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On the recognition of *Passiflora hibiscifolia* (Passifloraceae, section Dysosmia)

Sobre el reconocimiento de *Passiflora hibiscifolia* (Passifloraceae, sección Dysosmia)

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Abstract:

Background and Aims: *Passiflora* section *Dysosmia* is considered one of the most complicated groups in the passionflower genus, due in part to the difficulty of accurately delimiting taxa. One such example, currently recognized as *Passiflora ciliata* var. *hibiscifolia*, has undergone a series of nomenclatural changes based on varying taxonomic opinions since its circumscription in 1789. Few researchers have thus far objectively investigated the uniqueness of this taxon or its affinity with other similar taxa in the section. The objective of this study was to characterize the taxon currently known as *P. ciliata* var. *hibiscifolia* and provide evidence for its taxonomic recognition.

Methods: Intensive morphological studies were carried out using 217 herbarium specimens, including type material, supplemented by 27 iNaturalist observations.

Key results: The results show significant, consistent macro- and micromorphological differences between the taxon known as *P. ciliata* var. *hibiscifolia* and all other taxa within section *Dysosmia*.

Conclusions: The entity studied here is distinct enough to warrant recognition at the rank of species as *Passiflora hibiscifolia*.

Key words: Central America, Mexico, nomenclature, systematics, taxonomy.

Resumen:

Antecedentes y Objetivos: *Passiflora* sección *Dysosmia* es considerado uno de los grupos más complicados dentro del género de pasionaria, debido en parte a la dificultad en delimitar adecuadamente sus taxa. Uno de esos ejemplos, actualmente reconocido como *Passiflora ciliata* var. *hibiscifolia*, ha sufrido una serie de cambios nomenclaturales basados en diversas opiniones taxonómicas desde su circunscripción en 1789. Hasta el presente, pocos investigadores han estudiado objetivamente la naturaleza única de este taxon o su afinidad con otros taxa similares en la sección. El objetivo de este estudio fue caracterizar el taxon actualmente conocido como *P. ciliata* var. *hibiscifolia* y proveer evidencia para su reconocimiento taxonómico.

Métodos: Se realizaron estudios morfológicos intensos de 217 especímenes de herbario, incluyendo material tipo, además de 27 observaciones en iNaturalist.

Resultados clave: Los resultados muestran diferencias significativas consistentes a nivel macro y micro morfológico entre el taxon conocido como *P. ciliata* var. *hibiscifolia* y todos los demás taxa en la sección *Dysosmia*.

Conclusiones: La entidad estudiada es suficientemente distinta para concederle el reconocimiento de especie como *Passiflora hibiscifolia*.

Palabras clave: Centroamérica, México, nomenclatura, sistemática, taxonomía.

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Introduction

Passionflowers (*Passiflora* L., Passifloraceae) are an easily recognizable group due to their many, and often striking, morphological features. The genus is represented in the New World tropics by at least 580 recognized species (Ocampo Pérez and Coppens d'Eeckenbrugge, 2017) with potentially many more undescribed. Section *Dysosmia* DC., one of the infrageneric groups accepted by Feuillet and MacDougal (2003) in subgenus *Passiflora* supersection *Stipulata* Feuillet & J.M. MacDougal, is among the most widespread and taxonomically complicated in the genus and can be found from the southern United States of America through Argentina and throughout the West Indies. Mexico is a hotspot of diversity within section *Dysosmia*, which harbors 12 of the 30 taxa currently recognized in the section (Vanderplank, 2013) including two major species complexes: *Passiflora ciliata* Aiton and *P. foetida* L.

Like other members of supersection *Stipulata*, and subgenus *Passiflora* more generally, section *Dysosmia* has showy flowers, large involucral bracts, and conspicuous stipules. Unique to the section, however, are a suite of characters that are found nowhere else in the genus, including highly divided bracts and stipules and ubiquitous glands across the vegetative features. The latter are responsible for the often fetid or pungent smell associated with many of the taxa that belong to this section. These features may indeed represent synapomorphies for the section, but no phylogenetic studies to date have focused on *Dysosmia* in its entirety or aimed to test the assumptions of monophyly.

One of the oldest names attributed to section *Dysosmia*, *Passiflora hibiscifolia* Lam. (Fig. 1), was first described in 1789 by Jean-Baptiste Lamarck from material cultivated at the Jardin des Plantes ("Jardin du Roi") in Paris, France. Lamarck (1789) believed that the material for this plant originated in South America, but Killip (1938) surmised its origin to be somewhere in Central America based on the distribution inferred from herbarium collections known at the time. Subsequent taxonomic combinations based on this basionym (see Taxonomy below) have shuffled the rank and specific affinity of the taxon from a species of *Passiflora*, to that of a segregate genus, *Dysosmia* (DC.) M. Roem. (Roemer, 1846), to a variety of *P. foetida* (Killip, 1938). In his synopsis of the section, Vanderplank (2013) recognized the

taxon as *P. ciliata* var. *hibiscifolia* (Lam.) Vanderpl., largely on account of its glabrous leaves (as *P. ciliata* (*sensu lato*) has), and is the currently accepted name.

