Synopsis of Himatanthus (Apocynaceae, Rauvolfiodieae: Plumerieae) species from Peru
Carlos Amasifuen Guerra, Piero G. Delprete, Andrea Spina

To cite this version:
Carlos Amasifuen Guerra, Piero G. Delprete, Andrea Spina. Synopsis of Himatanthus (Apocynaceae, Rauvolfiodieae: Plumerieae) species from Peru. Phytotaxa, Magnolia Press 2016, 283 (1), pp.65-73. 10.11646/phytotaxa.283.1.4 . hal-01940160
Synopsis of *Himatanthus* (Apocynaceae, Rauvolfioideae: Plumerieae) species from Peru

CARLOS A. AMASIFUEN GUERRA¹, PIERO G. DELPRETE ²* & ANDREA P. SPINA³

E-mail: carlos.amasifuen@gmail.com
²Herbier de Guyane, Institut de Recherche pour le Développement (IRD), UMR AMAP, Boîte Postale 90165, 97323 Cayenne Cedex, French Guiana, France
E-mail: piero.delprete@ird.fr
³Rua Capitão Leônidas Marques 894, 81540-470 Curitiba, PR, Brazil
E-mail: apspina2001@yahoo.com.br
*Author for correspondence

**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 semi-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 disc (Endress & Bruyn 2000, Woodson 1937), and can be distinguished from each other by the characteristics cited by Woodson (1937, 1939, 1948), Plummel (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* (Benthan 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), hypocrateriform 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. Lancellatae* 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; Rodríguez 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
cymose or thyrsiform, multiflorous; veins joined by a series of marginal loops. congested at branch tips, blades chartaceous, subcoriaceous to thickly coriaceous, margins often revolute; secondary to 30 m tall, with white latex.

Shrubs or trees ex Roemer & Schultes (1819: 221).

Calyx

Himatanthus in Peru. HIMATANTHUS

Taxonomic treatment

We present the following treatment in an attempt to clarify previous taxonomic confusion of the genus Himatanthus occurring in Peru: 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: Himatanthus articulatus, Himatanthus revolutus (Huber 1915: 200) Spina & Kinoshita (in Spina et al. 2013: 1307), and Himatanthus 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 Himatanthus tarapotensis and Himatanthus phagedaenicus exhibit a simple brochidodromous venation. The angle of the secondary veins with respect to the midrib is useful in distinguishing Himatanthus revolutus, with secondary veins nearly or exactly perpendicular to the midrib (80–90°), while they are at 70–80° in Himatanthus phagedaenicus and 50–70° in Himatanthus 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 Himatanthus phagedaenicus and Himatanthus revolutus versus 35–45 mm long in Himatanthus 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 Himatanthus tarapotensis and Himatanthus revolutus. Finally, the follicles are 27–29 cm long in Himatanthus tarapotensis, 16–26 cm long in Himatanthus phagedaenicus, and 12.5–25.5 cm long in Himatanthus 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, 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


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 thyrsiform, multiflorous; bracts large, showy, caducous, with numerous glands at base. Flowers 5-merous. Calyx small, persistent, lobes small, unequal, imbricate. Corolla hypocrateriform, 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 subsessile, 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, dehiscing 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-eucamptodromus*; 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 round, sometimes short-acuminate, margin revolute; venation smooth in young stems, striate in older stems. .......................... 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*


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, oblancoelate 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, Rio 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).

**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).


**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 oblong-elliptic, 10.5–18.5(–20) x 3–5 cm, base cuneate, apex acute to acuminate, 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* 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, Sº de Paranáquara, Brésil, Néo-RB, Syn-U.” Plumel’s (1991: 79) citation of *Ducke 11399* at RB was not a valid neotypification because he had already neotyped 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: Dto. San Juan, Localidad de Quistococha, km 4.5 en la carretera Iquitos–Nauta, 23 September 2015 (II), N. Mitidieri & U. Mozombite 16 (USM).


**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.


**Acknowledgments**

This study is part of a doctoral dissertation of the first author, developed at the Escuela Doctoral Franco Peruana en Ciencias de la Vida, Universidad Peruana Cayetano Heredia and École Doctorale GAIA Biodiversité, Agriculture, Alimentation, Environnement, Terre, Eau, Université de Montpellier, France. We thank the directors and curators of the herbaria listed in the Material & Methods for loan of material, providing digital images, and for providing working space during our visits. This project was supported by a Franco-Peruvian doctoral fellowship from the National Council for Science, Technology and Technological Innovation (Consejo Nacional de Ciencia, Tecnología e Innovación Tecnológica, CONCYTEC) of the Peruvian Government, and the French Embassy in Peru. The Institut de Recherche pour le Développement (IRD) also supported this project by sponsoring field work in Peru through the Laboratorio Mixto Internacional Andino Amazónico en Química de la Vida led by Michel Sauvain, travel expenses to the Herbier de Guyane (CAY), Cayenne and field work in French Guiana by the first author. The Research Institute of the Peruvian Amazon (Instituto de Investigaciones de la Amazonía Peruana, IIAP) allowed us to carry out part of the fieldwork at its biological station within the Allpahuayo Mishana National Reserve. Permission to study and collect in the Peruvian Amazon were granted by the Servicio Nacional Forestal y de Fauna Silvestre (SERFOR) and the Servicio Nacional de Areas Naturales Protegidas (SERNANP) of Peru. Nicole Mitidieri, Ricardo Zárate and Tony Mori collected and donated part of the specimens included in this study. Marcos Ríos also contributed fertile specimens as part of Project IRB 27 (Inventario Rápido Biológico) Tapiche-Blanco of the Rio Tapiche, a remote area of the Peruvian Amazon. We would like to thank Joseph Kirkbride (Smithsonian Institution, Washington, USA), John Wiersema (U.S. National Arboretum, USDA-ARS, Beltsville, USA), Mary Endress (Zurich University, Switzerland), Michael Nee (Missouri Botanical Garden, St. Louis, USA), and the anonymous reviewers for valuable comments and corrections to the manuscript.

**References**


http://dx.doi.org/10.1590/S0101-3122200600100009


http://dx.doi.org/10.1016/S0378-8741(99)00158-0


http://dx.doi.org/10.1007/BF02857781


http://dx.doi.org/10.1007/BF02857781


http://dx.doi.org/10.1248/cpb.42.1198


http://dx.doi.org/10.1590/S0101-3122200600100009


