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Research Article

Revision of Manettia (Rubiaceae) in Paraguay

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Manettia Mutis is a Neotropical genus comprising over 100 species, many of which are only known from their original descriptions or, at most, from revisions dating back over 100 years. Recent review studies have remained unpublished for several years. Conventional taxonomic methods are followed. Here, we present a brief history of *Manettia* and its current taxonomic status in the Flora of Paraguay. As a result of taxonomic and morphological studies, four species are recognised: *Manettia cordifolia, M. paraguariensis, M. rojasiana* and *M. tweedieana.* A dichotomous key for identification, distribution data and preliminary assessments of their states of conservation in Paraguay are presented. A complete description of *M. rojasiana* is also provided, confirming the presence of distyly.

Keywords: flora of Paraguay, Manettia, Rubiaceae, Spermacoceae, taxonomy

Introduction

Paraguay is located in the centre of the South American continent, between 18°28′ and 27°30′ south latitude and 54°19′ and 62°38′ west longitude (De Egea et al. 2012, Peña-Chocarro and De Egea 2018). The Paraguay River divides Paraguay into two large geographic regions: the eastern region, characterised by mesophilic formations, and the western region, or Chaco, characterised by mainly xerophytic formations (Spichiger et al. 2011). The two regions overlap in an extensive hygrophilous ecotonal area along the Paraguay River (Spichiger et al. 2011). Since the 1970s, excessive human activity has dramatically accelerated the degradation of natural vegetation, mainly in eastern Paraguay. The main threat to plant species conservation is the establishment of extensive agricultural and livestock farming, which is mainly oriented towards promoting monocultures with high economic yields (Spichiger et al. 2011).

Paraguay's flora consists of 197 families, 1356 genera and around 5296 species, 330 of which are endemic (Zuloaga et al. 2019). In Paraguay, the family Rubiaceae is represented by 37 genera and 132 species (Bacigalupo et al. 2008). The most diverse tribe in the country is the Spermacoceae, comprising around 10 genera and 67 species (Gauto and Salas 2024). Of these taxa, *Manettia* Mutis has its southernmost representatives

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in the country. The genus has a Neotropical distribution and belongs to the tribe Spermacoceae (Rubiaceae), comprising between 125 and 130 species of vines (Lorence and Dwyer 1993, Gauto et al. 2022a, 2022b). *Manettia* is closely related to the shrubby genus *Bouvardia* Salisb. These genera share similar floral morphology (funnel-shaped corolla) and winged seeds (Bremer and Manen 2000, Kårehed 2008, Groeninckx et al. 2009, Bremer and Erikson 2009, Kiehn and Berger 2020, Gauto et al. 2022a, Zuntini et al. 2024). It is distributed from central to South America, extending as far as the central region of Argentina (Gauto et al. 2022a).

In the checklist of the southern cone of America, four species of the genus are recognised for Paraguay (Bacigalupo et al. 2008): *Manettia cordifolia* Mart., *M. luteorubra* (Vell.) Benth., *M. rojasiana* Chodat and Hassl., and *M. tweedieana* K. Schum. However, subsequent analysis of herbarium specimens has revealed that *M. luteorubra* was in fact a misidentification, with *M. paraguariensis* Chodat being the correct identification (Macias 1998, Cordeiro Marinero et al. 2012, Gauto et al. 2022a, 2022b).

The aim of this work is to provide a synoptic review of the genus *Manettia* in Paraguay. It includes a brief analysis of its taxonomic history, a taxonomic treatment of the genus including a complete description of *M. rojasiana*, geographic distribution, and a preliminary assessment of its conservation status.

Material and methods

The taxonomic treatment followed standard practices in botanical taxonomy. A total of approximately 228 specimens (see appendix) were analyzed from the following institutions: BAA, BAB, BM, CORD, CTES, F, FCQ, G, K, LIL, MA, MBM, MO, SI, SP P, PY. Observations and measurements were conducted using a stereomicroscope and a digital caliper. When necessary, herbarium specimens were rehydrated in warm water with soap prior to examination. High quality images from online databases such as JSTOR (https://www.jstor.org/) and SpeciesLink (https://specieslink.net/search/) were also studied. Additional information on old publications, authors, and collectors was also gathered in BHL (2025).

Coordinates not originally provided on specimen labels were georeferenced based on the locality data indicated by collectors. The conservation status of the species was assessed according to the IUCN Red List criteria (ver. 3.1 2012), applied at the national scale, limiting the analysis to confirmed records found on Paraguayan territory. The extent of occurrence (EOO) was estimated by determining the area (in km²) delimited by a minimum convex polygon, using the online tool GeoCAT (Bachman et al. 2011). Geographic distribution maps were generated using QGIS ver. 3.32.1 (QGIS Development Team 2018). Species distributions patterns were determined according to the terrestrial ecoregions proposed by Olson et al. (2001).

Results and discussion

The genus Manettia in the flora of Paraguay

The history of the genus *Manettia* in Paraguay began almost at the same time as the first studies of its flora, thanks to the contributions of the Swiss medical Emile Hassler who resided in Paraguay between 1883 and 1937 (Stafleu and Cowan 1979). Hassler was one of the founders and supporters of the study of the flora of Paraguay. He collected a significant number of specimens on Paraguayan territory and his main collection is deposited at the Geneva herbarium (35 000 specimens) (Stafleu and Cowan 1979). He collaborated closely with Robert Hippolyte Chodat, Botanist of the Geneva herbarium (Cabrera and Willink 1980, Stafleu and Cowan 1976) and with Teodoro Rojas, a renowned Paraguayan botanist, assistant director of the botanical garden of Asunción and curator of its herbarium (Cabrera and Willink 1980, Stafleu and Cowan 1983).

Manettia hassleriana Chodat and *M. paraguariensis* were the first new species from Paraguay to be described by a Swiss botanist (Chodat 1899). The former was later classified as a variety of *M. cordifolia*, i.e. *M. cordifolia* var. *hassleriana* (Chodat) Chung. Currently, it is treated as a synonym of *M. tweedieana* (Gauto et al. 2022a). A few years ago, *M. paraguariensis* was considered by Hassler (1904) to be a synonym of *M. luteo-rubra* and later as a variety of the same species by Chung (1967) (i.e. *M. luteo-rubra* var. *paraguariensis* (Chodat) Chung). *M. paraguariensis* is currently considered a valid species. Chodat (1899) also mentioned *M. ignita* (Vell.) K. Schum. and *M. gracilis* Cham. and Schltdl. in Paraguay; however, both species are currently excluded from the country's flora. These two species were reported based on *M. cordifolia* specimens (Table 1). Later, Chodat and Hassler (1904) described *M. rojasiana*, a species with a bicolorous corolla that is unique in the genus for its urceolate form.

