



Synopsis of *Himatanthus* (Apocynaceae, Rauvolfioideae: Plumerieae) species from Peru

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Abstract

The delimitation of *Himatanthus* (Apocynaceae) species has long been problematic, and much confusion remains as to which names and species delimitations should be adopted. In order to recognize and clarify the species of *Himatanthus* occurring in Peru, herbarium specimens were examined, coupled with detailed field observations. The present study recognizes three species in Peru: *H. revolutus*, *H. tarapotensis* and *H. phagedaenicus*. A key to identify the species, as well as descriptions, synonymy, specimens cited, and taxonomic comments are presented.

Key Words: Apocynaceae, *Himatanthus*, Neotropics, Plumerieae, Rauvolfioideae, South America, taxonomy.

Introduction

Himatanthus Willdenow ex Roemer & Schultes (1819: xiii; Apocynaceae) is currently recognized as a neotropical genus of nine species, characterized by alternate leaves, presence of colleters in the axils of the petiole and at the base of the floral bracts; terminal, thyrsoid inflorescences consisting of dichotomous cincinni with a reduced axis subtended by two deciduous, petaloid floral bracts, corolla infundibuliform, sinistrorsely convolute, stamens inserted near the base of corolla tube, anthers free from the style head, gynoecium hemi-syncarpous composed of two carpels, style head cylindrical or obconical with two round apices, ovary semi-inferior without nectariferous disc, two opposite, woody follicles, and seeds with a concentric wing (Spina 2004, Spina *et al.* 2013). Endress and Bruyn (2000) positioned *Himatanthus* in subfamily Rauvolfioideae (= Plumerioideae), tribe Plumerieae, along with nine other genera. Recently, Endress *et al.* (2014) confirmed the position of the genus in tribe Plumerieae, subtribe Plumeriinae, along with *Plumeria* Linnaeus (1753: 209) and *Mortoniella* Woodson (1939: 257–259). These three genera have the following common characteristics: semi-inferior ovary, style head without a basal collar, and absence of a nectariferous disk (Endress & Bruyn 2000, Woodson 1937), and can be distinguished from each other by the characteristics cited by Woodson (1937, 1939, 1948), Plumel (1990, 1991), and Morales (2005).

Himatanthus and *Plumeria* have a complex, intertwined taxonomic history. For about eighteen years after its description, *Himatanthus* was treated as a monotypic genus with a *H. rigidus* Hoffmannsegg ex J.A. Schultes (1819: 221), which was described from material collected in the state of Pará, Brazil. However, Müller Argoviensis (1860) in *Flora Brasiliensis*, overlooked this genus and recognized only species in *Plumeria*.

In 1937, following the evaluation of *Plumeria* and *Himatanthus* by Woodson (1937: 189–224), the delimitation of *Himatanthus* was expanded to include other species, and its geographic distribution was extended from Panama throughout South America. In his study, Woodson recognized that certain species of *Plumeria* ranging from southern Panama to southern Brazil, are distinguishable from the other species from Central America, southern Mexico and the Antilles, by their large petaloid bracts, and he transferred the corresponding species to *Himatanthus*, increasing the

number of species from one to seven. According to his treatment, four species are restricted to Brazil: *H. attenuatus* (Benth 1841: 245) Woodson (1937: 197); *H. lancifolius* (Müller Argoviensis 1860: 41) Woodson (1937: 200); *H. obovatus* (Müller Argoviensis 1860: 40) Woodson (1937: 201–202); and *H. phagedaenicus* (Martius in Spix & Martius 1831: 1128) Woodson (1937: 199). The other three species recognized by Woodson are distributed from southern Panama throughout southern South America: *H. articulatus* (Vahl 1798: 20) Woodson (1937: 196–197) occurring in Panama, Venezuela, Guyana, Surinam, French Guiana and Brazil; *H. bracteatus* (A. de Candolle 1844: 394) Woodson (1937: 200) in Guyana and Brazil; and *H. sucuuba* (Spruce ex Müller Argoviensis 1860: 40) Woodson (1937: 198–199) occurring in Bolivia, Brazil and Peru. Woodson produced a tentative key to the species of *Himatanthus*. However, he did not have much confidence in its reliability, and stated the following:

