular at base, forming a white star-like pattern (with the 5 lobes) in *S. wilson-brownei* (Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Guianas, Peru, Brazil, Bolivia and Paraguay; open savannas, forest undercanopy, and rocky outcrops).....8. *Sipanea*

### 1. CHALEPOPHYLLUM

*Chalepophyllum* Hook.f. in Benth. & Hook.f., Gen. Pl. 2: 50. 7–9 Apr 1873.

Hook.f. in Hooker's Ic. Pl. 12: 43–44, tab. 1148. Apr. 1873; K.Schum. in Martius et al., Fl. Brasil. 6(6): 245–246, tab. 111, fig. 4. 1889; Steyerl. in Mem. New York Bot. Gard. 10: 192–194, fig. 70A–F. 1964; Steyerl. in Lasser & Steyerl., Fl. Venezuela 9(1): 322–326, fig. 52. 1974; Delprete et al. in Steyerl. et al., Fl. Venez. Guayana 8: 541–542, fig. 437. 2004.

Type: *Chalepophyllum guyanense* Hook.f.

*Subshrubs* to *shrubs*; distal internodes, base of petioles and base of peduncles often covered by a resinous exudate produced by stipular colleters. *Stipules* free at base, broadly triangular to subtruncate, older stipules sometimes becoming bifid at apex, with the basal 2/3 covered by dense colleters inside. *Leaves* opposite, sessile to short-petiolate; blades ovate, obovate, oblong or spatulate; subcoriaceous; domatia in tuft of hairs, or absent. *Inflorescences* axillary, reduced-cymose, 1–7 flowered. *Flowers* heterostylous, 5-merous, fragrant. *Hypanthium* obconical or turbinate. *Calyx* tube extremely reduced, lobes subequal to unequal, large, oblong-triangular, ovate-lanceolate, oblong-lanceolate, lanceolate, elliptic to oblong-spatulate, with 3–5 minute colleters at each lobe sinus. *Calycophylls* absent. *Corolla* infundibuliform, white to cream-white, sometimes with the tube pale green outside; tube obconical, externally strigose, internally pubescent throughout or only at mouth, with a pubescent ring at orifice inside; lobes left-contorted, ovate, margin entire, round, obtuse, acute or short-acuminate at apex. *Pollen* (3)4-colporate; exine foveolate-reticulate, perforate. *Ovary* with a stalked placenta; stalk inserted at the middle of the septum, terminating with a narrow oblong-ellipsoid extension; ovules dorsoventrally peltate on the placental extension. *Short-styled flowers*: stamens

included, inserted at upper portion of corolla throat; filaments short; anthers narrowly oblong; style included, short, style branches oblong. *Long-styled flowers*: stamens included, inserted at medio-basal portion of corolla throat; filaments short; anthers narrowly oblong; style exerted well beyond corolla mouth, style branches oblong. *Fruits* capsular, dehiscent septically, thinly woody, the valves secondarily splitting at apex. *Seeds* many, vertical, 3–5-angular, irregularly elliptic or irregularly oblong to fusiform in outline, compressed, wings extremely reduced and concentric, or absent.

**Notes about publication dates:** Joseph Dalton Hooker (1873) published the genus *Chalepophyllum* in Bentham & Hooker's *Genera Plantarum*, vol. 2, page 50. In this work he only published the genus name, followed by the citation "*Hook. f. Ic. Pl. t. 1148*", and after the description he wrote that it has one species from Guyana, without citing the species name. The title page of volume 2 of *Genera Plantarum* states the publication date of 1873. Stafleu and Cowan (1976: 179) indicated that the part where page 50 is included was published on 7–9 April 1873.

Hooker published the name *Chalepophyllum guyanense* Hook.f. on page 43 and on plate 1148 of volume 2 of his *Icones plantarum*. The title page of this volume states the publication date as 1876. Below this binomial Hooker cited "*Chalepophyllum*, *Hook. f. in Benth. and Hook. f. Gen. Pl. ii. 50.*" Stafleu and Cowan (1979: 294–296) gave several publication dates of Hooker's *Icones plantarum* for volume 2 and plate 1148. On page 294, they gave the date of publication of plate 1148 as 1876 (as stated in the title page). Then on page 296, they gave the publication date of plate 1148 as April 1873. Above the dates of publication on page 296, they stated "...those [dates] of the parts of volumes 11–13 are cited here from manuscript annotations in the copies of the libraries at the Royal Botanical Gardens, Kew, and of the Botany Department of the British Museum (Natural History), London."

Therefore, both *Genera plantarum* and *Icones plantarum* must be cited for the name *Chalepophyllum* as places of publication, as it is impossible to know which of these publications was published first.

**Distribution and ecology:** Guayana Shield in Venezuela, Guyana and northern Brazil; scrub formations in sandy savannas, wet savannas with *Stegolepis* and Rapateaceae, white-sand savannas, open dwarf *Bonnetia* forests, and sandy valleys, at 300–1430 m altitude. Only one species is here recognized.



1-1. *Chalepophyllum guyanense* Hook.f., Ic. Pl. 12: 43, tab. 1148. 1873. (Figures 4A–B, 6–9).

Type: GUYANA. Without locality, s.d., R.H. Schomburgk s.n. (holotype K [without barcode; see details below]; photo-K at NY).

*Chalepophyllum guyanense* var. *guyanense* in Mem. New York Bot. Gard. 10: 192. 1964

(=) *Chalepophyllum guyanense* var. *cuneatum* Steyermark, Mem. New York Bot. Gard. 10: 193. 1964.

Type: VENEZUELA. Bolívar: Ilu-Tepui, Gran Sabana, near Kavanayén, 1300 m, 30 Mar. 1952 (fl, fr), B. Maguire 33700 (holotype NY [barcode 00131039]; isotypes G [barcode G00389737], GH [barcode GH00095916], K [without barcode], P [barcode P02273576], US [barcode US00137690]).

(=) *Chalepophyllum longilobum* Steyermark, Mem. New York Bot. Gard. 10: 193. 1964.

Type: GUYANA. Pakaraima Mountains, Mount Ayan-ganna, occasional at forest edges between Ayanganna and Chinowieng, 1000–1200 m, 7–8 Feb. 1955, B. Maguire, W.M.C. Bagshaw & C. Maguire 40637 (holotype NY [barcode 00131041]; isotypes US [barcode 00137691], VEN [Acc. No. 49511]).

*Subshrubs* to *shrubs* 0.4–4 m tall; branches puberulent. *Stipules* broadly triangular to subtruncate, 2–5(–6) × 2–3 mm, shallowly obtuse when young or sometimes becoming bifid at apex when older, glabrous or puberulent outside, glabrous at distal portion and with the basal 2/3 covered by dense colleters inside. *Leaves* with petioles 3–7 mm long, 1–1.5 mm thick, glabrous; blades round, broadly elliptic, elliptic to obovate, 2–10 × 1.3–5.5 cm, obtuse to acute at base, truncate, obtuse or round at apex, coriaceous, dark green and shiny above, pale green below, drying brown to olive-green; glabrous above, densely puberulent below, margin sometimes minutely revolute, veins densely puberulent; secondary veins 7–13 each side, tertiary venation densely reticulate, impressed above and evident below; tuft-domatia always present. *Inflorescences* subsessile to long pedunculate, reduced-cymose, 1–7-flowered; peduncle 0.2–5.7 cm long; distal

bracts orbicular to broadly triangular, 1–5 × 1–3.5 mm; bracteoles scaliform or absent. *Flowers* with pedicels 1–3 mm long, glabrous to minutely puberulent. *Hypanthium* obconical or turbinate, 1–1.5 × 1–1.3 mm, glabrous or minutely puberulent. *Calyx* tube extremely reduced or absent; lobes subequal to unequal, oblong-triangular, ovate-lanceolate, oblong-lanceolate, lanceolate, elliptic to oblong-spathulate, 2–17 × 1–3.5 mm, glabrous to sparsely puberulent, with 3–5, oblong to linear, 0.25–0.5 mm long, colleters at each lobe sinus. *Corolla* infundibuliform, white to cream-white sometimes with tube reddish or greenish at base, 17–31 mm long; tube infundibuliform, 10–18 mm long, 1–1.4 mm wide at base, 3–4.5 mm wide at mouth, glabrous outside, densely yellow-pubescent at mouth inside; lobes ovate, narrowly ovate to oblong-elliptic, 7–15 × 4–5.5 mm, round, obtuse, acute or short-acuminate at apex, glabrous outside, basally yellow-pubescent inside. *Short-styled flowers* (Delprete & Benjamin 12860D; tube 18 mm long, lobes 11 mm long): stamens included, inserted at 3 mm below corolla mouth; filaments 0.7 mm long; anthers narrowly oblong, 3 × 0.2–0.3 mm, acute at both ends; style included, about half the length of the corolla tube, 5.5–6.5 mm long, glabrous, style branches oblong, 1 mm long. *Long-styled flowers* (Steyermark 59670; tube 12 mm long, lobes 8 mm long): stamens included, inserted at 5–7 mm from base of corolla; filaments 0.5–0.7 mm long; anthers narrowly oblong, 2.5–3 × 0.2–0.3 mm, round to acute at base, acuminate at apex; style exerted well beyond corolla mouth, 11–18 mm long, style branches oblong, 1.2 mm long. *Capsules* ovoid to ellipsoid, 7–17 × 5–7 mm, obtuse to acute at base, rounded at apex, dark brown, appressed-puberulent, to sparsely pubescent. *Seeds* 2.5–4 × 2–3 mm.

**Notes:** Joseph Dalton Hooker (1876: 43–44, pl. 1148), along with the description of *Chalepophyllum guyanense*, cited “Hab. British Guiana, Schomburgk [Sic!]” without indicating the herbarium of deposit. A specimen at K has the handwritten label “12 last smallest, Remijia? British Guiana, Schomburgk.” On the sheet of the specimen are drawn beautiful pencil sketches of flowers in anthesis, dissected corolla, young ovary and seeds that are almost identical to those illustrated in Plate 1148. This specimen is the holotype and, at the time I studied it, it did not have a barcode.

Steyermark (1964) distinguished *Chalepophyllum longilobum* Steyermark from *C. guyanense* by the corolla

**Figure 6.** *Chalepophyllum guyanense*. A. Branch with inflorescences. B. Inflorescences with flowers in anthesis and flower buds. C–D. Stipule variation on the same branch. C. Entire stipule. D. Bifid stipule. E. Dissected long-styled flower. F. Dissected short-styled flower. G. Capsule. A–D: drawn from Delprete & Araujo 7429 (CAY); E: drawn from Steyermark 59670 (F); F: drawn from Delprete & Benjamin 12860D (CAY); G: drawn from Delprete & Araujo 7428 (CAY). Illustration by Piero Delprete.

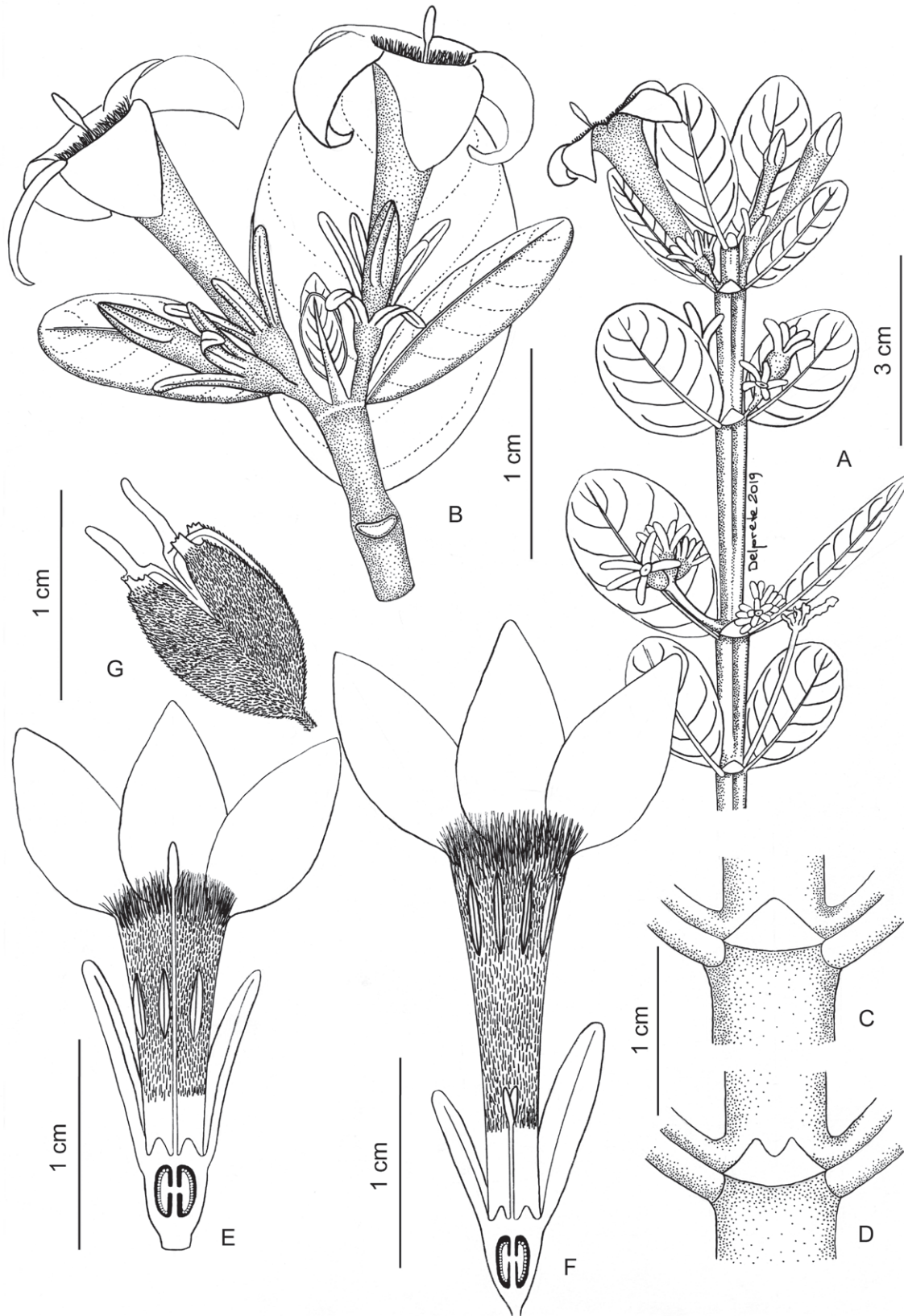


Figure 6.

lobes 14–15 mm long (vs. 6–12 in *C. guyanense*) and the seeds 2.8–3 mm long (vs. 3–4 mm long). In the same publication, he also published *Chalepophyllum guyanense* var. *cuneatum* Steyermark., which he differentiated from the typical variety by having leaf blades obovate and acute at base (vs. oblong-obovate, rounded or narrowed at base). Recent collections demonstrated that the characters used by Steyermark to distinguish these three taxa are morphologically and geographically overlapping (Delprete et al. 2004), and they are here treated as synonymous. Also, Steyermark (1964, 1974) and other authors wrote the specific epithet as “*guyanense*”, but it was originally published by J.D. Hooker (1873) as *guyanense* and must be maintained as such.

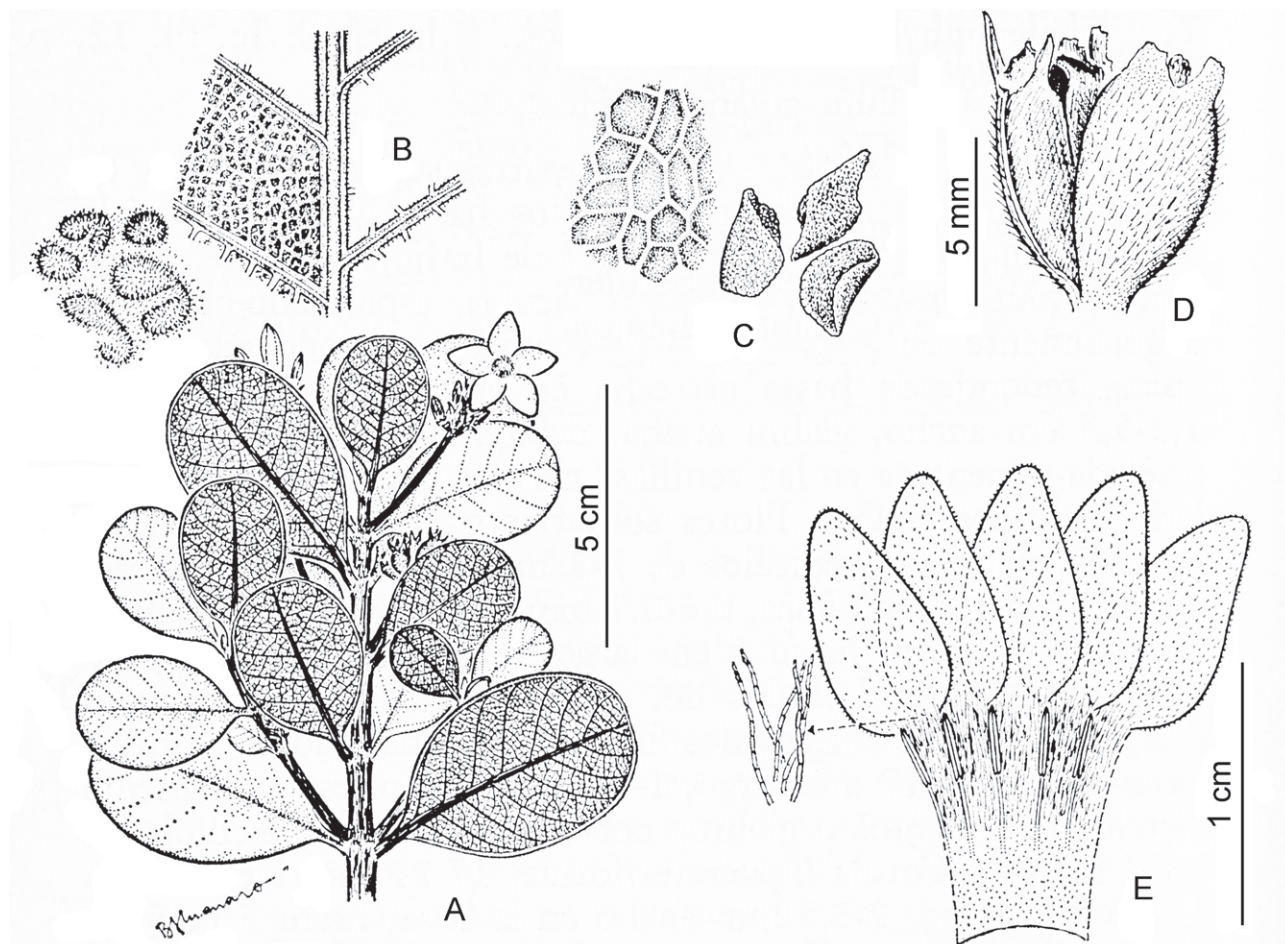
**Distribution and ecology:** Endemic to the Guiana Shield, in Venezuela, Guyana and northern Brazil (Fig-

ure 9); growing in scrub formations in sandy savannas with Rapateaceae Melastomataceae, Piperaceae and *Drosera*, wet savannas with *Stegolepis* and *Drosera*, white-sand savannas, open dwarf *Bonnetia* forests, and sandy valleys, at 300–1430 m altitude.

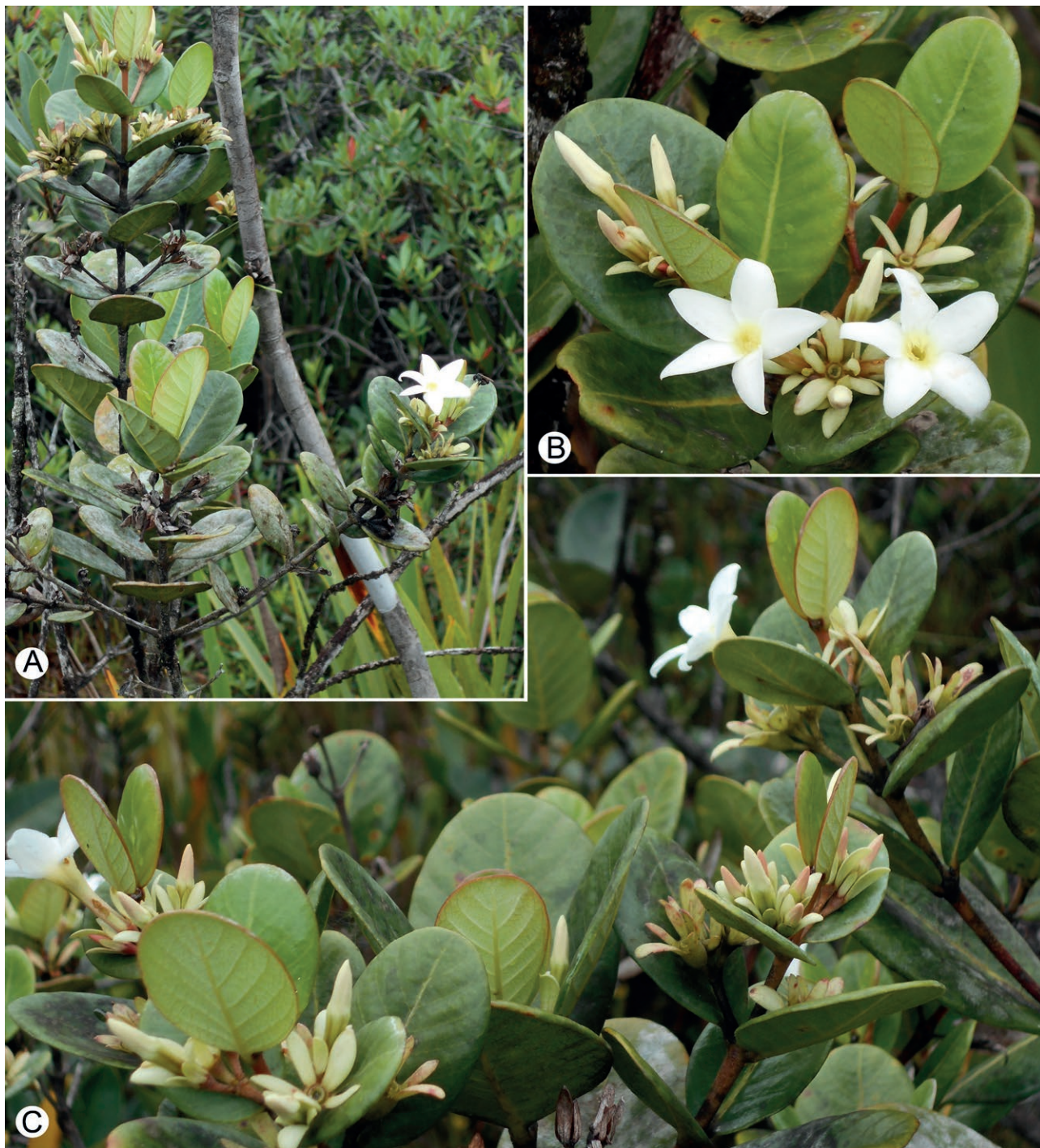
**Phenology:** Flowering and fruiting throughout the whole year.

**Suggested conservation status: Least Concern (LC).**

This species is known from many localities in Venezuela, Guyana and northern Brazil. The size of the populations in all the localities is unknown. Personal observations in its natural environment were made in Venezuela in 2000, and in Guyana in 2016; the populations in these two localities were healthy, with more than 50 individuals, and with no immediate threats. In addition, this species



**Figure 7.** *Chalepophyllum guyanense*. A. Branch with inflorescences and infructescences. B. Detail of leaf blade abaxial side, showing reticulate-foveolate surface, and high magnification detail of depressed areoles. C. Seeds and detail of the testa. D. Dehisced capsule. E. Dissected corolla of short-styled flower, and detail of multicellular present at corolla mouth. Illustration by Bruno Manara (Reproduced with permission from Flora de Venezuela vol. 9(1), fig. 52. 1974).



**Figure 8.** *Chalepophyllum guyanense*. **A.** Habit. **B.** Detail of inflorescence with flower buds and flowers in anthesis. **C.** Detail of distal portion of branches with flower buds and flowers in anthesis (note leaf revolute margin). Photos taken by Piero Delprete on June 2016, in the Kaieteur National Park, Guyana (plants not collected).

grows in several protected areas, and in at least in three national parks: the Canaima National Park, Venezuela, the Kaieteur National Park, in Guyana, and the Monte

Roraima National Park, in northernmost Brazil. Therefore, taking into account the numerous sites of occurrence, including many remote and preserved areas, and

its healthy populations, this species is here treated as Least Concern (LC) following IUCN criteria (IUCN 2012, 2019).

**Specimens examined: VENEZUELA: Bolívar:** Gran Sabana, ca. km 167, S of El Dorado along hwy to Santa Elena, 24 km S of La Ciudadella, 1300 m, 4 Dec. 1973 (fl), *G. Davidse et al.* 4825 (MO, NY); 2 km N of San Rafael de Kamoioren, km 174, area seasonally inundated with white-sand soil, dominated by Melastomataceae, Rapateaceae, Piperaceae, *Drosera*, 5°39'N, 61°24'W, 1300 m, 27 Dec. 2000, *P.G. Delprete & A.C. Araujo* 7424 (imm fr) (CAY, NY, UFG, VEN), 7426 (imm fr) (CAY, L, MO, US), 7428 (fl, fr) (CAY, GB, NY, UFG, VEN), 7429 (fl, imm fr) (BR, F, NY, P, UFG, VEN); Piar, extremo N de la Gran Sabana, Carretera El Dorado-Santa Elena de Uirén, ca. 100 km S of El Dorado, 5°40'N, 61°30'W, 1300 m, 3 Apr. 1985 (fl), *B.K. Holst et al.* 2158 (MO); Distr. Roscio, Sabana ca. 10 km N del Kamá-meru, mano derecho de la Carretera Sta. Elena de Uirén-Luepa, 5°29'N, 61°18'W, 1180 m, 4 Mar. 1983 (fr), *O. Huber et al.* 7330 (P, US); Dtto. Piar, sabana arbustiva ubicada en el paso entre Ptari-tepui y Soropán-tepui, al N de Kavanayén, 5°42'N, 61°45'W, 1370 m, 28 Jun. 1983 (fl, fr), *O. Huber & C. Alarcon* 7713 (NY [2 sheets], US, VEN); Dtto. Piar, sabanitas ubicadas sobre altiplanicie al NE del Aprada-tepui, ca. 40 km al ENE de Urimán, 5°30'N, 62°20'W, 930 m, 12 Dec. 1984 (fl, fr), *O. Huber et al.* 9904 (NY, US, VEN); *ibid.*, 5°40'N, 62°50'W, 900 m, 12 Dec. 1984 (fl, fr), *O. Huber et al.* 9918 (NY, VEN); Dtto. Roscio, sabanas y arbustales en la cuenca superior meridional del Río Kamurán, ca. 20–25 km NW del Ilu-tepui, 5°37'N, 61°13'W, 1000 m, 18 Jun. 1985 (fl, fr), *O. Huber & C. Alarcon* 10616 (NY, VEN); Dtto. Sifontes, sabana arbustiva sobre planicie ubicada a la ribera izquierda (Sur) del Río Yuruaní medio, ca. 5 km al franco Sur del Wadakaoué-tepui, 5°17'N, 60°53'W, 1050 m, 5 Sep. 1986 (fl, imm fr), *O. Huber* 11765 (NY, US, VEN); Mun. Gran Sabana, [Canaima National Park], Sierra de Lema, 70 km NNE de Kavanayén, 1650 m, 30 Jan. 1988, *O. Huber* 12497 (US, VEN); Mun. Gran Sabana [Canaima National Park], herbazal y arbustal tepuyano en el sector occidental de la Sierra de Leme, a lo largo de un afluente oriental del Río Carrao alto, ca. 70 km al NNE de Kavanayén, 5°58'N, 61°37'W, 1250 m, 31 Jan. 1988 (fr), *O. Huber* 12518 (INPA, U, US); ca. 1 km S of Military Base, just N of turnoff to Kavanayen by VEN-10, 24 Jul. 1983 (fl), *R. Kral & Á.C. González* 70383 (MO); Gran Sabana, ca. 1 km E of Cavanayen, 26 Jul. 1983 (fl, fr), *R. Kral & A.C. Gonzalez* 70500 (NY); Guayana venezolana, Kavanayen, 28 May 1945 (fl), *T. Lasser* 1824 (NY, VEN); Gran Sabana, km 137 along El Dorado-Santa Elena rd, 1420 m, open savanna, 16 Nov. 1978 (fl, fr), *J.L. Luteyn et al.* 6278 (NY); Ilu-Tepui, Gran Sabana, between Urupata and Enemasic, 1000 m, 8 Feb. 1952 (fl, young fr), *B. Maguire*

33244 (NY, US, VEN); Ilu-Tepui, Gran Sabana [Canaima National Park], Mesa Grande, savanna thickets and bush islands, area dominated by *Stegolepis* and *Bonnetia*, 1600 m, 12 Mar. 1952 (fl), *B. Maguire* 33357 (NY, P, VEN); Ptari-tepui, SW slop forest and savanna, 1500 m, 17 Dec. 1952 (fl), *B. Maguire & J.J. Wurdack* 33922 (IAN, NY, US, VEN); Ptari-tepui, slopes and rocks in vicinity of “Cave Rock,” below S face of mountain, savanna S of Ptari-tepui, 1.5 hours from “Cave Rock” by foot, soil moist with scattered shrubs, 1600–2000 m, 14–19 Aug. 1970 (fl), *H.E. Moore Jr. et al.* 9731 (F, NY); Gran Sabana, treeless wet savanna, ca. 16 km E of the mission at Kavanayen, 1340 m, 19 Dec. 1979 (fl, fr), *J. Pruski & J.A. Steyermark* 1417 (NY); Gran Sabana, Parque Nacional Canaima, Carretera Fuerte, Luepa-Santa Helena, km 168, 19 Mar. 1993 (fl), *N. Ramírez* 3552 (MO), 3553 (MO); Gran Sabana, Parque Nacional Canaima, Carretera Fuerte, Luepa-Santa Helena, 20 Mar. 1993 (fl, fr) *N. Ramírez* 3742 (MO); Gran Sabana, Parque Nacional Canaima, Carretera Fuerte, Luepa-Kavanayen, desvío hacia Rinoriwo, 23 Mar. 1993 (fl, fr) *N. Ramírez* 4077 (MO); Gran Sabana, between Mission of Santa Teresita de Kavanayén NW to Río Karuai, on large mesa, 1220 m, 26 Oct. 1944 (fl), *J.A. Steyermark* 59359 (F, NY, US, VEN); Ptari-tepui, dry sandy and rocky sandstone exposure on level ground adjacent to swamp on plateau-portion of SE facing slopes, 1600 m, 1 Nov. 1944 (fl), *J.A. Steyermark* 59670 (F, NY, US, VEN); vicinity of Misia Kathy Camp, on mesa between Ptari-tepui and Sororopán-tepui, 1615 m, 15–17 Nov. 1944 (fl, fr), *J.A. Steyermark* 60233 (F, NY, US); Uei-tepui, between SE slope and summit, between Luepa and Cerro Venamo, 1100–1300 m, 19 Apr. 1960 (fl), *J.A. Steyermark & S. Nilsson* 60348 (F, NY, US, VEN); near rd Campamento 150, at 150 km in valley of savanna of Río Uarama below Uarama-tepui, NE of Luepa, 1220 m, 24–25 Apr. 1960 (fl), *J.A. Steyermark & S. Nilsson* 60644 (NY, VEN); Gran Sabana [Canaima National Park], altiplanicie de suelo arenoso, formación Roraima, drenaje de las cabeceras del Río Aponguaou, sabana pantanosa entre Río Arautá-parú (km 148–150 S de El Dorado), 1350–1400 m, 20 Dec. 1970 (fl), *J.A. Steyermark et al.* 104111 (NY, P, VEN).

**GUYANA:** Upper Mazaruni River Region, Karowtipu Mountain, E end of mountain, 1000 m, 21 Apr. 1987 (fl), *B.M. Boom & D. Gopaul* 7604 (MO, NY); Cuyuni-Mazaruni Region, Utshi River, trail to Santa Elena (Venezuela), 5°39'N, 61°9'W, 980 m, 31 Jan. 1996 (fl), *H.D. Clarke* 918 (BRB, MO, NY, U); Paruima, 20 km W, wet savanna on Waukauyengtipu, 5°49'58"N, 61°14'5"W, 1430 m, 17 Jul. 1997 (fl), *H.D. Clarke et al.* 5809 (BRB, MO, NY, U, US); Potaro-Siparuni Region, Mount Ayan-ganna, camp on summit plateau, 2040 m, 23 Jun. 2001 (fl), *H.D. Clarke et al.* 9490 (US); Kaieteur Plateau, near

Kaieteur Falls, ca. 426 m, savanna and low savanna-forest, boggy area in savanna margin, 25 Feb. 1962 (fl, fr), *R.S. Cowan & T.R. Soderstrom* 1945 (NY, US, VEN); Potaro-Siparuni Region, Upper Potaro River, Chenapou Village, Aklapanan Savanna, motorbike trail from Chenapou Creek mouth towards Paramakatoi Village, eight hills from creek mouth (ca. 10 km), then small trail to the left, crossing a small waterfall, savanna frequently burned with *Pteridium arachnoides* (fern) and *Brocchinia micrantha* (Bromeliaceae), bordered by trees 2–3 m tall, on white-sand soil, 4°55'28"N, 59°34'33"W, 510 m, 16 Jun. 2016 (fl), *P.G. Delprete & P. Benjamin* 12860D (BRG, CAY, GB, NY); Kaieteur National Park, between airstrip and escarpment, ENE of airstrip, 5°11'N, 59°29'W, 450 m, 29 Mar. 1989 (fl), *L.J. Gillespie & H. Persaud* 916 (BRB, MO, NY, U, US); Kaieteur National Park, savanna along airstrip, 5°10'30"N, 59°29'W, 420–450 m, 7 May

1989 (fl), *L.J. Gillespie et al.* 1349 (MO, NY, US); Potaro-Siparuni Region, Kaieteur Falls National Park, 5°12'N, 59°29'W, 500 m, 7 May 1988 (fl), *W. Hahn et al.* 4092 (BRB, CAY, MO, NY, P, U, US); Potaro-Siparuni Region, Kaieteur Falls National Park, 5°10'N, 59°29'W, 500 m, 12 Apr. 1988 (fr), *W. Hahn et al.* 4461 (BRB, MO, P, U, US); Potaro-Siparuni Region, Kaieteur plateau, 3 km WNW from Falls along Kaieteur-Kuribrong trail, seepage bog and xeromorphic scrub forest mosaic on pink sand with frequent sandstone outcrops, 5°12'N, 59°30'W, 540 m, 22 Jul. 1993 (fl, fr), *T.W. Henkel & R. Williams* 2357 (MO, NY, U, US); Cuyuni-Mazaruni Region, Pakaraima Mts., base camp 11.4 km NE Imbaimadai Partang R., 1 km E, 5°48'N, 60°14'W, 675–700 m, 25 May 1992 (fl). *B. Hoffman et al.* 1849 (CAY, F, MO, NY, U, US); Pakaraima Mountains, between Koatse River and Chenoweing Village, 5°27'N, 60°04'W, 700–800 m, 12 Nov. 1992 (fl), *B.*

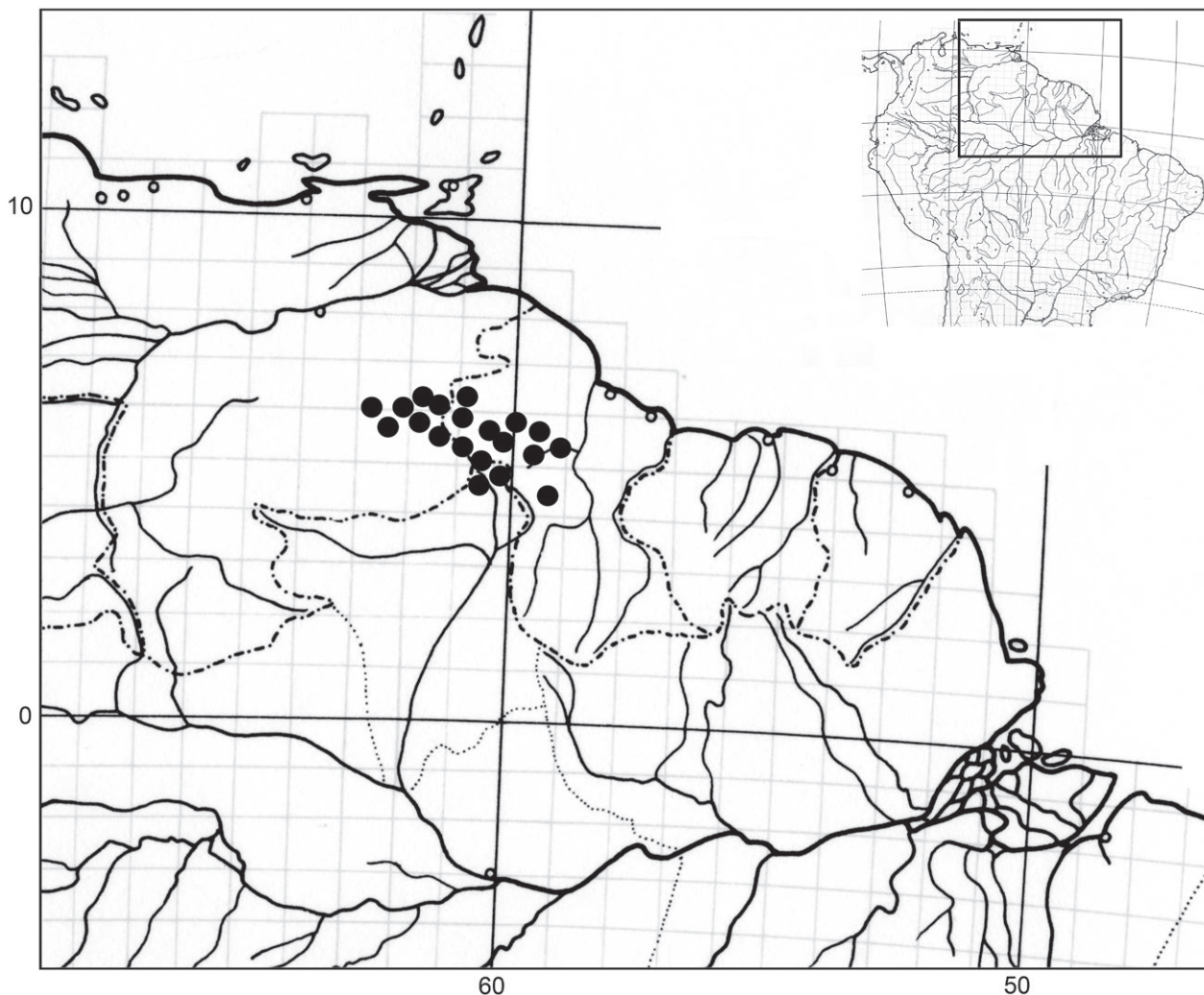


Figure 9. Distribution of *Chalepophyllum guyanense*.

*Hoffman & T. Henkel* 3356 (BRB, MO, US); Potaro-Siparuni Region, Kaieteur Falls National Park, around airstrip, 5°10'N, 59°29'W, 300 m, 16 Jul. 1993 (fl), *C.L. Kellogg et al.* 972 (BRB, MO, U, US); Potaro-Siparuni Region, Kaieteur Falls, vicinity of Kaieteur airstrip, 5°11'N, 59°29'W, 450 m, 8 Oct. 1987 (fl, fr), *L.P. Kvist et al.* 101 (MO, NY, U, US); Pakaraima Mountains, Mount Aymatoi (sandstone), 5°55'N, 61°0'W, 1150 m, 15 Oct. 1981 (fl), *P.J.M. Maas et al.* 5716 (MO, NY, P, U, US); Kaieteur Plateau, 3 May 1944 (fl, fr), *B. Maguire & D.B. Fanshawe* 23169 (F, MO, NY, P, RB, U, US); Upper Mazaruni River, occasional in savanna, Samwarakna-tipu (Holitipu), 1100 m, 10 Nov. 1951 (fl, fr), *B. Maguire & D.B. Fanshawe* 32559 (NY, RB); Cuyuni-Mazaruni Region, Mt. Holitipu, on eroded sandstone and white sand, forested creek below peak, 5°56'N, 61°05'W, 1150–1240 m, 1 Jun. 1990 (fl, fr), *T. McDowell & D. Gopaul* 3023 (F, MO, NY, P, US); E of Arabaru Creek, Kobadai Savanna, 5°27'N, 60°39'W, 500 m, 16 Jul. 1991 (fl), *T. McDowell* 4597 (BRB, MO, U, US); Potaro-Siparuni Region, Kaieteur National Park, Upper Mure Mure Basin, savanna on trail to Menzies landing, 5°15'27"N, 59°30'40"W, 480 m, 28 Mar. 2014 (fl, fr), *F.A. Michelangeli* 2565 (NY); Pakaraima Mountains, Ireng River at Kurutuik Falls, 5°05'N, 59°59'W, 670 m, 23 Oct. 1994 (fl), *P. Mutchnick et al.* 188 (BRB, MO, US); Cuyuni-Mazaruni Region, vicinity of Chinoweng Village, savanna and mixed forest, also *Bonnetia-Moronobea* associations along creeks, 5°32'N, 60°7'W, 650 m, 21 Feb. 1987 (fl, fr), *J.J. Pipoly et al.* 10478 (CAY, NY, US); Ayanganna Plateau, ca. 3 km N of Koatse River, due S of mountain central depression, 5°38'N, 60°4'W, 650–670 m, 27 Feb. 1987 (young fr), *J.J. Pipoly & G. Samuels* 10739 (F, MO, NY, U, US); Ayanganna Plateau, N of mountain center, 5°28'N, 60°4'W, 650–700 m, 1 Mar. 1987 (young fr), *J.J. Pipoly & G. Gharbarran* 10846 (BRB, MO, NY, U, US); Kako River vicinity, above Kako Village, near Camp 3, ca. 22 km air distance E of Tulameng Summit, 5°33'27"N, 60°59'35"W, 520 m, 26 Jul. 2010 (fl, young fr), *K.M. Redden et al.* 7089 (F, MO, US); Kaieteur Savannah, in thickets among *Brocchinia*, by Indian trail, ca. 400 m, 4 Sep. 1934 (fl, fr), *N.Y. Sandwith* 1346 (K, NY, U); Kaieteur Savanna, sandy and gravelly place, 370 m ["1100 ft"], 30 Aug. 1933 (fl, fr), *G.T. Tutin* 676 (BM, RB, U, US); Potaro-Siparuni Region, Boy Scout Lookout & Johnsons Lookout, 5°10'46"N, 59°29'1"W, 466 m, 30 Aug. 2006 (fr), *K.J. Wurdack et al.* 4195 (P, U); Cuyuni-Mazaruni Region, Kato River, 490 m, 19 May 2009 (fl, fr), *K.J. Wurdack et al.* 5073 (US); Cuyuni-Mazaruni Region, below 1st escarpment (of four) of Kamakusa Mt., Partang Airstrip (presently non-operational) and vicinity, 734 m, 19 May 2012 (fl, fr), *K.J. Wurdack et al.* 5672 (US).

**BRAZIL. Roraima:** Uiramutã, Parque Nacional do Monte Roraima, Monte Caburaí, vegetação herbácea-arbustiva com afloramento e campos de Rapateaceae, 5°10'22"N, 60°13'57"W, 1322 m, 6 Nov. 2014 (fl, fr), *R. Forzza et al.* 8128 (INPA, RB); Uiramutã, Parque Nacional do Monte Roraima, Monte Caburaí, campos arbustivos com rapateaceae, 5°10'22"N, 60°13'57"W, 1320 m, 6 Nov. 2014 (fl, fr), *G. Martinelli et al.* 18392 (MG, NY, RB); Uiramutã, Parque Nacional do Monte Roraima, Monte Caburaí, campos de Rapateaceae intercalados com floresta ambrófila, 5°10'22"N, 60°13'57"W, 1322 m, 6 Nov. 2014 (fl, fr), *M. Nadruz et al.* 2861 (RB); Uiramutã, Parque Nacional do Monte Roraima, Monte Caburaí, imediações do marco de fronteira B-BG/11A, 5°10'22"N, 60°13'57"W, 1400 m, 6 Sep. 1998 (fl, fr), *L.A. Pessoni* 335 (UFRR).

#### Excluded Species

*Chalepophyllum coriaceum* Gleason in Gleason & Killip, *Brittonia* 3: 192. 1939.

Type: VENEZUELA. Bolívar: Mount Auyan-Tepui, 2200 m, Dec. 1937 (fl, fr), *G.H.H. Tate* 1179 (holotype NY [barcode 00131038]; isotype VEN [not found]).

(=) *Maguireothamnus speciosus* (N.E.Br.) Steyererm. (see below).

*Chalepophyllum latifolium* Standl., *Publ. Field Columbian Mus., Bot. Ser.* 7: 379. 1931.

Type: VENEZUELA. Amazonas: Summit of Mount Duida, s.d. (fl, fr), 1320 m, *G.H.H. Tate* 730 (holotype NY [barcode 00131040]; isotype F [Acc. No. 603528]).

(=) *Maguireothamnus tatei* (Standl.) Steyererm. (see below).

*Chalepophyllum pungens* Standl. & Steyererm., *Fieldiana, Bot.* 28: 568. 1953.

Type: VENEZUELA. Amazonas: On open granitic rocks at Puerto Ayacucho, 100 m, 18 May 1940 (fr), *Ll. Williams* 12970 (holotype F [Acc. No. 1078932]; isotypes F [Acc. No. 1609002], US [barcode 00137692], VEN [Acc. No. 15136]).

(=) *Acanthella sprucei* Hook.f. in Bentham & J.D.Hooker (1867: 749; Melastomataceae).

Standley and Steyermark (1953: 568, 570) described *Chalepophyllum pungens* Standl. & Steyermark., using specimens with open capsules and seeds, and cited as the type *Llewelys Williams 12970* at F. There are two sheets of *Williams 12970* at F, which are kept together in the same folder. Sheet with Accession No. 1078932 is annotated in Standley's handwriting "Type. *Chalepophyllum pungens* Standl. & Steyermark." and that with Accession No. 1609002 is annotated in Standley's handwriting "Iso-Type. *Chalepophyllum pungens* Standl. & Steyermark."

*Chalepophyllum speciosum* N.E.Br., Trans. Linn. Soc. London II, 6: 33. 1901.

Type: VENEZUELA. Bolívar: F.V. McConnell & J.J. Quelch 653 (first-step lectotype, designated by Steyermark (1964: 223), **second-step lectotype** K [without barcode, with label "New York Botanical Garden Neg. No. N.S. 3240 (1953)"], **here designated**; isolecotype BM [barcode BM000614299].

(=) *Maguireothamnus speciosus* (N.E.Br.) Steyermark. (see below).

Brown (1901: 33) described *Chalepophyllum speciosum* and cited three syntypes "McConnell & Quelch 100, 305, 653." Steyermark (1964: 223) among the specimens studied for this species cited "McConnell & Quelch 653 (photo of holotype of *Chalepophyllum speciosum*, from K at NY)." Although Steyermark cited this collection as holotype, according to Art. 7.11 and 9.10 of the *Code* (Turland et al. 2018) is a correctable error, and it is here treated as an inadvertent first-step lectotypification of *McConnell & Quelch 653* at K because there are two specimens of *McConnell & Quelch 653* at K. At the time they were studied, these specimens did not have barcodes. The specimen with the label "New York Botanical Garden Neg. No. N.S. 3240 [1953]," which has eight branchlets with flowers is here designated the second-step lectotype of this taxon. The other specimen with three branchlets with flowers, and without the NYBG label, is an isolecotype.

*Chalepophyllum tatei* Standl., Publ. Field Columbian Mus., Bot. Ser. 7: 380. 1931.

Type: VENEZUELA. Amazonas: Mount Duida, summit of Peak N. 7, 2130 m, Aug. 1928–Apr. 1929 (fl, fr), G.H.H. Tate 623 (holotype NY [barcode 00131042]; isotype F [Acc. No. 603541]).

(=) *Maguireothamnus tatei* (Standl.) Steyermark. (see below).

## 2. DENDROSIPANEA

*Dendrosipanea* Ducke, Arch. Inst. Biol. Veg. 2(1): 69. 1935 Emend. Steyermark. in Mem. New York Bot. Gard. 10: 195–199, fig. 71. 1964; Steyermark. in Lasser & Steyermark, Fl. Venezuela 9(1): 326–330, fig. 53. 1974; Delprete & Steyermark. in Steyermark et al., Fl. Venez. Guayana 8: 571, fig. 454. 2004; Delprete, Phytotaxa 382(1): 125–135. 2018.

Type: *Dendrosipanea spigelioides* Ducke

*Shrubs* or *treelets*. *Stipules* free or basally adnate to petioles, deltoid, acuminate or bifid, with basal 2/3 covered by dense colleters intermixed with hairs inside. *Leaves* opposite, subsessile to short-petiolate; blades oblong, spatulate or oblanceolate, subcoriaceous; domatia absent. *Inflorescences* terminal or terminal on distal axillary branches, cymose, sometimes frondose, few- to many-flowered. *Flowers* distylous, 5-merous. *Hypanthium* obconical, turbinate to narrowly obovoid. *Calyx* funnel-shaped, tube extremely reduced or absent with lobes free at base, persistent; lobes subequal to unequal, deltoid, narrowly triangular, oblong, narrowly oblong, lanceolate, or spatulate, with 1–4 minute colleters each lobe sinus. *Calyxophylls* absent. *Corolla* hypocrateriform, actinomorphic, white to cream-white, sometimes with tube green; tube narrowly infundibuliform, glabrous or sparsely appressed-strigulose or hirtellous outside, basal portion glabrous and medio-distal portion villous inside, with a dense ring of yellow hairs at mouth inside; lobes left-contorted, sometimes asymmetrical, ovate, narrowly ovate, oblong to ovate-oblong, margin entire, obtuse to acute at apex. *Pollen* 4-colporate; exine foveolate or foveolate-reticulate, perforate. *Short-styled flowers*: stamens included or partially exerted, inserted at distal portion of corolla throat; filaments short; anthers linear; style included, much shorter than corolla tube, style branches oblong. *Long-styled flowers*: stamens included, inserted at basal portion of corolla throat; filaments short; anthers linear; style barely exerted (only branch tips beyond corolla mouth), style branches oblong. *Ovary* with a fleshy placental extension adnate along the entire length of the septum; ovules irregularly peltate on the longitudinal placental extension. *Fruit* capsular, dehiscent septically, thinly woody. *Seeds* antrorsely peltate along the central placenta, minute, 3–5-angular or irregularly-shaped; testa reticulate.

**Taxonomic observations:** Ducke (1935) published the new genus *Dendrosipanea* Ducke, positioned it in the Rondeletieae, and described it as having loculicidal capsules. Steyermark (1964: 195–196) corrected Ducke's error, as its capsules are septicidal. *Dendrosipanea* is most similar to



*Sipanea*, in having terminal multiflorous inflorescences, distylous flowers (although a few species of *Sipanea* remain to be confirmed to be distylous), corolla lobes contorted to the left, and capsular fruits. *Dendrosipanea* differs from *Sipanea* by being a shrub or treelet with septicial capsules, while species of *Sipanea* are prostrate, decumbent or erect herbs or subshrubs (in a few species the stem may be woody at base) with loculicidal capsules. In the molecular phylogenetic analysis of Delprete and Cortés B. (2004) *Dendrosipanea* was retrieved at a basal position on the tree, suggesting that the woody habit is ancestral within the tribe, while *Sipanea* was found in a distant clade.

**Geographic distribution and ecology:** A genus of three species, distributed in Amazonian Colombia, Venezuela and Brazil, growing on white-sand savannas, sometimes seasonally inundated.

#### Key to *Dendrosipanea* species

1. Leaf blades mostly round or broadly obtuse (rarely acute) at apex, primary and secondary veins impressed above and prominent below; inflorescence shortly branched, 3–7 cm long, including peduncle and flowers (corollas 17–24 mm long; tube 9–14 mm long, 2–2.2 mm wide at base, 3–4 mm wide at mouth); lobes ovate, obtuse at apex... 2. *D. revoluta*
  1. Leaf blades obtuse to acute or acuminate at apex, primary and secondary veins not impressed above and slightly prominent below; inflorescences long-branched, 6–16 cm long, including peduncle and flowers; lobes ovate to narrowly ovate or oblong to ovate-oblong, acute or obtuse to acute at apex ..... 2
  2. Corollas 19–22.5 mm long; tubes 11–14 mm long, 1.6–1.9 mm wide at base, 2–2.8 mm wide at mouth; lobes ovate to narrowly ovate, 7.5–8.5 × 4.5–4.8 mm, acute at apex ..... 1. *D. prancei*
  2. Corollas 27–30 mm long; tubes 16–20 mm long, 2–2.5 mm wide at base, 3.5–4.5 mm wide at mouth; lobes oblong to ovate-oblong, 12–16 × 5–7.5 mm, obtuse to acute at apex .. ..... 3. *D. spigelioides*
- 2-1. *Dendrosipanea prancei* Delprete, Phytotaxa 382(1): 127, fig. 1. 2018. (Figures 4C–D, 10–11).

Type: BRAZIL. Amazonas: Basin of Rio Negro, Rio Uneixi [ca. 0°32'S, 65°3'W, ca. 30 m alt.], 5 km above mouth, periodically flooded savanna on

sand, 8 Nov. 1971 (fl), G.T. Prance, P.J.M. Maas, D.B. Woolcott, O.P. Monteiro & J.F. Ramos 16199 (holotype INPA [Acc. No. 34418]; isotypes F [Acc. No. 1841650], MO [Acc. No. 2728504], NY, R [Acc. No. 180261], S [Acc. No. 10-28034], U [U0016880], US [Acc. No. 2868603]). (Figures 4C–D, 10–11).

*Shrubs* or *treelets*, 1–1.3 m tall; leafy branchlets terete to slightly tetragonal, glabrous, red, distal nodes slightly resinous, resin produced by the stipules. *Stipules* free or basally adnate to petioles, ovate-triangular to broadly triangular, 2–3 × 2–4.5 mm, bifid at upper third to half the length, lobes narrowly triangular to acuminate and reduced to two teeth in older stipules, glabrous outside, glabrous at distal portion and basal 2/3 covered by dense colleters intermixed with wavy sericeous hairs inside; margins glabrous or sometimes hispidulous-ciliolate. *Leaves* subsessile to short-petiolate; petioles 2–5 mm long, glabrous throughout; blades elliptic, oblong-elliptic to narrowly oblong-elliptic, 4–10 × 1.3–3 cm, acute to decurrent at base, acute at apex, subcoriaceous, dark green and shiny above, pale green below when fresh, drying brown above and pale brown below; glabrous throughout, margins scarcely or not revolute, primary and secondary veins not impressed above and slightly prominent below; secondary veins 6–11 each side of midrib. *Inflorescences* cymose, frondose, long-branched, 6–14 cm tall, (including peduncle and flowers), 3–8 cm broad, terminal branches scorpioid, expanding at fruit maturity; rachis glabrous; peduncle 2.5–5.5 cm long; secondary branches subtended by a pair of leaf-like bracts; these similar in shape to regular cauline leaves, (2.5–)3.5–7 × 0.9–2.2 cm; each flower with 1 bracteole inserted on the opposite side of the branch; bracteoles sessile, oblong-lanceolate, 1–1.5 × 0.5–0.8 mm, acuminate at apex, often with 1–2 tiny teeth on each side, glabrous, sparsely ciliolate. *Flowers* with pedicels 3–8 mm long, glabrous. *Hypanthium* turbinate to narrowly obovoid, 1.5–1.7 × 1.2–1.5 mm, glabrous. *Calyx* lobes subequal to unequal, oblong to narrowly oblong, 1.5–5 × 0.4–0.7 mm, round to acute at apex, glabrous or sparsely strigillose outside, sericeous at base inside, margins glabrous, with 2–4, linear, 0.3–0.4 mm long, colleters at each lobe sinus. *Corolla* 19–22.5 mm long; tube narrowly infundibuliform, 11–14 mm long, 1.6–1.9 mm wide at base, 2–2.8 mm wide at mouth, glabrous or with a few appressed-strigulose hairs

**Figure 10.** *Dendrosipanea prancei*. **A.** Branch with terminal, frondose inflorescence. **B–C.** Stipule shapes present on the same branch. **D.** Detail of inflorescence branch, with secondary branches subtended by two leaf-like bracts (i.e., pherophylls). **E.** Flower in anthesis. **F.** Dissected long-styled flower, with stamens inserted at basal portion of corolla tube. **A–D:** drawn from Prance et al. 16199 (F, S); **E–F:** drawn from Prance et al. 15472 (US). Illustration by Piero Delprete (Reproduced from fig. 1 of Delprete (2018) with permission of copyright holder Magnolia Press).

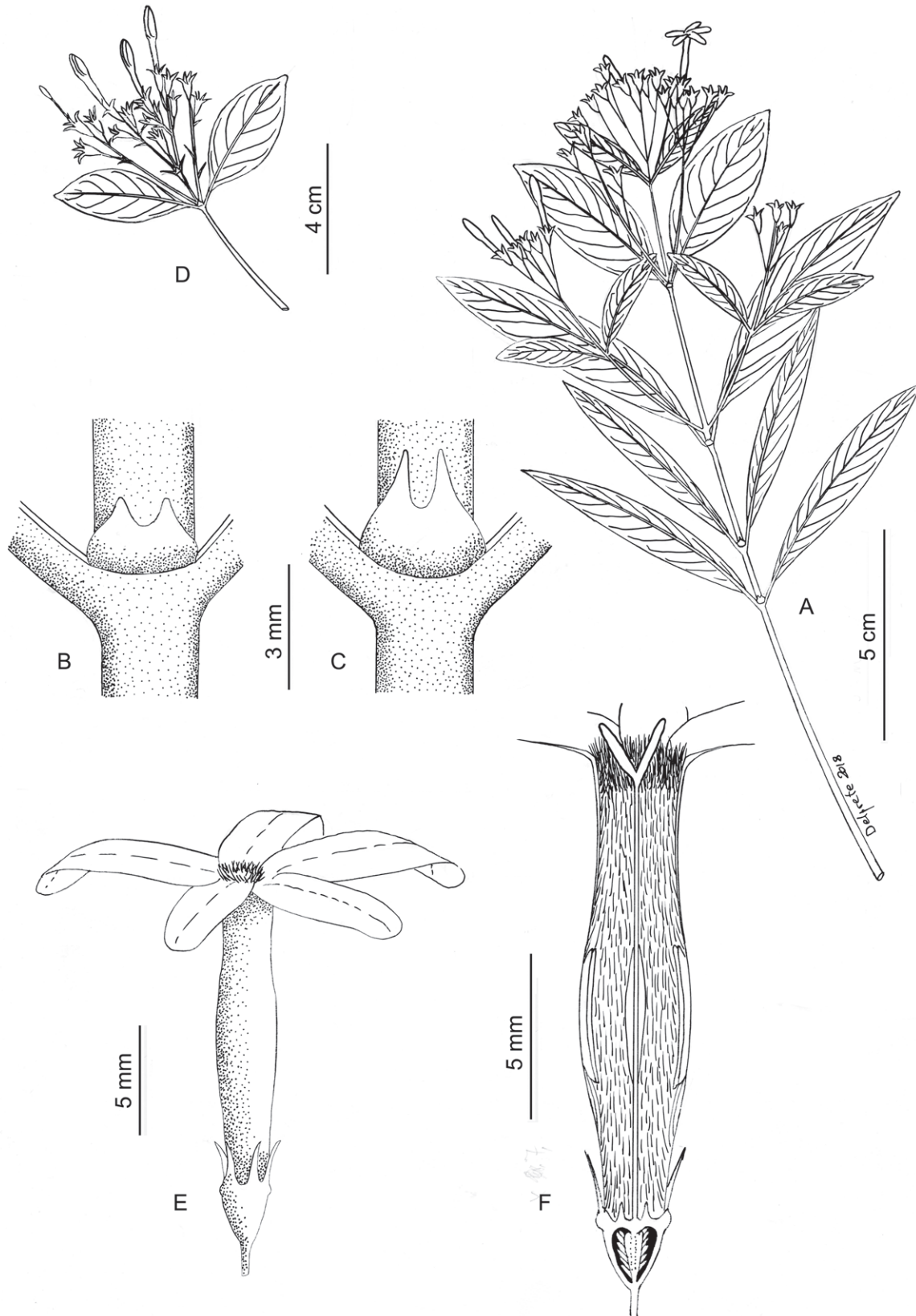


Figure 10.

outside, villous and densely yellow-pubescent at mouth inside; lobes ovate to narrowly ovate, 7.5–8.5 × 4.5–4.8 mm, sometimes slightly asymmetrical and of slightly different width on the same corolla, acute at apex, glabrous outside, densely papillose inside, margins glabrous. *Short-styled flowers* unknown. *Long-styled flowers* (Prance et al. 15472): stamens included, inserted at 2.7 mm from the base of corolla; filaments 3.7 mm long; anthers linear-oblong, 3.5–3.7 × 0.2–0.3 mm, acute at both ends; style barely exerted (only branch tips beyond corolla mouth), 14–15 mm long, glabrous, style branches oblong, 2 mm long. *Infructescences, capsules and seeds* unknown.

**Notes:** *Dendrosipanea prancei* Delprete is similar to *D. spigelioides* in having leaf blades acute at apex (vs. round, broadly obtuse or rarely acute) at apex in *D. revoluta*), with primary and secondary veins not impressed

above and slightly prominent below (vs. impressed above and prominent below in *D. revoluta* Steyerem.); the former differs from the latter by the long-branched inflorescence, 6–16 cm long including peduncle and flowers (vs. shortly branched, 3–7 cm long including peduncle and flowers in *D. spigelioides*), corollas 19–22.5 mm long, tubes 11–14 mm long, 1.6–1.9 mm wide at base, 2–2.8 mm wide at mouth, and lobes ovate to narrowly ovate, 7.5–8.5 × 4.5–4.8 mm, acute at apex (vs. corollas 27–30 mm long, tubes 16–20 mm long, 2–2.5 mm wide at base, 3.5–4.5 mm wide at mouth, lobes oblong to ovate-oblong, 12–16 × 5–7.5 mm, obtuse to acute at apex in *D. spigelioides*).

**Distribution and ecology:** Only known from the Rio Uneixi Basin, affluent of the Rio Negro, state of Amazonas, Brazil, and the Department of Guainía, Amazonian Colombia (Figure 11); on white-sand savan-

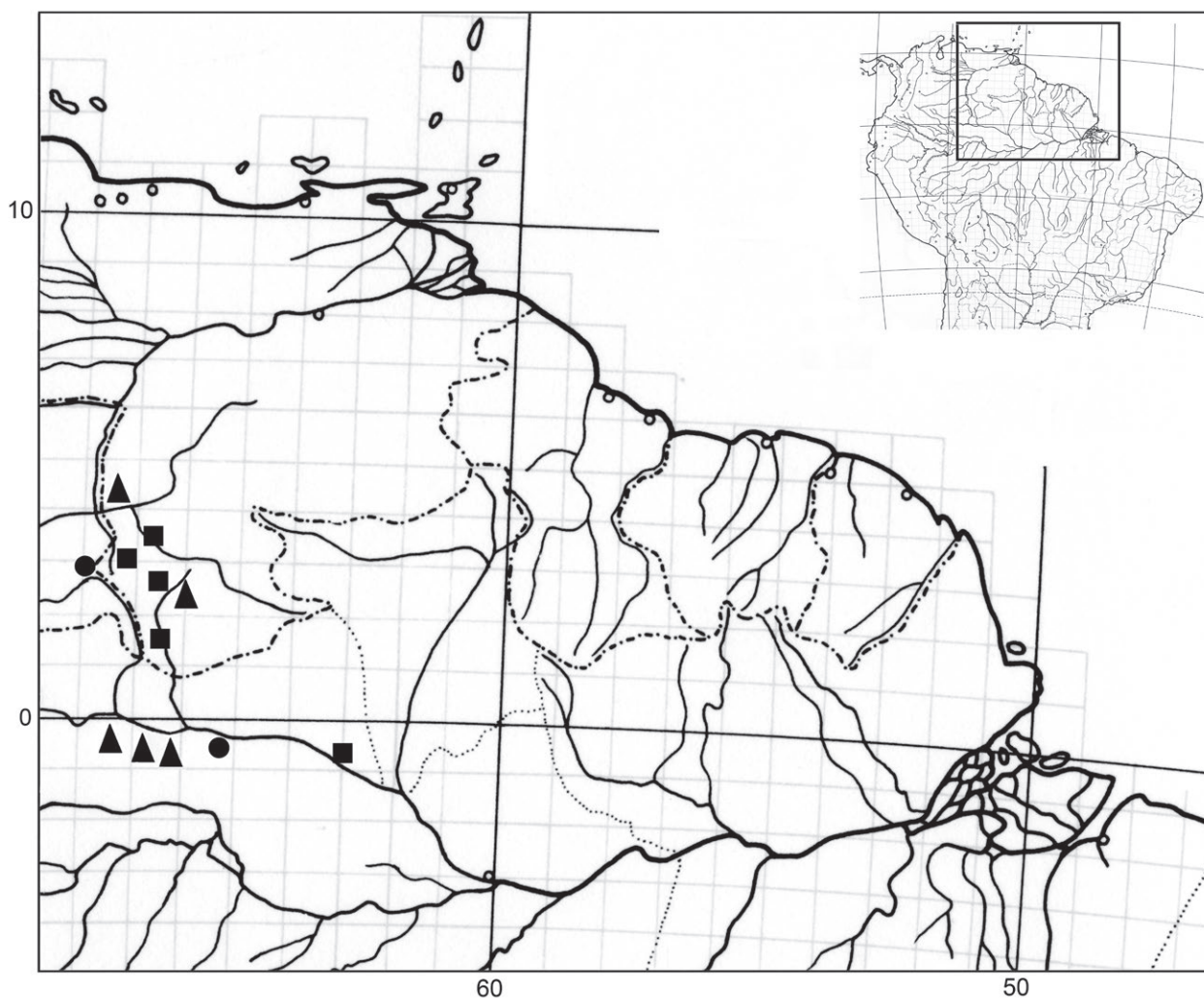


Figure 11. Distribution of *Dendrosipanea prancei* (circles), *D. revoluta* (squares), and *D. spigelioides* (triangles).

nas, seasonally flooded by black-water rivers, at 30–110 m altitude.

**Phenology:** Flowering specimens were collected in October and November.

**Suggested conservation status: Vulnerable (VU).**

This species is quite rare and is only known from two collections made in 1971 near the Rio Uneixi, an affluent of the Rio Negro, state of Amazonas, Brazil, and one recent collection from the Municipality of Inirida, Department of Guainía, Amazonian Colombia. The two localities are quite remote and very distant from each other.

The labels of the two 1971 collections near the Rio Uneixi (ca. 0°32'S, 65°3'W, ca. 30 m alt.) do not report population sizes, nor the rarity of the species. Personal observations of the vegetation surrounding the Rio Uneixi were made in February 2018. The region of the Rio Uneixi was inhabited by sparse indigenous communities, and the vegetation was fairly well preserved. During the dry season, the white-sand savannas of this region are subjected to frequent extensive fires (pers. obs.), often started by the local communities. After extensive searches made in several local savannas in February 2018, this species was not found. It is possible that, as it flowers in October–November, the species was not evident in February.

The single collection in Colombia was made in 2005 near the Caño Pato, 3°8'14"N, 67°47'34"W, an affluent of the Río Inirida. It is a isolate locality, nevertheless, ca. 50 km from a main road. The specimen label reports that the species was growing in a seasonally flooded forest undercanopy, but did not report the size of the population. It is expected that the locality has the potential of being altered, as it is not far from a main road. Therefore, this species is Vulnerable (VU) following IUCN criteria (IUCN 2012, 2019).

**Additional specimens examined (paratypes):**

**COLOMBIA. Guainía:** Mun. Inirida, km 50 de la carretera Huesito (Río Inirida – Puerto Caribe – Río Guainia), Sector de Caño Pato, bosque abierto con sotobosque denso sobre llanura alluvial, 3°8'14"N, 67°47'34"W, 110 m, 3 Oct. 2005 (fl, imm fr), *D. Cárdenas & A.L. Bermudez 16831* (COAH, NY).

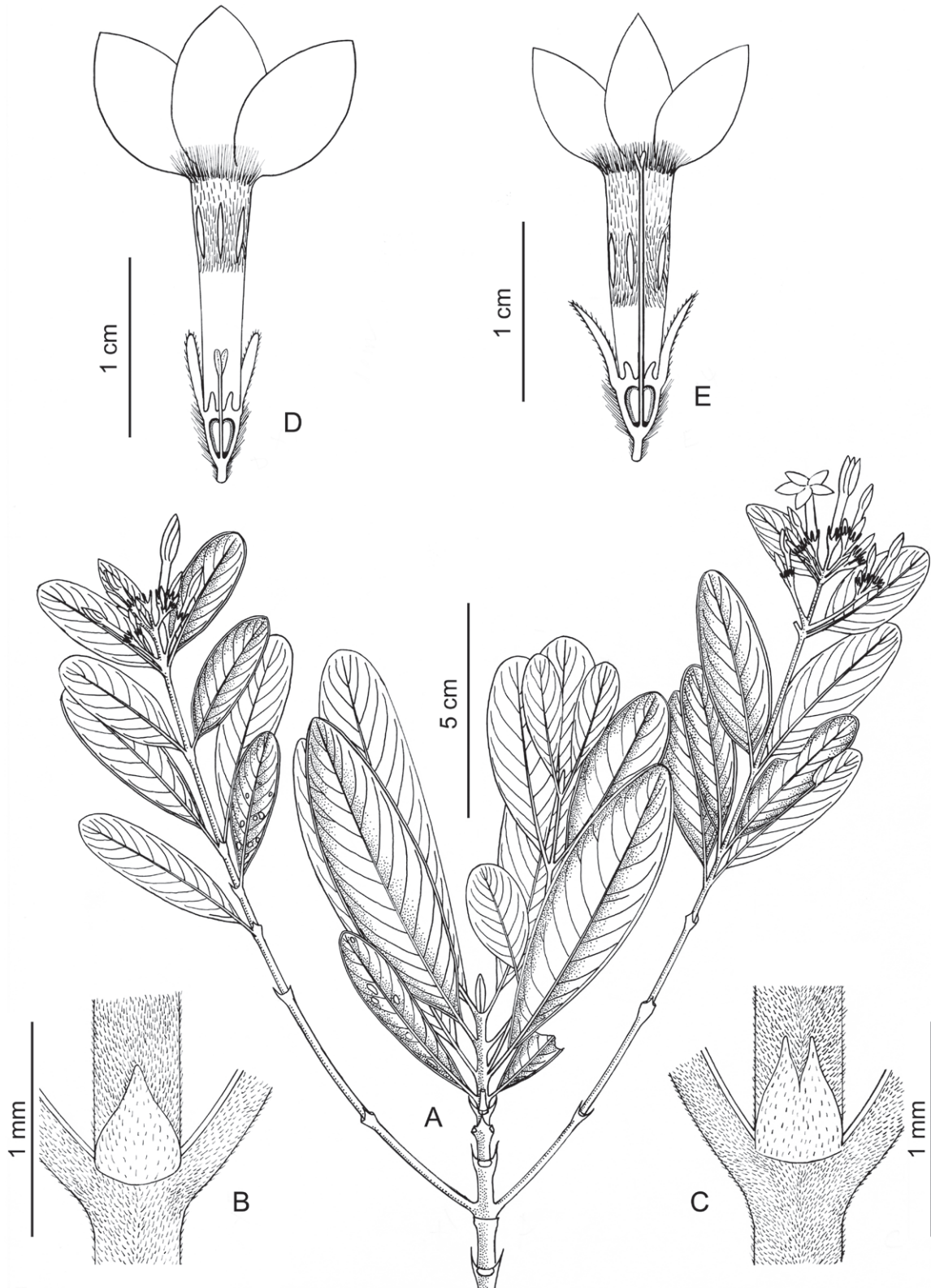
**BRAZIL. Amazonas:** Basin of Rio Negro, Rio Uneixi [ca. 0°32'S, 65°3'W, ca. 30 m alt.], 100–200 km above mouth, black-water flooded savanna forest on sand, shrub 1.3 m tall, corolla tube green, lobes white with yellow hairs at center, 21 Oct. 1971 (fl), *G.T. Prance et al. 15472* (INPA, MG, NY, U, US).

2-2. *Dendrosipanea revoluta* Steyerl., Mem. New York Bot. Gard. 10: 196, fig. 71. 1964. (Figures 11–12).

Type: VENEZUELA. Amazonas: Savanna on right bank of Río Pacimoni, 50 km above mouth, frequent, 100–140 m, 7 Feb. 1954 (fl), *B. Maguire, J.J. Wurdack & G.S. Bunting 37592* (holotype NY [00131229]; isotypes P [P00729464], RB [Acc. No. RB 115187, barcode 00543545], US [00137732], VEN [Acc. No. 49433]).

*Shrubs* 0.5–4 m tall; leafy branchlets terete to slightly tetragonal, hirtellous, distal nodes slightly resinous. *Stipules* free at base, ovate-triangular to broadly triangular (at wider nodes), 2–4 mm × 2–5.5 mm, acuminate or bifid to half the length, irregularly strigose outside, sparsely pubescent at distal portion and basal 2/3 covered by dense colleters intermixed with straight sericeous hairs inside; margins hispidulous ciliate.

*Leaves* subsessile to short-petiolate; petioles 2–9 mm long, glabrous or sparsely hispidulous above, hirtellous below; blades narrowly oblong or oblanceolate-spathulate, 3–10 × 1–3.5 cm, cuneate at base, round to broadly obtuse or rarely acute at apex, subcoriaceous, dark green and shiny above, pale green below when fresh, drying pale brown above and pale olive-green below; glabrous or sparsely asperous-hirtellous above, densely pubescent below, margin minutely revolute, primary and secondary veins impressed above and prominent below, veins glabrous above and densely strigillose below; secondary veins 7–9 each side of midrib. *Inflorescences* cymose, often frondose, shortly branched, 3–7 cm long (including peduncle and flowers, 2–3 cm broad, expanding at fruit maturity; rachis sparsely to densely strigillose; peduncle 2–3 cm long; secondary branches often subtended by a pair of leaf-like bracts; these, (when present) similar in shape of regular cauline leaves, 2–3.5 × 0.8–1.5 cm; flowers subtended by 1 bracteole, these sessile, oblong-lanceolate, 2–3.5 × 0.4–0.8 mm, acute at apex, sparsely strigillose. *Flowers* with pedicels 1–5 mm long, sparsely to densely strigillose or hispidulous. *Hypanthium* turbinate, 2–3 × 1.5–2.5 mm, strigillose. *Calyx* lobes subequal to unequal, narrowly oblong-lanceolate, oblanceolate to spatulate-oblong, 2–9 × 0.7–3.5 mm, sparsely to moderately hispidulous outside, glabrous or hispidulous on distal portion and with a row of trichomes at base inside, margins hispidulous-ciliate, with 1–2, linear, 0.4–0.5 mm long, colleters at each lobe sinus. *Corolla* 17–24 mm long; tube narrowly infundibuliform, 9–14 mm long, 2–2.2 mm wide at base, 3–4 mm wide at mouth, sparsely strigillose or hirtellous outside, basal portion glabrous or papillose, the medio-distal portion villous and densely



**Figure 12.** *Dendrosipanea revoluta*. A. Branch with inflorescences. B–C. Stipule variation on the same branch. B. Entire stipule. C. Bifid stipule. D. Dissected short-styled flower. E. Dissected long-styled flower. A–C, E: drawn from Wurdack & Adderley 42972 (US); D: drawn from Maguire et al. 36672 (US). Illustration by Piero Delprete.

yellow-pubescent at mouth inside; lobes ovate, 8–11 × 4–6 mm, obtuse at apex, sparsely strigulose or glabrate outside, glabrous inside, margins basally ciliate. *Short-styled flowers* (Maguire et al. 36672): stamens included, inserted at 5 mm below corolla mouth; filaments 0.7–0.8 mm long; anthers linear, 2.2–3.1 × 0.2–0.3 mm, acuminate at both ends; style included, 2.5 mm long, glabrous, style branches oblong, 1 mm long. *Long-styled flowers* (Wurdack & Adderley 42972): stamens included, inserted at 7 mm below corolla mouth; filaments 0.7–0.8 mm long; anthers linear, 2.5–2.6 × 0.2–0.3 mm, acuminate at both ends; style barely exerted (only branch tips beyond corolla mouth), 8.5–9 mm long, style branches oblong, 0.5–0.6 mm long. *Infructescence* a compound dichasium, 4.5–6.5 cm long, terminal branches scorpioid, 2.5–3.5 cm long. *Capsules* oblong-turbinate, (5–)7–10 × 3–5 mm, acute at base, round at apex, disk exceeding the calyx, dark brown, strigillose. *Seeds* irregularly polyhedral, 1.2–1.8 × 0.7–1 mm, yellowish-brown to pale brown.

**Distribution and ecology:** Occurring in the Venezuelan state of Amazonas, in the basins of the Río Atabapo and Río Pacimoni, and one collection in the Municipality of Barcelos, state of Amazonas, Brazil (Figure 11); growing in white-sand savannas seasonally flooded during the rainy season near black water rivers, at 100–200 m altitude. It is probable that this species might occur also in adjacent Colombia (Guainía Department).

**Phenology:** Flowering specimens were collected in February, March, June, October and November; with flowers and immature fruits in February and March; and with mature fruits in May.

**Suggested conservation status: Near Threatened (NT).** Known by numerous collections in the basins of Río Atabapo and Río Pacimoni, Venezuelan state of Amazonas, and one collection in the distant Municipality of Barcelos, in the Brazilian state of Amazonas. In Venezuela it was collected in 1953, 1957, 1959, 1979, 1980, 1981, 1989, 1995, and 1996. While the single collection from the surroundings of Barcelos, Brazil, was made in 1985. All of these localities are quite remote, and apparently without any immediate threat. However, Amazonian white-sand savannas are often subjects of frequent fires during the dry season. The population sizes are unknown. Using the coordinates of all collection localities, the EOO of this species is of ca. 40,000 km<sup>2</sup>. Two localities in the Casiquiare Department, Venezuela, are now included within the Alto Orinoco-Casiquiare Biosphere Reserve. Therefore, taking into account that the localities of occurrence might be subjects of frequent

fires, and that the last collection of this species was made in 1996, it is classified as Near Threatened (NT) following IUCN criteria (IUCN 2012, 2019).

**Specimens examined: VENEZUELA: Amazonas:** shrubby white-sand savanna just W of Santa Cruz de Atabapo, 3°13'N, 67°23'W, 100 m, 30 Nov. 1995 (fl), P.E. Berry et al. 5779 (MO, VEN); lower Río Guasacavi (black-water river), 0–1 km W of mouth of Río Temi, 3°14'0"N, 67°23'38"W, 100 m, 6 Mar. 1996 (fl), P.E. Berry et al. 5996A (MO, VEN); Depto. Atabapo, SE bank of the middle part of Caño Yagua at Cucurital de Yagua, 3°36'N, 66°34'W, 120 m, 8 May 1979 (fr), G. Davidse et al. 17395 (MO, NY, US, VEN); Depto. Atabapo, pequeña sabana a ca. 5 km S del caserío Puruname, en el Río Puruname bajo, 3°22'N, 66°30'W, 100 m, 8 Mar. 1980 (imm fr), O. Huber 5075 (NY, VEN); Depto. Río Negro, extensa sabana en la margen derecha del bajo Río Pasimoni, 1°35'N, 66°33'W, 125 m, 8 Feb. 1981 (fl, imm fr), O. Huber & E. Medina 5850 (NY, VEN); Depto. Casiquiare, sabanas ubicadas al W de la Serra Cariche, ca. la altura de Cariche en la ribera izquierda del Río Orinoco, 2°57'N, 66°23'W, 120 m, 17 Feb. 1981 (imm fr), O. Huber 6098 (NY, VEN); Depto. Casiquiare, Ríos Pacimoni-Yatua, savanna on R bank of Río Pacimoni, 60 km above mouth, 29 Nov. 1953 (fl), B. Maguire et al. 36672 (IAN, NY, US, VEN, paratype); Sabana Pacimoni, R bank of Río Pacimoni, 50 km above mouth, 100 m, 2 Oct. 1957 (fl), B. Maguire et al. 41665 (NY, P, U, US, paratype); Depto. Atabapo, Laja Cúcuta, Río Atacavi, Pica 1, Frente No. 3, individuo de 80 cm, dominante en sabana amazónica arbustiva, flores blancas, 3°12'N, 67°24'W, 100 m, Nov. 1989 (fl, imm fr), J. Velazco 1056 (NY, PORT, US); Río Atabapo, Sabana Manacal, 15 km above Guarinumó, 125 m, 12 Jun. 1959 (fl), J.J. Wurdack & L.S. Adderley 42972 (IAN, NY, US, VEN, paratype).

**BRAZIL: Amazonas:** Mun. Barcelos, Rio Aracá, a 13 horas de barco de Barcelos, beira do Rio, 0°0'–20'S, 63°0'–30'W, 28 Jul. 1985 (fl), J.A. Silva et al. 386 (INPA, NY [2 sheets]).

2-3. *Dendrosipanea spigelioides* Ducke, Arch. Inst. Biol. Veg. 2(1): 70, figs. 8–9. 1935. (Figures 11, 13).

Emend. Delprete & Steyerl. in Steyerl. et al., Fl. Venez. Guayana 8: 571. 2004.

Type: BRAZIL. Amazonas: Rio Curicuriary [now Rio Curicuriari; ca. 0°12'S, 66°47'W, ca. 60 m alt.], affluent of the Upper Rio Negro, ["abaixo das cachoeiras, margem inundavel"], 19 Oct. 1932

(fl, fr), *A. Ducke s.n.* (RB 24426) (holotype RB [mounted on 4 sheets, 00706257 (Sheet No. 1, fl), 00706256 (Sheet No. 2, fl), 00706258 (Sheet No. 3, fl), 00543546 (Sheet No. 4, fr)]; isotypes F [Acc. No. 779985], IAN [Acc. No. 50581], NY [2 sheets, 1731845 and 131230], INPA [Acc. No. 246872], P [P00729463], S [Acc. No. S05-1746], U [U0016882], US [00137733]).

(=) *Dendrosipanea wurdackii* Steyerl., Mem. New York Bot. Gard. 10: 198, fig. 72a–g. 1964

Type: VENEZUELA. Amazonas: Río Guainía, occasional in Sabana El Venado, on left bank above of Caño Pimichín [2°74'N, 67°56'W], above Pimichín, 140 m, 14 Apr. 1953 (fl), *B. Maguire & J.J. Wurdack* 35558 (holotype NY [barcode 00131231]; isotype VEN [Acc. No. 49443]).

*Shrubs* 2–4 m tall; leafy branchlets terete to slightly tetragonal, glabrous or sparsely strigillose, distal nodes lightly resinous. *Stipules* free or basally adnate to petioles, ovate-triangular to broadly triangular, 2.5–3 × 2–4.5 mm, acuminate or bifid to half the length, glabrous or sparsely strigillose outside, sparsely pubescent at distal portion and basal 2/3 covered by dense colleters intermixed with straight sericeous hairs inside; margins hispidulous ciliate. *Leaves* subsessile to short-petiolate; petioles 3–10 mm long, glabrous above, glabrous or sparsely strigillose below; blades elliptic-lanceolate, oblong-lanceolate, lanceolate-ovate, narrowly oblong-lanceolate, 4–13 × (1–)2.5–4.5 cm, acute at base, acute or acuminate at apex, subcoriaceous, dark green and shiny above, pale green below when fresh, drying brown above and olive-green below; glabrous above, glabrous and with veins glabrous or sparsely strigillose below, margins scarcely or not revolute, primary and secondary veins not impressed above and slightly prominent below; secondary veins (6–)7–12 each side of midrib. *Inflorescence* cymose, frondose, long-branched, 6–16 cm long (including peduncle and flowers), 3–13 cm broad, terminal branches scorpioid, expanding at fruit maturity; rachis glabrous or sparsely strigillose; peduncle 2–5 cm long; basal secondary branches subtended by a pair of leaf-like bracts; these similar in shape of regular caul-

ine leaves, 3–5.5 × 1–2 cm; each flower with 1 bracteole inserted on the opposite side of the branch; bracteoles sessile, oblong-lanceolate, 1–2 × 0.3–0.7 mm, acuminate at apex, often with 1–2 tiny teeth on each side, sparsely strigillose, sparsely ciliate. *Flowers* with pedicels 3–5 mm long, glabrous or sparsely strigillose. *Hypanthium* turbinate, 2–3 × 1.7–2 mm, glabrous or sparsely strigillose. *Calyx* lobes subequal or unequal, deltoid to narrowly triangular, 1–3.5 × 0.9–1.2 mm, glabrous or sparsely strigillose outside, short-sericeous inside, margins hispidulous-ciliate, with 2–4, linear, 0.3–0.5 mm long, colleters at each lobe sinus. *Corolla* 27–30 mm long; tube narrowly infundibuliform, 16–20 mm long, 2–2.5 mm wide at base, 3.5–4.5 mm wide at mouth, glabrous or very sparsely appressed-strigillose outside, basal portion glabrous or papillose, the medio-distal portion villos and densely yellow-pubescent at mouth inside; lobes oblong to ovate-oblong, 12–16 × 5–7.5 mm, often slightly asymmetrical and of different width on the same corolla, obtuse to acute at apex, glabrous outside, glabrous inside, margins glabrous. *Short-styled flowers* (*Maguire & Wurdack* 35558, type of *D. wurdackii* Steyerl., corolla tube 16–20 mm long, lobes 14–16 × 4–5 mm): Stamens included, inserted 6 mm below corolla mouth; filaments 2.5–3.5 mm long; anthers linear-oblong, 2.8–3.1 × 0.2–0.3 mm, acute at both ends; style included, 3–3.5 mm long, glabrous, style branches oblong-lanceolate, 1–1.3 mm long. *Long-styled flowers* (*Ducke* 356, corolla tube 18 mm long): Stamens included, inserted 5–6 mm from the base of corolla tube; filaments 4–4.5 mm long; anthers linear-oblong, ca. 4 × 0.2–0.3 mm, acuminate at both ends; style barely exerted (only branch tips exerted beyond corolla mouth), 16.5–20.3 mm long, glabrous, style branches oblong-elliptic, 2–3 mm long, round at apex. *Infructescences* a compound dichasium, 6–16 cm long, terminal branches scorpioid, 6–9 cm long. *Capsules* turbinate to oblong-turbinate, (6–)8–11.5 × (4–)5–5.7 mm, acute at base, round at apex, disk exceeding the calyx, brown, strigillose. *Seeds* irregularly polyhedral or irregularly-shaped, uncinated, dorso-ventrally compressed to tronco-conical, 1–2 × 0.6–1.3 mm, pale brown.

**Taxonomic notes:** Ducke (1935), along with the description of *Dendrosipanea spigelioides* Ducke, indi-

**Figure 13.** *Dendrosipanea spigelioides*. **A.** Branch with inflorescence and flowers in anthesis. **B.** Dissected corolla of long-styled flower, with exerted style. **C.** Dissected corolla of short-styled flower, with included style. **D.** Longitudinal section of ovary, disk and calyx, showing fleshy placental extension adnate along the entire length of the septum, and peltate ovules. **E.** Septicidal capsule, half portion showing septum and long disk. **F–G.** Stipule variation on the same branch. **F.** Entire stipule. **G.** Bifid stipule. **A, D, F, G:** drawn from *Ducke* 356 (F); **B:** drawn from *Ducke* 356 (S); **C:** drawn from *Maguire & Wurdack* 35558 (NY); **E:** drawn from *Ducke s.n.* (RB 24426) (RB). Illustration by Piero Delprete.

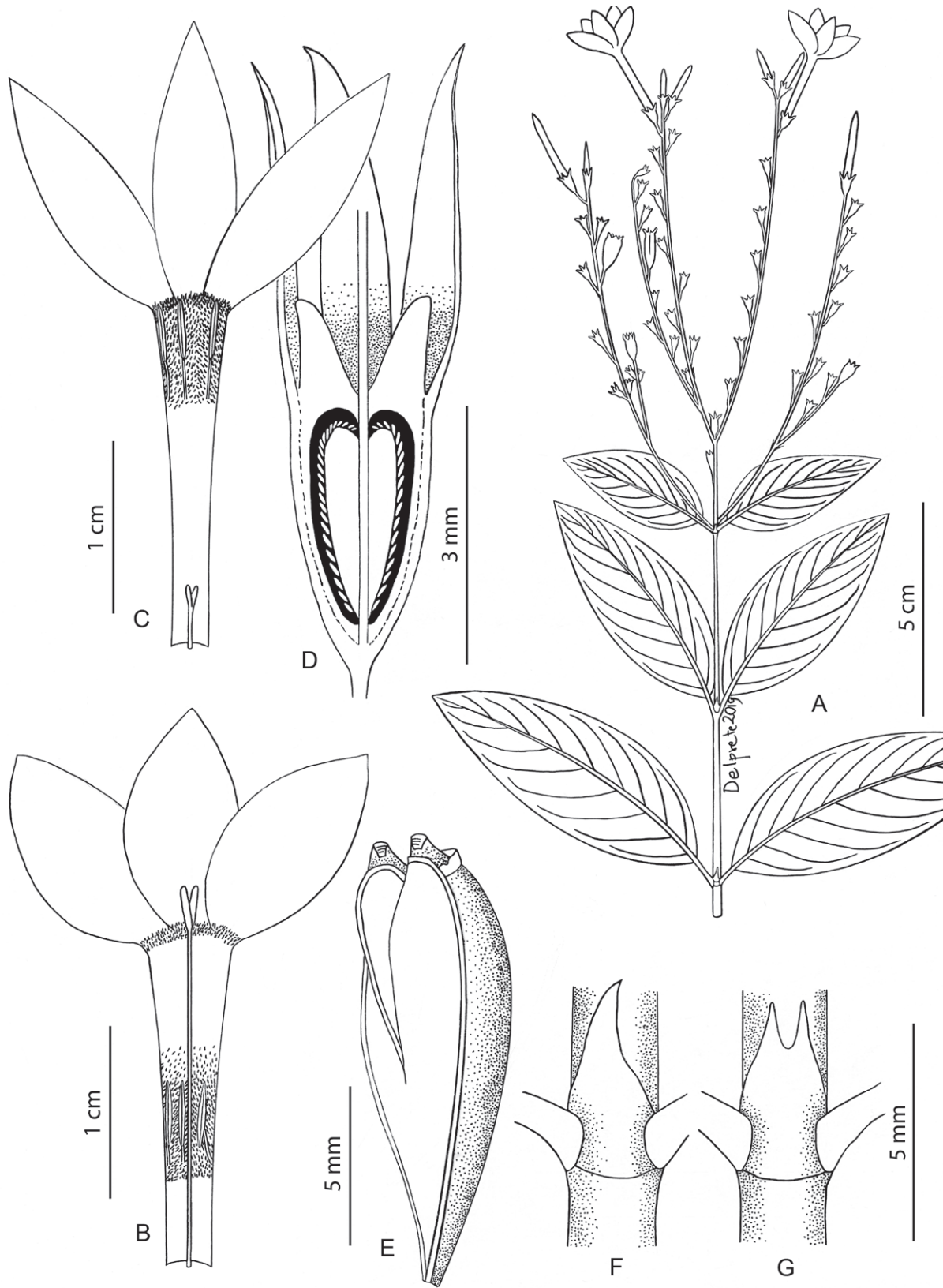


Figure 13.



cated his own unnumbered collection with the RB accession No. 24426, without indicating the herbarium of deposit. At the time of the publication he worked at the Botanical Garden of Rio de Janeiro (RB) and he did not use his own collection numbers, but rather the RB accession numbers, as it was commonly done in those days at that institution. This gathering was subsequently distributed, and duplicate specimens with RB accession No. 24426 are now at F, INPA, NY, P, RB, S and US. Steyermark (1964: 199) cited the type of this name as “Brazil. Amazonas: Rio Curicuriary affluentis Rio Negro superioris; ad ripas inundatas; 19 October 1932, A. Ducke 24426 (isotype NY). - The isotype specimen at NY shows minor variations from the description of the species. According to the material examined, this species has a larger, more laxly branched inflorescence than either of the other two species of the genus.” Article 9.10 of the *Code* (Turland et al. 2018) states that “The use of a term defined in the *Code* (Art. 9.1, 9.3 and 9.5–9.9) as denoting a type, in a sense other than that in which it is so defined, is treated as an error to be corrected (for example, the use of the term lectotype to denote what is in fact a neotype).” Because Ducke in the protologue of *D. spigelioides* cited “leg. A. Ducke, 19-10-1932, H.J.B.R. n° 24.426,” Steyermark assumed that Ducke cited a sole specimen at RB, which, according to him, was the holotype. With this assumption, Steyermark (1964) by citing “A. Ducke 24426 (isotype NY)” was correct in using the term isotype as he assumed that it was a duplicate of the holotype at RB, hence it cannot be corrected. At RB are present four sheets with accession No. 24426; these sheets are kept together in the same folder, and only one of them (sheet No. 1, with barcode 00706257), has the original label handwritten by Ducke (the other three sheets have no label); therefore, according to Art. 8.3 of the *Code* (Turland et al. 2018), they are a single specimen with multiple preparations. To each sheet has been assigned a different barcode. This specimen, mounted on four sheets, is the holotype of *Dendrosipanea spigelioides*.

Steyermark (1964) separated *Dendrosipanea wurdackii* from *D. spigelioides* based on the shape and size of the calyx lobes and details of the pubescence of both vegetative and reproductive structures. However, according to Delprete and Steyermark (2004a, p. 571), the variation in these characters is continuous, and these taxa are here confirmed to be synonymous.

**Distribution and ecology:** It has been collected in Amazonian Venezuela on white-sand savannas, along streams, and adjacent seasonally flooded forests, usually

in hummocks locally called “tatucos”, and Brazil, near the Rio Curicuriari, Upper Rio Negro Basin (Figure 11); growing in seasonally flooded white-sand savannas, and seasonally flooded low vegetation or forests at river margins, at 90–200 m altitude.

**Phenology:** Flowering specimens were collected in February, April, June, July, October and November; with flowers and mature fruits in February.

**Suggested conservation status: Vulnerable (VU).** A rare species known by three collections in Amazonian Venezuela, and three collections in contiguous Amazonian Brazil, always on white-sand savannas. In Brazil it was collected in the state of Amazonas in 1932 (type of *D. spigelioides*) and 1936 (paratype of *D. spigelioides*) near the Rio Curicuriari, ca. 0°12'S, 66°47'W, and in 1987 near the Rio Içana, ca. 0°23'N, 67°33'W, in the Municipality of São Gabriel da Cachoeira.

In Venezuela it was collected in the state of Amazonas, in 1953 (type of *D. wurdackii*) in the savanna El Venado, basin of the Río Guainía, near Caño Pimichín, ca. 2°74'N, 67°56'W; in 1982 in a savanna at ca. 15–20 km S of Tama-Tamá, ca. 2°31'N, 66°16'W; and in 1992, in a savanna near the town of San Juan de Ucata, 4°20'25"N, 67°44'12"W.

None of the specimen label report the size of the populations of this species, and no recent observations has been made in the collection localities to assess their state of preservation. During the dry season, Amazonian white-sand savannas are subject to frequent fires, often started by the local communities. Therefore, this species is classified as Vulnerable (VU) following IUCN criteria (IUCN 2012, 2019).

**Specimens examined: VENEZUELA: Amazonas:** Edge of lagoon below Raudal de Ucata, above town of San Juan de Ucata, 4°20'25"N, 67°44'12"W, 120–150 m, 20 Jun. 1992 (fl), *P.E. Berry et al.* 5162 (MO, VEN); Dto. Río Negro, ca. 15–20 km S of Tama-Tamá, transecto desde sabana de arena blanca con drenaje laterítico hasta bosque medio denso inundado, con tatucos, 2°31'N, 66°16'W, 90 m, 5 Nov. 1982 (fl, young fr), *F.M. Guánchez* 1996 (MO, TFAV).

**BRAZIL: Amazonas:** Rio Curicuriari [ca. 0°12'S, 66°47'W, ca. 60 m alt.], above waterfalls, flooded river margin, 23 Feb. 1936 (fl, fr), *A. Ducke* 356 (F, MO, NY, R, US); Mun. São Gabriel da Cachoeira, Rio Içana, Jauacanã, arbusto, na mata de igapó, 0°23'N, 67°33'N, 2 Nov. 1987 (fl), *C. Farney & W. Rodrigues* 1861 (MO, NY).

### 3. LIMNOSIPANEA

*Limnosipanea* Hook.f., Ic. pl. 11: 38, pl. 1050. 1868

K.Schum. in Mart. et al., Fl. Bras. 6(6): 252–256, tab. 123. 1889; Steyerl. in Mem. New York Bot. Gard. 17: 282–284. 1967; Steyerl. in Lasser and Steyerl., Fl. Venezuela 9(1): 384–390, fig. 61. 1974; Delprete and Steyerl. in Steyerl. et al., Fl. Venez. Guayana 8: 638–639, figs. 500–501. 2004; Delprete in J.A. Rizzo, Fl. Goiás Tocantins 40(2): 619–629, fig. 54. 2010.

Type: lectotype (designated by Steyerl. (1967: 282), see notes below): *Limnosipanea spruceana* Hook.f.

*Herbs*, terrestrial, semi-aquatic (amphibious) or aquatic (in *L. spruceana*); erect, prostrate or decumbent; ephemeral to short-lived (2–4 months life span) when terrestrial or semi-aquatic, or perennial when growing in permanently submersed areas; aerial portion (i.e., not submerged) of stems sparsely pubescent. *Stipules* reduced to a line between the petioles, sometimes obsolete, persistent, withering on the stem (no abscission layer is formed); with 1 to 3 colleters inserted just below the margin, on the internal side, with the tips exerted beyond the stipule margin, or, when stipules obsolesce, 1 or 2 colleters inserted at the sinuses between leaf bases; in submersed stems, stipules and colleters absent. *Leaves* opposite or whorled, sessile, membranaceous or chartaceous, domatia absent; homophyllous with 2–3 per node in terrestrial plants; heterophyllous in aquatic or semi-aquatic plants, submerged leaves (when present) 3–6(–8) per node, linear to acicular, aerial leaves 2–5 per node per node, linear to lanceolate. *Inflorescence* terminal, cymose, few–many-flowered, frondose or not, or uniflorous. *Flowers* homostylous, (4–)5(–6)-merous. *Hypanthium* narrowly ellipsoid to narrowly obovoid, densely hispid. *Calyx* persistent; tube extremely reduced or absent; lobes free or nearly so, subequal, oblong, lanceolate to linear, aristate at apex (arista caducous) or not, with 1 minute colleter in each lobe sinus. *Calycophylls* absent. *Corolla* hypocrateriform, white, cream-white, pinkish-white, pink to lilac; tube externally glabrous or strigose, internally villous, with a pubescent ring at orifice; lobes left-contorted, ovate or oblong-ovate, margin entire or undulate, obtuse or round at apex. *Stamens* exerted; filaments attached near the mouth of the corolla tube, glabrous; anthers yellow, narrowly elliptic or oblong, round at base and at apex, dorsifixed near the middle. *Pollen* 3(4)-colporate, exine shallowly foveolate or shallowly reticulate-foveolate, without perforations or finely perforate. *Ovary* with a stalked placenta; stalk inserted at the middle of the sep-

tum, terminating with a hemi-ellipsoid extension; ovules inserted on the placental extension. *Style* exerted, filiform, glabrous; branches oblong or ovate. *Fruits* capsular, dehiscent loculicidally, crustaceous. *Seeds* many per locule, horizontal, small, 3–5-angular; testa foveolate.

**Notes on designation of lectotype species:** Joseph Dalton Hooker (1868: 38. t. 1050) published *Limnosipanea* Hook.f., and described three species in this genus: *L. spruceana* Hook.f., *L. schomburgkii* Hook.f., and *L. palustris* (Seem.) Hook.f., without indicating the type species. Standley (N. American Fl. 32(2): 94. 10 May 1921) indicated *L. spruceana* as the type of the genus, without any explanation. Article 10.7 Ex. 11 of the *Code* (Turland et al. 2018) states that “In considering the typification of *Achyranthes* L. [...] in the *North American Flora*, Paul C. Standley (in J. Wash. Acad. Sci. 5: 72. 1915) selected *A. repens* L. as type stating that “there seems, moreover, no doubt as to the type of the genus *Achyranthes* under the *American Code* of nomenclature”, noting that, as a result, “the name *Achyranthes* must be used in a sense other than that in which it has generally been employed in recent years”. As a result of this published statement of acceptance of the *American Code*, not only is Standley’s selection of *A. repens* superseded by that of *A. aspera* L. by Hitchcock (in Sprague, Nom. Prop. Brit. Bot.: 135. 1929), but types cited in Standley’s other publications (e.g. in Britton, N. Amer. Fl. 21: 1–254. 1916–1918) are supersedable under Art. 10.5.” As Standley followed a clearly mechanical method and accepted the *American Code*, his species lectotypification of *Limnosipanea* should be superseded. Searching subsequent specialized literature, the following type species citation for *Limnosipanea* is that by Steyerl. (Mem. New York Bot. Gard. 17(1): 282. 1967), who designated *L. spruceana* as the type of the genus, which is here followed.

**Distribution:** Genus ranging from Panama through Colombia, Venezuela, Guyana, Brazil to Bolivia. The three species of this genus are terrestrial or semi-aquatic (amphibious), commonly found in seasonally inundated fields, at margins of small water courses, and swamps with *Mauritia flexuosa* L.f. palms, or in permanently inundated areas (aquatic habit). Two species of this genus can assume different habit and can be heterophyllous, depending on the habitat where they grow. For example, when *L. spruceana* grows as a partially submerged plant in inundated areas, the submerged leaves are whorled, 3–6(–8) per node, linear to acicular, and the aerial leaves are opposite or whorled, 2–5 per node, lanceolate to ovate. On the other hand, when the same species grows in areas not inundated, the plants are terrestrial and the

leaves are homophyllous and similar to those of the aerial portion of the partially submerged plants.

*Limnosipanea*, and particularly *L. spruceana*, is often overlooked as a genus of Rubiaceae because the stipules are so reduced that they appear to be absent, its semi-aquatic habit and whorled leaves, which are unusual in this family.

#### Key to *Limnosipanea* species

1. Leaves homophyllous or heterophyllous, 2–6(-8) per node; submerged leaves (when present) 3–6(-8) per node, linear to acicular, without evident secondary veins or sometimes with 1 secondary vein on each side of midrib; aerial leaves 2–6 per node, linear to lanceolate, with 1–2(-3) secondary veins on each side of midrib..... 3. *L. spruceana*
  1. Leaves homophyllous, whorled, 3–4 per node, at basal nodes and opposite and ternate at distal nodes, or leaves opposite throughout the whole plant; leaf blades ovate, narrowly ovate, oblong-ovate, elliptic to lanceolate, without evident secondary veins (rarely with 1–2 secondary veins on each side of midrib) ..... 2
  2. Plant prostrate or decumbent; leaves 3–4 per node at basal nodes and opposite at distal nodes, or opposite throughout the whole plant; flowers with pedicels (0.5–)1–2.5 mm long; corollas 11.5–16(-18) mm long, pink to lilac, tube 7–9 mm long, glabrous outside, lobes 4.5–8 × 2–4 mm; capsule pedicellate, sparsely hispid..... 1. *L. erythraeoides*
  2. Plant erect; leaves commonly opposite throughout the whole plant, or rarely ternate; flowers commonly sessile (rarely short-pedicellate in central flowers); corollas 5.7–10 mm long, white to pinkish-white, tube 3.5–6.5 mm long, strigose outside, lobes 2.2–3.5 × 0.7–0.9 mm; capsule sessile, hispid-setose..... 2. *L. palustris*
- 3-1. *Limnosipanea erythraeoides* (Cham.) K.Schum. in Martius & A.G.Eichler, Fl. Bras. 6(6): 253, tab. 123. 1889. (Figures 14–15).

(=) *Sipanea erythraeoides* Cham., Linnaea 9: 242. 1834. Original type: BRAZIL: “Brasilia inter tropicos”, s.d., Sellow s.n. (B, destroyed). **Neotype (here designated)**: BRAZIL. Goiás: Near Caiapônia, “in arenosis humidiusque, Aldeia dos Cayapos” [sandy humid savanna, near the indigenous village of the Cayapos (now the town of Caiapônia, ca. 16°57'S, 51°48'W)], Aug. 1826 (fl), *L. Riedel 409* (BR [barcode 00000824532]; isoneotypes BM [barcode BM000614341], FI [barcode FI018882], P [barcode P00729267], US [Acc. No. 254488]).

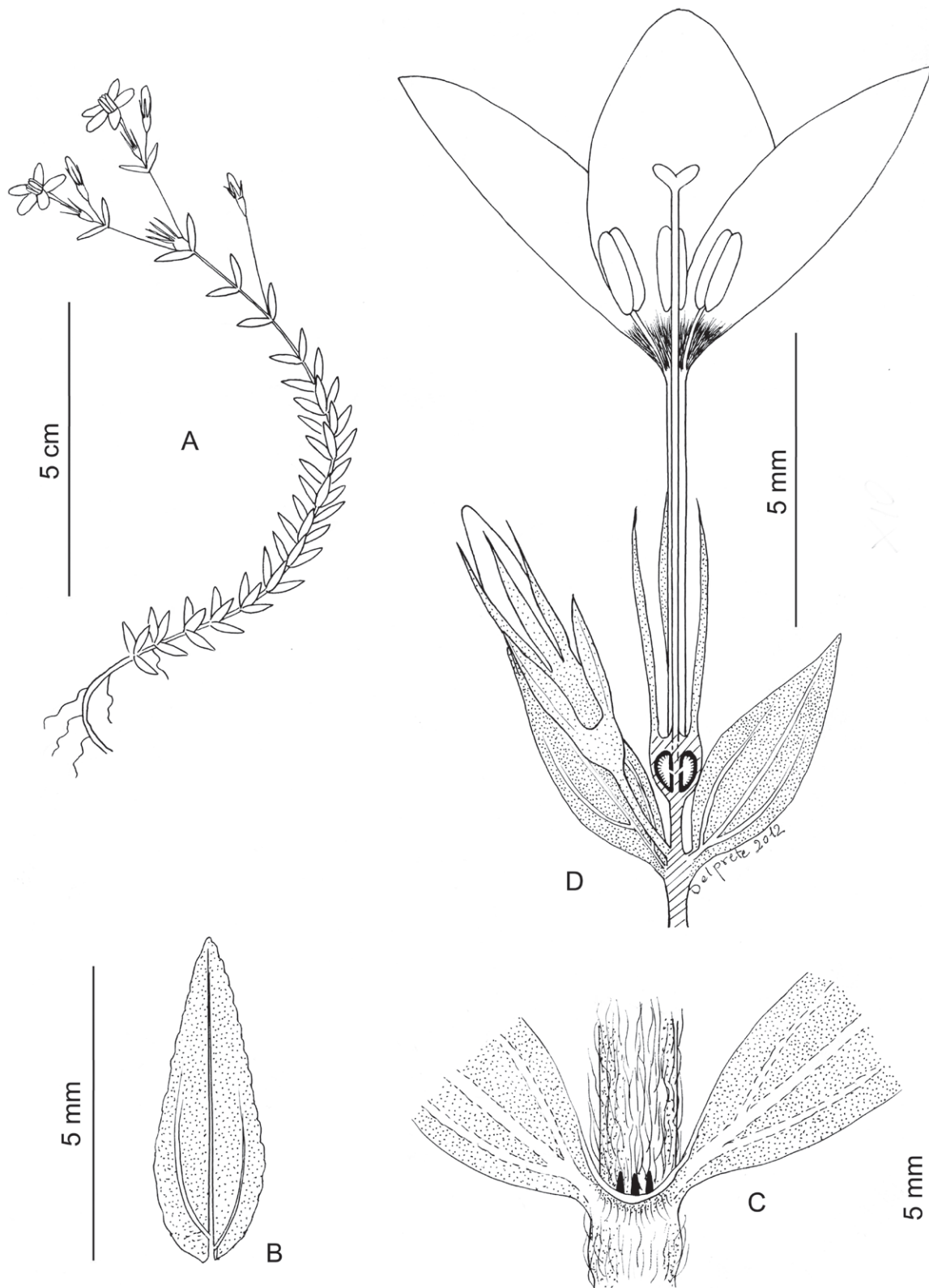
*Herb*, terrestrial or semi-aquatic (amphibious), prostrate or decumbent, single-stemmed or sparsely branched; main

stems 8–20 cm long; stems sparsely to densely appressed pubescent. *Stipules* reduced to a line between the petioles, sparsely appressed pubescent, with 2 or 3 colleters inserted just below the margin on the internal side, with the tips exerted beyond the margin. *Leaves* homophyllous, 3–4 per node at basal nodes and opposite at distal nodes, or opposite throughout the whole plant, sessile; blades ovate, narrowly ovate, elliptic to lanceolate, 2.5–8(-10) × 0.5–3.5 mm, acute to obtuse at base, acute to obtuse at apex, chartaceous to membranaceous, pale green, drying olive-green, glabrous above and below, only the midvein evident (rarely with 1–2 secondary veins evident on each side). *Inflorescences* 1–3-flowered, or 2–3-chotomous and pauciflorous, 3–15 mm long, frondose, with leaf-like bracts subtending secondary branches; bracteoles subtending each flower elliptic-lanceolate, narrowly lanceolate to linear, 1.5–2.5 × 0.2–0.4 mm, glabrous. *Flowers* pedicellate; pedicels (0.5–)1–2.5 mm long. *Hypanthium* narrowly obovoid, 1–1.5 mm long, hispid, with white, erect hairs 0.3–0.7 mm long. *Calyx* lobes narrowly lanceolate, narrowly oblanceolate to linear, 2.8–4.5 × 0.3–0.5 mm, glabrous throughout, sometimes with a few hispid hairs at margins, with 1 deltoid, 0.1 mm long colleter at each lobe sinus. *Corolla* hypocrateriform, 11.5–16(-18) mm long, pink to lilac; tube narrowly cylindrical, 7–9 mm long, glabrous outside, sparsely villose at mouth inside, glabrous below; lobes ovate to oblong-ovate, 4.5–8 × 2–4 mm, obtuse to round at apex, glabrous. *Filaments* 1.5–2 mm long, anthers oblong-elliptic, 0.2–0.3 × 0.1 mm. *Style* 10–13 mm long, glabrous; style branches ovate, 0.2–0.3 mm long. *Capsules* pedicellate, globose, 2.5–3 × 2.5–3 mm, sparsely hispid. *Seeds* 0.2–0.5 × 0.2–0.5 mm, strongly foveolate.

**Taxonomic observations:** Chamisso (1834: 242) in the protologue of *Sipanea erythraeoides* Cham. cited the gathering “Brasilia inter tropicos. Sellow.” When he published this name he worked at Berlin. The original material at B was destroyed during WW2 (R. Vogt, pers. comm.). In addition, no original specimen with this name collected by Sellow is present at M (A. Fleischmann, pers. comm.). After exhaustive searches in several other herbaria, no original material of *S. erythraeoides* collected by Sellow could be found. Therefore the specimen *Riedel 409* at BR, barcode 00000824532, is here designated the neotype of this name, and the duplicates of this gathering at BM, FI, P, and US are isoneotypes.

This species is easily distinguishable from the others of the same genus, by its prostrate or decumbent habit, pedicellate flowers, and pink to lilac corollas.

**Geographic distribution and ecology:** Species restricted to Brazil. It has been collected in the states of Bahia, Goiás, Distrito Federal, Mato Grosso, Mato Gros-



**Figure 14.** *Limnosipanea erythraeoides*. **A.** Habit. **B.** Leaf. **C.** Node with base of two leaves, and extremely reduced stipule with three partially exerted colleters. **D.** Dissected flower, with a flower bud, subtended by two leaves. **A–D:** drawn from *Macedo 5537* (US). Illustration by Piero Delprete.

so do Sul, Minas Gerais, Rondônia and São Paulo (Figure 15). Ephemeral to short-lived (2–4 months life span), prostrate herb, terrestrial or semi-aquatic, commonly found in inundated open fields, at margins of small water courses, and swamps with *Mauritia flexuosa* L.f. palm communities.

**Phenology:** Flowering and fruiting from June to November, which in Central Brazil correspond to the dry season, with one collection in December which corresponds to the beginning of the rainy season.

**Suggested conservation status: Least Concern (LC).** This species occurs in numerous Brazilian states (see geographic distribution and specimens cited). It is a prostrate herb, commonly found in seasonally inundated open fields, at margins of small water courses,

and swamps. The size of the populations is unknown. In addition, it is poorly collected due to its small size and short life span. Taking into account the numerous sites of occurrence, this species is here treated as Least Concern (LC) following IUCN criteria (IUCN 2012, 2019).

**Specimens examined: BRAZIL: Bahia:** Near Salvador, “Habitat in aquaticis uliginosis ad Soteropolin, Prov. Bah.”, Dec. [1818], *C.F.P. Martius Iter Brasil.* 2884 (M M0198161); without locality, “Prov. Bahiensis”, s.d. [Oct.–Nov. 1818], *C.F.P. Martius Iter Brasil.* 2885 (M M0198163); between Lages and Caetitê, “Habitat in campis humidis ad Lages et Caetitê [ca. 14°4’S, 42°28’W]”, Oct.–Nov. [1818], *C.F.P. Martius Iter Brasil.* 2886 (M M0198162). **Distrito Federal:** Ca. 25 km E of Brasília, low gallery forest, creek margin, wet soil, 21 Aug. 1964 (fl), *H.S. Irwin & T.R. Soderstrom* 5429 (NY,

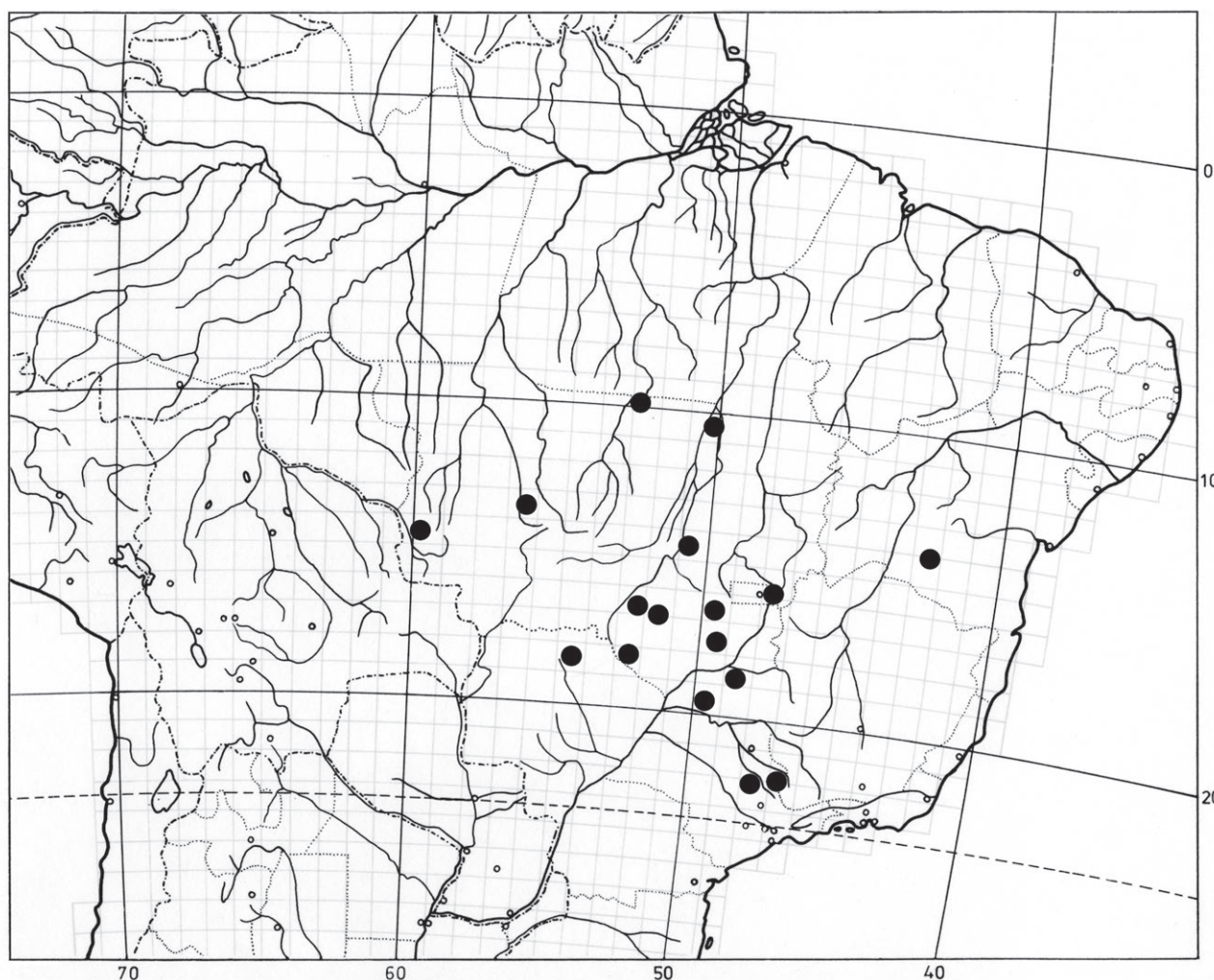


Figure 15. Distribution of *Limnosipanea erythraeoides*.

UB). **Goiás:** Rd. Aruanã–Araguapaz, at 22.4 km from Aruanã [ca. 14°55'S, 51°1'W], swamp near the river, with *Bacopa myriophylloides* and *Drosera*, amphibious plant, 15 Nov. 1999 (fl), C.P. Bove et al. 594 (R); rd. Caiapônia–Iporá, 54 km from jct, at river margin, inside water, submersed leaves red, emerged leaves green, 19 Nov. 1999 (fl), C.P. Bove et al. 672 (HUNI, R); Mun. Goiânia, Dec. 1936 (fl), A.C. Brade 15461 (RB); rd. Caiapônia–Jataí, left margin, near spring with sulphur water, 14 Oct. 1968 (fl), S. Fonseca & E. Onishi 1542 (F, RB, UB); without locality, 21 Dec. 1873 (fl), A. Glaziou s.n. (P P00729458); Pouso Alto, nos pantanos, 24 Aug. 1894 (fl, fr), A. Glaziou 21340 pro parte (mixed collection; mixed with some individuals of *Acisanthera pulchella*, Melastomataceae) (R); “Ponte Lavrado à Cuba,” 18 Aug. 1894 (fl), A. Glaziou 21692 (BR, P [2 sheets], R, S); Mun. Jataí, locality Balsamo, 19 Jul. 1951 (fl), A. Macedo 3334 (S, US); Mun. Quirinópolis, Serra da Confusão do Rio Preto, Faz. Boa Sorte [ca. 18°26'S, 50°26'W], no meio da vereda, em local alagado, 757 m, 8 Aug. 2014 (fl, fr), I.L.M. Resende 3363 (SPF); Mun. Quirinópolis, Serra da Confusão do Rio Preto, Faz. Boa Sorte, no meio da vereda, em local alagado, 757 m, 3 Oct. 2014 (fl, fr), I.L.M. Resende 4027 (SPF); Goiânia, near EFO-MARGO, base of Morro de Santo Antônio, 5 Sep. 1968 (fl), J.A. Rizzo & A.M. Barbosa 2127 (NY, UB, UFG); Mun. Morrinhos, rd. Morrinhos–Caldas Novas [ca. 17°43'S, 49°4'W], Córrego Samambaia, 29 Aug. 1970 (fl), J.A. Rizzo & A.M. Barbosa 5457-A (UFG); “Goyaz,” without locality, 1816–1821 (fl, fr), A. Saint-Hilaire Catal. C1 747 (P [P00729269]). **Mato Grosso:** Poconé, Rodovia Transpantaneira, 178.4 km de Cuiabá, Pantanal, solo úmido, 116 m, 16°37'42”S, 56°46'17”W, 1 Dec. 2005 (fl), R.M. Harley et al. 55369 (HUEFS); Coxim [ca. 18°30'S, 54°45'W], May 1911 (fl), F.C. Hoene 3220 (R), 3222 (R), 3223 (R), 3225 (R); Barra do Rio Camaré, Juruena, Ilha do meio do rio, Jan. 1912 (fl), F.C. Hoene 5181 (R); Porto Velho do Rio Arinos, planta rasteira das margens do rio e de um lago, Nov. 1914 (fl), J.G. Kuhlmann 1486-K (F, R); 1° de Fevereiro, Rio Cautario, margens do rio, Jan. 1919 (fl), J.G. Kuhlmann 2362-K (B†, R; photo-B at MO, NY); Mun. Santa Cruz do Xingu, Parque Estadual do Xingu, limite NE do parque, subindo o Rio Fontourinha, 9°42'19”S, 52°21'16”W, 250 m, 1 Mar. 2011 (fl), D.C. Zappi et al. 3037 (RB). **Minas Gerais:** Uberlândia, Clube Caça e Pesca Itororó [ca. 18°55'S, 48°17'W], campo úmido, borda do brejo, 13 Aug. 1993 (fl), A.A. Arantes 44 (HUFU); Uberlândia, Clube Caça e Pesca Itororó, 29 Sep. 1994 (fl), A.A. Arantes 203 (HUFU); “Inter Tejuco et Rio Paranahyba,” s.d. (fl), W.J. Burchell 5814 (BR, P); Mun. Campina Verde, Arenitos, várzea, sandy soil, 19 Jun. 1989 (fl), A. Macedo 5537 (NY, US); Mun. Campi-

na Verde, brejo, 19°32'8”S, 49°29'11”W, 2 Jul. 2005 (fl), A. Macedo 5913 (NY, US); “Habitat in rudis campis uliginosis ad Buritizaes, crescit Chap. do Par., Provinciae MG”, Sep. [1818], C.F.P. Martius Iter Brasil. 2907 (M M0198164); “Prov. Minas Geraes”, without locality, s.d. [February–Sep. 1818], C.F.P. Martius Iter Brasil. 2908 (M M0198160); “olho d'agoa” [Olho d'Água], 1816–1821 (fl, fr), A. Saint-Hilaire s.n. (P P00729270); “Minas Gerais,” without locality, 1816–1821 (fl, fr), A. Saint-Hilaire Catal. C1 977bis (P [P00729272]); “Minas Gerais,” without locality, 1816–1821 (fl, fr), A. Saint-Hilaire Catal. B1 1817 (P [P00729271]), 1929 (P [P00729274]); Campina Verde, Faz. São João do Lajeado, 20 Jul. 2003 (fl, fr), J.F. dos Santos 5841 (US). **Rondônia:** Rio Guaporé, Fazenda Santa Rosa, mata, 11 Jun. 1952 (fl, fr), G.A. Black & E. Cordeiro 52-14823 (IAN). **São Paulo:** Without locality, 1833 (fl), C. Gaudichaud Herbar Imperial du Brésil N. 99 (P); São Carlos, brejos dos cerrados [ca. 22°S, 47°53'W], 22 Apr. 1963 (fl), M. Kuhlmann 3077 (RB, SP); Mogy-Guaçu [Mogi Guaçu, ca. 22°22'S, 46°56'W], 27 Jul. 1889 (fl, fr), A. Lofgren 1337 (SP). **Tocantins:** Mun. Lagoa da Confusão, Ilha do Bananal, Parque Nacional do Araguaia, área ca. 3 km da sede do parque, Lago Rufino, solo escuro, floresta de galeria mesofítica, 10°26'48”S, 50°28'25”W, 210 m, 21 Mar. 1999 (fl), M. Aparecida da Silva et al. 4034 (RB). **Without state:** Without locality, s.d., A. Glaziou s.n. (P [barcode 00729458]).

3-2. *Limnosipanea palustris* (Seem.) Hook.f., Ic. pl. 11: 38. 1868. (Figures 16A-E, 17).

(=) *Sipanea* [as “*Sipania*”] *palustris* Seem., Bot. Voy. Herald 136. 1854; non *Sipanea palustris* (A. Rich.) J.H.Kirkbr., Brittonia 49: 360. 1997, *comb. illeg. superfl.* (= *Sipanea wilson-brownei* R.S.Cowan); non *Bertiera palustris* A.Rich. ex DC. (Sep. 1830: 392 [see *Neobertiera palustris*, below]).

Type: PANAMÁ: Near Panama City, swamps, s.d. [1846–1849], B.C. Seemann 347 (**lectotype** BM [barcode BM 000614301], **here designated**; isolecotype K [without barcode]; photo-BM at BM, MO, NY, US).

(=) *Limnosipanea schomburgkii* Hook.f., Ic. pl. 11: 38. 1868.

Type: GUYANA. [“Roraima”, sic!], Rovuma River, s.d. [1842–1843], R.H. Schomburgk ser. II, 464 (= M.R. Schomburgk 744) (**lectotype** BM [BM000614338], **here designated**; isolecotypes F [Acc. No. 766892], G [2 sheets, barcodes G00379139,

G00379140], K [without barcode], P [barcode P00729461], US [barcode 00588519]; photo-P at NY; photo-G at F [Neg. No. 25681]).

(=) *Limnosipanea schomburgkii* var. *robustior* Pilg., Bot. Jahrb. Syst. 30: 198. 1901 [title page of the volume reports “1902” but the third page of the same volume reports that “Heft 2 (pp. 129–288)” was published in “2 July 1901”].

Type: BRAZIL. Mato Grosso: Near Cuiabá “gesellig in kleinen Complexen auf trockner Wiese bei Cuyabá,” Apr. 1899 (fl), *R. Pilger 400* (holotype B [barcode B100673663]).

*Herbs*, terrestrial or semi-aquatic (amphibious), erect, 5–40 cm tall, single-stemmed or sparsely branched; stems sparsely to densely appressed pubescent, or pubescent and with two kinds of hairs, antrorsely appressed and spreading intermixed. *Stipules* reduced to a line between the petioles, sparsely appressed-pubescent, with 1 to 3 colleters inserted just below the margin on the internal side, with the tips exerted beyond the margin. *Leaves* homophyllous, opposite or ternate, or sometimes ternate at basal nodes and opposite at distal nodes of the same plant, sessile; blades narrowly ovate, oblong-ovate, elliptic to lanceolate, 5–18 × 1–8 mm, round, obtuse to subobtuse at base, acute at apex, chartaceous, pale green below, drying olive-green, glabrous or sparsely appressed pubescent above and below, midvein strigose to glabrate above and below, margins sometimes ciliate; secondary veins 2–4 each side of midrib. *Inflorescence* 0.5–12 cm long, 2–4-dichotomously branched, with one flower at the base of each bifurcation, 2–many flowered; frondose, with leaf-like bracts subtending secondary branches; bracteoles subtending flowers elliptic-lanceolate to narrowly lanceolate, 4–6.5 × 1–1.5 mm, strigose-pubescent, margins ciliate. *Flowers* sessile or short-pedicellate in central flowers. *Hypanthium* narrowly ellipsoid to narrowly obovoid, 0.7–1 mm long, densely hispid, with white, erect hairs ca. 1 mm long. *Calyx* lobes narrowly lanceolate to linear, 2.5–5 × 0.3–0.6 mm, sparsely hirsute outside, glabrous inside, with 1 broadly triangular to deltoid, 0.05–0.1 mm long colleter at each lobe sinus. *Corolla* hypocrateriform, white to cream-white, 5.7–10 mm long; tube narrowly cylindrical, 3.5–6.5 mm long, strigose outside, sparsely villose at mouth

inside, glabrous below; lobes oblong-ovate, 2.2–3.5 × 0.7–0.9 mm, obtuse to round at apex, glabrous on both sides. *Filaments* 1.5–1.7 mm long; anthers oblong, 0.7–0.8 × 2.5–3 mm. *Style* 5.5–7.5 mm long, glabrous, style branches narrowly oblong, 0.5–0.8 mm long. *Capsules* sessile, globose, 2.5–3.5 × 2–2.5 mm, hispid-setose. *Seeds* 0.2–0.4 × 0.2–0.4 mm, strongly foveolate.

**Taxonomic observations:** Seeman (1854: 136) did not indicate his collection number or the herbarium of deposit for *Sipanea* [as “*Sipania*”] *palustris* Seem. Delprete (2010b: 624) indicated the type of this name as “Seeman 347 (holótipo, K; isotipo K, fotos em NY).” Lorence et al. (2012: 138) indicated as type “Seeman 347 (foto MO! ex BM)”. According to the *Code*, as they were published after 2001, both Delprete’s and Lorence’s statements cannot be interpreted as inadvertent lectotypifications because they did not include “here designated” or a similar expression. Therefore, the specimen *Seeman 347* at BM, barcode BM 000614301, is here designated as the lectotype of this taxon.

Hooker (1868: 38) along with the description of *Limnosipanea schomburgkii* Hook.f. cited the gathering “Schomburgk 464 (744)” without citing the herbarium of deposit. Hooker’s citation corresponds to the gathering *R.H. Schomburgk ser. II, 464* (= *M.R. Schomburgk 744*). A specimen at BM, barcode BM000614338, has the label “464, Schomburgk, Coll. 1842-3, Roraima, Brit. Guiana” is here designated as the lectotype of this name. Duplicate specimens are at F, G, K (with the handwritten label “464 (744), Sipanea, Roraima, British Guiana, Schomburgk 1843”), P and US are isolectotypes.

Pilger (1901) described *Limnosipanea schomburgkii* var. *robustior* Pilg. and cited the collection *Pilger 400* from Mato Grosso, Brazil. As he worked at Berlin, and there is only a specimen of *Pilger 400* in that herbarium, it is the holotype specimen. This variety fits within the morphological variation of the species and no variety is recognized in *L. palustris*.

Steyermark (1967: 282) differentiated *Limnosipanea schomburgkii* by the entire calyx lobes, opposite leaves, and its occurrence in “Southern Venezuela, probably British Guiana [Guyana] and Brazil” keeping *L. palustris* separated because of the bi-aristate calyx lobes, whorled leaves (3–4 per node), and restricted to Panama. As already stated by Delprete (2010b), after a detailed analysis of specimens from the whole distribution, these charac-

**Figure 16.** A–E. *Limnosipanea palustris*. A. Habit. B. Flower in anthesis. C. Dissected corolla. D. Longitudinal section of ovary and calyx. E. Dehiscent capsule. F–L. *Limnosipanea spruceana* var. *spruceana*. F. Habit. G. Dehiscent capsule. H. Longitudinal section of ovary and calyx, with colleters at lobe sinuses. I. Seeds. J. Dissected corolla. K. Young fruit subtended by two leaf-like bracts. L. Node with whorled leaves. Illustration by Bruno Manara (Reproduced with permission from *Flora de Venezuela* vol. 9(1), fig. 61. 1974, as *L. schomburgkii* Hook.f.).

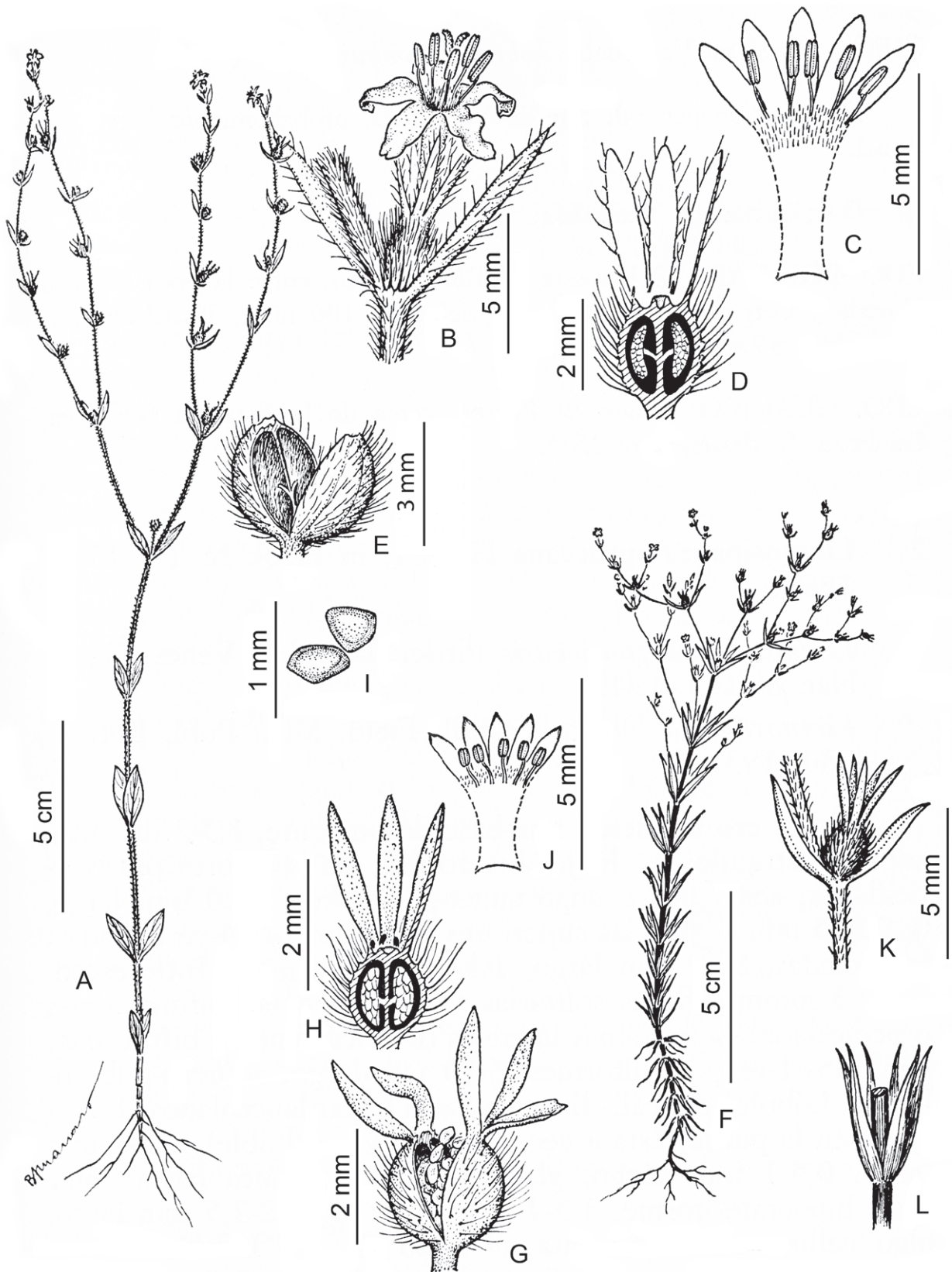


Figure 16.



ters were found to be variable throughout the geographic range, and the two taxa are treated as synonymous.

**Distribution and ecology:** Distributed in Panama, Colombia, Venezuela, Guyana, and Brazil, on the Guiana and Brazilian Shields (Figure 18). Short-lived semi-aquatic or terrestrial herb, sprouting just after the water of the flooded area has dissipated, in seasonally inundated areas in open savannas and along streams, at 100–1200 m altitude.

*Limnosipanea palustris* (Seem.) Hook.f. has been collected at least six times in populations intermixed with *L. spruceana* var. *spruceana*: **COLOMBIA: Guaviare:** Río Guaviare, San José del Guaviare [ca. 2°34'N, 72°38'W], sabana, 240 m, 13 Nov. 1939 (fl, fr), *J. Cuatrecasas* 7714 (COL, F, US, mixed collection). **Meta:**

Río Meta, Orocué, 140 m, sabana, 3 Nov. 1933 (fl, fr), *J. Cuatrecasas* 4363 (COL, F, P, US; mixed collection); **VENEZUELA: Bolívar:** Morichal, 2 km E of Río Orinoco, between Río Horeda and Cerro Gavilan (Cerro Carichana), 100 m, 17 Dec. 1955 (fl, fr), *J.J. Wurdack & J.V. Monachino* 39942 (F, MO, NY, S, US, VEN; mixed collection), 39944 (NY, VEN; mixed collection). **GUYANA:** Rupununi District, Chaakoitou, 29 Oct. 1979 (fl, fr), *P.J.M. Maas & L.Y.T. Westra* 4100 (*L. palustris*; K, MO, NY, P, S, U), 4101 (*L. spruceana*; BBS, F, NY, S, U).

**Phenology:** In Guyana, flowering and fruiting during the dry season, from August to October. In Central Brazil, flowering and fruiting from the end of the rainy season to the beginning of the dry season, from April to June.

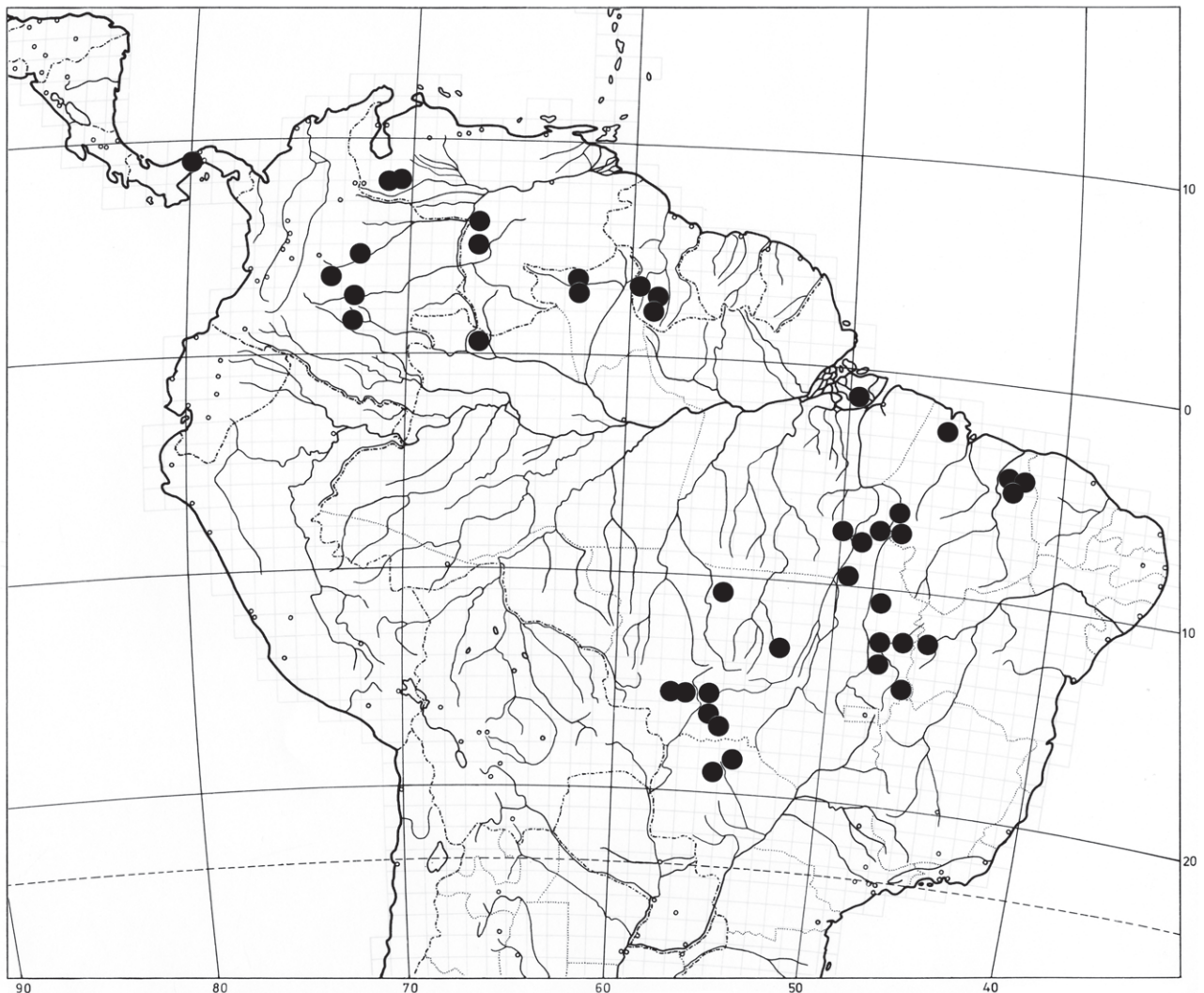


Figure 17. Distribution of *Limnosipanea palustris*.

**Suggested conservation status: Least Concern (LC).** Species ranging from Panama, Colombia, Venezuela, Guyana to Brazil. In Brazil it has been collected in the states of Amazonas, Bahia, Goiás, Maranhão, Mato Grosso, Pará, Piauí, Roraima, and Tocantins. It is a short-lived, semi-aquatic or terrestrial herb, usually found in seasonally inundated areas in open savannas and along streams. The size of the populations is unknown. In addition, it is poorly collected due to its small size and its short life span. Considering the numerous sites of occurrence, without imminent threats, this species is here treated as Least Concern (LC) following IUCN criteria (IUCN 2012, 2019).

**Specimens studied: COLOMBIA: Arauca:** Mun. Arauca, corregimiento Caracol, Vda. La Maporita, Finca La Maporita, 6,933297 N, -70,461718 W, 117 m, sabana alta abierta, 10 Dec. 2015 (fl, fr), *J.C. Arias et al. 3070* (COL); Mun. Arauca, corregimiento Caracol, Vda. La Maporita, Finca La Maporita, 6,946514 N, -70,452555 W, 122 m, sabana alta abierta, 11 Dec. 2015 (fl, fr), *J.C. Arias et al. 3100* (COL). **Casanare:** Río Meta, Orocué [ca. 1°48'N, 72°45'W], 140 m, sabana, 3 Nov. 1933 (fl, fr), *J. Cuatrecasas 4363 pro parte* (Mixed collection; COL, F [2 sheets], P, US). **Guaviare:** Río Guaviare, San José del Guaviare, sabana, 240 m, 13 Nov. 1939 (fl, fr), *J. Cuatrecasas 7714 pro parte* (Mixed collection; COL, F, US). **Meta:** 73 km W of Las Gaviotas, along rd to Puerto Gaitán [ca. 4°18'N, 72°4'W], low lying savanna along drainage channel now dried to mud at this time of the year, 210 m, 30 Dec. 1973 (fl, fr), *G. Davidse 5386* (COL, F, NY); Boca de Monte, Llanos de San Martín [ca. 3°41'N, 73°41'W], 300 m, open savanna, 16 Aug. 1950 (fl, fr), *S. Galen Smith & J.M. Idrobo 1389* (COL, F), 1398 (US); Cabuyaro, 10 Jan. 1899 (fl, fr), *T.A. Sprague 57* (BM); Llano de San Martín, La Quebradita, 200 m, 16 Aug. 1950 (fl, fr), *J. Triana 3248(2)* (COL, F). **State Unknown:** without locality, 1844 (fl, fr), *J. Goudot s.n.* (P P00728115).

**VENEZUELA. Amazonas:** Depto. Atures, 56 km NE of Puerto Ayacucho, 170 m, 22 Nov. 1984 (fl), *R. Kral et al. 71775* (NY, TFAV, US). **Apure:** “plaines marecageuses entre l'Apure et l'Arauca,” 1894 (fr), *F. Geay s.n.* (P [P00729254]); “savane marecageuses du Guaritico,” 1894 (fr), *F. Geay s.n.* (P [P00729253]); Depto. Paez, Módulo F., Corrales de la Unellez, Carretera a La Victoria, 28 Dec. 1985 (fl), *B. Stergios & P. Stergios 8802* (PORT, US). **Bolívar:** “Orenoque” [Río Orinoco], 1844 (fr), *J. Goudot s.n.* (FI-Webb); Morichal, 2 km E of Río Orinoco, between Río Horeda and Cerro Gavilan (Cerro Carichana), 100 m, 17 Dec. 1955 (fl, fr), *J.J. Wurdack & J.V. Monachino 39942 pro parte* (Mixed collection;

F, NY, S, US, VEN), 39944 (NY, VEN). **Guárico:** Dto. Infante, Parque Nacional Aguaro-Guariquito, Morichal Charcote, 9°24'-32'N, 67°64'-68'W, 70 m, Dec. 1981 (fl), *F. Delascio, R. Montes & G. Davidse 11121* (NY, US, VEN); Dto. Infante, Parque Nacional Aguaro-Guariquito, Saladillal Los Galapagos, 9°04'-08'N, 67°52'-56'W, 60 m, Dec. 1981 (fl, fr), *F. Delascio et al. 11234* (MO, NY, VEN).

**GUYANA:** Rupununi Distr., Kuyuwini Landing, Kuyuwini River, savanna, 1 km S of river, 2°05'N, 59°15'W, 150–250 m, 9 Oct. 1992 (fl, fr), *M.J. Jansen-Jacobs et al. 2796* (CAY, F, MO, NY, P, U, US); Rupununi Distr., Dadanawa, savanna, near pond, 2°49'N, 59°31'W, 120 m, 19 Aug. 1995 (fl), *M.J. Jansen-Jacobs et al. 4781* (P, U, US); Rupununi Distr., Dadanawa, savanna, near pond, 2°49'N, 59°32'W, 120 m, 19 Aug. 1995 (fl), *M.J. Jansen-Jacobs et al. 5376* (BBS, MO, NY, U, US); Rupununi Distr., Chaakoitou, near Mountain Point, just S of Kanuku Mts., 2°56'N, 59°40'W, 29 Oct. 1979 (fl, fr), *P.J.M. Maas & L.Y.T. Westra 4100* (F, K, MO, NY, P, S, U).

**BRAZIL: Amazonas:** Frechal, Maruay, entre pedras graníticas, Sep. 1927 (fl, fr), *P. Luetzelburg 20448* (R); Rio Piriá, Sep. 1959 (fl, fr), *N.T. Silva 555* (IAN). **Bahia:** Near Rio Piau, ca. 150 km SW of Barreiras, 14 Apr. 1966 (fl, fr), *H.S. Irwin et al. 14789A* (UB). **Goiás:** Mun. Cavalcante, RPPN Serra do Tombador, trilha do Borá, 13°42'2”S, 47°46'32”W, 900 m, 17 Apr. 2013 (fl, fr), *E. Barboza et al. 3694* (MBM); Mun. Campos Belos, estrada para Pouso Alto, ca. 18 km a direita da Usina Mosquito, 12°55'29”S, 46°25'6”W, 680 m, 26 Apr. 2001 (fl), *M.L. Fonseca et al. 2612* (RB, US); Serra do Morcego [ca. 15°S, 46°W], near Córrego Estrema, ca. 38 km NE of Formosa, 800 m, 21 Apr. 1966 (fl), *H.S. Irwin et al. 15198* (NY); “Bresil Central, Salinas”, May–Jun. 1844 (fl, fr), *M.A. Weddell 2026* (P), 2054 (P), *s.n.* (P 00729260). **Maranhão:** Perizes, campo, 6 Jul. 1954 (fl, fr), *G.A. Black et al. 54-16543* (IAN); Itapicurú, campo alto, 8 Jul. 1954 (fl, fr), *G.A. Black et al. 54-16658* (IAN, RB); Mun. Carolina, margem esquerda do Rio Farinha, próximo a ponte na BR-010, 6°51'49”S, 47°28'6”W, 150 m, 25 Apr. 2008 (fl, fr), *G.P. Silva et al. 13338* (CEN); Mun. Carolina, estrada Carolina–Babaçulândia, km 8.2, margem direita do Rio Tocantins, kms marcados da Igreja São Francisco, Bairro Brejinho, 7°18'25”S, 47°30'18”W, 170 m, 22 May 2010 (fl, fr), *G.P. Silva et al. 15288* (CEN); perto de Carolina [ca. 7°19'S, 47°28'W], campo cerrado, 26 May 1950 (fl), *J.M. Pires & G.A. Black 2164* (IAN), 2280 (IAN); Mun. Santa Elena [ca. 2°13'S, 45°18'W], near locality Queimados, Campos da Chapada, terra firme, 9 Jul. 1978 (fl, fr), *N.A. Rosa & O.C. Nascimento 2564* (IAN, MG, NY, RB, UEC, UFG). **Mato Grosso:** Chapada dos Guimaraes, Alto do Paredão, acima do Assentado, 10

May 1983 (fl, fr), *J. Barcia et al. 1460* (R); Cuiabá, Sep. 1984 (fl, fr), *G.M. Barroso s.n. (RB 225234)* (RB); Mun. Itaúba, Resgate de Flora da UHE Colíder, floresta do Planalto do Parecis, região ecótono entre Floresta Amazonica e Cerrado, L 0672562, 8783385, 268 m, 27 Apr. 2017 (fl, fr), *M.E. Engels et al. 5359* (RB, TANG); Mun. Porto Estrela, Fazenda Salobrinha, 14 May 1995 (fl, fr), *G. Hatschbach et al. 62745* (US); Serra do Roncador, wet campo, ca. 60 km N of Xavantina, 550 m, 24 May 1966 (fr), *H.S. Irwin et al. 15951* (NY, US [2 sheets]); Cuiabá, Morrinho de Santo Antonio, loco aperto humido parce graminoso, 26 Apr. 1894 (fl), *G.O.A. Malme 1578* (F, R, S [2 sheets], US); Cuiabá, 3 May 1894 (fl), *G.O.A. Malme 1578t* (F, S [2 sheets]); Cuiabá, “in arenosis apertis humidis in consortio *Poteranthera*, *Acisanthera*, etc.,” Jun. 1902 (fl), *G.O.A. Malme 1654* (F, S); near Cuiabá, Aricá, in campo argiloso-arenoso humido, 8 May 1903 (fl, fr), *G.O.A. Malme 1654a* (S); near Cuiabá, Aricá, 17 Jun. 1903 (fr), *G.O.A. Malme 1654b* (S); Cuiabá, in arenosis apertis, 9 Jun. 1902 (fr), *G.O.A. Malme 1694* (S); Santa Anna da Chapada [now Chapada dos Guimarães], 31 May 1903 (fr), *G.O.A. Malme 3413* (S); Poconé, Estrada para Porto Cercado, km 18, campo de murundum, sazonalmente alagável, seco no momento da coleta, 22 Apr. 1993 (fl, fr), *A.L. do Prado 2009* (UEC); Poconé, Estrada Poconé–Porto Cercado, km 18, campo de murundum, sazonalmente alagável, seco no momento da coleta, 22 Apr. 1993 (fl, fr), *A.L. do Prado 2035* (UEC); Poconé, Rodovia Poconé–Porto Cercado, proximidade da entrada para Baía Acurizal, 2 km após o sítio, campo de murundum, sazonalmente alagável, seco no momento da coleta, 22 Nov. 1992 (fl, fr), *A.L. do Prado et al. 2767* (UEC); Mun. Poconé, behind Poconé Agriculture Exposition Center, seepage area, 16 Jun. 1979 (fl, fr), *G.T. Prance & G.B. Schaller 26249* (NY, UFMT); Pantanal de Poconé, Faz. Nossa Senhora Aparecida, campo de murunduns, May 2007 (fl), *L. Rebellato 196* (UFMT); Pantanal Mato-Grossense, District of Poconé, highway Poconé–Porto Cercado, at km 16.9, 16°21’S, 56°29’W, 120 m, 15 Jul. 1992 (fl), *M. Schessi 2627b* (UFMT). **Mato Grosso do Sul:** Coxim [ca. 18°30’S, 54°45’W], campos humidus, May 1911 (fl, fr), *F.C. Hoene 11414* (ex *Com. Rondon N. 3231*) (F, SP). **Pará:** Ilha de Marajó, Rio Camará, Fazenda Gurupatuba, campina, 8 Jul. 1950 (fl, fr), *G.A. Black 50-9900* (IAN); [Ilha de] Marajó, Rio Camará, Jutuba, Sep. 1902 (fl, fr), *V.C. de Miranda s.n. (MG 3200)* (MG); Conceição do Araguaia [ca. 7°33’S, 49°42’W], beira de campo, 24 Jun. 1953 (fr), *R.L. Frões 29911* (IAN). **Piauí:** Mun. Campo Maior [ca. 4°50’S, 42°10’W], Baixão da Cobra, 25 May 2002 (fl), *C.G. Lopes et al. 149* (TEPB); Mun. Piracuruca, Parque Nacional Sete Cidades, área A1 do levantamento fitos-

sociológico, campo limpo úmido, 4°3’45’’S, 41°43’24’’W, 12 May 2007 (fl, fr), *M.R.A. Mendes 17* (TEPB); Mun. Piracuruca, Parque Nacional Sete Cidades, Córrego Barreiro, Ponto 56, campo úmido com afloramentos rochosos, solo arenoso, 4°3’45’’S, 41°43’24’’W, 153 m, 23 Jul. 2007 (fl, fr), *R.C. Mendonça & C. Fagg 6124* (RB); Mun. Piracuruca, Parque Nacional Sete Cidades, campo limpo úmido, solo hidromórfico argiloso, 4°5’9’’S, 41°43’38’’W, 22 Aug. 2006 (fl, fr), *C.B.R. Munhoz et al. 3132* (RB). **Roraima:** Mun. Boa Vista, Estação Ecológica de Maracá [ca. 3°24’N, 61°41’W], campo, solo arenoso, 23 Nov. 1978 (fl, fr), *J. Lima de Souza 307* (BM); [“Rio Branco”], campo bei Serra do Mel [ca. 4°11’N, 60°52’W], Surumu, Sep. 1909 (fl, fr), *E. Ule 8326* (L, MG). **Tocantins:** Mun. Porto Nacional [ca. 10°42’S, 48°25’W], rd. towards Fazenda dos Buritis, cerrado, 21 May 2000 (fl, fr), *E.A. Anunciação & A.V.C. Gonçalves 901* (HTO, UFG); “inter Porto Real et Santa Anna” [between Porto Nacional and Santa Ana], s.d. [1829], *W.J. Burchell 8945* (L, P, U); “inter Funil et S. João, ad fluv. Tocantins” [between Funil et S. João, near the Tocantins River], s.d. [1829], *W.J. Burchell 8945* (BR); “São Pedro de Alcantara”, 8 May 1829 (fl), *W.J. Burchell 8945* (NY) [labels of *W.J. Burchell 8945* report three different collection localities]; Mun. Porto Nacional, near access rd. to Caneta, 29 May 2001 (fl), *C.G. Oliveira Jr. et al. 14* (HTO); Varedão do Relâmpago, duas léguas de Carolina (Maranhão), 28 May 1950 (fl, fr), *J.M. Pires & G.A. Black 2391* (IAN, U), *2409a* (IAN); Mun. Couto de Magalhães [ca. 8°17’S, 49°14’W], Rio Araguaia, campos gerais, terreno úmido, 5 Jul. 1953 (fl, fr), *R.L. Frões 30128* (IAN, U); Mun. Pium [ca. 10°S, 49°W], 10 km from Barreira da Cruz, near city of Pium, local úmido, 12 Jun. 1974 (fl, fr), *J.A. Rizzo 9861* (UB, UFG); Mun. São Salvador do Tocantins, Canteiro de obras do UHE São Salvador, left margin of Rio Tocantins, Fazenda Serrinha, 330 m, 12°48’S, 48°14’W, 14 Jun. 2006 (fl, fr), *G.P. Silva et al. 10661* (CEN, HUTO, UFG).

3-3. *Limnosipanea spruceana* Hook. f., *Icon. Pl.* 11: 38, pl. 1050. 1868. (Figures 4E–F, 16F–L, 17–21).

For types, synonyms, and varieties, see below.