Several other taxa with gross morphological similarities to *P. ciliata* var. *hibiscifolia* are found throughout Mexico and Central America, including *P. liebmännii* Mast. While this particular name has been synonymized with the taxon of interest in the past (Killip, 1938; Vanderplank, 2013), other names have not been critically investigated in this manner. Furthermore, while the taxon's glabrous vegetative features and red fruit clearly ally this taxon with *P. ciliata* (*sensu lato*), the taxonomic affinity between the two has remained unclear.

The objective of this study is to evaluate the biological distinctness of the organism currently known as *P. ciliata* var. *hibiscifolia* and provide evidence for its taxonomic recognition.

Materials and Methods

A total of 217 herbarium specimens, including the holotype of *Passiflora hibiscifolia* (Fig. 2), and 27 verified iNaturalist observations (iNaturalist Network, 2018) were examined for this study. In addition, type material for several other morphologically similar taxa was also investigated: *P. foetida* var. *maxonii* Killip, *P. foetida* var. *nicaraguensis* Killip, *P. foetida* var. *subpalmata* Killip, *P. liebmännii*, and the current parent taxon, *P. ciliata*. The herbaria consulted were ASU, B, C, DUKE, E, F, IND, LINN, MEXU, MO, NY, P, RSA, TEX-LL, and US (codes follow Thiers, 2018). Coordinates from these observations were curated and mapped using SimpleMappr.net (Shorthouse, 2010). All examinations were made using an Olympus SZ61 stereomicroscope (Olympus, Center Valley, USA) and micrographs were taken with an Olympus SC30 camera (Olympus, Center Valley, USA).

Results and Discussion

Intensive morphological investigations revealed that the taxon currently recognized as *Passiflora ciliata* var. *hibiscifolia* possesses a suite of traits that are absolutely unique to the entity (Table 1). Among the most distinguishable traits are ubiquitous spheroidal, lepidote glands (Fig. 3) on the abaxial surface of the leaves which are always glabrous and deeply 3-5-lobed. The suite of



Figure 1: *Passiflora hibiscifolia* Lam. ($\equiv$ *P. ciliata* Aiton var. *hibiscifolia* (Lam.) Vanderpl.), A. flower (photo by Diana Fuentes); B. leaves and mature fruits (photo by Alexis López Hernández).



Figure 2: Holotype specimen of *Passiflora hibiscifolia* Lam. (P-P00307573), available from Muséum National d'Histoire Naturelle (MNHN, 2018).

exclusive and consistent micro- and macromorphological traits indicate that this taxon is distinct from all other members of section *Dysosmia*, including the species to which it is currently assigned, *P. ciliata* (*sensu stricto*). On account of this evidence, and following the guidance of the Unified Species Concept (de Queiroz, 2007), this taxon deserves recognition at the rank of species as *Passiflora hibiscifolia*.

Passiflora hibiscifolia is easily recognizable by its unique morphological features and is the most regularly encountered *Dysosmia* taxon in the state of Oaxaca (Mex-

ico). Confirmed individuals of this taxon are also found in the Mexican states of Chiapas, Guerrero, Jalisco, Michoacán, Morelos, Nayarit, Puebla, Tabasco, and Yucatán (Fig. 4). One of these collections from the state of Puebla, Liebmann 4078 collected in 1842, became the basis for Masters’ *Passiflora liebmannii* (Masters, 1872) but unequivocally represents *P. hibiscifolia* based on the uncommon traits that they share. The name *Passiflora hibiscifolia*, though, has priority over *P. liebmannii* in accordance with Article 11 of the current International Code of Nomenclature (Turland et al., 2018).

Table 1: Comparison of *Passiflora hibiscifolia* Lam. with other morphologically similar taxa.

Trait	<i>Passiflora hibiscifolia</i> Lam.	<i>P. ciliata</i> Aiton (<i>sensu stricto</i>)	<i>P. foetida</i> L. var. <i>maxonii</i> Killip	<i>P. foetida</i> L. var. <i>nicaraguensis</i> Killip	<i>P. foetida</i> L. var. <i>subpalmata</i> Killip
Stem pubescence	Glabrous	Glabrous	Pilosulous	Glabrous	Glabrous
Stipules	Glabrous	Glabrous	Pubescent	Glabrous	Pubescent
Foliar pubescence	Glabrous	Glabrous	Pilosulous	Glabrous	Hirsutulous
Leaf lobing	3-5 lobed	3- to sub 5-lobed	3-5 lobed	3-lobed	3-5 lobed
Foliar glands	Lepidote, spheroidal	Capitate long-stipitate (margins only)	Pyriform long-stipitate	Capitate long-stipitate (margins only)	Pyriform long-stipitate
Leaf margins	Entire to sparingly crenate	Coarsely dentate to ciliate	Ciliate	Ciliate	Ciliate
Involucral bracts	Bi- to tripinnatisect	Bi- to tripinnatisect	Bi- to tripinnatisect	Bi- to tripinnatisect	Bipinnatisect
Perianth color	Lavender	Pink-white	“Pale purple”	Pink-white	Unknown
Fruit color	Red	Red	Red	Red	Unknown