“Although leaf characters have been employed almost exclusively in this purely tentative treatment, it probably is inevitable that their use may have to be modified greatly as additional material, so greatly needed, finds its way into our collections. It should be borne in mind by those who attempt to use the following key that it is offered quite provisionally, and is designed merely as a basis for the re-establishment of the genus *Himatanthus*.” (Woodson, 1937: 195)

Plumel (1990, 1991) distinguished *Himatanthus* from *Plumeria* by the woody branches (vs. fleshy in *Plumeria*), di- or tri-chasial inflorescences (vs. multi-chasial), large, enveloping, persistent bracts (vs. poorly developed, caducous), lobed calyx, with unequal, acute or lanceolate lobes, sometimes obsolete or absent (vs. with equal lobes), hypocateriform corolla (vs. infundibuliform), thin style head [i.e., cylindrical to narrowly obconical], with a faintly developed collar (vs. globose), thin and digitate stigmas (vs. globose, separate), seeds with a circular, laterally asymmetrical wing (vs. with a terminal wing), and reticulate seed tegument (vs. plicate, rugose). He subdivided *Himatanthus* into two subgenera, *H.* subgen. *Obovatae* Plumel (1990: 105; 1991: 5 = *H.* subgen. *Himatanthus*) and *H.* subgen. *Lanceolatae* Plumel (1990: 105; 1991: 7). By examining type specimens Plumel (1990, 1991) was able to expand upon Woodson’s species delineations. Consequently, he resurrected several species that Woodson previously treated as synonyms. Plumel proposed several new combinations in *Himatanthus*, and ultimately recognized 13 species and eight varieties in the genus. In his key to species, except for two couplets, Plumel used only leaf characters. Our research however, indicates that these leaf characters can vary within a species and sometimes even within an individual.

Subsequently, Spina (2004) performed a taxonomic revision of *Himatanthus* as part of an unpublished doctoral dissertation, using morphological and molecular characters. She recognized nine species and rejected the subgeneric classification proposed by Plumel (1990, 1991). She confirmed the similarities and close relationships of *Himatanthus*, *Mortoniella* and *Plumeria*; however, the molecular phylogenies presented in her thesis were inconclusive, as only a small number of taxa were included. Therefore, the separation and delimitation of these genera remain to be tested. Nevertheless, chromosome numbers supply significant characters in separating these closely related genera, as Williams & Stutzman (2008) reported $2n = 18$ in *Himatanthus*, $2n = 36$ in *Plumeria*, and $2n = 32$ in *Mortoniella*.

Consequently, as the monophyly of *Himatanthus* has never been tested with molecular phylogenies, the generic delimitations proposed by Woodson (1937, 1939), Plumel (1990, 1991), Spina (2004), Spina *et al.* (2013), and Endress *et al.* (2014) are here adopted, and the species delimitations of Spina (2004) and Spina *et al.* (2013) are followed.

***Himatanthus* in Peru**

To date there has been a total of six species of *Himatanthus* cited for Peru (Brako & Zarucchi 1993; Ruokolainen & Tuomisto 1998; Ulloa *et al.* 2004; Rodriguez *et al.* 2006; Tropicos, 2016): *H. articulatus*, *H. bracteatus*, *H. lancifolius*, *H. phagedaenicus*, *H. sucuuba*, and *H. tarapotensis* (K. Schumann ex Markgraf 1932: 339) Plumel (1990: 112). Our research indicates that there are fewer species in the country. The proliferation of names, in our opinion, is because a few morphological features help differentiate the species of *Himatanthus* and these have been variably interpreted for species delimitation and identification of herbarium specimens.