Based on Paraguayan specimens, Wernham (1919) described two new species: *M. angustifolia* Wernham and *M. sublanata* Wernham. Both species were later classified as synonyms, with the former being classified as *M. tweedieana* (Gauto et al. 2022a) and the latter as *M. cordifolia* (Bacigalupo et al. 2008).

More recently, Gauto et al. (2022b) presented an update on the nomenclature of certain *Manettia* species occurring in Argentina. As part of this update, *M. paraguariensis* and *M. tweedieana* were neotypified, while *M. rojasiana* was lectotypified. *Manettia*'s taxonomic history and present treatment are summarised in.

Taxonomic treatment

Manettia Mutis (Mutis 1771, p. 553–554, 558)

Type species: *Manettia reclinata* L.

An exclusively Neotropical genus comprising between 125 and 130 species. There is no modern revision for the genus in Paraguay or neighbouring countries. In Argentina,

Table 1. Names referring to *Manettia* in Paraguay indicated in the main treatments and flora reviews and their comparisons with the proposed in this work

Author	Cited species	Present study
Hassler 1899	*M. paraguariensis* (*Hassler 2511*), as a new species.	= *Manettia paraguariensis*, accepted.
	M. hassleriana (*Hassler 2509*), as a new species.	= *M. tweedieana*
	M. gracilis (*Hassler 1237*).	*M. gracilis*: excluded; *Hassler 1237=M. cordifolia*
Hassler 1904	*M. hassleriana*	= *M. tweedieana*
	M. gracilis	= excluded
	M. rojasiana (syntypes *Hassler 5409, Hassler 8282*), as a new species.	*M. rojasiana*, accepted; *Hassler 8282: lectotype*
	M. luteo-rubra (Hassler 4502)	= excluded; *Hassler 4502=M. paraguariensis*
	M. ignita var. glabra K. Schum. *(Hassler 7026)*	= *M. cordifolia*
	M. ignita var. micans (Poepp.) K. Schum. *(Hassler 8327)*	
	M. ignita var. *angustifolia* K. Schum. *(Hassler 8327a)*	
	M. micans var. *cordifolia (Hassler 6246)*	
Wernham 1919	*M. rojasiana* Chod. & Hassler. (Hassler 8282, 5405, 10269, 10527)	accepted
	Manettia cordifolia Mart. (*Hassler 6426*)	
	M. cordifolia var *filiformis* (*Fiebrig 4636*), as a new variety	= *M. cordifolia*
	M. sublanata (*Hassler 8841*), as a new species.	
	M. angustifolia (Fiebrig 5734), as a new species.	= *M. tweedieana*
	M. inflata Sprague *(Hassler 4502, Fiebrig 5416, Hassler 8906, Balanza 2133)*	= *M. paraguariensis; Hassler 4502!, Fiebrig 5416!, Hassler 8906!, Balanza 2133!*
Chung 1967, 1968	*M. rojasiana* Chod. & Hassl. (*Hassler 5405, 8282, 10269, 10527, Woolson 1556*)	= accepted
	Manettia cordifolia Mart. (*Hassler 4132, 6246, 8841a; Jorgensen 7269, Morong 512*)	
	M. cordifolia Mart. var cordifolia fo. incana (Schum.) Chung. *(Balanza 2135, Hassler 8841, Jorgensen 4132)*, as a new combination.	= *M. cordifolia*
	M. cordifolia var. glabra (Cham. & Schl.) Standl. *(Fiebrig 4636, Hassler 8327, 11200, 1237, 4435, 7026, 11783, Balansa 2134)*	
	M. cordifolia var. hassleriana (Chod.) Chung., as a new combination *(Fiebrig 5734)*	= *M. tweedieana*
	M. luteorubra var. paraguariensis Chung. *(Balansa 2133, Hassler 4502, 8906, West 852, Rojas 5042, Fiebrig 5416, Lindman A1847, Jorgensen 4311, 7270)*.	= *M. paraguariensis*
Bacigalupo et al. 2008	*M. rojasiana* Chodat & Hassl. (*Bacigalupo 1149*)	= Accepted
	M. luteorubra (Vell.) Benth. *(Jimenez 1223)*	= Excluded; *Jimenez 1223= M. paraguariensis*
	M. cordifolia Mart. *(Hassler 11783)*	= Accepted
	M. tweedieana (Fiebrig 5734)	= Accepted

the genus has been treated floristically (Gauto et al. 2022a), and a review has been completed for this country (Gauto, unpublished data). The most comprehensive studies were carried out by Wernham (1919); however, numerous proposals for taxonomic rearrangements have been introduced over the years by various authors (Chung 1967, 1968, Steyermark 1978, Macias 1998). Currently, four *Manettia* species are recognized in Paraguay, none of which are endemic. However, some species exhibit very restricted distributions (e.g. *M. tweedieana*) or has a unique flower morphology (e.g. *M. rojasiana* with urceolate corolla).

Manettia cordifolia Mart. (Martius 1824, p. 95)

Basionym: *Manettia ignita* (Vell.) K. Schum. var. *cordifolia* (Mart.) K. Schum. (Schumann 1889, p. 171).

Type: Brazil, Minas Gerais. Villa Rica, s.d., C. F. P. Martius s.n. (lectotype: M barcode M0198125, images!); isolectotypes: BR barcode BR0000016153028!, M barcode M0198128, images!, M barcode M0198129, images!, M barcode M0198134, images!, designated by Gauto et al. (2022b, p. 430).

Synonyms: *Manettia cordifolia* Mart. var. *filiformis* Wernham (Wernham 1919, p. 20). *M. cordifolia* var. *glabra* (Cham. and Schl.) Standl. (Standley 1931, p. 263). **Type**: Paraguay, North, between R. Apa and R. Aquidaban, Villa Sana. K. A. G. Fiebrig 4636 (holotype: BM barcode BM001191261!; isotype: K barcode K000173726!,)

Manettia sublanata Wernham (Wernham 1918, p. 14). **Type**: Paraguay, Dpto. Cordillera. Cordillera de Villa Rica, Ene 1905, É. Hassler 8841 (holotype: BM barcode BM001191268!; isotypes: G barcode G00436370, images!, G barcode G00436371, images!, GH barcode GH00096359, images!, K barcode K000173724!, NY barcode NY00132210, images!, UC barcode UC929600, images!).

Iconography: Gauto et al., (2022a).

Distribution

Manettia cordifolia is present in the departments of Concepción, Amambay, San Pedro, Capital, Central, Cordillera, Caaguazú, Guairá, Paraguarí, Alto Paraná, Itapúa, and Misiones (Map 1), and in the ecoregions Alto Parana Atlantic Forest, Cerrado, and Humid Chaco (Olson 2001).