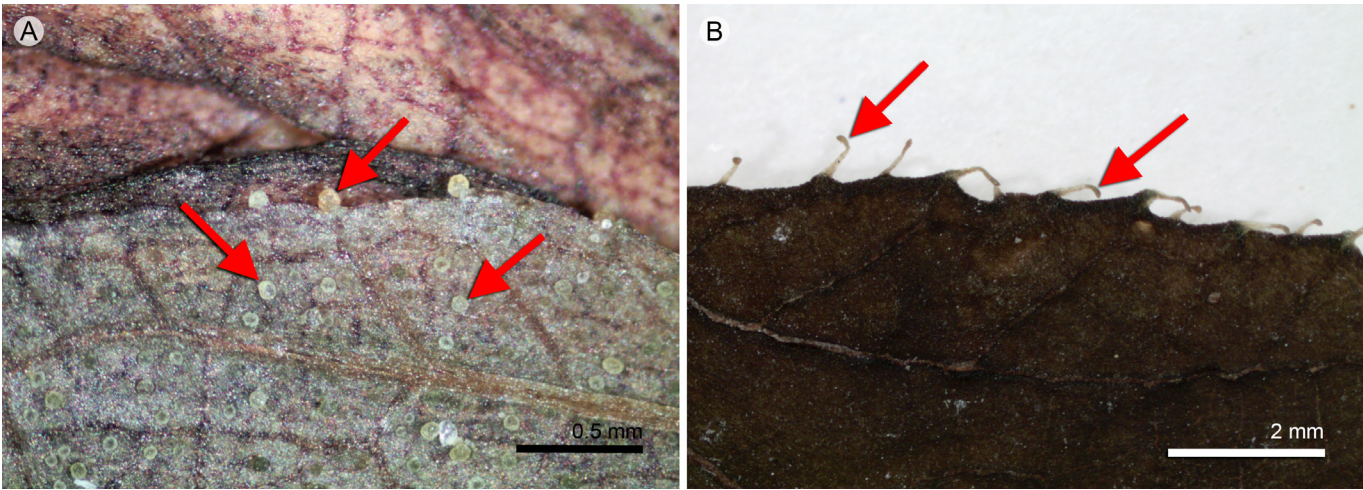


Figure 3: A comparison of some *Passiflora* L. gland types. A. lepidote glands (arrows) of *Passiflora hibiscifolia* Lam. (MacDougal 314, DUKE); B. capitate long-stipitate glands (arrows) of *P. ciliata* Aiton (*sensu stricto*) (Britton 2880, NY).

