



A rediscovery for the Colombian flora: *Passiflora mariquitensis* Mutis ex L.Uribe (Passifloraceae), a species lost for more than two centuries

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Abstract

Passiflora mariquitensis Mutis ex L.Uribe, a Colombian endemic species that belongs to the subgenus *Astrophea* (DC.) Masters, was rediscovered in a disturbed forest in Mariquita (Tolima), where it has not been reported since 1784. We redescribe the species, providing data on morphology, ecology, and geographic distribution. It can be recognized from *P. pittieri*, its relative species, mainly by 6 or 10 lateral nerves to each side of the leaf, the yellow-white color of the four series of corona filaments, and the presence of rings in the nectary chamber. *Passiflora mariquitensis* is Critically Endangered due to its restricted occurrence, and conservation actions are urgent.

Keywords

Andes, *Astrophea*, Critically Endangered, endemic species, *Capreolata*, Tolima

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Introduction

Colombia is comprised of five main biogeographic regions. Among these, the Andean region shows a highly varied topography with three long mountain ranges that separate two major inter-Andean valleys from the other regions. As a result of this habitat diversification, the Colombian flora comprises one of the most diverse groups of vascular plants worldwide, with more than 40,000 documented species (Myers et al. 2000; Kreft and Jetz 2007). Colombia is particularly rich in Passifloraceae Juss. ex Roussel, with approximately 180 species from genera such as *Ancystrothyrus* Harms, *Dilkea* Mast., *Passiflora* L. (Ocampo et al. 2007, 2010; Restrepo et al. 2019), although the addition of the genera *Piriqueta*

Aubl., and *Turnera* L. in the family (Chase et al. 2016) could make the number of species reported from the country exceed 200. Of these, 61 species are endemic to Colombia, and up to 96 percent are found in the Andean region. As this region is the most densely populated and disturbed area in the country, the endemic Passifloraceae are at a high risk of extinction (Hernández and García 2006; Ocampo et al. 2007, 2010; Hernández et al. 2015). Hence, Colombia is considered to be the “Garden of Eden” of passionflowers due to their high diversity and interaction with multiple organisms, including their pollinators (Ocampo et al. 2010).

The genus *Passiflora* is split into six subgenera and

distributed predominantly in the Neotropics from coastal zones to 4,300 m above sea level in the Andes and within the páramo and puna ecosystems (Ulmer and MacDougal 2004; Krosnick et al. 2009; Buitrago et al. 2018). The subgenus *Astrophea* (DC.) Masters includes 61 species of shrubs, trees, or lianas confined to tropical areas of South America, with three species extending north into Mesoamerica (Escobar 1990, 1994; Mezzonato-Pires et al. 2019). This subgenus has a chromosome number of $n = 12$ (Löve 1987), divided into two supersections, five sections, and two series (Feuillet and MacDougal 2003). The dates of divergence and diversification for the subgenus *Astrophea* have been estimated to be about 13.8 Mya (Muschner et al. 2012), 10.77 Mya (Abrahamczyk et al. 2014), and up to approximately 20.59 Mya (Sader et al. 2019). In the supersection *Astrophea* (DC.) J. M. MacDougal & Feuillet, the section *Capreolata* J. M. MacDougal & Feuillet (formerly *Dolichostemma* Killip) has 18 species, with seven species in Brazil at the center of their diversity; the next most diverse country is Colombia with six species (Escobar 1990; Ocampo et al. 2010; Hilgenhof 2012). The species of the section *Capreolata* include vigorous lianas which are very easy to recognize by their weak tendrils, minute stipules, unlobed leaves, foliar nectaries at the apex of the petiole, corona distributed in 3–5 series of filaments that are white, yellow or orange and marked with dark red, and a tubular operculum of more than 1 cm (Feuillet and MacDougal 2003). On the other hand, the general similarity in most organs frequently complicates the identification of some species, so that the experts of the section *Capreolata*, such as Killip (1938), Escobar (1990, 1994), Feuillet (2002, 2010), and Feuillet and MacDougal (2003), have considered it an exceedingly difficult group. Furthermore, in several cases, these experts, as well as amateurs, may have underestimated the infraspecific variation in widely distributed species, splitting well-known species into several species distinguished only by a few morphological characters.

Passiflora mariquitensis Mutis ex Uribe was collected and illustrated during the Royal Botanical Expedition to the New Kingdom of Granada (1783–1816). It was collected in the municipality of San Sebastián de Mariquita (Tolima) in 1783, in the riparian forests of the Guali River in 1784, and in the municipal forest of Mariquita between 1760–1790 (Mutis 1958). This species was documented based on the descriptions of Juan Eloy Valenzuela between 1783 and 1784 (Valenzuela 1983) and José Celestino Mutis in 1784 (Mutis 1958) from fresh materials, and an iconography of four paintings by Francisco Javier Matis, under the vernacular name in Spanish of *bejuco capafrayle* (Mutis 1958). A century and a half later, *Passiflora mariquitensis* was officially published by Uribe (1954) from a painting stored in the herbarium of the Royal Botanical Garden of Madrid in Spain (MA 2027). No other observation of fertile plants of the species has been reported in or outside Colombia since 1784. Although Escobar (1990, 1994) considered it as

synonymous with *P. pittieri* Mast., based on a revision of a sterile specimen collected in Mariquita in 1984 and from the available iconography, she questioned the taxonomic status of *P. mariquitensis*. However, Ocampo et al. (2007, 2010) maintained *P. mariquitensis* as a valid species until it could be well documented and its taxonomic name verified. The history of *P. mariquitensis* leaves the name unresolved and suggests that a greater effort in exploration, collection, and characterization is required to determine this species' validity. In this context, we document the rediscovery of *P. mariquitensis* in the area where it was originally described and in newly found areas where it was suspected to occur. Additionally, to assess its current taxonomical and conservation status, this species is described, illustrated, and compared with its most similar species. We gathered information from living materials and herbaria specimens, as well as from descriptions in the literature.