*Herbs*, terrestrial, semi-aquatic (amphibious) or aquatic, polymorphic, commonly ephemeral, rarely perennial when growing in permanently submerged areas; erect or decumbent, single-stemmed or sparsely branched; terrestrial plants 10–30 cm tall; semi-aquatic or aquatic plants with stems 7–65 cm long, submerged portion up to 50 cm long, glabrous, aerial portion 5–15 cm long, appressed-strigose to appressed-pubescent or

rarely glabrous; perennial plants growing in permanently flooded areas (i.e., with natural springs) with the submerged stem woody at base. *Stipules* reduced to a line between the petioles or obsolete, glabrous outside, without colleters or with 1 or 2 colleters inserted just below the margin on the internal side, included or with the tips slightly exerted beyond the margin, or, when stipules obsoletes, 1 or 2 colleters inserted at leaf sinuses; in submerged stems, stipules and colleters absent. *Leaves* homophyllous or heterophyllous, dimorphic when basal portion of plant is submerged; on submerged plants, the *submerged leaves* 3–6(–8) per node, with blades linear to acicular, 5–20 × 0.4–0.7 mm, glabrous, without secondary veins (rarely with 1 secondary vein each side); the *aerial leaves* 2–5 per node, with blades linear to lanceolate, 3.5–12 × 0.3–5 mm, glabrous, with 1–2(–3) secondary veins on each side of midrib; in plants entirely terrestrial (i.e., never partially submerged), the leaves are homophyllous and similar to those of the aerial portion of the partially submerged plants. *Inflorescences* simple, unbranched, with 1–5 flowers, or branched, 2–3-chotomously branched, with one flower at the base of each bifurcation, 2–18.5 cm long, 2–multiflorous; bracteoles subtending flowers narrowly lanceolate to linear, 2–4.5 × 0.4–1.5 mm, glabrous or sparsely pubescent. *Flowers* commonly sessile, the central ones (at the base of a bifurcation) subpedicellate. *Hypanthium* narrowly ellipsoid to narrowly obovoid, 0.5–1 × 1–1.3 mm, glabrous or sparsely to densely hispid, with white hairs 0.5–0.7 mm long. *Calyx* lobes lanceolate to linear, 1.5–5.5 × 0.3–0.6 mm, aristate at apex (arista caducous) or not, glabrous throughout, sometimes with a few hispid hairs at margins, with 1 narrowly triangular to linear, 0.1 mm long colleter at each lobe sinus. *Corolla* hypocrateriform, 3–11.2 mm long, white to cream-white, rarely pale violet; tube narrowly cylindrical or narrowly imbutiform, 2–4.7 mm long, glabrous outside, with a ring of yellow hairs at mouth, glabrous below, inside; lobes ovate to oblong-ovate, 1–6.5 × 0.5–2.2 mm, obtuse to round at apex, glabrous on both sides. *Filaments* 0.4–0.8 mm long; anthers oblong, 0.5–0.7 × 0.2–0.4 mm. *Style* 2.5–5 mm long, glabrous; style branches oblong, 0.3–0.5 mm long. *Capsules* ovoid to subglobose, 2–4 × 1.5–2.5 mm, hispid-setose, glabrate, or glabrous. Seeds 0.2–0.3 × 0.2–0.3 mm, strongly foveolate.

**Phenology:** This species has a very short life span, and it is common to find flowers and fruits on the same individual. Its phenology varies according to the geographic positions of the populations, and corresponds to the local seasons. In the region north of the Equator (Colombia, Venezuela, Guyana, and Brazil: Roraima),

it is flowering and fruiting from September through December. In the region south of the Equator (Brazil: Amazonas, Goiás, Mato Grosso, Minas Gerais, Pará, Rondônia, and Tocantins; Bolivia: Santa Cruz) it is flowering and fruiting from May through July (August).

**Distribution and ecology:** Distributed on the Guiana and Brazilian Shields, in Colombia, Venezuela, Guyana, Brazil, and Bolivia; short-lived, semi-aquatic or terrestrial herb, coming up just after the water of the flooded area has dissipated, in seasonally inundated areas in open savannas, along streams, and *Mauritia* palm swamp communities (in Venezuela called “morichales” or “canguchales”, and in Brazil called “buritizais”), at 50–900 m altitude.

**Suggested conservation status:** See under varieties.

**Habit variation:** *Limnosipanea spruceana* is a polymorphic herb (Figure 18), single-stemmed or sparsely branched, that could be terrestrial and 7–25 cm tall (Figure 18F), or semi-aquatic (amphibious) or aquatic, with the submerged portion to 40 cm long and aerial portion to 25 cm long (including inflorescence) (Figure 18A–E). The leaves can also be dimorphic (Figure 18C–D), if some of them are submerged or not. In plants partially submerged, the leaves below water (Figure 18C) (when present) are 3–6(–8) per node, linear to acicular, 5–20 × 0.4–0.7 mm, without secondary veins (rarely with 1 secondary vein on each side of the midrib); while the aerial leaves (Figure 18D) are 2–5 per node, linear to lanceolate, 3.5–12 × 0.3–5 mm, with 1–2(–3) secondary veins each side of the midrib. In terrestrial plants (i.e., not partially submerged), the leaves are homophyllous and similar to those of the aerial portion of the partially submerged plants.

The variation in life span, habit and leaf shape is correlated with the water level present during a given season. In localities seasonally inundated, during the rainy season the water level varies from 0.3 to 2 m in depth, and might reach up to 4–5 m in depth in Amazonian savannas (Figure 19A–B). As the precipitations decrease, the water level gradually drops until the soil is still moist but no longer flooded; at this precise moment the terrestrial form of this species appears (Figure 18F), sometimes forming large stands, visible from a distance due to their characteristic red stem. In this form, the leaves are opposite or whorled, 3–5 per node, and linear to lanceolate. This form is particularly short-lived (Figure 18E–F), and can grow, disperse seeds and die within 3–4 months (pers. obs.; P.G. Delprete et al. 7433–7437).

In permanently flooded areas, as in localities with natural springs, the submerged portion of the stem could

be up to 40 cm long, not branched, green, with the basal portion leafless, with adventitious roots at each node, and the distal submerged portion with whorled leaves, 3–6(–8) per node, linear to acicular (Figure 18C), and without adventitious roots (Figure 18A–D). The aerial portion of these plants is 10–25 cm long (Figure 18A), including inflorescences, branched, with stems and rachis red-vinaceous, and leaves opposite or whorled, 3–5 per node, linear to lanceolate (Figure 18D). This form is perennial (pers. obs.; B.S. Marimon & P.G. Delprete BS-975).

In other cases, in seasonally flooded areas, with water 20–30 cm deep during the rainy season, plants of *Limnosipanea spruceana* are seasonally semi-aquatic (amphibious), with dimorphic leaves (Figure 18E); the submerged portion of the plants has simple or sparsely branched stems, with 3–6(–8) leaves per node, linear to acicular; while the aerial portion is 10–20 cm long (including inflorescences), with 2–5 leaves per node, linear to lanceolate. At the end of the rainy season, when the water is completely gone, the portion of stem that was submerged is laying on the ground, decumbent, with the distal portion erect (Figure 18E); at this stage, the whole stem and the rachis are red, due to sun exposure. This form is particularly short-lived, and can grow, disperse seeds and die within 3–4 months (pers. obs.; e.g., B.S. Marimon & P.G. Delprete BS-976).

#### Key to the varieties of *Limnosipanea spruceana*

1. Corollas 3–6(–7) mm long, with tubes 2–3(–3.5) mm long, lobes ovate to oblong-ovate, 1–3(–3.5) × 0.5–0.7 mm; filaments 0.4–0.8 mm long; anthers 0.5–0.7 mm long; style 2.5–5 mm long.....3a. *L. spruceana* var. *spruceana*
  1. Corollas 8.5–11.2 mm long, with tubes 3.5–4.7 mm long, lobes oblong to oblong-ovate, 4.5–6.5 × 1.5–2.2 mm; filaments 1.3–1.8 mm long; anthers 1 mm long; style 6.5–9 mm long..... 3b. *L. spruceana* var. *macrantha*
- 3-3a. *Limnosipanea spruceana* Hook.f. var. *spruceana*,  
Icon. Pl. 11: 38, pl. 1050. 1868. (Figures 4E–F, 16F–L,  
18–21).

Type: BRAZIL. Pará: “Amazon R., marshy and sandy places near Pará” [Santarem, at the mouth of the Tapajos River], Aug. 1850 (fl), R. Spruce 1027 (lectotype K [without barcode], designated by Delprete (2010b: 627); isolectotypes P [barcode 00729466], RB [ex P, barcode 00543629]; possible isolectotypes (without collector number) BM [barcode BM000614344], E [2 sheets, barcodes E00499997, E00499998], F [2 sheets, Acc. Nos. 768300 and 971288], FI-Webb [barcode FI004806], MPU [barcode MPU 021333], P [barcode 00729465]; S [Acc. No. S05-474]; photo-B and photo-K at NY).

(=) “*Sipanea* [as “*Sipania*”] *limnophila* Spruce” cited in synonymy by J.D. Hooker (1868: 38, tab. 1050), not valid, *pro syn.*

Type: BRAZIL. Pará: [Santarem, at the mouth of the Tapajos River], marshy and sandy places “near Pará”, Aug. 1850 (fl), R. Spruce 1027 (lectotype K [without barcode], here designated; isolectotypes P [barcode 00729466], RB [ex P, barcode 00543629]; probable isolectotypes (without collector number) BM [barcode BM000614344], P [barcode 00729465]; possible isolectotypes (without collection number) E [2 sheets, barcodes E00499997, E00499998], F [2 sheets, Acc. Nos. 768300 and 971288], FI-Webb [barcode FI004806], MPU [barcode MPU 021333], S [Acc. No. S05-474; photo-B and photo-K at NY).

(=) *Limnosipanea kuntzei* Standl., Publ. Field Columbian Mus., Bot. Ser. 7: 280. 1931.

Type: BOLIVIA. Velasco, 200 m, Jul. 1892 (fr), O. Kuntze s.n. (holotype US [Acc. No. 701742, barcode 00137736]; isotypes NY [2 sheets, barcodes 000132101 and 000132102).

(=) *Limnosipanea ternifolia* Pittier, Bol. Soc. Venez. Ci. Nat. 8: 144. 1943.

Type: VENEZUELA. Guárico: Llanos de Calabozo, Laguna de Palo Seco, entre la Encrucijada y la Mis-

**Figure 18.** *Limnosipanea spruceana* var. *spruceana*. **A–D.** Perennial form growing in permanently flooded areas, with heteromorphic leaves. **A.** Habit, with basal submerged portion with adventitious roots, medial submerged portion leafless, distal submerged portion with acicular leaves, and aerial portion with whorled leaves and terminal inflorescence. **B.** Basal portion of the submerged portion of the stem with adventitious roots at each node. **C.** Distal submerged portion of the stem with whorled, acicular leaves. **D.** Aerial portion of the stem with whorled, lanceolate leaves. **E.** Form growing in seasonally flooded area, at the end of the rainy season (water completely dissipated), with decumbent stem; basal portion of stem, originally submerged, leaning on the ground, and distal portion of the stem erect, with opposite or whorled leaves. **F.** Terrestrial, short-lived form, found in seasonally inundated localities, with homomorphic leaves basally opposite and distally ternate. **A–D:** drawn from Marimon & Delprete BS-975 (CAY); **E:** drawn from Marimon & Delprete BS-976 (CAY); **F:** drawn from Cuatrecasas 7714 (F). Illustration by Piero Delprete.

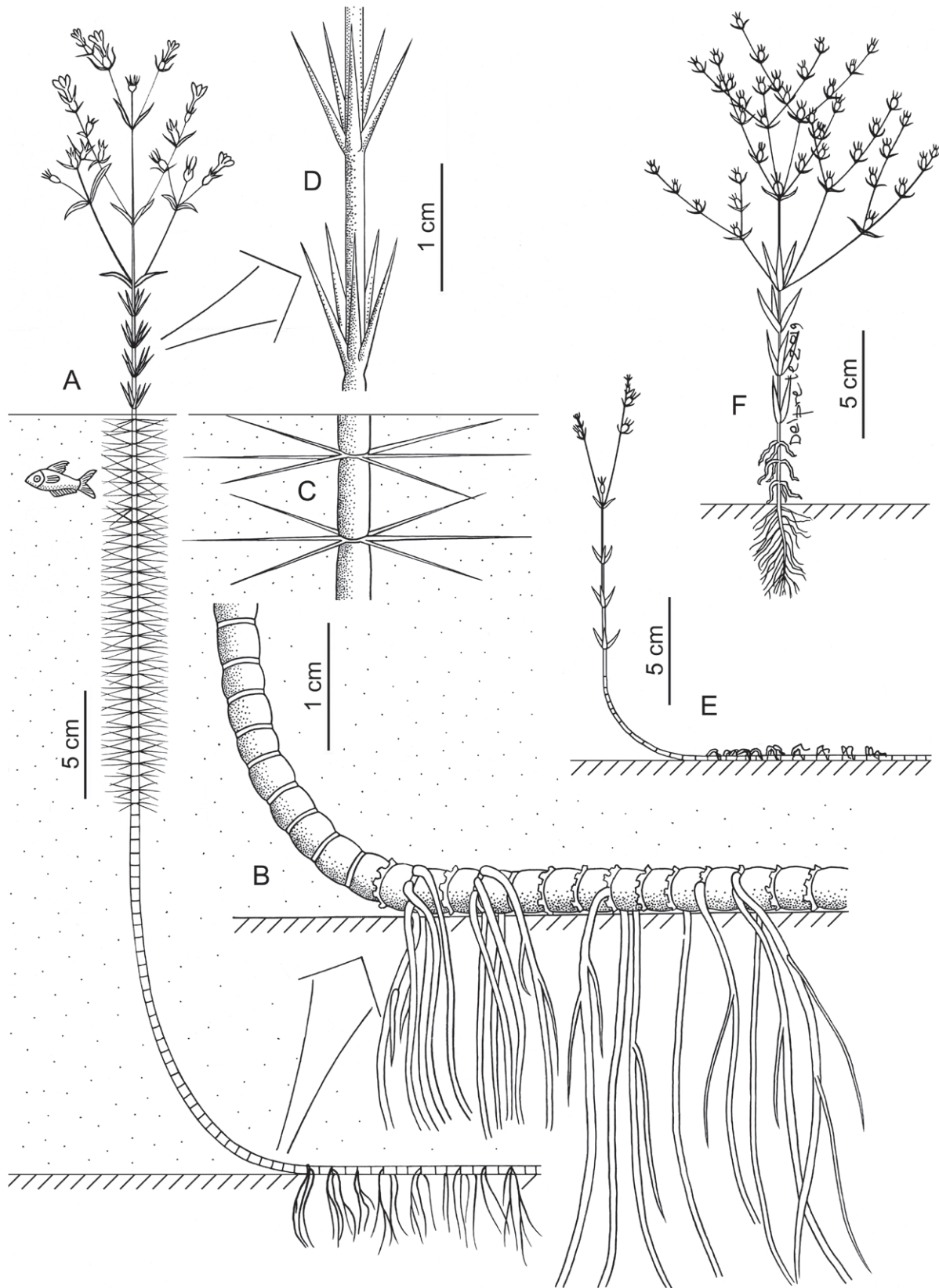
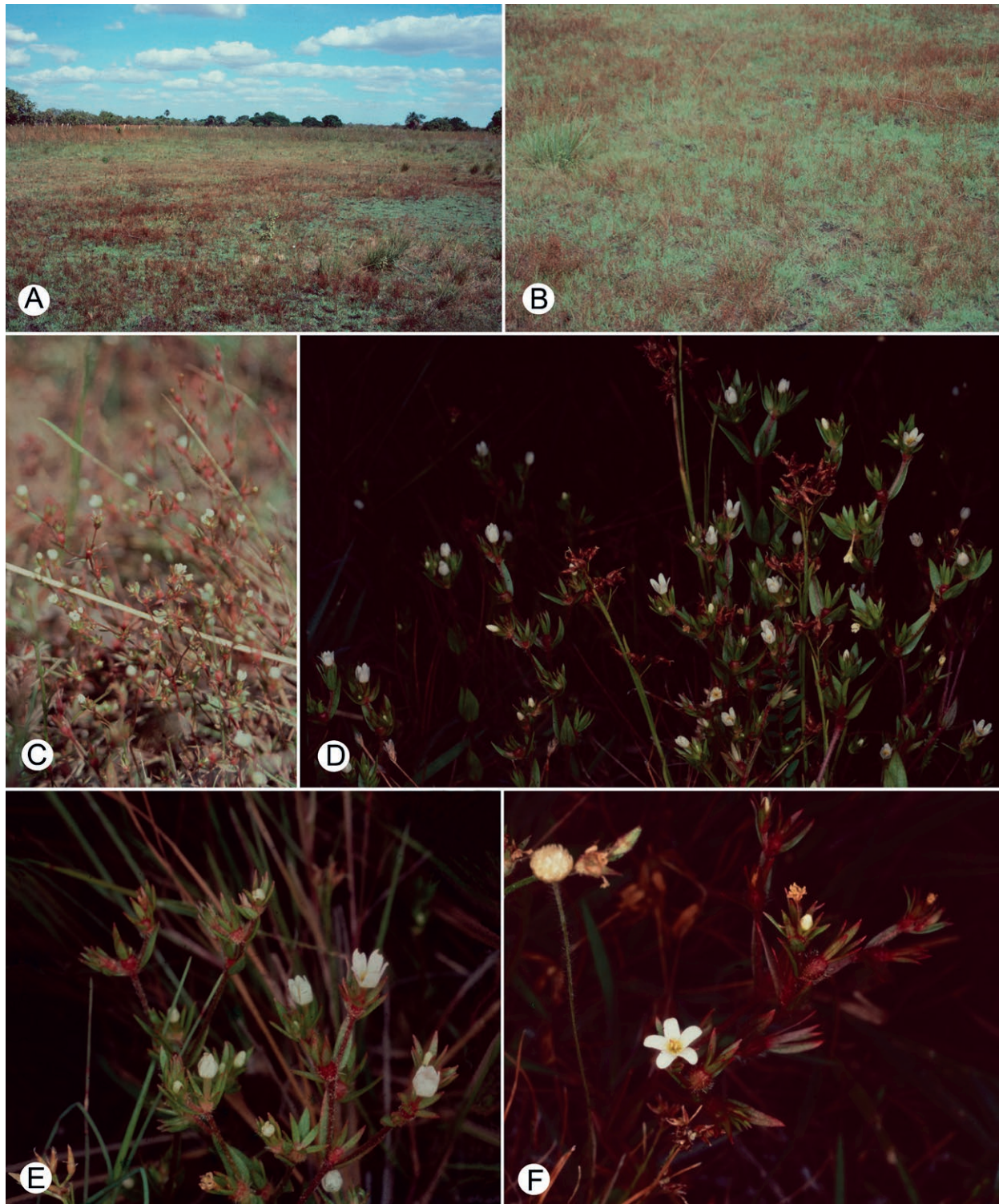


Figure 18.



**Figure 19.** *Limnosipanea spruceana* var. *spruceana*. **A.** General environment. During the rainy season (July–November) the water level reach 2–3 m in depth above the ground; the plants start growing in November–December, when the water above ground has almost completely dissipated, and the seedlings are fully or partially submersed. At the moment that these photos where taken, the soil was moist but without standing water. The red patches are populations of *L. palustris*. **B.** Detail of populations of *L. palustris* (red patches). **C–D.** Habit. **E.** Detail of branches with flower buds and corollas about to open. **F.** Detail of a branch with a flower in anthesis. Photos taken by Piero Delprete on 3 January 2001, in Mun. Puerto Ayacucho, Amazonas state, Venezuela, where *Delprete et al.* 7433–7437 were collected.

ión de Arriba, en terrenos periodicamente anegados, “10 Nov. 1941” [19 Feb. 1942] (fl, fr), *H. Pittier 14952* [same as *T. Lasser 130* (US, VEN, paratypes)] (holotype VEN [Acc. No. 15510]; isotypes F [Acc. No. 1268454], US [barcode 00137737]). While Pittier (1843: 144–145) in the publication reported the collection date “10 November 1941”, the specimen label at VEN reports the collection date “19 February 1942”.

(=) *Limnosipanea guaricensis* Pittier, Bol. Soc. Venez. Ci. Nat. 8: 145. 1943.

Type: VENEZUELA. Guárico: Llanos de Calabozo, en cienaga, Laguna de Palo Seco, cerca de la Misión de Arriba, en terrenos temporalmente anegados, “10 November 1941” [21 Feb. 1942] (fl, fr), *T. Lasser 145* (holotype VEN [Acc. No. 15508]). While Pittier’s (1943: 145) publication reports the collection date “10 November 1941” the specimen label at VEN reports the collection date “21 February 1942”.

*Herbs*, terrestrial, semi-aquatic (amphibious) or aquatic, polymorphic, commonly ephemeral, or perennial when growing in permanently submerged areas; erect or decumbent, single-stemmed or sparsely branched; terrestrial plants 10–30 cm tall; semi-aquatic or aquatic plants with stems 7–65 cm long, submerged portion up to 50 cm long, aerial portion 5–15 cm long, appressed-strigose to appressed-pubescent or rarely glabrous; perennial plants growing in permanently flooded areas (i.e., with natural springs) with the submerged stem woody at base. *Leaves* homophyllous or heterophyllous, dimorphic when basal portion of plant submerged; on submerged plants, the *submerged leaves* 3–6(–8) per node, with blades linear to acicular, 5–20 × 0.4–0.7 mm, glabrous, without secondary veins (rarely with 1 secondary vein on each side of midrib); the *aerial leaves* 2–5 per node, with blades linear to lanceolate, 3.5–12 × 0.3–5 mm, glabrous, with 1–2(–3) secondary veins each side; in plants entirely terrestrial, (i.e., never partially submerged), the leaves are homophyllous and similar to those of the aerial portion of the partially submerged plants. *Inflorescences* simple, not branched, with 1–5 flowers, or branched, 2–3-chotomously branched, with one flower at the base of each bifurcation, 2–18.5 cm long, 2–multiflorous; bracteoles subtending flowers narrowly lanceolate to linear, 2–4.5 × 0.4–1.5 mm, glabrous or sparsely pubescent. *Hypanthium* narrowly ellipsoid to narrowly obovoid, 0.5–1 × 1–1.3 mm, sparsely to densely hispid, with white, erect hairs 0.5–0.7 mm long, or glabrous. *Calyx* lobes lanceolate to linear, 1.5–5.5 × 0.3–0.6 mm, aristate at apex (arista

caducous) or not, glabrous throughout, sometimes with a few hispid hairs at margins, with 1, narrowly triangular to linear, 0.1 mm long, colleter at each lobe sinus. *Corolla* hypocrateriform, 3–6(–7) mm long, white, cream-white to pink, rarely pale violet; tube narrowly cylindrical or narrowly imbutiform, 2–3(–3.5) mm long; lobes ovate to oblong-ovate, 1–3(–3.5) × 0.5–0.7 mm, obtuse to round at apex, glabrous on both sides. *Filaments* 0.4–0.8 mm long; anthers oblong, 0.5–0.7 × 0.2–0.4 mm. *Style* exerted 0.7–1.5 mm beyond corolla mouth, 2.5–5 mm long, glabrous; style branches oblong, 0.3–0.5 mm long. *Capsules* ovoid to subglobose, 2–4 × 1.5–2.5 mm, hispid-setose, glabrate, or glabrous. *Seeds* 0.2–0.3 × 0.2–0.3 mm, strongly foveolate.

**Notes:** Hooker (1868: 38), along with the original description of *Limnosipanea spruceana* cited two collections made by Spruce in the Brazilian Amazon: 1) “*Sipanea* [sic] *limnophila*, Spruce 1027”, and 2) “Amazon River, marshy and sandy places near Pará [now Belém], Spruce (1851).”

Steyermark (1967) erroneously cited the type of *Limnosipanea spruceana* as “Vicinius Santarem, Prov. Pará, Brazil, August 1850, Spruce 677” without making any reference to the gathering cited by Hooker in the original publication, and without citing the herbarium of deposit. Because of these errors, Steyermark’s typification is invalid. Therefore, a new lectotypification was necessary, selecting a specimen out the gatherings cited by Hooker. Delprete (2010b: 627) designated the specimen *Spruce 1027* preserved at K, where Hooker worked, as the lectotype for this taxon. The lectotype specimen bears the label “1027 *Sipanea limnophila* sp. n., Santarem marshy and sandy valley inundated by the Tapajos [River], [...], Spruce 1851.” The information “*Sipanea limnophila* sp. n. [nom. illeg., pro syn.]” and “Spruce 1851” are in darker ink, and were probably written by an unknown author, and “1851” refers to the collection date. A duplicate specimen of *Spruce 1027* at RB is an isolectotype. The specimen has a label with the heading “Herb. Mus. Paris,” the stamp “Ex Herbario Musei Parisiensis” and the handwriting (author unknown) “Spruce 1027.”

Hooker (1868: 38) cited “*Sipanea* [as “*Sipanea*”] *limnophila* Spruce” in synonymy under *Limnosipanea spruceana* and cited the gathering *Spruce 1027* for both names. Therefore, *L. limnophila* is not a valid name.

For additional information about the synonymy of *Limnosipanea spruceana* and *L. ternifolia* Pittier, see Delprete & Steyermark (2004b).

**Distribution and ecology:** Distributed on the Guiana and Brazilian Shields, in Colombia, Venezue-



la, Guyana, Brazil, and Bolivia (Figure 20). Short-lived semi-aquatic or terrestrial herb, coming up just after the water of the flooded area has dropped, in seasonally inundated areas in open savannas, along streams, and *Mauritia* palm swamps, or a perennial herb when growing in permanently submerged areas; growing at 50–900 m altitude.

**Phenology:** See phenology of the species (above).

**Suggested conservation status: Least Concern (LC).** This variety has the same geographic distribution as the species, and ranges from Colombia, Venezuela, and Guyana, to Bolivia and Brazil. In Brazil it is known by numerous collections from the states of Amazonas, Goiás, Mato Grosso, Minas Gerais, Pará, Rondônia, Roraima and Tocantins. It is a terrestrial, semi-aquatic (amphibious) or aquatic, polymorphic herb, commonly short-lived, or perennial when growing in permanently inundated areas.

Personal observations of a large population were made in January 2001 (Delprete *et al.* 7433–7437) at about 45 km north of the city of Puerto Ayacucho, state of Amazonas, Venezuela. That area was seasonally inundated, with water levels reaching 2–3 m above the ground during the rainy season, which in that region spans from July to October. At the time the locality was visited, at the beginning of the dry season, the water had receded, the soil was moist, without standing water, and it was dominated by herbs 30–70 cm tall. According to the information supplied by the locals, the area was subjected to sporadic cow grazing during the dry season; however, the cows were not present at that moment. The population of this species covered an area of several hectares and was estimated to be of several thousands individuals. Apparently the population was not impacted by the sporadic cow grazing, because, due to the ephemeral life span, the plants succeeded in germinating, growing and dispersing seeds before the cows were allowed in the area.

Two populations were personally observed in June 2007 in the state of Mato Grosso, Brazil. One population, near the town of Nova Xavantina (Marimon & Delprete BS-975), was growing in a permanent lagoon, with crystal-clear water originating from natural springs. The water depth ranged from 15 to 70 cm deep. The population was composed of perennial, amphibious individuals, with the submerged portion of the stem 10–50 long, and the aerial portion with flowers in anthesis. The population was quite healthy, esteemed to be a few hundred individuals, although their exact number was not counted.

The other population observed in the state of Mato Grosso was located in the municipality of Barra do Gar-

ça, along the road BR-158 (Marimon & Delprete BS-976). That area was seasonally inundated, with water levels reaching 20–30 cm above the ground during the rainy season, observed by watermarks on local vegetation, which in that region spans from the end of September to May. At the time it was visited, 10 June 2007, the water had receded, the soil was moist, without standing water, and was dominated by small herbs. The population covered an area of numerous hectares and was esteemed to be of several thousand individuals. In the area, numerous cow footprints were observed, although no cow was seen at that moment. As observed in the seasonally inundated area in Venezuela, apparently the population was not impacted by the presence of cows.

Taking into account the vast extent of occurrence (EOO > 20,000 km<sup>2</sup>), numerous sites of occurrence, and the above observations, this species is here treated as Least Concern (LC) following IUCN criteria (IUCN 2012, 2019).

**Specimens examined: COLOMBIA: Casanare:** Río Meta, Orocué, 140 m, sabana, 3 Nov. 1933 (fl, fr), *J. Cuatrecasas* 4363 *pro parte* (Mixed collection; F [2 sheets], P, US); Mun. Paz de Ariporo, Corr. La Hermosa, Finca Nicaragua, Congrial, llanura aluvial de desborde, 5°36'35"N, 70°21'48"W, 115 m, 8 Nov. 2004 (fl, fr), *J.G. Ramírez Arañzo et al.* 9259 (COL). **Guaviare:** Río Guaviare, San José del Guaviare [ca. 2°34'N, 72°38'W], sabana, 240 m, 13 Nov. 1939 (fl, fr), *J. Cuatrecasas* 7714 *pro parte* (Mixed collection; COL, F, US). **Meta:** Serranía entre los Ríos Ariari y Meta, Llano Grande, matas de monte, 320 m, 26 Nov. 1939 (fl), *J. Cuatrecasas* 7885 (COL, F, US).

**VENEZUELA: Amazonas:** Depto. Atures, Mun. Puerto Ayacucho, ca. 45 km N of Puerto Ayacucho, on rd towards Parhueña, area seasonally inundated, field dominated by grasses and small herbs 30–70 cm tall, 5°45'N, 67°30'W, 150 m, 3 Jan. 2001 (fl, imm fr), *P.G. Delprete et al.* 7433 (CAY, GB, L, MO, NY, P, ufg, VEN), 7434 (B, BR, K, US, VEN), 7435 (CAY, G, GB, MO, P, US, VEN), 7436 (F, K, MG, NY, UFG, VEN), 7437 (L, MO, VEN). **Bolívar:** Dtto. Cedeño, km 12 de la carretera Caicara del Orinoco-Puerto Ayacucho, S of Caicara del Orinoco, 6°50'N, 66°30'W, 100 m, 18 Nov. 1984 (fl), *G. Aymard & B. Stergios* 3313 (NY, PORT); Dtto. Roscio, sabanas húmedas, morichales y bosques de Galeria en el Hato La Divina Pastora, ca. 8 km N de Santa Elena de Uairén, 4°42'N, 61°2'W, 840 m, 6 Oct. 1982 (fl, fr), *O. Huber & C. Alarcon* 6701 (NY, US, VEN); Morichal, 2 km E of Río Orinoco, between Rio Horeda and Cerro Gavilan (Cerro Carichana), 100 m, 17 Dec. 1955 (fl, fr), *J.J. Wurdack & J.V. Monachino* 39942 *pro parte* (Mixed

collection; F, NY, S, US, VEN), 39944 (NY, VEN). **Guárico:** Ca. 32 km SSE of Calabozo, on Finca Becerra, in and around morichal with standing water, morichal dominated by *Mauritia flexuosa*, 65 m, 6 Nov. 1973 (fl, fr), *G. Davidse 3791* (MO, NY, VEN); Dto. Infante, Parque Nacional Aguaro-Guariquito, Congriales de La Gorra, entre La Esperanca y Mesa de Cambao, 9°12'–16'N, 67°48'–60'W, 60 m, Dec. 1981 (fl, fr), *F. Delascio et al. 11204* (MO, NY, VEN); Llanos de Calabozo, near Mision de Arriba, sandy soil, 10 Nov. 1941 (fl, fr), *T. Lasser 130* (US, VEN, paratypes); Morichal La Becerra, al S de la Estación Biológica, vía paso del Caballo, 5 Nov. 1988 (fl), *P. Suárez S. 42* (NY, VEN).

**GUYANA:** Rupuruni Distr., Dadanawa, Rupuruni River, around pond, 2°50'N, 59°30'W, 100–150 m, 23 Sep. 1992 (fl, fr), *M.J. Jansen-Jacobs et al. 2615* (BBS, CAY, K, NY, P, U, US); Rupuruni Distr., Chaakoitou, near Mountain Point, just S of Kanuku Mts., 2°56'N, 59°40'W, 29 Oct. 1979 (fl), *P.J.M. Maas & L.Y.T. Westra 4101* (BBS, F, NY, S, U).

**BRAZIL: Amazonas:** Mun. Humaitá, lagoa temporária entre igarapés Retiro e Bom Futuro, N da estrada para Manaus, a 15 km da cidade, vegetação flutuante aparecendo 20 cm acima da água, 7°31'S, 63°10'W, 11 May 1980 (fl), *J.D. Gemtchujnicov & A. Janssen 366* (US); Mun. Humaitá, lagoa temporária entre igarapés Retiro e Bom Futuro, campo N da estrada 319, 657 km, vegetação flutuante aparecendo 20 cm acima da água, 7°31'S, 63°10'W, 11 May 1980 (fl), *A. Janssen & J.D. Gemtchujnicov 368* (INPA, MG, RB, SP). **Goiás:** Mun. Uruaçu, 13 km NE of village of Água Branca, 27 km from BR-153 (Belém–Brasília), region of Fazenda Amarra Cachorro, campo limpo de murundum, trans. para o cerrado em toda direção, solo areno-argiloso encharcado no local, camada de turfa, area inundated by the dam of Serra da Mesa, 14°22'S, 49°1'W, 470 m, 6 Aug. 1992 (fl), *B.M.T. Walter et al. 1956* (CEN). **Mato Grosso:** Vila Bela da Santíssima Trindade, Rod. MT-246, Pontes e Lacerda-Vila Bela da Santíssima Trindade, 35 km após ponte sobre rio na saída de Pontes e Lacerda, margem esquerda, estrada de acesso a propriedade particular, 1 km rumo ao sul, 15°8'6"S, 59°37'44"W, 239 m, 18 Jun. 2012 (fl, fr), *L.M. Borges et al. 766* (RB, SPF); Road Barra do Garças–Xavantina, 25 km from Xavantina, standing water and margin of ponds, white fl., herb, rooted under water, 9 Jun. 1966 (fl), *D.R. Hunt & J.F. Ramos 5902* (NY, P, R, SP, UB), 5904 (NY, SP, UB); near Cuiabá, Aricá, 5 Jun. 1894 (fl, fr), *G.O.A. Malme 1662* (F, R, S[2 sheets], US), 8 May 1903 (fl, fr), 2260 (F, S), 8 May 1903 (fl), 3260 (F, R); Mun. Nova Xavantina, town of Nova Xavantina, Rua da Palha, Lagoa do Saibro, lagoa natural com água cristalina, com nascentes nas margens, água de 15–70

cm de profundidade, erva anfibia, monocaule, porção submersa de 10–50 cm de compr., caule submerso verde, com raízes adventícias brancas, caule emerso e raquis vermelho-vinoso, corolas brancas, 14°40'34"S, 52°20'2"W, 280 m, 8 Jun. 2007 (fl), *B.S. Marimon & P.G. Delprete BS-975* (B, BR, C, CAY, F, G, GB, K, L, MG, MO, NY, NX, P, RB, S, UFMT, US); Mun. Barra do Garças, estrada Barra do Garças–Nova Xavantina (BR-158), km 747, campo sazonalmente inundado, neste momento sem água em cima do solo, pela vegetação é possível deduzir que a água chegou a 20–30 cm de profundidade, erva anfibia, monocaule, porção que era submersa (agora deitada no chão) de 10–20 cm, porção emersa de 10–20 cm, caule e raquis completamente vermelhos porque expostos ao sol, corolas brancas, 15°27'17"S, 52°12'6"W, 300 m, 10 Jun. 2007 (fl), *B.S. Marimon & P.G. Delprete BS-976* (B, BR, C, CAY, F, G, GB, K, L, MG, MO, NY, NX, P, RB, S, UFMT, US); Mun. Poconé, estrada Poconé–Porto Cercado, ca. 4 km após o Rio Bento Gomes, herbácea, flores alvas, frutos jovens avermelhados, frequente em pequenas ondulações do terreno com acúmulo de matéria orgânica, 27 May 1988 (fl, fr), *Pantanal do Poconé 25* (UFMT); Poconé, Estrada para Porto Cercado, Faz. Santa Carmen, km 18, campo de murundum com mata, sazonalmente alagável, seco [no momento da coleta], 22 Apr. 1993 (fl, fr), *A.L. Prado 2022* (UEC); Poconé, Estrada Poconé–Porto Cercado, Faz. Santa Carmen, km 18, campo sazonalmente alagável, nível de água 5 cm, 13 May 1992 (fl, fr), *A.L. Prado et al. 2783* (UEC). **Mato Grosso do Sul:** Coxim [ca. 18°30'S, 54°45'W], campos húmidos, May 1911 (fl, fr), *F.C. Hoene 3233* (R), 3234 (R). **Minas Gerais:** “ante Pirapora” [near town of Pirapora, ca. 17°20'S, 44°56'W], s.d. [1820], *J.E. Pohl 3326* (F [Acc. No. 869868], W [3 sheets; Acc. Nos. W-0072337, W-0072339, W-0072340]) (see below for discussion). **Pará:** Óbidos, campos ao NE do Lago Mariapixy, 19 Jul. 1912 (fl), *A. Ducke s.n. (MG 12014)* (MG); [Ilha do Marajó] Currálinho [ca. 1°48'S, 49°47'W], campo natural, 22 Aug. 1948 (fl, fr), *J.M. Pires 1263* (IAN); Canaã dos Carajás, Serra da Bocaina – Serra dos Carajás, Lagoa do Buritiranal, margem da lagoa de canga, secando, 6°18'43"S, 49°52'21"W, 692 m, 23 Jun. 2015 (fl), *N.F.O. Mota et al. 3406* (BHCB); Santarem, Aug. 1850 (fl, fr), *R. Spruce 677* (B†, M [barcode M-0198159], NY [barcode 00132103], RB [without collection number, RB 17398]; photo-B at F; erroneously cited by Steyermark (1967) as the type of *L. spruceana*). **Rondônia:** [“Guaporé”], Rio Guaporé, Fazenda Santa Rosa, planta aquática, 11 Jun. 1952 (st), *G.A. Black & Cordeiro, E. 52-14889* (IAN). **Roraima:** Rio Cantá, campina, 8 Oct. 1951 (fl, fr), *G.A. Black 51-13865* (IAN); Boa Vista (“Rio Branco”), Oct. 1913 (fl, fr), *J.G. Kuhlmann 851* (RB [2 sheets]); Manaus–Vene-

zuela road (BR-174), estrada Manaus-Boa Vista, between Mucajá and Boa Vista, W side of Rio Branco opposite Serra Grande, damp savanna on sand, 21 Nov. 1977 (fl), *W.C. Steward et al.* 142 (NY); Manaus-Venezuela road (BR-174), Malacacheta, E of Boa Vista, wet savanna on sand, 4 Dec. 1977 (fl, fr), *W.C. Steward, I. Araujo, W.R. Buck, J.F. Ramos & J. Ribamar* 251 (INPA, NY, P). **Tocantins:** Mun. Santa Isabel, Ilha do Bananal, Parque Nacional do Araguaia, caminho para Riozinho, campo de murundum, solo periodicamente inundável, 20 Jun. 1979 (fl, fr), *F. Cardoso da Silva et al.* 242 (UB).

**BOLIVIA: Santa Cruz:** Prov. Velasco, Parque Nacional Noel Kempff Mercado, pampa húmeda SW del campamento, 13°33'3"S, 61°3'31"W, 200 m, 25 May 1994 (fl, fr), *E. Gutiérrez et al.* 1132 (MO, NY); Prov. Velasco, Estancia Flor de Oro, W side of the Río Guaporé (Río Iténez), flat, grazed grass savanna near airstrip, with regularly spaced brush-covered and/termite mounds with *Cybistax antisyphilitica*, *Brosimum gaudichadii*, *Curatella americana*, *Simarouba*, on fine recent alluvium, 13°33'S, 61°1'W, 190 m, 21 Jun. 1991 (fl, fr), *M. Nee* 41158 (MO, NY); Velasco, Parque Nacional Noel Kempff Mercado, Pampa Toledo, 5–10 km NE del Campamento Los Fierros, sobre el camino a Tarbo, pampa húmeda, con islas arbóreas termiteras, 200 m, tallos rojizos, flor rosada, fruto pubescente y rojizo, 1 Jul. 1993 (fl, fr), *M. Saldias et al.* 2897 (US).

**Specimens with erroneous locality: BRAZIL:** “Rio de Janeiro: São João da Barra, dans les boursiers [in swamps]”, 6 Feb. 1876 (fl, fr), *A. Glaziou* 9887a (P [P00729291], R [Acc. No. 10468, barcode R010049086]).

The specimen labels of *Glaziou* 9887 and *Glaziou* 9887a report a dubious collection locality, with different collection dates and different ecologies. The labels of both gatherings indicate that they were collected in São João da Barra [ca. 21°38'24'S, 41°3'3"W], which is a coastal town at the northern portion of the State of Rio de Janeiro, mostly “floresta de tabuleiro” and “restinga” vegetation. The gathering *Glaziou* 9887 is *Sipanea pratensis* var. *dichotoma*; which is a variety that does not occur in the state of Rio de Janeiro (see discussion under this variety). The label of the specimen of *Glaziou* 9887a at R (Acc. No. 10468, barcode R010049086) has the heading “PLANTAS DO BRASIL CENTRAL, GLAZIOU N°” and the handwritten text “9887a. *Limnosipanea Spruceana* Hook., Flora Bras. VI, VI, p. 253. São João da Barra (Rio de Jan. [Rio de Janeiro]), 6 de Fevereiro de 1876. Herbacea flores rosas.”

The specimen of *Glaziou* 9887a at P, barcode P00729291, has two labels. At the lower left corner is a label handwritten by Glaziou in pencil reporting “N.

9887a. São João da Barra, dans les boursiers (Rio\_J), 6 fevrier 1876. Fl. roses.” The other label, at the lower right corner, has the printed heading “HERB. MUS. PARIS” and the text, handwritten in black ink by Glaziou “*Limnosipanea Spruceana* Hook. BRÉSIL (Rio Janeiro) São João da Barra, dans les boursiers [in swamps], 6 fevrier 1876, Fl. roses, n. 9887a” and the lower printed text “Herbier de A. Glaziou, donné par Mme SIMART, sa fille, en 1907.” [Glaziou herbarium, donated by Mrs. Simart, his daughter, in 1907].

The specimens *Glaziou* 9887a at P and R are *Limnosipanea spruceana* var. *spruceana*. Schumann (1889) did not cite the gathering *Glaziou* 9887a in *Flora Brasiliensis*. This variety is a terrestrial, semi-aquatic or aquatic herb, usually found in seasonally or permanently inundated areas, along streams and in swamps. It ranges from Colombia, Venezuela, the Guianas, to north-central Brazil. In Brazil it has been collected in the states (arranged from North to South) of Roraima, Amapá, Amazonas, Pará, Tocantins, Rondônia, Mato Grosso, Goiás, and Minas Gerais. The closest collection to the state of Rio de Janeiro was made by Pohl in 1820 (*J.E. Pohl* 3326 (F, W)) near Pirapora [ca. 17°20'S, 44°56'W], a town on the margin of the São Francisco River, in the northern portion of the state of Minas Gerais; this is the only collection reported from this state, and the southernmost collection of this species (see below). The town of Pirapora is about 630 km air distance from São João da Barra. It is well-known among botanists (Santos, 2016; Sleumer, 1954; Smith, 1966; Wurdack, 1970) that for numerous specimens Glaziou reported localities where he never was, and included Amazonian collections in his herbarium citing them as collected by him in Rio de Janeiro. Therefore, although there is no direct evidence that *Glaziou* 9887a has not been collected in São João da Barra, I assume that this specimen has a label reporting an erroneous collection locality, and I conclude that this taxon does not occur in the state of Rio de Janeiro. Schumann (1889, p. 253) under *Limnosipanea spruceana* cited the collection “ante Pirapora: Pohl n. 3326” without citing the Brazilian state. Most likely, this gathering was collected near the town of Pirapora, state of Minas Gerais, and, as far as I know, is the only collection of this species from that state, and is the southernmost record of this specie. The nearest collection, *B.M.T. Walter et al.* 1956 (CEN), is from the Municipality of Uruaçu, 14°22'S, 49°1'W, state of Goiás, and was made in the area that is now inundated by the dam of Serra da Mesa. Therefore, particular attention is given to the gathering *Pohl* 3326. Pohl (1976, Portuguese translation), in his travel diary reports that he was at the “Fazenda Pirapora”, now the town of Pirapora, state of Minas Gerais, on

20–21 Jul. 1820, however he did not report the collection of any specific plant.

There are three sheets of *Pohl* 3326 at W. Sheet with accession number W-0072339, has eight plants mounted on it and one label with the heading “HERB. MUSEI PALAT. VINDOB. (Botanische Abtheilung des K. K. Naturhist. Hofmuseums Wien.)” with the handwritten text “3326, *Limnosipanea* sp., Thurnheisera galioides, Brasilia. Pohl.” Specimen with accession number W-0072340, has ten plants mounted on it and one label with the printed heading “HRB. MUSEI PALAT.

VINDOB. (Botanische Abtheilung des K. K. Naturhist. Hofmuseums Wien.)” and the handwritten text “3326, ante Pirapora, Pohl.” Specimen with accession number W-0072337 has thirteen plants mounted on it and three labels, without the heading of the Wien Museum. The label at the bottom center has the text handwritten by Schumann “*Limnosipanea Spruceana* HKpt [? sic]” and the stamp “determ. C. Schumann”. The label at the bottom right corner has the handwritten text “3326, *Limnosipanea* sp., Hb. Bras., Thurnheisera galioides, Ante Pirapora. Pohl.” The third label, positioned above the other

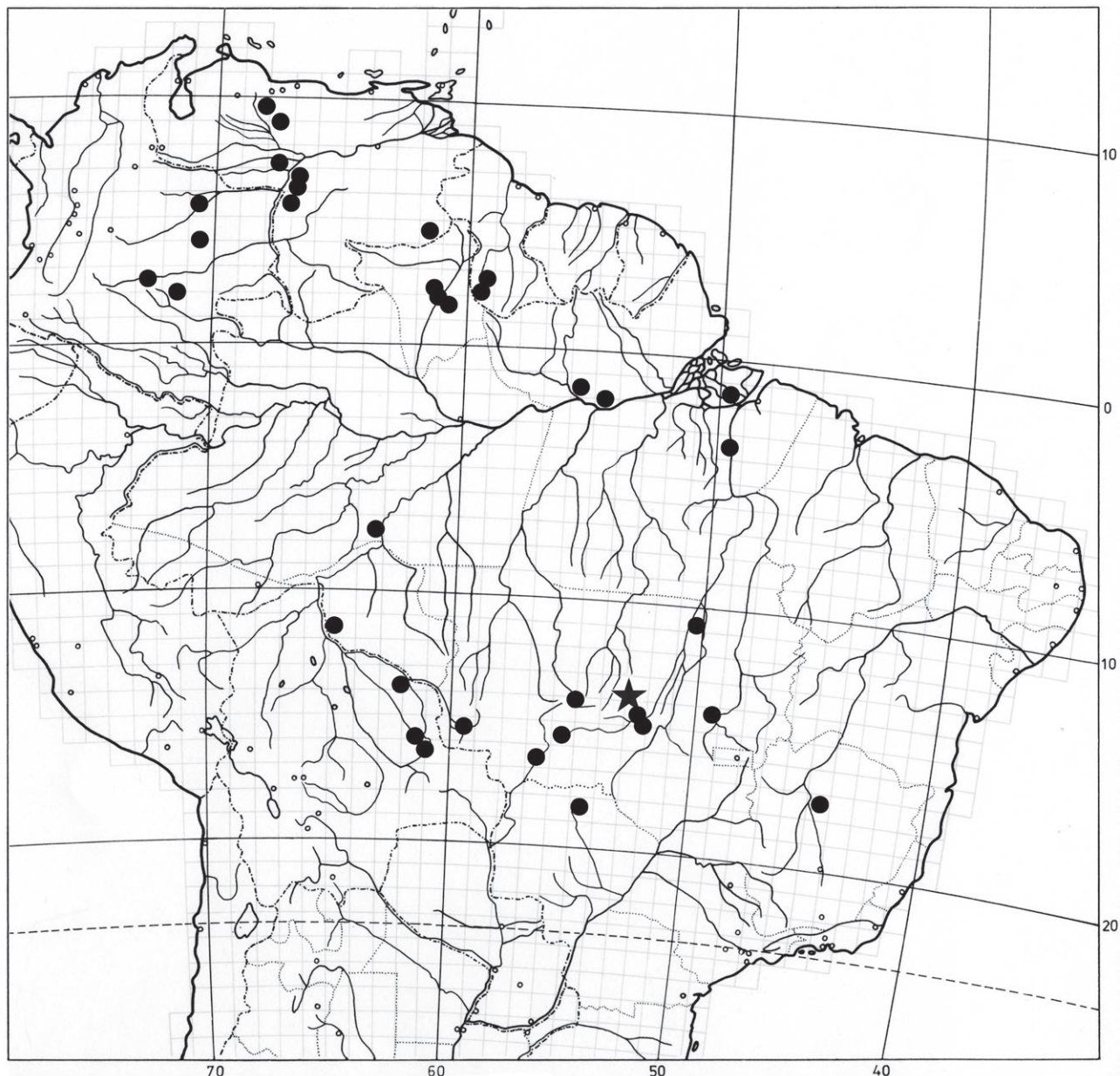


Figure 20. Distribution of *Limnosipanea spruceana* var. *spruceana* (circles) and *L. spruceana* var. *macrantha* (star).

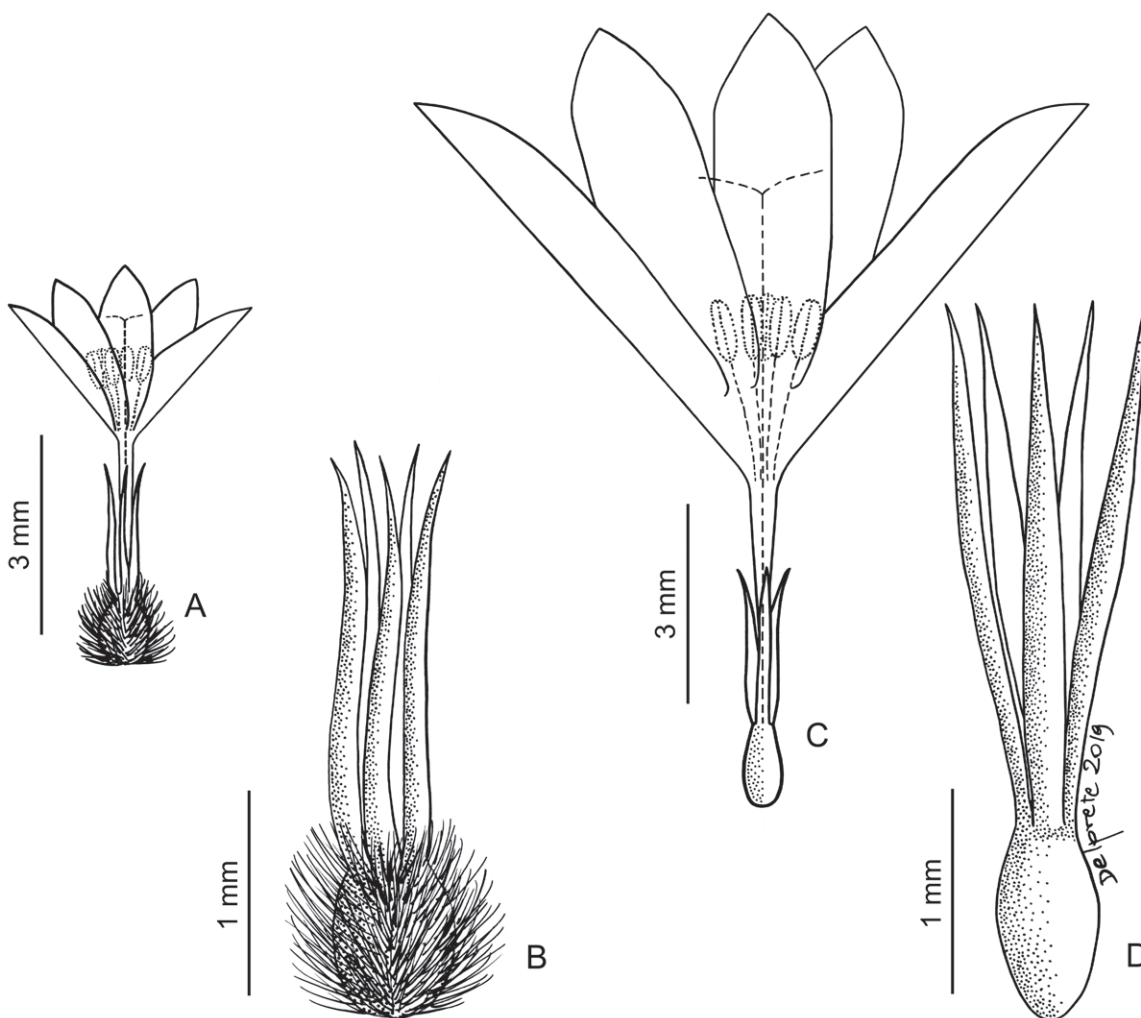
two labels, also has the stamp “determ. C. Schumann” (with “determ.” stroke through), and the text, handwritten by Schumann, “Hiervon wären einige Stengel für das Berliner Herbar sehr erwünscht”, which means “From this one [the sheet] some stems [plants] would be very appreciated by the Berlin Herbarium” (English translation by Bruno Wallnöfer). In other words, Schumann asked to extract some of the plants from this sheet to be deposited in the herbarium in Berlin [now B]. But apparently he didn’t receive any, because nothing was detached from the sheet, in which case this would have been annotated by the herbarium curators on that sheet (interpretation of the text and observations by Bruno Wallnöfer).

At F there is one specimen of *Pohl 3326*, Acc. No. 869868, with a single plant preserved in an enve-

lope glued on the sheet. This sheet has a label with the printed heading “HERB. MUSEI HIST. NATUR. VINDOBON. (Botanische Abtheilung des K. K. Naturhist. Hofmuseums Wien.)” indicating that this specimen was extracted from one of the sheets at W. Such label also has the handwritten text (author unknown) “*Limnosipanea Spruceana*, Pohl 3326, Brazil.”

3-3b. *Limnosipanea spruceana* Hook.f. var. *macrantha* Delprete, var. nov. (Figures 20–21).

Type: BRAZIL. Mato Grosso: Mun. Nova Xavantina, Drainage of the Upper Rio Araguaia, periodically flooded campo, ca. 30 km S of Xavantina



**Figure 21.** Flower comparison of *Limnosipanea spruceana* var. *spruceana* and var. *macrantha*. **A–B.** *L. spruceana* var. *spruceana*. **A.** Flower in anthesis. **B.** Detail of hypanthium and calyx. **C–D.** *L. spruceana* var. *macrantha*. **C.** Flower in anthesis. **D.** Detail of hypanthium and calyx. **A–B:** drawn from Marimon & Delprete BS-976 (CAY); **C–D:** drawn from Irwin et al. 17014 (NY). Illustration by Piero Delprete.

[ca. 14°54'31"S, 52°16'36"W], ca. 400 m, herb with ascending stems to ca. 20 cm long, 12 Jun. 1966 (fl), H.S. Irwin, R. Souza, J.W. Grear & R. Reis dos Santos 17014 (holotype UB [Acc. No. 43389]; isotypes F [Acc. No. 1677438], IAN [Acc. No. 130279], MO [Acc. No. 3172561], NY, RB [Acc. No. 145574], US).

**Diagnosis:** *Limnosipanea spruceana* Hook.f. var. *macrantha* Delprete differs from the typical variety by the aerial portion of the stem glabrous (vs. appressed-strigose to appressed-pubescent or glabrous in var. *spruceana*); hypanthium ellipsoid, 1–1.1 × 0.5–0.7 mm (vs. narrowly ellipsoid to narrowly obovoid, 0.5–1 × 1–1.3 mm); corollas 8.5–11.2 mm long (vs. 3–6(–7) mm long), with tube 3.5–4.7 mm long (vs. 2–3(–3.5) mm long) and lobes oblong to oblong-ovate, 4.5–6.5 × 1.5–2.2 mm (vs. ovate to oblong-ovate, 1–3(–3.5) × 0.5–0.7 mm); filaments 1.3–1.8 mm long (vs. 0.4–0.8 mm long); anthers narrowly ellipsoid, 1.0 × 0.4 mm (vs. oblong, 0.5–0.7 × 0.2–0.4 mm); and style 6.5–9 mm long (vs. 2.5–5 mm long). (Figure 21).

**Description:** *Herbs*, semi-aquatic (amphibious) or aquatic, erect or decumbent (when the submerged part of the stem laying on the ground after the water receded), single-stemmed; stem 35–50 cm long, submerged portion up to 34 cm long, glabrous (laying on the ground after the water has receded), aerial portion 10–15 cm long, glabrous. *Leaves* heterophyllous, dimorphic; *submerged leaves* 3–6(–8) per node, with blades linear to acicular, 5–14 × 0.2–0.5 mm, glabrous, without secondary veins; *aerial leaves* 3–5 per node, with blades linear, narrowly lanceolate to lanceolate, 4–6.5 × 1–2 mm, glabrous, with 1–2 secondary veins each side. *Inflorescence* 2–8.5 cm long, simple, not branched, with 1–3 flowers, or 2- or 3-chotomously branched, with 3 to many flowers, with one flower at the base of each bifurcation; bracteoles subtending flowers narrowly lanceolate to linear, 2.2–3.5 × 0.1–0.2 mm, glabrous, or absent. *Hypanthium* ellipsoid, 1–1.1 × 0.5–0.7 mm, glabrous. *Calyx* lobes narrowly lanceolate to linear, 2.3–3.2 × 0.3–0.6 mm, acute at apex, glabrous throughout, with 1, narrowly triangular, 0.1 mm long, colletar at each lobe sinus. *Corolla* hypocrateriform, 8.5–11.2 mm long, tube white, lobes pale reddish-violet, turning white after anthesis; tube narrowly cylindrical, flaring near the mouth, 3.5–4.7 mm long; lobes oblong to oblong-ovate, 4.5–6.5 × 1.5–2.2 mm, obtuse to acute at apex, glabrous on both sides. *Filaments* 1.3–1.8 mm long; anthers narrowly ellipsoid, 1.0 × 0.4 mm. *Style* exerted 3–5 mm beyond corolla mouth, 6.5–9 mm long, glabrous; style

branches oblong to narrowly oblanceolate, 0.6 mm long. *Capsules* and *seeds* unknown.

**Distribution and ecology:** Only known from the type collection from a locality ca. 30 km S of Nova Xavantina, Mato Grosso, Central Brazil (Figure 20), growing in seasonally inundated campos at ca. 400 m altitude (Brazilian Shield).

**Phenology:** Specimens with flowers were collected in June.

**Suggested conservation status: Critically Endangered (CR) or Extinct (EX).** Only known by the type collection made in 1966 at ca. 30 km S of Nova Xavantina, Mato Grosso, Central Brazil. The number of individuals of the population is unknown. The natural vegetation of this area has been destroyed by agriculture, mostly for establishment of soybean plantations. There is no recent field study to check if this variety is still extant or not. Considering that the area of occurrence is highly impacted by agricultural practices, this variety might be either Critically Endangered or Extinct following IUCN criteria (IUCN 2012, 2019).

#### Excluded species

*Limnosipanea parviflora* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 11(5): 220. 1936

Type: BRAZIL. Minas Gerais: Without locality, s.d. [1816–1821] (fl), A. *Saint-Hilaire* B2-2141 (holotype P [barcode P02285103]; isotype fragment F; photo-P at BR).

(≡) *Perama parviflora* (Standl.) J.H. Kirkbr. & Steyererm. in Steyererm. & Kirkbride in Brittonia 29(2): 195. 1977

This species was originally positioned in *Limnosipanea* by Standley (1936). In agreement with Steyererm. and Kirkbride (1977), because of the bilobed calyx, included stamens, clavate stigma, and hemilenticular seeds, among other characters, it is correctly placed in the genus *Perama* Aubl.

#### 4. MAGUIREOTHAMNUS

*Maguireothamnus* Steyererm., Mem. New York Bot. Gard. 10: 220. 1964.

Steyererm. in Lasser & Steyererm., Fl. Venezuela 9(1): 308–318, fig. 50. 1974; Delprete & Steyererm. in Steyererm. et

al., Fl. Venez. Guayana 8: 642–644, figs. 504–506. 2004.  
Type: *Maguireothamnus speciosus* (N.E. Br.) Steyererm.

*Shrubs.* *Stipules* with a basal sheath adnate with the petioles, free portion narrowly triangular to linear, sometimes with an apical colleter, subcoriaceous to coriaceous, with a row of 3–7 colleters on each side, inserted just below the margin (internal side) or on the margin of the basal sheath. *Leaves* opposite, sessile, subsessile or short-petiolate; blades ovate, obovate, oblong, oblanceolate to lanceolate, thinly to thickly coriaceous; domatia absent. *Flowers* axillary, solitary, 5-merous, homostylous, subtended by two leaf-like bracts, with a fragrance reminiscent of gardenia. *Hypanthium* oblong-obconical, obconical, narrowly obconical to narrowly obovoid, glabrous, minutely puberulent, densely pubescent, antrorse-hispidulous, antrorse-hispid to densely spreading strigose. *Calyx* tube extremely reduced or absent; lobes large, subequal or unequal, elliptic, narrowly-elliptic, oblong, narrowly lanceolate to linear, persistent (eventually braking off in very old capsules), with 5–7 colleters inside each lobe sinus. *Calycophylls* absent. *Corolla* hypocrateriform, actinomorphic, white to cream-white; tube long, externally glabrous, internally puberulent, with a pubescent ring at orifice inside; lobes left-contorted, ovate, lanceolate to oblong, margin entire, obtuse, acute or short-acuminate at apex. *Stamens* included; filaments attached near the mouth of the corolla tube, inserted just below the mouth, short, equal; anthers subsessile, elongate, dehiscent by longitudinal slits, dorsifixed near the base. *Pollen* 3(4)-colporate; exine smooth, not perforate, finely foveolate or finely and sparsely perforate. *Style* exerted well beyond the corolla mouth, terete, antrorse-papillose at distal portion; style branches elliptic, papillose on adaxial side. *Ovary* with a stalked placenta; stalk inserted at the middle of the septum, terminating with an oblong-ellipsoid extension; ovules inserted on the placental extension. *Fruit* capsular, dehiscent loculicidally, thinly woody, crowned by the persistent calyx lobes. *Seeds* many per locule, vertical, laterally compressed, reddish-brown, irregularly fusiform to rhomboid in outline, margin irregularly fringed; testa reticulate-foveolate.

**Distribution and ecology:** A genus endemic to the tepuis of the Guiana Shield, in Venezuela, Guyana and northern Brazil (Roraima); growing on exposed sandstone outcrops, open scrub formations, *Bonnetia roraimae* forests, shrubby savannas, and open wet savannas, on sandy soils, at 1300–2600 m altitude. Three species are here recognized in the genus. The flowers have a fragrance reminiscent of gardenias and are most likely pollinated by hawk-moths.

#### Key to *Maguireothamnus* species

1. Leaf blades 1–3.5 × 0.3–2 cm; capsules hispidulous to hispid (Venezuela: Amazonas: Cerro Duida, Cerro Sipapo, Cerro Huachamacari, Cerro Marahuaca-Atuhua-Shiho)..... 3. *M. tatei*
1. Leaf blades 2.5–6.5 × 0.4–2.5 cm; capsules glabrous (vestiture of densely pubescent form of *M. jauaensis* unknown, probably densely pubescent)..... 2
2. Leaf blades glabrous throughout; hypanthium obconical, narrowly obovoid to oblong-obovoid, 5.5–6 × 3.5–5 mm, glabrous or minutely puberulent; corolla lobes oblong, oblong-elliptic, or lanceolate to linear-lanceolate, 2.3–5 × 0.7–1.5(–2) cm, acute to acuminate at apex (Guyana, and Venezuela: Bolívar: Auyan-tepui, Ptari-tepui, Chimantá Massif, Angasina-tepui, Mount Roraima, Carrao-tepui, Churi-tepui)..... 2. *M. speciosus*
2. Leaf blades densely antrorse-pubescent throughout, glabrous above and densely antrorse-pubescent below, or glabrous throughout; hypanthium oblong-obconical, 4–5 × 2.5–3 mm, densely pubescent or glabrous; corolla lobes oblong-ovate to obovate, 2–2.5 × 0.8–1.1 cm, round or obtuse at apex (Venezuela: Bolívar: Cerro Jáua)..... 1. *M. jauaensis*

4-1. *Maguireothamnus jauaensis* (Steyererm.) Steyererm. in Lasser & Steyermark, Fl. Venez. 9(1): 311. 1974. (Figures 22–23).

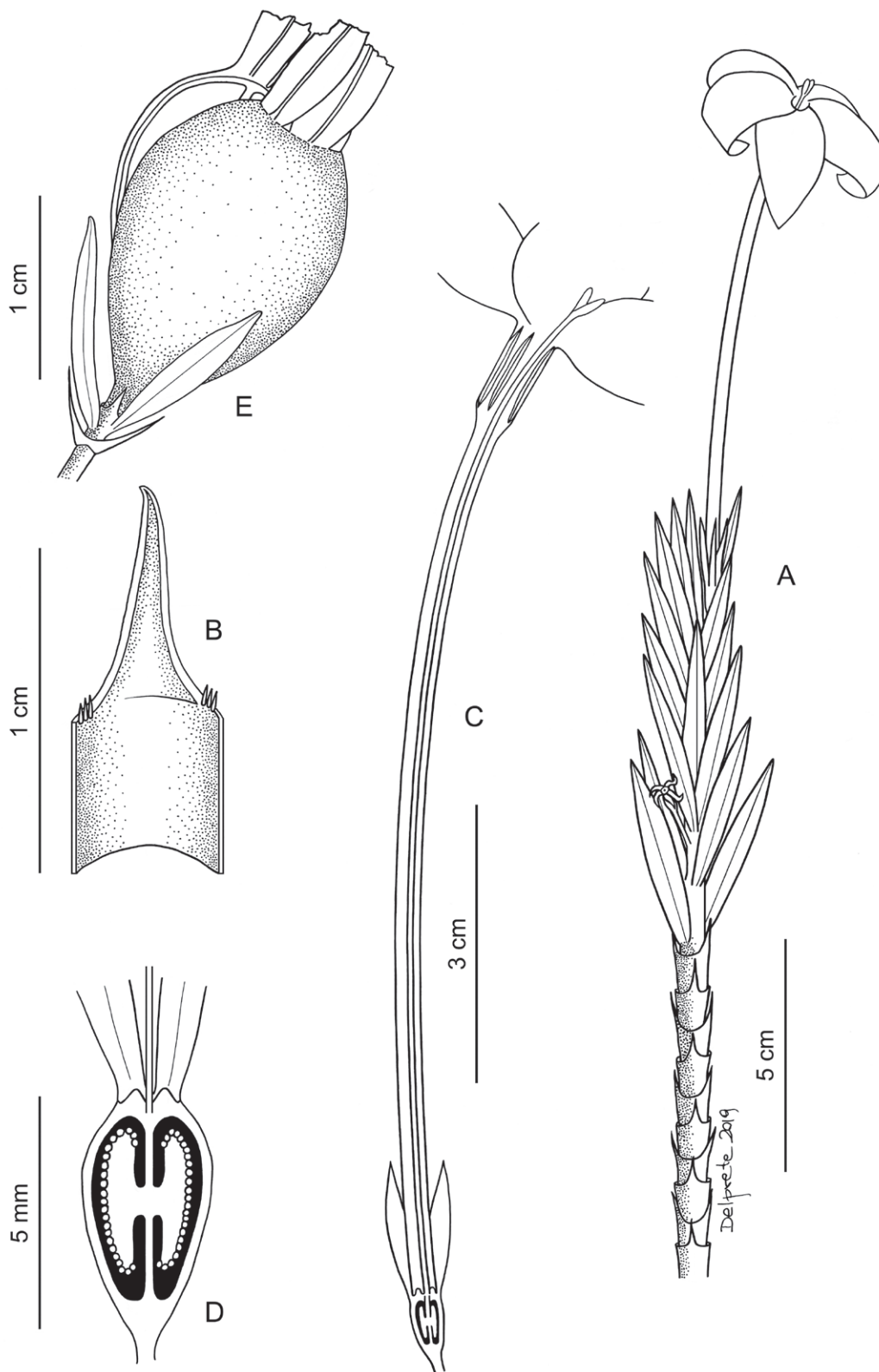
(=) *Maguireothamnus speciosus* subsp. *jauaensis* Steyererm. in Mem. New York Bot. Gard. 23: 883. 1972.

Type: VENEZUELA. Bolívar: Cerro Jáua, summit of the Central-Occidental portion, 60 km NE of Sanidad Mission Camp of Río Canaracuni, 4°45'N, 64°26'W, 1922–2100 m, 22–27 Mar. 1967 (fl), J.A. Steyermark 97837 (holotype VEN [Acc. No. 71474]; isotypes NY [barcode 00132137], U [barcode 0006070]).

(=) *Maguireothamnus jauaensis* (Steyererm.) Steyererm. var. *breweri* Steyererm. in Lasser & Steyermark, Fl. Venez. 9(1): 311. 1974

Type: VENEZUELA. Bolívar: Meseta de Jáua, Cerro Jáua, selva de galería al borde del tributario del Río Marajano, in savanna north of campsite, 4°48'N, 64°34'W, 1750 m, 4 March 1974 (fl), J.A. Steyermark, V. Carreño Espinoza & C. Brewer-Carías 109765 (holotype VEN [Acc. No. 97817]).

*Shrubs*, 0.5–2 m tall; internodes of young branchlets densely antrorse-pubescent or glabrous. *Stipules* basal



**Figure 22.** *Maguireothamnus jauaensis*. **A.** Branch with one flower in anthesis. **B.** Stipule, inner side, with three colleters on each side. **C.** Longitudinal section of flower in anthesis. **D.** Longitudinal section of ovary. **E.** Capsule. **A-D:** drawn from *Huber 12981* (US). Illustration by Piero Delprete.



sheath glabrous or puberulent outside, appressed puberulent inside; free portion narrowly triangular, gradually tapering at apex,  $6.3\text{--}10 \times 2\text{--}4$  mm, subcoriaceous, densely antrorse-pubescent or glabrous outside, glabrous inside; with a row of 3–4 colleters on each side, inserted just below the margin (internal side) of the basal sheath. *Leaves* erect, imbricate, sessile or subpetiolate; petioles to 1.5 mm long, densely antrorse-pubescent; blades lanceolate-elliptic or narrowly elliptic,  $2.5\text{--}4.5 \times 0.4\text{--}1$  cm, attenuate to acute at base, acute at apex, coriaceous, dark green above, pale green below, drying olive-green (or brown, when preserved in alcohol before drying), densely antrorse-pubescent throughout, or glabrous above and densely antrorse-pubescent below, or glabrous throughout; margins strongly revolute; secondary and tertiary venation submerged within the lamina. *Bracts* subtending flowers lanceolate to oblong-lanceolate,  $15\text{--}30 \times 5\text{--}6$

mm, acute at apex, subcoriaceous, glabrous or sparsely pubescent, margins glabrous. *Flowers* with pedicels 2–4 mm long, sparsely pubescent or glabrous. *Hypanthium* oblong-obconical,  $4\text{--}5 \times 2.5\text{--}3$  mm, glabrous or densely pubescent (fide Steyermark, 1974: 311). *Calyx* lobes 5, pale green, oblong-lanceolate,  $14\text{--}23 \times 4\text{--}5$  mm, acute at apex, subcoriaceous, glabrous, margins glabrous, with 5–6, narrowly-lanceolate,  $0.5\text{--}0.6$  mm long, colleters at each lobe sinus. *Corolla* 10–13 cm long; tube pale yellowish-green, long-cylindrical, slightly wider at mouth (anther portion), 9–10.5 cm long, 2–3 mm wide for most length, 3.5–5 mm wide near the mouth, glabrous outside, completely glabrous or basal portion puberulent, the rest glabrous from base to 2–2.2 cm below the mouth and villous above inside; lobes white, oblong-ovate to obovate,  $2\text{--}2.5 \times 0.8\text{--}1.1$  cm, round or obtuse at apex, glabrous outside, glabrous (microscopically papil-

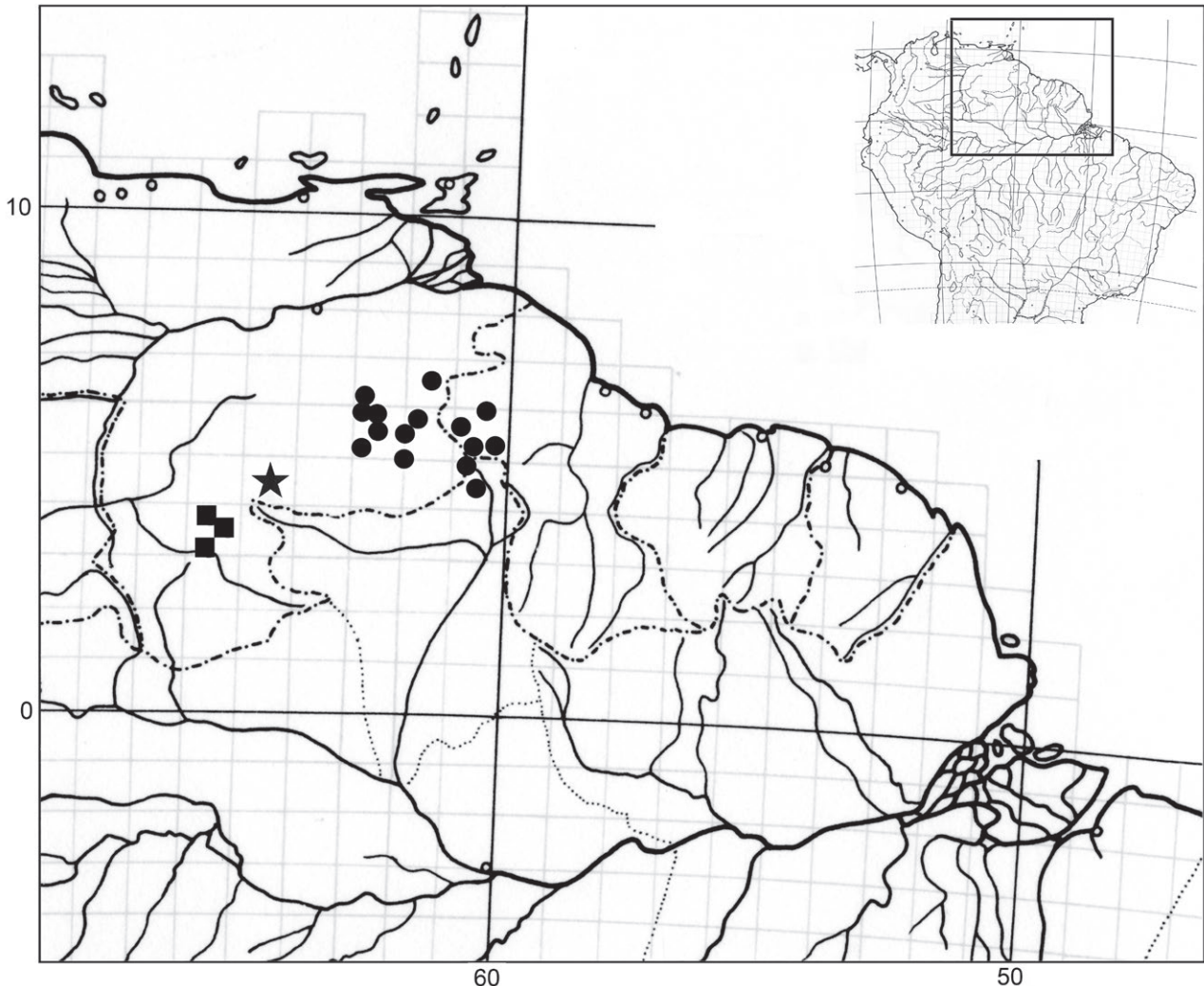


Figure 23. Distribution of *Maguireothamnus jauaensis* (star), *M. speciosus* (circles), and *M. tatei* (squares).

lose) inside. *Anthers* subsessile, elongate, 6.5–7 × 0.8–1 mm, base round, apex acuminate. *Style* 10.5–12 cm long, exerted 10.5 mm beyond corolla mouth, glabrous for most of the length and papillose at distal 1.8–2 cm below style branches; style branches broadly ovate-spathulate, 2 mm long. *Capsules* obovoid, 1.5 × 1.1 cm, acute at base, round at apex, dark brown, glabrous (vestiture of densely pubescent form unknown). *Seeds* unknown.

**Taxonomic observations:** Steyermark (1974: 311–312) described *Maguireothamnus jauaensis* var. *breweri* Steyermark and noted that most of its vegetative parts are densely pubescent while the calyx lobes are glabrous. He differentiated it from the typical variety by the leaves, branches, and stipules densely pubescent (vs. leaves glabrous above, branches and stipules glabrous), corolla lobes “0.7–1.3 × 0.3–0.4 cm” (vs. 2.5–3.5 × 0.7–1.6 cm; see comments below), round at apex (vs. acute to subobtuse at apex). On the other hand, he observed that (translated from Spanish) “All intermediary populations of *M. jauaensis* show the same characters that could be useful to separate this taxon from the other species of the genus, as the stipules narrowly triangular tapering towards the apex, the interior of the corolla throat glandular-puberulent at lower portion, and the well-developed peduncle.” In the same page, he reported the presence of intermediary populations between the two varieties, with vegetative and reproductive parts less pubescent, and corolla throat either glandular-puberulent or glabrous at base inside.

Steyermark (1974: 311) described the corolla lobes of *Maguireothamnus jauaensis* var. *breweri* as 0.7–1.3 × 0.3–0.4 cm, and round at apex. This variety is known only from the holotype specimen at VEN. The specimen Steyermark et al. 109765 has one flower at the tip of a small branch mounted on the sheet, and two loose flowers included in the attached envelop. All the corolla lobes of this specimen are completely wrinkled-up, and is impossible to know their real length when fully expanded. Most likely Steyermark’s measurements were made on these wrinkled-up lobes; therefore, the corolla lobes dimensions supplied by Steyermark for this variety are unreliable.

Steyermark (1974: 312) indicated that *Maguireothamnus jauaensis* var. *breweri* is similar to *M. tatei* because of the pubescent hypanthium and midrib ending at leaf apex, the paler or silvery color of the leaves below and the expanded leafy portion of the branches; and is similar to *M. speciosus* because of the glabrous calyx lobes. Delprete and Steyermark (2004c: 643) treated *M. jauaensis* var. *breweri* as a synonym of *M. speciosus* ssp. *jauaensis*, without further comments; however, recent studies, with more material available,

allowed me to reach a different conclusion. As already pointed out by Steyermark, populations on Cerro Jáua are extremely variable in terms of vestiture of vegetative and reproductive parts. On the type specimens of var. *jauaensis* (Steyermark 97837), the leaves are glabrous throughout, while in the type specimen of var. *breweri* (Steyermark et al. 109765) the leaves are densely antrorse-pubescent throughout. However, two collections from the same locality (Huber 12981 and Steyermark et al. 109333) have intermediate characters, as their leaves are glabrous above and densely antrorse-pubescent below, and their corolla throats are either glabrous (Huber 12981) or glandular-puberulent at lower portion (Steyermark et al. 109333). Therefore, all the above-cited collections and the names involved are here treated as synonymous and as part of a highly variable species endemic to Cerro Jáua.

**Distribution and ecology:** Known by four gatherings from Cerro Jáua (now part of the Jaua-Sarisariñama National Park), Bolívar, Venezuela, at 1750–2100 m altitude (Figure 23).

**Phenology:** Flowering specimens were collected in February, March and November; those collected in November have flowers in anthesis and mature capsules.

**Suggested conservation status: Critically Endangered (CR).** This species is endemic to Cerro Jáua, a tepui included in the Jaua-Sarisariñama National Park, Bolívar state, Venezuela. It is known from four collections made in 1967, 1974 and 1989, at 1750–2100 m altitude. The size of the populations is unknown. The label of the type of *Maguireothamnus speciosus* ssp. *jauaensis* (Steyermark 97837) reports that the specimen was collected on the summit of the Central-Occidental portion of Cerro Jáua, at 1922–2100 m, with coordinates “4°45’N, 64°26’W”. However, these coordinates are erroneous, because they fall outside Cerro Jáua. Therefore, this locality is eliminated from the EOO calculation. Using the three collections localities within Cerro Jáua, the EOO of this species is of 1.89 km<sup>2</sup>. Taking into account the extremely small area of occurrence, which is inside a national park, this species is treated as Critically Endangered (CR) following IUCN criteria (IUCN 2012, 2019).

**Specimens examined: VENEZUELA. Bolívar:** Distrito. Cedeño, Meseta de Jáua, Cerro Jáua, sector centro-meridional, cabeceras del Río Marajano, afluente del Río Cácaro, 4°48’N, 64°32’W, 1750–1800 m, 20 Nov. 1989 (fl, imm fr), O. Huber 12981 (US, VEN); Meseta de Jáua, Cerro Jáua, cumbre, porción SW, selva al borde del Río

Marajano, 4°48'50"N, 64°34'10"W, 1750–1800 m, 22 Feb. 1974 (fl), J.A. Steyermark et al. 109333 (NY, US, VEN).

4-2. *Maguireothamnus speciosus* (N.E.Br.) Steyermark, Mem. New York Bot. Gard. 10: 223. 1964. (Figures 4G–H, 23–24).

(≡) *Chalepophyllum speciosum* N.E.Br. in Trans. Linn. Soc. London ser. 2, 6: 33, pl. 5, figs. 10–17. 1901.

Type: VENEZUELA. Bolívar: F.V. McConnell & J.J. Quelch 653 (first-step lectotype, designated by Steyermark (1964: 223), **second-step lectotype** K [without barcode, with label “New York Botanical Garden Neg. No. N.S. 3240 (1953)”], **here designated**; isolecotype BM [barcode BM000614299]; photo-K at NY).

(=) *Chalepophyllum coriaceum* Gleason in Gleason & Killip, Brittonia 3: 192. 1939.

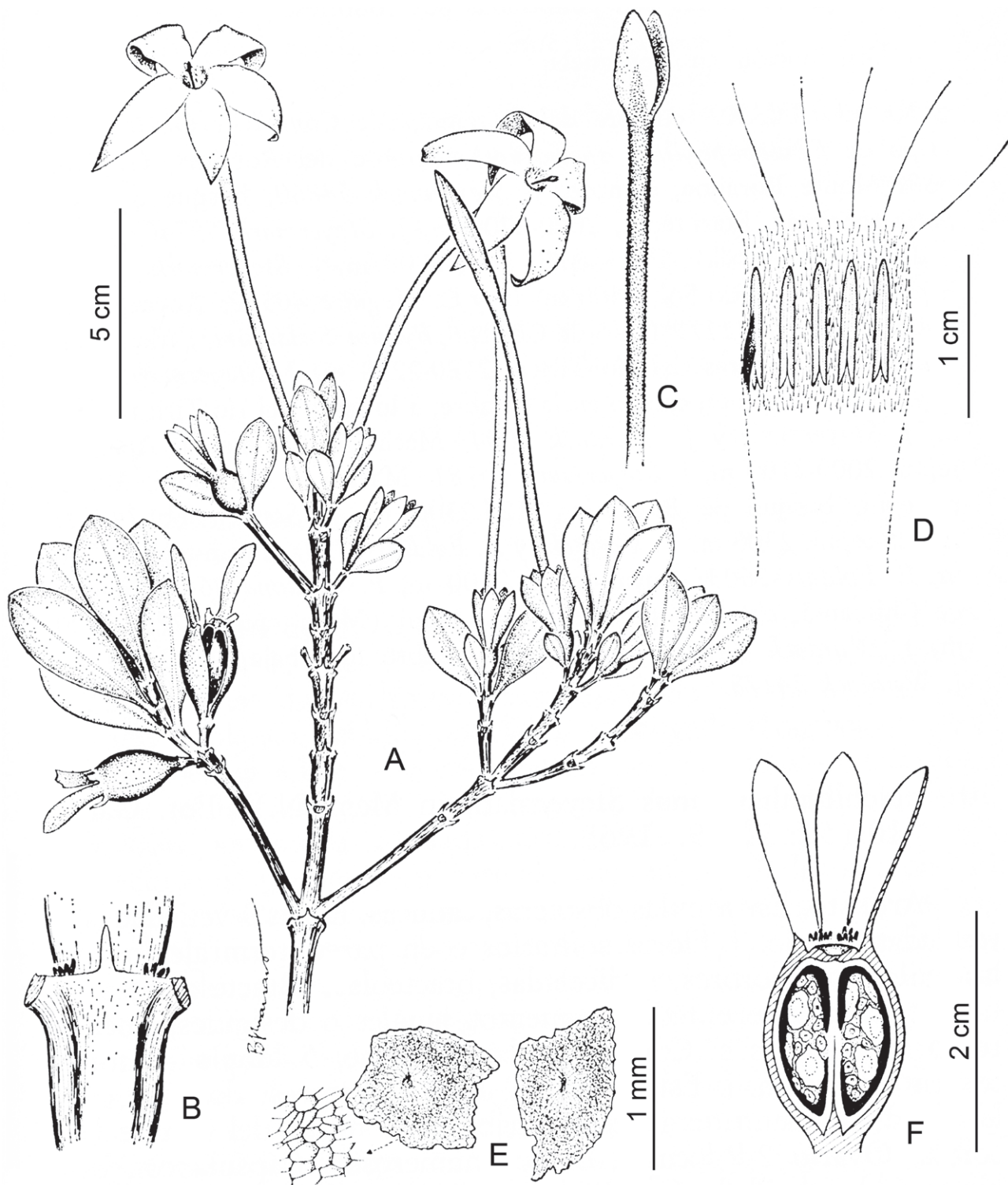
Type: VENEZUELA. Bolívar: Mount Auyan-Tepui [ca. 5°54'N, 62°32'W], 2200 m, Dec. 1937 (fl, fr), G.H.H. Tate 1179 (holotype NY [2 sheets, barcode 00131038]; isotype VEN [not found]).

*Shrubs* 0.5–3 m tall, erect or rarely partially prostrate; bark gray; internodes of young branchlets glabrous. *Stipules* basal sheath glabrous or puberulent outside, sparsely to densely sericeous inside; free portion narrowly triangular, gradually tapering at apex or broadly triangular at base and aristate at apex, 2–10 × 2–3 mm, sometimes with an apical colleter, subcoriaceous to coriaceous, glabrous (rarely strigose) outside, sericeous throughout or only at base inside; with a row of 5–7 colleters on each side, inserted near the margin on internal side of the basal sheath. *Leaves* erect and imbricate, sessile or short petiolate; petioles (when present) to 4 mm long, glabrous; blades oblong, obovate to oblanceolate, 2.5–6.5 × 0.8–2.5 cm, obtuse to acute at base, obtuse, round to acute at apex, coriaceous, dark green and shiny above, pale green below, drying olive-green, glabrous throughout; margin often minutely revolute; secondary and tertiary venation submerged within the lamina, sometimes with 2–3 secondary veins on each side of midrib, barely visible above. *Bracts* subtending flowers round, or broadly to narrowly obovate, (0.7–)9.5–1.6 × (0.3–)0.6–1 cm, round at apex, coriaceous. *Flowers* with pedicels 2–5(–8) mm long. *Hypanthium* obconical, obovoid to oblong-obovoid, 5.5–6 × 3.5–5 mm, glabrous or minutely puberulent. *Calyx* lobes oblong-ovate, narrowly-elliptic to linear, 10–32 × 2–7 mm, acute to acuminate at apex, subcoriaceous, glabrous or with sparse hairs at apex, with 5–7, narrowly-lanceo-

late to oblong-lanceolate, 0.5–0.7 mm long, colleters at each lobe sinus. *Corolla* 9–17 cm long; tube pale green, sometimes reddish at base, long-cylindrical and slightly wider near the mouth (anther portion), (6.5–)8–13 cm long, 2–4 mm wide for most length, 6–7 mm wide near the mouth, glabrous outside, glabrous from base to 1–1.5 cm from the mouth and densely pubescent to villous above inside; lobes white to cream-white, with one margin pink to brick-colored, oblong, oblong-elliptic, lanceolate to linear-lanceolate, 2.3–5 × 0.7–1.5(–2) cm, acute to acuminate at apex, glabrous outside, pubescent at base inside. *Anthers* subsessile, elongate, 6–8 × 0.8–1.1 mm, base round, apex acuminate. *Style* 7.5–15 cm long, exerted 15–20 mm beyond corolla mouth, glabrous for most of the length and papillose on the distal portion; style branches oblong-spathulate, 2.5–3 mm long. *Capsules* ovoid to ellipsoid, 1.5–2.7 × 0.8–1.5 cm, obtuse to acute at base, round at apex, dark brown, glabrous. *Seeds* 4–5 × 2–3 mm.

**Taxonomic observations:** Brown (1901: 33) described *Chalepophyllum speciosum* and cited three syntypes “McConnell & Quelch 100, 305, 653.” Steyermark (1964: 223) cited “McConnell & Quelch 653 (photo of holotype of *Chalepophyllum speciosum*, from K at NY.” Although Steyermark cited this collection as holotype, according to According to Art. 7.11 and 9.10 of the Code (Turland et al. 2018) is a correctable error, and it is here treated as an inadvertent first-step lectotypification of McConnell & Quelch 653 at K because there are two specimens of McConnell & Quelch 653 at K. At the time they were studied, these specimens did not have barcodes. The specimen bearing the label “New York Botanical Garden Neg. No. N.S. 3240 [1953],” which has eight branchlets with flowers is here designated the second-step lectotype of this taxon. The other specimen with three branchlets with flowers, and without the NYBG label, is an isolecotype.

Leaf shapes, corolla dimensions, and vestiture are variable within populations of *Maguireothamnus* species. Steyermark (1972b) recognized two subspecies under *M. speciosus*, and distinguished ssp. *jauaensis*, endemic to Cerro Jáua, by the lower half of the corolla tube puberulent inside (vs. lower half glabrous inside in the typical subspecies), among other characters. Two years later, Steyermark (1974) elevated *M. speciosus* subsp. *jauaensis* Steyermark to species level. Delprete and Steyermark (2004c: 642–643) returned the taxon to subsp. *jauaensis*, recognizing two subspecies in *M. speciosus*. However, recent studies with more material available showed that the specimens from Cerro Jáua are distinct from *M. speciosus* and are here treated as a distinct species (see above).



**Figure 24.** *Maguireothamnus speciosus*. **A.** Branch with capsules, flower buds, and flowers in anthesis. **B.** Node with stipule and partially exserted colleters. **C.** Distal portion of style with partially opened lobes. **D.** Distal portion of corolla tube, base of corolla lobes, and included stamens. **E.** Seeds with detail of reticulated testa. **F.** Longitudinal section of hypanthium, ovary, and calyx, with internal colleters. Illustration by Bruno Manara (Reproduced with permission from *Flora de Venezuela* vol. 9(1), fig. 50. 1974).

**Distribution and ecology:** Endemic to the tepuis of the Guayana Shield, in Guyana and Venezuela, state of Bolívar (Auyan-tepui, Ptari-tepui, Chimantá Massif, Angasina-tepui, Mount Roraima, Carrao-tepui, and Churi-tepui), and the Brazilian contiguous state of Roraima (Mount Roraima and Serra do Sol) (Figure 24). Growing on exposed sandstone outcrops, open scrub formations, *Bonnetia roraimae* forests, shrubby savannas, and open wet savannas, on sandy soils, at 1300–2600 m altitude.

**Phenology:** Flowering specimens were collected in January, February, May, and August; specimens with flowers and fruits in May and August.

**Suggested conservation status: Least Concern (LC).** This species occurs on numerous tepuis, at 1300–2600 m altitude, present in Guyana, Venezuela (state of Bolívar), and the contiguous Brazilian state of Roraima. In Venezuela, it has been collected on the Auyan-tepui, Ptari-tepui, Chimantá Massif, Angasina-tepui, Mount Roraima, Carrao-tepui, and Churi-tepui. Some of these tepuis are included within the Canaima National Park. On Mount Roraima, which also is within the Canaima National Park, where the triple border between Venezuela, Guyana and Brazil is located. This species has been collected in the three countries. Taking into account the numerous collection sites, and the large extent of occurrence, including many remote, preserved areas, this species is treated as Least Concern (LC) following IUCN criteria (IUCN 2012, 2019).

**Specimens examined: VENEZUELA: Bolívar:** Altiplanicie of Auyan-tepui, SW Sector, along small river, headwaters of Río Churún, high tepui scrub and low tepui forest along river and among sandstone outcrops, 5°48'N, 62°33'W, 1850 m, 23–25 Apr. 1996 (fl), *W.R. Andersson & O. Huber 13856* (MO, NY [2 sheets], VEN); Auyantepui, 2100 m, Jan. 1949 (fl), *F. Cardona 2669* (US); Dto. Roscio, Mun. Dalla Costa Roraima [ca. 7°18'N, 61°30'W], 270–300 m, 22 Aug. 1982 (fl, fr), *A. Castillo 1811* (U, VEN); Summit of Cerro Roraima, rock outcrops and pool, shrub in wet areas, 29–30 Sep. 1982 (fl, fr), *S.E. Clemants 2459* (NY); parte central del plató de Auyantepui, 1900 m, Apr. 1956 (fl), *E. Foldats 2603* (F); Valle Encantado, lado derecho del Salto Angel [ca. 5°58'N, 62°32'W], Auyantepuy, 15 Aug. 1968 (fl, imm fr), *E. Foldats 7108* (FT); Disto. Piar, Auyan-tepui summit, E edge of massif, 5°53'N, 62°26'W, 1740 m, open area with large flat rocks and low vegetation, some patches of *Bonnetia roraimae*, 27 May 1986 (fl, fr), *B.K. Holst 2994* (MO, NY, U, US); Disto. Piar, Ptari-tepui, summit,

5°46'N, 61°47'W, 2300 m, nearly flat summit with much exposed sandstone, patches of low vegetation and shrub islands with *Bonnetia roraimae* dominant, 27 May 1986 (fl, fr), *B.K. Holst 3596* (MO, US); Disto. Piar, Macizo del Chimantá, sector centro-noroeste del Chimantá-tepui, cabeceras orientales del Caño Chimantá, 5°18'N, 62°9'W, 2000 m, 26–29 Jan. 1983 (fr), *O. Huber & J.A. Steyermark 6863* (US, VEN); Disto. Piar, altiplanicie del Auyan-tepui, Sector SSW de la meseta, al W de la cumbre Sur, vegetación sobre rocas de arenisca y arbustales, 5°48'N, 62°32'W, 2070 m, 27 Aug. 1983 (fr), *O. Huber et al. 8055* (NY, US, VEN); Disto. Piar, altiplanicie del Auyan-tepui, sector SE, ca. 5 km al ESE del Churún-merú (Salto Churún), 5°51'N, 62°30'W, 10 Dec. 1983 (fl, fr), *O. Huber & E. Medina 8528* (MO, NY, VEN); Disto. Piar, Macizo del Chimantá, altiplanicie meridional del Abacápá-tepui, ubicada en el sector SW del Macizo, 5°10'N, 62°16'W, 2200 m, 31 Jan.–2 Feb. 1984 (fl), *O. Huber & N. Dezzeo 8602* (MO, NY, VEN); Disto. Piar, Macizo del Chimantá, sección septentrional del Apacará-tepui, en el extrem N del macizo, 5°25'N, 62°11'W, 2350 m, 3–5 Feb. 1984 (fl), *O. Huber & M. Colella 8703* (MO, NY, VEN); Disto. Roscio, Cumbre del Yuruaní-tepui, ca. 12 km al NNE del Kukenán-tepui, 5°19'N, 60°51'W, 2200 m, 29 Feb. 1984 (fl), *O. Huber 9082* (NY, VEN); Disto. Roscio, Kukenán-Tepui, cumbre del sector más septentrional algo separado del macizo principal, vegetación herbáceo-arbustiva sobre rocas de arenisca abiertas y alrededor de lagunas, 5°16'N, 60°48'W, 2500 m, 28 Apr. 1984 (fl), *O. Huber 9436* (NY, US, VEN); Disto. Piar, altiplanicie ubicada en la sección más septentrional del Brazo Occidental del Auyantepui, ca. 25 km al SE de Canaima, 6°6'N, 62°43'W, 1650 m, 13 Nov. 1984 (fl), *O. Huber 9720* (NY, US, VEN); Disto. Piar, Cumbre del Ptari-tepui, ca. 22 km al NNW de la Misión de Kavanayén, 5°54'N, 61°47'W, 2400 m, 19 Nov. 1984 (fl), *O. Huber 9822* (NY, VEN); Disto. Piar, altiplanicie del Auyan-tepui, sector N del Brazo Oriental, a lo largo de un valle afluyente (derecho) del Río Churún, 6°1'N, 62°26'W, 1900 m, 17 Jan. 1986 (fl), *O. Huber 11181* (NY, VEN); Disto. Piar, cumbre del Angasina-tepui (Adanta-tepui), cabeceras altiplanicie poco inclinada hacia el NE con saban arbustiva en el sector Nor-occidental, ca. 40 km al WNW de la Misión de Wonkén, 5°3'N, 62°7'W, 2100 m, 4 Mar. 1986 (fl, fr), *O. Huber 11362* (NY, US, VEN); Kukenan-tepui, summit, large open rocky areas, boggy areas, small patches of forest, 5°13'N, 60°18'W, 2550 m, 10 Apr. 1988 (fl), *R. Liesner 23047* (MO, NY); Disto. Piar, Macizo del Chimantá, setor SSE, altiplanicie sur-oriental del Acopántepui, cabecera del Río Arauác, praderas húmedas y arbustales enanos sobre turberas, 5°11'N, 62°0'W, 1920 m, 14–16 Feb. 1984 (fl), *J.L. Luteyn et al. 9475* (NY, U,

US, VEN); Disto. Piar, Macizo del Chimantá, sector SE, amplia altiplanicie en la sección nor-oriental del Acopán-tepui, levemente inclinada hacia el NE, en las cabeceras del Río Yunék, 5°12'N, 62°5'W, 1950 m, 8–11 Feb. 1985 (fl), *J.J. Pipoly et al.* 7210 (MO, NY, VEN); Disto. Piar, Macizo del Chimantá, sector centro-meridional, Amplio valle ubicado entre el borde nor-oriental del Torono-tepui y la sección central del Chimantá-tepui, drenando hacia el S, 5°16'N, 62°9'W, 2100 m, 11–15 Feb. 1985 (fl), *J.J. Pipoly et al.* 7245 (MO, NY, VEN); Plateau of Auyan-tepui, SW section of plateau, W of southern summit, 5°48'N, 62°32'W, 2070 m, 27 Aug. 1983 (fl, fr), *G.T. Prance & O. Huber* 28243 (MO, NY, US, VEN); Plateau of Auyan-tepui, Central Northern section of Eastern Branch, 5°57'N, 62°25'W, 1940 m, 27 Aug. 1983 (fl), *G.T. Prance & O. Huber* 28272 (FT [2 sheets], NY); Mun. Gran Sabana, Chimantá Massif, SSE sector, SE summit of Acopán-tepui, headwaters of Río Arauák, 5°11'N, 62°0'W, 1920 m, 6–8 Apr. 1989 (fl), *J. Pruski & O. Huber* 3556 (NY); Mun. Gran Sabana, Chimantá Massif, summit of central NE portion of Murey(Eruoda)-tepui, in the NE sector of the massif, 5°23'N, 62°3'W, 2550 m, 1–3 Apr. 1989 (fl), *J. Pruski & O. Huber* 3582 (MO, NY); Chimantá Massif, central section, rocky and swampy savanna between W and E branches of headwaters of Río Tirica, 2120–2210 m, 11 Feb. 1955 (fl), *J.A. Steyermark & J.J. Wurdack* 743 (F, NY, US); Chimantá Massif, vicinity of Summit Camp along Río Tirica, 1925 m, 20 Feb. 1955 (fl), *J.A. Steyermark & J.J. Wurdack* 1004 (NY [2 sheets], US, VEN); summit of Mount Roraima, on NW portion N and NW of Summit Camp, 2620–2740 m, 27 Sep. 1944 (fl), *J.A. Steyermark* 58860 (IAN [frag], F, NY [2 sheets], US); summit of Carrao-tepui, 2470–2500 m, 7 Dec. 1944 (fl), *J.A. Steyermark* 60896 (F); Ptari-tepui, *Bonnetia roraimae* forest on SW-facing shoulder, 2000–2200 m, 2 Nov. 1944 (fl), *J.A. Steyermark* 59740 (F, MO, NY); Ptari-tepui, S-facing slope, vicinity of Cave Rock, 1800–1900 m, 2 Nov. 1944 (fl), *J.A. Steyermark* 59801 (F, NY); Chimantá Massif, *Bonnetia* forest, NW part of Summit of Abácapa-tepui, 2125–2300 m, corolla tube pale green, corolla lobes white with one edge bordered rose, flowers very fragrant, 13 Apr. 1953 (fl), *J.A. Steyermark* 74881 (F, MO, NY [2 sheets]); Chimantá Massif, rocky plateau on SE-facing upper shoulder of Apacará-tepui, below summit, 2000–2100 m, 20 Jun. 1953 (fl bud), *J.A. Steyermark* 75781 (F, NY); Auyan-tepui, cumbre de la parte del brazo NE (division occidental del cerro), sabana de suelo de arenisca al S y alrededor de la avioneta de Jimmy Angel, 1800 m, 7 May 1964 (fl), *J.A. Steyermark* 93501 (F, NY, P, U); Cerro Roraima, cumbre NE de Venezuela inmediatamente al S del hito que marca los límites con Guyana, Brasil y Venezuela, El Valle, head-

waters of Río Arabapó, 5°12'N, 60°42'W, 2750–2800 m, 26 Aug–2 Sep. 1976 (fl), *J.A. Steyermark et al.* 112493 (F, NY, US, VEN); cumbre del Ptari-tepui, N de la Misión de Santa Teresita de Kavanayén, 5°45'N, 61°45'W, 2360–2420 m, 23 Feb. 1978 (fl), *J.A. Steyermark et al.* 115732 (F, MO); Dto. Sucre, Meseta de Jáua, cumbre, sección oriental-central, afloramiento de piedra arenisca en sitios expuestos con vegetación herbácea y arbustos achaparrados, 4°35'N, 64°15'W, 2020 m, 14 Feb. 1981 (fl, fr), *J.A. Steyermark et al.* 124334 (NY); Dto. Piar, Macizo del Chimantá, sector centro-noreste del Chimantá-Tepui, cabeceras orientales del Caño Chimantá, 5°18'N, 62°9'W, 2000 m, 26–29 Jan. 1983 (fl), *J.A. Steyermark, O. Huber & V. Carreño E.* 128081-A (MO, NY, U, VEN); Dto. Piar, Macizo del Chimantá, altiplanicie en la base meridional de los farallones superiores del Apacará-Tepui, sector N del macizo, 5°20'N, 62°12'W, 2200 m, 30 Jan–1 Feb. 1983 (fl), *J.A. Steyermark et al.* 128311 (MO, NY, U, VEN); Dto. Piar, Macizo del Chimantá, pequeñas altiplanicies en la base septentrional de los farallones superiores del Amurí-Tepui (Sector W del Acopán-Tepui), 5°10'N, 62°7'W, 1850 m, 2–5 Feb. 1983 (fl), *J.A. Steyermark et al.* 128668 (MO, NY, U, VEN); Dto. Piar, Macizo del Chimantá, cumbre sur-occidental del Amurí-tepui (Sector W del Acopán-tepui), small wooded area of dwarf forest bordering and below rocky open savanna, 2170 m, 6 Feb. 1983 (fl), *J.A. Steyermark et al.* 128765 (MO); Dto. Piar, cabeceras del affluent derecho superior del Río Tirica (Caño del Grillo), 5°18'N, 62°3'W, 2450 m, 7–9 Feb. 1983 (fl), *J.A. Steyermark et al.* 128916 (MO, NY, U, VEN); Dto. Piar, Macizo del Chimantá, sector SSE, altiplanicie sur-oriental del Acopán-tepui, cabeceras del Río Aruác, 1920 m, 14 Feb. 1984 (fl), *J.A. Steyermark et al.* 129900 (US, VEN); parte superior de Auyantepui, 2300 m, Apr. 1956 (fl), *V. Vareschi & E. Foldats* 4858 (F); Churi-tepui (Muru-tepui), NW cumbres, 2100–2200 m, 24 Jan. 1953 (fl), *J.J. Wurdack* 34178 (NY, P); Churi-tepui (Muru-tepui), NW cumbres, 2250–2300 m, 26 Jan. 1953 (fl), *J.J. Wurdack* 34209 (F, NY, U, US).

**GUYANA:** Cuyuni-Mazaruni Region, Mt. Maringma, summit, scrub forest and tepui bog on peat and sandstone, with *Bonnetia*, *Ilex*, and *Brocchinia*, 5°13'N, 60°35'W, 2110 m, 15 Jun. 2004 (fl), *H.D. Clarke et al.* 11703 (MO, NY, US); Cuyuni-Mazaruni Region, 1 km N of tip of northern prow of Roraima, El Dorado Swamp, open scrub and low trees on white sand and boulders, 5°15'N, 60°35'W, 2000–2200 m, 25 Feb. 1989 (fl), *W. Hahn & D. Goupal* 5516 (BRG, MO, NY, US); Mazaruni-Potaro Region, Guyana-Venezuela border, Roraima summit, La Proa Camp, E of border, near Lake Gladys, mostly rocky areas with ravines and lake, 14 Apr. 1988 (fl), *R.L. Liesner* 23309 (MO); Upper Mazaruni District,

N slope of Mt. Roraima, 5°16'N, 60°43'W, 2300 m, 14 Feb. 1985 (fl), *J. Rentz 14277* (U); Cuyuni-Mazaruni Region, Summit of Kamakusa Mountain (i.e., on top of 4th escarpment of four), impenetrable elfin forest to 3 m, extremely dense and wet, rich in epiphytes, with *Bonnetia* (2 spp.), *Brocchinia* cf. *tatei*, Malpighiaceae, Melastomataceae, Cyperaceae spp., *Weinmannia*, *Ilex* cf. *retusa*, 5°52'52"N, 6°6'10"W, 1686 m, 7 Jun. 2012 (fl), *E. Tripp et al. 3186* (P, US); N ridge of Mt. Roraima, small swampy areas on gently sloping land, *Heliampora*, Xyridaceae, Eriocaulaceae, soil humus-poor fine silty-sand, area windswept and often cloud-covered, with frequent rain, 5°15'40"N, 60°44'40"W, 2065–2430 m, 26 Mar. 1978 (fl), *J.F. Warrington et al. 42* (E, K, U).

**BRAZIL. Roraima:** Summit of Serra do Sol (Ueitupui) [ca. 5°1'N, 60°36'W], 2300 m, 28 Dec. 1954 (fl, fr), *B. Maguire & C.K. Maguire 40392* (IAN, NY [2 sheets], RB); Mt. Roraima (Guyana and N Brazil border), summit, 24 Nov. 1927 (fl), *G.H.H. Tate 388* (NY); Mun. Boa Vista, Monte Roraima, substrato rochoso, 2600–2870 m, 5 Dec. 1983, *E.L. Sette et al. 14* (MIRR); Monte Roraima, 9 Apr. 1973 (fl), *E.F. Terezo 23* (IAN); Monte Roraima, 10 Apr. 1973 (fl), *E.F. Terezo s.n.* (INPA No. 60513); Felsenregion, 2500 m, Jan. 1910 (fl), *E. Ule 8781* (L, MG).

4-3. *Maguireothamnus tatei* (Standl.) Steyerl., Mem. New York Bot. Gard. 10: 227. 1964. (Figures 23, 25).

(≡) *Chalepophyllum tatei* Standl., Publ. Field Columbian Mus., Bot. Ser. 7 (4): 380. 1931.

Type: VENEZUELA. Amazonas: Mount Duida, summit of Peak N. 7, 2130 m, Aug. 1928–Apr. 1929 (fl, fr), *G.H.H. Tate 623* (holotype NY [barcode 00131042]; isotype F [Acc. No. 603541, Negative No. 72096]).

(=) *Chalepophyllum latifolium* Standl., Publ. Field Columbian Mus., Bot. Ser. 7: 379. 1931.

(≡) *Maguireothamnus tatei* (Standl.) Steyerl. var. *latifolium* (Standl.) Steyerl., Mem. New York Bot. Gard. 10: 228. 1964.

Type: VENEZUELA. Amazonas: Summit of Mount Duida (Cerro Yennamadi), [ca. 3°30'N, 65°37'W],

1320 m, Aug. 1928–Apr. 1929 (fl, fr), *G.H.H. Tate 730* (holotype NY [barcode 00131040]; isotype F [Acc. No. 603528]).

*Shrubs* 0.5–3 m tall, erect; bark gray; internodes of young branchlets antrorse-hispidulous or glabrate on older internodes. *Stipules* basal sheath densely strigose outside, sparsely to densely sericeous at base and glabrous distally inside; free portion narrowly triangular to linear, gradually tapering at apex or broadly triangular at base and aristate at apex, 0.7–17.5 × 2–3 mm, subcoriaceous to coriaceous, sometimes with an apical colletter, densely strigose outside, glabrous inside; with a row of 5–7 colletters on each side, inserted on the margin of the basal sheath. *Leaves* erect and imbricate, sessile or subpetiolate; petioles to 1 mm long, glabrous or sparsely hirtellous; blades very variable in shape and size (Figure 25E–L), lanceolate-elliptic, elliptic, oblanceolate-oblong to obovate, 1–3.5 × 0.3–2 cm, acute, obtuse to subcordate at base, obtuse, round to acute at apex, coriaceous, dark green and shiny above, pale green below, drying olive-green or pale brown, glabrous throughout or lamina glabrous and midrib sparsely to densely strigillose above and below; margins narrowly to strongly revolute or planar; secondary and tertiary venation submerged within the lamina, sometimes with 2–3 secondary veins on each side of midrib, barely visible above. *Bracts* subtending flowers lanceolate to oblong-lanceolate, 7.5–17 × 2–3 mm, acute at apex, chartaceous to subcoriaceous, glabrous or sparsely hispidulous, margins glabrous or hispidulous-ciliate. *Flowers* with pedicels 1–3 mm long, densely strigose. *Hypanthium* obconical to narrowly obovoid, 2–3 × 1.5–2 mm, antrorse-hispidulous, antrorse-hispid to densely spreading strigose (hairs white). *Calyx* lobes pale green to whitish, oblong-lanceolate, linear-lanceolate to linear, 8–21 × 1.5–4 mm, attenuate, acute to acuminate at apex, glabrous or sparsely hispidulous, margins hispidulous-ciliate, and with 5–6, narrowly-lanceolate, 0.4–0.5 mm long, colletters at each lobe sinus. *Corolla* 8–14.5 cm long; tube pale green, greenish-yellow to cream-white, long-cylindrical and and slightly wider near the mouth (anther portion), 6.5–11 cm long, 2–3 mm wide for most length, 6–7.5 mm wide near the mouth, glabrous outside, glabrous from base to 1.2–1.5 cm below the mouth and villous above inside; lobes white to cream-white, lanceolate to oblong-lanceolate, 1.5–3.6 × 0.7–1.6 cm, sub-obtuse, acute to acuminate at apex, gla-

**Figure 25.** *Maguireothamnus tatei*. **A.** Branch with flowers in anthesis and capsule. **B.** Nodes with permanent, overlapping stipules. **C.** Longitudinal section of flower in anthesis. **D.** Capsule. **E–I.** Leaf variation within the species. **A, C, E:** from *Tate 730* (F); **B, F:** drawn from *Maguire & Politi 28449* (US); **D:** from *Maguire & Politi 27541* (F); **G:** drawn from *Steyermark 58030* (F); **H–I:** from *Huber 13287* (US). Illustration by Piero Delprete.

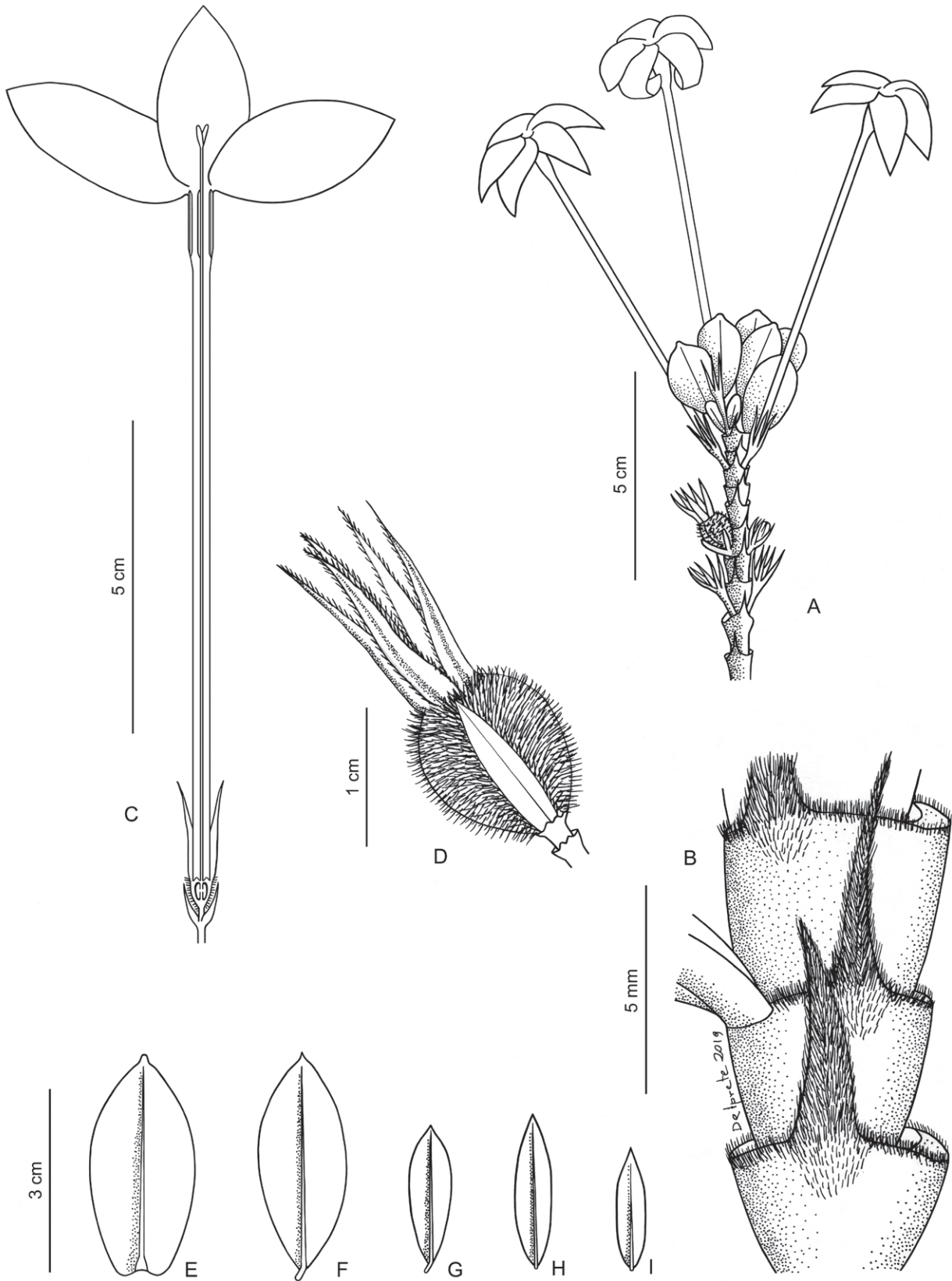


Figure 25.



brous outside, glabrous (microscopically papillose) inside. *Anthers* subsessile, elongate, 6.5–7.5 × 0.8–1 mm, base round, apex acuminate. *Style* 7–12.7 cm long, exerted 10–17 mm beyond corolla mouth, glabrous for most of the length and papillose on distal 2.7–5 cm below style branches; style branches oblong-spathulate, 2–2.5 mm long. *Capsules* obovoid, ovoid to ellipsoid, 1–2.5 × 0.8–1 cm, obtuse to acute at base, round at apex, dark brown, hispidulous to hispid (hairs 0.7–1 mm long). *Seeds* 2.5–3 × 1.5–2.5 mm.

**Distribution and ecology:** Endemic to the tepuis of the Venezuelan state of Amazonas, on Cerro Duida, Cerro Sipapo, Cerro Huachamacari, and Cerro Marahuaca-Atuhua-Shiho (Figure 23). Growing on exposed sandstone outcrops, open scrub formations, tepui slope and summit scrubs, meadows, and open savannas, at 1300–2555 m altitude.

**Phenology:** Flowering from August to February, and fruiting from November to January.

**Suggested conservation status: Least Concern (LC).** This species is known from numerous collections from two main regions within the state of Amazonas, southern Venezuela, at altitudes of 1230–2650 m. The first region corresponds with the nearby tepuis Cerro Duida, Cerro Huachamacari, and Cerro Marahuaca-Atuhua-Shiho; most of them are part of the Duida-Marahuaca Massif, which is included within the Duida-Marahuaca National Park. The second region corresponds to the distant tepui Cerro Sipapo, ca. 4°57'N, 67°20'W, 1500 m, which is about 200 km NW of the other region, and is not within a protected area. The size of the populations is unknown. Therefore, considering its large extent of occurrence (EOO), and that most of the collections were made within a national park, which is without any imminent threat, this species is classified as Least Concern (LC) following IUCN criteria (IUCN 2012, 2019).

**Specimens examined: VENEZUELA: Amazonas:** Depto. Atabapo, Cerro Duida (“Yennamadi”), sector meridional, herbazal arbustivo sobre ladera suavemente inclinada cerca del borde S de la meseta, 3°19'N, 65°38'W, 2100 m, 19 Nov. 1991 (fr), *O. Huber 13281* (US, VEN); Depto. Atabapo, Cerro Duida (“Yennamadi”), sector meridional, herbazal abierto en un pequeño valle y arbustales densos sobre colinas bajas cerca del borde S de la meseta, 3°17'N, 65°38'W, 2060 m, 20 Nov. 1991 (fl), *O. Huber 13287* (US, VEN); Depto. Atabapo, open rocky plateau of Cerro de Marahuaca, above Salto Los Monos on

tributary of headwaters of Río Iguapo, 3°37'N, 65°23'W, 2555 m, 27 Feb. 1985 (fl), *R.L. Liesner 18040* (MO, NY, VEN); Depto. Atabapo, gallery forest and open area on Plateau of Huachamacari, 3°50'N, 65°43'W, 1720 m, 1 Mar. 1985 (fl), *R.L. Liesner 18066* (MO, VEN); Cerro Sipapo (Paráque), [ca. 4°57'N, 67°20'W], near Savanna Camp, 1500 m, 6 Dec. 1948 (fr), *B. Maguire & L. Politi 27541* (F, NY, RB); Cerro Sipapo (Paráque), between Savanna Camp and West Peak, 1500–1800 m, 20 Dec. 1948 (fl), *B. Maguire & L. Politi 27801* (NY [2 sheets], VEN); Cerro Sipapo (Paráque), near Savanna Camp, 1500 m, 19 Jan. 1949 (fl), *B. Maguire & L. Politi 28449* (FT, NY [2 sheets], US, VEN); Cerro Sipapo (Paráque) [ca. 4°57'N, 67°20'W], occasional on North Mountain, 1500 m, 25 Jan. 1949 (fr), *B. Maguire & L. Politi 28582* (IAN, NY [2 sheets], P, U); Cerro Duida, Río Cunucunuma, N slopes and ridges of Caño Negro basin, 2000–2300 m, 23 Nov. 1950 (fr), *B. Maguire et al. 29695* (NY [2 sheets]); Cerro Huachamacari, Río Cunucunuma, cumbre, 1700 m, 4 Dec. 1950 (fl), *B. Maguire et al. 29810* (F, NY); Cerro Huachamacari, Río Cunucunuma, summit of E ridge [ca. 3°55'N, 65°30'W], 1820 m, 8 Dec. 1950 (fr), *B. Maguire et al. 30058* (NY [2 sheets], P, U, US); Cerro Huachamacari, Río Cunucunuma, W rim of ridge N. 1, summit camp, [ca. 3°55'N, 65°30'W], 1900 m, 11 Dec. 1950 (fr), *B. Maguire et al. 30129* (NY, P, U, US); Cerro Huachamacari, Río Cunucunuma, along SE escarpment, [ca. 3°55'N, 65°30'W], 1900 m, 11 Dec. 1950 (fl buds), *B. Maguire et al. 30142* (FT, NY, US, VEN); Cerro Huachamacari, Río Cunucunuma, between Summit Camp and E escarpment, [ca. 3°55'N, 65°30'W], 1800–1950 m, 16 Dec. 1950 (fl), *B. Maguire et al. 30263* (NY [2 sheets], US, VEN); Parque Nacional Duida-Marahuaca, cumbre del Cerro Duida, esquina SE, 2200 m, Mar. 1993 (fl), *B. Stergios et al. 15768* (NY, PORT, VEN); Cerro Duida, SE-facing slopes along Caño Negro (tributary of Caño Iguapo), 1700 m, 25–26 Aug. 1944 (fl), *J.A. Steyermark 58030* (IAN [frag], NY, US, VEN); summit of Cerro Duida, Savana Hills, 1025–1200 m, 2 Sep. 1944 (fl), *J.A. Steyermark 58240* (F, NY, US); summit of Cerro Duida, on high moist ridge top, 1820–2075 m, 4 Sep. 1944 (fl), *J.A. Steyermark 58335* (F, NY, IAN [frag]), 58348 (F); Depto. Atures, Serranía Sipapo, cumbre, sección septentrional, vegetación tipo sabana a lo largo de un riachuelo, 5°0'N, 67°30'W, 1500 m, 17 Feb. 1981 (fl), *J.A. Steyermark et al. 124538* (NY, VEN); Depto. Atabapo, Cerro Marahuaca-Huha, cumbre altiplanicie no arbolada, mas o menos plana, con piedras expuestas, río abajo, 3°40'N, 65°30'W, 2580 m, 31 Jan. 1982 (fr), *J.A. Steyermark et al. 125914* (MO, NY, US, VEN); Depto. Atabapo, Cerro Marahuaca-Fhuif, cumbre, zona pantanosa no arbolada en la altiplanicie, río arriba, 3°35'N, 65°20'W, 2480–2500 m, 2 Feb. 1982 (fl), *J.A. Steyermark et al. 126073* (MO,

NY, VEN); Depto. Atabapo, Cerro Marahuaca-Atuhua-Shiho, cumbre, parte aislada al SW del cerro, vegetación no arbolada en terreno pendiente, 3°30'N, 65°20'W, 2450–2480 m, 9–10 Feb. 1982 (fl), J.A. Steyermark et al. 126338 (F, MO, NY, US, VEN); Depto. Atabapo, Cerro Duida, cumbre, cerca de escarpa oriental, sabana pantanosa dominada por *Eliamphora* y *Brewcaria*, 3°25'N, 65°40'W, 1230 m, 10 Feb. 1982 (fl), J.A. Steyermark et al. 126399 (NY, VEN); Depto. Atabapo, Cerro Marahuaca, summit on undulating plateau with islands of shrubs and *Marahuaca*, with stream branch leading to Salto de Monos and SE edge to Caño Iguapo, S and SE of Summit Camp, 3°37'N, 65°23'W, 2520–2650 m, 26–27 Feb. 1985 (fl), J.A. Steyermark & B. Holst 130685 (MO, NY, U, VEN), 130731 (MO, NY); Mount Duida, slopes of Rudge 25, 1830–2000 m, 1928 (fl), Tate G. H. H. 427 (NY, frag-F [ex NY]); Mount Duida, 1928–1929 (fl), G.H.H. Tate 1016 (NY, frag-F [ex NY]); Estación D-21, NNE of Savana Hills Camp of Tate, Cerro Duida, inmediatamente al N de La Esmeralda, en el Río Orinoco, 3°10'N, 65°31'W, 1500 m, 2 Feb. 1975 (fl), S.S. Tillett et al. 751-49 (NY, U, VEN), 751-49a (NY, U, VEN).

##### 5. NEBLINATHAMNUS

*Neblinathamnus* Steyer., Mem. New York Bot. Gard. 10(5): 229. 1964.

Steyer. in Mem. New York Bot. Gard. 23: 309. 1972; Steyer. in Lasser and Steyermark, Fl. Venezuela 9(1): 318–322, fig. 51. 1974; Steyer. in Ann. Missouri Bot. Gard. 76: 968. 1989; Delprete and Steyer. in Steyermark et al., Fl. Venez. Guayana 8: 659–660, fig. 520. 2004.

Type: *Neblinathamnus argyreus* Steyer.

*Shrubs*. Stipules basally adnate to the petioles, minute, broadly to shallowly triangular to truncate, sometimes shallowly bilobed, often bilobed at apex, or rarely constituted of two free lobes on each side of the stem; with a row of 7–9 sparse colleters on margin in shallowly triangular to truncate stipules, or with a row of 4–5 colleters on margin of each lobe in stipules bilobed or constituted of two free lobes. *Leaves* opposite or ternate, short-petiolate or sessile; blades elliptic, obovate or oblong, thinly coriaceous; domatia absent. *Inflorescence* axillary, sometimes appearing terminal when on apical node, with 1–2 flowers, or cymose, (2–)3–5-flowered. *Flowers* heterostylous, 5-merous, short-pedicellate, subtended by two small, setaceous bracts. *Hypanthium* obovoid, oblong-ovoid, turbinate or narrowly obovoid, sparsely to densely hirtellous. *Calyx* lobes erect, equal

to subequal, spatulate, lanceolate, linear-acuminate, or linear-spatulate, with 2–3 colleters at each lobe sinus. *Calycophylls* absent. *Corolla* hypocrateriform, actinomorphic; corolla green to yellowish-green, or tube red and lobes yellowish or greenish; tube externally glabrous or hirtellous, internally puberulent throughout or pubescent at mouth, with a pubescent ring at orifice inside; orifice annular thickening absent; lobes left-contorted, narrowly ovate, ovate, elliptic or oblong, margin entire, obtuse or rounded at apex. *Pollen* 3-colporate; exine foveolate-reticulate, perforate. *Short-styled flowers*: stamens included, inserted at distal portion of corolla throat; filaments short; anthers linear; style included, style branches linear. *Long-styled flowers*: stamens included, inserted at medio-basal or median portion of corolla throat; filaments short; anthers narrowly oblong or linear; style as long as corolla tube, style branches barely exerted beyond corolla mouth or exerted, style branches narrowly ovate, narrowly lanceolate or linear. *Ovary* with a stalked placenta; stalk inserted at the middle of the septum, terminating with an oblong-ellipsoid extension; ovules inserted on the placental extension. *Fruit* capsular, dehiscent loculicidally, thinly woody. *Seeds* horizontal or vertical, minute, 3-5-angular, laterally compressed; testa reticulate-foveolate.

**Geographic distribution:** A genus of two species restricted to the Venezuelan and Brazilian sides of the Cerro de la Neblina Massif, hence the generic name.

**Morphological notes:** Steyermark (1964, 1974) wrote that the stipules of *Neblinathamnus* are obsolete and caducous, but they are instead shallowly triangular to truncate, shallowly bilobed, or constituted of two free lobes, and persistent.

##### Key to *Neblinathamnus* Species

1. Leaf blades obovate, obovate-oblong, narrowly oblong to linear-oblong, 1–2.5(–3.3) × 0.5–1.3(–1.5) cm, round, sometimes mucronate at apex; flowers 1–2 per axil; corolla tube 10.5–14.5(–16) mm long..... 1. *N. argyreus*
1. Leaf blades oblong-elliptic to ovate-lanceolate, (2.5–)3–6 × (0.8–)1–3 cm, acute to obtuse at apex; inflorescence cymose, (2–)3–5-flowered; corolla tube 9–12 mm long..... 2. *N. brasiliensis*

5-1. *Neblinathamnus argyreus* Steyer., Mem. New York Bot. Gard. 10(5): 229, fig. 77. 1964. (Figures 26–27).

Type: VENEZUELA. Amazonas: Cerro de la Neblina [ca. 0°53'N, 65°59'W], Río Yatua, along escarpment,

1200 m, shrub 2 m tall, corolla greenish, 16 Nov. 1957 (fl, fr), *B. Maguire, J.J. Wurdack, Keith & C.K. Maguire 42120* (holotype NY [barcode 00132332]; isotypes P [barcode P00729462], US [barcode 00137734], VEN [Acc. No. 49441]).

(=) *Neblinathamnus glabratus* Steyer., Mem. New York Bot. Gard. 10(5): 231. 1964.

Type: VENEZUELA. Amazonas: Cerro de la Neblina, Río Yatua, occasional along W escarpment edge, summit, 1700–2000 m, 30 Dec. 1953 (fl, fr), *B. Maguire, J.J. Wurdack & G.S. Bunting 37011* (holotype NY [barcode 00132335]; isotypes F [Acc. No. 1589377], VEN [Acc. No. 49435]).

*Shrub* 0.3–2 m tall, erect; internodes of young branchlets hispidulous-hirtellous or densely hispidulous. *Stipules* shallowly triangular to truncate, 0.3–0.6 × 1–1.5 mm, sometimes shallowly bilobed, subcoriaceous, hispidulous-hirtellous or sparsely to densely hispidulous outside, sericeous-pubescent inside, with a row of 7–9 sparse colleters on margin. *Leaves* shortly petiolate; petioles 2–3 mm long, glabrous or hispidulous; blades obovate, obovate-oblong, narrowly oblong to linear oblong, 1–2.5(–3.3) × 0.5–1.3(–1.5) cm, cuneate to acute at base, round and sometimes mucronate at apex, coriaceous, dark green and shiny above, silvery to whitish below, drying brown above and pale to dark olive green below, glabrous and rugose above, tessellate and foveolate, with a silvery appearance, foveolate with tufts of vermiform hairs and margins hispidulous-ciliate, below; midrib impressed above, prominent and appressed-hispidulous below; margins narrowly revolute; secondary veins 5–7 on each side of midrib, impressed above and prominent below; tertiary venation obsolete above and finely reticulate below. *Flowers* axillary, 1–2 per axil. *Bracteoles* subtending flowers setaceous, linear to very narrowly lanceolate, 1–3 × 0.1–0.4 mm, hispidulous. *Flowers* pedicellate; pedicels 1.5–2.5 mm long during anthesis, hispidulous-hirtellous or densely hirtellous. *Hypanthium* obovoid to oblong-ovoid, 2–2.5 × 1.7–2 mm, sparsely to densely hirtellous. *Calyx* lobes subequal, linear, linear-lanceolate to linear-spathulate, 4–7 × 0.3–1 mm, acute to acuminate at apex, sparsely to moderately hirtellous or hispidulous, with 2 or 3 linear, 0.2–0.3 mm long, colleters at each lobe sinus. *Corolla* 15–22 mm long,

green to yellowish-green, or tube red and lobes green to yellowish-green; tube narrowly cylindrical and slightly wider at mouth, 10.5–14.5(–16) mm long, 1–2 mm wide at lower third, 2–3 mm wide at mouth, glabrous or sparsely hirtellous outside, glabrous from base to 3–4 mm below the mouth and puberulent above, portion corresponding with the anthers with vermiform, multicellular hairs, inside; lobes ovate to oblong-ovate, 4.5–6 × 3.5–5 mm, round, obtuse or acute at apex, glabrous outside, glabrous (microscopically papillose) inside. *Short-styled flowers* (*Stein et al. 1636*; corolla tube 14 mm long, lobes 5.5–6 mm long): stamens included, inserted at 3 mm below corolla mouth; filaments 0.7 mm long; anthers narrowly oblong, 2.5 × 0.25–0.3 mm, acute at both ends, tips reaching corolla mouth; style included, 10.5 mm long, 5/7 of corolla tube, glabrous, style branches linear, 2.5–2.7 mm long, acuminate at tip. *Long-styled flowers* (*Luteyn & Steyermark 9437*; corolla tube 10.5 mm long, lobes 4.5 mm long): stamens included, inserted at 4 mm below corolla mouth; filaments 0.8–1 mm long; anthers narrowly oblong, 2 × 0.15–0.2 mm, acute at base, apiculate at apex; style as long as the corolla tube, 10.5 mm long, style branches narrowly ovate, 0.7 mm long, round at tip. *Capsules* with pedicels to 4 mm long, subturbinate to obovoid-subglobose, 4–5 × 3.5–4 mm, acute to obtuse at base, round to truncate at apex, brown, densely hirtellous or hispidulous. *Seeds* oblong-elliptic, 1–1.5 × 0.6–0.9 mm, yellowish rust brown.

**Notes:** Steyermark (1964: 231–232; 1974: 319) differentiated *Neblinathamnus argyreus* from *N. glabratus* by the corolla tube sparsely hirtellous outside (vs. completely glabrous outside in *N. glabratus*), leaf blades obovate or oblong-obovate, foveolate-tessellate and with tufts of vermiform papillae, giving a whitish appearance below (vs. narrowly oblong or linear-oblong, foveolate-tessellate but without tufts of white hairs below), corolla green to yellowish-green (vs. red or tube red with lime-yellow lobes), and flowers mostly solitary or sometimes in pairs (vs. flowers in pairs). At the same time, Steyermark (1964: 231–232) stated “That there are pronounced differences between *N. argyreus* and *N. glabratus* is apparent. Although it is quite possible that additional collections may break down the differences which appear to exist on the basis of the present material at hand, it is also evident that the differences now manifested can be

**Figure 26.** *Neblinathamnus argyreus*. **A.** branch with flowers in anthesis and flower buds. **B–C.** Stipule variation within the same branch. **B.** Truncate stipule. **C.** Shallowly bilobed stipule. **D.** Dissected long-styled flower; style as long as corolla tube with narrowly ovate branches. **E.** Dissected short-styled flower; style included with linear branches. **F.** Dehiscent capsule. **A–D:** drawn from *Luteyn & Steyermark 9437* (F); **E:** drawn from *Stein et al. 1636* (F); **F:** drawn from *Liesner et al. 16102* (US). Illustration by Piero Delprete.

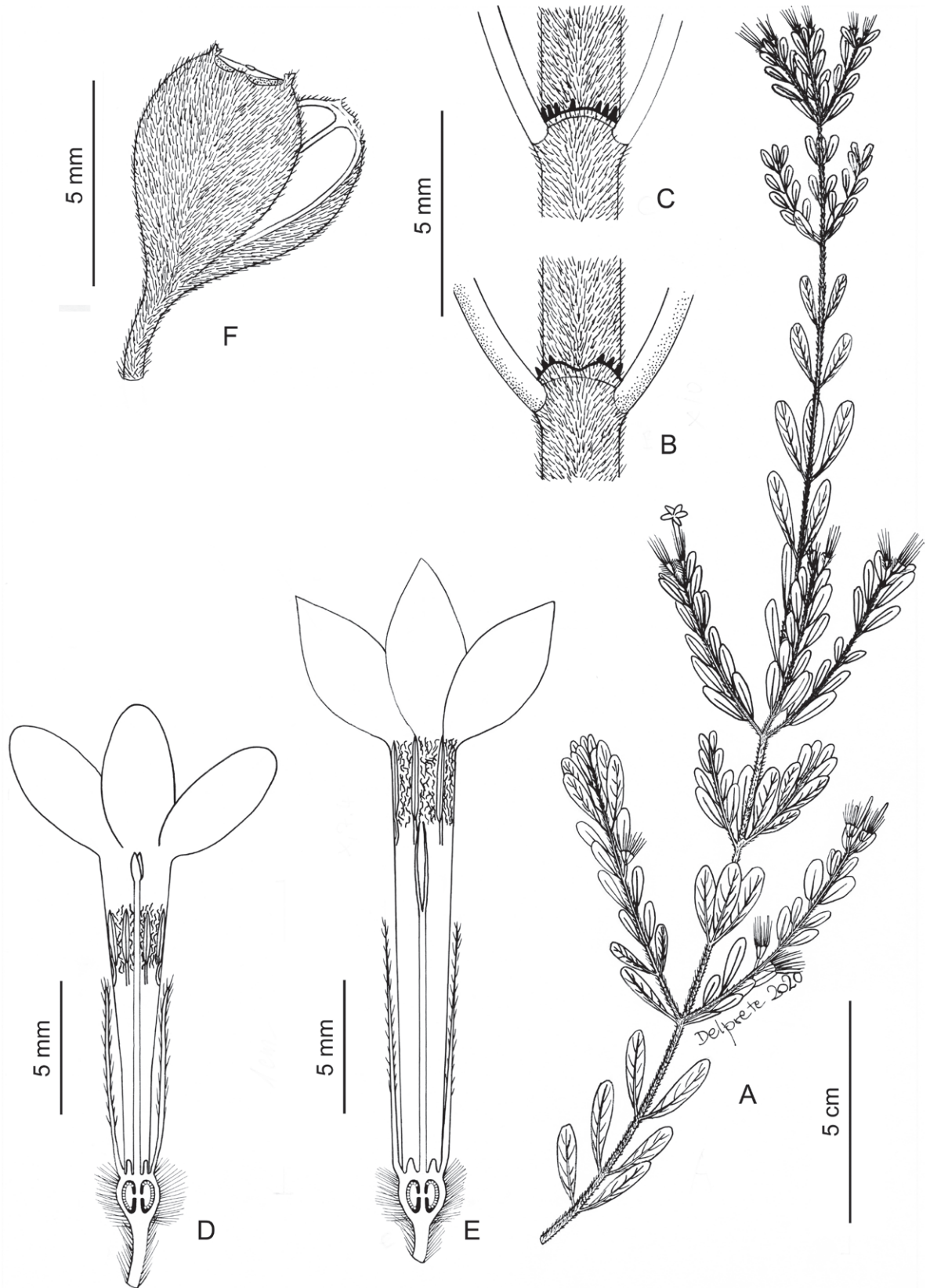


Figure 26.

best be expressed as specific taxa.” Delprete and Steyermark (2004d: 660) synonymized the two taxa and wrote “Steyermark distinguished *N. glabratus* by details of leaf shape and pubescence and by the absence of vermiform trichomes on its lower leaf surface. However, as he predicted in his description of *N. glabratus*, recent collections have shown that these characters intergrade. Consequently these names are here considered as synonymous.” In addition, the types of these two taxa were collected in two nearby localities near Río Yatua, Cerro da Neblina, Venezuela. After a detailed analysis complemented by additional material, the conclusion reached by Delprete and Steyermark is here confirmed, and the two taxa are maintained as synonymous.

**Distribution and ecology:** Endemic to Serranía de la Neblina (Figure 27), state of Amazonas, southernmost Venezuela, in open scrub forests, escarpments and summits of tepuis. The Neblina Massif divides northern Brazil from southern Venezuela, and is present on both countries, with most part in Venezuela. This portion of the Guiana Shield highlands is known as “Tepuis”, includes numerous unique habitats, and is a region rich in

endemic species. So far, this species has been found only in Venezuela. On the Brazilian side, where the highest point of the mountain (3014 m), as well as for Brazil, is located, remains poorly explored due to the difficult access. This species grows on exposed sandstone outcrops, open scrub formations and escarpments, at 1600–1900 m altitude.

**Phenology:** Flowering specimens were collected from November to February and April, and fruiting specimens in December and February.

**Suggested conservation status: Least Concern (LC).** Cerro de la Neblina is a protected area, with the Serranía de la Neblina National Park on the Venezuelan side, and the Pico da Neblina National Park on the Brazilian side. This species has been collected only on the Venezuelan side, at altitudes of 1600–1900 m. The size of its populations is unknown. As all the collections were made within a remote, well-preserved national park, which is without any imminent threat, this species is treated as Least Concern (LC) following IUCN criteria (IUCN 2012, 2019).



Figure 27. Distribution of *Neblinathamnus argyreus* (circles) and *N. brasiliensis* (squares).

**Specimens examined: VENEZUELA: Amazonas:** Río Negro, Camp III, Neblina Massif, NW Plateau, 13.5 km ENE of Cerro de la Neblina Base Camp, 0°54'N, 66°4'W, 1750–1850 m, 16–18 Feb. 1984 (fr), *R.L. Liesner 16102* (MO, NY, US); Cerro de la Neblina, altiplanicie en la cumbre del brazo nor-occidental, al N del campamento base a lo largo del Río Mawarinuma, afluente del Río Baria, 0°52'N, 66°5'W, 1880 m, 7–8 Feb. 1984 (fl), *J.L. Luteyn & J.A. Steyermark 9437* (F, MO, NY, US); Cerro de la Neblina, uppermost escarpment slopes S of Camp 3, 1700 m, 27 Dec. 1953 (fl), *B. Maguire et al. 36960* (NY, SP, paratype); Cerro de la Neblina, Río Yatua, occasional, NW Cumbre, 1900 m, 20 Dec. 1953 (fl), *B. Maguire et al. 37011-A* (IAN, NY, RB, paratype); Cerro de la Neblina, frequent in open areas 6–8 km N of Cumbre Camp, 1800–1900 m, 10 Jan. 1954 (fl), *B. Maguire et al. 37175* (NY [2 sheets], paratype); Cerro de la Neblina, escarpment edge above Cañon Grande, E of Cumbre Camp, locally abundant, 1800 m, 22 Nov. 1957 (fl), *B. Maguire et al. 42171* (COL, F, NY, P, S, US, VEN, paratype); Cerro de la Neblina, 6.5 km SSW of base camp, southern extension of range, ridge top with Bromeliads, *Heliamphora* and low shrubs, 0°47'N, 66°11'W, 1600 m, 18 Apr. 1984 (fl), *B.A. Stein et al. 1636* (F, MO, NY, US); Cerro de la Neblina, altiplanicie en la cumbre del brazo nor-occidental, al N del campamento base a lo largo del Río Mawarinuma, afluente del Río Baria, rocky margins, 0°52'–53'N, 66°5'W, 1880 m, 7–8 Feb. 1984 (fl), *J.A. Steyermark & J.L. Luteyn 129788* (F, MO, NY, U; same as *Luteyn & Steyermark 9437*).

5-2. *Neblinathamnus brasiliensis* Steyer., Mem. New York Bot. Gard. 23: 309. 1972. (Figures 4I, 27–28).

Type: BRAZIL. Amazonas: Rio Negro, Rio Cauaburi, Rio Maturacá, on slopes of Serra Pirapucú [Serra da Neblina, ca. 0°48'24"N, 66°0'19"W], plant 1 m tall, calyx green, corolla with red base and green lobules, 1300 m, 26 Jan. 1966 (fl, fr), *N.T. Silva & U. Brazão 60907* (holotype NY [barcode 00132333]; isotypes COL [Acc. No. 129225, barcode COL000004628], F [Acc. No. 1713895], S [Acc. No. S05-1759], US [barcode 00137735]).

(=) *Neblinathamnus aracamunianus* Steyer., Ann. Missouri Bot. Gard. 76: 968. 1989.

Type: VENEZUELA. Amazonas: Depto. Río Negro, [Neblina-Aracamuni Massif], Cerro Aracamuni, summit, Popa Camp, savanna at edge of tepui, shrub 0.5 m tall, corolla tube red with lobes greenish-

white, 1°26'N, 65°47'W, 1550 m, 19 Oct. 1987 (fl), *R. Liesner & F. Delascio 22153* (holotype MO [Acc. No. 3663774]; isotypes NY [barcode 00007410], VEN [Acc. No. 82233]).

*Shrub* 0.5–1 m tall, erect; internodes of young branchlets strigillose-hirtellous or appressed hirtellous. *Stipules* bilobed or constituted of two free lobes, lobes ovate, deltoid to broadly triangular, 1.2–1.5 × 0.7–0.8 mm, subcoriaceous, hispidulous-hirtellous or sparsely to densely hispidulous outside, appressed-hispidulous inside, with a row of 4–5 colleters on margin of each lobe. *Leaves* shortly petiolate; petioles 1.5–3 mm long, densely appressed strigillose-hirtellous or moderately to densely appressed hirtellous; blades oblong-elliptic to ovate-lanceolate, (2.5–)3–6 × (0.8–)1–3 cm, acute to obtuse at base, obtuse to acute at apex, coriaceous, dark green and shiny above, whitish pale green below, drying brown above and pale to dark olive green below, lamina glabrous, midrib sulcate and strigillose or with sparse appressed hairs above, tessellate and foveolate, foveolate with tufts of short vermiform hairs and margins glabrous, below; midrib impressed above, prominent and appressed-hispidulous below; margins narrowly revolute; secondary veins (4–)5–7 on each side of midrib, obscure, inconspicuous to obsolete above, inconspicuous to slightly prominent, appressed-hispidulous or glabrescent in older leaves) below; tertiary venation obsolete above, finely reticulate below and impressed, the areoles in depressed foveolate areas with circles of minute white trichomes. *Inflorescences* axillary, sometimes appearing terminal when axillary on apical node, cymose, (2–)3–5-flowered. *Bracteoles* subtending flowers subulate, setaceous, 1.5–3 × 0.1–0.4 mm, sparsely hispidulous. *Flowers* pedicellate; pedicels 1–3 mm long during anthesis, densely tomentose-strigillose. *Hypanthium* turbinate or narrowly obovoid, 1.8–2 × 1.4–1.5 mm, densely substrigillose-hirtellous. *Calyx* lobes green, equal to subequal, linear, linear-acuminate or linear-spathulate, sometimes wider near the apex, (4–)5–7 × 0.3–0.7 mm, acuminate to subacute at apex, sparsely hispidulous to hispidulous outside, glabrous inside, margins sparsely hispid-ciliate, with 2 or 3 linear, 0.2–0.3 mm long, colleters at each lobe sinus. *Corolla* 15–18 mm long, tube red and lobes green to yellowish- to whitish-green; tube narrowly cylindrical and slightly wider at mouth, 9–12 mm long, 1.4–1.8 mm wide at lower third, 2.2–2.5 mm wide at mouth, glabrous outside, glabrous from base to 3–4 mm below the mouth and puberulent above, portion corresponding with the anthers with vermiform/multicellular hairs inside; lobes 5, elliptic-oblong or ovate-oblong, 5–6 × 2.5–3.7 cm, round or obtuse at

apex, glabrous outside, glabrous (microscopically papillose) inside. *Short-styled flowers*: unknown. *Long-styled flowers*: stamens inserted at 1 or 3–4 mm from corolla tube base, filaments 1–3 mm long; anthers linear, 2–2.5 × 0.2 mm, round at base, acute at apex; style exerted, 10–13 mm long (style branches exerted beyond corolla mouth), glabrous, branches narrowly lanceolate to linear, 2–3 mm long, acuminate at apex. *Capsules* broadly obconical to obovoid, 4–5 × 3–4 mm, acute to obtuse at base, round to truncate at apex, brown, densely subhirsutellous. *Seeds* unknown.

**Notes:** Steyermark (1972a: 309) described *Neblinathamnus brasiliensis* Steyermark as having “3–4 leaves per node” [foliis 3–4-verticillatis] but the leaves of type specimens of this species are opposite or ternate. In the same description he also wrote that the corolla throat is densely villous-puberulent above 5 mm from the base [“intus supra basin 5 mm dense villosulo-puberulenti”], but in all the specimens examined the corolla throat is glabrous from base to 3–4 mm below the mouth and puberulent above, and the portion corresponding with the anthers is covered with vermiform/multicellular hairs.

Steyermark (1989: 968) along with the description of *Neblinathamnus aracamunianus* Steyermark added “*Neblinathamnus* was originally described by Steyermark (1964) with two species known, *N. argyreus* from Venezuela on Cerro de la Neblina and *N. glabratus* [= *N. argyreus*] from adjacent northern Brazil on Serra Pirapucú [sic! Type material of *N. glabratus* was collected on Serra da Neblina, as *N. argyreus*]. This third species differs from the other two in its shorter corolla; larger leaf blades with subacute or obtuse apices; and shorter, spatulate-linear, subacute calyx lobes, which are more dilated at the apex, dorsally pubescent, and more abundantly ciliolate.” However, with this statement it is clear that Steyermark confused his new species with a third species already described by him, *N. brasiliensis*, which is from Serra Pirapucú, near Pico da Neblina, at the Venezuelan-Brazilian border, and with which he did not make a comparison with his fourth new species. Delprete and Steyermark (2004d: 660) synonymized the two taxa without any further comment. A comparative analysis of the type specimens of both taxa confirmed that the morphological features *N. brasiliensis* and *N. aracamunianus* are widely overlapping. In addition, although located in different countries, both Cerro

Aracamuni (Venezuela) and Serra Pirapucú (Brazil) are parts of the Cerro da Neblina Massif, therefore geographically close (Figure 27), and the two taxa are here confirmed to be synonymous.

**Distribution and ecology:** Only known from the type specimens. Endemic to Cerro da Neblina Massif, occurring both on the Venezuelan (Cerro Aracamuni) and on the Brazilian side (Serra Pirapucú) (Figure 27). Growing on meadows along escarpments on tepui summits, at 1300 and 1550 m altitude.

**Phenology:** The gathering collected in January has flowers and mature capsules, and that collected in October only has flowers.

**Suggested conservation status: Least Concern (LC).** As explained for the other species of this genus, Cerro de la Neblina is protected by two national parks on the Venezuelan and on Brazilian sides. This is a rare species, only known by the two type gatherings, at 1550 m on the Venezuelan side, and at 1300 m on the Brazilian side. The size of the populations is unknown. As the collections were made within remote, well-preserved national parks, which are without any imminent threat, this species is treated as Least Concern (LC) following IUCN criteria (IUCN 2012, 2019).

## 6. NEOBERTIERA

*Neobertiera* Wernham, J. Bot. 55: 169. 1917.

Emend. Sandwith, Kew Bull. Misc. Inf. 1931: 470. 1931; emend. Steyermark, Mem. New York Bot. Gard. 17: 289–290. 1967; emend. Delprete, Phytotaxa 206: 118–132. 2015; Delprete, Phytotaxa 392: 225–231. 2019.

Type: *Neobertiera gracilis* Wernham.

*Perennial herbs*, subshrubs or shrubs. *Stipules* basally adnate with the petioles, broadly ovate, ovate, oblong-ovate or narrowly triangular, acuminate or bifid at apex; pubescent, and with numerous colleters either in a row or as two groups on each side at medio-basal portion inside. *Leaves* opposite, petiolate; blades elliptic, oblong-elliptic to oblanceolate, chartaceous; domatia absent. *Inflorescences* terminal, many-flowered, laxly cymose to densely glomerulate or subcapitate (extremely reduced cyme),

**Figure 28.** *Neblinathamnus brasiliensis*. **A.** Branch with flowers in anthesis, flower buds and capsule. **B.** Node with bilobed stipule. **C.** Dissected long-styled flower; style exerted with linear branches. **D.** Capsule, before dehiscence. **A–D:** drawn from *Silva & Brazão 60907* (F). Illustration by Piero Delprete.

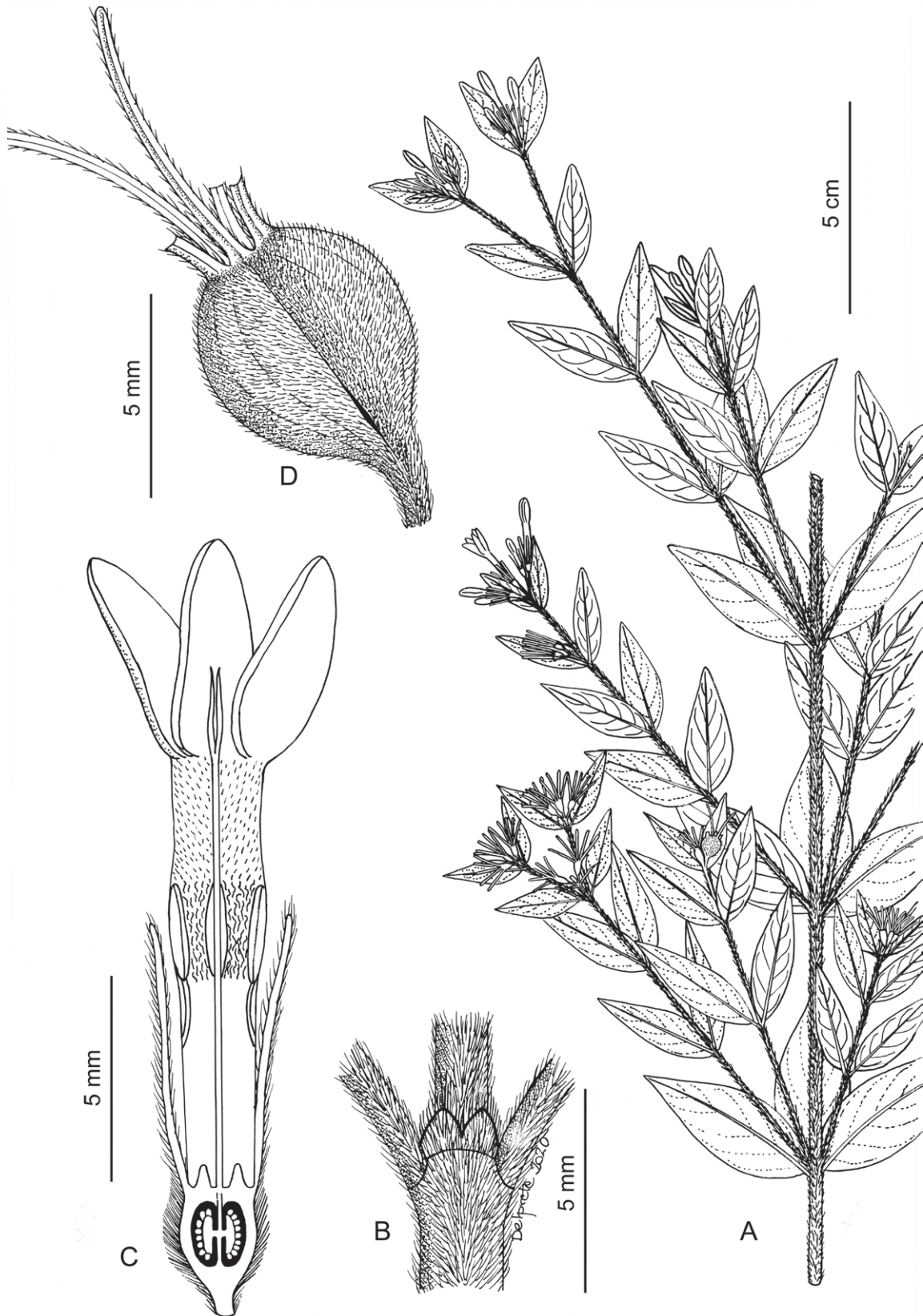


Figure 28.



when laxly cymose with ultimate branches scorpioid, (more evident when fully expanded), when glomerulate to densely cymose with lateral branches terminating in flowering glomerules. *Flowers* commonly distylous, rarely tristylous, 4-5-merous. *Hypanthium* globose, broadly obovoid to obovoid, appressed strigose, trichomes simple or basally tuberculate (tubercles multicellular in *N. montedouradensis*). *Calyx* tube extremely reduced or absent; lobes free, frequently unequal, erect, narrowly lanceolate, linear-lanceolate to narrowly lanceolate, acute at apex, with 1 or 2 colleters in each calycine sinus. *Calycophylls* absent. *Corolla* hypocrateriform, white (“orange” [?] in *N. montedouradensis*), tube appressed strigose-sericeous outside, puberulent inside, with a narrow line of sparse yellow moniliform hairs at mouth; lobes left-contorted, thickened at base, narrowly oblong or oblong-ovate, margin entire, round or acute at apex. *Pollen* 3-colporate; exine foveolate, perforate. *Short-styled flowers*: stamens included, filaments inserted around the middle or at distal portion of corolla tube; anthers linear; style included, much shorter than corolla tube, style branches narrowly oblong or elliptic. *Long-styled flowers*: stamens included, filaments inserted at the middle or near the base of corolla tube; anthers linear or narrowly sagittate; style about the same length as the corolla tube (tip of branches barely exerted) or exerted beyond corolla mouth, style branches narrowly oblong, narrowly lanceolate to linear. *Ovary* with a stalked placenta; stalk inserted at the middle or medio-basal portion (*N. montedouradensis*) of the septum, with a hemi-elliptic extension; ovules inserted on the placental extension. *Fruits* indehiscent, globose, falling off as dispersal units, leaving a tiny round scar on the infructescence rachis, crustaceous, appressed strigose, trichomes simple or basally tuberculate in *N. montedouradensis*. *Seeds* many, inserted on the stalked placenta, small, tetrahedral.

**Notes about generic emendations:** Wernham (1917) described *Neobertiera* with a single species, *N. gracilis*, and positioned it in the tribe Hamelieae. His description and discussion are erroneous because he stated that its fruits are berries with a few globose seeds. He also stated that the inflorescence of *Neobertiera* is similar to those of a section of *Bertiera*, hence the generic name. In addition, he described the sole species as having “Stamina 4, infra corollae fauce inserta” (although the stamens of the

holotype specimen are inserted at the distal portion of the corolla, and not at the corolla mouth) and “Anthers 1.5 mm, filaments slightly shorter, [...] style 1.6 mm long, stigmatic branches 0.7 mm.” He also wrote, with a pencil, on the holotype specimen “filaments inserted at mid-tube”, contrasting with what he wrote in the publication. Therefore, Wernham’s original description of this species was made using short-styled specimens (Jenman 2388).

Both Sandwith (1931: 470) and Steyermark (1967: 289–290) did not notice the distyly in *Neobertiera gracilis*, although they had ample material at hand. Sandwith (1931: 470) saw several collections of this species at K and described it as “a very pretty herb or low shrub, 1–5 ft. [30–150 cm] high, with pure white flowers. The flowers were described by Wernham as tetramerous, but even on his own type specimen at least two of the calyces are pentamerous, while pentamery is obvious on the material at Kew.” Therefore, Sandwith correctly emended the merosity of the genus. In fact all the species successively described in this genus are pentamerous.