One of the most frequently reported species of *Himatanthus* in Peru is *H. sucuuba* (e.g., Macbride 1959, Acevedo 1998, Alonso *et al.* 1998, Vásquez 1997, Ruokolainen & Tuomisto 1998, Vásquez & Phillips 2000, Pitman *et al.* 2002, 2003 a, b, Pennington *et al.* 2004, Tropicos 2016). However, our study indicates that this species does not occur in the country. Rather, *H. sucuuba* has a complex and often misinterpreted taxonomic history with many studies in the field of ethnobotany (e.g., Bourdy *et al.* 2000, Shanley *et al.* 2011, Odonne *et al.* 2013), leaf anatomy (Larrosa & Duarte

2005), morphology (Amaro *et al.* 2006), biochemistry (e.g., Perdue & Blomster 1978, Endo *et al.* 1994, Miranda *et al.* 2000, Wood *et al.* 2001, Silva *et al.* 2007, 2010), and ecology (e.g., Spichiger *et al.* 1990, Ferreira *et al.* 2007, 2009 a, b) reporting its presence in Peru. However, Spina (2004) and Spina *et al.* (2013) treated *H. sucuuba* as a synonym of *Himatanthus articulatus*, which is a species that does not occur in Peru. Therefore, as most of the above publications did not cite voucher specimens, it is impossible to know which species was/were actually studied. Following the species delimitations of Spina (2004) and Spina *et al.* (2013), we find that there are three species of *Himatanthus* occurring in Peru: *H. phagedaenicus*, *H. revolutus* (Huber 1915: 200) Spina & Kinoshita (in Spina *et al.* 2013: 1307), and *H. tarapotensis*. For the differentiation of the three species present in Peru, most vegetative characters are of little use, taking into account the broad variation within each species (Spina 2004). For example leaf bases are cuneate, and the apices are either acute or acuminate for all species in Peru. Similarly, the number of secondary veins can vary from 12 to 24 in all Peruvian species. On the other hand, venation type and angle of the secondary veins with respect to the midrib can provide some diagnostic characters that can be used for distinguishing the species. *Himatanthus revolutus* has a mixed type of brochidodromus-eucamptodromus venation, whereas *H. tarapotensis* and *H. phagedaenicus* exhibit a simple brochidodromous venation. The angle of the secondary veins with respect to the midrib is useful in distinguishing *H. revolutus*, with secondary veins nearly or exactly perpendicular to the midrib (80–90°), while they are at 70–80° in *H. phagedaenicus* and 50–70° in *H. tarapotensis*.

Reproductive features are a reliable source of significant diagnostic characteristics to distinguish species of *Himatanthus* (Spina 2004). For example, the corollas are 45–70 mm long in *H. phagedaenicus* and *H. revolutus* versus 35–45 mm long in *H. tarapotensis*. *Himatanthus phagedaenicus* is easily distinguished by its corolla tube and lobes of approximately the same length and style head with trichomes, whereas the corolla lobes are longer than the tube and the style heads glabrous in *H. tarapotensis* and *H. revolutus*. Finally, the follicles are 27–29 cm long in *H. tarapotensis*, 16–26 cm long in *H. phagedaenicus*, and 12.5–25.5 cm long in *H. revolutus*.

Material and Methods

This study is based on examination of herbarium specimens using a dissecting microscope, digital images, direct field observations, and consultation of specialized literature. Herbarium specimens of *Himatanthus* were studied either by visiting and/or through loans from the following herbaria: AMAZ, B, BM, BR, C, CAY, COL, F, G, IAN, INPA, K, L, M, MBM, MG, MO, NY, P, R, RB, S, UB, USM, UEC, Z. For the species in Peru, 26 individuals from 11 localities, corresponding to various habitats, were collected. Herbarium specimens of these individuals were deposited at AMAZ, MBM and USM. Descriptions and measurements are based on herbarium specimens identified by Spina (2004), as well as 26 gatherings recently collected in Peru. The measurements reported here for vegetative, floral and fruiting characters were obtained from fresh material. Geographical distributions and ecological preferences were obtained from the information on specimen labels and field observations. Species delimitations, synonymies, geographical distributions, and specimens examined, were obtained from Spina (2004), and Spina *et al.* (2013), complemented by new collections and field observations.