Conservation status

An estimated Extent of Occurrence (EOO) of 124 689 km^2, and Area of Occupancy (AOO) of 104 km^2 places it below the 'Endangered' (EN) threshold under criterion B2. However, the species is found in 12 departments and in many different types of vegetation, including several protected areas. Despite ongoing threats, such as deforestation and land-use change, in some areas of its distribution, the species is classified as 'Vulnerable' (VU) under criterion B2ab (iii).

Notes on typification

Gauto et al. (2022a) typified this species based on a specimen that clearly exhibits its distinctive characteristics, such as cordate bracts and red funnel-shaped corolla.

Additional specimen examined

Paraguay, Alto Paraná, Hernandaria, Sta Teresa, n/d Bertoni 4277 (CTES, LIL); Alto Paraná, Reserva Biológica Itabó, Bosque Bajo, 28 Mar. 1979, Caballero Marmori G. 269 (CTES); dpto. Alto Paraná, Italó, a km de hospedaje, 5 July 1987, Degen R. 269 (CTES); In Alto Paraná, regione fluminis 1909, K. Fiebrig 6169 (SI); Dpto. Alto Paraná. Loc. Ñacunday, 18 Nov. 1950, J. E. Montes 9780 (CTES - LIL); Amambay loc. Bella Vista, 22º07'27.67″S, 56º07'27.67″W, 24 Nov. 1994, Krapovickas A. et al. 44997 (CTES); Asunción Trinidad, 25º 15'86″S, 57º34'47.91″W, 85 m a.s.l., 19 Dec. 1943, T. Rojas 10743 (LIL); Asunción, Jardín Botánico, 24 July 1972, A. Schinini 5023 (CTES); Paraguay dep. central, between Asuncion and Limpio, Paso nande yara, humid chaco forest with altered soil due to human use, 5 Sept. 1979, Soejarte D. D. et al. 5102 (F); Canindeyú. zona de río Piratiy - 30 km NW de salto Guaira, 17 Feb. 1993, G. Carballo 3047 (CTES); Concepción, Apa River, tall forest, 12 May 2000, E.M. Zardini and D. Quintana 54473 (FACEN); Concepción, trail from Bella Vista Norte to Sargento Jose E. Lopez. Chaco forest 22º10'09″S, 56º30'59″W, 10 May 2000, E. M. Zardini and M. Vera 54248 (FACEN); Cordillera, Cerro caacupe 8 km del pueblo, 20 May 1975, Arenas A. 1207 (SI, CTES); Cordillera, R. Mandunirá, 2 June 1986, Degen R. 31 (CTES); Cordillera, caacupé, pendiente boscosa cordillera Ascurra, 14 May 1946, T. Rojas 13378 (SI - LIL); Cordillera: Cerro Ybitú Silla, 1 km S of tobatí. In forest, 28 June 1988, E. Zardini y R. Degen 5208 (CTES - MO - US); Cordillera, General Bernardino Caballero, Cerrado forest on sandstone, 9 July 1993, E. M. Zardini y T. Tilleria 36563 (LPB - MO - AS); Encarnación, Mboy caí, 19 Nov. 1945, Bertoni 2396 (CTES, LIL); Encarnación, Mbasicae, 29 Mar. 1949, Bertoni 4041 (CTES); Guaira, Villa Rica, sur le bord des ruisseauxe, 18 Feb. 1876, Balansa B. 2135 (P); Villa Rica, Mar. 1931, Jorgensen 7269 (F); Guairá, Loc. Borja, 18 Februari 1953, J. E. Montes 16191 (CTES - LIL); Guairá, Azucarera de Tebicuary, Ayo. Ihacá, 12 Jan. 1973, Schinini, A. 5863 (SI - CTES); Guaira. Mbocyaity - Melgarejo. 2 km on arroyo Gerbasia Gallery Forest, 6 July 1992, E. M. Zardini and T. Tilleria 32343 (FCQ). Itapúa, Natalio 25. Balneario, en arroyo 25. Bosque de ribera, 9 May 2003, F. Gonzalez Parini et. al. 1704 (CTES); Itapúa, Cordillera San Rafael. Distrito Alto Vera, 13 Nov. 2001, F. Gonzalez y M. Soloaga 482 (CTES - FCQ); Itapua. ruta 6, 5 km N de Artigas, 22 Mar. 1993, A. Schinini et. al. 27671 (CTES); Itapua, Yacyreta dam Island reserve, Oculto. Palm savanna, 7 Dec. 2002, E. M. Zardini y R. Gamarra 59452 (CTES); Iter ad 'Yerbales' montium 'Sierra de Maracayú': In regione fluminis Capibary Paraguay, no date , E. Hassler 4435 (P - F); Amer. Merid. 6 Jan. 1905, Bompland 599 (CTES, P); Misiones, Ayolas Kueju puesto 6 (sobre el viejo desvio a San Cosme y Damian a 4 km. prop. sr. Leiva), 24 Apr. 1983, Duré R. 193 (CTES); Misiones, Santiago, Est. La Soledad, Monte Bajo, 20 Oct. 1967, A. Lourteig 2074 (SI); Misiones, Santiago, Est. La Soledad, Monte Bajo, 20 Oct. 1967, A. Lourteig 2070 (SI); Misiones, estancia La soledad, Santiago dep. Misiones, T. M. Pedersen 5929 (SI - L - WAG); Orilla S del rio Aquidaban, paso horqueta, 17 Dec. 1986, L. Perez et. al. 1577 (CTES); ea. Soledad, 3 km S de Santiago, 3 Feb. 1988, A. Schinini and R. Vani 26007 (CTES); Paraguarí, estero del Ypoá, Carapeguá, Arroyo Mbaey, dry forest on clay soil and gallery forest along creek, 27 Jan. 1993, E. Zardini and T. Tilleria 34889 (LPB - MO - AS); Paraguari dans les bosquets, 9 May 1974, Balansa B. 2134 a (P); in regione cursus superioris fluminis Apa 1901 - 1902, E. Hassler 8327 (LIL - F); Paraguay 1913 Hassler E. 11783 (F); Paraguaria centralis, in regione lacus ypacaray 1913, E. Hassler 11785 (L); no date, P. Jorgensen 4132 (LIL - F); San Pedro around Rosario Paranaense Forest, 25 June 2001, E. M. Zardini and L. Guerrero 56754 (FACEN - LPB - MO)

***Manettia paraguariensis* Chodat. (Chodat 1899, p. 82)**

Basionym: *Manettia luteorubra* (Vell.) Benth. var. *paraguariensis* (Chodat) I. C. Chung (Chung 1967, p. 276).