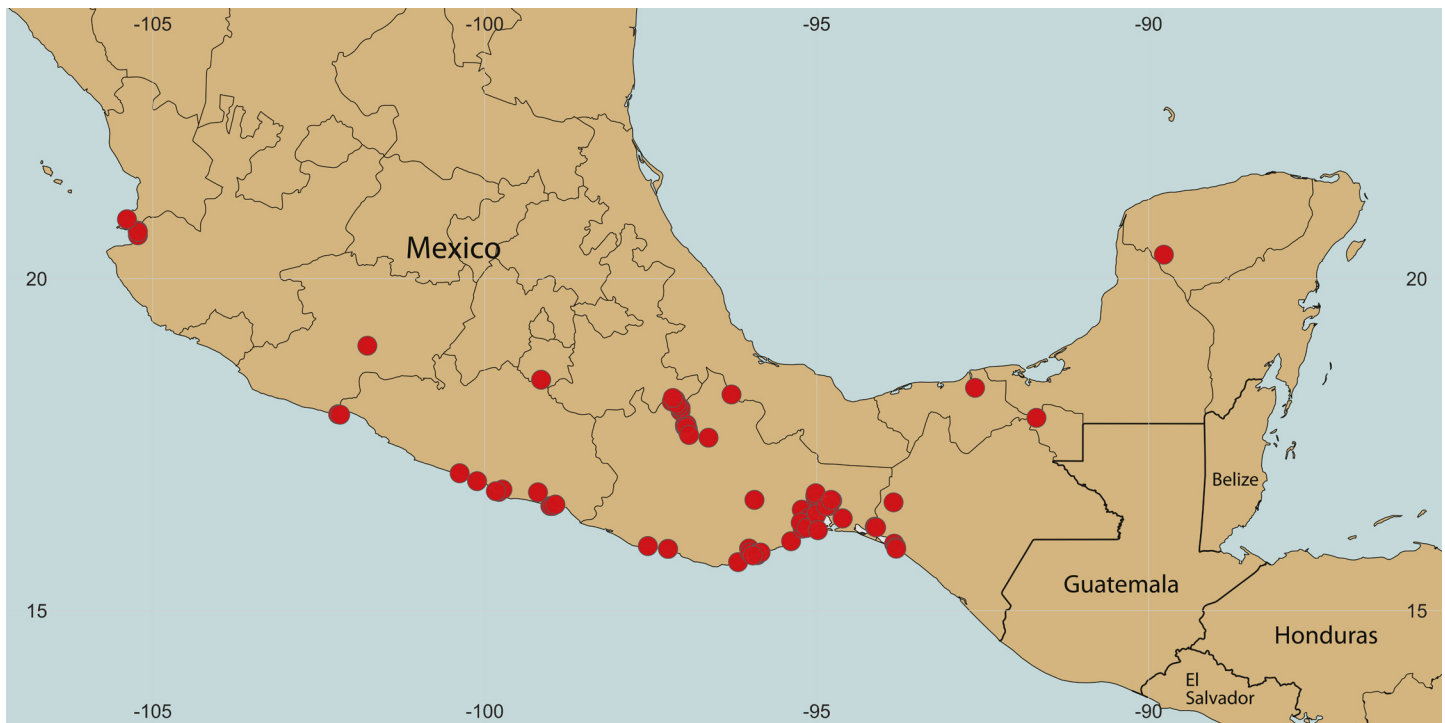


Figure 4: The known distribution (circles) of *Passiflora hibiscifolia* Lam. based on confirmed herbarium specimens and iNaturalist observations. Map rendered using SimpleMappr.net (Shorthouse, 2010).

This species is clearly closely related to *P. ciliata* based on the glabrous vegetative features and red fruit but differs in several ways, namely the lepidote foliar glands, the lavender perianth, deep purple coronal filaments, and the entire to sparingly crenate leaf margins in *P. hibiscifolia*. By comparison, *P. ciliata* (*sensu stricto*) has capitate long-stipitate foliar glands (restricted to the margins), a pink-white perianth, magenta corona filaments, and often coarsely dentate or ciliate leaf margins. The suite of traits of the latter species are also found in another taxon, *P. foetida* var. *nicaraguensis*, and likely represents the same organism (Svoboda, 2018).

Other taxa, namely *P. foetida* var. *maxonii* and *P. foetida* var. *subpalmata*, appear similar based on gross vegetative morphology but differ in having pubescent leaves and pyriform long-stipitate glands. Vanderplank (2013) included several pubescent specimens in his circumscription of *P. hibiscifolia* (as *P. ciliata* var. *hibiscifolia*), but this is in direct conflict with the protologue and type specimen which both indisputably represent a completely glabrous plant. Therefore, this name is confined to glabrous specimens with the morphological features mentioned above.

Taxonomy

Passiflora hibiscifolia Lam., *Encycl.* 3(1): 39. 1789. TYPE: FRANCE. Île-de-France, department of Paris, cultivated at the Jardin des Plantes ("Jardin du Roi"), Paris, original material presumably from Mexico, 13.IX.1779, J.-B. Lamarck s.n. (holotype: P!).

≡ *Dysosmia hibiscifolia* (Lam.) M. Roem., *Fam. Nat. Syn. Monogr.* 2(2): 149. 1846.

= *Passiflora liebmännii* Mast., *Fl. Bras.* 13(1): 547. 1872. TYPE: MEXICO. Puebla, municipality Coxcatlán, Venta Salada, V.1842, F. M. Liebmann 4078 (*Passiflore* 41) (holotype: CI, isotype: US!).

≡ *Passiflora foetida* L. var. *hibiscifolia* (Lam.) Killip, *Publ. Field Mus. Nat. Hist., Bot. Ser.* 19: 507. 1938.

≡ *Passiflora ciliata* Aiton var. *hibiscifolia* (Lam.) Vanderpl., *Bot. Mag.* 30(4): 358. 2013.

Plant completely glabrous throughout; stems terete; stipules deeply divided with pyriform long-stipitate glands; petioles with few short-stalked glands; leaves deeply 3-lobed when immature, developing 5(-7) lobes at matu-

riety, 5-10 cm wide, 4-8 cm long, margins entire to sparingly crenate, bearing short-stalked obconical glands, abaxial surface with spheroidal, lepidote glands; involucre bracts bi- to tripinnatisect, the ultimate segments gland-tipped; flowers lavender-white, 3.5-4.5 cm in diameter, sepals ovate-lanceolate, awned, petals oblong-lanceolate; corona in 5 series, the outermost magenta (inner fourth) and purple (outer third) with white between (Fig. 1A); androgynophore mostly red; ovary ovoid; fruits globose, deep red at maturity (Fig. 1B); seeds oblong, punctate, black-brown at maturity.

Distribution: found throughout southern Mexico, with a concentration in the state of Oaxaca (Fig. 4).

Habitat: most commonly in coastal dunes, secondary forest edges, sandy roadsides, and dry stream beds. Elevation 0 to 1069 m (273 m average).

Phenology: budding, flowering, and fruiting year-round.