Steyermark (1967: 234–235) in the key to the Rondeletieae genera included: *Gleasonia*, *Sipaneopsis*, *Cuaticasiasiodendron* [= *Arachnothryx*], *Rondeletia*, *Arachnothryx*, *Pteridocalyx*, *Neobertiera*, *Maguireothamnus*, *Neblinanthus* [as “*Neblinanthus*”], *Sipanea*, *Limnosipanea*, *Chalepophyllum*, and *Dendrosipanea*. He did not describe the fruits of *Neobertiera*, but considering all the other genera of his widely delimited Rondeletieae are capsular, he probably assumed that its fruits are not berries.

*Neobertiera* has been traditionally reported as having homostylous flowers, with filaments inserted at the distal portion of the corolla tube (Wernham 1917; Sandwith 1931; Steyermark 1967). However, Delprete (2015a) after a detailed observations showed that all the species of *Neobertiera* are distylous and that the filaments are not always inserted at the distal portion of the corolla tube. In long-styled flowers the stamens are inserted near the base of the corolla tube, and in short-styled flowers the filaments are inserted at median or in distal portions of the corolla tube, and their vascular tissue could be easily traced all the way to the base of the corolla. Delprete (2015a) therefore emended the description of *Neobertiera*, by reporting for the first time that the genus is heterostylous, and described three additional species. Delprete (2019b) described a new species, *N. montedouradensis*, from the state of Pará, Amazon Basin, which represents

**Figure 29.** *Neobertiera gracilis*. **A.** Branch with inflorescences. **B.** Node with bifid stipule. **C.** Detail of a lateral branch of a fully developed inflorescence. **D.** Dissected short-styled flower, with stamens inserted at the upper portion of the corolla tube. **E.** Dissected long-styled flower, with stamens inserted at the middle of the corolla tube. **F.** Fruit. **A–B:** drawn from Maguire & Fanshawe 22964 (F); **C:** drawn from Gleason 6 (US) **D:** drawn from Grewal & Persaud 110 (L); **E:** drawn from Schultz & Wessels Boer LBB 10223 (L); **F:** drawn from Smith 2106 (US). Illustration by Piero Delprete (Reproduced from fig. 6 of Delprete (2015a) with permission of copyright holder Magnolia Press).

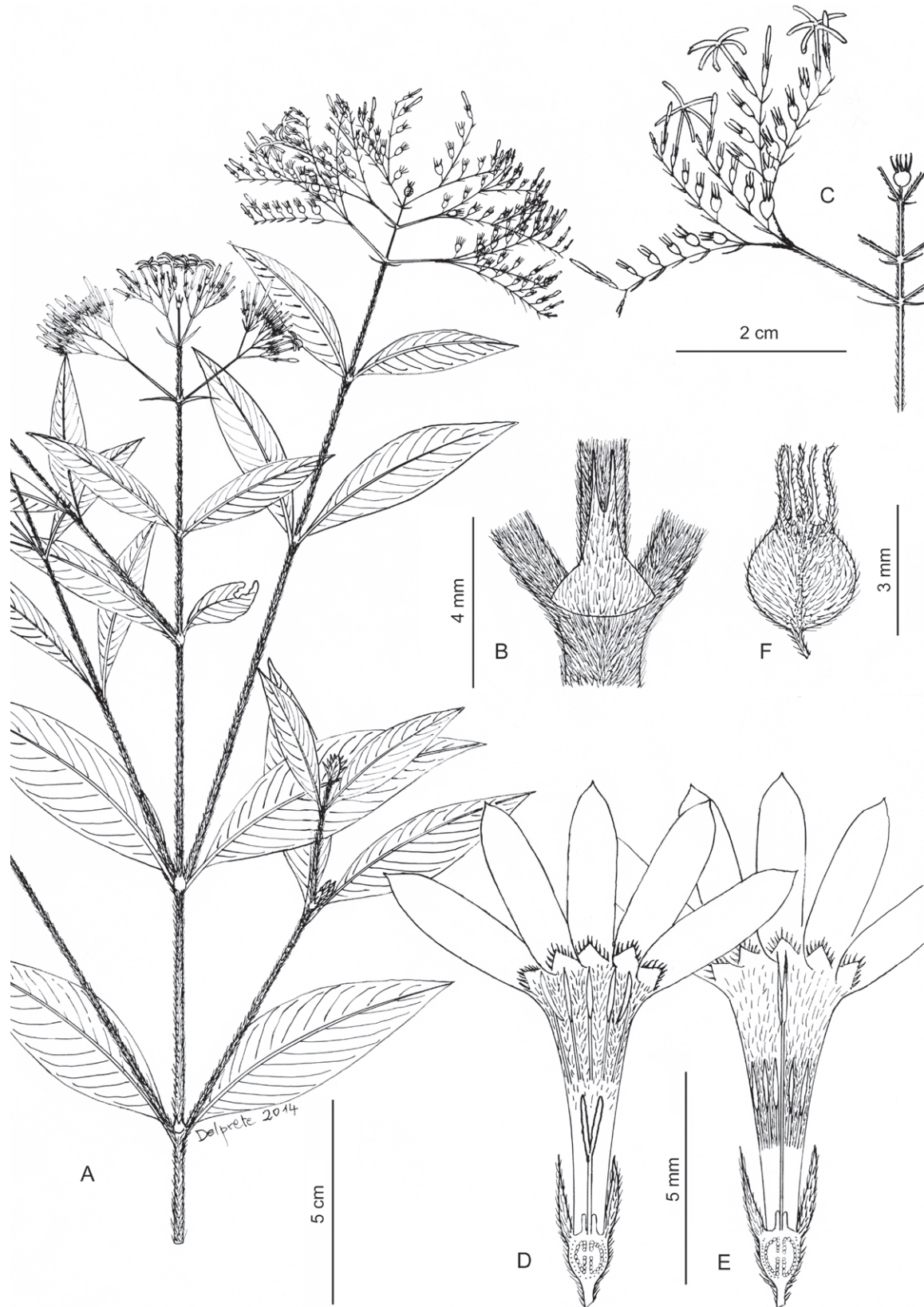


Figure 29.

a significant range extension and the first record of this genus for Brazil. The new species is unique within the genus by having hypanthia and fruits with trichomes conspicuously tuberculate at base, requiring an expansion in the generic description. In addition, he published a new combination for a species occurring in French Guiana.

**Geographic distribution:** A genus of five species endemic to the Guiana Shield (Funk & Berry, 2005), with two species probably restricted to Guyana, two species probably restricted to French Guiana, and one species from the Brazilian states of Pará and Amapá, at the southeastern edge of the Guiana Shield.

Key to *Neobertiera* species

1. Inflorescence subcapitate, an extremely reduced cyme; corolla tube 3–3.2 mm long, lobes 0.9–1 × 0.5–0.6 mm..... 2. *N. micrantha*
  1. Inflorescence densely to laxly cymose or glomerulate; corolla tube 4.5–10.5 mm long, lobes 3–7 × 1–2.7 mm..... 2
  2. Inflorescence glomerulate to densely cymose during anthesis, lateral branches cymose, extremely reduced, terminating with glomerules ..... 5. *N. palustris*
  2. Inflorescence laxly cymose during anthesis, lateral branches dichotomously divided, with one flower at the base of each bifurcation, ultimate branches scorpioid, more evident when fully expanded..... 3
  3. Stipules narrowly triangular, acute at apex; leaves broadly ovate to elliptic, round to obtuse at base; hypanthium with hairs basally tuberculate; corolla 14–15.5 mm long, tube 9.5–10.5 mm long, lobes ovate to oblong-ovate..... 3. *N. montedouradensis*
  3. Stipules ovate to broadly ovate, acuminate or bifid at apex; leaf blades narrowly elliptic, elliptic, lanceolate or oblong-elliptic to oblanceolate, acute-decurrent at base; hypanthium with hairs not basally tuberculate; corolla 7–7.7 or 9.5–13.5 mm long, tube 4–7.5 mm long, lobes oblong or narrowly oblong ..... 4
  4. Rachis slender to filiform; corolla 9.5–13.5 mm long, tube 4.5–7.5 mm long, lobes narrowly oblong, 5–6 × 1.2 mm ..... 1. *N. gracilis*
  4. Rachis stout; corolla 7–7.7 mm long, tube 4–4.5 mm long, lobes oblong, 3–3.2 × 1.1–1.2 mm..... 4. *N. pakaraimensis*
- 6-1. *Neobertiera gracilis* Wernham, J. Bot. 55: 169. 1917. (Figures 4J, 29–30).

Emend. Sandwith, Kew Bull. Misc. Inf. 1931: 470. 1931; emend. Steyermark, Mem. New York Bot. Gard. 17: 289–290. 1967; emend. Delprete, Phytotaxa 206. 127, fig. 2, 6. 2015.

Type: GUYANA. Macouria River, Nov. 1886 (fl), G.S. Jenman 2388 (holotype BM [barcode 000543796]; isotype K? n.v.).

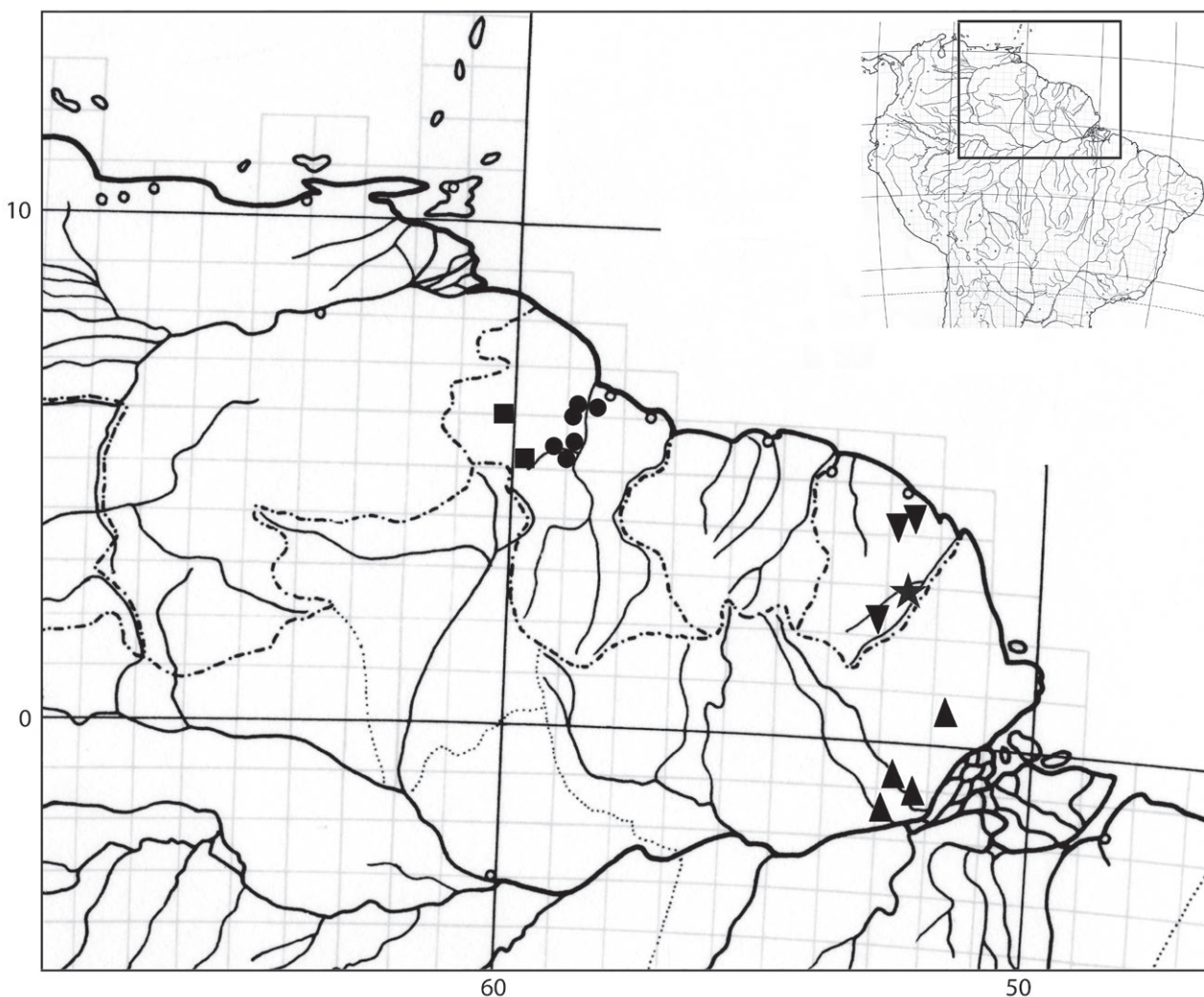
*Perennial herbs or shrubs*, 0.5–4 m tall, erect, sparsely branched; branches densely appressed strigose. *Stipules* broadly to narrowly ovate, 3–4.5 × 2.5–3.5 mm, acuminate or bifid at apex, lobes narrowly triangular to linear, sometimes with an apical colletter, appressed strigose-pubescent outside, appressed antrorse-pubescent at medio-basal portion and intermixed with 5–6 colletters on each side inside, margins strigose. *Leaves* petiolate; petioles 3–9 mm long, appressed-strigose-pubescent; blades elliptic, oblong-elliptic to oblanceolate, 4.5–13.5 × 2–5 cm, acute-decurrent at base, acute at apex, chartaceous, drying pale brown above and olive-green below, sparsely appressed strigose above and below, midvein densely strigose above and below; secondary veins 9–14 on each side of midrib. *Inflorescences* laxly cymose during anthesis; peduncles 2–3.5 cm long; rachis slender to filiform, appressed white-pubescent, 5.5–7.5 cm long when inflorescences fully expanded, with 2–3 pairs of lateral branches; lower lateral branches 1.5–4 cm long (excluding corollas); lateral branches dichotomously divided, with one pedicellate flower at the base of each bifurcation, ultimate branches scorpioid when fully expanded; bracteoles opposite to the insertion of each flower, linear-lanceolate, 1.5–2 × 0.2–0.4 mm, appressed-pubescent. *Flowers* 4-5-merous, pedicellate; pedicels filiform, 0.5–1(–1.5) mm long. *Hypanthium* obovoid to broadly obovoid, 0.7–1.1 × 0.7–1.1 mm, appressed strigose. *Calyx* lobes frequently unequal, narrowly lanceolate, 2.5–5 × 0.2–0.3 mm, appressed strigose outside, and with 2, oblong, 0.1 mm long, colletters at each lobe sinus. *Corolla* white, 9.5–13.5 mm long; tube narrowly cylindrical, slightly wider at mouth, 4.5–7.5 mm long, appressed strigose-sericeous outside, puberulent inside, with a narrow line of yellow, moniliform hairs at mouth inside; lobes narrowly oblong, 5–6 × 1–2 mm, acute at apex, glabrous on both sides. *Long-styled flowers* (Gleason 6 (US) measured on specimen): stamens inserted at 0.6–1 mm from base of corolla tube; filaments 0.3–0.5 mm long; anthers linear, 0.9–1.5 × 0.1–0.2 mm; style about the same length or slightly longer than the corolla tube, 5–7.5 mm long, glabrous; style branches narrowly oblong to linear, 0.8–1.5 mm long, acute at apex, densely papillose when receptive. *Short-styled flowers* (Grewal & Persaud 110 (U)): stamens inserted at distal portion of corolla, at 5.5–6 mm from base of corolla tube in flowers with corolla tube 7.5–8.5 mm long; filaments ca. 1 mm long; anthers linear, 1.5 × 0.2 mm, acute at both ends; style much short-

er than corolla tube, 4–4.5 mm long, glabrous; style branches narrowly oblong, 1.4 mm long, densely papillose when receptive. *Fruits* 2.5–3 mm diam., sparsely strigose-sericeous. *Seeds* ca. 0.3 mm long, microscopically foveolate (barely visible at 50× magnification).

**Notes:** Wernham (1917) in the introduction of the article where he described *Neobertiera gracilis* wrote “The types of all the novelties described are in the National Herbarium [BM].” Therefore the specimen *Jenman 2388* at BM, barcode 000543796, is the holotype of this name. He described the locality of the type specimen as “British Guiana, Macouria River (not far west of Cayenne), *Jenman 2388*.” The Macouria River is in Guyana, but he confused this river with the village of Macouria, which is located, as he stated, “not far west of

Cayenne” and is in French Guiana. Therefore, the type specimen of *Neobertiera gracilis* was collected in Guyana, not French Guiana.

Delprete (2015a) cited the collections *Irwin et al. 54918*, *Schultz & Wessels Boer s.n. (LBB 10223)* and *Schultz J.P. s.n. (LBB 10471)* under *Neobertiera gracilis*; however, a further analysis of additional duplicates revealed that these collections have apically dehiscent capsules (which can be observed only in very advanced stage of maturity) and hypanthium and capsules with hairs basally tuberculate. Therefore, these three gatherings belong to *Sipanea stahelii*, which, although it belongs to another genus, is a very similar species. In addition, as these collections were studied for the description of *N. gracilis*, the above species description differs from that published by Delprete (2015a).



**Figure 30.** Distribution of *Neobertiera gracilis* (circles), *N. micrantha* (star), *N. montedouradensis* (triangles), *N. pakaraimensis* (squares), and *N. palustris* (inverted triangles).

**Distribution and ecology:** Endemic to the Potaro-Siparuni Region, Guyana (Figure 30). It has been collected at the edge or inside wet forests, often near waterfalls, in alluvial or white-sand soils; at 25–120 m elevation. Delprete (2015a) stated that this species occurs in Guyana and Suriname; however, because of the re-identifications of the Suriname gatherings *Irwin et al. 54918*, *Schultz & Wessels Boer LBB 10223* and *Schultz LBB 10471* as *Sipanea stahelii* Bremek., this species is confirmed to be endemic to Guyana.

**Phenology:** Most specimens examined have flower buds, flowers in anthesis and mature fruits on the same inflorescence or at least on the same individual; these specimens were collected in April, June, July, August, September and November. The two specimens collected in June and July have flowers in full anthesis and some flower buds, but no fruits.

**Suggested conservation status: Vulnerable (VU).** This species is known from 19 collections from several localities in Guyana. Most of them are historical collections made from 1881 to the first half of 1990s. None of these localities are within protected areas, except one collection made in 1881 just below Kaieteur, which is now within the Kaieteur National Park. The size of the populations is unknown, and no recent observations in its natural environment are available. Because of this, Delprete (2015a) assigned this species to the category of Data Deficient (DD).

The extent of occurrence (EOO) of this species, using the collection localities with available or estimated coordinates is of ca. 19,700 km<sup>2</sup>, and its most recent collection was made in 1990. Also, recent information (Delprete, pers. obs.) confirmed that within the EOO are present indiscriminate, often illegal, gold hunters' activities, either by mining, panning, or by dragging the bottom of rivers with dredgers. Because the localities where it has been collected are threatened by these human activities, this species is here assigned to the Vulnerable (VU) category, following IUCN criteria (IUCN 2012, 2019); however, future field studies might show that it is even more endangered.

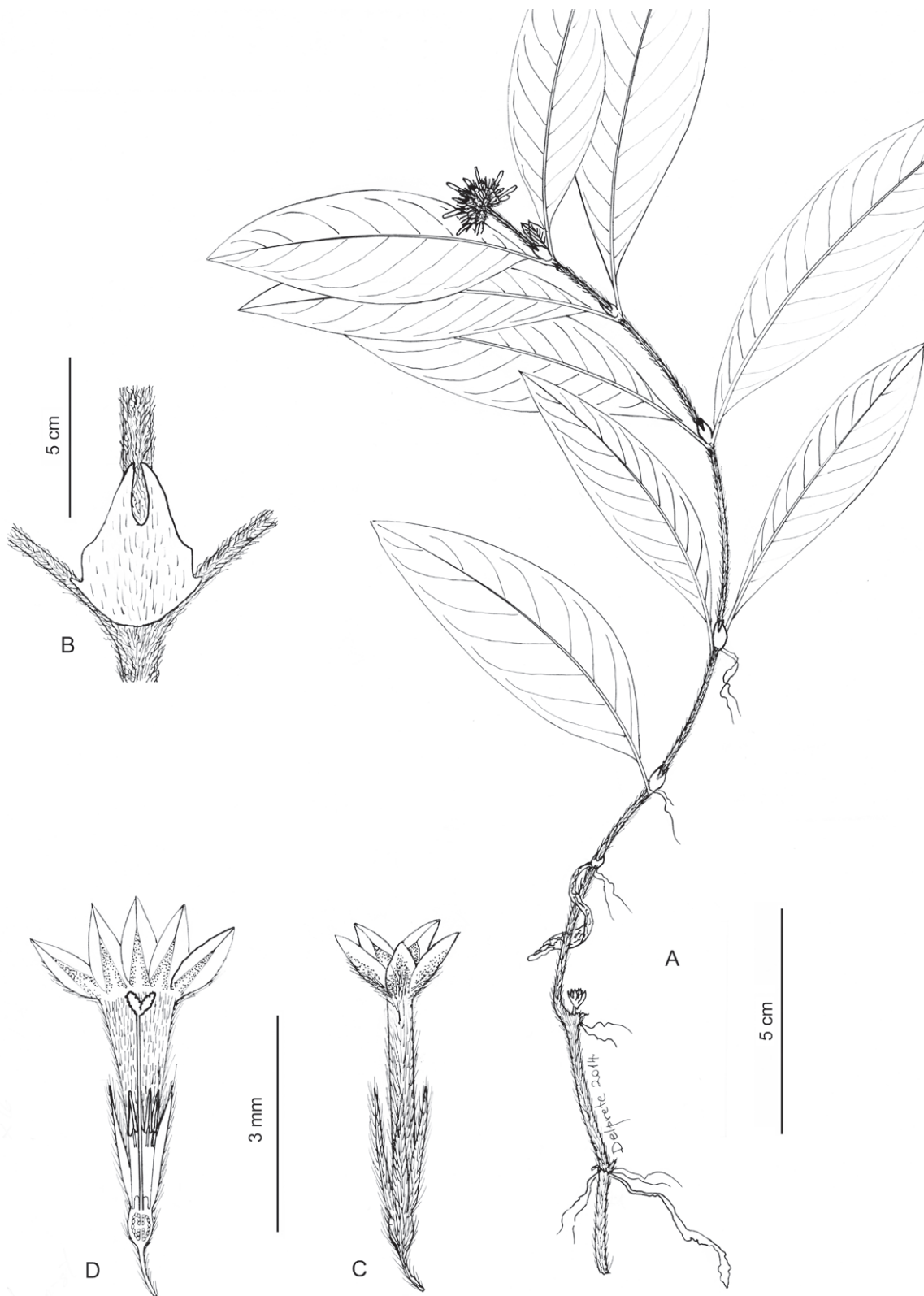
**Specimens examined: GUYANA:** Rockstone, Jun. 1904 (fl, fr), *A.B. Bartlett 8547* (K, U); Moraballi Creek [ca. 6°11'N, 58°50'W], Essequibo River, 3 Oct. 1938 (fl-fr), *Forest Department of British Guiana F120 (Record N. 2729)* (K [2 sheets]); Tumatumari [ca. 5°22'N, 59°0'W], 18–20 Jun. 1921 (fl), *H.A. Gleason 6* [= *Appun 331*] (NY, US); Rockstone, 13–30 Jul. 1921 (fl), *H.A. Gleason 483* (NY, US); Potaro River, Amatuk Mountain [ca. 5°18'N,

59°18'W], 1–2 Apr. 1958 (fl, fr), *V. Graham 193* (K); Rockstone, Essequibo River, 25 m, 20 Apr. 1976 (fl), *M.S. Grewal & R. Persaud 110* (U); Potaro River, below Kaieteur [ca. 5°10'N, 59°28'W], Sep.–Oct. 1881, *G.S. Jenman 945* (K); Demerara River, Mar. 1898 (fl), *G.S. Jenman 7338* (K); Potaro River, Garraway Stream [ca. 5°16'N, 59°9'W], 25 Apr. 1944 (fl, fr), *B. Maguire & D.B. Fanshawe 22964* (F, MO, NY, S, U, US); Moraballi Creek [ca. 6°11'N, 58°50'W], Essequibo River, May 1932 (fl), *E.B. Martyn 381* (K); Potaro-Siparuni Region, from camp on Elizabeth Creek, ca. 1 km along rd to NE and along creek, 5°18'N, 59°5'W, 120 m, 16 Oct. 1990 (fl, fr), *T. McDowell & D. Goupal 3571* (MO, NY, US); Northwest District, vicinity of Matthews Ridge [ca. 7°30'N, 60°10'W], Forest Dept. Camp at White Creek, 8 km SSW of Matthews Ridge, weed at edge of recently cleared field, 31 Aug. 1976 (fl), *S. Mori et al. 8261* (NY); Essequibo River, Moraballi Creek, near Bartica [ca. 6°24'N, 58°37'W], near sea level, 14 Sep. 1929 (fl), *N.Y. Sandwith 256* (K, NY, RB, U); Basin of the Essequibo River, Head Falls, 6°7'N, 20 Sep. 1937 (fl), *A.C. Smith 2106* (F, NY, U, US); Potaro road, Jun. 1910 (fl, fr), *F.A. Stockdale 8775* (K); ca. 83 miles, Bartica–Potaro road, Amatuk Falls [ca. 5°18'N, 59°18'W], 26 Aug. 1933 (fl, fr), *T.G. Tutin 602* (BM, K, US); Potaro River, Amatuk Mountain [ca. 5°18'N, 59°18'W], ca. 67 m, 23 Jul. 1959 (fl), *B.A. Whitton 5* (K).

6-2. *Neobertiera micrantha* Delprete, *Phytotaxa* 206: 123, figs. 1, 2. 2015. (Figures 30–31).

Type: FRENCH GUIANA. Commune de Camopi, Upper Oyapock River Basin, Roche Touatou, small creek in forest, S slope of Roche Touatou (inselbergs), herb 0.5 m tall, stem hirsute, reddish-brown, erect, with age becoming decumbent and rooting at basal nodes, inflorescence terminal, corolla white, 2°57'N, 52°32'W, 120 m, 22 May 1995 (fl, fr), *G. Cremers & J.J. de Granville 14097* (holotype CAY [barcode 079885]; isotypes CAY [barcode 079886], MO [Acc. No. 05000971, barcode MO-1508681], NY [barcode 03212820], P [barcode P007229247], U [barcode U010672], US [Acc. No. 3349483]).

*Perennial herbs*, 0.5 m tall, erect or basally decumbent, sparsely branched; branches densely appressed strigose; horizontal portion of stem rooting at basal nodes and internodes. *Stipules* oblong-ovate to broadly oblong-ovate, 4.5–6 × 4–5 mm, bifid at apex; each lobe narrowly triangular, ca. 2 mm long, appressed-strigose outside, basal portion appressed antrorse-pubescent intermixed with 5–6 colleters on each side and glabrous at distal por-



**Figure 31.** *Neobertiera micrantha*. **A.** Habit. **B.** Node with bifid stipule. **C.** Flower in anthesis. **D.** Dissected long-styled flower, with stamens inserted at lower portion of the corolla tube. Drawn from *Cremers & Granville 14097* (CAY). Illustration by Piero Delprete (Reproduced from fig. 1 of Delprete (2015a) with permission of copyright holder Magnolia Press).

tion inside, margins strigose. *Leaves* petiolate; petioles 4–10(–1.5) mm long, sparsely appressed-strigose; blades narrowly elliptic, elliptic to ovate, 4.5–9 × 1.5–3.5 cm, acute-decurrent at base, acute to obtuse at apex, chartaceous, drying dark olive-green to brown above, pale olive-green to olive-green below, sparsely appressed short-strigose above, glabrous to sparsely sericeous below, midvein and secondary veins densely strigose above, densely strigose-sericeous below; secondary veins 8–11 on each side of midrib. *Inflorescences* always subcapitate during and after anthesis; peduncles 1.5–2 cm long; rachis thin, appressed white-pubescent; flowering portion capitate (extremely reduced cyme); bracts subtending the head lanceolate, 2–3 × 1–2 mm; bracteoles subtending each flower, linear-lanceolate, 1–1.5 × 0.2–0.5 mm, glabrous, margins appressed-strigose. *Flowers* 5-merous, pedicellate; pedicels thin, 0.5–1.3 mm long. *Hypanthium* globose to broadly obovoid, 0.5–0.7 × 0.5–0.7 mm, appressed strigose. *Calyx* lobes slightly unequal, lanceolate, 1.5–2.2 × 0.3–0.5 mm, appressed strigose outside, with 1, oblong, 0.1 mm long, colleter at each lobe sinus. *Corolla* white, 3.9–4.2 mm long; tube narrowly cylindrical, 3–3.2 mm long, sparsely appressed-sericeous outside, densely pubescent inside (hairs microscopically moniliform), with a narrow line of sparse, yellow, moniliform hairs at mouth inside; lobes 5, ovate, 0.9–1.0 × 0.5–0.6 mm, round at apex, glabrous on both sides. *Long-styled flowers*: stamens inserted at 0.9 mm from the base of corolla tube; filaments 0.4 mm long; anthers narrowly sagittate, 0.7 × 0.2 mm; style about the same length as the corolla tube (with branch tips barely exerted), 3–3.2 mm long, glabrous; style branches elliptic, 0.3 mm long, densely long-papillose when receptive. *Short-styled flowers* unknown. *Fruits* 1.2–1.5 mm diam., sparsely strigose-sericeous. *Seeds* ca. 0.3–0.4 mm long, pale brown, microscopically foveolate (barely visible at 50× magnification).

**Distribution and ecology:** Known only from the type gathering, collected in 1995 near Roche Touatou (Figure 30), a group of small inselbergs located on the Upper Oyapock River Basin, French Guiana, near a small creek, in the undercanopy of primary forest, at 120 m altitude.

**Phenology:** Specimens with flowers and fruits were collected in May.

**Suggested conservation status: Critically Endangered (CR).** Known by a single collection near Roche Touatou, Upper Oyapock River Basin, French Guiana. The number of individuals of this population was not reported by the collectors. Due to the remote locality and the unknown number of individuals of the population, Delprete (2015) treated the conservation status of this species as Data Deficient (DD).

Roche Touatou is a group of granitic inselbergs, ca. 2°57'N, 52°32'W, situated at about 35 km SW of the town of Camopi, a community of about 1800 inhabitants. The town is within the zone of free adhesion of the French Guiana Amazonian Park. The region surrounding Camopi is mostly covered by tropical rainforest, with deforested patches of land cultivated by the local population. In addition, such a region is subject to illegal gold mining, which, aside from the destruction of natural vegetation, also cause mercury pollution of fresh water and aquatic fauna, both of them vital sources of the local population. As this species is known by a single collection in forest undercanopy, and in view of the threat of illegal gold mining, this species is Critically Endangered (CR) following IUCN criteria (IUCN 2012, 2019).

6-3. *Neobertiera montedouradensis* Delprete, *Phytotaxa* 392: 226, fig. 1. 2019. (Figures 30, 32).

Type: BRAZIL. Pará: Mun. Almeirim, Monte Dourado, Estrada Perimetral, mata de terra firme, solo argiloso, [ca. 0°52'S, 52°33'W], 27 Nov. 1978 (fl), *M.R. Santos 414* (holotype MG [Acc. No. 72269]).

*Shrub*, 0.4–3.5 m tall; branches sparsely appressed golden-pubescent. *Stipules* narrowly triangular, 2.5–4.5 × 1.7–2 mm, entire (not lobed), acute at apex, appressed-strigose outside, glabrous, with a row of golden hairs and a row of colleters at base inside, margins golden-pubescent ciliate. *Leaves* petiolate; petioles 7–17 mm long, densely appressed golden-pubescent; blades broadly ovate to elliptic, 3.5–8.7 × 1.9–3.5 cm, round, obtuse to acute-decurrent at base, acuminate at apex, chartaceous, drying dark brown above and rust-brown below, sparsely appressed strigose above and below, midvein and secondary veins densely appressed golden-pubescent below;

**Figure 32.** *Neobertiera montedouradensis*. **A.** Branch with a young, unexpanded inflorescence. **B.** Branch with a fully expanded inflorescence. **C.** Node with entire stipule. **D.** Dissected long-styled flower, with stamens inserted at lower portion of the corolla tube, and exerted style. **E.** Longitudinal section of flower, with corolla removed; note stalked placenta and hypanthium with basally tuberculate hairs. **F.** Basal portion of one hypanthium hair, longitudinal section. **A–F:** drawn from *M.R. Santos 414* (MG). Illustration by Piero Delprete (Reproduced from fig. 1 of Delprete (2019b) with permission of copyright holder Magnolia Press).

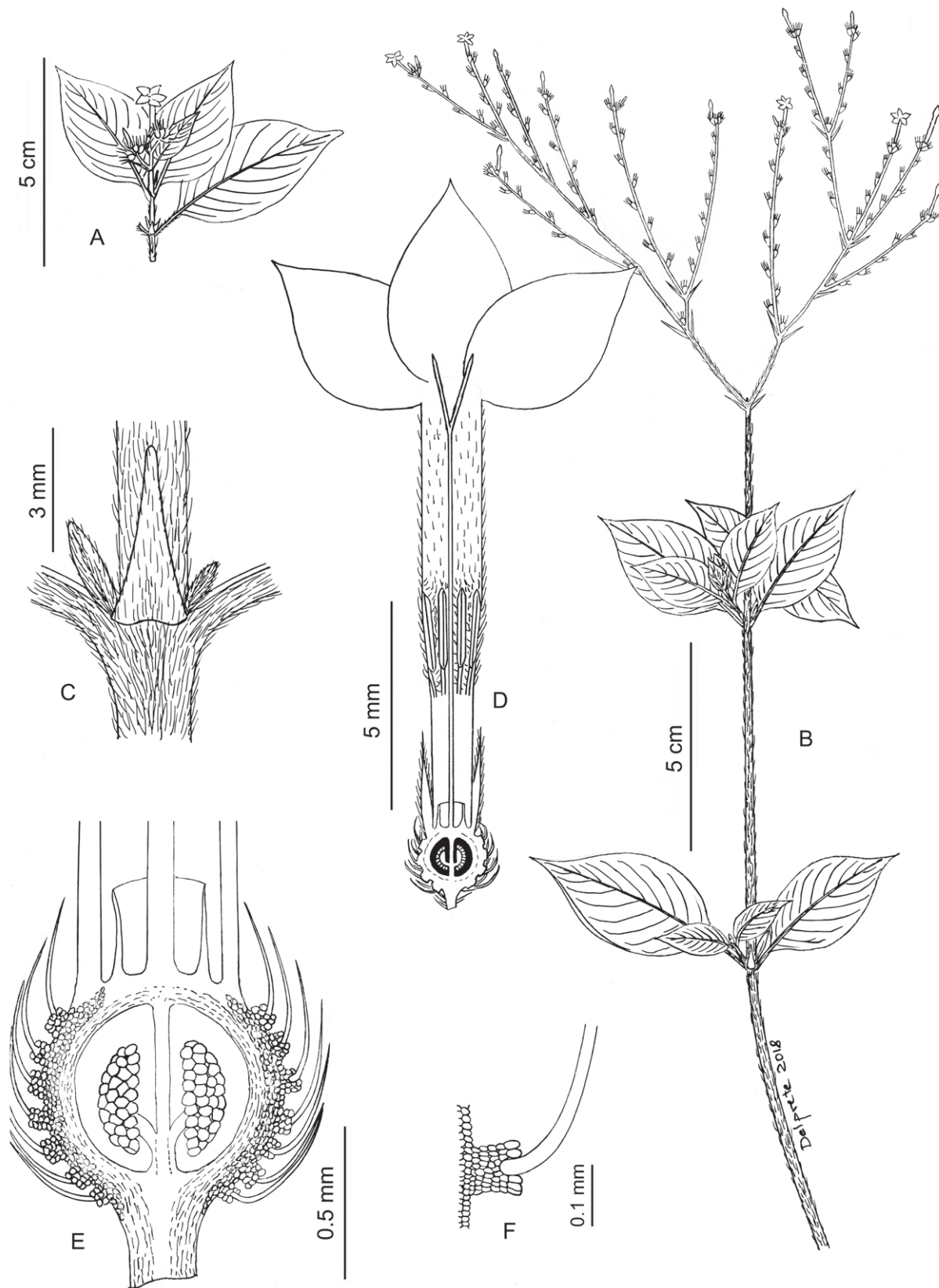


Figure 32.



secondary veins 8–9 each side of midrib, complanar or slightly depressed above, prominent below. *Inflorescence* densely cymose at initial stage of anthesis, expanding to compound laxly cymose during anthesis; peduncles initially 2–3 cm long and expanding to 4.7 cm long during final stage of anthesis; rachis stout to filiform, sparsely appressed golden-pubescent, 10–15.5 cm long when fully expanded, lateral branches 3 times dichomously divided, with one sessile to subsessile flower at the base of each bifurcation, ultimate branchlets scorpioid when fully expanded, 7–10-flowered; bracts subtending secondary and tertiary branches linear-lanceolate, 2.7–4 × 0.3–0.4 mm, sparsely appressed-pubescent; bracteoles opposite to the insertion of each flower, linear-lanceolate, 1.7–2.2 × 0.2–0.3 mm, sparsely appressed-pubescent. *Flowers* 5-merous, subpedicellate; pedicels 0.3–0.4 mm long, appressed strigose. *Hypanthium* globose to obovoid, 0.8–0.9 × 0.8–0.9 mm, densely appressed strigose; hairs basally tuberculate, basal tubercles multicellular. *Calyx* lobes frequently unequal, linear-lanceolate to narrowly lanceolate, 2.2–2.6 × 0.3–0.5 mm, sparsely appressed strigose outside, and with 1, oblong, 0.2 mm long, collector at each lobe sinus. *Corolla* pink (see Notes, below), 14–15.5 mm long; tube narrowly cylindrical, slightly wider at medio-distal portion, 9.5–10.5 mm long, sparsely appressed pubescent outside, glabrous at base, densely spreading pubescent at portion surrounding stamens and sparsely appressed pubescent at distal portion inside, glabrous at mouth; lobes 5, ovate to oblong-ovate, 4.5–5.2 × 2.2–2.7 mm, acute at apex, glabrous outside, papillose inside. *Long-styled flowers*: stamens inserted 3 mm from the base of corolla tube; filaments 0.6 mm long; anthers linear, 1.8 × 0.2 mm, acute at both ends; ovary 2-locular, placenta stalked, inserted at medio-basal portion of the septum; ovules many, inserted on the placental extension; style slightly longer than the corolla tube, ca. 13 mm long, glabrous, style branches almost completely exerted, linear, 1.5–1.8 mm long, acute at apex, densely papillose when receptive. *Short-styled flowers* (*Pires & Silva 110* (HAMAB)): stamens inserted at distal portion of corolla, at 3.5 mm below corolla mouth; filaments 0.5 mm long; anthers linear, 1.7 × 0.2 mm, round at both ends; style much shorter than corolla tube, ca. 5 mm long, glabrous; style branches narrowly oblong-lanceolate, 1.5 mm long, densely papillose when receptive. *Fruits* 2.5–3 mm diam., densely appressed strigose; hairs basally tuberculate, basal tubercles multicellular. *Seeds* unknown.

**Notes:** *Neobertiera montedouradensis* Delprete is unique within the genus by having hypanthium and fruit with hairs basally tuberculate (Fig. 32E–F). Hypanthia and fruits with basally tuberculate hairs are present

in a few species of *Sipanea*, e.g., *S. stahelii* and *S. wilson-brownei*. While the fruits of *Neobertiera* are indehiscent, those of *Sipanea* are loculicidal capsules.

On the specimen label of *M.R. Santos 414*, the flowers of *N. montedouradensis* are described as orange [“flor alaranjada”]; however, this is probably erroneous, as the labels of *Sarquis et al. 62* and *Forza & Leal 5928* indicate that the corollas of this species are pink.

*Neobertiera montedouradensis* is most similar to *N. pakaraimensis* because of its leaf blades chartaceous, with 8–10 secondary veins on each side of midvein, and inflorescences compoundly cymose during anthesis; the former differs from the latter by the narrowly triangular, entire stipules (vs. ovate to broadly ovate, bifid in *N. pakaraimensis*), leaf blades broadly ovate to elliptic, 3.5–8.7 × 1.9–3.5 cm, round, obtuse to acute-decurrent at base, acuminate at apex (vs. narrowly elliptic, lanceolate to narrowly oblong-elliptic, 4–10 × 0.7–2.5 cm, acute-decurrent at base, acute and acuminate at apex), hypanthium with hairs basally tuberculate (vs. with hairs not basally tuberculate), corollas 14–15.5 mm long, with tube 9.5–10.5 mm long, and lobes ovate to oblong-ovate, 4.5–5.2 × 2.2–2.7 mm, acute at apex (vs. 7–7.7 mm long, with tube 4–4.5 mm long, lobes oblong, 3–3.2 × 1.1–1.2 mm, round to obtuse at apex).

**Distribution and ecology:** Originally described from a single specimen collected near the town of Monte Dourado, state of Pará, in terra firme forest on clay soil, near the Jari River, a river running between the Brazilian states of Pará and Amapá. Three additional gatherings have recently been found in HAMAB and MG, one collected near the type locality, and the other two from the contiguous state of Amapá, near the Jari River, and in the Serra do Navio, in the center of the state (Figure 30); all these collections were also made at the edge of a terra firme forest.

**Phenology:** Three gatherings with flowers and fruits were collected in June and August, and one with only flowers was collected in November.

**Suggested conservation status: Critically Endangered (CR).** This species was originally described from a single specimen collected near the town of Monte Dourado [ca. 0°53’S, 52°36’W], near the Jari River, state of Pará. An expedition to the town of Monte Dourado was made during the first week of November 2018 to search for this species. Although a considerable portion of the forests surroundings this town was destroyed and replaced by eucalyptus plantations, several patches of well-preserved forests are still present in a radius of sev-

eral kilometers from the town; nevertheless, after three days of extensive searches in numerous primary and secondary forests of this region, the species was not found. Along with its original description Delprete (2019b) suggested a conservation status of Critically Endangered (CR) following IUCN criteria (IUCN 2012, 2017).

Three additional gatherings of this species have recently been found in HAMAB and MG, one from a locality between Monte Dourado and Almerim, at 1°15'6"S, 52°38'10"W, state of Pará, and the other two from the contiguous state of Amapá, at ca. 0°53'S, 52°22'W and 0°55'N, 51°52'W, extending the extent of occurrence of the species (EOO) to ca. 5,600 km<sup>2</sup>. The number of individuals are not reported in the specimen labels. Taking into account the aggressive forest destruction still ongoing around the town of Monte Dourado and in the other localities in the state of Amapá, it is difficult to predict how long these forest patches will last. Therefore, this rare species is maintained as Critically Endangered (CR) following IUCN criteria (IUCN 2012, 2019).

**Specimens examined: BRAZIL. Amapá:** Mun. Mazagão, margem esquerda do Rio Jari, Morro do Felipe IV [ca. 0°53'S, 52°22'W], beira da floresta mista primária-secundária, 16 Aug. 1985 (fl), *M.J.P. Pires & N.T. Silva 546* (HAMAB); Serra do Navio, Mineração Pedra Branca do Amapari, Ramal Serra da Canga, 0°55'N, 51°52'W, arbusto aproximadamente de 2 m de altura, flores roxas claras, 29 Aug. 2003 (fl, fr), *R.S.F.R. Sarquis et al. 62* (HAMAB [2 sheets], IAN, MG). **Pará:** Mun. Almeirim, Distrito de Monte Alegre, Área de Manejo da Orsa Florestal, Platô 2, floresta de terra firme, borda de mata, 1°15'6"S, 52°38'10"W, 250 m, arbusto 40–60 cm, ramos e nervuras vináceos, cálice verde, corola rósea, frutos verdes, 31 Jun. 2010 (fl, imm fr), *R.C. Forzza & E.S. Leal 5928* (K n.v., MG, RB).

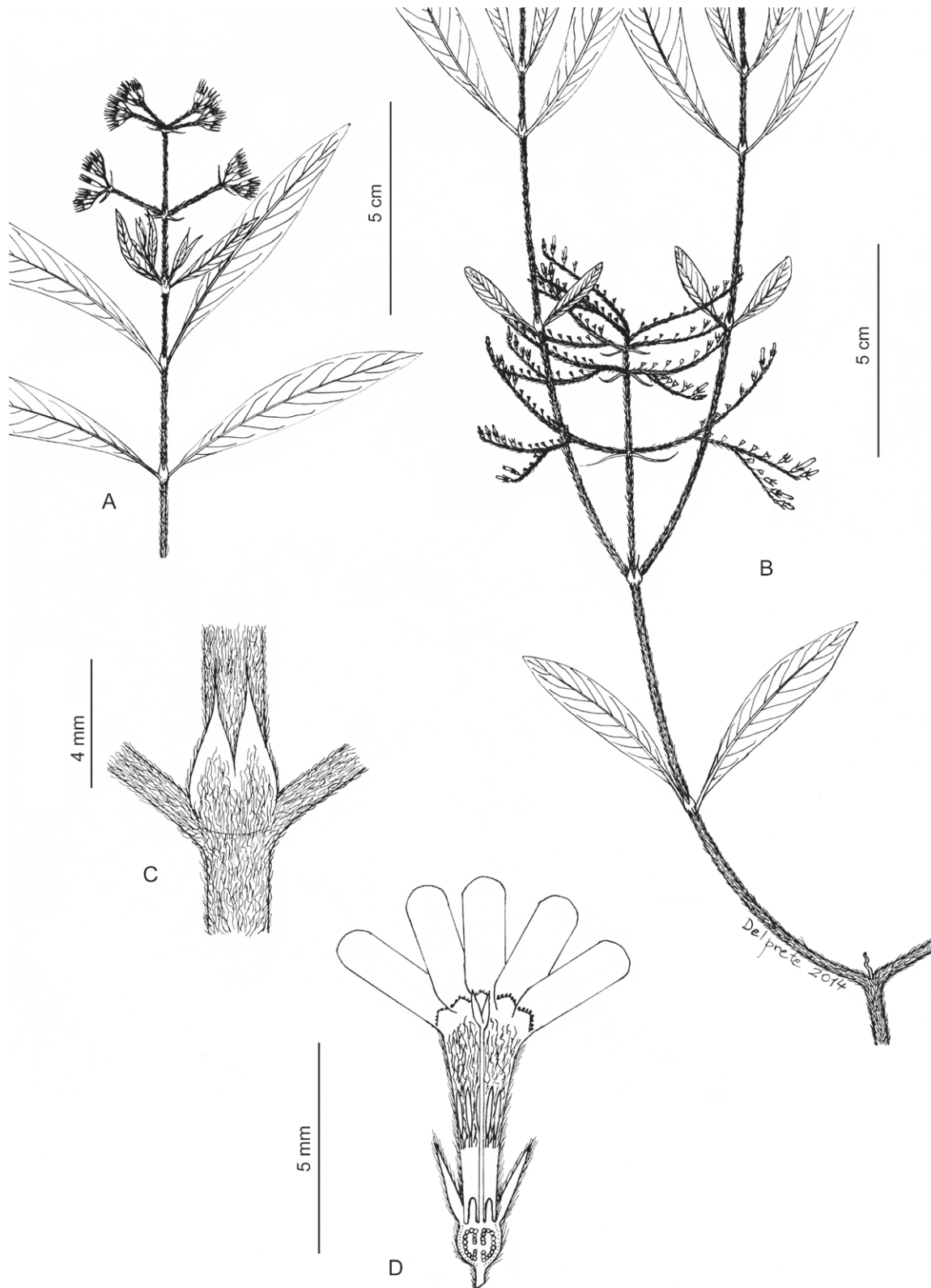
6-4. *Neobertiera pakaraimensis* Delprete, Phytotaxa 206: 126, figs. 2, 5. 2015. (Figures 30, 33).

Type: GUYANA. Potaro-Siparuni Region, Pakaraima Mountains, Mount Wokomung, across slope to SW 0.5 km from headwaters of Wusupubaru Creek, montane slope forest, W aspect, upper canopy 20–35 m, 2-storied, epiphytes abundant, incl. 0.5 hectare tree fall, shrub 0.5 m [tall], filaments white, 5°3'N, 59°53'W, 975–1125 m, 17 Feb. 1993 (fl), *T.W. Henkel, M. Chin & W. Ryan 1449* (holotype CAY [barcode 079485]; isotypes BBS [barcode BBS0032627], CAY [barcode 079486], F [Acc. No. 2232663], INPA [Acc.

No. 214891], MO [Acc. No. 04926765], NY [barcode 03212819], U [barcode 0248751], US [barcode 00699048]).

*Shrubs*, 0.5–4 m tall, erect or basally decumbent, sparsely branched; branches sparsely to densely appressed strigose; rooting at basal nodes and internodes. *Stipules* ovate to broadly ovate, 4–5.5 × 2.5–3 mm, bifid at medio-distal portion, appressed-strigose outside, basal portion antrorse-pubescent intermixed with 2–3 colleters on each side and glabrous at distal portion inside, margins pubescent. *Leaves* petiolate; petioles 6.5–11.5 mm long, densely appressed-strigose; blades narrowly elliptic, lanceolate to narrowly oblong-elliptic, 4–10.5 × 0.7–2.5 cm, acute-decurrent at base, acute or acuminate at apex, chartaceous, drying dark brown above and olive-green below, sparsely appressed strigose above, sparsely short- to long-strigose below, midvein and secondary veins densely strigose below; secondary veins 8–10 each side of midrib, evident only below, immersed in the lamina above. *Inflorescence* laxly cymose during anthesis; peduncles 1.7–4 cm long; rachis stout, appressed white-pubescent, 5.5–6.5 cm long when fully expanded, with 1–3 pairs of lateral branches; lower lateral branches 2.5–3.5 cm long (excluding corollas); lateral branches dichotomously divided, with one pedicellate flower at the base of each bifurcation, ultimate branches scorpioid when fully expanded; bracteoles opposite to the insertion of each flower, linear-lanceolate, 1.5–2 × 0.2–0.4 mm, appressed-pubescent. *Flowers* 4–5-merous, pedicellate; pedicels 1–1.5 mm long, densely appressed strigose. *Hypanthium* globose to obovoid, ca. 1 × 1 mm, appressed strigose. *Calyx* lobes frequently unequal, narrowly lanceolate to narrowly oblong-lanceolate, 2–3 × 0.3–0.4 mm, appressed strigose outside, and with 1 oblong, 0.1 mm long, colleter at each lobe sinus. *Corolla* white, 7–7.7 mm long; tube narrowly cylindrical, slightly wider at mouth, 4–4.5 mm long, appressed strigose-sericeous outside, puberulent inside, with a narrow line of yellow, moniliform hairs at mouth inside; lobes 5, oblong, 3–3.2 × 1.1–1.2 mm, round to obtuse at apex, glabrous on both sides. *Long-styled flowers*: stamens inserted 1.8 mm from the base of corolla tube; filaments 0.7–1 mm long; anthers linear, 1.2 × 0.2 mm, acute at both ends; style slightly longer than the corolla tube, 4.5–5 mm long, glabrous; style branches partially exerted, narrowly oblong, 0.9–1 mm long, acute at apex, densely papillose when receptive. *Short-styled flowers*: unknown. *Fruits* and *seeds* unknown.

**Notes:** Specimens of this taxon have incorrectly been identified as *Sipaneopsis cururuensis* (Henkel et al. 1449,



**Figure 33.** *Neobertiera pakaraimensis*. **A.** Branch with a young inflorescence. **B.** Branch with a fully developed inflorescence. **C.** Node with bifid stipule. **D.** Dissected long-styled flower, with stamens inserted at the middle of the corolla tube. **A–D:** drawn from Henkel *et al.* 1449 (CAY). Illustration by Piero Delprete (Reproduced from fig. 5 of Delprete (2015a) with permission of copyright holder Magnolia Press).

McDowell & Stobey 3853, *Mutchnick et al.* 156); however, *S. cururuensis* is known only from the type gathering from the Tapajos River Basin [ca. 5°18'N, 59°18'W], south of the Amazon River, and can be distinguished from *Neobertiera pakaraimensis* by the generic characters of *Sipaneopsis* (e.g., corolla opening before sexual parts mature, corolla lobes with a basal appendage covered with a tuft of hairs, and homostylous flowers).

In the description of *Neobertiera pakaraimensis*, Delprete (2015a) wrote that the corollas are “4.8–5 mm long” with tubes “4.5 mm long” and lobes “oblong, 3–3.2 × 1.1–1.2 mm”. While the corolla lobes shape and dimensions were correctly reported, the corollas of this species are 7–7.7 mm long with tubes 4–4.5 mm long.

**Distribution and ecology:** Endemic to Guyana (Figure 30), growing at elevations of 120–1125 m. It is known by four collections: two on the Pakaraima Mountain Range, eastern portion of the Roraima Massif, at 975–1125 m elevation, one on islands at Amatuk Falls, at 720 m, and one near the Eping River, at 120 m; growing at river margins inside wet forest.

**Phenology:** The collections with flowers in anthesis were made in October and February, and one collection with flowers and fruits in September.

**Suggested conservation status: Endangered (EN).** Delprete (2015) at the time of the original description of this species, was aware of only two nearby collection localities, and assigned this species to the category of Endangered (EN) following IUCN criteria. Currently, this rare species is known from three localities: two on the Pakaraima Mountain Range, at 975–1125 m elevation, one near Amatuk Falls on the Potaro River, at 720 m, and one near the Eping River, at 120 m. The size of the populations is unknown, and the Extent of Occurrence (EOO) is ca. 4,100 km<sup>2</sup>. None of these localities are within protected areas, and no recent observations to assess their conservation status have been made. The basin of the Potaro River is subject to indiscriminate, often illegal, gold hunters' activities, either by mining, panning, or by dragging the bottom of rivers with dredgers (Delprete, pers. obs.). Because the localities where it has been collected are threatened by these human activities, this species is here confirmed to be Endangered (EN), following IUCN criteria (IUCN 2012, 2019).

**Specimens examined: GUYANA:** Kuyuni-Mazaruni Region, Eping River, common along river, 6°0'N, 60°10'W, 120 m, 6 Feb. 1991 (fl), *T. McDowell & A. Stobey* 3853 (BRG, CAY, MO, NY, U, US); Potaro-Siparuni

Region, Pakaraima Mountains, upper Ireng watershed, Sukabi River, E branch to Kukunang Falls, 5°7'N, 59°57'W, 720 m, 21 Oct. 1994 (fl), *P. Mutchnick et al.* 156 (MO, NY, US); Potaro-Siparuni Region, islands at Amatuk Falls [ca. 5°18'N, 59°18'W; Potaro River], 7 Sep. 2006 (fl, fr), *K.J. Wurdack et al.* 4290 (US).

6-5. *Neobertiera palustris* (A.Rich. ex DC.) Delprete, *Phytotaxa* 392: 228. 2019. (Figures 4K, 30, 34–35).

(=) *Bertiera palustris* A.Rich. ex DC., *Prodr.* 4: 392. Sep. 1830. [A.Rich., *Mem. Fam. Rubiacées* 174. Dec. 1830; reimpr. in *Mem. Soc. Hist. Nat. Paris* 5: 254. 1834]. – *Sipanea palustris* (A.Rich. ex DC.) J.H.Kirkbr., *comb. illeg.*, *Brittonia* 49: 360. 1997; non *Sipanea palustris* Seem. (1853 [= *Limnosipanea palustris* (Seem.) Hook.f.]).

Type: FRENCH GUIANA. “In paludosis, rivis sylvium, inter Conana et Ynéri, mayo et junio florens, augusto fructif.” s.d. [May–Jun. 1781–1785], *L.C.M. Richard s.n.* (holotype P [barcode P02273205]; photo-P at F).

(=) *Neobertiera glomerata* Delprete, *Phytotaxa* 206: 124, figs. 2–4. 2015

Type: FRENCH GUIANA. Commune de Montsinery, Route D-5, trail to Bagne des Annamites, ca. 1 km from Route D-5, forest seasonally flooded, plants growing at the edge of trail, with roots near the water, herb 40–70 cm tall, erect, rooting at basal nodes, leaves chartaceous, corolla white, 4°50'3"N, 52°31'2"W, 10 m, 18 Apr. 2012 (fl), *P.G. Delprete & G. Quenette* 11860 (holotype CAY [barcode CAY214218]; isotypes GB, K, L, MG, MO, NY, P, RB, US).

*Perennial herbs or shrubs*, 0.4–1.5 m tall, erect or basally decumbent, sparsely branched; branches densely appressed strigose; rooting at basal nodes and internodes. *Stipules* ovate to broadly ovate, 2.5–4.5 × 2.5–4.5 mm, acuminate or bifid at apex, appressed-strigose outside, basal portion antrorse-pubescent with group of 7–11 colleters on each side and glabrous at distal portion inside, margins pubescent. *Leaves* petiolate; petioles 7–30 mm long, appressed-strigose-pubescent; blades elliptic, oblanceolate to obovate, 9–14.5 × 3–5.8 cm, acute-decurrent at base, acute at apex, chartaceous, drying dark olive-green to brown above and pale olive-green to olive-green below, sparsely appressed strigose above, appressed strigose below, midvein densely strigose above

and below; secondary veins 13–15 each side of midrib. *Inflorescences* glomerulate to densely cymose during anthesis, densely cymose after anthesis; peduncles 1.3–3.5 cm long; rachis stout, appressed white-pubescent, 2.5–4 cm long (excluding corollas), with 2–3 pairs of very short lateral branches; lower lateral branches 0.4–1.2 cm long (excluding corollas); lateral branches cymose, condensed, terminating in flowering glomerules; bracteoles subtending each flower, linear-lanceolate, 2.5–3 × 0.4–0.6 mm, densely appressed-strigose. *Flowers* 5-merous, sessile to subpedicellate; pedicels, when present, stout, to 1 mm long. *Hypanthium* obovoid to broadly obovoid, 0.9–1.5 × 0.9–1.5 mm, appressed strigose. *Calyx* lobes slightly unequal, lanceolate, 2.5–3.5 × 0.4–1.1 mm, appressed strigose outside, and with 1 oblong, 0.2–0.25 mm long, colleter at each lobe sinus. *Corolla* white, 11.8–13.3 mm long; tube narrowly cylindrical, slightly wider at mouth, 8–9 mm long, sparsely appressed-sericeous outside, puberulent inside (hairs moniliform), with a narrow line of sparse, yellow, moniliform hairs at mouth inside; lobes 5, oblong-ovate to oblong-ellipsoid, 3.8–4.3 × 2.3–2.5 mm, round at apex, glabrous on both sides. *Long-styled flowers*: stamens inserted 2–3 mm from base of corolla tube; filaments 0.5–0.7 mm long; anthers narrowly sagittate, 0.8–1 × 0.1–0.2 mm; style about the same length as corolla tube (tip of branches barely exerted), 8–9 mm long, glabrous; style branches narrowly oblong, 1.4–1.7 mm long, densely papillose when receptive. *Short-styled flowers*: stamens inserted 3–4 mm from base of corolla tube; filaments 0.7–1.1 mm long; anthers linear, 1.4–1.5 × 0.2–0.3 mm, acute at both ends; style much shorter than corolla tube, 4.5–5 mm long, glabrous; style included, branches narrowly oblong, 0.5–0.6 mm long, densely papillose when receptive. *Fruits* 3–4 mm diam., sparsely strigose-sericeous. *Seeds* 0.3–0.4 mm long, black, microscopically foveolate (barely visible at 50× magnification).

**Notes:**—Achille Richard described *Bertiera palustris*, which was first published in Candolle's *Prodromus* (Sep. 1830: 392), and re-published three months later in Richard's *Mémoire sur la famille des Rubiacées* (Richard Dec. 1830: 174), based on a collection made by his father, L.C.M. Richard, in French Guiana. Steyermark (1967: 321–322) excluded this taxon from *Bertiera* and explained, “I have examined a sheet in the Paris Herbarium corre-

sponding to the type specimen from Richard's Herbarium. This specimen has crustaceous capsules and globose non-angled seeds. Furthermore, the inflorescence is regularly branched and does not have a secondly arranged dichasial flowering axis as occurs in the other species of the genus. The specimen obviously pertains to another genus, but at the present time I am unable to assign it to a definite genus. The bifid stipules and herbaceous habit are, likewise, extraneous to the genus *Bertiera*.”

Robbrecht *et al.* (1993: 135) in a survey of *Bertiera* excluded *B. palustris* from the genus with the comment “doubtful, see Steyermark, Mem. New York Bot. Gard. 17: 321 (1967).”

Kirkbride (1997) wrote “In my opinion *S. [Sipanea] wilson-brownei* and *B. palustris* are the same species. The epithet *palustris* has priority over *wilson-brownei*, and so must be transferred to the genus *Sipanea*.” Accordingly, he proposed the new combination *Sipanea* (sect. *Sipanea* subsect. *Nudae* Steyerm.) *palustris* (A. Rich. ex DC.) J.H. Kirkbr. However, the binomial *Sipanea palustris* was already published [*Sipanea palustris* Seem. (Seeman, 1853) = *Limnosipanea palustris* (Seem.) Hook.f.], and renders Kirkbride's combination illegitimate. He cited the type of *Bertiera palustris* as “(holotype: P-n.v. [Field Museum of Natural History Photograph 37285]),” which is the specimen with barcode P02273205 at P.

A close examination of the holotype specimen of *Bertiera palustris* at P showed that all the features correspond to the recently described *Neobertiera glomerata* Delprete. Both Steyermark and Kirkbride did not notice that the fruits of this specimen are indehiscent and fall off as dispersal units, which excludes this specimen from *Sipanea*, which has dehiscent, permanent capsules, and places it in *Neobertiera*. Therefore, Delprete (2019b) published the new combination *Neobertiera palustris* (A. Rich. ex DC.) Delprete for this species.

Several collections of this species from French Guiana have been previously been identified as “*Neobertiera gracilis*”, but they are *N. palustris*. *Neobertiera gracilis* does not occur in French Guiana.

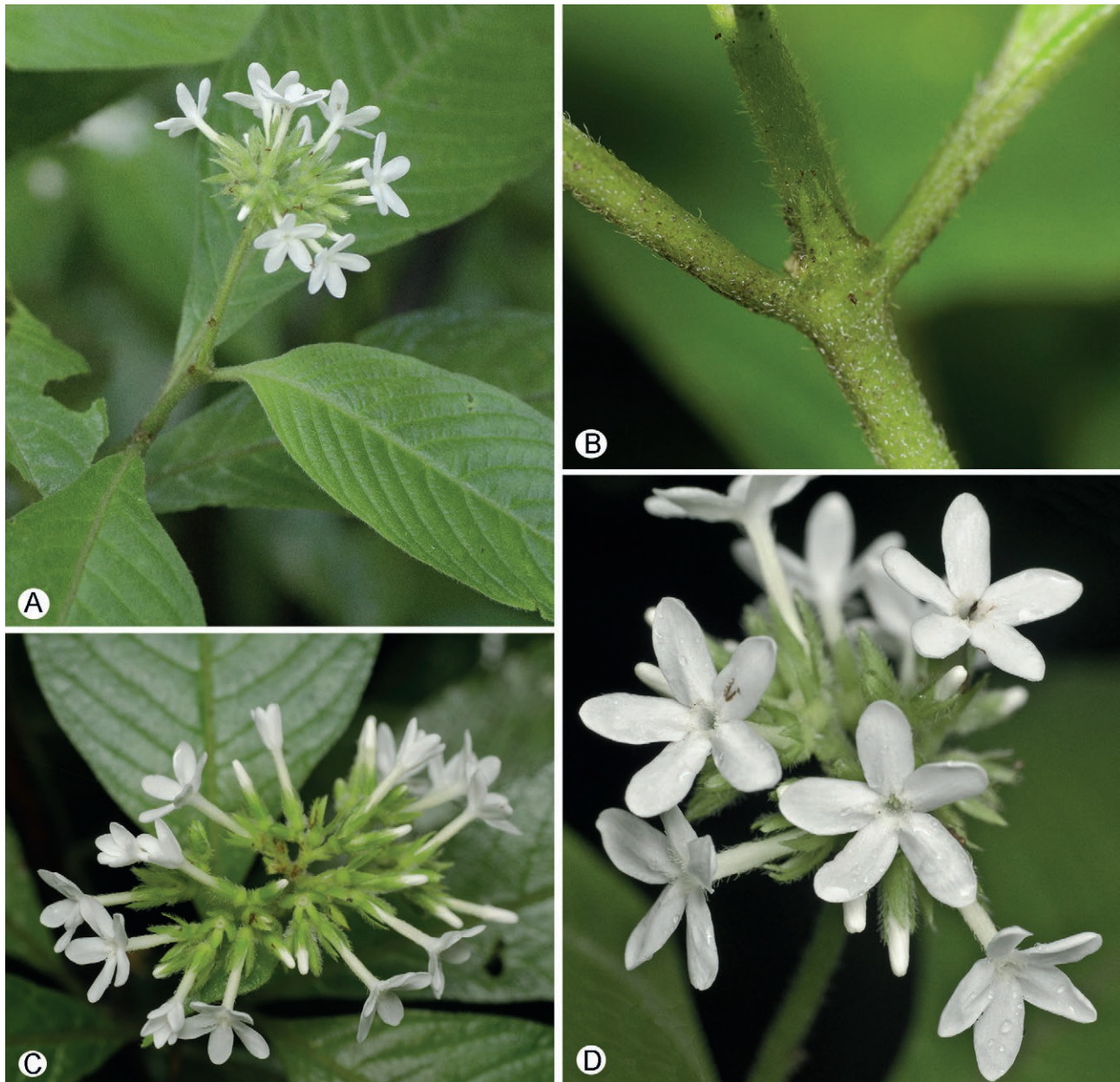
**Distribution and ecology:** Apparently endemic to French Guiana (Figure 30). Known from a few collections in coastal forests, mostly in sites along Route National 2, the historic collection “inter Conana et Ynéri”, and one recent collection near the village of Tampak

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**Figure 34.** *Neobertiera palustris*. **A.** Branch inflorescence and old infructescence. **B.** Node with stipule. **C.** Dissected long-styled flower, with stamens inserted at the middle of the corolla tube. **D.** Dissected long-styled flower, with stamens inserted at lower portion of the corolla tube. **E.** Dissected short-styled flower, with stamens inserted at the upper portion of the corolla tube. **F.** Fruit. **A–C:** drawn from Delprete & Quenette 11860 (CAY); **D:** drawn from Granville 2888 (CAY); **E:** drawn from Feuillet 3635 (CAY); **F:** drawn from Granville 2888 (UB). Illustration by Piero Delprete (Reproduced from fig. 3 of Delprete (2015a) with permission of copyright holder Magnolia Press).



Figure 34.



**Figure 35.** *Neobertiera palustris*. A. Flowering branch. B. Node with stipule. C. Inflorescence. D. Close-up of inflorescence. Photos taken by Gwenaël Quenette on 18 April 2012, along Trail to Bagnes des Annamites, French Guiana, where *Delprete & Quenette 11860* was collected (Reproduced from fig. 4 (as *Neobertiera glomerata* Delprete) of Delprete (2015a) with permission of copyright holder Magnolia Press).

(Commune de Camopi), Camopi River, Upper Oyapock River Basin. Growing in the undercanopy of primary forest, often near standing or slowly running water, at 10–90 m altitude.

**Phenology:** Specimens with flower buds were collected in February, with flowers in anthesis and no fruits

in March, and with flowers in anthesis and mature fruits in May and June.

**Suggested conservation status: Endangered (EN).** This species is known from several localities in French Guiana. According to personal observations made in 2012 and 2014, the populations of this species are always

very small, with less than 50 individuals. Taking into account this species relatively small populations, Delprete (2015) suggested the Endangered (EN) category for this species, following IUCN criteria. Several personal visits to the localities of occurrence of this species were made in 2016 and 2018, but it was not found. Therefore, this species is maintained in this category following IUCN criteria (IUCN 2012, 2019).

**Specimens examined (paratypes): FRENCH GUIANA:** Commune de Montsinery, Route D-5, trail to Bagne des Annamites, ca. 1 km from Route D-5, 4°50'3"N, 52°31'2"W, 10 m, 19 Feb. 2014 (fl buds), P.G. Delprete & J.C. da Silva 12293 (CAY, L, NY); Commune de Camopi, near the village of Tampak, base of Montagne Couronné, 3°10'3"N, 52°32'16"W, 100 m, 25 Feb. 2014 (fl buds), P.G. Delprete et al. 12310 (CAY, K, MG, NY, P, US); Route Nationale 2, P.K. 58, bord de piste forestiere, 4°35'N, 52°20'W, 25 Mar. 1986 (fl), C. Feuillet 3635 (CAY, MO, P); Montagne Maripa, Route Nationale 2, P.K. 75, 10 May 1979 (fl, fr), J.J. de Granville 2888 (CAY, NY, P, U, UB); Commune de Montsinery, along the trail between D-5 and Bagne des Annamites, 8 Jun. 2008 (fl), J.J. de Granville & M. Rome 17592 (CAY, K, MO, P, NY, US).

## 7. PTERIDOCALYX

*Pteridocalyx* Wernham, J. Bot. 49: 317. 1911.

Wernham, J. Bot. 51: 218. 1913; Steyerm., Mem. New York Bot. Gard. 17: 234 [key to genera], 289–290 [discussion under *Neobertiera*] 1967; Delprete, Phytotaxa 391: 81–91. 2019.

Type: *Pteridocalyx appunii* Wernham.

*Shrub*, single-stemmed. *Stipules* basally adnate to the petioles, ovate to narrowly triangular, acuminate or bifid at apex, strigose outside, strigose intermixed with colleters on medio-basal portion inside. *Leaves* opposite, petiolate; blades elliptic-lanceolate, chartaceous; domatia absent. *Inflorescence* terminal, cymose, many-flowered, ultimate branches scorpioid, more evident when fully expanded; bracts and bracteoles small, lanceolate. *Flowers* distylous, 5-merous. *Hypanthium* oblong-obovoid. *Calyx* tube absent or extremely reduced, lobes small, linear-lanceolate to very narrowly oblanceolate; with 1 or 2 colleters at each lobe sinus; with 1 or 2 expanded, petaloid lobes (i.e., calycophylls) per flower. *Calycophylls* stalked, blades ovate to narrowly ovate, white, palmately-veined. *Corolla* hypocrateriform, white during anthesis,

turning yellowish-white after anthesis; lobes left-contorted, oblong-ovate to ovate, margin entire. *Pollen* 3-colporate; exine foveolate-reticulate, perforate. *Short-styled flowers*: stamens included, filaments inserted at distal portion of corolla tube; anthers linear; style included, much shorter than corolla tube. *Long-styled flowers*: stamens included, filaments inserted near the base of corolla tube; anthers linear; style about the same length of the corolla tube, with tips of branches barely exerted or exerted just beyond corolla mouth. *Ovary* with a stalked placenta; stalk inserted at the distal most portion of the septum near the roof of the locule, with a pendulous, narrowly cylindrical extension; ovules inserted on the pendulous placental extension. *Fruit* capsular, dehiscent septically, thinly woody; calycophylls often breaking off before full maturity capsule (i.e., before seed dispersal). *Seeds* many, horizontally inserted along the longitudinal placenta, small, globose; testa foveolate.

**Distribution and ecology:** A genus of a single species endemic to the Upper Potaro River Basin, central Guyana.

**Morphological observations:** Delprete (2019a) described the placenta of *Pteridocalyx* as “longitudinally adnate along the central septum”. However, further examination of ovaries from several additional specimens revealed that the placenta has instead a minute stalk inserted at the distalmost portion of the septum (i.e., near the roof of the locule), and terminates with a pendulous, narrow cylindrical extension almost as long as the locule on which are inserted numerous ovules. Because of these placental features and the presence of calycophylls, *Pteridocalyx* is unique within the Sipaneeae.

*Pteridocalyx* is similar to *Neobertiera* in having cymose inflorescences with scorpioid terminal branches, corolla lobes with a basal triangular area of glandular hairs inside, and ovary with a stalked placenta; the former differs from the latter by the presence of calycophylls (vs. lacking in *Neobertiera*), placenta with a stalk inserted at the at distalmost portion of the septum, terminating with a pendulous cylindrical extension (vs. with a stalk inserted at the middle of the septum, terminating in a hemi-ellipsoid, oblong-ellipsoid or hemi-elliptic extension), oblong-ellipsoid to narrowly oblong, 6–14 × 2–3 mm, septicidal capsules (vs. globose, 1.2–4 mm diam., indehiscent fruits), and globose seeds (vs. tetrahedral). No phylogenetic studies are available to test the relationships between *Pteridocalyx* and members of the Sipaneeae (study in progress).

*Pteridocalyx* is also similar to *Dendrosipanea* by being shrubs or treelets 1–2 m tall, with ovate-triangular



stipules acute or bifid at apex, terminal inflorescences, 5-merous, distylous flowers, hypocrateriform corollas with lobes left-contorted, and septicidal capsules. The former differs from the latter by the presence of 1–2 calycophylls per flower (vs. calycophylls absent in *Dendrosipanea*); corolla tube pale brown or white and brownish at medial portion, lobes pink, with a basal white triangle of glandular hairs on adaxial side at base (the rest glabrous) forming a white star-like pattern with the 5 lobes (Figure 37D), at mouth (vs. corolla white to cream-white, sometimes tube green, lobes without a basal white triangle of glandular hairs on adaxial side); placenta with a stalk inserted at the distal most portion of the septum, with a pendulous, narrowly cylindrical extension almost as long as the locule, and the ovules inserted on the cylindrical extension (vs. placenta with a fleshy extension adnate along the entire length of the septum, and ovules irregularly peltate on the longitudinal placental extension); capsules oblong-ellipsoid to narrowly oblong, crustaceous (vs. oblong-turbinate, thinly woody); seeds globose, testa foveolate (vs. 3–5-angular or irregularly-shaped, testa reticulate).

7-1. *Pteridocalyx appunii* Wernham, J. Bot. 49: 318. 1911. (Figures 4L, 5A–B, 36–39).

Type: GUYANA. “Demerara” [Potaro-Siparuni Region, Upper Potaro River], Kaieteur Falls [5°10'N, 59°28'W], [day & month unknown] 1872 (fl, fr), C. Appun s.n. (holotype BM [barcode BM000099002]).

(=) *Pteridocalyx minor* Wernham, J. Bot. 51: 218. 1913.

Type: GUYANA. Potaro-Siparuni Region, Potaro River, “Sheenabowa” [Chenapou Village, 4°55'N, 59°34'W, ca. 470 m], Sep.–Oct. 1881 (fl), G.S. Jenman 1282 (holotype K [barcode K000173940]).

*Shrub* 1–2 m tall, with a central, thin stem, sparsely branched towards the top; young branches reddish, older stems and branches pale gray; young branches densely appressed strigose. *Stipules* ovate to narrowly triangular, 2.2–3 × 4–6 mm, acuminate or bifid at apex, sometimes entire at early stage and becoming bifid at apex at

later stage, apical teeth (when present) to 1.5 mm long, appressed strigose-pubescent outside, strigose-pubescent intermixed with 15–17 colleters at medio-basal portion and glabrous distally inside, margins short-strigose. *Leaves* with petioles 1.5–5 mm long, appressed-strigose-pubescent; blades elliptic to elliptic-lanceolate, 9–16 × 3–5.5 cm, acute to decurrent at base, acuminate at apex, chartaceous, shiny and dark green above and dull pale green below when fresh, pale brown above and olive-green below when dry, sparsely pubescent above, pubescent below, midrib and secondary veins sericeous-pubescent below; secondary veins 10–12 on each side of midrib. *Inflorescence* cymose when young (up to anthesis), expanding during and after anthesis, appressed-pubescent, with 1–3 pairs of lateral branches; lateral branches 2–6 cm long when fully expanded, dichotomously divided, with one flower at the base of each bifurcation, ultimate branches scorpioid, more evident when fully expanded; bracts subtending branchlets lanceolate, 2–4 × 0.5–1 mm, appressed-pubescent; bracteoles subtending flowers 1–2(–3), linear-lanceolate, 1–3 × 0.2–0.7 mm, appressed-pubescent. *Flowers* sessile or rarely sub-pedicellate, secundiflorous. *Hypanthium* oblong-obovoid, 1.5–2 × 1.1–1.3 mm, acute-decurrent at base, round to truncate at apex, appressed strigose-pubescent. *Calyx* tube absent (lobes free) or extremely reduced, to 0.2 mm long; smaller lobes white when fresh, cream-white to beige when dry, linear to linear-lanceolate, 2–4.5 × 0.4–0.7 mm long, sparsely appressed strigose-pubescent outside, margins hispidulous; with 1 or 2 colleters in each calycine sinus, oblong, 0.15–0.2 mm long. *Calycophylls* 1–2 per flower, pure white when fresh, cream-white to beige when dry, varying in size and shape within the same calyx; smaller calycophylls without a distinguishable stalk, linear, narrowly oblanceolate to narrowly oblong-oblanceolate, 4.5–9.5 × 0.8–1.5 mm, acute at apex, sparsely hispidulous along veins and sometimes at margins, with 3 veins (including midrib); larger ones with stalks 2–5 mm long, blades narrowly elliptic, elliptic to ovate, 4–13 × 5–9 mm, acute, obtuse to round at base, acute to obtuse at apex, sparsely hispidulous along veins and sometimes at margins, with 5–7 veins (including midrib). (Figs. 37, 39). *Corolla* 14–19 mm long, tube pale brown or white and brownish at medial portion, lobes pink, with a basal white triangle of glandular hairs inside; tube narrowly cylindrical, slightly wider at

**Figure 36.** *Pteridocalyx appunii*. **A.** Branch with inflorescence. **B–C.** Stipule shapes present on the same branch. **D.** Flower in anthesis. **E.** Dissected long-styled flower, with stamens inserted at basal portion of corolla tube. **F.** Dissected short-styled flower, with stamens inserted at distal portion of corolla tube. **G.** Mature capsule. **A–E:** drawn from P.G. Delprete & P. Benjamin 12813 (CAY); **F:** drawn from P.G. Delprete & P. Benjamin 12824 (CAY); **G:** drawn from P.G. Delprete & P. Benjamin 12836 (CAY). Illustration by Piero Delprete (Reproduced from fig. 1 of Delprete (2019a) with permission of copyright holder Magnolia Press).

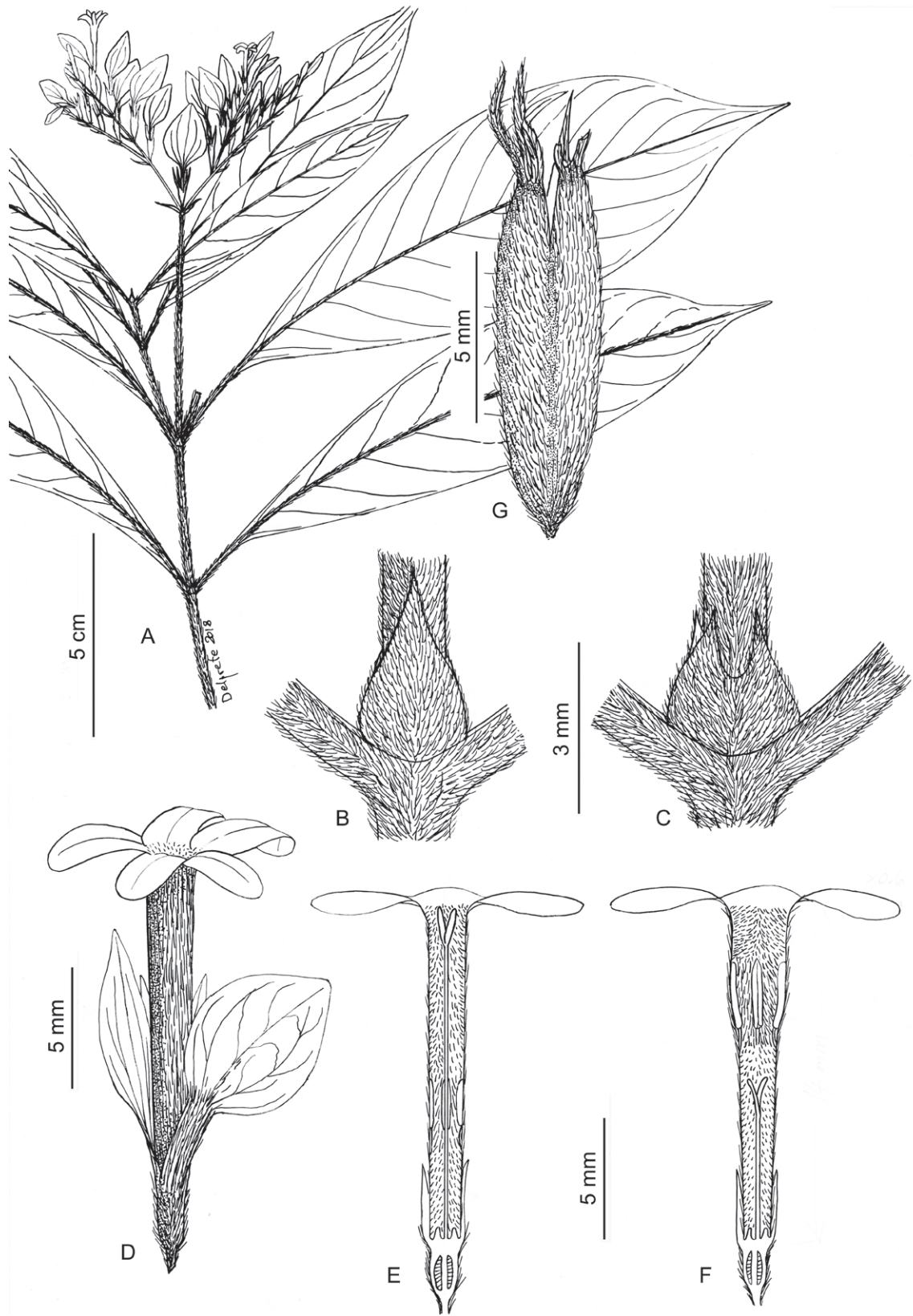
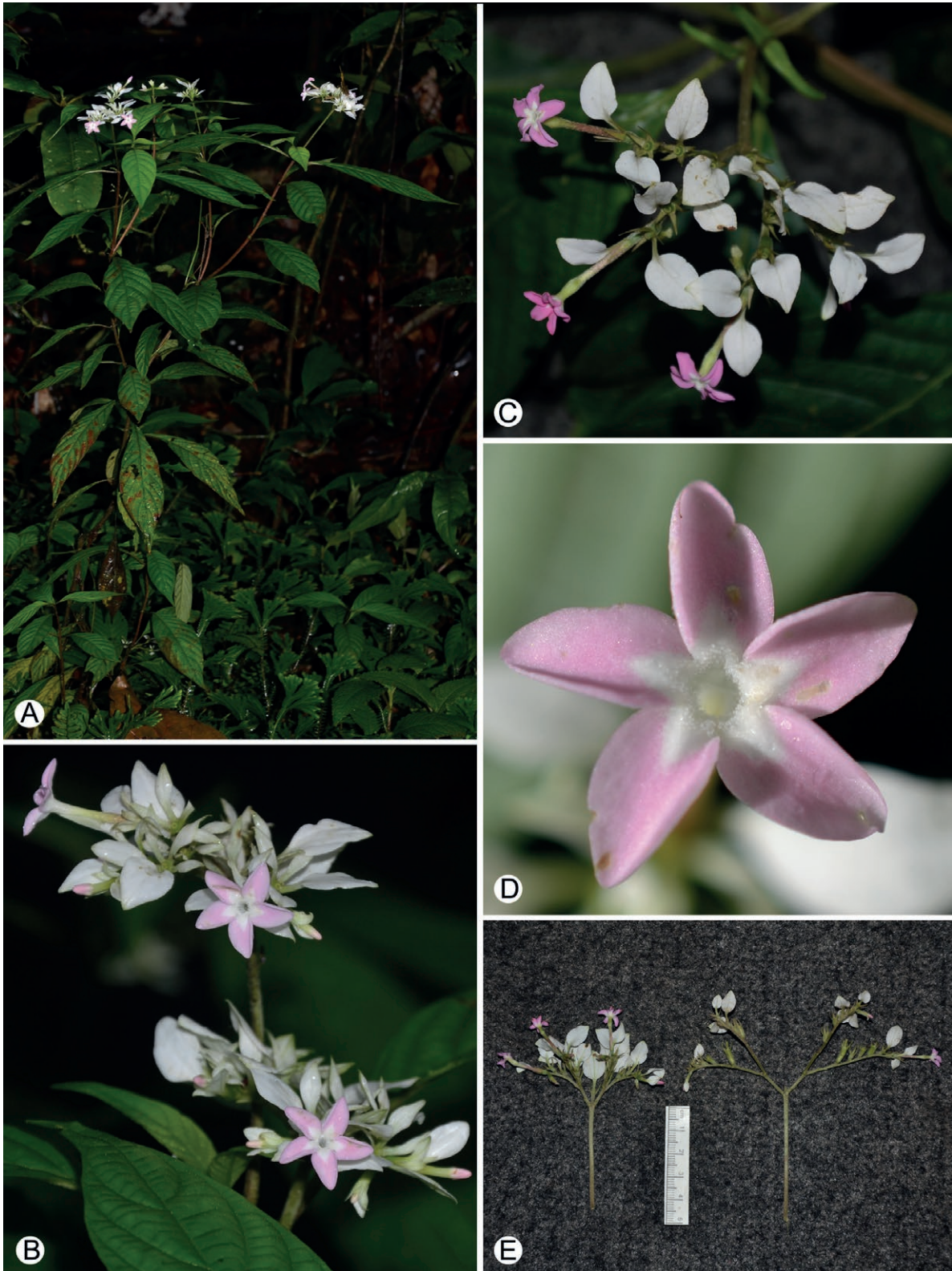


Figure 36.



**Figure 37.** *Pteridocalyx appunii*. A. Habit. B. Inflorescences, side view. C. Inflorescence, top view. D. Corolla, top view. E. Inflorescence and infructescence from the same plant. Photos taken by Piero Delprete, Upper Potaro River, near Chenapou Village, Guyana, where *Delprete & Benjamin 12813* was collected. (Reproduced from fig. 2 of Delprete (2019a) with permission of copyright holder Magnolia Press).

mouth, 10.5–13.5 mm long, 0.7–0.8 mm wide for most length, 1.3–1.5 mm wide at mouth, appressed strigose-sericeous outside, sparsely glandular-puberulent inside; lobes oblong-ovate to ovate, 3.5–5.5 × 1.7–3 mm, obtuse to acute at apex, glabrous outside, with a basal triangular area of glandular hairs inside (Figure 37B & D), the rest glabrous. *Long-styled flowers*: stamens inserted at 3–4 mm from base of corolla tube; filaments 0.5–0.7 mm long; anthers linear, 1.8–2 × 0.2–0.3 mm, acute at both ends; style about the same length as corolla tube (tips of branches exerted) or barely exerted, 11–15 mm long, glabrous; style branches linear, 1–1.2 mm long, densely papillose when receptive. *Short-styled flowers*: stamens inserted at 5.5–6 mm below corolla mouth; filaments 0.3–0.5 mm long; anthers linear, 2.5–2.7 × 0.2–0.3 mm, acute at both ends; style included, 6–6.5 mm long, glabrous; branches narrowly lanceolate, 1.5 mm long, acute, densely papillose when receptive. *Capsules* oblong-ellipsoid to narrowly oblong, 6–14 × 2–3

mm, acute-decurrent at base, round to truncate at apex, crustaceous, sparsely strigose-sericeous, pale green when young, turning pale brown when dry. *Seeds* globose, 0.3–0.4 mm in diam., foveolate.

**Morphological observations:** Wernham (1911: 318) described the calyx tube of *P. appunii* Wernham as “3–4 mm long”; however, in the type specimen the calyx tube is either absent (lobes free) or extremely reduced, to 0.2 mm long, as in all other specimens studied.

Wernham (1913: 218) separated *Pteridocalyx minor* Wernham from *P. appunii* by the stipules entire (vs. divided at apex in *P. appunii*), calycophyll blades 4 × 5 mm (vs. 11–13 × 7–9 mm), and corolla tubes 16 mm long (vs. 10–11 mm long). However, although he described *P. minor* as having “corolla tube 16 mm long, 1 mm wide, lobes 5.5 × 2 mm”, the holotype specimen at K has corolla tube 11 mm long and lobes 3.5 × 1.5 mm, which largely correspond to the measurements supplied by him

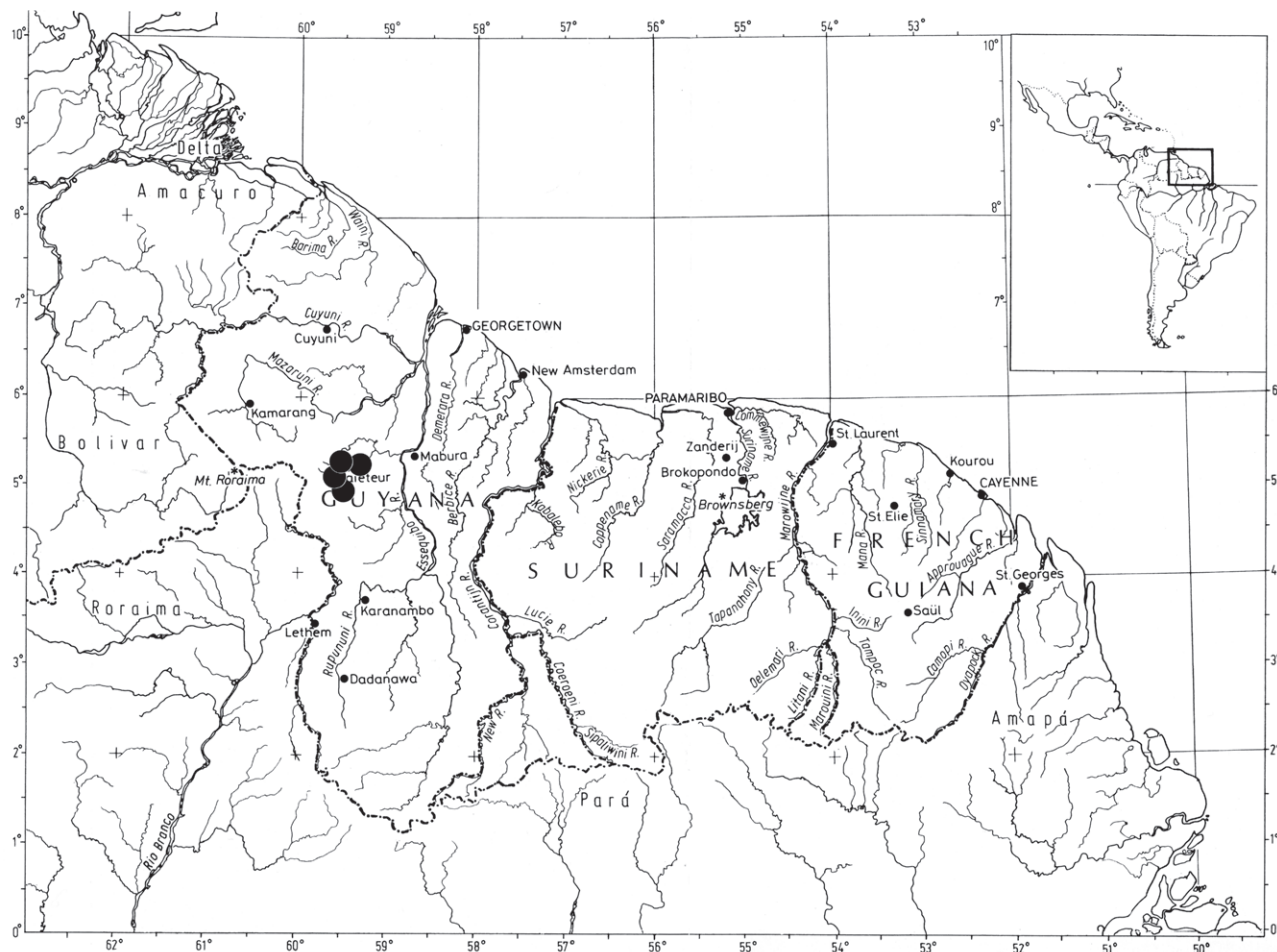


Figure 38. Distribution of *Pteridocalyx appunii*.

for *P. appunii*, i.e., “corolla tube 10–11 mm long, lobes 4–5 × 2 mm.” (Wernham, 1911: 318).

In addition, recent personal observation of herbarium specimens and natural populations near the Chenapou Village, Upper Potaro River, Guyana, demonstrated that the stipules can be either entire or bifid at the apex on the same branch, often being entire when young and becoming bifid at an older stage.

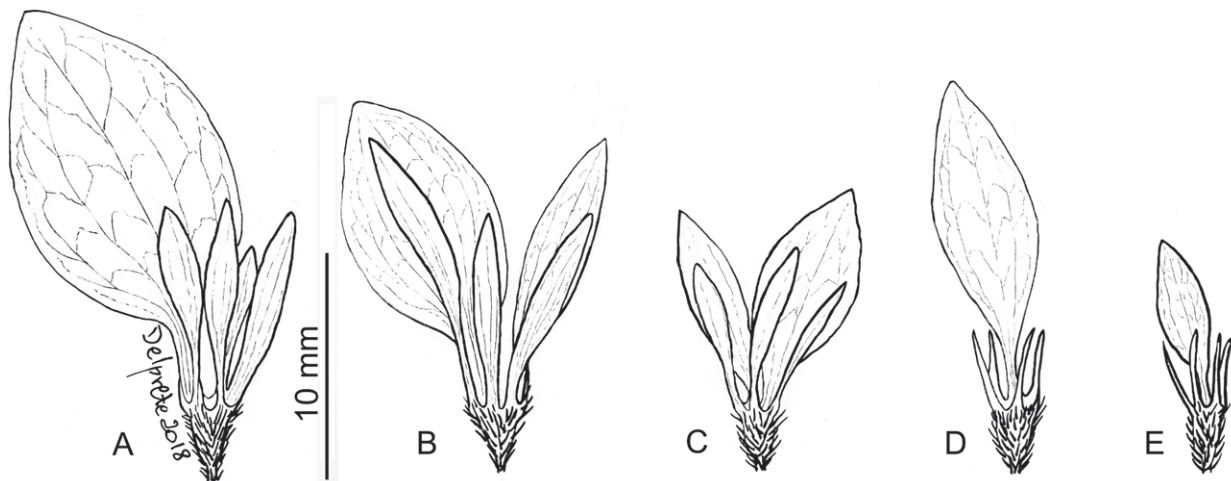
Finally, petaloid calyx lobes (calycophylls) can be one or two per flower, sometimes with one or two additional less expanded lobes, and can vary in shape and size within the same inflorescence (Figures 37, 39), with blades ranging from narrowly elliptic, elliptic to ovate and 4–13 × 5–9 mm within the same inflorescence. The largest ones are found on the basal flowers and the smaller ones on the distal flowers of the same inflorescence branch. All morphological characters used by Wernham to distinguish *P. minor* from *P. appunii* are widely overlapping, and the two taxa are conspecific.

**Distribution and ecology:** Endemic to the Upper Potaro River basin, above and below Kaieteur Falls (Figure 38), central Guyana, at 200–500 m altitude. *Pteridocalyx appunii* is a shade-loving species, found in the undercanopy of tall forests, in alluvial or lateritic soils, either seasonally inundated, e.g., mora forest (dominated by *Mora excelsa* Benth.), or not inundated although constantly humid, e.g., bulletwood forest (dominated by *Manilkara bidentata* (A. DC.) A. Chev.).

**Phenology:** Flowering specimens were collected in June, September, October and November; the sole col-

lection with mature capsules is the type of *Pteridocalyx appunii*, which was collected at an unknown date in 1872.

**Conservation status: Endangered (EN).** Delprete (2019a) wrote “Until recently *Pteridocalyx* was a genus known from only a few historical collections made in 1872, 1881 and 1907, preserved in BM and K. A gathering of 1992 remained unidentified until recently. All these collections are from the Upper Potaro River basin, above and below Kaieteur Falls, located within the Kaieteur National Park, central Guyana, which is an area botanically poorly collected. During my field expedition of 2016, I observed several populations of approximately 100–200 individuals along the trails bordering the Potaro River and its affluents, near Chenapou Village, in forests seasonally inundated or never inundated. Because of the difficult terrain in the forests away from the trails, the only populations that I examined are those bordering the rivers. Therefore, the AOO (Area of Occupancy) of this taxon is difficult to estimate, and the EOO (Extent of Occurrence) is less than 20,000 km<sup>2</sup>. Although this monospecific genus is endemic to the Upper Potaro River basin, no imminent threats were detected in 2016, as the forests bordering the rivers surrounding Chenapou Village are fairly well preserved, except for selective logging of certain large trees, even though they do not have any official conservation status. In addition, the only way to access the area surrounding the Potaro River above Kaieteur National Park is by canoe, which renders impossible any considerable timber exploitation on this portion of the river, aside from sparse extraction by the local indigenous community, including the forests surrounding the



**Figure 39.** *Pteridocalyx appunii*. Calycophyll variation within the same inflorescence branch. A. Basal flower. B–D. Intermediate flowers, from base towards distal portion. E. Distal flower. A–E: drawn from *Delprete & Benjamin 12813* (CAY). Illustration by Piero Delprete (Reproduced from fig. 3 of Delprete (2019a) with permission of copyright holder Magnolia Press).

Chenapou Village. In conclusion, because of the small populations observed and the relatively restricted area of occurrence, this taxon is here treated as Vulnerable (VU) based on criterion D1 of IUCN (2012, 2017)."

As a result of a renewed analysis regarding the conservation status, here presented, it should be emphasized that the collection localities of this species are within a small area, including the most recent collections. Its Extent of Occurrence (EOO) is here calculated to be of ca. 174 km<sup>2</sup>, which is slightly larger than criteria B1 for Critically Endangered (CE) and falls within the Endangered (EN) category. Therefore, although Delprete's (2019a) discussion and conservation status is recent, considering the EOO here calculated, and the vicinity of Chenapou Village, which impacts the populations of the species, *Pteridocalyx appunii* is here re-classified as Endangered (EN) following IUCN (2012, 2019) criteria.

**Specimens examined:** GUYANA: Potaro-Siparuni Region, Potaro River, Holmia [ca. 4°58'N, 59°35'W], Nov. 1907 (fl), A.W. Bartlett 8763 (K); Potaro-Siparuni Region (Region 8), Upper Potaro River, Chenapou Village, trail from village to Karisparu Landing, tall Mora forest seasonally inundated, on alluvial soil, 4°58'40"N, 59°34'14"W, 450 m, 12 Jun. 2016 (fl), P.G. Delprete & P. Benjamin 12813 (BRG, CAY, K, MG, MO, NY, US), 12814 (B, BBS, BR, BRG, L, P, US), 12815 (BRG, CAY, K, GB, NY, P, US); Potaro-Siparuni Region, Upper Potaro River, Chenapou Creek (affluent of Potaro River), Chenapou Creek Mouth, secondary forest, on lateritic soil, 4°58'25"N, 59°34'47"W, 420 m, 13 Jun. 2016 (fl), P.G. Delprete & P. Benjamin 12824 (BRG, CAY, GB, L, MG, MO, NY, RB, W); Potaro-Siparuni Region, Upper Potaro River, Chenapou Village, Paramakatoi trail, parallel to Chenapou Creek, going from Chenapou Village to Paramakatoi Village, bulletwood forest on lateritic soil, never inundated, 4°57'26"N, 59°35'1"W, 440 m, 14 Jun. 2016 (imm fr), P.G. Delprete & P. Benjamin 12836 (BRG, CAY, G, MO, NY, RB, US); Potaro-Siparuni Region, Potaro River, left margin on portage trail on second set of rapids above Chenapou, 5°0'40"N, 59°38'22"W, 430–490 m, 18 Mar. 2014 (fl), F.A. Michelangeli et al. 2307 (MO, NY); Potaro-Siparuni Region, Micobe, mixed forest on brown and white sand, shady places, 5°20'N, 59°30'W, 200 m, 20 Oct. 1992 (fl), S. Tiwari & A. Mengarini 487 (BRG [3 sheets], CAY).

## 8. SIPANEA

*Sipanea* Aubl., Hist. Pl. Guiane 1: 147. 1775 K.Schum. in Martius et al., Fl. Brasil. 6(6): 247–252, fig. 122. 1889

Wernham, J. Bot. 55: 171–175. 1917; Steyer., Mem. New York Bot. Gard. 17: 261–282. 1967; Steyer. in Lasser and Steyermark, Fl. Venezuela 9(1): 357–384, figs. 58–60. 1974; Delprete and Steyer. in Steyermark et al., Fl. Venez. Guayana 8: 828–832, fig. 640–647. 2004; Delprete in J.A. Rizzo, Fl. Goiás Tocantins 40(3): 1140–1152, fig. 106. 2010.

Type: *Sipanea pratensis* Aubl.

*Virecta* L.f., Suppl. 17. 1781

Type: *Virecta biflora* L.f. [= *Sipanea biflora* (Rottb.) Cham & Schltdl.]

Non *Virecta* Smith in A.Rees, *nom. superfl.* (= *Virectaria* Bremek.).

*Ptychodea* Willd. ex Cham. & Schlecht., Linnaea 4: 168. 1829

Type: the two specific binomials published by Chamisso and Schlechtendal (1829: 128) are illegitimate, because are cited in synonymy under two validly published names in *Sipanea*.

From Chamisso & Schlechtendal (1829: 168): "Addimus synonyma Herbarii Willdenowianii ad *Sipaneas* Humboldtianas: *Sipanea dichotoma* H.B.Kh. 3. p. 110. est *Ptychodea pedunculata* Hb. Willd. n. 4123. – *Sipanea glomerata* H.B.Kh. l.c. est *Ptychodea sessiliflora* Hb. Willd. n. 4123."

**Note:** The citation "Hb. Willd. N. 4123" represents the genus number in the Willdenow Herbarium, where "4123" in the number of *Sipanea*, and is cited for both *P. pedunculata* and *P. sessiliflora*.

*Herbs*, erect, trailing, prostrate or decumbent, often rooting at basal nodes, sometimes mat-forming, rarely floating on water in inundated areas (*S. biflora*), or *subshrubs* (stems woody at base), erect or decumbent. *Stipules* free or basally adnate to the petioles, sometimes sheathing at base, truncate to broadly transversally elliptic, broadly to narrowly triangular, suborbicular, subulate, linear, rarely setaceous or reduced to a line between the petioles; adaxial side with a few to several colleters inserted on each side or irregularly spread near the base or at median portion or just below the margin, or inserted along the margin. *Leaves* opposite, sessile, subsessile to short-petiolate, rarely with axillary brachyblasts with numerous smaller leaves (e.g., *S. galioides*); blades ovate, narrowly ovate, rhombic-

ovate, elliptic, oblong-elliptic, oblong-lanceolate, linear-lanceolate to linear, membranaceous, chartaceous or thinly subcoriaceous; domatia absent. *Inflorescences* terminal, sometimes appearing axillary as a result of the reiteration of an axillary bud subtending the inflorescence, paniculate, cymose or corymbose, usually not frondose or rarely frondose, pauci- to multi-florous or uniflorous; in several species (e.g., *S. pratensis*, *S. glomerata*, *S. hispida*) inflorescences initially condensed, subcapitate, and in later stages the rachis elongates and the secondary branches expand from subcapitate to scorpioid at fruit maturity. *Bracteoles* subtending the flowers or opposing the flowers, commonly present or rarely absent. *Flowers* distylous, (4-)5(-6)-merous. *Hypanthium* globose, subglobose, ovoid, obovoid, narrowly obovoid to broadly turbinate, glabrous or pubescent, sometimes with hairs basally tuberculate (e.g., *S. wilson-brownei*, *S. ovalifolia*, *S. prancei*). *Calyx* persistent; lobes free or rarely shallowly connate at base, oblong-lanceolate, lanceolate, linear to setaceous; with 1 or 2 colleters in each calycine sinus. *Calyco-phylls* absent. *Corolla* hypocrateriform, narrowly infundibuliform, narrowly campanulate to campanulate, white, pinkish-white, cream-white, pink, or pale purple, sometimes the lobes with a white basal triangular area forming a star shape at mouth with the five lobes; tube glabrous, puberulent, short-pubescent or hirsute, or lower half glabrous and distal portion pubescent outside, glabrous, or puberulent or pubescent at stamens insertion and the rest glabrous, or puberulent or pubescent throughout inside; corolla mouth glabrous or with sparse hairs (Sect. *Nudae*), or with a pubescent ring of white hairs (Sect. *Virecta*), or with a pubescent ring of yellow hairs (Sect. *Sipanea*) at orifice inside; lobes left-contorted, round, broadly ovate, obovate, elliptic-ovate or lanceolate, sometimes slightly asymmetrical, in several species (e.g., *S. galioides*, *S. pratensis*) varying in size and shape within the same population and/or on the same plant, round, obtuse or acute, sometimes mucronate, at apex. *Pollen* 3-colporate; exine foveolate-reticulate or finely foveolate, perforate. *Long-styled flowers*: stamens included or exerted beyond the corolla mouth; filaments inserted near the base, at about the middle, or at medio-distal portion of the corolla tube, anthers narrowly oblong-elliptic to linear; style about the same length as the corolla tube with tips of branches barely exerted or exerted just beyond corolla mouth. *Short-styled flowers*: stamens included, inserted at the distal or medio-distal portion of the corolla tube, anthers narrowly oblong-elliptic, very narrowly lanceolate or linear; style included, much shorter than corolla tube. *Ovary* with stalked placenta;

stalk inserted at median or medio-basal portion of the septum, with a narrowly oblong-elliptic extension (in certain species the stalk is very short, appearing as if the ovules are inserted on the central septum); ovules many per locule, inserted on the placental extension. *Fruit* capsular, dehiscent loculicidally, crowned by the permanent calyx, thinly woody to crustaceous, glabrous or pubescent, rarely with hairs basally tuberculate (e.g., *S. wilson-brownei*, *S. ovalifolia*). *Seeds* many per locule, perpendicular to the placental extension or acropetally imbricate, minute, irregularly globose, subglobose, ellipsoidal, polyhedral, tetrahedral, rhomboidal, or trigonous, faintly to strongly angular; testa reticulate-foveolate, smooth or rugulose-verrucose.

**Distribution:** A genus of 17 species, occurring in Nicaragua, Costa Rica, Panama, Colombia, Venezuela, the Guianas, Brazil, Ecuador, Peru, Bolivia and Paraguay.

#### History of *Sipanea* sections

Schumann (1889: 249; 1891: 38-39) divided *Sipanea* into two sections: 1) Sect. *Eusipanea* K.Schum., characterized by multiflorous or rarely uniflorous inflorescences with elongating cincinni, and crustaceous-subwoody capsules, where he included *S. glomerata* and *S. pratensis*; 2) Sect. *Panisea* K.Schum., with 1-2(-3)-florous inflorescences, and papyraceous capsules, where he included only *S. biflora*.

Steyermark (1967, 1974) divided *Sipanea* into two sections:

1) Sect. *Sipanea*, characterized by "Stipules prominent, tapering to a long triangular or subulate-setaceous apex; mainly erect to ascending herbs with relatively stout firm stems, large leaf-blades, and usually 3-20- or more-flowered terminal or rarely axillary, once or twice dichasial branched inflorescences with monochasial branches; capsule usually thick-walled, difficult to break." He subdivided this section into two subsections: 1a) Subsect. *Nudae*, with "Orifice of corolla mouth glabrous or at least not yellow villous" (*S. ayangannensis*, *S. stahelii*, *S. wilson-brownei*), and 1b) Subsect. *Luteovillosae*, with "Orifice of corolla within densely yellow-villous" (*S. glaberrima*, *S. glomerata*, *S. pratensis*, *S. hispida*, *S. glabrata*, *S. pubinoda*, *S. galioides*).

2) Sect. *Virecta*, characterized by "Stipules low, shallow, rounded, or broadly triangular, at most acute at apex, or obsolete; usually creeping, prostrate herbs with slender weak rooting stems, often prostrate vegetative stems, or with ascending to erect flowering axes; leaf blades relatively small and thin; inflorescences axillary or terminal, usually 1-3(-5)-flowered; capsules thin-

walled, easily broken or splitting.” He subdivided this section into two subsections: 2a) Subsect. *Cryptotricha*, with “Orifice of corolla within white-villous, the hair mass not projecting; one colleter at sinus between bases of calyx lobes; inflorescence mainly 2–3-flowered, axillary or terminal” (*S. micrantha*, *S. ovalifolia*, *S. gleasonii*, *S. biflora*, *S. cowanii* [= *S. biflora*]); and 2b) Subsect. *Phanerotricha*, with “Orifice of corolla within densely yellow-villous, the mass of hairs projecting beyond orifice; two squamellae [i.e., colleters] usually present at sinus of calyx-lobes; inflorescence mainly 1–2-flowered, falsely terminal” (*S. acinifolia* [= *S. veris*], *S. veris*)

In the molecular phylogenetic study of the tribe Sipaneeae of Delprete and Cortés B. (2004), nine taxa of *Sipanea* were included. The sections and subsections of *Sipanea* proposed by Steyermark (1967, 1974) were not supported, as species with different habits (i.e., prostrate or erect) were found side by side on the same monophyletic clades. On the other hand, species with similar corolla mouth vestiture were found grouping together, indicating a possible sinapomorphic character for monophyletic sections within the genus. For example, in the strict consensus tree from the combined trnL-F and ITS analysis, *S. stahelii* and *S. wilson-brownei*, both with glabrous corolla mouth, were found as sister taxa of one clade, although with low support (bootstrap value (BV) = 58). On the same tree, *S. biflora*, the sole species with white-pubescent corolla mouth included in the analysis, was found at the base of the sister clade, which in turn is a sister clade with a strongly supported clade (BV = 97) with *S. pratensis*, *S. glomerata*, *S. galioides*, *S. acinifolia* (= *S. veris*), *S. hispida* and *S. veris*, all with yellow-pubescent corolla mouth. However, the number of species sampled in *Sipanea* was about half the species recognized in the genus, and the phylogenies obtained could not be treated as conclusive. Therefore, further analyses with a larger species sampling is necessary to confirm these groupings.

Steyermark’s (1967, 1974) *Sipanea* sections were used in his dichotomous keys, which are practical for identifying species within the genus. However, in this case I prefer to recognize sections that are at least indicated to be monophyletic in the molecular phylogenetic study of Delprete and Cortés B. (2004). Therefore, in the present treatment three sections are recognized within *Sipanea*, which are characterized by the internal vestiture at the corolla mouth: 1) Section *Sipanea*, with a ring of yellow hairs; 2) Section *Virecta*, with a ring of white hairs; 3) Section *Nudae*, glabrous or with sparse white hairs. In the present treatment, species are organized according to these three sections, and within each section they are arranged in alphabetical order.

### *Inflorescence expansion after anthesis*

After detailed study of numerous populations of *Sipanea glomerata*, *S. hispida*, and *S. pratensis* var. *dichotoma*, it was observed that the inflorescences are initially condensed, subcapitate (i.e., extremely shortly-branched), and later, during and after anthesis the rachis elongates and the secondary branches also elongate from subcapitate to scorpioid. Therefore, this inflorescence expansion is generally treated as a variation correlated with different stages of development, and might be observed even on the same individual. However, in *S. pratensis* two varieties with allopatric distributions and different fruit shapes are here recognized: var. *pratensis*, with inflorescences initially congested-cymose, appearing fasciculate, secondary branches that do not elongate in later stages, flowers and fruits congested-cymose, appearing fasciculate, without a subsecond monochasium of dichasial appearance, infructescences remain congested-cymose, appearing fasciculate, and capsules about as long as broad, 4–4.5 × 3–4.5 mm, strongly costate; var. *dichotoma*, with inflorescence axes that elongate to various lengths during and after anthesis, producing a subsecond monochasium of dichasial appearance, infructescences show some degree of expansion, often with scorpioid secondary branches (See *S. pratensis* for further discussion), and capsules longer than broad, (3–)4.5–8 × 1.5–3 mm, smooth or faintly costate.

### Sectional classification of *Sipanea*

#### 8A. *Sipanea* section *Sipanea*

Type: *S. pratensis* Aubl. [Steyermark (1967: 268) wrote that the type of *S. sect. Sipanea* is *S. wilson-brownei* Cowan, but the type of this section is *S. pratensis*]

*Sipanea* sect. *Eusipanea* K.Schum. in Martius et al., Fl. Bras. 6(6): 249. 1889.

Type: *Sipanea pratensis* Aubl.

*Sipanea* sect. *Sipanea* subsect. *Luteovillosae* Steyermark., Mem. New York Bot. Gard. 17: 261, 270. 1967.

Type: *Sipanea pratensis* Aubl.

*Sipanea* sect. *Virecta* subsect. *Phanerotricha* Steyermark., Mem. New York Bot. Gard. 17: 263, 266. 1967.

Type: *Sipanea acinifolia* Spruce ex Sprague (= *S. veris* S.Moore).



*Herbs*, prostrate or decumbent, or *subshrubs* with basal portion woody, erect, ascending or decumbent; corolla mouth with a ring of yellow hairs.

Species included:

- 8-1. *Sipanea galioides* Wernham
- 8-2. *Sipanea glaberrima* (Bremek.) Steyerem.
- 8-3. *Sipanea glomerata* Kunth in Humb. & Bonpl.
- 8-4. *Sipanea hispida* Benth. ex Wernham
- 8-5. *Sipanea pratensis* Aubl.
- 8-6. *Sipanea veris* S. Moore

**8B. *Sipanea* section *Virecta*** (Rottb.) Steyerem., Mem. New York Bot. Gard. 17: 263. 1967

*Virecta* L.f., Suppl. Pl. 17, 134. 1782 ["1781"].

Type: *Virecta biflora* (Rottb.) L.f [= *Sipanea biflora* (Rottb.) Cham. & Schltdl.].

*Sipanea* sect. *Panisea* K.Schum. in Martius et al., Fl. Bras. 6(6): 249. 1889

Type: *Sipanea biflora* (Rottb.) Cham. & Schltdl.

*Sipanea* sect. *Sipanea* subsect. *Cryptotricha* Steyerem., Mem. New York Bot. Gard. 17: 263, 264. 1967

Type: *Sipanea biflora* (Rottb.) Cham. & Schltdl.

*Herbs*, prostrate, rarely decumbent; corolla mouth with a ring white hairs.

Species included:

- 8-7. *Sipanea biflora* (Rottb.) Cham. & Schltdl.
- 8-8. *Sipanea carrenoi* Steyerem.
- 8-9. *Sipanea gleasonii* Steyerem.
- 8-10. *Sipanea micrantha* Sandwith
- 8-11. *Sipanea ovalifolia* Bremek.
- 8-12. *Sipanea setacea* Steyerem.

**C. *Sipanea* section *Nudae*** (Steyerem.) Delprete, **sect. et stat. nov.**

*Sipanea* sect. *Sipanea* subsect. *Nudae* Steyerem. in Mem. New York Bot. Gard. 17: 261, 268. 1967

Type: *S. wilson-brownei* Cowan

*Herbs or subshrubs*, erect or decumbent; corolla mouth glabrous or with sparse white hairs.

Species included:

- 8-13. *Sipanea ayangannensis* Steyerem.
- 8-14. *Sipanea prancei* Steyerem.
- 8-15. *Sipanea saxicola* J.H.Kirkbr.
- 8-16. *Sipanea stahelii* Bremek.
- 8-17. *Sipanea wilson-brownei* Cowan

#### Key to *Sipanea* species

In the following key, priority is given to the three sections supported as monophyletic in the phylogenetic analysis of Delprete and Cortés B. (2004). The three sections can be distinguished by the vestiture or lack of vestiture at the corolla mouth. Due to the short life-span of the species in this genus, flowers and fruits are commonly found on the same individual; therefore, both flower and fruits traits are used in the key below. Also, as the habit of certain species is quite variable, certain species appear multiple times in the key.

1. Corolla mouth with a ring of white or yellow hairs; herb, prostrate or decumbent, or subshrub (basal portion woody), erect, ascending or decumbent; stipules truncate, broadly transversely elliptic, broadly to narrowly triangular, deltoid to triangular-lanceolate, or rarely shortly suborbicular, triangular-lanceolate, ovate to broadly ovate, linear, or setaceous ..... 2
1. Corolla mouth glabrous or with sparse white hairs; herbs or subshrubs, erect or decumbent; stipules reduced to a line between the petioles, or subulate (base triangular and medio-distal portion narrowly triangular to linear, in *S. ayangannensis*), narrowly oblong, transversely ovate, or narrowly triangular to almost linear (Section *Nudae*) ..... 15
2. Corolla mouth with a ring of yellow hairs; herbs, prostrate or decumbent, or subshrubs (basal portion woody), erect, ascending or decumbent; stipules truncate, or broadly to narrowly triangular, rarely shortly suborbicular (Section *Sipanea*) ..... 3
2. Corolla mouth with a ring white hairs; herbs, prostrate or rarely decumbent; stipules broadly transversely elliptic to truncate, ovate to broadly ovate, linear, broadly triangular, deltoid to triangular-lanceolate, or setaceous (Section *Virecta*) ..... 10
3. Plant erect or ascending ..... 4
3. Plant prostrate or decumbent ..... 8
4. Plant entirely glabrous, except corolla throat ..... 2. *S. glaberrima*
4. Plant with some kind of vestiture ..... 5
5. Stems often with axillary brachyblasts bearing numerous smaller leaves; leaf blades linear-lanceolate to linear, 1.3–

- 4.3 × 0.2–0.9(–1.2) cm, 5–8 times longer than wide; leaf secondary veins 2–3(–4) on each side of midrib..... 1. *S. galioides*
5. Stems commonly without axillary brachyblasts; leaf blades ovate, broadly elliptic, oblong-lanceolate, ovate-lanceolate, oblong-elliptic, lanceolate to narrowly oblong-lanceolate, 1.2–9.5 × 0.5–5 cm, 2–3 times longer than wide; leaf secondary veins 3–11 on each side of midrib..... 6
6. Stems densely hirsute or villous; leaf blades sparsely to densely strigose above; corollas (8.5–)9.5–16.5 mm long, tube (6–)7–12.5 mm long, lobes 2.5–5 × 1.5–3 mm ..... 4. *S. hispida*
6. Stems sparsely to densely appressed or spreading pubescent or sericeous; leaf blades densely sericeous or sparsely to densely appressed pubescent to glabrate above; corollas 14–28 mm long, tube (8–)10–17 mm long, lobes (2.5–)4–11 × (2–)2.5 × 7 mm..... 7
7. Leaf blades densely sericeous or sparsely to densely appressed pubescent to glabrate above, densely sericeous or sparsely appressed pubescent or glabrous below, midrib and secondary veins appressed-strigose below; inflorescences 5–8-flowered, a single head subtended by two leaf-like bracts, or made of three pedunculate heads; hypanthium narrowly obovoid, 2.5–3 × 2–2.5 mm, densely sericeous; calyx lobes 7–13 mm long ..... 3. *S. glomerata*
7. Leaf blades appressed pubescent to densely short- to long-pubescent (hairs 0.3–2 mm long) above, densely appressed pubescent or villous or short- to long-hirsute (hairs 0.3–2 mm long) below; inflorescences 4–8-flowered, congested-cymose (appearing fasciculate), rarely with secondary branches to 4 mm long, sometimes subtended by 2 or 4 leaf-like bracts (var. *pratensis*), or 4–37-flowered, evidently branched during anthesis (var. *dichotoma*); hypanthium turbinate to narrowly obovoid, 0.7–1.5 × 0.5–0.9 mm, appressed pubescent to sericeous; calyx lobes 2.3–6 mm long ..... 5. *S. pratensis*
- 8(3). Stems often with axillary brachyblasts bearing numerous smaller leaves; leaf blades linear-lanceolate to linear, 5–8 times longer than wide..... 1. *S. galioides*
8. Stems commonly without axillary brachyblasts; leaf blades ovate, ovate-lanceolate to rhombic-ovate, elliptic, oblong-elliptic, oblong-lanceolate, lanceolate, narrowly lanceolate to narrowly oblong-elliptic, 2–3 times longer than wide... 9
9. Perennial herb or subshrub, terrestrial or epipetric; stems often woody at basal internodes; stipules 2–6 × 0.6–1.5 mm, appressed pubescent to sericeous outside; leaf blades 1.5–7.5 × 0.5–2.5 cm, chartaceous, secondary veins 3–8 on each side of midrib; inflorescences 4–8-flowered, congested-cymose (appearing fasciculate, rarely with secondary branches to 4 mm long), sometimes subtended by 2 or 4 leaf-like bracts (var. *pratensis*), or 4–37-flowered evidently branched during anthesis (var. *dichotoma*)..... 5. *S. pratensis*
9. Delicate herbs, prostrate or trailing, rarely decumbent, often forming thick patches; stems thin, herbaceous; stipules 0.5 × 0.5–0.8 mm, strigulose or glabrate outside; leaf blades 0.5–2.6 × 0.2–1.7 cm, membranaceous to papyraceous, secondary veins 2–3 on each side of midrib; inflorescences 1–2-flowered..... 6. *S. veris*
- 10(2). Stipules setaceous, 0.1 mm wide ..... 12. *S. setacea*
10. Stipules broadly transversely elliptic to truncate, ovate, broadly ovate, broadly triangular, deltoid to triangular-lanceolate, 0.4–2 mm wide..... 11
11. Leaf blades 5–17 × 3–7 cm; corolla campanulate, white, 4–6.5 mm long, tube obconical, 2.5–3 mm long, lobes 1.5–3 × 1–1.5 mm ..... 10. *S. micrantha*
11. Leaf blades (0.4–)1.2–5 × (0.35–)0.8–3 cm; corolla hypocrateriform, narrowly infundibuliform to narrowly campanulate, white, pinkish-white, pink, deep pink to pale purple, 4.3–21(–29) mm long, tube caniculate or cylindrical to narrowly obconical, 2.5–13(–15) mm long, lobes 1.5–8.5(–14) × 1.5–5.5(–7) mm ..... 12
12. Hypanthia and capsules with hairs conspicuously tuberculate at base..... 13
12. Hypanthia and capsules with hairs not tuberculate at base (slightly inflated at base in *S. prancei*)..... 14
13. Hypanthium 1.3–1.7 × 1–1.5 mm; calyx lobes setaceous, 4–4.5 × 0.1–0.2 mm; corollas narrowly infundibuliform, 12–14 mm long, tube 7.5–9.5 mm long, lobes 4–8 × 2.5 × 3 mm; inflorescences 2–3-flowered..... 9. *S. gleasonii*
13. Hypanthium 0.7–0.8 × 0.7–0.8 mm; calyx lobes linear to linear-lanceolate, 2.5–4 × (0.1–)0.2–0.4 mm; corollas narrowly campanulate, 4.3–5.3 mm long, tube 2.8–3.6 mm long, lobes 1.5–1.8 × 1.2–1.3 mm; inflorescences 3–5-flowered ..... 11. *S. ovalifolia*
14. Leaf blades ovate, rhombic-ovate or rarely oblong, (0.4–)1.2–5 × (0.35–)0.8–2.8 cm; stipules broadly triangular, 0.3–1.2(–2) × 0.7–0.9(–1.2) mm, glabrous or sparsely strigillose outside; leaf secondary veins (3–)4–6 on each side of midrib; calyx lobes linear-lanceolate to setaceous, 1–5 × 0.2–0.6 mm; corolla tube 5–13(–15) mm long, lobes 3–8.5(14) × 2–5.5(–7) mm; capsules subglobose, 3–5 × 3–5 mm ..... 7. *S. biflora*
14. Leaf blades ovate-lanceolate, elliptic to elliptic-oblong, 0.7–2.3 × 0.4–0.9 cm; stipules deltoid to triangular-lanceolate, 2–3 × 0.5–2 mm, densely strigose outside; leaf secondary veins 2–4 on each side of midrib; calyx lobes linear-lanceolate, 4.5–5.5 × 0.5–0.7 mm; corollas tube 10–13 mm long, lobes 5.5–6.5 × 4–5 mm; capsules narrowly oblong-elliptic, 8–9 × 2–3 mm..... 8. *S. carrenoi*
- 15(1). Stipules reduced to a line between the petioles of the same node or very shallowly transversally ovate, 0.5–3 mm long, sometimes with a central seta..... 16

15. Stipules deltoid, narrowly triangular to almost linear, or subulate (base triangular and medio-distal portion narrowly triangular to linear in *S. ayangannensis*), (2-)3.5-5 mm long, without central seta..... 17
16. Herbs or subshrubs, to 50 cm tall, terrestrial; stipules reduced to line between petioles and crowned by 5-7 colleters; leaf blades ovate to elliptic, 2-7.5 × 1-4.5 cm, secondary veins 5-7 on each side of midrib; calyx lobes linear to setaceous, 2.2-3 × 0.1-0.2 mm; corolla 8.5-11 mm long, tube 5.7-7.5 mm long, lobes ovate, 2.7-3.5 × 1.4-1.5 mm; capsules globose, 2.5-3 × 2.5-3 mm..... 14. *S. prancei*
16. Herbs, 15-20 cm tall, terrestrial or epipetric; stipules transversely oblong to reduced to a line between petioles; leaf blades narrowly obovate, 9-12 × 2.5-4.3 cm, secondary veins 8-9 on each side of midrib; calyx lobes very narrowly elliptic to almost linear, 7-10 × 0.6-0.8 mm; corolla 14-16.5 mm long, tube 9-10.5 mm long, lobes obovate, 5-6 × 3-4 mm; capsules globose to very broadly ellipsoid, 5.5-6 × 4-5.5 mm ..... 15. *S. saxicola*
- 17(15). Bracteoles opposing each flower linear to acicular, 0.8-2.5 × 0.1-0.3 mm; calyx lobes linear to acicular, 1.5-3 × 0.2-0.5 mm ..... 16. *S. stahelii*
17. Bracteoles opposing each flower elliptic, narrowly elliptic, lanceolate, narrowly lanceolate to linear-lanceolate, 3.5-7 × 0.5-1.7 mm; calyx lobes oblong-lanceolate, oblanceolate, lanceolate to linear, 3.5-8 × 0.3-1.7 mm ..... 18
18. Stipules subulate, base triangular and medio-distal portion narrowly triangular to linear, entire; leaf blades lanceolate-elliptic, 4-5.5 × 1.7-2.2 cm, acute at apex, secondary veins 5-7 on each side of midrib; corolla tube 14.5 mm long, lobes 10.4 × 4.3 mm; hypanthium with hairs not basally tuberculate..... 13. *S. ayangannensis*
18. Stipules deltoid or narrowly triangular to almost linear, commonly entire or sometimes becoming bifid at apex at later stage, apical teeth to 2 mm long; leaf blades elliptic to elliptic-lanceolate, 2.5-10.5(-14.5) × 1-4(-5.5) cm, acuminate at apex, secondary veins 6-10 on each side of midrib; corolla tube (7-)9.5-15 mm long, lobes 4-9.5(-14) × 2-6(-8) mm; hypanthium with hairs basally tuberculate.... ..... 17. *S. wilson-brownei*

#### 8A. *Sipanea* section *Sipanea* Aubl.

Type: *Sipanea pratensis* Aubl. [Steyermark (1967: 268)

wrote that the type of *S. sect. Sipanea* is *S. wilson-brownei* Cowan, but the type of this section is *S. pratensis*]

- 8-1. *Sipanea galioides* Wernham, J. Bot. 55: 172. 1917. (Figures 5C, 40-41).

Type: GUYANA. Roraima Region, Spelemoota, Arapoo River, 1 Dec. 1884, *E.F. Im Thurn* 29 (holotype BM [barcode 000614317]; isotypes K [without barcode], US [barcode 00137725]; photo-K at NY). [Section *Sipanea*].

*Perennial herb* 10-50 cm tall, prostrate, decumbent or ascending, with (1)3-20(-50) stems departing from a central taproot; stems simple (rarely a few secondary branches), to 200 cm long, usually reddish; young branches thin, 0.6-1.5 mm thick, terete, sparsely to densely antrorse strigose-hirtellous or antrorse sericeous (hairs white, 1-1.5 mm long). *Stipules* basally adnate to the petioles, sheathing, free portion truncate or broadly triangular to triangular at base and narrowly triangular to linear distally, or narrowly triangular, 1.5-3.3 × 0.6-1.5 mm, acute to acuminate, densely antrorse-strigose outside (hairs white, 1-1.5 mm long, longer hairs on the narrowly triangular lobe); glabrous, slightly thickened at margin inside; margin with 2 colleters on each side of the central lobe. *Leaves* sessile to subpetiolate, often with axillary brachyblasts with numerous smaller leaves; blades linear-lanceolate to linear, 1.3-4.3 × 0.2-0.9(-1.2) cm, 5-8 times longer than wide, acute to decurrent at base, obtuse to acute at apex, papyraceous to thinly subcoriaceous, dark green above and pale green below when fresh, olive-green when dry, sparsely strigose above, densely strigose or glabrous with midrib and secondary veins antrorse-strigose below; secondary veins 2-3(-4) on each side of midrib, obsolete above, prominent below; margins narrowly revolute. *Inflorescences* terminal, pedunculate, congested-cymose, commonly 5-flowered or rarely 1- or 3-flowered; lateral axes 5-10 mm long (excluding corollas), with 1 central flower and 2 flowers on each lateral axis; peduncles 0.7-3.7 cm long, sparsely to densely antrorse strigose-hirtellous or antrorse sericeous (hairs white, 1-1.5 mm long); bracts subtending inflorescence (when present) 2, leaf-like,

**Figure 40.** *Sipanea galioides*. **A.** Habit with short fertile branches, and long stoloniferous branches for vegetative reproduction. **B.** Sterile branch. **C.** Reproductive branch. **D.** Dissected short-styled flower, with stamens inserted at distal portion of corolla tube, and included style. **E.** Spinulose style branches of short-styled flower. **F.** Dissected long-styled flower, with stamens inserted at median portion of corolla tube, and exserted style. **G.** Corolla lobes variation within the same population. **H.** Capsule. **A, B:** drawn from Delprete & Araujo 7430 (CAY); **C:** drawn from Delprete & Araujo 7430 (CAY); **D-E:** drawn from Delprete & Araujo 7412A (CAY); **F-G:** drawn from Delprete & Araujo 7412C (CAY); **H:** drawn from Steyermark 111276 (US). Illustration by Piero Delprete.

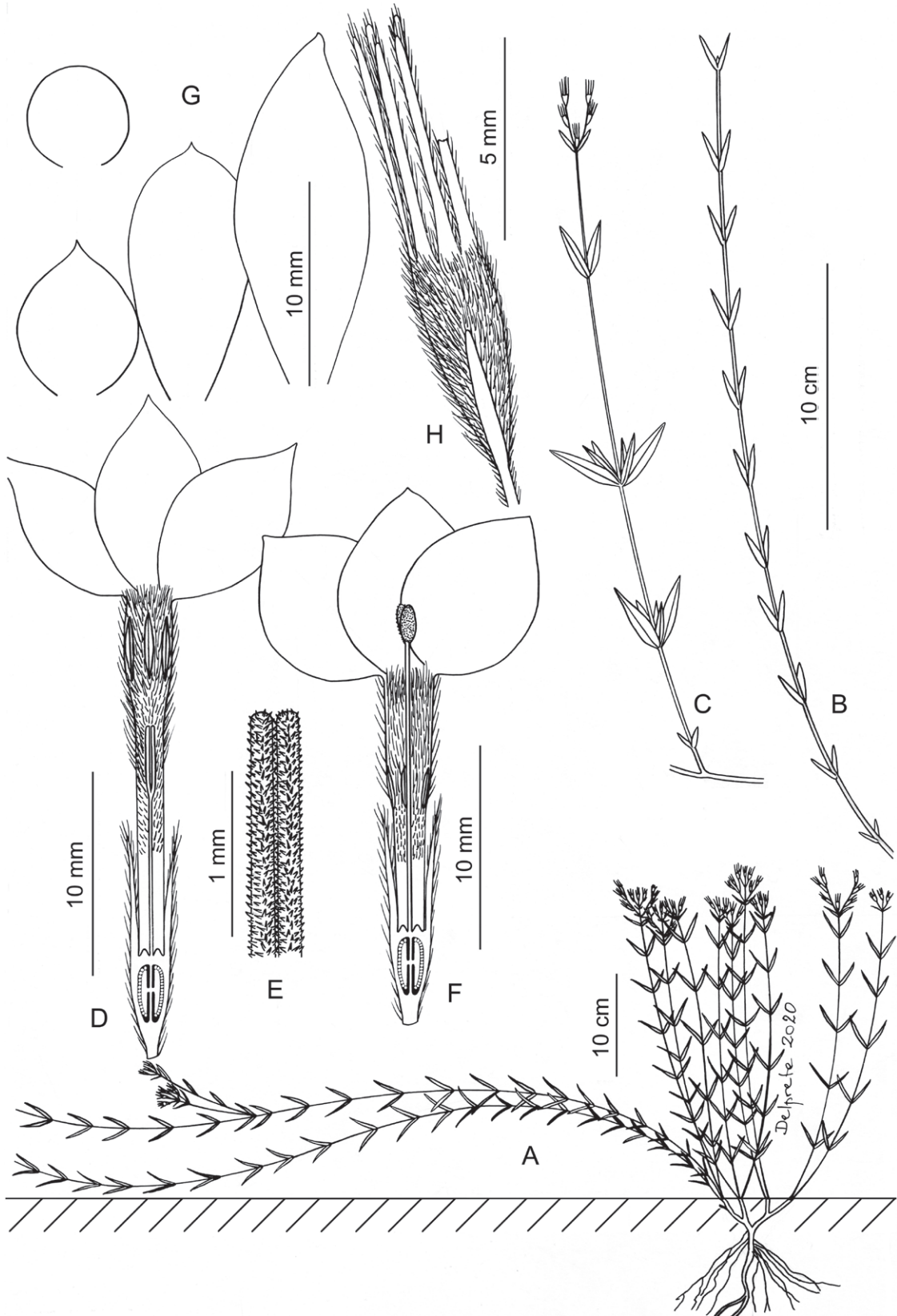


Figure 40.

linear-lanceolate to linear,  $3.3\text{--}6 \times 0.4\text{--}0.8$  mm, acute at apex, sparsely strigose above, densely strigose or glabrous with midrib and secondary veins antrorse-strigose below, or bracts absent; bracteoles subtending flowers linear-lanceolate to linear,  $4\text{--}6 \times 0.2\text{--}1$  mm, densely antrorse-strigulose. *Flowers* distylous, 5(6)-merous, central flower sessile, those on lateral branches sessile to subsessile. *Hypanthium* turbinate to narrowly obovoid,  $1.7\text{--}2 \times 1\text{--}1.7$  mm, acute at base, round at apex, sparsely to densely antrorse setose-strigulose. *Calyx* lobes equal or subequal, green to reddish-green when fresh, linear,  $4\text{--}8 \times 0.3\text{--}0.7$  mm, acuminate at apex, densely white-strigose outside, margins strigose-ciliate, glabrous inside; with 1 colleter in each calycine sinus, linear,  $0.2\text{--}0.4$  mm long. *Corolla* hypocrateriform,  $(18.5\text{--})22.5\text{--}27.5(-28)$  mm long, pink, pale pink, whitish-pink, or tube pink and lobes white during anthesis, turning whitish-pink to white after anthesis, with a dense ring of yellow hairs exerted beyond mouth; tube  $(13\text{--})15\text{--}18$  mm long, gradually expanding towards the mouth,  $0.7\text{--}1.2$  mm wide at base,  $2\text{--}3$  mm wide at mouth, glabrous at medio-basal portion and densely strigose, sometime only in lines, at medio-distal portion outside, glabrous at basal portion, densely puberulous above and densely yellow-pubescent at distal portion inside, the yellow pubescence exerted beyond corolla mouth; lobes 5(6), round, broadly ovate, obovate, elliptic-ovate to lanceolate, varying in shape and size within the same population (Figure 40G), sometimes unequal or of different shape on the same corolla, sometimes asymmetric,  $(5.5\text{--})7.5\text{--}10.5 \times 3\text{--}6(-7.5)$  mm, round, subobtuse to acute or apiculate at apex (Figure 40G), glabrous throughout. *Long-styled flowers* [Delprete & Araujo 7412A *pro parte* (corolla tube  $14.5\text{--}15$  mm long); Delprete & Araujo 7412C (corolla tube  $13$  mm long)]: stamens inserted at  $7.5\text{--}8$  mm from base, about the middle of corolla tube; filaments  $0.7\text{--}1$  mm long; anthers narrowly oblong-elliptic,  $2.5\text{--}3 \times 0.2\text{--}0.3$  mm, acute at both ends; style exerted  $1.5\text{--}3.5$  mm beyond corolla mouth,  $17\text{--}17.5$  mm long, glabrous; style branches oblong,  $1\text{--}1.3$  mm long, round at tip, papillose-aculeate. *Short-styled flowers* [Delprete & Araujo 7412A *pro parte* (corolla tube  $17.5$  mm long)]: stamens inserted at  $3.5$  mm below corolla mouth; filaments  $2.5$  mm long; anthers narrowly oblong-elliptic,  $3 \times 0.2\text{--}0.3$  mm, acute at both ends; style included,  $12$  mm long, glabrous; branches linear,  $3$  mm long, round at tip, papillose-aculeate. *Infructescences* cymose, slightly more expanded than inflorescences. *Capsules* cylindrical-oblong to oblong-turbinate,  $5\text{--}7.5 \times 2\text{--}4$  mm, acute at base, round to acute at apex, thinly woody, faintly costate, densely to sparsely antrorse-strigulose or antrorse-hispid, (hairs  $1\text{--}1.5$  mm long), green to reddish-green when young,

turning beige to pale brown when dry. *Seeds* irregularly trigonous-rhomboid or subglobose, faintly or strongly angular,  $(0.4\text{--})0.5\text{--}0.7$  mm in diam., testa foveolate.

**Notes:** Wernham (1917) in the introduction of the article where he described *Sipanea galioides* wrote “The types of all the novelties described are in the National Herbarium [BM].” Therefore the specimen *Im Thurn 29* at BM, barcode 000614317, is the holotype of this name.

The type specimen at US has the typewritten label “Mt. Roraima Expedition, British Guiana, Oct.-Jan., 1884–5” with the handwritten note “*Sipanea pratensis* Aublet, N. 29, Spelemonta [sic! Spelemoota], Arapoo R.” which corresponds entirely with the information supplied on the holotype specimen label and in the original publication. On the same sheet an additional handwritten label reports the collector as “E. Jenman.” Because collection date and locality are identical to those of the holotype, the US specimen should be cited as “*E.F. Im Thurn 29*” and is an isotype.

*Sipanea galioides* is similar to *S. pratensis*, the former differing from the later by the combination of the following characters: stems commonly simple or rarely branched, often with axillary brachyblasts topped by numerous smaller leaves (vs. commonly branched, without brachyblasts in *S. pratensis*), leaf blades papyraceous to thinly subcoriaceous, with margins narrowly revolute, and  $2\text{--}3(-4)$  secondary veins on each side of midrib (vs. chartaceous, margin planar, with  $3\text{--}8$  secondary veins on each side of midrib), inflorescences  $(1\text{--})3\text{--}5$ -flowered (vs. congested,  $4\text{--}8$ -flowered, or evidently branched,  $4\text{--}37$ -flowered), hypanthium  $1.7\text{--}2 \times 1\text{--}1.7$  mm, sparsely to densely antrorse setose-strigulose (vs.  $0.7\text{--}1.5 \times 0.5\text{--}0.9$  mm, appressed pubescent to sericeous), corolla tube  $(13\text{--})15\text{--}18$  mm long (vs.  $(8\text{--})10\text{--}17$  mm long). In addition, *Sipanea galioides* is restricted to Venezuela (Amazonas and Bolívar) and Guyana, at  $(125\text{--})700\text{--}2200$  m altitude, while *S. pratensis* is widely distributed in Colombia, Venezuela, the Guianas, and northern Brazil (Roraima, Amapá, Pará, Amazonas, and Maranhão), and is an extremely variable species in terms of habit, leaf shape, inflorescence architecture, flower size, and fruit shape, found in extremely different environments from near sea level to  $1200$  m altitude.

**Phenology:** Individuals of this species are commonly found with flowers and fruits on the same inflorescence. Flowering and fruiting mostly during the rainy season, from November–December through May.

**Distribution and ecology:** Restricted to Venezuela (Amazonas and Bolívar) and Guyana (Figure 41). Pros-

trate, decumbent or ascending herb (stems sometimes woody at basal nodes), usually growing in open dry, sandy savannas, savannas with sparse trees, white-sand savannas, rocky savannas, seasonally flooded area with *Mauritia flexuosa*, bare laterritic slopes of savannas, borders of dwarf forests, riparian forests, open tepui slopes, or on rocky outcrops; at (125-)700–2200 m altitude.

**Suggested conservation status: Least Concern (LC).** This species is known from numerous localities in Venezuela, mostly in the state of Bolívar, at altitudes of 700–2200 m, and a couple of collections in the state of Amazonas at about 125 m altitude, as well as several collections from Guyana, at altitudes of (80-)700–1830 m. In Venezuela, most collection localities are within the Canaima National Park, state of Bolívar. In Guyana,

several collections are from the Mount Roraima Massif, which includes the Pakaraima Mountains, and is contiguous with the Canaima National Park. During a botanical expedition in Venezuela in December 2000, several healthy populations of this species (*Delprete & Araujo 7412A, 7412C, 7414, 7427*) were personally observed in the municipalities of Gran Sabana and Cavanayen, which are both currently included within the Canaima National Park. The number of individuals in each population was not reported. Considering that this species is known by numerous collections, and many of the localities are within a well-preserved national park, without any imminent threat, this species is positioned in the Least Concern (LC) category, following IUCN criteria (IUCN 2012, 2019).

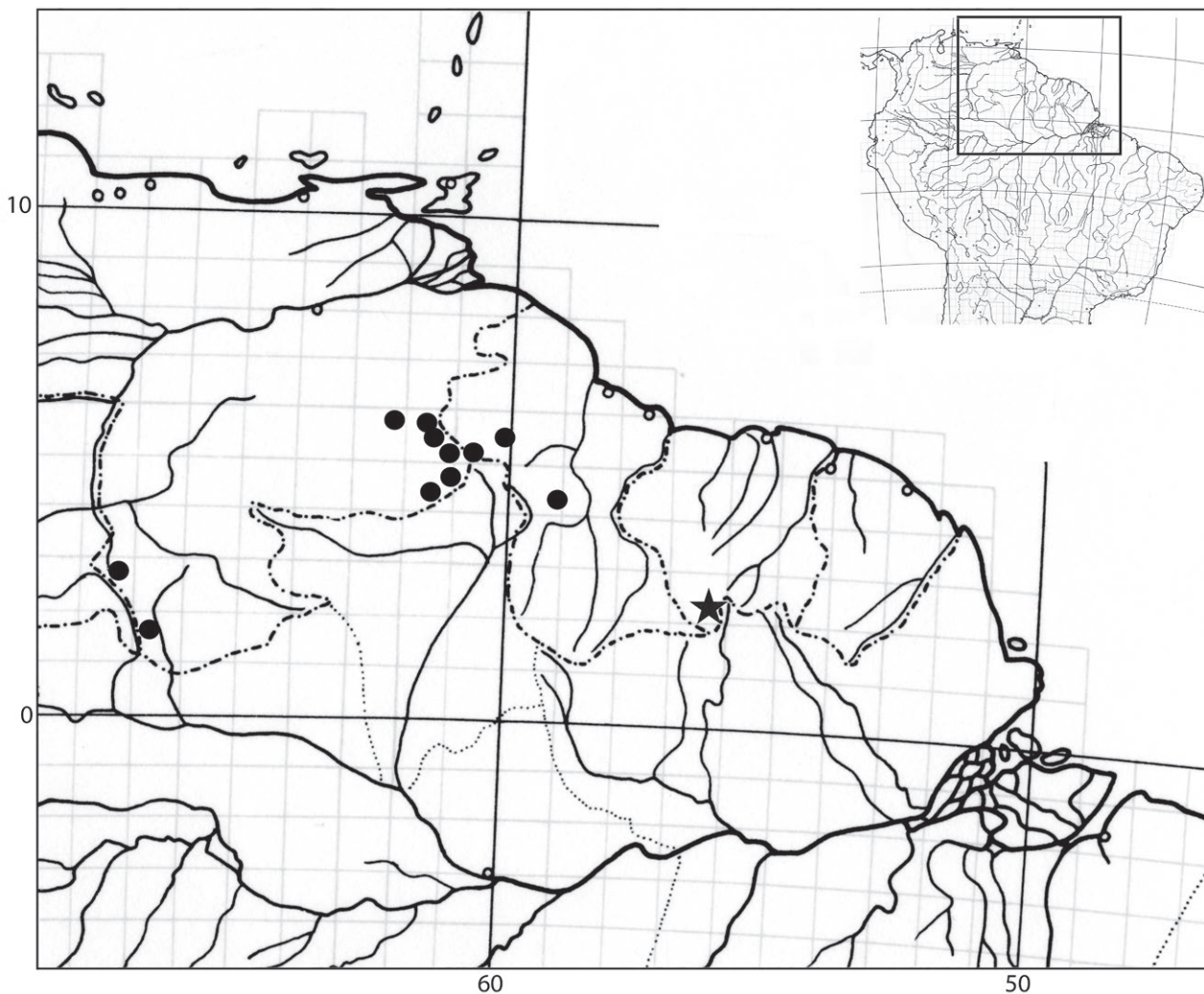


Figure 41. Distribution of *Sipanea galioides* (circles) and *S. glaberrima* (star).

**Specimens examined: VENEZUELA. Amazonas:** Mun. Guainía, along road from Maroa to Yavita, ca. 700 m from Yavita, 2°54'42"N, 67°26'55"W, evergreen, moist forest, decumbent herb, many-branched from base, corolla turning from white to pinkish, 19 Feb. 1998 (fl, fr), *P. Acevedo-Rodriguez et al.* 10266 (MO, PORT, US); Ríos Sipapo y Autana, 1952 (fl), *Herbier S.M. Roi Léopold III N. 332* (BR); Río Negro, rock outcrop and forest around it, Mamurividi, Zona 10, Estación Climatológica of Ministerio del Ambiente on Río Pasimoni, 1°32'N, 66°32'W, 125 m, 3 Apr. 1984 (fl, fr), *R. Liesner 17201* (CAY [2 sheets], MG). **Bolívar:** Distr. Roscio, sabana inundable en la base del Cerro Roraima, 5°13'N, 60°45'W, 2200 m, 26 Mar. 1984 (fl), *G. Aymard & J. Luteyn 2432* (NY, PORT, VEN); Calzeta de la Botella, 150 m, 14 Apr. 1957 (fl), *A.L. Bernardi 6505* (NY [2 sheets]); La Gran Sabana, km 145 along hwy, 2 km S of La Ciudadela, open savanna dominated by *Trachypogon*, *Echinolaena*, and *Paspalum*, soil with top 20 cm sand and organic material mixture, 1 m of white sand, below which is yellow sand, 1300 m, 3 Dec. 1983 (fl), *G. Davidse 4680* (MO, NY, VEN); Mun. Gran Sabana, Parque Nacional Canaima, Tarotá, 5°47'8"N, 61°36'55"W, 1320 m, 1 May 2002 (fl), *F. Delascio et al.* 18203 (NY, VEN); Mun. Gran Sabana, Parque Nacional Canaima, savanna with herbaceous vegetation dominated by Gramineae, Cyperaceae, Orchidaceae and *Lycopodium*, white sand soil, full sunny exposure, growing on mounds and in areas with low, slowly flowing water, 5°58'N, 61°24'W, 1300 m, 20 Dec. 2000 (fl), *P.G. Delprete & A.C. Araujo 7412A* (CAY, pickled flowers only); Mun. Cavanayen, 2 km E of village, disturbed herbaceous-shrubby vegetation near small creek, herbaceous layer dominated by Gramineae, Cyperaceae, Xyridaceae and sparse Melastomataceae, small population of sparse individuals, perennial herb, erect, suberect to prostrate with axillary brachyblasts with smaller leaves, 1200 m, 5°35'N, 61°44'W, 21 Dec. 2000 (fl), *P.G. Delprete & A.C. Araujo 7412C* (CAY, pickled flowers only); Mun. Gran Sabana, ca. 15 km S of Kama-Meru Camp, open field frequently burned, with some degree of moisture dominated by Cyperaceae and Poaceae, 5°20'N, 61°13'W, 1170 m, 22 Dec. 2000 (fl), *P.G. Delprete & A.C. Araujo 7414* (CAY, MO, VEN); Mun. Gran Sabana, 2 km N of San Rafael de Kamoioren, km 174, area seasonally inundated with white-sand soil, dominated by Melastomataceae, Rapateaceae, Piperaceae and *Drosera*, 5°39'N, 61°24'W, 1300 m, 27 Dec. 2000 (fl, fr), *P.G. Delprete & A.C. Araujo 7427* (CAY, GB, NY, VEN), 7430 (BR, CAY, P, US, VEN); km 119–122 S of El Dorado, 1100 m, 16 Mar. 1974 (fl), *A. Gentry, G. Morillo & B. de Morillo 10462* (MG, NY); Distr. Roscio, sabana arbustiva sobre cuevas de piedemonte al WSW del Ilu-

Tepui, en la region del Río Caraurín medio, 5°18'N, 61°0'W, 1150 m, 27 Jun. 1983 (fl), *O. Huber & C. Alarcón 7701* (NY, VEN); Distr. Roscio, extensas sabanas abiertas sobre altiplanicie en la region del Alto Río Arabapó, ca. 10 km SW del Uei-Tepui (Cerro El Sol), 4°56'N, 60°41'W, 1100 m, 21 Jan. 1985 (fl), *O. Huber 9998* (NY, VEN); Alto Caroni, near Sta. Elena de Uairen, 25 Apr. 1946 (fl, fr), *T. Lasser 1457* (NY, US, VEN); Kavanayen, en sabanas, Guayana Venezolana, 30 May 1946 (fl, fr), *T. Lasser 1893* (NY); 17 km E of El Pauji by rd. and 64 km W of Santa Elena by road, 4 km N of hwy, Río las Ahallas, 4°30'N, 61°30'W, 850 m, 1 Nov. 1985 (fl), *R. Liesner 19267* (MO, NY, VEN); Dist. Piar, 2–5 km W of Amaruay-Tepui, savannas between Tepui and Río Acanán Guarumo, 5°56'N, 62°17'W, 470 m, 4 May 1986 (fl), *R. Liesner 20594* (MO, NY); Gran Sabana, 5 km S of San Ignacio de Yuruani, wet savanna on slope, 4°59'N, 61°10'W, 850 m, 9 May 1988 (fr), *R. Liesner 24412* (MO, NY); km 121 along El Dorado-Santa Elena rd., wet dwarf forest, 1310 m, 16 Nov. 1978 (fl, young fr), *J.L. Luteyn et al.* 6264 (NY, US, VEN); Gran Sabana, savanna 1–5 km NW of Misión at Kavanayen, 1300 m, 4 Apr. 1952 (fl), *B. Maguire 33733* (NY, US); road S of El Dorado, km 98, along edge of rain forest, 450 m, 18 Dec. 1979 (fl), *J. Pruski & J.A. Steyermark 1368* (NY, US, VEN); Gran Sabana, dry, open, rocky savanna on Roraima sandstone near km marker 164 S of El Dorado, 20 Dec. 1979 (fl), *J. Pruski & J.A. Steyermark 1441* (NY); Gran Sabana, vía Kavanayen, El Jardín (Guamu-Loma de Guamu), entre el campamento Parupa y Cavanayen, ca. 65 km E del Fuerte Luepa, 1350 m, 7 Oct. 1984 (fl, fr), *N. Ramírez 976* (NY, VEN); vicinity of road campamento 150 at km 150 in valley of savanna of Río Uarama below Uarama-Tepui, NE of Luepa [ca. 5°50'N, 61°30'W], 1220 m, 24–25 Apr. 1960 (fl), *J.A. Steyermark & S. Nilsson 537* (NY, VEN), 694 (NY, VEN); Mount Roraima, forested SW-facing quebrada near Rondón Camp, 2040 m, 25 Sep. 1944 (fl), *J.A. Steyermark 58649* (NY); dense forest along Río Karuai, between Santa Teresita de Kavanayén and base of Ptari-Tepui, 1220 m, 18 Nov. 1944 (fl), *J.A. Steyermark 60297* (NY, US, VEN); Carretera El Dorado hacia Santa Elena de Uairen, km 198 al S de El Dorado, 1200–1400 m, 7–10 Dec. 1972 (fl, young fr), *J.A. Steyermark et al.* 106626 (NY, US, VEN); km 121 S of El Dorado on rd. to Sta. Elena, bordering dwarf forest, 1200 m, 29 Dec. 1974 (fl, young fr), *J.A. Steyermark 111276* (US); Gran Sabana, Las Delicias, Sta. Elena, Feb. 1946 (fl), *F. Tamayo 2769* (US).

**GUYANA:** Potaro-Siparuni Region, Surama, 4°10'N, 59°5'W, 80 m, 1 Dec. 1995 (fl), *D. Clarke 698* (MO, US); Cuyuni-Mazaruni Region, Utshi River to Great Falls trail, on Kamarang River, 5°40'N, 61°6'W, 910 m, 30 Jan. 1996 (fl), *D. Clarke 876* (CAY, MO, NY, U, US); Cuyu-

ni-Mazaruni Region, Pakaraima Mountains, savanna between Koatse River and Chinowieg Village, white-sand savanna, 5°27'N, 60°4'W, 700–800 m, 12 Nov. 1992 (fl), *T.W. Henkel & B. Hoffman 217* (MO, US); Mount Roraima Expedition, 1000 m, fall of 1894 (fl), *J.J. Quelch & F. McConnell 195* (K), 198 (K); Mount Roraima, stony slopes on sandy soil, Philipp Camp, 5200–6000 ft [1585–1830 m], 7 Nov. 1927 (fl, fr), *G.H.H. Tate, 288* (NY); Atkinson, St. Cuthbert's Trail, 4.5 mi from Highway, fringe of xeromorphic scrub/palm marsh woodland, 26 Feb. 1969 (fl), *U.G. Bio 106 [University of Guyana, Biology, course 106] 74* (NY).

8-2. *Sipanea glaberrima* (Bremek.) Steyer., Mem. New York Bot. Gard. 17: 270. 1967. (Figures 41–42).

(≡) *Sipanea pratensis* var. *glaberrima* Bremek., Recueil Trav. Bot. Néerl. 33: 707. 1936 [reimpr. Meded. Bot. Mus. Herb. Rijks Univ. Utrecht 35: 707. 1936].

Type: SURINAME. Upper Sipaliwini River, Great Savannah, 2°N, 56°W, 23 Oct. 1935 (fl), *H.E. Rombouts 223bis* (holotype U [barcode 0006310]; photo-U at NY). [Section *Sipanea*].