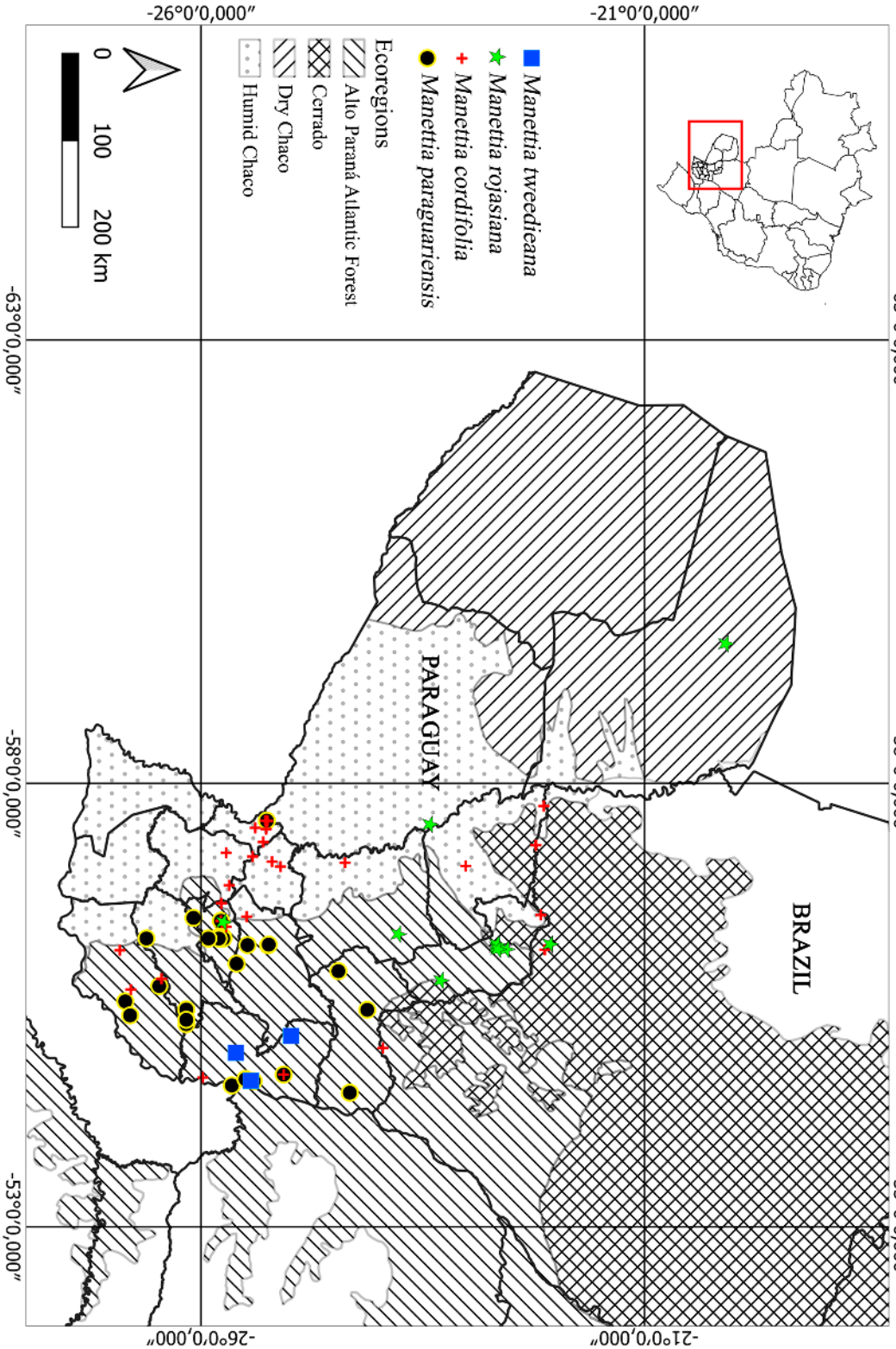
Type: Paraguay, Itapúa, 2 km S de Bella Vista, 7-X-1993, A. Krapovickas and C. L. Cristóbal 44482 [neotype: CTES barcode CTES0554093!, designated by Gauto et al. (2022b, p. 431); isotype: G 45050/1 (not seen)].

Synonym: *Manettia inflata* Sprague (Sprague 1904, p. 385). **Type**: Specimen cultivated at the Kew botanical garden (holotype: K!; isotype P01900490, images!)

Iconography: Gauto et al., (2022a)

Distribution

Manettia paraguariensis is present in the states of Canindeyú, Caaguazú, Alto Paraná, Guairá, Caazapà, Itapúa, and in the ecoregions Alto Paraná Atlantic Forest and Humid Chaco (Olson 2001) (Map 1).



Map 1. Distribution of *M. cordifolia*, *M. paraguariensis*, *M. tweedieana* (in Paraguay) and *M. rojasiana* (Paraguay and Brazil), in relation to the terrestrial ecoregions of the world (Olson et al. 2001). Abbreviations for the states: AM = Amambay, AP = Alto Paraguay, APN = Alto Paraná, CA = Caázapá, CE = Central, CN = Canindeyù. CO = concepcion, CR = Cordillera, GU= Guairá, IT = Itapúa, MI = Misiones, MS = Mato Grosso do Sul, PA = Paraguarí, SP = San Pedro. Abbreviations for the terrestrial ecoregions of the world: ce = Cerrado, ap = Alto Paraná Atlantic Forest, dc = Dry Chaco, hc= Humid Chaco.

Conservation status

Based on an estimated Extent of Occurrence (EOO) of 57 233 km^2, and Area of Occupancy (AOO) of 104 km^2, by far exceeding the threshold established for threatened categories under criterion B1, the species is considered as 'Least Concern' (LC).

Notes

Manettia luteorubra is a validly published name that has long been used to identify specimens of *M. paraguariensis* (Delprete 2005, Bacigalupo et al. 2008) *Manettia luteorubra* was excluded from the flora of Argentina due to a more detailed analysis (Gauto et al. 2022a). It is found in the states of Goiás, Mato Grosso, Minas Gerais, Espírito Santo, Rio de Janeiro, and São Paulo (Macias 1998, Bacigalupo et al. 2008).