Additional specimens examined: HONDURAS. Atlántida, unknown municipality, La Fragua, 20 m, 7.XII.1927, *P. C. Standley* 52665 (type of *Passiflora foetida* var. *nicaraguensis*; F, US). MEXICO. Chiapas, municipality Chiapilla, hwy 190 between Tehuantepec and Tuxtla Gutiérrez, Central Depression region, 18.V.1995, *K. Gould and J. Williams* 138 (TEX); 50 km al SE de Tuxtla Gutiérrez, camino a La Angostura, 630 m, 21.IV.1987, *E. Martínez S. and A. Reyes G.* 20194 (MEXU, RSA, TEX). Municipality Cintalapa, near Comitancillo, 11.I.1945, *E. J. Alexander* 314 (NY). Municipality Ocozacoautla de Espinosa, 10 km E de La Ventosa, 21.XI.1984, *O. Téllez V. et al.* 8163 (MEXU). Municipality Tonala, NW of Puerto Arista, 3 m, 22.VI.1972, *D. E. Breedlove* 25574 (MEXU, MO); loc. cit., 19.X.1972, *D. E. Breedlove and R. F. Thorne* 20852 (MEXU, MO, NY); Puerto Arista, 2.VI.1964, *R. Lent* 1 (MO). Guerrero, municipality Acapulco de Juárez, N of Pie de la Cuesta, NW of Acapulco, 5.I.1944, *F. A. Barkley* 14171 (BRIT, MEXU, MO, NY, RSA, TEX); Viveros El Huayacán, La Poza, 22.V.1979, *W. L. Forment* 763 (MEXU), 767 (MEXU); terreno al O de Viveros El Huayacán, La Poza, 28.VIII.1980, *W. L. Forment* 1140 (MEXU); San Pedro de las

Playas, orilla de la Laguna de Tres Palos, 1 m, 6.VII.1966, *D. García S. s.n.* (MEXU); Isla de la Rogusta, Acapulco, V.1951, *D. Ramírez C. s.n.* (MEXU); Puerto Marqués, Acapulco, IX.1952, *D. Ramírez C. s.n.* (MEXU); 3 km SE de Puerto Marqués, 10 m, 28.V.1986, *J. C. Soto N. and F. Solórzano G.* 12856 (MEXU). Municipality Arcelia, lower Barranca de la Guacamaya, 27.XI.1937, *Y. Mexia* 8911 (B, US). Municipality Copala, 64 km E of San Marcos on hwy 200, 17.VII.1993, *D. Seigler et al.* 13919 (MEXU). Municipality Coyuca de Benítez, cerca de la barra, Laguna Matilda, 2 m, 28.III.1984, *G. Espinosa* 89 (MEXU); Boca de Mitla, Laguna de Mitla, 5 m, 30.VIII.1984, *L. Lozada P.* 2 (MEXU); Isla Magueyes, 4 m, 30.X.1984, *L. Lozada P.* 194 (MEXU); El Dorado II, Laguna de Mitla, 0 m, 5.III.1984, *L. Lozada P.* 331 (MEXU); Boca de Mitla, Laguna de Mitla, 1 m, 7.VII.1985, *L. Lozada P.* 515 (MEXU). Municipality Cruz Grande, brecha a Playa del Sol, 5 km NE de La Huacana, 30.IV.1982, *E. Martínez S. and J. Villaseñor* 475 (MEXU, MO). Michoacán, municipality La Huacana, camino revestido a 80 km E de Acapulco, en la carretera Acapulco Pinotepa Nacional, 23.III.1982, *E. Martínez S. and O. Téllez* 110 (DUKE). Oaxaca, district Cuicatlán, municipality Cuicatlán, 550 m, 24.III.1920, *C. Conzatti* 3911 (MEXU). Municipality San Juan Bautista Cuicatlán, Papala to Cuyamecalco, 1000 m, XII.1945, *G. Aguirre B.* 12 (NY); Río de San José El Chilar, 627 m, 17.73278°, -96.94278°, 26.X.2001, *C. A. Cruz-Espinosa and E. San Pedro* 659 (MEXU); 3 km N de San José El Chilar, orilla del Río Chilar, 700 m, 17.68528°, -96.93639°, 10.X.2002, *C. A. Cruz-Espinosa and E. San Pedro* 1511 (MEXU); Cuicatlán, 610 m, 17.79944°, -96.96453°, 23.XII.1940, *F. A. Miranda-González* 979 (MEXU); barranca del Río Chico, E de (San Juan Bautista) Cuicatlán, 14.IX.1948, *F. A. Miranda-González* 4621 (MEXU); vicinity of Cuicatlán, 8-24.X.1894, *E. W. Nelson* 1632 (US); near Tomellín, 4-5.IX.1905, *J. N. Rose et al.* 10056 (US); 1 km O de Dominguillo, 750 m, 18.IV.1987, *A. Salinas T. and C. H. Ramos* F-3978B (RSA); 1.5 km O de Dominguillo, 750 m, 18.05°, -97.05°, 1.VII.1987, *A. Salinas T. et al.* 4160 (MEXU, MO). Municipality Valerio Trujano, Valerio Trujano, a orillas del Río Apoala, 692 m, 17.76942°, -96.98417°, 16.X.2004, *G. Juárez G. and F. Marini* 608 (MEXU); 1.5 km O de Tomellín, 1000 m, 18.05°, -97.05°, 30.VI.1987, *A. Salinas T. et al.* 4143 (MEXU). District Ixtlán, municipality San Juan Quiotepec, Río de Quiotepec, 18.XII.2004, *C. A. Cruz-Espinosa* 2185 (MEXU). District