Methods

Data collection sources. Four botanical fieldtrips to the Department of Tolima (Colombia) were conducted in 2004, 2005, 2019, and 2020. Fieldtrips were planned to visit known localities of *Passiflora mariquitensis* mentioned in the works of Uribe (1954, 1955) and in the botanical field notes of José Celestino Mutis (Mutis 1958) and Eloy Valenzuela during the Royal Botanical Expedition to the New Kingdom of Granada (Valenzuela 1983). Our collected specimens were deposited at the Herbarium José Cuatrecasas Arumi of the Universidad Nacional de Colombia (VALLE). The specimens representative of section *Capreolata* stored at major herbaria in Colombia (CAUP, CHOCO, COL, COAH, CUV, FAUC, FMB, HUA, HUQ, JBB, JAUM, MEDEL, PSO, SURCO, TOLI, TULV, VALLE, and UIS), in other countries (K, MA, MOL, UCR, P, and USM), and in high-resolution images of type collections available in the Global Plant Initiative (GPI) on JSTOR (DUKE, F, GH, QCA, MO, NY, TEX, and the US) were examined to establish the morphologically most similar species to *P. mariquitensis*. All herbarium acronyms follow Index Herbariorum (Thiers 2020). The database of field and herbaria data was supplemented with information published in species descriptions by Killip (1938), Escobar (1990, 1994), Feuillet (2002, 2010), and Vanderplank et al. (2014), as well as in the list of Passifloraceae for Colombia (Ocampo et al. 2007, 2010).

Morphological description. A list of 81 morphological characteristics previously evaluated by Ocampo and Coppens d'Eeckenbrugge (2017) and following the descriptive terminology proposed by Puri (1947, 1948) and Tillett (1988) were employed to establish the morphological description of *P. mariquitensis*. Additionally, a dataset and photographs of one specimen of *Passiflora pittieri* from Costa Rica, with morphological measurements, were included to create a more accurate species description.

Conservation status. Fieldtrip, herbaria, and data from the literature were used generate a dot distribution map of collections of *P. mariquitensis* and its most similar species using ArcMap v. 10.3. Conservation status was assessed according to International Union for the Conservation of Nature categories and criteria (IUCN 2019). Extent of Occurrence (EOO) and Area of Occupancy (AOO) were obtained using the Geospatial Conservation Assessment Tool, GeoCAT (Bachman et al. 2011). The AOO was calculated using a 2 km² grid.

Results

During the collecting trips in the municipality of San Sebastián de Mariquita we collected six individuals with morphological characteristics occurring in species of *Passiflora* subgenus *Astrophea*. These plants were growing in disturbed habitats along roads and in riparian and secondary forests. Of the six specimens collected, only three were fertile plants belonging to the section *Capreolata*; they were identified as *P. mariquitensis*, *P. pittieri*, and *P. mutisii* Killip. These were found growing on the understory of “Mariquita Forest”, a Tropical Humid Forest (Bh-T), and in the riparian forest of Rio Sucio on top of shrubby vegetation. No specimens were found on the riparian forests of the Guali River, where originally various specimens of *P. mariquitensis* were recorded by the Royal Colombian Botanical Expedition. Nonetheless, this area was devastated by an avalanche caused by a volcanic eruption in 1985 and is currently occupied by pastures for livestock farming. In our revisions of herbaria, only four paintings representing the section *Capreolata* were found; they were labeled as *P. mariquitensis* in the herbarium of the Royal Botanical Garden of Madrid in Spain (MA 2026, 2026a, 2026b, and 2027).

Passiflora mariquitensis and its most similar species (*P. pittieri* and *P. mutisii*) were characterized *in situ* using fertile living material following a list of 81 characteristics and complemented with measurements from examined iconographies and herbarium specimens. As a result, we identified 11 quantitative and 25 qualitative traits (Table 1), allowing us to confirm the morphological difference of *P. mariquitensis* with its most similar species and to resolve its current taxonomic status. The shape acute leaf or round at the base and the yellow-white color of the four series of corona filaments, presence of rings in the nectary chamber, and a greenish-yellow operculum are characters exclusive to *P. mariquitensis*. Compared to the specimen of *P. pittieri* from Costa Rica, the specimens collected in a riparian forest (Rio Sucio) match *P. pittieri* (VALLE 16845, Appendix) but with some differences in the shape of the leaf apex (caudate-abruptly acuminate), number of lateral nerves on each side of the leaf (11 or 14), absence of peduncle bifurcation on the tendrils, pink color at the base of the first and second corona filament series, greenish-white styles, and ovate seeds with its margin entire, truncated slightly at the apex, slightly acute at the base,

and ornamentation coarsely reticulate. In MA 2026 (as *P. mariquitensis*), these morphological characteristics evaluated by F.J. Matis shows that this illustration corresponds to *P. pittieri* (VALLE 16845) from a riparian forest in Rio Sucio. The internal flower description of *P. mutisii* from the painting MA 2028 (F.J. Matis) and the dried specimen MA 2279 (J.C. Mutis) is very limited (Uribe 1955; Appendix). However, characters such as the greenish-white color mottled with red on the adaxial surface and the greenish color on the abaxial surface of the sepal, the greenish-yellow color of the abaxial surface of the petal with a white border, yellow biseriate filaments of the corona, and glabrous styles allowed us to distinguish between *P. mariquitensis* and *P. pittieri*. Moreover, a sterile dried specimen collected by L.A. Escobar et al. 4547 (HUA 8665) labeled as *P. mariquitensis* and later confirmed as *P. cf. pittieri*, corresponds to *P. mutisii* according to our morphological characterization.

No dried specimens of *P. mariquitensis* were mentioned by Valenzuela (1983) and Mutis (1958), and as none were found in the herbaria reviewed by us, our collection (Velázquez et al. 01) is the first and only herbarium specimen of *P. mariquitensis*, reflecting the rarity of the species.

Below, we summarize the information gathered from fieldtrip collections, analysis of herbaria specimens, and literature review.

Passiflora mariquitensis Mutis ex L. Uribe

Figures 1, 2

New record. COLOMBIA • Department of Tolima, San Sebastián de Mariquita municipality, bosque de Mariquita, parte alta, 751 m a.s.l.; 05°11'23"N, 074°55'15"W; 3 Oct. 2019; A. Velázquez et al. 01 (VALLE 16844).