Additional specimen examined

Paraguay, Alto Paraná, in regione fluminis alto Paraná, Oct. 1909, K. Fiebrig 5416 (SI – LIL); Alto Paraná: itabo, Reserva biológica de Itaipú. Selva cerca del río Itabo, 24 May 1989, R. Kiesling et al. 7203 (SI); Alto Paraná, Puerto Bertoni, Mayo 1938, T. Rojas 8019 (LIL); Alto Paraná, C.F.A.P. Puerto Stroessner, 25º30′S, 54º40′W, 16 Oct. 1991, R. Spichiger y P. A. Loizeau RS 5054 (CTES – G); Hernandaria, Sta Teresa, 14 July 1949, Bertoni 4292 (CTES – LIL); Alto Paraná. Hernandarias, 20 km N de Hernandarias, 10 Jan. 1974, A. Schinini 8098 (CTES); Alto Paranà, Itabò, Reserva Biológica Itaipu. Sendero Tangarà, 24 Apr. 1989, M. Ortiz 1410 (FCQ), Alto Paranà, Itabò, Reserva biológica Itaipu. Sendero Tangarà, 25 Apr. 1989, M. Ortiz 1331 (FCQ); Alto Paraná, a 29 km de Puerto Stroessner, 9 Dec. 1992, F. Casas 7349 (NY); Alto Paraná, pto. Stroessner, esc. Técnica forestal, 27 Jan. 1982, F. Casas 5651 (NY); Alto Paraná, Itapúa, entre capitán Meza y Puerto Triunfo, 17 Jan. 1980, F. Casas 3700 (NY); Amambay, Itapopo, 8 June 1993, N. Soria 6279 (NY); asunción abaí montes picada (Trinidad Asunción), May 1932, T. Rojas 5815 (SI). Caaguazú, estancia primera, Septembre 1927, T. Rojas 5042 (SI); Caaguazú, distrito de Tajao, Bosque Deagradado, 27 July 2002, F. Gonzalez Parini 1155 (CTES – FCQ); Caaguazú, Distrito de Tajao, Bosque Degradado, 28 Aug. 2002, F. Gonzalez 1189 (CTES – FCQ); Caaguazú, Ruta 2. Parque Guayakí, 26 Sept. 1967, A. Krapovickas et. Al. 13534 (CTES); dpto. Caaguazú, Ruta 2. Parque Guayakí, 22 May 1987, E. Zardini et. Al. 2441 (CTES – MO – MBM); Caa guazu, Flora caaguazuensis, in vicinii caa guazú, February 1905, E. Hassler 8906 (F – V – NY); Caazapá, SW base of cordillera de Caá Guazu, dpto. Caazapá 600 m a.s.l., 15 Mar. 1937, J. West 8525 (SI); Caazapá, Tavaí, tall forest 1 km N of hospital, 26º10′S, 55º27′W, 29 Oct. 1988, E. Zardini 7765 (CTES – MO – MBM); Parque guayaki, km 160, 26 Sept. 1967, A. G. Schulz 16164 (CTES); Caazapá, Tavai. Five kms S of Destacamento, on Constancio Trociuk Ranch, tall forest, 30 Oct. , E. Zardini 7831 (CTES – MO – FCQ); Caazapá – distr. Yuty. Loc. 15 km S de Capitindy, 10 Sept. 1987, M. M. Arbo et al. 2813 (CTES – F – MO – MBM); Caazapá, P.N. Caaguazù. Interior y borde de Bosque, 25 July 1998, F. Mereles et al. 7273 (FCQ), Caazapá, Tavai. Prop. Del sr. Trosiuk, 16 Mar. 1989, N. Soria 3328 (MO – FCQ); Caazapá, Tavai, Yacare-ry, 26-10′S, 55-20′W, 4 Dec. 1988, I. Basualdo 1984 (MO – FCQ); Caazapá, Tavai, Pacuri, Comunidad mbya, 26º10′S, 55º20′W, 22 Dec. 1988, I. Basualdo 2096 (MO – FCQ), Caazapa, yuti, desvio a 3 de mayo, 10 September 1987, E. Zardini et al. 2945 (MBM). Canindeju, dpto. Kanendiju, Col. Fortuna, 8 km de Kuruguaty, 8 May 1974, Pastor Arenas 695 (SI – CTES – F); Canindeyu, campo mbariguiry. Campo cerrado, Suelo Arenoso, 24º27′7″S, 55º52′55″W, 23 Aug. 2002, F. G. Parini et al. 1140 (FCQ); Canindeyu, Reserva Mbaracayu, 13 June 1992, I. Basualdo 4161 (FCQ); Canindeyú. Loc. Jejui-ui ? (49500/28900 utm), 1 May 1996, B. Jimenez and M. Peña 1223 (CTES – S – FMB); Iter ad yerbales, motium sierra de Maracayú , E. Hassler 4502 (P – NY); Canindeyú, Guadalupe, 28 Oct. 1978, M. Bernardi 18255 (NY); Canindeyú, entre la paloma y saltos de Guaira, 16 Dec. 1982, F. Casas 7594 (NY); Canindeyu, Villarica, nd, P. Jorgensen 4371 (NY); Canindeyú, Torrin, 26 Aug. 1985, G. Hatschbach and A. C. Cervi 49802 (MBM); Canindeyú. Loc. Guadalupe, ca 30 NW de puerto Adela, 360 m a.s.l.., 17 Dec. 1982, A. Schinini 23168 (CTES); central, ruta 7 en desvio km A 289.3. camino a Asuncion, 28 Nov. 1967, O. Boelcke 13418 (CTES – BAA); ruta 2 km A 252, 28 Nov. 1967, O. Boelcke 13484 (CTES – BAA – MBM); Col. Presidente Gonzales, 1 Aug. 1893, Lindman C. A. M. A1847 (F); Guaira, Villa Rica, Paraguay, 25º46′33.82″S, 56º26′58.53″W, 183 m a.s.l.., May 1931, P. Jorgensen 4311 (SI – LIL – F); Guaira, Vega Cué, dpto. Guairá, 13 May 1987, Schmeda 921 (CTES); Guairá, dpto. Del Guairá. Loc. Monte Santa Clara Iturbe, 26º05′10.29″S, 56º28′58.68″W, 121 m a.s.l.., 15 July 1952, J. E. Montes 15898 (CTES – LIL); Guira reta Bosque Ribereño, alto del rio Tebicuary, 10 Dec. 2003, C. Vogt and T. Rios 101 (PY – FCQ); Guaira, cordillera de Ybytyruzu, Melgarejo cerro acati 2 KM S of Melgarejo on aº Tacuara, 25º45′S, 56º16′W, 10 July 1992, E. Zardini and L. Guerrero 32553 (FCQ); Guaira, cordillera de Ybytyruzu. Melgarejo cerro acati 8 KM S of Melgarejo, forest on slopes, 25º48′S, 56º16′W, 10 July 1992, E. Zardini and T. Tilleria 32666 (MO – FCQ); Guaira, tororo: Cerro Polilla , 52º55′,S 56º16′W, 13 Nov. 1988, M. Ortiz 830 (MO – FCQ); Guaira, tororo: Prop. Raul Alvarenga 25º55′S, 56º15′W, 13 May 1988, N. Soria 2694 (MO – FCQ); Guaira, Tororo: Aº Polilla 25º55′S, 56º15′W, 14 Dec. 1988, N. Soria 2839 (MO – FCQ); Guairá, Cordillera de Ybytyruzù Road Melgarejo-Antena, 6 km N of Antena 25º45′S, 56º15′ W, 14 July 1989, E. Zardini 13412 (MO – FCQ); Guairá, Coordillera de Ybytyruzù, road melgarejo, elgarejo 5 km N of antena tall forest, 25º48′S, 56º15′W, 9 Sept. 1989, E. Zardini 14061 (FCQ); Guairá, cordillera del Ybytyruzù, Forest, 10 kms S of Melgarejo, 25º55′S, 56º15′W, 28 May 1989, E. Zardini and C. Velasquez 12386 (FCQ); Villa Rica, May 1931, P. Jorgensen 7270 (F); Orayo-Bossado, à l'est de la cordillère de Villa-Rica Paraguay, 20 Sept. 1874, B. Balansa 2133 (P); Itapua, Pirapó, centro de desarollo forestal, Bosque Alto 26º51′18.96″S 55º32′28.89″W, 163 a.s.l., 21 Apr. 1983, R. Duré 178 (SI – CTES); Itapúa, 15 Sept.