*Herbs*, height unknown, erect, entirely glabrous, except corolla throat; young branches thin, 1.3–1.6 mm thick, terete, glabrous. *Stipules* basally adnate to the petioles, free portion truncate and mucronate, or broadly triangular at base and narrowly triangular distally, 1.5–2 × 1.3–1.5 mm, distal triangular portion 0.7–0.9 mm long, slightly thickened at margin inside; margin with 3 colleters on each side of the central lobe. *Leaves* short-petiolate; petioles 2.5–3 mm long, glabrous; blades elliptic to narrowly ovate, 3–3.7 × 1.3–1.5 cm, obtuse to acute and shortly decurrent at base, acute at apex, chartaceous, olive-green when dry, glabrous throughout; secondary veins 7 on each side of midrib, obsolete above, prominent below. *Inflorescences* terminal, pedunculate, dichotomously branched, 25-flowered, 6.7 × 2.5 cm (excluding corollas), lateral axes 2.8 cm long, scorpioid; peduncle 3.9 cm long; bracts subtending secondary branches leaf-like, elliptic, 9.5–10.5 × 6 mm, acute; bracteoles subtending flowers narrowly lanceolate, 1–7 × 0.2–0.6 mm. *Flowers* sessile, 5-merous; distyly not observed. *Hypanthium* turbinate, 1–1.5 × 0.6 mm, acute at base, round at apex. *Calyx* lobes subequal, linear-lanceolate, 3.5–4 × 0.1–0.3 mm, acuminate; with 1 colleter in each calycine sinus, linear, 0.3 mm long. *Corolla* hypocrateriform, 15.3–15.5 mm long, color unknown, with a dense ring of yellow hairs exerted beyond mouth; tube 12.5 mm

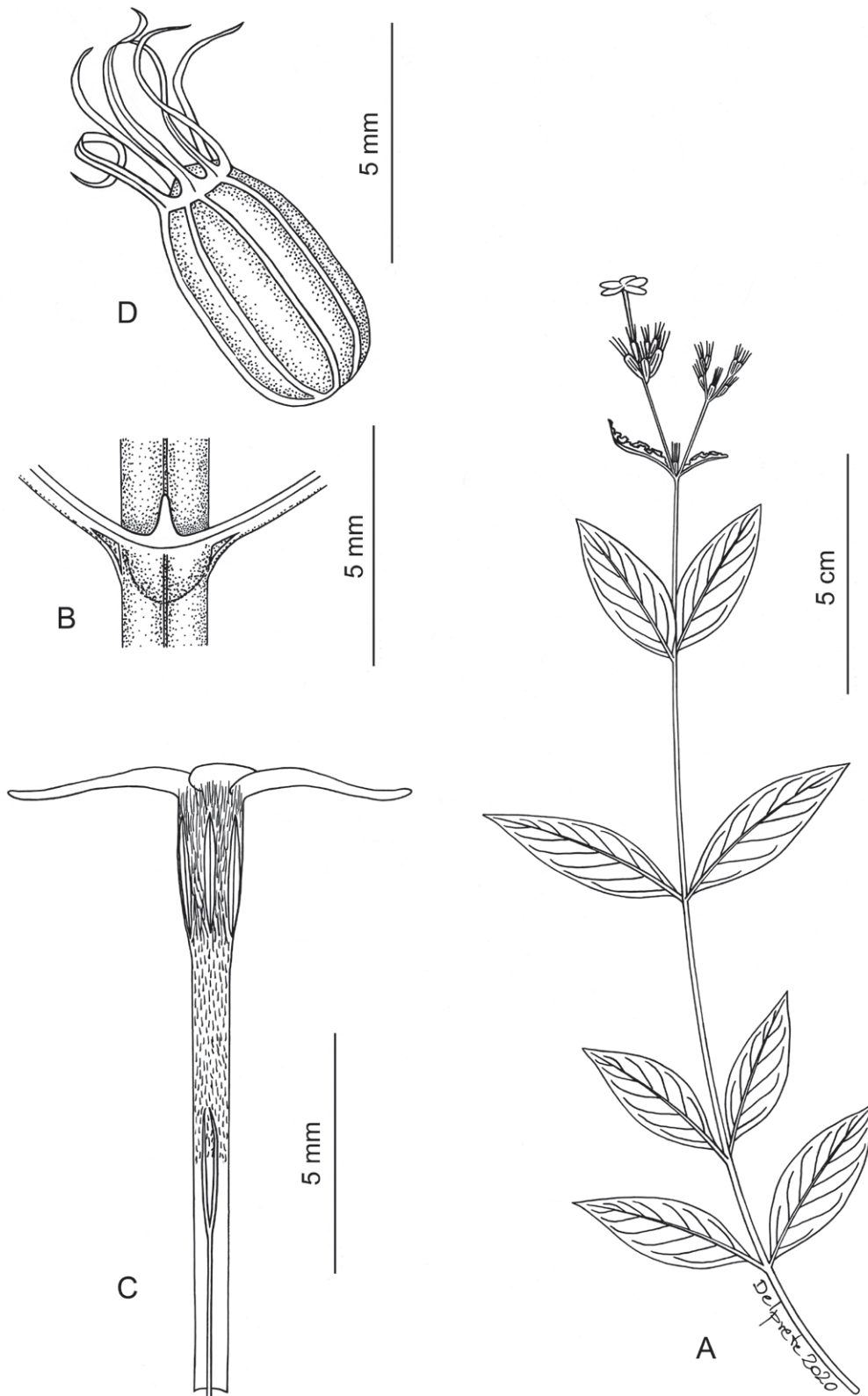
long, gradually expanding towards the mouth, 0.7 mm wide at base, 1.5 mm wide at mouth, glabrous at basal 5 mm, densely puberulous above (up to stamen insertions) and densely yellow-pubescent at distal portion inside, the yellow pubescence exerted beyond corolla mouth; lobes broadly obovate to oblong-elliptic, 3–3.5 × 2.3–2.5 mm, obtuse at apex. *Short-styled flowers* (*Rombouts 223bis* (corolla tube 12.5 mm long)): stamens inserted 3 mm below corolla mouth; filaments 0.2–0.3 mm long; anthers narrowly oblong-elliptic, 2–2.2 × 0.2 mm, acute at both ends; style included, 6 mm long; branches linear, 2–3 mm long, acute at apex. *Long-styled flowers* unknown. *Infructescences* dichotomously branched, with scorpioid secondary branches, lateral axes 2.8 cm long. *Capsules* oblong, 5–5.8 × 2.7–3 mm, round at base, obtuse at apex, thinly woody, strongly costate, turning beige when dry. *Seeds* irregularly tetrahedral, faintly angular, 0.4–0.5 mm in diam., testa foveolate, rugulose.

**Notes:**—Bremekamp (1936: 707) described *Sipanea pratensis* var. *glaberrima* Bremek., and wrote “This variety is known in one specimen only, a plant collected by Mr. Rombouts in the Great Savanna (Lat. 2°N, Long. 56°W) in the midst of plants belonging to the *forma typica*.” Steyermark (1967: 270) upgraded Bremekamp’s variety to species rank, and stated “This is a distinct species, easily recognized by having all parts of the plant glabrous,” and provided a complete species description.

*Sipanea glaberrima* (Bremek.) Steyer. is unique within the genus by being completely glabrous, except for the pubescence at corolla throat. It is most similar to *S. pratensis* var. *dichotoma*, with which is sympatric, because of the erect habit, branched inflorescences, flower size, and oblong, costate capsules. As the two taxa are sympatric, a varietal rank for *S. glaberrima* is incompatible with the variety concept adopted in the present treatment (secondary variation with a morphological-geographical correlation, where sympatric varieties are not allowed; see section Species and Variety Concepts, above); therefore, it is here treated as a distinct species. Aside from being completely glabrous, *S. glaberrima* differs from *S. pratensis* by the stipules truncate and mucronate, 0.5–2 mm long, glabrous (vs. broadly triangular at base and very narrowly triangular to linear distally, 2–6 mm long, appressed pubescent to sericeous outside).

**Distribution and ecology:** Only known by the single type specimen collected in southernmost Suriname, in the Great Savanna of Sipaliwini, at 2°N, 56°W (Figure 41). Growing in sunny exposure, in the midst of a population of *S. pratensis* var. *dichotoma*.





**Figure 42.** *Sipanea glaberrima*. **A.** Branch with terminal inflorescence. **B.** Node with stipule and petioles. **C.** Dissected short-styled flower, with stamens inserted at distal portion of corolla tube, and included style. **D.** Capsule. **A–D:** drawn from *Rombouts 223bis* (U, holotype). Illustration by Piero Delprete.

**Phenology:** The sole specimen known, collected in October, has flowers in anthesis and mature capsules in the same inflorescence.

**Suggested conservation status: Critically Endangered (CE).** This species is known by a single specimen collected in 1935 in the Great Savanna of Sipaliwini, which in 1972 became a Nature Reserve, and is located at the southern border of Suriname, contiguous with the Tumucumaque Mountains National Park, Brazil. Most of the reserve consists of savanna formation, with vast grassy field and sometimes with sparse trees. The number of individuals of this species is unknown. Large tropical savannas are subject to frequent fires, which is the case of the single collection locality of this species. Following criteria B1, B2a, and C2a, this species is treated as Critically Endangered (CE), following IUCN criteria (IUCN 2012, 2019).

8-3. *Sipanea glomerata* Kunth in Humb. & Bonpl., Nov. Gen. Sp. 3: 398. 21 Nov. 1821 [“1820”]. (Figures 5D, 43–44).

Type: VENEZUELA. Amazonas: Near Atures, on the Orinoco River, s.d. [15–17 Apr. 1800], *A.J.A. Bonpland & F.W.H.A. Humboldt 862* (**lectotype**, B-W [barcode B-W 04123-01 0] **here designated**; B†; possible isoelectotype photo-B [Negative No. F0BN000060] at F and NY). [Section *Sipanea*].

(=) “*Ptychodea sessiliflora*” in Cham. & Schldl. in Linnaea 4: 168. 1829, *nom. illeg. superfl. pro syn.*

Type: VENEZUELA. Amazonas: Near Atures, on the Orinoco River, s.d. [15–17 Apr. 1800], *A.J.A. Bonpland & F.W.H.A. Humboldt 862* (**lectotype**, B-W [barcode B-W 04123-01 0] **here designated**; B†; possible isoelectotype photo-B [Negative No. F0BN000060] at F and NY).

(=) *Sipanea glomerata* var. *paucinervia* Steyerl., Mem. New York Bot. Gard. 17: 282. 1967

Type: VENEZUELA. Amazonas: On granitic dome, about 30 km above Playa Alta, 200 m, 28 Dec. 1950 (fl, fr), *B. Maguire, R.S. Cowan & J.J. Wurdack 30458* (holotype NY [barcode 00133312]).

*Herbs or subshrubs* (basal internodes woody), 0.3–1 m tall, erect, branched; young branches tough, terete to slightly tetragonal, 3–4 mm thick, sparsely to densely

appressed or spreading yellowish- or beige-pubescent or sericeous (hairs 1–2.5 mm long). *Stipules* adnate to the petioles, sheathing, free portion broadly to shallowly triangular at base and narrowly triangular to linear distally, 4–13 × 1–2.5 mm, acuminate, densely strigose or villos outside, glabrous and slightly thickened at margin inside; with 5–6 colleters inserted just below the base of the central lobe inside or 6–7 colleters inserted along the margin. *Leaves* sessile to short-petiolate; petioles (when present) to 2 mm long, densely sericeous; blades broadly elliptic, oblong-lanceolate to lanceolate, 3.5–9.5 × 1–4.5 cm, acute at base, acuminate at apex, chartaceous, dark green above and pale green or yellowish-green below when fresh, olive-green when dry, lamina densely sericeous or sparsely to densely appressed pubescent to glabrate above, densely sericeous or sparsely appressed pubescent or glabrous below, midrib and secondary veins appressed-strigose; secondary veins 5–11 on each side of midrib, strongly ascending, commonly impressed above and prominent below. *Inflorescence* terminal, pedunculate, a single head subtended by two leaf-like bracts, or trichotomous with three pedunculate heads; heads 1–1.5 × 1–1.5 cm during anthesis, 5–8-flowered; peduncles 0.7–5 cm long, sparsely to densely appressed-antrorse or spreading sericeous (hairs 1–2 mm long); bracts subtending the heads 3–6; external bracts broadly ovate to shallowly elliptic, lobed or lacinate, 3–4 mm long, or entire, lanceolate, 7–9 mm long, acuminate, densely sericeous outside; inner bracts entire, lanceolate, 9.5–14 × 1.8–5 mm, acuminate, densely sericeous outside, margins ciliate, glabrous inside; bracteoles subtending flowers lanceolate to narrowly lanceolate, 8–12 × 1.1–1.7 mm, sparsely to densely sericeous outside, glabrous inside, ciliate-sericeous at margins. *Flowers* distylous, 5-merous, subsessile to short-pedicellate; pedicels to 1.5 mm long. *Hypanthium* narrowly obovoid, 2.5–3 × 2–2.5 mm, acute at base, round at apex, densely sericeous. *Calyx* lobes subequal, green to yellowish-green when fresh, oblanceolate, lanceolate to subulate, 7–13 × 0.7–1.2 mm, enlarging to 15–17 mm long on fruits, acuminate, sericeous-strigose outside (hairs 0.4–1 mm long), margins long-ciliate, glabrous inside; with 1–2 colleters in each calycine sinus, narrowly conical, acute at apex, 0.4–0.5 mm long. *Corolla* hypocrateriform, 19–25 mm long, white, with a dense ring of yellow hairs exerted beyond mouth; tube 12–17 mm long, gradually expanding towards the mouth, 0.9–1.2 mm at base, 2.8–3 mm wide at mouth, glabrous at medio-basal portion and densely white-sericeous at medio-distal portion outside, glabrous at basal portion, densely puberulous above and densely yellow-pubescent at distal portion inside, the yellow pubescence exerted beyond corolla mouth; lobes obovate to broadly obo-

vate, 7–8 × 3.5–5.5 mm, round to subacute at apex, glabrous throughout. *Long-styled flowers* [Ll. Williams 13016 (corolla tube 12 mm long)]: stamens inserted at 4.5–5.5 mm from base of corolla tube; filaments 0.5 mm long; anthers linear, 2.5 × 0.2 mm, acute at both ends; style exerted 2–3 mm beyond corolla mouth, 14–15 mm long, glabrous; style branches obovate, 1–1.3 mm long, round at apex. *Short-styled flowers* [Holt & Blake 799 (corolla tube 15 mm long), Zarucchi 1675 (corolla tube 17 mm long)]: stamens inserted at 4–4.5 mm below corolla mouth; filaments 0.3–0.5 mm long; anthers linear, 2.5–3 × 0.2–0.3 mm, acute at both ends; style included, 6–9 mm long, glabrous; branches linear, 2.3–2.8 mm long, acute at apex. *Infructescence* a condensed single head or tricotomous with three condensed heads, similar to inflorescence. *Capsules* oblong-ovoid to narrowly ovoid, 6–9 × 3–4.5 mm, round at base, acute at apex, crustaceous, densely gray-sericeous (hairs 0.4–1 mm long), pale green when young, turning beige when dry. *Seeds* irregularly tetrahedral, subangular, 0.6–0.8 mm in diam., testa foveolate, rugulose-verrucose.

**Notes:** After exhaustive searches in P, P-JU and P-Bonpl., no original specimen of *Sipanea glomerata* Kunth could be found. See discussion under *Sipanea pratensis* var. *dichotoma* for further information regarding the complex history of the specimens collected by Bonpland and Humboldt and described by Kunth. An original specimen of *S. glomerata* was found at B-W, with barcode B-W 04123-010. This specimen has two handwritten labels: “*Sipanea glomerata* H.B.Kth. 3 p. 310. – ! Schum.” and “germin. an 8 [Germinal (22 March–20 April) 1800], orinoco, No. 862. Pent. lia [Pentandria monogynia], πρσοχύδης – psonatur (W.) – in Guiana d. Aturès – (Humboldt).” On the lower right corner of the sheet it is handwritten “Humboldt. W.” and on the upper right corner is handwritten “Pt. [*Ptychodea*] sessiliflora.” On the sheet is mounted a branch with numerous leaves, and an inflorescence with a flower in anthesis. Aside with the branch are present several inflorescence fragments, including one loose flower in anthesis. This specimen is here designated the lectotype of *S. glomerata*. This specimen is also here designated as the lectotype of the illegitimate superfluous name “*Ptychodea sessiliflora*” that was cited by Chamisso & Schlechtendal (1829: 168) as a synonym of *Sipanea glomerata*. The image of this specimen is avail-

able at: <https://ww2.bgbm.org/Herbarium/specimen.cfm?Barcode=BW04123010>.

Humboldt donated to Kunth about 3000 original specimens from the Bonpland and Humboldt collection (Stauffer et al. 2012), which Kunth took with him to Berlin, after he finished writing the *Genera Plantarum*. Kunth’s private herbarium comprised nearly 70,000 specimens, which were all destroyed during WWII in 1943. Francis Macbride, of the Field Museum, took photographs of type specimens in numerous European herbaria before they were destroyed during WWII. One of these photographs is of a specimen of *S. glomerata*, which has the label handwritten by several authors “*Sipanea glomerata* Kunth in Humb. et Bonpl. 3 p. 398. *Ptychodea sessiliflora* Willd. herb. ! Schum., Hb. Kunth, Ex herb. Humb.” Most likely, that specimen was part of the original material used by Kunth to describe this species, however the label does not indicate any locality or collection number, which renders impossible to connect this image to the specimen of *Bonpland & Humboldt* 862 present in B-W. Macbride’s photograph of this specimen is available at: <https://fm-digital-assets.fieldmuseum.org/36/440/60.jpg>

Steyermark (1967: 281–282; 1974: 364–365) distinguished the typical variety of *Sipanea glomerata* from var. *paucinervia* Steyermark by having “upper surface of leaf-blades densely sericeous with crowned appressed hairs” (vs. “glabrous or sparsely appressed-pilose with more scattered hairs” in var. *paucinervia*), “leaf blades 2.5–4.5 cm broad” (vs. 1–2.2 cm broad), and “lateral nerves of leaf-blades 7–11 on each side” (vs. “5–6”). Delprete and Steyermark (2004e: 829–830) did not recognize any variety in this species, without any comment. After a detailed study of ample material from throughout its geographic range, I confirmed that the characters used by Steyermark to differentiate the two varieties are widely overlapping and no varieties are here recognized in this species.

**Distribution and ecology:** Distributed in the Amazon Region of Colombia, Venezuela, Surinam, and Brazil (Mato Grosso, Roraima, Pará, and Amazonas) (Figure 44). Often found in large stands, in open savannas with sparse trees and shrubs, or on forested and open igneous granitic outcrops, gravelly savannas, sometimes in secondary vegetation (in Brazil called “capoeira”), in sunny or semi-shady exposures, in sandy, granitic or lateritic soils; at 80–200 m altitude.

**Figure 43.** *Sipanea glomerata*. **A.** Branch with terminal young inflorescence. **B.** Node with sheathing stipule and leaf bases. **C.** Dissected long-styled flower, with stamens inserted at medio-distal portion of corolla tube, and exerted style. **D.** Dissected short-styled flower, with stamens inserted at distal portion of corolla tube, and included style. **E.** Capsule. **A–C:** drawn from Williams 13016 (US); **D:** drawn from Holt & Blake 799 (US); **E:** drawn from Maguire et al. 36046 (US). Illustration by Piero Delprete.

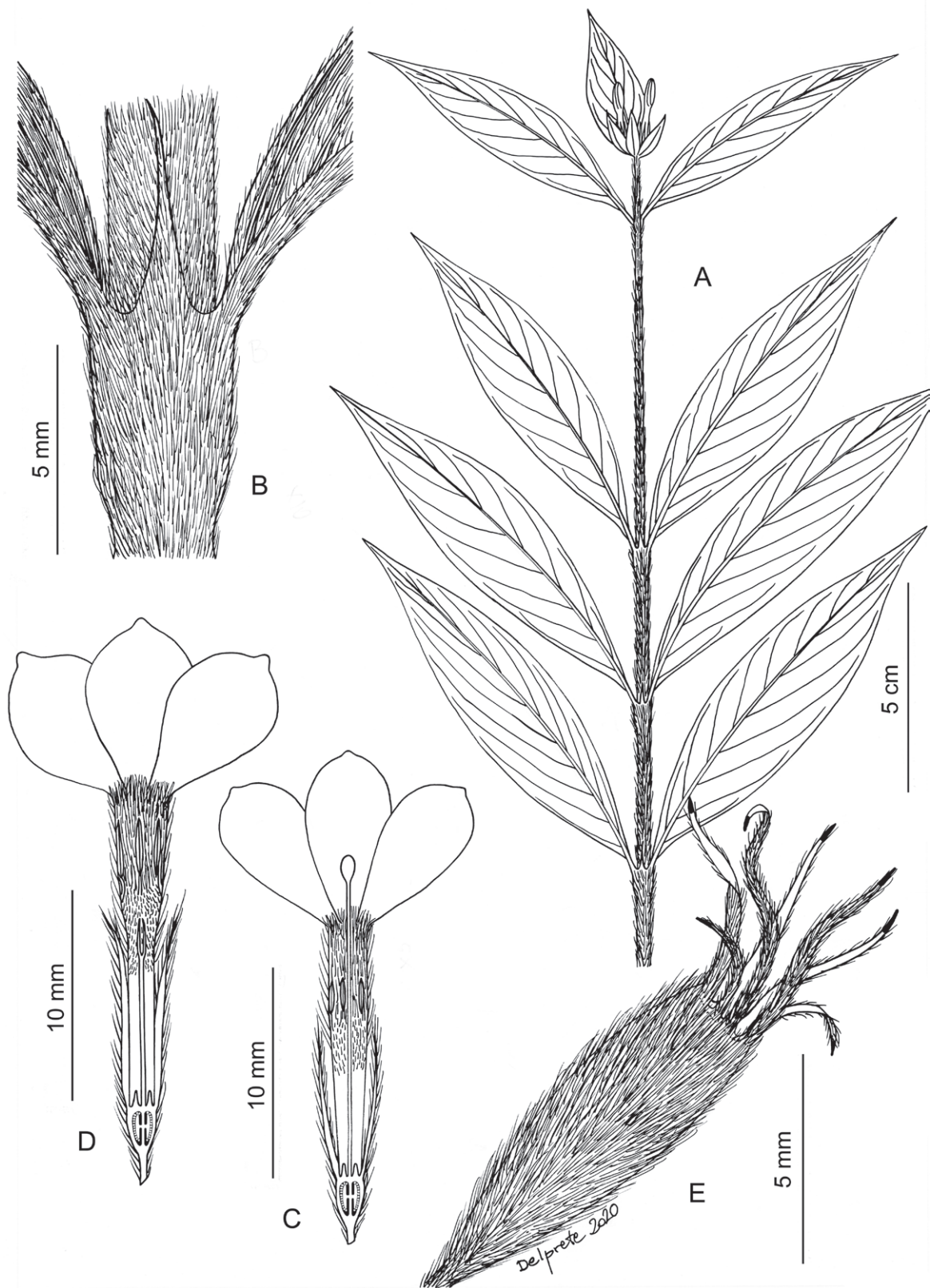


Figure 43.

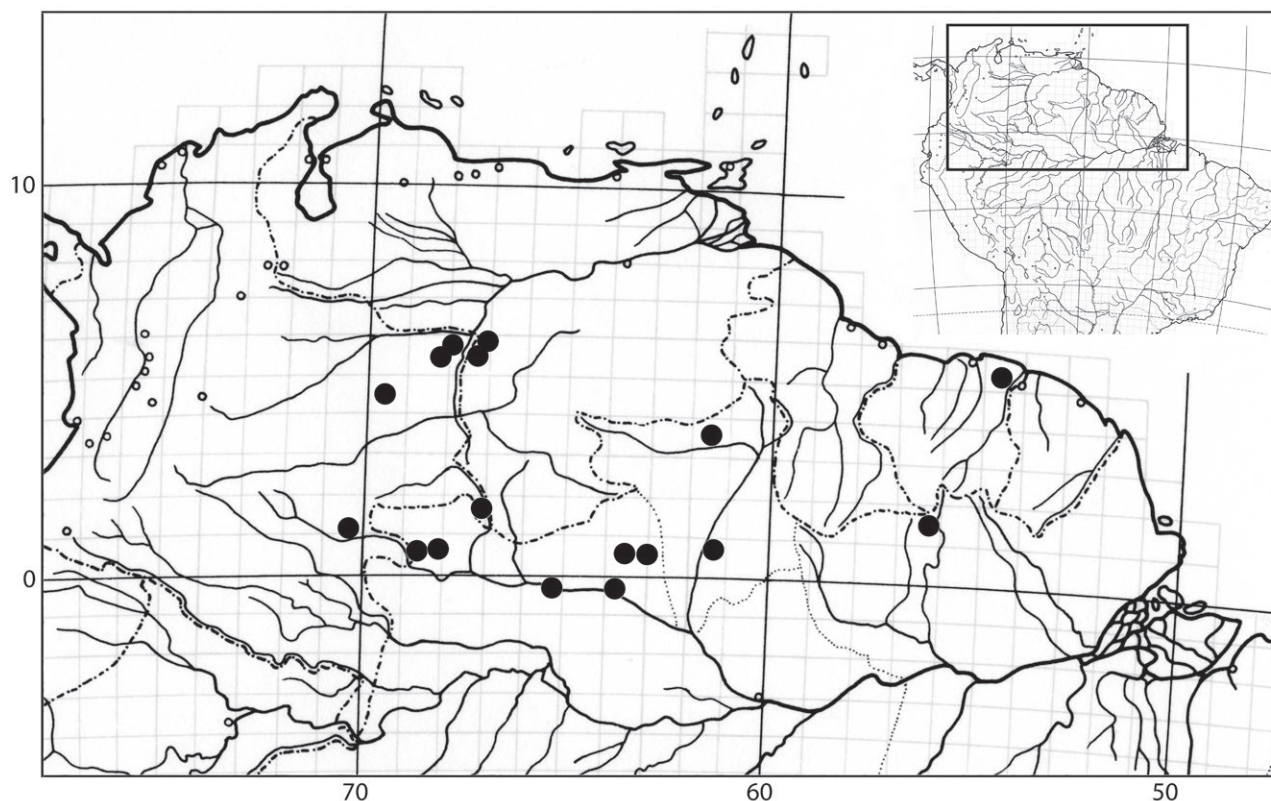


Figure 44. Distribution of *Sipanea glomerata*.

**Notes:** *Sipanea glomerata* is similar and has been often confused with *S. hispida*. The former can be distinguished from the latter by the stems sparsely to densely appressed or spreading, pubescent or sericeous (vs. densely hirsute or villous in *S. hispida*), leaf adaxial side densely sericeous or sparsely to densely appressed pubescent to glabrate (vs. sparsely to densely strigose), leaf abaxial side densely sericeous or sparsely appressed pubescent or glabrous (vs. densely villose-sericeous), inflorescence a single head usually subtended by two leaf-like bracts, or trichotomous and made of three pedunculate heads (vs. cymose, dichotomous or rarely trichotomous), calix lobes 7–13 × 0.7–1.2 mm in flowers, enlarging to 15–17 mm long in fruits (vs. 4–6 × 0.3–0.6 mm), corollas 19–25 mm long, white (vs. 8.5–15(–16.5) mm long, pink), corolla tubes 12–17 mm long (vs. 6–10(–12.5) mm long), and corolla lobes 7–8 × 3.5–5.5 mm (vs. 2.5–5 × 1.5–3 mm).

**Phenology:** Individuals of this species are commonly found with flowers and fruits. Flowering and fruiting the whole year around.

**Uses:** In Venezuela (Amazonas: Sanariapo), an infusion made with the whole plant of this species is used for stomach problems (*Ll. Williams 16002*).

**Suggested conservation status: Least Concern (LC).** This species has been collected in numerous localities in Colombia, Venezuela, Surinam, and northern Brazil. It is often found in large stands in secondary vegetation and along roadsides (pers. obs. in Venezuela and Brazil). Considering that this species is known by numerous collections, and is often found as a ruderal in secondary vegetation, it is positioned in the Least Concern (LC) category, following IUCN criteria (IUCN 2012, 2019).

**Specimens examined: COLOMBIA: Guainía:** Immediately S of Casuarito, lajas along the Río Orinoco, in cracks on laja and grassy pockets, 5°40'N, 67°37'W, 90 m, 22 Jun. 1984 (fr), *G. Davidse & J.S. Miller 26391* (NY); Río Negro, San Felipe and vicinity, below confluence of Río Guainía and Río Casiquiare, 1°50'N, 67°0'W, 200 m, 26 Oct. 1952 (fl), *R.E. Schultes et al. 18065* (NY, US), 18094 (US). **Vaupés:** Río Vaupés, Cerro de Mitú, 20 Aug. 1960 (fr), *R.E. Schultes & I. Cabrera 22716* (NY); Mitú and vicinity [ca. 1°11'N, 70°10'W], granitic slope of Cerro de Mitú, side facing Mitú, 28 May 1976 (fl), *J.L. Zarucchi 1675* (MO, US). **Vichada:** Corregimiento Cumaribo, carretera Cumaribo-Santa Rita, camino entre

Palmarito y Chaparral, en morichal, 4°25'W, 69°48'W, 150 m, 12 Dec. 1993 (fl, fr), *C. Sastre et al.* 9082 (P), 9083 (COL); "prope Maypures, flumen Orenoco" [Maipures, Río Orinoco, ca. 5°12'N, 67°50'W], Jun. 1854 (fl), *R. Spruce* 3665 (BR, P).

**VENEZUELA: Amazonas:** Bords de l'Orenoque, savane Atures, s.d. (fr), *J. Chaffanjon* 171 (P); Mission Camp, ornamental plant with white flowers, 4 Apr. 1950 (fl), *H.M. Curran* 209 (NY); Depto. Atures, ca. 23 km NE of Puerto Ayacucho along the rd to El Burro, laja and savanna at its base, 5°51'N, 67°29'W, 80–150 m, 17 Apr. 1979 (fl), *G. Davidse & O. Huber* 15248 (MO, NY, VEN); Depto. Atures, ca. 4.5 km N of Puerto Venado, just E of Samariapo, 5°15'N, 67°47'W, 85 m, 25 Apr. 1979 (fl), *G. Davidse et al.* 16766 (MO, US, VEN); near Puerto Ayacucho, 100 m, 30 Sep. 1960 (fl), *E. Foldats* 3529 (NY); bords de l'Orenoque, entre Atures et San Fernando de Atabapo, 17 May 1887 (fr), *A. Gaillard* 7 (P); 22–23 km N of Samariapo on rd. to Puerto Ayacucho, 100 m, forest edge, 5°39'50"N, 67°37'25"W, 29 Jun. 1975 (fl), *A. Gentry & P. Berry* 14571 (BM, MO); Puerto Ayacucho, 100 m, May 1931 (fl), *E.G. Holt & E.R. Blake* 799 (NY, US); alrededores de Puerto Ayacucho, ca. 12 km S, laja granítica, derecho de la carretera Puerto Ayacucho-Samariapo, 5°34'N, 67°35'W, 80–250 m, 20 Jul. 1977 (fl), *O. Huber & S.S. Tillett* 923 (NY); Great Rapids of the Río Orinoco, Puerto Ayacucho, crystalline laja 1–1.5 km E of Hotel Amazonas, 100–120 m, 7 Nov. 1953 (fl, fr), *B. Maguire et al.* 36046 (NY, US); sobre laja granítica, ca. 3.5 km al N de Puerto Ayacucho, margen de la carretera Puerto Ayacucho-El Burro, 80 m, 14 Oct. 1988 (fl, fr), *G.A. Romero* 1693 (NY, S, TFAV), 17 Oct. 1988 (fl, fr), 1756 (NY); transecto entre bosque inundado (rebalse) y Cerro Caribe (afloramiento granítico al N de San Juan de Ucata), 4°20'N, 67°49'W, 70–100 m, 22 Oct. 1989 (fl, fr), *G.A. Romero et al.* 2168 (NY); Depto. Atures, Montaña Fría, entre poblaciones de Puerto Ayacucho y Sanariapo, 180 m, 26 Jul. 1967 (fl), *L. Ruiz-Terán* 4327 (MERF, MG); Depto. Atures, forested areas and igneous outcrops along Río Coromoto, at Tobogán de la Selva, 35 km SE of Puerto Ayacucho, 5°22'N, 67°33'W, 150 m, 14 May 1980 (fl), *J.A. Steyermark et al.* 122563 (MO, NY); Depto. Atures, Tobogán de la Selva, Río Coromoto, 35 km SE of Puerto Ayacucho, among igneous exposures, 5°27'N, 67°33'W, 7 Sep. 1985 (fl), *J.A. Steyermark et al.* 131518 (MO, NY, VEN); Puerto Ayacucho, orilla del Riachuelo El Bagre, 100 m, 20 May 1940 (fl), *Ll. Williams* 13016 (US); sabana abierta de Sanariapo [ca. 5°14'N, 67°47'W], parte inferior, 120 m, 3 Jul. 1942 (fl), *Ll. Williams* 16002 (US).

**SURINAME:** Fluv. Corantjin [Courantyn River], Apihollo Savanna, 29 Jan. 1911 (fl), *J.F. Hulk* 56 (U); Via secta

ab Moengo [ca. 5°37'N, 54°24'W], tapoe ad Grote Zwiebelzwamp, km 6.7 in savanna, 5 Oct. 1948 (fl), *J. Lanjouw & J.C. Lindeman* 657 (U); *ibid.*, km 15.7–15.9 in savanna, 15 Oct. 1948 (fl), *J. Lanjouw & J.C. Lindeman* 844 (U).

**BRAZIL. Amazonas:** Rio Negro, Tapuruquara [ca. 0°24'S, 65°2'W], capoeira, 25 Apr. 1948 (fl, fr), *G.A. Black* 48-2481 (IAN); Barcelos, Serrinha, afloramento rochoso, próximo do Rio Aracá, 0°25'3"N, 63°22'58"W, 59 m, 20 Aug. 2014 (fl, fr), *F.N. Cabral et al.* 1217 (INPA); Rio Negro, Uaupés, Taracua [ca. 0°41'N, 69°32'W], arredores, 3 Mar. 1959 (fl, fr), *P. Cavalcante* 738 (MG); Mun. Barcelos, margem do Rio Araça, pouco abaixo da foz do Rio Jauari, 0°25'N, 63°25'W, 20 Jul. 1985 (fl), *I. Cordeiro* 245 (INPA, MG, NY, US); Barcelos, Rio Aracá, acima da comunidade de Bacuquara, afloramento de granito [inselberg] localmente chamado Serrinha, 0°11'20"N, 63°10'5"W, 110 m, 17 Apr. 2014 (fl), *R.C. Forzza et al.* 7961 (INPA, RB); Rio Negro, Tapurucoara [ca. 0°24'S, 65°2'W], 6 Apr. 1947 (fl, fr), *R.L. Frões* 22076 (IAN); Rio Uaupés, local Ipanoré, uma hora de motor de popa acima de Taraquá, Estrada para Urubuquara, ca. 0°18'N, 68°40'W, caatinga, 17 Nov. 1987 (fl), *M.L. Kawasaki* 171 (INPA); Basin of Rio Negro, Tapuruquara [ca. 0°24'S, 65°2'W], beside road to airport, capoeira, 16 Oct. 1971 (fl), *G.T. Prance et al.* 15315 (NY, S, US); Rio Negro, Tupuruquara, terra firme, solo argiloso, erva ereta muito comum no local, 20 May 1973 (fl), *M.F. Silva et al.* 1740 (INPA, US); Tyler-Duida Expedition, Rio Negro, Santa Isabel [now Santa Isabel do Rio Negro, ca. 0°24'S, 65°2'W], 8 Sep. 1928 (fl), *G.H.H. Tate* 98 (NY, US); Mun. Barcelos, Serra do Aracá, platô, solo arigiloso e pedregoso, subarbusto, 0°55'18"N, 63°26'48"W, 28 Aug. 2001 (fl), *A. Vicentini et al.* 1913 (INPA); Upper Rio Negro River, 1907–1908 (fr), *L. Weiss & H. Schmidt s.n.* (NY [2 sheets, 02690184 and 02690185]). **Pará:** Mon. Óbidos, Rio Parú de Oeste (Tiriós), campo, 21 Jun. 1960 (fl, fr), *P. Cavalcante* 794 (IAN, MG); Região dos Tiriós, Rio Paru do Oeste [ca. 1°31'S, 56°02'W], 16 Mar. 1962 (fl), *E.J. Fittkau & D. Coelho s.n.* (INPA No. 12773) (INPA, RB), 17 Mar. 1962 (fl), *s.n.* (INPA 12805) (INPA). **Roraima:** Local Anauá [ca. 0°57'N, 61°22'W], 7 Nov. 1973 (fl, fr), *B.G.S. Ribeiro* 391 (IAN); Morro Tepequem [ca. 3°45'N, 61°45'W], 3 Feb. 1975 (fl, fr), *B.G.S. Ribeiro* 692 (IAN), 698 (IAN).

8-4. *Sipanea hispida* Benth. ex Wernham, *J. Bot.* 55: 173. 1917. (Figures 45–46).

K.Schum. in Martius et al., *Fl. Brasil.* 6(6), fig. 122 (as *Sipanea pratensis*). 1889.

Type: BRAZIL. Amazonas: Rio Negro, São Gabriel da Cachoeira [ca. 0°7'N, 67°5'W], Jan.–Aug. 1852,

*R. Spruce 2051* (first-step lectotype, designated by Steyermark (1967: 279), **second-step lectotype** BM [barcode 000614346], **here designated**; isolectotypes E [barcode E00505240], F [Acc. No. 767786], FI-Webb [barcode FI004807], G [2 sheets; barcodes G00436761, G00436762], K [without barcode], LD [barcode 1220003], M [barcode M-0189372], NY [barcode 00133313], P [barcode P00748149], RB [Acc. No. 17401, barcode 00543715]; frag F [Acc. No. 635362]; photo-K at NY). [Section *Sipanea*].

(=) *Sipanea trianae* Wernham, J. Bot. 55: 174. 1917

Type: COLOMBIA. [Villavicencio, Susumuco, 400 m, 1000 m; see Kirkbride (1982: 305)], s.d. (fl, fr), *J.J. Triana 1776* (holotype BM [barcode 000614328]; isolectotypes E [barcode 00285373], P [barcode P00748116 “entre Susumuco y Villa Vicencio”], US [Acc. No. 1481047, barcode 00137730]; photo-US, photo-K and photo-BM at NY).

(=) *Sipanea brasiliensis* Wernham, J. Bot. 55: 174. 1917

Type: BRAZIL. Minas Gerais: on a dry bank near Sabara, Sep. [1840] (fl, fr), *G. Gardner 5009* (holotype, BM [barcode 000614348]).

(=) *Sipanea pratensis* var. *major* Hassl., Repert. Spec. Nov. Regni Veg. 14: 170. 1915

(=) *Sipanea hispida* Benth. ex Wernham var. *major* (Hassl.) Steyermark, Mem. New York Bot. Gard. 17: 280. 1967

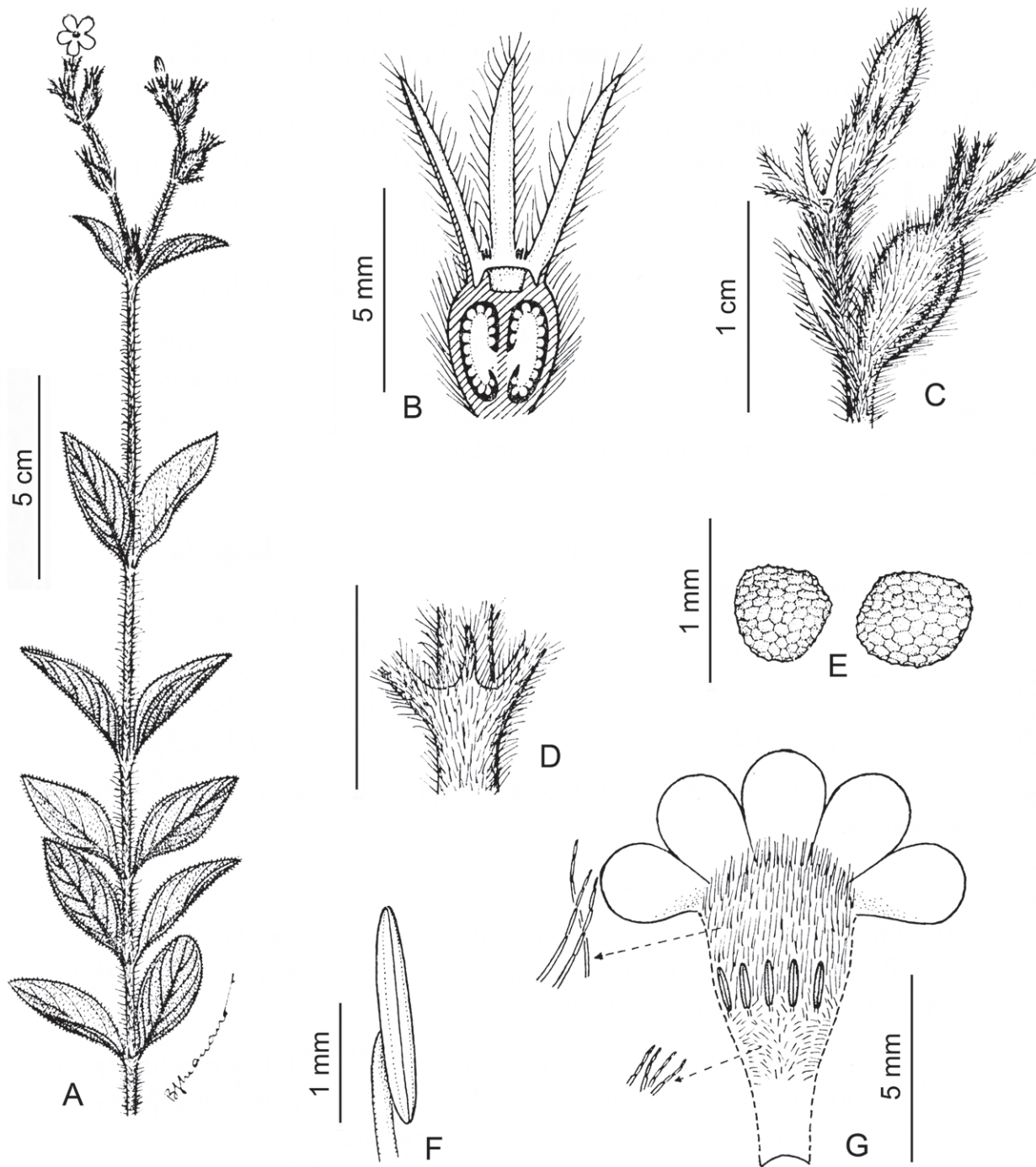
Type: PARAGUAY. Upper Apa River, Nov. [year unknown], *E. Hassler 7733* (**lectotype**, G [2 sheets, barcode G00307684], **here designated**; isolectotypes, [4 sheets, G00307683, G00307685, G00307685, G00307726], BM [barcode 000549052], MPU [barcode MPU021334], NY [barcode 00133326], P [3 sheets, barcodes P00729402, P00753869, P00753870], S [Acc. No. 10-27662]).

(=) *Sipanea glabrata* Wernham, J. Bot. 55: 173. 1917

Type: BRAZIL. Mato Grosso: “Santa Anna da Chapada” [now Chapada dos Guimarães], 28 Jun. 1902 (fl, fr), *A. Robert 333* (**lectotype**, BM [barcode 000614333], **here designated**; photo at NY).

*Perennial herbs* or *subshrubs* (basal internodes woody), 0.1–1.2 m tall, terrestrial, erect; young branch-

es terete not geniculate, green or rarely reddish, densely hirsute or villous (hairs long, spreading). *Stipules* adnate to the petioles, sheathing, free portion broadly to shallowly triangular at base and narrowly triangular to linear distally, 4–13 × 1–2.5 mm, densely strigose or villous outside, glabrous and slightly thickened at margin inside; with 5–6 colleters inserted just below the base of the central lobe inside or 6–7 colleters inserted just below the margin inside; margin densely strigose or villous. *Leaves* sessile to short-petiolate; petioles to 5 mm long, densely antrorse or spreading strigose or villous; blades ovate, ovate-lanceolate, narrowly elliptic to oblong-elliptic, 1.2–7.5 × 0.6–3 cm, acute to round at base, acute at apex, chartaceous to membranaceous, dark green above and pale green below when fresh, olive-green when dry, lamina sparsely to densely strigose above, densely villose-sericeous below, midrib and secondary veins densely antrorse or spreading strigose or villous; secondary veins 5–7 on each side of midrib, slightly impressed above, prominent below. *Inflorescences* cymose, dichotomous or rarely trichotomous, with a solitary branch at axil of each branching, 5–20-flowered, slightly expanding after anthesis, 5–16(–24) cm long, peduncle 1–8 cm long, densely hirsute or villous, simple, without later branches, or with 1–3 pairs of lateral branches; lateral branches 3–14(–18) cm long when fully expanded, dichotomously branched, ultimate branches scorpioid, 3–7-flowered; bracts subtending branchlets lanceolate, 7–10 × 0.7–2 mm, densely hirsute or villous; bracteoles opposing each flower narrowly triangular to linear, 3–7 × 0.4–0.7 mm, densely hirsute or villous. *Flowers* heterostylous, 5-merous, commonly sessile, the central ones at base of inflorescence bifurcations with pedicels to 1.5 mm long, glabrous or puberulous. *Hypanthium* obconical to obovoid, 2.5–5 × 1.5–2 mm, acute at base, round at apex, densely antrorse hispid or sericeous, hairs slightly enlarged-tuberculate at base. *Calyx* lobes subequal to unequal, green when fresh, linear to lanceolate, 4–6 × 0.3–0.6 mm, sparsely antrorse hispidulous to sericeous; with 1–2 colleters in each calycine sinus, linear, 0.3–0.4 mm long. *Corolla* hypocrateriform, (8.5–)9.5–16.5 mm long, pink, with a wide ring of yellow hairs at tube distal portion inside and at corolla mouth; tube (6–)7–12.5 mm long, narrowly cylindrical at lower portion and slightly expanded at point of stamen insertions, 1–1.2 mm at base, 1.5–2 mm wide at mouth, sparsely sericeous outside, glabrous or puberulent below stamen insertion and densely antrorse-pubescent in area surrounding stamens inside; lobes oblong to obovate, 2.5–5 × 1.5–3 mm, round at apex, reflexed at anthesis, glabrous, margins villous-pubescent. *Medium-styled flowers*: (in corolla tubes 7.5–9 mm long): stamens inserted



**Figure 45.** *Sipanea hispida*. A. Habit. B. Longitudinal section of hypanthium, ovary and calyx. C. Inflorescence branchlet, with flower bud and capsule. D. Node with stipule and petioles. E. Seeds. F. Stamen. G. Dissected corolla, and detail of hairs at distal and medio-basal portion of the corolla tube. Illustration by Bruno Manara (Reproduced with permission from Flora de Venezuela vol. 9(1), fig. 58. 1974).

below the tips of the style branches, at 3–3.5 mm (3/10 to 1/2 of the corolla tube) from base; filaments 0.5–0.7 mm long; anthers linear, 2.1–2.5 × 0.2–0.3 mm, round or acute at base, acute at apex; style included, as long

as the middle of the anther or as the upper tip of the anthers, 4–5 mm long (4.5/10 to 7/10 of the corolla tube), glabrous; style branches linear, 1–1.5 mm long, acute at apex. *Short-styled flowers* (in corolla tubes 7.5–12.5 mm



long): inserted above or at the same height of the tips of the style branches, at 3–8.5 mm (2/5 to 7/10 of the corolla tube) from base; filaments 0.5–0.7 mm long; anthers linear, 2–2.5 × 0.2–0.3 mm, round or acute at base, acute at apex; style included, shorter than the points of stamen insertions, style 2–7.5 mm long (2/5 to 3/5 of the corolla tube), glabrous; branches linear, 1–1.5 mm long, acute at apex. *Infructescence* cymose, dichotomous or rarely trichotomous, slightly more expanded than the inflorescence. *Capsules* elliptic-oblong to oblong, 6–11 × 3–5 mm, acute at base and at apex, crustaceous or thinly woody, pale green when young, turning pale brown-beige when dry, densely antrorse hispid or hirsute, hairs slightly enlarged at base. *Seeds* trigonous or rhomboid-suborbicular, 0.2–0.5 mm in diam., compressed, angular or irregularly tetrahedral, testa foveolate.

**Notes:** Schumann (1889) included “*S. hispida* Spruce ms.” (later validly published by Wernham (1917), see below), along with several other species, in a very broadly delimited *Sipanea pratensis*. In fact, Schumann’s figure of *S. pratensis* (Schumann, 1889, tab. 122) is instead *S. hispida*. Schumann’s erroneous and much too broad delimitation of *S. pratensis* caused great confusion among Rubiaceae specialists. For additional information about the confusion between these two species, see discussion under *Sipanea pratensis*.

Hassler (1915: 170) described *Sipanea pratensis* var. *major* Hassl., citing the gathering Hassler 7733, without indicating the herbarium of deposit. At G are present six sheets of Hassler 7733. The two sheets with barcode G00307684 have the following letter glued on the first sheet “Geneve, le 22 mars 1909. Cher Monsieur, Après avoir examiné à nouveau votre *Sipanea* et l’avoir comparé aux échantillons que nous avons, j’ai constaté que votre numéro 5691 est à peu près identique à R. Spruce, nr. 2051 auquel Schumann a mis le nom de *S. dichotoma* H.B.K., nom qu’il a ensuite relégué dans la synonymie de son *S. pratensis*, qui deviant ainsi une espèce excessivement polymorphe. Votre bien dévoué, Aug. de Candolle.” The text of this letter shows the confusion present in those days between *Sipanea pratensis* and *S. hispida*, and might also explain why Hassler positioned his new variety in *S. pratensis*. The two sheets with barcode G00307684 are here treated as a single specimen with multiple preparations (Art. 8.3 of the ICN; Turland et al. 2018), which is here designated as the lectotype of *S. pratensis* Aubl. var. *major*.

Wernham (1917) in the introduction of the article where he revised *Sipanea*, wrote “The types of all the novelties described are in the National Herbarium [BM].” Therefore, the specimen Gardner 5009 at BM,

barcode 000614348, is the holotype of *S. brasiliensis* Wernham (1917: 174), and the specimen Triana 1776 at BM, barcode 000614328, is the holotype *Sipanea trianae* Wernham.

Wernham (1917) along with the description *Sipanea glabrata* Wernham cited two gatherings, collected by A. Robert near the town of Santa Anna da Chapada (now Chapada dos Guimarães), Mato Grosso, Brazil, with collection numbers 333 and 364. Both collections are mounted on the same BM sheet, with a different barcode number.

Steyermark (1967: 282) commented for *Sipanea glabrata* Wernham, “I have examined the holotype and paratype collections deposited in the British Museum (BM).” However, as he did not annotate these specimens it is impossible to know which he intended for “holotype” and which for “paratype”. Therefore, the specimen Robert 333, with barcode BM 000614333, is here designated as the lectotype of this taxon because it is a more complete specimen, with flowers and fruits. Also, Wernham separated *S. glabrata* from *S. hispida* by the “nearly glabrous leaves, the obsolete stipules, and the very small corolla-limb, barely half a centimeter in diameter.” However, the leaves of both Robert 333 and 364 have veins densely appressed pubescent above and below, while the lamina are either glabrous or sparsely puberulent. All the characters used by Wernham to distinguish *S. glabrata* overlap with the morphological variation of *S. hispida*, and the two taxa are here treated as synonymous.

Steyermark (1967: 279) cited the type of *S. hispida* as “Rio Negro, prope São Gabriel da Cachoeira, Amazonas, Brazil, Jan–Aug. 1852, R. Spruce 2051 (lectotype),” which is one of the gatherings cited by Wernham (1917), although without citing the herbarium of deposit; therefore, Steyermark’s citation should be treated as a first-step lectotypification. The specimen Spruce 2051 at BM, barcode 000614346, is here designated the second-step lectotype of this name.

Steyermark (1967: 279–280) wrote: “*Sipanea hispida* sometimes approaches pubescent extremes of *S. pratensis* var. *dichotoma*, but the two have a different type of inflorescence; in *S. hispida* the ultimate branches of the inflorescence have the fruits much more widely separated and more strongly hispid with enlarged tuberculate bases [although they only slightly enlarged at base], whereas in *S. pratensis* var. *dichotoma* the fruits are much closer together, and much less hispid with shorter more erect and relatively fewer trichomes. Moreover, in *S. hispida* the capsules are longer, and the pubescence of the vegetative parts are denser, longer, and more villous. Where the ranges of two taxa approach one another, apparently hybrid populations are encountered. Thus,

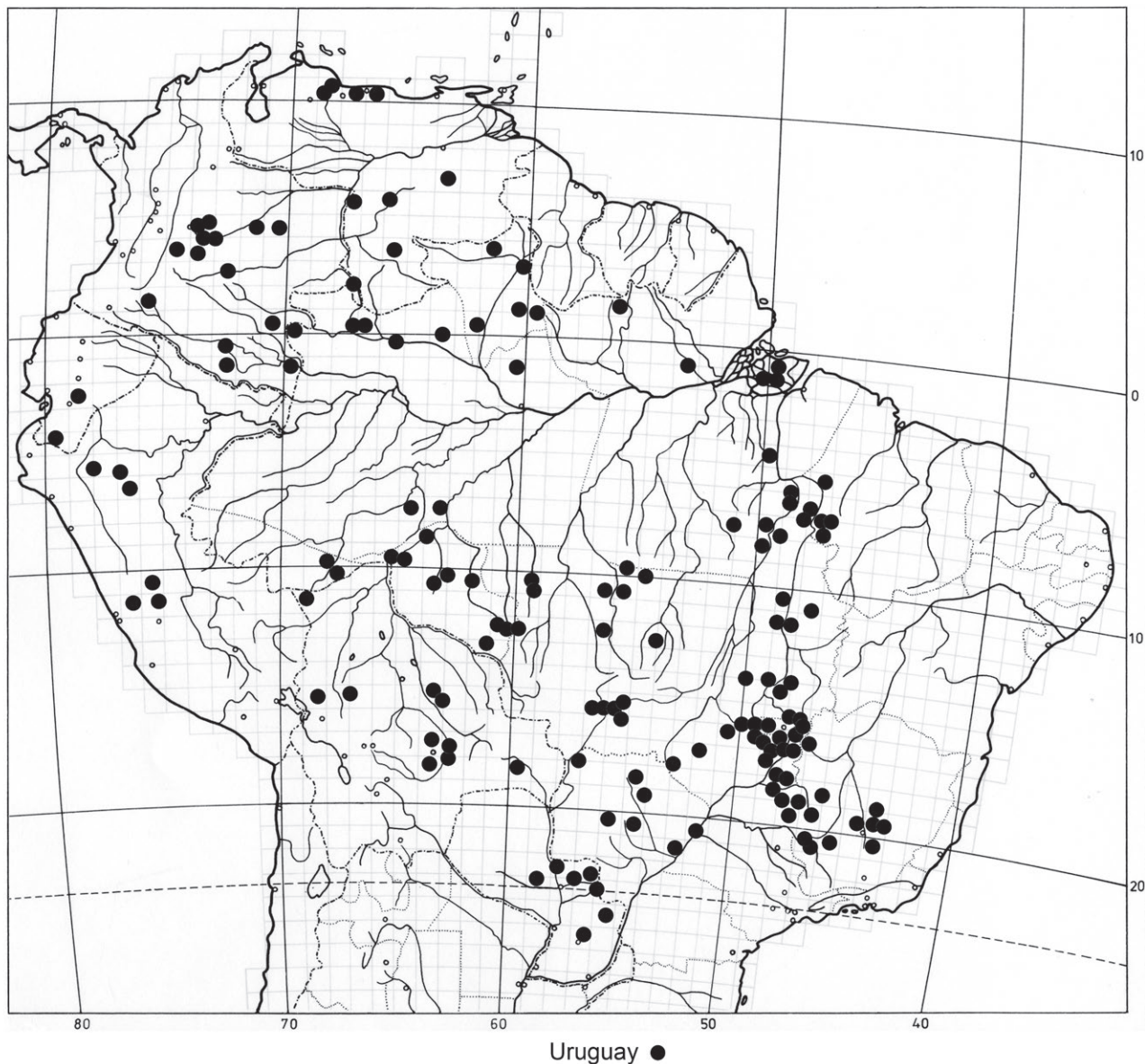


Figure 46. Distribution of *Sipanea hispida*.

same inflorescence. In order to assess the presence of heterostyly in this species, the flowers of more than 50 collections from throughout its geographic distribution were examined. In all flowers studied, the style is included and shorter than the upper tip of the anthers. Also, two forms were detected: short-styled flowers, with stamens inserted above or at the same height of the tips of the style, at 2/5 to 7/10 from the base of the corolla tube; and medium-styled flowers, with stamens inserted below the tips of the style, at 3/10 to 1/2 from the base of the corolla tube.

collected the whole year around, with flowering peak during the rainy season.

**Suggested conservation status: Least Concern (LC).** This species has been collected in numerous localities in Colombia, Venezuela, Peru, Bolivia, Brazil, and Paraguay. In Brazil it is very common in the Cerrado Biome, in savanic formations in the Amazon Basin, in the states of Acre, Amazonas, Distrito Federal, Goiás, Maranhão, Mato Grosso, Minas Gerais, Pará, Rondônia, Roraima, and Tocantins. It is also found forming large

stands in secondary vegetation and along roadsides (pers. obs. in Brazil). Considering that this species is known by numerous collections, and is also found as a ruderal species, it is Least Concern (LC), following IUCN criteria (IUCN 2012, 2019).

**Specimens examined: COLOMBIA. Amazonas:**

Corregimiento de Araracuara [ca. 0°36'S, 72°23'W], trucha al Río Yará, al NE del corregimiento, en pié de monte, 200–300 m, 18 Apr. 1986 (fl, fr), *G. Galeano et al.* 911 (COL); La Pedrera [ca. 1°19'S, 69°34'W], ca. 2 km en el camino entre La Pedrera y Taparacá, borde del camino en sitio abierto, 230 m, 11 Mar. 1990 (fl), *G. Galeano et al.* 2039 (NY); Araracuara, entre el campamento y el aeropuerto, 220 m, 3 Aug. 1977 (fl, fr), *J.M. Idrobo* 8874 (COL); Río Igara-Parana, prairie a bovines entretenue regulierment, sur sable et grès (La Chorrera [ca. 1°26'S, 72°47'W]), 19 Sep. 1973 (fl, fr), *C. Sastre* 2259 (COL, P). **Caquetá:** Mun. Valparaiso, vereda La Esmeralda, tierra firme, 1°16'20"N, 75°42'46"W, 220 m, 18 Oct. 2010 (fr), *D. Cárdenas et al.* 40542 (NY). **Cundinamarca:** Ubalá B [ca. 4°44'N, 73°32'W], Inspección de Policía San Pedro de Jagua, Vereda Soya, marge derecha Río Zaguea, s.d. (fl, fr), *J.L. Fernandez et al.* 16310 (COL); Cáqueza [ca. 4°24'N, 73°56'W], 1810 m, 23 May 1940 (fl, fr), *H. Garcia Barriga* 8465 (COL). **Guaviare:** San José del Guaviare [ca. 2°34'N, 72°38'W], sabana, 240 m, 4 Nov. 1939 (fl), *J. Cuatrecasas* 7412 (COL, US). **Guainía:** San Felipe, across river from San Carlos de Río Negro (Venezuela), on grassy Wall of fort, 1°55'N, 67°5'W, 120 m, 12 Nov. 1977 (fl, fr), *R. Liesner* 3395 (COL, MO). **Meta:** E del Río Manacacías, potrero sobrepastoreado, 5 Jun. 1963 (fl), *J. Blydenstein* 992 (COL); San Juan de Arama [ca. 3°22'N, 73°52'W], Campamento Los Micos, 350 m, 9 Aug. 1972 (fl, fr), *E. Echeverry & R. Jaramillo M.* 2261 (COL); Las Lagartijas, plateau between Río Papa-mene and Río Duda, Colombia-Urube trail, 7 km SW of Uribe, clearing on hilltop, 3°12'N, 74°29'W, 1100 m, 19 Dec. 1942 (fl, fr), *F.R. Fosberg* 19418 (P, US); Llanos Orientales, alrededores de Villavicencio [ca. 4°8'N, 73°37'W], 450 m, cerca de Peralonso, 24–28 Jul. 1946 (fl), *R. Jaramillo et al.* 289 (COL, US); Villavicencio, grassy llano, 450 m, s.d., *F.W. Pennell*, 1450 (MO, NY); chemin longeant le Río Guatiquia, 15 km en amont de Villavicencio, 4 Mar. 1971 (fl, fr), *C. Sastre* 920 (COL, P); Mun. Puerto Lopez [ca. 4°5'N, 72°57'W], Hacienda Llano Grande, laguna, 7 Mar. 1971 (fl), *C. Sastre & P. Pinto* 1007 (COL, P); Ranch Menegua, ca. 100 km S and E of Villavicencio, 15 Jul. 1945 (fl, fr), *H. Schiefer* 800 (US [2 sheets]); frente al Hato Yopare, Carimagua, 200 m, 5 Oct. 1995 (fl), *P. Torrijos O. & R. Serna I.* 102 (COL); Andes de Bogotá, Pusumuco y Villavicencio, [400] 800–1000 m, Jan. 1856 (fl, fr), *J.J. Triana*

3248 (COL, P). **Vaupés:** Mun. Mitú, Comunidad Indígena de Acaricuara, Paca, sector de sabanetas y catingas de 6 a 8 m de altura, com presencia de varillales, sobre arenas blancas, 0°42'29"N, 70°14'14"W, 200 m, 2 Jun. 2009 (fr), *D. Cárdenas et al.* 22627 (COAH, NY); Mun. Mitú, alrededores de Mitú, camino hacia el Cerro Urania, bosque de rebalse intervenido, 8 Jan. 2000 (fl, fr), *R. Cortés* 1579 (NY); Mun. Mitú, camino entre Bogotá Cachivera y Acaricuara, bosque de catinga alta sobre arena blanca, 16 Jan. 2000 (fl, fr), *R. Cortés* 1649 (NY [2 sheets]); Río Kuduyarí, Pacuativa, 380 m, 19–20 Oct. 1952 (fl), *H. García-Barriga* 14901 (COL [2 sheets]); Bajo Vaupés, Mitú y sus alrededores, 8 Mar. 1944 (fr), *G. Gutierrez & R.E. Schultes* 943 (NY), 14 Mar. 1944 (fl), 1010 (COL); Río Vaupes, a Mitu, 320 m, 7–8 Nov. 1952 (fr), *H. Humbert & A. Fernandez* 27241 (P); Río Vaupés, Mitú and vicinity, 250 m, 8 Sep. 1951 (fl, fr), *R.E. Schultes & I. Cabrera* 13957 (NY, S, US); Río Kuduyarí (tributary of Río Vaupés), middle and lower course, 230–270 m, 16 Oct. 1952 (fl, fr), *R.E. Schultes & I. Cabrera* 17864 (NY [2 sheets], US); Río Vaupés, Mitú and vicinity, 1°0'N, 70°5'W, 9 May 1953 (fl, fr), *R.E. Schultes & I. Cabrera* 19251 (NY, US); Río Vaupés, Mitú and vicinity, Sep.–Oct. 1966 (fl, fr), *R.E. Schultes* 24242 (COL). **Vichada:** Mun. El Viento [ca. 4°35'N, 71°4'W], Centro de Las Gaviotas, sabana no inundable, 170 m, 20 Jul. 1995 (fl), *F. Cortés P. & H. Dueñas G.* 322 (COL); near Saracuré, Región bocas Río Muco y San José de Ocuté [ca. 4°14'N, 70°19'W], 13 May 1945 (fl, fr), *F. di Giovanni s.n.* (COL 000410421); hacienda de Hector Pérez, Saracuré, on the Río Vichada, ca. 40 km W of San José de Ocuté, dry grassy llanos, 100 m, 18 Jan. 1944 (fl, fr), *F.J. Hermann* 10959 (US).

**VENEZUELA. Amazonas:** Alto Orinoco, La Esmeralda [3°10'N, 65°32'W], rather rare in the Savannas along the river, 14 Jul. 1951 (fl, fr), *L. Croizat* 84 (NY [2 sheets]); Dto. Atures, near Puerto Ayacucho, ca. 3 km N of town, sabana arenosa, on L side of rd towards El Burro, 5°43'N, 67°30'W, 85 m, 29 Jan. 1978 (fl, fr), *O. Huber & J. Cerda* 1480 (NY [2 sheets], VEN); Dto. Atures, faldas orientales del Cerro Yaví, Laguna de Maguari, 5°45'N, 65°48'W, 300 m, 17 Aug. 1978 (fl, fr), *O. Huber & J. Cerda* 2261 (NY, VEN). **Bolívar:** Morichal 1 km E of ranch house, 6°45'N, 63°30'W, 420 m, s.d., *J.J. Wurdack & N.G.L. Guppy* 34 (NY). **Carabobo:** El Paito, 1 Sep. 1951 (fl), *Hermano Gines* 4538 (US). **Miranda:** Path from Petare [ca. 10°28'N, 66°46'W] to La Guayrita, 900 m, 11 Dec. 1938 (fl, fr), *A.H.G. Alston* 5477 (BM); Los Teques [ca. 10°20'N, 67°2'W], in German Plantations (Parque de los Bárbaros), 1400–1500 m, 19 Oct. 1917 (fl), *H. Pittier* 7507 (NY, US, VEN). **Yaracuy:** El Amparo, 7 km N of Salom [ca. 10°11'N, 68°28'W], 1100–1200 m, 1 Dec. 1974 (fr), *J.A. Steyermark et al.* 111209 (NY, US, VEN).

**ECUADOR. Morona-Santiago:** Cantón Gualaquiza, Parroquia Bomboiza, road to Nueva Tarqui on S side of Río Cuyes, -3.441583°, -78.61631°, 850 m, 30 Jan. 2019 (fl, fr), *C. Persson et al.* 3284 (GB). **Zamora-Chinchipec:** Road Zumba – La Balsa, km 23, regularly burned pastures, 4°57'S, 79°8'W, 900 m, 25 May 2001 (fl), *J.E. Madson & C. Rosales* 8140 (AAU).

**BRAZIL. Acre:** Km 4 from Rio Branco [ca. 9°58'S, 67°48'W], on Rio Branco-Brasileia road, roadside, 16 Oct. 1980 (fl), *S.R. Lowrie et al.* 560 (INPA, NY, UB); Mun. Plácido de Castro, km 20, rod. AC-40 (Plácido de Castro-Rio Branco), beira da estrada, terra firme, 10°15'45"S, 67°36'46"W, 4 Feb. 2000 (fl), *I.S. Riveiro et al.* 327 (NY). **Amazonas:** Estrada Manaus–Caracarái, Reserva Biológica do INPA, capoeira, solo argiloso, 1978, *A. Anderson s.n.* (INPA 142512); São Gabriel da Cachoeira, 50 m N do Porto de Camanaus, terra firme, areia branca, 0°7'S, 67°4'W, 70 m, 7 Jan. 2003 (fr), *A. Antonelli* 245 (GB, R); Rio Negro, São Gabriel (Rio Uaupés), campo aberto, 30 Apr. 1948 (fl, fr), *G.A. Black* 48-2453 (IAN); Mun. Presidente Figueiredo, Balbina, Estrada de acesso ao antigo porto, vegetação aberta, degradada, 1°0'N, 59°0'W, 1 Aug. 2006 (fl), *J.G. de Carvalho-Sobrinho & K.M. Silva* 825 (INPA); Mun. Humaitá, Estrada Porto Velho–Humaitá, BR-319, km 675, campo, 7°31'S, 63°10'W, 70 m, 5 Apr. 1976 (fl, fr), *M.R. Estrela & W. Bellusci* 101-5476 (INPA); *ibid.*, 6 Apr. 1976 (fl, fr), *M.R. Estrela & W. Bellusci* 106-6476 (INPA); Jauareté [ca. 0°36'N, 69°11'W], Vaupés, Rio Negro, 22 Oct. 1945 (fr), *R.L. Frões* 21251 (IAN, NY); Rio Negro, Camanáos, 22–23 Dec. 1930 (fl, fr), *E.G. Holt & E.R. Blake* 570 (NY, RB); Mun. Humaitá, Fazenda Flávio Neri, S of BR-319, km 658, 7°31'S, 63°10'W, 27 Dec. 1979 (fl, fr), *A. Janssen & I. Gemtchujnicov* 96 (INPA, MG, RB, UB); Rio Negro, Umarituba [ca. 0°40'N, 67°15'W], 11 Sep. 1928 (fl, fr), *P. Luetzenburg* 22180 (R); Rio Negro, Comunidade Aparecida, opposite mouth of Igarapé Tuari, near abandoned portion of Perimetral Norte, open secondary vegetation along river, 0°20'N, 67°18'W, 6 Nov. 1987 (fl, fr), *P.J.M. Maas et al.* 6937 (INPA); Caatinga do Porto de Camanaus, campina alta, 19 Oct. 1978 (fl, fr), *P.I. Madison, S. Braga & H. Kennedy* PFE-447 (INPA); Rio Negro, acima de São Gabriel da Cachoeira, terra firme, capoeira, 21 Jul. 1979 (fl, fr), *L.A. Maia et al.* 722 (INPA); Pr. Rio Negro, s.d. [Nov. 1819–Jan. 1820], *C.F.P. Martius s.n.* (*Herb. Reg. Monac. Duplum* 186) (FI-Webb); Estrada Manaus–Porto Velho, BR-319, km 530, 21 Apr. 1976 (fl, fr), *O.P. Monteiro & J. Ramos* 835 (INPA); Lábrea [ca. 7°15'S, 64°47'W], na estrada do aeroporto, capoeira baixa de terra firme, 19 Jun. 1976 (fl, fr), *C.D.A. Mota, s.n.* (INPA 60348); Rio Purus, km 1–4 rd. Lábrea-Humaitá, 5 Nov. 1968 (fr), *G.T. Prance et al.* 8187 (INPA,

MG, NY, S, US); Rio Negro, São Felipe, km 2 da Perimetral Norte, mata de caatinga, 21 May 1975 (fl, fr), *N.T. Silva* 3862 (IAN), 3863 (IAN); Mun. Humaitá, Estrada Humaitá-Jacarecanga, km 150, 60 km S, campo natural, solo arenoso, 21 Jun. 1982 (fl, fr), *L.O.A. Teixeira et al.* 1256 (INPA, MG, NY, RB); Uaupés, terreno aberto, 26 Dec. 1964 (fr), *S. Vogel* 332 (INPA). **Distrito Federal:** Planaltina, CPAC, rod. BR-020, próximo ao Banco de Proteínas, 47°42'W, 1175–1200 m, 17 Apr. 1985 (fl), *S.P. Almeida* 1001 (IBGE); Parque Nacional de Brasília [ca. 15°38'S, 48°1'W], 4 Feb. 1992 (fl), *M.A.G. Barros et al.* 2234 (IBGE, UB), 2278 (IBGE, UB); Centro Olímpico da UnB, 7 Jun. 1985 (fl–fr), *L. Branco s.n.* (UB); Bacia do Rio Descoberto, caminho para a cidade Eclética, 19 May 1999 (fl, fr), *K. Calago & S. Silva* 144 (CEN); Brasília, 15 Jun. 1979 (fr), *F. Chagas e Silva* 188 (IBGE); Brasília, próximo do MBTC, 6 Jul. 1985 (fl), *C.O. Córdova s.n.* (UB); Barragem do Paranoá, 15°45'S, 47°47'W, 31 May 1983 (fl–fr), *C. Cunha* 14 (UB); Brazlandia [“Brasilândia”], prox. Brasília, 20 Dec. 1960 (fl, fr), *R. Delforge s.n.* (RB108700) (RB); Parque Nacional de Brasília, campo limpo, 14 Dec. 2006 (fl), *E.B.A. Dias et al.* 264 (CEN), 326 (CEN), 342 (CEN); Chacara Tororó, 26 Jun. 1985 (fl), *A.M. Dos Santos, s.n.* (UB); Brasília, area do Zoobotânico, 17 Jan. 1967 (fl, fr), *A.P. Duarte* 10189 (RB, US); Fazenda Santa Cecília, Núcleo Rural Rajadinha II, mata de galeria inundável, solo argiloso, 15°45'59"S, 47°38'12"W, 992 m, 22 Nov. 2012 (fl), *M.H. Fernandes & B.R. Teixeira* 275 (CEN); Incra, Nucleo Rural, 9 Nov. 1971 (fl), *M.B. Ferreira* 587 (HEPH); Convenio Florestal de Brasília, 29 May 1960 (fl, fr), [without initials] *Gomes* 773 (RB); Bacia do Rio São Bartolomeu, 20 Dec. 1979 (fl), *E.P. Heringer et al.* 2963 (IBGE, MG, NY, UEC), 9 Jan. 1980 (fl–fr), 3090 (IBGE, MG, UB), 17 Mar. 1980 (fr), 3826 (IBGE, MG, NY, US); foz do Córrego Torto com o lago, 17 Jul. 1979 (fl–fr), *E.P. Heringer* 6941 (IBGE); Rio São Bartolomeu, 25 Oct. 1965 (fl), *E.P. Heringer* 10765 (IAN, NY [2 sheets], RB, UB); Córrego Papuda, 5 Jun. 1979 (fl), *A.E. Heringer Salles* 98 (IBGE, NY); E of Lagôa Paranoá, 975 m, 9 Dec. 1965 (fl), *H.S. Irwin et al.* 11144 (IAN, NY, UB, US); Córrego Landim, ca. 25 km N of Brasília, 850 m, 27 Jan. 1966 (fl), *H.S. Irwin et al.* 12066 (IAN, NY, S, UB); Cachoeira Piripiripau, ca. 15 km S of Planaltina, 20 Feb. 1970 (fl, fr), *H.S. Irwin et al.* 26440 (NY [2 sheets], RB); 1 km S of Planaltina, ca. 15°38'S, 47°40'W, ca. 900 m, 26 Jan. 1972 (fl), *J.H. Kirkbride* 1697 (C, NY, P, R, UB, US); pastagem perto do Lago Paraim, 15°7'S, 47°0'W, 800 m, 24 May 1980 (fl–fr), *J.H. Kirkbride* 3485 (UB); perto da DF-18, ca. 16 km E da BR-251, 16°1'S, 47°26'W, 15 Oct. 1980 (fl), *J.H. Kirkbride* 3655 (NY, RB, UB[2 sheets]); Córrego bananal, 15°35'S, 47°55'W, 900 m, 19 Apr. 1983 (fl–fr), *J.H. Kirkbride* 5229

- (INPA, NY, RB, UB, US), *D.A.M. Netto 14* (NY, UB), *M.L.M. Thomé s.n.* (UB); Parque Nacional de Brasília, entorno da antiga pista de ultra leve, Cerrado ralo., 15°44'53"S, 47°55'34"W, 4 Jan. 2015 (fl), *C.R. Martins 1403* (CEN); Parque Nacional de Brasília, margem da Lagoa da Meditação, solo compactado, 15°44'1"S, 47°55'39"W, 30 Nov. 2016 (fl), *C.R. Martins 2318* (CEN); Córrego Santa Rita, divisa com estado de Goiás, 19 Mar. 1992 (fl), *E. Melo & F. França 619* (UB); Brasília, Fundos da QI 29 Lago Sul, entrada pelo condomínio Morada Sul, 17 Mar. 1992 (fl-fr), *A.E. Morbeck & D. Alvarenga 51* (IBGE); Córrego Bananal, a esquerda da pastagem e Estrada DF-02, 15°25'S, 47°55'W, 19 Apr. 1983 (fr), *Novato et al. 14* (NY); Centro Olímpico da UnB, entre a quadra de futebol e o lago, 18 Nov. 1981 (fl), *M.A.F. Oliveira s.n.* (UB); Brasília, Rio São Bartolomeu, 28 Mar. 1963 (fl, fr), *E. Pereira 7420* (RB); Brasília, Parque Florestal, 12 Apr. 1963 (fl-fr), *J.M. Pires 9007* (UB); Fundação Zoobotânica, 30 Apr. 1963 (fl-fr), *J.M. Pires et al. 9514* (RB, UB); 5 km N de Brazlândia, 24 Apr. 1982 (st), *J.P. Pires 235* (CEN); Reserva Biológica de Águas Emendadas, campo úmido próximo ao Córrego Fumal, 10 Dec. 1982 (fl), *A.E. Ramos 168* (HEPH, INPA, UFMT); Lagoa Bonita, ca. 30 km NE de Brasília, 21 Jan. 1983 (fl), *A.E. Ramos 178* (CEN, HEPH, INPA, UFMT); Parque Nacional de Brasília, 15°53'S, 47°56'W, 28 Nov. 1990 (fl), *P.C.M. Ramos 340* (UB); Samambaia, 15°52'S, 48°3'W, 1150 m, 22 Apr. 1996 (fr), *J.M. Rezende 405* (CEN); Brasília, Parque Nacional, 13 Apr. 1963 (fl, fr), *J. Sacco 2014* (R [3 sheets]); DF-100 sentido BsB - Formosa, Fazenda Só Frango, ao lado da Fazenda Itapeti, 15°56'S, 47°22'W, 27 Nov. 2002 (fl), *A.A. Santos, J.B. Pereira & J.M. Rezende 1708* (CEN); Brasília, Parque Nacional, 13 Apr. 1963 (fr), *E. Santos & J. Secco 1781* (NY); Parque Nacional de Brasília, Trilha Cristal Água, Cerrado sensu stricto perturbado, 18 Jan. 2007 (fl, fr), *J.R. Santos, C.A.F. Neiva & L.M.G. Nogueira 969* (CEN); Centro Olímpico da UnB, May 1983 (fl-fr), *A.F. Neto 5* (UB), 1984, *M.N. Sato 23* (UB); Brasília, 15 Jul. 1979 (fr), *F.C. Silva 188* (NY, UB); Reserva Ecológica do IBGE, 15°57'S, 47°52'W, 25 Apr. 1988 (fr), *M.A. da Silva et al. 581* (IBGE, RB, US); Reserva Ecológica do IBGE/ Fazenda Água Limpa, UnB, cerca ao S da reserva, 15°57'S, 47°53'W, 8 Jan. 1990 (fl), *M.A. da Silva & E.C. Lopes 924* (IBGE); Mun. Guarará, Condom. Lúcio Costa, Reserva Ecológica do Guarará, 15°48'26"S, 47°59'3"W, 1120 m, 22 Nov. 2001 (fl), *M.A. da Silva 6049* (IBGE, UFG); Brazlândia, Fazenda Velho Barreiro, 24 Jun. 1985 (fl-fr), *H.B. Souza s.n.* (UB); Centro Olímpico da UnB, beira do Lago Norte, 15 Jun. 1983 (fl-fr), *J.L. Sousa 15* (UB); Reserva Ecológica do IBGE, 15 Dec. 2015 (fl, fr), *V.C. Souza, T.B. Flores, G.D. colletta, R.L.G. Coelho & M.A.S.S.C. Souza 39639* (RB, SP); Parque Mansões de Recreio Estrela Dalva 7, 40 km em linha reta ao S do centro de Brasília (8 km em linha reta ao N de Luziânia), 7 Dec. 1987 (fl), *Taxonomy Class of the UnB 1236* (UB); Brasília, margem esquerda do Lago Paranoá, capoeira, campo sujo, latossolo vermelho, 20 Jun. 2001 (fl, fr), *Taxonomy Class of the UnB s.n.* (INPA); Universidade de Brasília, Campus Universitário, centro Olímpico, 13 Jun. 1984 (fl, fr), *S.C. Ulhoa 22* (NY, UB), 1984 (fl, fr), *M.N. Sato 23* (NY); Fazenda Sucupira, após a área de estudo do SPSB, campo sujo, 2 Mar. 2007 (fl, fr), *G.D. Vale, J.B. Pereira & C.G. Fontes 352* (CEN, RB); Planaltina, 3 km W da DF-130, próximo ao Córrego Saco dos Pilões, afluente do Rio São Bartolomeu, 15°44'S, 47°41'W, 1100 m, 20 May 1992 (fr), *B.M.T. Walter et al. 1425* (CEN, NY, RB).
- Goiás:** Mun. Goiás, Serra do Brumado, cerrado, 30 Mar. 1996 (fl, fr), *M.B. Alcântara et al. s.n.* (NY, UFG 18972); Serra dos Pireneus, ca. 15 km (straight line) N of Corumbá de Goiás, 1230 m, 16 Mar. 1973 (fl), *W. Anderson 10463* (MO, NY, UB, US); Goiania, Dec. 1936 (fl, fr), *A.C. Brade 15462* (RB); prope urbem Goyaz [now town of Goiás, also known as "Goiás Velho", 15°56'S, 50°8'W], s.d. (fl, fr), *W.J. Burchell 6497* (BR); Mun. Mineiros, Parque Nacional das Emas [ca. 18°S, 53°W], próx. à ponte E.J. Amaral, 15 Feb. 1995 (fl, fr), *I.B. Cassimiro 29* (NY, UFG); Mun. Luziânia, Hidrelétrica de Corumbá III, area de influencia, 16°40'35"S, 47°59'25"W, 868 m, campo limpo úmido, 11 Dec. 2007 (fl), *C.H.G. Cezare et al. 574* (UB); Mun. Caldas Novas [ca. 17°44'S, 48°37'W], 3 km da Alternativa 15, 580 m, 27 Apr. 1993 (fl-fr), *S.P. Cordovil et al. 286* (CEN, NY); Mun. Cocalzinho, BR-414, direção para Niquelândia, 100 m antes do trevo para Brasília, floresta densa, 1180 m, 15°45'30"S, 48°45'14"W, 16 Dec. 2004 (fl), *P.G. Delprete & L.F. da Silva 9171* (NY, UB, UFG); Mun. Cocalzinho, Parque Estadual dos Pireneus, formação rupestre desde a base até o topo do Morro Cabeludinho, 15°48'40"S, 48°48'54"W, 1280–1320 m, 10 Dec. 2005 (fl, fr), *P.G. Delprete et al. 9395* (CAY, NY, RB, SPF, UB, UFG); Mun. Pirenópolis, Serra dos Pireneus, margem da estrada sentido Vereda do Cristal, 15°49'22"S, 48°53'20"W, 1040 m, 18 Mar. 2006 (fl), *P.G. Delprete et al. 9545* (CAY, HTO, NY, RB, UB, UFG); Mun. Cocalzinho, Parque Estadual dos Pireneus, ca. 700 m depois do portal do parque do lado de Cocalzinho, campo limpo estacionalmente encharcado, 15°47'56"S, 48°49'7"W, 1170–1180 m, 15 May 2006 (fl), *P.G. Delprete & L.B. Bosquetti 9780* (BR, RB, UFG); Mun. Pirenópolis, Serra dos Pireneus, estrada para Vereda dos Cristais, entre o mata-burro e a casa de Fernando Maduenho, campo limpo, 15°49'19"S, 48°53'22"W, 950–1000 m, 16 Mar. 2007 (fl), *P.G. Delprete et al. 10022* (MBM, UB, UFG); Mun. Pirenópolis, Serra

- dos Pireneus, em direção do Portal São Lázaro, entre a Cachoeira do Coqueiro e a Cachoeira da Santa, área de nascentes, com solo constantemente encharcado, 15°47'29"S, 48°54'1"W, 1020 m, 27 May 2007 (fl), P.G. Delprete & V.L. Gomes-Klein 10202 (UFG); Mun. Pirenópolis, Serra dos Pireneus, estrada para a subida da serra desde Pirenópolis, primeira estrada a direita em direção da Cachoeira da Andorinha, bosque estacional semicaducifolio na beira do riacho, 15°50'23"S, 48°55'36"W, 800 m, 19 Aug. 2007 (fl), P.G. Delprete et al. 10301 (UFG); Mun. Pirenópolis, Serra dos Pireneus, estrada para a subida da serra desde Pirenópolis, primeira estrada a direita em direção da Cachoeira da Andorinha, vegetação na beira do riacho, 15°50'23"S, 48°55'36"W, 800 m, 21 Dec. 2007 (fl), P.G. Delprete & Estudantes da UFG 10513 (CAY, NY, RB, UB, UFG); Mun. Caldas Novas, estr. para Alternativa 4, ca. 5,7 km da estr. UHE-Corumbá-Caldas Novas, 17°54'S, 48°3'W, 9 Feb. 1993 (fl-fr), T.A.B. Dias et al. 289 (CEN); Mun. Caldas Novas, estr. para UHE-Corumbá-Caldas Novas, ca. 13 km, 17°58'S, 48°35'W, 12 Feb. 1993 (fl), T.A.B. Dias et al. 390 (CEN); estr. Brasília-Unai, 17 Oct. 1965 (fl, fr), A.P. Duarte 9350A (RB [2 sheets], US); Mun. Mossâmedes, Fazenda do Jander (Estância Quinta da Serra), Serra Dourada, cerrado típico, 16°2'S, 50°3'W, 4 Feb. 2009 (fl, fr), J.E.Q. Faria et al. 409 (CEN); Mun. Mineiros, Parque Nacional das Emas, 22 Dec. 1991 (fl), H.D. Ferreira 3021 (UFG); Mun. Pirenópolis, brejo próx. do córrego, 8 Jan. 1999 (fl), H.D. Ferreira 3671 (UFG), 3672 (UFG); Mun. Luziânia, Sítio Novo, 24 Nov. 1971 (fl-fr), M.B. Ferreira 939 (HEPH); Mun. Corumbá de Goiás, ca. 4 km da cidade, estrada para Aparecida, 1060 m, 15°54'S, 48°45'W, 13 Mar. 2002 (fl, fr), M.L. Fonseca et al. 3182 (CEN, IBGE, RB); "Goyaz," Nov. 1839 (fl), G. Gardner 3224 (BM, FI-Webb); without locality, 1841 (fl), 3224 (K); Planalto de Goyaz, Retiro do Bananal, 16 Feb. 1898 (fl, fr), A. Glaziou 21519 (BR, MPU, P [3 sheets], S); Mun. Mossâmedes, Serra Dourada, rd. Goiânia-Goiás, 17 Mar. 1994 (fl, fr), V.L. Gomes-Klein et al. [additional collectors not cited] 2210 (NY, UFG); Mun. Jataí, Bom Sucesso, 17 Nov. 1973 (fl, fr), G. Hatschbach & C. Koczicki 33340 (C, MBM, MO); Mun. Uruaçu [ca. 14°S, 49°W], rod. para Niquelândia, Fazenda Guaporé, 550 m, 19 Jan. 1992 (fl, fr), G. Hatschbach et al. 56231 (C, MBM, MO); Mun. Catalão, rod. BR-050, Córrego Capão d'Antas [ca. 18°10'S, 47°56'W], 6 Feb. 1994 (fl), G. Hatschbach et al. 59871 (FLOR, MBM); Samambaia, Rio Corumbá, 8 Jan. 1967 (fl-fr), E.P. Heringer 11263 (MG, RB, UB); Mun. Caldas Novas, 12 km W of Caldas Novas, on rd Caldas Novas-Morrinhos, on side rd leading to Hotel Pousada Rio Quente, 17°44'S, 48°45'W, 23 Dec. 1974 (fl-fr), E.P. Heringer & G. Eiten 14200 (NY, UB, US); Serra de Caldas Novas, Termas do Rio Quente, 4 Jan. 1977 (fl), E.P. Heringer 16714 (IBGE, UB); Mun. Corumbá de Goiás, 26 Mar. 1978 (fl), E.P. Heringer, A.E.H. Salles & F.C. Silva 17017 (IBGE, UB, UEC p.p. [UEC 118192]); Luziânia, 4 Feb. 1983 (fl), E.P. Heringer 18435 (IBGE, RB, US); 23 km E of Caiapônia, on rd to Montevidéu, 4 Feb. 1959 (fl, fr), H.S. Irwin 2576 (NY, US); Serra do Caiapó, ca. 48 km S of Caiapônia, on rd to Jataí, 800–1000 m, 17°12'S, 51°47'W, 23 Oct. 1964 (fl), H.S. Irwin & T.R. Soderstrom 7264 (NY); Serra dos Pireneus, ca. 20 km S of Corumbá de Goiás, ca. 20 km of Corumbá de Goiás, 1000 m, 3 Dec. 1965 (fl), H.S. Irwin et al. 11011 (IAN, NY, UB); Serra dos Pireneus, 30 km N of Corumbá de Goiás, on rd to Niquelândia, in Valley of Rio Corumbá, ca. 1150 m, 18 Jan. 1968 (fl), H.S. Irwin et al. 18816 (IAN, NY, UB); Serra Dourada, lower slopes, pasture, ca. 30 km SE of Goiás Velho, 14°S, 50°W, 650 m, 22 Jan. 1966 (fl, fr), H.S. Irwin, R. Souza & R. Reis dos Santos 11978 (NY); ca. 15 km SE of Guará, on rd to Tupirama, ca. 500 m, 21 Mar. 1968 (fl), H.S. Irwin et al. 21605 (IAN, NY, RB, UB, US), 21612 (IAN, NY, RB, UB, US); Contraforte Central, ca. 24 km NE of Catalão, 875 m, 22 Jan. 1970 (fl), H.S. Irwin 25101 (UB); ca. 15 km S of Niquelândia [ca. 14°28'S, 48°27'W], ca. 750 m, 22 Jan. 1972 (young fr), H.S. Irwin, W.R. Anderson et al. 34756 (NY, UB, US); ca. 17 km S of Niquelândia, ca. 750 m, 23 Jan. 1972 (young fr), H.S. Irwin et al. 34901 (NY, UB, US); Abadiana, Fazenda S. Mateus, 11 Apr. 1968 (fl), A.M. Lima 69 (RB, UB); Mun. Jataí, localidade Queixada, 10 Dec. 1948 (fl), A. Macedo 1466 (NY, S, US); 20 km from Jataí on rd to Goiânia, 1 Oct. 1963 (fl), B. Maguire et al. 56988 (MG, NY, UB); Mun. Luziânia, Santo Antônio do Descoberto, 27 Mar. 1980 (fl), R.C. Mendonça 101 (IBGE); Mun. Leopoldo de Bulhões, 16°34'S, 48°43'W, 20 Mar. 1989 (fl), R.C. Mendonça 1320 (IBGE, UB, US); Mun. Pirenópolis, Parque Estadual dos Pireneus, 28 Feb. 2004 (fl, fr), S.C. Miranda 1003 (UFG); Mun. Aparecida de Goiânia, Chacara Jatobá, 26 Dec. 2002 (fl), J.F.B. Pastore 203 (CEN); Mun. Corumbá de Goiás, Serra de Salto Corumbá, 15°50'59"S, 48°45'41"W, 988 m, 15 Feb. 2016 (fl, fr), J.R.L. Paz 49 (UB); km 18 N of Aragarças, ca. 15°51'S, 52°15'W, 14 Jan. 1968 (fl), D. Philcox & A. Ferreira 4037 (NY, P, RB, UB); Villa Boa [now town of Goiás], s.d. (fl), J.E. Pohl s.n. (BR 824753) (BR); "Megaponte" [sic! Meiaponte, now town of Pirenópolis], s.d., J.E. Pohl 1130 (878d) (NY, W); Mun. Padre Bernardo, Fazenda Lagoa Santa, 18 Nov. 1993 (fl, fr), C.E.B. Proença 1059 (UB); Paraúna, caminho para ponte de pedra, Ponto 7, 17°10'22"S, 50°50'4"W, 673 m, 17 Jan. 2013 (fr), C.E.B. Proença et al. 4327 (UB, UC, UEG); Mun. Luziânia, Canteiro de obras do AHE Corumbá IV, margem direita do Rio Corumbá, 860 m,

- 16°20'S, 48°11'W, 9 Dec. 2002 (fl, fr), *J.M. Rezend et al.* 691 (CEN); rd. Goiânia-Inhumas, km 14, transição cerrado-cerradão, 17 Apr. 1968 (fl), *J.A. Rizzo & A.M. Barbosa* 468 (UFG); Mun. Goiânia, rod. para Guapó, etr. BR-19, 30 Dec. 1968 (fl), *J.A. Rizzo & A.M. Barbosa* 3229 (NY, UB); Mun. Goiânia, saída Sul, 31 Dec. 1968 (fl-fr), *J.A. Rizzo & A.M. Barbosa* 3268 (NY, UFG, UB); mun. desconhecido, esquerda do Ribeirão Dourado, próx. à cabeceira, 29 Jan. 1969 (fl, fr), *J.A. Rizzo & A.M. Barbosa* 3419 (UFG); Mun. Goiânia, rod. GO-07 (Goiânia-Guapó), 31 Jan. 1969 (fl-fr), *J.A. Rizzo & A.M. Barbosa* 3617 (UB); Mun. Morrinhos, rod. para Caldas Novas, Córrego Samambaia, 28 Mar. 1970 (fl,fr), *J.A. Rizzo & A.M. Barbosa* 4918-A (UFG), 25 Apr. 1970 (fl,fr), 5081 (UFG), 25 Apr. 1970 (fl,fr), 5102 (UFG), 28 Nov. 1970 (fl), 5759-A (UFG), 6 Mar. 1971 (fl, fr), 6023-A (NY, UFG); Mun. Goiandira, Fazenda do Chapéu, 18°0'S, 48°8'W, 22 Jan. 2005 (fl), *J.A. Rizzo et al.* 12860 (UFG), 26 Feb. 2005 (fr), 12983 (UFG); Mun. Pirenópolis, Terra Nostra, 6 May 2003 (fl), *A.S. Rodrigues, J.R. Pará, M.M. Santiago & S.M. Delgado* 115 (CEN); "Province de Goyaz", without locality, s.d. [1816-1821], *A. Saint-Hilaire Catal. CI No. 729* (P [2 sheets]); Mun. Niquelândia, 1.5 km após a ponte sobre o Rio Tocantinzinho, sentido Colinas do Sul-Niquelândia, 17 Dec. 1999 (fr), *A.A. Santos et al.* 612 (CEN); Mun. Chapa dos Viadinhos, Rio dos Brancos, prox. Estrada entre São Gabriel de Goiás e São João da Aliança, campo rupestre, 18 Mar. 1976 (fl, fr), *J. Semir* 4261 (NY); Mun. Caldas Nova, alternativa 4 regua de leitura da vazão da hidrometria, 660 m, 17°56'S, 48°33'W, 27 Feb. 1996 (fl, fr), *G.P. Silva et al.* 3379 (CEN); Mun. Cristalina, margem do Rio Arrependido, a NW da área de empréstimo, 850 m, 16°13'S, 47°20'W, 6 Mar. 2002 (fr), *G.P. Silva et al.* 6038 (CEN); Mun. Santo Antônio do Descoberto, margem direita do Rio Descoberto, próx a Barra com o Córrego Engenho das Lages, 900 m, 16°5'S, 48°16'W, 17 Feb. 2003 (fl, fr), *G.P. Silva et al.* 7100 (CEN); Mun. Niquelândia, Niquelândia, Avenida Bernardo Sayao, lote 51, 14°4'S, 48°4'W, 600 m, 6 Apr. 1988 (fl-fr), *L.A. Skorupa & J.N. Silveira* 341 (CEN); nos cerrados abertos perto de Goyaz [now town of Goiás], Jan. 1893 (fl, fr), *Ule, E.* 430 (P); Mun. Niquelândia, estrada de terra para Barro Alto, 7 km após a entrada, 14°34'S, 48°41'W, 30 Nov. 1999 (fl), *S.M. Verboonen et al.* 135 (CEN). **Maranhão:** Mun. Imperatriz, behind Rodobrás station on S side of city of Imperatriz, opem meadow with thick grass and herbs 1-1.5 m tall, 5°33'S, 47°28'W, 6 Jan. 1970 (fl, fr), *G. Eiten & L.T. Eiten* 10207 (US); Mun. São Pedro dos Crentes, margem esquerdo do Ribeirão da Mata, Estrada Estreito-São Pedro dos Crentes, km 75, mata de galeria, solo argiloso, 6°54'17"S, 46°55'43"W, 280 m, 9 Jan. 2008 (fl, fr), *G.P. Silva & G.A. Moreira* 12469 (CEN); Mun. Carolina, Estrada Carolina-Barra do Ouro, km 4, margem esquerda do Rio Lages, mata ciliar, solo arenoso, 7°22'33"S, 47°27'57"W, 150 m, 18 Jan. 2008 (fl, fr), *G.P. Silva & G.A. Moreira* 12760 (CEN); Mun. Carolina, Parque Nacional Chapada das Mesas, acesso no km 596 da BR-230, 19 km E em Estrada vicinal, Ribeirão Cancela, solo arenoso, 7°6'53"S, 47°17'13"W, 192 m, 12 Apr. 2016 (fl, fr), *M.F. Simon et al.* 2929 (CEN). **Mato Grosso:** Mun. Aripuanã, margem MT-420, 5 km da cidade, 10°12'29"S, 59°24'26"W, floresta ombrofila alterada, 3 Jul. 1997 (fr), *G.F. Árbocz et al.* 4056 (UFMT); estrada Ranchão da Lagoa Engenho Velho, 15°47'11"S, 56°4'17"W, 140 m, 24 Feb. 1977 (fr), *S. Assunção & A. Duarte* s.n. (BR 824589) (BR); Cuiabá, margem esquerda do Ribeirão dos Barbados, muito frequente no Cerrado, solo argilo-arenoso, 5 Mar. 1977 (fl, fr), *S. Assunção & A. Duarte* 652 (UFMT), 653 (INPA); Chapada dos Guimarães [ca. 15°27'S, 55°45'W], Colégio Evangélico de Burití, margem do Rio Monjolinho, 6 May 1983 (fl, fr), *J. Barcia et al.* 1289 (R [2 sheets], US), 1294 (R [2 sheets]); Itauba, Resgate de Flora da UHE Colider, Lot G de supressão, 21 L 0681275, 8779614, 270 m, Floresta do Planalto dos Parecís, região ecotono entre floresta amazonica e cerrado, 30 Jan. 2015 (fl, fr), *A.Z. Bronholi et al.* 11-240 (RB); Chapada dos Guimarães, São Vicente, Cachoeirinha, 22 Mar. 1983 (fl, fr), *L. Carreira et al.* 613 (MG, NY); Mun. Poconé, Estrada nova para Boqueirão, Cerrado, 3 Apr. 1982 (fl, fr), *C.N. da Cunha & A.L. Prado* 473 (UFMT); Chapada dos Guimarães, proximo à Cachoeira da Noiva, 1 Mar. 1983 (fl, fr), *C.N. da Cunha et al.* 748 (MG, UFMT); Alto Paraguai, Região Sul, Estrada Cuiabá-Barra do Bugres, km 47, Fazenda São Pedro, caminho para subida da serra do Limboso, 2 Apr. 1983 (fl), *C.N. da Cunha et al.* 886 (MG, UFMT); rd. from Juruena to Aripuanã, 94 km NW of Juruena, 26 May 1998 (fl), *Dubs, B.* 2451 (K, S, UFMT, US); Rio Branco, Fazenda Rio Vermelho, próximo à Vila Boa União, 28 Nov. 1984 (fr), *M. Emmerich et al.* 5530 (IAN, R [3 sheets], US); Itaúba, Resgate de Flora de UHE Colider, Floresta do Planalto do Parecís, região de ecotono entre floresta amazonica e cerrado, 21 L 0672676, 8783487, 383 m, 9 May 2017 (fl, fr), *M.E. Engels et al.* 5255 (RB); Chapada dos Guimaraes, arredores da cidade, cerrado, solo argilo-arenoso, 15°17'25"N, 55°48'15"W, 793 m, 10 Feb. 1978 (fl, fr), *F. Ehrendorfer* 2405 (UFMT); Mun. Batagunçu, Porto XV, 14 Feb. 1970 (fl, fr), *G. Hatschbach* 23537 (C, INPA, NY); Mun. Terenos, Cachoeirão, Cerrado junto a córrego, 13 Aug. 1970 (fl, fr), *G. Hatschbach* 24610 (NY); Mun. Rio Verde, Serra da Pimenteira, 28 Aug. 1973 (fl, fr), *G. Hatschbach* 32445 (C, US), 8 Feb. 1975 (fl, fr), 35962 (C, NY); Mun. Poconé, Rod. BR-070, km 584, 4 May 1995 (fl, fr), *G. Hatschbach*

- et al.* 62218 (MBM, US); Cuiabá, Cox. da Ponte, campos húmidos, May 1911 (fl, fr), *F.C. Hoene 4800* (R); Serra do Roncador, wet campo and gallery margin, ca. 60 km N of Xavantina, 550 m, 25 May 1966 (fl), *H.S. Irwin et al. 15982* (NY); Campina, Serra do Amolar, 7 May 2003 (fl, fr), *L. Junior et al. 333* (UFMT); 11 km S de Ponta Porá, 21 Feb. 1968 (fl, fr), *A. Krapovickas et al. 14115* (C, P); Santa Cruz, Rio Jamary, Dec. 1918 (fl, fr), *J.G. Kuhlmann 2364* (R [2 sheets], RB); Rio Garças, barranco pedregoso, 6 May 1958 (fl, fr), *A. Lima 58-3133* (RB [2 sheets]); Capão Secco, prope S. Anna da Chapada [now Chapada dos Guimarães], in nemoribus vel uliginosis, 14 Jan. 1894 (fl), *C.A.M. Lindman A2731* (S [2 sheets]); Mun. Varzea Grande, lot. 13 de Setembro, 3 Feb. 1994 (fl, fr), *M. Macedo & R. Godinho s.n. (UFMG 3596)* (INPA); Cuyabá [now Cuiabá], 27 Dec. 1893 (fl), *G.A. Malme s.n. (S)*, 29 May 1894 (fl, fr), *G.A. Malme s.n. (S [2 sheets])*; Mun. Rosário Oeste, Sesc Serra Azul, antiga Fazenda Santo Antonio, matas da trilha a Cachoeira da Serra Azul, 14°29'44"S, 55°42'20"W, 343 m, 26 May 2015 (fl, fr), *G. Martinelli et al. 18506* (CEN, RB); Xavantina, marsh, 1 km from Olaria, 4 km from Xavantina, 14°38'S, 52°14'W, 5 Mar. 1968 (fl), *D. Philcox & A. Ferreira 4476* (NY); Mt. Santo Antonio de Laverger, mata alagada, 25 Mar. 1982 (fl, fr), *A.L. Prado & H. Freitas Leitão Filho 329* (UFMT); Cuyabá [now Cuiabá], Jan. 1827 (fl, fr), *L. Riedel 764 (Herb. Hort. Petropol. 137)* (BR); "Santa Anna da Chapada" [Now Chapada dos Guimarães], 28 Jun. 1902 (fr), *A. Robert 364* (BM 000614334, paratype of *S. glabrata*), 364b (K); Poconé, Cotia [ca. 15°58'S, 56°28'W], entre Livramento e Poconé, km 39, em frente à Fazenda Assombrada (de seu Gigi), cerrado aberto, 19 Oct. 1983 (fl), *N. Saddi, C.T. Rizzini & [initials unknown] Mattos Filho 3383* (RB); Mun. Chapada dos Guimarães, rodovia entre Cuiabá e Chapada, 21 Nov. 1982 (fl), *J.U. Santos & Rosário, C.S. 420* (HAMAB, IAN, INPA, MG, UFMT); Salobre, Jan.–Feb. 1940 (fl), *M. Santos s.n. (R 150197)*; Faz. Mandioré, Brasil/Bolivia, Serra do Amolar, 2 Apr. 2003 (fl, fr), *M.C.V. Santos et al. 288* (UFMT); Colíder, Resgate de Flora da UHE Colíder, Lote B de Supressão, [ca. 10°59'S, 55°46'W], 9 Dec. 2014 (fl), *S. Sardelli et al. 237* (RB); Colíder, Resgate de Flora da UHE Colíder, lote B de supressão, [ca. 10°59'S, 55°46'W], 259 m, 19 Dec. 2014 (fl), *L.F. Sardelli et al. 265* (RB); Mun. Rio Branco, Fazenda Rio Vermelho, prox. à vila Boa União, 28 Nov. 1984 (fl, fr), *J.D. Silva & M. Emmerich 1002* (CEN); Mun. Luciara, 8–16 km N de Luciara, Estrada em direção da fazenda Três Pontas do Araguaia, 140 m, savanna parquet, beira da estrada, 19 Mar. 1997 (fr), *V.S. Souza et al. 14628* (UFMT); Mun. Alta Floresta, Fazenda Pontal, ca. 90 km SSW (em linha reta) de Alta Floresta, transição savanna florestada-floresta onbrófila aberta, 10°33'19"S, 56°15'54"W, 19 Apr. 1997 (fr), *V.S. Souza et al. 15109* (UFMT); Mun. Alta Floresta, Fazenda Brasil, ca. 80 km SSW (em linha reta) de Alta Floresta, 10°32'S, 56°20'W, 21 Apr. 1997 (fr), *V.S. Souza et al. 15225* (UFMT); Mun. Matupá, Sítio Amutum, ca. 50 km NE de Amutá, 9°49'S, 54°40'W, contato floresta estacional-floresta ombrófila, 26 Apr. 1997 (fr), *V.S. Souza et al. 15742* (UFMT); Mun. Tapurah, Fazenda São Jacó, 12°30'S, 56°15'W, contato floresta estacional-floresta ombrófila, 8 Jun. 1997 (fl), *V.S. Souza et al. 17423* (UFMT); Mun. Aripuanã, Estrada velha Aripuanã-Castanheira, arredores de Serra Morena, 10°17'–19'S, 59°12'–18'W, savanna arborizada sobre solo arenoso (fl), *V.S. Souza et al. 18488* (UFMT); Mun. Maracapu, Fazenda Santo Antonio, Propriedade do Dr. Alfredo Neder, 590 m, 29 Dec. 1973 (fr), *D. Sucre 10580* (RB [4 sheets], US). **Mato Grosso do Sul:** Corumbá, povoado do Amolar, Capoeirinha, 18°1'22"S, 57°30'15"W, 29 Nov. 2010 (fl, fr), *R. Borges et al. 1083* (RB); Bataguçu [Bataguassu, ca. 21°42'S, 52°25'W], beira da Estrada várzea aluvional do Rio Paraná, brejo, 20 Nov. 1982 (fr), *I. Cordeiro et al. 982* (UFMT); Mun. Três Lagoas, Retiro dos Telhados, 30 km da cidade, 20°47'S, 51°41'W, 21 May 1964 (fr), *J. Correa Gomes Jr. 1752* (UB); Mun. Três Lagoas, Córrego da Onça, Faz. Iamaguti, 22°S, 49°W, 7 Jul. 1964 (fl, fr), *J. Correa Gomes Jr. 2076* (UB); Mun. Aquidauana [ca. 20°28'S, 55°47'W], Piraputanga, 18 Feb. 1970 (fl, fr), *G. Hatschbach 23793* (US); Coxim [ca. 18°30'S, 54°45'W], campos húmidos, May 1911 (fl, fr), *F.C. Hoene 4297* (R), 4298 (R); Mun. Paranaíba, Rod. MS-306, margem do Córrego Fundo, local brejoso, 22 Mar. 2001 (fl, fr), *M.D. Moraes et al. 607* (CEN); Mun. Tacuru [ca. 23°37'S, 55°0'W], ca. 10 km W of Tacurú, 8 Feb. 1994 (fl, fr), *T.M. Pedersen 15974* (C); Mun. Bataguçu, local Rio Pardo, rodovia MS-276, 5 km N de Bataguçu, 21°40'42"S, 52°24'8"W, 22 Apr. 2002 (fl), *V.J. Pott et al. 5385* (CEN, HMS); Corumbá, Serra do Amolar, Estrada do Taquaral, floresta estacional semidecídua, 18°2'58"S, 57°29'53"W, 320 m, 29 Nov. 2010 (fl, fr), *A. Quinet et al. 2153* (RB); Mun. Campo Grande, edge of brejo, ca. 15 km E os Campo Grande, 4 Jul. 1946 (fr), *J.R. Swallen 9608* (US). **Minas Gerais:** Lagoa Santa, s.d. (fl, fr), [without initials] *Becker 229* (RB); Lagoa Santa [ca. 19°37'S, 43°53'W], Dec. 1937 (fl, fr), *C.E.M. Burret & A.C. Brade 15972* (RB); Carassa [Serra do Caraça, ca. 20°5'S, 43°29'W], 1843 (fl, fr), *P. Clausen 134* (P); without locality, 1841 (fl), *P. Clausen 621* (FI-Webb); without locality, 1838 (fl, young fr), *P. Clausen 642* (C, P [2 sheets]); without locality, s.d. (fl, fr), *P. Clausen 720* (414) (FI-Webb); Uberlândia, Estação Ecológica do Panga [ca. 19°9'–11'S, 48°23'–24'W], Cerrado secundário, herbáceo, 10 Apr. 1992 (fr), *FEPP 13* (NY), 15 May 1992 (fr), *FEPP 100* (NY), 26 Jun. 1992 (fl, fr), *FEPP 230* (NY); São



- Roque de Minas [ca. 20°14'S, 46°21'W], ca. 1 km from the town, towards Serra da Canastra, campo cerrado, 12 Jan. 1994 (fl, fr), *A.M. Giullietti et al. CFCR 13576* (NY); Santa Luzia do Rio das Velhas [now Santa Luzia, ca. 19°46'S, 43°51'W], vieille route de Sabara, 25 Nov. 1893 (fl, fr), *A.F.M. Glaziou 20358* (C, P, R); Mun. Perdizes, Estação Ambiental Galheiro, Península, 13 Feb. 2004 (fl), *E.K.O. Hattori et al. 200* (UB); Mun. Perdizes, Estação Ambiental Galheiro [ca. 19°21'S, 47°17'W], Céu Cavallo, 13 Feb. 2004 (fl), *E.K.O. Hattori et al. 216* (UB); Mun. Lagoa Santa, barrancas humidas, Nov. 1915 (fl, fr), *F.C. Hoene 6456* (R); Mun. São Roque de Minas, Serra da Canastra, 3 km from São Roque de Minas to Araxá, 20°19'S, 46°31'W, 2 Nov. 1996 (fl–fr), *A. Ibáñez García & S. Bridgewater A480* (UB); wet campo, ca. 35 km NE of Patrocínio [ca. 18°56'S, 46°59'W], 1000 m, 29 Jan. 1970 (fl), *H.S. Irwin et al. 25636* (UB); ca. 12 km N of Patrocínio, cerrado and gallery forest, 1000 m, 31 Jan. 1970 (fl), *H.S. Irwin, E. Onishi, S.F. da Fonseca, R. Souza, R. Reis dos Santos & J. Ramos 25766* (NY, RB, UB, US); ca. 2 km N of Paracatú, rocky hillside, 700 m, 3 Feb. 1970 (fl), *H.S. Irwin et al. 25926* (UB); São Gonzalo do Abaeté [ca. 18°20'S, 45°49'W], 7 Jan. 1989 (fl, fr), *A. Krapovickas & C.L. Cristobal 42819* (C); Riacho Fundo [now Santana do Riacho, 19°10'S, 43°42'W], Mar. 1835 (fl, fr), *P. Lund s.n.* (C); prope Curvello, Mar–Apr. 1835 (fl, fr), *Lund, P. s.n.* (C); Cachoeira Dourada, margem do Rio Parnaíba, 14 Aug. 1945 (fl, fr), *H.L. Mello Barreto s.n.* (RB [2 sheets]); Mun. Lagoa Santa, Santa Luzia, vallo em capoeirinha, 17 Dec. 1937 (fl, fr), *H.L. Mello Barreto & A.C. Brade 10158* (R); Mun. Lagoa Santa, vallo no cerrado, 6 Jan. 1940 (fl), *H.L. Mello Barreto 10515* (R, US); Mun. Perdizes, Estação Ambiental Galheiro, cerrado próximo da caixa d'água, 20 Dec. 2002 (fl), *S. Mendes et al. 361* (UB); Mun. Caeté, Campo dos Coelhoos, entre União e Curralinho, campo pedregoso, 26 Nov. 1942 (fl), *G. Mendes Magalhães 2299* (US); Mun. Monte Carmelo [ca. 18°43'S, 47°29'W], Alagoas, Brejo Seco, 3 Jun. 1940 (fr), *J.E. de Oliveira 45* (IAN, US); Mun. São Roque de Minas, Vargem Grande, 20°20'9"S, 46°25'20"W, 6 Jan. 2008 (fl), *C. Proença & S.A. Harris 3473* (UB); without locality, Nov. 1828 (fl, fr), *L. Riedel 876* (*Herb. Hort. Petropol. 138*) (P, RB); Serra do Curral, Nova Lima, BH, 13 Mar. 1955 (fr), *L. Roth 1729* (RB); Mun. Unai, mata abaixo do vertedouro, mata ciliar de encosta, solo argilo-arenoso, 16°13'13"S, 47°19'29"W, 25 Jun. 2002 (fr), *A.A. Santos et al. 1289* (CEN); Mun. Ibiá, cerrado, rd. MG-230, 2 km from BR-262, 19°34'51"S, 46°29'47"W, 2 Mar. 1989 (fl, fr), *B.M.T. Walter et al. 42* (US); Mun. Pratinha, cerrado, dirt rd. connecting BR-262 and town of Pratinha, 5 km from BR-262, 19°38'4"S, 46°28'39"W, 2 Mar. 1989 (fl, fr), *B.M.T. Walter et al. 67* (SP, UB, US); Mun. Cabeceira Grande, região da ponte sobre o Rio Preto, 29 km from jct with BsB/Unai/Palmital, towards Palmital, divisa DF/MG, campo sujo, 16°2'15"S, 47°18'34"W, 850 m, 14 Feb. 2002 (fl, fr), *B.M.T. Walter et al. 5026* (CEN, US); Lagoa Santa, s.d. (fl), *E. Warming s.n.* (C [2 sheets]); Lagoa Santa, Oct. 1863 (fl), *E. Warming s.n.* (P P00748135); Lagoa Santa, 26 Nov. 1863 (fl), *E. Warming s.n.* (C). **Pará:** São Geraldo do Araguaia [ca. 6°24'S, 48°32'], campo cerrado, morro 3, margem da Cachoeira do Isidoro, 15 Jun. 1995 (fl, fr), *M.N. Bastos & M.R. Cordeiro 2205* (IAN, MG); without locality, “planta que nasce em terra prêta misturada com areia e barro, Fl. Março et Abril”, “Brésil, Pará, donné par l’herbier du Muséum lusitanique”, s.d. (fr), *Collector Unknown s.n.* (P [P00729409]); Mun. Anajás [ca. 0°59'S, 49°56'W], Rio Anajás, Fazenda Santa Quitéria, 20 Aug. 1982 (fr), *M.R. Cordeiro & N.A. Sena 1717* (IAN); Mun. Anajás, cidade de Anajás, ao lado do aeroporto, 20 Aug. 1982 (fr), *M.R. Cordeiro & N.A. Sena 1755* (IAN); Prainha [ca. 1°48'S, 53°28'W], Rio Marapy, Campo Alto, 15 May 1903 (fl), *A. Ducke s.n.* (MG 3575) (MG); Mun. Conceição do Araguaia [ca. 7°33'S, 49°42'W], campos gerais, 24 Jun. 1953 (fl, fr), *R.L. Frões 29913* (IAN); Reserva Florestal de Gorotire (Kayapó Indian Reservation), surroundings of Gorotire Village at Rio Fresco, 7°47'S, 51°7'W, 200 m, 19 Jan. 1983 (fl, fr), *G.K. Gottsberger & D.A. Posey 11-19183* (US); Rio Tiriós, Taperamba, 21 May 1962 (fl, fr), *E. Oliveira 1973* (IAN, UB); Rio Tiriós, lado esquerdo, parte norte ocidental do Pará, 24 May 1962 (fl, fr), *E. Oliveira 2002* (IAN); Mun. Conceição do Araguaia, 2 km W of town along hwy PA-287, 8°15'S, 49°18'W, 300 m, 24 Feb. 1980 (fl, fr), *T. Plowman et al. 9077* (IAN, INPA, MG, NY, UB, US); Mun. Palestina do Pará, inicio da mata do Rio Gameleira, mata, solo-areno-argiloso, 6°7'8"S, 48°25'2"W, 160 m, 18 Apr. 2004 (fr), *G.P. Silva et al. 8794* (CEN); Marajó Island, Cuanta do Anajás, Rio Anajás, between Anajás and Vista Alegre, 0°57'S, 49°48'W, 4 Nov. 1987 (fr), *G.T. Prance et al. 30292* (HAMAB, INPA, MG); Rio Tocantins, Jacundá [ca. 4°27'S, 49°6'W], barranco da beira do rio, varzea alta, 17 May 1977 (fl, fr), *M.G. Silva & R. Bahia 3104* (INPA, MG, RB, UB); Mun. Breves, Comunidade São Pedro, capoeira baixa, 1°33'41"S, 50°27'0"W, 30 Jul. 2011 (fl, fr), *M.G.C. Souza & M.R. Pietrobom 1213* (IAN). **Rondônia:** Margins of forest on terra firme, along Rio Pacaás Novos [ca. 10°S, 63°W], between the first and second cachoeiras, 220 m, 18 Mar. 1978 (fr), *W.R. Anderson 12174* (INPA, NY, UB, US); Ouro Preto do Oeste [ca. 10°44'S, 62°13'W], mata da CEPLAC, estrada para Embratel, 11 Jul. 1986 (fl, fr), *J. Augusto et al. 1738* (R [3 mounted sheets, 2 unmounted]); Cerejeiras, ramal de acesso ao Parque Estadual de Corumbiara, beira de estrada antropizada, 13°7'26"S,

61°12'16"W, 204 m, 20 Apr. 2013 (fl, fr), *A.P.B. Avaroma & F.C.P.S. Justiniano 679* (RB); Porto Velho, Fazenda Papai e Mamãe, campo cerrado, 9°39'28"S, 65°9'60"W, 132 m, 7 May 2013 (fr), *N.C. Bigio et al. 850* (RB); Estrada Guajará Mirim-Abunã, trecho entre km 45–60, linha 4A do INCRA, 1 Feb. 1983 (fl, fr), *L. Carreira et al. 476* (INPA, MG, NY); BR-364, area brejosa com buriti, 12°23'3"S, 60°37'24"W, 348 m, 19 Jan. 1999 (fl), *R. Farias et al. 304* (HUEFS, UB); Mun. Vilhena, Fazenda Vilhena do Pensamento, 12°18'18"S, 60°23'13"W, cerrado, solo arenoso, 25 May 1997 (fl, fr), *I.S. Miranda & P.J.D. Silva 1576* (IAN, MG); Basin of Rio Madeira, track between Mutumparaná and Rio Madeira, 3 Jul. 1968 (fl, fr), *G.T. Prance et al. 5518* (INPA, MG, NY, S, US); Madeira-Mamoré Railroad, km 217–9, 2–4 km E of Abunã, savanna, 18 Nov. 1968 (fl), *G.T. Prance et al. 8592* (INPA, MG, NY, P, S, US); Vilhena, arredores do aeroporto [ca. 12°41'S, 60°5'W], campo cerrado, 4 Jan. 1979 (fl), *M.G. Silva & A. Pinheiro 4139* (INPA, MG, NY, UB); Mun. Ariquemes, Mineração Mibrasa, Setor Alto Candeias, km 128, 10°35'S, 63°35'W, SW of Ariquemes, 11 May 1982 (fl, fr), *L.O.A. Teixeira et al. 359* (INPA, MG, NY, RB, US), 13 May 1982 (fl, fr), *419* (MG, NY, RB, US). **Roraima:** along Mucaí-Caracará road, BR-174, km 17, 8 Nov. 1977 (fl, fr), *L. Coradin & M.R. Cordeiro 1012* (IAN, NY, US); Mun. São Luiz do Anauá, Estrada Perimetral Norte (BR-210), 2 km da cidade de São Luiz, 1°5'N, 60°10'W, afloramento rochoso, 26 Aug. 1987 (fl), *C.A.C. Ferreira 9228* (INPA, NY); Ilha de Maracá, sandy savanna at Santa Rosa at the E side of Island, 3°20'N, 61°25'W, 8 Oct. 1987 (fl, fr), *J. Pruski et al. 3424* (INPA, NY); Fazenda Canada, margem direita do Rio Uraricuera, campo alagado temporariamente, 7 Feb. 1979 (fl), *N.A. Rosa 3071* (MG, NY). **Tocantins:** Mun. Palmas [ca. 10°11'S, 48°20'W], Bosque de Biodiversidade, Campus Unitins, 1 Dec. 1999 (fl), *Arnaldo 1893* (HTO, UFG); Mun. Porto Nacional, Faz. Ribeirão Manduca, margens da Carreira Comprida [agora submersa], cerrado fechado, 14 Dec. 1999 (fl), *Arnaldo 2175* (HTO, UFG); Mun. Santa Rosa, Rod. Santa Rosa-Silvanópolis (TO-050), ca. 15 km de Santa Rosa, floresta de galeria com solo encharcado, 11°13'20"S, 48°10'39"W, 250 m, 3 Nov. 2005 (fl), *P.G. Delprete et al. 9242* (HPL, HTO, UFG); Mun. Darcinoópolis, L margin of Rio Totantins, Córrego Pequi, gallery forest, 6°50'2"S, 47°32'5"W, 160 m, 19 Apr. 2008 (fr), *J.B. Pereira et al. 13083* (CEN); Mun. Couto de Magalhães, Estrada de Pequizeiro a Couto de Magalhães, 30 km antes de Couto de Magalhães, mata secundária, 11 Jan. 1974 (fl), *J.A. Rizzo 9538* (UFG, UB); Mun. Barra do Ouro, Fazenda Campo Grande, ca. 15 km do Rio Manoel Alves, plintossolo, 7°30'45"S, 47°32'56"W, 180 m, 4 Mar. 2005 (fr), *G.P. Silva et al.*

9783 (CEN); Mun. Ipueiras, próx. Rio Tocantins, margem da lagoa, 11°14'50"S, 48°27'31"W, 6 Dec. 2001 (fl), *E.A. Soares 1842* (HTO); ca. 15 km S of Araguaína, ca. 300 m, 16 Mar. 1968 (fl), *H.S. Irwin et al. 21275* (NY, UB, US). **State Unknown:** without locality, s.d. (fl, fr), *Collector Unknown s.n.* (BR 824748) (BR); without locality, s.d. (fl, fr), *Collector Unknown s.n.* (ex herbario *Musei imperialis lusitaniae communicata*) (P [P00729401]); "Bresil", without locality, *Collector Unknown s.n.* (FI-Webb 080085); "Bresil", without locality, [Viagem Filosófica], s.d., *A.R. Ferreira s.n.* (ex herb. *Lusitanic.*) (Herb. Lus. M. Geoffroy) (P P00748147); without locality, s.d. (fl), *A. Glaziou 21519* (C); without locality, s.d., *A. Glaziou 19725* (C, P); "Andrequecé," Oct. 1855 (fl), *G.T. Reinhardt s.n.* (C); "Brésil central", 1844 (fr), *M.A. Weddell 1984* (P).

**PERU. Junín:** San Ramón [ca. 11°7'S, 75°21'W], 900–1300 m, 9 or 12 Jun. 1929 (fl), *E.P. Killip & A.C. Smith 24788* (NY, US); Pichis Trail, Porvenir, 1500–1900 m, 3–4 Jul. 1929 (fl), *E.P. Killip & A.C. Smith 25909* (NY, US); Puerto Yessup [ca. 10°27'S, 74°54'W], 400 m, 10–12 Jul. 1929 (fl), *E.P. Killip & A.C. Smith 26270* (NY, US). **Loreto:** Florida, Río Putumayo, at mouth of Río Zubineta, 180 m, forest clearing, Oct.–Dec. 1931 (fl, fr), *G. Klug 2285* (BM, NY, S, US). **Pasco:** Prov. Oxapampa, Central Selva, Palcazu Valley, Izcozacín, above PEPP Project Camp, forestry experimental strip in old secondary forest, clay soil, 31 Mar. 1986 (fr), *J. Salick 7302* (NY). **San Martín:** Zepelacio, near Moyobamba [ca. 6°2'S, 76°58'W], 1200–1600 m, mountain forest, Jan. 1934 (fr), *G. Klug 3543* (NY, S, US); Mount La Campana, 1 Sep. 1925 (fl), *D. Melin 253* (S); Dtto. Lamas [ca. 6°25'S, 76°32'], bosque bajo, orilla de camino, 1000 m, 6 Apr. 1972 (fl, fr), *J. Schunke-Vigo 5349* (NY [2 sheets], US); Tarapoto [6°29'S, 76°22'W], 1855–1856 (fl), *R. Spruce 4602* (BM, NY); San Roque, 1350–1500 m, Jan–Feb. 1930 (fl, fr), *Ll. Williams 7409* (US); Río Negro, open places among ferns, 1400 m, 18 Jan. 1961 (fr), *F. Woytkowski 6224* (NY).

**BOLIVIA. Beni:** Prov. Ballivian, Isla de Espiritu, Rio Yacuma, 200 m, sabana húmeda, 13 Apr. 1981 (fl, fr), *G. Beck 5376* (UB). **La Paz:** Mapiri Region, San Carlos, 850 m, 1 Apr. 1927 (fl, fr), *O. Buchtien 1433* (BR, C, NY, S); Mapiri, Jul.–Aug. 1892 (fl, fr), *M. Bang 1488* (BM, NY [2 sheets], R, US); Mapiri [ca. 15°18'S, 68°13'W], 830 m, May 1886 (fl, fr), *H.H. Rusby 2461* (BM, NY [3 sheets], P, US). **Pando:** Nicolás Suárez, cerca de Porvenir [ca. 11°5'S, 68°54'W], en los entornos y dentro de un curiche, 21 Jan. 1983 (fl, fr), *J. Fernández Casas & Susanna 8366* (NY). **Santa Cruz:** Prov. Chiquitos, ca. 10 km W of Roboré to San Pedro, then NE onto serrania, from 0.5–5 km, mosaic of Cerrado, dry forest and large rock outcrops,

18°15'S, 59°49'W, 400–600 m, 5 Feb. 1995 (fl, fr), *J.R. Abbott & B. Mostacedo 16094* (NY); between Río Pirai and Río Cuchi, campos, 550 m, Jan. 1911 (fr), *T. Herzog 1438* (S); Prov. Núflor de Chávez, between kms 15 and 30 from Ascensión de Guarayos on rd to Urubicha, roadside at edge of deciduous woodland rich in *Orbignya* palms, 15°30'S, 63°5'W, 4 Aug. 1983 (fl, fr), *M.J.G. Hopkins et al. 141* (NY); Santa Cruz [Santa Cruz de la Sierra, 17°47'S, 63°12'W], Dec. 1891 (fl), *S. Moore 801* (BM); Prov. Guarayos [formerly part of Prov. Núflor de Chávez], 11 km N of Ascensión de Guarayos on rd. to Urubichá, forest on flat, somewhat swampy Quaternary river or lake deposit, 15°47'S, 63°9'W, 190 m, 13 Jul. 1991 (fl, fr), *M. Nee 41709* (NY); Prov. Ichilo, 3 km SW of El Hondo, “potrerillo”, Cerrado savanna vegetation S of the buildings, sandy soil, 17°40'20"S, 63°27'25"W, 400 m, 12 Feb. 1994 (fl), *M. Nee 44897* (NY); Santa Cruz, Jun. 1865 (fl, fr), *R.W. Pearce s.n.* (BM); Prov. Sara, campos de Buena Vista [ca. 17°40'S, 63°44'W], 500 m, 27 Mar. 1921 (fl), *J. Steinbach 5481* (NY); Prov. Sara, campos de Buena Vista, 450 m, 8 Mar. 1925 (fl, fr), *J. Steinbach 6965* (BM, NY, S); San José [now San José de Chiquitos, 17°51'S, 60°45'W], 600 m, 2 Feb. 1902 (fr), *R.S. Williams 383* (BM, NY); Santa Cruz, Chiquitos, Santiago de Chiquitos, ca. 1 km del pueblo, alrededores del campo militar, cerrado con arbustos y arboles disperses, suelo arenoso y afloramientos rocosos (campo rupestre), pocas plantas el lugar más húmedo, arenoso, 18°21'5"S, 59°36'8"W, 590 m, 12 Apr. 2008 (fl, fr), *J.R.I. Wood et al. 24433* (UB).

**PARAGUAY. Amambay:** Entre Bellavista y San Carlos [San Carlos del Apa], estero húmedo próximo al Apa, 12 Feb. 1982 (fl), *J. Fernandez Casas & J. Moleiro 6268* (NY); Zwischen Río Apa und Río Aquidaban, Caballero-rué, 1908–1909 (fl, fr), *K. Fiebrig 4799* (BM); Parque Nacional Cerro Corá, 22°40'S, 56°5'W, open savannah dominated by *Anadenanthera*, *Gochnatia*, *Styrax*, many myrtaceous shrubs, etc., 1 Nov. 1983 (fl, fr), *W. Hahn 1769* (US); Cerro Corá, Arroyo Aceite, 40 km de P.J. Caballero, sobre la barranca del arroyo, 24 Feb. 1968 (fl), *A. Krapovicic et al. 14179* (C); Parque Nacional Cerro Corá, 22°39'S, 56°3'W, open campos, S side of Cerro Tujá-og, 20 Feb. 1982 (fl, fr), *J.C. Solomon et al. 7137* (MO, US); Bella Vista, 15 Dec. 1983 (fl, fr), *R. Vanni et al. 293* (C); Parque Nacional Cerro Corá, 300 m, 21 Jan. 1981 (fl, fr), *M. Vavrek 134* (MO, US). **Canindeyú:** Serra de Maracayú [ca. 24°20'S, 55°3'W], yerbales, 1898–1899 (fl, fr), *E. Hassler 5961* (BM, MPU, NY, P); 65 km S of Capitán Bado, on frontierline [ca. 23°16'S, 55°32'W], cerrado-pantanal, 550 m, 29 Mar. 1983 (fr), *J.E. Simonis 227* (UB). **Concepción:** Arroyo Trementina, 15 km E of Paso Barreto, gallery forest “chaco” type, 23°2'39"S, 57°0'41"W, 210 m, 1 Jul. 1994 (fl, fr), *E.M. Zardini &*

*L. Guerrero 39905* (NY); Yaguareté Forest, inundated savanna on black soil, 23°47'48"S, 56°6'42"W, 210 m, 18 Jan. 1996 (fl, fr), *E.M. Zardini & L. Guerrero 44323* (P). **San Pedro:** Distr. Lima, Estancia Carumbé [ca. 25°33'S, 56°40'W], 24 Nov. 1969 (fl, fr), *T.M. Pedersen 9383* (C, P); Alto Paraguay, Primavera, 6 Jun. 1958 (fl, fr), *A.L. Woolston 991* (C [2 sheets], MG, NY, S, US). **Province Unknown:** Without locality, s.d. (fr), *S.G. Weddell 3272* (P [2 sheets]), 3274 (NY).

**URUGUAY:** “Banda Oriental del Uruguay”, s.d. [1816–1821] (fl), *A. Saint-Hilaire Catal. C2 No. 2278* (P [2 sheets, P00729293, P00729294]).

#### Hybrid forms between *S. hispida* and *S. pratensis*

**var. *dichotoma*:** Intermediate forms, as already indicated as “introgression” by Steyermark (1967: 275–276), are found in a few specimens from Colombia, where both taxa occur, are here interpreted as hybrid forms between *S. hispida* and *S. pratensis* var. *dichotoma*. Two gatherings from Colombia show intermediate characters between these two taxa, as spreading pubescence, typical of *S. hispida* (vs. appressed pubescent in *S. pratensis*) and corolla tubes 11–14 mm long, typical of *S. pratensis* var. *dichotoma* (vs. 6–10(–12.5) mm long in *S. hispida*). This combination of intermediate characters is present in the following gatherings:

**COLOMBIA: Cundinamarca:** Caqueza, 1810 m, 23 May 1940 (fl–fr), *H. García Barriga 8466* (COL, US). **Meta:** Los Llanos, Río Metica, Puerto López, 380 m, 14 Oct. 1938 (fl–fr), *J. Cuatrecasas 3567* (US).

8-5. *Sipanea pratensis* Aubl., Hist. Pl. Guiane 1: 148, tab. 56. 1775. [Section *Sipanea*] (Figures 5E–F, 47–50).

For synonyms and types see under varieties.

*Perennial herb* or *subshrub* (basal internodes woody), 0.3–1.5 m tall, terrestrial or epipetric on inselberg or granitic outcrops, basal portion sometimes woody, prostrate, decumbent, ascending or erect, often forming large patches (var. *pratensis*) or large populations (var. *dichotoma*); stems to 1.8 m long, rarely or often geniculate, sometimes rooting at basal nodes; young branches thin to stout, 0.6–3.3 mm thick, terete or sometimes slightly quadrangular in older stems, sparsely to densely, appressed or spreading, pubescent or sericeous (hairs whitish or beige, 0.8–2 mm long). *Stipules* adnate to the petioles, sheathing, free portion truncate to broadly triangular at base and very narrowly triangular to linear distally, 2–6 × 0.6–1.5 mm, appressed pubescent to sericeous outside (hairs whitish or beige,

1.5–2 mm long); glabrous inside, slightly thickened at margin inside; with 2–3 colleters inserted at margin on each side of the central lobe; margins pubescent to sericeous. *Leaves* sessile to short-petiolate; petioles (when present) to 5 mm long, hirsute-pubescent, villous, appressed-pubescent or strigose-sericeous (hairs 1–2 mm long); blades broadly ovate, ovate, ovate-elliptic, elliptic, oblong-elliptic, oblong-lanceolate, lanceolate, narrowly lanceolate to narrowly oblong-elliptic, 1.5–7.5 × 0.5–2.5 cm, round, obtuse to acute at base, rarely decurrent, acute to acuminate at apex, chartaceous, dark green above and pale green below when fresh, olive-green when dry, appressed pubescent to densely short- to long-pubescent above, (hairs 0.3–2 mm long) above, densely appressed pubescent or villous or short- to long-hirsute below (hairs 0.3–2 mm long); secondary veins 3–8 on each side of midrib, obsolete or slightly impressed above, prominent below. *Inflorescence* terminal, sessile or pedunculate, congested-cymose, appearing fasciculate, rarely with secondary branches to 4 mm long, 4–8-flowered, sometimes subtended by 2 or 4 leaf-like bracts, with heads 0.4–1.5 × 0.3–1.5 cm (corollas excluded) during anthesis (var. *pratensis*), or evidently branched during anthesis (var. *dichotoma*), 4–37-flowered, 1–10 × 0.8–7 cm (excluding corollas) during anthesis, with lateral axes 0.5–7 cm long, more or less elongating during and/or after anthesis, 1–10 cm long (excluding corollas), scorpioid; peduncles (when present) to 7.5 cm long, sparsely to densely, appressed or spreading, pubescent or sericeous (hairs whitish or beige, 1.5–2 mm long), bracts subtending secondary branches (when present) lanceolate, oblong-lanceolate, narrowly lanceolate to linear, 2.5–7 × 0.5–1.2 mm. *Flowers* distylous, (4)5(6)-merous, sessile to subsessile; pedicels (when present) to 0.7 mm long. *Hypanthium* turbinate to narrowly obovoid, 0.7–1.5 × 0.5–0.9 mm, acute at base, round at apex, appressed pubescent to sericeous. *Calyx* lobes free, equal, subequal or unequal, lanceolate, narrowly oblong-lanceolate to linear, 2.3–6 × 0.2–0.6 mm, acuminate at apex, green to yellowish-green when fresh, sparsely to densely appressed pubescent to sericeous, sometimes almost glabrous outside, margins long-ciliate, glabrous inside; with 1–2 colleters in each calycine sinus, linear, 0.2–0.4 mm long. *Corolla* hypocrateriform, 14–28 mm long, pale to dark pink, or tube pink and lobes white during anthesis, turning paler to almost white after anthesis, with a dense ring of yellow hairs exerted beyond mouth; tube (8–)10–17 mm long, gradually expanding towards the mouth, 0.4–0.7 mm wide at base, 1.5–3 mm wide at mouth, glabrous at medio-basal portion and sparsely to densely appressed pubescent at medio-distal portion or completely glabrous outside, glabrous at basal portion,

densely puberulous above and densely yellow-pubescent at distal portion inside, the yellow pubescence exerted beyond corolla mouth; lobes round, broadly elliptic, elliptic, obovate, oblong-elliptic to oblanceolate, sometimes varying in shape and size within the same population, sometimes unequal or of slightly different shape within the same corolla, (2.5–)4–11 × (2–)2.5–7 mm, round, obtuse to acute, rarely apiculate when subobtuse or acute, or indented when obtuse or round at apex, glabrous throughout. *Long-styled flowers*: stamens inserted at 6–7 mm from base or about the middle of corolla tube; filaments 0.5–0.8 mm long; anthers narrowly oblong-elliptic to linear, 1.8–2.5 × 0.2–0.3 mm, acute at both ends; style exerted 1–2.5 mm beyond corolla mouth, (9.5–)15–16.5 mm long, glabrous; style branches narrowly oblong to oblong-ovate, (0.6–)1–1.5 mm long, round at apex. *Short-styled flowers*: stamens inserted at 2.5–5.5 mm below corolla mouth; filaments 0.2–0.7 mm long; anthers linear to narrowly oblong-elliptic, 1.7–3 × 0.2–0.3 mm, acute at both ends; style included, 6–8 mm long, glabrous; branches linear, 1.5–3 mm long, round or acuminate at apex. *Infructescences* with mature fruits congested-cymose, appearing fasciculate, rarely with secondary branches to 4 mm long (var. *pratensis*), or dichotomously branched, more or less expanded, with scorpioid secondary branches (0.5–)1–10 cm long (var. *dichotoma*). *Capsules* nearly as broad as long, subglobose, ovoid to obovoid, 4–4.5 × 3–4.5 mm, round or acute at base, round at apex, strongly costate when dry (var. *pratensis*), or longer than broad, cylindrical-oblong to oblong-narrowly ovoid, (3–)4.5–8 × 1.5–3 mm, round to acute at base, round at apex, commonly smooth or faintly to strongly costate when dry (var. *dichotoma*); thinly woody, sparsely to densely pubescent to sericeous (hairs 0.5–1.5 mm long) to almost glabrate (very sparsely pubescent), pale green when young, turning beige to pale brown when dry. *Seeds* irregularly tetrahedral, faintly to strongly angular, (0.4–)0.5–0.7 mm in diam., testa foveolate, rugulose-verrucose.

**Distribution and ecology:** Distributed in Colombia, Venezuela, the Guianas, and northern Brazil (Roraima, Amapá, Pará, Amazonas, Maranhão); an extremely variable species in terms of habit, leaf shape, inflorescence architecture, flower size, and fruit shape; prostrate, decumbent, ascending or erect herb or subshrub, often forming extended patches (var. *pratensis*) or large populations (var. *dichotoma*) in open savannas, white-sand savannas, brown-sand savannas, on granitic inselbergs, granitic outcrops, swampy margins in savannas, seasonally inundated savannas, open field savannas with *Trachypogon*, or savannas with sparse

trees of *Curatella americana* L. and *Byrsonima crasifolia* (L.) Kunth, margins of semi-shady forest, creek margins in forests, margins of forest trails, *Mauritia* palm swamps, road margins, and disturbed, secondary or roadside vegetation; in sunny or semi-shady exposures; on sandy, granitic or lateritic soils; from near sea level to 1200 m altitude.

**Suggested conservation status: Least Concern** (See discussion under varieties).

**Notes:** *Sipanea pratensis* has gone through several re-delimitations by Rubiaceae specialists, due to the different interpretations of morphological characters or because several authors did not examine the type specimens. Because of these various re-delimitations, a brief taxonomic history of this species is considered necessary.

Aublet (1775) described *Sipanea pratensis* from specimens that he collected in open savannas of French Guiana. These plants have congested inflorescences that remain congested at fruit maturity (see description of *S. pratensis* var. *pratensis*).

Schumann (1889) delimited *Sipanea pratensis* very broadly, including *S. dichotoma*, *S. trichantha*, “*S. vinca* Martius. Ms.! in hb. Monac. [nom. illeg. synon.]”, “*S. hispida* et *acinifolia* Spruce Ms.! in Pl. exicc. n. 2051, 4602 et n. 3652” [*S. hispida* was later validly published by Wernham (1917), and *S. acinifolia* was later validly published by Sprague (1905)], *Virecta pratensis* (Aublet) Vahl, “*Virecta dichotoma* Spreng.! Eclog. II. 11”, and “*Ptychodea dichotoma* Willd., hb.”, without recognizing any variety. The figure labelled *Sipanea pratensis* (Schumann, 1889, tab. 122) is instead *S. hispida*. Schumann’s too broad delimitation of *S. pratensis* gave raise to considerable confusion that was later clarified by subsequent authors, although a certain degree of confusion as to the separation of *S. pratensis* from *S. hispida* still persists among contemporary rubiologists. *Sipanea hispida*, as it has been convincingly demonstrated by recent authors (Steyermark, 1967, 1974; Delprete & Steyermark, 2004e; Delprete, 2010c), is a distinct species, ranging from Colombia, Peru, Ecuador, Bolivia, and most of Brazil to Paraguay.

Wernham (1917) succinctly revised *Sipanea* and kept *S. pratensis* as a distinct species, without varieties, stating that “this species, the type of the genus, may be regarded as the parent-species of the four preceding [i.e., *S. galioides*, *S. spraguei*, *S. veris*, *S. biflora*], which, like it, are more or less slender and even delicate plants, inclined to creep or straggle, smooth and tending to glabrousness; they are distinguished also by the relatively large corolla limb.”

Standley (1921: 93–94) in *North American Flora* delimited *Sipanea pratensis* including *S. dichotoma* Kunth in synonymy, without recognizing any variety. He stated that *S. pratensis* occurs in “Trinidad and the Guianas; reported from Dominica.” However, as far as I know, this species does not occur in Dominica.

Bremekamp (1934a: 127–132) in *Flora of Surinam* treated *Sipanea pratensis* as widely delimited, although with a narrower delimitation than that of Schumann (1889), including *S. dichotoma* and *S. trichantha* in synonymy, without recognizing any variety. In addition, he described *S. coppenamensis* Bremekamp (1934: 258), from material collected along the Coppename River (Suriname), distinguished from *S. pratensis* by its “leaves distinctly petiolate” (vs. “sessile” in *S. pratensis*), ovary and calyx sparsely hairy (vs. densely villous), and calyx lobes less than a third the length of the corolla tube (vs. “about half as long as the corolla tube”). A detailed analysis of numerous specimens throughout the geographic range demonstrated that the characters used by Bremekamp to distinguish *S. coppenamensis* from *S. pratensis* are widely overlapping, and these two names are here treated as synonymous.

Bremekamp (1936: 707) later described *Sipanea pratensis* var. *glaberrima* Bremek. using a single collection of completely glabrous individuals from the Sipaliwini “Great Savanna (2°N, 56°W, Suriname) growing in the midst of plants belonging to the *forma typica* [*S. pratensis* sensu Bremekamp, which included var. *pratensis* and var. *dichotoma*, as later recognized by Steyermark].”

Lemée (1954 [“1953”]: 506) in *Flore de la Guyane française* treated *Sipanea pratensis* as narrowly delimited, with terminal, congested inflorescences, without citing any synonym.

Steyermark (1967) recognized numerous varieties and forms in *Sipanea pratensis*, and expressed his concepts about subspecific ranks as follows: “After a prolonged study of numerous specimens, it is believed in the best interests of taxonomy to render the great variation expressed by the assignment of varietal and formal categories. No subspecies are given, since there does not appear to be any definite geographic range indicated within the variations, and the differences manifest appear to intergrade in various portions of the variable characters.” (Steyermark, 1967: 271). In other words, Steyermark allowed varieties and forms to be morphologically and geographically overlapping throughout their geographical ranges. However, according to the concepts adopted by in the present treatment, only one subspecific rank is used, the variety, which is defined by a set secondary morphological characters correlated with geographical distribution, which corresponds to Steyermark’s subspecies concept.

Steyermark (1967, 1974) characterized the typical variety of *Sipanea pratensis* by “no part of the inflorescence elongating, the flowers or fruits all fasciculate-congested [i.e., reduced-cymose], without a subsecund monochasial or dichasial appearance, [...] capsules subglobose to ovoid, mainly 4–4.5 mm long, nearly as broad as long,” while he distinguished var. *dichotoma* by the “lateral axis of inflorescence more or less elongating, producing a subsecund monochasial or dichasial appearance, [...] capsules cylindrical-oblong, 4–8 mm long, longer than broad.” (Steyermark, 1967: 271). After a detailed study of several hundred specimens of *S. pratensis* throughout its geographic distribution, these characters are here confirmed to be diagnostic of these two varieties, and are correlated with geographical ranges; therefore these two varieties are here recognized.

Aside from *Sipanea pratensis*, in several other species, a certain degree of expansion of the inflorescence has been observed from condensed during anthesis to much expanded starting from the final stage of anthesis to fruit maturity, as, for example in *S. glomerata* and *S. hispida*, which have young inflorescences condensed to subcapitate, expanding into cymose with scorpioid secondary branches when the capsules reach full maturity. However, this variation in inflorescence expansion is present in various degree throughout the range, and has no correlation with any geographic distribution. Therefore, in several species the degree of inflorescence expansion is treated as a developmental stage, and no varieties are recognized in *S. glomerata* and *S. hispida*.

Bremekamp's (1936) *Sipanea pratensis* var. *glaberrima*, which was treated as a distinct species by Steyermark (1967), is here maintained as such because the plant is completely glabrous, except for the corolla throat pubescence, although it is known only from the type specimen collected “in the midst of a population” of *S. pratensis* var. *dichotoma*. For additional information see discussion under *S. glaberrima* (Bremek.) Steyerm.

Finally, there is a certain tendency for the populations of *Sipanea pratensis* growing on inselbergs and white-sand savannas to have a prostrate-decumbent habit and smaller leaves (i.e., approaching *Sipanea galioides* in general habit); however, these morphological features intergrade with those of nearby populations with ascending or erect habit and larger leaves, occurring at the edges of these formations, and in other open populations occurring in open fields on lateritic soils. Therefore, variation in habit and leaf size are interpreted as morphological variation influenced by ecological factors, and leaf shape and size cannot be used as taxonomic characters for supporting subspecific ranks within this species.

#### Key to varieties of *Sipanea pratensis*

1. Inflorescences congested-cymose, appearing fasciculate, or rarely with secondary branches to 4 mm long during anthesis, sometimes subtended by 2 or 4 leaf-like bracts (i.e., pherophylls), no part of the inflorescence elongating during and/or after anthesis (without a subsecund monochasial or dichasial appearance); infructescences congested, appearing fasciculate, rarely with secondary branches to 4 mm long; capsules nearly as broad as long, subglobose, ovoid to obovoid, 4–4.5 × 3–4.5 mm, strongly costate [Guyana, Suriname, French Guiana, Brazil (Amapá, Pará), mostly coastal areas] .8-5a. *S. pratensis* var. *pratensis*
1. Inflorescence congested-cymose, appearing fasciculate, or obviously dichomously branched during anthesis, expanding after anthesis, with lateral axes 0.5–7 cm long, excluding corollas, more or less elongating during and/or after anthesis, scorpioid, producing a subsecund monochasial or dichasial appearance; infructescences dichotomously branched, more or less expanded, with scorpioid secondary branches (0.5–)1–10 cm long; capsules longer than broad, cylindrical-oblong to oblong-narrowly ovoid, (3–)4.5–8 × 1.5–3 mm, smooth or faintly costate [Colombia, Venezuela, Trinidad, Guyana, Suriname, French Guiana, Brazil (Amapá, Amazonas, Maranhão, Pará, Roraima)]. .....8-5b. *S. pratensis* var. *dichotoma*

8-5a. *Sipanea pratensis* Aubl. var. *pratensis*, Hist. Pl. Guiane 1: 148, tab. 56. 1775. (Figures 5E-F, 47–49).

Type: FRENCH GUIANA. “in pratis Caiënnæ & Guianæ” [open fields of Cayenne and French Guiana] and “se trouve en abondance dans les savanes qui sont autour de la ville de Caiënnæ [...] presque toujours en fleur & en fruit,” [it is found in the savannas that surround the city of Cayenne [...] almost always in flower and fruit], s.d. [1762–1764], *J.B.C. Aublet s.n.* (Lectotype P-JJR 8: 281, designated by Lanjouw & Uittien (1940: 158); isolectotype BM [barcode BM000614306], specimens with N. “1” [excluding the specimen with N. “2”; see Nomenclatural Notes below]; photo-BM at NY). [Section *Sipanea*].

(=) *Sipanea copenamensis* Bremek., Recueil Trav. Néerl. 31: 258. 1934.

Type: SURINAME. Coppename River, near Turcotabbetje, 26 Jul. 1921 (fl), *J.W. Gonggrijp 58* (B.W. 5326) (holotype U [2 sheets, barcodes 0006308 and 0006309]; photo-U at NY).

*Perennial herb* 0.3–1 m tall, terrestrial or epipetric (on inselberg or granitic outcrops), prostrate, decum-

bent, ascending or erect, often forming extended patches; stems often geniculate, basal portion prostrate, rooting at nodes; young branches thin, 0.6–1(–1.3) mm thick, terete or sometimes slightly quadrangular in older stems), sparsely to densely, appressed or spreading, pubescent or sericeous (hairs whitish or beige, 1.5–2 mm long). *Leaves* with blades ovate-elliptic, elliptic, oblong-elliptic, oblong-lanceolate, lanceolate to narrowly lanceolate, 1.5–4.5 × 0.5–1.8 cm, obtuse to acute, sometimes decurrent, at base, acute to acuminate at apex; secondary veins 3–7 on each side of midrib, obsolete above, prominent below. *Inflorescences* sessile or pedunculate, congested-cymose (appearing fasciculate), or rarely with secondary branches to 4 mm long, sometimes subtended by 2 or 4 leaf-like bracts; heads 0.4–1.5 × 0.5–1.5 cm (corollas excluded) during anthesis, 4–8-flowered, no part of the inflorescence elongating during and/or after anthesis, without a subsecund monochasial or dichasial appearance; peduncles (when present) to 4.5 cm long, sparsely to densely, appressed or spreading, pubescent or sericeous (hairs whitish or beige, 1.5–2 mm long); external bracts (when present) 4–7, lanceolate, oblong-lanceolate to narrowly lanceolate, 2.5–5.5 × 0.5–1.2 mm, acute to acuminate, sparsely to densely antrorse-pubescent outside, sometimes absent; bracteoles subtending flowers (when present) lanceolate to narrowly lanceolate, 2–2 × 0.4–0.7 mm, appressed pubescent to sericeous outside (hairs whitish or beige, 1.5–2 mm long), sometimes absent. *Hypanthium* 1–1.5 × 0.7–0.9 mm, acute at base, round at apex, appressed pubescent to sericeous. *Calyx* lobes narrowly lanceolate to linear, 2.5–5 × 0.3–0.6 mm. *Corolla* 17.5–25.5 mm long; tube (10–)12.5–17 mm long, 0.4–0.5 mm wide at base, 1.5–2.8 mm wide at mouth; lobes broadly elliptic, elliptic, obovate, oblong-elliptic to oblanceolate, (sometimes varying in shape and size within the same population), sometimes unequal or of slightly different shape within the same corolla, 5–9 × 2.5–5.5 mm, round, obtuse to acute, rarely apiculate when subobtusate or acute, or indented when obtuse or round at apex. *Long-styled flowers* [Delprete 12882 (corolla tube 13 mm long), Granville et al. 15909 (corolla tube 12.5 mm long)]: stamens inserted at 6 mm from base or about the middle of corolla tube; filaments 0.7–0.8 mm long; anthers linear, 2.3–2.4 mm long; style

exserted 1–2 mm beyond corolla mouth, 14–18 mm long; style branches narrowly oblong to oblong-ovate, 1–1.3 mm long, round at apex. *Short-styled flowers* [Delprete 12882 (corolla tube 13 mm long), Delprete 12886 (corolla tube 10 mm long)]: stamens inserted at 2.5–3.5 mm below corolla mouth; filaments 0.2–0.3 mm long; anthers linear, 1.7–2.8 × 0.2–0.3 mm, acute at both ends; style included, 6–8 mm long, glabrous; branches linear, 1.5–3 mm long, round at apex. *Infructescences* with mature fruits congested-cymose, appearing fasciculate, rarely with secondary branches to 4 mm long. *Capsules* subglobose, ovoid to obovoid, nearly as broad as long, 4–4.5 × 3–4.5 mm, round at base, strongly costate when dry, sparsely pubescent to sericeous (hairs 0.5–1 mm long), pale green when young, turning beige to pale brown when dry.

**Nomenclatural notes:** A short biography of Aublet and full typification of the Rubiaceae taxa described by him, including *Sipanea pratensis*, was recently published by Delprete (2015b). Aublet (1775), for each species supplied the localities and habitat where they grew, without citing any collection number. Therefore, according to the *Code* (Turland et al. 2018), Aublet's specimens cannot be treated as single gatherings, and lectotypes or isolectotypes should be designated. Lanjouw and Uittien (1940) reported the discovery of an additional set of Aublet's specimens within the Jean-Jacques Rousseau herbarium (P-JJR). Most importantly, in Section 6 of their article, entitled (translated from French) "Types of genera and species of Fusée Aublet in the herbarium of Jean Jacques Rousseau in possession of Henri Denaiffe at Carignan (Ardenne), France," they listed all the Aublet's specimens found in this herbarium. As the title of this section begins with "Types", according to Art. 9.10 of the *Code* their statement should be treated as an error to be corrected, and the types citations in this section should be recognized as lectotypifications. There are two Aublet specimens of *S. pratensis*, one at P-JJR and the other at BM. Lanjouw and Uittien (1940: 158) cited the P-JJR specimen as "Hb. Denaiffe vol. VIII, no. 281: une branche portant des fleurs ressemblant à la planche [one branch with flowers, resembling the plate]." On sheet P-JJR 8: 281 is mounted one much-branched speci-

**Figure 47.** *Sipanea pratensis* var. *pratensis*. **A.** Habit, with flowers in anthesis and capsules. **B.** Node with sheathing stipule and leaf bases. **C.** Dissected short-styled flower, with stamens inserted at distal portion of corolla tube, and included style. **D.** Dissected long-styled flower, with stamens inserted at medio-distal portion of corolla tube, and exserted style. **E–I.** Corolla lobes variation within the species. **J.** Infructescence with mature capsules. **K.** Mature capsule. **A–B, D:** drawn from Delprete 12882 (CAY); **C:** drawn from Delprete 12886 (CAY); **E:** drawn from Hoff 5068 (CAY); **F:** drawn from Billiet & Jadin 5751 (CAY); **G:** drawn from Albertini 18 (CAY); **H:** drawn from Billiet & Jadin 4403 (CAY); **I:** drawn from Moretti 1191 (CAY); **J:** drawn from Delprete 12885 (CAY); **K:** drawn from Rova et al. 2018 (CAY). Illustration by Piero Delprete.

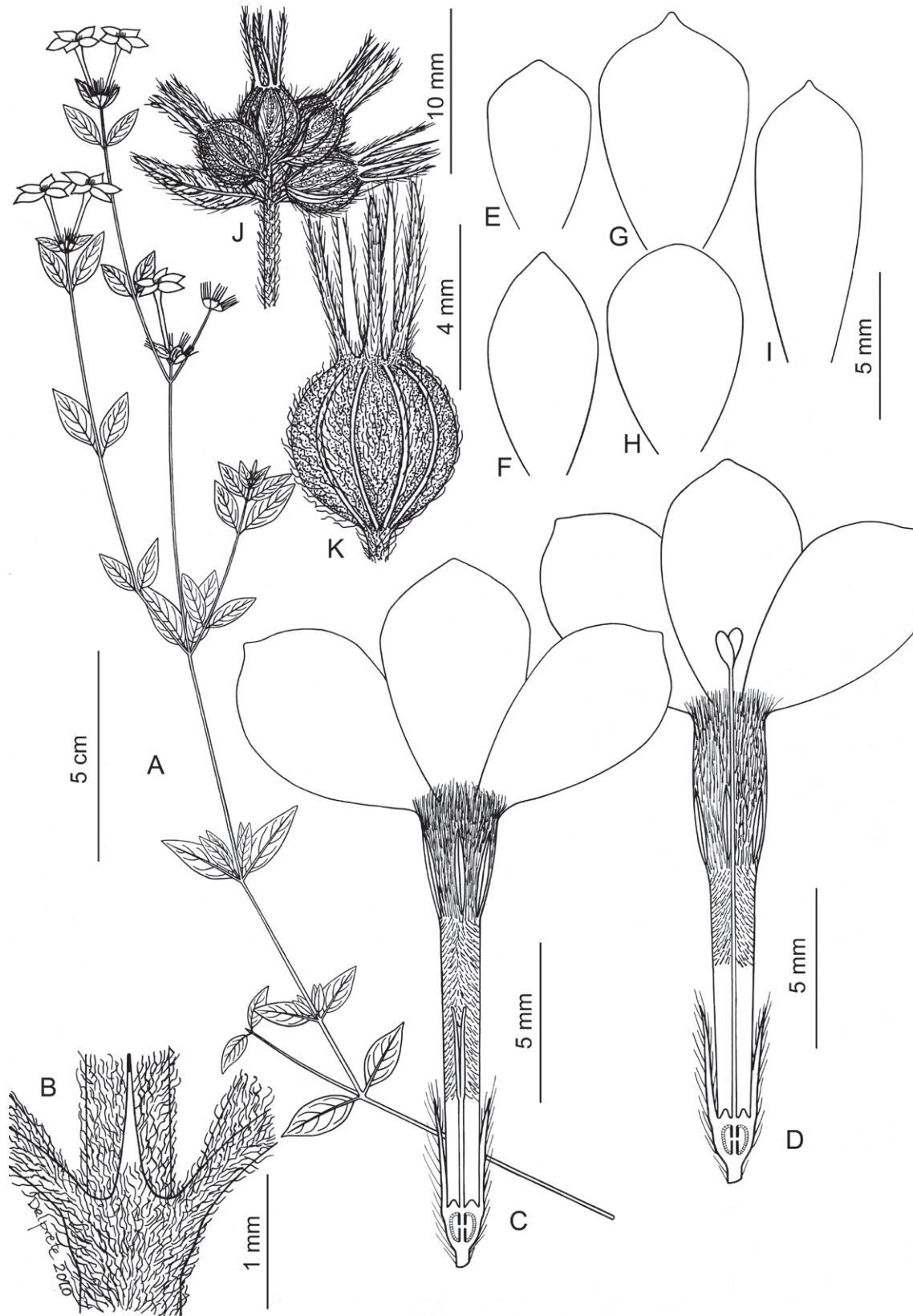


Figure 47.



men, with numerous leaves and several inflorescences with flower buds and flowers in anthesis. At the upper-left corner there is a label, handwritten by Aublet, which states “Classis V, pentandria monogynia, *Sipanea pratensis*, hist. guia. franc. 148, T. 56.” Therefore, sheet P-JJR 8: 281 is the lectotype of *S. pratensis*.