Identification. Woody liana shrub with weak tendrils. Stem angulate, striate, glabrous. Tendrils green, glabrous. Stipules linear-subulate, 1.5–3 mm long, 0.5 mm wide, green, soon deciduous. Petioles strongly grooved, 1.5–2.5 cm long, 0.3 cm wide, green, glabrous, laterally with 2 flattened glandules at the apex. Leaves unlobed, oblong, 9–19 × 4.4–6.6 cm wide, obtuse, subobtuse or somewhat emarginate at the apex, obtuse or round at the base, penninerved (lateral nerves 6 or 10 on each side), coriaceous, entire and undulate at the margins, glabrous, green. Peduncles solitary, once or twice bifurcate (somewhat slender tendril in bifurcation), 2–5.5 cm long, 0.2–0.3 cm wide, glabrous, green. Pedicels green, 0.8–1.2 cm long, 0.3 cm wide, glabrous. Bracts setaceous, alternate disposition, 1–1.5 mm long, 0.5 mm wide, green. Flowers fragrant, semierect to pendent, 3.3–3.5 cm long (from the base of the nectary chamber to the ovary apex) × 6.0–7.2 cm wide. Nectary chamber glabrous, 6–7 × 9–10 mm, green outside and greenish-yellow inside, nectary ring (annulus) greenish-yellow. Hypanthium campanulate, 3–4 mm long × 10–11 mm diameter (at the base of the sepals), glabrous, green outside, and inside. Sepals oblong, 3.3–4 × 0.8–1.1 cm wide, adaxial surface white,

Table 1. Summary and comparison of morphological characters between *P. mariquitensis*, *P. mutisii*, and *P. pittieri* as described by various authors.

Organ	<i>P. mariquitensis</i>	<i>P. mutisii</i>	<i>P. pittieri</i>	<i>P. pittieri</i>
	Description by Mutis (1784) and Uribe (1954) From living specimens	Description by Mutis (1785) and Killip (1938) Dried specimens (MA 2279, holotype), living specimens and iconography (MA 2028) Mariquita (Mariquita Forest)	Description by Masters (1897) and this study From dried specimens and living specimens	Description by Velásquez and Ocampo (2019) From living specimens and iconographies (VALLE 16845) Mariquita (riparian forest in Sucio River)
	Mariquita (Mariquita Forest)	Mariquita (Mariquita Forest)	Costa Rica—Belize, Guatemala, Nicaragua, Panama, and Colombia Appendix 1	Mariquita (riparian forest in Guali River)
Stipule	1.5–2 mm	Appendix 1 1.5–2 mm	Appendix 1 2–4 mm	1.5–2.5 mm
Petiole	2.2–2.5 × 0.3 cm	1.5–2.3 × 0.3 cm	1.4–1.6 × 0.3 cm	1.2–1.6 × 0.3 cm
Leaf	9–19 × 4.4–6.6 cm Oblong 7 or 10 lateral nerves on each side Obtuse, subobtusate or somewhat emarginate at the apex Obtuse or round at the base	15–18 × 5–6 cm Oblong 6 or 8 lateral nerves on each side Obtuse, subobtusate or somewhat emarginate at the apex Obtuse or round at the base	7–18 × 3.2–7 cm Oblong to obovate 8 or 12 lateral nerves on each side Subcaudate to acuminate at the apex Acute at the base	11–30 × 5–12 cm Oblong to obovate 11 or 14 lateral nerves on each side Acute or aristate at apex Acute, round or somewhat round at base
Peduncle	2–4 × 0.2–0.3 cm Solitary, once bifurcate Tendrill absent in peduncle bifurcation	2.5–5.5 × 0.2–0.3 cm Solitary, once or twice bifurcate A somewhat slender tendrill in peduncle bifurcation	1–5 × 0.2–0.3 cm Solitary, once or twice bifurcate A somewhat slender tendrill in peduncle bifurcation	1.2–3.6 × 0.2–0.3 cm Solitary, once bifurcate A somewhat slender tendrill in peduncle bifurcation
Flower	3.3–4 × 0.8–0.9 cm Adaxial surface white	3.3–3.6 × 1–1.1 cm Adaxial surface white	3.2–4.2 × 0.8–1.5 cm Adaxial surface white	3.4–3.7 × 1–1.1 cm Adaxial surface white
Sepal	Abaxial surface green with white border 3.1–3.7 × 0.6–0.8 cm Abaxial surface green	Abaxial surface green with white border 3.4–4.5 × 0.7–1.3 cm Abaxial surface white	Abaxial surface green with white borders 4.3–4.6 × 1.0–1.3 cm Abaxial surface white	Abaxial surface green with white borders 2.5–4.8 × 0.6–1.4 cm Abaxial surface white
Petal				
Corona	4 series of filaments First series 2.2–2.4 cm long First series subdoblabriform and dilated at apex, acute 1st: yellow, white at the base 2nd: yellow at the apex, white 3rd: yellow at the apex, white 4th: white	2 series of filaments First series 1.3–2.3 cm long First series ligulated 1st: orange 2nd: orange 3rd: yellow at the apex, white 4th: white	4–5 series of filaments First series 1.5–1.7 cm long First series subdoblabriform, dilated at apex, acute 1st: orange at the apex, orange-tinged red, white at base 2nd: orange at the apex, orange-tinged red, white at base 3rd: orange at the apex, orange-tinged red, white-tinged pink at base 4th: orange at the apex, white-tinged pink 5th: pink-tinged red	5 series of filaments First series 1.4–1.5 cm long First series subdoblabriform, dilated at apex, acute 1st: orange at apex, orange-tinged red, white at base 2nd: orange at apex, orange-tinged red, pink at base 3rd: orange at apex, orange-tinged red, pink at base 4th: orange at apex, pink-tinged red 5th: pink-tinged red
Nectar chamber	Not observed	Nectary ring (annulus)	Absent	Absent
Operculum	Greenish-white	Greenish-yellow	Not observed	Pink to red
Androgynophore	Not observed	Greenish to yellow	Pink to red, green base	Pink to red, green at the base
Style	Greenish-white Pubescent	Greenish-white Pubescent	Greenish-pink Pubescent	Greenish-white Pubescent
Fruit	Unknown	Unknown	6–7 × 3–3.3 cm	6–6.3 × 4–4.1 cm
Seed	Unknown	Unknown	0.7–1.1 × 0.7–0.8 cm Ovate, pale brown Margin entire to slightly crenate Acute, prominent at the apex Truncated to slightly acute at the base Reticulate ornamentation	0.9–1.0 × 0.7–0.8 cm Oblong, pale brown Margin entire Slightly truncate at the apex Slightly acute at the base Coarsely reticulate ornamentation