The clarification of the species of *Himatanthus* in Peru has become urgent and necessary due to the many ongoing studies in the country focusing on medicinal properties, ecological preferences, and factors influencing herbivory in *Himatanthus*. We present the following treatment in an attempt to clarify previous taxonomic confusion of the genus in Peru.

Taxonomic treatment

Himatanthus Willdenow ex Roemer & Schultes, Syst. Veg., ed. 15 bis, 5: XIII, 221. 1819. Type: *H. rigidus* Willdenow ex Roemer & Schultes (1819: 221).

Shrubs or trees to 30 m tall, with white latex. *Stems* terete, with conspicuous leaf scars. *Leaves* alternate, often congested at branch tips, blades chartaceous, subcoriaceous to thickly coriaceous, margins often revolute; secondary veins joined by a series of marginal loops. *Inflorescences* terminal or pseudo-lateral by reiteration of axillary buds, cymose or thyriform, multiflorous; *bracts* large, showy, caducous, with numerous glands at base. *Flowers* 5-merous. *Calyx* small, persistent, lobes small, unequal, imbricate. *Corolla* hypocateriform, large, white; tube narrow, straight,

glabrous inside; lobes convoluted in bud, spreading or reflexed at anthesis. *Stamens* inserted at the lower portion of the corolla tube; anthers sessile, lanceolate, basally sagittate. *Ovary* apocarpous, topped by a fusiform or cylindrical stigmatic head; ovules numerous in each locule. *Fruit* consisting of two separate, banana-like follicles, straight or curved, drying at maturity, dehiscent by a ventral slit. *Seeds* dry, compressed, with a papery, concentric wing.

Geographic distribution: *Himatanthus* has nine species widespread throughout South America, one of them (*H. articulatus*) extending to Panama.

Key to the species of *Himatanthus* occurring in Peru

- 1 Leaf venation brochidodromous-eucamptodromous; secondary veins at 80–90° angle with the midrib 2. *H. revolutus*
 1 Leaf venation brochidodromous; secondary veins at 50–80° angle with the midrib 2
- 2 Secondary veins at 50–70° angle with the midrib; corolla tube 15–20 mm long, lobes 20–25 mm long; style head glabrous; follicles 27–29 cm long 3. *H. tarapotensis*
 2 Secondary veins at 70–80° angle with the midrib; corolla tube 20–35 mm long, lobes 25–35 mm long; style head pubescent; follicles 16–26 cm long 1. *H. phagedaenicus*

1. *Himatanthus phagedaenicus* (Martius) Woodson, Ann. Missouri Bot. Gard. 25: 199. 1937 [“1938”] (as “*phagedaenica*”). ≡ *Plumeria phagedaenica* Martius in Spix & Martius, Reise Bras. 3: 1128. 1831.

Type:—BRAZIL. Amazonas: Manaus, Cachoeira, prope Barra do Rio Negro [now Manaus], s.d., C.F.P. Martius 2778 (first-step lectotype, designated by Plumel (1991: 65); second step-lectotype, here designated: M [barcode M-0183348], photos at F, INPA, MO, RB).

Small or medium-size trees, 2–15 m tall; young stems dark brown with bright brown spots, older stems grayish; periderm smooth in young stems, striate in older stems. *Leaves* with petioles 20–35(–45) mm long, glabrous; blades obovate, oblanceolate or elliptic, 15–23(–27.5) x 7–9.5(–11) cm, coriaceous, base cuneate, apex acute, obtuse-emarginate or round, sometimes short-acuminate, margin revolute; venation brochidodromous; secondary veins at 70–80° angle, 14–23 on each side of midrib; tertiary veins slightly evident on both sides. *Bracts* 20–30 mm long, glabrous. *Calyx* 4–8 x 2 mm; lobes ovate, 0.5–1(–1.5) mm long, unequal in size, with 3 or all reduced. *Corolla* 45–70 mm long; tube 25–35 x 2–3 mm, pilose inside at distal 6–10 mm of corolla tube; lobes elliptic, 25–35 x 8–12 mm. *Stamens* 2.5 mm long, inserted at 2–2.5 mm from the base of corolla tube. *Style head* obconical, pubescent, without protuberance, 2.0 mm long, with 2 short apices 0.2–0.5 mm long. *Follicles* 16–26 x 2–3 cm; pericarp striate with two lateral prominent ribs, yellowish. *Seeds* 50 x 25–40 mm, with apical wing larger than basal and lateral wings; seminal nucleus 25–30 x 10 mm; hilum 10 mm long.