Steyermark (1967: 272) cited the type of *Sipanea pratensis* as follows: “Photo of type from BM, (1) Guiana, Aublet, (2) Cayenne, von Rohr.” Two collections are mounted on the BM sheet, barcode 000614306, with most of the branches collected by Aublet, and one branch collected by Julius von Rohr. Aublet’s specimens are identified with No. 1, and are represented by one large, much-branched specimen with several inflorescences with flowers in anthesis and flower buds (mounted at the center-left of the sheet), one branch with an inflorescence and a couple of flowers in anthesis (mounted near the right margin of the sheet), and a small sterile branch with a couple of nodes (mounted on the upper right corner of the sheet). Rohr’s specimen, identified with No. 2, is a single branch (mounted on top of the distal nodes of the largest Aublet specimen) with two terminal inflorescences, one with flowers in anthesis, and the other with flower buds. At the bottom of the sheet, handwritten in pencil, probably by Solander, is “*Sipanea pratensis* Aublet!” And on the back of the sheet, handwritten by Solander is “Guiana. F. Aublet. 1, Cayenne. Jul. v. Rohr. 2”, and there is a printed label saying “New York Botanical Garden, Neg. No. N.S. 553 [1952].” Following the type citation of Lanjouw and Uittien (1940: 158), the three specimens with No. 1 on the BM sheet are the isolectotype of *S. pratensis*. Whereas, the specimen with No. 2 was collected by Rohr and is not original material.

**Hybridization between varieties:** One gathering from the Upper Oyapock River, State of Amapá, Brazil, presents transitional characters between *S. pratensis* var. *dichotoma* and var. *pratensis*, and was collected in an intermediate locality of the distribution of the two varieties. In these specimens the inflorescences are congested during anthesis and slightly expanded, with lateral branches 6–9 mm long at fruit maturity (typical of var. *dichotoma*), while the fruits are globose and costate (typical of var. *pratensis*). This collection is:

**BRAZIL: Amapá:** Upper Oyapock River, Brazilian side [“rive brésilienne”], Roche Mon Père [ca. 3°17’N, 52°12’W], 19 Feb. 1968 (fl, fr), R.A.A. Oldeman & C. Sastre 309 (CAY, P, U).

**Distribution and ecology:** Distributed in Guyana, Suriname, French Guiana, and the Brazilian states of

Amapá and Pará (Figure 49). Perennial herb, prostrate, decumbent or ascending (exceptionally erect), often forming extended patches in open savannas and at forest margins, at edges of and on inselbergs, road margins, and disturbed vegetation, in sunny exposures, on white or brown sand, and on granitic or lateritic soils; from near sea level to 750 m altitude.

**Phenology:** Due to the rapid phenology of this species it is common to find individuals with flowers and fruits. Flowering and fruiting the whole year around.

**Suggested conservation status: Least Concern (LC).** This variety is most common in French Guiana and in the contiguous Brazilian state of Amapá, and is less frequent in Guyana, Suriname, and the Brazilian state of Pará. It often forms large patches in open savannas and forest margins, at edges of and on inselbergs, and is also found as a ruderal species quite common at road margins, and in disturbed vegetation. Taking into account that it is a ruderal species known from numerous collections, it is here positioned the Least Concern (LC) category, following IUCN criteria (IUCN 2012, 2019).

**Vernacular names:** FRENCH GUIANA: arajada (Arawak, *Capus* 215), ka?api?i (Wayapi, *Grenand* 1228), ka?api?ipilã, sə?əkea (Wayapi, *Sastre* 4458), Peruβia (Palikur, *Granville* 4295), Peruβia, winikei (Palikur, *Berton* 153), winikwei (Palikur, *Berton* 162).

**Uses:** One herbarium label (*Albertini* 18) reports that it is used in French Guiana to cure conjunctivitis in humans and cataracts in dogs.

**Specimens examined: GUYANA:** Potaro-Siparuni Region, Kato, 4°40’N, 59°55’W, 750 m, savanna and low forest vegetation on pale red clay soils, 11 Mar. 1989 (fl, fr), *W. Hahn et al.* 5587 (NY); East Coast Water Conservancy, SE of Georgetown, canal SE of Lamaha Stop-off, 27 Nov. 1919 (fl), A.S. *Hitchcock* 16981 (NY, S, US); without locality, s.d. (fl), *J.P.B. von Rohr s.n.* (C [2 sheets]); without locality, s.d. (fl), *J.P.B. von Rohr* 43 (C); without locality, s.d. (fl), *E. Rudge s.n.* (BM 000614350) (BM).

**SURINAME:** Doetabikinosoe, Marowynne River, Pedrosoengue-val, 1 Jul. 1939 (fr), *G. Stahel* 73 (NY, U).

**FRENCH GUIANA:** Piste de Saint-Elie, sideroad vegetation, 5°20’N, 53°0’W, 27 Apr. 1994 (fl), *S. Albertini* 18 (CAY); Haut Oyapock, petite ile entre Eureupou Crique et Riv. Motoura, Jan. 1948 (fl), *E. Aubert De la Rüe s.n.* (P P00729323); Haut Oyapock, Roche Sikini [ca. 3°15’N, 52°16’W], zone dénudé en foret, Vallée riv. Siki-



**Figure 48.** *Sipanea pratensis* var. *pratensis*. A. Habitat on roadside vegetation. B. Habit. C. Detail of inflorescences, top view. D. Detail of inflorescence, side view. E. Short-styled and long-styled flowers longitudinally dissected, from the same population. Photos taken by Piero Delprete on 19 April 2017, Commune de Matoury, RN 2, pk 10–11, French Guiana, where *Delprete 12882–12884* were collected.

- ni, 50 m, 16 Mar. 1949 (fl), *E. Aubert De la Rüe s.n.* (P [3 sheets, P00729314, P00729324, P00729326]); without locality, 1961 (fl, fr), *A. Aubreville s.n.* (P [P00719295]); N° 3, without locality, 1961 (fl), *A. Aubreville s.n.* (P [P00729316]); Savane Gallion, near Carrefour Gallion, 4°47'N, 52°25'W, 7 Jul. 2004 (fl), *L. Barrabé & F. Crozier 55* (CAY, NY); Charvein, savane blanche, 26 Oct. 1913 (fl), *R. Benoist 126* (P); Pariacabo, 10 Jul. 1914 (fl), *R. Benoist 1414* (P); Oyapock River Basin, Crique Gabaret, 3°55'N, 51°48'W, 11 May 1997 (fl, fr), *M.-E. Berton 153* (CAY); Oyapock River Basin, Commune de Saint-George, edge of private house, 3°53'N, 51°48'W, 10 May 1997 (fl, fr), *M.-E. Berton 162* (CAY); Le Gallion (RN2), 18 Oct. 1981 (fl, fr), *F. Billiet & B. Jadin 1034* (BR, CAY, U); Kourou, piste vers la Montagne de Singes, 24 Oct. 1981 (fl), *F. Billiet & B. Jadin 1142* (BR, CAY); Kourou, savane récemment brûlé, 27 Oct. 1982 (fl), *F. Billiet & B. Jadin 1423* (BR); Piste FRG, km 87 de la RN1, PK 16, 5°11'N, 52°55'W, 13 Feb. 1988 (fl), *F. Billiet & B. Jadin 4403* (AAU, BM, BR, CAY, RB); Route RN2 Cayenne-Regina, PK 67, 4°29'N, 52°19'W, 5 m, 10 Feb. 1993 (fl), *F. Billiet & B. Jadin 5751* (BR, CAY, MO, P); Le Larivot, mangrove à *Avicennia*, 4°53'N, 52°20'W, 14 Nov. 1998 (fl), *F. Billiet & B. Jadin 7099* (BR, CAY); Campo de Passoura, 21 Oct. 1954 (fl, fr), *G.A. Black & Klein 54-17108* (IAN); Campo de Passoura, 25 Oct. 1954 (fl, fr), *G.A. Black & [without initials] Klein 54-17216* (IAN); Savane Gabrielle, degrade d'Escole, 4°41'N, 52°18'W, 4 Aug. 1993 (fl, fr), *P. Blanc & P. Birnbaum BB-93-42* (CAY, NY, U); trail to Bagne des Annamites, 31 Jan. 2003 (fl), *G. Bourdy 3034* (CAY); Route de Monsinery, Kamuyene Kamuyene, 12 Apr. 2005 (fl), *G. Bourdy 3124* (CAY); vicinity of Cayenne, 13 May 1921 (fl, fr), *W.E. Broadway 186* (US), 398 (CAY, US); Savane incluse Agami, 5°15'28"N, 52°48'37"W, 8 Mar. 1995 (fl), *L. Cadamuro & F. Solacroup 399* (CAY); Savane incluse Agami, 5°13'19"N, 52°48'59"W, 8 Mar. 1995 (fl, fr), *L. Cadamuro 424* (CAY); Savane Nicole, 5°15'10"N, 52°46'41"W, 23 Mar. 1995 (fl, fr), *L. Cadamuro & F. Solacroup 496* (CAY); Carrière Roche-Nicole, 23 Feb. 1994 (fl), *L. Cadamuro 621* (CAY); Arawak Village of Sainte Rose de Lima, 23 May 1981 (fl), *F. Capus 215* (CAY), 24 Sep. 1981 (young fr), 229 (CAY); Cayenne, s.d. (fl), *Collector Unknown s.n. (FI-Webb 080083)* (FI-Webb); Savanna W of Cayenne, 26 Oct. 1954 (fl), *R.S. Cowan & B. Maguire 38016* (NY); Savane de Charvin, white sand overlaying laterite-clay, 19 Dec. 1954 (fl, young fr), *R.S. Cowan 38869* (NY, U); Savane Bordelaise, Route du Tour de l'Île, 25 Feb. 1977 (fl), *G. Cremers 4349* (CAY, US); Massif des Emerillons, N inselberg, 350 m, 20 Sep. 1980 (fl, fr), *G. Cremers 6741* (CAY [2 sheets], P [2 sheets], U, UB); Route du Tour de l'Île de Cayenne, R.N. 2, PK 13, 28 Mar. 1986 (fl), *G. Cremers 9404* (CAY); Bassin de l'Approuague, Savane Roche (Inselberg) Virginie, 4°11'N, 52°9'W, 140 m, 12 Feb. 1991 (fl), *G. Cremers & P. Petronelli 11865* (CAY, P, US); Bassin du Bas-Oyapock, Savane Roche (Inselberg) Quatorze de Juillet, 3°58'N, 51°52'W, 50 m, 16 Apr. 1991 (fl), *G. Cremers 12163* (CAY, NY, P, U, US); Savane de Corossony, Piste de Saint-Elie, 5°23'N, 53°0'W, 10 m, 26 Mar. 1992 (fl), *G. Cremers & M.N.C. Bastos 12872* (CAY, MG); Bassin de l'Approuague, Savane Roche (Inselberg) Anabelle, 4°0'N, 52°16'W, 120 m, 10 May 1997 (fl), *G. Cremers 15250* (CAY); Savane de bord de Piste St. Elie, 7 Feb. 1990 (fl), *DEA Paris VI 136* (CAY); Piste de St. Elie, 5°20'N, 53°2'W, 18 Sep. 2005 (fl), *C. Delnatte & C. Girod 141* (CAY), 172 (CAY); Piste de St. Elie, PK 2, savane inondée, 5°22'N, 52°59'W, 8 m, 8 Jan. 2006 (fl), *C. Delnatte et al. 509* (CAY); Macouria, Savane Marivat, locality Maya, 4°56'59"N, 52°26'30"W, 15 m, 1 Apr. 2006 (fl), *C. Delnatte, S. Gonzalez, & F. Crozier 713* (CAY); Cayenne, Source de Baduel, 4°55'30"N, 54°18'40"W, 14 m, 24 Jun. 2006 (fl), *C. Delnatte 859* (CAY); Commune de Roura, Reserve Naturelle Volontaire de Trésor, Route de Kaw, 4°36'N, 52°16'W, 30–200 m, savanna dominated by grasses and sedges with sparse mounts with shrubs 3–5 m tall, 8 Feb. 1999 (fl), *P.G. Delprete & F. Crozier 7157* (CAY); Commune de Kourou, Savane des Pères, ca. 2 km from Station Radar-Télémessure of CSG, towards Kourou, right side, savanna with sparse trees of *Byrsonima crassifolia* and *Curatella americana*, mostly grassy field, seasonally inundated, at the moment with water 5–30 cm deep, 5°7'7"N, 52°39'4"W, 30 m, 5 Jul. 2009 (fl), *P.G. Delprete 10586* (CAY, GB, MO, NY, US), 10605 (CAY, F, G, L, MO, US); Commune de Macouria, Savane de Matiti, open field savanna dominated by graminaceae and cyperaceae, with sparse shrubs and small trees, including *Palicourea rigida*, area slightly elevated, not flooded, on rocky-lateritic soil, 5°4'10"N, 52°35'47"W, 10–20 m, 12 Jul. 2009 (fl), *P.G. Delprete 10651* (CAY, NY, US); Commune de Macouria, Savane de Matiti, savanna permanently flooded, with dense shrubs, mostly Melastomaceae, vines and small herbs, at the moment with water 10–20 cm deep, 5°4'10"N, 52°35'47"W, 10 m, 12 Jul. 2009 (fl), *P.G. Delprete 10678* (CAY, GB, MO, P, US); Commune de Monsinery, Savane de Monsinery, across the road from Centre de Diffusion Internationale de Guyane, grassy savanna with sparse treelets and shrubs, sometimes with sparse islets of shrubby vegetation, 4°53'39"N, 52°30'25"W, 20 m, 18 Jul. 2009 (fl), *P.G. Delprete 10704* (CAY, L, K, MO, P, US); Commune de Iracoubo, Savanne de Trou Poisson, road towards Kaja Nostra Hotel, grassy savanna dominated by poaceae and cyperaceae, with sparse trees and shrubs, seasonally

- inundated, 5°25'27"N, 53°5'19"W, 10 m, 19 Jul. 2009 (fl), *P.G. Delprete 10746* (CAY, K, US); Commune de Iracoubo, Savanne de Trou Poisson, road continuing after Kaja Nostra Hotel, ca. 2 km after the hotel, open field grassy savanna dominated by poaceae and cyperaceae 10–40 cm tall, soil of fine white sand, 5°24'25"N, 53°5'43"W, 20 m, 30 Jan. 2010 (fl), *P.G. Delprete & O. Vrignaud 10845* (CAY, MO, P); Commune de Iracoubo, Savanne de Trou Poisson, road continuing after Kaja Nostra Hotel, ca. 1.5 km after the hotel, open field savanna with sparse grasses and many species of small herbs, soil of fine white sand, very impregnated with water due the abundant rainy season, 5°24'25"N, 53°5'43"W, 20 m, 27 Apr. 2012 (fl), *P.G. Delprete 11880* (CAY, K); Commune de Montsinery, road RD-5, ca. 1 km before the bridge on Crique Aguille, on road between Port Inini and Village Patawa, secondary vegetation at edge of roadside, 4°50'60"N, 52°30'58"W, 10 m, 12 Oct. 2014 (fl, fr), *P.G. Delprete 12619* (CAY); Commune de Kourou, Savane des Pères, ca. 2 km from Station Radar-Télémesure of CSG, towards Kourou, right side, open field herbaceous savanna with sparse trees of *Byrsonima crassifolia* and *Curatella americana*, seasonally inundated, at the moment soil moist but not inundated, 5°7'7"N, 52°39'4"W, 20–30 m, 21 Mar. 2015 (fr), *P.G. Delprete et al. 12625* (CAY); Commune de Sinnamary, Region of Pripri de Yiyi, Maison Nature, going E from Maison Nature, secondary vegetation resembling savanic vegetation (once forested), with sparse tall shrubs, 5°25'8"N, 53°2'48"W, 20 m, 18 Apr. 2015 (fl), *P.G. Delprete 12633* (B, CAY, MO, NY, P), *12634* (CAY, L, NY, P), *12635* (CAY, MO, NY, P), *12636* (CAY, MO, NY, P); Commune de Matoury, Route Nationale 2 (RN2), between PK 10 and PK 11, roadside vegetation with herbs and small shrubs, soil gravelly-lateritic, 4°48'48"N, 52°21'10"W, 10 m, 19 Apr. 2017 (fl), *P.G. Delprete 12882* (B, CAY, F, MO, P), *12885* (BR, CAY, L, MO, NY, P, S, US), *12886* (CAY, G, MO, NY, RB), *12887* (B, BR, CAY, F, G, GB, MG, MO, P, NY, RB, S, US); Commune de Saint George de l'Oyapock, roadside vegetation on Route Nationale 2 (RN2), at ca. 1 km outside Saint-George, 3°54'13"N, 51°48'47"W, 10 m, 28 May 2018 (fl), *P.G. Delprete 12892* (CAY, F, MO, NY, P); Commune de Regina, Savane Roche Virginie (Inselberg), vegetation growing at the edges and on organic substance accumulating on the granitic inselberg, 4°11'55"N, 52°9'5"W, 150 m, 19 Feb. 2019 (fl), *P.G. Delprete & J.C. da Silva 12902* (CAY, F, MO, NY, P, US), *12904* (CAY [2 sheets], F, L, INPA, MG, MO, NY, P, R, RB, UB, US); route Saint Laurent du Maroni–Mana, 21 km de Saint Laurent, savane, 21 Jan. 1974 (fl), *B. Descoings & C. Luu 20478* (P); Mts. de Kaw, Trésor Reserve, near main trail, 4°35'N, 52°16'W, 210–378 m, 30 Jan. 2003 (fl), *R.C. Ek 1390* (CAY, U); Piste St. Elie, km 15.5, roadside vegetation, 25 Sep. 1982 (fl), *C. Feuillet 190* (CAY); Inselberg Borne N. 4 (border between French Guiana and Brazil), 13 Apr. 1983 (fl), *C. Feuillet 845* (CAY); Montagne de Kaw, Piste Roura-Kaw, PK 8, 4°33'N, 52°9'W, 26 Nov. 1985 (fl), *C. Feuillet 2882* (CAY, P); Piste St. Elie, Savane Corossony, 5°23'N, 53°0'W, 27 Dec. 1986 (fl), *C. Feuillet 4037* (CAY); Bassin de l'Arataye, Montagne des Nouragues, 4°3'N, 52°42'W, lisiere se savane roche (inselberg), 27 Aug. 1987 (fr), *C. Feuillet 4363* (CAY); E of Cayenne, Route de Montabo, PK 3.5, 14 Apr. 1982 (fl), *A. Fournet 147* (CAY, P); Sauts de l'Oiapoque [?], 1900 (fl), *F. Geay 889* (P); SW of Cayenne, near airport, open savanna, 50 m, 21 Feb. 1985 (fl), *A. Gentry & E. Zardini 50266* (CAY, MO); Savane Roche Malmaison [inselberg], 4°58'25", 52°26'20"W, 18 Sep. 2008 (fl, fr), *S. Gonzalez & M. Chaix 1440* (CAY); Savane de Tonate, 5 Feb. 1978 (fl), *J.J. de Granville 2855* (CAY, P, UB); Montagne de Kaw, Camp Caiman, vegetation secondaire sur laterite, 13 Jun. 1979 (fl), *J.J. de Granville & G. Cremers 2947* (CAY, P, U, UB); Massif des Emerillons, zone central, inselberg [ca. 3°15'N, 53°5'W], 300 m, 11 Sep. 1980 (fl), *J.J. de Granville 3817* (CAY [2 sheets], NY, P, U, UB); Region of Oyapock River estuary, SE slope of Montagne des Trois Pitons, inselberg, 250 m, 21 Jan. 1981 (fl), *J.J. de Granville 4295* (CAY); Inselberg à l'extrémité NW des Monts de la Trinité [ca. 4°35'N, 53°21'W], 6 Aug. 1981 (fl), *J.J. de Granville 4775* (BR, CAY [2 sheets], P, UB); Montagnes de la Trinité, NW inselberg, [ca. 4°40'N, 53°20'W], 350 m, 17 Jan. 1984 (fl) *J.J. de Granville et al. 6109* (CAY, MO, NY, P, U, US); Upper Camopi River Basin, Mont Belvédère [ca. 2°24'N, 53°6'W], inselberg on S slope, 300 m, 21 Nov. 1984 (fl), *J.J. de Granville 6926* (B, BR, CAY [2 sheets], G, MO, NY, P, U, US); Upper Marouini River Basin, Roche Koutou, 2°53'N, 54°4'W, 220 m, 15 Aug. 1987 (fl, fr), *J.J. de Granville et al. 9307* (CAY, US); Upper Marouini River Basin, Camp N. 3, Roche N. 1, Akouba Booka goo Soula, lisiere de savane roche (inselberg margin), 500 m SW, 2°36'N, 54°1'W, 160 m, 26 Aug. 1987 (fl, fr), *J.J. de Granville et al. 9729* (B, CAY, MO, NY, P, U, US); Upper Marouini River Basin, Roche N. 3 Monpé Soula, 2°39'N, 54°5'W, 200 m, 1 Sep. 1987 (fl, fr), *J.J. de Granville et al. 9916* (CAY [2 sheets], MO, NY, P, US); Savanne Renner, 5°20'N, 52°53'W, 3 m, 18 Apr. 1996 (fl, fr), *J.J. de Granville 14377* (CAY, MO, P); Monts d'Awara, central inselberg, 2°49'0"N, 53°22'0"W, 6 Jul. 2002 (fl, fr), *J.J. de Granville et al. 15060* (B, CAY, K, MO, NY, P); Ile de Cayenne, Crique Cabassou, 4°54'N, 54°18'W, 14 Aug. 2002 (fl, fr), *J.J. de Granville & F. Crozier 15619* (CAY, MO); Upper Wanapi River Basin, central dome of inselberg, 2°31'0"N, 53°49'20"W, 14 Apr. 2004 (fl, fr), *J.J. de Granville et al.*

- 15909 (CAY, MO, P, U); Mont Saint Marcel, zone SE du massif, inselberg, 2°23'N, 53°0'W, 300 m, 18 Jul. 2002 (fl), *J.J. de Granville et al.* 15291 (B, CAY [2 sheets], K, MO, NY, P), 15319 (B, CAY [2 sheets], NY, P); Upper Marouini River, Inselberg D.Z., 2°36'30"N, 54°1'45"W, 200 m, 21 Jun. 2004 (fl, young fr), *J.J. de Granville & F. Crozier* 16302 (CAY, MO, P, U), 180 m, 1 Jul. 2004 (young fr), *J.J. de Granville & F. Crozier* 16568 (CAY, MO, P); Commune de Macouria, route de la Carapa, locality Maya, 4°56'59"N, 52°26'30"W, 9 m, 2 Aug. 2005 (fl, fr), *J.J. de Granville & O. Tostain* 17038 (CAY, MO); Site Ariane 4, Crique Karouabo, C.S.G., 5°14'N, 52°47'W, 8 m, 11 May 2007 (fl, fr), *J.J. de Granville & O. Tostain* 17343 (CAY); Savane Matiti, zone du projet d'implantation d'éoliennes, 5°5'15"N, 52°35'50"W, 4 m, 12 Aug. 2008 (fl, fr), *J.J. de Granville* 17626 (CAY, MO); Trois Saut, Inselberg of Mont St. Marcel [ca. 2°23'N, 53°1'W], 16 Mar. 1976 (fl), *P. Grenand* 1228 (CAY [2 sheets]); Savane de Montsinery, 23 Mar. 1982 (fl), *P. Grenand* 2066 (CAY [2 sheets], P); Route Cayenne-Rochambeau, 17–21 Jul. 1962 (fl), *F. Hallé* 441 (CAY [3 sheets], P, U, US); Trou Poisson, s.d. (fl), *V. Hequet* 1150 (CAY); Savane Lambert, s.d. (fl), *V. Hequet* 1240 (CAY); Ile de Cayenne, Route de Baduel, garden, 4°56'N, 52°19'W, 10 m, 23 Apr. 1987 (fl), *M. Hoff* 5068 (CAY); Savane Matiti, 5°5'N, 52°37'W, 10 m, 13 Dec. 1988 (fl), *M. Hoff & J.J. de Granville* 5474 (B, CAY); Savane Mamaribo, R.N. 1, 1 km E, 5°31'N, 53°22'W, 10 m, 26 May 1989 (fl), *Hoff, M. & G. Cremers* 5618 (CAY); Kourou, Passoura, Parcelle I, 13 Apr. 1956 (fl), *J. Hoock s.n.* (P [P00729335]); Route de Sinnamary, 19 May 1956 (fl), *J. Hoock s.n.* (P [P00729338]); without locality, Relevé N. 1, 22 Mar. 1962 (fl, fr), *J. Hoock s.n.* (IAN, NY, P [P00729336], U, US); without locality, relevé n. 3, 6 Apr. 1962 (fl), ORSTOM – IFAT s.n. (P [7 sheets; P00729444–P00729450], R); Route de l'Est [RN2], 1 km after the bridge on the Conté River, 20 Apr. 1975 (fl), *H. Jacquemin* 1625 (CAY); Kaw Mountains, Trésor, Favard Creek, savanna, 4°36'N, 52°18'W, 7 m, 8 Feb. 1996 (fl), *M.J. Jansen-Jacobs et al.* 5114 (CAY, P, U); Kourou, Savane des Pères, 5°7'N, 52°39'W, 10 m, 24 Jul. 2000 (fl, fr), *G. Kallin* 115 (CAY [3 sheets]); [Cayenne], Route de Montabo, Jardin des Alexandres, 4 Apr. 1986 (fl, young fr), *Kodjoed, J.F.* 106 (CAY [3 sheets]); Savane Bordelaise, 25 Jan. 1983 (fl), *J.-N. Labat* 212 (P); Kourou, Savane de Combi, pépinière du Cirad, 31 Dec. 2010 (fl), *O. Lachenaud* 1014 (BR, CAY); Savane-roche Virginie, route Regina-St. George, 4°11'44"N, 52°9'8"W, 59 m, 7 Apr. 2014 (fl), *O. Lachenaud* 1739 (BR, CAY, MO, P); Bassin de l'Approuague-Arataye, Montagne des Nouragues, 4°3'N, 52°42'W, 100 m, lisière se savane roche (inselberg), Feb. 1990 (fl), *D. Larpin* 864 (CAY, P); without locality, 1792 (fl, fr), *J.B. Leblond s.n.* (P00729382); Savane Sinnamary, exploitation maraichère de Benoit Girard, s.d., *A. Leclerc* 36 (CAY), 37 (CAY), 77 (CAY); Montagne des Cheveaux, S of Cayenne (30 km along rd), 4°43'N, 52°25'W, 50 m, 23 Jan. 1978 (fl), *A.J.M. Leeuwenberg* 11628 (CAY, NY, WAG); Cayenne, 1857–1859 (fl), *E.J.F. Leguillou s.n.* (P [2 sheets; P00729305, P00729308]); without locality, s.d. (fl, fr), *J.P. Leprieur s.n.* (P [2 sheets, P00729395, P00729396]); without locality, s.d. [1835] (fl), *J.P. Leprieur s.n.* (BM [000614351], FI-Webb [080082], P [P00729393]); Mt. Sineri, 1838 (fl, fr), *J.P. Leprieur* 36 (P); without locality, s.d. (fl), *J.B.L.T. Leschenault de la Tour* 392 (P [2 sheets]); Kourou, Route de Tonate, 25 Jan. 1974 (fl), *J.P. Lescure* 42 (CAY, P); Ile de Cayenne, Circuit du Lac du Rorota, 10 Feb. 1974 (fl), *J.P. Lescure* 81 (CAY, P [2 sheets]); Terrain de l'IRAT, Cabassou, 5 Apr. 1976 (fl), *J.P. Lescure* 599 (CAY [2 sheets], P, U); Cayenne, s.d. (fl), *J. Martin* 77 (P); without locality, 1842 (fl), *E.M. Mélinon* 42 (P); Ile de Cayenne, Cabassou, Station IRAT, 9 Dec. 1982 (fl), *H. Merlier* GY-242 (CAY); Monts d'Awara, central inselberg, 2°48'59"N, 53°21'59"W, 24 Mar. 2006 (fl), *J.F. Molino & D. Sabatier* 2252 (CAY); [Maroni River Basin], Sauts du Litany, Antekume Pata, 5 Aug. 1980 (fl), *C. Moretti* 1191 (CAY); Savannas of Gallion, ca. 20 km SW of Cayenne, 4°46'N, 52°24'W, 26 Apr. 2001 (fl, fr), *S.A. Mori, E.F. Hecklaum, B.W. Keeley, T.A. Lobova & H.P. Pekham* 25198 (CAY, NY, P); Nouragues Filed Station, ca. 7 km from Saut Pararé on the Arataï River, near Crique Cascade, 1.2 km SW of Camp Inselberg, 4°5'N, 52°41'W, 120 m, 13 Aug. 2004 (fl), *S.A. Mori, T. Lobova, N. Pitcairn, C. Geiselman & B. Vlášáková* 25776 (CAY, NY); Ile de Cayenne, bord de route du Tour de l'Ile, Carrefour de la Route de Stoupan, prairies inondables, 24 Jan. 1968 (fl), *R.A.A. Oldeman & C. Sastre* 2 (CAY, IAN, NY, P, U, US); Fleuve Oyapock, Savane Canot Fandé-Fandé, 5 Jul. 1969 (fl, fr), *R.A.A. Oldeman B-2473* (CAY [2 sheets], NY, P, U); fleuve Oyapock, savane roche (inselberg) Canari Zozo, 7 Jul. 1969 (fl), *R.A.A. Oldeman B-2484* (CAY [2 sheets], NY, P [2 sheets], U); Lower Oyapock River, downstream from Saut Fourmi, 3 Jun. 1970 (fl), *R.A.A. Oldeman B-3353* (CAY, NY, P); Ile de Cayenne, route forestière près du pont des cascades, 16 Apr. 1971 (fl), *R.A.A. Oldeman B-3885* (CAY [2 sheets], P); Ile de Cayenne, base of Mt. Matoury, 30 Jul. 1965 (fl, fr), *R.A.A. Oldeman* 1499 (CAY, P, U); Ile de Cayenne, S.M.A., near Camp Tigre, left side of Route de Cabassou, 8 Mar. 1971 (fl, fr), *R.A.A. Oldeman* 3217 (CAY [2 sheets], P, U, US); savanne aux environs de Kourou, May–Jun. 1969 (fl, fr), *J. Petitbon* 59 (P); without locality, 1826 (fl, fr), *P.A. Poiteau s.n.* (P [3 sheets; P00729387–P00729389]); Ile de Cayenne, Cabassou, Station IRAT, 14 Feb. 1983 (fl), *M.F. Prévost* 1252 (CAY, P, UB); Station de

la Piste de St. Elie (ECEREX), PK 15.7, 5°17'N, 53°3'W, 24 Mar. 2000 (fl), *M.F. Prévost* 3830 (CAY, NY, P); Piste de St. Elie, 20 Mar. 1994 (fl), *Y. Purwanto* 79 (CAY); Cayenne, école d'agriculture de Suzini, entre les monts Bourda et St. Martin, 29 Feb. 1976 (fl), *A. Raynal & C. Tirel* 18302 (NY, P, U); Savane du Gallion, ca. 20 km SSE de Cayenne, 4 Mar. 1976 (fl), *A. Raynal & C. Tirel* 18452 (NY, P, U); in pratis Guyane, s.d. [1781–1785] (fl), *L.C.M. Richard s.n.* (P P00729306); in pratis, campestribus, s.d. [1781–1785] (fl), *L.C.M. Richard s.n.* (P P00729383); without locality, s.d. [1781–1785] (fl), *L.C.M. Richard s.n.* (P P00729384); old airstrip at Le Gallion, ca. 10 m SW of Rochambeau airport along RN2, 4°47'N, 52°24'W, 8 Mar. 1994 (fl), *J.H.E. Rova et al.* 1901 (CAY, GB, NY, S); Route de St.-Elie, savanna along rd at km 1.5, 5°22'N, 53°0'W, 15 Mar. 1994 (fl), *J.H.E. Rova et al.* 1980 (CAY, GB, S), 1981 (CAY, GB, S); Savane de Organabo, 5 km E of Organabo on RN 1, 5°32'N, 53°25'W, 20 Mar. 1994 (fl), *J.H.E. Rova et al.* 2018 (CAY, GB, S); Cayenne, 1859 (fl), *P.A. Sagot s.n.* (P [2 sheets] P00729301, P00729304); Cayenne, 1859 (fl), *P.A. Sagot* 1246 (P [P00729303]); Bassin de l'Arataye, Montagne des Nouragues, S slope, 4°3'N, 52°42'W, vegetation herbacea de Savane roche

(inselberg), 16 Jan. 1988 (fl, fr), *C. Sartou* 168 (CAY), 8 Jan. 1988 (fl, fr), *C. Sartou* 191 (CAY); Savane de Kourou, savane à *Byrsonima crassifolia*, 7 Jul. 1972 (fl, fr), *C. Sastre* 1328 (CAY [2 sheets], IAN, NY, P, U); Maroni River, Saut Lassédédé (between Beligui and Loca), 17 Apr. 1975 (fl), *C. Sastre et al.* 3822 (CAY, P); Haut Oyapock, Mont Saint Marcel, inselberg, [ca. 2°25'N, 53°0'W], 300–450 m, 20 Mar. 1976 (fl), *C. Sastre* 4458 (CAY, P, US); Savane Changement, 6 km from Sinnamary, PK 79, 16 Apr. 1976 (fl), *C. Sastre* 4772 (CAY [2 sheets], P); Matiti, savane seche a *Byrsonima verbascifolia*, sur sable gris, 12 Aug. 1961 (fl), *R. Schnell* 11067 (P); Pariacabo, 14 Aug. 1961 (fl), *R. Schnell* 11123 (P [2 sheets]); Stoupan, savane de la ferme Petit, Jul. 1948 (fl), *Service Forestier* 3034 (U); route Larivot, Jan. 1950 (fl), *Service Forestier* 3493 (P); Mont Joly, Aug. 1950 (fl), *Service Forestier* 3591 (P); La Madelaine, Jan. 1951 (fl), *Service Forestier* 3680 (P); without locality, s.d. (fl), *Service Forestier* 3685 (P); Region Littorale, Digue Yiyi, 5°25'N, 53°4'W, 2 m, 26 May 1992 (fl), *D. Toriola-Marbot & M. Hoff* 92 (CAY); RN 1, Savane Yiyi, 5°24'N, 53°2'W, 7 m, 25 Jun. 1992 (fl, fr), *D. Toriola-Marbot* 281 (CAY); Station de l'Arataye, Approuage River Basin, 4°2'N, 52°42'W, 200 m, 26 Mar. 1987

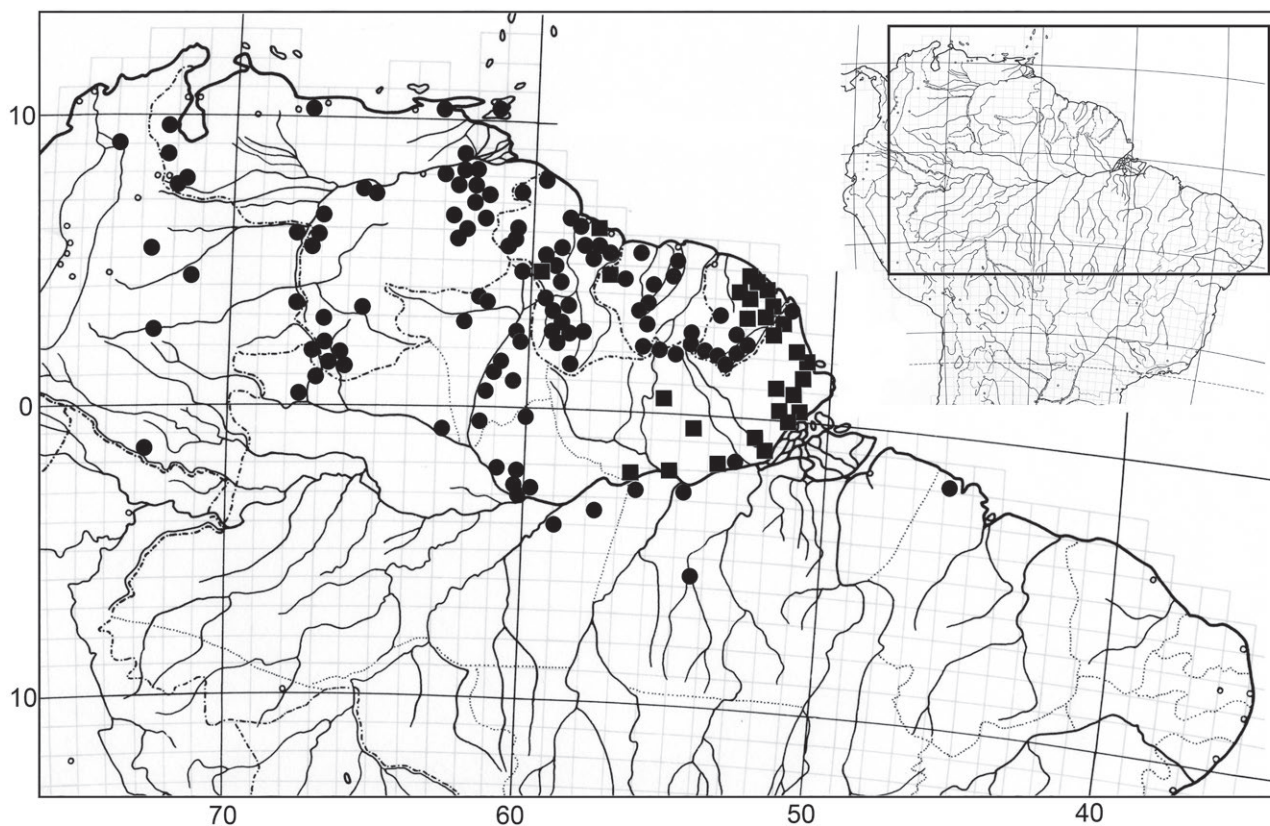


Figure 49. Distribution of *Sipanea pratensis* var. *pratensis* (squares) and *S. pratensis* var. *dichotoma* (circles).

(fl), *J.F. Villiers 4022* (CAY); Arataye River, 60 km WSW of Regina, 6 km N of Saut Pararé, 14 Feb. 1988 (fl), *J.F. Villiers 4334* (CAY); Inselberg Roche-Dachine, 3°28'N, 53°13'W, 220 m, 2 Apr. 1997 (fl), *J.F. Villiers & C. Sartou 6001* (CAY [3 sheets], NY, P); Inselberg Mont Chauve, 3°49'N, 53°44'W, 265 m, 13 Apr. 1997 (fl), *J.F. Villiers & C. Sartou 6094* (CAY, P); end of road overlooking Kaw, 4°30'N, 52°4'W, 13 Sep. 1987 (fr), *A.L. Weizman & W. Hahn 311* (NY, U); "Guyane", s.d. (fl), *Collector Unknown 174* (FI).

**BRAZIL. Amapá:** Rod. Perimetral Norte, km 162, beira da estrada, 5 Jun. 1992 (fl), *O. Alencar & B. Santos 007* (HAMAB); entre km 105 e Local Areal, 5 km E de Porto Grande [ca. 0°42'N, 51°24'W], posto ao Norte, 18 Oct. 1979 (fl, fr), *D.F. Austin et al. 7110* (INPA, MG, NY, US); Macapá [ca. 0°22'N, 51°3'W], campina, 30 Oct. 1949 (fl), *G.A. Black 49-8251* (IAN); Oiapoque, esquerda do Campo de Aviação [3°51'N, 51°47'W], 7 Oct. 1949 (fl), *G.A. Black 49-8444* (IAN, P, U); Mun. Amapá, Fazenda Tucunaré, campo com manchas de campina, apresentando ilhas espalhadas, 19 Apr. 1950 (fl), *G.A. Black & I. Lobato 50-9462* (IAN), 50-9469 (IAN, INPA); 6 km N of Porto Grande, Cerrado close to Cerrado-mata transition zone, 0°44'N, 51°20'W, 6 Aug. 1993 (fl, fr), *S. Bridgewater et al. S121* (HAMAB, INPA); Porto Grande, BR-210, área antropizada, 0°40'29"S, 51°30'1"W, Apr. 2014 (fl), *A.L.R. Cardoso 1305* (MG); Mun. Mazagão, próximo a entrada de Vila Santa Clara, 28 May 2001 (fl), *N.V. Costa Neto & O.T. Silveira 511* (HAMAB); Mun. Calçoene, cerrado na margem do Rio Cassiporé, 3°46'N, 51°9'W, 31 Aug. 2002 (fl), *Costa S.V. Neto & M.S. Silva 1019* (HAMAB); Mun. Tartarugalzinho, Rio Tartarugalzinho [ca. 1°30'N, 50°54'W], erva de 30 cm, 12 Aug. 2004 (fl), *S.V. Costa Neto et al. 1561* (HAMAB); Serra do Navio, Rio Amapari, forest of lower slope of Observatorio Ore Body, 70–300 m, 8 Nov. 1954 (fl), *R.S. Cowan 38152* (NY); Serra do Navio, Rio Amapari, Terezinha-Reservatorio trail, wet lowland forest, 75 m, 13 Nov. 1954 (fl), *R.S. Cowan 38317* (IAN, NY, RB, U); Mun. Macapá, km 43, área de baixada, 20 Mar. 1982 (fl, fr), *M. Dantas 948* (IAN); Amapá [2°3'N, 50°47'W], campo, 27 Jun. 1904 (fl, fr), *A. Ducke s.n.* (MG 4804) (MG); Oiapoque, Clevelandia, pasto, 23 Apr. 1960 (fl, fr), *W.A. Egler 1405* (MG, NY); Rio Oiapoque, Roche Mon Pére [ca. 3°17'N, 52°12'W], among loose rocks in soil-filled depression on large granitic outcrop, 3°33'N, 52°5'W, 17 Aug. 1960 (fl, fr), *W.A. Egler 47652* (Irwin collection number) (IAN, MG, NY, US); Porto de Santana [ca. 0°2'S, 51°51'W], 29 Jan. 1961 (fl), *M. Emmerich & A.G. Andrade 694* (R); Porto Grande, Rodovia Perimetral Norte, trecho Porto Grande-Serra do Navio, localidade Mungubas, ca. 59 km da BR-156, na entrada

de Porto Grande, 0°38'55"S, 51°50'51"W, 89 m, 21 Jul. 2010 (fl, fr), *C.N. Fraga 2955* (MG, RB); Mun. Macapá, Rio Macacorai, 6 Jul. 1951 (fl), *R.L. Frões & G.A. Black 27265* (IAN, U); Rio Araguari, perto da Cachoeira do Paredão, terra firme, 25 Jul. 1951 (fl), *R.L. Frões & G.A. Black 27691* (IAN); "Guyana Brasileira", Counany [ca. 2°51'N, 51°7'W], 18 Oct. 1895 (fl), *J. Huber Herb. Amaz. 1103* (RB 15627) (RB); Rio Oiapoque, Cachoeira Cacheri, immediately W of mouth of Cricú River, wet sandy soil, 3°43'N, 51°58'W, 15 Aug. 1960 (fl), *H.S. Irwin & W.A. Egler 47543* (IAN, MG, NY [2 sheets], US); Rio Araguari, 20 minutes downriver from Porto Platón, 0°44'N, 51°22'W, 16 Sep. 1961 (fl, fr), *H.S. Irwin et al. 50965* (IAN, NY); Cuxibi, a 150 km de Serra do Navio, entre pastos, 15 Jun. 1966 (fl), *A. Lourteig 1783* (P, R, US); Rio Oiapoque, second-growth woodland along rd between Oiapoque and Clevelandia, frequent, 19 Jul. 1960 (fl), *B. Maguire et al. 47066* (NY); Mun. Calçoene, BR-156, 12 km W of Calçoene, 2°28'N, 51°0'W, 8 Dec. 1984 (fl, fr), *S.A. Mori & R. Cardoso 17266* (HAMAB, MG, US); Mun. Calçoene, BR-156, vicinity of government road camp "Carnot", 53 km WNW of Calçoene, 2°33'N, 51°16'W, 10 Dec. 1984 (fl), *S.A. Mori et al. 17334* (HAMAB, MG, NY); São Joaquim do Pacuí, margem de estrada, 28 Feb. 1981 (fl), [without initials] *Mozart s.n.* (HAMAB No. 2172); Mazagão, BR-156, as proximidades de Vila de Santa Clara, cerrado, 22 Sep. 2001 (fl, fr), *S.V. Neto & G.A.R. Melo 591* (HAMAB); Pracuúba, BR-156, Flexal, beira da estrada em campo aberto, 1°42'N, 50°53'W, 26 Feb. 2001 (fl), *L.A. Pereira, F. Cesarino, S.M. Alfaia, & J.P. Reis 98* (HAMAB, INPA); Amapá, BR-156, crescendo na beira da estrada, 2°3'N, 50°53'W, 13 Mar. 2001 (fl), *L.A. Pereira & M.A.C. Santos 166* (HAMAB, INPA); Mazagão, Estrada do Jari, BR-210, solo arenoso de campo aberto, 0°20'S, 51°52'W, 23 Mar. 2001 (fl), *L.A. Pereira & J.P. Reis 295* (HAMAB, IAN); Mun. Pracuúba, área de campo cerrado, subarbusto 20 cm altura, 16 Jun. 1983 (fl), *L.C. Pinto, Jonas & H.P. Belo 21* (HAMAB); Rio Oiapoque, near Mt. Carupina, 3°33'N, 51°37'W, 10–30 m, 16 Oct. 1960 (fl, fr), *J.M. Pires & L.Y.T. Westra 48878* (Irwin collection number) (IAN, NY, US); Rio Araguari, Porto Platón, 18 Sep. 1961 (fl), *J.M. Pires 51049* (Irwin collection number) (IAN, MG, NY); Mun. Macapá, km 38 para Matapi, 2 Feb. 1955 (fl, fr), *J.M. Pires & N.T. Silva 4795* (IAN); road to Amapá, km 48, 0°17'N, 51°5'W, 7 Jul. 1962 (fl), *J.M. Pires & P.B. Cavalcante 51977* (Irwin collection number) (IAN, MG, NY, US); Colonia do Torrão, forest at border of igarapé, 2°25'N, 51°15'W, 28 Aug. 1962 (fl), *J.M. Pires & P.B. Cavalcante 52622* (Irwin collection number) (IAN, MG, NY); km 104 da BR-156-Macapá, campo cerrado, 5 May 1979 (fr), *B.V. Rabelo s.n.* (Museu Ângelo Costa Lima N. 1412) (MG);

Oiapoque, Aeroporto, campina de areia branca, 20 Mar. 1982 (fl), B.V. *Rabelo RN 1545* (UB); Mun. Macapá, km 104 da BR-156, campo cerrado, 5 May 1979 (fl), B.V. *Rabelo s.n.* (HAMAB No. 1412); Mun. Oiapoque, Aldeia do Manga, Tribo Karipuna, capoeira próximo da Aldeia, 20 Aug. 1981 (fl), B.V. *Rabelo 1303* (HAMAB); Mun. Oiapoque, aeroporto, campina de areia branca, 20 Mar. 1982 (fl), B.V. *Rabelo 1545* (HAMAB); BR-156, km 103, campina de areia branca, 29 Feb. 1984 (fl), B.V. *Rabelo et al. 2544* (HAMAB); Ferreira Gomes [ca. 0°51'N, 51°10'W], cerrado, 23 Jul. 2009 (fl, fr), A.E.S. *Rocha 1131* (HAMAB, MG); Calçoene, savanna, Estrada para Cunanin, 27 Jun. 2010 (fl, fr), A.E.S. *Rocha & S.V.C. Neto 1327* (HAMAB, MG); Mun. Amapá, perto do aeroporto, terreno úmido, campo, erva rasteira, occasional à margem da Estrada, 25 Aug. 1978 (fl), W. *Rodrigues 10059* (INPA); Mun. Amapá, quadrícula SB-22-VA, ponto 44, campos naturais de terra firme, 9 Apr. 1982 (fl), N.A. *Rosa et al. 4201* (MG, NY); Mun. Pracuúba, Vila Porto Franco, cerrado, subarbusto 35 cm altura, 1 Jul. 2002 (fl), M.A.C. *Santo & M.H.A. Martins 283* (HAMAB); Porto Grande, savana, 10 Oct. 103 (fl), M.V.B. *Soares & W.L.S. Silva 103* (MG); Mun. Pracuúba, ruderal, 9 May 1987 (fl), C. *Souza & B.V. Rabelo C-50* (HAMAB). **Pará:** Mun. Faro, Fazenda Santa Olimpia, Campo Umirí, 6 Dec. 1950 (fl), G.A. *Black & P. Ledoux 50-10577* (IAN, U); Óbidos, em torno da Serra do Escama, perto do Lago Pauxí, 22 May 1957 (fl), G.A. *Black & W.A. Egler 57-19454* (IAN), P. *Cavalcante 224* (MG); Prainha [ca. 1°48'S, 53°28'W], capoeira, 10 May 1903 (fl), A. *Ducke s.n. (MG 3601)* (MG); campos a E de Faro, 21 Aug. 1907 (fl, fr), A. *Ducke s.n. (MG 8436)* (MG); Mun. Almeirim [ca. 1°31'S, 52°34'W], Estrada de acesso a Monte Dourado, saindo da cidade, 12 May 2005 (fl), L.C.B. *Lobato 3246* (MG); arredor do Campo de Aviação, margem do Rio Parú, 2 Jun. 1974 (fl), N.A. *Rosa 6* (IAN); Região do Rio Jari, Água Branca, km 3, campo cerrado, 28 Jul. 1969 (fl, fr), N.T. *Silva 2491* (IAN, NY, UB); Mun. Óbidos, Estação Ecológica do Grão Pará, trilha 3, 0°38'33"N, 55°41'47"W, 22 Jan. 2009 (fl), M.G.C. *Souza & G. Teixeira 456* (MG), 24 Jan. 2009 (fl), 533 (MG); Macau airstrip, 1.5 h upstream from Lageira airstrip, on Rio Maicuru, 0°55'S, 54°26'W, 270 m, 24 Jul. 1981 (fl, fr), J.J. *Strudwick et al. 3481* (INPA, MG, MO).

8-5b. *Sipanea pratensis* var. *dichotoma* (Kunth) Steyerem. in Mem. New York Bot. Gard. 17: 273. 1967. (Figures 49–50).

(=) *Sipanea dichotoma* Kunth in Humb. & Bonpl., Nov. Gen. Sp. 3 (quarto): 397. 21 Nov. 1819 ["1820"].

Type: VENEZUELA. "Atures, cataractam Orinocensium," [Atures, Orinoco waterfalls], s.d. [15–17 Apr. 1800], A.J.A. *Bonpland & F.W.H.A. Humboldt 855* (**lectotype** P [barcode P00729459], **here designated**; isolectotype B [barcode B-W 04124-1 0]).

(=) "*Ptychodea pedunculata*" in Cham. & Schldl. in Linnaea 4: 168. 1829, *nom. illeg. superfl. pro syn.*

Type: VENEZUELA. "Atures, cataractam Orinocensium," s.d. [15–17 Apr. 1800], A.J.A. *Bonpland & F.W.H.A. Humboldt 855* (**lectotype** B [barcode B-W 04124-1 0]) **here designated**; isolectotype P [barcode P00729459]). This name was cited by Chamisso & Schlectendal (1829: 168) as a synonym of *Sipanea dichotoma* Kunth.

(=) *Sipanea trichantha* Miq., Linnaea 18(3): 293. 1845 ["1844"].

Type: SURINAME: Onoribo, s.d. (fl, fr), H.C. *Focke 60* (**lectotype** U [barcode U00116946], **here designated**).

(=) *Sipanea colombiana* Wernham, J. Bot. 55: 174. 1917

Type: COLOMBIA. [Norte de Santander]: Ocaña, Crecenoche, 300 m, May [1846–1852] (fl), L. *Schlim 548* (holotype BM [barcode 000614320]; isotypes BR [barcode BR824758], K [without barcode], P [2 sheets, barcodes P00729397 and P00748109]; photo-K NYBG Neg. No. 3247]; photo at NY).

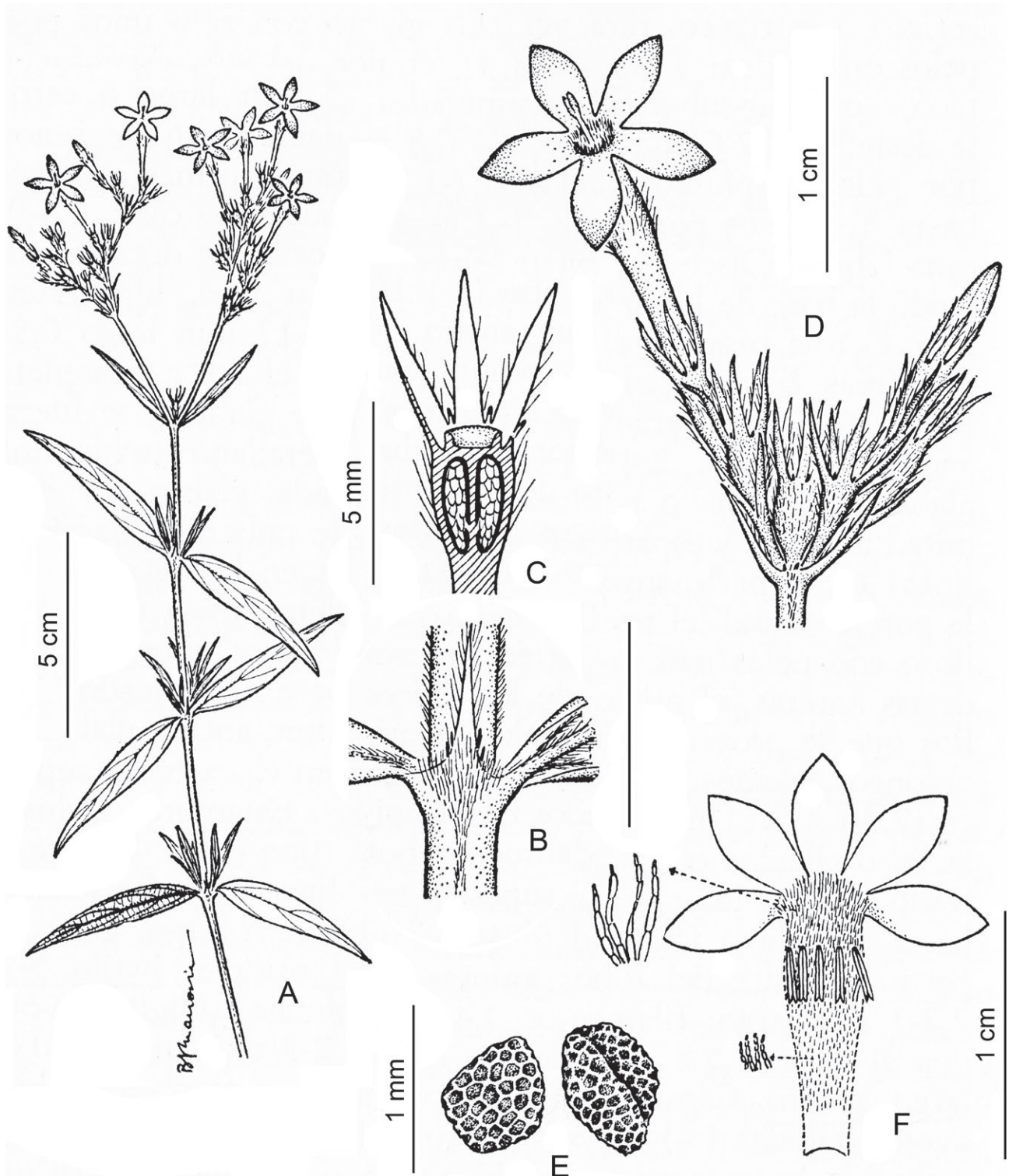
(=) *Sipanea pratensis* var. *dichotoma* f. *brachycarpa* Steyerem., Mem. New York Bot. Gard. 17: 276. 1967

Type: VENEZUELA. Amazonas: Danta (Tapir) Falls, Rio Cuao, Río Orinoco, 125 m, 19 Nov. 1948 (fl, fr), B. *Maguire & L. Politi 27324* (holotype VEN not found; isotypes NY [2 sheets, barcodes NY00133317, and NY 00133318], US [barcode 00137727]).

(=) *Sipanea pratensis* var. *dichotoma* f. *glabriloba* Steyerem., Mem. New York Bot. Gard. 17: 276. 1967

Type: VENEZUELA. Amazonas: Yavita–Pimichín trail, near Yavita, Río Atabapo, 125–140 m, 10 Jun. 1959 (fl, fr), J.J. *Wurdack & L. Adderley 42916* (holotype NY [barcode 0013323]; isotypes S [Acc. No. 10-27872], US [Acc. No. 2320890, barcode 00137728]).





**Figure 50.** *Sipanea pratensis* var. *dichotoma*. A. branch with terminal inflorescence. B. Node with stipule and leaf bases. C. Longitudinal section of hypanthium, ovary and calyx (note colleter at each calyx lobe sinus). D. Inflorescence branchlet. E. Seeds. F. Dissected corolla with detail of hairs at mouth and corolla throat. Illustration by Bruno Manara (Reproduced with permission from *Flora de Venezuela* vol. 9(1), fig. 59. 1974).

(=) *Sipanea pratensis* var. *dichotoma* f. *glabrior* Steyererm., Mem. New York Bot. Gard. 17: 277. 1967

Type: VENEZUELA. Bolivar: Cerro San Borjas, 100–300 m, 12 Dec. 1955 (fl), J.J. Wurdack & J.B. Monachino 39823 (holotype NY [barcode 00133324]; isotype VEN [Acc. No. 65160]).

(=) *Sipanea pratensis* var. *dichotoma* f. *breviflora* Steyererm., Mem. New York Bot. Gard. 17: 277. 1967

Type: VENEZUELA. Bolivar: Cerro between Las Nieves and base of slopes SE of Cerro Picacho, N of Las Nieves, 45 km N of Tumeremo, Altiplanicie de Nuria, 100–300 m, 1–11 Feb. 1961 (fl, fr), J.A. Steyermark 89276 (holotype VEN [Acc. No. 64017]; isotypes NY [4 sheets, barcodes NY00133319, NY00133320, NY00133321, NY00133322]). Steyermark (1967: 277) cited the type of forma *breviflora* as “Steyermark 89276 (holotype VEN).” Therefore, although the VEN specimen Acc. No. 64017 was annotated by Steyermark as isotype, it is the holotype of this taxon.

(=) *Sipanea pubinoda* Steyererm., Mem. New York Bot. Gard. 17: 278. 1967

Type: VENEZUELA. Amazonas: Capibuará, Alto Casiquiare, 120 m, 29 May 1942 (fl, fr), L.L. Williams 15656 (holotype VEN [Acc. No. 16075]; isotypes NY [without barcode], RB [Acc. No. 108624, barcode 00364140], US [2 sheets, barcodes 00604080 and 00137729]; photo at NY).

*Perennial herb* or *subshrub* (basal internodes woody), 0.3–1.5 m tall, basal portion sometimes woody, terrestrial or epipetric (on inselbergs), erect or ascending, rarely decumbent, often forming large populations; stems to 1.8 m long, rarely geniculate, sometimes rooting at nodes; young branches thin to stout, 1–3.3 mm thick, terete, sparsely to densely, appressed or spreading, pubescent or sericeous (hairs whitish or beige, 0.8–2 mm long). *Leaves* with blades broadly ovate, ovate, ovate-elliptic, elliptic, oblong-elliptic, oblong-lanceolate, lanceolate, narrowly lanceolate to narrowly oblong-elliptic, 1.8–7.5 × 0.5–2.5 cm, round, obtuse to acute, rarely decurrent, at base, acute to acuminate at apex; secondary veins 4–8 on each side of midrib, obsolete or slightly impressed above, prominent below. *Inflorescences congested-cymose during anthesis*, 4–8-flowered, heads 0.5–1.8 × 0.3–1.5 cm (excluding corollas) during anthesis, moderately or much expanding and obvi-

ously branched during and/or after anthesis; peduncle (when present) to 7.5 cm long; bracts subtending secondary branches lanceolate, oblong-lanceolate to narrowly lanceolate, 3–5.5 × 0.5–1.1 mm, acute to acuminate at apex, sparsely to densely antrorse-pubescent outside; bracteoles subtending flowers (when present) lanceolate to narrowly lanceolate, 2–3.5 × 0.4–0.5 mm, acute to acuminate at apex, sparsely to densely antrorse-pubescent outside; *inflorescences evidently branched during anthesis*, 4–37-flowered, 1–10 × 0.8–7 cm (excluding corollas) during anthesis, with lateral axes 0.5–7 cm long, more or less elongating during and/or after anthesis, 1–10 cm long (excluding corollas), scorpioid, producing a subsecund monochasial of dichasial appearance; peduncle (when present) to 7.5 cm long, sparsely to densely, appressed or spreading, pubescent or sericeous (hairs whitish or beige, 1.5–2 mm long); bracts subtending secondary branches (when present) lanceolate, oblong-lanceolate, narrowly lanceolate to linear, 2.5–7 × 0.5–1.2 mm, acuminate at apex, sparsely to densely antrorse-pubescent outside, sometimes absent; bracteoles subtending flowers (when present) lanceolate, narrowly lanceolate to linear, 2–7 × 0.4–0.7 mm, appressed pubescent to sericeous outside (hairs whitish or beige, 1.5–2 mm long). *Hypanthium* 0.7–1.5 × 0.5–0.9 mm. *Calyx* lobes lanceolate, narrowly oblong-lanceolate to linear, 2.3–6 × 0.2–0.5 mm. *Corolla* 14–28 mm long; tube (8–)10–17 mm long, 0.4–0.7 mm wide at base, 1.5–3 mm wide at mouth; lobes broadly elliptic, elliptic, obovate, oblong-elliptic to oblanceolate, (sometimes varying in shape and size within the same population), sometimes unequal or of slightly different shape within the same corolla, (2.5–)4–11 × (2–)3–7 mm, obtuse to acute, rarely apiculate when subobtuse or acute, at apex. *Long-styled flowers* [Delprete & Marjanom 12441 (corolla tube 14 mm long), Delprete & Benjamin 12861 (corolla tube 14 mm long), Jansen-Jacobs et al. 1114 (corolla tube 8 mm long)]: stamens inserted at 6–7 mm from base or about the middle of corolla tube; filaments 0.5–0.7 mm long; anthers narrowly oblong-elliptic, 1.8–2.5 mm long, acute at both ends; style exserted 1.5–2.5 mm beyond corolla mouth, (9.5–)15–16.5 mm long; style branches narrowly oblong to oblong-ovate, (0.6–)1.3–1.5 mm long, round at apex. *Short-styled flowers* [Delprete & Marjanom 12440 (corolla tube 12.5 mm long), Delprete & Marjanom 12596 (corolla tube 14 mm long)]: stamens inserted at 4–5.5 mm below corolla mouth; filaments 0.5–0.7 mm long; anthers linear to narrowly oblong-elliptic, 2.5–3 × 0.2–0.3 mm, acute at both ends; style included, 6–8 mm long, glabrous; branches linear, 2–3 mm long, acuminate at apex. *Infructescences* with mature fruits dichotomously branched, more or

less expanded, with scorpioid secondary branches (0.5–)1–10 cm long. *Capsules* longer than broad, cylindrical-oblong to oblong-narrowly ovoid, (3–)4.5–8 × 1.5–3 mm, round to acute at base, thinly woody, commonly smooth or faintly costate when dry, sparsely to densely pubescent to sericeous (hairs 0.5–1.5 mm long) to almost glabrate, pale green when young, turning beige to pale brown when dry.

**Taxonomic notes:** The fate of the botanical specimens gathered by Bonpland and Humboldt has been discussed by several authors (Delprete 2001; Hiepko 2006; Kirkbride & Wiersema 2020; Lack 2004a, 2004b, 2009, 2018; Stauffer et al. 2012). Humboldt divided these collections in several sets. The main set, although incomplete, is currently kept in the Bonpland Herbarium (P-Bonpl.) at the Museum of Natural History in Paris. Bonpland was initially in charge of writing the descriptions for the *Nova genera et species plantarum*, but after several months he renounced to this task. Then, Humboldt invited Carl Ludwig Willdenow (1765–1812) to take up this huge task, to whom he sent a set in Berlin, but he died shortly after. Subsequently, Humboldt invited Carl Sigismund Kunth (1788–1850), then in Berlin, to take up this enormous work. Kunth arrived in Paris in 1813, and started immediately to write the descriptions for the *Nova genera*. Three years later, in 1816, Bonpland emigrated from France to Argentina, with his personal herbarium, which was a third, incomplete set of the collections that he made with Humboldt. Therefore, Kunth and Bonpland were both in Paris from 1813 to 1816, and, as far as I know, it is not possible to exclude the possibility the Kunth was able to study the specimens in Bonpland's personal herbarium during that period. Kunth went to La Rochelle, just before Bonpland's departure, to convince him to leave his personal set and his field book in France, but he was only able to obtain Bonpland's field book ("Journal Botanique"). Bonpland returned his personal herbarium from Argentina in 1832, which arrived in Paris in 1833, and was then integrated in the P general herbarium in 1837. These specimens have the label "Herbier de l'Amérique équatoriale, donné par M. A. Bonpland."

No original specimen of *Sipanea dichotoma* was found in P-Bonpl. and P-JU, but two specimens were found at P and B-W. This is not surprising, as the absence of original specimens in P-Bonpl. has puzzled many botanists (Stauffer et al. 2012). For example, out of the about 350 monocotyledon names described by Kunth, Stauffer et al. (2012) reported that 235 original specimens are not present in P-Bonpl. The P specimen of *S. dichotoma*, with barcode P00729459, has the

label "germ. an 8. Orinoco, no. 855. Pent.<sup>ia</sup>, in Guainia. Atures" handwritten by Bonpland, where "germ. an 8" means that it was collected in the month of Germinal (March–April) and the 8<sup>th</sup> year of the French Republican calendar, which corresponds to 1800. This specimen has a second label with the printed heading "Herb. Mus. Paris" and the print "Herbier de l'Amérique équatoriale, donné par M. A. Bonpland" at the bottom of the label. On the second label it is handwritten (author unknown) "Hedyotis, Sipanea pratensis Aubl., K. Schum. Fl. Bras. VI, pars VI, p. 249." Therefore, this specimen was part of the set that Bonpland returned to Paris from Argentina. It has a simple branch with a few nodes with leaves and axillary brachyblasts, and a terminal, dichomously branched inflorescence with a few open capsules. It is here designated the lectotype of *Sipanea dichotoma*. The image of this specimen is available at: <https://science.mnhn.fr/institution/mnhn/collection/p/item/p00729459>

The original specimen of *S. dichotoma* at B-W, with barcode B-W 04124 -01 0, is inside a folder with the label "Pentandria Monogynia, Ptychodea pedunculata, floribus terminalibus pedunculata, Habitat ad Orinocum" handwritten by Willdenow. On the sheet there are three labels. The first two labels are handwritten by two unknown authors "Sipanea dichotoma H. B. Kth. 3. p 110" and "855 Pent.<sup>ia</sup>, Orinoco (Humboldt)". The third label has "Sipanea pratensis Aubl." handwritten by K. Schumann and the the print "det. Schumann in Fl. Bras." At the lower right corner is handwritten directly on the sheet "Humboldt. W." meaning that this is a specimen that Humboldt sent to Willdenow. This specimen has the same collection number of P00729459, to which is similar by bearing a small branch with a few leafy nodes, and two branched inflorescences with open capsules. This specimen is the isolectotype of *S. dichotoma*. This specimen is also original material of "Ptychodea pedunculata", an illegitimate superfluous name that Chamisso & Schlechtendal (1829: 168) cited as a synonym of *Sipanea dichotoma*. The image of this specimen is available at: <https://ww2.bgbm.org/Herbarium/specimen.cfm?Barcode=BW04124010>

Kunth (in Humboldt & Bonpland (1821 ["1820"]: 397 (quarto)) described *Sipanea dichotoma* as having hypoc crateriform, pink corollas with a tube longer than the calyx, 5-lobed, yellow-pubescent at mouth, with 5 included stamens, and a bilobed style. As both specimens of *Bonpland & Humboldt 855* only have open capsules, Kunth might have used another specimen to describe the flowers, or he might have used Bonpland's field book to complete the description of this species.

Miquel (1844: 49–50), in the introduction of his *Symbolae ad Floram Surinamensem* wrote that Hendrik

Focke (1802–1858) had a profound botanical knowledge, and made excellent herbarium specimens, pickled flowers, drawings made from living plants, and detailed species descriptions. Miquel wrote that he used these specimens and accompanying information for the description of taxa in the *Symbolae ad Floram Surinamensem*. Miquel (1845: 293–294) along with the description of *Sipanea trichantha* Miq. stated that this species is frequent in Suriname, without citing the collection locality or the herbarium of deposit. He started the species description with “Annua? ex cl. Focke perennae, [...]”, which means that is an annual species that, according to Focke, might also be perennial. Therefore, as explained above, original collection to be considered for type designation of new taxa described by Miquel should be specimens collected by Focke in Suriname.

Steyermark (1967: 274) for *S. trichantha* cited “Suriname: [...] *Hostmann* 663 (photo of type of *Sipanea trichantha*),” and in the following page (1967: 275) he wrote “*Sipanea trichantha* Miq., described from Suriname, is conspecific *S. dichotoma* H.B.K. The photo of the type of *S. trichantha* (*Hostmann* 663 from the Delessert Herb.) shows loosely moderately villous stems with elongated leaves with a short, appressed pilosity on the lower nerves and midrib. The lower surface appears glabrate, while the upper surface appears appressed-pilose with short hairs. The photo shows elongate, setaceous calyx-lobes which appear to measure 3.5–4.5 mm long. The corolla lobes in bud appear to show slight pilosity along the outer margins. The characters shown by the photo of the *S. trichantha* type fall within the range of variation matched by various other collections from Suriname with similarly elongated leaves, similar type of inflorescence, calyx-lobes, and corolla-tube, which are to be identified with *S. dichotoma* H.B.K. (= *S. pratensis* var. *dichotoma*), tending toward the variation with longer, slender, calyx-lobes.” However, as discussed above, Miquel stated that all his species descriptions were based on specimens collected by Focke. Therefore, Steyermark’s citation of *Hostmann* 663 at G the as the type of *S. trichantha* cannot be interpreted as an inadvertent neotypification, and should be superseded by a specimen collected by Focke.

According to Stafleu and Cowan (1981), Friedrich Miquel (1811–1871) worked at Utrecht during 1859–1871, his herbarium and types are mostly at U, and additional specimens are present at E, K, L, and P. Accordingly, Ek (1991: 38) confirmed that Focke collected in Suriname and sent his collections to Miquel. At U are present two specimens collected by Focke with the labels “*Sipanea trichantha* sp.” handwritten by Miquel. One specimen, barcode U0016947, has a label “*Sipanea trichantha* [...]

a forte dichotoma HBK, Surinami, Para, poste Wran, s. April, legit Il. C. Focke 153.” The other specimen, barcode U00116946, has the label “*S. trichantha* Miq., *Sipanea pratensis* Aubl., Onoribo, Surinami, in Martu [sic, Martius?] 1023, Focke 60.” The latter specimen, barcode U00116946, collected by Focke near the town of Onoribo, has three branches with flowers in anthesis and fruits, and is here designated the lectotype of *Sipanea trichantha*.

**Distribution and ecology:** Distributed in Colombia, Venezuela, the Guianas, and northern Brazil, in the states of Roraima, Amapá, Amazonas, Pará, and Maranhão (Figure 49). Often forming large populations, in white-sand savannas, brown-sand savannas, on granitic inselbergs, granitic outcrops, swampy margins in savannas, seasonally inundated savannas, open field savannas or savannas with sparse trees of *Curatella Americana* and *Byrsonima* spp., margins of semi-shady forest, creek margins in forests, margins of forest trails, disturbed or secondary vegetation, roadside vegetation; in sunny or semi-shady exposures; on sandy, granitic or lateritic soils; from near sea level to 1200 m altitude.

**Phenology:** Due to the short life span of this species, it is common to find individuals with flowers and fruits. Flowering and fruiting the whole year.

**Suggested conservation status: Least Concern (LC).** This variety is amply distributed in Colombia, Venezuela, the Guianas, and Amazonian Brazil (Roraima, Amapá, Amazonas, Pará, Maranhão). It is most common in various kinds of savannas (see ecology, above), and is also a ruderal species growing at margins of forest trails, in secondary vegetation, and roadside vegetation, often forming large populations. As it is quite common in savannic vegetation and is a ruderal species known by numerous collections, this variety belongs to the Least Concern (LC) category, following IUCN criteria (IUCN 2012, 2019).

**Vernacular names:** VENEZUELA: clavel del agua (Spanish, *Williams* 11770), clavel de pozo (Spanish, *Williams* 11953). SURINAME: nepoko (Karib, *Gonggrijp & Stahel* 805), witbaka (N.E., *Gonggrijp & Stahel* 805). BRAZIL. Roraima: malva do campo (*Jaccoud s.n. (INPA* 285)).

**Specimens examined: COLOMBIA: Amazonas:** Rio Igara-Parana (affl. Río Putumayo), corr. La Chorrera, territoire des indiens Witoto Jitomagaró, famille Kuiru, 17 km en aval de La Chorrera [ca. 1°27’S,

72°45'W], 25 Dec. 1973 (fr), *J. Gasche & J. Desplats* 91 (P), Parcelle 107, 3 Apr. 1974 (fr), 1268 (P), Parcelle 124, 26 Jun. 1974 (fl, fr), *C. Sastre* 3507 (P). **Casanare:** Tauramena [ca. 5°1'N, 72°45'W], sabanas o llanos al S de la población, 550 m, 30 Jun. 1961 (fl), *L. Uribe Uribe* 3757 (US). **Guainía:** Mun. Inírida, Corregimiento de Cacaual, Río Atabapo, Comunidad de Pato Corona, bosque de tierra firme, 3°21'11"N, 67°19'48"W, 10 May 2007 (fl-fr), *D. Cárdenas et al.* 20642 (COAH, NY); Mun. Inírida, Caño Chaquita, sabanas naturales de arenas blancas inundadas, 3°31'12"N, 67°39'11"W, 9 Jul. 2008 (fl-fr), *D. Cárdenas et al.* 21658 (COAH, NY). **Magdalena:** Bajo Magdalena, Sep. 1916 (fl, fr), *M.T. Dawe* 445 (US); 17 km N of El Banco [ca. 9°0'N, 73°58'W], on rd to Chimichagua, very abundant in sabana, 1 Aug. 1938 (fl, fr), *O. Haught* 2216 (NY, US); La Jagua, 100 m, 3 Aug. 1943 (fl, fr), *O. Haught* 3587 (US). **Meta:** Puerto Gaitán, Estación Carimagua, region de Core-Alegría, 4°35'N, 71°18'W, 200–300 m, sabanas arenosas, 10 Jan. 1995 (fl), *F. González & R. Serna* 3378 (NY). **Vaupés:** San José del Guaviare [ca. 2°33'N, 72°38'W], sabana, 240 m, 4 Nov. 1939 (fl-fr), *J. Cuatrecasas* 7411 (US); Río Negro, San Felipe [ca. 1°54'N, 67°4'W], 200 m, 13–25 Nov. 1952 (fl, fr), *H. Humbert* 27496 (P). **Vichada:** Raudal San Borja [ca. 6°2'N, 67°25'W], Ventanas, margen izquierda del Río Orinoco, 100 m, 17 Mar. 1971 (fl, fr), *P. Pinto & C. Sastre* 1291 (P).

**VENEZUELA: Amazonas:** Dpto. Río Negro, selvas pluviales a 8 km SE de San Carlos de Río Negro, por la carretera que va a Solano, 1°10'N, 67°0'W, 12 Apr. 1985 (fl), *G. Aymard et al.* 3507 (MO, MY, PORT); Depto. Atures, Puerto Ayacucho [ca. 5°39'N, 67°37'W], near MARNR fish culture station in fields and woods south of the station, area of many granite outcrops, 90 m, 21 Jan. 1985 (fl), *B.M. Boom & A.L. Weitzman* 5283 (NY); Depto. Río Negro, San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, 1°56'N, 67°3'W, 119 m, 24 Jan. 1985 (fl, fr), *B.M. Boom et al.* 5340 (INPA, MO, NY, US); bords de l'Orenoque, Cerro Carichand, s.d. (fl), *J. Chaffanjon* 101 (P [2 sheets]); San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, 1°56'N, 67°3'W, 119 m, near secondary radar construction site, 5.3 km NNE of San Carlos de Río Negro on Solano Rd., on bulldozed white sand, 23 Mar. 1981 (fl), *H.L. Clark et al.* 7835 (INPA, NY); Alto Orinoco, La Esmeralda [ca. 3°10'N, 65°31'W], scarce in the savanna, 14 Jul. 1951 (fl), *L. Croizat* 86 (NY); Puerto Ayacucho, 24 Mar. 1950 (fl), *H.M. Curran* 136A (NY), 140 (NY); Depto. Río Negro, km 11 NE of San Carlos de Río Negro, along rd to Solano, 1°53'N, 67°2'W, 75 m, 24 Jun. 1984 (fr), *G. Davidse & J.S. Miller* 26493 (NY), 26533 (MO, NY); Depto. Río Negro,

Mamurividi, laja along Río Pasimoni, E bank, 1°50'N, 66°38'W, 75 m, 27 Jun. 1984 (fl, fr), *G. Davidse & J.S. Miller* 26710 (MO, NY, US); Depto. Río Negro, Mucuripari, small laja along the lower part of the Río Baria, 1°20'N, 66°26'W, 80 m, 28 Jun. 1984 (fl, fr), *G. Davidse & J.S. Miller* 26770 (MO, NY, US); Depto. Casiquiare, Culimacare, Indian village on the N bank of the Brazo Casiquiare, 1°58'N, 66°50'W, 75 m, 27 Jun. 1984 (fl), *G. Davidse & J.S. Miller* 26730 (MO, NY, US); Depto. Río Negro, Río Pasimoni, between its mouth and its junction with the Río Baria and the Río Yatua, 1°10'–27'N, 66°25'–32'W, 80 m, inundated forest along river, 22–23 Jul. 1984 (fl), *G. Davidse* 27706 (NY); Depto. Río Negro, lower part of the Río Baria, 1°27'–35'N, 66°32'–35'W, 80 m, inundated forest along river margin, 23–25 Jul. 1984 (fl), *G. Davidse* 27807 (NY); Depto. Atures, Mun. Puerto Ayacucho, Setor Corocito, ca. 3 km N of Puerto Ayacucho, on the road toward El Burro, sabaneta inundable con pequeños arboles (3–7 m) esparcos, vegetation dominated by Poaceae and Cyperaceae, 5°42'N, 67°35'W, 85 m, 5 Jan. 2001 (fl), *P.G. Delprete et al.* 7438 (CAY, MO, P, TFAV, VEN), 7439 (L, NY, TFAV, VEN), 7440 (F, TFAV, VEN), 7441 (CAY [2 sheets], TFAV, VEN), 7442 (VEN); Dpto. Atures, 9 km por arriba del Raudal Remo, 4°34'N, 67°18'W, 120 m, May 1989 (fl), *E. Foldats & J. Velazco* 9528 (NY); bords de l'Orenoque, Savane d'Atures, 28 Jul. 1887 (fr), *A. Gaillard* 77 (P); bords de l'Orenoque, bois humides des bords de l'Atabapo, 31 Aug. 1887 (fl), *A. Gaillard* 191 (P); San Carlos, Río Negro, 100 m, 28–29 Jan. 1930 (fl), *E.G. Holt & W. Gehriger* 305 (US), 312 (NY, US), 329 (NY, RB, US); San Carlos, Río Negro, 100 m, 27 Jan. 1931 (fl), *E.G. Holt & E.R. Blake* 640 (NY, US); terreno situado entre la carretera hacia Samariapo y la pista de aterrizaje del Aeropuerto de Puerto Ayacucho, entre las macollas elevadas de la "cowfoothill" sabana, 5°37'N, 67°36'W, 75 m, 13 Apr. 1977 (fl), *O. Huber* 555 (NY); entre la carretera hacia Samariapo y la pista de aterrizaje del aeropuerto de Puerto Ayacucho, sabana semi-inundada de tierra negra SW de la Estación, 5°37'N, 67°36'W, 75 m, 23 May 1977 (fl, fr), *O. Huber* 779 (NY, US, VEN); terreno situado entre la carretera hacia Samariapo y la pista de aterrizaje del aeropuerto de Puerto Ayacucho, sabana húmeda a lo largo de un pequeño arroyo casi sin agua, al pié de la Laja Grande, 5°37'N, 67°36'W, 75 m, 6 Dec. 1977 (fl), *O. Huber* 1283 (NY); Depto. Atures, ca. 30 km N of Puerto Ayacucho, Sabana de Rincones de Cachorro, 5°48'N, 67°20'W, 80 m, 23 May 1979 (fl), *O. Huber* 3785 (US); Depto. Río Negro, carretera San Carlos-Solano, entre km 4 y 20, 1°56'W, 67°3'W, 120 m, 15 Sep. 1980 (fl, fr), *O. Huber & E. Medina* 5654 (NY, US); Depto. Atures, 56 km NE of Puerto Ayacucho, 170 m, 22 Nov. 1984 (fl, fr), *R. Kral et*

al. 71760 (NY); Dpto. Casiquiare, near Chapezon, between Boca de Casiquiare and Solano, large but flat laja with many depressions with patches of grasses and sedges and patches of shrubs, 9 Nov. 1987 (fl), *R. Liesner & G. Carnevali* 22930 (NY); Río Orinoco, Río Cuao, near Danta (Tapir) Falls, 125 m, 19 Nov. 1948 (fl, fr), *B. Maguire & L. Politi* 27326 (MO, NY); mouth of Cano Arapacua, Río Pacimoni, 120 m, 8 Apr. 1953 (fl, fr), *B. Maguire & J.J. Wurdack* 34918 (NY, UB, US); Ríos Pacimoni, Yatua, Casiquiare, Piedra Catipan, 100–140 m, 30 Nov. 1953 (fl), *B. Maguire et al.* 36474 (NY [2 sheets], US, VEN); Río Negro, slopes of Piedra Nunca (just N of Piedra Cocuy), 200–250 m, 10 Apr. 1953 (fl), *B. Maguire & J.J. Wurdack* 34951 (NY); Depto. Atures, near Puerto Ayacucho [ca. 5°39'N, 67°37'W], 120 m, 17 Jan. 1968 (fl), *L. Ruiz-Terán* 4286 (NY); Depto. Río Negro, near San Carlos de Río Negro [ca. 1°50'N, 67°5'W], 120 m, 17 Jan. 1968 (fl-imm fr), *L. Ruiz-Terán* 4968 (BR, NY, US); San Carlos de Río Negro, ca. 4–5 km along track running eastwards out of the village from airstrip, sandy soil, 120 m, 8 Mar. 1984 (fl, fr), *B.L. Stannard* 67 (U); Selvas pluviales y de rebalse del Río Pasimoni, entre la boca y Piedra Arapacoa, 1°50'N, 66°45'W, 175 m, 20–30 Oct. 1986 (fl, fr), *B. Stergios et al.* 9537 (MO, NY, PORT); Piedra Aracapua y laguna adyacente, selvas de rebalse (Iguapó), Misión Proyecto Vavilov, 1°51'5"N, 66°35'11"W, 3 Nov. 1994 (fl, fr), *B. Stergios et al.* 16213 (NY, PORT, US); San Carlos de Río Negro, sabana y selva alrededores del aeropuerto, 125 m, 17–18 Apr. 1970 (fl), *J.A. Steyermark & G. Bunting* 102712 (NY, P); 10–30 km E of Puerto Ayacucho towards Gavilan, 5°35'N, 67°22'W, 120 m, 11 Jun. 1977 (fl), *J.A. Steyermark et al.* 113887 (NY); Puerto Ayacucho, 100 m, 18 May 1940 (fl), *Ll. Williams* 12979 (US), Apr. 1940 (fl), *Ll. Williams* 13450 (US); camino de Yavita, sitios abierto a lo largo del camino, 128 m, 22 Jan. 1942 (fl, fr), *Ll. Williams* 13876 (S, US), 2 Feb. 1942 (fl, fr), *Ll. Williams* 14147 (NY, S, US); sabana de Atures, 120 m, 26 Jun. 1942 (fl), *Ll. Williams* 15914 (US). **Bolívar:** Mun. Uriman, Campo de Uriman, Morichal, 400 m, 7 Sep. 1954 (fl), *L. Bernardi* 1683 (MER, NY); Río Carrao, Alto Caroní, playos del Salto Hacha, 6°15'N, 62°51'W, 350 m, Mar. 1954 (fl), *F. Cardona Puig* 2871 (NY, US, VEN); Via Upata, Río Caroni, 25 Aug. 1947 (fl), *H.M. Curran* 216 (NY); 61 km SE of Upata (20 km SE of Villa Lola), *Trachypogon* savanna on low hills with very widely spaced *Curatella americana*, 2 Dec. 1973 (fl), *G. Davidse et al.* 4625 (MO, NY); Dto. Piar, Kamarata, disturbed *Trachypogon* savanna around village, 5°42'N, 62°21'W, 470 m, 23 Nov. 1982 (fl), *G. Davidse & O. Huber* 22519 (NY); Mun. Sucre, sabana gramínea abierta dom. por *Tragopogon*, 7°30'N, 65°16'W, 50 m, Jul. 1990 (fl), *L. Delgado* 1246 (NY, PORT, US, VEN); Mun. Piar, sabana gramínea arbustiva densa, 7°4'N, 62°5'W, 100 m, Apr. 1994 (fl), *L. Delgado* 2201 (NY, PORT, US, VEN); Mun. ASC. Farreras, Maripa-Aripao, 7°29'N, 65°20'W, 80 m, Feb. 1990 (fl), *S. Elcoro* 680 (NY, PORT); Distrito Pilar, sabanas en los alrededores del Hato Terecay, ca. 16 km N de El Manteco, 7°28'N, 62°27'W, 300 m, 24 Sep. 1982 (fl), *O. Huber & C. Alarcón* 6592 (NY, US, VEN); N of Guasipati [ca. 7°40'N, 61°57'W], 1 km S of Santa Rosa, 260 m, 19 Mar. 1974 (fl, fr), *A.H. Gentry et al.* 10752 (MO, US); Villa de Upata [ca. 8°10'N, 62°24'W], dans la savanne, 1864 (fl), *R. Grosourdy* 43 (P); Mun. Sifontes, Tumeremo, Via Los Guaicas, roadside, 7°13'N, 61°26'W, 160 m, 19 Feb. 2000 (fl, fr), *C. Knab-Vispo* 1185 (NY); La Gran Sabana, 2 km W of Kamarata, 450 m, 22 Feb. 1967 (fl), *T. Koyama & G. Agostini* 7228 (NY [2 sheets]); Mun. Piar, entre El Miamo y El Palmar, 7°40'N, 61°46'W, 240 m, Apr. 1986 (fl), *E. Sanoja* 1027 (NY); Reserva Forestal Imataca, Pica de la CGV que conduce al medio Río Botanamo (cerca de la confluencia con le Río Corumo) desde la carretera Casa Blanca-Anacoco, selva pluvial, 19–20 Feb. 1983 (fl), *B. Stergios et al.* 5392 (MO, NY, PORT); between Ciudad Bolívar and Río Caroní, sandy openings along small stream in savana, 100 m, 31 Jul. 1944 (fl), *J.A. Steyermark* 57576 (NY, US); vicinity of Urimán, large savanna, 300 m, 30 Apr. 1953 (fl, fr), *J.A. Steyermark* 75281 (NY, US, VEN); Altiplanicie de Nuria, more or less level forest in vicinity of Quebrada Agua Linda, 8–11 km E of Campamento Nuria, E of Hato de Nuria, near pica 35 and 106, 19 Jul. 1960 (fl), *J.A. Steyermark* 86515 (NY); Río Toro (Río Grande), between Río La Reforma and Puerto Rico, N of El Palmar, 200–250 m, 12 Dec. 1960 (fl), *J.A. Steyermark* 87966 (F, NY [3 sheets], US); NW of Camp, 5 km from Hato de Nuria, E of Miamo, Altiplanicie de Nuria, 400 m, avanna bordering morichal, 400–450 m, 10 Jan. 1960 (fl), *J.A. Steyermark* 88332 (NY [3 sheets]); 261 km SW of Caicara del Orinoco, small stream in savanna, 6°10'N, 67°16'W, 110 m, 5 Sep. 1985 (fl), *J.A. Steyermark et al.* 131389 (MO, NY); Distrito Piar, vicinity of Guadequen (Buadequen), Río Acanán (affluent of Río Carrao), W of Cerros Los Hermanos, brushy draw at head of low place of savanna by forest border, 5°56'N, 62°17'W, 470 m, 13–3 and 20 May 1986 (fl), *J.A. Steyermark et al.* 131970 (MO, NY, US, VEN); Bajo Caura, Guayapo, 100 m, 12 Apr. 1939 (fl, fr), *Ll. Williams* 11770 (US); Bajo Caura, 100 m, 21 Apr. 1939 (fl, fr), *Ll. Williams* 11953 (US). **Delta Amacuro:** Río Amacuro, Venezuela-Guyana frontier, Sierra Imataca, downstream from mouth of Yarakita River, 65–80 m, 9 Nov. 1960 (fl), *J.A. Steyermark* 87445 (NY [3 sheets]). **Monagas:** Carretera de Barrancas a Temblador, Puente sobre el Río Uracoa, 8°49'N, 62°27'W, 50 m, vegetación de morichal, 19 Apr. 1973 (fl), *G. Agostini & T. Agostini*

1663 (NY, U, US [2 sheets], VEN); between Montaña de Aguata and Colorado, along Río Caripe, E of Caripe [ca. 10°10'N, 63°30'W], 700–800 m, 19 Apr. 1945 (fl), *J.A. Steyermark* 62237 (NY [2 sheets], US, VEN); Caripito [ca. 10°6'N, 63°6'W], praderas megatermicas, 11 Mar. 1948 (fl), *F. Tamayo* 3492 (NY, US, VEN); open swampy margins of Laguna Grande, just S of La Pica, 3 Oct. 1955 (fl), *J.J. Wurdack & J.V. Monachino* 39556 (NY). **Tachira:** W of El Piñal [San Rafel del Piñal, 7°31'N, 71°57'W], W of bridge over Río Frio, 250–300 m, 27–30 Aug. 1966 (fl), *J.A. Steyermark & M. Rabe* 96664 (NY, U); Montañas de Guafitas, just W and N of El Piñal, sandy steep slopes, ridges and quebradas, 7°32'30"N, 71°58'20"W, 250–300 m, *J.A. Steyermark et al.* 119526 (NY). **Zulia:** Perijá, 30 m, 3 Jan. 1951 (fl, fr), *Hermano Gines* 1569 (US). **State unknown:** Without locality, s.d. (fl), *L. Ruíz Terán* 4295 (NY).

**TRINIDAD:** Erin Savanna, 20 Dec. 1977 (fl, fr), *C.D. Adams* 14323 (NY); Piarco Savanna [ca. 10°35'N, 61°20'W], S of Arouca, 27 Feb. 1920 (fl, fr), *E.G. Britton et al.* 86 (NY); Piarco Savannah, 12 Dec. 1919 (fl, fr), *W.E. Broadway s.n.* (US 1047665) (US); Piarco Savannah, S of Arouca, 27 Feb. 1920 (fl, fr), *W.E. Broadway* 86 (US); Piarco Savannah, 10 Mar. 1929 (fr), *W.E. Broadway* 7142 (BM, US [2 sheets]); locality unknown, s.d. (fl), *Collector Unknown* 3125 (US); 3 miles S of Cunupia, along the Southern Main Road, 40 m, treeless savanna dominated by *Axonopus & Andropogon*, 8 Aug. 1970 (fl), *G. Davidse* 2602 (US); Piarco Savanna, 100 ft [30 m], 19 Jun. 1963 (fl), *M.B. Kalloo B-643* (NY), 21 Feb. 1971 (fl), *B-984* (NY); Erin Savanna, 11 Aug. 1977 (fl), *D. Philcox & E. Ramcharan* 8167 (NY, P); Erin Savanna, open savanna, 65 m, 25 Aug. 1962 (fl, fr), *J.W. Purseglove* 6462 (K, NY, US); Piarco Savanna, 7 Dec. 1891 (fl), *E. Warming* 126 (C, US), s.d., 127 (C), 7 Dec. 1891 (fl), 150 (C, US); St. George, Mausica Savanna, 2–2.5 mi S of D'Abadia P.O., 25 Aug. 1959 (fl), *G.L. Webster* 9887 (S); St. Patrick, Erin Savanna, E of Buenos Ayres, 26 Aug. 1959 (fl, fr), *G.L. Webster et al.* 9921 (S); Pitch Lake, Sep. 1901 (fl), *F. Went* 1045 (U).

**GUYANA:** Waruni-Ituni Savannahs, along Berbice-Rupununi Cattle Trail, 1919 (fl, fr), *A.A. Abraham* 27 (NY); Waruni-Ituni Savannahs, along Berbice-Rupununi Cattle Trail, 24 May 1919 (fl, fr), *A.A. Abraham* 129 (NY); Kaieteur Plateau, Potaro River, 1300 ft, May 1926 (fl, fr), *A.H.G. Alston* 549 (NY); Koriabo River, savanna, 20–22 Jul. 1934 (fl-fr), *W.A. Archer* 2361 (US); Upper Mazaruni River Region, vicinity of Kako, an Akawaio Indian Village on the Kako River near its junction with the Mazaruni River, 5°45'N, 60°35'W, 500 m, 14 Apr. 1987 (fl), *B.M. Boom & D. Gopaul* 7289 (MO, NY); Immatumari, sandy soil, s.d., *A.J. Cheong* 3 (US); Upper

Demerara-Berbice Region, Mabura Hill, 60 km N on Mabura Hill-Linden Hwy, 5°50'N, 58°30'W, 60 m, 4 Jan. 1996 (fl), *H.D. Clarke* 769 (CAY, NY, U, US); Upper Takutu-Upper Essequibo Region, Sand Creek to Shea Village, 2°58'N, 59°31'W, 28 May 1996 (fl), *H.D. Clarke* 1762 (U, US), 1792 (NY); Upper Takutu-Upper Essequibo Region, Maparri River, base of waterfall, 3°20'N, 59°15'W, 2 Jun. 1996 (fl), *H.D. Clarke* 1879 (MO, US); Upper Takutu-Upper Essequibo Region, Bat Mountain, 2°10'N, 59°10'W, 25 Jul. 1996 (fl), *H.D. Clarke* 2459 (MO, US); Upper Takutu-Upper Essequibo Region, Makarapan Mountain, base of S side, 1 m S of camp, 3°56'59"N, 58°52'3"W, 100 m, 29 Sep. 1997 (fl), *H.D. Clarke et al.* 6943 (NY); Cuyuni-Mazaruni Region, Ataro River, below falls of Wayalayeng Village, 5°14'8"N, 60°30'37"W, 488 m, 29 Jun. 2004 (fl, fr), *H.D. Clarke et al.* 12260 (P); Warenero [?], Berbice, brown sand savanna, Oct. 1973 (fl, fr), *A. Cooper* 37 (U); St. Cuthbert's Mission, Mahaica River, white sand savanna, Sep. 1966 (fl), *D.H. Dans* 28 (NY); N Rupununi, savanna, Apr. 1968 (fl), *D.H. Dans* 755 (NY), 902 (NY); Pomeroun District, Moruka River, Mora Landing, 14 Aug. 1921 (fl, fr), *J.S. De La Cruz* 975 (NY, US), 26 Aug. 1921 (fl), 1057 (NY, US); between Demerara and Berbice Rivers, 5°50'N, 15–19 Jul. 1922 (fl, fr), *J.S. De La Cruz* 1578 (NY, US), 1603 (NY, US), 1604 (NY, US); Upper Rupununi River, near Dadanawa, 24–29 Jul. 1922 (fl), *J.S. De La Cruz* 1800 (NY); Pomeroun District, Moruka River, Mora Landing, 21–23 Aug. 1922 (fl, fr), *J.S. De La Cruz* 1816 (NY, US); vicinity of Bartica, on Essequibo River, 6°25'N [58°37'W], 3–12 Sep. 1922 (fl), *J.S. De La Cruz* 1860 (NY, US); Upper Mazaruni River, ca. 60°10'W, 22 Sep.–6 Oct. 1922 (fl, fr), *J.S. De La Cruz* 2118 (NY, US), 2239 (NY, US), 2392 (NY, US); Demerara River, Malali, ca. 5°35'N, 30 Oct.–5 Nov. 1922 (fl, fr), *J.S. De La Cruz* 2630 (NY, US); Upper Mazaruni River, Kamakusa, ca. 59°50'W, 23–29 Nov. 1922 (fl, young fr), *J.S. De La Cruz* 2765 (MO, NY, US); Northwest District, Waini River, 8°20'N, 59°40'W, 3–18 Apr. 1923 (fl, fr), *J.S. De La Cruz* 3573 (NY, US); Northwest District, Wanama River, 7°45'N, 60°15'W, 10–23 May 1923 (fl, fr), *J.S. De La Cruz* 3882 (NY, US), 4047 (NY, US); Kaieteur Falls, Potaro River, 23 Oct.–3 Nov. 1923 (fl, fr), *J.S. De La Cruz* 4448 (NY, US); Potaro-Siparuni Region, Upper Potaro River, Chenapou Village, Aklapanan Savanna, motorkike trail from Chenapou Creek mouth towards Paramakatoi Village, eight hills from creek mouth (ca. 10 km), then small trail to the left, crossing a small waterfall, savanna frequently burned, dominated by *Pteridium arachnoideum* and *Brocchinia micrantha*, on white-sand soil, 4°55'28"N, 59°34'33"W, 510 m, 16 Jun. 2016 (fl, imm fr), *P.G. Delprete & P. Benjamin* 12860B (BRG, CAY, MO); Potaro-

- Siparuni Region, Upper Potaro River, Chenapou Village, disturbed vegetation around village, frequently cut, on lateritic-sandy soil, 4°59'0"N, 59°34'35"W, 470 m, 17 Jun. 2016 (fl, imm fr), *P.G. Delprete & P. Benjamin* 12861 (B, BRG, CAY, K, L, MG, MO, NY, P, US), 12863 (BR, BRG, CAY, F, K, US); Potaro-Siparuni Region, Iwokrama Rainforest Reserve, N of Surama Lake, trail to Lake Surama, frequently burned savanna, brown sand, 4°10'N, 59°3'W, 200 m, 15 Mar. 1995 (fl), *C. Ehringhaus et al.* 60 (CAY, NY, U, US); Rupununi Distr., S Kanuku Mountains, Sand Creek Village, 6 Feb. 1985 (fl), *C. Feuillet* 1628 (CAY); Rupununi River, Sand Creeek, Sep. 1948 (fl), *Forest Department of British Guiana* BW 156 (NY); Cock of the Rock, Dec. 1948 (fl, imm fr), *Forest Department of British Guiana* BW 649 (NY); Rocky hillside, 0.5 mi N of Camp 1, 6 .1952 (fl, imm fr), *Forest Department of British Guiana* Field No. G318 (Record No. 7397) (NY); Parakara Savanna, 8 Dec. 1952 (fl), *Forest Department of British Guiana* Field No. G633 (Record No. 7648) (NY); Upper Takutu-Upper Essequibo Region, Baboon Hill, 1.5 km S of Sand Creek Village, 3°0'N, 59°13'W, 120–150 m, 21 Jun. 1989 (fl, fr), *L.J. Gillespie et al.* 1734 (NY, U, US); Upper Takutu-Upper Essequibo Region, SE Kanuku Mountains, Mt. Ishtaban, upper slopes, 3°15'N, 59°25'W, 500–700 m, 26 Jun. 1989 (fl), *L.J. Gillespie et al.* 1895 (NY); Upper Demerara-Berbice Region, ca. 27 km from Ituni, along Ituni-Kwakwa rd., 5°22'N, 58°7'W, 30–60 m, 16 Jan. 1990 (fl, fr), *L.J. Gillespie et al.* 2965 (CAY, NY, U, US); second-growth thickets along Potaro River, Tumatumari [ca. 5°22'N, 59°0'W], 18 Jun–8 Jul. 1921 (fl), *H.A. Gleason* 44 (NY, US), 45 (NY, US); Rockstone, in and about the village, 13–30 Jul. 1921 (fl), *H.A. Gleason* 703 (NY, US); 2 miles S of St. Ignatius, near Takutu, grassland with scattered trees, dominant: *Curatella*, *Byrsonima*, *Trachypogon*, *Fimbristylis*, 115 m, 1 Aug. 1963 (fl-fr), *R. Goodland* 265 (NY [2 sheets], US); Stand 7, SE of Kumu Creek, high lateritic outcrops, sand and gravel, grassland with scattered trees, dominant: *Curatella*, *Byrsonima*, *Trachypogon*, *Fimbristylis*, 350 ft [ca. 106 m], 14–15 Aug 1963 (fl-fr), *R. Goodland & P.F. Maycock* 422 (NY); Stand 21, Nappi Flats, grassland with scattered trees, dominant: *Curatella*, *Byrsonima*, *Trachypogon*, *Fimbristylis*, 350 ft [ca. 100 m], 11 Sep. 1963 (fl), *R. Goodland & R. Persaud* 653 (NY); Inasa Creek, grassland with scattered trees, dominant: *Curatella*, *Byrsonima*, *Trachypogon*, *Fimbristylis*, 115 m, 20 Sep. 1963 (fl-fr), *R. Goodland* 846 (US); Rupununi Savanna, natural pond near Karanambo Ranch, 3°45'N, 59°19'W, 100–250 m, 21 Nov. 1992 (fl, fr), *A.R.A. Görts-van Rijn et al.* 361 (CAY, NY, U [2 sheets]); Savanna beyond Aratak Mission across Kamuni Creek from Santa Mission, 6°30'N, 58°23'W, 0–200 m, 28 Nov. 1992 (fl, fr), *A.R.A. Görts-van Rijn et al.* 453 (CAY, P, U); Junction of Mazaruni and Cuyuni Rivers, at Kalacoon, Jun. 1927 (fl), *E.H. Graham* 101 (NY); Ituni trail by goat farm, 1 Jul. 1976 (fl, fr), *M.S. Grewal* 212 (U); Potaro-Siparuni Region, Kaieteur Falls National Park, around guest house, 5°10'N, 59°29'W, 500 m, 18 Apr. 1988 (fl), *W. Hahn et al.* 4744 (NY, U, US); St. Ignatius, Rupununi, most marginal land between savanna and marsh, 14 Jul. 1958 (fl, imm fr), *S.G. Harrison* 1283 (NY); Upper Demerara-Berbice Region, lower 3 km of Macouria River, N and S banks, 6°25'N, 58°34'W, 0–15 m, 7 Dec. 1992 (fl), *T.W. Henkel & M. Chin* 335 (NY, U, US); Essequibo Island-West Demerara Region, lower 7 km of Tiger Creek, 6°30'N, 58°39'W, 0–15 m, 12 Dec. 1992 (fl, fr), *T.W. Henkel & M. Chin* 472a (INPA, NY); Potaro-Siparuni Region, Kaieteur Pateau, 3 km WNW from falls along Kaieteur-Kuribong trail, 5°12'N, 59°30'W, 540 m, 22 Jul. 1993 (fl), *T.W. Henkel & R. Williams* 2390 (NY, U, US); Est Berbice Region, Berbice Savanna near Takama Army Base, 5°43'N, 57°57'W, 100 m, 14 Aug. 1993 (fl, fr), *T.W. Henkel et al.* 2515 (CAY, MO, NY, US); Upper Takutu-Upper Essequibo Region, S Rupununi savanna, 5 km S of Aishton along rd to Marudi Mountains, 2°23'N, 59°18'W, 200 m, 9 Sep. 1993 (fl, fr), *T.W. Henkel et al.* 2799 (CAY, MO, NY, U, US); Upper Takutu-Upper Essequibo Region, South Rupununi Savanna, Aishalton village, 2°31'N, 59°20'W, 200 m, 3 Aug. 1993 (fl, fr), *T.W. Henkel & R. James* 3970 (NY, U, US); Potaro-Siparuni Region, Pakaraima Mts., Upper Ireng River watershed, Kaatnang River, near base of Malakwalai-Tipu, 4°48'N, 60°12'W, 700 m, 9 Jul. 1994 (fl), *T.W. Henkel & M. Chin* 5489 (CAY [2 sheets], NY, U, US); Upper Takutu-Upper Essequibo Region, northern Rupununi Savanna, 2.5 km NW of Karanambo Ranch, 3°45'N, 59°19'W, 100–120 m, 11 Mar. 1992 (fl, fr), *B. Hoffman* 1248 (CAY, NY, U, US); Cuyuni-Mazaruni Region, Pakaraima Mountains, Kurupung River, landing at base of Makrega Falls, 6°7'N, 60°20'W, 85 m, 18 Jul. 1992 (fl), *B. Hoffman* 2075 (MO, NY, US); Upper Takutu-Upper Essequibo Region, NW Kanuku Mountains, 12 km ESE of Nappi Village in foothills, 3°23'N, 59°29'W, 170 m, 10 Feb. 1993 (fl, fr), *B. Hoffman* 3664 (MO, US); Kaieteur Savanna, 1936 (fl), *G. Hollister s.n.* (NY); Rupununi District, Lethem, stream bank 1 mile N of city, 14 Apr. 1956 (fl), *H.S. Irwin* 570 (US); Rupununi District, Lethem, Swail S of Lethem, near Takutu River, 15 Apr. 1956 (fl, fr), *H.S. Irwin* 620 (US), 622 (US); Rupununi Savanna, Lethem, 3°23'N, 59°47'W, 80 m, 27 Oct. 1987 (fl, fr), *M.J. Jansen-Jacobs et al.* 552 (CAY, NY, P [2 sheets], U, US); Rupununi Savanna, Mora Savanna, near Toroebroe Creek, 3°23'N, 59°29'W, 145 m, 21 Nov. 1987 (fl, fr), *M.J. Jansen-Jacobs et al.* 1114 (CAY, U, US); Rupununi Savanna, Nappi Village, 3°25'N, 59°35'W, 110 m, 1



- Dec. 1987 (fl, fr), *M.J. Jansen-Jacobs et al. 1379* (CAY, NY, P, U, US); Essequibo River, Gunn's Savanna, 1°39'N, 58°38'W, 240–260 m, 3 Sep. 1989 (fl, fr), *M.J. Jansen-Jacobs et al. 1434* (CAY, MO, NY, U), 26 Sep. 1989 (fl, fr), 1836 (CAY, NY, U); Rupununi District, Kuyuwini Landing, Kuyuwini River, savanna, 10 Feb. 1991 (fl, fr), *M.J. Jansen-Jacobs et al. 2512* (CAY, NY, P, U); Rupununi District, Kuyuwini Landing, Kuyuwini River, savanna, 29 Oct. 1992 (fl), *M.J. Jansen-Jacobs et al. 3156* (CAY, NY, P, U, US); Rupununi District, Manari, savanna, 3°26'N, 59°46'W, 80 m, 12 Jul. 1995 (fl), *M.J. Jansen-Jacobs et al. 4419* (CAY, NY, P, U); Kanuku Mountains, Moco Moco River, 3°18'N, 59°39'W, 140–180 m, 14 Jul. 1995 (fl), *M.J. Jansen-Jacobs et al. 4463* (MO, U, US); South Rupununi District, Wakadanawa Savanna, 1°60'N, 59°34'W, 290 m, 8 Sep. 1997 (fl, fr), *M.J. Jansen-Jacobs et al. 5424* (MO, NY, P, U); Corentyne River, Nov. 1879 (fl), *G.S. Jenman 294* (P); Bartica, Nov. 1888 (fl, fr), *G.S. Jenman 4723* (BM, NY [mounted on the same sheet with *Jenman 5453*], US); Potaro River, Kaieteur Savannah, Sep.–Oct. 1881 (fl), *G.S. Jenman 855* (P); Mazaruni River, Aug. 1889 (fl, fr), *Jenman, G.S. 5453* (BM, NY, US); Rupununi River, Ruimatter, Oct. 1889 (fl, fr), *G.S. Jenman 5520* (US); Japacourna [?], Jan–Feb. 1901 (fl, fr), *G.S. Jenman 7829* (NY); creek 2 miles S of Araquoi, 2 Nov. 1957 (fl, fr), *C.D.K. Kooch 88* (NY, U); Bartica, Waipiole Luce, 7 Oct. 1922 (fl), *H. Lang 133* (US); Rupununi Savanna, in directionem borealem de montibus Kanuku, maurisie-laagte a.d. voet v.d. Manakaparuheuvels ten z.o. van Jawarie, 14 Feb. 1959 (fl fr), *J. Lanjouw 760* (U); Cuyuni River, Camaria Road, 15–30 m, 12 Feb. 1951 (fl, fr), *Lorkie, J.R. 214* (S); Rupununi District, Manari, 3°28'N, 59°41'W, 21 Oct. 1979 (fl, fr), *P.J.M. Maas & L.Y.T. Westra 3702* (U), 22 Oct. 1979 (fl), 3754 (S, MO, NY, U); Sand Hills, W of Abary River, 5°55'N, 57°54'W, 4 Oct. 1981 (fl), *P.J.M. Maas et al. 5512* (MO, NY, P, S, U); Rupununi River, Monkey Pond Landing, SW of Mt. Makarapan, 3°53'N, 58°55'W, 10 Sep. 1988 (fl), *P.J.M. Maas et al. 7346* (MG, MO, U, US), 11 Sep. 1988 (fl), 7380 (CAY, U, US); Kaieteur Plateau, savannas, 14 May 1944 (fl), *B. Maguire & D.B. Fanshawe 23472* (NY); Mount Ayanganna, Pakaraima Mountains, between Ayanganna and Chinowieng, 1000–1200 m, 7–8 Feb. 1955 (fl), *B. Maguire et al. 40639* (NY); Southern Pakaraima Mountains, Kamana Savanna, en route to Kopinang Falls, pebbly red laterite, 28 Aug. 1961 (fl), *B. Maguire et al. 45974A* (NY); Ando Savanna, Sukabi River (affl. Ireng River), 800 m, 16 Sep. 1961 (fl, fr), *B. Maguire et al. 46184A* (MO, NY); Waranama Ranch, Wiruni Ituni Savannah, Sep. 1929 (fl, fr), *E.B. Martyn 86* (NY); Upper Takutu-Upper Essequibo Region, woods between Lake Surama and Surama Village, 4°9'N, 59°3'W, 65–75 m, 22 Feb. 1990 (fl), *T. McDowell et al. 1984* (CAY, NY); East Berbice-Corentyne Region, Baba Grant Sawmill landing, along banks of Corentine River, above Cow Falls, 5°0'N, 57°42'W, 10–25 m, 21 Apr. 1990 (fl, fr), *T. McDowell & D. Gopaul 2403* (CAY, NY, U, US); Cuyuni-Mazaruni Region, Waramaden, around village and between airstrip and creek, 5°48'N, 60°44'W, 490 m, 12 Jun. 1990 (fl, fr), *T. McDowell & D. Gopaul 3209* (CAY, MO, NY, US); Potaro-Siparuni Region, in woods along creek at SW of Eagle Mt., along Potaro-Konawaruk Rd., 5°12'N, 59°7'W, 107–152 m, 12 Oct. 1990 (fl, fr), *T. McDowell & D. Gopaul 3506* (CAY, MO, NY, U, US); Cuyuni-Mazaruni Region, along road from Ariching airstrip to Mazaruni River 6°10'N, 60°7'W, 137 m, 22 Feb. 1991 (fl, fr), *T. McDowell 4055* (MO, NY, U, US); Cuyuni-Mazaruni Region, route to Crommer's Farm, 2 km SE of Haiamatiupu, 5°27'N, 60°31'W, 550 m, 21 Jun. 1991 (fl-imm fr), *T. McDowell & B. Hoffman 4761* (NY); Mazaruni River, settlement, 8 Aug. 1933 (fl, fr), *C.D. Mell & R.C. Mell 226* (NY, US); on rd. to St. Cuthbert's Mission, ca. 10 km in from the Linden-Soesdyke Hwy, ca. 50 km S of Georgetown, open savannah, 8 Aug. 1976 (fl), *S.A. Mori et al. 8039* (NY, US); Mazaruni-Potaro District, Bartica-Potaro Road, 24 miles S of Bartica at Forest Service "24 mile Camp", 50–125 m, 20 Aug. 1976 (fl), *S.A. Mori et al. 8183* (NY, US); East Berbice-Corentyne Region, Baranka Landing, Piruru Savanna, 5°11'21"N, 57°17'7"W, 20 m, 1 Apr. 1995 (fl, fr), *P. Mutchnick 1143* (NY, U, US); Upper Mazaruni District, Kamarang River, Waramadong, 2800 m, 6 Oct. 1938 (fl, fr), *A.S. Pinkus 21* (NY, US); Mazaruni-Potaro Region, Pakaraima Mts., N of Imbaimadai, 5°43'N, 60°18'W, 518 m, 20 Jun. 1986 (fl), *J.J. Pipoly & K. Alfred 7880a* (US); Mazaruni-Potaro Region, Pakaraima Mts., Imbaimadai Creek, W of Imbaimadai, 5°42'N, 60°18'W, 500 m, 22 Jun. 1986 (fl), *J.J. Pipoly & K. Alfred 7969* (CAY, NY, P, U, US); East Berbice-Corentyne Region, S Awara Savanna, ca. 35 mi S of Torani Canal, on Canje River, 3 mi SE of Digitima Creek 5°43'N, 57°32'W, 0–25 m, 18 Dec. 1986 (fl), *J.J. Pipoly et al. 9385* (NY); East Berbice-Corentyne Region, Left (S) bank of Upper Canje River, W of Digitima Creek, 5°36'N, 57°35'W, 1–25 m, 19 Dec. 1986 (fl), *J.J. Pipoly et al. 9457* (MO, NY, US); Upper Demerara-Berbice Region, ca. 15 km E of Rockstone, on Linden-Rockstone rd., secondary *Eperua* forest, *Dimorpan-dra* thickets & Savannas, deep white sand, sandy loam, loamy sand, 5°58'N, 58°30'W, 1–50 m, 19 Dec. 1986 (fl), *J.J. Pipoly & G. Gharbarran 9575* (NY); East Berbice-Corentyne Region, Canje River, 0.75 km N of Ekwarun River, disturbed tall evergreen forest on brown loamy sands, 5°20'N, 57°38'W, 1–25 m, 9 Apr. 1987 (fl, fr), *J.J. Pipoly et al. 11332* (CAY, MO, NY, US); Bartika [now

Bartical], along road in the jungle 12–15 miles from the town, 28 Aug. 1935 (fl), *D. Potter 5341* (BR); Upper Mazaruni District, Kamarang, footpath in the village and along airstrip, man-made savanna, 5°52'N, 60°37'W, 525 m, 18 Oct. 1985 (fl), *H.E. Robinson 85-0054* (NY, US); Cuyuny River, sides of portage road at lower Camaria Landing, 23 Nov. 1929 (fl), *N.Y. Sandwith 655* (NY, RB); without locality, s.d. (fl), *R.H. Schomburgk s.n.* (FI-Webb); without locality, s.d. (fl), *R.H. Schomburgk s.n.* (P P00748113); Berbice, moist savannahs, 1837 (fl), *R.H. Schomburgk Ser. I, 15* (BM, BR, P, U [2 sheets], US [2 sheets]); without locality, moist savannahs, 1837 (fl, fr), *R.H. Schomburgk Ser. I, 95* (BM, BR, FI-Webb, NY, P, US); Pirara, 1838 (fl, fr), *R.H. Schomburgk Ser. I, 723* (FI-Webb, mounted on the same sheet with two branches of *Declieuxia chiococcoides* Kunth); Basin of Rupununi River, near mouth of Charwair Creek, ca. 2°35'N, 1–4 Nov. 1937 (fl, fr), *A.C. Smith 2390* (NY, P, S, U, US); without locality, s.d., *F.L. Splitgerber s.n.* (P P00729339); West-Demerara, Mabura Hill, 180 km SSE of Georgetown, Demerara Landing, 7 km up the Great Falls, 5°20'N, 54°40'W, 0–50 m, 14 Jun. 1988 (fl), *H. ter Steege & G.J. ter Steege 407* (CAY, U, US).

**SURINAME:** Potaro River, Kangaruna Landing, Oct. 1922 (fl, fr), *A.A. Abraham 349* (U); Tumuc-Humac Mountains, Talouakem, 2°31'N, 54°45'W, 430–530 m, open vegetation at base of granite, 9 Aug. 1993 (fl, fr), *P. Acevedo-Rodriguez et al. 5958* (CAY [2 sheets], MO, NY, U, US); without locality, 1841 (fl, fr), *M. Berthoud-Coulon 176* (BM, NY [2 sheets]); Coppename River, Aug. 1901 (fl), *H. Boon 1077* (U), Sep. 1901 (fl), *1147* (U); Suriname River, 1908 (fl, fr), *Coll. Indigen. s.n. (U 001806)* (U), *s.n. (U 0016988)* (U); without locality, s.d. (fl), *Collector Unknown [probably Hostmann] s.n. (BR 825740)* (BR, probable type material of *S. trichantha*); Brokopondo, Brownsberg Nature Park, trail to Mazaruni Val., primary forest, light gaps, 4°56'N, 55°11'W, 400–450 m, 23 Jan. 1999 (fl, fr), *P.G. Delprete & Flora of the Guianas Symposium Tour Participants 7082* (BBS, CAY, MO, NY, P, U, US); Sipaliwini Distr., Sipaliwini Village, savanna N of the the airstrip, with sparse trees of *Curatella americana* (3–5 m tall), herbaceous layer dominated by grasses and sedges, with many species of flowering plants, 2°1'39"N, 56°7'23"W, 240 m, 16 Apr. 2014 (fl, imm fr), *P.G. Delprete & G.P. Marjanom 12349* (BBS, CAY, GB, K, L); Sipaliwini Distr., Sipaliwini Village, trail from the Sipaliwini Village to the Sipaliwini River, secondary forest with sparse trees 25–30 m tall and canopy 15–20 m tall, herb 50–130 cm tall, found as sparse individuals in large standing of more than 100 individuals, 2°1'14"N, 56°7'23"W, 250 m, 16 Apr. 2014 (fl, imm fr), *P.G. Delprete & G.P. Marjanom 12386* (B, BBS, CAY, F, GB, K, L,

MO, US); Sipaliwini Distr., Sipaliwini Village, trail from the Sipaliwini airstrip towards the Sipaliwini Nature Reserve, ca. 2 km of the airstrip, savanna with sparse *Curatella Americana* trees (3–5 m tall) and herbaceous layer dominated by grasses and sedges, white-sand soil, herb 70–100 cm tall, 2°1'53"N, 56°6'53"W, 230 m, 18 Apr. 2014 (fl, imm fr), *P.G. Delprete & G.P. Marjanom 12440* (BBS, CAY, F, G, L, K, NY, P), *12441* (B, BBS, BR, C, CAY, F, GB, L, K, MO, NY, P, RB, S, US); Sipaliwini Distr., Sipaliwini Village, trail from the Sipaliwini Village to the Sipaliwini River, secondary forest with sparse trees 25–30 m tall and canopy 15–20 m tall, herb 50–130 cm tall, vegetation at the edge of the trail, fine gray sandy soil, 2°1'14"N, 56°7'23"W, 250 m, 19 Apr. 2014 (fl, imm fr), *P.G. Delprete & G.P. Marjanom 12449* (B, BBS, CAY, K, L, MG, MO, NY, P, US), *12450* (BBS, BR, CAY, F, G, GB, RB, S, US); Sipaliwini Distr., Sipaliwini Village, small savanna on the other side of the Sipaliwini River with respect to the Sipaliwini Village (S of the village), savanna with rolling hills, with sparse with sparse trees of *Curatella Americana* and a few other species, grass layer dominated by grasses and sedges, 2°1'6"N, 56°7'23"W, 220–230 m, 20 Apr. 2014 (fl, imm fr), *P.G. Delprete & G.P. Marjanom 12466* (BBS, C, CAY, FT, L, P); Sipaliwini Distr., Sipaliwini Village, disturbed area around the village, adventitious plants, 2°1'28"N, 56°7'29"W, 240 m, 26 Apr. 2014 (fl, imm fr), *P.G. Delprete & G.P. Marjanom 12596* (BBS, CAY, L, P); Zanderij-complex, kleihoudende zand-savanne, 31 Jul. 1952 (fl, fr), *I.J.G. Dirven LP297* (U); Lobin-savanna inter Zanderij I et Hannover, Aug. 1958 (fl), *J. van Donselaar & W.A.E. van Donselaar 319* (NY); Paramaribo, in pratis et cortis cultis, 2 Jul. 1902 (fl), *E. Essed 93* (U); Saramacca District, Experimental Farm Coebiti, 5°20'N, 55°30'W, 10 Nov. 1981 (fl), *A.P. Everarts 524* (CAY, U, US); Dam, langs de spoorbaan, 9 Nov. 1950 (fl, fr), *J. Florschütz & P.A. Florschütz 156* (U); Brokobotovale in de Boven-Saramacca, 7 Feb. 1951 (fl, fr), *J. Florschütz & P.A. Florschütz 1214* (NY, U); Paka Paka (Saramacca), naar Ebbatop (v. Asch v. Wijks-Geb.), bij km 8, granitic plateau, 10 Feb. 1951 (fl), *J. Florschütz & P.A. Florschütz 1309* (BR, C, NY, U); Warrak-savanna on W bank of Maratakka River, 7 Apr. 1951 (fl, fr), *J. Florschütz & P.A. Florschütz 1943* (C, NY, U); without locality, s.d. (fl, fr), *H. Focke s.n. (U 0016948)* (U); Para, poste Wran, Apr. [without year] (fl, fr), *H. Focke 153* (U); South Central Suriname, Kaysergebte Airstrip [ca. 3°5'N, 56°28'W], sandy soil along airstrip, 2 Dec. 1961 (fl, fr), *R. Freund & S. Freund R-28-B* (US); Powakka Savanne, 1936 (fl, fr), *J. Frickers & H.J. Müller 7* (U), 22 (U); Palaime Savanne, Boven Tapanahoni, 2 May 1952 (fl, fr), *D.C. Geijskes s.n. (U 0016949)* (U); Coppename River, Cabalebas Creek, 26

- Jan. 1915 (fl), *J.W. Gonggrijp & G. Stahel 805* (U); Massif de Tumuc-Humac, Inselberg Talouakem, N slope, 2°29'N, 54°45'W, 550 m, herbaceous vegetation de savane roche (inselberg), 9 Aug. 1993 (fl), *J.J. de Granville et al. 12160* (BBS, CAY, MO, P, U, US); Voltzberg, base of inselberg, 4°41'N, 56°8'W, 200 m, 28 Jan. 1999 (fl), *J.J. de Granville et al. 13739* (BBS, CAY, NY, P); Central Suriname Nature Reserve, Voltzberg, Top I, 4°41'N, 56°11'W, 245 m, 13 Apr. 2002 (fl), *A. Gröger et al. 1306* (U); Jodensavanne (fluv. Suriname), 14 Jun. 1957 (fl, fr), *Heyligers, P.C. 342* (U); without locality, s.d. (fl, fr), *F.W.R. Hostmann & A. Kappler 507* (BM, FI-Webb, NY, P, S); "In Surinam", s.d. (fl), *F.W.R. Hostmann 663* (P [2 sheets, P00729342 and P05030245]); without locality, s.d., *F.W.R. Hostmann 663a* (MO [Acc. No. 5448229], FI-Webb [Acc. No. 080089], G [without barcode], S [Acc. No. S05-478], U [barcode 0016778]); Zuid Rivier, 3°10'–20'N, 56°29'–49'W, Kayser Airstrip, 25 km above confluence with Lucie River, 270 m, 1 Jul. 1963 (fl), *H.S. Irwin et al. 53958* (NY, P, S); Zuid Rivier, 3°10'–20'N, 56°29'–49'W, 2 km above confluence with Lucie River, 220 m, 3 Jul. 1963 (fl, fr), *H.S. Irwin et al. 54056* (NY, RB, UB, US); Wilhelmina Geberte, savanna ca. 2 km N of Lucie River, 3°20'–32'N, 56°26'–49'W, 225 m, 16 Jul. 1963 (fl, fr), *H.S. Irwin et al. 54214* (NY); Wilhelmina Geberte, forested hill 9 km N of Lucie and 12 km W of Oost River, 3°36'–41'N, 56°30'–34'W, 275 m, 16 Jul. 1963 (fl, fr), *H.S. Irwin et al. 54223* (F, NY, RB); Zuid Rivier, 3°10'–20'N, 56°29'–49'W, Kayser Airstrip, 45 km above confluence with Lucie River, 270 m, 22 Sep. 1963 (fl), *H.S. Irwin et al. 55946* (MO, NY [2 sheets], RB, UB, US), 55963 (MO, NY, S); along railway near LBB, Zanderij, white-sand savanna, 2 Mar. 1976 (fl, fr), *J. Jansma s.n. (LBB 15525)* (U); nieuwe weg van Zanderij, naar Matta Zand, 9 Dec. 1955 (fl), *A.M.E. Jonker-Verhoef & F.P. Jonker 151* (U); Zanderij, vliegveld, 30 Dec. 1955 (fl), *A.M.E. Jonker-Verhoef & F.P. Jonker 323* (U); ad fl. Tapanahoni, Oct–Nov. [without year] (fl), *A. Kappler 2084* (P); Joden Savanne – Mapane Creek area, Suhoza (Suriname River), 19 Dec. 1960 (fl, fr), *K.U. Kramer & W.H.A. Hekking 2380* (U); Zanderij [ca. 50 km S of Paramaribo], savanna, 26 Dec. 1960 (fl), *K.U. Kramer & W.H.A. Hekking 2503* (U); Saramacca Distr., Tafelberg [ca. 3°54'N, 56°10'W], Lareco-savanne, 300 m, 25 Feb. 1961 (fl), *K.U. Kramer & W.H.A. Hekking 3032* (U); Paramaribo, Oct. 1972 (fl), *C. Kock s.n.* (U); Potaro-Siparuni Region, Kaie-teur Falls, close to the falls and the government house, disturbed scattered shrubby vegetation on white sand and exposed bedrock, terrestrial and epipetric, 5°11'N, 59°29'W, 425 m, 6 Oct. 1987 (fl, fr), *L.P. Kvist et al. 3* (CAY, NY, P, U, US); Kleisavanne I, bij Vierkinderen, 5 Sep. 1948 (fl), *J. Lanjouw & J.C. Lindeman 183a* (U), 198 (U); Coppename River, near Raleighfalls, 10 Sep. 1933 (fl), *J. Lanjouw 755* (U); via secta ab Moengo tapoe ad Grote Zwiebelzwamp, km 11.5 in savanna, 9 Oct. 1948 (fl), *J. Lanjouw & J.C. Lindeman 757* (U); Indigenous Village, Kalebas Creek, 1 Oct. 1933 (fl), *J. Lanjouw 1006* (INPA, U); Savannah near Brownsweg, Nov. 1933 (fl, fr), *J. Lanjouw 1251* (U); Tibiti Savanne, 5 Jan. 1949 (fl), *J. Lanjouw & J.C. Lindeman 1601* (IAN, NY, U, US), 6 Jan. 1949 (fl), 1618 (IAN, NY, U), 1619 (U), 1621 (U); Jodensavanne, bij ruine, 12 Apr. 1949 (fl), *J. Lanjouw & J.C. Lindeman 2999* (U), 3000 (U); Zanderij, zandsavanne B, 10 Mar. 1949 (fl), *J. Lanjouw & J.C. Lindeman 3270* (NY, U); savanne langs spoorbaan bij km 100, 16 Mar. 1949 (fl), *J. Lanjouw & J.C. Lindeman 3315* (U), 3316 (U); Blanche Marie Vallen, Upper Nickerie River, 100 m, Apr. 1984 (fl, fr), *H. Lardinois 25* (BR); Kasiwinika, yearly burned clay savanna near Kopie, 15 Jul. 1953 (fl, fr), *J.C. Lindeman 4263* (U); Maratablow bij Esparracreek, bogere savanne, 8 May 1965 (fl, fr), *P.J.M. Maas & J.A. Tawjoeran s.n. (LBB 5215)* (U); 3 km ZO van basiskamp, 2 km beneden Blanche Marievallen, Nickerierivier, 19 Jun. 1965 (fl, fr), *P.J.M. Maas & J.A. Tawjoeran s.n. (LBB 10910)* (U); W-oever van Nickerie River, 3 km N van Kamisavallen, struiksavanne, 2 Jul. 1965 (fl, fr), *P.J.M. Maas & J.A. Tawjoeran s.n. (LBB 11037)* (U); Sanderij, Savanna II, 3 Jun. 1944 (fl), *B. Maguire & G. Stahel 23663* (NY); Wilhelmina Geberte, 3°34'–36'N, 56°30'–34'W, 9 km N of Lucie and 12 km W of Oost River, 275 m, 16 Jul. 1963 (fl, fr), *B. Maguire et al. 54223* (NY, UB, US); Berseba, small savanna, 12 Sep. 1954 (fl, fr), *A.M.W. Mennega 13* (U); Boven Tanjimama, 20 Nov. 1954 (fr), *A.M.W. Mennega 491* (U); clay savanna Berseba, near Republiek, 14 Nov. 1974 (fl, fr), *A.M.W. Mennega & J. Koek-Noorman 894* (U); vicinity of Blanche Marie Waterfall, on Nickerie River, along the entrance road to the Blanche Marie Guest House, 4°45'20"N, 56°54'19"W, 60 m, 3 Feb. 1998 (fl, fr), *J.S. Miller et al. 9300* (MO, U), 9306 (MO, U); western part of Great Sipaliwini Savanna, near bank of the 4-Gebroeders Creek, transect D near base camp, 283 m, 4 Jan. 1968 (fl), *F.H.F. Oldenburger et al. 674* (U); Coesterie Creek (Coesewijne), creek bank, Jan. 1978 (fl, fr), *J. Procter 4700* (U, UB); Upper Coppename River, in Monte Volzberg, 50 m, 21 Aug. 1920 (fl, fr), *A. Pulle 226* (U); Upper Coppename River, in summit Monte Volzberg, 250 m, 22 Aug. 1920 (fr), *A. Pulle 250* (U); Skull Point, near Bartica, 9 Apr. 1956 (fl), *J.R. Ramsammy 13* (US); Awarra Savanne aan de Maratakka, 2 Mar. 1971 (fl, fr), *D. Reeder s.n. (LBB 13464)* (U); Corantyne River, Wonotobo Falls, 6 Aug. 1935 (fl, fr), *H.E. Rombouts 101* (U); Upper Sipaliwini River, savanna, 23 Oct. 1935 (fl, fr), *H.E. Rombouts 223* (U); Upper Sipaliwini River, savanna near Kamp II, 6 Dec. 1935 (fl),

*H.E. Rombouts* 332 (U); Upper Tapanahoni River, Idenburg Rapids, granitic islet, 13 Sep. 1936 (fl, fr), *H.E. Rombouts* 603 (C, U); Litani River, Mt. Knopaiamoi [ca. 2°28'N, 54°30'W], 12 Aug. 1937 (fl), *H.E. Rombouts* 807 (BR, U); Upper Litani River, bij oorsprong granite, 8 Nov. 1937 (fl), *H.E. Rombouts* 885 (IAN, U); without locality, s.d. (fl, fr), *J.P. Schultz s.n.* (U 0016944) (U); along Zuidrivier, near confluence with Lucie River, 3 Jul. 1963 (fl, fr), *J.P. Schultz s.n.* (LBB 10023) (U); Zuidrivier, savanna near Kayser Landing, 13 Aug. 1963 (fl, fr), *J.P. Schultz s.n.* (LBB 10432) (U); Voltzberg (Boven-Wayombo), op dun verwerings-laagje, 22 Apr. 1956 (fl), *J.P. Schultz* 7610a (U); Upper Coppename River, near Raleigh Falls, 23 Sep. 1956 (fl, fr), *J.P. Schultz* 7819 (U); without locality, s.d. [1837–1838] (fl), *F.L. Splitgerber s.n.* (BM 000614321) (BM); Wilhemina Geberte, 11 May 1926 (fr), *G. Stahel* 7049 (U [2 sheets]); Corantyne River, Wonotobo Falls, 14 Oct. 1916 (fl, fr), *G. Stahel & J.W. Gonggrijp* 3157 (U); Makatui Savanna, ca. 3.5 km SW of Aishalton, 2°30'N, 59°15'W, white sand savanna, 18 Nov. 1982 (fl), *A.L. Stoffers et al.* 360 (MO, U); near Aishalton Hospital, 2°30'N, 59°15'W, along savanna pond on clay, 18 Nov. 1982 (fl), *A.L. Stoffers et al.* 388 (U); near Aishalton Hospital, 2°30'N, 59°15'W, white sand savanna, 19 Nov. 1982 (fl, fr), *A.L. Stoffers et al.* 435 (NY, S), 440 (C, CAY, MG, MO, RB, U); 5 km SE of Aishalton Hospital, near Lake Awakawau, 2°30'N, 59°15'W, white sand savanna, on clay, 20 Nov. 1982 (fl), *A.L. Stoffers et al.* 508 (CAY, MO, U); Suriname River, near Misikai, 13 Jul. 1908 (fr), *J.H.A.T. Tresling* 128 (MG, U); Suriname River, “jp. pr. coth. Kwemba” 25 Jul. 1908 (fl), *J.H.A.T. Tresling* 225 (U); Suriname River, near Kapiyai, 5 Aug. 1908 (fr), *J.H.A.T. Tresling* 287 (U); Upper Suriname River, 19 Sep. 1908 (fr), *J.H.A.T. Tresling* 449 (U); Suriname River, Gran Rio, 20 Sep. 1908 (fr), *J.H.A.T. Tresling* 469 (U), 21 Sep. 1908 (fr), *J.H.A.T. Tresling* 471 (U); without locality, s.d. (fl), *J.E. Tulleken* 152 (MO); Marowini River, Jul. 1904 (fl, fr), *G.M. Versteeg* 614 (U); Brokopondo Distr., Brownsberg National Park, 5 Nov. 1973 (fl), *C. Vreden s.n.* (LBB 14723) (U); Brokopondo, Brownsberg Nature Reserve Plateau weg, 4°55–57'N, 55°11–12'W, 475–500 m, 23 Jul. 1979 (fl, fr), *G.L. Webster* 24103 (U); Para, between Hannover and the Onverwacht-Zanderij road, 5°28'N, 55°10'W, 20 m, 10 Jul. 1979 (fl, fr), *G.L. Webster* 24034 (U); Para District, prope Berlijn, Sep. 1901 (fr), *F. Went* 386 (U); along Affobaka road near Berg en Dal, S of Blauwe Berg, 20 Dec. 1962 (fl, fr), *J.G. Wessel Boer* 400 (U); along Kabel railroad, at km 116 near Brownsberg, on white sand, 14 Feb. 1963 (fl, fr), *J.G. Wessel Boer* 684 (U); inter Flum. Coppename Dextrum et montes Emma dictos, 4°10'N, 56°20'W, 20 May 1963 (fl, fr), *J.G. Wessel Boer* 14010 (U); Nat. Res. Brinckheuvel, Saban pasi

savanne, 16 Jan. 1968 (fl), *J.T. Wildschut & P.A. Teunissen s.n.* (LBB 12175) (U); “Surinam: Hmenge [? illegible], 1864 (fl, fr), *H.R. Wullschlaegel s.n.* (BR 824613) (BR); Paramaribo, 1851 (fl, fr), *H.R. Wullschlaegel* 257 (BR).

**FRENCH GUIANA:** Upper Tampoc River, Saut Pier Kourou, on islets just below the waterfall, 6 Apr. 1977 (fl), *G. Cremers* 4636 (CAY [2 sheets], P, U); Tumuc Humac, layon Orstom Koulimapopann-Mitaraka (border between French Guiana and Brazil), p.k. 7.5, great inselberg, 550 m, 6 Aug. 1972 (fl, fr), *J.J. de Granville* 1129 (CAY [2 sheets], P); Tumuc Humac, base of Toukouchipann, N slope, 480 m, 22 Aug. 1972 (fl, fr), *J.J. de Granville* 1339 (CAY, P); Haut Oyapock, Mont St. Marcel [ca. 2°36'N, 53°1'W], inselberg on S slope, 300–350 m, 30 Jul. 1975 (fl), *J.J. de Granville* 2603 (CAY); Upper Mana River, Saut Ananas, 12 Aug. 1981 (fl), *J.J. de Granville* 4820 (BR, CAY, P, UB); Oyapock River Basin, Roche Touatou (Inselberg), vegetation herbacée de savane-roche [herbaceous vegetation on inselberg], 2°57'N, 52°32'W, 160 m, 16 May 1995 (fl, fr), *J.J. de Granville & G. Cremers* 12935 (B, CAY [2 sheets], K, MO, P, U, US [some duplicates of this collection have the label “Montagne Emérillons, alt. 160 m, 3°15'N, 53°5'W” but this label is wrong]); Upper Mana River, Saut Ananas, bord d'un sentier en sous-bois clair, 31 Aug. 1962 (fl), *F. Hallé* 741 (CAY, NY, P, U, US); Maripasoula, Massif du Mitaraka, Crique Alama, Inselberg Sommet Cloche, éperon de roche affleurante au nord du dome, 2°13'40"N, 54°28'10"W, 500 m, 5 Mar. 2015 (fl), *O. Poncy* 2869 (B, CAY, MO, P); Mitaraka Sud, sommet inselberg, border of inselberg, 2°16'N, 54°31'W, 660 m, 4 Mar. 2001 (fl), *C. Sartou* 807 (CAY, MO, P); Tumuc-Humac (border Brazil-French Guiana-Suriname), Montagne Paloulouiméem-peu, E slope, 450–500 m, granitic inselberg, 2 Aug. 1972 (fl, fr), *C. Sastre* 1538 (CAY [2 sheets], IAN, NY, P); Massif Mitaraka, Mitaraka S, versant S, granitic slopes, 550 m, 17 Aug. 1972 (fl, fr), *C. Sastre* 1713 (CAY [2 sheets], P); Upper Maroni River (Litany), Antecum-Pata (Malavate) [ca. 3°19'N, 54°4'W], 21 Apr. 1975 (fl), *C. Sastre et al.* 3855 (CAY, MO, P); gros saut rivière Portal (Mana), 29 Mar. 1949 (fl), *Service Forestier s.n.* (P00729315) (P); Mana River, Station Rivière Forestal, 29 May 1949 (fl), *Service Forestier* 4544 (CAY [2 sheets], P).

**BRAZIL: Amapá:** Massif Tumuc-Humac, Inselberg Talouakem, 2°29'N, 54°45'W, 650 m, 11 Aug. 1993 (fr), *J.J. de Granville et al.* 12244 (BBS, CAY, MO, P, US); Mun. Oiapoque, Aldeia do Manga [ca. 3°43'N, 51°43'W], tribo Karipuna, 20 Aug. 1981 (fl, imm fr), *B. Rabelo* 1303 (NY). **Amazonas:** Rio Cuieras, at junction with Rio Negro [ca. 2°47'S, 60°27'W], campina on white sand, 5 Mar. 1976 (fl), *A.B. Anderson* 237 (INPA), 238 (INPA); Manaus, Taracua Campo, 10 Dec. 1962 (fl), *A.G.*

- Andrade & M. Emmerich* 1455 (R [3 sheets]), 1456 (R); without locality, 2°55'46"S, 59°58'24"W, 138 m, 28 Aug. 2010 (fl), *A. Antonelli et al.* 431 (INPA); Manaus, rod. AM-010, Manaus-Itacoatiara, km 26, Reserva Florestal Adolfo Ducke [ca. 3°0'S, 59°56'W], prox. ao alojamento, 11 Feb. 2000 (fl-fr), *E.A. Anunciação & E.C. Pereira* 810 (INPA, UB); Itacoatiara, rod. AM-010, Manaus-Itacoatiara, km 227, MIL-Madeira, beira da estrada em direção ao Mun. de Silves, km 22, 7 Mar. 2000 (fl), *E.A. Anunciação et al.* 833 (INPA); Ilha do Piranadé, Rio Negro above Barcelos, 9 Feb. 1944 (fl), *J.T. Baldwin Jr.* 3307 (F, IAN, NY, US); Rio Negro, Barcelos [ca. 0°58'S, 62°55'W], capoeira, 23 Apr. 1948 (fl, fr), *G.A. Black* 48-2430 (IAN, U [2 sheets]); Rio Içana, Tunuí, floresta de caatinga, 10 May 1948 (fl, fr), *G.A. Black* 48-2595 (IAN, P), Rio Içana, Camrão, capoeira, 7 May 1948 (fl, fr), *G.A. Black* 48-2627 (IAN); 72 km NNE of Manaus, Distrito Agropecuário, Fazenda Dimona of the WWF/INPA MCS Project, 2°19'S, 60°5'W, 50–125 m, mata de terra firme, 26 Aug. 1991 (fl, fr), *B.M. Boom & M. Pacheco* 8486 (INPA, NY); Estrada Manaus-Itacoatiara, km 64, picada do INPA, 800 da rodovia, lagoa ao lado da picada, solo úmido-arenoso, 2 Feb. 1969 (fl, fr), *Byron & D. Coelho* 69-126 (INPA, US); 2 km S of Maués [ca. 3°23'S, 57°43'W], near Maués River, deserted farm and nearby forest, disturbed open area on terra firme, 26 Apr. 1974 (fl), *D.G. Campbell et al.* P22132 [Prance collection number] (INPA, MO, NY, R, S, U, US); Maués airport road, between Maués and airport, 27 Apr. 1974 (fl), *D.G. Campbell et al.* P22173 [Prance collection number] (INPA, NY, US); Reserva Florestal Adolpho Ducke, Manaus-Itacoatiara, km 26, 2°53'S, 59°58'W, 9 Dec. 1994 (fl), *M.T.V. Campos et al.* 580 (INPA, NY); Estrada do Aleixo, Lajes, solo de terra firme, 19 May 1975 (fl), *L. Carreira* 64 (INPA); Mun. Presidente Figueiredo, Balbina, Estrada de acesso ao antigo porto, vegetação aberta, degradada, 1°0'N, 59°0'W, 1 Aug. 2006 (fl), *J.G. de Carvalho-Sobrinho & K.M. Silva* 824 (INPA), 826 (INPA); Manaus, antiga estrada de de São Raimundo, terra úmida, 7 Dec. 1954 (fl, imm fr), *J. Chagas s.n.* (INPA 330) (INPA), (MG No. 254545) (MG), *s.n.* (MG 21681) (MG); Manaus, margem do Igarapé do Parque 10, 6 Dec. 1955 (fl), *J. Chagas s.n.* (INPA 3049) (IAN, INPA, MG), 23 Jul. 1956 (fl), *J. Chagas s.n.* (INPA 3971) (INPA, MG); Manaus, Cachoeira Grande dos Bilhares, 16 Mar. 1959 (fl), *J. Chagas s.n.* (INPA 7220) (INPA), (MG 25061) (MG), *s.n.* (MG 25134) (MG), *s.n.* (MG 25068) (MG), *s.n.* (INPA 330) (IAN 109888) (IAN), *s.n.* (INPA 7220) (RB), 11 Apr. 1958 (fl), *s.n.* (INPA 6342) (IAN, INPA, RB); Reserva Florestal Adolpho Ducke, Manaus-Itacoatiara, km 26, 2°53'S, 59°58'W, 9 Dec. 1994 (fl), *M.A. Costa & J.R. Nascimento* 43 (INPA, MG, NY); Manaus, RDS do Tupé, campinara-na, prox à comunidade Agrovila, trilha que segue a 4 km a dentro da mata de terra firme, 2°98'22"S, 60°21'8"W, 35 m, 31 May 2015 (fl), *L.O. Demarchi, J. Alves & M.C. Melo* 409 (INPA); Parintins, Tribo Sateré Maué, mata secundária, Araticu, 8 May 2005 (fl), *P.A. Ferreira* 26 (INPA); Região de Parintins, Lago do Jurutí, 18 Jan. 1957 (fl, fr), *R.L. Frões* 33079 (IAN, US); Parintins, pastagem de terra firme, 2°53'14"S, 56°40'40"W, 26 Jan. 2009 (fl), *A.K.L. Galvão et al.* 35 (INPA); Acampamento da D.B.F.F./W.W.F., km 41, Res. 1501, 25 Jul. 1985 (fl, fr), *M.V.B. Garcia* 008 (R); Igarapé da Bolívia, woods along stream near turnoff of Caracará Road from Itacoatiara Road, ca. 8 km from Manaus, 14 Dec. 1974 (fl), *A. Gentry & J. Ramos* 13298 (INPA, MO); Santarém, Dto. Alter do Chão, Lago Verde dos Muiraquitãs, Igapó do Caranazal, margem do igapó, 2°31'17"S, 54°55'54"W, 2 Oct. 2015 (fl), *L.L. Giacomini et al.* 2680 (RB); Manaus, Reserva Florestal A. Ducke, Estrada Manaus-Itacoatiara, km 26, 2°53'S, 59°58'W, 4 Dec. 2001 (fl), *M. Groppo Jr. et al.* 916 (INPA); Manaus, margem do igarapé da Normandia, 28 Oct. 1954 (fl), [initials unknown] *Jaccoud s.n.* (INPA No. 285) (IAN, MG); Cachoeira do Tarumã Mirim, 7 Dec. 1974 (fl), *W. Junk* 175 (INPA); Cacaupirêra, margem direita do Rio Negro, campo arenoso na terra firme, com argila branca, explorada para tijolos, 28 Jun. 1986 (fl), *M.L. Kawasaki et al.* 2 (INPA); Igarapé Tarumã, N of junction of Rio Negro and Igarapé Tarumã, white sand, black water igapó, 3°2'S, 60°8'W, 23 Nov. 1977 (fl), *S. Keel & J. Guedes* 300 (MG, NY, RB, S, U); Manaus, road Manaus-Itacoatiara, km 13.5–14, along roadside, 22 Feb. 1969 (fl), *H. Kennedy* 126 (INPA); "Manãos, civ. Amazonas" [Manaus], Oct. 1912 (fl), *J.G. Kuhlmann s.n.* (RB2842) (S 10-27921); Uucajatuba, Rio Paurary, afluyente do Rio Maués, 17 Mar. 1924 (fl, fr), *J.G. Kuhlmann* 1648 (RB 110698) (RB [3 sheets]); estrada Manaus-Caracará, km 585, campina, 29 Jun. 1979 (fl), *J. Lima* 464 (INPA); Road to Praia Dourada, ca. 10 km NW of Manaus, 30 Aug. 1980 (fl), *J. Lowe* 3953 (INPA); near the ferry, other side of the Rio Negro from Manaus, roadside herb, 28 Sep. 1980 (fl), *J. Lowe* 4028 (INPA); Boa Vista road, 55 km N of Manaus, herb in road cutting, 17 Apr. 1981 (fl, fr), *J. Lowe* 4080 (INPA); Road AM-010, km 246 (25 km WNW of Itacoatiara), 10 Jun. 1981 (fl), *J. Lowe* 4271 (INPA); Manaus, Fazenda Aurora, 22 Aug. 1922 (fl, fr), *P. Luetzelburg* 22041 (R), 22073 (R); Tunuy, Rio Içana, 21 Oct. 1927 (fl, fr), *P. Luetzelburg* 22412 (R); Manaus, Jardim Zoológico, secondary vegetation along creekside, 18 Apr. 1971 (fl), *P.J.M. Maas & H. Maas* 278 (INPA); Manaus, Arquipélago das Anavilhanas, Foz do Rio Cuieras, solo argiloso-arenoso, 4 Mar. 1976 (fl, fr), *M.E. Medri* 51 (INPA); Manaus, igarapé da Cachoeira Grande dos Bilhares, 26 Sep. 1955 (fl), *F.C.*

- Mello s.n.* (MG 25352) (MG), (INPA 2040) (IAN, INPA); Manaus, campina nos fundos do Conjunto dos Jornalistas, solo arenoso, 5 Jun. 1984 (fl), *F.E. Miranda & M.C.C. Miranda* 817 (INPA); estrada Manaus–Itacoatiara, Reserva Florestal Ducke, próximo ao campo de futebol, 12 Mar. 1977 (fl), *O.P. Monteiro & R. Lisboa* 1339 (INPA); Mun. Prainha, sub-base do Projeto RADAM/BRASIL, capoeira baixa de terra firme, 29 Sep. 1976 (fl, fr), *C.D. Mota s.n.* (INPA); Cucuí, 26 Apr. 1975 (fl, fr), *O.C. Nascimento et al.* 198 (IAN, RB, US); Rio Negro, L margin, 50 km acima de Manaus, Campo Amélia, Faz. Belo Horizonte, campo natural de terra firme, dominado por *Antonia ovate*, *Bulbostylis* spp. e *Curatella americana*, solo argiloso, 18–19 Aug. 1985 (fl), *B. Nelson et al.* 1414 (NY, UFMT, US); Manaus, área da Fenologia de EEST (Estação Experimental de Silvicultura Tropical), BR-174, 45 km de Manaus, 10 Dec. 1996 (fl, fr), *A. Nitta & A. Yoshida* 17565 (INPA); 90 km NNE of Manaus, Distrito Agropecuário, Reserva 1501 (km 41), 2°24'26"–2°25'31"S, 59°43'40"–59°45'50"W, 50–125 m, mata de terra firme, 26 Aug. 1991 (fl, fr), *A.A. Oliveira et al.* 176 (INPA, NY); Manaus, campina atrás do Conjunto dos Jornalistas, solo arenoso, 5 Jun. 1984 (fl), *N. de Paula et al.* 16 (INPA); Manaus, Reserva Florestal Adolfo Ducke, floresta de terra firme, 2°33'35"S, 59°35'7"W, 17 Sep. 2013 (fl), *M.C. Pessoa et al.* 855 (INPA); Manaus, Reserva Florestal Adolpho Ducke, caminho para Harpia, terra firme, clareira, solo areno-argiloso, 21 Oct. 2015 (fl), *R.B. Pinto et al.* 528 (INPA); Rio Içana, Tunuí, pé da serra, terreno pedregoso, 24 Oct. 1947 (fl, fr), *J.M. Pires* 756 (IAN); Parintins, 11 Mar. 1946 (fl, fr), *J.M. Pires & G.A. Black* 1143 (IAN); Manaus-Itacoatiara Highway, km 64, Reserva Florestal Walter Egler, beside small lake, trailing herb, corolla pale purple, 13 Dec. 1966 (fl), *G.T. Prance et al.* 3623 (INPA, NY, S); vicinity of Manaus, Tarumã Grande, 1 km N from the junction of Rio Negro and Manaus, Rio Negro, Baía do Bueussu, 15 km above Manaus, 18 Mar. 1969 (fl), *G.T. Prance et al.* 10436 (F, INPA, MG, NY, S, US); Campo Amélia, Faz. Belo Horizonte, entre Igapó Acajatuba e margem direita do Rio Negro, extenso campo gramíneo de terra firme, solo argiloso, 21 Apr. 1986 (fl), *G.T. Prance et al.* 30048 (NY, US); Reserva Florestal Adolpho Ducke, Manaus-Itacoatiara, km 26, ramal para a torre, terra firme, 28 Apr. 1988 (fl, fr), *J.F. Ramos* 1890 (IAN, INPA, NY); Manaus, Bilhares-Chapada, campo aberto, solo arenoso, úmido, 30 Dec. 1958 (fl, fr), *W. Rodrigues* 770 (IAN, INPA, MG); Manaus, Igarapé Passarinho, terra firme, solo arenoso, descampado, 21 Nov. 1961 (fl, fr), *W. Rodrigues & J. Chagas* 3607 (INPA, US); Manaus, Cachoeira Alta do Tarumã, Igarapé do Passarinho, terra firme, solo arenoso, descampado, 30 Nov. 1961 (fl), *W. Rodrigues & J. Chagas* 3640 (INPA); Rio Tiririca, afluente do Rio Preto, terreno úmido, sujeito a inundação temporária, 1 Jun. 1964 (fl), *W. Rodrigues & D. Coelho* 5866 (INPA); Parintins, Comunidade Vinte Quilo da Tribo Mawé, 24 Nov. 2009 (fl, fr), *O.A. Santos* 221 (INPA); Région de Manaus, clarière herbeuse sur sable claire, Oct. 1958 (fl), *R. Schnell* 9223 (P); Manaus, Cachoeira Grande, 30 Mar. 1982 (fl, fr), *C.A.W. Schwacke* 181 (coll. III) (R); Mun. Presidente Figueiredo, km 189 da BR-174, 4 Oct. 1998 (fl), *J.A. Silva et al.* 857 (INPA); Rio Xié, prox. a Cachoeira de Cumati [ca. 1°18'N, 67°15'W], capoeira de solo argiloso, 9 May 1973 (fl, fr), *M.F. Silva et al.* 1404 (INPA, US); Estrada Manaus-Caracarái, trecho perdido, 11 Mar. 1978 (fl), *N.T. Silva* 4583 (MG, NY); Manaus, atrás do Conjunto dos Jornalistas, campina perturbada, solo arenoso, 5 Jun. 1984 (fl), *H.C. de Souza* 19 (INPA); “Prov. Rio Negro, prope Barra [now city of Manaus]”, Dec. 1850–Mar. 1851 (fl), *R. Spruce* 994 (NY), *s.n.* (NY 02693444, BM 000614335, FI-Webb 080079, P [2 sheets, P00748125, P00748124], RB 17399 [2 sheets], C); “Barra” [Manaus], Dec. 1850 (fl), *R. Spruce* 1132 (P); prope Panuré ad Rio Uaupés, Oct. 1852–Jan. 1853 (fl), *R. Spruce* 2908 (P); Mun. Nova Olinda [Nova Olinda do Norte, ca. 3°53'S, 59°5'W], Lower Rio Mari Mari, below Rio Pará, Laranjal, along river and Igarapé, sandy soil, 1 Jul. 1983 (fl), *C. Todzia et al.* 2286 (INPA, MG, NY, RB, US); SWW of Manaus, en route from Cacau Pirera to Manacapuru, along rd. AM-070, sunny place, roadside, 50–60 m, 6 Aug. 1987 (fl), *S. Tsugaru* B-757 (NY); Manaus, Jan. 1901 (fl), *E. Ule* 5374 (MG). **Maranhão:** Turiaçu [ca. 1°39'S, 45°22'W], km 6 da BR-106 Maracaçumé-Sta. Helena, Fazenda Maracaçumé Agro Industrial Grupo Mesbla, solo arenoso, 1 Dec. 1978 (fl, fr), *N.A. Rosa & H. Vilar* 2780 (MG, NY). **Pará:** Rio Parú, Parú do Oeste, Missão Tiriyo, arredores da Missão, 2°20'N, 55°45'W, 23 Feb. 1970 (fl), *P. Cavalcante* 2491 (MG, NY, US); Rio Tiriós, parte norte ocidental do E Pará, 12 May 1962 (fl, fr), *E. Oliveira* 1843 (IAN, UB); Rio Arapiuns, Campo da Raposa, 8 Jun. 1952 (fl), *J.M. Pires & N.T. Silva* 4226 (IAN); Mun. Juruti [ca. 2°9'S, 56°05'W], erva comum a margem do rio em locais úmidos, 3 Jun. 2014 (fl, fr), *R.P. Salomão et al.* 1384 (MG); Sete Varas airstrip on Rio Curua [ca. 5°20'S, 54°30'W], open savanna bordered by medium-sized forest and low scrub, 8 Aug. 1981 (fl, fr), *J.J. Strudwick et al.* 4348 (MG). **Roraima:** Boa Vista [ca. 2°49'N, 60°40'W], 8 Jul. 1955 (fl), *M. Alvarenga s.n.* (RB 90577) (RB); Caracarái, Parque Nacional do Viruá, na margem da Estrada Perdida, 1°25'35"N, 60°59'0"W, 62 m, área alagada, solo argiloso, 17 Jul. 2010 (fl), *T.D.M. Barbosa & S.M. Costa* 1138 (INPA); Caracarái, Parque Nacional do Viruá, na margem da Estrada Perdida, 1°26'4"N, 60°58'51"W, 63 m, área alagada, solo

- argiloso, 19 Jul. 2010 (fl), *T.D.M. Barbosa & S.M. Costa* 1178 (INPA); Mun. Boa Vista, Igarapé Aguas Boas, 20 Aug. 1951 (fl, fr), *G.A. Black* 51-12816 (IAN, U); entre Igarapé Azul e Branco e a Estrada Boa Vista-Caracarái, 17 Sep. 1951 (fl, fr), *G.A. Black* 51-13562 (IAN); Ilha de Maracá, erva lenhosa, flores róseas, 19–26 Jun. 1997 (fl, fr), *L. Carreira et al.* 1224 (MG); NE Roraima, ca. 110 km NE of Boa Vista, 8 km SW of Bonfim, Fazenda Valparaíso, 133 m, savannas (campo) with moist sandy soil, 20 Oct. 1977 (fl), *L. Coradin & M.R. dos R. Cordeiro* 820 (IAN, INPA, NY); along Boa Vista–Mucajaí road (BR-174), km 2, 3 Nov. 1977 (fl), *Coradin, L. & M. dos R. Cordeiro* 965 (INPA); Along Mucajaí–Caracarái road (BR-174), km 17, dry, sandy soil, roadside, 8 Nov. 1977 (fr), *L. Coradin & M.R. dos R. Cordeiro* 1012 (INPA); Caracarái, Parque Nacional do Viruá, Estrada Perdida, 1°48'67"N, 61°1'57"W, Jun. 2006 (fl), *F.R.C. Costa* 1255 (INPA); Caracarái, Parque Nacional do Viruá, campina, às margens de rio de água preta, 1°3'0"N, 61°14'59"W, 23 Mar. 2011 (fl), *S.M. Costa* 941 (INPA); Caracarái, Parque Nacional Viruá, campinarana (emergentes até 15 m), solo arenoso, inundado periodicamente, Lat. 1.48219, Long. -61.0207, 64 m, 30 May 2010 (fl, fr), *N.C. Dávila & F.N. Cabral* 6178 (INPA), 6179 (INPA); Caracarái, Parque Nacional Viruá, vegetação secundária, Lat. 1.816, Long. -61.128, 2 Jun. 2010 (fl), *N.C. Dávila et al.* 6211 (INPA); Caracarái, Parque Nacional do Viruá, Estrada Perdida, área aberta, alagada, com solo arenoso, 22 Jul. 2010 (fl), *G.C. Delgado Jr. et al.* 106 (INPA); Caracarái, Parque Nacional do Viruá, Rio Anauá, localidade Campinho, campina aberta, solo hidromorfo, 12 Mar. 2007 (fl), *C.A.C. Ferreira et al.* 12979 (INPA); Caracarái, Estação Ecológica de Niquiá, floresta de terra firme, 0°48'5"N, 61°39'37"W, 50 m, 25 Mar. 2012 (fl), *R.C. Forzza et al.* 7007 (RB); SEMA Estação, open grassy savanna close to estação, savanna with *Curatella americana*, 3°22'N, 61°20'W, 7 Jul. 1986 (fl), *M.J.G. Hopkins* 545 (MG); Rorainópolis [ca. 0°56'N, 60°25'W], Rio Xipariná, área alterada no igapó, sazonalmente inundada, 6 Mar. 2010 (fl), *M.J.G. Hopkins & E.L. da Encarnação* 1978 (INPA); Ilha de Maracá, Mun. Alto Alegre, near Estação Ecológica de Maracá, 3°22'N, 61°20'W, 12 Jul. 1986 (fl), *A. Henderson & R. Pereira de Lima* 545 (NY, US); Caracarái, Parque Nacional Viruá, Estrada perdida, near BR-174, along stagnant water channel dominated by *Mauritia flexuosa*, 5 Apr. 2013 (fl), *J.E. Householder* 2576 (INPA); Margem do Igarapé da Normandia, 28 Oct. 1954 (fl), [initials unknown] *Jaccoud s.n.* (INPA No. 285) (INPA, MG, RB); Amajari, Serra do Tepequém, submontana, savanna, 3°45'45"N, 61°42'57"W, 723 m, 3 Dec. 2013 (fl, fr), *D.L. Komura et al.* 1769 (INPA), 6 Dec. 2013 (fl, fr), 1778 (INPA); Manaus, Oct. 1912 (fl), *J.G. Kuhlmann* 37 (RB); Boa Vista, Jul. 1913 (fl, fr), *J.G. Kuhlmann* 814 (RB); Estrada Caracarái, Boa Vista, km 59, beira da Estrada, solo argiloso-arenoso, 28 Jun. 1979 (fl, fr), *J. Lima* 450 (INPA); Mun. Caracarái, Jualpiri, várzea, 30 Jun. 1979 (fl, fr), *J. Lima* 467 (INPA); Mun. Boa Vista, 5 km N do alojamento, campo de terra firme, gramíneo, com *Curatella* e *Byrsonima*, solo areia quartzosa, 16 May 1987 (fl), *J. Lima & B. Nelson* 734 (INPA, NY, U); Serra do Xiriry, campos serranos, Aug. 1927 (fl), *P. Luetzelburg* 20708 (R); Serra da Moça, campos húmidos, Aug. 1927 (fl), *P. Luetzelburg* 20811 (R), 20816 (R); Serra do Murupú, campos húmidos, Aug. 1927 (fl), *P. Luetzelburg* 20821 (R); Serra do Camelo, campos húmidos, Aug. 1927 (fl, fr), *P. Luetzelburg* 20868 (R); Valle do Rio Quinó, Igarapé do Ignacio, campos húmidos, Sep. 1927 (fl), *P. Luetzelburg* 21502 (R); Igarapé Ouato, campos húmidos, Sep. 1927 (fl), *P. Luetzelburg* 21588 (R); Boa Vista, Apr. 1952 (fl, fr), *D. Magalhães* 1 [= *G.A. Black* 51-12816] (IAN); Serra Tepequem, occasional in savanna below airstrip, 700–800 m, 2 Dec. 1954 (fl), *B. Maguire & C.K. Maguire* 40147 (NY); Caracarái, Rio Catrimani, 4 km acima da boca do Rio Branco, 0°28'39"N, 61°45'0"W, 45 m, 26 Mar. 2012 (fl, fr), *G. Martinelli et al.* 17518 (RB); Caracarái, Parque Nacional do Viruá, Estrada Perdida, após a primeira bueira, campinarana alagada, 22 Jul. 2010 (fl), *A. Melo et al.* 399 (INPA); Caracarái, Parque Nacional do Viruá, margem do Rio Iruá, 23 Aug. 2012 (fl), *A. Melo et al.* 1016 (INPA); Rod. RR-205, km 67, savan arbórea aberta, 23 Jun. 1994 (fl), *I.S. Miranda* 187 (INPA); Boa Vista, Lago Redondo, campo aberto, mal drenado, solo arenoso, 29 Jun. 1994 (fl), *I.S. Miranda* 242 (INPA), 257 (INPA [2 sheets]); Estrada Velha para a Vila do Cantá, savanna arbustiva, solo arenoso, 27 May 1995 (fl), *I.S. Miranda* 715 (INPA); Lago Redondo, à esquerda do km 1 da estrada para Vila São Francisco, campo úmido, 6 Oct. 1995 (fl), *I.S. Miranda* 881 (INPA); Mutum, Igarapé do Rebenque, subindo a serra, savanna, 13 Oct. 1995 (fl, imm fr), *I.S. Miranda* 1122 (INPA); Alto Alegre, Estação Ecológica de Maracá, Grade do PPBio, trilha No. 1, ilha de savanna arborizada, 3°22'45"N, 61°26'32"W, 128 m, 18 May 2012 (fl), *P.O. Perdiz et al.* 1354 (INPA, RB); Caracarái, Parque Nacional do Viruá, Estrada de acesso à sede do Parque, sentido sede-guarita, floresta ombrófila densa, 1°29'24"N, 61°0'10"W, 10 Aug. 2013 (fl, imm fr), *P.O. Perdiz et al.* 1931 (INPA); Rorainópolis, Rio Xipariná, Comunidade Xixuaú, 0°38'56"S, 61°27'10"W, 7 Sep. 2013 (fl), *M.C. Pessoa & E.A. Santos* 826 (INPA); Caracarái, Parque Nacional do Viruá, floresta de terra firme, 20 Sep. 2013 (fl), *M.C. Pessoa & J. Maciel* 858 (INPA); Caracarái, campo, *J.M. Pires et al.* 14330 (IAN, M); rd. Rio Uraricoera-Tepequem, grassy campo, 9 Feb. 1967 (fl, fr), *G.T. Prance et al.* 4245 (F,

INPA, MG, NY, P, R, S); foothills of Serra da Lua, 2°25'–29'N, 60°11'–14'W, 10 Jan. 1969 (fl), *G.T. Prance et al.* 9183 (F, INPA, MG, NY, S); Reserva Florestal Ducke, Manaus-Itacotiara, km 26, 2°53'S, 59°58'W, ramal para a torre, 28 Apr. 1988 (fl, fr), *J.F. Ramos 1890* (RB); Ilha de Maracá, SEMA Ecological Reserve, Santa Rosa Area, 3°22'N, 61°25'W, damp campo below the station, 23 Feb. 1987 (fl, fr), *J.A. Ratter et al.* R-5393 (INPA, NY, U); Ilha de Maracá, SEMA Ecological Reserve, Santa Rosa Area, ca. 4 km NE of Station buildings, 3°22'N, 61°25'W, scrubby transition zone between campina forest and seasonally inundated campo, 1 Feb. 1988 (fr), *J.A. Ratter et al.* R-6189 (NY); Estrada Boa Vista-Venezuela, perto do Igarapé Jacitara, campo alagado com buritizal, 1 May 1979 (fl), *I.A. Rodrigues et al.* 803 (IAN); Normandia, 6 Nov. 1954 (fl), *W. Rodrigues 11* (IAN, INPA, MG, RB); margem do Igarapé Canan, 22 Nov. 1954 (fl), *W. Rodrigues 145* (INPA); Mun. Boa Vista, Estação Ecológica de Maracá, campo, 19 Nov. 1978 (fl), *J.L. dos Santos 260* (INPA [2 sheets]); Boa Vista, Estrada do Cantá, 2°50'N, 60°40'W, beira da Estrada, solo argiloso, 31 Jul. 1986 (fr), *J.A. Silva et al.* 550 (INPA, MG, UB); Boa Vista, Estrada da Serra Grande, 2°50'N, 60°40'W, beira da Estrada, solo argiloso, 2 Aug. 1986 (fr), *J.A. Silva et al.* 585 (INPA, MG, UB); Aldeia da Raposa, 1 Apr. 1964 (fl, fr), *M. Silva 262* (MG); **State Unknown:** Without locality, s.d. (fl, fr), *Collector Unknown s.n.* (BR 824757) (BR).