Figure 1. *Passiflora mariquitensis* Mutis ex L.Uribe. **A.** Branch with leaves, flowers, and young buds. **B.** Detail of a gland at the petiole apex. **C.** Minute stipule. **D.** Peduncle bifurcated with two young buds. **E.** Schematic detail of a longitudinal section of the flower. Drawn by Benjamin Cárdenas (A. Velásquez et al. 01, VALLE 16844).

abaxial surface green with white border (two of them green), glabrous, reflexed. Petals white, linear-oblong, $3.1\text{--}4.5 \times 0.6\text{--}1.3$ cm wide, glabrous, reflexed. Corona filaments in four series, yellow to white at the base; the outermost $1.6\text{--}1.9$ cm long, subdolabriform, dilated at the apex to a width of 4 mm tapering gradually to the

base (2 mm), those of the second series spatulate, $5\text{--}8 \times 1$ mm wide; the third series gradually shorter, $4\text{--}6$ mm long; the inner series 4 mm long, minute, filiform, white. Operculum tubular, membranaceous, erect, exserted above apex of hypanthium, ca $1.0\text{--}1.1$ cm high, minutely denticulate at the margin, greenish-yellow. Limen

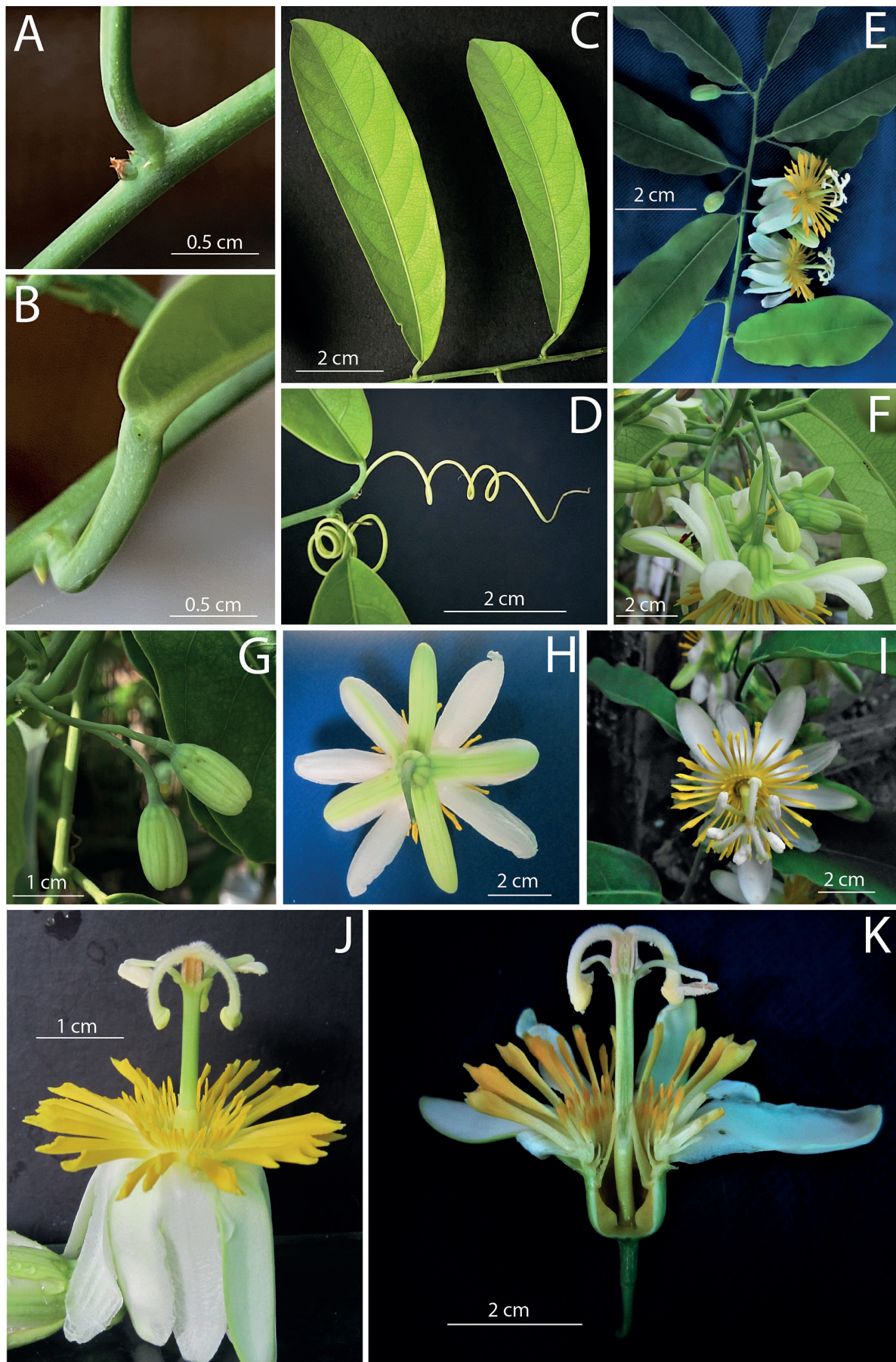


Figure 2. *Passiflora mariquitensis*. **A.** Minute stipule. **B.** Petiole and flattened glandular-related taxas at the apex. **C.** Juvenile leaves. **D.** Tendrils. **E.** Branch with leaves, flowers, and young buds. **F.** Buds and flower. **G.** Peduncle, pedicel, bracts, and young buds. **H.** Adaxial flower. **I.** Flower, front view. **J.** Flower, side view. **K.** Detail of a longitudinal section of the flower. Photos by Adriana Velásquez and John Ocampo (A. Velásquez et al. 01, VALLE 16844).

absent. Androgynophore greenish to yellow, $3.3\text{--}3.6 \times 0.3$ cm in diameter. Gynophore absent, 1.5–1.6 mm long, green. Staminal filaments greenish-white, 1.0–1.1 cm long. Anthers white, 5–6 mm long. Pollen white to deep yellow. Ovary oblong truncated, 5–6 mm long, 9 or 10 ribbed, densely tomentose, olive-green. Styles greenish-white, 0.8–1.0 cm long, hairy. Stigmas greenish-yellow, 2–3 mm in diameter. Fruit unknown.