Distribution:—From Venezuela, Guyana, Suriname, and French Guiana to Amazonian Colombia, Peru and Brazil.

Taxonomic notes:—Martius (in Spix & Martius 1831), when he described *Plumeria phagedaenica* Martius (in Spix & Martius 1831: 1128) did not cite any collection number or herbarium of deposit. Müller Argoviensis (1860: 40, tab. 11, fig. 1) cited the same gathering indicated by Martius, also without collection number or herbarium of deposit. Woodson (1937: 199) cited the type of this name as: “Brazil: Amazonas: sylvis ad Rio Cachoeira prope Barra do Rio Negro, Oct., year lacking, Martius 2778 (M, type).” Plumel (1991: 65) cited the type as “Martius 2778, Manaus, holo-M” which is a first-step lectotypification. There are two specimens of this taxon collected by Martius at M, and only one, with barcode M-0183348, has Martius’ collection number “2778”, which is here selected as a second-step lectotype.

Selected specimens examined:—PERU. **Loreto:** Between Quistococha and Santo Tomas, 14 km from Iquitos, 18 August 1981 (fl), Moore *et al.* [additional collectors unknown] 123 (F); Prov. Maynas, across lake Quistococha, opposite Fish Experiment Station, W of Iquitos, 17 November 1975 (fl), C. Davidson 3567 (MO, NY); Dtto. Alto Nanay, Río Nanay, Quebrada Anguilla, upland never inundated, 29 March 1978 (fr), M.Y. Rimachi 3494 (F, MO); Prov. Requena, Quebrada Yanayacu-Río Tapiche, 19 October 2014 (fl), M. Ríos, T. Mori, N. Pitman, L. Torres & C. Vriesendorp 4553 (F, USM, MBM).

2. *Himatanthus revolutus* (Huber) Spina & Kinoshita, Taxon 62: 1307. 2013. ≡ *Plumeria revoluta* Huber (as “*Plumiera*”), Bull. Soc. Bot. Genève, ser. 2, 6: 200. 1915. ≡ *Himatanthus bracteatus* var. *revolutus* (Huber) Plumel, Compt. Rend. Séances Soc. Biogéogr. 66(3): 114. 1990.

Type:—BRAZIL. Amazonas: Região do Alto Ariramba [Campos de Ariramba], campinarana, 21 December 1906, *A. Ducke s.n. (MG 8039)* (lectotype, here designated: G [barcode G00164788], photos at INPA, MO, NY; not at MG).

Himatanthus stenophyllus Plumel, Compt. Rend. Séances Soc. Biogéogr. 66(3): 116. 1990.

Type:—BRAZIL. Amazonas: Mun. Manaus, estrada Manaus–Itacoatiara, km 28, 6 December 1983, *M.M. Plumel & D.F. Coelho 8391* (holotype P [barcode P00076082]; isotype INPA [barcode INPA112835]).