**Specimens with erroneous locality: BRAZIL:** “Rio de Janeiro: São João da Barra, dans les bois”, 10 February 1876 (fl, young fr), *A. Glazou 9887* (C [2 sheets, without barcode], P [P00748138], R [Acc. No. 10469]).

The specimens *Glazou 9887* and *Glazou 9887a*, belonging to two different species, have labels reporting a collection locality in the state of Rio de Janeiro, with different collection dates and different ecologies. The labels of both gatherings indicate that the specimens were collected in São João da Barra [ca. 21°38'24'S, 41°3'3"W], which is a coastal town in the northern portion of the State of Rio de Janeiro, mostly with restinga vegetation and patches of “floresta de tabuleiro”. The gathering *Glazou 9887* is *Sipanea pratensis* var. *dichotoma*. The label of the specimen *Glazou 9887* at R [Acc. No. 10469, barcode R010053882] has the heading “PLANTAS DO BRASIL CENTRAL, GLAZIOU N°” and the handwritten text “9987. *Sipanea pratensis* var. *trichantha*, K. Sch. Flora Bras. VI. VI, 255. São João da Barra (Rio de Jan. [Rio de Janeiro]), 10 de Fevereiro de 1876. Herbacea flores rosas.” The specimen of *Glazou 9887* at P, barcode P00748138, has two labels. At the lower left corner is a label handwritten by Glazou in pencil reporting “São João da Barra [...] 10 fevrier 1876. Herb. fl. rose.”

The other label, at the lower right corner, has the printed heading “HERB. MUS. PARIS” and the text, handwritten in black ink by Glazou “*Sipanea pratensis* Aubl. var. *trichantha*. BRÉSIL (Rio Janeiro) São João da Barra, dans les bois, 10 fevrier 1876, Herbacé – fl. rose, n. 9887” and the lower heading “Herbier de A. Glazou, donné par Mme SIMART, sa fille, en 1907.” There are two specimens of *Glazou 9887* at C, without barcode, and without indication of locality or collection date. Each specimen has a label with the printed heading “Herbarium Eug. Warming” and the handwritten text “*Sipanea pratensis* Aubl. [Legit] Glazou 9887, [determ.] Schumann.” The specimens of *Glazou 9887* at C, P, and R, correspond with *S. pratensis* var. *dichotoma*; however, Schumann (1889) in *Flora Brasiliensis* did not cite the gathering *Glazou 9887* under *S. pratensis* or any other species of *Sipanea*. This variety ranges throughout the Guiana Shield and the Amazon Basin, in Colombia, Venezuela, the Guianas, and northern Brazil (Roraima, Amapá, Pará, and Maranhão). The southernmost collection of this variety is reported from Nova Olinda do Norte [ca. 3°53'S, 59°5'W, *Todzia et al.* 2286], in the Brazilian state of Amazonas, which is more than 2000 km air distance from São João da Barra [ca. 21°38'S, 41°3'W], state of Rio de Janeiro, which is also a completely different habitat, with remnants of “floresta de tabuleiro” and “restinga” vegetation. Glazou collected in the states of Rio de Janeiro, São Paulo, Espírito Santo, Minas Gerais and Goiás (Lanjouw & Stafleu 1957; Urban, 1906), and never set foot in the Amazon Basin. It is well-known among botanists (Santos, 2016; Sleumer, 1954; Smith, 1966; Wurdack, 1970) that for numerous specimens Glazou reported localities where he never was, and included Amazonian collections in his herbarium citing them as collected by him in Rio de Janeiro. Therefore, the specimen labels of *Glazou 9887* are treated as reporting an erroneous collection locality.

8-6. *Sipanea veris* S. Moore, Trans. Linn. Soc. 2, 4: 368. 1895. (Figures 51–53).

Type: BRAZIL. Mato Grosso: Rio dos Bugres, near the confluence with the Paraguay River, “in apertis arenosis ad ripas fl. dos Bugres, itaque ad confluentes fl. Paraguay et dos Bugres prope Santa Cruz,” 1891–1892 (fl), *S. Moore 435* (**Lectotype** BM [barcode 000614332], **here designated**; isoelectotypes K [without barcode], NY [barcode 01085914]; photo-BM at NY). [Section *Sipanea*].

(=) *Sipanea acinifolia* R. Spruce ex Sprague, Trans. Proc. Bot. Soc. Edinb. 22: 433. 1905



Type: COLOMBIA. Vichada: Maipures, Río Orinoco [border between Colombia and Venezuela], “Prope Maypures, ad flumen Orenoco”, Jun. 1854 (fl), *R. Spruce* 3652 (**lectotype** LD [Acc. No. 1219703], **here designated**; isoelectotypes K [without barcode], MPU [barcode MPU021332], P [barcode P007294432, as “3652 (299)”] RB [Acc. No. 15356, barcode 00364227]).

(=) *Sipanea spraguei* Wernham, *J. Bot.* 55: 172. 1917.

Type: VENEZUELA. Bolívar: Río Orinoco, Caicara, near a clump of moriche palms, Nov. 1898 (fl), *C.J. Sprague* 7 (holotype BM [barcode 000614324]; isotype K [without barcode]).

*Herbs*, prostrate or sometimes decumbent, rooting at nodes, commonly forming thick patches; stems thin, 0.5–0.8 mm thick, terete or slightly quadrangular, green, sparsely strigulose. *Stipules* adnate to the petioles, sheathing, free portion truncate, shallowly triangular or shortly suborbicular, 0.5 × 0.5–0.8 mm, truncate to shallowly obtuse at apex, membranaceous, strigulose or glabrate outside, glabrous, slightly thickened at margin inside; with 5–6 colleters inserted along the margin. *Leaves* very variable in size, often varying in size on the same individual, petiolate; petioles 0.5–6 mm long, olive-green when dry, strigulose below, glabrous or glabrate above, commonly canaliculate, not winged, sparsely appressed strigose; blades ovate, ovate-lanceolate to rhombic-ovate, 0.5–2.6 × 0.2–1.7 cm, subacute, cuneate to obtuse at base, obtuse to acute at apex, membranaceous to papyraceous, grass-green above and dull pale green below when fresh, olive-green above and below when dry, lamina glabrous or sparsely strigulose above (hairs 0.5 mm long) with midrib and secondary veins sparsely short strigose above, with midrib and secondary veins sparsely strigose below, margin glabrous or appressed-strigulose ciliate; secondary veins 2–3 on each side of midrib, obsolete above, slightly prominent below. *Inflorescences* terminal or subaxillary, originally terminal, uniflorous or 2-flowered, sessile to short-pedunculate, peduncle (when present) to 4.5 mm long, appressed strigose; bracts and bracteoles lacking. *Flowers* distylous, 5(6)-merous, sessile to short-pedunculate; pedicels (when present) to 1 mm long, sparsely strigulose. *Hypanthium* obovoid, 1.5–3.5 × 2–2.2 mm,

acute to obtuse at base, round to obtuse at apex, densely appressed-strigillose. *Calyx* lobes subequal or unequal, green to reddish-green when fresh, linear-lanceolate, (2-)3–7.5 × 0.1–0.6 mm, acute to acuminate at apex, sparsely strigulose outside, especially along the midvein, margins sparsely appressed ciliate; with 1–2 colleters in each calycine sinus, narrowly conical, acute at apex, 0.2–0.4 mm long. *Corolla* hypocrateriform, (14-)16–23.5 mm long, variable in size throughout the geographic range, sometimes varying in size within the same population or on the same individual, pale to intense pink, turning paler after anthesis, lobes basally white, nonglandular, forming a white ring at mouth, with a dense ring of yellow hairs exerted beyond the mouth; tube (8-)10–13.5 mm long, cylindrical and gradually expanding towards the mouth, 0.9–1.1 mm at base, 2–3 mm wide at mouth, glabrous and shortly strigillose in lines outside, lower half glabrous and puberulous above, and yellow-villous where anthers are inserted, densely yellow-villous at corolla mouth; lobes 5(6), obovate, broadly obovate to round, 6–10 × 4.5–8 mm, obtuse to subacute at apex, glabrous throughout. *Long-styled flowers* [*Molina & Barkley* 161 (corolla tube 10 mm long)]: stamens inserted at 3.7 mm below corolla mouth; filaments 0.3 mm long; anthers linear, 1.7 × 0.2 mm, acute at both ends; style exerted to 1.5 mm beyond corolla mouth, glabrous; style branches obovate, 1 mm long, round at apex, papillose. *Short-styled flowers* [*Beck et al.* 9898 (corolla tube 13.5 mm long), *Haugh* 2622 (corolla tube 12.5 mm long), *Velez* 2713 (young fruits, US)]: stamens inserted at 3–3.5 mm below corolla mouth; filaments 0.3 mm long; anthers linear, 1.8 × 0.2 mm, acute at both ends; style included, 7–7.5 mm long, glabrous; branches linear to very narrowly lanceolate, ca. 2 mm long, acute at apex. *Infructescences* terminal or subaxillary, originally terminal, uniflorous or 2-flowered, similar to inflorescence. *Capsules* oblong-elliptic, 7 × 3 mm, round at both ends, crustaceous, densely antrorse hispidulous-strigillose, pale green when young, turning pale brown when dry. *Seeds* irregularly polyhedral, ca. 0.5 mm in diam., testa foveolate.

**Notes:** Moore (1895: 368–369) described *Sipanea veris* and cited his own gathering *Moore* 435, without mentioning the herbarium of deposit. Steyermark (1967: 266–267) cited *Moore* 435 as type, without indicating any herbarium. Delprete (2010c: 1150) cited a speci-

**Figure 51.** *Sipanea veris*. **A.** Habit. **B.** Node with sheathing stipule and partially exerted colleters, and leaf bases. **C.** Dissected short-styled flower, with stamens inserted at distal portion of corolla tube, and included style. **D.** Dissected long-styled flower, with stamens inserted at distal portion of corolla tube, and exerted style. **A–B, D:** drawn from *Molina & Barkley* 18-V-161 (US); **C:** drawn from *Haught* 2622 (US). Illustration by Piero Delprete.

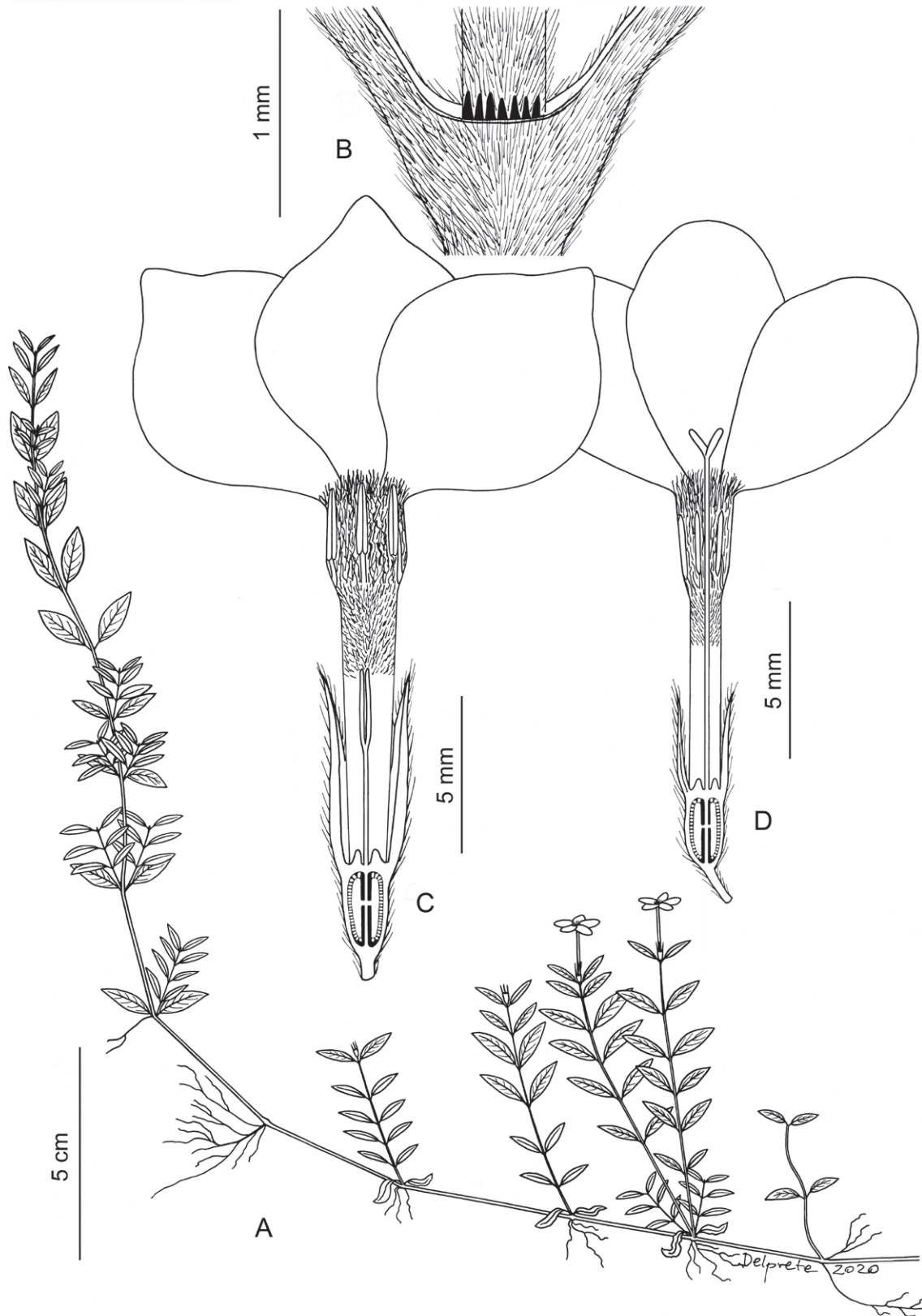


Figure 51.



**Figure 52.** *Sipanea veris* – Color plate. **A.** Habitat; vegetation frequently cut down, in front of a house; ground about 5 m above river level at the time of collection; during the rainy season (June–September) the water level is 0.5–1 m above the ground. **B.** Habit. **C.** Detail of habit, with plants in anthesis. **D–F.** Corolla variation in lobe shapes and merosity. **D.** Corolla with four equal lobes. **E.** Corolla with five equal lobes. **F.** Corolla with five unequal lobes (two wider than the others). Photos taken by Piero Delprete on 7 January 2001, Mun. San Fernando de Atabapo, locality Súpiro, at the margin of the Orinoco River, Venezuela, where *Delprete et al.* 7457–7459 were collected.

men at BM as holotype; however, this citation cannot be treated as an inadvertent lectotypification because, as being published after 2001, it should have been accom-

panied by “here designated” or a similar expression. Therefore, the BM specimen, barcode 000614332, is here designated the lectotype of this name.

Sprague (1905: 433–434) described *S. acinifolia* Spruce ex Sprague as having corolla tubes sparsely pubescent outside and cited two gatherings “Orinoco: Caicara, *Sprague*, No. 383; Maypures, *Spruce*, No. 3562” without mentioning any herbarium. Steyermark noted that both gatherings cited by Sprague have corolla tubes externally glabrous; therefore, to be in agreement with Sprague’s protologue, he designated as type of *S. acinifolia* “Vicinius Santarem, Prov. Para, Brazil, Nov–Mar. 1849–1850, *R. Spruce* 329 (lectotype)”, which has corolla tube sparsely pubescent outside. As the corolla outer vestiture is here considered a variable character within the species, specimen *Spruce* 3652 at LD [Acc. No. 1219703] is here designated as the lectotype of *S. acinifolia*.

Wernham (1917), in the introduction of the same article where he published the revision of *Sipanea* wrote “The types of all the novelties described are in the National Herbarium [BM].” Therefore the specimen *Sprague* 7 at BM, barcode 000614324, is the holotype of *Sipanea spraguei* Wernham. In the same article he also treated *Sipanea acinifolia* as a synonym of *S. veris*.

Steyermark (1967: 266–267) explained that the difference in size and vestiture of leaves and corollas of *Sipanea veris* and *S. spraguei* are overlapping in several specimens, therefore he treated them as synonymous. A conclusion with which I concur.

Steyermark (1967: 263; 1974: 361) distinguished *Sipanea acinifolia* from *S. veris* by having corolla tube externally sparsely strigillose (vs. externally glabrous throughout in *S. veris*), and leaf blades more or less densely strigose beneath (vs. glabrous or nearly so beneath, only the midrib and lateral nerves strigose in *S. veris*), although admitting that “there is little or no demarcation within these intergradations, and it is believed at this time, until further collections are available, justifiable to encompass the variability of leaf pubescence in *S. acinifolia* as one taxon.”

Delprete and Steyermark (2004e: 828–832) treated *S. veris* and *S. acinifolia* as synonymous, without any comment. After an analysis of numerous specimens from throughout the geographic range, I concluded that the variation in external corolla vestiture is a trivial character that can vary even within the same population, and it is here confirmed that these two names are conspecific. Therefore, Steyermark’s typification of *S. acinifolia* is superseded, and the lectotype of this name is here selected from the two gatherings cited by Sprague. Specimens of *Spruce* 3562 are at K, LD and MPU. The specimen at LD, Acc. No. 1219703, has Spruce’s handwritten label “3652 (299) *Sipanea acinifolia* sp. n., Prope Maypures, ad flumen Orenoco, coll. R. Spruce, Junio 1854” and is here designated the lectotype of this name.

**Distribution and ecology:** Distributed in the Amazon Basin, in the “Llanos del Orinoco” or Orinoquía” of Colombia and Venezuela, as well as Brazil and Bolivia (Figure 53). Spreading herbs, sometimes forming small patches, growing in seasonally flooded areas, in open savannas, at river margins, or at edges of forests and *Mauritia* palm swamps, in sunny or semi-shady exposures, in sandy soils, or soils with sand and clay intermixed with organic material; at 70–450 m altitude.

**Phenology:** Flowering specimens were collected from January through June, and from October through December. Specimens with flowers and fruits were collected in March, April, July and October.

**Suggested conservation status: Least Concern (LC).** This species is amply distributed in Colombia, Venezuela, the Guianas, and Amazonian Brazil (Roraima, Amapá, Amazonas, Pará, Maranhão). It is most frequent in the various kinds of savannas and forest edges (see Distribution and Ecology, above), and is also a common ruderal species growing at margins of forest trails, in secondary vegetation, and roadside vegetation, often forming large patches. Because of its wide geographic distribution, common occurrence in savannic vegetation and as a ruderal species, this species belongs the Least Concern (LC) category, following IUCN criteria (IUCN 2012, 2019).

**Specimens examined: COLOMBIA: Boyacá:** Near mouth of Río Güira (Río Meta), 150 m, wet soil, partly shaded, 22 Feb. 1939 (fl), *O. Haught* 2622 (NY, US); Cañada Castero, 20 km de Santa Elena, piste Mani-Sta. Elena, 25 Feb. 1971 (fl), *C. Sastre* 863 (P); Caño Casimena, 16 km de Santa Elena, 26 Feb. 1971 (fl), *C. Sastre* 883 (P). **Casanare:** Río Meta, Orocué [ca. 4°47’N, 71°20’W], 140 m, 3 Nov. 1938 (fl, fr), *J. Cuatrecasas* 4378 (US). **Guainía:** Ribeiras del Río Inírida, sitio Sabanita, a medio camino entre “Raudal Alto” y “Morichal,” 180–200 m, 7 Feb. 1953 (fl), *A. Fernández* 2184 (US). **Guaviare:** San José del Guaviare [ca. 2°33’N, 72°38’W], Río Guaviare, sabana, 240 m, 13 Nov. 1939 (fl, fr), *J. Cuatrecasas* 7722 (US). **Meta:** Mun. Puerto Gaitán, cerca al Río Manacacias, 4°18’N, 72°5’W, 220 m, en sabana, 9 Dec. 1993 (fl), *R. Cortés et al.* 1103 (P); 2 km E of Puerto Gaitán, in the flood-plain of Río Manacacias, low lying savanna and scattered secondary forest along river bank, 150 m, 31 Dec. 1973 (fl), *G. Davidse & F. Llanos* 5408 (F, MO, NY); margen derecho del Río Manacacias, frente a Puerto Gaitán, formación Serrania, ca. 200 m, 26 Mar. 1971 (fl), *E.P. Pinto & O.P. Bernal* 1575 (P). **Vaupés:** Río Vaupés, a Mitu [1°11’N, 70°10’W], 320 m, 7–8 Nov. 1952

(st), *H. Humbert & A. Fernandez s.n.* (P P06772733), (fl), *s.n.* (P P06772734). **Vichada:** Hacienda de Hector Pérez, Sacuraré, on the Río Vichada, ca. 40 km W of San José de Ocuté, 18 Jan. 1944 (fl), *F.J. Hermann 10964* (F, NY, US); Parque Nacional El Tuparro, La Linea Roja, just S of Río Toro, open savanna and wooded edge of small stream, 5°32'N, 68°32'W, 100 m, 12 Mar. 1985 (fl, fr), *J.L. Zarucchi & C.E. Barbosa 3684* (COL, FMB, MO, NY).

**VENEZUELA. Amazonas:** Orinoco River, southern part of Isla del Raton, savannah, grass vegetation, light shade, 5°2'N, 67°46'W, 90 m, 22 Nov. 1965 (fl), *F.J. Breteler 4786* (MER, NY, U, US, WAG); carretera Puerto Ayacucho–Sanariapo, 100 m, s.d., *G. Bunting et al.*

3543 (U, VEN); San Fernando de Atabapo [ca. 4°3'N, 67°38'W], 29 Mar. 1950 (fl), *H.M. Curran 109* (NY); Isla Ratón, area seasonally inundated, dominated by Poaceae, soil of sand intermixed with rich organic material and clay, at moment of collection soil moist but not inundated, 5°4'N, 67°48'W, 90 m, 6 Jan. 2001 (fl), *P.G. Delprete et al. 7446* (CAY, MO, NY, P, TFAV, US, VEN), 7447 (CAY, F, L, NY, TFAV, VEN), 7448 (B, CAY, K, TFAV, VEN), 7449 (CAY, P, TFAV, US, VEN), 7450 (CAY, VEN); Mun. San Fernando de Atabapo, Community of Minicia Nuevo, caserío near river margin, open, sunny exposed area, soil with sand and clay intermixed, 3°56'N, 67°27'W, 130 m, 7 Jan. 2001 (fl), *P.G. Delprete et*

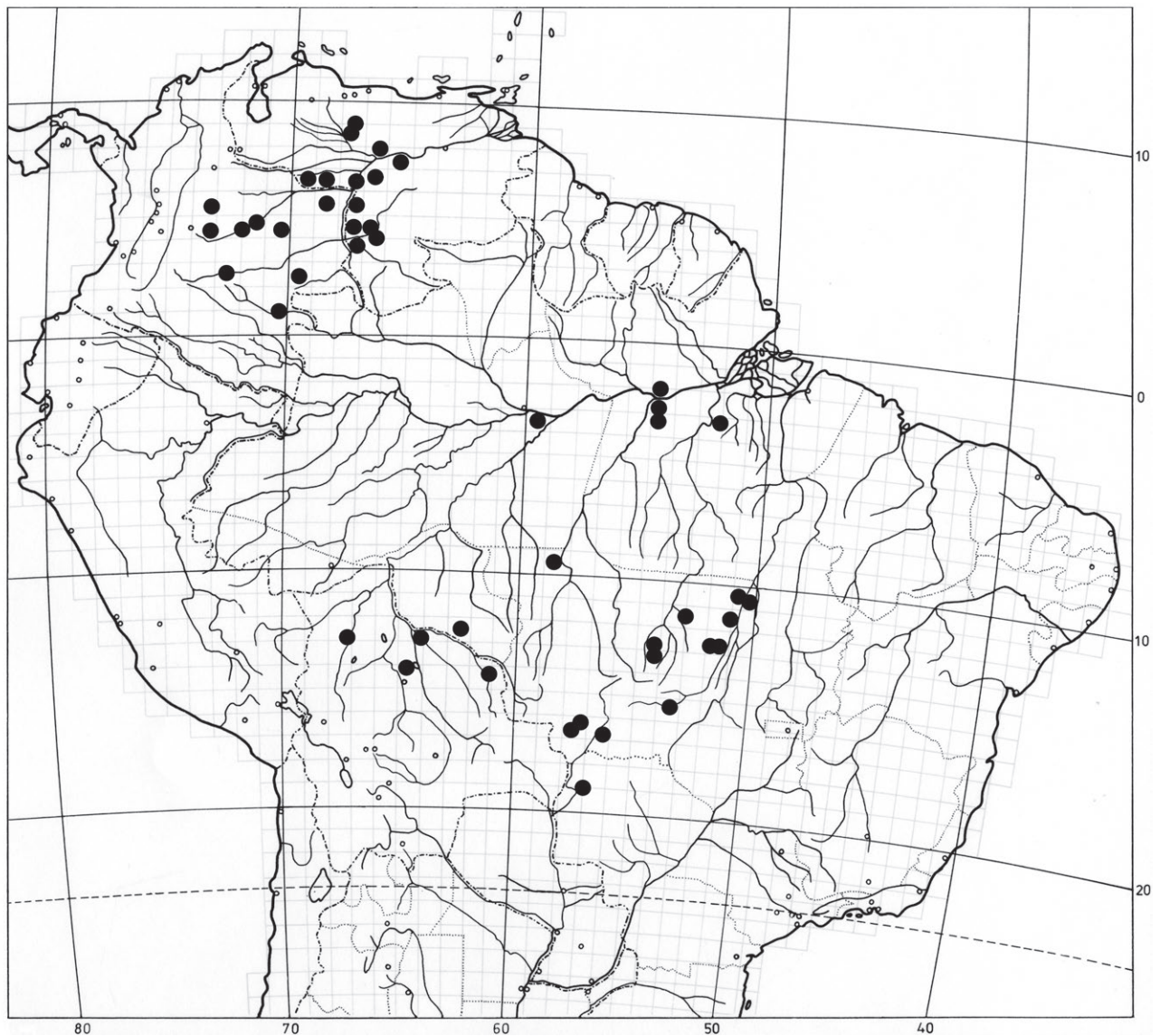
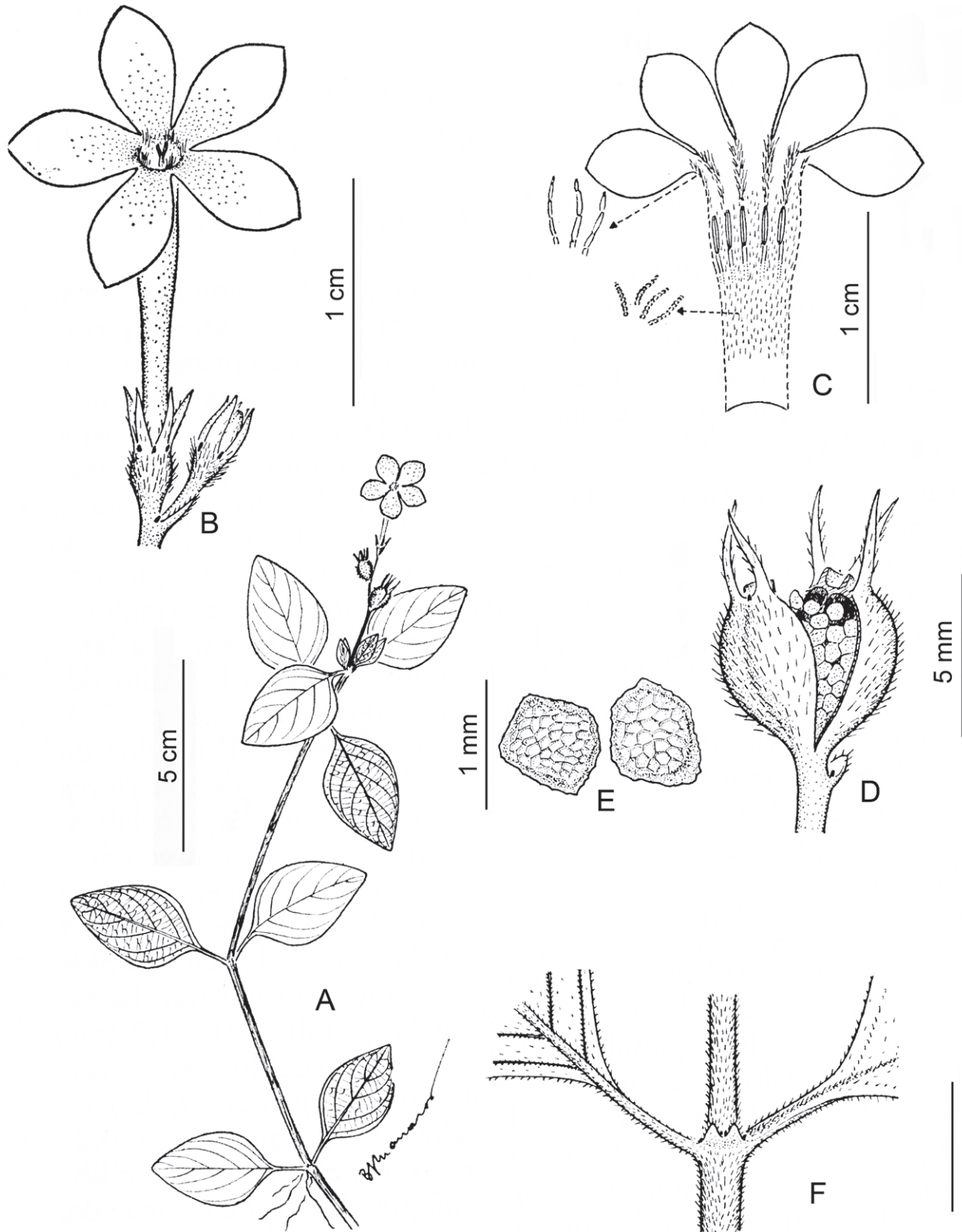


Figure 53. Distribution of *Sipanea veris*.

*al.* 7454 (CAY, P, TFAV, US, VEN), 7455 (CAY, MO, NY, TFAV, VEN), 7456 (B, K, L, TFAV, VEN); Mun. San Fernando de Atabapo, locality Súpiro, at the margin of the Orinoco River, vegetation frequently cut down on front of a house, soil about 5 m above river level at the time of collection, during the rainy season (June–September) the water level increases to 0.5–1 m above soil level (and the plants are submersed), soil of clay and sand intermixed, 3°56'N, 67°27'W, 120 m, 7 Jan. 2001 (fl), *P.G. Delprete et al.* 7457 (CAY, MO, TFAV, US, VEN), 7458 (L, NY, P, TFAV, VEN), 7459 (BR, K, NY, TFAV, VEN); [Parque Nacional Cerro Yapacana, ca. 4°0'N, 66°35'W], Cerro Yapacana, upper Río Orinoco, 100 m, Apr. 1931 (fl), *E.G. Holt & E.R. Blake* 774 (BR, NY); Depto. Atabapo, near Canaripó, L margin (S) of Río Ventuari, ca. 20 km from junction with Río Orinoco, sabana inundada con *Caraipa* y montículos de termiteros hasta 2 m de alto, 4°3'N, 66°49'W, 98 m, 31 May 1978 (fl), *O. Huber* 1974 (NY, VEN); clearing at Santa Barbara, at junction of Ríos Orinoco and Ventuari, 100 m, 8 Jan. 1951 (fl), *B. Maguire et al.* 30811 (NY [2 sheets], VEN); Alto Río Orinoco, Santa Barbara, at junction of Ríos Orinoco and Ventuari, 120 m, 16 Mar. 1953 (fl), *B. Maguire & J.J. Wurdack* 34479 (NY [2 sheets], UB, VEN); orilla del Río Orinoco en los alrededores de San Fernando, 250 m, terrenos arenosos y húmedos, 24 Nov. 1948 (fl), *J.A. Molina & F.A. Barkley* 18-V-161 (US); gallery forest along Caño Cataniapo, 14 km S of Puerto Ayacucho, 75 m, 4 May 1977 (fl, fr), *J.A. Steyermark & O. Huber* 113871 (F, VEN); silvestres en formación, graminiforme e chaparral sobre pequeñas planicies y/o lajas graníticas, en el Tobogancito, alrededores de Puerto Ayacucho, al sur, 16 Apr. 1986 (fl), *B. Truillo et al.* [additional collectors unknown] 20441 (MG, VEN); along trail between San Fernando de Atabapo and Río Orinoco, 125 m, 29 May 1959 (fl), *J.J. Wurdack & L.S. Adderley* 42664 (NY [2 sheets], US, VEN). **Apure:** Dtto. Muñoz, Hato El Polvero, 79 km S de Elorza, sabanas de banco adyacentes al Caño Cicuture (afluente del Alto Río Cinaruco), 6°38'N, 69°37'W, 80 m, 28 Apr. 1987 (fl), *G. Aymard et al.* 5666 (MO, NY); Dtto. Pedro Camejo, near Río Meta, at Fundo El Algarrobo, 25 airline km WNW of Buena Vista, Morichal de La Madera, 6°13'N, 68°49'W, 70 m, 16–18 Feb. 1978 (fl), *G. Davidse & A. González* 14188 (MO, NY, P, VEN); Puerto Paez [ca. 6°12'N, 67°27'W], 8 May 1946 (fl), *I. Velez* 2713 (US). **Bolívar:** Dtto. Cedeño, km 12–120 de la carretera Caicara del Orinoco–Puerto Ayacucho, s de Caicara del Orinoco, 6°50'N, 66°30'W, 100 m, 18 Nov. 1984 (fl), *G. Aymard & B. Stergios* 3286 (MO, NY, PORT); Caicara [ca. 7°50'N, 66°10'W], Estero Santa Rita, 60 m, 4 Jun. 1984 (fl), *S. Lopez-Palacios et al.* 4334 (MERF, NY, VEN); Distrito Cedeño, 14 km SW of Caicara del Ori-

noco, wet savanna, 2 Sep. 1985 (fl), *J.A. Steyermark et al.* 131116 (MO, VEN); Guayapo [ca. 7°20'N, 65°11'W], Bajo Caura, 100 m, 20 Apr. 1939 (fl, fr), *Ll. Williams* 11917 (F, IAN, US); sítios bajos y periódicamente anegados, en la sabana de El Tigre, 90 m, 20 Jun. 1940 (fl, fr), *Ll. Williams* 13411 (US). **Guárico:** Hato Flores Moradas, 60 km S of Calabozo, *s.d.*, *L. Aristeguieta & Hernández* 2324 (VEN); Dtto. Infante, Parque Nacional Aguaro-Guariquito, Aguas Muertas, orillas del Río San Bartolo, 8°92–96'N, 67°52–60'W, 50 m, Dec. 1981 (fl), *F. Delascio et al.* 11282 (NY); Carretera Santa Rita–Cabruta, *s.d.*, *B. Trujillo* 5507 (VEN). **State Unknown:** without locality, 7 Apr. 1921 (fl), *M. Grisol s.n.* (P P00729413).

**BRAZIL. Amazonas:** Mun. Nova Olinda [Nova Olinda do Norte], lower Rio Mari, below Rio Pará, Laranjal, along river and igarapé, sandy soil, 1 Jul. 1983 (fl, fr), *C. Todzia et al.* 2288 (INPA, MG, NY). **Mato Grosso:** Parque Nacional do Xingú [now Parque Indígena do Xingú], Rio Tutuarí, margem alagável do rio, Sep. 1965 (fl), *D. Coelho s.n.* (INPA 15866) (INPA); Cidade de Barra dos Bugres, beira do Rio Paraguai, mata de beira do rio, solo arenoso, 15°5'S, 57°10'W, 160 m, 27 Aug. 1984 (fl), *L. Coradin et al.* 6996 (CEN); Serra do Roncador, Mun. Barra do Garças, Córrego do Gato, 210 km along new road NNE of village of Xavantina, 50 km due S of Royal Society–Royal Geographic Society Base Camp, base camp at 12°51'S, 51°45'W, 450 m, 9 Sep. 1968 (fl, fr), *G. Eiten & L.T. Eiten* 8649 (RB, UB), 4 Oct. 1968 (fl, fr), 9074 (NY, SP, US); without locality, 11°27'S, 50°19'W, 25 Nov. 1977 (fl), *C.T. Falcão* 5096 (RB [2 sheets]); Nova Ubitatã, Estação Ecológica (ESEC) Rio Ronuro, Cruz de Malta I, margem direita do Rio Ronuro, floresta estacional semididicial, transição Cerrado–Amazônia, mata ciliar, 13°5'32"S, 54°25'19"W, 323 m, Oct. 2018 (fl), *D.R. Giacoppini et al.* 486 (CNMT); Córrego do Gato, ca. 51 km S of Base Camp (12°49'S, 51°46'W), drying up margin of small lake, 3 Oct. 1968 (fl), *R.M. Harley, R. Souza & A. Ferreira* 10443 (NY, P, RB, U, UB); 1° de Fevereiro, margem do Rio Cautario, Jan. 1919 (fl), *J.G. Kuhlmann* 2362 (RB [2 sheets]); Rio Sangrador, in nemore uliginoso, 9 Dec. 1893 (fl), *C.A.M. Lindman* A2443 (S [2 sheets]); Fazenda Espírito Santo, Sesc Pantanal [ca. 16°30'S, 56°30'W], borda Cerrado, 15 Nov. 2003 (fl), *G.A. Lima Jr.* 31 (UFMT); 0.5 km E of km 235.5 of Xavantina–Cachimbo road, 18 Dec. 1967 (fl), *D. Philcox et al.* 3656 (NY, P, UB); Poconé, Fazenda Ipiranga, seco, 25 Jul. 1991 (fl), *A.L. Prado* 959 (UEC); Poconé, Fazenda Ipiranga, ca. 4 km a esquerda no km 10 da rodovia transpantaneira, borda de campo, sazonalmente alagável, 21 Jul. 1991 (fl), *A.L. Prado* 5103 (UFMT); Pantanal de Poconé, Fazenda Nossa Senhora Aparecida, campo inundável, solo argilo-arenoso, 15 Nov. 2003 (fl), *L. Rebellato & L.*



**Figure 54.** *Sipanea biflora*. A. Habit. B. Portion of inflorescence. C. Dissected corolla with detail of hairs at mouth and corolla throat. D. Dehiscent capsule. E. Seeds. F. Node with bilobed stipule and leaf bases. Illustration by Bruno Manara (Reproduced with permission from Flora de Venezuela vol. 9(1), fig. 60. 1974).

*Ferraz* 212 (UFMT); Rio Xingú, Oct. 1947 (fl), *H. Sick B-416* (RB); ca. 66 km S of Base Camp, along rd, 9 Sep. 1968 (fl), *R. Souza in Richards* 6878 (NY, P, RB, U); Mun. Luciara, lake 2 km NW of Luciara, cerradão forest and marsh, 11°11'S, 50°44'W, 8 Oct. 1985 (fl), *W.W. Thomas et al.* 4303 (INPA, MG [2 sheets], NY [2 sheets]), SPF; Jacaré (acampamento), Rio Xingu, 15 Jan. 1948 (fl), *M. Victorino* 1 (R 3 sheets); Cotriguaçu [ca. 9°51'S, 58°24'W], Fazenda São Nicolau, 3 Mar. 2011 (fl), *M.C. Vilela-Santos & L.F. Barbosa* 4832 (IAN); Pantanal de Poconé, Pirizal, Fazenda Aparecida, campo de pastagem, 18 Nov. 2000 (fl), *D.A.A. Vilhalva & E.C. Arruda* 95 (UFMT). **Mato Grosso do Sul:** Mun. Corumbá, Fazenda Marilândia [ca. 19°S, 57°W], campo arenoso seco, 7 Oct. 1953 (fl), *E. Pereira et al.* 245 (NY, R, RB); Mun. Corumbá, Fazenda Campo Dora, Vazante, 10 Jun. 1994 (fl), *G. Hatschbach et al.* 60916 (C, MBM, US). **Pará:** Mun. Santarém, Praia do Lago Verde de Alter do Chão, 2°29'2"S, 54°56'56"W, 3 Apr. 2016 (fl), *T. André et al.* 82 (RB); Belterra, Praia de Porto Novo, 29 Oct. 1947 (fl), *G.A. Black* 47-1841 (IAC, IAN, U); Santarém, emboadura do Rio Tapajós, lado direito, campo arenoso com vegetação arbustiva, 12 Dec. 1966 (fl), *P. Cavalcante & M. Silva* 1727 (IAN, MG, RB); Bôa Esperança, abaixo da Cachoeira, capoeira, margem esquerda, 29 Dec. 1951 (fl, fr), *J.M. Pires* 3644 (IAN); Parque Nacional Tapajós, km 60 da estrada Itaituba–Jacarecanga, margem esquerda do rio, capoeira de várzea, 23 Nov. 1978 (fl, fr), *M.G. Silva & C. Rosário* 3904 (MG, NY, UB); Santarém, campos de Maracá, soil peaty, Nov. 1849 (fl), *R. Spruce* 299 (C, K, P, S, MPU); in vicinibus Santarém, Nov. 1849–Mar. 1850 (fl), *R. Spruce s.n.* (FI-Webb, P); Vitória do Xingu, 3°12'54"S, 52°6'46"W, 20 Feb. 2015 (fl), *C.R.D. Vieira*, *PSACF\_EX05366* (RB). **Rondônia:** São Francisco, Porto Murinho, Reserva Biológica Guaporé [ca. 12°30'S, 62°53'W], Rio São Miguel, permanently flooded wetland dominated by *Mauritia flexuosa*, 150 m, 1 Oct. 2013 (fl), *J.E. Householder* 3025 (INPA). **Tocantins:** Mun. Santa Isabel, Ilha do Bananal, moist edges of campo, growing in large masses, 25 Jul. 1968 (fl), *P.W. Richards* 6515 (NY, P, RB, U, UB). **State Unknown:** Without locality, s.d. (fl, fr), *L. Riedel* 141 (BR).

**BOLIVIA: Beni:** Prov. Ballivian, en la zona de influencia del Río Yacuma, Isla de Espiritu, [14°9'S, 64°23'W], 200 m, sabana húmeda, 16 Oct. 1980 (fl), *G. Beck* 5102 (UB); Prov. Itenez, S side of Río Guaporé, “campo verde” ca. 15 km ESE of Costa Marques [Estado de Rondônia, Brazil], flat grassland with scattered tortuous trees, 12°30'S, 64°8'W, 150 m, 31 Mar. 1987 (fl), *M. Nee* 34644 (NY, P, SP). **La Paz:** Prov. Iturrealde, Luisita, W del Río Benio, pastizal al lado del Río Muqui, sabana húmeda, 13°5'S, 67°15'W, 180 m, 22 Feb. 1984 (fl), *G. Beck & R.*

*Haase* 9898 (US). **Santa Cruz:** Prov. Velasco, Reserva Ecológica El Refugio, Campamento La Toledo, a 5 km de la casa, pampa inundada estacionalmente, 14°45'42"S, 61°8'26"W, 220 m, 29 Oct. 1996 (fl), *M. Garvizu & A.M. Carrión* 234 (MO); Prov. Velasco, Parque Nacional Noel Kempff Mercado, pampa húmeda Los Fierros, con termiteros atualmente seca sin incendio recente, atualmente inundada, 14°48'41"S, 60°23'45"W, 225 m, 15 Oct. 1993 (fl), *T. Killeen et al.* 5562 (MO, NY); Prov. Velasco, Reserva Ecológica El Refugio, pampa inundada estacionalmente, 14°45'42"S, 61°8'26"W, 200 m, 19 Oct. 1994 (fl), *T. Killeen et al.* 7012 (NY).

**8B. *Sipanea* section *Virecta*** (Rottb.) Steyererm., Mem. New York Bot. Gard. 17: 263. 1967.  
*Virecta* L.f., Suppl. Pl. 17, 134. 1782 [“1781”].

Type: *Virecta biflora* (Rottb.) L.f. [= *Sipanea biflora* (Rottb.) Cham. & Schltdl.].

*Sipanea* sect. *Panisea* K.Schum., Martius et al., Fl. Bras. 6(6): 249. 1889.

Type: *Sipanea biflora* (Rottb.) Cham. & Schltdl.

*Sipanea* sect. *Sipanea* subsect. *Cryptotricha* Steyererm., Mem. New York Bot. Gard. 17: 263, 264. 1967.

Type: *Sipanea biflora* (Rottb.) Cham. & Schltdl.

Herbs, prostrate, rarely decumbent; corolla mouth with a ring of white hairs.

8-7. *Sipanea biflora* (Rottb.) Cham. & Schltdl., Linnaea 4: 168. 1839. (Figures 5G, 54, 55).

(≡) *Rondeletia biflora* Rottb., Descr. Rar. Pl. Surin. 7-8. 1776 [Rottb., Acta Lit. Univ. Hafn. 1: 276, tab. 2, fig. 2. 1778; Ed. 2: 8. 1798]. - *Virecta biflora* (Rottb.) L. f., Suppl. Pl. 134. 1782 [“1781”]. - *Rondeletia biflora* A. Rich., Mém. Fam. Rubiacées 191. Dec. 1830 [reimpr. Mém. Soc. Hist. Nat. Paris, ser. 3, 5: 271. 1834], isonym. **Lectotype (here designated):** Drawing commissioned by Christen Friis Rottbøll in the library archives of the Natural History Museum, Copenhagen, the plant and analysis on the right side of the drawing [illustrated in Moraes, Dobreff & Reinhammar, Phytotaxa 165(1): Fig 21. 16 Apr 2014].

(=) *Sipanea radicans* Endl., Atakt. Bot. 7, fig. 7. 1833



Type: BRAZIL. Bahia: Without locality, s.d., *J.S. Blanchet s.n.* (**lectotype** W [Acc. No. W0072693], **here designated**).

(=) *Sipanea cowanii* Steyerl., Mem. New York Bot. Gard. 17: 265. 1967.

Type: GUYANA. Kaieteur Plateau, near Johnson's View, vicinity of Kaieteur Falls, and along western rim of Potaro Gorge, 425 m, 18 Feb. 1962, *R.S. Cowan & T.R. Soderstrom 1863* (holotype US [Acc. No. 2438240, barcode 00137724]; isotypes NY [barcode 00133310], VEN [Acc. No. 309636]; photo-US at NY).

(=) *Manettia hydrophila* Dwyer, Ann. Missouri Bot. Gard. 67: 280. 1980.

Type: PANAMA. Veraguas: Mouth of Río Concepción, in swamp, 4 Dec. 1967 (fl, fr), *W.H. Lewis, T.B. Croat & J.L. Hawcker 2822* (holotype MO [Acc. No. 312080]).

*Herbs*, terrestrial on forest floor, prostrate or sometimes decumbent on terrestrial habitats, or floating or semi-submersed in flooded areas, rooting at nodes, commonly forming thick patches, very variable in leaf and corolla size and shape; stems thin, 1.5–2 mm in diam., terete or slightly quadrangular, green, sparsely antrorse-pubescent or sparsely strigulose. *Stipules* adnate to the petioles, broadly triangular, 0.3–1.2(–2) × 0.7–0.9(–1.2) mm, shallowly obtuse to subacute or very rarely bifid at apex, membranaceous, glabrous or sparsely strigillose outside, glabrous, with a line near the base with a row of 2–6 colleters inside; margins hispid. *Leaves* very variable in size, often varying in size on the same individual, petiolate; petioles 4–18 mm long, green when fresh, commonly canaliculate, not winged or sometimes narrowly winged on both sides, sparsely short-strigose to shortly villous; blades ovate, rhombic-ovate or rarely oblong, (0.4–)1.2–5 × (0.35–)0.8–2.8 cm, truncate, round to cuneate, sometimes decurrent, rarely asymmetric, at base, obtuse to acute at apex, membranaceous to papyraceous, grass-green above and dull pale green below when fresh, olive-green above and below when dry, lamina glabrous, sparsely strigulose-puberulous or strigillose above with midrib and secondary veins sparsely short puberulous-strigulose above, glabrous, with midrib and secondary veins sparsely short puberulous-strigulose or strigillose below, margin sparsely appressed pubescent to appressed-strigulose ciliate; secondary veins (3–)4–6 on each side of midrib, ascending, weakly evident above,

slightly prominulous below. *Inflorescences* terminal or subaxillary, originally terminal, cymose, monochasial or rarely dichotomous, 1–3(–7)-flowered, short to long-pedunculate, rachis thin to almost capilliform, peduncle 5–15 mm long, glabrous; bracts subtending terminal cyme lanceolate, 1.5–3 × 0.2–0.4 mm, acute or acuminate at apex, glabrous, sparsely ciliate at margins; bracteoles subtending central flowers subulate, 0.5–1.5 mm long. *Flowers* distylous, (4)5-merous, pedicellate or sessile; pedicels of lateral flowers 5–15 mm long, those of central flower absent (flower sessile) or 1–1.5 mm long, appressed-pubescent and ciliate at apex. *Hypanthium* obconical, obovoid or subglobose, 1.5–2 × 0.7–1.2 mm, acute obtuse at base, round to obtuse at apex, sparsely appressed-strigillose at distal half (glabrous below), or appressed-strigillose throughout. *Calyx* lobes subequal or unequal, green when fresh, linear-lanceolate to setaceous, 1–5 × 0.2–0.6 mm, acuminate at apex, glabrous or puberulent, with a few sparse hairs or appressed-pubescent, margins with a few antrorse-ascending or appressed hairs; with 1 colleter in each calycine sinus, conical, obtuse at apex, 0.25–0.3 mm long. *Corolla* hypocrateriform, (8–)15–21(–29) mm long, very variable in size throughout the geographic range, sometimes varying in size within the same population or on the same individual, pink deep pink to pale purple turning paler after anthesis, lobes with a basal narrowly triangular area with white, glandular hairs, forming a white star-shaped area at mouth, with a ring of white hairs at mouth; tube cylindrical, 5–13(–15) mm long, 1–1.1 mm wide throughout, or slightly widening distally, 1–1.2 mm at base and to 1.4–2 mm wide at mouth, glabrous or glabrate at lower half and sparsely short-pubescent outside, lower half glabrous and shortly puberulous above, and white-villous near the anthers, with papillose hairs inside, densely white-villous at corolla mouth; lobes oblong-obovate, obovate to round, 3–8.5(–14) × 2–5.5(–7) mm, obtuse to round at apex, glabrous throughout. *Long-styled flowers* (*Henkel et al. 4607, Wessel-Boer 636, Sastre et al. 8150*; corolla tubes 7.5–13.5 mm long): stamens inserted at 3.7–5.5(–9) mm below corolla mouth; filaments 0.5–0.7 mm long; anthers narrowly oblong to linear, 1.5–2.5 × 0.15–0.2 mm, acute at both ends; style about the same length as corolla tube (tips of style branches exerted) or exerted to 1.5 mm beyond corolla mouth, glabrous; style branches linear, acute or very narrowly lanceolate and acuminate at apex, 0.8–2 mm long. *Short-styled flowers* [*Pipoly & Gharbarran 10147*; corolla tubes 12–12.5 mm long]: stamens inserted at 4–4.5 mm below corolla mouth; filaments 0.5–0.7 mm long; anthers linear, 2.2 × 0.2 mm, acute at both ends; style included, 5 mm long, glabrous; branches linear, 1.2

mm long, acute at apex. *Infructescences* terminal or subaxillary, originally terminal; seemingly lateral due to the reiteration of an axillary bud subtending the inflorescence, cymose, monochasial or rarely dichotomous, with 1–3(–7) fruits, similar to inflorescence. *Capsules* subglobose, 3–5 mm in diam., round at both ends, crustaceous, sparsely appressed puberulent or sparsely hispidulous-strigillose, pale green when young, turning pale brown when dry. *Seeds* irregularly polyhedral, irregularly rhomboid to irregularly globose, 0.5 mm in diam., testa foveolate.

**Notes:** This species was originally described as *Rondeletia biflora* by Rottbøll (1776: 7–8), who stated that he used material collected by Rolander in Suriname. This species was later re-named *Virecta biflora* by Linnaeus filius (1782 [“1781”]: 134), without citing *Rondeletia biflora* Rottb. Linnaeus filius certainly referred to the species described by Rottbøll, based on the habit, the floral characters, and the specific epithet. Article 41.4 of the Code (Turland et al. 2018) states that “If, for a name of a genus or lower-ranked taxon published before 1 January 1953, no reference to a basionym is given but the conditions for its valid publication as the name of a new taxon or replacement name are fulfilled, that name is nevertheless treated as a new combination or name at new rank when this was the author’s presumed intent and a potential basionym (Art. 6.10) applying to the same taxon exists.” Therefore, the binomial *Virecta biflora* should be treated as a new combination, and its type is the type of *R. biflora*, its basionym. Chamisso and Schlechtendal (1829: 168) published the new combination *Sipanea biflora* (Rottb.) Cham. & Schltld., citing both *Rondeletia biflora* Rottb. and *Virecta biflora* L.f. as synonyms. Richard (1830: 191) cited *Virecta biflora* as a synonym of his *Rondeletia biflora*. Since *V. biflora* is a new combination based on *R. biflora* Rottb., this is an indirect reference to *R. biflora*, which is the basionym of Richard’s *R. biflora*. Therefore, *R. biflora* (Rottb.) A.Rich. has the same type as *R. biflora* Rottb., and is an isonym without nomenclatural status (Art. 6 Note 2; Turland et al. 2018).

Moraes et al. (2010: 183) treated *Virecta biflora* L.f. as a name independent of *Rondeletia biflora* Rottb., but they did not take into account article 41.4 and cited the lectotype of the Linnaean name as “C.G. Dahlberg s.n. (SBT 4.2.7.83)”. However, as explained above, *Virecta biflora* should be treated as a new combination, and the type is the the type of *R. biflora* Rottb. They designated the lectotype of *Rondeletia biflora* as the specimen “D. Rolander s.n. (SBT 4.2.6.60).” Along with their lectotypification they wrote “Specimen SBT 4.2.6.60 was attributed to Rolander by P.J. Bergius, who also annotated

“*Rondeletia* (*biflora*), ... Friis Rottb. in act. litt. Hafn. 1778. p. 276. \* t. 2. f. 2.” Further, on the reverse side of the sheet, there is an annotation of “*Geophila reniformis* Cham. & Schlechtend.” by J.E. Wikström. Specimen SBT 4.2.7.83 that has the following handwritten text on it: “e Surinamo. Dahlb. (written by C.P. Thunberg), followed by “Thunberg.” (probably written by P.J. Bergius) and “scripsit” (by J.E. Wikström); just below “*Sipanea biflora* Linn. fil., si *Virecta virens* Vhal.” by J.E. Wikström, and on the bottom right, “*Virecta*” (by J.E. Wikström), “*virens*” (written by C.P. Thunberg), and “Vahl.” and “Thunberg scripsit” (by J.E. Wikström); the writing in the lowermost right-hand corner is a note probably written by Bergius about the number of male and female parts, viz. “5 andria. Iginia.” This specimen is not the same as the one represented in the drawing by Rottbøll. In *Index Kewensis*, there is an entry for *Virecta virens* Vahl, *Symb. Bot.* 2: 38. 1791, indicating it is a synonym of *Sipanea biflora* (Rottb.) Cham. & Schltld. In fact, Vahl (1791) mistakenly quoted “*virens*. VIRECTA. Lin. S. V. pag. 197.” and cited *Rondeletia biflora* Rottb. as a synonym, while Vahl (1798) referred it to “*Virecta biflora*. Lin. Syst. Veget. pag. 197,” thus correctly citing the information by Murray, *Syst. Veg.* (ed. 14): 197. 1784. Nevertheless, *Virecta virens* L. [Pl. Surin.: 7. 1775. Specimen: SURINAME. Loco non indicato, (fl.), C. G. Dahlberg 77 (LINN 212.1)] is not a validly published name, since in *Plantae Surinamenses*, *Virecta* was not given a separate generic description, being validly published only in *Suppl. Pl.*: 17. 1782. The reprint in *Amoen. Acad.*, Schreber ed. 8 (166): 254. 1785, amended *V. virens* L. as a synonym of *V. biflora* L. f.. However, by comparing the two collections by Dahlberg and that of Rolander, it is clear the *V. virens* is a different species. According to Rottbøll (1776), *Rondeletia biflora* is not in Rolander’s manuscript, thus one cannot assume it is the same species as “*Rondeletia repens* Rol.” (Mss. p. 395), nom. invalid., non *R. repens* L., *Syst. Nat.* (ed. 10) 2: 928. 1759.”

Moraes et al. (2010: 183) wrote that specimen SBT 4.2.6.60 was attributed to Rolander by P.J. Bergius, but there is no information on the specimen or in related literature that can prove that it was collected by Rolander. They also noted that “this specimen is not the same as the one represented in the drawing by Rottbøll.” In fact, a detailed analysis demonstrated that specimen SBT 4.2.6.60 does not belong to *Rondeletia biflora*, but is instead *Coccocypselum guianense* (Aubl.) K.O.Schum. (Basionym: *Tontanea guianensis* Aubl.). This is supported by the fact that the specimen has axillary, long-pedunculate inflorescences, with a fascicle of 6–7 sessile fruits; while in *Rondeletia biflora* (= *Sipanea biflora*) the inflorescences are terminal (or rarely subaxillary, origi-

nally terminal and becoming subaxillary by the reiteration of an axillary bud), cymose, commonly with 1–2 pedicellate flowers (or exceptionally with 3(–7) flowers). In fact, in figure 2 of table 2 of *Rondeletia biflora* published by Rottbøll (1778) the plant is depicted with three 2-flowered inflorescences. The identification of specimen SBT 4.2.6.60 as *Coccocypselum guianense* was further confirmed by Cristina Bestetti Costa, a specialist that wrote a monograph on *Coccocypselum* (Costa 2004). Therefore the lectotypification of *Rondeletia biflora* by Moraes et al. (2010) is erroneous and is here superseded.

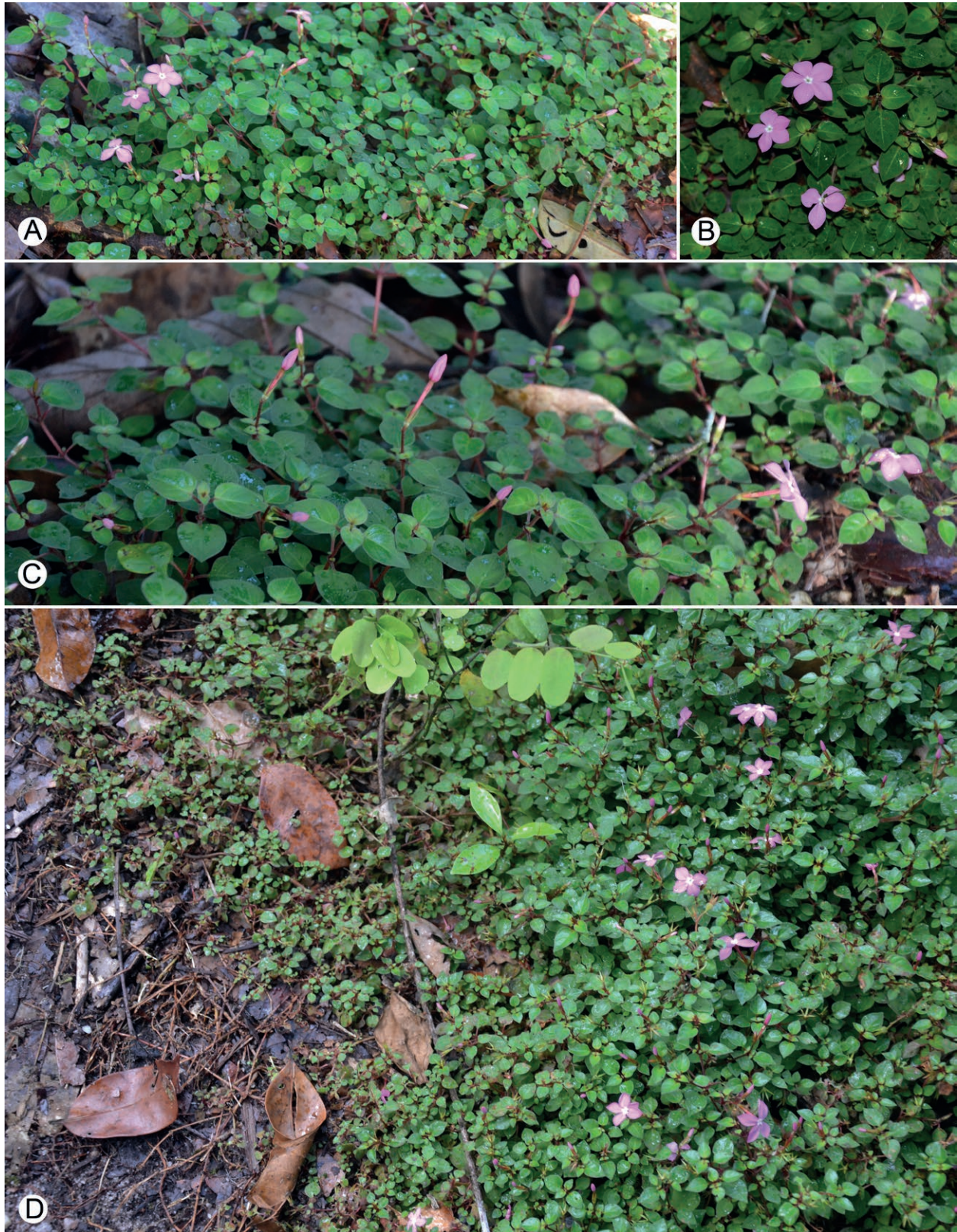
According to Stafleu & Cowan (1983: 930–931), Kristen Friis Rottbøll studied botany with Linnaeus in 1756–1757, was director of the Botanical Garden in Copenhagen in 1770–1797, and his “herbarium and types are at C, with some further material in LINN.” Rottbøll (1776) first published the description of *Rondeletia biflora* in his *Descriptionis Rariorum Plantarum*. Moraes et al. (2010: 183) cited that Table 2 Figure 2 was published in Rottbøll’s 1776 publication; however, no plate is included in that publication. The illustration of *Rondeletia biflora* was first published two years later by Rottbøll (1778) in Table 2, Figure 2 of *Descriptiones Plantarum quarundam Surinamensium*, in *Acta Literaria Universitatis Hafniensis*. As figure 2 of table 2 of Rottbøll (1778) was published after the original description, it cannot be treated as original material. Therefore, original material of *Rondeletia biflora* is either a specimen collected by Rolander and examined by Rottbøll, or an illustration that was available to him by 1776.

Two specimens of *Rondeletia biflora* were located at C. Both of them were without barcode at the time they were studied. Both of them have the stamp “HB VAHL-II” on the upper right-hand corner on the back of the sheet, confirming that they were in Martin Vahl’s Herbarium. In Vahl’s vast card catalogue, intended for his *Enumeratio Plantarum*, he positioned the species in the genus *Virecta*. On the card dedicated to *Virecta biflora* he wrote “biflora V. [Virecta] foliis ovatis pedunculis bifloris – *Rondeletia biflora*, caulis filiformis repente; pedunculis bifloris – Rottb. descr. pl. Surinamensium pag. 7 tab. 2 fig 2. \* *Virecta biflora* Lin. Suppl. pag. 134 S.V. – Habitat Surinami humidis Ø - [followed by the plant description].” One C specimen is composed by two branches with numerous adventitious roots at each node, and numerous leaves; one branch has at least one fruit, and the other branch has a flower in anthesis. On the back of the sheet, on the lower portion, is Vahl’s handwritten note “*Virecta biflora* Rottb. Des. pag. 7 no. 6 tab. 2 fig. 2.” This specimen much resembles the plant depicted in figure 2 of table 2 of Rottbøll’s 1778 publication. However, on this specimen the collection local-

ity or the collector’s name is not indicated, and there is no evidence that it was studied by Rottbøll. The other C specimen of *R. biflora* is a very small branch with a few leaves, one flower, and one young fruit. On the back of the sheet, on the lower portion, is Vahl’s handwritten note “*Virecta biflora* Linn. Suppl. – *Rondeletia biflora* Rott. Descr. Sur. 7 ns. 6 tab. 2 fig 2.” On this specimen the locality and collector’s name is also not supplied, and there is no evidence indicating that it was studied by Rottbøll. In conclusion, because it cannot be proven with certainty that the two C specimens were collected by Rolander nor that they were examined by Rottbøll, they cannot be treated with certainty as original material.

In Table 2 Figure 2 of Rottbøll’s 1778 publication is depicted a ramified branch with numerous adventitious roots, leaves acute at base, and three terminal 2-flowered inflorescences, each of them with one terminal flower in anthesis, and a fruit just below it. In the lower portion of the figure are depicted flowers in anthesis (side view and dissected), one unopened fruit, and one open capsule. As this figure was published two years after Rottbøll’s 1776 publication where he first described *Rondeletia biflora*, it cannot be treated as original material.

The only entities that can be treated as original material of *Rondeletia biflora*, available to Rottbøll by 1776 are the right portion of the drawing commissioned by Rottbøll, and the right portion of the copper plate engraving corresponding to Table 2 Figure 2 of Rottbøll’s 1778 publication. The original copper plate engraving has been lost (Henning Knudsen, pers. comm.). Therefore the only original material left is the drawing commissioned by Rottbøll. The drawing commissioned by Rottbøll was reproduced in Figure 21 of Moraes et al. (2014) and is an ink drawing of two different species, and is similar to Table 2 Figure 2 of Rottbøll’s 1778 publication. On the left side of the drawing is *Eriocaulon fasciculatum* Rottb. and on the upper margin is depicted a series flower and fruits of that species. On the right side of the drawing is depicted a plant of *Rondeletia biflora* with several branches and adventitious roots. On the lower right portion of the drawing is glued a rectangular piece of paper with the same series of parts depicted in Table 2 Figure 2 of Rottbøll’s 1778, which is to say flowers in anthesis (side view and dissected), one unopened fruit, and one open capsule. Aside from the small piece of paper glued on the sheet, it is possible to see that Figure 21 of Moraes et al. (2014) is a photograph of the original drawing by the calligraphy of the letters present on the drawing, which differs from that of the letters on Table 2 Figure 2 of Rottbøll’s 1778 publication. Rottbøll’s commissioned drawing (reproduced in Figure 21 of Moraes et al. (2014)) was present in the



**Figure 55.** *Sipanea biflora*. A. Habit. B. Detail of habit with flowers in anthesis. C. Detail of habit with flower buds. D. Habit, showing variation in leaf size within the same population. Photos by Piero Delprete in the Kaieteur National Park on 22 June 2016, Guyana, plants not collected.

archives of the library of the Natural History Museum of Copenhagen. That Museum is currently under restructuring and reorganization. The librarian responsible for the archives at the time that the drawing commissioned by Rottbøll was photographed has retired, and a new librarian has not yet been appointed. In addition, as the museum is being renovated, the library and archives are currently closed to the public. Henning Knudsen, the person temporarily responsible of the library and the archives of that institution, informed me that Rottbøll's original copper plates were historically destroyed and melted to produce new copper plates. Therefore, the portion of the drawing commissioned by Rottbøll (reproduced in Figure 21 of Moraes et al. (2014)), representing the plant on the right side of the drawing and the small piece of paper with the flower and fruit series is here designated as the lectotype of *Rondeletia biflora*.

Endlicher (1833: 7, fig. 7) described *Sipanea radicans* Endl. and cited a gathering collected by Blanchet in the state of Bahia, Brazil, without indicating the herbarium of deposit. A specimen at W, Acc. No. W0072693, has two handwritten labels "Hb. Endl., *Sipanea radicans* Endl., Bahia, Blanchet" and "*Sipanea biflora* L. fil., determ. C. Schumann." This specimen is here designated the lectotype of this name.

Steyermark (1967) separated *S. cowanii* from *S. biflora* by the hypanthium densely strigose (vs. glabrous except for sparse hairs on upper half in *S. biflora*), upper leaf moderately appressed-pubescent (vs. upper surface glabrous), and capsules moderately to inconspicuously strigillose (vs. glabrous except for a few inconspicuous short hairs). A detailed study of specimens of *S. biflora* from throughout the geographic range, and personal field observations in Guyana, French Guiana, and Brazil,

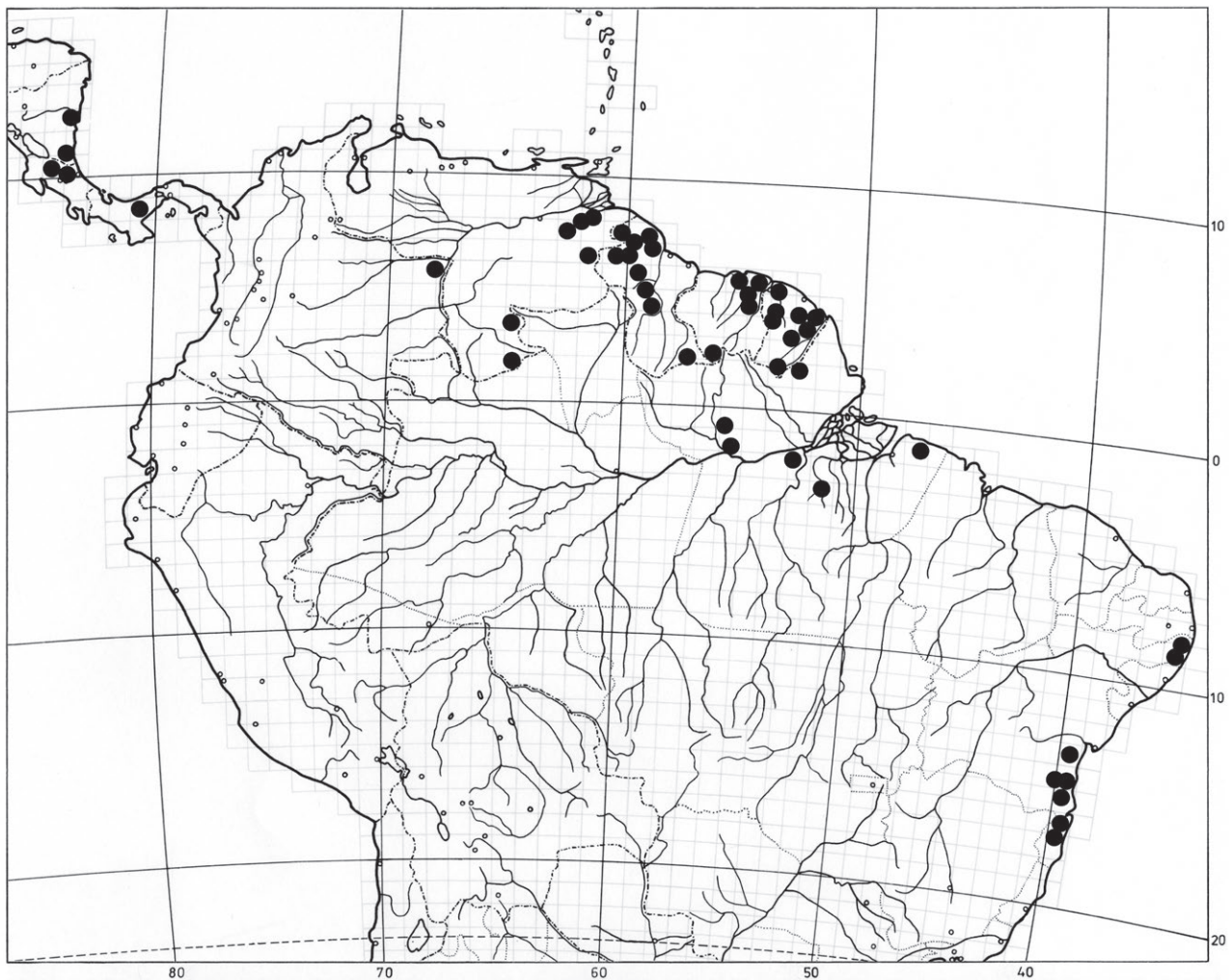


Figure 56. Distribution of *Sipanea biflora*.

revealed that the vestiture of this polymorphic species is highly variable (see below), and the characters used by Steyermark to separate the two taxa are broadly intergrading. Therefore, the two names are here treated as synonymous.

**Notes on variation in vegetative parts and corolla dimensions:** After detailed study of herbarium specimens of more than 300 collections from throughout the geographic range, I concluded that the variations in leaf shape and size, hypanthium vestiture, corolla tube and lobes shape and dimensions of this species is not correlated with any geographical pattern. A certain clinal variation is observed in leaf dimensions, which are generally smaller at higher elevations. Leaves and corollas of *Sipanea biflora* are widely variable in the same patch and often on the same plant. To convey the degree of variation of this species, a detailed field study of three populations occurring in Suriname and Guyana is presented below:

**Suriname:** Sipaliwini District. Sipaliwini trail from Sipaliwini Village towards Sipaliwini Nature Reserve. Primary forest with canopy 15–25 m tall, with some large emergent trees, lateritic and white sand soil, 2°21'N, 56°6'45"W, 220 m, 19 Apr. 2014 (fl, fr), *P.G. Delprete & G. Marjanom 12446* (B, BBS, BR, CAY, K, L, MO, P, RB, US) and 12447 (BBS, C, CAY, F, G, GB, K, NY, MG, ). **Plant description:** Decumbent herbs, rooting at basal nodes, forming patches several meters wide, area seasonally inundated. **Leaves:** blades ovate narrowly ovate to rhombic, 0.6–3.4 × 0.4–2.1 cm. **Corollas:** tubes 7–8.5 mm long; lobes oblong, obovate to broadly ovate, 3.5–5 × 1–2.5 mm.

**Guyana:** Potaro-Siparuni Region, Kaieteur National Park, trail between Guest House and Johnson's view, evergreen wet forests, thin sandy soil, mixed with bare rocks, 5°11'N, 59°29'W, 420–450 m, 23 Jun. 2016 (fl, fr). Populations studied and photographed, but no specimen collected (Figure 55). **Plant description:** prostrate to somewhat decumbent herbs, rooting at basal nodes, forming dense patches 0.5–2 meters wide, growing on leaf litter accumulated on white-sand soil. **Leaves:** blades ovate, narrowly ovate to rhombic, 0.4–3.5 × 0.3–3 cm. **Corollas:** tubes 8.3–13.5 mm long; lobes ovate to oblong-ovate, 5–10 × 3–5 mm.

**Guyana:** Potaro-Siparuni Region. Upper Potaro River, Chenapou Village, trail between Kamo Creek and Urakak Creek, Mora forest on white sand, soil moist but not inundated, 4°59'43"N, 59°34'6"W, 220 m, 18 Jun. 2016 (fl, fr), *P.G. Delprete & P. Benjamin 12869* (BRG, CAY, MO, NY). **Plant description:** prostrate to somewhat decumbent herbs, rooting at basal nodes, forming patches

0.5–1.5 meters wide, growing on leaf litter accumulated on white-sand soil. **Leaves:** blades ovate to narrowly ovate, 0.6–3.2 × 0.4–2.8 cm. **Corollas:** tubes 8–12.5 mm long; lobes narrowly ovate to oblong-ovate, 6–11 × 3–4.5 mm.

In addition, a few gatherings have exceptionally large flowers. For example, *Hoffman & Marco 2324* (CAY, U), from Pakaraima Mountains, Guyana, has corolla tubes 13.5–15 mm long and lobes 11.5–14 × 5–7 mm; however, the rest of the vegetative and reproductive characters are well within the species morphological range. At the other extreme, several specimens of *Sipanea biflora* have exceptionally small flowers. For example, *Versteeg 863* (U), from Tapanahoni River, Suriname, has corolla tubes 5.5–6.5 mm long.

**Notes on variation in stamen insertion and style presentation:** As a result of a detailed analysis of numerous natural populations and herbarium specimens, *Sipanea biflora* is here confirmed to be distylous. In addition, there is a certain degree of variation in stamen insertion and style length within the two morphs. For example, in long-styled flowers the style could be either about the same length as the corolla tube or exerted just beyond the corolla mouth, and the stamens could be inserted at variable height of the corolla tube. To demonstrate this variation, a few examples are presented below.

*Long-styled flowers with stamens inserted at distal portion of corolla tube:* **Guyana:** Akarai Mts., *Henkel et al. 4607*: corolla tube 7.5 mm long; stamens inserted 3.7 mm below corolla mouth; filaments 0.5 mm long; anthers narrowly oblong, 1.5 × 0.15 mm, acute at both ends; style about the same length as corolla tube (tip of branches exerted), 7.5 mm long, glabrous; style branches linear, 0.8 mm long, acute at apex. **Suriname:**–Brownsberg, *Wessel-Boer 636*: corolla tube 10.5 mm long; stamens inserted 4.5 mm below corolla mouth, filaments 0.7 mm long; anthers 2.5 mm long; style about the same length as corolla tube (tip of branches exerted) style branches very narrowly lanceolate, 2 mm long, acuminate at apex. **French Guiana:** Lawa River, *Papichon, Sastre et al. 8150*: corolla tube 13.5 mm long; stamens inserted 5.5 mm below corolla mouth; filaments 0.7 mm long; anthers narrowly oblong, 2 × 0.2 mm, acute at both ends; style exerted 3 mm beyond corolla mouth, 17 mm long, glabrous; style branches linear, 1.7 mm long, acute at apex.

*Long-styled flowers with stamens inserted at about the middle of corolla tube:* **Suriname:** Upper Demerara River, *Jenman s.n.* (US Acc. No. 223383): corolla tube 15 mm long; stamens inserted 9 mm below corolla mouth; filaments 0.5 mm long; anthers linear, 2 × 0.2 mm,

acute at both ends; style exerted 1.5 mm beyond corolla mouth, 16.5 mm long, glabrous; style branches linear, 1.5 mm long, acute at apex.

*Short-styled flowers with stamens inserted at distal portion of corolla tube:* **Guyana:** Kaieteur Falls National Park, *Pipoly & Gharbarran 10147*: corolla tube 12.5 mm long; stamens inserted at 4–4.5 mm below corolla mouth; filaments 0.5–0.7 mm long; anthers linear, 2.2 × 0.2 mm, acute at both ends; style included, 5 mm long, glabrous; branches linear, 1.2 mm long, acute at apex.

**Distribution and ecology:** A species broadly distributed, ranging from Nicaragua, Costa Rica, Panama to Colombia, Venezuela, the Guianas, and Amazonian Basin and Atlantic forest of Brazil (Figure 56). Commonly found in riparian forests, semideciduous forests, evergreen lowland forests to lower mountain forests; growing on the forest floor, usually in areas rich in organic material and leaf litter, in lateritic soils or white-sand; sometimes found as aquatic/amphibian plant floating or semi-submersed in seasonally flooded area or in muddy soils of wet forests; at 5–750 m altitude.

**Phenology:** Due to the short life span of this species, it is common to find flowers and fruits on the same gathering. In Central America, specimens with flowers and fruits were collected in March, June, July, September, November and December. In South America, specimens with flowers and fruits were collected the whole year around.

**Suggested conservation status: Least Concern (LC).** A species distributed from Nicaragua, Costa Rica, Panama, Colombia, Venezuela, the Guianas, to the Amazonian Basin and Atlantic forest of Brazil. It is rare in Panama (collected in 1967) and Colombia (collected in 1854), where it is known only by a single collection in each country, and where it is locally endangered (or extinct?). This shade-loving species is most common on forest floor, and less frequent as an aquatic/amphibian plant in seasonally flooded, shaded areas, and sometimes often forming large patches. Because of its wide geographic distribution and its numerous collections, it is placed in the Least Concern (LC) category, following IUCN criteria (IUCN 2012, 2019).

**Specimens examined: NICARAGUA: Río San Juan:** San Juan del Norte, Río Indio, Caño La Paloma, 11°3'N, 83°53'W, 5 m, 1 Dec. 1982 (fl), *M. Araquistán 3357* (MO, P); entre el pueblo de San Juan del Norte Nuevo y la casa de Ramón Castillo, viajando por el Caño

San Juanillo, 10°55'N, 83°49'W, 5 m, 7 Jul. 1994 (fl), *R.M. Rueda et al. 1847* (MO).

**COSTA RICA: Alajuela:** Llanura de San Carlos, Lagunas Lagarto Lodge, 7 km N of Boca Tapada, 37 km N of Pital, 10°41'N, 84°10'W, 90 m, 6 Jun. 2000 (fl), *G.E. Crow 9835* (CR, MO, NHA n.v.); San Carlos, Boca Tapada, Lagunas Lagarto Lodge, 7 km N of Boca Tapada, pantano en bosque, agua no muy profunda, 10°40'48"N, 84°10'48"W, 90 m, 27 Jul. 1996 (fl), *B.E. Hammell 20356* (INB n.v., MO). **Limón:** Inundated forest at northern base of SW-most extension of Cerro Coronel, inundated lowland dominated by *Symphonia*, *Camptosperma*, *Manicaria* and *Cyclathaceae* understory, small clearing in forest for rice field, 10°40'30"N, 83°39'30"W, 5 m, 19 Sep. 1986 (fl, fr), *G. Davidse & G. Herrera 31444* (MG, MO); Refugio Barra de Colorado, forest and pastures between Río Cirripocito and Río Sardina, marshy sites along carril in primary forest, 10°38'N, 83°45'W, 12 Nov. 1988 (fl), *M.H. Grayum et al. 9018* (MO); Refugio Barra de Colorado, forest and pastures between Río Cirripocito and Río Sardina, muddy sites along trail in low, disturbed forest, 10°38'N, 83°45'W, 12 Nov. 1988 (fl), *M.H. Grayum 9755* (F, INBIO n.v., MO); E of Cerro Coronel, opposite Laguna Danto, *Raphia* swamp, in standing water, 10°41'N, 83°38'W, 5 m, 20 Sep. 1986 (fl), *W.D. Stevens & O.M. Montiel 24668* (MO); ca. 2 km S of Río Colorado, along new rd and ca. 1 km E; inundated forest with *Manicaria* and clumped *Sphaeradenia* dominant, margin of swamp forest, 10°40'N, 83°40'W, 5 m, 19 Mar. 1987 (fl, fr), *W.D. Stevens, G. Herrera & O.M. Montiel 25080* (CAY, MG, MO).

**PANAMA: Veraguas:** Mouth of Río Concepción, swamp, 4 Dec. 1967 (fl, fr), *W.H. Lewis et al. 2822* (MO, type of *Manettia hydrophila* Dwyer).

**COLOMBIA: Vichada:** “prope Maypures, flumen Orenoco” [Now Maipures, ca. 5°12'N, 67°50'W, on Río Orinoco], Jun. 1854 (fl), *R. Spruce 3620* (BM, BR, NY, P).

**VENEZUELA: Amazonas:** Río Metacuni, Frente No. 5, selvas ribereñas y del banco, bajo del Salto “Pura Wàniti'ma”, 22 Jan. 1990 (fl, fr), *B. Stergios & J. Velazco 14114* (MO, NY, PORT, VEN); Mun. Río Negro, 1°49'N, 64°16'W, 427 m, Nov. 1992 (fr), *A. Valera 152* (MO, NY, PORT). **Bolívar:** Región de Urimán, selva pluvial de Alto Río Chirca, 750 m, Aug. 1953 (fl, fr), *L. Bernardi 950* (MER, NY); 32 km E of El Palmar, moist virgin forest, 4 Jun. 1960 (fl, fr), *J.A. Steyermark 86259* (NY, VEN); Altiplanicie de Nuria, forest trail between El Cruzero and slightly beyond pica 101, ESE of Villa Lola, 315 m, 15 Jul. 1960 (fl), *J.A. Steyermark 86390* (NY, P, US, VEN); low wet woods along trail at base of Cerro Pauji [ca. 8°8'N, 62°32'W], along Quebrada 94 at km 94 S of El Dorado, 250 m, 27 Jul. 1960 (fl), *J.A. Steyermark 86713* (NY, VEN), *86731* (NY, VEN); near El Palmar, 8°5'N,

61°50'W, 75 m, 23 Nov. 1967 (fl, fr), *J.G. Wessel Boer* 2078 (NY, U). **Delta Amacuro:** Depto. A. Diaz, bosques húmedos primarios del medio Río Grande, 60 km al NE de El Palmar, 15 Mar. 1987 (fl, imm fr), *G. Aymard* 5440 (MO, PORT, VEN); E of Río Grande, directly E of El Palmar, swampy mature forest, 6 Jul. 1975 (fl, fr), *A. Gentry & P. Berry* 14979 (MO, NY, U); Río Amacuro, Venezuela-Guyana frontier, Río Amacuro, Sierra Imat-aca, in low places along water at Salto de Quebradero, upstream from San Victor, 65–80 m, 2 Nov. 1960 (fl), *J.A. Steyermark* 87252 (F, NY [3 sheets], VEN).

**GUYANA:** Kaieteur, 29 Dec. 1948 (fl), *D.J. Atkinson* 39 (BM); Upper Takutu-Upper Essequibo Region, Kuyuwini River, area near camp, disturbed vegetation, 2°5'N, 59°17'W, 240 m, 19 Jul. 1996 (fl), *D. Clarke* 2309 (MO, US); Upper Takutu-Upper Essequibo Region, Kassikai-tyu River, 0–1 km N of landing at terminus of trail from Kuyuwini River, 1°50'N, 59°5'W, 240 m, 18 May 1997 (fl), *D. Clarke* 4658 (MO, US); Potaro-Siparuni Region, Upper Potaro River, Chenapou Village, between Kamo Creek and Urakak Creek, mora forest on white sand, not inundated (terra firme), 4°59'43"N, 59°34'6"W, 450 m, 18 Jun. 2014 (fl), *P.G. Delprete & P. Benjamin* 12869 (BRG, CAY, MO, NY); Loc. Mapuera Camp, Riverside, Acarai Mountains [ca. 1°50'N, 57°30'W], 25 Oct. 1952 (fl), *Forest Department of British Guiana Field No. G-495 (Record No. 7510)* (NY); Potaro-Siparuni Region, Kaieteur Falls National Park, mostly evergreen forest to 20 m, 5°10'N, 59°29'W, 500 m, thin brown-white sand-gravel substrate, 29 Mar. 1988 (fl, fr), *L.J. Gillespie & H. Persaud* 973 (MO, US); Cuyuni-Mazaruni Region, Aurora, creek ca. 1 km WSW of camp, 1 km W of camp along 10,400 line, 6°47'N, 59°45'W, 70 m, 16 Oct. 1989 (fl, fr), *L.J. Gillespie & S. Tiwari* 2387 (MO, NY, US); Potaro-Siparuni Region, Kaieteur Falls National Park, mostly evergreen forest to 20 m, 5°10'N, 59°29'W, 500 m, thin brown-white sand-gravel substrate, 29 Mar. 1988 (fl, fr), *W. Hahn et al.* 4023 (MO, NY, US); Potaro-Siparuni Region, Kaieteur National Park, Kaieteur Gorge, W bank of Potaro River, 0.75 km from falls, 5°11'N, 59°28'W, 200–250 m, sandstone and conglomerate with medium stature forest, 50–100 m upslope from river, 13 Jul. 1993 (fl, fr), *T.W. Henkel & R. Williams* 2187 (MO, NY, US); Upper Takutu-Upper Essequibo Region, Acarai Mountains, Watuwau Creek, 8–10 km upstream of junction with Chodikar River, 1°22'N, 58°42'W, 250 m, 22 Feb. 1994 (fl, fr), *T.W. Henkel et al.* 4607 (CAY, MO, NY, U, US); Cuyuni-Mazaruni Region, Pakaraima Mountains, Meanu River, at foot of Marali Falls, on rocks, growing in mixed herb, bryophyte, pteridophyte community, 6°15'N, 60°26'W, 150–200 m, 6 Aug. 1992 (fl), *B. Hoffman & G. Marco* 2324 (CAY, MO, NY, U, US); near

Kaieteur Falls, Potaro River, Essequibo County, 17 Jan. 1954 (fl), *H.S. Irwin* BG-94 (US); Upper Demerara River, s.d. (fl), *G.S. Jenman s.n. (US 00634732)* (US); Demerara, s.d. (fl, fr), *G.S. Jenman* 4096 (US); Demerara River, Mar. 1898 (fl), *G.S. Jenman* 7306 (K); Potaro-Siparuni Region, Kaieteur Falls, trail between Gouvernement Guesthouse and Johnson's view, open, shrubby vegetation mixed with patches of forests, thin sandy soil, mixed with bare rocks, 5°11'N, 59°29'W, 420 m, 12 Oct. 1987 (fl, fr), *L.P. Kvist et al.* 227 (NY, U, US); Potaro-Siparuni Region, line from Kaieteur to Tukeit, 5°13'N, 59°27'W, 90–450 m, mixed forest, alluvial sand and gravel, growing on rocks, 15 Jul. 1991 (fl), *K. Lance & C. Bird* 18 (MO, US); Upper Mazaruni River, Kurupung [ca. 6°28'N, 59°10'W], 19 Nov. 1922 (fl, fr), *H. Leng* 159 (NY, paratype of *S. cowanii*); Potaro River Gorge, damp rock ledges, mixed forest, trail Tukeit to Kaiatuk Plateau, 29 Apr. 1944 (fl, fr), *B. Maguire & D.B. Fanshawe* 23086 (NY); N of Tina-mu Falls [ca. 6°41'N, 58°59'W], Cuyuni River, Essequibo, on mossy dead log, 7 Mar. 1931 (fl, fr), *E.B. Martyn* 292 (K); Upper Takutu-Upper Essequibo Region, along track leading to airstrip village between Buro-Buro River and savanna, 4°8'N, 59°4'W, 70–80 m, 20 Feb. 1990 (fl, fr), *T. McDowell et al.* 1934 (CAY, MO, U, US); Barima-Waini Region, along trail between Baramita airstrip toward Millionaire, 7°22'N, 60°28'W, 91 m, mixed forest, low-land brown mud, red clay soil, 3 Apr. 1991 (fl, fr), *T. McDowell et al.* 4189 (CAY, MO, NY, U); Potaro-Siparuni Region, Kaieteur Falls National Park, trail to Johnson's View, cliff area proceeding S, on W side of Potaro River, cloud and elfin forest, on sandstone, on rock wall, 5°11'N, 59°28'W, 360–400 m, 28 Jan. 1987 (fl, fr), *J.J. Pipoly & G. Gharbarran* 10147 (NY, P, U, US); without locality, s.d., *J.P.B. Rohr s.n. ("dedit Vahl")* (C [2 sheets]); gorge below Kaieteur Falls, ravine above Tukeit, 167 m, 1 Sep. 1937 (fl, fr), *N.Y. Sandwith* 1274 (K); Kaieteur Falls, top of precipices at edge of savannah, 400 m, 8 Sep. 1937 (fl, fr), *N.Y. Sandwith* 1437 (K, U); Cuyuni River, Arawak Matope, damp sand at edge of creek, 29 Jul. 1933 (fl), *T.G. Tutin* 399 (BM, U, US).

**SURINAME:** Sipaliwini District, trail from Sipaliwini Village towards Sipaliwini Nature Reserve, primary forest with canopy 15–25 m tall, with some large emergent trees, lateritic and white sand soil, 2°2'1'N, 56°6'45"W, 220 m, 19 Apr. 2014 (fl, fr), *P.G. Delprete & G. Marjanom* 12446 (B, BBS, BR, CAY, L, K, MO, P, RB, US), 12447 (BBS, C, CAY, F, G, GB, K, MG, NY); Bergakkij lands, 1835 (fl, fr), *H.C. Focke* 61 (U); without locality, s.d. (fl, fr), *F.W.R. Hostmann & A. Kappler* 150 (S); without locality, s.d. (fl), *F.W.R. Hostmann* 1121 (BM, P, U); Spoorlijn bij km 129.5 bij Kabel in bos, 25 Feb. 1956 (fl, fr), *A.M.E. Jonker-Verhoef & F.P. Jonker* 621 (U);



in sylvis humidis ad fl. Marowyne, Aug. 1846 or 1847 (fl), *A. Kappler 1890* (C, FI-Webb, P [2 sheets], S, U); Joden Savanne [ca. 5°25'N, 54°59'W], Mapanecreek area, Kamp 8, 21 Dec. 1960 (fl, fr), *K.U. Kramer & W.H.A. Hekking 2437* (U); Brokopondo Distr., Brownsweg [ca. 5°0'N, 55°9'W], ad viam ferream prope km 115–116, 5 Apr. 1961 (fl, fr), *K.U. Kramer & W.H.A. Hekking 3200* (C, F, U); road Afobaka-Brownsveg, N of Brokopondo Lake, 10 Nov. 1974 (fl, fr), *P.J.M. Maas et al. 2332* (NY, U); Paramaribo, “in umbrosis Surinami prope Paramaribo”, May 1838 (fl, fr), *F.L. Splitgerber 937* (L); Brownsberg, Wallibase creek, 1 Jul. 1924 (fl, fr), *G. Stahel & J.W. Gonggrijp BW 6552* (U); without locality, s.d. (fl, fr), *Sulityerber s.n.* (P P00729417); Tapanahoni River, Sep. 1904 (fl), *G.M. Versteeg 863* (U); from Brownsberg at Kabel railroad to Mazaroni Peak, in desne forest, frequent in very wet, muddy places, 11 Feb. 1963 (fl, fr), *J.G. Wessel Boer 636* (NY, U).

**FRENCH GUIANA:** Saint Jean du Maroni [ca. 5°24'N, 54°4'W], lieux humides sous bois, 8 Jul. 1914 (fl), *R. Benoist 862* (P); Piste de Saint Laurent vers Paul Isnard, km 15, forêt primaire, 10 Nov. 1983 (fl, fr), *F. Billet & B. Jadin 1996* (BR, CAY); Beira do Rio Cassa, 9 Nov. 1954 (fl, fr), *G.A. Black et al. 54-17651* (IAN); Bassin de l'Approuague, Rivière Kourouaï, jonction de la Kourouaï et la R.N. 2, 4°25'N, 51°56'W, 16 Oct. 1996 (fl), *M. Blanc 141* (CAY, MO, NY, P); Projet de route d'Apatou, entre 2 et 3 km E de la Crique Sparouine, Plateau Bastien, 5°15'50"N, 54°13'40"W, 130 m, forêt dense a sol bien drainé, 10 May 2004 (fl), *B. Bordenave & L. Betian 7363* (CAY, MO); Bassin de l'Approuague, R.N. 2, Crique Kapiri, 4°7'N, 52°5'W, 5 m, forêt inondable primaire, 12 Jan. 1991 (fl, fr), *G. Cremers 11505* (CAY); D.Z. 5, Route Régina–Saint-George, Bassin de l'Approuague, petite crique dans une forêt de basse altitude, 1 Dec. 1995 (fl), *G. Cremers & J.J. de Granville 14290* (CAY); piste forestière de St. Laurent à Paul Isnard, entre PK 10 et 40, 14 Feb. 1983 (fl, fr), *C. Feuillet 735* (CAY, P, UB); Upper Camopi River, ca. 1.5 km NE of Mont Belvédère, 4 Dec. 1984 (fl), *J.J. de Granville 7119* (CAY [2 sheets], MO, P); route Regina–Saint George, Bassin de l'Approuague, forêt ripicole sur sable, 4°2'N, 52°1'W, 100 m, 26 Nov. 1995 (fl, fr), *J.J. de Granville & G. Cremers 13154* (CAY, K, MO, P, U); Projet routier entre Saint-Georges et le pont transfrontalier sur l'Oyapock, zone Crique Mazy, forêt sur flat, 3°52'20"N, 51°49'30"W, 5 m, 8 Dec. 2005 (fl, fr), *J.J. de Granville et al. 17184* (CAY, MO); Maroni River, s.d. (fl, fr), [initials unknown] *Hachenheim 150* (P); Région Organabo, Mana [ca. 5°40'N, 53°46'W], 8 Aug. 1962 (fl, fr), *F. Hallé 504* (P); Saül, Piste Sophie, dans un ruisseau sous bois, 7 Sep. 1962 (fl, fr), *F. Hallé 805* (US), *805a* (P); Haut Oyapock,

Trois Sauts [ca. 2°14'N, 52°52'W], végétation secondaire, 11 Jul. 2006 (fl, fr), *C. Haxaire 1028* (CAY, MO); Camp Arataï, right bank of the Arataï River, a short distance from the mouth of the Approuague River, ca. 3°59'N, 52°34'W, 20 Feb. 2003 (fl), *S.A. Mori 25584* (CAY, NY); Basse Crique Kourouaïe (affluent basse Approuague), ca. 700 en mont du deuxième camp, 13 Jan. 1970 (fl, fr), *R.A.A. Oldeman B-2724* (CAY [2 sheets]); Basse Crique Kourouaïe (affluent basse Approuague), ca. 900 en mont des Deux Fourches (dé fouca), rive droite, 15 Jan. 1970 (fl, fr), *R.A.A. Oldeman B-2750A* (CAY [2 sheets]); Route de Paul Isnard, km 40, selectively logged forest, 5°44'N, 53°58'W, 100 m, 18 Mar. 1994 (fl, fr), *J.H.E. Rova et al. 2005* (CAY, MO, NY, S); Fleuve Approuague[Basin], Rivière Arataye, Saut Pararé, layon X, 25 Aug. 1977 (fl), *C. Sastre 5765* (CAY, P); Fleuve Lawa, Papaichon, layon de la source, 3°49'N, 54°10'W, 80–120 m, 30 Aug. 1986 (fl, fr), *C. Sastre et al. 8150* (CAY, P, US); Prés de Saint Laurent [du Maroni], bas-fonds humides, 21 Aug. 1961 (fl), *R. Schnell 11375* (P); Znieff Abattis Kotica, 4°1'23"N, 54°18'50"W, 82 m, 15 Jan. 2012 (fl, fr), *P. Silland & R. Girault 372* (CAY); Znieff du flat à palmiers bâches de la Waki [Waki River], 3°10'50"N, 53°28'39"W, 129 m, 16 Aug. 2012 (fl, fr), *P. Silland et al. 835* (CAY).

**BRAZIL: Alagoas:** Mun. Matriz do Camaragibe [ca. 9°9'S, 35°31'W], Usina Serra d'Água, mata atlântica, 31 Oct. 2009 (fr), *Chagas-Mota & J.W.A. Silva 6357* (MAC); Ibatiguara, Usina Serra Grande, Mata Coimbra, mata atlântica, 8°38'32"S, 35°55'46"W, 13 Oct. 2010 (fl), *R.P. Lyra-Lemos et al. 12082* (MAC). **Amapá:** ca. 1–3 km N of Cachoeira Tres Saltos, 2°12'–13'N, 52°52'–53'W, 12 Sep. 1960 (fr), *H.S. Irwin et al. 48214* (IAN, NY, US). **Bahia:** Mun. Una, Reserva Biológica do Mico-leão (IBAMA), entrada no km 46 da Rod. BA-001 Ilhéus-Una, 15°9'S, 39°6'W, Picada paralela ao Rio Maruim, 8–12 Mar. 1993 (fl), *A.M. Amorim et al. 1156* (CEPEC, NY, US); without locality, s.d. (fl, fr), *J.S. Blanchet s.n.* (P P00729425); without locality, 1835 (fl, fr), *J.S. Blanchet 1439* (FI-Webb); without locality, s.d. (fl), *J.S. Blanchet 1639* (P); Mun. Porto Seguro, Estação Biológica Pau-Brasil [ca. 16°22'S, 39°10'W], CEPLAC, erva crescendo na sombra da mata, 19 Apr. 1982 (fl), *A.M. Carvalho et al. 1189* (CEPEC, UB); Mun. Ilhéus, Mata da Esperança, acesso pelo Banco da Vitória, trilha que dá acesso à represa, 14°46'60"S, 39°50'0"W, 22 Jan. 2010 (fl, fr), *L. Danau et al. CEPEC 228* (HUEFS, RB); Porto Seguro, BR-5, km 21, Fazenda Iraipe, 6 Sep. 1961 (fl), *A.P. Duarte 6168* (RB); Una, Posse, 17 Dec. 1966 (fl, fr), *L. Emygdio [de Mello] et al. 2474* (R [3 sheets]); Faz. Olhos d'Água do Laranjeiras, 11 Jan. 1976 (fr), *Gusmão, E.F. de 269* (RB, UB); Mun. Cravolândia, rd. Ilha Formosa de Cravolândia-Ubaira, ca. 8.5 km, 13°28'5"S, 39°39'25"W, 5 May 2007

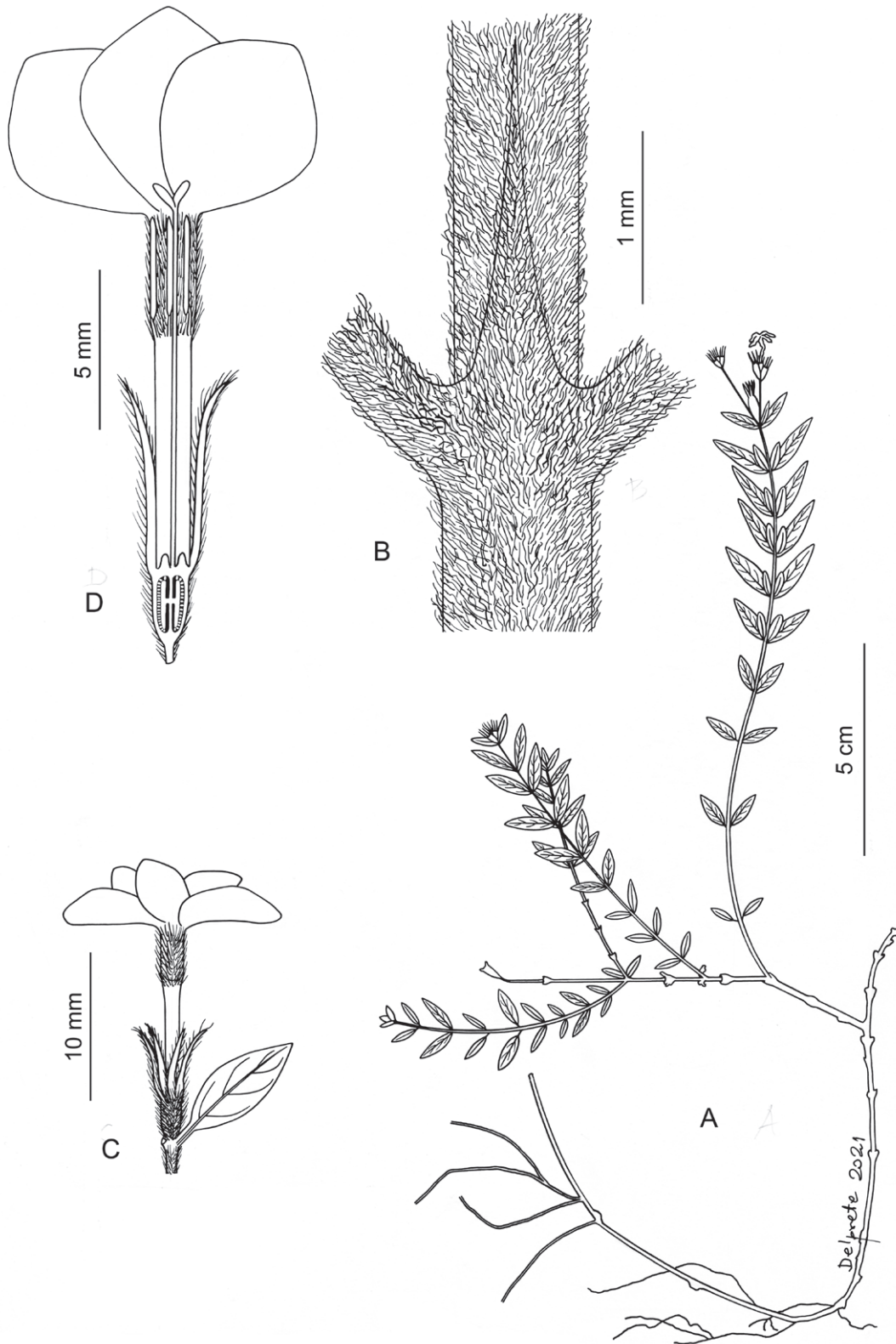
(fl, fr), *J. Jardim et al.* 5097 (CEPEC, NY); near the Ilheus River ["in viis umbrosis silvarum primaevorum prope fluvium Ilheos"], s.d. (fl, fr), [initials unknown] *Klaenzze* 114 (BR 824571) (BR); Cruz de Cosme, s.d. (fl, fr), *B. Luschnath* 87 (C.F.P. *Martius Herb. Fl. Bras. N.* 594); Cruz de Cosme, Feb. 1835 (fl, fr), *B. Luschnath* 87 (C.F.P. *Martius Herb. Fl. Bras. N.* 1315) (BR, FI, NY); without locality, s.d. (fl, fr), *B. Luschnath* 100 (BR 824559) (BR); Cruz de Cosme, s.d. (fl, fr), *Collector Unknown* (probably *Luschnath*; C.F.P. *Martius Herb. Fl. Bras. N.* 594, p. 309) (NY 02690175); without locality, 1851 (fl, fr), C.F.P. *Martius s.n.* (*Herbar. Florae Brasil. No.* 594) (P); Mun. Una, km 27 da Rod. São José-Una (Jct. with BR-101), prox. Fazenda Piedade, 20 Jul. 1981 (fr), *L.A. Mattos et al.* 1291 (IPA, NY); Mun. Ilheus, rd. between Sururú and Vila Brasil, 6–14 km from Sururú, 12 km SE of Buerarema, ca. 100 m alt., mata em destruição, 27 Oct. 1979 (fl, fr), S.A. *Mori & F. Benton* 12892 (CEPEC, UB); Ilheus, Faz. Pirataquise, 12 Mar. 1944 (fl, fr), *H. Pimenta Velloso* 837 (R [2 sheets]); "in humidis pr. Ilhéos" [near Ilheus], May 1821 (fl, fr), *L. Riedel* 142 (*Herb. Hort. Petropol.* 139) (BR, P); Igrapiúna, Faz. Michelin, 28 Feb. 2001 (fl, fr), S. *Sampaio* 24 (MBM); Mun. Una, Reserva Biológica do Mico-leão (IBAMA), entrada no km 46 da Rod. BA-001 Ilhéus-Una, 15°9'S, 39°6'W, Picada da Bandeira, 25 Jul. 1996 (fl), S.C. *de Sant'Ana et al.* 615 (MO, NY); Mun. Teixeira de Freitas, Vale do Rio Alcobaça, 15 Aug. 1972 (fl), T.S. *dos Santos* 2374 (CEPEC, NY); Mun. Porto Seguro, Parque Nacional Monte Pascoal, 3 km S of entrance along rd on N side of Park, 16°51'S, 39°16'W, 6 Feb. 1999 (fl, fr), W.W. *Thomas et al.* 12065 (CEPEC, MO, NY). **Pará:** Mun. Vitória do Xingu, 3°11'44"S, 51°46'52"W, 15 Jun. 2014 (fl, fr), B.S.P. *da Costa PSACF\_EX03392* (RB); Mun. Vitória do Xingu, 3°11'59"S, 51°47'3"W, 30 Jun. 2014 (fl, fr), B.S.P. *da Costa PSACF\_EX03439* (RB); Obidos, Igapó do Curuçambá, 8 Aug. 1912 (fr), A. *Ducke s.n.* (*Herb. Amaz.* 12166) (MG, RB); S. Manuel, Tapajóz, paludicola, fl roseas, Mar. 1912 (fl, fr), F.C. *Hoene* 5202 (R); Rio Maracanã, Igarapé Açu, beira do Igarapé do Prata, 24 Sep. 1903 (fl, fr), J. *Huber s.n.* (*Herb. Amaz.* 3809) (MG, RB); Mun. Óbidos, Flota de Trombetas, floresta de transição de cerrado para floresta ombrófila submontana, 0°58'10"S, 55°31'3"W, Apr. 2008 (fl, young fr), L.C.B. *Lobato* 3452 (MG); rodovia Belém-Brasília, km 54–62, 29 Nov. 1959 (fl, fr), E. *Oliveira* 184 (IAN); Mun. Peixe Boi, estrada de ferro de Bragança, campo alagado, 22 Jun. 1951 (fl), J.M. *Pires* 3381 (IAN, U); vicinity of Cachoeira, km 96, varzea forest, 30 Oct. 1965 (fl, fr), G.T. *Prance & T.D. Pennington* 1867 (IAN, MO, NY, S, US). **Without State:** without locality [probably state of Bahia], s.d. (fl, fr), P. *Clausen* 6 (BR); without locality, s.d. (fl, fr), *Collector Unknown s.n.* (BR [barcode 824568]), s.n. (BR

[barcode 824574]); without locality [probably state of Bahia], s.d. (fl, fr), J.S. *Blanchet s.n.* (C), s.n. (BM [barcode 000614331]); without locality, s.d. (fl, fr), C.F.P. *Martius s.n.* (NY [barcode 02690174]); without locality, s.d. (fl), C.F.P. *Martius Herb. Florae Brasil.* 594 (L [barcode L0275963]); without locality, s.d. (fl, fr), F. *Sellow s.n.* (BM [barcode 000614345]), s.n. (S [Acc. No. 10-27501]), s.n. (S [Acc. No. 10-27503]).

8-8. *Sipanea carrenoi* Steyerl., Ann. Missouri Bot. Gard. 71: 333. 1984. (Figures 57–58).

Type: VENEZUELA. Bolívar: Gran Savana [Canaima National Park], at base of Salto del Aponguao [5°34'59"N, 61°19'12"]; also known as Salto Aponwao or Salto Chinak-Merú], 42.5 km NE of Misión de Santa Teresita de Kavanayén, open densely covered slopes at base of salto, 1130 m, 22 Feb. 1978 (fl, fr), J.A. *Steyermark, V. Carreño E., G.C.K. Dunsterville & E. Dunsterville* 115598 (holotype, VEN [Acc. No. 195063]; isotypes, MO [barcode 3223163], NY [barcode 00133309]). [Section *Virecta*].

*Herbs*, prostrate, trailing or sprawling, rooting at nodes; stems trailing, to 47 cm long, thin, 1.5–2 mm thick, terete, densely or sparsely antrorse- or subspreading-pubescent. *Stipules* adnate to the petioles, deltoid to triangular-lanceolate, 2–3 × 0.5–2 mm, acute at apex, membranaceous, densely strigose outside, glabrous, with 3–5 colleters at median portion inside; margins strigose. *Leaves* subsessile to short-petiolate; petioles 0.5–1.5 mm long, olive-green when dry, not winged, margins-pilose-ciliate; blades ovate-lanceolate, elliptic to elliptic-oblong, 0.7–2.3 × 0.4–0.9 cm [Steyermark (1984: 333) wrote "1–2 mm by 0.6–0.9 mm"], acute-decurrent at base, obtuse to subacute at apex, thinly subcoriaceous, dark brown above and brownish-olive green below when dry, lamina glabrous on both sides, midrib and secondary veins glabrous, margins narrowly revolute; secondary veins 2–4 on each side of midrib, obsolete to impressed above, prominulous below. *Inflorescences* terminal or appearing axillary (due to the reiteration of an axillary branch originating from a lateral bud at the base of the terminal inflorescence), a condensed dichotomous cyme, 3–7-flowered, rarely uniflorous, sessile to pedunculate, subtended by 2 leaf-like bracts (pherophylls), these ovate, elliptic to narrowly ovate, 0.4–1.5 × 0.3–0.6 cm; peduncle (when present) to 1.1 cm long, sparsely antrorse- or subspreading-pubescent; bracteoles subtending flowers linear-lanceolate, 3–4 × 1–1.5 mm, glabrous. *Flowers* probably distylous, 5-merous, sessile to



**Figure 57.** *Sipanea carrenoi*. **A.** Habit. **B.** Node with stipule and petioles. **C.** Flower in anthesis. **D.** Dissected long-styled flower, with stamens inserted at distal portion of corolla tube, and exserted style. **A–B:** drawn from Steyermark et al. 115598 (MO); **C–D:** drawn from Steyermark et al. 115598 (NY). Illustration by Piero Delprete.

short-pedunculate; pedicels (when present) to 1.5 mm long, sparsely antrorse-pubescent to antrorse-strigillose. *Hypanthium* narrowly obovoid, 2–2.5 × 1–1.5 mm, acute at base, round to obtuse at apex, densely antrorse-strigillose. *Calyx* lobes subequal, linear-lanceolate, 4.5–5.5 × 0.5–0.7 mm, acuminate at apex, glabrous, margins sparsely antrorse-pubescent; with 1 colleter in each calycine sinus, conical, obtuse at apex, 0.3 mm long. *Corolla* hypocrateriform, 16.5–19.5 mm long, pink, turning pinkish-white at end of anthesis, with a dense ring of white hairs included below corolla mouth; tube cylindrical and slightly expanding towards the mouth, 10–13 mm long, 0.8–1 mm at base, 1.2–1.3 mm wide at mouth, sparsely antrorse-pubescent at distal portion and glabrous below outside, glabrous except densely white-villose just below corolla mouth inside; lobes round, suborbicular to obovate, 5.5–6.5 × 4–5 mm [Steiermark (1984:

333) wrote “6–6.5 mm by 5–7 mm”], round to obtuse at apex, glabrous throughout. *Long-styled flowers* (type): stamens inserted at ca. 4 mm below corolla mouth; filaments 0.2 mm long; anthers linear, ca. 3 × 0.2 mm, acute at both ends; style as long as corolla tube, 11–13 mm long, glabrous; style branches obovate, 1 mm long, round at apex. *Short-styled flowers* unknown. *Infructescence* terminal or subaxillary (originally terminal), a condensed dichotomous cyme with 3–7-fruits, rarely a single fruit, similar to inflorescence. *Capsules* narrowly oblong-elliptic, 8–9 × 2–3 mm, acute at base, round at apex, crustaceous, densely antrorse hispidulous-strigillose, pale brown when dry. *Seeds* unknown.

**Notes:** This species is most likely distylous, as are the rest of the *Sipanea* species. In the only collection known, the style is as long as the corolla tube (style

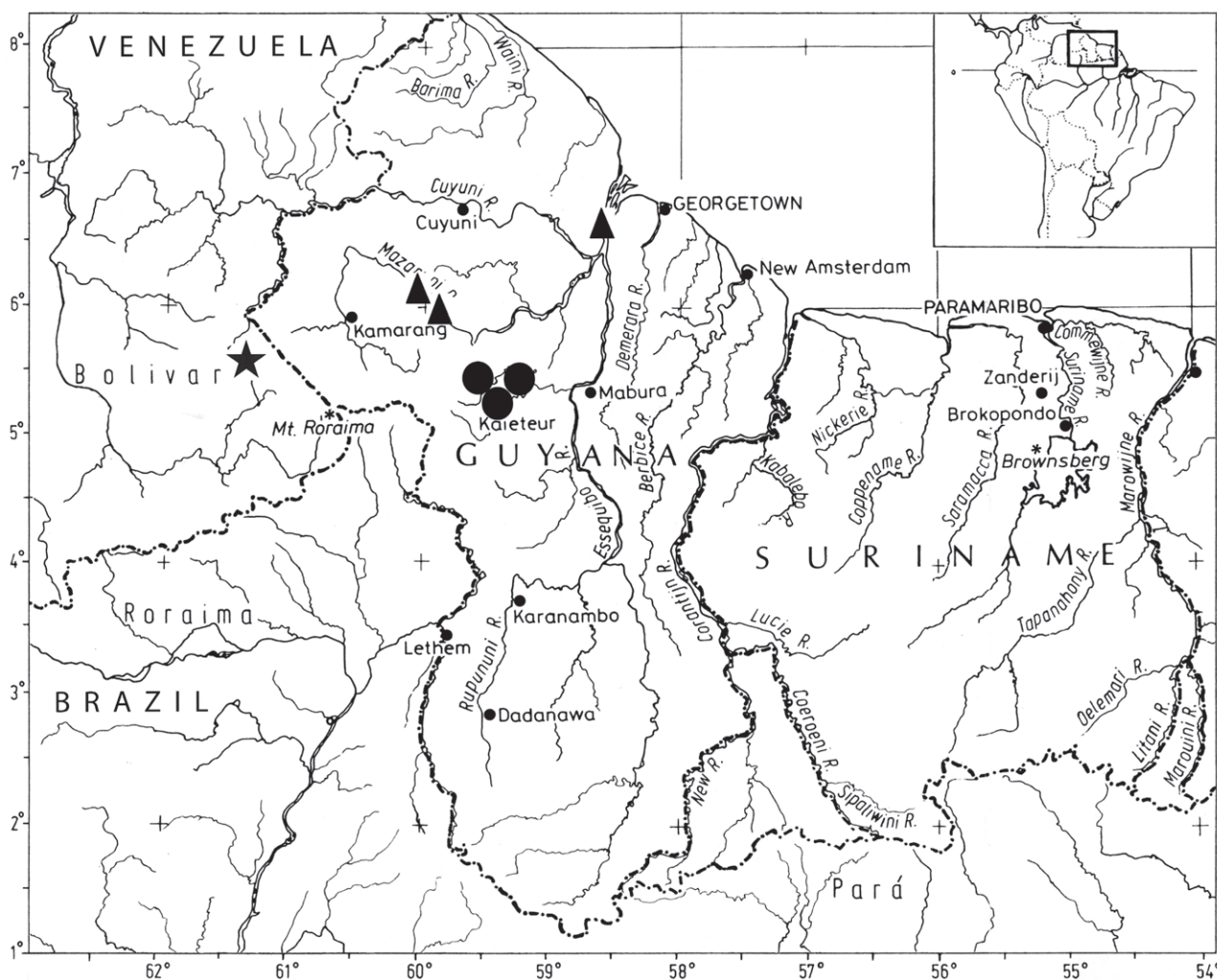


Figure 58. Distribution of *Sipanea carrenoi* (star), *S. gleasonii* (circles), and *S. micrantha* (triangles).

branches barely exerted), and stamens inserted ca. 4 mm below corolla mouth, which led me to conclude that these are long-styled flowers, pending future collection to confirm the heterostylous condition of this species.

Steyermark (1984) compared *S. carrenoi* Steyermark with *S. pratensis*, and stated that the former differs in the creeping, rooting habit of the stems and the densely crowded, smaller, glabrous, obtuse to subacute leaves with fewer secondary veins. However, because of the dense ring of white hairs included below the corolla mouth, he should have positioned this species in his section *Cryptotricha*. Within this section, although Steyermark's sections are not recognized in the present treatment, it is similar to *S. biflora* as here delimited (including *Sipanea cowanii* Steyermark.), because of the creeping habit, thin stem, and small, membranous leaves, from which it differs by the stipules deltoid to triangular-lanceolate, 2–3 × 0.5–2 mm, densely strigose outside (vs. broadly triangular, 0.3–2 × 0.7–1.2 mm, glabrous or sparsely strigillose outside in *S. biflora*), leaf blades ovate-lanceolate elliptic to elliptic-oblong, 0.7–2.3 × 0.4–0.9 cm (vs. ovate, rhombic-ovate or rarely oblong, (0.4–)1.2–5 × (0.35–)0.8–2.8 cm), calyx lobes linear-lanceolate, 4.5–5.5 × 0.5–0.7 mm (vs. linear-lanceolate to setaceous, 1–5 × 0.2–0.6 mm), and capsules narrowly oblong-elliptic, 8–9 × 2–3 mm (vs. subglobose, 3–5 mm in diam.).

Because of the creeping habit, the ovate-lanceolate, elliptic, elliptic-oblong to rhombic, 0.5–2.6 cm long, leaf blades, the corolla tubes (8–)10–13.5 mm long, and the capsules oblong-elliptic, *S. carrenoi* is most similar to *S. veris* (including *S. acinifolia*), of Section *Sipanea*, from which it differs by the ring of white hairs included below corolla mouth (vs. ring of yellow hairs exerted beyond corolla mouth in *S. veris*), stipules deltoid to triangular-lanceolate, 2–3 × 0.5–2 mm (vs. broadly triangular or shortly suborbicular, 0.5 × 0.5–0.8 mm), inflorescences 3–7-flowered (vs. 1–2-flowered), and corolla lobes 5.5–6.5 × 4–5 mm (vs. 6–10 × 4.5–8 mm).

**Distribution and ecology:** Only known from the type, collected in the Gran Sabana, Venezuela, near Salto de Apongua, at 42.5 km NE of the Mission of Santa Teresita de Kavanayen (Figure 58). Growing in open densely covered slopes, on moist sandstone slopes below waterfall, at 1130 m altitude.

**Phenology:** The sole gathering, with flowers and mature capsules, was collected in February.

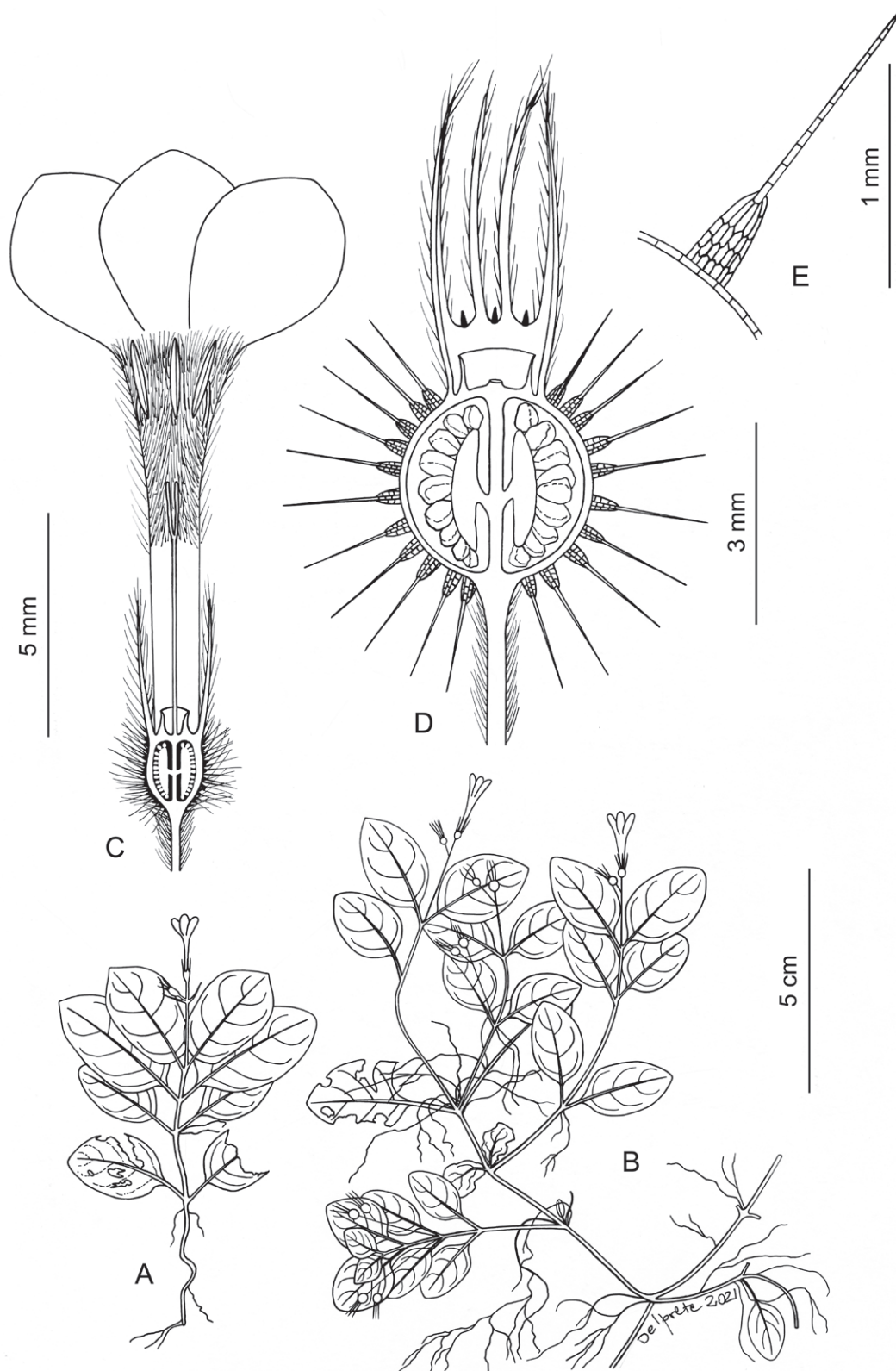
**Suggested conservation status:** **Critically Endangered (CE).** An extremely rare species only known from

the type collection, gathered near Salto de Apongua (also known as Salto Aponwao or Salto Chinak-Merú). This beautiful waterfall is formed by the homonymous river, and is included within the Canaima National Park, southern Venezuela. The size of its population(s) is unknown, and is suspected to be quite small, because although the area of the park has been intensely collected for decades, it was found only once. Also, this waterfall, located within the national park, is frequently visited by tourists groups, causing a considerable impact on the vegetation of this locality. Because of its rarity, the most likely small population, and the considerable human pressure on the locality of occurrence, this species is treated as Critically Endangered (CE) following IUCN criteria (IUCN 2012, 2019).

8-9. *Sipanea gleasonii* Steyermark., Mem. New York Bot. Gard. 17: 265. 1967. (Figures 58–59).

Type: GUYANA: [Potaro-Siparuni Region] Tumatumari [ca. 5°22'N, 59°0'W], dense upland forest, 18 Jun.–8 Jul. 1921 (fl, fr), H.A. Gleason 431 (holotype NY [barcode 00133311]; isotype US [Acc. No. 1122933, barcode 00137726]). [Section *Virecta*].

*Herbs*, prostrate, rooting at basal nodes; stems 3–10 cm long, thin, terete or slightly quadrangular, green, densely antrorse-strigose. *Stipules* adnate to the petioles, broadly triangular to broadly ovate, 0.5–2 × 0.8–1.2 mm, round to obtuse at apex, membranaceous, glabrous or sparsely strigose outside, glabrous, with 3–5 colleters at median portion or 7–10 irregularly distributed colleters inside; margins irregularly fringed, long-pubescent. *Leaves* petiolate; petioles 3.5–15 mm long, green when fresh, winged on both sides (extension of decurrent blade), sparsely antrorse-strigose pubescent; blades ovate to elliptic-oblong, 1.6–5 × 1–3 cm, obtuse to acute and decurrent at base, obtuse at apex, membranaceous, grass-green above and dull pale green below when fresh, olive-green above and below when dry, lamina sparsely appressed pubescent above (hairs 0.7–1 mm long), midrib and secondary veins sparsely sericeous-pubescent, margin sparsely setaceous-pubescent ciliate; secondary veins 3–4 on each side of midrib, ascending, weakly evident above, slightly prominulous below. *Inflorescences* terminal or simingly axillary (due to the reiteration of an axillary branch originating from an axillary bud at the base of the inflorescence), long-pedunculate, with a terminal 2–3-flowered cyme; rachis filiform, almost capilliform, peduncle 0.9–3.5 cm long, densely strigillose; bracts subtending terminal cyme linear-lanceolate



**Figure 59.** *Sipanea gleasonii*. A–B. Habit (both plants drawn to same scale). C. Dissected short-styled flower, with stamens inserted at distal portion of corolla tube (partially exerted), and included style. D. Longitudinal section of fruit. E. Detail of one hair, basally tuberculate. A–B, D–E: drawn from *Gleason 112* (US, paratype); C: drawn from *McDowell et al. 4824* (US). Illustration by Piero Delprete.

to setaceous,  $2\text{--}3.5 \times 0.2\text{--}0.3$  mm, acuminate at apex, sparsely antrorse-hispidulous, ciliate at margins; bracteoles subtending flowers (when present) linear,  $2.5\text{--}2.7 \times 0.2$  mm, acuminate, sparsely antrorse-hispidulous. *Flowers* probably distylous, 5-merous, pedicellate; pedicels of lateral flowers 2–11 mm long, those of central flower 0.7–3 mm long, sparsely antrorse-hispidulous. *Hypanthium* subglobose to broadly obovoid,  $1.3\text{--}1.7 \times 1\text{--}1.5$  mm, obtuse at base, round at apex, densely antrorse hispid-strigose; hairs basally tuberculate, thin, 0.7–1.1 mm long. *Calyx* lobes subequal, green when fresh, setaceous,  $4\text{--}4.5 \times 0.1\text{--}0.2$  mm, acute at apex, glabrous, margins hispidulous-ciliate, hairs 0.5–0.7 mm long, antrorse-ascending to appressed; with 1 colleter in each calycine sinus, linear, 0.3 mm long. *Corolla* narrowly infundibuliform, 12–14 mm long, pale pink to white, with a ring of white sericeous hairs at mouth; tube narrowly obconical, gradually expanding towards the mouth, 7–9.5 mm long, 1 mm wide at base, 2–2.5 mm wide at mouth, lower half glabrous and upper half sparsely antrorse-pubescent outside, lower 4.5 mm glabrous and densely white-villous above inside; lobes oblong to oblong-obovate to broadly ovate,  $4\text{--}8 \times 2.5\text{--}3$  mm, obtuse to round at apex, glabrous throughout. *Long-styled flowers* unknown. *Short-styled flowers* (*Gleason 112* – corolla tube 9 mm long; *McDowell et al. 4824* – corolla tube 9.5 mm long; *Tutin 541* – corolla tube 7–8.5 mm long): stamens inserted at 2.5 mm below corolla mouth; filaments 0.6–0.9 mm long; anthers partially exerted (only tip exerted), narrowly oblong to linear,  $1.4\text{--}1.8 \times 0.2\text{--}0.3$  mm, acute at both ends; style included, 5.5–7 mm long, glabrous; branches linear, 1–1.6 mm long. *Infructescences* terminal or singly axillary, due to the reiteration of an axillary branch originating from an axillary bud at the base of the inflorescence, long-pedunculate, with a terminal 2–3-fruited cyme, rachis filiform, almost capilliform, similar to inflorescences. *Capsules* globose, 2.8–3 mm in diam., round at both ends, crustaceous, pale green when young, turning pale brown when dry, densely erect-hispid; hairs basally tuberculate, 1–1.5 mm long. *Seeds* irregularly tetrahedral-globose, 0.5–0.7 mm in diam., testa foveolate.

**Notes:** This species is only known from a few flowering specimens, and each of them has only one or a few flowers. In all the flowers of the specimens examined the style is included, and the anthers are inserted near the corolla mouth, indicating that most likely they are short-styled forms. Additional collections with more flowers are needed to confirm its distylous condition.

*Sipanea gleasonii* is similar to *S. ovalifolia* because of the creeping habit, thin stems rooting at nodes and

internodes, broadly ovate to broadly triangular stipules, leaf blades ovate to elliptic oblong,  $1.6\text{--}5 \times 1\text{--}3$  cm long, few-flowered inflorescences, hypanthium and capsules with basally tuberculate hairs, and corollas with a ring of white hairs at mouth; the former differs from the latter by the leaves with 3–4 secondary veins on each side of midrib (vs. 3–6 secondary veins on each side of midrib in *S. ovalifolia*), inflorescences 2–3 flowered (vs. 3–5-flowered), hypanthium  $1.3\text{--}1.7 \times 1\text{--}1.5$  mm (vs.  $0.7\text{--}0.8 \times 0.7\text{--}0.8$  mm), calyx lobes setaceous,  $4\text{--}4.5 \times 0.1\text{--}0.2$  mm (vs. linear to linear-lanceolate,  $2.5\text{--}4 \times (0.1\text{--})0.2\text{--}0.4$  mm), and corollas narrowly infundibuliform 12–14 mm long with tubes 7.5–9.5 mm long and lobes  $(4\text{--})5\text{--}8 \times 2.5 \times 3$  mm (vs. corollas narrowly campanulate, 4.3–5.3 mm long with tube 2.8–3.6 mm long and lobes  $1.5\text{--}1.8 \times 1.2\text{--}1.3$  mm).

**Distribution and ecology:** Endemic to lower Potaro-Siparuni Region, central Guyana, from where it is known from a few collections (Figure 58). Growing on forest floor, on brown, sandy soils, at 137–200 m altitude.

**Phenology:** Due to its short life span, it is common to find flower and fruits on the same individual. Such specimens were collected in February, May, June–July and November.

**Suggested conservation status: Critically Endangered (CR).** This species is endemic to the lower Potaro-Siparuni Region, central Guyana. It is known from three collections, including the type, made in 1921 and 1933 near the town of Tumatumari [ca.  $5^{\circ}22'N$ ,  $59^{\circ}0'W$ ], and a few other localities in the lower Potaro-Siparuni Region. For all these localities, the population sizes of this species are unknown. The region surrounding the town of Tumatumari has fertile soils, which have been devoted to agricultural exploitation; the area has also been profoundly impacted by timber extraction used by several local factories producing matches, pencils and tooth-picks. Currently the area is also greatly impacted by mining activities, and the natural vegetation surrounding Tumatumari has mostly been destroyed, and only a few patches of secondary vegetation are present.

The two most recent collections of this species were made in 1991, one along the North Fork River, near Porkknoker Works, at  $5^{\circ}9'N$ ,  $59^{\circ}8'W$  (*McDowell 4824*), and the other at the nearby village of Micobe, at  $5^{\circ}20'N$ ,  $59^{\circ}30'W$  (*Tiwari & Mengharini 515*), at 137 and 200 m altitudes, respectively. Both of these localities are heavily impacted by gold hunting activities, either by mining, panning, or dragging the bottom of rivers with dredgers; and the forest surrounding the village of Micobe is partially destroyed.

In conclusion, all the localities where this species has been collected are profoundly impacted by human activities, where the natural forests have been destroyed or reduced to meager secondary remnants. Considering all the above, this species is Critically Endangered (CR), following IUCN criteria (IUCN 2012, 2019).

**Specimens examined:** GUYANA: Berbice or Demerara County, along the Berbice-Rupununi Cattle Trail, 1919 (fl), A.A. Abraham 306 (NY); [Potaro-Siparuni Region], Tumatumari [ca. 5°22'N, 59°0'W], dense upland forest, 18 Jun.–8 Jul. 1921, H.A. Gleason 112 (NY, US, paratype); Potaro-Siparuni Region, along North Fork River, 0.5–1.5 km N of Konawark Rd., near Porkknoker works, forest floor, 5°9'N, 59°8'W, 137 m, 28 May 1991 (fl), T. McDowell 4824 (MO, NY, U); Potaro-Siparuni Region, Micobe, mixed forest on brown sand, 5°20'N, 59°30'W, 200 m, 21 Oct. 1991 (fl), S. Tiwari & A. Mengharini 515 (NY, US); Tiger Creek, Tumatumari [ca. 5°22'N, 59°0'W], wet clay in Mora forest near the creek, 300 ft. [ca. 90 m], 24 Aug. 1933 (fl, fr), T.G. Tutin 541 (BM, U, US);

8-10. *Sipanea micrantha* Sandwith, Bull. Misc. Inform. Kew 1928(9): 378. 1928. (Figures 58, 60).

Type: GUYANA. Mazaruni River, Kamakusa [ca. 5°57'N, 59°54'W, ca. 80 m], Sep. 1925 (fl), A.A. Abraham 404 (holotype K [without barcode]; isotype NY [barcode 00133314]). [Section *Virecta*].

*Herbs*, prostrate, rooting at nodes; stems to 35 cm long, thin, 0.3–0.5 mm thick, terete, green, appressed antrorse-pubescent. *Stipules* adnate to the petioles, broadly transversely elliptic to truncate, 0.3–0.4 × 0.4–0.6 mm, membranaceous, appressed antrorse-pubescent outside, glabrous, with 3–5 colleters inserted just below the margin inside, tips exserted beyond margin; margins long-hispid. *Leaves* petiolate; petioles 2–6 mm long, narrowly winged, sparsely antrorse-pubescent; blades ovate to rhombic-ovate, 5–17 × 3–7 mm, acute to obtuse at base, acute at apex, chartaceous, brownish olive-green when dry, lamina glabrous above, glabrous and with midrib and secondary veins with secondary veins sparsely strigose below, margin glabrous; secondary veins 2–3 on each side of midrib, ascending, weakly evident above, slightly prominulous below. *Inflorescences* terminal or subaxillary (originally terminal), pedunculate, rachis capilliform, with a terminal (1)2-flowered cyme, peduncle 1.2–1.8 cm long, appressed antrorse-pubescent; bracteoles subtending flowers linear-lanceolate, 0.9–1 × 0.2 mm, acute at apex, sparsely appressed-puberulent. *Flowers* most likely disty-

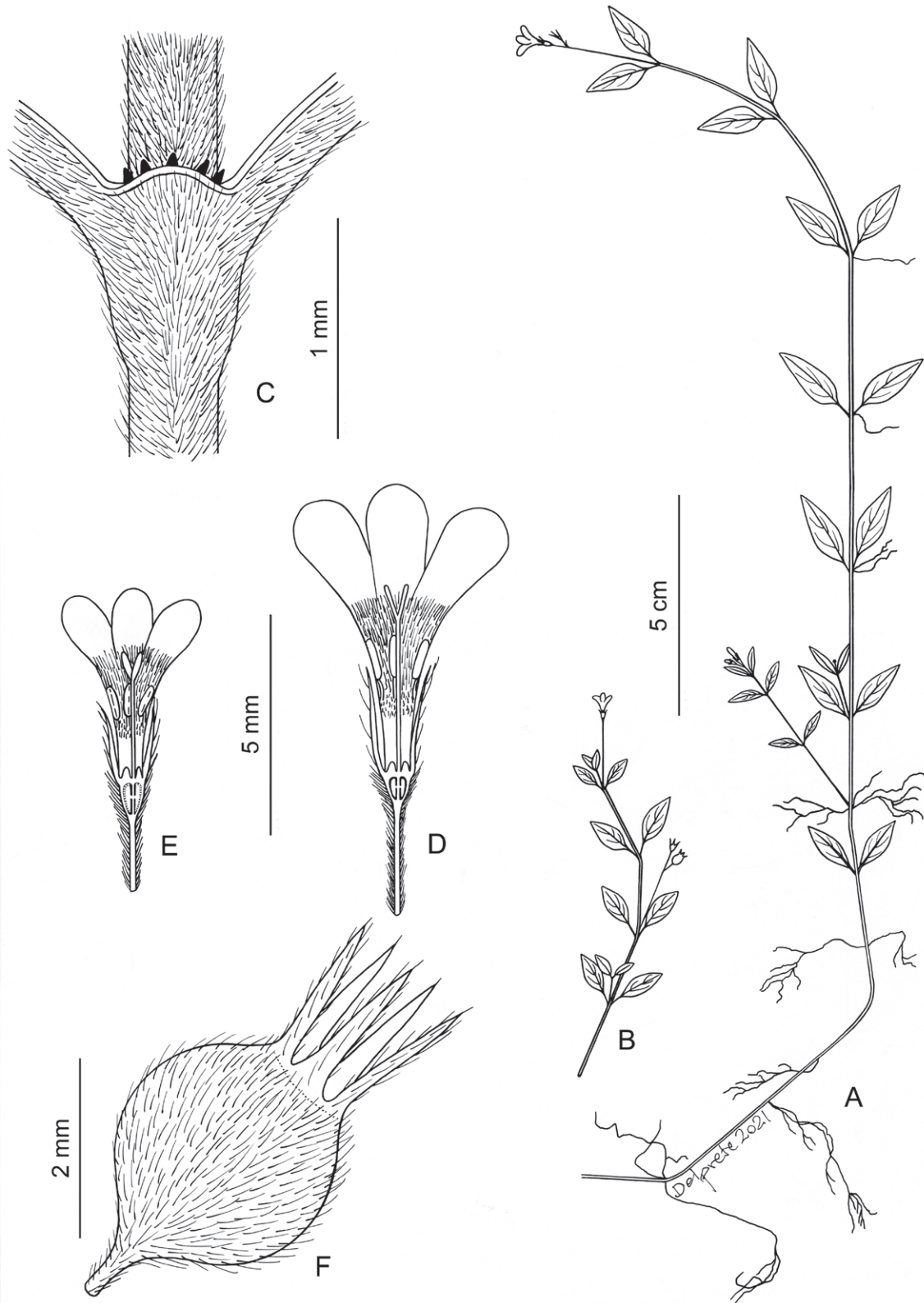
lous (only one flower dissected), (4)5-merous, pedicellate; pedicels of terminal flower 3–6 mm long, those of lateral flowers 1.5–2 mm long, appressed antrorse-pubescent. *Hypanthium* obovoid, 0.7–0.8 × 0.7 mm, acute at base, round at apex, glabrous or with a few appressed hairs. *Calyx* lobes subequal, linear-lanceolate, 1.3–1.7 × 0.2–0.3 mm, acute at apex, with a few appressed-pubescent hairs; with 1 colleter in each calycine sinus, conical, obtuse at apex, 0.1 mm long. *Corolla* campanulate, 4–6.5 mm long, white, with a ring of white hairs at mouth; tube obconical, 2.5–3.5 mm long, 0.5–0.6 mm wide at base, 1.5–2 mm wide at mouth, glabrous outside, lower half glabrous and shortly puberulous above, and white-villous in the areas where anthers are located inside; lobes oblong-ovate to oblong-obovate, 1.5–3 × 1–1.5 mm, obtuse to round at apex, puberulent inside, glabrous outside. *Long-styled flowers*: Stamens included, inserted 0.7–1 mm above base of corolla tube, filaments 0.4–0.6 mm long, anthers narrowly oblong, 0.75–1.2 × 0.15 mm; style about the same length as corolla tube (tips of style branches exserted), 2.5–3.3 mm long, style branches 0.6–0.7 mm long. *Short-styled flowers* unknown. *Infructescences* terminal or subaxillary (originally terminal), pedunculate, rachis capilliform, with a terminal (1)2-fruited cyme, similar to inflorescences. *Capsules* ovoid to subglobose, 2.5 mm in diam., round at both ends, crustaceous, glabrous or with a few appressed hairs. *Seeds* not seen.

**Notes:** Sandwith (1928) described *Sipanea micrantha* and cited Abraham 404 at K as the type of this taxon; therefore this specimen is the holotype. He also cited Jenman 2416 as the paratype of this taxon, without indicating the herbarium of deposit; this specimen has not been traced.

*Sipanea micrantha* is similar to *S. veris* in the creeping habit, thin stems, shallow stipules, leaf blades 5–17(–26) mm long, and inflorescences 1–2-flowered; the former differs from the latter in the hypanthium 0.7–0.8 × 0.7 mm (vs. 1.5–3.5 × 2–2.2 mm in *S. veris*), calyx lobes 1.3–1.7 × 0.2–0.3 mm (vs. (2–)3–7.5 × 0.1–0.6 mm), corolla campanulate, with a ring of white hairs at mouth, 4–6.5 mm long (vs. hypocrateriform, with a ring of yellow hairs at mouth, (14–)16–23.5 mm long) with tube obconical, 2.5–3.5 mm long and lobes 1.5–3 × 1–1.5 mm (vs. tube cylindrical, (8–)10–13.5 mm long and lobes 6–10 × 4.5–8 mm), and capsules ovoid to subglobose, 2.5 mm in diam. (vs. oblong-elliptic, 7 × 3 mm in diam.).

**Distribution and ecology:** A very rare species occurring in the Mazaruni River Basin, Guyana (Figure 58). Growing on forest floor, at 76–122 m altitude.





**Figure 60.** *Sipanea micrantha*. A–B. Habit (both plants drawn to same scale). C. Node with sheathing stipule with partially exerted colleters, and petioles. D–E. Dissected long-styled flowers, with stamens inserted at distal portion of corolla tube, and exerted style (drawn to same scale). F. Capsule. A, C–D: drawn from McDowell 3779 (US); B, E–F: drawn from Abraham 404 (K). Illustration by Piero Delprete.

**Phenology:** The three collections, with flowers and fruits, were made in September and November.

**Suggested conservation status: Critically Endangered (CR).** This is a very rare species known from three localities in the Mazaruni River Basin, Guyana. It might be undercollected due to the minute size of its leaves and flowers. The first collection (*Jenman 2416*) was made in 1886, near the town of Bartica, at the triple confluence of the Cuyuni, Mazaruni and Essequibo Rivers; the corresponding specimen was cited by Sandwith (1928) but it was not traced. During the 20th century, Bartica underwent considerable expansion and the surrounding forest was generally eliminated; nevertheless, some patches of secondary forest are still present in the vicinities of the town.

The second collection, the type gathering of this species (*Abraham 404*), was made in 1925 near the town of Kamakusa, ca. 5°57'N, 59°54'W, at the edge of the Mazaruni River. The current status of conservation of the forest surrounding this town is unknown but is probably precarious, as the general area is subjected to mining activities.

The third and most recent collection (*McDowell 3779*) was made in 1990, also near the Mazaruni River, at 2–6 km upstream from Eping River Camp (Golden Star Resources, 6°5'N, 60°7'W). The current state of conservation of the forest at this locality is unknown. However, as the specimen label indicates, the area is subject of gold mining activities.

Summarizing the above discussion, the three localities where this species was collected are heavily impacted by human activities, and the population sizes are unknown, as no recent field observation in these localities has been made. Therefore, this species is estimated to be Critically Endangered (CR), according to IUCN criteria (IUCN 2012, 2019).