Passiflora mariquitensis can be recognized from its most similar species, *P. pittieri*, mainly by the presence of 6 or 10 lateral nerves on each side of the leaf (vs 8 or 14), the yellow-white color of the four series of corona filaments (vs orange-tinged red-white, 4 or 5 series), the presence of rings in the nectary chamber (vs absent), a greenish-yellow operculum (vs pink to red), and a self-incompatible flower (vs self-compatible).

Phenology. Flower opening time in *P. mariquitensis* occurs early in the morning from 6:00 to 8:00 hours, and flowering takes place from February to May and again in October. Carpenter bees of the genera *Eulaema*, *Euglossa*, and *Bombus* were observed visiting open flowers and sipping nectar. However, the size of these insects does not match the length of the androgynophore, and pollen was not observed on their wings and thorax. Moreover, bumblebees (*Xylocopa* sp.), birds *Coereba flaveola* (Linnaeus, 1758), and *Amazilia tzacatl* (La Llave, 1833) were seen landing on the flowers, sipping nectar and dusted with pollen on their thorax and head; they may be associated as pollinators as has been reported in other *Passiflora* species with similar floral morphology. Ten manual self-pollinations during three consecutive flowering seasons were carried out unsuccessfully, suggesting that *P. mariquitensis* is probably a self-incompatible species and needs cross-pollination.

Distribution and habitat. *Passiflora mariquitensis* was observed as a woody liana shrub, along roadsides in the understory of the secondary tropical rainforest known as “Mariquita Forest.” This species grows in the understory on areas with soils derived from volcanic ash with a high content of organic matter and stony gravelly texture. Using data from Ideam (2019) we report that an annual mean temperature of 22.7°C (range $19.4\text{--}30.7^\circ\text{C}$), annual rainfall of 2,713 mm, and 5–6 h of sunshine per day are the climatic preferences of *P. mariquitensis*. Figure 3 is a dot map of the spatial distribution of *P. mariquitensis* based on the four known records of the species obtained from our recent field collections and the literature (Mutis 1958; Valenzuela 1983) between 1783–1784, as well as its closest relatives. *Passiflora mariquitensis* is endemic to the Colombian department of Tolima and in particular near the municipality of San Sebastián de Mariquita (hence the name). The pattern of geographical distribution shows that *P. mariquitensis* and *P. mutisii* are sympatric species that currently occur only in the Mariquita Forest in Tolima between 537 and 751 m a.s.l. in foothills on the eastern flank of the Central Cordillera. On the other hand, *P. pittieri* grows in lowlands in riverside forests of the Sucio and Guali rivers between 434–489 m a.s.l. and 1–3 km from San Sebastián de Mariquita.

Conservation status. *Passiflora mariquitensis* is known only from four individuals in Mariquita Forest, and two of them were found 236 years ago. Hence, this species should be considered Critically Endangered (B1a, D) according to IUCN (2019) guidelines. Within criterion B, the rediscovered species is classified as B1a, as its area of occupancy (AOO = 12 km^2) is estimated as less than 100 km^2 and its habitat is disturbed due to deforestation and other human activities and the plants

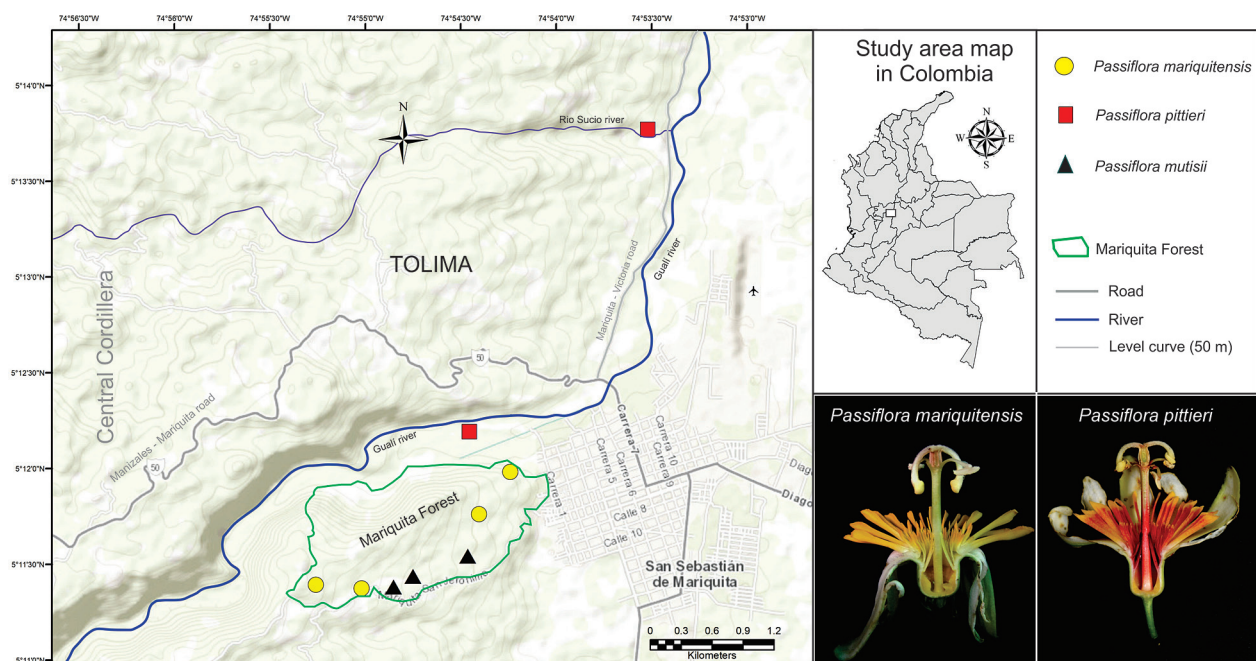


Figure 3. Geographical distribution of *P. mariquitensis* (yellow circles) and its most similar species *P. mutisii* (black triangles) and *P. pittieri* (red squares) in Colombia. Photos of *P. mariquitensis* and *P. pittieri* by Adriana Velásquez from plant collected in Mariquita.

occurring in a single location (EOO is not measurable). Criterion D is applicable because the population size is very small and estimated at fewer than 50 mature individuals; just four plants were observed during the Royal Botanical Expedition to the New Kingdom of Granada in 1784 (Valenzuela 1983) and during our collecting trips in 2004, 2005, 2019, and 2020 (Fig. 3).