Small or medium-size trees, 3–12 m tall; young stems dark brown, older stems brown; periderm smooth in young stems, rugose, striate in older stems. *Leaves* with petioles 15–20 mm long, glabrous; blades oblanceolate, 10.5–18.5(–20) x 3–5 cm, base cuneate, apex acute to obtuse, margin revolute, chartaceous; venation brochidodromous-eucamptodromous; secondary veins at 80–90° angle, (8–)13–17(–23) on each side of midrib; tertiary veins slightly evident in both sides. *Bracts* 20–25 mm long. *Calyx* 5–7 x 2 mm; lobes ovate, 0.1–1(–2.5) mm long, unequal in size, 1, 4 or all reduced. *Corolla* 45–70 mm long; tube 20–30 x 2–3 mm, pilose inside at distal 1/2 of corolla tube; lobes obovate, 25–40 x 5–8 mm. *Stamens* 2.5 mm long, inserted at 1.5–2 mm from base of corolla tube. *Style head* obconical, 1.5–2 mm long, glabrous, with 5 striations, with 2 apices 0.2 mm long, flat. *Follicles* 12.5–25.5 x 3 cm; pericarp striate with two lateral prominent ribs, dark brown. *Seeds* 30–50 x 25–30 mm, with apical, basal and lateral wings of the same size; seminal nucleus 30–50 x 25–30 mm; hilum 15 mm long.

Distribution:—From Venezuela, Guyana, Suriname, French Guiana, to Amazonian Colombia, Peru and Brazil.

Taxonomic notes:—This species has not been previously reported from Peru in any of the literature cited above. The identification of this species was recently made, from a new record collected in the Loreto District.

Huber (1915) described *Plumeria revoluta* Huber (1915: 200) and cited the gathering “Hab. in regione fl. Arirambae superioris in fruticetis “Campina rana” dictis, 21 décembre 1906, leg. A. Ducke (8039).” However, he did not indicate this collection as type and did not cite the herbarium of deposit. In addition, “8039” is not a collection number, but is the accession number of this specimen of the Museu Goeldi (MG), because at that time Ducke did not use collection numbers; therefore, this gathering should be cited as “*A. Ducke s.n. (MG 8039)*.”

Plumel (1990: 114–116) reduced *Plumeria revoluta* to a variety of *Himatanthus bracteatus* (A. de Candolle 1844: 394) Woodson (1937: 200), and cited the type as “Ducke A. 11358, MG BM” without any explanation. This citation is a first-step neotypification, because he cited MG and BM herbaria. A year later, Plumel (1991: 79) explained that, because he was unable to find *Ducke s.n. (MG 8039)*, he designated a neotype. The neotype was cited as “Ducke 11399 RB, S^m de Paranaquara, Brésil, Néo- RB, Syn- U.” Plumel’s (1991: 79) citation of *Ducke 11399* at RB was not a valid neotypification because he had already neotypified the name on *Ducke 11358* in his previous publication (Plumel 1990).

Recently, Spina *et al.* (2013) found a specimen of *Ducke s.n. (MG 8039)* at G, citing it as “Holotype: [...], Ducke s.n. (G! photos: INPA!, MO!, NY!).” Their citation as holotype is incorrect, as Huber (1915: 200) did not cite the herbarium of deposit. It cannot be recognized as a lectotypification because, according to the *International Code of Nomenclature for algae, fungi, and plants* (ICNafp), it must now state “here designated” (or equivalent) to be valid. In addition, as Spina *et al.* (2013) had found a specimen of *Ducke s.n. (MG 8039)*, according to Art. 9.19 of the ICNafp (McNeill *et al.* 2012) Plumel’s (1990) neotypification on *Ducke 11358* is superseded. Also, after an exhaustive search of *Ducke s.n. (MG 8039)* at MG, we are convinced that it is lost. Therefore, we here designate *Ducke s.n. (MG 8039)* at G, barcode G00164788, as the lectotype of *Plumeria revoluta*.

Specimen examined:—PERU: Loreto: Dtto. San Juan, Localidad de Quistococha, km 4.5 en la carretera Iquitos–Nauta, 23 September 2015 (fl), *N. Mitidieri & U. Mozombite 16* (USM).

3. *Himatanthus tarapotensis* (K. Schumann ex Markgraf) Plumel, Compt. Rend. Séances Soc. Biogéogr. 66(3): 112. 1990. ≡ *Plumeria tarapotensis* K. Schumann ex Markgraf, Notizbl. Bot. Gart. Berlin-Dahlem 11: 339. 1932.