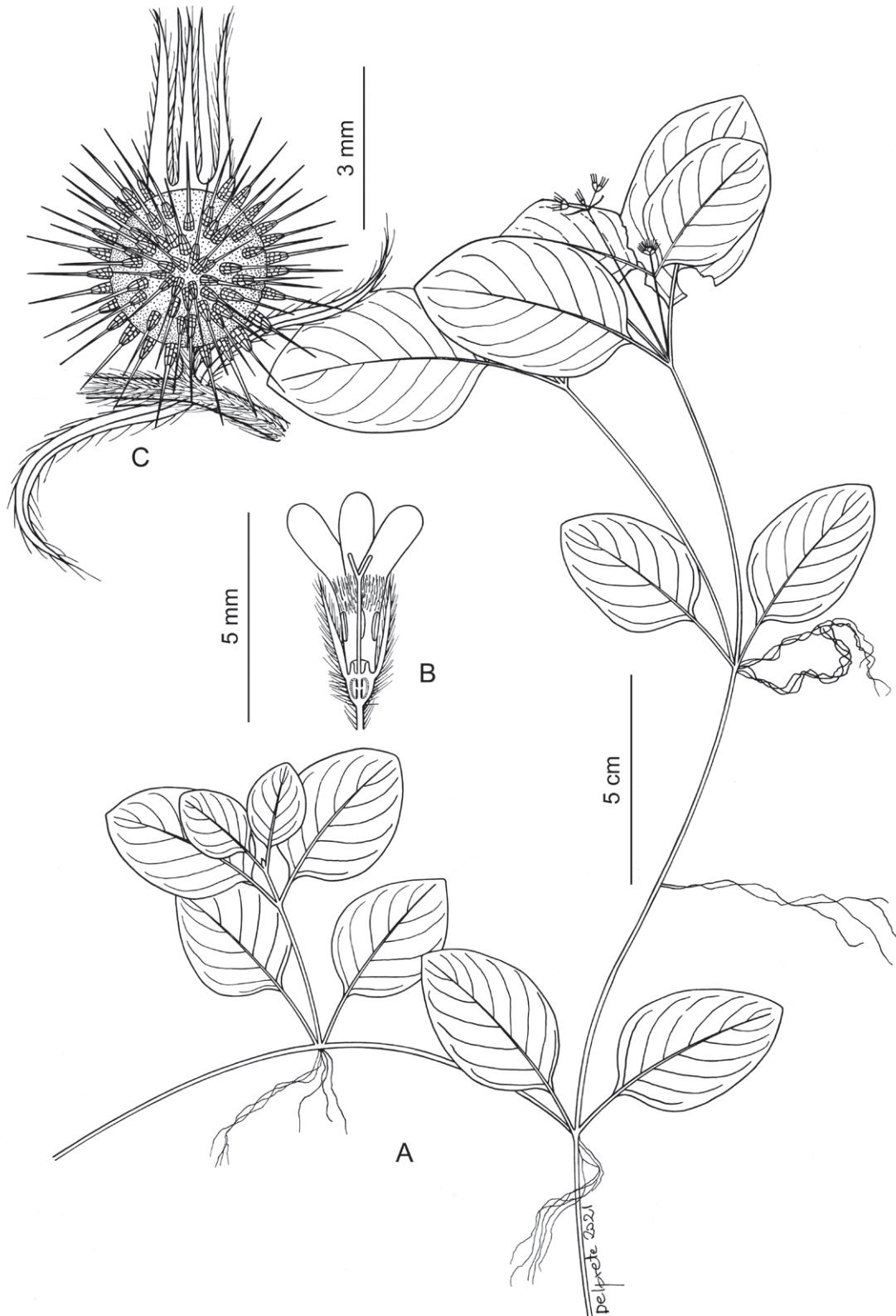
**Specimen examined: GUYANA:** Bartica Grove [ca. 6°24'N, 58°37'W], Nov. 1886, *G.S. Jenman 2416* (cited by Sandwith (1928), not found); Cuyuni-Mazaruni Region, ranging 2–6 km upstream from Eping River Camp (Golden Star Resources), 6°5'N, 60°7'W, 76–122 m, 15 Nov. 1990 (fl), *T. McDowell 3779* (MO, US).

8-11. *Sipanea ovalifolia* Bremek., Rec. Trav. Bot. Neerl. 31: 259. 1934. [Section *Virecta*]. (Figures 61–63).

**Note:** For types and conservation status, see under varieties.

*Herbs*, prostrate, rooting at basal nodes and internodes; stems thin, terete or slightly quadrangular, green,

pubescent, antrorsely appressed pubescent (var. *ovalifolia*) or spreading to ascendingly villous (var. *villosissima*). *Stipules* adnate to the petioles, broadly ovate to broadly triangular, 0.4–0.7 × 0.8–1.2 mm, obtuse at apex, membranaceous, sparsely to densely antrorse-pubescent outside (hairs 1.5–1.7 mm long), glabrous, with 3–4 colleters inserted just below the margin inside, tips exerted beyond margin; margins long-hispid. *Leaves* petiolate; petioles 5–20 mm long, narrowly winged or not winged, sparsely to densely antrorse-pubescent or villous; blades broadly ovate, ovate to oblong-ovate, 1.7–4.7 × 1.2–3.2 cm, truncate, broadly obtuse to round at base, obtuse, round to subobtuse at apex, membranaceous, dark green above and pale green below when fresh, olive-green above and below when dry, sparsely appressed pubescent or lamina glabrous and veins sparsely appressed pubescent (hairs appressed, 0.4–1.3 mm long; var. *ovalifolia*), or lamina and veins villous (hairs erect, 1.5–2.5 mm long; var. *villosissima*) above, lamina and veins sparsely appressed pubescent, or lamina sparsely appressed pubescent and veins densely appressed pubescent, or lamina glabrous and secondary veins sparsely appressed pubescent below (hairs 0.6–1.3 mm long; var. *ovalifolia*), or lamina and veins villous below (hairs erect, 1.3–2.5 mm long; var. *villosissima*), margin ciliate; secondary veins 3–6 on each side of midrib, ascending, weakly evident above, prominulous below. *Inflorescences* terminal or subaxillary (originally terminal), long-pedunculate, with a terminal 3–5-flowered cyme, rachis filiform, almost capilliform; peduncle 2–4 cm long, antrorsely appressed-pubescent or antrorsely appressed-sericeous (hairs 0.5–1.2 mm long; var. *ovalifolia*), or ascendingly villous (hairs 1.3–1.5 mm long; var. *villosissima*); bracts subtending terminal cyme and bracteoles subtending flowers very similar, narrowly lanceolate to linear, 1.5–2.5 × 0.2–0.3 mm, acute at apex, glabrous, hispid at margins. *Flowers* distylous, 5-merous, subsessile to pedicellate; in 3-flowered cymes, pedicel of central flower 0.7–1.5 mm long and those of lateral flowers 1.3–3 mm long, in 4–5-flowered cymes pedicels 0.5–2 mm long, sparsely to densely antrorse-hispidulous. *Hypanthium* subglobose to broadly obovoid, 0.7–0.8 × 0.7–0.8 mm, obtuse at base, round at apex, densely antrorse-strigose, hairs basally tuberculate (hairs 0.7–1.3 mm long). *Calyx* lobes subequal, green when fresh, linear to linear-lanceolate, 2.5–4 × (0.1–)0.2–0.4 mm, acute at apex, densely antrorse-hispid (hairs antrorse-ascending to appressed, 0.6–0.7 mm long); with 1 colleter in each calycine sinus, conical, obtuse at apex, 0.1 mm long. *Corolla* narrowly campanulate, 4.3–5.3 mm long white, with a ring of sericeous white hairs at mouth; tube basally urceolate, constricted just below the mouth,



**Figure 61.** *Sipanea ovalifolia* var. *ovalifolia*. **A.** Habit. **B.** Dissected long-styled flowers, with stamens inserted at median portion of corolla tube, and exserted style. **C.** Fruit. **A:** drawn from Wessel Boer 1554 (U). **B:** drawn from Florshutz & Florshutz 1242 (U). **C:** drawn from Oldeman B-2190 (CAY). Illustration by Piero Delprete.

2.8 mm long (var. *ovalifolia*) or narrowly obconical, constricted at medial portion and slightly wider at mouth, 3–3.6 mm long (var. *villosissima*), glabrous outside, lower half (cylindrical portion) glabrous and upper half white-puberulent, and densely white-villous near the mouth inside; lobes ovate to oblong-obovate, 1.5–1.8 × 1.2–1.3 mm, obtuse to round at apex, glabrous on both sides. *Long-styled flowers* (Cremers 6460, Pulle 222; corolla tubes 2.8–3.5 mm long): stamens inserted at medio-basal portion of corolla tube; anthers subsessile, oblong, 0.7–0.9 × 0.2 mm, acute at both ends; style as long as corolla tube (tip of branches exerted), 3–3.5 mm long, glabrous; branches obovate, 0.6 mm long, round at apex. *Short-styled flowers* unknown. *Infructescences* terminal or subaxillary (originally terminal), long-pedunculate, with a terminal 3–5-fruited condensed cyme, rachis filiform, almost capilliform, similar to inflorescence. *Capsules* globose, 2.5–2.8 mm in diam., round at both ends, crustaceous, pale green when young, turning pale brown when dry, densely erect hispid-strigose; hairs basally tuberculate, 0.9–1.5 mm long. *Seeds* irregularly tetrahedral, 0.5–0.6 mm wide, testa foveolate.

**Notes:** Steyermark (1984: 159–160) distinguished *Sipanea ovalifolia* var. *villosissima* Steyermark from the typical variety “in having dense villous pubescence which covers the stems, petioles, peduncles, and the calyx lobes with hairs 1–2.5 mm long, the var. *ovalifolia* having only appressed pubescence.” Detailed studies with more material available supported the distinction of these varieties. For *S. ovalifolia* var. *villosissima* the only specimens available are the type specimens. Variety *villosissima* was recently photographed at Mount Itoupé, the type locality, by Sebatién Sant (Parc Amazonien de Guyane). In those photographs the villous vestiture of vegetative parts is quite evident, and proved that this variety is most likely endemic to this locality. Unfortunately the plants photographed in Mount Itoupé were not collected. Additional characters that can be used to distinguish these two varieties are found in the shape of the corollas, which are compared in the key below. Also, var. *ovalifolia* is known from Suriname and French Guiana, at 10–180 m altitude, while var. *villosissima* is only known from Mount Itoupé, Central French Guiana, at 600–700 m altitude.

Key to varieties of *Sipanea ovalifolia*

1. Stems, petioles and peduncles antrorsely appressed-pubescent or antrorsely appressed-sericeous; leaf lamina glabrous or sparsely appressed-pubescent and veins sparsely appressed-pubescent above (hairs appressed, 0.4–1.3 mm long), lamina glabrous and veins sparsely to densely

appressed-pubescent below (hairs appressed, 0.6–1.3 mm long); corolla tube urceolate, constricted just below the mouth, 2.8 mm long; corolla lobes oblong-ovate, 1.5 × 1.3 mm (Suriname and French Guiana, at 10–180 m altitude)..

.....*S. ovalifolia* var. *ovalifolia*

1. Stems, petioles and peduncles spreading to ascendingly villous; leaf blades villous above (hairs erect, 1.5–2.5 mm long) and below (hairs erect, 1.3–2.5 mm long); corolla tube narrowly obconical, constricted at medial portion and slightly wider at mouth, 3–3.6 mm long; corolla lobes ovate, 1.5–1.8 × 1.2 mm (Central French Guiana, Mount Itoupé, at 600–700 m altitude).....  
.....*S. ovalifolia* var. *villosissima*

8-11a. *Sipanea ovalifolia* Bremek. var. *ovalifolia*, Rec. Trav. Bot. Neerl. 31: 259. 1934. (Figures 61, 62A–C, 63).

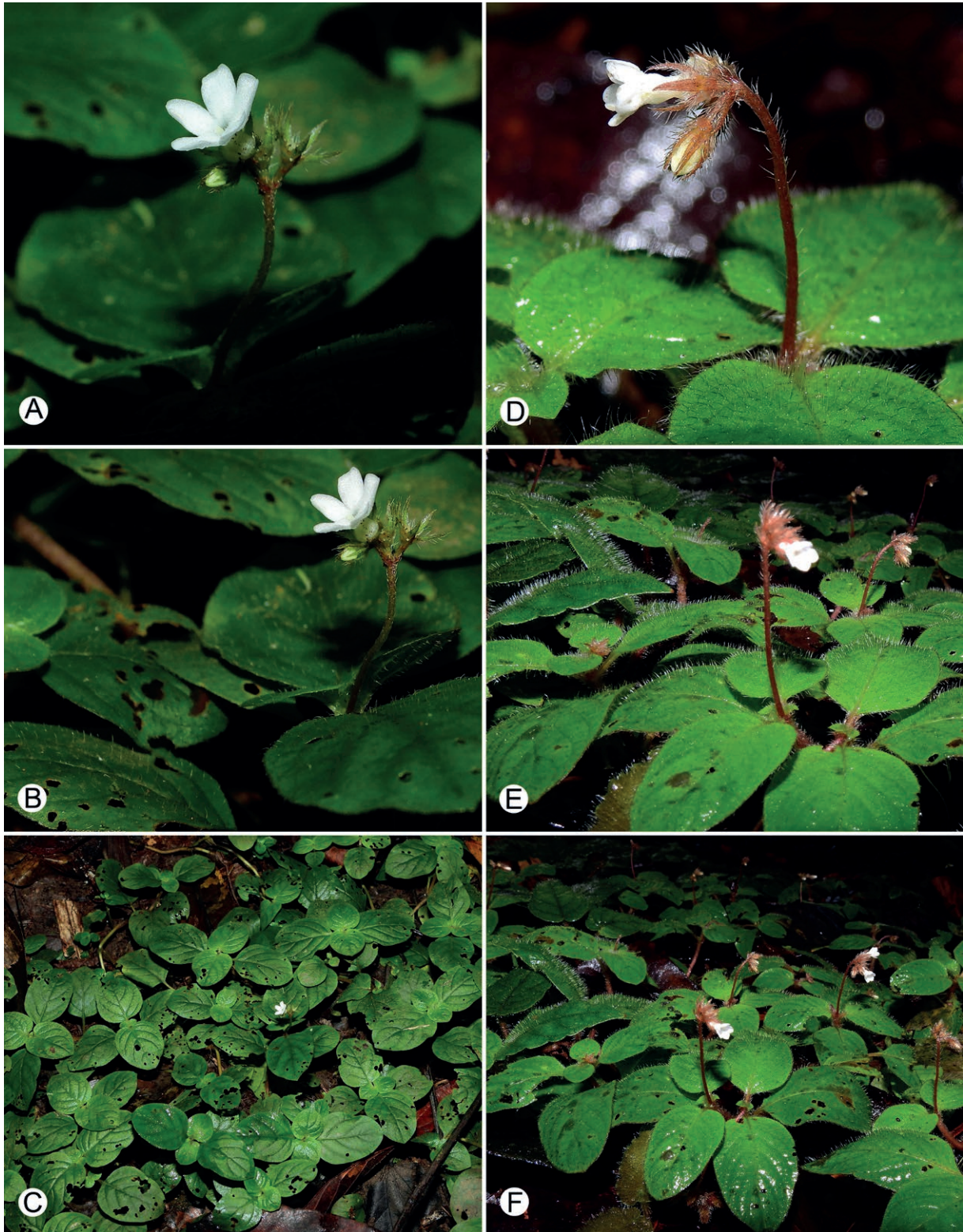
Type: SURINAME: Saramacca River, 16 Mar. 1903, A.A. Pulle 222 (holotype U [2 sheets, barcodes 0006311 and 0006312]; isotype NY [barcode 00133315]).

**Notes:** The specimen *Pulle 222* at U is mounted on two sheets that are kept together; therefore, according to Art. 8.3 of the *Code* (Turland et al. 2018), it should be treated as a single specimen with multiple preparations. The specimen *Pulle 222* at NY is annotated as holotype by Steyermark (May 1965), but the holotype is at U.

*Stems* antrorsely appressed-pubescent or antrorsely appressed-sericeous. *Leaves* with petioles 7–20 mm long, narrowly winged or not winged, antrorsely appressed-pubescent; blades broadly ovate, ovate to oblong-ovate, 1.7–4.7 × 1.2–3.2 cm, truncate, round, obtuse to obtuse-subacute at base, obtuse, round to obtuse, often microscopically mucronate at apex, lamina glabrous or sparsely appressed-pubescent and veins sparsely appressed-pubescent above (hairs appressed, 0.4–1.3 mm long), lamina sparsely appressed-pubescent and veins sparsely to densely appressed-pubescent below (hairs appressed, 0.6–1.3 mm long); secondary veins 3–6 on each side of midrib. *Peduncles* antrorsely appressed-pubescent or antrorsely appressed-sericeous (hairs 0.5–1.2 mm long). *Corolla* 4.3 mm long; tube urceolate, constricted just below the mouth, 2.8 mm long; lobes oblong-obovate, 1.5 × 1.3 mm, obtuse to round at apex.

**Vernacular name:** FRENCH GUIANA: Yüemapilä (Wayapi, *Granville 2486*).

**Distribution and ecology:** A variety known from several collections in Suriname and French Guiana (Fig-



**Figure 62.** *Sipanea ovalifolia*. A–C. *S. ovalifolia* var. *ovalifolia*. A. Inflorescence with one flower in anthesis. B. Detail of inflorescence and several leaves (note sparsely short-pubescent leaves). C. Habit. D–F. *S. ovalifolia* var. *villosissima* Steyerl. D. Inflorescence with one flower in anthesis. E. Detail of inflorescence and several leaves (note villous leaves). F. Habit. Photos by Sebastien Sant. A–C: from Gros-Saut, Papaïchton, Abounami River, French Guiana, plants not collected; D–F: from Mont Itoupé, E slope, French Guiana, plants not collected.

ure 63). Growing on forest floor, in Mora forest, frequently in humid or swampy places; at 10–180 m altitude.

**Phenology:** Specimens with flowers and fruits were collected in February, June, July and August, which corresponds with the local rainy season.

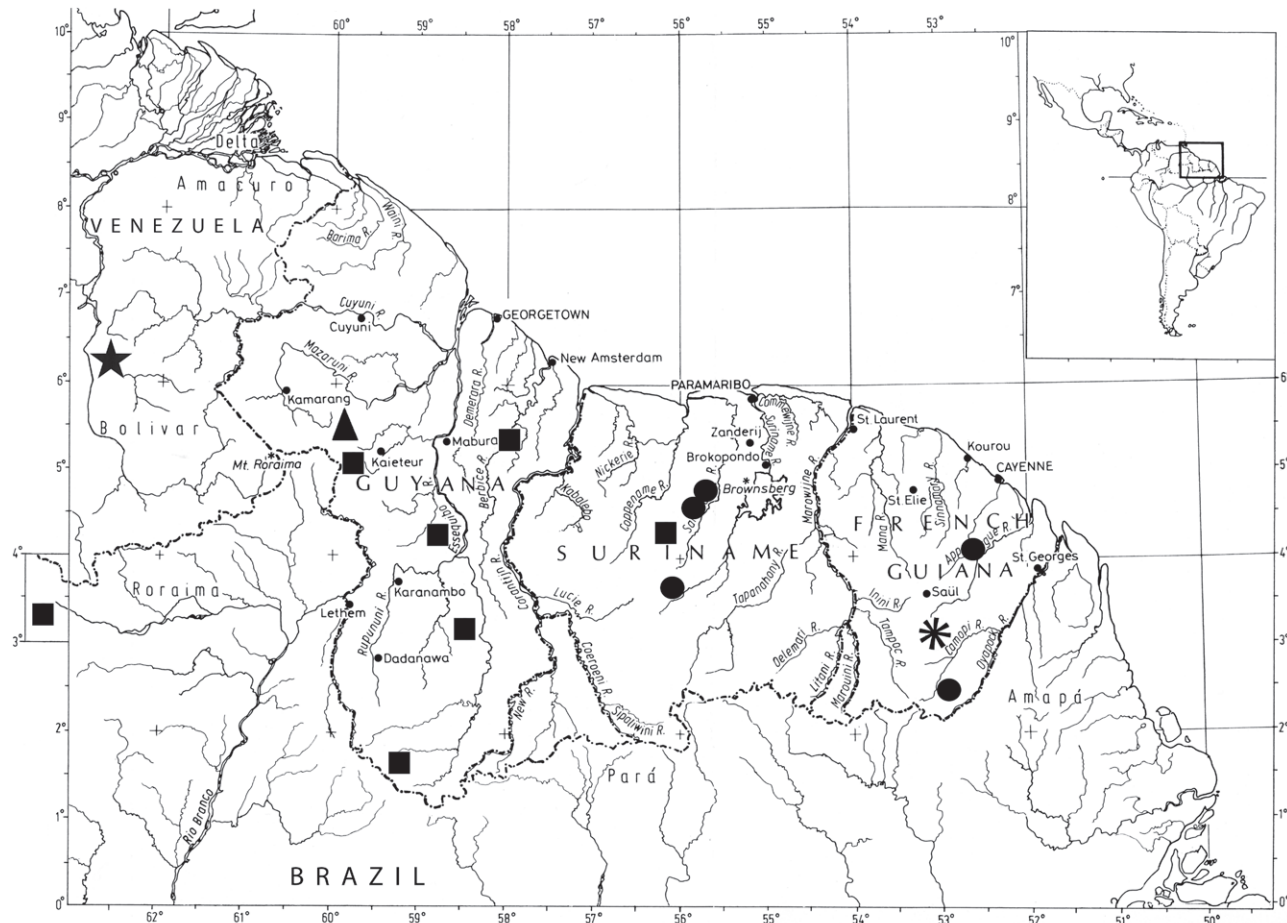
**Suggested conservation status: Near Threatened (NT).** This variety is a rare, shade-loving, prostrate herb, growing on the forest floor, known from five collections in Suriname and two in French Guiana. In Suriname it has been collected in 1903 (type), 1908, 1933, 1951, and 1963. These collections were made in remote localities, none of which has recently been visited by botanists, therefore the status of preservation of these forest areas is unknown. The most recent collection was made in 1963, in a forest south of Kappel Savanna [ca. 3°48'N, 56°8'W], a white-sand savanna surrounded by forest, located in central Suriname. A floristic survey of that savanna was published by Kramer & Donselaar (1968),

but the current status of preservation of the forest south of it is unknown.

In French Guiana, it is known from two collections made in localities far away from each other: the first one (*Oldeman B-2190*) was made in 1969, in the Approuage River Basin, Ipoucin Creek, Camp Salvat [ca. 4°9'N, 52°27'W], at ca. 100 m elevation; the second one (*Graville 2486*) was made in 1975, in the Upper Oyapock River Basin, near the Takululi Creek [or Euleupousing Creek], ca. 1 km W of Saut Cambrouze [Cambrouze falls, ca. 2°20'N, 52°58'W], at ca. 180 m elevation; The size of the populations in these three localities is unknown, and their forests are apparently well preserved.

In conclusion, all the collections of this species have been made in remote, uninhabited localities, and it is supposed that they do not have any immediate threats, although this remains to be confirmed.

**Specimens examined: SURINAME:** Lijn van Paka Paka (Saramacca) [ca. 4°37'N, 55°40'W], ca. 5 km from



**Figure 63.** Distribution of *Sipanea ovalifolia* var. *ovalifolia* (circles), *S. ovalifolia* var. *villosissima* (asterisk), *S. setacea* (star), *S. ayangannensis* (star), and *S. prancei* (squares).

Ebbatop (v. Asch v. Wijck-Geb.), 9 Feb. 1951 (fl, fr), *J. Florschütz & A. Florschütz 1242* (U); Suriname River, near Ketokvorsoe, 23 Aug. 1908 (fl), *J.H.A.T. Tresling 367* (U [U0016826], paratype); S of Kappel Savanna [ca. 3°48'N, 56°8'W], near Tafelberg, in swampy place near creek in dense forest, 12 Jun. 1963 (fl, fr), *J.G. Wessels Boer 1554* (NY, U).

**FRENCH GUIANA:** Upper Oyapock River Basin, Takululi Creek [or Crique Euleupousing], affluent of Ipsi Creek, ca. 1 km W of Saut Cambrouze [ca. 2°20'N, 52°58'W, ca. 180 m], forêt sur flat, 19 Jul. 1975 (fl, fr), *J.J. de Granville 2486* (CAY [2 sheets], US); Approuage River Basin, Ipoucin Creek, Camp Salvat [ca. 4°9'N, 52°27'W, ca. 100 m], 25 Feb. 1969 (fl), *R.A.A. Oldeman B-2190* (CAY, NY, P, U).

8-11b. *Sipanea ovalifolia* var. *villosissima* Steyerl., *Brittonia* 38: 159. 1984. (Figures 62D–F, 63).

Type: FRENCH GUIANA. [Région des Emérillons] Sommet Tabulaire [Mount Itoupé, ca. 3°1'–5'N, 53°5'W], central zone, W slope, 600–700 m, ca. 40 km SE of Saül, 26 Aug. 1980 (fl), *G. Cremers 6460* (holotype P [ex CAY] [barcode P00076246]; isotypes CAY [ex P, 2 sheets, barcodes CAY024971 and CAY024972], VEN [Acc. No. 161727]).

**Notes:** Steyerl. (1984: 159), in the original publication of *Sipanea ovalifolia* var. *villosissima* Steyerl. stated that the holotype specimen of this variety was at CAY. However, as explained by Cremers (2001), in 1998 the holotypes of 31 taxa were transferred from CAY to P, and the corresponding isotypes were transferred from P to CAY. Therefore, the two isotype sheets at P (not reported in the original publication) of this variety are now at CAY, and the holotype specimen of this taxon is at P [barcode P00076246]. To confirm this, both isotype sheets at CAY have the label “*HERBARIUM MUSEUM PARISIENSIS*” and have the paper that at that time was used at P.

*Stems* spreading to ascendingly villous. *Leaves* with petioles 5–11 mm long, narrowly winged, villous; blades ovate to oblong-ovate, 2.2–3 × 1.2–1.7 cm, round, obtuse to acute at base, obtuse to acute at apex, lamina and veins villous above (hairs erect, 1.5–2.5 mm long), lamina and veins villous below (hairs erect, 1.3–2.5 mm long); secondary veins 5–6 on each side of midrib, ascending. *Corolla* 4.5–5.3 mm long, white; tube narrowly obconical, constricted at medial portion and slightly wider at mouth, 3–3.6 mm long; lobes ovate,

1.5–1.8 × 1.2 mm, obtuse to round at apex, glabrous on both sides.

**Distribution and ecology:** A variety only known from Mount Itoupé, central French Guiana (Figure 63). Growing on forest floor, in humid places, at 600–700 m altitude.

**Phenology:** Specimens with flowers and fruits were collected in August.

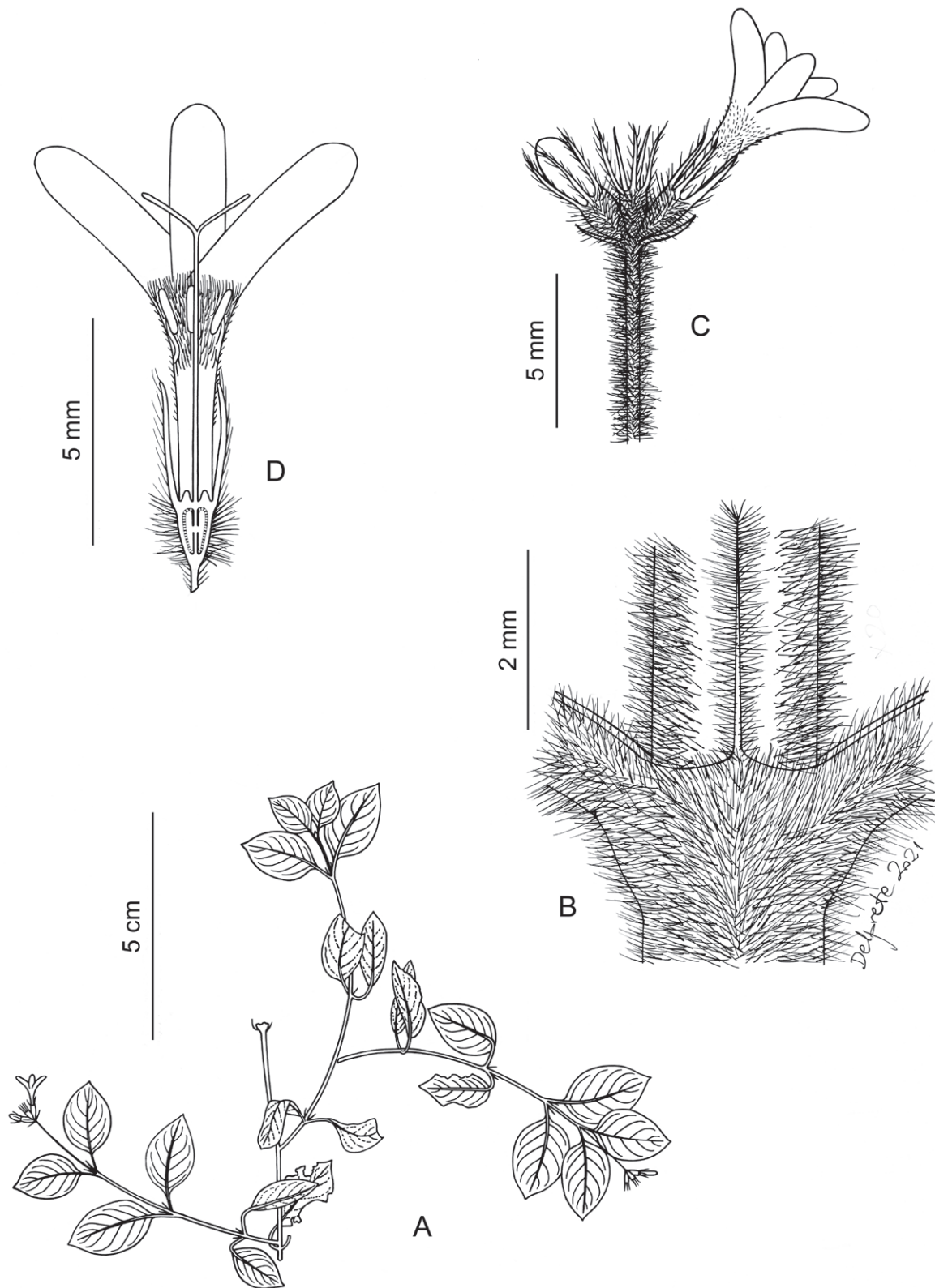
**Suggested conservation status: Near Threatened (NT).** This variety only known by the type specimens (*Cremers 6460*) was made in 1980 on the slopes of Sommet Tabulaire [or Mount Itoupé; ca. 3°5'N, 53°5'W], at 600–700 m altitude.

Mount Itoupé (or Sommet Tabulaire) is included within the French Guiana Amazonian Park (Parc Amazonien de Guyane). Scientific expeditions to this table mountain have been made in 2010, 2014, 2016 and 2017, and the pristine condition of its forests was confirmed. This variety has been photographed by Sébastien Sant (Parc Amazonien de Guyane) on 9 March 2017 during an expedition to Mount Itoupé, confirming its presence in this locality; unfortunately the plants photographed were not collected. Although there are apparently no immediate threats for this rare variety in such remote locality, the AOO is most likely extremely small, therefore it is here positioned in the Near Threatened (NT) category, following IUCN criteria (IUCN 2012, 2019).

8-12. *Sipanea setacea* Steyerl., *Ann. Missouri Bot. Gard.* 74: 114. 1987. (Figures 63–64).

Type: VENEZUELA. Bolivar: Dtto. Piar, Cerro Venado, 20 km E of Canaima, Cumbre Norte, “hierba escasa sobre rocas húmedas”, 6°17'N, 62°41'W, 1300 m, 31 Aug. 1983 (fl), *O. Huber, G.T. Prance & C. Alarcón 8246* (holotype NY [barcode 00133327]; isotype VEN not traced). [Section *Virecta*].

*Herbs*, creeping, growing on wet rocks, rooting at basal nodes and internodes; stems thin, 0.5 mm diam., terete or slightly quadrangular, green, densely spreading or loosely antrorse-pubescent (hairs 0.2 mm long). *Stipules* adnate to the petioles, truncate, with a central seta or two unequal setae, 2–3 × 0.1 mm, densely pilosulous; internal side not observed. *Leaves* petiolate; petioles 3.5–4.5 mm long, densely spreading or loosely antrorse-pubescent; blades ovate to elliptic-ovate, 1.2–2 × 0.9–1.2 cm, obtuse to subacute at base, acute at apex,



**Figure 64.** *Sipanea setacea*. A. Habit. B. Node with setaceous stipule and petioles. C. Inflorescence with a flower in anthesis. D. Dissected long-styled flowers, with stamens inserted at distal portion of corolla tube, and exserted style. A–D: drawn from *Huber et al.* 8245 (NY, holotype). Illustration by Piero Delprete.



membranaceous, reddish-brown when dry (specimen pressed with alcohol 30–50%), densely subappressed-pubescent on both sides (hairs 0.2–0.3 mm long); secondary veins 5–6 on each side of midrib, ascending, weakly evident above, prominulous below. *Inflorescences* terminal, pedunculate, rachis filiform, almost capilliform, with a terminal 3-flowered cyme, peduncle 1–1.7 cm long, densely spreading or loosely antrorse-pubescent; terminal cyme subtended by two bracts, these linear-acicular, 2.2–2.4 × 0.1 mm [Steyermark (1987: 114) wrote “2.2 cm long × 0.1 cm wide”], margins setose-ciliate (hairs 0.3–0.5 mm long). *Flowers* most likely distylous, 5-merous, subsessile; pedicels to 0.5 mm long. *Hypanthium* narrowly obovoid, 1.5 × 0.8 mm, acute at base, round at apex, densely villosulous with spreading white, non-tuberculate hairs 0.4–0.5 mm long. *Calyx* lobes subequal, subulate or subsetaceous, 2.5–2.6 × 0.3–0.4 mm, densely antrorse-pubescent (hairs 0.3–0.4 mm long); with 1 colleter in each calycine sinus, setiform, 0.15–0.2 mm long. *Corolla* infundibuliform, 7.5 mm long, “purple” (“corola morada” fide Huber *et al.* 8246), with a ring of white-sericeous hairs at mouth; tube narrowly obconical, 4 mm long, 0.7 mm wide at base, 1.5 mm wide at mouth, sparsely puberulent outside, shortly pubescent near the base of the stamens inside; lobes narrowly oblong, 3.5 × 1–1.5 mm, obtuse apex, moderately pilose outside. *Long-styled flowers*: stamens inserted at medio-distal portion of tube, filaments 0.6 mm long; anthers narrowly oblong, 1 mm long; style exerted beyond corolla mouth, glabrous, style branches linear, 1.5 mm long. *Short-styled flowers* unknown. *Infructescences, capsules and seeds* unknown.

**Notes:** Only the holotype specimen of *Sipanea setacea* Steyererm. was studied for this species. It only has one flower in anthesis, which was not dissected. Therefore, it is impossible to confirm if this species is heterostylous. In the sole flower observed, the style is exerted beyond the corolla mouth, and the included stamens were observed through the transparent dried corolla. Therefore, it is assumed that this is the long-styled form of this species.

Steyermark (1987: 115) wrote that the bracts subtending the inflorescence of *S. setacea* are “subulate, acuminate, 2.2 cm long, 0.1 cm wide”; however, these bracts are linear-acicular, 2.2–2.4 × 0.1 mm.

Steyermark (1987: 115) about *S. setacea* stated: “In its setaceous stipules and pubescent exterior of the corolla lobes, this species differs from other members of sect. *Virecta* subsect. *Cryptotracha*, but resembles them in habit, slender stem, and small leaves. From *S. ovalifo-*

*lia* Bremekamp [...], it differs in the shorter peduncle and petioles, longer corolla and corolla lobes, 3-flowered inflorescence on a shorter peduncle, shorter, non-tuberculate hairs of the hypanthium, narrower leaves, and purple instead of white corollas. From *S. micrantha* Sandw. it may be distinguished by the spreading pubescence of stems and peduncles, broader ovate leaves with pubescent upper surface, loosely pubescent calyx lobes, and 3-flowered inflorescence. From *S. gleasonii* Steyererm. it is differentiated by the subsessile flowers, shorter petiole, calyx lobes, hypanthium, and corolla tube, smaller leaf blades, shorter foliar pubescence, and non-tuberculate hairs of the hypanthium. Finally, from *S. cowanii* Steyererm. it differs in the densely spreading hairs of the hypanthium, the shorter corolla and calyx lobes, and the 3-flowered inflorescence.” Steyermark’s *Sipanea* sect. *Sipanea* subsect. *Cryptotracha* Steyererm. is here included in *Sipanea* sect. *Virecta*, as here delimited. Although Steyermark’s subsection is not maintained, I concur with his comparisons of similar species, and *S. setacea* is here confirmed to be a distinct species.

**Distribution and ecology:** Only known from the type, collected in open scrub vegetation on tepui summit of Cerro Venado, ca. 6°17’N, 62°41’W, Bolivar state, Venezuela, at 1300 m altitude (Figure 63).

**Phenology:** The sole gathering, with flowers in anthesis, and without fruits, was collected in August.

**Suggested conservation status: Vulnerable (VU).** A species only known by the type specimen, collected in 1983 on Cerro Venado, ca. 6°17’N, 62°41’W, Bolivar state, Venezuela. Cerro Venado is located at ca. 20 km east of the town of Canaima, on the other side of Carrao River, and is included within the Canaima National Park. The specimen label reports that it was a rare plant growing on humid rocks of the North Peak, at 1300 m altitude. This species might be undercollected because of its diminutive size. The population size is unknown, as it was not indicated in the specimen label and no recent field work has been made in this locality. Because of its rarity, it is treated as Vulnerable (VU) following IUCN criteria (IUCN 2012, 2019), pending future field studies to confirm the size and health of its population(s).

**8C. *Sipanea* section *Nudae* (Steyererm.) Delprete, sect. et stat. nov.**

*Sipanea* sect. *Sipanea* subsect. *Nudae* Steyererm., Mem. New York Bot. Gard. 17: 261, 268. 1967

Type: *S. wilson-brownei* Cowan

Herbs or subshrubs, erect or decumbent; corolla mouth glabrous or with sparse white hairs.

8-13. *Sipanea ayangannensis* Steyerl., Mem. New York Bot. Gard. 17: 269. 1967. (Figures 63, 65).

Type: GUYANA. Upper Mazaruni River Basin, Mount Ayanganna [ca. 5°24'N, 59°57'W], on shoulder of E flank, about Thompson Camp, 1418 m, "Small herb; leaves medium green, papery; calyx green, corolla tube red, limb pinkish-white, slightly irregular; frequent, dense scrub and low forest (8–10 m)", 12 Aug. 1960 (fl), S.S. Tillett, C.L. Tillett & R. Boyan 45114 (holotype NY [barcode 00133308]). [Section *Nudae*].

*Herbs*, decumbent, rooting at basal nodes; young branches slightly geniculate at least at basal nodes, densely antrorse-strigose (hairs yellowish-beige). *Stipules* adnate to the petioles, subulate, base triangular and medio-distal portion narrowly triangular to linear, 2.5–4 × 1.5–2 mm, densely strigillose outside, margins glabrous or sparsely antrorse-strigillose; internal side and presence of colleters not observed. *Leaves* often unequal in size on the same node, petiolate; petioles 4–6 mm long, densely antrorse-strigose (hairs yellowish-beige); blades lanceolate-elliptic, 4–5.5 × 1.7–2.2 cm, acute to decurrent at base, acute at apex, chartaceous, brown above and olive-green below when dry, lamina densely appressed-strigose above, sparsely strigose below, midrib and secondary veins strigose; secondary veins 5–7 on each side of midrib, slightly impressed above, prominent below. *Inflorescences* cymose, dichotomous, 5–7-flowered, condensed at initial stage of anthesis, 4–6 cm long (including peduncle and flowers in anthesis), expanding during and after anthesis; peduncle 1.3–2 cm long during anthesis and 2.7 cm long after anthesis, densely griseous-strigose; lateral branches 0.5–1 cm long, 3–5-flowered; bracts subtending branchlets narrowly lanceolate to linear, 4–6 × 0.3–0.5 mm, sparsely antrorse-strigose outside, margins antrorse-strigose; bracteoles opposing each flower narrowly lanceolate to linear-lanceolate, 3.5–7 × 0.5–0.7 mm, sparsely antrorse-strigose outside, margins antrorse-strigose. *Flowers* most likely distylous, 5-merous; the flower at base between the two branches with pedicels 0.7 mm long, densely antrorse-strigose; the other flowers sessile to subsessile. *Hypanthium* broadly turbinate to obovoid, 1.5–2 × 1.3–1.5 mm, acute to obtuse at base, round at apex, not tuberculate, densely

antrorse-strigose; hairs 0.7–1 mm long, not tuberculate. *Calyx* lobes subequal, oblong-lanceolate to oblanceolate, unequal, 5.5–7 × 0.7–1 mm, evidently veined, glabrous, midvein and margins strigose-ciliate; with 1 colleter in each calycine sinus, conical, obtuse at apex, 0.2 mm long. *Corolla* hypocrateriform, 24.9 mm long, corolla tube red, lobes pinkish-white, with a glabrous white ring at mouth; tube subcylindrical, gradually wider towards the mouth, 14.5 mm long, 0.6 mm wide at base, 1.5 mm wide at mouth, hirsutulous at medio-basal portion and densely griseous-strigose at distal portion outside, glabrous at basal 2.5 mm, villosulous above, puberulent at anther portion; lobes elliptic-oblong to obovate-oblong, 10.4 × 4.3 mm, round at apex, margins glabrous or sparsely ciliate. *Long-styled flowers* unknown. *Short-styled flowers* (Tillett et al. 45114): stamens inserted at 5.5–6.5 mm below corolla mouth; filaments 3 mm long, glabrous; anthers linear, 2 × 0.2–0.3 mm; style included, 6.5 mm long, glabrous; branches narrowly lanceolate, ca. 1 mm long, acute at apex. *Infructescences*, *capsules* and *seeds* unknown.

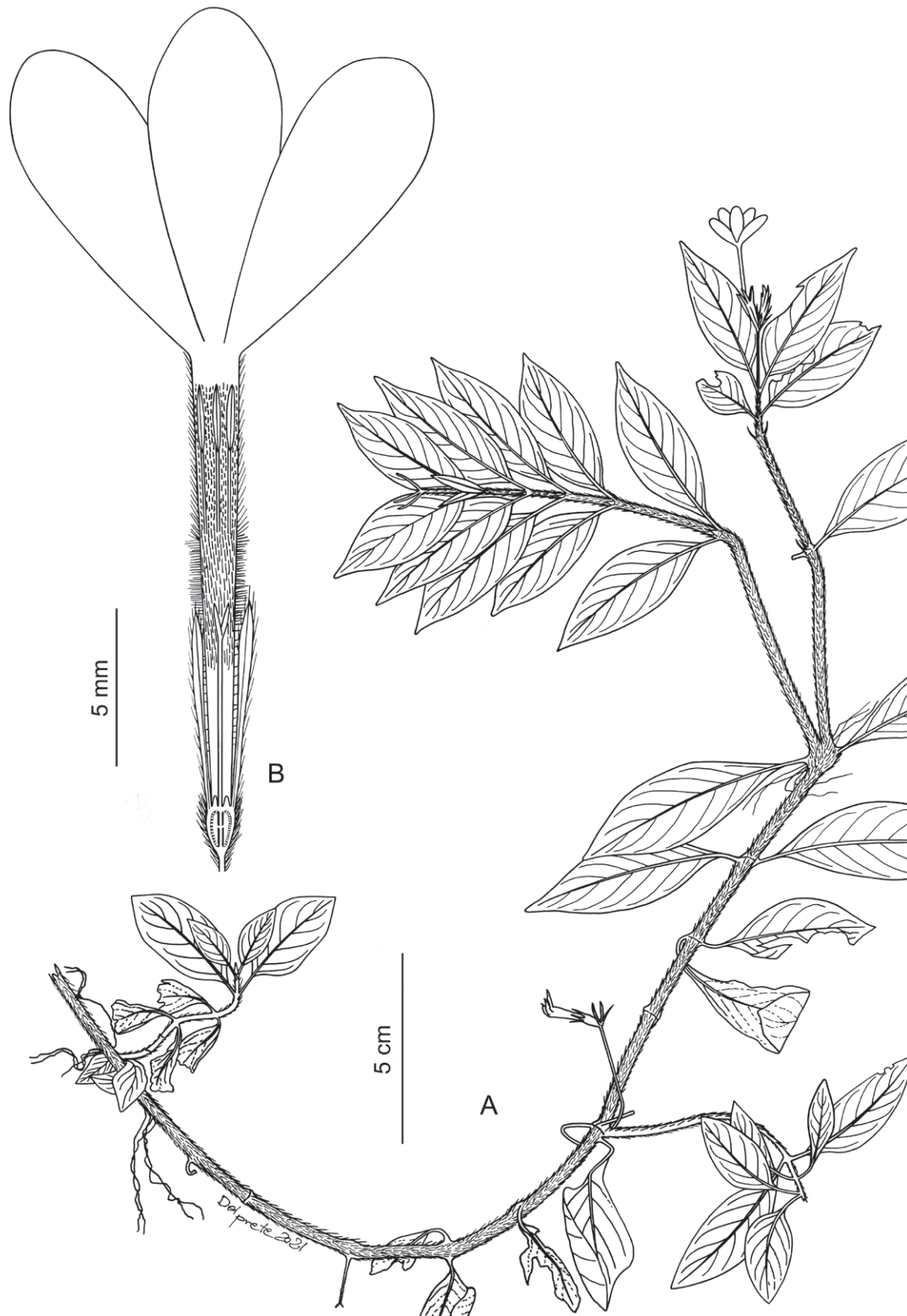
**Notes:** Steyerl (1967: 269) in the original description of *Sipanea ayangannensis* Steyerl. wrote that the corolla tube is 18 mm long and the corolla lobes are 9–9.5 × 4.5–4.7 mm. However, the sole corolla in anthesis of the holotype specimen has a tube 14.5 mm long and lobes 10.4 × 4.3 mm.

Steyerl (1967: 269–270) also wrote: "This species is distinct from *S. stahelii* and *S. wilson-brownei* in the larger corolla tube, prominently ciliate corolla-lobes, prominently strigose midrib of the calyx-lobes, externally hirsutulous spreading hairs of the corolla-tube throughout most its length, and obsolete calycine squamellae [i.e., colleters] or these not manifest." I concur with these observations.

**Distribution and ecology:** Only known from the type, collected on Mount Ayanganna, Guyana (Figure 63); growing in dense scrub and low forest, at 1418 m altitude.

**Phenology:** The sole flowering collection was made in August.

**Suggested conservation status: Critically Endangered (CR).** A species only known by the type, collected in 1960 on the shoulder of the East flank of Mount Ayanganna, Guyana, at 1418 m altitude. Mount Ayanganna is part of the Pakaraima Mountain range, and is sandstone tepui reaching 2041 m altitude. One flank of the mountain is slanted, while the other flank has sev-



**Figure 65.** *Sipanea ayangannensis*. A. Habit. B. Dissected short-styled flower, with stamens inserted at distal portion of corolla tube, and included style. A–B: drawn from Tillett *et al.* 45114 (NY, holotype). Illustration by Piero Delprete.

eral escarpments, these being an alternation of plateaux and steep slopes. Mount Ayanganna is also considered a national landmark, and each year, on 23 February, members of the Guyana Defense Force climb to its top and hoist the national flag to celebrate the anniversary of Guyana as a republic. It is also recognized as a center of biodiversity, with a high number of endemic frogs and plant species, many of which have recently been described (e.g., MacCulloch & Lathrop 2005; Cobb et al. 2007; Skog & Clark 2015; Wurdack & Michelangeli 2019). A description of the ascension, observations about the local vegetation, and endemic species, as well as botanical collections made by Bruce Hoffman and collaborators in October–November 1992 is available in Alexander et al. (2014).

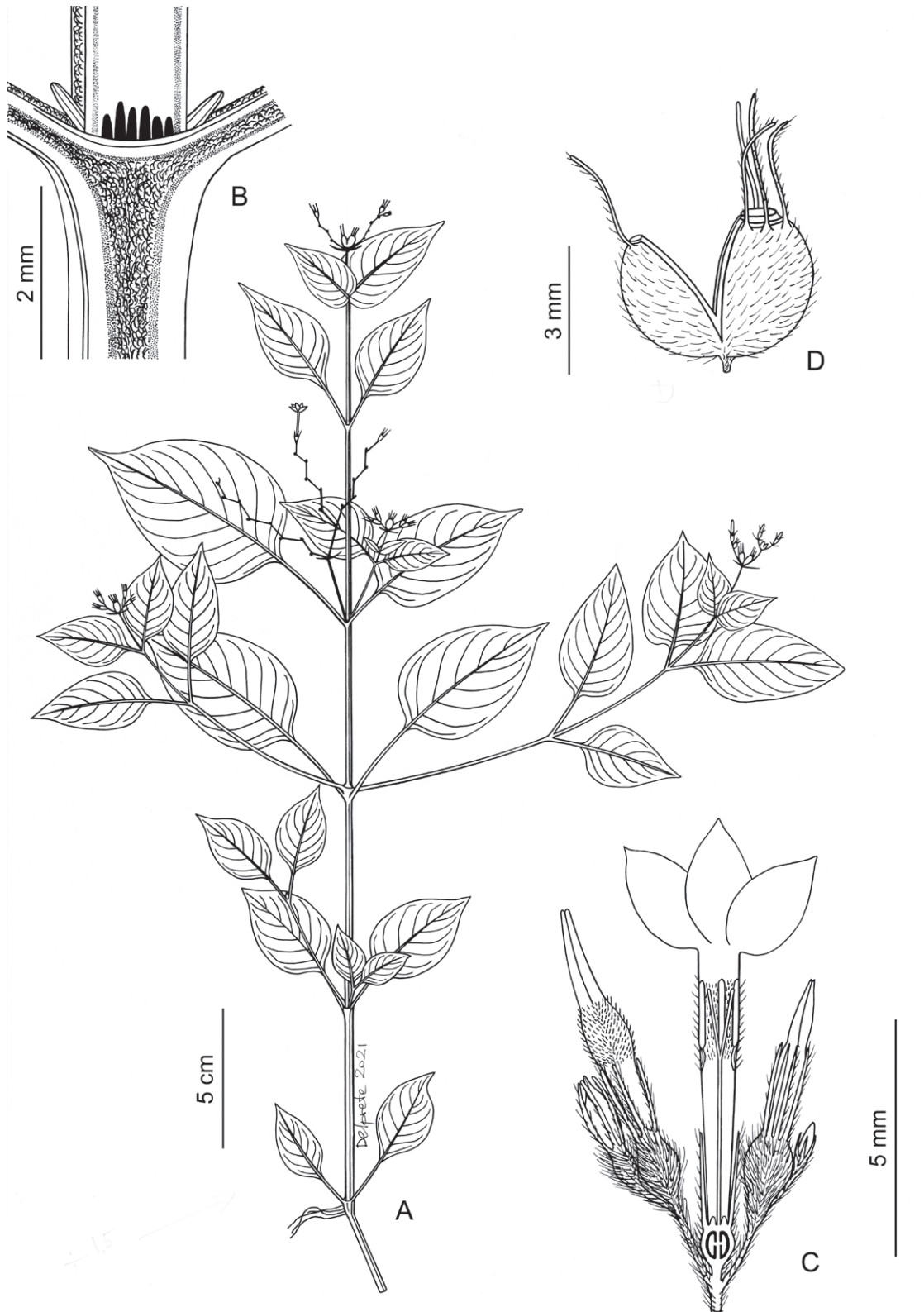
The label of the type specimen reports this species as a small herb, locally frequent, growing in dense scrub and low forest (8–10 m tall). The population size was not reported. Although several botanical expeditions have been made on Mount Ayanganna, in 1955 (e.g., *Maguire et al.* 40637), 1987 (e.g. *Pipoly et al.* 11177), 1992 (e.g., *Henkel & Hoffman* 154), and 2001 (e.g., *Clarke et al.* 9490), this species remains known only from the type collection. The Pakaraima Mountain range is known to be an area of indiscriminate gold and diamond mining, and Mount Ayanganna is not included in a protected area. Therefore, because of its rarity, and the potential of gold mining exploitation in the area, this species is treated as Critically Endangered (CR) following IUCN criteria (IUCN 2012, 2019; area of occurrence < 10 km<sup>2</sup>, and a single known locality).

8-14. *Sipanea prancei* Steyerl., *Brittonia* 33: 400. 1981. (Figures 63, 66).

Type: BRAZIL. Roraima: [Yanomami Indigenous Territory], Indian trail from Surucucu to Uaicá, near Maitá Indian Village, 3°20'N, 63°24'W, terra firme forest, 14 Feb. 1971 (fl, fr), *G.T. Prance, W.C. Steward, F.P. Harter, J.F. Ramos, W.S. Pinheiro & O.P. Monteiro* 10528 (holotype NY [barcode 00133316]; isotypes INPA [Acc. No. 28860], MG [Acc. No. 42032], MO [Acc. No. 2988539], R [Acc. N. 180079], S [Acc. No. 10-28005], U [1574627], US [Acc. No. 2801068], VEN [Acc. No. 134008, 2 sheets]). [Section *Nudae*] (Figures 63, 66).

*Herbs* or *subshrubs* (basal internodes woody), to 50 cm tall, erect, sparsely branched; stems with pubescence in two lines on the internal margins of two opposite sides, antrorsely appressed-pubescent, the other

two sides glabrous. *Stipules* reduced to a line between the petioles, with 5–7 colleters intermixed with a few hairs. *Leaves* petiolate; petioles 0.3–3.7 cm long, antrorse appressed-strigose, often with curved hairs; blades ovate to elliptic, 2–7.5 × 1–4.5 cm, acute-decurrent to obtuse and shortly decurrent at base, acute or acuminate at apex, membranaceous, drying olive-green, sparsely strigose above and below, midrib and secondary veins densely to sparsely antrorse-strigose above and below (hairs 0.7–1 mm long); secondary veins 5–7 each side. *Inflorescences* laxly cymose during anthesis, dichomously branched, (3–)5–32-flowered, (1.5–)3–6 cm long when fully expanded; rachis thin, filiform, with pubescence in two lines on two opposite sides, antrorse appressed pubescent, the other two sides glabrous; peduncles 1–3 cm long; with two lateral branches dichotomously divided into two terminal branchlets; ultimate branchlets scorpioid when fully expanded, 3–8-flowered; or rarely the whole inflorescence extremely reduced, unbranched, (2–)5–8-flowered (on the same plant of the other dichomously-branched inflorescences), or with two small 1–2(–3)-flowered branches, inflorescences 3–5-flowered; bracteoles opposite to the insertion of each flower, linear to narrowly lanceolate, 1.7–4 × 0.2–0.4 mm, glabrous or sparsely appressed-pubescent. *Flowers* distyly not observed (see Morphological Observations, below), 5-merous, sessile. *Hypanthium* obovoid to subglobose, 0.7–0.9 × 0.5–0.7 mm, densely antrorse-pubescent; hairs inflate at base, not tuberculate. *Calyx* lobes subequal, linear to setaceous, 2.2–3 × 0.1–0.2 mm, margins sparsely appressed-ciliate; with 1 colleter in each calycine sinus, narrowly conical, acute at apex, 0.2 mm long. *Corolla* hypocrateriform, 8.5–11 mm long, tube pale green to greenish-white and lobes pink, with a glabrous white ring at mouth; tube narrowly cylindrical, slightly wider at median portion, at the area with anthers, 5.7–7.5 mm long, 0.5–0.7 mm wide at base, 1–1.2 mm at medio-distal portion, the anther position, and at mouth, sparsely pilose at distal portion and glabrous below outside, antrorse pubescent at medio-distal portion inside, with a thickened, glandular ring at mouth; lobes ovate, 2.7–3.5 × 1.4–1.5 mm, obtuse to acute at apex, glabrous outside, papillose inside. *Stamens* inserted 3.7–4.3 mm above the base of corolla tube [Steyerl (1981: 400) wrote “at 6 mm from base”]; filaments 0.5 mm long; anthers linear, 1.2–1.5 × 0.1–0.2 mm. *Style* not completely elongated, included, filiform, 4–4.5 mm long; style branches still appressed against each other, linear, 1.5 mm long. *Infructescences* laxly cymodichomously branched, (3–)5–32-fruited, rachis filiform, similar to or slightly larger than inflorescence. *Capsules* globose, 2.5–3.5 mm diam., crustaceous, sparsely antrorse-strigose; hairs



**Figure 66.** *Sipanea prancei*. A. Habit. B. Node with stipule reduced to a line between petioles, exserted colleters, basal portion of petioles, and axillary vegetative buds. C. Terminal portion of inflorescence, with a flower in anthesis (dissected) and flower buds. D. Dehiscent capsule. A, B, D: drawn from *Jansen-Jacobs et al. 6010 (CAY)*. C: drawn from *Daniels & Jonker 906 (U)*. Illustration by Piero Delprete.

0.9–1 mm long, inflated at base, not tuberculate. *Seeds* irregularly polyhedral with smooth angles, 0.4–0.6 mm in diam.; testa foveolate.

**Morphological observations:** Several collections of *Sipanea prancei* were studied; however, most of them only have one or a few flowers in anthesis. Because of this, the flowers of only three collections were analyzed. In the specimens studied, the corolla tubes are 6.5–7.5 mm long, and the stamens are inserted at about the middle of the corolla tube (1/2 to 3/5 from base, i.e., 3.7–4 mm from the base). In the flowers analyzed, the style is slightly longer than the points of insertion of the stamens, with the style branches still appressed against each other or opened. With the material at hand it is impossible to confirm the heterostyly of this species. Additional specimens with flowers in anthesis are wanted to determine the possible distylous condition of this species. The three specimens analyzed provided the following proportions:

**Suriname:** *Daniels & Jonker 906* (U): Corolla tube 7.5 mm long; stamens inserted at 4 mm from the base of the corolla tube (3/5 of corolla tube); style 4.5 mm long, branches opened.

**Guyana:** *Jansen-Jacobs et al. 6010* (CAY, U; two flowers analyzed): Corolla tube 6.5 mm long; stamens inserted at 3.8 mm from the base of the corolla tube (3/5 of corolla tube); style 4.5 mm long, branches not opened.

**Guyana:** *Kennedy & Ek 4759* (US): Corolla tube 7.3 mm long; stamens inserted at 3.7 mm from the base of the corolla tube (1/2 of corolla tube); style 4 mm long, branches not opened.

**Notes:** Steyermark (1981: 400) wrote that *Sipanea prancei* Steyermark. “is most closely related to *S. stahelii* Brem., from which it differs in the absence of conspicuously enlarged tuberculate-based hairs on the fruiting hypanthium, the longer hairs of the hypanthium, the conspicuously appressed pilose midrib and nerves on both upper and lower leaf surfaces, the elongate ciliate hairs on the leaf margins, and the shorter corollas. From *S. gleasonii* Steyermark. and *S. ovalifolia* Brem. it differs in the absence of the white villous pubescence within the orifice of the corolla tube, and the different habit, inflorescence, and leaf blades.” I concur with Steyermark’s statements.

*Sipanea prancei* and *S. stahelii* Bremek. are also similar to *Neobertiera gracilis*, because of the dichotomously branching inflorescence with a thin, filiform rachis, and globose fruits. However, *Neobertiera* has indehiscent crustaceous fruits falling off as dispersal units, whereas *Sipanea* has persistent loculicidal capsules with wind-dispersed seeds.

**Distribution and ecology:** Known by several collections from Guyana and Suriname, and the type specimen collected in the nearby Brazilian state of Roraima (Figure 63). Found in forests on granitic rocks, forested slopes, along trails in lowland forests, and secondary vegetation, at 75–500 m altitude.

**Phenology:** Specimens with flowers and fruits were collected in February, August and September.

**Suggested conservation status: Vulnerable (VU).** Known from several collections from remote localities in Suriname and Guyana, and one in the contiguous Brazilian state of Roraima. In Brazil it is only known by the type collection made in 1971 in the northern portion of Roraima, along the indigenous trail from Surucucu to Uaicá villages, near the Maitá Indigenous Village (ca. 3°20’N, 63°24’W), in *terra firme* forest. This locality is now within Yanomami Indigenous Territory.

In Suriname it is known from two collections made in 1959 on the Emmaketen Mountains, ca. 4°5’N, 56°12’W, at 325 and 350 m altitude.

In Guyana it is known from eight collections from five different localities. The first collection was made in 1992 in the Upper Demerara-Berbice Region, Mabura, DTL Concession, West Pibiri Compartment, Pibiri Creek and vicinity, 5°20’N, 58°30’W, 0–75 m, in secondary vegetation. Two collections were made in the Potaro-Siparuni Region, one in 1994 on the Pakaraima Mountains, Upper Ireng River, Julong Falls, and the other in 1997 near the Iwokrama Mountains, at 60 m elevation, inside the Iwokrama Forest Reserve (ca. 4–5°N, 58–59°W). Three collections were made in the Upper Takutu-Upper Essequibo Region in 1999 on the Wassarai Mountains, 1°35’N, 59°14’W, at 215, 300 and 715 m altitude. The most recent collection was made on 20 September 1999 along the Rewa River, Spider Mountain, Upper Essequibo River, 3°08’N, 58°32’W, at 400–500 m, in an open spot within forest growing on rock.

The only collection of this species from a preserved area was made in 1997 at the base of the Iwokrama Mountains, inside the Iwokrama Forest Reserve, Guyana. No recent field observation has been made to assess the conservation status of the localities where it has been collected in Brazil, Suriname and Guyana. Using all the collection localities, the extent of occurrence (EOO) of this species is calculated to be of ca. 151,000 km<sup>2</sup>. Several collection sites in Guyana and Suriname within the EOO are influenced by indiscriminate, often illegal, gold hunting activities. Because the localities where it has been collected are threatened by these human activities,

it is here treated as Vulnerable (VU), following IUCN criteria (IUCN 2012, 2019).

**Specimens examined: SURINAME:** Emmaketen Mountains [Emma Range, ca. 4°5′–13′N, 56°11′–12′W], on bank of waterfall 1 km E of Main Camp, 350 m, 1 Sep. 1959 (fl, fr), A.G.H. Daniéls & F.P. Jonker 906 (U); Emmaketen Mountains, on top of a large granite boulder, trail upstream of Main Camp, 325 m, 7 Sep. 1959 (fl, fr), A.G.H. Daniéls & F.P. Jonker 946 (U).

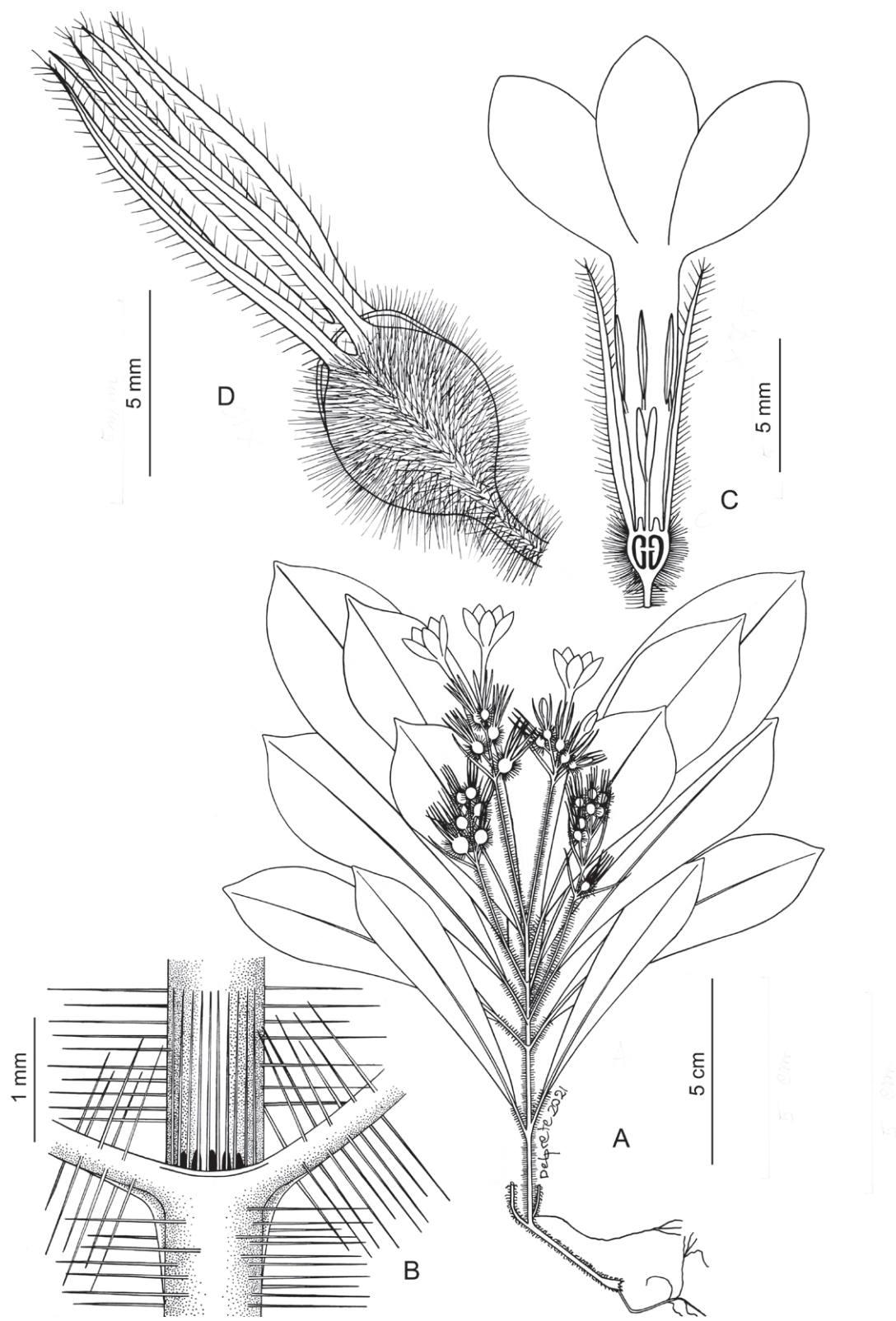
**GUYANA:** Potaro-Siparuni Region, Iwokrama Rainforest Reserve, Iwokrama Mountains, 4.5 km transect from Karupurani-Annai Rd., to camp, dense forest on brown sand, with *Mora*, *Carapa* and *Socratea*, 4°20′15″N, 58°48′37″W, 60 m, 27 Mar. 1997 (fl, fr), D. Clarke et al. 4350 (MO, NY, US); Upper Takutu-Upper Essequibo Region, Wassarai Mountains, 0.2–0.5 km N of camp at base of mountains, semi-disturbed forest at base of escarpment on brown sandy clay and boulders, with *Euterpe*, *Jacaratia* and *Cecropia*, 1°35′57″N, 59°14′17″W, 300 m, 27 Aug. 1999 (fl, fr), D. Clarke et al. 7992 (MO, NY, US); Upper Takutu-Upper Essequibo Region, Wassarai Mountains, summit of unnamed peak, 8 km S of S. Kassikaityu River, dense forest on reddish sandy clay, with *Couratari*, *Pouteria* and *Inga*, 1°34′57″N, 59°14′17″W, 715 m, 31 Aug. 1999 (fl, fr), D. Clarke et al. 8092 (MO, NY, US); Upper Takutu-Upper Essequibo Region, Wassarai Mountains, near camp, along creek at base of highest peak in Wassarai Mountains (1230 m), dense forest on brown sandy clay, with *Inga*, *Socratea* and *Cecropia*, 1°34′8″N, 59°14′18″W, 275 m, 17 Sep. 1999 (fl, fr), D. Clarke, R. Williams & C. Perry 8744 (MO, NY, US); Upper Essequibo River, Rewa River, Spider Mountain, forest on rock, open spot, 3°08′N, 58°32′W, 400–500 m, 20 Sep. 1999 (fl, fr), M.J. Jansen-Jacobs et al. 6010 (CAY, NY, P, U [2 sheets]); Upper Demerara-Berbice Region, Mabura, DTL Concession, West Pibiri Compartment, Pibiri Creek and vicinity, secondary vegetation, 5°20′N, 58°30′W, 0–75 m, 3 Nov. 1992 (fl, fr), H. Kennedy & R. Ek 4759 (U, US); Potaro-Siparuni Region, Pakaraima Mountains, Upper Ireng River, 15–20 km upriver from Cipo settlement, Julong Falls, creekside and falls spray zone, waterfall meadow, 5°0′N, 59°57′W, 60 m, 2 Nov. 1994 (fl, fr), P. Mutchnick et al. 361 (MO, US).

8-15. *Sipanea saxicola* J.H. Kirkbr., Brittonia 49: 362, fig. 3. 1997. (Figures 67–68).

Type: BRAZIL. Pará: Mun. Oriximiná, 15 km NW of Cachoeira Porteira, Rio Cachorro, Serra do Cachorro [ca. 0°58′S, 57°10′W], terra firme, afloramento rocho-

so, “saxicola, ciófila, crescendo nas grutas formadas por rochas de salitre, local seco; pecíolos avermelhados, folhas levemente discoloradas, inflorescência com brácteas verdes, calice verde, corola rósea, estames alvos, frutos imaturos verdes”, 150 m, 8 Jun. 1980 (fl, fr), G. Martinelli, C. Davidson & C.D.A. Mota 7074 (RB203259) (holotype RB [Acc. No. 203259, barcode 00543717]; isotypes BRIT [barcode 24069], INPA [Acc. No. 101666], MG [Acc. No. 101066], MO [barcode 2292872], NY [2 sheets, barcodes 00658722 and 1747355], RB [2 sheets; barcodes 00543717 and 00560065], SPF [SPF 00163000], UB [Acc. No. 61930, barcode UB0040404], US [barcode 00512891]). [Section *Nudae*].

*Herbs* 15–20 cm tall, terrestrial or epipetric, erect, with a central taproot; young branches terete, green, spreading erect-pubescent (hairs thin, 0.9–1.2 mm long). *Stipules* reduced to a line between the petioles or very shallowly transversally ovate, 0.5–3 mm tall, sometimes with a central seta 0.5–0.7 mm long, glabrous outside, glabrous inside, with 5–8 colleters inserted in a row just below the margin inside, 1–2.2 mm long; margins with long-pubescent hairs (ca. 1.5 mm long). *Leaves* petiolate; petioles 0.2–1.5 cm long, reddish when fresh, winged on one or both sides (extensions of decurrent blade), sparsely spreading erect-pubescent; blades narrowly obovate, 9–12 × 2.5–4.3 cm, acute to decurrent at base, acute to obtuse at apex, membranaceous, grass-green above and dull pale green below when fresh, olive-green above and below when dry, lamina sparsely spreading erect-pubescent throughout, margin erect-pubescent, hairs thin, erect-sericeous; secondary veins 8–9 on each side of midrib, weakly evident. *Inflorescences* terminal, modified dichasia, 8–20-flowered, 5–11 cm long, expanding after anthesis, rachis thin, almost capilliform during anthesis, slightly thicker at fruiting stage, peduncle terete, 3–7 cm long, sparsely pubescent, with 1–3 pairs of lateral branches; lateral branches 0.5–4 cm long during anthesis, increasing in length when fully expanded (fruiting stage), scorpioid, more evident when fully expanded, 3–9-flowered; bracts subtending branches narrowly elliptic, 3–9 × 0.6–1.1 mm, acute at apex, sparsely erect-pubescent (hairs thin, erect-sericeous, 0.9–1.2 mm long), ciliate-pubescent at margins; rarely inflorescences simple, unbranched, 3–4-flowered (e.g., *Ferreira 9718*); bracteoles opposing each flower linear-lanceolate, 3–6 × 0.5–0.7 mm, sparsely pubescent, midvein and margins ciliate-pubescent, (hairs thin, erect-sericeous). *Flowers* distylous, 4- or 5-merous, pedicellate; pedicels 1.5–3 mm long, terete, sparsely erect-pubescent (hairs thin, erect-sericeous). *Hypanthium* globose, 1–1.5



**Figure 67.** *Sipanea saxicola*. A. Habit. B. Node with stipule reduced to a line between petioles, exserted colleters, and basal portion of petioles (note long, erect trichomes). C. Dissected short-styled flower, with stamens inserted at median portion of corolla tube, and included short style. D. Dehiscent capsule with permanent calyx lobes. A–D: drawn from *Martinelli et al. 7074* (MG). Illustration by Piero Delprete.



× 1.5–2 mm, round at both ends, densely spreading erect-pubescent (hairs thin, 0.9–1.2 mm long). *Calyx* lobes subequal, green when fresh, very narrowly elliptic to almost linear, 7–10 × 0.6–0.8 mm, acute at apex, sparsely pubescent, margins spreading pubescent; with 1 colleter in each calycine sinus, linear, 0.1 mm long. *Corolla* hypocrateriform, 14–16.5 mm long, pink, with a glabrous white ring at mouth; tube narrowly cylindrical, gradually expanding towards the mouth, 9–10.5 mm long, 1–1.5 mm wide at base, 2.5–4 mm wide at mouth, lower half glabrous and upper half sparsely pubescent outside, glabrous inside; lobes obovate, 5–6 × 3–4 mm, obtuse at apex, glabrous throughout. *Long-styled flowers* unknown. *Short-styled flowers* (Martinelli et al. 7074; Coelho et al. 213): stamens inserted at 4–5 mm below corolla mouth, about the middle of the tube; filaments

0.3–0.5 mm long; anthers linear, 2.5–3 × 0.2 mm, round at base, acute at apex; style included, 3–5 mm long, glabrous; branches narrowly oblong-ovate, 2.5–3.5 mm long, acute at apex. *Infructescences* terminal, modified dichasia, 8–20-fruited, with 1–3 pairs of lateral branches, more expanded than the inflorescences, rachis capilliform or slightly thicker; lateral branches scorpioid, 3–9-fruited. *Capsules* globose to very broadly ellipsoid, 5.5–6 × 4–5.5 mm, round at base and at apex, crustaceous, erect-pubescent; hairs thin, sericeous, 0.9–1.2 mm long, pale green when young, turning pale brown-beige when dry. *Seeds* irregularly globose to subglobose, 0.35–0.4 mm in diam., testa reticulate-foveolate.

**Distribution and ecology:** Endemic to Serra do Cachorro, Municipality of Oriximiná, state of Pará, Bra-

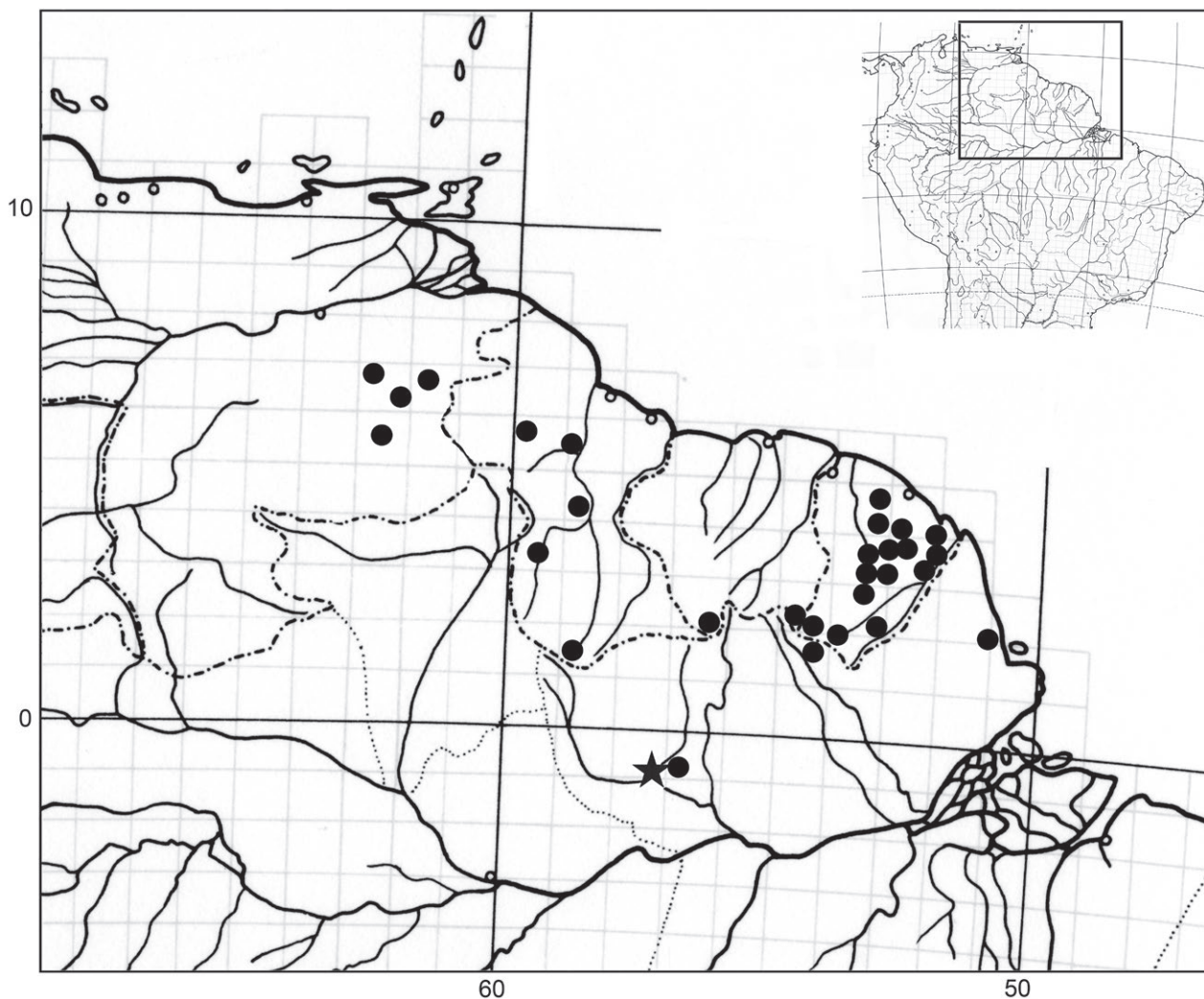


Figure 68. Distribution of *Sipanea saxicola* (star) and *S. wilson-brownei* (circles).

zilian Amazon (Figure 68). Growing on sandy soils, or sandy soil with saltpeter accumulation, at ca. 150 m altitude.

**Phenology:** It is common to find flowers and fruits on the same individual or even in the same inflorescence. Specimens were collected in May, June and November.

**Suggested conservation status: Critically Endangered (CR).** A species known by three collections near and at the base of the Serra do Cachorro, Municipality of Oriximiná, state of Pará, Brazil. The Serra do Cachorro is a tabular mountain at ca. 0°58'S, 57°10'W, and ca. 3 km from Rio Cachorro, a tributary of Rio Trombetas. This mountain has been visited by at least three botanical expeditions in 1980, 1985, and 1987. The Serra do Cachorro is now included inside the Faro State Forest, which is in the municipalities of Faro and Oriximiná. The label of the 1985 collection describes this species as a creeping herb growing on the sandy margins of the Rio Cachorro, which flows near the Serra do Cachorro. The label of the type specimen and that of the 1987 collection report it as an herb growing on sandy soil with saltpeter accumulation, at the base of Serra do Cachorro. The size of the populations was not reported on the specimen labels. Because of its rarity, the probably small populations, and its extent of occurrence (EOO) less than 100 km<sup>2</sup>, this species is treated as Critically Endangered (CR) following IUCN criteria (IUCN 2012, 2019).

**Specimens examined: BRAZIL. Pará:** Mun. Oriximiná, Serra do Cachorro [ca. 0°58'S, 57°10'W], Rio Cachorro, afluente da margem direita do Rio Trombetas, planta rasteira com flor lilás e botões florais esverdeados, 20 Nov. 1985 (fl, fr), L.S. Coelho *et al.* 213 (INPA, NY); Mun. Oriximiná, Serra do Cachorro, 3 km do Rio Cachorro, afluente do Rio Trombetas, encosta da serra, crescendo sobre arenito e salitre, 0°58'S, 57°10'W, 28 Nov. 1987 (fl, fr), C.A.C. Ferreira (as "C.A. Cid") 9718 (INPA, MG, MO, RB).

8-16. *Sipanea stahelii* Bremek., Recueil Trav. Bot. Néerl. 31: 258. 1934. (Figures 69–71).

Emend. Steyerl., Mem. New York Bot. Gard. 17: 268–269. 1967.

Type: SURINAME. Wilhelmina Range ["Wilhelminageberte"], 20 Jun. 1926, G. Stahel 7168 (**lectotype**

U [barcode 0006313], **here designated**; isolectotypes U [3 sheets, barcodes U 006314, U 006315, U 0006316]. [Section *Nudae*].

*Herbs* or *subshrubs* (basal internodes woody), 0.25–4 m tall, unbranched or sparsely branched, erect or decumbent, sometimes basal internodes prostrate, rooting at basal nodes; stems terete, reddish, terminal internodes slightly quadrangular, sparsely antrorsely-appressed sericeous-pubescent. *Stipules* adnate to the petioles, broadly to shallowly triangular at base, narrowly triangular to almost linear distally, 3.5–4 × 1.5–2 mm, acuminate, sparsely appressed sericeous-pubescent outside, sparsely pubescent, with 6–9 colleters in a row just below the margin or concentrated just below the base of the central lobe inside; margins pubescent. *Leaves* of the same node often unequal, petiolate; petioles 0.7–3 cm long, sparsely antrorsely-appressed sericeous-pubescent; blades ovate, elliptic to oblong-elliptic, 3.5–9 × 1.2–4.7 cm, obtuse and shortly decurrent at base, acute to acuminate at apex, chartaceous or rarely membranaceous, dark green above and pale green below when fresh, drying reddish-brown above and pale brown to olive green below, lamina glabrous or very sparsely pubescent above, sparsely pubescent below, midrib and secondary veins glabrous or sparsely to densely antrorse-pubescent above, sparsely to densely antrorse-pubescent, red to reddish, slightly prominent below; secondary veins 6–10 each side. *Inflorescences* laxly cymose during anthesis, dichomously branched, (13–)16–48-flowered, 4.5–13 cm long when fully expanded, with a pair of lateral branches dichotomously divided into two terminal branchlets (for a total of four terminal branchlets), rarely with two pairs of lateral branches dichotomously divided for a total of 8 terminal branchlets; rachis filiform; ultimate branchlets scorpioid when fully expanded, 4–8-flowered; peduncles 1.8–6.5 cm long; basal branches subtended by bracts narrowly lanceolate, 2.5–6 × 0.3–2.5 mm, or subtended by two leaf-like bracts (i.e., pherophylls), elliptic, up to 4 × 2 cm; rachis filiform, uniformly sparsely antrorse appressed pubescent; bracteoles opposite to insertion of each flower, linear to acicular, 0.8–2.5 × 0.1–0.3 mm, sparsely appressed-pubescent. *Flowers* distylous, 5-merous, subsessile to shortly pedicellate; pedicels 0.3–1.2 mm long, sparsely to densely pubescent. *Hypanthium* subglobose, 0.7–1.1 × 0.8–0.9 mm, densely antrorse-pubescent; hairs basally tuberculate. *Calyx* lobes subequal or unequal, linear to acicular, 1.5–3 × 0.2–0.5 mm, acuminate, glabrous, margins sparsely appressed-ciliate; with 1 colleter in each calycine sinus, conical or linear, obtuse at apex, 0.2–0.3 mm long. *Corolla* hypocrateriform, 15–20 mm long, tube pale

green to greenish-white, lobes pink to lavender, with a thickened glabrous white ring at mouth; tube narrowly cylindrical, gradually wider towards the mouth, 10.5–12 mm long, 0.6–0.8 mm wide at base, 1.2–1.5 mm wide at mouth, sparsely pubescent at medio-distal portion and glabrous below outside, basal portion glabrous and puberulent at anthers position inside; lobes elliptic, oblong-elliptic to oblong-obovate, 4.5–8 × 1.8–3 mm, obtuse to subacute at apex, glabrous outside, papillose inside. *Long-styled flowers* (Schultz & Wessels Boer LBB 10223 and Florschütz & Maas 3116): stamens inserted at 2–3 mm from base of corolla tube; filaments 0.5–1 mm long; anthers linear, 1.2–2 × 0.1–0.2 mm; style about the same length or slightly longer than the corolla tube, 11–12.5 mm long, glabrous; style branches linear to filiform, 1.5–2 mm long, acuminate at apex, densely papillose when receptive. *Short-styled flowers* (Maguire 24314): stamens inserted at distal portion of corolla, at 4–4.5 mm below corolla mouth; filaments ca. 1 mm long; anthers linear, 1.8–2 × 0.2 mm, obtuse at both ends; style much shorter than corolla tube, 5–5.5 mm long, glabrous; style branches linear, 1.4 mm long, densely papillose when receptive. *Infructescences* laxly cymose, dichomously branched, 16–48-fruited, with a pair of lateral branches dichotomously divided into 2 terminal branchlets for a total of 4 terminal branchlets, or with 2 pairs of lateral branches dichotomously divided for a total of 8 terminal branchlets; ultimate branchlets scorpioid when fully expanded, 4–8-fruited. *Capsules* apically loculicidally dehiscent at full maturity, globose, 3.7–4.5 × 3.5–4 mm, crustaceous, antrorse-pubescent; hairs basally tuberculate, more evident in fresh or rehydrated specimens, 0.4–0.6 mm long, basal tubercles conical, 0.2–0.3 mm long. *Seeds* irregularly polyhedral, subcompressed, with smooth angles, 0.6–0.9 mm in diam.; testa foveolate-reticulate.

**Notes:** Bremekamp (1934b: 258) along with the protologue of *Sipanea stahelii* Bremek. cited the gathering “Wilhelmina Range, Stahel 7168” without citing the herbarium of deposit. At U, where he worked, there is a type folder with four sheets of *Stahel 7168*, each sheet has a different label, and these specimens are not consecutively numbered. According Art. 8.3 of the *Code* (Turland et al. 2018) “A specimen may be mounted as more than one preparation, as long as the parts are clearly

labelled as being part of that same specimen, or bear a single, original label in common. Multiple preparations from a single gathering that are not clearly labelled as being part of a single specimen are duplicates, irrespective of whether the source was one individual or more than one.” Therefore, these four sheets are duplicate specimens, and one of them should be designated lectotype. The specimen with barcode 0006313 has Stahel’s original field label “510, 7168, 20 VI 26” and was annotated as holotype by Steyermark in 1965. However, Steyermark (1967: 268) cited the gathering without specifying that there are four sheets, and without designating a lectotype. Therefore, specimen 0006313 is here designated the lectotype of this name.

*Sipanea stahelii* is similar to *S. wilson-brownei*, and the two species have sometimes been confused in herbaria. Both of them can be found as herb, subshrub or shrub (basal internodes woody), 0.25–2(–4) m tall, with stipules adnate to the petioles, triangular at base and narrowly triangular to almost linear distally, leaves with 6–10 secondary veins on each side, inflorescences dichomously branched with scorpioid terminal branchlets, and hypanthia and fruits with hairs basally tuberculate. *Sipanea wilson-brownei* differs from *S. stahelii* by the inflorescence rachis thin but not filiform (vs. filiform in *S. stahelii*), bracteoles opposing each flower elliptic, narrowly elliptic, lanceolate, narrowly lanceolate to narrowly oblong-lanceolate, 3.5–7 × 0.3–1.7 mm (vs. linear to acicular, 0.8–2.5 × 0.1–0.3 mm), hypanthium narrowly obconical, narrowly ovoid to obovoid, 1–1.5 × 0.7–1.5 mm (vs. subglobose, 0.7–1.1 × 0.8–0.9 mm), calyx lobes oblong-lanceolate, lanceolate to narrowly lanceolate, 3.5–8 × 0.5–1.7 mm (vs. linear to acicular, 1.5–3 × 0.2–0.5 mm), corolla tube pink or red, sometimes reddish-green at base, and lobes pink, often with a median linear white area (microscopically glandular) at base, the 5 lobes sometimes forming a white star-like pattern (vs. tube pale green to greenish-white and lobes pink to lavender), and capsules subglobose, broadly ovoid, ovoid to narrowly ovoid, 3.5–7 × 3–5 mm (vs. globose, 3.7–4.5 × 3.5–4 mm).

*Sipanea stahelii* is also similar to *S. prancei*, from which it differs by the hypanthia and fruits with hairs conspicuously tuberculate at base (vs. with hairs slightly tuberculate at base in *S. prancei*), and the corollas 15–20 mm long, with tubes 10.5–12 mm long and lobes 4.5–8

**Figure 69.** *Sipanea stahelii*. **A.** Habit. **B.** Node with stipule and basal portion of petioles. **C.** Dissected long-styled flower, with stamens inserted at median portion of corolla tube, and exerted style. **D.** Dissected short-styled flower, with stamens inserted at distal portion of corolla tube, and included short style. **E.** Dehiscent capsule with permanent calyx lobes. **F.** Detail of basally tuberculate hair present on the capsule. **A, B, D:** drawn from Maguire 24314 (US). **C:** drawn from Schultz & Wessel Boer LBB 10223 (US). **E–F:** drawn from Irwin et al. 54918 (US). Illustration by Piero Delprete.

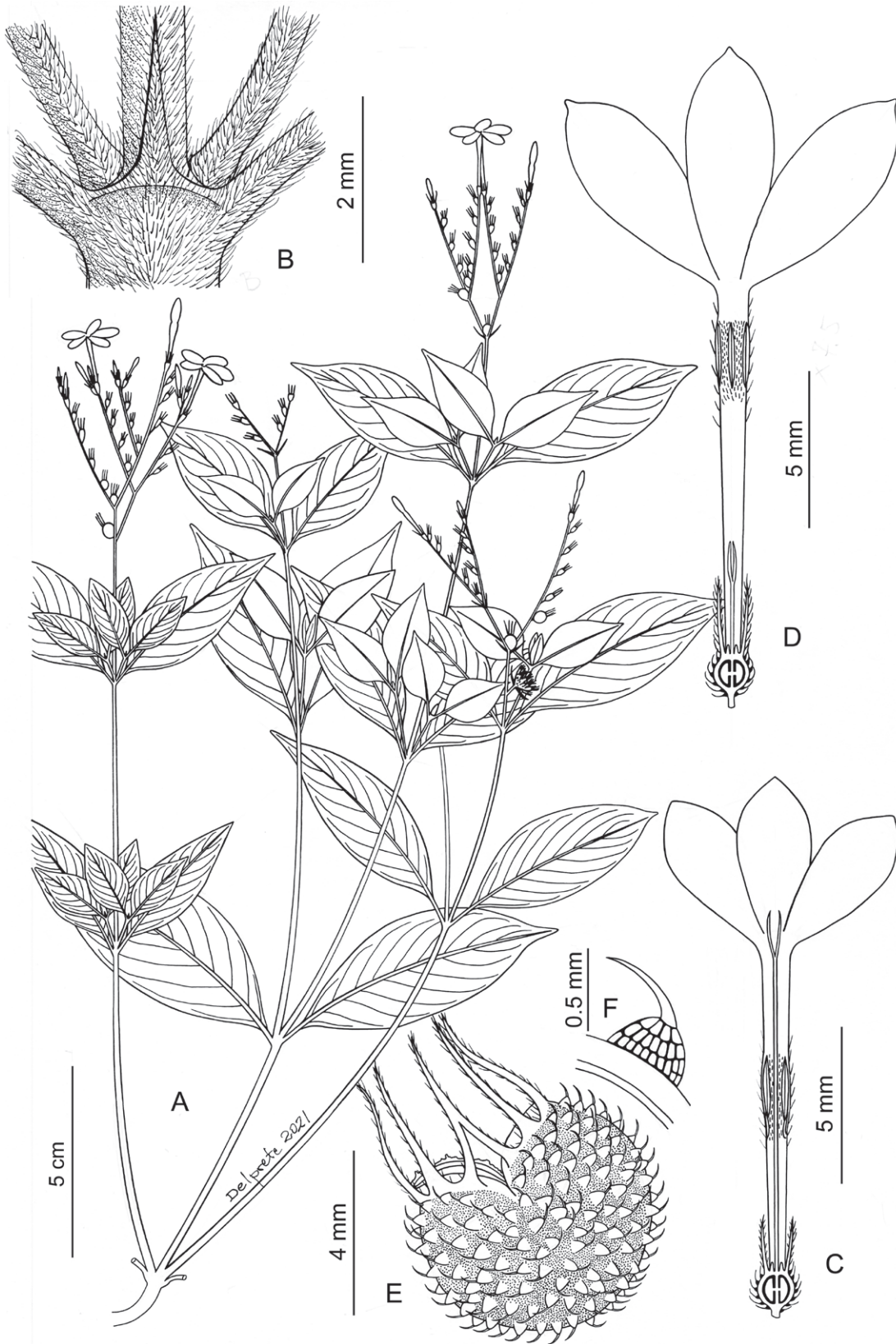


Figure 69.



**Figure 70.** *Sipanea stahelii*. **A.** Habit. **B.** Inflorescence, side view. **C.** Flower in anthesis (note glabrous mouth). **D.** Inflorescence with flowers in anthesis, top view. **E.** Inflorescence with flower buds, flower in anthesis, and young fruits. Photos taken by Hervé Galliffet on 28 April 2019, Sentier Roche Bateau, Saül, French Guiana (reproduced with permission from the author, plants not collected).

× 1.8–3 mm (vs. corollas 8.5–11 mm long, with tubes 5.7–7.5 mm long and lobes 2.7–3.5 × 1.4–1.5 mm).

*Sipanea prancei* and *S. stahelii* are also similar to *Neobertiera gracilis*, because of the erect habit, inflorescences dichotomously branched with a thin, filiform rachis, and globose fruits. *Neobertiera* differs from *Sipanea* by the indehiscent fruits falling off as dispersal units, while in *Sipanea* the fruits are persistent, loculicidal capsules, and the wind-dispersed seeds are released at capsule dehiscence. Due to the above-mentioned similarities, Delprete (2015) erroneously cited the Suriname collections Irwin *et al.* 54918, Schultz & Wessels Boer *s.n.* (LBB 10223) and Schultz *J.P. s.n.* (LBB 10471) under *Neobertiera gracilis* Wernham. However, after detailed observations of additional duplicate specimens, these three collections have apically dehiscent capsules, and hypanthium and capsules with basally tuberculate hairs (vs. with hairs basally inflated but not basally tuberculate in *N. gracilis*). The dry fruits of *Sipanea stahelii* at

the initial stage of maturity seem to be indehiscent, which lead to the misidentification of Delprete (2015). The dehiscence of these capsules takes place only at the final stage maturity, which was observed in recently analyzed duplicates, confirming that these three Surinamese collections belong to *S. stahelii*.

**Common name:** FRENCH GUIANA: alakua?a (Wayampi).

**Distribution and ecology:** Known only from several collections from Suriname and two collections from French Guiana (Figure 71). Growing in forests under-canopy on forested slopes, and top of table mountains, at (200–)390–1027 m altitude.

**Phenology:** Specimens with flowers were collected in March, and with flowers and fruits in July and August.

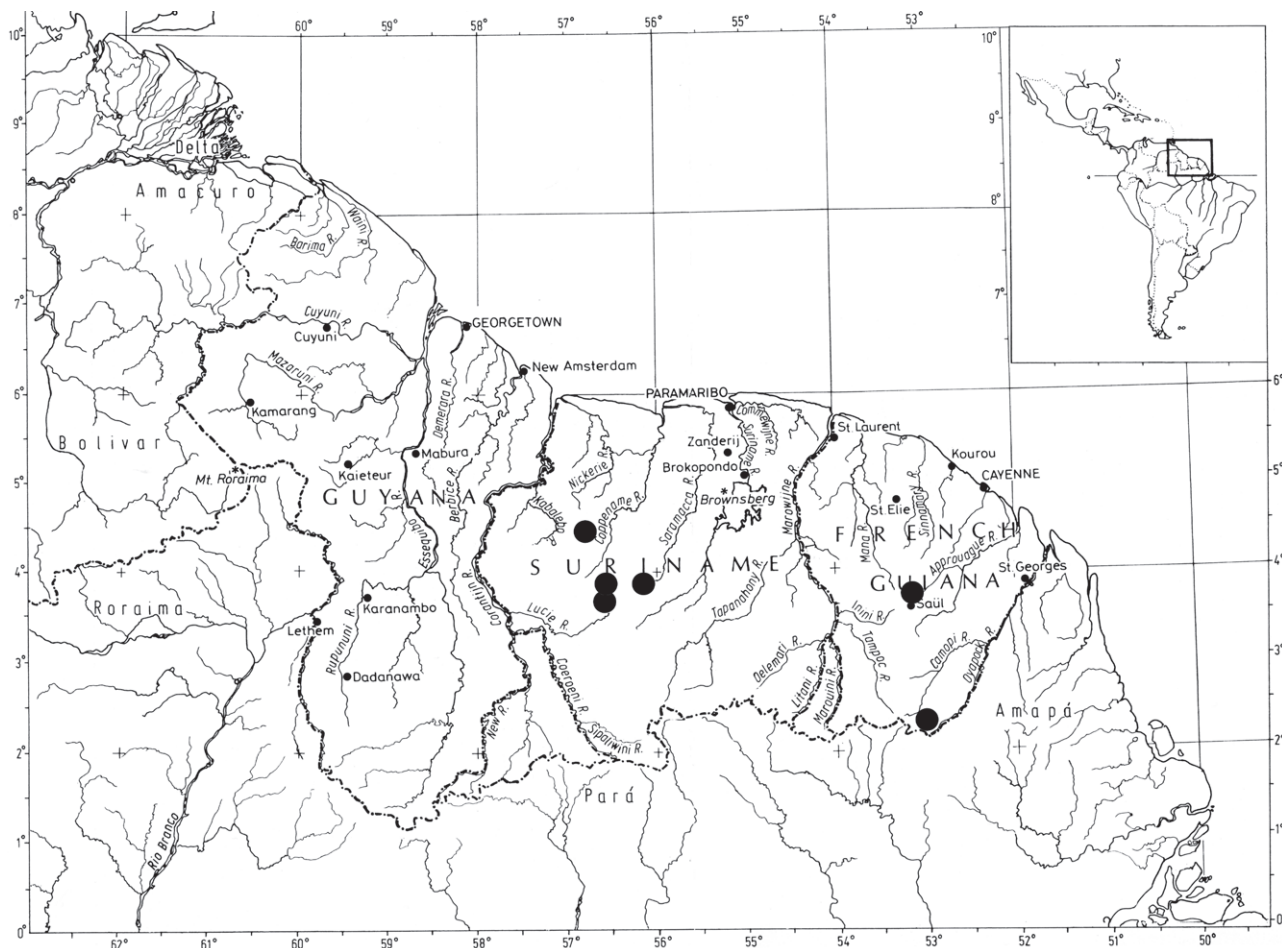


Figure 71. Distribution of *Sipanea stahelii*.

**Suggested conservation status: Vulnerable (VU).**

This species is known from several collections from Suriname and two from French Guiana. In Suriname it is known from six collections from three localities. The first collection was made in 1944 on the flank of Tafelberg Mountain (“Table Mountain”), ca. 3°54’N, 56°10’W, at 390 m altitude. Four collections were made in 1963 on the Wilhelmina Mountains (“Wilhelminageberte”): at 1 km SE of Juliana Top at 800 m; at 3.5 km SSE of Juliana Top, 3°30’–36’N, 56°30’–34’W, at 500 m; on a nameless top SE of camp km 14 in line to Lucie River, at 700 m; and on Top 1059, SE of Julianatop, at 900 m. The most recent collection in Suriname was made in 1965 on the Bakhuis Mountains, ca. 4°21’N, 56°45’W, at 1027 m. Tafelberg Mountain is one of the highest mountains in Suriname, and is included in the Central Suriname Nature Reserve. The Wilhelmina Mountains, which include Julianatop, ca. 3°41’N, 56°32’W, 1280 m, the highest mountain in Suriname, are also part of the Central Suriname Nature Reserve. This reserve is a UNESCO World Heritage Site. The Bakhuis Mountains, a continuation of the Wilhelmina Mountains, are outside of the Nature Reserve, are rich in bauxite, nickel and copper, and have been the focus of several potential mining projects, which have not been realized due to local protests.

In French Guiana, this species is known from two collections. The first one was made in 1975 on Mont Saint Marcel, at 500 m altitude. Mont Saint Marcel, ca. 2°23’N, 53°1’W, with its 645 m altitude, is one of the highest mountains in French Guiana and is included within the French Guiana Amazonian Park (Parc Amazonienne de Guyane). Numerous sites of illegal gold mining sites are present within the park, although most of them are at low altitudes and in the central zone of French Guiana, while Mont Saint Marcel is located at the southern limit of the French Guiana.

The second collection of *Sipanea stahelii* in French Guiana was made in 1994 on Monts Belvédère, 3°38’N, 53°10’W, at 200–400 m altitude, located at 1.8 km from the town of Saül. This small mountain is inside the free-adhesion area of the French Guiana Amazonian Park, which means that it is under limited human pressure; for example, locals are allowed to fish and hunt in this area. On the other hand, no gold mining is allowed in the immediate vicinity of the town of Saül.

The number of individuals of populations present in Suriname and French Guianas is not reported in the specimen labels, and no recent field work has been made to access the status of conservation on the above described localities. The extent of occurrence (EOO) of this species is of ca. 40,000 km<sup>2</sup>. It is tempting to say

that the localities within the Central Suriname Nature Reserve are without any immediate threat because the collection localities of this species are at 390–1027 m altitudes; while illegal gold mining is usually present at lower altitudes. This species is known from five distant localities and has a large EOO. Because the last collection of this species was made in 1994, and some localities might be impacted by illegal gold mining, it is estimated to be Vulnerable (VU) following IUCN criteria (IUCN 2012, 2019).

**Specimens examined: SURINAME:** In montibus Bakhuis inter flum. Kabalebo et Coppename Sinistrum, Bakhuis Mountains [ca. 4°21’N, 56°45’W], top of 1027 m, 3 Mar. 1965 (fl), *J. Florschütz & P.J.M. Maas 3116* (NY, U); Wilhelmina Geberte, forested lower slopes of Frederick Top, 3.5 km SSE of Juliana Top, 3°30’–36’N, 56°30’–34’W, 500 m, 20 Aug. 1963 (fl, fr), *H.S. Irwin et al. 54918* (MO, NY, P, S, U, US); Wilhelmina Mountains, 1 km SE of Juliana Top [ca. 3°41’N, 56°32’W], headwaters of West River, frequent on forested slopes and granitic peak, 800 m, 27 Aug. 1963 (fl-fr), *H.S. Irwin et al. 55129* (F, NY [2 sheets], RB, UB, US); Tafelberg (“Table Mountain”), [ca. 3°54’N, 56°10’W], base of N escarpment, 390 m, 11 Aug. 1944 (fl, fr), *B. Maguire 24314* (NY, U, US), 15 Sep. 1944 (fr), *24774* (F, NY); Wilhelmina Mountains, top 1059, SE of Julianatop, 900 m, 24 Jul. 1963 (fl), *J.P. Schultz & J.G. Wessels Boer s.n. (LBB 10223)* (BBS [2 sheets], MO, U); Wilhelmina Mountains, nameless top SE of camp km 14 in line to Lucie River, 700 m, 24 Jul. 1963 (fl), *J.P. Schultz s.n. (LBB 10471)* (BBS, K, NY, U).

**FRENCH GUIANA:** Upper Oyapock River, Mont Saint Marcel [ca. 2°23’N, 53°1’W], NE Summit, forêt basse broussailleuse, 500 m, 31 Jul. 1975 (fr), *J.J. de Granville 2624* (CAY [3 sheets]); vicinity of Saül, Monts Belvédère, 3°38’N, 53°10’W, 200–400 m, 27 Mar. 1994 (fl), *J.H.E. Rova et al. 2068* (S).

8-17. *Sipanea wilson-brownei* Cowan, Cowan et al. in *Brittonia* 7: 412. 1952. (Figures 5H, 68, 72–73).

Type: GUYANA. Komo Creek, Dec. 1948 (fl, fr), *G. Wilson-Browne 637* (holotype NY [barcode 00133328]; isotypes U [barcode 000317], US [barcode 00137731]). [Section *Nudae*].

*Herbs, subshrubs or shrubs* (basal internodes woody), 0.25–2 m tall, terrestrial or epipetric, dichotomously branched, erect or decumbent, rooting at basal nodes; young branches geniculate or slightly geniculate at least at basal nodes, reddish, sparsely to densely antrorse-

pubescent or antrorse-sericeous. *Stipules* adnate to the petioles, deltoid, narrowly triangular or broadly to shallowly triangular to truncate at base and narrowly triangular to narrowly oblong-triangular distally, 2–6.5 × 1–3.5 mm, acute or acuminate at apex, sometimes becoming bifid at apex at later stages, apical teeth (when present) to 2 mm long, equal or sometimes unequal, sparsely to densely appressed-pubescent to appressed strigose-pubescent, sparsely antrorse-sericeous or rarely glabrous outside, glabrous and with 3–7 colleters at base or a 3–4 colleters on each side at base inside; margins sparsely to densely pubescent or sericeous. *Leaves* petiolate; petioles 3–28 mm long, sparsely antrorse-pubescent or antrorse-sericeous; blades elliptic to elliptic-lanceolate, 2.5–10.5(–14.5) × 1–4(–5.5) cm, acute to decurrent at base, acuminate at apex, chartaceous, dark green above and dull pale green or reddish below when fresh, dark reddish-brown or olive-green above and pale brown below when dry; lamina glabrous or sparsely antrorse-puberulent above, glabrous, sparsely to densely appressed-puberulent or appressely hispidulous on secondary and tertiary veins below, midrib and secondary veins sparsely to densely appressed-puberulent, often reddish below; secondary veins 6–10 on each side of midrib, complanar above, prominent below. *Inflorescences* condensed-cymose (capitate) to shortly cymose at initial stage of anthesis, pauci- or multiflorous, 2.5–5.5 cm long (excluding corollas), expanding during and after anthesis to 8 cm long; peduncle 2–3.3 cm long, sparsely to densely antrorse-puberulent or antrorse-sericeous, with 1–3 pairs of lateral branches; rachis thin (i.e., not filiform), slightly thicker in infructescences, secondary branches cymose, 0.8–4 cm long during anthesis, dichotomously divided, ultimate branchlets scorpioid, more evident when fully expanded, 3–9-flowered; bracts subtending the flowering portion of secondary branches broadly to narrowly obovate, lanceolate, lanceolate, narrowly lanceolate to linear, 4.5–9 × 0.5–2 mm, glabrous, or with very few hairs, or sparsely antrorse-sericeous outside, margins antrorse-pubescent or antrorse-sericeous; bracteoles opposing each flower elliptic, narrowly elliptic, lanceolate, narrowly lanceolate to narrowly oblong-lanceolate, 3.5–7 × 0.3–1.7 mm, glabrous, or with very few hairs, or sparsely antrorse-pubescent outside, margins ciliate-pubescent or antrorse-sericeous. *Flowers* distylous, 5-merous, subsessile to pedicellate; pedicels 0.5–1 mm long, sparsely to densely antrorse-puberulent to densely antrorse-pubescent (strigose) or densely antrorse-sericeous. *Hypanthium* narrowly obconical, narrowly ovoid to obovoid, 1–1.5 × 0.7–1.5 mm, acute to obtuse at base, round to obtuse at apex, densely antrorse-strigose or densely antrorse-pubescent; hairs basally

tuberculate, 0.7–1.4 mm long. *Calyx* lobes subequal or unequal, green to reddish when fresh, oblong-lanceolate lanceolate to narrowly lanceolate, (2.5–)3.5–8 × 0.5–1.7 mm, glabrous, margins sericeous or long-hispidulous; with 1 colleter in each calycine sinus, narrowly conical, acute at apex, 0.2–0.3 mm long. *Corolla* hypocrateriform, 12.5–28 mm long, tube pink or red, sometimes reddish-green at base, lobes pink, often with a median linear white area (microscopically glandular) at base, sometimes forming a white star-like pattern with the 5 lobes, with a glabrous white ring at mouth; tube narrowly cylindrical, slightly wider at mouth, (7–)9.5–15 mm long, 0.5–1 mm wide for most length slightly wider at the distal portion below the mouth (at anther position in short-styled flowers), 0.8–2 mm wide at mouth, sparsely spreading or appressed antrorse-pubescent or antrorse-sericeous outside, densely puberulent from middle to distal portion of corolla tube, glabrous below and above inside; lobes elliptic, narrowly elliptic, narrowly obovate to obovate, 4–9.5(–14) × 2–6(–8) mm, round, obtuse or acute, rarely mucronate at apex, glabrous throughout (with a median linear white area (microscopically glandular) at base above, or microscopically glandular above and glabrous below. *Long-styled flowers* (*Cremers* 12781): stamens inserted at 3.5–4.5 mm from base corolla tube; filaments 0.5–1 mm long; anthers linear, 2–2.5 × 0.2–0.3 mm, round at base, acute at apex; style about the same length as corolla tube (tip of branches exerted) or exerted, 8.5–15 mm long, glabrous; style branches linear, 1–1.5 mm long, acute at apex. *Short-styled flowers* (*Granville* 14801, *Granville* 13588, *Ferreira et al.* 7630 [Oriximiná]): stamens inserted at 4–7 mm below corolla mouth; filaments 0.3–0.5(–0.7) mm long; anthers linear, 1.7–2.5 × 0.2 mm, round or acute at base, acute, often apiculate at apex; style included, 3.5–5.5 mm long, glabrous; branches narrowly lanceolate to linear, 1–1.3 mm long, acute at apex. *Infructescences* slightly or much expanded with respect to the inflorescence size, with lateral branches scorpioid, (2–)3.5–6.5 cm long; bracteoles persistent, even after the corresponding capsules have fallen off. *Capsules* broadly ovoid, ovoid to narrowly ovoid, 3.5–7 × 3–5 mm, round at base, obtuse to subacute at apex, crustaceous, sparsely ascending or spreading pubescent; hairs basally tuberculate, 0.9–1.4 mm long; pale green when young, turning pale brown to reddish-brown when dry pale green when young, turning pale brown when dry. *Seeds* irregularly tetrahedral-globose, 0.6–0.7 mm in diam., testa foveolate.

**Morphological notes:** *Sipanea wilson-brownei* Cowan is highly variable in terms of corolla size, like several other species of the genus. Sometimes the corolla size



varies even within the same individual; for example, in *Jansen-Jacobs et al. 1611* (U), the corollas vary from 12.5 mm long (tube 9 mm long and lobes 3.5–3.7 × 1.1–1.3 mm) to 18 mm long (tube 11 mm long and lobes 6–7 × 2.9–3.2 mm). This species is also variable in vestiture of vegetative and reproductive parts. Young branches, stipules and petioles can be sparsely to densely antrorse-pubescent or antrorse-sericeous. The leaf lamina can be glabrous or sparsely antrorse-puberulent above, glabrous or sparsely to densely appressed-puberulent or appressed-hispidulous, with midrib, secondary and tertiary veins sparsely to densely antrorse or spreading puberulent.

*Sipanea wilson-brownei* is similar to *S. stahelii* and has sometimes been confused in herbarium specimens. For comparison and differentiation of this two species, see discussion under *S. stahelii*.

Two collections from a single locality in the state of Pará, Brazil, differ from the specimens from all other collection localities. The locality is within the municipality of Oriximiná, at ca. 0°58'48"S, 56°59'23"W, at 14 km north of the waterfall called Cachoeira Porteira, at the edge of Rio Trombetas. The two collections C.A.C. *Ferreira & J. Ramos 1074* and C.A.C. *Ferreira 7630* differ from all the other specimens by having inflorescences with both the bracts subtending the branched portion of secondary branches and the bracteoles opposing each flower sparsely antrorse-sericeous outside (vs. glabrous or with very few hairs outside in all other specimens), the corolla tubes 9.5–10 mm long (vs. 10–15 mm long), the corolla lobes 4–4.5 × 3 mm, round to obtuse at apex (vs. 4.5–14 × 2–8 mm, obtuse to acute, sometimes mucronate at apex), and the capsules 3.5 × 3 mm (vs. 5–7 × 2.8–5.5 mm). The features peculiar to these two collections from the municipality of Oriximiná are here interpreted as morphological variation of a variable, wide-ranging species.

**Distribution and ecology:** A species distributed throughout the Guiana Shield, in Amazonian Venezuela (Amazonas, Bolívar), Guyana, Suriname, French Guiana and Amazonian Brazil (Amapá and Pará) (Figure 68). A species adapted to a wide range of habitats, commonly found in the undercanopy of lowland forests, lower to higher montane, common among igneous outcrops and over sandstones, in forests of mountain summits, or high altitude cloud forest with *Clusia*, *Bonnetia*, *Helico-*

*nia*, *Cecropia*, Rubiaceae and Myrtaceae, or in dense forest on brown sand and laterite, with *Caryocar*, *Sloanea* and *Aparisthium*, or in semi-shady places of forested mountain slopes and in forests at the edges of inselbergs, often found at edges of forest creeks, and sometimes also found in secondary vegetation; on granitic, sandy, lateritic or clay soils, brown sand, or soils with a superficial layer of forest litter, at 50–1500 m altitude.

**Vernacular name:** FRENCH GUIANA: Pililaãga (Wayampi; *Sastre 4480*).

**Phenology:**—It is quite common to find fruits at the basal portion and flowers at the distal portion of the same inflorescence. However, specimens at the early stages of anthesis might not have developing fruits present. Flowering and fruiting specimens were collected the whole year around.

**Conservation status: Least Concern (LC).** A species widely distributed in southern Venezuela (Amazonas, Bolívar), Guyana, Suriname, French Guiana and eastern Amazonian Brazil (Amapá and Pará), adapted to a wide range of habitats and soil types (see Distribution and ecology, above), and ranging from 50 to 1500 m altitude. Because of its vast extent of occurrence (EOO > 500,000 km<sup>2</sup>) and its numerous collection localities, some of them included within protected areas, this species belongs to the Least Concern (LC) category, following IUCN criteria (IUCN 2012, 2019).

**Specimens examined: VENEZUELA: Bolívar:** Carretera El Dorado, ca. km 88, Nov. 1958 (fl, fr), *L. Aristequieta 3722* (NY, US, VEN); entre el km 88 y el 126, 8 Apr. 1970 (fl, fr), *A. Fernández 1100* (F, MY); 105 km de El Dorado hacia Santa Helena, 29 Dec. 1956 (fl), *E. Foldats 2679* (F); La Escalera, 107–118 kms S of El Dorado, bosque montano, 5°50'N, 61°30'W, 450 m, 2 Apr. 1985 (fl, fr), *B.K. Holst et al. 2052* (MO, VEN); N portion of Cerro Uroi, Río Uroi [ca. 6°18'5"N, 62°3'47"W], Río Chicanán [ca. 6°44'N, 61°37'W], 250–400 m, 12 Sep. 1962 (fl, fr), *B. Maguire et al. 53733* (F, NY [2 sheets], RB, UB, US); along forested dirt road between km 109 and 125, between El Dorado and Cerro Uei, 800–1000 m, 30 Apr. 1960 (fl, fr), *J.A. Steyermark & S. Nilsson 837* (NY, US, VEN).

**Figure 72.** *Sipanea wilson-brownei*. **A.** Habit. **B.** Dissected long-styled flower, with stamens inserted at median portion of corolla tube, and exerted style. **C.** Dissected short-styled flower, with stamens inserted at distal portion of corolla tube, and included short style. **D.** Dehiscid capsule with permanent calyx lobes. **E.** detail of basally tuberculate hair present on the capsule. **A:** drawn from *Granville & Crozier 13588* (CAY). **B:** drawn from *Clarke et al. 4158* (CAY). **C:** drawn from *Clarke 2554* (CAY). **D–E:** drawn from *Mori & Smith 25056* (CAY). Illustration by Piero Delprete.



Figure 72.

**GUYANA:** Potaro-Siparuni Region, Iwokrama International Rainforest Reserve, Iwokrama Mountains, summit of highest peak, 4°20'N, 58°46'W, 1000 m, 23 Sep. 1996 (fl), *H.D. Clarke 2554* (CAY, MO, U, US); Upper Tukutu-Upper Essequibo Region, Kamao Mountains, 2 km N of camp on Kamao River, scrub forest on granitic outcrop, 1°32'50"N, 58°50'4"W, 520 m, 9 Nov. 1996 (fl, fr), *H.D. Clarke 2992* (MO, US); Potaro-Siparuni Region, Iwokrama Rainforest Reserve, Karupukari-Annai Rd, below summit of unnamed peak, dense forest on brown sand and laterite, 4°28'N, 58°47'W, 500–600 m, 20 Mar. 1997 (fl), *H.D. Clarke et al. 4158* (CAY, MO, NY, U, US); Cuyuni-Mazaruni Region, Pakaraima Mountains, transect 4 km along NE Plateau of Mout Ayanganna, 5°24'N, 59°57'W, 1100–1500 m, 6 Nov. 1992 (fl, fr), *T.W. Henkel & B. Hoffman 154* (MO, US); Upper Tukutu-Upper Essequibo Region, NW of Kanuku Mountains, top to Nappi Mountain, 12 km S of Nappi village, 3°18'N, 59°33'W, 750–950 m, 8 Feb. 1993 (fl, fr), *B. Hoffman & R. Foster 3549* (BRG, F, MO, US); Kanuku Mountains, Nappy Mt., 3°19'N, 59°34'W, 700–960 m,

11 Nov. 1987 (fl, fr), *M.J. Jansen-Jacobs et al. 884* (CAY, MO, NY, P, U, US); Kamao River, Toucan Mountain, forest on mountain slope, 1°33'N, 58°50'W, 260–360 m, 16 Sep. 1989 (fl), *M.J. Jansen-Jacobs et al. 1611* (CAY, MO, NY, P, U, US); Potaro-Siparuni Region, ridge of Eagle Mountain, near trail of Golden Star, upper plateau of ridge, 5°12'N, 59°7'W, 300–685 m, 10 Oct. 1990 (fl, fr), *T. McDowell & D. Gopaul 3478* (MO, US); Cuyuni-Mazaruni Region, Mount Ayanganna, E side on steep slopes, cloud forest dominated by *Clusia*, *Bonnetia*, Myrtaceae and Rubiaceae, 5°27'N, 59°57'W, 1250–1300 m, 12 Mar. 1987 (fr), *J.J. Pipoly et al. 11177* (CAY, INPA, MO, NY, US).

**SURINAME:** Sipaliwini District, Sipaliwini Village, trail from village towards the Sipaliwini Nature Reserve, ca. 2 km from village, primary forest with canopy 15–25 m tall, lateritic soil and white sand, 2°2'1"N, 56°6'45"W, 220 m, 17 Apr. 2014 (fl), *P.G. Delprete & G.P. Marjanom 12408* (CAY); Massif de Tumuc-Humac, Inselberg Talouakem, 2°29'N, 54°45'W, 10 Aug. 1993 (fl, fr), *J.J. de Granville et al. 12225* (CAY, US).



**Figure 73.** *Sipanea wilson-brownei*. Inflorescence with flowers in anthesis, flowers buds, and immature fruits. Photo taken by Scott Mori at Pic Matécho, central French Guiana, on 8 September 2000 (reproduced with permission from the author), gathering *Mori & Smith 25056*.

**FRENCH GUIANA:** Bassin de l'Approuague, Savane Roche (inselberg) Virginie, lisiere de savane roche, 4°11'N, 52°9'W, 50 m, 12 Feb. 1991 (fl), G. Cremers & P. Petronelli 11857 (CAY, P, U, US); Montagnes de la Trinité, Bassin de la Mana, 4°35'N, 53°21'W, 440 m, 17 Mar. 1992 (fl, fr), G. Cremers 12781 (CAY, P, U, US); Région des Emerillons, Mont Bakra, forêt primaire, 3°18'N, 52°57'W, 550 m, 14 Apr. 1993 (fl, fr), G. Cremers 13075 (CAY, B, MO, NY, P, U, US); Crique Jean-Pierre, Bassin de l'Approuague, 4°17'N, 52°12'W, 75 m, 5 Dec. 1994 (fl, fr), G. Cremers et al. 13537 (BR, CAY, MO, NY, P, US); along rd between Cayenne and Regina, pk 93, 4°18'N, 52°10'W, 21 Feb. 1993 (fl, fr), T.B. Croat 74314 (CAY, MO); Réserve Naturelle des Nouragues, forêt basse sur inselberg, 4°5'30"N, 52°42'W, 300 m, 17 Oct. 2007 (fl, fr), C. Delnatte et al. 1507 (CAY, MO, P); Mun. Saint George de l'Oyapock, site of future road to the bridge French Guiana–Brazil, ecological corridor, ca. 2 km from the Oyapock River, primary disturbed forest, at forest disturbed edge, 3°52'33"N, 51°49'35"W, 50 m, 2 Jul. 2009 (fl), P.G. Delprete 10575 (CAY); Mun. Saint George de l'Oyapock, on the road to future bridge to Brazil, primary forest with canopy 30–35 m tall, on rich lateritic soil, 3°52'33"N, 51°49'35"W, 50 m, 8 Jul. 2009 (fl), P.G. Delprete 10629 (CAY, F, G, L, MO, NY, P); Route National 2, pk 91, near Regina, 5 Apr. 1992 (fl, fr), Deroin, T. 133 (CAY, P); Grégoire, abbatis N. 11, 3 Jun. 1972 (fl, fr), G. Deward 237 (CAY [2 sheets], P); Montagne des Nouragues, Bassin de l'Arataye, forêt basse sur inselberg, 4°3'N, 52°42'W, 23 Aug. 1987 (fl, fr), C. Feuillet 4264 (CAY), 25 Aug. 1987 (fl, fr), 4301 (MO, P, US); Station Hydrologique de la Crique Grégoire, vers le saut, Haute Sinnamary, 21 Jan. 1974 (fl), J.J. de Granville B-5104 (CAY, US); Tumuc Humac Range, layon Koulimapopann-Mitaraka (frontier), pk 7.5, grande savane roche (inselberg) sur crête granitique, 500 m, 6 Aug. 1972 (fl, fr), J.J. de Granville 1135 (CAY, P, VEN); trail from Saül to Carbet Mais, granitic hill 2 km N of Carbet Mitan, 7 Jul. 1979 (fl), J.J. de Granville & G. Cremers 3030 (CAY, NY, P, UB); Pic Matécho, S summit, 30 km NE of Saül, 520 m, 22 Jan. 1980 (fl, fr), J.J. de Granville 3368 (CAY [2 sheets], NY, P, U, UB); Massif des Emerillons, zone centrale, affleurement granitique, 10 Sep. 1980 (fl, fr), J.J. de Granville 3808 (CAY, P, U, UB); Monts Bakra, versant Sud, at 3.5 km W of Pic Coudreau [ca. 3°17'N, 52°55'W], 450 m, 1 Oct. 1980 (fl, fr), J.J. de Granville 4047 (CAY [2 sheets], P, U [2 sheets], UB); granitic inselberg at NW limit of Monts de la Trinité, 4 Aug. 1981 (fr), J.J. de Granville 4746 (CAY, P, UB); Montagnes Trinité, N summit, 350 m, 13 Jan. 1987 (fl, fr), J.J. de Granville et al. 5953 (BR, CAY, G, MG, MO, NY, P, S, U, US); *ibid.*, 400 m, J.J. de Granville et al. 5974 (CAY);

Région des Emerillons, Mont Bakra, Pic Coudreau, forêt basse sur inselberg, 3°18'N, 52°57'W, 650 m, 19 Apr. 1993 (fl, fr), J.J. de Granville & G. Cremers 11825 (CAY, MO); Montagnes de la Trinité, S zone, Bassin de la Mana, forêt basse sur inselberg, 4°34'N, 53°21'W, 350 m, 14 Jan. 1998 (fl, imm fr), J.J. de Granville & F. Crozier 13588 (B, CAY, K, MO, NY, P, U, US); Pic Matécho, zone sommitale 2, 3°45'N, 53°2'W, 400 m, forêt basse sur inselberg, 15 Sep. 2000 (fl, fr), J.J. de Granville et al. 14079 (CAY, MO, NY); Monts Bakra, 1.5 km W of Pic Coudreau, forêt basse sur inselberg, 3°18'N, 52°57'W, 520 m, 16 Jun. 2002 (fl, fr), J.J. de Granville et al. 14801 (CAY, MO, P, US); Chemin de fer Gare-Tigre-Saint Elie, de pk 11 à pk 17, forêt primaire, 4°54'N, 53°11'W, 20 m, 7 Apr. 1990 (fl, fr), M. Hoff et al. 6536 (CAY, MO, NY, P, U); Montagnes des Nouragues, Bassin de l'Approuague-Arataye, 4°3'N, 52°42'W, 260 m, Oct. 1989 (fl), D. Larpin 697 (CAY); Pic Matécho, ca. 22.5 km NE of Les Eaux Claires, 3°45'N, 53°2'W, 515 m, on rock outcrop, 8 Sep. 2000 (fl, fr), S.A. Mori & N.P. Smith 25056 (CAY, NY); Saül, Roche Bateau trail, ca. 2 km SE of the village, 3°37'N, 53°12'W, 200 m, 15 May 2006 (fl), S.A. Mori et al. 25857 (CAY); Route de l'Est (RN2), près de Regina, végétation secondaire, 4°18'N, 52°12'W, 17 Sep. 1999 (fl, fr), M.-F. Prévost & D. Barthélémy 3699 (CAY, MO, NY, P, U); Pic Coudreau du Sud, Bassin de la Malani, 2°14'53"N, 54°19'40"W, 320 m, 7 Feb. 2013 (fl), H. Richard & F. Bagadi 703 (CAY, P); Haut Oyapock, Mont Saint Marcel [ca. 2°23'N, 53°1'W], près du sommet, 300–450 m, 21 Mar. 1976 (fl), C. Sastre 4480 (CAY, L, P); Haut Oyapock, Mont Saint Marcel, ilet sablonneux de la Crique Camp Poivre, 300–450 m, 24 Mar. 1976 (fl), C. Sastre 4526 (CAY, NY, P); Fleuve Approuague, Rivière Arataye, Saut Pararé, sommet d'un inselberg, 375 m, 22 Oct. 1978 (fl, fr), C. Sastre 6225 (CAY, NY, P, U, US); Les Nouragues Reserve, Montagnes des Nouragues, Bassin de l'Approuague-Arataye, 4°3'N, 52°42'W, 120 m, 15 Mar. 2002 (fl, fr), E.J. Tepe et al. 561 (CAY).

**BRAZIL. Amapá:** Territoire contesté franco-brésilien, place de Carsevenne [Calçoene? ca. 2°29'N, 50°57'W], terrain aurifère, 1898 (fl), F. Geay s.n. (P P00748134); Upper Jari River, margin of an inselberg, "2°28'N, 54°46'W" [these coordinates are incorrect, because they fall in southern Suriname], 500 m, 24 Aug. 1993 (fl), J.J. de Granville et al. 12437 (CAY, MO, US); margem do Rio Vila Nova, solo umido, 8 Dec. 1976 (fl buds), B.G.S. Ribeiro 1654 (UB); Tumuc-Humac Region, Paloulouiméempeu Mountain [ca. 2°20'N, 54°38'W], E slope, 550 m, 2 Aug. 1972 (fl, fr), C. Sastre 1539 (CAY, IAN, NY, P, U). **Pará:** Mun. Oriximiná, a 200 m da margem esquerda da estrada da Cachoeira Porteira, paralela ao Rio Trombetas, km 14 [ca.

0°58'48"S, 56°59'23"W], Igarapé das Pedras, mata ciliar, solo humoso, 19 Jun. 1980 (fl), C.A.C. Ferreira [as "C.A. Cid"] & J. Ramos 1074 (INPA, MG, NY [2 sheets], RB, UB, US); Mun. Oriximiná, BR-163, estrada que dá acesso à Perimetral Norte, a 14 km de Cachoeira Porteira [ca. 0°58'48"S, 56°59'23"W], mata de terra firme, solo argiloso, 9 Aug. 1986 (fl), C.A.C. Ferreira [as "C.A. Cid"] 7630 (F, INPA, MG, MO, NY, US).

### Excluded species

*Sipanea angustifolia* A.Rich. ex DC., Prodr. 4: 414. Sep. 1830, *nom. illeg. pro syn.* under *Virecta multiflora* Sm. (in A.Rees, The Cyclopaedia, vol. 37, Part I. 1817).

(-) *Sipanea angustifolia* A.Rich., Mém. Fam. Rubiacées 196. Dec. 1830; reimpr. A.Rich., Mem. Soc. Hist. Nat. Paris 5: 276. 1834].

Type: ANGOLA. Without locality, s.d., *Collector Unknown s.n.* (lectotype P [P03947412] designated by Verdcourt (1953b: 314).

(≡) ***Pentas angustifolia*** Verdc., Bull. Jard. Bot. État Bruxelles 23: 312. 1953.

**Notes:** Verdcourt (1953b: 312) published the new combination "*Pentas angustifolia* (A. Richard) Verdcourt" citing "*Sipanea angustifolia* A. Rich. ex DC., Prodr. IV, p. 414 (1830); Mém. Soc. Hist. Nat., Paris, p. 276 (1834)." However, *Sipanea angustifolia* A. Rich. was published in Candolle's *Prodromus* (Sep. 1830, p. 414) in synonymy under *Virecta multiflora* Sm. Therefore, the combination "*Pentas angustifolia* (A. Rich. ex DC.) Verdcourt" is based on an illegitimate name, and the correct authority for this taxon is *P. angustifolia* Verdc. In addition, Verdcourt indicated the type of *Pentas angustifolia* as "Angola: sine loco, no collector's name (T.) (P)." The citation "(T.) (P.)" means that the type is in the Paris general herbarium. Below the description, he observed that "*Sipanea angustifolia* has always been misinterpreted and referred to *Virecta* by all authors; yet the excellent type is available at Paris. No one could have looked at it since there is no possible doubt as to its identity." With this statement, Verdcourt designated the lectotype of this name, which is specimen with barcode P03947412 at P.

*Virecta elatior* DC., Prodr. 4: 415. Sep. 1830.

(-) *Sipanea elatior* A. Rich. ex DC., Prodr. 4: 415. Sep. 1830, *nom. illeg. pro syn.* [*Sipanea elatior* A.Rich.

Mém. Fam. Rubiacées 196. Dec. 1830, *nom. superfl.*; reimpr. Mém. Soc. Hist. Nat. Paris 5: 276. 1834].

Type: ANGOLA. Without locality, s.d., J.J. da Silva s.n. (holotype P [barcode 00539269]).

(≡) ***Otomeria elatior*** (DC.) Verdc. in Bull. Jard. Bot. État Bruxelles 23: 18. 1953.

**Notes:** Verdcourt (1953a) published the new combination "*Otomeria elatior* (A.Rich. ex DC.) Verdcourt" (Verdcourt 1953a: 18) citing "*Sipanea elatior* A. Rich. ex DC., Prodr. IV, p. 415 (1830), *Virecta elatior* A. Rich. ex DC., loc. cit., *Pentas elatior* Benth. ex Walp., Repert., IV, p. 57 (1846)" along with two heterotypic synonyms. However, "*Sipanea elatior* A. Rich." was published in Candolle's *Prodromus* (Sep. 1830) in synonymy under *Virecta elatior* DC. (Sep. 1830: 415), and is an illegitimate superfluous name. Therefore, the authority of "*Otomeria elatior* (A.Rich. ex DC.) Verdcourt (1953a: 18)" is erroneous, and the correct authority for this taxon is *O. elatior* (DC.) Verdc. Verdcourt (1953a: 22) cited the type as "Angola: s.l., unknown collector (T.) (P)." Below the description, he explained "This extremely variable plant has long been known by Hiern's name, but is so certainly the long misunderstood *Sipanea elatior* of Richard that a name change is unavoidable. An excellent specimen which I have accepted as the type exists in the herbarium at Paris. It was collected by an unknown traveler in Angola, and formed part of a collection that was seized from Lisbon by Napoleon during the invasion of Portugal. The collection was carried off to Paris without notes of any kind." Later, Verdcourt (1976: 214) cited the type of *Virecta elatior* as "Angola, da Silva [s.n.] (P, holo!)." Most likely, the collector cited as "da Silva" was Joaquim José da Silva, who collected in Angola before 1804 (Hettie Vegter 1986). The P sheet, barcode P 00539269, has a label with the handwriting (author unknown) "Herb. Mus. Par. - *Sipanea elatior* A. Rich. - Potius *Virecta elatior* DC., Prodr. IV, p. 415. - Angola." Just above this label, there is a label reporting "Holotypus vel Lectotypus, *Otomeria elatior* (A. Rich. ex DC.) Verdcourt, Determinavit N. Hallé, 30 mars 1965." This specimen is the holotype *Virecta elatior* DC.

*Sipanea carnea* Jacques, Rev. Hort., sér. 2, vol. 2 ["vol. 5 (26)"]: 302. May 1843.

*Sipanea carnea* Neumann, *nom. illeg. superfl.*, in Rev. Hort., sér. 2, vol. 2 ["vol. 5 (32)"]: 445, fig. 15. Nov. 1843

(=) *Pentas carnea* (Jacques) Benth., Curtis's Bot. Mag. 17: tab. 4086. 1844. – *Virecta carnea* (Jacques) Baill., Hist. Pl. 7: 331. 1880. Type: Locality of original collection unknown, "Herbier de Jacques," cultivated, s.d., Jacques s.n. (**Lectotype**, P [barcode P04959285], **here designated**).

(=) *Pentas lanceolata* (Forssk.) Deflers, Voy. Yemen 142. 1889.

**Notes:** Jacques (May 1843: 302–303) in the introduction "*Plantes figurées dans ce numéro*" [Plants illustrated in this issue] of *Revue Horticole*, sér. 2, vol. 2, fascicle 26, described *Sipanea carnea* Jacques as a plant originally either from Madagascar or South America, sent to the *Jardin des Plantes* (Paris) in 1841 by Mr. Pervillé. Jacques was referring to the same plant described and illustrated in the same volume by Neumann, in a fascicle published six months later. Jacques described the species as an herb 30 cm tall, with ovate to lanceolate leaves, terminal multiflorous corymbs, and corolla pale pinkish-violet, with narrowly cylindrical tube. He did not mention any collection or herbarium of deposit. According to Stafleu & Cowan (1979: 404), Jacques might have had "Some material (cult. Plants from Neuilly garden) in Webb herbarium at FI." However, after exhaustive searches at FI and FI-Webb, no original material of *S. carnea* was found. In P there are four specimens labeled *S. carnea*:

1) Specimen with barcode P04959285 has a label with the heading "MUSEUM NATIONAL D'HISTOIRE NATURELLE – CULTURE" with the handwritten text "Sipanea carnea Nem. – Herbier de Jacques." At the lower left corner is a label (author unknown) with the handwritten annotation "Sipanea carnea." The specimen is a branch with numerous leaves and inflorescences with flowers in anthesis. This specimen is original material and is here designated the lectotype of *Sipanea carnea*.

2) Specimen with barcode P04959286 has a label with the heading "HERB. MUS. PARIS" and the printed text "herbier d'Édouard Spach, donné au Muséum par sa famille, en juillet 1879." At the lower left corner is a label (author unknown) with the handwritten annotation "Sipanea carnea det. Brongn. (*Pentas carnea* Lindl) S. Par 1841 seminibus borbonides." The specimen is composed of two branches with numerous leaves and terminal inflorescences. This specimen is not original material of *Sipanea carnea*.

3) Specimen with barcode P04959287 has a label with the heading "HERB. MUS. PARIS" and the printed text "Herbier donné par M. Houillet, Jardinier en chef des Serres. (1869. N° 1.)" At the lower left corner is a

label (author unknown) with the handwritten annotation "Sipanea carnea Ad. Brong. – *Pentas carnea* Bot. veg. 1844., S. ch., en herb. Houllun, Ile Bourbon. Juillet 1844, hort. Paris, Pervillé." The specimen is composed of two branches with numerous leaves and terminal inflorescences. This specimen is not original material of *Sipanea carnea*.

4) Specimen with barcode P04959288 has a label with the heading "HERB. MUS. PARIS" and the printed text "Herbier d'Adrien de Jussieu, donné au Muséum par ses enfants, en 1857." At the lower left corner is a label (author unknown) with the handwritten annotation "Sipanea carnea. ad. Br. – *Pentas carnea* Lindl. H.P. (Serr. Ch.) Mars 1846." The specimen is composed of two branches with numerous leaves and terminal inflorescences. This specimen is not original material of *Sipanea carnea*.

In the fascicle 32 of the same volume where Jacques (May 1843: 302–303) first published *Sipanea carnea*, J.H.F. Neumann (Nov. 1843: 445), six month later, described and illustrated *S. carnea*. He described the species as a herbaceous plant from South America, with corymbose inflorescence, corolla tube four times longer than the calyx, with (4)5 lobes, filiform style longer than the corolla, and pale violet corollas. The beautiful illustration, drawn by the same author, corresponds entirely with the species description. Neumann did not indicate a collection or herbarium, and, according to Stafleu & Cowan (1981: 731), he did not keep a personal herbarium.

The following year, Bentham (1844: tab. 4086) published the new genus *Pentas* Benth., with the species *P. carnea* Benth. and *P. parviflora* Benth. Along with the description of *P. carnea*, he wrote "Our stoves have lately exhibited a fine flowering plant, under the name of *Sipanea carnea*, well worthy of general cultivation. Mr. Makoy, of Liege, I believe, introduced it to England: at least, the Royal Botanic Garden of Kew is indebted for the possession of it to that liberal cultivator. A slight examination of the flowers, however, show that it has nothing to do with *Sipanea*, and that it is one of the Hedyotideae;—a new genus, to which Mr. Bentham has given the name of *Pentas* [...] although not so stated, there is every reason to believe the plant is from tropical Africa". Bentham (1844: tab. 4086) cited *S. carnea* in synonymy under *P. carnea*. Bentham's citation is an indirect reference to *S. carnea* Jacques, and it should be treated as the publication of the new combination *Pentas carnea* (Jacques) Benth., which has the same type of *S. carnea*.

## 9. SIPANEOPSIS

*Sipaneopsis* Steyerl., Mem. New York Bot. Gard. 17: 284–289. 1967

Steyerl. in Lasser & Steyerl., Fl. Venezuela 9: 272–282. 1974; J.H. Kirkbr., Acta Amazonica 10: 113–115. 1980; Delprete & Steyerl. in Steyerl. et al., Fl. Venez. Guayana 8: 833–835, figs. 648–650. 2004.

Type: *Sipaneopsis rupicola* (K.Schum.) Steyerl.

*Subshrubs* or *shrubs*, rarely *herbs*, erect, ascending or rarely decumbent. *Stipules* persistent, free or adnate to petioles, sometimes basally sheathing, free portion broadly to narrowly triangular, or base broadly triangular and distal portion linear, acuminate, bilobed or bifid at apex, or topped by 2–7 linear lobes (*S. morichensis*, *S. rupicola*), with (1)2–11 colleters at medio-basal portion or just below the margin inside, tips exserted. *Leaves* opposite, short-petiolate; blades ovate, elliptic, lanceolate or linear, chartaceous or subcoriaceous; domatia absent. *Inflorescence* terminal, cymose, few- to many-flowered. *Flowers* homostylous, 5-merous or very rarely 6-merous. *Hypanthium* subglobose, globose, broadly turbinate, turbinate, subcampanulate-urceolate, broadly-obovoid, obovoid-turbinate, obconical or oblong-obovoid, scabrous, densely hispid, densely hispidulous strigillose, densely to sparsely strigose, sericeous-strigose or sericeous. *Calyx* persistent; lobes free or shallowly connate at base, small, ovate, narrowly ovate, narrowly lanceolate to linear-lanceolate. *Calycophylls* absent. *Corolla* campanulate at initial and intermediate stages of flowering with tube short and lobes already opened and erect, at ultimate stage of anthesis the corolla becoming hypocrateriform with tube completely elongate and lobes reflexed and perpendicular to the tube; corolla pink during anthesis and turning pinkish-white to white at final stage of anthesis; tube externally hirsute, internally pubescent, without a pubescent ring, with 5 triangular appendages at the base of the corolla lobes, the appendages fleshy, covered by dense tufts of strigose hairs 0.3–0.4 mm long; lobes left-contorted or rarely imbricate, obovate, ovate or round, margin entire, obtuse or round at apex. *Stamens* included, filaments extremely short, attached at the middle of the corolla tube; anthers subsessile, linear, acute at both ends, dorsifixed near the base. *Pollen* 4(5)-colporate; exine shallowly foveolate, perforate. *Ovary* with a stalked placenta; stalk inserted at the middle of the septum, terminating with a globose extension; ovules inserted on the globose extension. *Style* included or with branch tips exserted, filiform, glabrous; branches lanceolate to nar-

rowly lanceolate. *Fruit* indehiscent, globose, subglobose or urceolate, thinly woody to crustaceous, crowned by the permanent calyx lobes, falling off as a dispersal unit, leaving a round scar on the infructescence rachis. *Seeds* minute, horizontal, spherical to ellipsoidal.

**Flowering modality:** The flowering process of *Sipaneopsis* is unique within the Rubiaceae, and it can be appreciated in Figures 80 and 82. It was described in detail by Delprete (2015a, 2017). An inflorescence with flowers in different developmental stages of *Sipaneopsis maguirei* is shown in Figure 80B–C. During the initial stage of anthesis the flowers are still very small; however, their corolla lobes are already open and erect, although not fully expanded, before tube elongation (Figure 82A–B); at this stage the triangular appendages present at the base of the corolla lobes are appressed against each other, forming a convex structure at the corolla mouth (Figure 82A–B), and obstructing the entrance of any visitors or pollinators. During successive stages of anthesis, the corolla tube and lobes elongate; the corolla lobes remain erect and the corolla lobe appendages are still appressed against each other (Figure 82C–F), continuing to obstruct the entrance of any visitors or pollinators. At the final stage of anthesis, the corolla lobes reflex outwards and become perpendicular to the tube (corolla hypocrateriform), the corolla lobe basal appendages become erect, not touching each other anymore (Fig. 82G–H), allowing visitors and pollinators to access the corolla tube and nectar disk. In addition, flowers of *Sipaneopsis* are protandrous, which means that after the lobes have become perpendicular to the corolla tube, on the first day the anthers reach full maturity and dehisce, releasing pollen, while the stigmatic branches are still appressed to each other and not receptive (Figure 82G). The following day the anthers are no longer releasing pollen, the stigmatic branches spread apart and are reflexed, and the stigmatic surface become receptive. For the above reasons, for species descriptions the corolla tube and lobes of *Sipaneopsis* species should be measured only when they are fully expanded and the lobes are perpendicular to the tube.

**Distribution and ecology:** A genus with eight species endemic to white-sand savannas, occurring mostly in the lowlands, although with a few collections from higher altitudes, of the Guayana Shield, ranging from Colombia to southern Venezuela and the Amazon basin of Brazil.

**Stipules variation within the same species:** Stipules are polymorphic in several species of *Sipaneopsis*, as they

can be entire, bifid or multifid in the same species. Also, in some species the stipules are entire at distal nodes and sometimes apically splitting with age, remaining entire or becoming bifid or multifid in older nodes of the same branch. In *S. cururuensis* they are consistently bifid with narrowly triangular lobes. In *S. duckei*, *S. maguirei* and *S. pacimoniensis* they are consistently entire and broadly to narrowly triangular. In *S. foldatsii* and *S. huberi* they are broadly to narrowly triangular, and rarely (*S. foldatsii*) or consistently (*S. huberi*) bifid at apex. In *S. rupicola* they are triangular, entire and caudate, or triangular at base with 2–3 linear lobes, or basal portion extremely reduced and topped by 6–7 linear lobes or by 2 longer lobes intercalated with shorter ones.

Key to *Sipaneopsis* species

Stipule shape and vestiture of vegetative parts are important characters for species identification in *Sipaneopsis*. As in several species stipules are polymorphic, a few species are present in multiple entries in the key below. Corolla measurements were made only when fully expanded, with the corolla lobes perpendicular to the tube, and the corolla lobe basal appendages erect, no longer touching each other.

1. Herbs, 10–12 cm tall, single-stemmed (Venezuela: Amazonas, Río Pacimoni) ..... 7. ***S. pacimoniensis***
1. Subshrubs or shrubs, (8–)18–200 cm tall, many-stemmed or branched, or ranging from herb to subshrub in *S. cururuensis* ..... 2
2. Stipules with 2 narrowly triangular lobes (i.e., stipules bifid) or with (1–)2–7 linear lobes ..... 3
2. Stipules entire ..... 9
3. Stipules with (1–)2–7 linear lobes ..... 4
3. Stipules with 2 narrowly triangular lobes (i.e., stipules bifid) ..... 5
4. Stipules ochroleucous-pubescent outside, with 1–4 linear lobes (Venezuela: Amazonas: Cerro Moriche) ..... 6. ***S. morichensis***
4. Stipules densely white-strigulose outside, with 2–3 linear lobes, or base reduced to a transversal line with 6–7 linear lobes (Colombia: Vaupés: Cerro Chiribiquete; Caquetá: Araracuara; Venezuela: Amazonas: Casiquiare) ..... 8. ***S. rupicola***
5. Leaf blade sericeous below; corollas 13–14 mm long, with tubes 9.5–10 mm long and lobes 4–4.5 mm long when fully expanded (Venezuela: Amazonas, Dpto. Río Negro) ..... 4. ***S. huberi***
5. Leaf blade glabrous, scabrous or strigose below; corollas 14.5–22 mm long, with tubes 11–16 mm long and lobes 3.5–7 mm long when fully expanded ..... 6
6. Young stems strigulose; leaf blade glabrous or sparsely to densely strigose, or densely sericeous-strigose with mid-vein and secondary veins white- or ochroleucous-strigose below; corollas 14.5–16.2 mm long, with tubes 11–11.5 mm long and lobes 3.5–4.7 mm long when fully expanded (Colombia: Vaupés: Cerro Chiribiquete; Caquetá: Araracuara; Venezuela: Amazonas: Casiquiare) ..... 8. ***S. rupicola***
6. Young stems glabrous, sparsely to densely strigose, or sparsely to densely scabrous; leaf blade glabrous, sparsely to densely strigose, or sparsely to densely scabrous below; corollas 17.5–22 mm long, with tubes 12–16 mm long and lobes 4.2–7 mm long when fully expanded ..... 7
7. Young stems and leaf lamina sparsely to densely scabrous below; stipules always bifid; stamens inserted at 9–9.5 mm below corolla mouth, filaments 3.5–4 mm long (Brazil: Pará, Tapajos River Basin) ..... 1. ***S. cururuensis***
7. Young stems and leaf lamina glabrous or sparsely to densely strigose or densely hispid-strigose below; stipules entire or rarely bifid at older nodes; stamens inserted 2–3.5 mm below corolla mouth, filaments 0.3–0.4 mm long (anthers subsessile) ..... 8
8. Leaf lamina glabrous and midrib appressed-strigose above, glabrous or sparsely strigose and midrib and secondary veins appressed strigose below; corollas 17.5–22 mm long, with tubes 12–16 mm long and lobes 4.5–7 mm long when fully expanded; fruits globose, 4–5 x 4–5 mm, appressed strigose (Brazil: Pará, Campos do Ariramba, and Amazonas, Serra do Aracá) ..... 2. ***S. duckei***
8. Leaf lamina densely hispid-strigose above and below; corollas 20.5–24 mm long, with tubes 14–16 mm long and lobes 6.5–8 mm long when fully expanded; fruits urceolate, 3.5 x 3 mm, densely sericeous (Venezuela: Amazonas, Río Atabapo) ..... 3. ***S. foldatsii***
9. Corollas 14.5–16.2 mm long, with tubes 11–11.5 mm long and lobes 3.5–4.7 mm long when fully expanded (Colombia: Vaupés: Cerro Chiribiquete; Caquetá: Araracuara; Venezuela: Amazonas: Casiquiare) ..... 8. ***S. rupicola***
9. Corollas 17.5–30 mm long, with tubes 12–22 mm long and lobes 4.5–9 mm long when fully expanded ..... 10
10. Stems thin; inflorescences 2–8(–13)-flowered (Venezuela: Amazonas, Dptos. Atabapo, Atures, Casiquiare; Brazil: Amazonas, Rondônia) ..... 5. ***S. maguirei***
10. Stems stout; inflorescences (12–)19–58-flowered ..... 11
11. Leaf lamina glabrous and midrib appressed-strigose above, glabrous or sparsely strigose and midrib and secondary veins appressed strigose below; corollas 17.5–22 mm long, with lobes 4.5–7 mm long when fully expanded; fruits globose, 4–5 x 4–5 mm, appressed strigose (Brazil: Pará,



Campos do Ariramba, and Amazonas, Serra do Aracá).....  
 .....2. *S. duckei*

11. Leaf lamina densely hispid-strigose above and below; There is absolutely no contrast in this character.; corollas 20.5–24 mm long, with lobes 6.5–8 mm long when fully expanded; fruits urceolate, 3.5 x 3 mm, densely sericeous (Venezuela: Amazonas, Río Atabapo)..... 3. *S. foldatsii*

- 9-1. *Sipaneopsis cururuensis* J.H. Kirkbr., Acta Amazon. 10: 113, figs. 19, 24. 1980. (Figures 74–75).

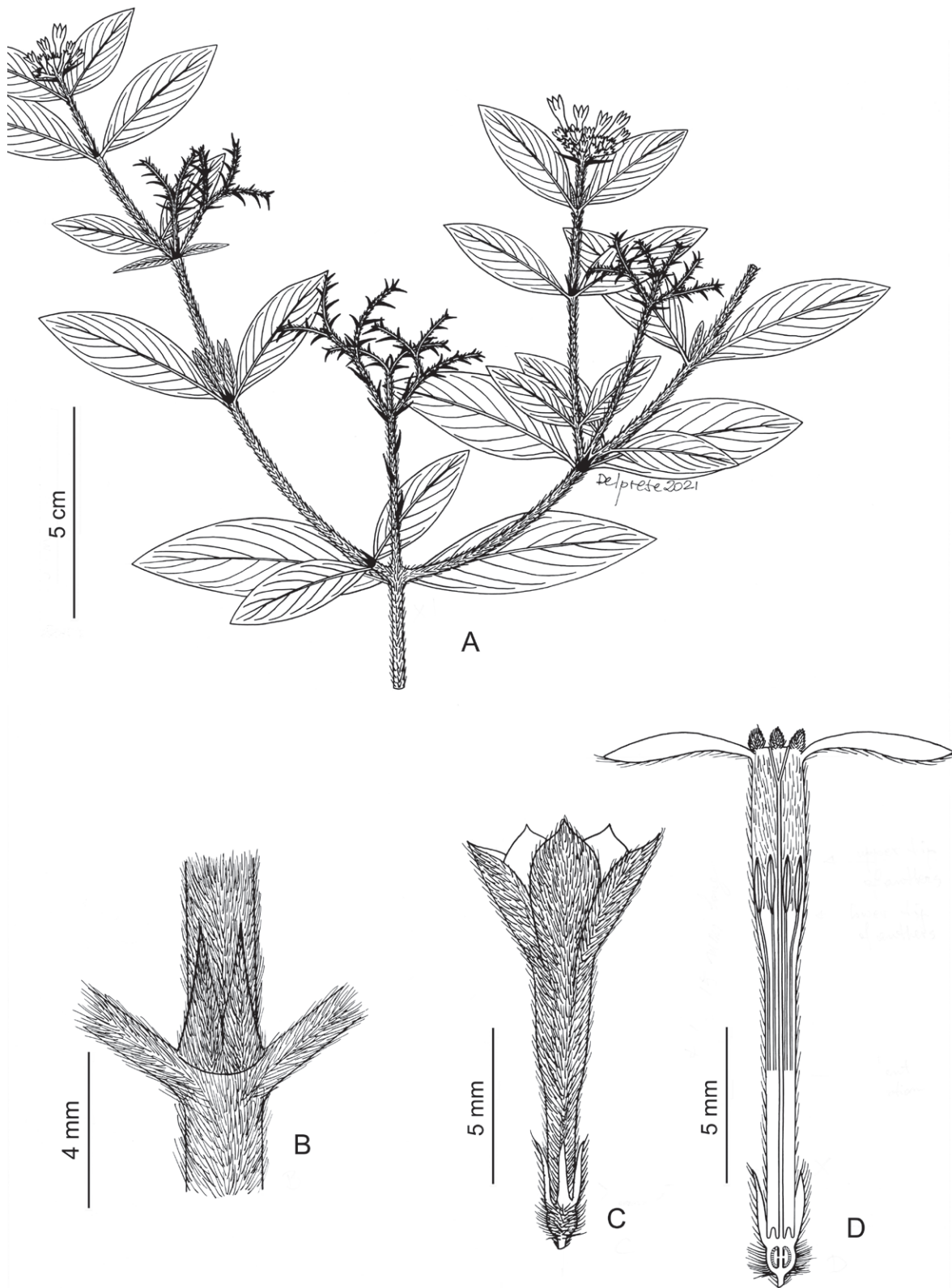
Type: BRAZIL. Pará: Upper Tapajós River Basin, Cururu River, Erereri [River, ca. 7°37'S, 57°37'W], 8 Feb. 1960 (fl, fr), W.A. Egler & Raimundo [R.R. Silva] 1265 (MG 24312) (holotype IAN [barcode and Acc. No. 123604]; isotypes MG [barcode unknown, Acc. No. 24312]; isotype fragment US [barcode 00074187]; photo-IAN at NY, UB, S).

*Herbs or subshrubs* 25–50 cm tall, basal portion sometimes prostrate, rooting at basal nodes; stems scabrous to densely scabrous; hairs antrorse, white or pale brown. *Stipules* free at base, bifid, the lobes narrowly triangular, acute at apex, 2–5 × 0.5–1 mm, scabrous to densely scabrous outside, sparsely scabrous and with a few colleters at base inside. *Leaves* petiolate; petioles 2–3 mm long, scabrous to densely scabrous; blades elliptic to narrowly elliptic, 4–7 × 1.5–2.5 cm, attenuate at base, acute at apex, papyraceous, dark green above, pale green below, drying brown above and pale brown below, sparsely scabrous above, scabrous to densely scabrous below; with 7–10 secondary veins each side. *Inflorescences* cymose, a compound dichasium with scorpioid terminal branches, 23–52-flowered, 2.5–5(–13) cm tall, (including peduncle and flowers), 3–4.5 cm broad, rachis scabrous to densely scabrous; peduncle 0.5–3(–6.5) cm long; with 9–14 terminal branchlets; branchlets secundiflorous, scorpioid, 7–14-flowered. *Flowers* with pedicels 0.4–0.6 mm long, scabrous to densely scabrous, subtended by one bracteole narrowly triangular to oblong-lanceolate, 2.2–5.8 × 1–2.4 mm, acute at apex, scabrous. *Hypanthium* globose, ca. 1 mm in diam., scabrous. *Calyx* lobes subequal, narrowly ovate, 2–2.3 × 0.5–0.7 mm, sparsely strigose outside, glabrous inside, acute at apex; with 1–2 colleters in each calycine sinus, narrowly oblong, 0.2 mm long. *Corolla* hypocrateriform, 18.2–20 mm long when fully expanded, tube cylindrical and slightly wider at mouth, 14–15.4 mm long when fully elongated, 0.8 mm wide at base, 1.2 mm wide at mouth, strigose outside, glabrous at base and sericeous at upper 3/4 inside; lobes irregularly imbricate in bud,

1–3 lobes interior, elliptic to oblong-ovate, 4.2–4.6 × 1.8–2 mm when fully expanded (perpendicular to the tube), broadly acute at apex, antrorse-strigose outside, glabrous inside. *Stamens* included, inserted at 9–9.5 below corolla mouth; filaments 3.5–4 mm long; anthers narrowly oblong, 1.6–1.7 mm long, acute at both ends. *Style* included, ca. 13 mm long, glabrous; style branches lanceolate, ca. 1 mm long. *Infructescences* a compound dichasium, 5–14.5 cm long, terminal branches scorpioid, 3–7 cm long; rachis scabrous to densely scabrous; peduncle 0.5–3(–6.5) cm long; fruits subtended by the persistent bracteoles. *Fruit* globose, 3–4 mm in diam., strigose to sparsely strigose. *Seeds* globose, 0.5–0.8 mm in diam.; testa reticulate-foveolate, cells polygonal.

**Notes:** In agreement with Kirkbride's (1980) discussion, *Sipaneopsis cururuensis* J.H. Kirkbr. is similar to *S. rupicola* (K. Schum.) Steyererm. and *S. morichensis* Steyererm. because of the lobed stipules, shorter corolla tubes and taller habit with respect to the other species of the genus, from which it could be distinguished by the scabrous leaves and stems (vs. glabrous in *S. rupicola* or villosulous in *S. morichensis*), and corolla lobes 4.2–4.6 mm long (vs. 3–3.5 mm long in *S. rupicola* or 4.5–6 mm long in *S. morichensis*).

*Sipaneopsis cururuensis* is also similar to *S. duckei* Delprete in being herbs or subshrubs with stout stems, leaves with 6–10 secondary veins on each side of midrib, inflorescences compound dichasia, corolla tube length (14–15.4 mm long in *S. cururuensis* and 12–16 mm long in *S. duckei*), and globose fruits. *Sipaneopsis cururuensis* differs from *S. duckei* in the young stems scabrous to densely scabrous (vs. hispid-strigose or appressed to spreading strigose in *S. duckei*), stipules consistently bifid (vs. entire or bifid), leaf blades sparsely scabrous above (vs. completely glabrous, or lamina glabrous and midrib appressed strigose, or lamina and midrib sparsely strigose above in *S. duckei*) and scabrous to densely scabrous below (vs. completely glabrous, or sparsely strigose and midrib and secondary veins sparsely to densely appressed strigose below), hypanthium globose, ca. 1 × 1 mm, scabrous (vs. globose, broadly obovoid to obovoid-turbinate, 1–5 × 0.8–1.5 mm, densely to sparsely strigose in *S. duckei*), corolla lobes elliptic to oblong-ovate, 4.2–4.6 × 1.8–2 mm when fully expanded (vs. roundish, obovate to elliptic, 4.5–7 × 2–4 mm when fully expanded in *S. duckei*), stamens inserted 9–9.5 mm below corolla mouth, filaments 3.5–4 mm long (vs. inserted 2–3 mm below corolla mouth, anthers sessile in *S. duckei*), fruits 3–4 × 3–4 mm (vs. 4–5 × 4–5 mm in *S. duckei*), and seeds globose, 0.5–0.8 × 0.5–0.8 mm (vs. irregularly ellipsoid to subglobose, 0.9–1.1 × 0.8–1 mm).