Discussion

The Royal Botanical Expedition to the New Kingdom of Granada between 1783 and 1816, which covered present-day Colombia, Ecuador, Panama, Venezuela, Peru, northern Brazil, and western Guyana, was the first botanical expedition in South America (Pérez et al. 1954). The project was headed by José Celestino Mutis, a Spanish priest, doctor, and naturalist, who, together with his team of botanists and painters, discovered and described 6,000 new species (Pérez et al. 1954). *Passiflora mariquitensis* was one of them, but was only validly published 170 years later by Uribe (1954), based on an iconography of two paintings numbered MA 2026 and MA 2027. The botanist Juan Eloy Valenzuela was the first to describe the species on 1 October 1783 from fresh material collected in the riparian forests of the Guali River (Uribe 1955; Valenzuela 1983); later, this species was illustrated by Francisco Javier Matis in iconographies numbered MA 2026 (color: branch with leaves, flowers, and fruit) and MA 2026a (gray copy of MA 2026). A year later in September to October 1784, Mutis examined new specimens from the forests around Mariquita (Uribe 1954, 1955; Mutis 1958), which were also illustrated by Matis under the numbers MA 2026b (gray: branch with leaves and fruit) and MA 2027 (color: branch with leaves and flowers). Also in 1784, José Celestino Mutis carefully examined all specimens illustrated by Matis (Mutis 1958) and made a description of the species with a meticulous comparison with previous descriptions of Valenzuela (1983). Therefore, the descriptions prepared by Mutis and Valenzuela partially coincide, but with remarkable differences in the coloration of the corona filaments (orange-tinged red vs yellow-white) and operculum (pink to red vs greenish-white), as well as in the form of the leaf at the base (acute vs obtuse). The description of *P. mariquitensis* by Uribe (1954), which was based on MA 2027, describes a corona in three series of yellow filaments; however, the greenish-yellow color of the operculum was not included. Presently, the three descriptions bring up some questions about our morphological description, which is based on living material (Fig. 2) and high-quality photographs of the iconography. These differences can be explained by the orange-tinged red color of the corona filaments and the pink to red color of the operculum and androgynophore observed in MA 2026 and MA 2027, either appearing or absent from the descriptions by Mutis (1958) and Uribe (1954, 1955). These inconsistencies might be based on the artistic work of Francisco Javier Matis when he illustrated

the iconographies, who was nonetheless recognized by Mutis and Humboldt as the most brilliant plant illustrator of his time (Mutis 1958). Matis kept the orange, pink, or red flower colorations present in the first illustration (MA 2026) of *P. mariquitensis* in MA 2027, probably following his painter instinct and not his training as a botanist. This supports the differences between the historical descriptions of *P. mariquitensis* and the proposal that the first description by Juan Eloy Valenzuela based on specimens 2026 and 2026b, corresponds to *P. pittieri*. In contrast, in the description proposed by Uribe (1954, 1955), three series of filaments of the corona are mentioned, although, in Mutis's 1760–1790 and Valenzuela's 1783–1784 descriptions (Mutis 1958; Valenzuela 1983), four series are declared and clearly observed in MA 2026 and MA 2027.

Our results suggest that the description presented in this work corresponds to the descriptions of *P. mariquitensis* by Mutis (1958) and Uribe (1954, 1955), with the exception in the number of corona filaments (three vs four), pink to red color on the androgynophore in the first one, and the operculum in the latter. However, these differences are supported by the inconsistency in some colors of the flower observed between the iconography and the botanical descriptions, as already mentioned above. We did not study the fruit of *P. mariquitensis* despite trying unsuccessfully 10 times to self-pollinate *P. mariquitensis* during three consecutive flowering seasons. In Mutis's description of the species, the fruit was included, although in his daily field notes, he wrote that he never saw the fruit in a living specimen that he examined (MA 2027). Therefore, Mutis probably described them from observations from MA 2026 and MA 2026b (Uribe 1954, 1955), which correspond to *P. pittieri*.

Passiflora pittieri, described by Masters (1897) from Costa Rica, is distributed from Belize in Central America to northwest-central Colombia from the sea level up to 1,100 m a.s.l. in foothills (Fig. 4). Enthusiasts appreciate this species as an ornamental plant for its abundant flowers and fruits through self-fertilization. Both the first description of *P. mariquitensis* by Juan Eloy Valenzuela in 1783 (MA 2026 and MA 2026b) and our specimen collected in the riparian forest of Rio Sucio, 3 km from Mariquita, corresponds to *P. pittieri*. Mutis in 1784 was faced with two different living specimens: the first one was collected by himself and the second one by F.J. Matis (no data from collection). Although Mutis doubted some morphological characters, he allowed Matis to eliminate these differences in illustrations MA 2026 and MA 2027, both of which represent *P. pittieri*. However, the taxonomy and knowledge of the genus *Passiflora* were insipient at that time, and only 29 new species had been described by Linnaeus (1753). Mutis kept the draft of the new species description for more than 25 years, and it was never published. Meanwhile, 306 taxa described by Mutis were published by Linnaeus, Humboldt and Bonpland, Cavanilles, and some botanists of the 20th century, such as Killip (1938) and Uribe (1954,