1988, T. M. Pedersen 15021 (SI – CTES – MBM); Itapúa, dep. Itapua, Loc. 2km S de Bella Vista, 7 Oct. 1993, A. Krapovickas and C. L. Cristobal 44482 (CTES); Itapúa, ruta 6, camino de Bella Vista a arq. Romero Pereira en el cruce de Pirapó, 26º48′S, 55º23′O, 25 Apr. 1992, O. Morrone and J. Pensiero 268 (FCQ); Itapúa, cordillera San Rafael, Distrito Alto Vera, 26º28′18″S, 55º42′51.2″W, 15 Oct. 2001, F. Gonzales 275 (FCQ).

Manettia rojasiana **Chodat and Hassl. (Chodat and Hassler 1904, p. 91) (Fig. 1)**

Basionym: *Lygistum rojasianum* (Chodat and Hassl.) B.L. Rob. (Robinson 1910, p. 405).

Type: Paraguay, no date, ST: Hassler 5405, no date; Paraguay. ST: Hassler 8282, no date; Paraguay, (lectotype: G barcode G00436363! designated by Gauto et al. 2022b (2022, p.

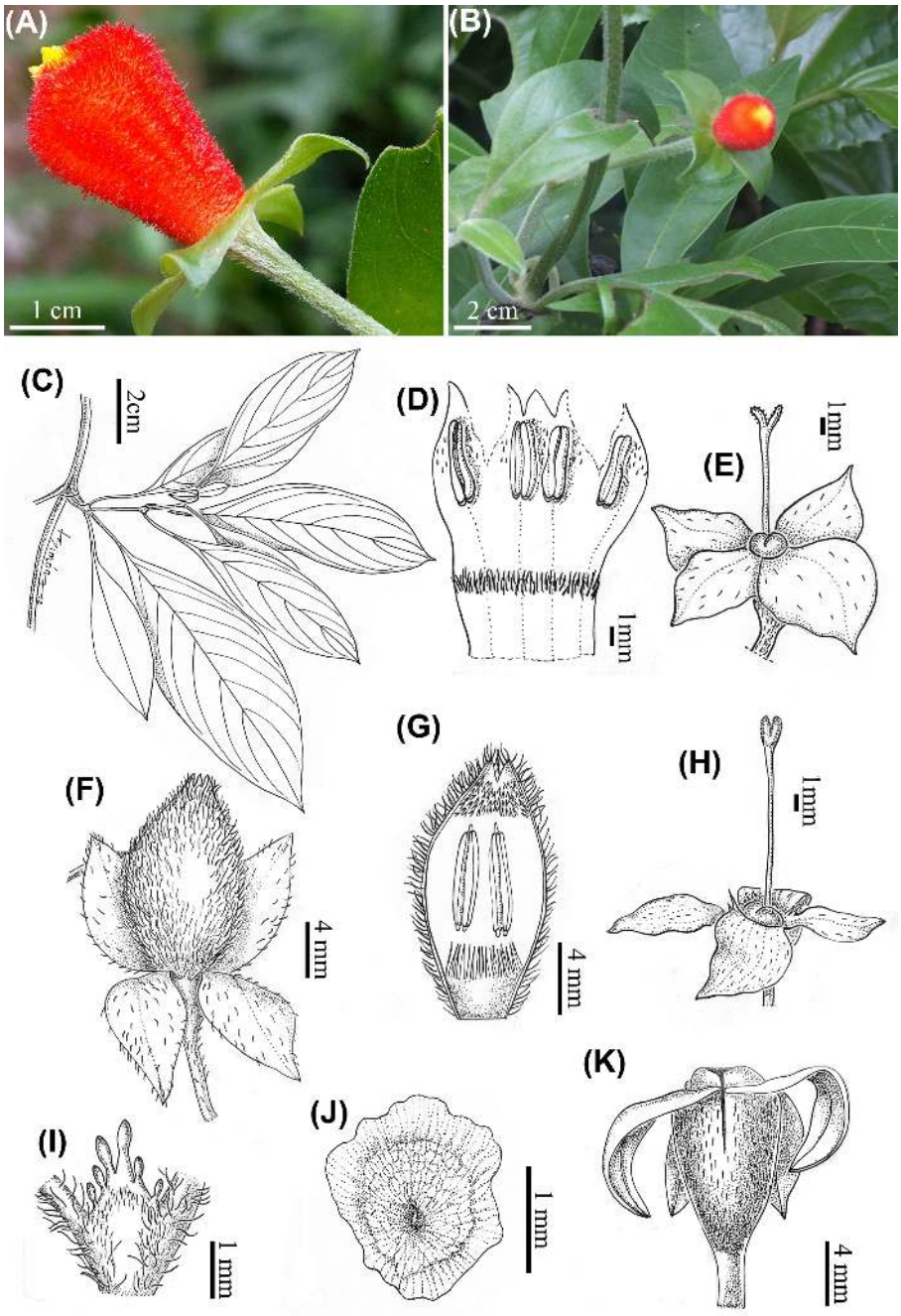


Figure 1. (A)–(K) *Manettia rojasiana*. (A)–(B) Photographs of M. rojasiana in the field, (C) leaves, (D) open corolla of brevistylus flower, (E) gynoecium of brevistylus flower, (F) general appearance of flower, (G) open corolla of longistylus flower, (H) gynoecium of longistylus flower, (I) stipule pubescent, (J) winged seed, (K) capsule-type fruit with persistent calyx lobes. Hahn 1204 (CTES—); Hatschbach 72982 (CTES—D,E). Drawn by Laura Simon. Photograph by L. Castillo.

431); isolectotypes: G barcode G00436362!, G barcode G00436366!, G barcode G00436361!).