Juchitán, municipality Asunción Ixtaltepec, hacia el Agua Tibia, 500 m en línea recta al N de Nizanda, 11 m, 16.66722°, -95.00972°, 22.VII.1999, *J. M. del Castillo* 2288 (MEXU); 3 km NO de Chivela, 16.XI.1982, *R. Cedillo T. and R. Torres C.* 1067 (LL, MEXU, MO). Municipality Juchitán de Zaragoza, 11 km NE de Juchitán hacia La Ventosa, 30 m, 16.5275°, -94.96194444°, 10.VI.2002, *L. Alvarado C. et al.* 63 (MEXU); 13 km al NE de Juchitán (de Zaragoza), carretera a La Ventosa, 24.V.1982, *R. Cedillo T. et al.* 1362 (LL, MEXU, MO); 0.5 mi E of Río de los Perros in Saltillo, VII.1980, *C. Greene* 8027 (IND); ejido La Ventosa Mojonera San Carlos, a orilla de la carretera panamericana, entre la Venta y la Ventosa, 38 m, 16.57236°, -94.87633°, 21.II.2007, *A. Nava Z. et al.* 1911 (MEXU). Municipality Matías Romero, 14 km S de Matías Romero en la carretera Transístmica, 100 m, 22.II.1978, *M. Sousa et al.* 9194 (MEXU). Municipality San Francisco del Mar, el rancho Faja de Oro, 5.4 km en línea recta, al NW de Montecillo Santa Cruz, 10 m, 16.39083°, -94.61194°, 27.XI.2001, *A. Franco et al.* 21 (MEXU); el rancho Faja de Oro, 3.75 km en línea recta al NW de Montecillo Santa Cruz, 10 m, 16.3875°, -94.60861°, 28.X.2001, *K. F. Martínez et al.* 51 (MEXU). Municipality San Miguel Chimalapa, 2 km SE de Vista Hermosa, hacia San Miguel Chimalapa, 13.III.1982, *R. Torres C. and R. Cedillo T.* 108 (DUKE, MEXU, MO, NY). Municipality of San Pedro Tapanatepec, 5 mi N of Oaxaca - Chiapas line, ca. 10 mi S of jct. of rte 200 and 190 (along rte 200), 16.25222°, -94.10639°, 17.VII.1971, *D. L. Spellman* 2103 (MO), 2104 (MO), 2106 (MEXU, MO), 2108 (MEXU, MO), 2109 (MO). Municipality Santiago Niltepec, along an irrigation canal off hwy 190, 60 mi E of Tehuantepec, 20.VII.1978, *M. Pennel et al.* 206 (MEXU, MO). District Juquila, municipality Santa Catarina Juquila, 17.VII.1910, *H. H. Rusby* 48 (NY, US). District Pochutla, municipality San Miguel del Puerto, Zimatán, 2 km N del puente, por la brecha a Xadani, 80 m, 15.875°, -96.00528°, 6.III.2000, *M. Elorsa C.* 2772 (MEXU). District Tehuantepec, municipality Magdalena Tlacotepec, 7 km NW de la entrada a Tlacotepec, 474 m, 16.51983965°, -95.2253161°, 26.IX.1984, *E. Cabrera C. and H. de Cabrera* 7363 (MEXU). Municipality San Mateo del Mar, San Mateo del Mar, 5 m, 11.I.1978, *D. Zizumbo and P. Colunga* 67 (MEXU, MO). Municipality San Pedro Huamelula, Playa Grande, 0.5 km N de la playa por el Arroyo Playa Grande, 5 m, 15.84472°, -95.90694°, 25.XI.1998, *M. Elorsa C.* 1157 (MEXU); 1 km N de Playa Grande, 40 m, 15.83417°, -95.89778°, 28.I.1999, *M. Elorsa C.* 1567 (MEXU); Playa Grande, 1 km N, 25 m, 15.85056°, -95.90361°, 11.I.2000, *M. Elorsa C.* 2647 (MEXU, MO); 1.5 km N de Playa Grande, sobre La Brecha, 40 m, 15.85417°, -95.90306°, 22.IV.1999, *C. Perret et al.* 310 (MEXU); Mascalaco, camino hacia la Laguna, 300 m W de Rancho Paraíso, 30 m, 15.87389°, -95.84639°, 12.IV.1997, *J. Rivera H. et al.* 382 (MEXU). Municipality Santa María Guienagati, La Chiviza, 3 km S de la Ollaga, 16.III.1983, *R. Torres C. et al.* 2561 (MEXU, MO). Municipality Santiago Astata, Barra de la Cruz, 2 km SE de camino hacia el campamento tortuguero, 5 m, 30.IV.1998, *M. Elorsa C.* 187 (MEXU); Barra de la Cruz, 25.5 km E de Laguna la Agüita y Cerro Pelón, 5 m, 22.I.1999, *M. Elorsa C.* 1530 (MEXU); 4 km E de Arroyo Jicara, 10 m, 3.II.1999, *M. Elorsa C.* 1627 (MEXU); Zimatán, 4 km SSE del puente, por la bocana del río, 15 m, 6.II.1999, *M. Elorsa C.* 1661 (MEXU); 1.6 km NO a la desviación de la carretera de Costera, 110 m, 17.III.1999, *M. Elorsa C.* 1926 (MEXU); 2.5 km SO de Río Viejo Zimatán, 45 m, 23.III.1999, *M. Elorsa C.* 1962 (MEXU); 2 km SE de camino hacia el campamento tortuguero, 5 m, 5.IV.1999, *M. Elorsa C.* 1982 (MEXU); 6 km SE por La Agüita, 10 m, 8.II.2002, *M. Elorsa C.* 2707 (MEXU); 1.5 km SE de Laguna del Cerrito, 0 m, 21.XII.1998, *S. Salas M.* 1910 (MEXU). Municipality Santo Domingo Tehuantepec, km 15 de la carretera Tehuantepec a Juchitán (de Zaragoza), 25.II.1981, *R. Cedillo T.* 562 (MEXU, NY); Ensenada Chipehua, 37 km SO de Salina Cruz, 3.V.1980, *S. González O.* 334 (MEXU); Buenos Aires on gravel road off hwy 190, ca. 15 km E of Tehuantepec, Isthmus of Tehuantepec, 17.V.1995, *K. Gould and J. Williams* 137 (TEX); 1.8 mi off hwy 190, 9 mi E of jct with hwy 185, 22.VII.1976, *L. Hess et al.* 1265 (ASU, MEXU, MO, NY); 9-10 km E of the village of La Ventosa, along the Pan-American highway (rte 190), 50 m, 16.VII.1959, *R. M. King* 1686 (NY, TEX, US); Salina Cruz, La Ventosa, 27.VII.1978, *J. M. MacDougall* 314 (DUKE, US); Tehuantepec, 28.III.1970, *T. MacDougall* 25.5 (NY); loc. cit., XII.1964, *T. MacDougall s.n.* (NY); loc. cit., 31.V.1964, *T. MacDougall s.n.* (NY); (San Pedro) Huilotepec, 4-11.V.1895, *E. W. Nelson* 2589 (US); Tehuantepec, 2.VI.1910, *C. R. Orcutt* 5272 (US); Tehuantepec, cerco de una casa, 20.II.1975, *G. Shapiro* 3 (MEXU); 7 mi S of jct. of rte 185 and 190, 16.4580556°, -94.9994444°, 17.VII.1971, *D. L. Spellman*