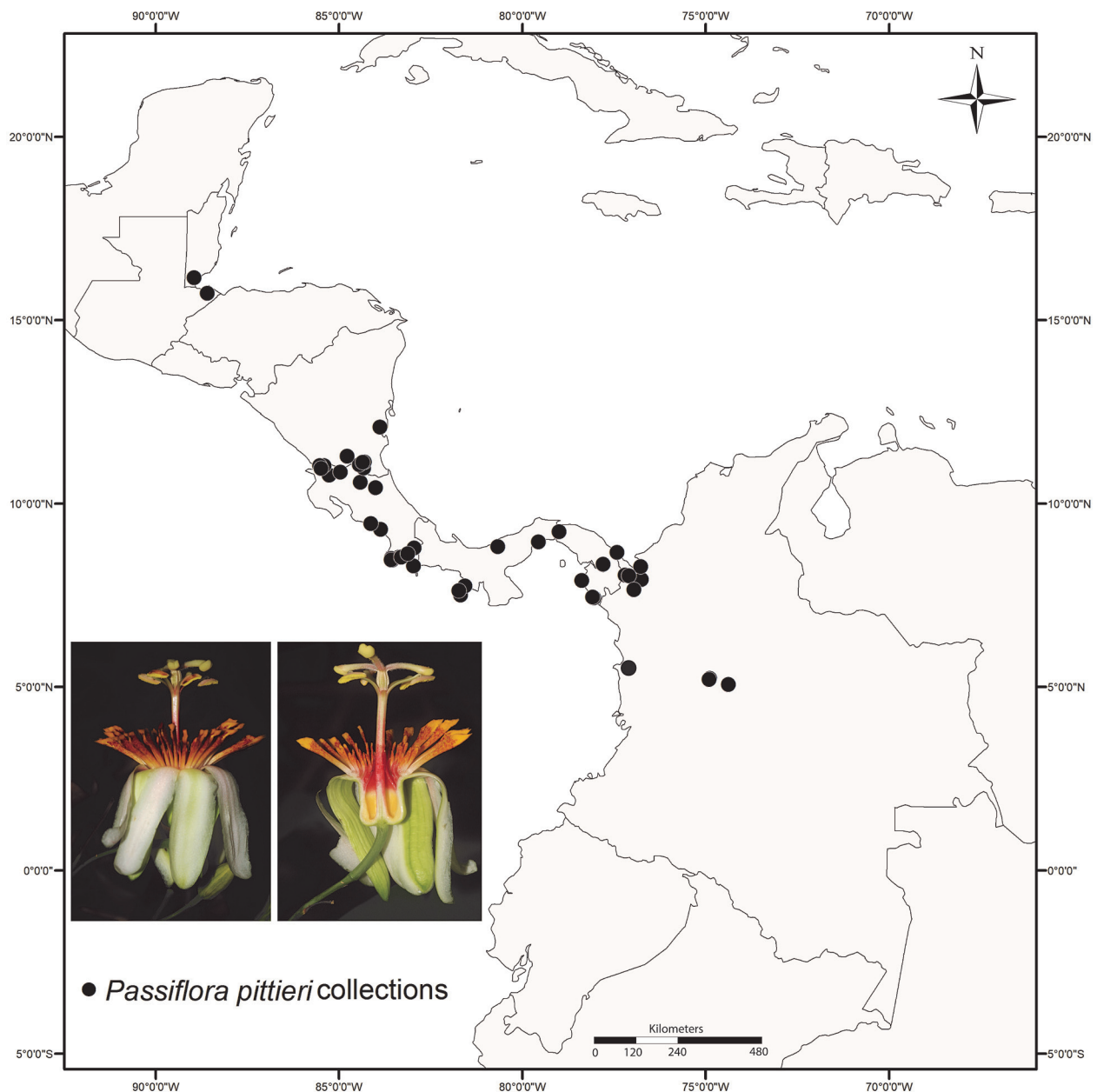


Figure 4. Dot distribution map of *P. pittieri* collections (black circles). Photos on map of *P. pittieri* by Miguel Molinari from plant collected in Costa Rica.

1955). The occurrence of *P. pittieri* in Mariquita is rare, and the collections reported in Colombia are mainly (six of eight) located on the other flank of the Andes near the border with Panama. The geographic distribution patterns of *P. pittieri* in the center of the Andean region of Colombia is not surprising, if we consider the sympatry of two related species, *P. mariquitensis* and *P. mutisii*, in the foothills of the inter-Andean valley of the Magdalena River and one specimen of *P. pittieri* observed in the municipality of Nocaima in Cundinamarca department (05°03'56"N, 074°23'02"W) at 1,100 m a.s.l. on the western flank of the Eastern Cordillera, and 60 km from Mariquita (photographs and videos from O. Enciso, pers. comm. 2020-7-21). The presence of all three related species could also be supported by the decades of deforestation and environmental degradation suffered by the

ecosystems in the Colombian Andean region, which has caused the extinction, reduction, or isolation of populations as a consequence of forest fragmentation.

Escobar (1990, 1994), one of the best-known specialists of *Passiflora*, questioned whether *P. mariquitensis* is a synonym of *P. pittieri* on the basis of her observations of MA 2026 and MA 2027 published by Uribe (1954, 1955) and from a sterile specimen collected in San Sebastián de Mariquita (L.A. Escobar *et al.* 4547, HUA 8665) labeled as *P. mariquitensis* and verified by herself as *Passiflora* cf. *pittieri*. Escobar concluded that MA 2026 and MA 2027 are the same species and match the description of *P. pittieri* but did not consider the differences in the shape of the leaves at the apex and base, the color of the corona filaments, and the internal structure of the flower in the description of *P. pittieri*

(Masters 1897). Likewise, the specimen *L.A. Escobar et al.* 4547 (HUA 8665) is a misdetermination and is *P. mutisii* according to our observations. Our results show that *P. mariquitensis* presents characters unique from other members of section *Capreolata*, which suggests that it is a valid species and that *P. pittieri* is the species morphologically most similar to it. Our newly collected specimens provide new information about the internal structures of the flower *P. mariquitensis*, which were previously unknown.

Passiflora mariquitensis is a Critically Endangered species, and its geographical distribution is restricted only to Mariquita Forest, part of “The Protected Forest Reserve of Quebradas El Peñón and San Juan.” Although *P. mariquitensis* occurs within a protected area, the pressure of illegal urban sprawl and deforestation places the protection of its habitats at risk. Conservation strategies and restoration efforts for the habitats of *P. mariquitensis* in Mariquita Forest are urgently needed, and these must be integrated into the more general landscape-level management that can be guaranteed by the coordination of governmental and non-governmental organizations. *Ex situ* conservation in botanical gardens and seedbanks, when they become available, are other strategies that must be implemented when critical habitats are vulnerable or destroyed. The rediscovery of *P. mariquitensis* and other *Passiflora* species in the last decade confirms that greater efforts to explore and collect the Colombian flora are needed, especially for those species where only the type specimen is known (Ocampo et al. 2015; Restrepo et al. 2019). *Passiflora mariquitensis* should not only be studied as an important member of an ecosystem but also in investigations that involve the probable use of its secondary metabolites and as a potential rootstock to solve biotic or abiotic problems that affect cultivated species of the genus *Passiflora* (Ocampo et al. 2010).