**Figure 74.** *Sipaneopsis cururuensis*. **A.** Branch with several inflorescences and infructescences (fruits fallen off). **B.** Node with stipule and basal portion of petioles. **C.** Flower at intermediate stage of anthesis. **D.** Flower at final stage of anthesis, with corolla lobes reflexed, and receptive stigmas. **A–D:** drawn from Egler & Raimundo 1265 (MG, isotype). Illustration by Piero Delprete.

A few specimens from Guyana, i.e., *Henkel et al.* 1449, *McDowell & Stobey* 3853, and *Mutchnick et al.* 156, have been incorrectly identified as *Sipaneopsis cururuensis*; however, *S. cururuensis* is known only from the type collection from the Tapajos River Basin, Brazilian state of Pará, south of the Amazon River, on the Brazilian Shield. Those specimens are *Neobertiera pakaraimensis* Delprete (2015: 126) instead. *Sipaneopsis* and *Neobertiera* are similar by having indehiscent fruits falling off as dispersal units; the former differ from the latter by the homostylous flowers, and the corolla lobes that open before tube elongation and possess basal appendage covered with a tuft of hairs; while in *Neobertiera* the flowers are distylous, and the corolla lobes open only after complete tube elongation and lack basal appendages.

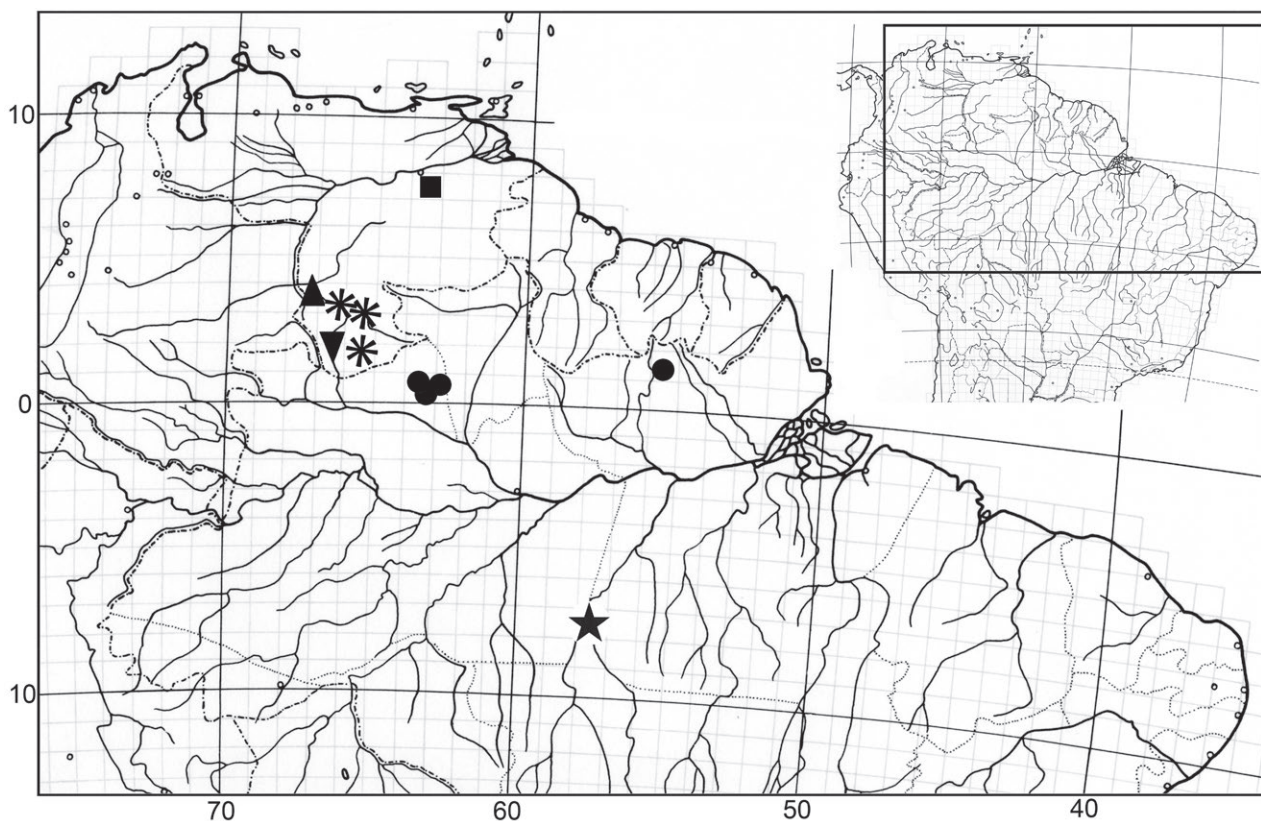
**Distribution and ecology:** A species only known by the type locality, in the Brazilian state of Pará, South of the Amazon River, along the Cururu River, in the upper Tapajos River basin (Figure 75).

**Phenology:** The type gathering, with flowers and fruits, was collected in February.

**Suggested conservation status: Critically Endangered (CR).** An extremely rare species only known from the type gathering, collected in 1960 near the Erereri River, ca. 7°37'S, 57°37'W, a small affluent of the Cururu River, Upper Tapajós River Basin, state of Pará, Brazil. This remote locality was botanically explored only once and remains poorly collected. The size of the population of this species is unknown and suspected to be quite small. Because it is known from a single locality, and most likely a small population, and the high possibility of local deforestation, it is treated as Critically Endangered (CR) following IUCN criteria (IUCN 2012, 2019).

9-2. *Sipaneopsis duckei* Delprete, *Phytotaxa* 282(1): 130, fig. 2. 2018. (Figures 5I–J, 75–76).

Type: BRAZIL. Pará: Mun. Oriximiná, Campos do Ariramba, campina inundavel do Rio Jaramacará, solo arenito, 90 m, 8 Jun. 1980 (fl, imm fr), *G. Martinelli* 6869 (RB 202995) (holotype MG [Acc. No. 92530]; isotypes INPA [Acc. No. 101497], NY [2 sheets, barcodes 02693457 and 01552866], RB



**Figure 75.** Distribution of *Sipaneopsis cururuensis* (star), *S. duckei* (circles), *S. foldatsii* (triangle), *S. huberi* (asterisks), *S. morichensis* (square), and *S. pacimoniensis* (inverted triangle).

[Acc. No. 202995, barcode 00364126], UB [Acc. No. unknown]).

*Subshrubs* to *shrubs* 0.3–1.6 m tall, erect, ascending or rarely decumbent, few- to many-branched; stems stout, woody; young branches sparsely hispid-strigose or appressed to spreading strigose; hairs 0.3–0.6 mm long. *Stipules* free at base or adnate to petioles and basally sheathing, free portion narrowly triangular to narrowly oblong-triangular, or base broadly triangular and distal portion linear to acicular, (2.5–)3–6.5 × 1.5–3.5 mm, or very rarely bifid at apex in older stipules, probably originating from a young entire stipule, the lobes (when present) narrowly triangular to linear, sometimes with a terminal colleter, hispid-strigose to spreading-strigose outside, spreading pubescent at base and glabrous distally or sericeous, with 4–7 colleters inserted just below the margin inside, tips exerted (populations in Serra Aracá), or sparsely pubescent at base and glabrous above or completely sericeous, with (1)4–7 colleters at medio-basal portion inside (populations of Campos do Ariramba). *Leaves* subsessile to petiolate; petioles to 5.5 mm long, hispid-strigose or appressed to spreading-strigose (hairs 0.3–0.5 mm long); blades ovate, narrowly ovate, elliptic-lanceolate, narrowly elliptic to narrowly oblong-elliptic, (2.5–)3.5–8.5 × (0.6–)1–3.5 cm, round, obtuse to attenuate at base, acute at apex, subcoriaceous, margins planar or narrowly revolute, dark green above and pale green below when fresh, drying dark brown above and pale brown below, lamina glabrous and midrib appressed strigose above or lamina and midrib sparsely strigose/scabrous above, lamina glabrous or sparsely strigose and primary and secondary veins sparsely to densely appressed strigose below; secondary veins 6–10 each side of midrib, strongly depressed above, prominent below. *Inflorescences* congested-cymose, branched portion reduced, dichotomously branched, (12–)19–58-flowered, 2.2–10 cm long (including peduncle and flowers), 1–3 cm broad (expanding after anthesis), sometimes frondose, i.e. subtended by leaf-like bracts (i.e., pherophylls), these (when present) narrowly ovate to lanceolate, 1–3.5 × 0.2–1 cm, acute at apex, lamina sparsely strigose and primary and secondary veins densely appressed-strigose below, margins strigose-ciliate; peduncle 0.7–7.5 cm long, densely strigose; bracts subtending secondary branches lanceolate, narrowly elliptic to narrowly oblong-elliptic, (1–)2–4.5 × (0.3–)0.5–1.5 mm, attenuate at base, acute at apex; terminal branchlets scorpioid, 0.5–15 mm long, elongating after anthesis, densely strigose. *Flowers* sessile to short-pedicellate, secundiflorous, central flower sessile to sub-pedicellate, with pedicels (when present) to 1.3 mm long, lateral flowers sessile; bracteoles 2 per flower, 1

opposing and the other subtending each flower, the one subtending the flower smaller than the one opposing the same flower, sessile, lanceolate to narrowly lanceolate, decreasing in size towards branch tip, 1.5–4.5 × 0.5–1.1, acute at apex, sparsely strigose, margins ciliate-strigose. *Hypanthium* globose, broadly-obovoid to obovoid-turbinate, 1–1.5 × 0.8–1.5 mm, densely to sparsely strigose. *Calyx* lobes equal or subequal, ovate, lanceolate to narrowly lanceolate, 1.5–3 × 0.3–0.7 mm, acute at apex, strigose outside, margins strigose-ciliate, glabrous inside; with 2 colleters in each calycine sinus, ellipsoid, acute at apex, 0.25–0.3 mm long. *Corolla* hypocrateriform, pink, 17.5–22 mm long when fully elongated; tube cylindrical, slightly wider at mouth, 12–16 mm long when fully elongated, 0.5–0.7 mm wide at base, 1.6–2 mm wide at mouth, sparsely appressed-strigose and distally more densely so outside, glabrous at basal 3–3.5 mm and sparsely pubescent at upper portion inside; lobes left-contorted, roundish, obovate to elliptic, 4.5–7 × 2–4 mm when fully expanded (perpendicular to the tube), round, obtuse to acute at apex, sparsely appressed strigose outside, glabrous and papillose inside. *Stamens* included, with anthers tips ca. 1–1.3 mm below corolla mouth or about the same length as the tube, inserted 2–3 mm below corolla mouth; filaments 0.3–0.4 mm long; anthers subsessile, oblong-elliptic, 1.5–2.1 mm long, acute at both ends. *Style* included, slightly shorter than or about the same length as the tube, 12–14 mm long when fully elongated, glabrous; style branches narrowly lanceolate, ca. 1 mm long. *Infructescences* a compound dichasium, 6.5–8.5 cm long, terminal branches scorpioid, 1.5–3 cm long. *Fruit* globose, 4–5 mm in diam., appressed strigose, larger than in flowers, 3–4.5 mm long. *Seeds* 6–8 per locule, irregularly ellipsoid to subglobose, 0.9–1.1 × 0.8–1 mm; testa rugose-foveolate, pale brown.

**Notes:** *Sipaneopsis duckei* is similar to *S. maguirei* in several aspects, e.g., stipules entire (not lobed), inflorescences congested-cymose, style included (slightly shorter than or about the same length as the tube), and seeds 6–8 per locule. The former differs from the latter in having stems stout, erect (vs. thin, reclining, decumbent or ascending in *S. maguirei*); stipules (2.5–)3–6.5 × 1.5–3.5 mm (vs. 1.5–3.5 × 1–2 mm); inflorescences 19–58-flowered (vs. 2–8(–13)-flowered); corolla 17.5–20 mm long and tube 12–14 mm long when fully elongated (vs. corolla 21–30 mm and tube 15–22 mm long when fully elongated); and fruits 4–5 × 4–5 mm (vs. 3.5–4 × 3.5–4 mm).

*Sipaneopsis duckei* is also similar to *S. rupicola* (K. Schum.) Steyerl. by being a subshrub to shrub with stout, strigose to strigulose branches, subcoriaceous leaves, and inflorescences 19–58-flowered. The former

differs from the later by the stipules entire or rarely bilobed at older nodes (lobes narrowly triangular to linear, sometimes with a terminal colleter), base broadly triangular and distal portion linear, or narrowly triangular to narrowly oblong-triangular, (2.5–)3–6.5 mm long, hispid-strigose to spreading-strigose outside; whereas, in *S. rupicola* the stipules are triangular, 4–5 mm long, entire and caudate, or triangular at base, with 2 or 3 acute lobes, or the base reduced to a line with 6 or 7 linear lobes, densely strigulose outside. In *Sipaneopsis duckei* the corollas are 17.5–22 mm long when fully expanded, tubes are 12–16 mm long when fully expanded, sparsely appressed-strigose and distally more densely so outside, glabrous at basal 3–3.5 mm and sparsely puberulous at upper portion inside; lobes are broadly obovate, (almost round), obovate to elliptic, 4.5–7 × 2–4 mm when fully expanded (perpendicular to the tube), round, obtuse to acute at apex, appressed strigose outside, papillose inside. In *S. rupicola* the corollas are 16–16.2 mm long when fully expanded; tubes are 11.5 mm long when fully expanded, sericeous-strigose (densely so near the mouth) outside, glabrous at basal 3.5–4 mm and puberulent above and papillose near the mouth inside; the lobes are left-contorted or irregularly imbricate (1 or 2 external), subequal, oblong-obovate, 4.5–4.7 × 2.2–2.5 mm when fully expanded, obtuse to round at apex, sparsely strigulose outside, glabrous inside.

**Eponimy:** The specific epithet of this taxon is dedicated to Adolpho Ducke (1876–1959), a major botanist and entomologist who collected for about 50 years in the Amazon basin of Brazil, often in remote places. This epithet is dedicated to him because he was the first botanist to make botanical collections in Campos do Ariramba, northern portion of the state of Pará, Brazil, where he made the first collection of this species. He described his difficult expedition to reach this locality that took place during 7–27 December 1906, going upstream on the Rio Trombetas, and then its affluent Rio Jaramacará, followed by several days on foot on difficult terrain, in an article published the following year (Ducke, 1907). He collected *Sipaneopsis duckei* Delprete (2018: 130) two days before reaching the open fields of Campos do Ariramba, in an area of *campinarana*, on 20 December 1906 (*A. Ducke s.n. (MG 8020)*, MG, R, RB). The gath-

ering *Martinelli 6869 (RB 202995)*, collected in the same locality, is designated the type of this taxon because it has duplicates deposited in several herbaria (MG, NY [2 sheets], RB, UB).

**Distribution and ecology:** A species occurring in two populations in Campos do Ariramba, state of Pará, and on Serra do Aracá (tepui formation), state of Amazonas, in the northernmost region of Amazonian Brazil (Figure 75). Endemic to white-sand savannas with sparse trees and shrubs, locally called *campinarana*, sometimes seasonally inundated; most collections were made at 80–100 m altitude, and one collection was made at 1200 m altitude on the plateau of the northern massif of Serra Aracá.

**Phenology:** Specimens with flowers in anthesis were collected in January, February, May, July, October and December. Three gatherings with flowers and fruits were collected in January, June and July.

**Suggested conservation status: Not Threatened (NT).** *Sipaneopsis duckei* is known from numerous collections from two distant areas of Amazonian white-sand savannas, Brazil. The two main areas are Campos do Ariramba, state of Pará, and Serra do Aracá (tepui formation), state of Amazonas, in the northern region of Amazonian Brazil. The extent of occurrence (EOO) is therefore not calculable, and the number of individuals per population is unknown. This species occurs in remote areas, without any imminent threat, as white-sand areas are not exploitable for agriculture or cow pastures because of their soils with very low nutrient content. White-sand areas are commonly subjected by seasonal fires during the dry season, and their vegetation is adapted to a fast regeneration. This species is therefore considered Not Threatened (NT) according to IUCN criteria (IUCN 2012, 2019).

**Specimens examined: BRAZIL. Amazonas:** Mun. Barcelos, Parque Estadual da Serra do Aracá, vegetação arbustiva com afloramentos e alagados, com pequena mata na margem de igarapé, 0°55'24"N, 63°25'58"W, 1220 m, 1 Sep. 2011 (fl), *R.C. Forzza et al. 6632* (INPA, MG, RB); Mun. Barcelos, Parque Estadual da Serra do Aracá, Serra do Aracá, acampamento do fosso,

**Figure 76.** *Sipaneopsis duckei*. **A.** Branch with two frondose inflorescences and one infructescence (note last fruit on the infructescence). **B.** Stipule. **C.** Detail of an inflorescence. **D.** Flower at early stage of anthesis. **E.** Flower at intermediate stage of anthesis. **F.** Flower at final stage of anthesis, with corolla lobes reflexed, and receptive stigmas. **G.** Indehiscent fruit, fallen off as dispersal unit. **A–B:** drawn from *Egler 273* (MG); **C, G:** drawn from *Rosa & Lira 2268* (MG); **D–F:** drawn from *Prance et al. 28853* (US). Illustration by Piero Delprete (Reproduced from fig. 2 of Delprete (2018) with permission of copyright holder Magnolia Press).

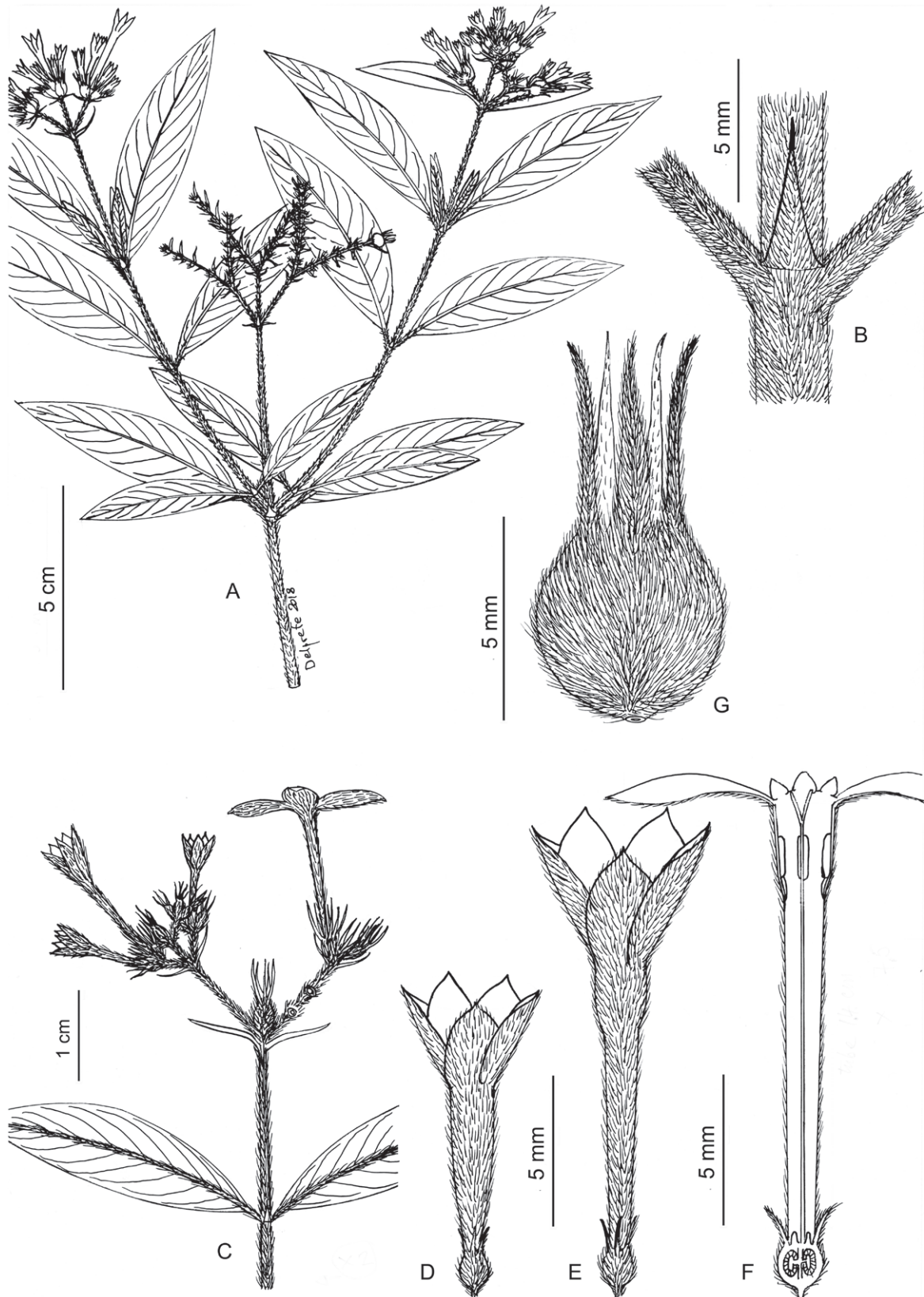


Figure 76.

0°51'47"N, 63°19'59"W, 1020 m, 19 Apr. 2014 (fl, fr), R.C. Forzza et al. 7999 (RB); Rio Aracá, afluente do Rio Negro, campinarana, solo arenoso, 24 Oct. 1952 (fl), R.L. Frões & G. Addison 29039 (IAN); Mun. Barcelos, campina, palmar de *Barcella odora* y sabana sobre arena blanca, en la ribera izquierda del Río Aracá medio, ca. 16 km al SE (en línea recta) de la boca del Río Januari, ca. 0°25'N, 63°23'W, 100 m, Jul. 1985 (fl), O. Huber et al. 10782 (INPA, NY); Mun. Barcelos, Parque Estadual da Serra do Aracá, campos de altitude sobre tepui, 0°52'15"N, 63°25'1"W, 1100 m, 1 Nov. 2011 (fl), G. Martinelli et al. 17267 (RB); Mun. Barcelos, Parque Estadual da Serra do Aracá, margem direita do Igarapé Preto, acima da Cachoeira do El Dorado, 1900 m, 17 Aug. 2011 (fl), M.A. Moraes & E. Fernandez 221 (RB); Mun. Barcelos, Serra do Aracá, Platô Sul, campo rochoso, próximo a curso d'água, 0°51'59"N, 63°19'56"W, 1000 m, 4 May 2016 (fl, fr), M.G.C. Nogueira et al. 498 (MG); base of Serra do Aracá, 0–3 km S of Central Massif, 3 km E of Rio Jauari, white-sand savanna, 0°49'N, 63°19'W, 6 Feb. 1984 (fl), G.T. Prance et al. 28853 (INPA, MG, MO, NY, UB, US); plateau of northern massif of Serra Aracá, 0°51–57'N, 63°21–22'W, 1200 m [confirmed by Prance, pers. comm.], 11 Feb. 1984 (fl), G.T. Prance et al. 28939 (F, INPA, MG, MO, NY, RB, UB, US); 3 km S of central massif of Serra Aracá, 0°49'N, 63°17'W [specimen label reports "65°17'W" which is a typographical error], 100 m, savanna on sand, dominated by *Lagenocarpus*, 18 Jul. 1985 (fl), G.T. Prance et al. 29680 (INPA, MG, NY, UFMT, US); N margin of Rio Aracá, near Serrinha, open savanna on sand, sedge dominated, subshrub with prostrate branches, corolla pink, 0°25'N, 63°23'W, 80 m, 25 Jul. 1985 (fl, fr), G.T. Prance et al. 29798 (HFSL, INPA, MG, NY, US); N margin of Rio Aracá, just above Igarapé Sauadaua, savanna on white sand, 0°13'N, 63°8'W, 80 m, 26 Jul. 1985 (fl), G.T. Prance et al. 29798 (NY; this specimen has different locality and coordinates than the other duplicates of Prance et al. 29798); 3 km S da parte central da Serra Aracá, no caminho entre a pista de baixo e a encostas, e a 8 km E do Rio Jauari, solo silicoso ao redor do campamento, campina lenhoso-graminóide [campina-rana], 0°49'N, 63°19'W, 13 Mar. 1984 (fl, imm fr), W.A. Rodrigues et al. 10653 [Aracá Inventory IL2-6] (INPA, NY); 3 km S da parte central da Serra Aracá, 8 km E do Rio Jauari, solo silicoso ao redor do campamento, campina lenhoso-graminóide [campina-rana], escandente até 0.3 m, 0°49'N, 63°19'W, 13 Mar. 1984 (fl, imm fr), W.A. Rodrigues et al. 10662 [Aracá Inventory IL7-18] (INPA, NY, RB); parte baixa ou pé da Serra Aracá, terreno arenoso ou catinga, planta de 60 cm, flores roseas, 21 Feb. 1977 (fl), N.A. Rosa & M.R. Cordeiro 1562 (MG, NY [2 sheets]); arredores do rio da Serra

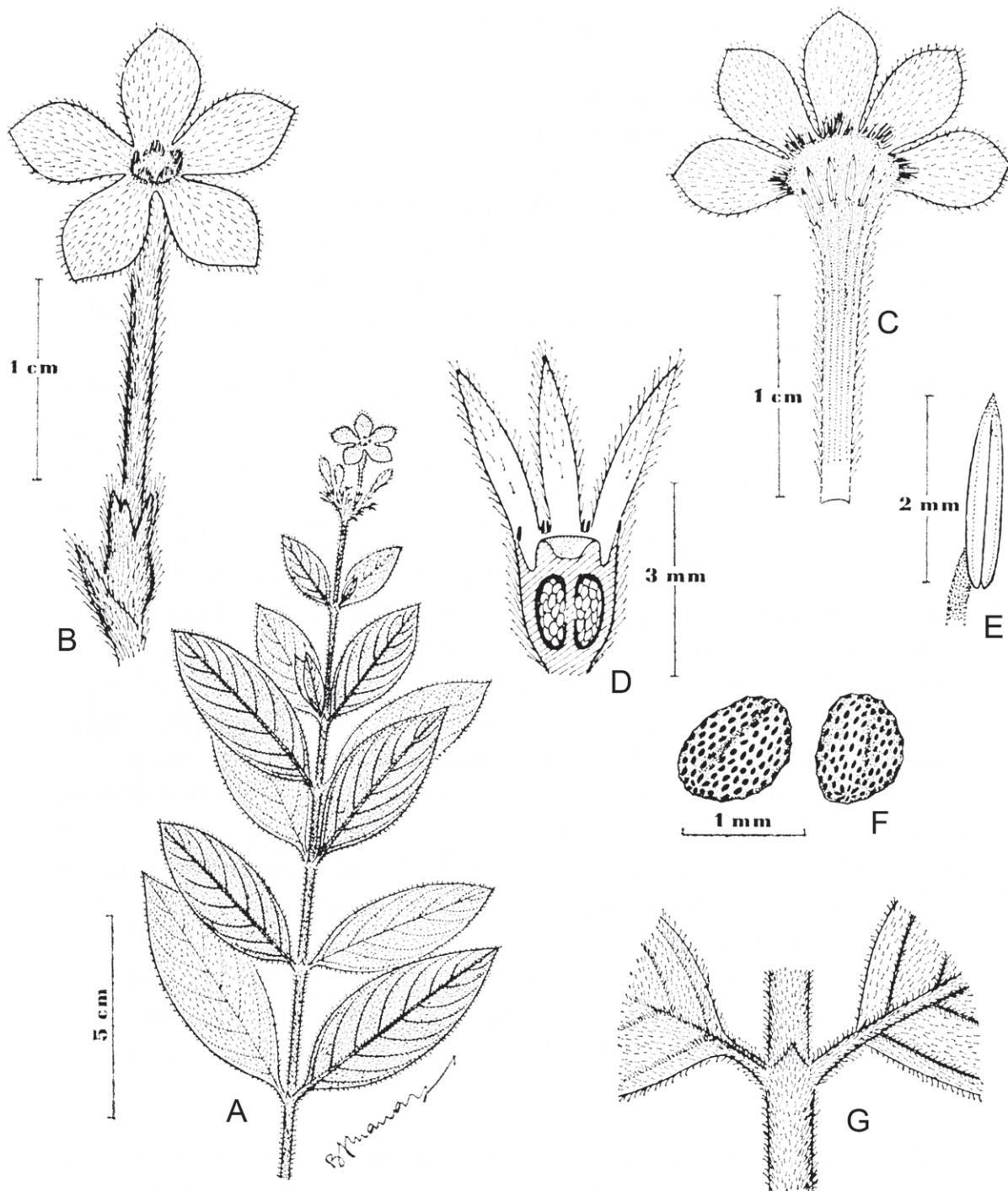
Aracá, erva de 50 cm, flores roseas, 28 Jan. 1978 (fl, fr), N.A. Rosa & S.B. Lira 2268 (MG, NY, UB). **Pará:** Campo do Jamaracará, perto do barracão, Região do Ariramba, 26 May 1957 (fl), G.A. Black et al. 57-19606 (IAN); Alto Ariramba, campinarana, 20 Dec. 1906 (fl), A. Ducke s.n. (MG 8020) (MG, R, RB; the first collection of this species); Mun. Óbidos, Jaramacará, 27 May 1957 (fl), W.A. Egler 273 (MG); Mun. Óbidos, Campos do Ariramba, campos near Igarapé Mutum and Rio Ariramba, white-sand soil, 4 Dec. 1987 (fl), C. Farney & E.F. Batista 2057 (F, NY, US); Mun. Óbidos, 91 km de Oriximiná, nos Campos de Ariramba, entre Rio Jaramacará e Igarapé Mutum, campina aberta, solo areno-pedregoso, ca. 1°10'S, 55°35'W, 4 Dec. 1987 (fl), C.A.C. Ferreira 9769 (INPA, MO, RB); Mun. Oriximiná, Campos do Ariramba, campinas da margem do Rio Jaramacará, afluente arenítico, 80 m, 8 Jun. 1980 (fl, imm fr), G. Martinelli et al. 6929 (INPA, RB).

9-3. *Sipaneopsis foldatsii* Steyerl., Mem. New York Bot. Gard. 17: 288. 1967. (Figures 75, 77).

Steyerl. in Lasser & Steyermark, Fl. Venez. 9: 280–281, fig. 46. 1974.

Type: VENEZUELA. Amazonas: Santa Cruz [ca. 3°15'N, 67°20'W], margen del Río Atabapo, cerca de la desembocadura del Río Atacavi, arbusto fruticoso, flores rosadas, crece en lugar pantanoso durante la estación de lluvias, 4 Sep. 1960 (fl, fr), E. Foldats 3678 (holotype VEN [Acc. No. 63682]).

*Subshrubs* 30–50 cm tall; stems erect or ascending (basal portion sometimes prostrate), densely appressed-strigose; hairs antrorse, white or pale brown. *Stipules* free at base, triangular to broadly triangular, 3–4 × 2–3 mm, acute at apex, rarely bifid at apex in older stipules, the lobes (when present) narrowly triangular, densely strigose outside, inside not seen. *Leaves* petiole; petioles 2–4 mm long, hispid-strigose; blades elliptic-lanceolate, 3–6 × 0.8–3 cm, acute to subobtusate at base, acute at apex, papery to subcoriaceous, dark green, slightly shiny above, pale green below, drying brown to dark olive green above and pale olive green below, densely hispid-strigose above and below; with 5–10 secondary veins each side. *Inflorescences* congested-cymose, expanding after anthesis, with branched portion extremely reduced, 21–39-flowered, 2–4.5 cm long (including peduncle and flowers), 0.6–0.8 cm broad, rachis appressed-strigose; hairs antrorse, white; peduncle 1.7–2.3 cm long. *Flowers* sessile to short-pedi-



**Figure 77.** *Sipaneopsis foldatsii*. **A.** Branch with terminal inflorescence. **B.** Flower at final stage of anthesis, side view. **C.** Dissected flower at final stage of anthesis, with stamens at distal portion of corolla tube. **D.** Longitudinal section of hypanthium, ovary, disk and calyx. **E.** Stamen. **F.** Seeds. **G.** Node with stipule and basal portion of petioles. Illustration by Bruno Manara (Reproduced with permission from Flora de Venezuela vol. 9(1), fig. 46. 1974).

cellate, subtended by one bracteole narrowly triangular to narrowly lanceolate, 1–2 × 0.2–0.4 mm, acute at

apex, appressed-strigose. *Hypanthium* broadly turbinate, ca. 2 × 1.7 mm, densely hispid, hairs erect. *Calyx*



lobes equal or subequal, narrowly lanceolate, 2.5–2.7 × 0.5–0.7 mm, densely hispid outside, margins ciliate with appressed rigid hairs, glabrous inside, acute at apex; with 2 colleters in each calycine sinus, narrowly ellipsoid, acute at apex, 0.2 mm long. *Corollas* hypocra-teriform, pink, 20.5–24 mm long when fully elongated; tube cylindrical and slightly wider at mouth, 14–16 mm long when fully elongated, 0.8 mm wide at base, 2 mm wide at mouth, densely antrorse-hispidulous outside, glabrous on basal 2.5 mm and puberulous at medio-distal portion inside; lobes left-contorted, obovate, 6.5–8 × 3–4 mm when fully expanded (perpendicular to the tube), obtuse to acute at apex, strigose-hispidulous outside, hispidulous inside. *Stamens* included, inserted at 3.5 mm from corolla mouth; filaments 0.4 mm long; anthers sessile, oblong-lanceolate, 2 mm long, round at base, acute at top. *Style* included, ca. 8.5 mm long, glabrous; style branches unknown. *Infructescences* cymose, 3.5–5 cm long, fruits subtended by persistent bracteoles; terminal branches scorpioid, 1.5–2 cm long. *Fruits* urceolate 3.5 × 3 mm, densely sericeous. *Seeds* ca. 12 per locule, ovoid to ellipsoid, 1 × 0.9 mm, foveolate, testa dark brown.

**Notes:** For differentiation of *Sipaneopsis foldatsii* from *S. rupicola*, see notes under the latter.

**Distribution and ecology:** A rare species only known by three collections from a locality near the town of Santa Cruz, at the margin of the Río Atabapo, state of Amazonas, Venezuela (Figure 75). Growing in white-sand savannas seasonally inundated, at about 100 m altitude.

**Phenology:** The three gatherings with flowers and fruits were collected in September and October.

**Suggested conservation status: Critically Endangered (CR).** A very rare species known by three collections from the same locality near the town of Santa Cruz (ca. 3°15'N, 67°20'W), which is at the margin of the Río Atabapo, at the junction of the Río Atacavi, State of Amazonas, Venezuela. The collections were made in September and October 1960, and the specimen labels report this species as a shrub locally abundant, growing in an area that is flooded during the rainy season. This locality is not within a protected area. The size of the population was not reported on the specimen labels, and no recent field observations have been made to assess the status of the conservation of this locality. Therefore, because of its rarity and the small Extent of Occurrence (< 100 km<sup>2</sup>), this species is estimated to

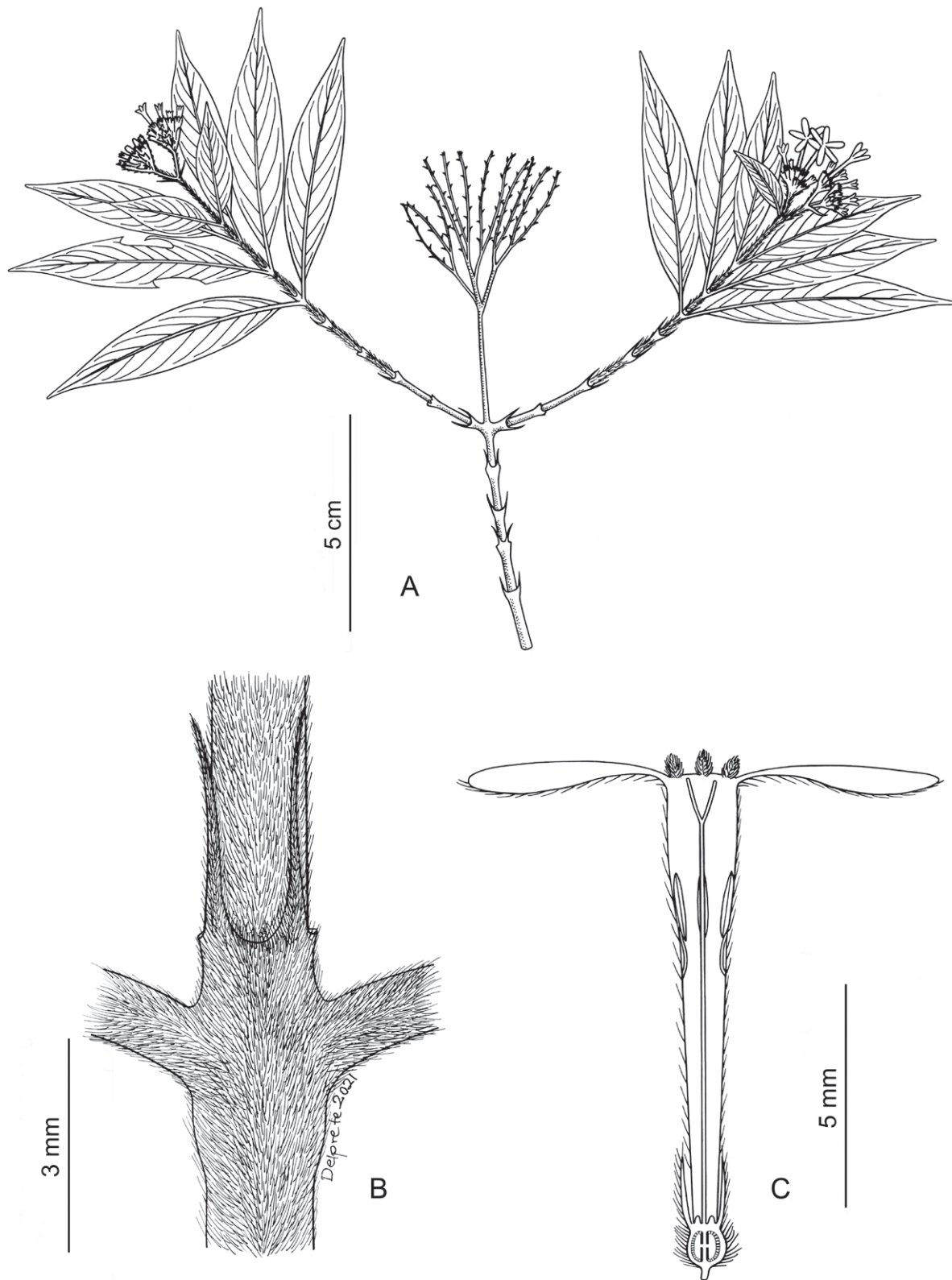
be Critically Endangered (CR) following IUCN criteria (IUCN 2012, 2019).

**Specimens examined: VENEZUELA. Amazonas:** Santa Cruz [ca. 3°15'N, 67°20'W], margen del Río Atabapo, cerca de la desembocadura del Río Atacavi, arbus- to de 50 cm de alto, flores rosadas, crece en lugar pantanoso durante la época de las lluvias, 4 Oct. 1960 (fl, fr), *E. Foldats* 3692 (VEN, paratype); Santa Cruz [ca. 3°15'N, 67°20'W], margen del Río Atabapo, cerca de la desembocadura del Río Atacavi, muy abundante, flores rosadas, crece en terrenos inundados durante la estación lluviosa, 9 Oct. 1960 (fl, fr), *E. Foldats* 3830 (VEN, paratype).

9-4. *Sipaneopsis huberi* Steyerl., *Ernstia* 23: 37, fig. 11. 1984. (Figures 75, 78).

Type: VENEZUELA. Amazonas: Depto. Río Negro, domo rocoso de gneiss granitoide, ubicado en la ribeira derecha del Río Siapa medio, ca. 15 km al E de la Punta N del Cerro Aracamuni, “Arbusto/frútice hasta 1 m de alto, poco frecuente, cáliz verde claro, corola rosada, haz verde muy oscuro mate, envéz verde claro seríceo, frutos globosos de ca. 0.5 cm de diam., verdes”, 1°41'N, 65°41'W, 350 m, 6 Feb. 1981 (fl, fr), *O. Huber & E. Medina* 5786 (holotype VEN [Acc. No. 309632]; isotypes MO [barcode 3235600], NY [barcode 00133329], U [barcode 0006318], US [barcode 00054383]).

*Shrubs* 50–100 cm tall; stems erect or ascending, terete, 1.5–2.5 in diam., densely antrorse-strigose. *Stipules* adnate to petioles and sheathing at basal 3 mm, free portion deltoid to narrowly triangular at base, distally bifid, each lobe linear, 2.5–3 × 0.2 mm, acute at apex, densely strigose outside, sparsely scabrous and with a few colleters at base inside. *Leaves* sessile to short-petiolate; petioles 1–4 mm long, hispid-strigose; blades lanceolate, elliptic-lanceolate to narrowly oblong-lanceolate, 2.5–7.7 × 0.9–2.3 cm, acute to narrowly cuneate at base, acuminate at apex, papyraceous, dark green above, pale green below, drying dark olive green above and pale olive green below, sericeous above and below; with 7–9 secondary veins on each side, impressed above and prominent below. *Inflorescences* congested-cymose when young and unexpanded, during anthesis a compound dichasium, 31–147-flowered, with 5–9 axes dichomously branched, 2–6.5 cm tall, 2–4 cm broad (including peduncle and flowers); terminal secondary branchlets scorpioid, 5–9-flowered, 1–2.5 cm long; rachis densely sericeous; peduncle 2–4 cm long, 1 mm thick, densely sericeous.



**Figure 78.** *Sipaneopsis huberi*. **A.** Branch with inflorescences in anthesis and an old infructescence with fruits fallen off. **B.** Node with stipule and basal portion of petioles. **C.** Flower at final stage of anthesis, with corolla lobes reflexed, dehisced anthers, and receptive stigmas. A–C: drawn from *Huber & Medina 5786* (U, isotype). Illustration by Piero Delprete.

*Flowers* secundiflorous, sessile to shortly pedicellate, subtended by one bracteole; bracteoles linear-lanceolate to setaceous, 2–4 mm long, densely antrorse-strigillose; pedicels to 0.5 mm long, densely sericeous. *Hypanthium* oblong-obovoid, ca. 1 × 1 mm, strigillose. *Calyx* lobes equal, linear-lanceolate, 1.5 × 0.2–0.5 mm, strigose outside, margins ciliate with appressed rigid hairs, glabrous inside, acute at apex; with 2 colletes in each calycine sinus, narrowly ellipsoid, acute at apex, 0.2 mm long. *Corolla* hypocrateriform, 13–14 mm long when fully elongated, densely strigillose outside; tube cylindrical and slightly wider at mouth, 9.5–10 mm long when fully elongated, 0.5 mm wide at base, 1–2 mm wide at mouth, hispidulous outside, glabrous inside; lobes irregularly left contorted in bud, obovate, 4–4.5 × 2.5–3 mm when fully expanded (perpendicular to the tube), round to obtuse at apex, strigose-hispidulous outside, hispidulous inside. *Stamens* included, inserted at 6 mm from base of corolla tube; filaments ca. 1.1 mm long; anthers positioned at upper ¼ of corolla tube, narrowly oblong, 1.5 mm long, round at base, apiculate at top. *Style* (not fully elongated) included, ca. 5.5 mm long, glabrous; style branches lanceolate, ca. 1 mm long. *Infructescences* a compound dichasium 5–8 cm long, with 5–9 axes dichomously branched, with 31–147 fruits, not all of them present at any given time, because falling off as they reach maturity; terminal branchlets scorpioid, 2–3 cm long. *Fruit* globose, ca. 5 mm in diam. *Seeds* unknown.

**Notes:** This species is similar to *Sipaneopsis rupicola* and *S. moricensis* Steyererm. because of its multifid stipules. According to Steyermark (1984c: 39) it is most similar to *S. rupicola* because of the leaf shape and inflorescence type, from which it differs by the calyx lobes densely strigose outside, the longer style, and the leaf blades densely strigose-sericeous on both sides.

*Sipaneopsis huberii* Steyererm. differs from *S. morichensis* by the stems densely antrorse-strigose (vs. densely ochroleucous-villous in *S. morichensis*), stipules densely strigose outside, with two linear lobes 2.5–3 mm long (vs. ochroleucous-villous (hairs spreading and/or acropetally oriented) outside, topped by (1–)3–4 linear lobes 8–10 mm long), leaf blades sericeous above and below (vs. ochroleucous-strigose above, densely ochroleucous-villous below), corolla 13–14 mm with tubes 9.5–10 mm long when fully elongated, hispidulous outside, and lobes strigose-hispidulous outside (vs. corolla 14.5–18 mm long with tubes 11–12 mm long when fully elongated, densely grayish-strigose outside, and lobes sericeous or appressed-pilose outside).

**Distribution and ecology:** Known from four col-

lections from the southern portion of the Venezuelan state of Amazonas (Figure 75). Growing on flat rocky outcrops (“lajas”) in savannas formations, at 200–420 m altitude.

**Phenology:** Specimens with flowers in anthesis were collected in February and November, and specimens with flowers and fruits in February and June.

**Suggested conservation status: Endangered (EN).**

A rare species known from four collections from four localities in the Río Negro Department, southern portion of Venezuelan state of Amazonas, Venezuela. The first collection, the type, was made in February 1981, on a rocky dome of granitic gneiss, 1°41'N, 65°41'W, 350 m, located at the margin of the Río Siapa Medio, ca. 15 km E the N pick of Cerro Aracamuni. The specimen label reports this species as an infrequent shrub.

The second collection, a paratype, was made in June 1981 in the central portion of the plateau of the Serranía del Vinilla, 2°26'N, 65°20'W, 420 m, in hilly savanna, at ca. 20 km SW of the town of Mavaca. The specimen label reports this species as a locally frequent subshrub growing in humid savanna.

The third collection was made in 1987 near the Río Siapa, near the base of Cerro Aracamuni, 1°39'N, 65°40'W, at 250 m altitude, growing on a flat rocky outcrop. The frequency of this species in this locality was not reported on the specimen label.

The fourth and most recent collection was made in February 1990 near the Río Metacuni, 3°2'N, 65°12'W, at 200–230 m altitude, also growing on a flat rocky outcrop. The frequency of this species at this locality was not reported.

All the above described localities are within preserved areas, either within the Parima Tapirapecó National Park, the Serra da Neblina National Park, or the Reserva de Biosfera. This region is inhabited by indigenous people of the Yanomami ethnic group, who are allowed to hunt and cultivate traditional crops within the region. The size of the populations was not reported on the specimen labels, and no recent field observations have been made to assess the conservation status of these localities. Due to its rarity, its extent of occurrence (EOO) of ca. 3500 km<sup>2</sup>, and human pressure in the area of occurrence, this species is treated as Endangered (EN) following IUCN criteria (IUCN 2012, 2019).

**Specimens examined: VENEZUELA. Amazonas:** Depto. Río Negro, sabana collinosa en el sector central de una altiplanicie en la Serranía del Vinilla, ca. 20 km SW of Mavaca, 2°26'N, 65°20'W, 420 m, 13 Jun. 1981 (fl,

fr), *O. Huber* 6192 (COL, INPA, NY, VEN, paratypes); Dpto. Río Negro, Río Siapa near base of Cerro Aracumuni, large, open laja surrounded by medium to tall forest, 1°39'N, 65°40'W, 250 m, 4 Nov. 1987 (fl), *R. Liesner* & *G. Carnevali* 22732 (MO, NY, U); Río Metacuni, selvas húmedas de tierra baja de rebalse y de lomerio bajo, de laja y piedra, 3°2'N, 65°12'W, 200–230 m, 2 Feb. 1990 (fl), *B. Stergios* & *J. Velazco* 14562 (NY, PORT).

9-5. *Sipaneopsis maguirei* Steyerl., Mem. New York Bot. Gard. 17: 287. 1967. (Figures 79–82).

Steyerl. in Lasser & Steyerl., Fl. Venez. 9: 277–278. 1974.

Type: VENEZUELA [“Colombia”]. Amazonas: Río Atabapo, between San Fernando de Atabapo and Caño Temi, Cacagual Savanna, 135 m, 13 Sep. 1957 (fl, fr), *B. Maguire*, *J.J. Wurdack* & *W.M. Keith* 41438 (holotype NY [barcode 00133330]; isotype NY [barcode 00133331]).

(=) *Sipaneopsis wurdackii* Steyerl., Mem. New York Bot. Gard. 17: 288. 1967

Steyerl. in Lasser, Fl. Venez. 9: 278–279. 1974.

Type: VENEZUELA. Amazonas: Savanna on L bank of Caño Hechimoni, 8 km above mouth, locally frequent, 100–130 m, 9 Feb. 1954 (fl), *B. Maguire*, *J.J. Wurdack* & *G.S. Bunting* 37639 (holotype NY [barcode 00133335]; isotype NY [barcode 00133336]).

*Subshrubs* (9–)18–40(–70) cm tall, few-stemmed, with a central perennial, woody taproot; stems thin, woody, ascending, reclining or rarely decumbent; young branches often reddish, canescent or sparsely to densely strigose; hairs 0.1–0.3 mm long, becoming glabrate with age. *Stipules* adnate to petioles, sheathing at basal 2–3 mm, free portion broadly to narrowly triangular, 1.5–3.5 × 1–2 mm, acute or acuminate at apex, canescent, strigulose or glabrous and strigulose on margins outside, sericeous with 2–3 colleters inserted on each side of the central lobe near the margin inside; margins pubescent. *Leaves* shortly petiolate to subsessile; petioles 1–3 mm long, appressed-strigulose (hairs 0.1–0.3 mm long), often reddish when fresh; blades narrowly oblong-lanceolate, oblanceolate, elliptic-lanceolate to linear-lanceolate, 1–6 × 0.4–1.5 cm, acute, obtuse to round at base, acute to acuminate at apex, papyraceous to subcoriaceous, dark green and slightly shiny above, pale green with when fresh, venation red-

dish to vinose-red above and below when fresh, blades drying brown above and pale olive green below, glabrous or sparsely strigulose above, glabrous and primary and secondary veins sparsely appressed pubescent or strigulose below; with 3–8 secondary veins on each side, slightly depressed above, prominent below; margins planar or narrowly revolute. *Inflorescences* congested-cymose, branched portion extremely reduced, 2–8(–13)-flowered, 3.5–4.5 cm tall, (including peduncle and flowers), 0.6–1.3 cm broad, short-strigose; terminal branchlets 0.5–0.7 cm long; peduncle 0.3–3.5 cm long, canescent or strigulose; bracts subtending basal secondary branches of inflorescence linear-lanceolate, 3.5–6 mm long, shortly strigose outside, margins hispidulous-ciliate. *Flowers* sessile to short-pedicellate, subtended by one bracteole, linear-lanceolate, 1–1.3 × 0.2–0.3 mm, acute at apex, sparsely hispid; central flower with pedicel 0.4–0.5 mm long, lateral flowers sessile. *Hypanthium* turbinate or subcampanulate-urceolate, 1–1.5 × 1.2–1.5 mm, densely gray-strigose or sericeous. *Calyx* lobes equal or subequal, lanceolate, 2–3 × 0.5–0.7 mm, acuminate, gray-strigose outside, margins hispidulous-ciliate, glabrous inside, acute at apex; with 1 colleter in each calcine sinus, narrow cylindro-conical, acute at apex, 0.3 mm long. *Corolla* hypocrateriform, pink, turning pale pink to white after anthesis, 21–30 mm long when fully elongated; tube cylindrical and slightly expanded towards the mouth, 15–22 mm long when fully elongated, 1 mm wide at base, 2 mm wide at mouth, densely strigose or canescent outside, glabrous at basal 3–3.5 mm and sparsely puberulous at upper portion inside; lobes left-contorted, obovate, 4.5–9 × 3–4.2 mm when fully expanded (perpendicular to the tube), obtuse to acute at apex, strigulose outside, glabrous or sparsely strigulose and papillose inside. *Stamens* included, anther tips 0.3–1(–3) mm below corolla mouth, filaments inserted at 3–7 mm below corolla mouth, 2–3 mm long; anthers oblong-lanceolate, 1.5–2.5 mm long, acute at top, acute or round at base. *Style* included or rarely partially exerted (only style branches tips exerted), slightly shorter than or about the same length as the tube, 15–20 mm long when fully elongated, glabrous; style branches narrowly lanceolate, 0.6–1 mm long. *Infructescences* congested-cymose, 4.5–5.5 cm long, terminal branches 1–1.5 cm long. *Immature fruits* reddish. *Fruits* subglobose, 3.5–4 × 3.5–4 mm, appressed-strigulose. *Seeds* 6–8 per locule, subglobose, 0.7–1 mm diam.; testa rugose-foveolate, dark brown.

**Notes:** In the original description of *Sipaneopsis wurdackii* Steyerl., Steyerl. (1967: 288) wrote

that the corollas are 15–25 mm long, with tubes 15–18 mm long and lobes 4.5–7 mm long. An error occurred in that description, as the tube and lobe length do not add up to the minimal length given for the corolla (i.e., 15 mm), or, most likely, the minimal length supplied by Steyermark might refer to corollas not completely expanded. Steyermark's inconsistency might be due to the fact that in *Sipaneopsis* the corolla lobes open before the tube is completely elongated (i.e., before anthesis), and they remain erect and slowly elongating while the corolla is still expanding, and they become perpendicular to the tube and finish their expansion only after the corolla tube is completely elongated. On the type specimens of *S. wurdackii* (Maguire *et al.* 37639), fully expanded corollas have tubes 16–18 mm long and lobes 5–6 mm long, adding up to corollas 21–24 mm long.

Steyermark (1967: 285; 1974: 273–274), in the key to species of *Sipaneopsis*, distinguished *S. maguirei* from *S. wurdackii* by the corolla lobes glabrous and papillose within (vs. densely strigillose within in *S. wurdackii*) and leaf blades 3–6 cm long (vs. 1–2.7 cm long). However, after careful examination of the type specimens and additional material from Venezuela, Delprete and Steyermark (2004f: 833–835) concluded that these characters are found on a continuous morphological and geographical gradient. For example, specimens of *Davidse et al.* 17391 (MO, US), identified by Steyermark as *S. wurdackii*, have linear leaves 2–4 × 0.3–0.4 cm, and corolla lobes glabrous and papillose within. Therefore, I confirm that the two taxa are conspecific.

**Distribution and ecology:** This is the most widespread and most collected species of the genus. Known from numerous gatherings in Venezuelan state of Amazonas and in the Brazilian state of Amazonas, one collection in the Brazilian state of Rondônia, and several collections in the Colombian departments of Guainía and Vaupés (Figure 81). Commonly found in Amazonian open field savannas, dominated by grasses and sedges, or shrubby savannas (Figure 80A), herbaceous layer with sparse shrubs and treelets, in Brazil called “campinas” or “campinaranas”, respectively; growing on white sand, on white sand intermixed with black granitic sand (“salt & pepper sand”), or on white sand intermixed with clay, sometimes associated with *Brocchinia prismatica* L.B. Sm., often in areas seasonally inundated; at 55–984 m altitude.

**Phenology:** Due to the extended flowering period, it is common to see flowers and fruits on the same inflorescence. Such specimens were collected the whole year around.

**Suggested conservation status: Least Concern (LC).** This species is amply distributed in Amazonian Colombia (Guainía and Vaupés), Venezuela (Amazonas) and Brazil (Amazonas and Rondônia), and is known from numerous collections. It grows in open fields or shrubby savannas within the Amazon Basin, in Brazil called “campinas” or “campinaranas” respectively, and in Colombia and Venezuela called “catingas”. It sometimes forms large populations with sparse individuals (pers. obs., e.g. Delprete *et al.* 7451–7453). Because of its wide extent of occurrence (EOO) and its numerous collections, this species belongs the Least Concern (LC) category, following IUCN criteria (IUCN 2012, 2019).

**Specimens examined: COLOMBIA. Guainía:** Mun. Puerto Inírida, comunidad de Caño Vitina, ecotono entre bosque y las sabanas naturales de arenas blancas, arbustal de hasta 6–8 m de altura, denso, alta radiación solar hasta el suelo, suelos con mal drenaje y encharcados en época de lluvias, alta presencia de flor de Inírida (*Guacamaya superba*), hierba de 35 cm, flores rosadas, 9 Jun. 2015 (fl), A. Barona *et al.* 862 (COAH); Mun. Inírida, Río Inírida, sabana de arena blanca, Caño Vitina (margen derecha del resguardo de Caranacoa), 10 km N de Inírida, hierba de 40 cm, tallos jóvenes y flores rosadas, 170 m, 3°56'N, 67°55'W, 8 Sep. 2002 (fl), D. Cárdenas & M. Avellaneda 13484 (COAH); Mun. Inírida, Sector del Caño Culebra, sabanas naturales de arena blanca, con presencia de Flor de Inírida (*Schoenoecephalum teretifolium* y *Guacamaya superba*), hierba de 20 cm, flor rosada, 3°46'49"N, 67°46'49"W, 120 m, 3 Mar. 2005 (fl), D. Cárdenas & G. López 16331 (COAH); Mun. Inírida, sector comprendido entre Caño Inírida y Caño Culebra, sabanas naturales de arena blanca, con presencia de arbustales y sabanas abiertas, hierba de 45 cm, flor lila, 3°48'32"N, 67°51'29"W, 120 m, 4 Mar. 2005 (fl), D. Cárdenas López 16435 (COAH); Mun. Inírida, Comunidad de Guamal, arbustal (catinga) sobre arenas blancas y sabanas naturales y pequeños bosques, hierba de 25 cm, flor rosada, 3°52'20"N, 67°51'08"W, 100–150 m, 5 Jan. 2007 (fl), D. Cárdenas & J.G. Ramírez 20466 (COAH); Mun. Inírida, Comunidad de Guamal, arbustal (catinga) sobre

**Figure 79.** *Sipaneopsis maguirei*. A. Habit. B. Node with stipule. C. Portion of a stem with a leaf pair. D. Inflorescence with flowers in different developmental stages. E. Inflorescence with fully expanded branches. F. Flower at initial stage of anthesis. G. Flower at intermediate stage of anthesis. H. Flower at final stage of anthesis. J. Fruit. A–J: drawn from Delprete *et al.* 7452. Illustration by Piero Delprete (Reproduced from fig. 2 of Delprete (2017) with permission of copyright holder Magnolia Press).

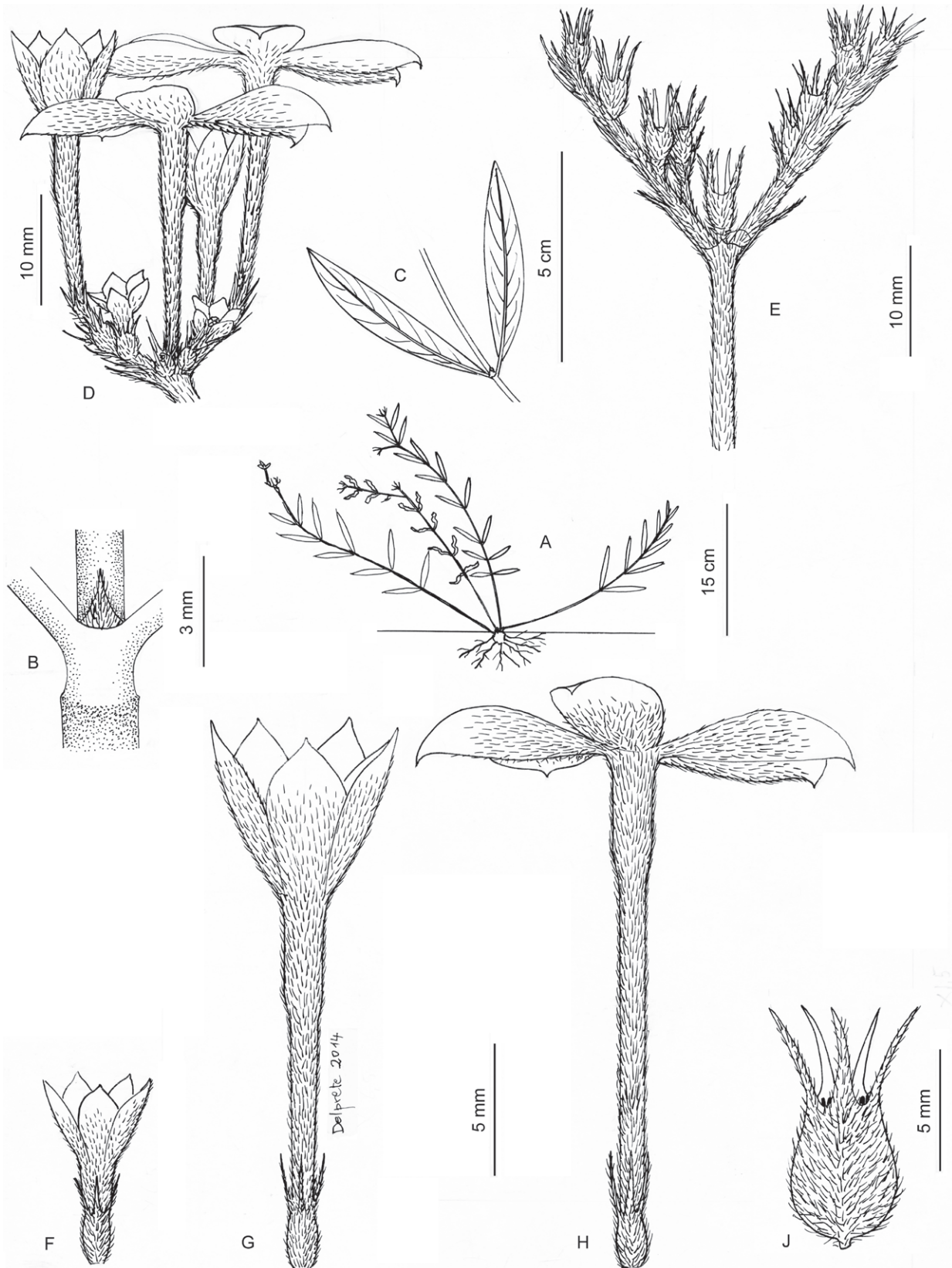
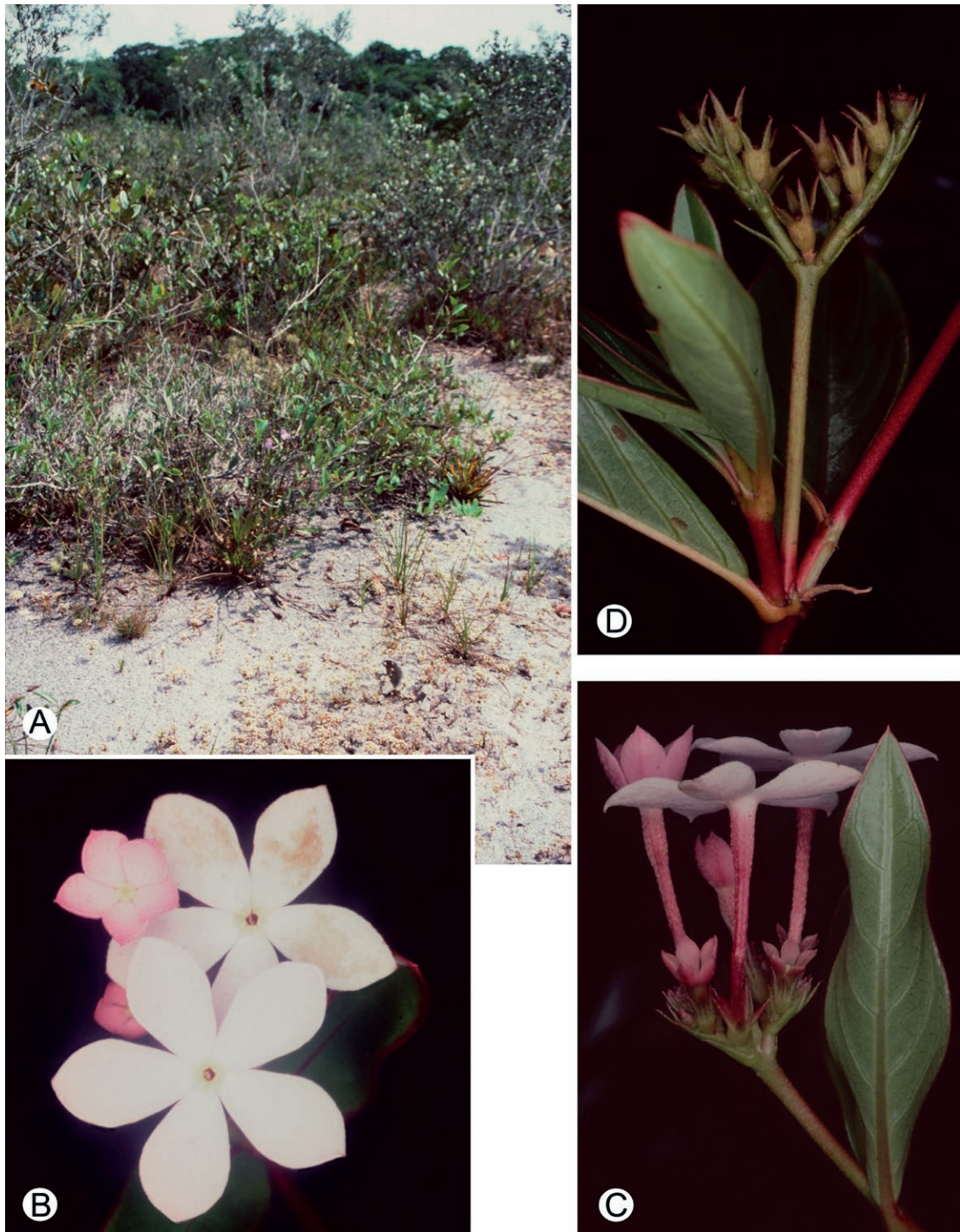


Figure 79.



**Figure 80.** *Sipaneopsis maguirei* **A.** Habitat. White-sand savanna with sparse vegetation. **B.** Inflorescence, top view. Note flowers at various stages of the flowering process. Young corollas pink, with lobes already opened and basal portion of lobes with appendages appressed against each other. The other two corollas completely expanded and opened, with lobes perpendicular to the tube, and basal appendages free from each other. **C.** Same inflorescence of B, side view. Note flowers at various stages of the flowering process. Short corollas, pink, with lobes already opened. One corolla at intermediate stage, with tube completely elongated, and lobes ascending (not completely reflexed). The other two corollas opened, with lobes perpendicular to the tube, and basal appendages free from each other. And two corollas with lobes completely expanded and perpendicular to the tube. **D.** Inflorescence with immature fruits. Photos taken by Piero Delprete on 7 January 2001, Mun. San Fernando de Atabapo, Amazonas State, Venezuela, where *Delprete et al.* 7451–7453 were collected.

arenas blancas y sabanas naturales y pequeños bosques, hierba de 25 cm, flor rosada, 3°52'20"N, 67°51'08"W, 100–150 m, 5 Jan. 2007 (fl), *D. Cárdenas & J.G. Ramírez* 20469 (COAH); Mun. Inírida, Corregimiento de Cacagual, comunidad Cacagual, sabana de arenas blancas con arbustales y matorrales, sufrutice de 20 cm, tallos rojizos, flores rosadas, 3°31'43"N, 67°25'53"W, 11 May 2007 (fl), *D. Cárdenas et al.* 20723 (COAH); Mun. Puerto Inírida, comunidad de Caño Vitina vegetación en sabana natural de arenas blancas, hierba de 30 cm, flores rosadas, 150 m, 3°43'48"N, 67°50'3"W, 1 Dec. 2013 (fl), *D. Cárdenas et al.* 44045 (COAH); Mun. Inírida, comunidad de Caño Vitina, sabanas naturales de arenas blancas, vegetación a borde de bosque, hierba de 25 cm, flor morada, 3°43'48"N, 67°50'3"W, 150 m, 8 Jun. 2015 (fl) (fl), *D. Cárdenas et al.* 44326 (COAH); Mun. Puerto Inírida, comunidad de Caño Vitina, sabanas naturales de arenas blancas, hierba de 15 cm, flores rosadas, 3°48'21"N, 67°49'19"W, 150 m, 9 Sep. 2014 (fl), *M. Rodríguez et al.* 1514 (COAH); Mun. Inírida, via Inírida–Caño Vitina, Sitio Curva de Los Pepes, sabanas naturales de arenas blancas, dominadas por varias especies de Cyperaceae, Xyridaceae y Rapateaceae, hierba, ejes de la inflorescencia, brácteas y tallos morados, flores

rosadas, 110 m, 3°48'45"N, 67°52'20"W, 7 Apr. 2006 (fl), *N.R. Salinas et al.* 601 (COAH). **Vaupés:** Mitú and vicinity [ca. 1°11'N, 70°10'W, ca. 180 m], lower Río Kubiyú, sandstone savanna, 1 Jul. 1976 (fl), *J.L. Zarucchi & M.J. Balick* 1796 (F, MO, US).

**VENEZUELA. Amazonas:** Depto. Casiquiare, Caño San Miguel, Sector Las Tinajas y el Caño Iqueven, sabanas (dominancia de Rapateaceae) con bosque bajo sobre suelos quartzosos, 2°39'N, 66°45'W, 160 m, 25 Apr. 1991 (fl), *G. Aymard* 9188 (MO, NY); Depto. Atabapo, SE bank of the middle part of Caño Yagua at Cucurbital de Yagua, inundated sabaneta, 3°36'N, 66°34'W, 120 m, 8 May 1979 (fl), *G. Davidse et al.* 17391 (MO, US); Mun. San Fernando de Atabapo, Indigenous Community of Minicia Nuevo, sabaneta inundavel, at the moment of collection with dry soil, exposed white sand intermixed black granitic sand ("salt & pepper sand"), vegetation dominated by sparse shrubs 2–3 m tall, 3°55'N, 67°26'W, 120 m, 7 Jan. 2001 (fl, imm fr), *P.G. Delprete et al.* 7451 (CAY, NY, TFAV, VEN), 7452 (CAY, MO, NY, TFAV, VEN), 7453 (CAY, MG, TFAV, VEN); Depto. Atabapo, sabanas y bosques ribereños en los alrededores de Canaripó, en la margen izquierda (S) del Bajo Río Ven-

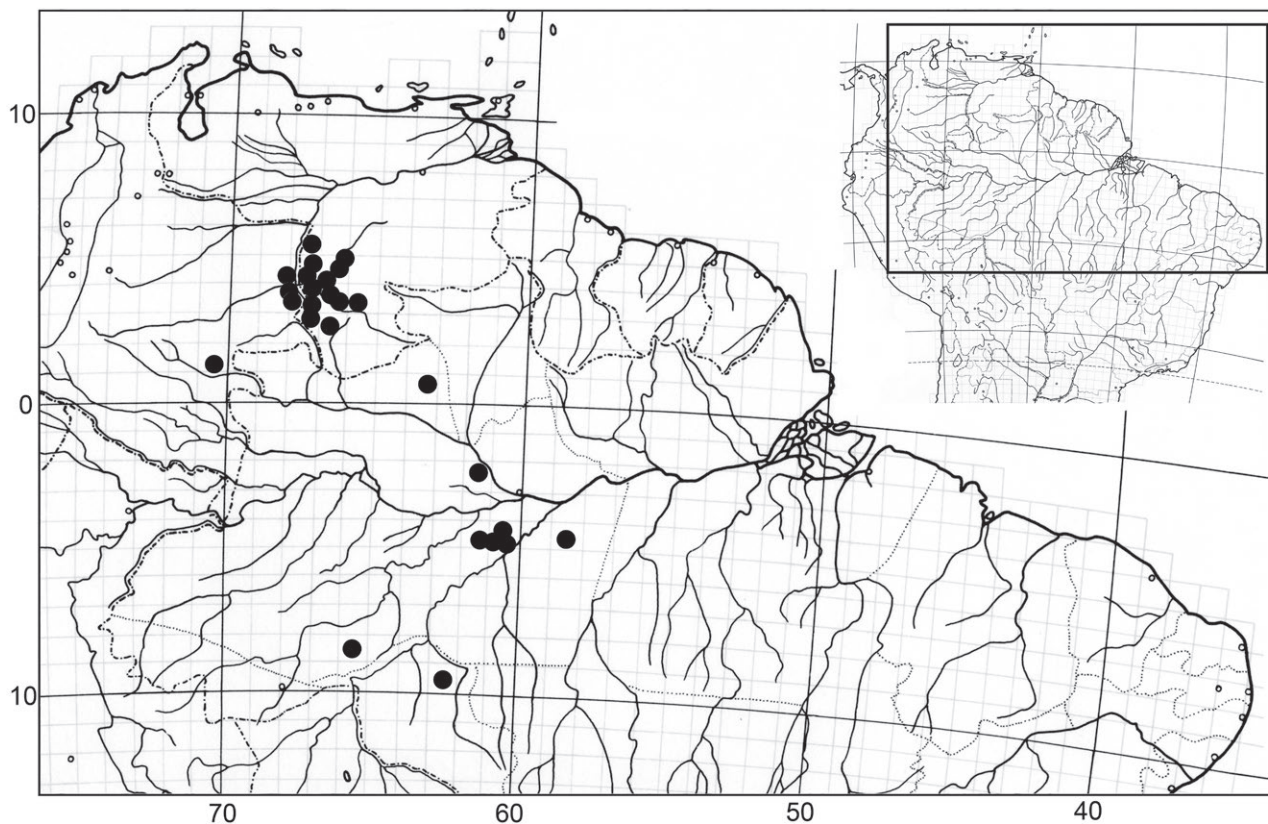
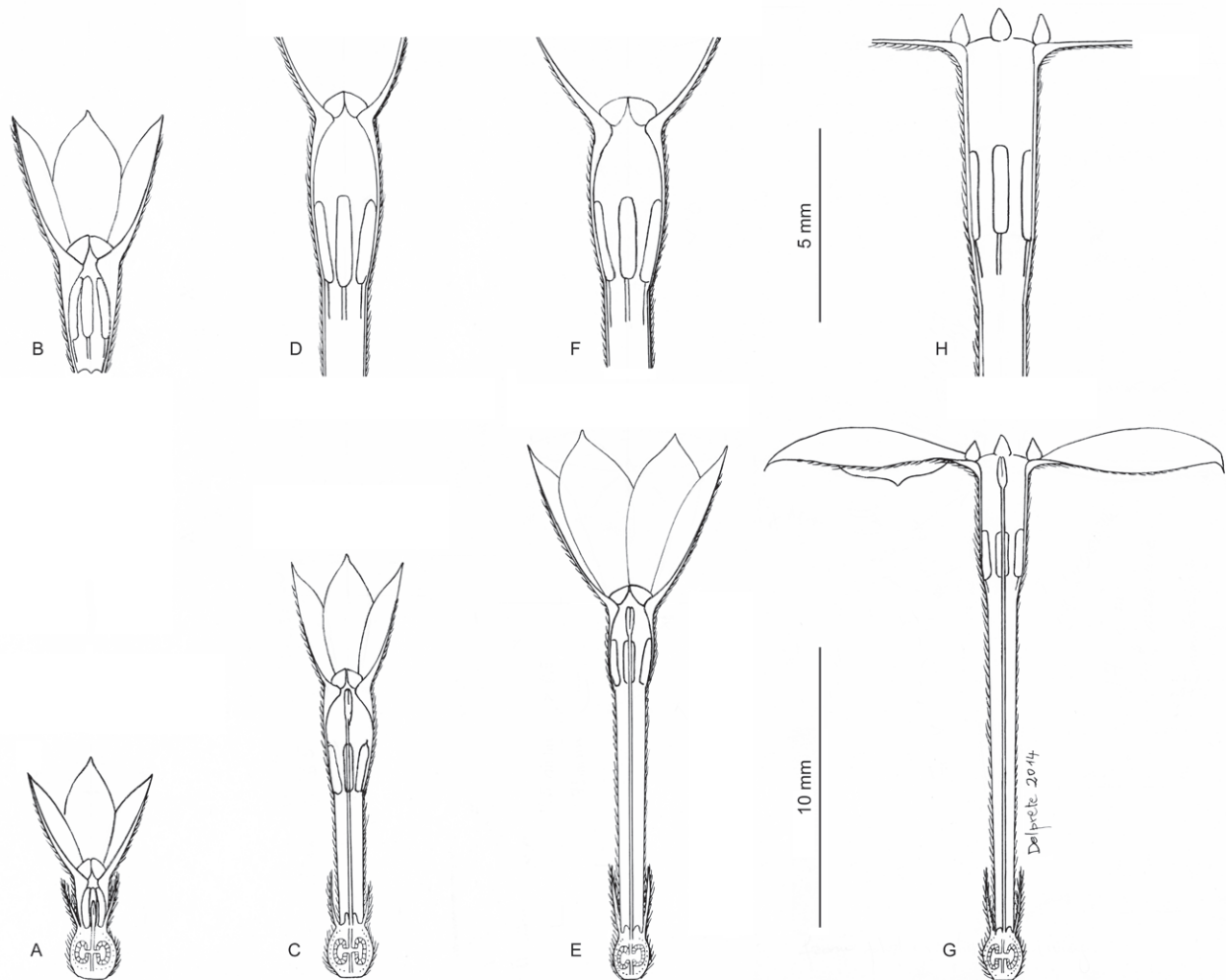


Figure 81. Distribution of *Sipaneopsis maguirei*.



tuari, ca. 20 km al E de la confluencia con el Río Orinoco, sabana inundada con hummocks (“tatucos”) por debajo de morichal al S de la pista de aterrizaje, 4°3’N, 66°49’W, 98 m, 30 May 1978 (fl), *O. Huber 1910* (NY); Depto. Atabapo, tercera sabana al pié del Cerro Yapacana, hierba común al borde de los motículos en la sabana anegadiza, cáliz rojo carmesí, corolla rosada, 3°38’N, 66°52’W, 100 m, 3 Jun. 1978 (fl), *O. Huber 2021* (NY); Depto. Atures, sabana en la ribera N (derecho),

del Río Ventuari, frente al caserío Carmelitas, 4°13’N, 66°30’W, 100 m, 22 Aug. 1978 (fl), *O. Huber 2420* (NY); Depto. Atabapo, sabana de Minicio, en la ribera S (Izquierda) del Río Orinoco, 3°56’N, 67°32’W, 23 Aug. 1978 (fl), *O. Huber 2512* (NY); Depto. Atabapo, sabanas en las cabeceras del Caño Yagua, 3°57’N, 66°27’W, 120 m, 26 Aug. 1978 (fl), *O. Huber 2691* (NY); Depto. Atabapo, pequeña sabanita distante 15 min al SE del Sitio Chipital, ubicado en la ribera izquierda (S) del Caño Yagua, ca.



**Figure 82.** *Sipaneopsis maguirei*, flowering process. **A, B.** Flower at initial stage of anthesis, with corolla lobe basal appendages appressed against each other. **C, D.** Longitudinal section of flower at intermediate stage of anthesis. **C.** Longitudinal section. **D.** Longitudinal section of distal portion of corolla tube and basal portion of lobes, with appendages appressed against each other. **E, F.** Longitudinal section of flower at successive intermediate stage of anthesis. **E.** Longitudinal section, with tube and lobes further elongated. **F.** Longitudinal section of distal portion of corolla tube and basal portion of lobes, with appendages appressed against each other. **G, H.** Longitudinal section of flower at final stage of anthesis, with mature anthers and style branches not receptive (still appressed to each other), allowing visitors and pollinators to access the corolla tube and nectar disk. **G.** Longitudinal section of flower, with lobes spreading perpendicularly to the tube, and erect appendages not touching each other. **H.** Longitudinal section of distal portion of corolla tube and basal portion of lobes, with appendages not touching each other. Drawing based on field observations, photographs and pickled flowers (Delprete *et al.* 7452). Drawn by Piero Delprete (Reproduced from fig. 3 of Delprete (2017) with permission of copyright holder Magnolia Press).

15 km (el línea recta) río arriba desde la boca, 3°29'N, 66°41'W, 120 m, 6 Dec. 1978 (fl), *O. Huber & S.S. Tillett 2900* (NY); Depto. Atabapo, extensas sabanas al NE y E del Cerro Cucurito, ribera SE del medio Caño Yagua, sabana de *Brocchinia prismatica*, 3°36'N, 66°34'W, 120 m, 17 Jan. 1979 (fl), *O. Huber 3111* (NY); Depto. Atures, sabana ubicada al pie SE del Cerro Moriche, 4°43'N, 66°22'W, 120 m, 19 Feb. 1979 (fl), *O. Huber 3199* (NY); Depto. Atabapo, Caño Caname (afrente derecho (oriental) del Medio Río Atabapo), sabanita al N del Medio Caño Caname, ca. 18 km E de la boca, 3°40'N, 67°22'W, 100 m, 29 Apr–4 May 1979 (fl), *O. Huber et al. 3748* (NY); Depto. Atures, sabana ubicada a ca. 5 km al S del Río Autana y ca. 15 km SSW del Cerro Autana, 4°45'N, 67°35'W, 100 m, 26 Jun. 1979 (fl, fr), *O. Huber 3830* (NY); Depto. Atures, sabana ubicada a ca. 8 km al E del Río Orinoco, ca. a la altura de Morganito, 5°6'N, 67°46'W, 90 m, 3 Jul. 1979 (fl), *O. Huber 4109* (NY); Depto. Atabapo, sabanas a ca. 30 km al W de la Seranía El Tigre, en la region del Alto Caño Yagua, 3°51'N, 66°27'W, 130 m, 29 Feb. 1980 (fl), *O. Huber 4854* (NY); Depto. Atabapo, sabana a ca. 10–12 km W de Esmeralda, en la ribera derecho (N) del Río Orinoco, 3°11'N, 65°37'W, 125 m, 7 Mar. 1980 (fl, fr), *O. Huber 5053* (NY); Depto. Casiquiare, sabana y caatinga abierta a ca. 2–3 km al SE del Bajo Río Guasacavi, 3°8'N, 67°30'W, 90 m, 10 Mar. 1980 (fl), *O. Huber 5127* (NY); Depto. Atabapo, pequeña sabana ubicada a ca. 2 km al S del Medio Río Puruname, al SE del caserío de Puruname, 3°20'N, 66°32'W, 100 m, 22 Jul. 1980 (fl, fr), *O. Huber & S. Tillett 5456* (INPA, NY); Depto. Atures, sabana ubicada en la ribera izquierda (S) del Río Guayapo medio, 4°14'N, 67°22'W, 100 m, 27 Jul. 1980 (fl), *O. Huber & S. Tillett 5499* (INPA, NY); Depto. Atures, sabanas ubicadas a ca. 4 km al N del Río Pipapo Medio, ca. 5 km al W del Macizo del Sipapo, 4°36'N, 67°12'W, 120 m, 28 Jul. 1980 (fl, fr), *O. Huber & S. Tillett 5589* (NY); Depto. Sasiquire, extensas sabanas ubicadas a ca. 20 km al NW de Yavita, en las cabeceras del Caño Pimichín, 3°1'N, 67°33'W, 120 m, 11 Feb. 1981 (fl), *O. Huber & E. Medina 5945* (NY); Río Orinoco, Savanna N. 3 at NW base of Cerro Yapacana [ca. 4°0'N, 66°35'], 130 m, 1 Jan. 1951 (fl), *B. Maguire et al. 30549* (F, NY, US, paratypes of *S. maguirei*); Río Atabapo, between San Fernando de Atabapo and Caño Temi, savanna 1 km W of Cacagual, 130 m, 19 Nov. 1953 (fl, fr), *B. Maguire et al. 36280* (NY, P, R, paratypes of *S. maguirei*); Río Guainía, Sabana El Venado, on L bank of Caño Pimichín [ca. 2°74'N, 67°56'W], frequent, 120–140 m, shrub to 0.2 m, corolla pink, 23 Nov. 1963 (fl), *B. Maguire et al. 36353* (NY, paratype of *S. wurdackii*); Río Guainía, Sabana El Venado, on L bank of Caño Pimichín [ca. 2°74'N, 67°56'W], frequent, 140

m, 14 Apr. 1953 (fl), *B. Maguire & J.J. Wurdack 35564* (F, NY, paratype of *S. wurdackii*); Cerro Yapacana, savanna 4, 3°45'N, 66°50'W, 140 m, forming herbaceous dense mat, 14 Mar. 1987 (fl), *K.J. Systma et al. 5122* (NY); Savannas near Santa Cruz, a small village on the Río Atabapo 1 km N of the confluence of the Río Temeni and the Río Atacavi, 17–18 Nov. 1979 (fl), *W.W. Thomas & G.K. Rogers 2680* (NY); area of San Fernando de Atabapo (4°2'N, 67°42'W), at the confluence of Atabapo and Guaviare Rivers with the Orinoco, Caño La Vieja, 10 km from Pozo Lucas and 20 km from San Fernando, along rd to Santa Barbara, 27 May–3 Jun. 1974 (fl), *S.S. Tillett et al. 745-319* (NY).

**BRAZIL. Amazonas:** Mun. Barcelos, Serra do Aracá, Platô da Serra do Aracá, Acampamento da Grotinha, vegetação sobre afloramento rochoso e sob solo arenoso, 0°52'4"N, 63°19'56"W, 984 m, 22 Aug. 2014 (fl), *F.N. Cabral et al. 1235* (INPA); [Mun. Humaitá], Estrada do Estanho, rd to Igarapé Preto, ca. 60 km SE of Transamazonian Hwy, 2 Jul. 1979 (fl), *C.E. Calderon et al. 2750* (INPA, US); Mun. Novo Aripuanã, Parque Estadual do Matupiri, savana arbustiva, inundação lençol raso periodicamente, solo arenoso, ca. 4°49'55"S, 61°0'12"W, 55 m, 28 Nov. 2012 (fl), *F.M. Costa & M.L.G. Mari 1920* (INPA); Maués, Campina Socoró, campina arbustiva alagável, p orte baixo, com densa cobertura de gramíneas baixas, 4°17'2"S, 58°34'40"W, 7 Aug. 2015 (fl), *L.O. Demarchi et al. 523* (INPA); Mun. Lábrea, Parque Nacional Matinguari, Campos do Rio Coti (acesso aéreo, em helicóptero), campinaranas gramíneo-lenhosa e arbustiva recém queimadas, 8°55'47"S, 65°23'45"W, 110 m, 26 Jul. 2014 (fl), *L.L. Giacomini & Y.F. Gouvêa 2131* (INPA); N margin of Rio Aracá, just above Igarapé Sauadaua, savanna on white sand, subshrub 30 cm tall, 26 Jul. 1985 (fl), *G.T. Prance et al. 29861* (INPA, NY); Canutama, Parque Estadual do Matupiri, campina gramíneo-lenhosa, solo hidromórfico areno-argiloso, 5°0'45"S, 61°16'15"W, 29 Oct. 2010 (fl), *E.M.B. Prata et al. 789* (INPA); Canutama, Reserva de Desenvolvimento Sustentável do Matupiri, campina gramíneo-lenhosa, solo hidromórfico areno-argiloso, 4°50'46"S, 60°31'46"W, 2 Nov. 2010 (fl), *E.M.B. Prata et al. 930* (INPA); Borba, Campina da Catuquira, vegetação savânica encharcável, com Poaceae, Rapateaceae, Cyperaceae, Humiriaceae, *Bactris campestris*, 4°54'13"S, 61°6'15"W, 30 m, 11 Jul. 2007 (fl), *P.L. Viana et al. 3042* (INPA); Parque Nacional do Jaú, Campina do Patauá, caminho para a cabeça do espermatozoide [ca. 2°15'S, 62°38'W], campo queimado, campina arbustiva, 5 Sep. 1998 (fl), *A. Vicentini & J.G. Loco 1391* (INPA, MO). **Rondônia:** Igarapé Preto, SC-20-XA-Ponto.30 [ca. 9°25'S, 62°30'W], 30 Jun. 1975 (fl), *J.C. Silva 120* (MG).

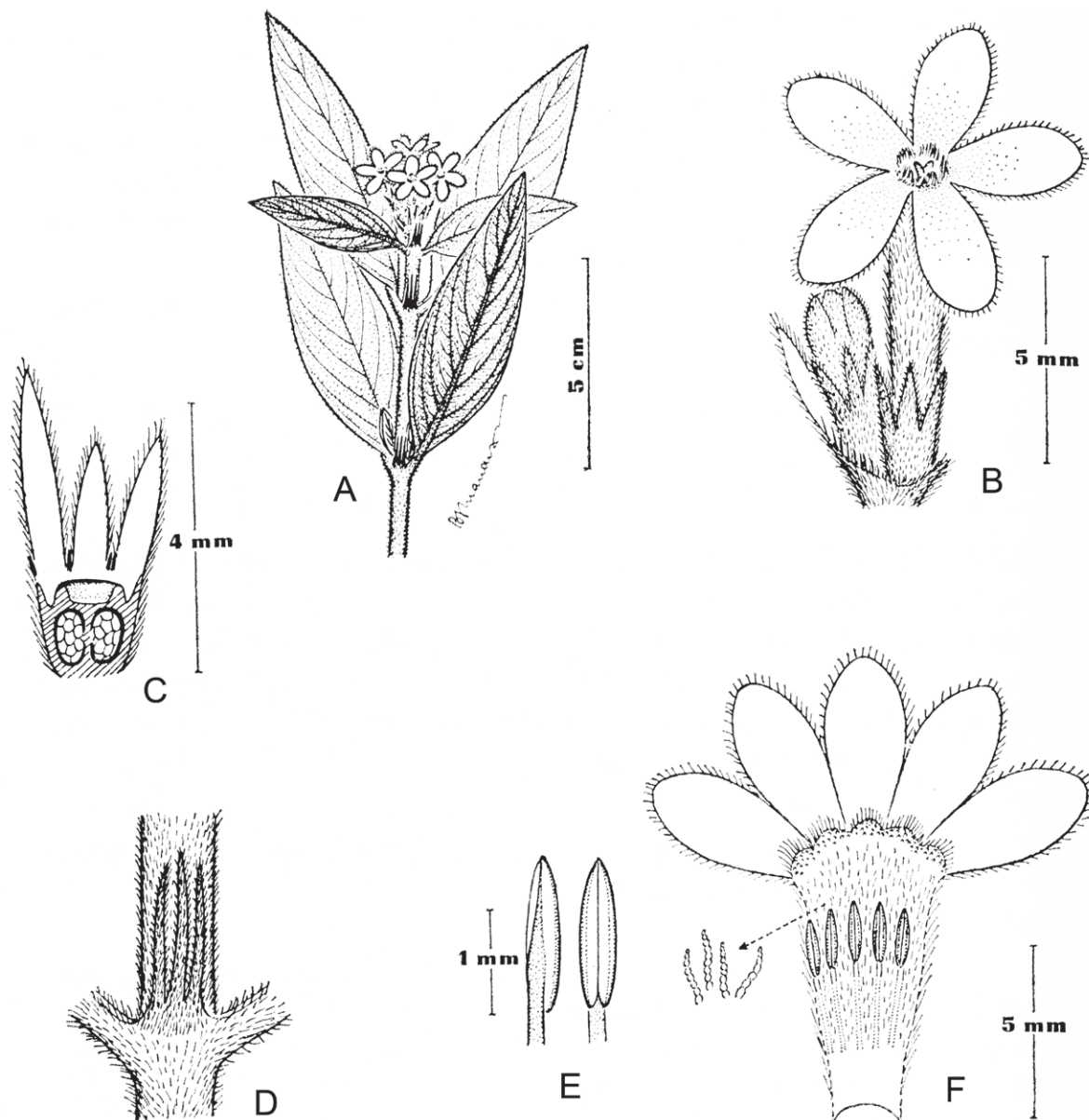
9-6. *Sipaneopsis morichensis* Steyerl., Mem. New York Bot. Gard. 17: 286. 1967. (Figures 75, 83).

Steyerl. in Lasser & Steyerl., Fl. Venez. 9: 275–277, fig. 45. 1974.

Type: VENEZUELA. Amazonas: Cerro Moriche [ca. 7°18'N, 63°23'W], Río Ventuari, 800 m, in montane caño savanna, shrub to 2 m tall, flowers pink, 14

Jan. 1951 (fl), B. Maguire, R.S. Cowan & J.J. Wurdack 30878 (holotype NY [barcode 00133333]; isotypes MICH [barcode 1108305], MO [barcode 1811402], NY [barcode 00133332], VEN [Acc. No. 65195]).

Shrubs to 2 m tall; stems erect; young branches stout, 4–5 mm in diam., villous, hairs ochroleucous. Stipules free or shallowly adnate to petioles, free portion broadly triangular at base, topped by 1–4 linear lobes



**Figure 83.** *Sipaneopsis morichensis*. A. Branch with terminal inflorescence. B. Flower at final stage of anthesis and flower bud. C. Longitudinal section of hypanthium, ovary, disk and calyx. D. Node with stipule and basal portion of petioles. E. Stamens, dorsal and ventral view. F. Dissected flower at final stage of anthesis, with stamens at median portion of corolla tube, and detail of moniliform hairs. Illustration by Bruno Manara (Reproduced with permission from Flora de Venezuela vol. 9(1), fig. 45. 1974).

8–10 mm long, villous, hairs ochroleucous, spreading or acropetally oriented outside, white-sericeous, with 6–7 colleters inserted just below the margin inside, with tips exerted; margins villous. *Leaves* with petioles 2–5 mm long, densely villous; blades broadly lanceolate, oblong-elliptic to narrowly ovate, 4.5–8.5 × 1.5–2.7 cm, acute to obtuse at base, acute at apex, chartaceous to subcoriaceous, dark green above, ochroleucous-villous below when fresh, drying brown above and beige-villous below, sulcate and hispidulous with midvein and secondary veins ochroleucous-strigose above, densely ochroleucous-villous below; with 8–11 secondary veins on each side, depressed above, prominent below, strongly ascending, terminating near the margin. *Inflorescences* congested-cymose, branched portion reduced during anthesis, 27–39-flowered, 3.5–4.5 cm tall, 2–3 cm broad (including peduncle and flowers), trichomously branched; terminal branchlets 3–7-flowered; rachis villous, hairs ochroleucous, spreading or acropetally oriented; peduncle 1–2.5 cm long, densely ochroleucous hirsute; bracts subtending the inflorescence subulate, 4–11 mm long, canescent outside, sometimes leaf-like, 2.5–2.7 × 0.8–1.4 cm. *Flowers* secundiflorous, sessile to subpedicellate, pedicels to 0.5 mm long, villous, hairs ochroleucous, spreading or acropetally oriented; subtended by one bracteole; bracteoles lanceolate to narrowly lanceolate, decreasing in size towards the tip, dimensions 3.5–5.5 × 1–1.5 mm, villous, hairs ochroleucous, spreading or acropetally oriented outside, glabrous inside. *Hypanthium* broadly obovoid, 1.5–1.7 × 1.5–1.7 mm, white-sericeous-strigose, hairs both acropetal and spreading. *Calyx* lobes equal or subequal, lanceolate, 2–2.5 × 0.5–0.7 mm, acute at apex, gray or ochroleucous sericeous outside (hairs 0.5 mm long), glabrous inside; with 1–2 colleters in each calycine sinus, narrowly ellipsoid, acute at apex, 0.25 mm long. *Corolla* hypocrateriform, pink, 14.5–18 mm long when fully elongated (lobes perpendicular to the tube); tube cylindrical and slightly wider at mouth, 11–12 mm long when fully elongated, 1.5 mm wide at base, 3–3.5 mm wide at mouth, densely grayish-strigose outside, glabrous at basal 3–3.5 mm and papillose-villosulous from filament insertion to corolla mouth inside; lobes left-contorted, subequal, oblong to narrowly obovate, 4.5–6 × 2–3.5 mm when fully expanded (perpendicular to the tube), round or ovate at apex, white-sericeous or appressed-pilose outside, glabrous and papillose inside. *Stamens* included, inserted 4–5 mm below corolla mouth; filaments 1.5 mm long; anthers oblong-lanceolate, 1.5 mm long, acute at top, round at base. *Style* included, 6.5–10 mm long, glabrous; style branches lanceolate, ca. 1 mm long. *Infructescences* a compound dichasium, 8.5–9 cm long, villous, hairs ochroleucous, spreading or acropetal-

ly oriented; terminal branches scorpioid, 2.5–3.5 cm long. *Mature fruits and seeds* unknown.

**Distribution and ecology:** Known from only two collections from Cerro Moriche, state of Amazonas, Venezuela, at 300–800 m elevation (Figure 75).

**Phenology:** The two flowering collections were made in January.

**Suggested conservation status: Critically Endangered (CR).** A species only known by two collections made in 1951 on Cerro Moriche, ca. 7°18'N, 63°22'W, at 300–800 m, state of Amazonas, Venezuela. Cerro Moriche is located not far from the Río Ventuari, and is an important center of biodiversity with a high degree of endemism. As a result of the same expedition to this locality in January 1951, the botanists B. Maguire, R.S. Cowan and J.J. Wurdack discovered numerous new taxa that were subsequently described [e.g., *Axonopus arundinaceus* G.A. Black (1957: 251), *Brocchinia cowanii* L.B. Smith (1957: 293), *Caraipa llanorum* subsp. *cordifolia* Kubitzki (1978: 104), *Cassia tetraphylla* var. *ventuarensis* Irwin (1964: 95), *Clidemia morichensis* J.J. Wurdack (1964: 183), *Clusia annularis* Maguire (1961: 23), *Gongylolepis paniculata* Maguire & Phelps (1953: 157), *Ilex savannarum* var. *morichei* Edwin (1965: 147), *Macrolobium discolor* var. *egranulosus* R.S. Cowan (1953: 292), *Navia crispa* L.B. Smith (1953: 378), *Navia hohenbergioides* L.B. Smith (1957: 298), *Navia semiserrata* L.B. Smith (1957: 309), *Orthaea thibaudioides* Maguire, Steyermark & Luteyn (1978: 173), *Perama galioides* forma *cinerea* Steyermark (1964: 243), *Phoradendron microstachyum* Kuijt (2003: 301), *Remijia argentea* Steyermark (1972a: 267), *Rudgea morichensis* Steyermark (1967: 424), *Siphanthera cowanii* J.J. Wurdack (1958: 97), *Stegolepis hitchcockii* subsp. *morichensis* Maguire (1965: 83)], including the present species.

The label of the type specimen (Maguire *et al.* 30878) reports *Sipaneopsis morichensis* Steyermark as a shrub growing near a small mountain creek at 800 m altitude, at the top of Cerro Moriche. The label of the paratype specimen (Maguire *et al.* 30868) describe it as a frequent shrub growing on the east flank of Cerro Moriche, between 300 and 800 m. The size of the populations was not reported on the specimen labels. Cerro Moriche is part of the “Monumento Natural Macizo Guao-Sipapo y Cerro Moriche” (Guao-Sipapo and Cerro Moriche Massif Natural Monument), a protected area that was established in 1990. Because of its rarity, small extent of occurrence (EOO) of < 100 km<sup>2</sup>, and small area of occupancy (AOO < 10 km<sup>2</sup>), this species is treat-

ed as Critically Endangered (CR) following IUCN criteria (IUCN 2012, 2019).

**Specimens examined:** VENEZUELA. Amazonas: Cerro Moriche [ca. 7°18'N, 63°22'W], frequent in E slope, 300–800 m, 13 Jan. 1951 (fl), *B. Maguire et al.* 30868 (NY, US, VEN, paratypes).

9-7. *Sipaneopsis pacimoniensis* Steyerl., Mem. New York Bot. Gard. 17: 289. 1967. (Figures 75, 84).

Steyerl. in Lasser & Steyerl., Fl. Venez. 9: 282. 1974.

Type: VENEZUELA. Amazonas: Infrequent in savanna on R bank of Río Pacimoni [Río Pasimoni, ca. 2°0'N, 66°43'W], 50 km above mouth, 100–140 m, 7 Feb. 1954 (fl), *B. Maguire, J.J. Wurdack & G. Bunting* 37570 (holotype NY [barcode 00133334]).

*Perennial herbs* 10–12 cm tall, single-stemmed, erect; young branches thin, densely appressed-canescens. *Stipules* free at base, triangular, 2.5–3 mm long, densely antrorse-strigose outside, inside not seen. *Leaves* shortly petiolate; petioles 1–2 mm long, densely antrorse strigulose; blades oblong-elliptic to narrowly ovate, 1.5–3 × 0.7–1.2 cm, acute to obtuse at base, acute to subacute at apex, chartaceous, blade colors when fresh unknown, drying dark reddish brown above and below, glabrous with midvein strigulose above, densely strigulose at midvein and secondary veins below; with 3–5 secondary veins on each side, ascending; margins strigulose-ciliate. *Inflorescences* cymose, 2–3-flowered; peduncle 1–2 cm long, canescens. *Flowers* 5-merous, sessile to subpedicellate, pedicels to 1.5 mm long, hispidulous; subtended by one bracteole linear-lanceolate, 3–4 mm long, acuminate, hispidulous outside, inside unknown. *Hypanthium* broadly subturbinate, 1.5 × 1.5 mm, densely hispidulous. *Calyx* lobes subequal, lanceolate, 1.7–2 × 0.7 mm, acute at apex, strigose-canescens outside, glabrous inside; with 1 colleter in each calycine sinus, narrow cylindroconical, acute at apex, 0.2 mm long. *Corolla* hypocrateriform, pink, 27.5–28.5 mm long when fully elongated; tube cylindrical and gradually wider near the mouth, 19 mm long when fully elongated, 0.7 mm wide at base, 2.5 mm wide at mouth, canescens-sericeous or canescens-strigose, densely so near the mouth outside, glabrous at basal 3.5 mm and puberulent above inside; lobes left-contorted in bud, subequal, obovate, 8.5–9.5 × 4.5–5.5 mm when fully expanded (perpendicular to the tube), obtuse and abruptly mucronate at apex, appressed-strig-

ulose outside, glabrous inside. *Stamens* included, inserted 4 mm below corolla mouth; filaments 3 mm long, papillose; anthers oblong-lanceolate, 1.8 mm long, acute at top, round at base. *Style* included (not fully elongated), 11.5 mm long, glabrous; style branches unknown. *Infructescences, fruits and seeds* unknown.

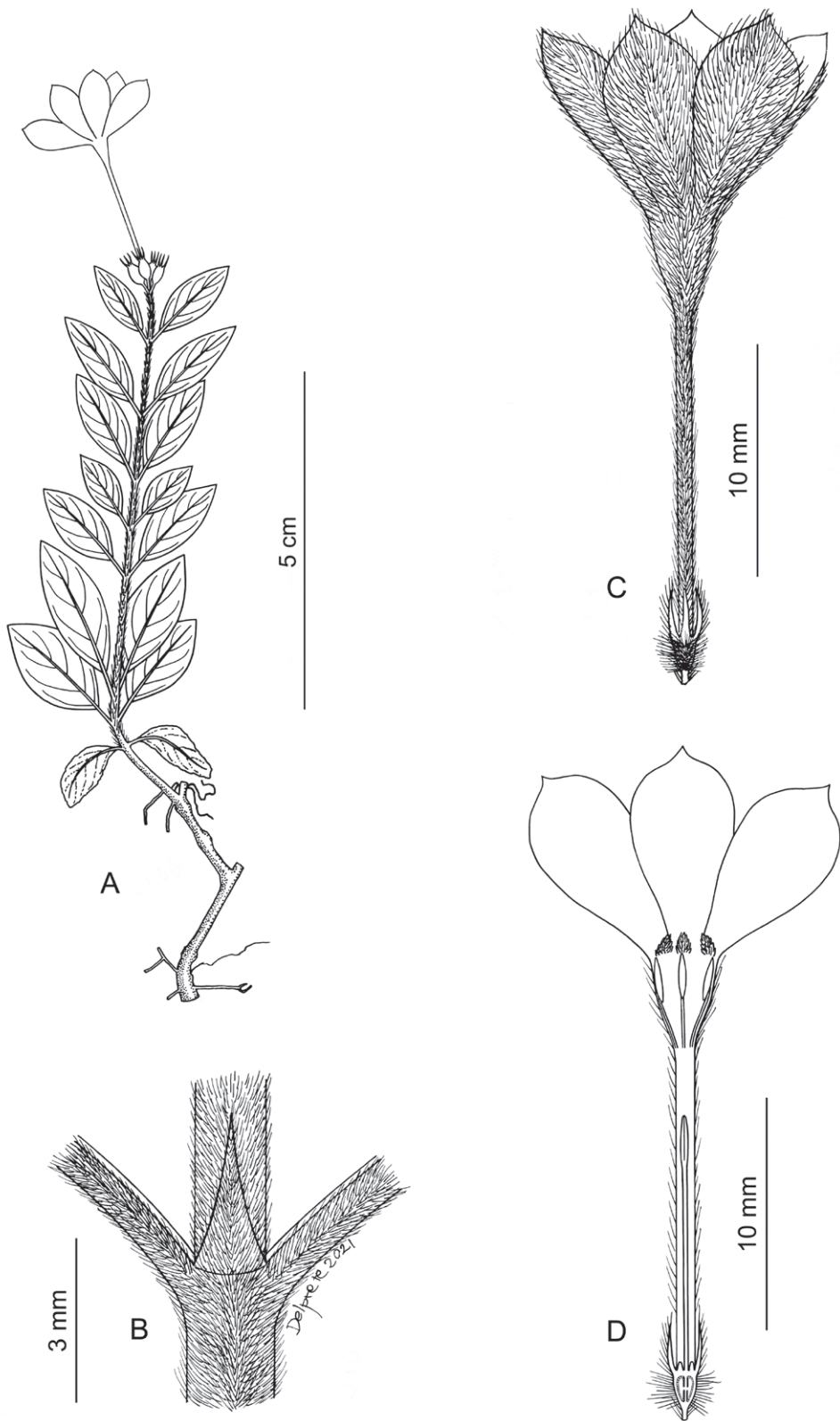
**Notes:** Steyerl. (1967: 289) wrote that *Sipaneopsis pacimoniensis* Steyerl. “differs from *S. foldatsii* in the dwarf stems, shorter internodes, shorter leaves, much larger corolla lobes, glabrous interior of corolla-lobes, and fewer lateral nerves of the leaf-blades.” Steyerl. (1967: 289; 1974: 282) also wrote that the corolla of *S. pacimoniensis* is 26 mm long, with a tube 17 mm long and lobes 8–9.5 mm long; however, the total of the tube plus the maximal length of the lobes add up to more than 26 mm. This species is only known from the holotype specimen preserved at NY, which has a single flower in full anthesis. Careful measurements of this specimen revealed that the corolla is 27.5–28.5 mm long, with tube 19 mm long and lobes 8.5–9.5 mm long.

Delprete and Steyerl. (2004f) in the key to species of *Sipaneopsis* differentiated *S. pacimoniensis* from *S. foldatsii* by the petioles 1–2 mm long (vs. 2–4 mm long in *S. foldatsii*), leaf blades 1.5–3 cm long, glabrescent except the midrib strigillose above, strigose below (vs. 3–7.5 cm long, densely hispid-strigose above and below), with 3–5 secondary veins on each side of the midrib (vs. 6–10 each side), and corolla lobes 8–9.5 mm long, glabrous adaxially (vs. 3.5–6.5 mm long, strigose-hispidulous adaxially).

**Distribution and ecology:** Only known from the type specimen, collected in a savanna on the right bank of Río Pacimoni, state of Amazonas, Venezuela, at 100–140 m altitude (Figure 75).

**Phenology:** The sole flowering collection was made in February.

**Suggested conservation status: Critically Endangered (CR).** A species only known from the holotype specimen collected in 1954 at about 50 km above the mouth of the Río Pacimoni, ca. 2°0'N, 66°43'W, at 100–140 m, state of Amazonas, Venezuela. This herb is 10–12 cm tall and reported as infrequent in a savanna near the Río Pacimoni. The size of the populations was not reported in the specimen label, and no recent observation has been made in the area to assess its conservation status. Because of it is known from a single collection locality, which is not within a protected area, this species is Critically Endangered (CR) following IUCN criteria (IUCN 2012, 2019).



**Figure 84.** *Sipaneopsis pacimoniensis*. **A.** Habit. **B.** Node with stipule and basal portion of petioles. **C.** Flower in anthesis, side view. **D.** Longitudinal section of flower at intermediate stage of anthesis, with corolla lobes not completely reflexed, and style not completely elongated. **A–D:** drawn from Maguire *et al.* 37570 (NY, holotype). Illustration by Piero Delprete.

9-8. *Sipaneopsis rupicola* (K.Schum.) Steyermark, Mem. York Bot. Gard. 17: 285, fig. 29g-m. 1967. (Figures 85-86).

Steyermark in Lasser & Steyermark, Fl. Venez. 9: 274-275. 1974. - *Rondeletia rupicola* K.Schum. in Martius et al., Fl. Bras. 6(6): 222. 1889.

Type: VENEZUELA. Amazonas: "ad flumina Casiquiare, Vasiva et Pacimoni," s.d. [1853-1854] (fl), R. Spruce 3392 (B†; **lectotype** BR [barcode 00532837], **here designated**; isoelectotypes C [without barcode], E [barcode 00285371], G [barcode G00436652], GH [barcode 00094363], L [barcode 1214530], LD [Acc. No. 1214530], K n.v., NY [barcode 00133193], P [barcode P00729443], RB [2 sheets, barcodes 00560059 and 00543699]; frag at F [Acc. No. 587152]; photo-B at F and NY; photo-K and photo-US at NY).

(=) *Rondeletia rupicola* var. *chiribiquetana* R.E. Schult., Bot. Mus. Leaflet 14: 46. 1949, **syn. nov.**

Type: COLOMBIA. Vaupés: Macaya-Ajaju River confluence, Mount Chiribiquete [ca. 1°19'N, 72°45'W], quartzitic base, summit, 1700-2100 feet [520-640 m], 15-16 May 1943 (fl, fr), R.E. Schultes 5448 (holotype GH n.v.; isotypes BR [barcode 00532837], COL [barcode 000004687]; UC [barcode 925799], US [barcode 00137636]).

*Subshrubs* to *shrubs*, 0.3-2 m tall, erect; young branches stout, strigulose. *Stipules* free at base, triangular, 4-5 mm long, entire and caudate, or base triangular topped by 2-3 acute lobes, or base reduced to a line 0.5-0.7 tall with 6-7 linear lobes, central one longer, 3-4 mm long, the lateral ones shorter, 1.2-1.7 mm long, or two longer ones intercalated with shorter ones, densely strigulose outside, white-sericeous with 10-11 colleters inserted just below the margin inside with tips exerted; margins strigulose. *Leaves* with petioles 3-4 mm long, sericeous-strigose; blades elliptic, narrowly ovate, narrowly elliptic to elliptic-lanceolate, rarely lanceolate, 2.7-6.5 × 0.8-1.5 cm, acute to obtuse at base, acute or acuminate at apex, subcoriaceous, margins narrowly revolute, dark green above and pale green below when fresh, drying dark brown above and pale brown, glabrous or sparsely strigose and sulcate with midvein

and secondary veins white-strigose above, glabrous or sparsely to densely strigose, or densely sericeous-strigose with midvein and secondary veins white- or ochroleucous-strigose below; with 7-9 secondary veins on each side, ascending. *Inflorescences* cymose, a compound dichasium with scorpioid secondary branches, 21-47-flowered, 3-4 cm long (including peduncle and flowers), 2.5-3 cm broad during anthesis (expanding after anthesis), with 2-3 main branches, each branch 1-3-furcate, ultimate branchlets 3-6-subsecundiflorous; peduncle 1.5-3 cm long, densely strigose. *Flowers* sessile or with pedicels 0.5 mm long; except for central flower with pedicel 1.5-2 mm long; subtended by bracteoles linear-lanceolate, decreasing in size towards the tip of the branch, 2-3.5 × 0.1-0.3 mm, acuminate, strigulose outside, glabrous inside. *Hypanthium* subglobose, 1.2-1.5 × 1 mm, strigose-sericeous. *Calyx* lobes subequal, lanceolate, 1-1.5 × 0.5-0.7 mm, acute at apex, sparsely to densely strigose outside, glabrous inside; with 1 colletter in each calycine sinus, narrowly conical (acute at apex), 0.2 mm long. *Corolla* hypocrateriform, pink, 14.5-16.2 mm long when fully expanded; tube cylindrical and slightly wider at mouth, 11-11.5 mm long when fully expanded, 0.7 mm wide at base, 1.5 mm wide at mouth, sericeous-strigose, densely so near the mouth outside, glabrous at basal 3.5-4 mm, puberulent above and papillose near the mouth inside; lobes left-contorted or irregularly imbricate, 1 or 2 external, subequal, oblong-obovate, 3.5-4.7 × 2.2-2.5 mm when fully expanded (perpendicular to the tube), obtuse to round at apex, sparsely strigulose outside, glabrous inside. *Stamens* included, inserted at 4.5 mm below corolla mouth; filaments 1.5-2 mm long; anthers oblong-lanceolate, 1-1.5 mm long, round at base, acute at top. *Style* as long as the corolla tube, with branch tips barely exerted, glabrous; style branches lanceolate, ca. 1 mm long. *Infructescences* a compound dichasium, 6.5-7.5 cm long, terminal branches scorpioid, 3-3.5 cm long. *Immature fruits* subglobose-urceolate, 3 × 2.5 mm (fide Steyermark, 1974: 275), strigose. *Seeds* 8-10 per locule, those inside immature fruits subglobose, 0.7-1 mm diam. (fide Steyermark, 1974: 275), rugose-foveolate. *Mature fruits and seeds* unknown.

**Morphological observations:** Steyermark (1967: 285-286; 1974: 274-275) described the corolla of *S. rupicola* as being 11 mm long, with tube 8-8.5 mm long

**Figure 85.** *Sipaneopsis rupicola*. A-B. Habit variation. A. Habit from Mount Chiribiquete (Colombia). B. Habit from Araracuara (Colombia). C-E. Stipule variation. F-G. Leaf shape variation and detail of vestiture on abaxial side. H. Flower bud (note lobes already opened at early stage). I. Flower in anthesis. A, D, E, F, H, I from Gutierrez & Schultes 654 (US); B, G from Sastre & Raichel 5150 (P); C from Williams 14897 (US). Illustration by Piero Delprete.

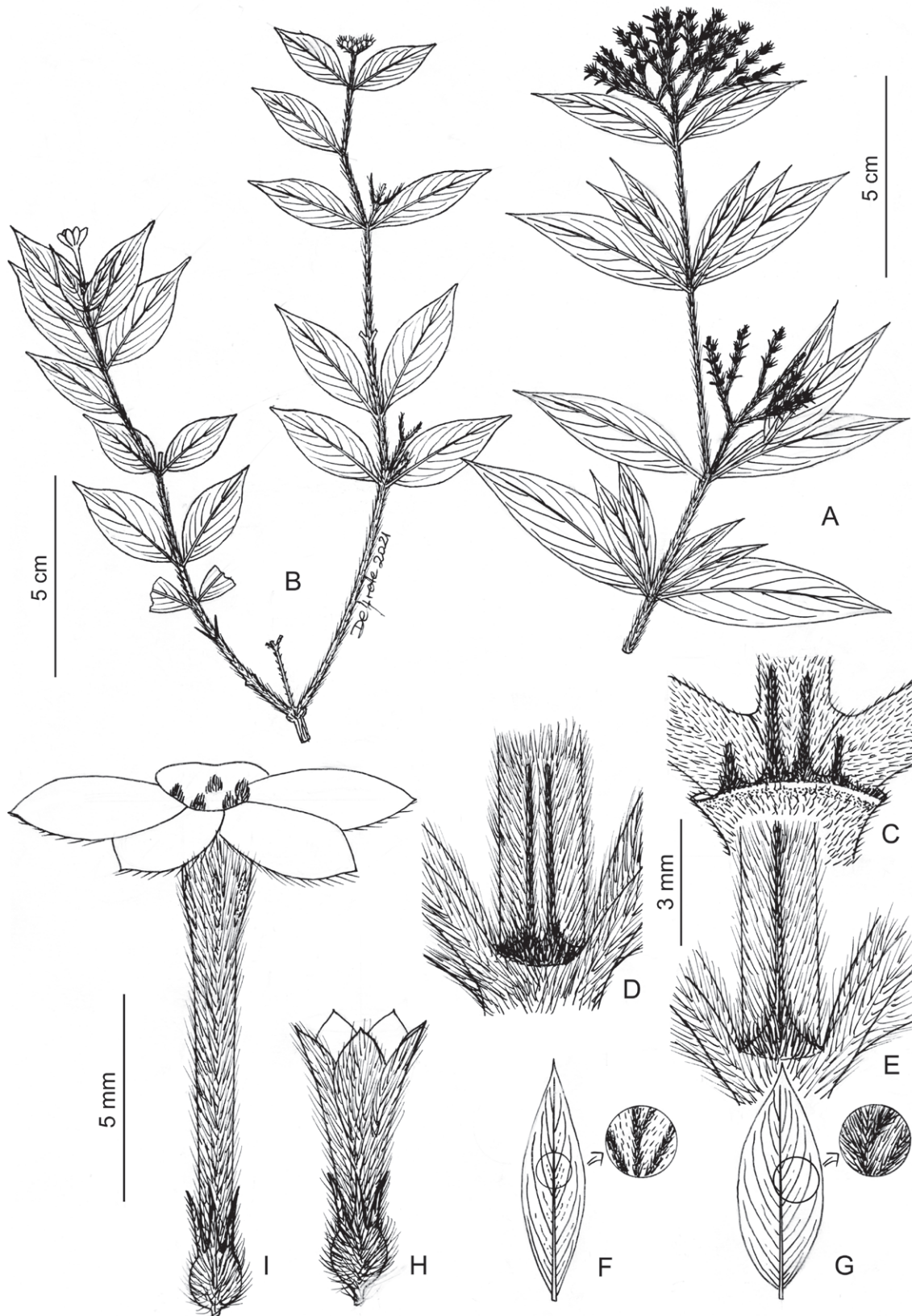


Figure 85.



and lobes  $3\text{--}3.5 \times 1.7\text{--}2$  mm, and style only 4 mm long; however, these measurements were made on flowers not completely expanded. The corollas and style are much larger when fully expanded, with corolla tubes 11–11.5 mm long and lobes  $3.5\text{--}4.7 \times 2.2\text{--}2.5$  mm, and style is as long as the corolla tube.

**Notes:** Schumann (1889: 222 [in *Flora Brasiliensis* the page is erroneously numbered as “224”]) published *Rondeletia rupicola* K. Schum. citing “*Sipanea rupicola* Spruce Ms. in *Pl. exsicc. n. 3392*” in synonymy. Art. 46.4 of the *Code* (Turland et al. 2018) states that “When a validly published name or its final epithet is taken up from and attributed to the author of a different “name” that has not been validly published, or one at a different rank likewise not validly published, only the author of the validly published name is cited (except as provided in Art. 46.7).” Therefore, “*Sipanea rupicola* Spruce” is not a name, and should not be referred to as such. It is here cited between quotation marks to show that it is not a name (see Art. 36.1, Exs. 1–8).

Schultes (1949: 46) separated *Rondeletia rupicola* var. *chiribiquetana* R.E. Schult. from the typical variety by the leaves elliptic-lanceolate,  $4\text{--}5 \times 1\text{--}1.3$  cm, acute at apex (vs. long-lanceolate,  $5\text{--}8 \times 1.5$  cm, acuminate at apex in the typical variety), bullate above, mid-

rib and secondary veins densely sericeous-strigillose (vs. glabrous or sparsely to densely strigose), and larger corolla lobes. Steyermark (1967: 285–286) and Delprete and Steyermark (2004f: 833–835) synonymized the two varieties without any comment. A detailed comparison of the specimens from throughout the geographic range of the species confirmed that the characters used by Schultes to differentiate the two varieties are found on a gradient. For example, examination of several collections demonstrated that leaf size is variable within the populations present on Cerro de Chiribiquete. Also, in the populations of Cerro de Chiribiquete the leaf abaxial side is densely sericeous-strigillose, while in those from the Colombian and Venezuelan lowlands the leaf abaxial is glabrous or sparsely to densely strigose, which could indicate a possibility of the recognition of two varieties. However, the collections from near Araracuara and Inírida (Colombia lowlands) have ovate-elliptic blades densely strigose below, which are here interpreted as an intermediate form between the two putative varieties. Also, corolla lobes in *Sipaneopsis* are already open in flower bud and gradually expand during the flowering process, reaching the full length only at final stage, when they are completely reflexed and perpendicular to the corolla tube. Corolla size and vestiture is consistent among all the collections examined. As a result of the

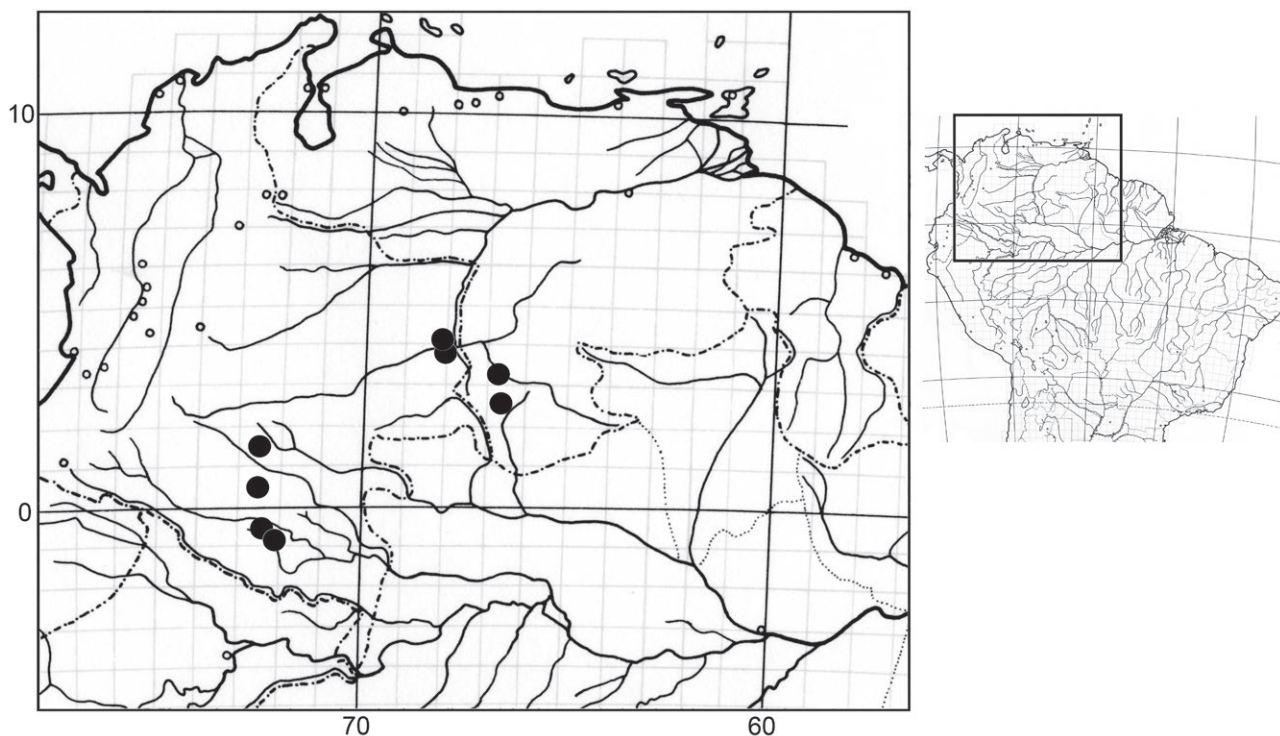


Figure 86. Distribution of *Sipaneopsis rupicola*.

above analysis, no variety is here recognized in *Sipaneopsis rupicola*.

Several herbarium specimens of *Sipaneopsis rupicola* have been incorrectly identified as *S. maguirei*, although these species differ in many characters. In *S. maguirei* the stems are thin, ascending or reclining (rarely decumbent), the stipules are entire (i.e., not lobed), broadly to narrowly triangular, the inflorescences are congested, 2–8-flowered, and fully elongated corollas are 21–30 mm long (tubes 15–22 mm long, lobes 4.5–9 mm long). Whereas, in *S. rupicola* the stems are stout, erect, the stipules can be entire and caudate or reduced at base and with 2–3 or 6–7 linear lobes, the inflorescences are cymose, compound dichasia with scorpioid secondary branches, 21–47-flowered, and fully elongated corollas are 14.5–16.2 mm long (tubes 11–11.5 mm long, lobes 3.5–4.7 mm long).

A few herbarium specimens of *Sipaneopsis rupicola* from Colombia have been incorrectly identified as *S. foldatsii*. In *S. foldatsii*, the stems and the leaves are densely appressed-strigose, the hypanthia are broadly turbinate, densely hispid, and fully expanded corollas are 20.5–24 mm long (tube 14–16 mm long, lobes 6.5–8 mm long). Whereas, in *S. rupicola*, the stems are strigulose and the leaves are glabrous or sparsely strigose (rarely densely strigose below), the hypanthia are subglobose, strigose-sericeous, and fully expanded corollas are 14.5–16.2 mm long (tube 11–11.5 mm long, lobes 3.5–4.7 mm long).

**Distribution and ecology:** Known from several collections in Amazonian Colombia and Venezuela (Figure 86). Growing on sandstone mountains (Tepuis), or on rocky or white-sand savannas, at 100–640 m altitude.

**Phenology:** Specimens with flowers were collected in January, February, March, April, July, September and November. Specimens with flowers and immature fruits were collected in May, June and September.

**Suggested conservation status: Endangered (EN).** A rare species known from several collections in Colombia and five in Venezuela. In Colombia, two collection were made in 1943 and 1949 (type of *Rondeletia rupicola* var. *chiribiquetana*) on Cerro de Chiribiquete, at 520–640 m, department of Vaupés. Cerro de Chiribiquete [ca. 1°31'N, 72°47'W] is a sandstone tepui located at the easternmost portion of the Guiana Shield, and is included within the Chiribiquete National Natural Park, which was declared a UNESCO World Heritage site in 2018. Three Colombian collections were made in the Vaupés department, in 1976, 1992 and 1994, near the locality of Araracuara [ca. 0°36'–55'S, 72°20'–23'W]. And two other

collections of *Sipaneopsis rupicola* where made in 1992 and 2007 in the municipality of Inírida, in the department of Guainía, in the same locality where *S. maguirei* grows.

In Venezuela, all the collections were made in the state of Amazonas. The first collection (type of *Rondeletia rupicola* K. Schum.) was made in 1853–1854 in a region cited on the specimen label as “Rivers Casiquiare, Vasiva and Pacimoni.” Judging by the three rivers cited, this region is now included within the Alto Orinoco-Casiquiare Biosphere Reserve. Two additional collections were made in 1942 and 1959 near Caño San Miguel (ca. 2°39'N, 66°45'W and ca. 2°37'N, 66°40'W), and two other collections were made in 1954 and 1957 along the Casiquiare River, near Piedra Tururumeri and near Piedra Araucaua, which are also within the Alto Orinoco-Casiquiare Biosphere Reserve.

Several localities where this species has been collected are within the Chiribiquete National Natural Park, in Colombia, and others within the Alto Orinoco-Casiquiare Biosphere Reserve, in Venezuela. The size of the populations was not reported in the specimen labels. Based on the collection localities, its EOO is of ca. 48,600 km<sup>2</sup>. Although several localities are present within preserved areas, several other collection localities in non-protected areas near human communities that could be impact its natural environment, this species is treated as Endangered (EN) following IUCN criteria (IUCN 2012, 2019).

**Specimens examined: COLOMBIA. Caquetá:** Río Caquetá, Araracuara [ca. 0°36'S, 72°23'W], camino a la Sabana, 2° Sabana de Tibeyes, suelo arenoso blanco, sobre rocas de arenisca, 5 Jan. 1976 (fl, fr), C. Sastre & H. Raichel D. 5150 (P [2 sheets]); Mun. Puerto Santander, trocha a La Chorrera, 20 km SW de Araracuara, sabana de areniscas (aduche) (Bh-T), hierba de 50 cm, flor rosada, 0°55'S, 72°20'W, 160–260 m, 2 Apr. 1994 (fl), Cárdenas et al. 4540 (COAH); Araracuara, areniscas de la Sabana de Aduche, arbusto de 2 m, flores rosadas, 25 Nov. 1992 (fl), J. Murillo et al. 215 (COAH, COL). **Guainía:** Mun. Inírida, comunidad de Guamal, arbustal (catinga), sobre arenas blancas y sabanas naturales y pequeños bosques, hierba de 70 cm, flor roja, creciendo en sabana, 3°52'20"N, 67°51'08"W, 100–150 m, 5 Jan. 2007 (fl), D. Cárdenas & J.G. Ramírez 20499 (COAH); Mun. Inírida, Río Atabapo, sector entre Maviso y comunidad de Chaquita, hierba de 80 cm, flores fucsia, en sabana, 4°2'15"N, 67°42'43"W, 9 May 2007 (fl), D. Cárdenas et al. 20522 (COAH). **Vaupés:** Cerro de Chiribiquete [ca. 1°19'N, 72°45'W], a un lado del Río Macaya, terreno muy pedregoso, 17 Jan. 1944 (fl), G. Gutiérrez & R.E. Schultes 654 (US).

**VENEZUELA. Amazonas:** Ríos Pacimoni-Yatua, Casiquiare, frequent in open areas on Piedra Turumeri, 110–220 m, 4 Feb. 1954 (fl), *B. Maguire et al.* 37512 (F, MO, NY); Ríos Pacimoni-Yatua, Casiquiare, locally frequent in clearing, Piedra Araucaua, Río Yatua, 110–550 m, 27 Sep. 1957 (fl, imm fr), *B. Maguire et al.* 41603 (F, NY, RB, SP); Guainía, margenes y alrededor de las lajas, Caño San Miguel, cerca de la Boca del Caño Ichana [ca. 2°39'N, 66°45'W], 127 m, 26 Mar. 1942 (fl), *Ll. Williams* 14897 (F, US); Caño San Miguel, between Limoncito and Caño Ikebenie, ca. 70 river km from mouth [ca. 2°37'N, 66°40'W], 120–130 m, 29 Jun. 1959 (fl, fr) *J.J. Wurdack & L.S. Adderley* 43253 (NY, UB, US).

#### 10. STEYERMARKIA

*Steyermarkia* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 216. 1940.

Standley & Williams, Fl. Guatemala, Fieldiana, Bot. 24: 203–204, fig. 10. 1975; D.H. Lorence in G. Davidse et al., Fl. Mesoamericana 4(2): 284. 2012.

Type: *Steyermarkia guatemalensis* Standl.

*Subsessile perennial herbs or subshrubs*, with a rosette of leaves condensed near the ground; stem short, woody. *Stipules* persistent, free at base, lanceolate to linear-lanceolate, attenuate or rarely shortly bifid at apex. *Leaves* opposite, condensed in rosettes, short-petiolate; blades narrowly obovate or oblanceolate, membranaceous or chartaceous; domatia absent. *Inflorescences* axillary, long-pedunculate, not frondose, capitate, subtended by bracts. *Flowers* homostylous, 4-merous. *Hypanthium* turbinate, densely antrorsely hispid, hairs white, long, slightly enlarged-tuberculate at base. *Calyx* persistent; tube extremely reduced; lobes large, erect, narrowly ovate-lanceolate to linear-lanceolate, densely long-hispid-sericeous outside; with a linear colleter in each calycine sinus. *Calycophylls* absent. *Corolla* hypocrateriform, actinomorphic, pink; tube externally hirsute, internally glabrous throughout, puberulent at mouth; lobes left-contorted, ovate, margin entire, round at apex. *Stamens* included; filaments attached on the upper part of the corolla tube, free at base, slender, short, equal, glabrous; anthers sessile, elongate, acute

at base, round at apex, dorsifixed near the base. *Pollen* 3-colporate; exine foveolate, perforate. *Style* partially exerted (branch tips exerted just above the corolla mouth), filiform; style branches oblong. *Ovary* with a stalked placenta; stalk inserted at the middle of the septum, with an oblong-hemielliptic extension; ovules many, inserted on the placental extension. *Fruit* capsular, dehiscent loculicidally, crustaceous. *Seeds* many per locule, horizontal, minute, globose.

**Geographic distribution:** A rare monotypic genus restricted to southern Mexico (Chiapas) and Guatemala.

**Notes:** Standley (1940) dedicated the name of this genus to Julian A. Steyermark (1909–1988), who collected the type specimens in Guatemala during the Stanley Field Expedition of 1939–1940. As Standley predicted, this monotypic genus is extremely rare. Later collections demonstrated that it occurs also in the contiguous Mexican state of Chiapas, and the only collection from Guatemala is the type gathering. Standley (1940) also indicated that *Steyermarkia* Standl. is most similar to *Sipanea*, from which it differs by being a plant reduced to a basal rosette of leaves, with large, 4-merous flowers, and globose seeds. On the other hand, *Sipanea* species are herbs or shrubs, erect or decumbent, with cauline leaves, with smaller, (4)5(6)-merous flowers, and angular seeds.

10-1. *Steyermarkia guatemalensis* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 216. 1940. (Figures 5K–L, 87–88).

Standl. & Williams, Fl. Guatemala, Fieldiana, Bot. 24(9): 203–204, fig. 10. 1975.

Type: GUATEMALA. Izabal: Río Dulce, 2–4 miles W of Livingston, on S side (L side going up-river) [ca. 15°46'54"N, 88°46'54"W], shaded moist limestone bluffs near base, 1–3 m above sea level, 16 Apr. 1940 (fl), *J.A. Steyermark* 39520 (lectotype F [Acc. No. 1035008], designated by Lorence (1999: 170); isolectotypes F [Acc. No. 1035009], MO [Acc. No. 1204537]).

*Stems* short, unbranched, to 18 cm long; internodes very short. *Stipules* 1.5–2 cm long, densely white-hir-

**Figure 87.** *Steyermarkia guatemalensis*. **A.** Habit of plant in bloom. **B.** Hypanthium and calyx (note partially exerted calycine colleters). **C.** Corolla partially dissected showing stamens and exerted style. **D.** Detail of outer surface of corolla. **E.** Young flower bud. **F.** Seed. **G.** Cross section of hypanthium and ovary. Upper right corner: Sketch of Dr. Julian Steyermark. Illustration by M. Pahl. (Reproduced with permission from Flora of Guatemala vol. 24, part 11, fig. 10. 1975).

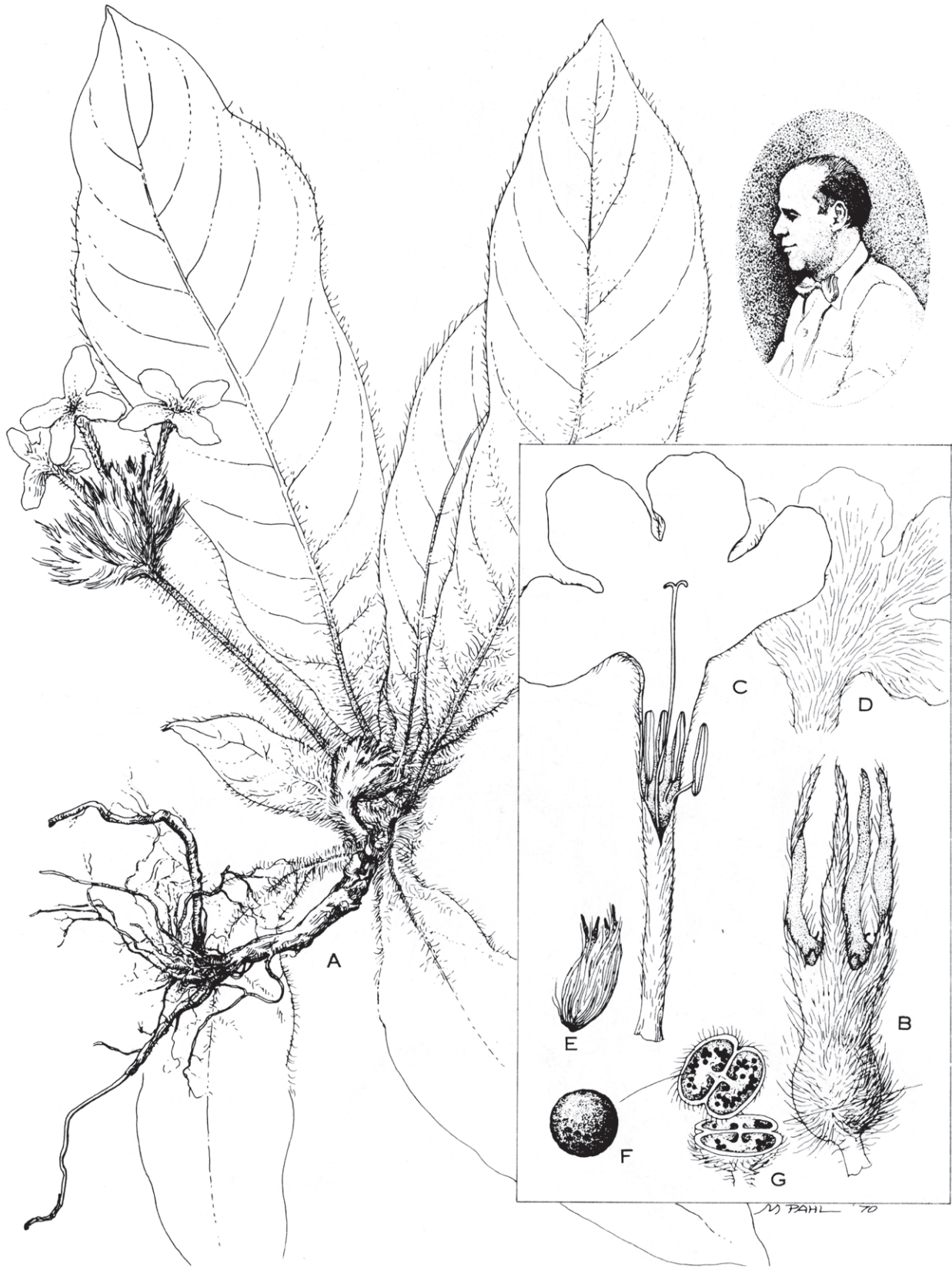


Figure 87.

sute outside, glabrous inside. *Leaves* with petioles 1–4 cm long, hirsute; blades 11.5–35 × 4–10 cm, attenuate at base, acute or acuminate at apex, chartaceous, dull green above, pale green and midrib white below, drying reddish brown above and olive green below, lamina densely long-hirsute and veins strigose above (hairs to 6 mm long), more densely hirsute below; with 15–20 secondary veins on each side of midrib. *Inflorescences* 10–12-flowered, with 3 head-like cymules, hirsute, rarely with an additional subterminal inflorescence; peduncle 9–16 cm long, long-hirsute, (hairs erect, beige, 3–4 mm long); bracts subtending the head narrowly lanceolate to narrowly ovate-lanceolate, 15–20 × 3–4 mm, long-attenuate, connate at base, with 2–3 colleters in each calycine sinus; bracteoles subtending the flowers narrowly lanceolate, 1.5–2 cm long, acuminate, long-hispid (hairs appressed antrorse, beige, 2–3 mm long) outside, glabrous inside. *Flowers* sessile or short-pedicellate. *Hypanthium* 1.5–2 × 1–1.5 mm. *Calyx* tube 0.5–1 mm long, densely long-hispid-sericeous outside (hairs white, 2–3 mm long), glabrous inside; lobes erect, 10–15 × 1–1.5 mm, acute at apex; with 1 colleter in each calycine sinus, linear, 0.7 mm long. *Corolla* 4.6–6 cm long; tube cylindrical and slightly wider at mouth, 3.5–4.5 cm long when fully expanded, 1.5 mm wide at base, 1.5–3 mm wide at mouth, with long-spreading hairs (3–4 mm long) outside, glabrous inside; lobes subequal, broadly ovate, 1.4–2 × 0.9–1.3 cm, round at apex, densely hispid, with long-

spreading hairs outside, glabrous and sparsely glandular at base inside. *Stamens* inserted near the base of corolla tube; filaments 4–6 mm long, glabrous; anthers narrowly oblong, 5–6 mm long, round at both ends. *Style* 3.5–4.5 cm long, glabrous; style branches oblong, 4–4.5 mm long, acute at tip. *Fruit* subglobose, 6.5–8 × 6.5–8 mm, densely long-hirsute. *Seeds* 90–110 per locule, globose to subglobose, 0.3–0.4 mm diam., foveolate, testa dark brown.

**Notes:** Standley (1940) along with the description of *Steyermarkia guatemalensis* Standl., cited as type *Steyermark* 39520 preserved at F. However, at F are present two specimens of *Steyermark* 39520, which are kept in separate type folders and have different accession numbers. Lorence (1999: 170) cited the F specimen with Acc. No. 1035008 as the holotype, and cited the F specimen with Acc. No. 1035009 and a MO specimen (without citing the accession number) as isotypes. According to Art. 7.11 and 9.10 of the *Code*, Lorence's citation of the specimen with Acc. No. 1035008 as the holotype is a correctable error, and should be treated as an inadvertent lectotypification on this specimen.

**Distribution and ecology:** Restricted to the state of Chiapas, southern Mexico, and known by a single collection in northern Guatemala (Figure 88). Growing on rock walls, in tropical rain forest understory, from near sea level to 550 m altitude.

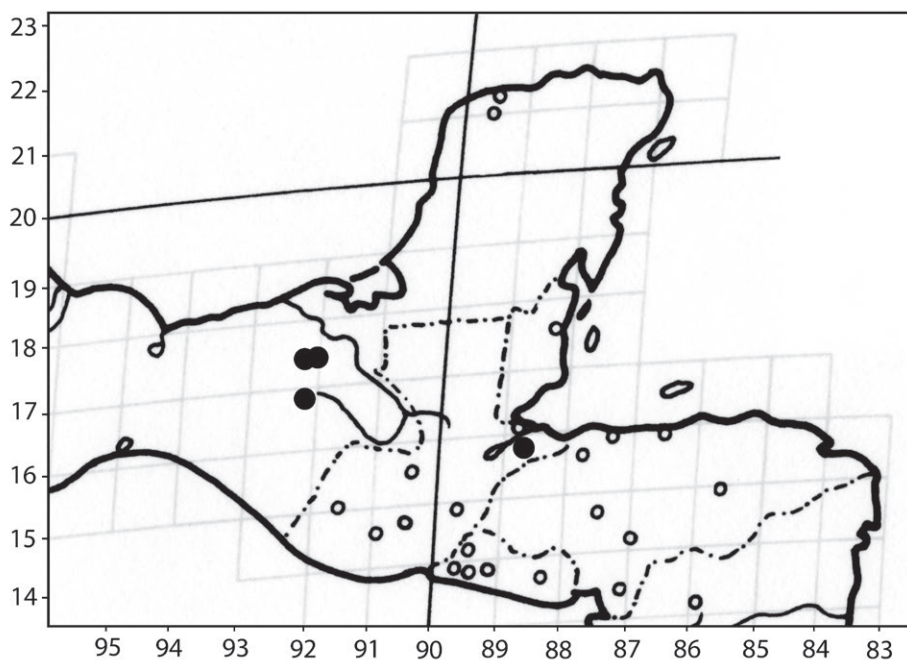


Figure 88. Distribution of *Steyermarkia guatemalensis*.

**Phenology:** Specimens with flowers were collected in April, October and December; and with flowers and fruits in April and May.

**Conservation status: Critically Endangered (CR) or Probably Extinct (EX).** This species is known from a single collection from Guatemala and four collections from the contiguous Mexican state of Chiapas. The sole collection from Guatemala (the type) was collected in 1940 in the community of Izabal, near Río Dulce, at 2–4 miles W of Livingston [ca. 15°46'54"N, 88°46'54"W], in shaded moist limestone bluffs. Standley and Williams (1975: 203–204) wrote that the habitat of *Steyermarkia* in Guatemala “may have been destroyed where the plants were collected more than 30 years ago.” In fact, the type specimen remains the sole record from this country, where it might be locally extinct.

In Mexico, this species was collected four times in the state of Chiapas. Two collections were made in nearby localities, one in 1973 in the municipality of Palenque, ca. 17°29'N, 92°2'W, on shaded cliff face, at 300 m, and the other in 1986 in the municipality of Chontal, 17°28'48"N, 92°4'48"W, on a vertical rock face in forest along a river, at 450 m. The other two collections were made in the municipality of Ocosingo, ca. 16°54'N, 92°5'W, in 1980 and 1981, in lower montane rain forest on a rock wall, at 550 m altitude. This species was last collected in 1986.

The extent of occurrence (EOO) of this species, counting the type locality in Guatemala, is of 11,700 km<sup>2</sup>. However, as stated by Standley and Williams in 1975, its natural environment in Guatemala has most likely been obliterated. Therefore, if the Guatemalan locality is excluded from the calculation, its EOO in Mexico is of 243 km<sup>2</sup>. Also, the size of the populations was not reported on the specimen labels, and none of the localities are within protected areas. In Mexico, the natural vegetation in the region between Ocosingo and Palenque is extremely fragmented due to agriculture and general human pressure. Because of the small area of occurrence, fragmented natural vegetation, and probably small populations, this species is treated as Critically Endangered (CR) following IUCN criteria (IUCN 2012, 2019). On a final sad note, considering that its last collection was made in 1986, and it is not cultivated in any garden, it is also possible that this species is Extinct (EX).

**Additional specimens examined: MEXICO: Chiapas:** Mun. Palenque [ca. 17°29'N, 92°2'W], on shaded cliff face, tropical rain forest adjacent to small cascading river at Agua Azul, 300 m, 24 May 1973 (fl, fr), *D.E. Breedlove* 35338 (CAS, MO, NY); Mun. Ocosingo [ca. 16°54'N, 92°5'W], lower montane rain forest, 70

km SW of Palenque, on road to Ocosingo along the Jol Uk'um, plant on rock wall, 550 m, 4 Dec. 1980 (fl), *D.E. Breedlove* 48293 (CAS, MO); Mun. Ocosingo [ca. 16°54'N, 92°5'W], lower montane rain forest, 70 km SW of Palenque, on road to Ocosingo along the Jol Uk'um, 550 m, 12 Apr. 1981 (fl, fr), *D.E. Breedlove* 50883 (CAS [2 sheets]); Mun. Chontal, rd between San Cristobal de las Casas and Palenque, 136 km NE of San Cristobal, Villa Paraiso, on vertical rock face in forest along river, 17°28'48"N, 92°4'48"W, 450 m, 10 Oct. 1986 (fl), *B.E. Hammel et al.* 15637 (BM, F, MO).

#### ACKNOWLEDGMENTS

This project started more than two decades ago, and, due to my moves to different institutions and numerous concurrent long-term projects, it was stopped and restarted several times. This gave me the opportunity to visit numerous herbaria and undertake precious field work in many Neotropical countries. My first field expedition dedicated to the Sipaneeae took place in Venezuela in December 2000 – January 2001, for which I wish to thank Gerardo Aymard (then at UNELLEZ-Guanare, Herbario Universitario (PORT), Mesa de Cavacas, Venezuela) for help during the application for the collecting permit, and Ana Claudia Araujo (at that time doctoral student at the University of São Paulo, Brazil, currently at the Natural History Museum, London, England), who helped during field work and processing herbarium specimens; that expedition gave me the opportunity to observe the unique flower modality of *Sipaneopsis maguirei* in a population growing in a white-sand savanna near San Fernando de Atabapo. Following that field trip, I compiled sufficient material for a molecular phylogenetic study of the Sipaneeae, which was accomplished in collaboration with Rocío Cortes-Ballén (then a doctoral student under my supervision at City University of New York (CUNY), New York, USA, and now professor at the Universidad Distrital, Bogotá, Colombia).

Important advancements towards this project were made while I was working as a Visiting Scientist at the National Herbarium of the Netherlands, Utrecht University branch, when I started the treatment of the Rubiaceae for the series *Flora of the Guianas*, in 2004; funds for that visiting fellowship were provided by the Netherlands Organization for Scientific Research NWO (grant B 85-368), and additional funds were granted from the Alberta Mennega Stichting and the Van Eeden Foundation for work in 2006 and 2008. My profound gratitude goes to Marion Jansen-Jacobs (U) for the efficient coordination of the project and for answering

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Important observations of several species of *Sipanea* and *Limnosipanea* in Central-Western Brazil, in the states of Goiás, Tocantins and Mato Grosso, were made during 2004–2008, while I was working as a Visiting Scientist at the Federal University of Goiás (UFG), with a fellowship from the Conselho Nacional de Pesquisa (CNPq) of the Brazilian Government (grant 309885/2003–5). Special help during that period was provided by Juliana Costa da Silva (now my wife), who accompanied me during numerous field expeditions and herbarium studies in this region.

Field work in French Guiana was made while working at the IRD, starting from 2009 to present; during this period, I received help from Gwenaël Quenette and Juliana Costa da Silva, who accompanied me during local field excursions, provided digital images, and helped processing herbarium and pickled specimens of *Neobertiera palustris* from a population growing along the trail to the Bagne des Annamites, French Guiana, in 2013–2014. Funds for field work, during which I had the occasion to study an additional population of *N. palustris* in the surroundings of the village of Camopi, upper Oyapock River basin, French Guiana, were provided by the LABEX CEBA (Laboratory of Excellence - Center for the Study of Biodiversity in Amazonia; Project TEKO); during this expedition, I was accompanied by Guillaume Odonne (CNRS), Damien Davy (CNRS), and Sophie Gonzalez (IRD), who are here acknowledged for help during field work.

In Suriname, important observations on populations of *Sipanea pratensis* var. *dichotoma* and *S. veris* were made during a multidisciplinary expedition, in April–May 2014, to the surroundings of the Sipaliwini village, coordinated by Antoine Fouquet (CNRS, Laboratoire Evolution et Diversité, Toulouse, France), who also obtained the collecting permits for the entire team. At the Sipaliwini village we were hosted by the Trio Indigenous tribe, which is here acknowledged. During that

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Field work in Guyana in 2016, during which I studied natural populations of *Pteridocalyx* in the surroundings of the Chenapou Village, *Chalepophyllum guyanense* and *Sipanea veris* in the Kaieteur National Park, Upper Potaro River. Funds for that expedition were provided by the LABEX CEBA (Laboratory of Excellence - Center for the Study of Biodiversity in Amazonia). During that expedition I was accompanied by Paul Benjamin, excellent field guide and based at the Chenapou Village, of the Patamona Indigenous people, and Sebastien Cally, at that time doctoral student studying opilions at the University of Toulouse, France, who are here acknowledged for their help during field work. Thanks are also due to the staff of the Biodiversity Center of the University of Guyana, Georgetown, especially Kaslyn Holder-Collins and Elford Liverpool for help in gathering field supplies, drying facilities, and their valuable collaboration. Thank are also due to the Environmental Protection Agency (E.P.A.) of Guyana, and especially Diana Fernandes for her assistance in the process of obtaining the collecting permit (No. 060716 BR004) and the export permit (No. 062716 SP007).

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## LIST OF NAMES TYPIFIED IN THIS VOLUME

Numbers between parentheses correspond to those given in the Numerical List of Taxa.

- Chalepophyllum speciosum* N.E.Br. (4-2)  
*Limnosipanea schomburgkii* Hook.f. (3-2)  
*Limnosipanea spruceana* var. *macrantha* Delprete (3-3b)  
 “*Ptychodea pedunculata*” (8-5b)  
 “*Ptychodea sessiliflora*” (8-3)  
*Rondeletia biflora* Rottb. (8-7)  
*Rondeletia rupicola* K.Schum. (9-8)  
*Sipanea acinifolia* R.Spruce ex Sprague (8-6)  
*Sipanea carnea* Jacques [= *Pentas lanceolata* (Forssk.) Deflers]  
*Sipanea dichotoma* Kunth (8-5b)  
*Sipanea erythraeoides* Cham. (3-1)  
*Sipanea glabrata* Wernham (8-4)  
*Sipanea glomerata* Kunth (8-3)  
*Sipanea hispida* Benth. ex Wernham (8-4)  
 “*Sipanea* [as “*Sipania*”] *limnophila*” (3-3a)  
*Sipanea* [as “*Sipania*”] *palustris* Seem. (3-2)  
*Sipanea pratensis* var. *major* Hassl. (8-4)  
*Sipanea radicans* Endl. (8-7)  
*Sipanea stahelii* Bremek. (8-16)  
*Sipanea trichantha* Miq. (8-5b)  
*Sipanea veris* S. Moore (8-6)

## NUMERICAL LIST OF TAXA

- 1-1. *Chalepophyllum guyanense* Hook.f.  
 2-1. *Dendrosipanea prancei* Delprete  
 2-2. *Dendrosipanea revoluta* Steyererm.  
 2-3. *Dendrosipanea spigelioides* Ducke  
 3-1. *Limnosipanea erythraeoides* (Cham.) K.Schum.  
 3-2. *Limnosipanea palustris* (Seem.) Hook.f.  
 3-3a. *Limnosipanea spruceana* Hook.f. var. *spruceana*  
 3-3b. *Limnosipanea spruceana* Hook.f. var. *macrantha* Delprete  
 4-1. *Maguireothamnus jauaensis* (Steyererm.) Steyererm.  
 4-2. *Maguireothamnus speciosus* (N.E. Br.) Steyererm.  
 4-3. *Maguireothamnus tatei* (Standl.) Steyererm.  
 5-1. *Neblinathamnus argyreus* Steyererm.  
 5-2. *Neblinathamnus brasiliensis* Steyererm.  
 6-1. *Neobertiera gracilis* Wernham  
 6-2. *Neobertiera micrantha* Delprete

- 6-3. *Neobertiera montedouradensis* Delprete  
 6-4. *Neobertiera pakaraimensis* Delprete  
 6-5. *Neobertiera palustris* (A.Rich.) Delprete

7-1. *Pteridocalyx appunii* Wernham

**A. *Sipanea* section *Sipanea***

- 8-1. *Sipanea galioides* Wernham  
 8-2. *Sipanea glaberrima* (Bremek.) Steyererm.  
 8-3. *Sipanea glomerata* Kunth  
 8-4. *Sipanea hispida* Benth. ex Wernham  
 8-5a. *Sipanea pratensis* Aubl. var. *pratensis*  
 8-5b. *Sipanea pratensis* Aubl. var. *dichotoma* (Kunth) Steyererm.  
 8-6. *Sipanea veris* S. Moore

**B. *Sipanea* section *Virecta***

- 8-7. *Sipanea biflora* (Rottb.) Cham. & Schltld.  
 8-8. *Sipanea carrenoi* Steyererm.  
 8-9. *Sipanea gleasonii* Steyererm.  
 8-10. *Sipanea micrantha* Sandwith  
 8-11a. *Sipanea ovalifolia* Bremek. var. *ovalifolia*  
 8-11b. *Sipanea ovalifolia* Bremek. var. *villosissima* Steyererm.  
 8-12. *Sipanea setacea* Steyererm.

**C. *Sipanea* section *Nudae***

- 8-13. *Sipanea ayangannensis* Steyererm.  
 8-14. *Sipanea prancei* Steyererm.  
 8-15. *Sipanea saxicola* J.H.Kirkb.  
 8-16. *Sipanea stahelii* Bremek.  
 8-17. *Sipanea wilson-brownei* Cowan

- 9-1. *Sipaneopsis cururuensis* J.H.Kirkb.  
 9-2. *Sipaneopsis duckei* Delprete  
 9-3. *Sipaneopsis foldatsii* Steyererm.  
 9-4. *Sipaneopsis huberi* Steyererm.  
 9-5. *Sipaneopsis maguirei* Steyererm.  
 9-6. *Sipaneopsis morichensis* Steyererm.  
 9-7. *Sipaneopsis pacimoniensis* Steyererm.  
 9-8. *Sipaneopsis rupicola* (K.Schum.) Steyererm.

10-1. *Steyermarkia guatemalensis* Standl.

LIST OF SPECIMENS EXAMINED

Specimens are arranged by collector in alphabetical order, followed by collector's number in increasing order, with species number in parentheses. Specimens without collector number, indicated by "s.n.", are included in the list if they can be identified by a herbarium accession number or barcode. For specimens with two collectors, both collectors are cited. For specimens with more than

two collectors, only the first collector is cited followed by "et al." Numbers in **bold** are type specimens.

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## PIERO GIUSEPPE DELPRETE



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