Description

Climbing plant; stems cylindrical subtetragonous, 1.3–3.6 mm in diameter, pubescent or puberulous. Leaves petiolate; petioles subcylindrical, 6.0–27.5 mm long., pubescent or tomentose. Stipules triangular, acute or acuminate at apex, with coléters, 1.77 × 1.23 mm; blade lanceolate, ovate or elliptic, discolorous, 18.0–97.9 × 11.1–40.0 mm., length/width ratio 1.62:1–2.45:1, acute at apex and base, glabrous or pubescent, abaxially glabrous or pubescent, with margin glabrous, membranaceous or papery; secondary nerves 3-–5, visible only on the abaxial side. Inflorescence a monocasium or dichasium, axillary, 1–2-florous, bracteate, foliate; bract sessile, elliptic–lanceolate, 17.2–29.1 × 3.6–9.7 mm, length/width ratio 2.5:1–3.2:1, pubescent. Flowers distylous; pedicels 16.5–44.5 mm. long, pubescent; flower and pedicel glabrous or pubescent, 16.5–44.5 mm long; hypanthium oblong, 2.7–4.0 mm, pubescent or tomentose; calyx 4-lobed, 6.5–17.8 mm, ovate, foliaceous, with intercalary teeth; corolla outside distinctly pubescent, reddish gradually transitioning to yellow towards base; corolla lobes triangular, 0.8 × 2 mm., patent. Corolla inside with a ring of hairs towards the base. Long-styled flower with urceolate corolla (Fig. 2A), 16.7 mm long; stamens 5.7–6.0 mm; anthers 4.3–4.9 mm long; style 12–20 mm; stigma included. Short-styled flower with tubular corolla, narrowed at base (Fig. 2B), 16.2 mm long; stamens 7.5–8.4 mm; anthers 4.1 mm long; stigma 5.5–6.0 mm long. In both kind of flowers the stigma is bilobate, glandulose. Floral nectary disc-shaped. Capsules oblong, 19.9–63.0 x 5.3 mm, pubescent; pedicel 7.6–12.4 mm long; seeds almost spherical in outline, 1.9 × 1.9 mm; exotesta winged, membranaceous, finely reticulate.

Phenology

Flowering in every month of the year.

Distribution

Manettia rojasiana is present in the states of Alto Paraguay, Amambay, San Pedro and Guairá in Paraguay, as well as in the state of Mato Grosso do Sul in Brazil, and in the ecoregions Alto Paraná Atlantic Forest, Cerrado, Dry Chaco, Humid Chaco and Pantanal (Olson 2001) (see Map 1).

Conservation status

Based on an estimated Extent of Occurrence (EOO) of 242 166 km² and an area of occupancy (AOO) of 56 km² *M. rojasiana* qualifies as 'Least Concern' (LC). However, due to loss and degradation of natural habitat through deforestation in the American Gran Chaco (Cardozo et al. 2013) and land-use change in several of these areas (Garcia Calabrese et al. 2017), in addition to a limited number of locations, it is suggested that the species should be classified as 'Endangered' (EN) under criterion B2ab(iii).

Notes on distribution and brevistyly

Manettia rojasiana was considered endemic to Paraguay (Bacigalupo et al. 2008) for a long time. Later, Peña Chocarro and De Egea (2018) excluded it from the endemic species of Paraguay, possibly because it was mentioned in studies in Mato Grosso do Sul, Brazil (Faria and Araujo 2010, Vasconcellos Barbosa 2018).

The protologue of *M. rojasiana* mentions '*a brevistyla form?*', leaving open the possibility that the species could be distylic., but the author provided no description of the fruits and seeds. However, upon detailed analysis of the specimens, the presence of a brevistyle morphotype is evident. This morphotype is described and illustrated here.

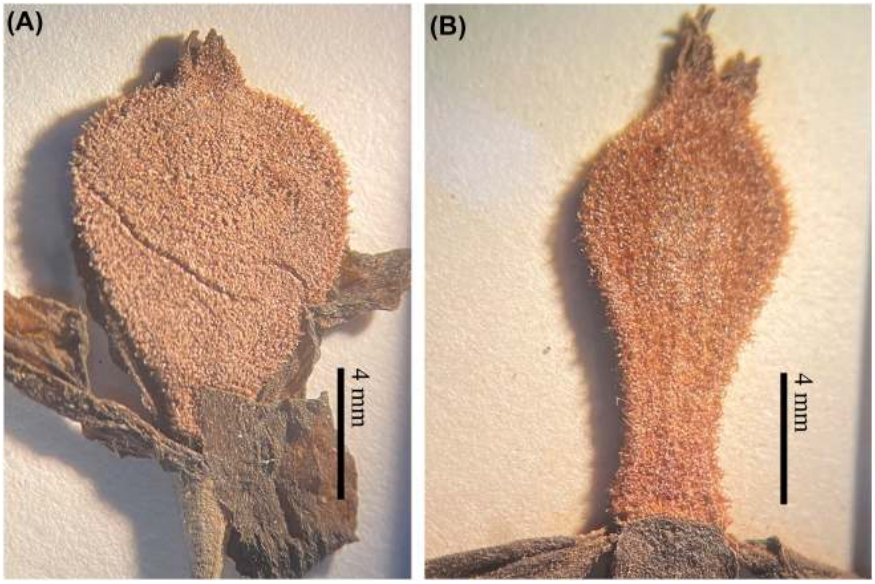


Figure 2. A–B *Manettia rojasiana*. (A) Overall appearance of brevistylus flower, from Hahn 1204 (CTES, MO), (B) overall appearance of longistylus flowers, from Krapovickas et al. 13993 (CTES).