We also found *P. mutisii* in our study, growing in the same area with *P. mariquitensis*. Mutis’s (1958) and Killip’s (1938) morphological descriptions of the flower are poorly detailed. However, *P. mutisii* has some morphological characteristics intermediate between *P. pittieri* and *P. mariquitensis*, which suggests that this could be a natural hybrid between these species, although the number of coronal rows is distinct and not intermediate. Hence, DNA barcoding of *P. mutisii*, as well as the other members of the section *Capreolata*, is needed for a better understanding of the morphological and genetic diversity of the species.

In conclusion, the morphological description of *P. mariquitensis* by Uribe (1954) was based on an old inconsistency generated by the illustrator Francisco Javier Matis in the coloring of some parts of the flower detailed in the iconographies MA 2026 and MA 2027. *Passiflora mutisii*, a Critically Endangered species, is reported here, and *P. mariquitensis* is a valid, extant, endemic species which must be preserved under *in situ* and *ex situ* conservation strategies and actions.

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Authors’ Contributions

JOV, AIV, and JO collected the specimens; AIV and JO characterized the living material; JO and JOV identified the specimens; AIV and JO photographed the living specimens; JO conducted the research, revised herbarium collections, prepared the distribution map, and wrote the manuscript.

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Appendix

Additional material of *Passiflora mutisii* and *P. pittieri* examined

***Passiflora mutisii* Killip.** COLOMBIA • Department of Tolima, Sebastián de Mariquita, alrededor de Mariquita; without geographic coordinates; 1760; *J.C Mutis* no data from collection (holotype MA 2279; isotype, US). • Same locality; without geographic coordinates; 1784; *J.C Mutis* & *F.J. Matis* no data from collection (iconography MA 2028). • Same locality, without geographic coordinates; 535–650 m a.s.l.; 8 Jun. 1984; *L.A. Escobar et al.* 4547 (HUA 8665, sterile).

***Passiflora pittieri* Masters.** BELIZE • Toledo, without locality; 16°09'50"N, 88°57'16"W; 3 Mar. 1945; *P.H. Gentle* 5248 (M0). COLOMBIA • Department of Tolima, San Sebastián de Mariquita municipality, bosques alrededor de Mariquita, without geographic coordinates; 1784; *F.J. Matis* no data from collection (iconographies MA 2026, 2026b). • Balneario Cancun, lado derecho de río sucio, 435 m a.s.l.; 05°13'47"N, 074°53'32"W; 21 Nov. 2019, *A. Velásquez* & *J. Ocampo* 02 (VALLE 16845).

- Antioquia, Turbo, 07°55'52"N, 076°44'46"W; 10–100 m; 25 Oct. 1983; *J. Brand & M. González 532* (JAUM, MO). • Parque Nacional Natural Los Katíos sectores Tilupo peye; 07°54'32"N, 077°06'18"W; 47 m a.s.l.; 12 Apr. 1982; *S. Zuluaga 898* (COL 294366). • Necoclí; 08°16'36"N, 076°46'00"W; 2 m a.s.l.; 1 May 1992; *Castaño et al. 135* (HUA). • Chocó, Unguía; 08°01'48"N, 077°05'60"W; 100–300 m a.s.l.; 19 Jul. 1975; *A. Gentry & L.E. Aguirre 15318* (COL 152651, MO). • Same department, Unguía; 08°02'00"N, 077°06'00"W; 900 m a.s.l.; 20 Jan. 1975; *A. Gentry & S. A. Mori 13728* (COL 165096, MO). • Nuquí, corregimiento Coquí, estribaciones de la Serranía de Baudó, Golfo de Tribuga; 05°35'06"N, 077°21'18"W; 5–100 m; 2 Feb. 1995; *J.C. Betancur et al. 6092* (COL 367239). COSTA RICA • Santo Domingo, Golfo Dulce; 08°32'12"N, 083°18'17"W; 1 Apr. 1896; *H. Pittier 9894* (isotype, US 115089); *J. Donnell Smith 7031* (isotype, K 323264). • Alajuela, Upala; without geographic coordinates; 10°51'36"N, 084°57'36"W; 100 m a.s.l.; 18 Nov. 1987; *G. Herrera 1340* (MO). • Guanacaste, Liberia; 10°57'36"N, 085°29'24"W; 650 m a.s.l.; 12 Apr. 2003; *B. Boyle et al. 7110* (ARIZ). • Heredia, Sarapiquí; 10°25'48"N, 084°00'00"W; 100 m a.s.l.; 9 Jun. 1983; *Chacón & I. Adolfo 949* (DUKE). GUATEMALA • Izabal, Puerto Barrios; 15°43'34"N, 088°35'38"W; 0 m a.s.l.; m, 25 Apr. 939; *P.C. Standley 73059* (F). NICARAGUA • Machuca; Río San Juan; 11°07'48"N, 084°18'36"W; 183 m a.s.l.; 5 Apr. 2005; *D. Urbina 3194* (HULE). • Atlántico Sur; 12°05'00"N, 083°53'00"W; 50 m a.s.l.; 26 Feb. 2002; *P. F. Foster 1689* (MICH). PANAMA • Chiriquí, without locality, 08°18'00"N, 082°58'00"W; 400–500 m a.s.l.; 24 Feb. 1973; *R. L. Liesner 197* (F, MO). • Darién; 07°27'00"N, 078°05'00"W; 0–100 m a.s.l.; 22 Jan. 1982; *S. Knapp & J. Mallet 3030* (MO, PMA). • Veraguas, Sona; 07°44'53"N, 081°34'26"W; 20 m a.s.l.; 1 Apr. 2002; *A. Ibáñez 1872AI* (MO).
- We determined that Bolivian specimens labeled as *P. pittieri* correspond to *Passiflora cauliflora* Harms. BOLIVIA • Santa Cruz, Velasco; 13°42'09"S, 061°31'59"W; 210 m a.s.l.; 4 Nov. 1994; *R. Guillén et al. 2560* (MO, USZ) and 14°40'00"S, 00°46'00"W; 700 m a.s.l.; 6 Oct. 1993; *M. Saldias et al. 3473A* (MO, USZ).