2110 (MEXU), 2111 (MO), 2112 (MO), 2116 (MO), 2117 (MO). District Teotitlán, municipality San Antonio Nahuatipam, cerro Nahualtepec, 3 km O de San Gabriel, por la terracería rumbo a Axusco, 1050 m, 18.15°, -97.183333°, 16.IV.1987, A. Salinas T. and C. H. Ramos F-3880 (MEXU, RSA, US); Cañada Bandera al SE de San Antonio Nahuatipam, 900 m, 28.V.1985, P. Tenorio L. et al. 8861 (MEXU, US). Municipality San Juan de los Cués, 3.5 km from San Juan de los Cués on gravel road, 575 m, 18.005°, -97.05083°, 9.V.2001, J. I. Calzada and M. Paredes F. 22981 (MEXU). Municipality San Martín Toxpalan, 15 mi past border on rte 135 from Tehuacán to Oaxaca, 650 m, 18.083333°, -97.08333°, 15.VII.1990, J. A. Soule and D. R. Brunner 2249 (MEXU, MO, TEX). District Tlacolula, municipality San Pedro Totolápan, 24 mi E of (San Pedro) Totolápan, 2400 m, 12.VIII.1962, G. L. Webster et al. 12996 (GH, MEXU, MO). District Tuxtepec, municipality Cosolapa, 6 km N de Las Margaritas, rumbo a San Luis del Río, 820 m, 16.X.1987, S. Acosta C. 788 (MEXU). Unknown municipality, estación San Antonio, 800 m, 13.XII.1907, C. Conzatti and C. Conzatti 2111 (MEXU); San Antonio, 762 m, 2.IX.1894, C. G. Pringle 4847 (E, MEXU, MO, NY, P, RSA, US); 10.I.1896, E. Seler 1665 (NY); San Antonio valley, 792 m, 1.IX.1894, C. L. Smith 245 (MO, RSA, US). Puebla, municipality Coxcatlán, rte 131, 1 mi N of Tlapa, 853 m, 20.VII.1978, J. M. MacDougal 285 (DUKE, US); 12 km SE de Coxcatlán, sobre la carretera a Teotitlán (de Flores Magón) on hwy 980, 31.III.1968, J. Rzedowski 25576 (MEXU); Río Salado, SO de Pueblo Nuevo, 1020 m, 22.V.1991, P. Tenorio L. and E. Martínez C. 17380 (MEXU). Municipality Tehuacán, Tehuacán, VI.1841, F. M. Liebmman 4079 (US). Tabasco, municipality Centla, Lagunas Pajaral I, II, 20 km S de Frontera, laguna que desemboca a Río San Pedrito, 7 m, 18.35445°, -92.615833°, 8.VII.1998, A. Novelo R. and L. Ramos V. 2702 (MO). Municipality Emiliano Zapata, 32 km SE de Blanca, 11 km NE de El Chable, 10.V.1982, E. Cabrera C. et al. 2660 (DUKE, MEXU, MO). Yucatán, municipality Progreso, Progreso, open place, 11-15.VIII.1932, W. C. Steere 3022 (type of *Passiflora foetida* var. *subpalmata*; US). Municipality Santa Elena, Uxmal, 3.I.1977, W. Schwabe s.n. (MEXU). NICARAGUA. Managua, municipality Managua, vicinity of Managua, mostly along the shore of Lake Managua, 24.VI.1923, W. R. Maxon 7219 (type of *Passiflora foetida* var. *maxonii*; US). UNITED KINGDOM. England,