Examined specimens

Paraguay, Amambay, Ea. San Francisco, camino a bella vista, 23°17′53.10″S, 55°40′27.06″W, 409 a.s.l., 10 Dec. 1992, E. Nicora 9818 (SI - CTES - PY - FCQ); Amambay, cerro Sarambí a 12 km de PN Cerro Corá 22°40′S, 56°03′W, 6 May 1989, Bacigalupo et al. 1149 (BAB - FCQ - SI); Dpto. de Amambay, Parambi'y a 40 km de P.J. Caballero, 22° 33′ 32,50″ S 56° 01′ 29,99″ W, 411 a.s.l., 12 June 1974, P. Arenas 792 (SI); dpto. Amambay, PN Cerro Corá, Deciduous forest to 25m tall, 22°40′S, 56°05′W, 7 May 1984, W. Hahm 2488 (CTES - MO - MBM - G - MBM - RB - SP - PY - FCQ); dpto. Amambay. P.N. Cerro Corá 22°39′08.68″S, 56°01′31.92″W, 270 a.s.l., 12 Dec. 1989, R. Vanni et al. 1349 (CTES); Dpto. Amambay, Camino de Sereno a la Colonia Yaguatí, 26 June 1993, N. Soria 6251 (CTES), dpto. Amambay, estancia Errante, ca 32 km SW de Bella Vista, 24 Aug. 1980, A. Schinini 20620 (CTES); Dpto. Amambay, PN Cerro Corá, semideciduous forest, Aspidosperma polyneuron, Tabebuia, Balfourodendron y Parapiptadenia domi - nant, soil red, somewhat sandy, 22°04′S, 56°05′W, 18 Mar. 1983, W. Hahm et al. 1204 (CTES - MO - MBM - G - PY); Amambay, Itapopo, propiedad del señor Galvan, 28 June 1993, N. Soria 6279 (FCQ); Amambay, P.N Cerro Corá camino a colonia Naranja Hai, 15 May 1995, N. Soria 6980a (FCQ); in altaplanitie et declivibus,sierra de Amambay 1907 - 1908, T. Rojas and E. Hassler 10527 (F - G); Alto Paraguay, Lima, Monte Picada, 20°05′06.90″S, 59°28′19.52″W, 119 a.s.l., Apr. 1921, T. Rojas 3679 (SI). Alto Paraná, Itaso, reserva biológica itaipu, Sendero Tangarà, 24 May 1989, M. Ortiz 1410 (FCQ); Canindeyú, yerbales mountain montium sierra de maracayú, in altoplanitie et decliviis, Nov. 1904, E. Hassler 5405 (F - P - NY - AMES); Concepción, 10 km N de Yby Yau, 23°25′17.13″S, 57°26′04.00″W, 74 a.s.l., Jan. 1992, N. Soria 5127 (FCQ); Guaira cordillera de Ybytyruzu, Road Antena- Melgarejo, 15 km N of antena tall, forest, 25°45′S, 56°20′W, 9 Sept. 1989, E. Zardini and A. Aguayo 14123 (FCQ); San Pedro Loma Hoby, 7 June 1954, A. Wolston 185 (SI); E. Hassler 8282 (SI - LIL - NY - P - US - F - AMES); dpto. San Pedro, Yaguareté Forest (sustainable forest systems site), Northern boundary, tall and los forest, 23°46′49″S, 56°11′49″W, 27 May 1997, S. E. Zardini and S. Zavala 46741 (CTES - MO); S. E. Villa San Pedro, montes Picada, 'yatebó?', nd, T. Rojas 2337 (SI - F); San Pedro, estancia Santa Librada, bosque degradado, 23°31′,S 50°21′W, 7 June 2002, F. Gonzales 872 (FCQ); San Pedro, línea ovetense 10 km NE de Choré, 3 Oct. 1987, Zardini E. and C. Benitez 3359 (FCQ); Paraguay, 18 Nov. 1968, A. Krapovickas et. al. 13993 (SI - CTES - BAA - MBM); Paraguay, Zardini y S. Zavala 46741 (CTES - MO)

Manettia tweedieana K. Schum. (Schumann 1889, p. 169)

Based on the same type: *Lygistum tweedieanum* (K. Schum.) Kuntze (Kuntze 1891, p. 288).

Type: Brazil. Rio Grande do Sul, São Francisco de Paula, José Velho, Mar 2003, R. Wasum 1652 (holotype: B†; neotype: MBM barcode MBM283005 [digital image]!; isotype: NY barcode NY778346 [digital image]! designated by Gauto *et al.* (2022b, p. 431).

Synonyms: *Manettia angustifolia* Wernham (Wernham 1918, p.22). **Type**: Paraguay. Dpto. Alto Paraná: Rio Alto Paraná, K. A. G. Fiebrig 5734 (holotype: BM barcode BM001191262!; isotypes: GH barcode GH00096454 [digital image]!, K barcode K000173722!, US barcode US00137828 [digital image]!).

Manettia hassleriana Chodat (Chodat 1899, p. 82). Manettia cordifolia Mart. var. hassleriana (Chodat) I.C. Chung (Chung 1968, p. 362). **Type**: Paraguay. Dpto. Concepción, Rio Apá, É. Hassler 2509 (holotype G).

Iconography: Gauto et al. (2022a).

Distribution

Manettia tweediana grows only in the Alto Paraná department, in the alto paraná atlantic forest ecoregion (Olson 2001) (Map 1).

Conservation status

Based on an estimated extent of occurrence (EOO) of 1275 km² and an area of occupancy (AOO) of 12 km² *M. tweedieana* qualifies for the 'Endangered' (EN) category. From Paraguay, there are only a few historical collections, most of which are more than 70 years old. A continuous decline in habitat quality has been identified, mainly due to causes such as anthropic pressure, which has led to the loss of 90% of the forest cover and high degree of fragmentation in Alto Paraná department (Peralta Kulik et al. 2018, Angelo at al. 2009). Therefore, under a preliminary regional assessment for Paraguay, the species could be considered as 'Endangered' (EN) under criteria B1ab(ii, iii)+2ab(ii, iii).

Examined specimens

Paraguay, Alto Paraná. loc. sta. Luisa, 24°59′07.04″S, 55°09′05.06″W, 250 a.s.l., 5 Aug. 1945, Bertoni 1665 (CTES - LIL); in regione fluminis alto Paraná, 25°36′27.20″S, 54°57′40.26″W, 252 a.s.l., Oct. 1909, K. Fiebrig 5734 (SI - LIL); Hernandarias, Loc. pto. Sauce, 25°26′18.53″S, 54°38′47.92″W, 217 a.s.l., 5 Aug. 1949, Bertoni 4402 (CTES - LIL); dep. Hernandarias, 24 July 1949 Bertoni 4341 (CTES - LIL); Paraguay, n.d., K. Fiebrig 4636 (F - B).

Key to the species of Manettia in Paraguay

1. Corolla urceolate or tubular and inflated at the base, 16.2–18.0 mm long, with reddish indumentum at the base, gradually turning to yellow towards the apex; corolla lobes glabrous inside; flowers distylous……2
– Corolla infundibuliform, 24–55 mm long; corolla lobes glabrous inside; flowers homostylous, completely red….3
2. Corolla tubular and inflated at the base, with the upper third yellow……..…*Manettia paraguariensis*
– Corolla urceolate or tubular at base but with the upper half urceolate, yellow only at the lobes…..…*M. rojasiana*
3. Bracts cordate, length/width ratio 1.14 – 1.60(2):1……..…*M. cordifolia*

– Bracts linear-lanceolate, length/wide ratio 2.77 – 3.28:1……..…*M. tweedieana*

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Conflict of interest – The authors declare no conflict of interest.

Author contributions

Silvana Yasmin Gauto: Conceptualization (equal); Data curation (equal); Investigation (equal); Methodology (equal); Project administration (equal); Validation (equal); Visualization (equal); Writing – original draft (equal). **Ana Maria Gonzalez:** Conceptualization (equal); Funding acquisition (equal); Resources (equal); Supervision (equal); Writing – review and editing (equal). **Roberto Manuel Salas**: Conceptualization (equal); Funding acquisition (equal); Resources (equal); Supervision (equal); Writing – review and editing (equal);

Data availability statement

This article has no additional data.

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