Type:—PERU. Loreto, Tarapoto, October 1902, *E. Ule 6473* (B destroyed; lectotype designated by Spina *et al.* (2013: 1307): G [barcode G00164786]; isolectotype MG [barcode MG006333]).

Small or medium-size trees, 7–15 m tall; young stems dark brown with yellowish spots, older stems deep brown; periderm smooth in young stems, flaky in older stems. *Leaves* with petioles 15–35 mm long, glabrous; blades narrowly elliptic, (16–)18–26(–29) x 4–6(–7) cm, base cuneate to decurrent, apex acute or acuminate, chartaceous, margin slightly revolute or undulate; venation brochidodromous; secondary veins at 50–70° angle, (11–)14–20 on each side of

midrib; tertiary veins emergent on adaxial side, immersed in the lamina and darker than lamina on abaxial side. *Bracts* 15–20(–25) mm long. *Calyx* 5–10 x 2 mm; lobes ovate, 0.1–0.5(–0.6–1) mm long, unequal in size, 3 or all reduced. *Corolla* 35–45 mm long; tube 15–20 x 2 mm, throat pilose at distal 1/3 of corolla tube, lobes obovate, 20–25 x 4–6 mm. *Stamens* 2–2.5 mm long, inserted at 1.5–2 mm from the base of corolla tube. *Style head* obconical, 1.5 mm long, glabrous, without protuberances, with 2 apices 0.5 mm long. *Follicles* 27–29 x 3.5–4.5 cm; pericarp striate, with two lateral prominent ribs, brown. *Seeds* 60 x 35 mm, with apical and basal wings smaller than lateral wings; seminal nucleus 35 x 10 mm; hilum 15 mm long.

Distribution:—From Colombia, Venezuela, and French Guiana to Amazonian Ecuador, Peru, Brazil and Bolivia.

Selected specimens examined:—PERU. **Amazonas:** Prov. Bagua, Quebrada Tambillo (opposite kms 280–282 of Marañón road), valley of Río Marañón, above Cascadas de Mayasi, 18 September 1962 (fl), *J.J. Wurdack 2048* (F, MO, NY, S). **Huánuco:** Dtto. Puerto Inca, Bosque Nacional de Iparia, a lo largo del Río Pachitea, 23 December 1968 (fl), *J.V. Schunke 2916* (G, NY); Prov. Leoncio Prado, localidad Rupa-Rupa, 25 October 2014 (fl) *R. Zárate, M. Sosa, E. Rengifo, R. Remusgo, S. Filomeno & M. Mori 20197* (MBM). **Junín:** La Merced, Río Seco, 1944 (fl), *J.J. Soukup 2496* (F); 10–24 August 1923 (st), *J.F. MacBride 5402* (F). **Loreto:** Reserva Nacional Allpahuayo-Mishana, 12 March 2014 (fl), *C.A. Amasifuen & R. Pua 3483* (AMAZ, USM), *3484* (MBM, USM), *3485* (MBM), *3486* (MBM), *3487* (AMAZ, MBM); Cerro Escalera, 30 July 2013 (fl), *T. Mori 1961, 1962, 1963* (MBM); Comunidad Tangarana, Río Atacuari, 5 February 2014 (fl), *C.A. Amasifuen, T. Mori, M. Panaifo & G. Panaifo 3478* (AMAZ, MBM, USM); localidad Jenaro Herrera, quebrada Supay, 21 July 2014 (fl), *C.A. Amasifuen, N. Villacorta & N. Macedo 3488* (AMAZ, MBM, USM); localidad Bagazán, quebrada Carahuayte, 24 July 2014 (fl), *C.A. Amasifuen, A. Vásquez & N. Macedo 3489* (AMAZ, MBM, USM); localidad Pebas, comunidad Pucaurquillo, 28 September 2014 (fl), *R. Zárate, D. Fagua & A. García 20153* (MBM); comunidad Santa Lucía de Pro, 30 September 2014 (fl), *R. Zárate, D. Fagua & P. Gonzales 20181* (MBM).

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