county of Oxfordshire, Honorable Mrs. Barrington's stove at Mongewell, VII.1791, (original material from Jamaica), *Unknown* s.n. (neotype of *Passiflora ciliata*; LINN-HS).

iNaturalist observations examined: MEXICO. Guerrero, municipality Copala, 16.574339°, -99.011536°, 15.III.2018, H. V. Bárcenas (username: horacio_barce-nas; iNaturalist ID: 10360363); 16.574585°, -98.978237°, 15.III.2018, D. Fuentes (username: dianafr; ID: 10393452). Jalisco, municipality Puerto Vallarta, 20.653407°, -105.225332°, 26.III.2017, M. C. Álvarez R. (username: cecilia_mayanjays; ID: 5874307); 20.722495°, -105.23058°, 17.I.2018, E. Canales (username: erendiracanales; ID: 9524959); 20.702344°, -105.224605°, 8.IV.2017, M. Guel A. (username: maribel_guel20; ID: 9872887); 20.653407°, -105.225332°, 17.I.2018, K. E. Peña J. (username: karenjoya; ID: 9529551). Michoacán, municipality Lázaro Cárdenas, 17.956181°, -102.208217°, 6.X.2017, W. Ostría (username: wero-ostría; ID: 8291767); 17.950494°, -102.178906°, 4.V.2017, H. Suzuki (username: hakikuchi; ID: 6096896). Morelos, municipality Tlaquiltenango, 18.477116°, -99.151407°, 7.VI.2013, username: annemirdl (ID: 325005). Nayarit, municipality Bahía de Banderas, 20.893697°, -105.389357°, 1.II.2017, A. López H. (username: alexiz; ID: 5115933). Oaxaca, district Juchitán, municipality Asunción Ixtaltepec, 16.571377°, -94.954319°, 10.V.2011, username: tereso30 (ID: 7605012). Municipality Heroica Ciudad de Juchitán de Zaragoza, 16.597207°, -94.82686°, 8.I.2007, username: tereso30 (ID: 7605025); 16.423098°, -95.016101°, 10.V.2017, A. Jossafat (username: abeljossafat; ID: 6168756); 16.574997°, -94.814415°, 22.V.2015, J. C. Pérez M. (username: charro; ID: 2663734). District Juquila, municipality Villa de Tututepec de Melchor Ocampo, 15.971396°, -97.543402°, 17.III.2018, H. V. Bárcenas (username: horacio_barce-nas; ID: 10710804); 15.92873°, -97.238402°, 18.III.2018, H. V. Bárcenas (username: horacio_barce-nas; ID: 10728801); 15.970324°, -97.514048°, 18.V.2018, H. V. Bárcenas (username: horacio_barce-nas; ID: 12695916); 15.971833°, -97.544243°, 17.III.2018, D. Fuentes (username: dianafr; ID: 10311329); 15.929715°, -97.241989°, 18.III.2018, D. Fuentes (username: dianafr; ID: 10311694); 15.92906°, -97.239655°, 18.III.2018, D. Fuentes (username: dianafr; ID: 10408089). District Pochutla, municipality Santa María Huatulco, 15.767418°, -96.130646°, 24.VI.2018, C.

Domínguez-Rodríguez (username: blakesito; ID: 13851296); 15.767322°, -96.130409°, 2.VII.2018, *C. Domínguez-Rodríguez* (username: blakesito; ID: 14114383); 15.767513°, -96.130516°, 3.VII.2018, *C. Domínguez-Rodríguez* (username: blakesito; ID: 14115527); 15.729802°, -96.184521°, 8.II.2015, *J. C. García M.* (username: juancarlosgarciamorales1; ID: 1232027). District Tehuantepec, municipality San Pedro Huamelula, 15.840556°, -95.970833°, 5.V.2018, *E. N. Tapia B.* (username: momoto-erick; ID: 12537177). Municipality Santo Domingo Tehuantepec, 16.324444°, -95.238889°, 8.V.2014, *J. C. García M.* (username: juancarlosgarciamorales1; ID: 1166121); 16.335481°, -95.235672°, 23.IV.2015, *J. C. García M.* (username: juancarlosgarciamorales1; ID: 1418031).

Author contribution

HTS identified specimens, verified the nomenclature and type specimens, carried out all examinations, and conceived and wrote the manuscript in its entirety.

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