

ARISTOLOCHIA PENTANDRA (ARISTOLOCHIACEAE) IN COLOMBIA: BIOGEOGRAPHIC IMPLICATIONS AND PROPOSED SYNAPOMORPHIES BETWEEN THE PENTANDROUS SPECIES OF *ARISTOLOCHIA* AND ITS SOUTH AMERICAN SISTER GROUP

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Abstract

González F., H. E. Esquivel., G. A. Murcia, N. Pabón-Mora: *Aristolochia pentandra* (Aristolochiaceae) in Colombia: biogeographic implications and proposed synapomorphies between the pentandrous species of *Aristolochia* and its South American sister group. *Rev. Acad. Colomb. Cienc.* **34** (133): 467-478, 2010. ISSN 0370-3908.

Flowers of most *Aristolochia* species possess six stamens and six carpels; however, the c 40 species of subsection *Pentandrae*, which grow in S United States, Mexico, N Central America, Cuba, and Jamaica, have flowers with five stamens and five carpels. The sister group of this subsection consists of five hexandrous species from subtropical and temperate areas of South America, thus matching the puzzling temperate South America-Temperate North America disjunction. The synapomorphies that support such sister-group relationship and the monophyly of subsection *Pentandrae* are described. An important range extension of *A. pentandra* Jacq., which was recently found in the Island of San Andrés (Colombia), is reported, and an update of the description and typification of this species is provided.

Key words: Aristolochiaceae, Caribbean Flora, Flora of Colombia, Flora of San Andrés Island, phytogeographic disjunctions, Piperales.

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Resumen

Las flores de muchas especies de *Aristolochia* poseen seis estambres y seis carpelos; no obstante, las cerca de 40 especies que conforman la subsección *Pentandrae* y que prosperan en el sur de los Estados Unidos, México, norte de Centro América, Cuba y Jamaica, poseen cinco estambres y cinco carpelos. El grupo hermano de esta subsección es un conjunto de cinco especies hexandras de Sur América subtropical y templada, lo cual constituye un caso más de la enigmática disyunción biogeográfica entre el centro y sur de América del Sur y la zona templada y subtropical de América del Norte. Se describen las sinapomorfías que evidencian dicha relación de grupo hermano y que sustentan la monofilia de la subsección *Pentandrae*; a la vez, se reporta una extensión en el areal de *A. pentandra*, la cual fue recientemente detectada en la isla de San Andrés (Colombia) y se actualiza la descripción y la tipificación de la especie.

Palabras clave: Aristolochiaceae, flora del Caribe, flora de Colombia, flora de la isla de San Andrés, disyunciones fitogeográficas, Piperales.

Introduction

With about 500 species, the genus *Aristolochia* is the largest and the most widely distributed of the family Aristolochiaceae. Two of the plesiomorphic characters of *Aristolochia* are the presence of a completely inferior ovary formed by the congenital fusion of six carpels, and the congenital fusion of the six stamens with the stylar portion of the carpels, forming the typical gynostemium in the genus (González, 1999b; González & Stevenson, 2000, 2002; Kelly & González, 2003). However, the number of stamens and carpels varies from 5 to 24 and 5 to 6, respectively. Interestingly, flowers with more than six stamens are found only in some African and Malesian species of subgenus *Pararistolochia*, and can occur without affecting the 6-merous gynoecium, whereas the pentandrous condition is always associated to the presence of five carpels (González & Stevenson, 2000, 2002) and is characteristic of a group of species, most of which are found in S United States and N Mexico. Traditionally, these species constitute the subsection *Pentandrae*, one of the two subsections of *Aristolochia* subgenus *Aristolochia* section *Gymnolobus* proposed by Duchartre (1854, 1864). Pfeifer (1970) recognized thirty five species; since then, at least ten additional species from Mexico have been described by Calzada *et al.* (1997), Ortega & Ortega (1995), Santana-Michel (1995, 2002, 2007), Santana-Michel & Lemus-Juárez (1996), and Santana-Michel & Solís-Magallanes (2007).

Alternatively, the pentandrous species of *Aristolochia* have been segregated into a separate genus, *Einomeia*, by Rafinesque (1828), which was later emmended by Klotzsch (1859), and later accepted as a distinct genus by Huber (1985, 1993), and Mabberley (2008). However, recent

phylogenetic analyses (González, 1997, 1999b; González & Stevenson, 2002; Wanke *et al.*, 2006, and Wagner, 2010) have shown that the pentandrous species of *Aristolochia* are nested inside subgenus *Aristolochia* (Fig. 1), which discourages the recognition of the pentandrous lineage as a distinct genus. Molecular and morphological evidence supports the monophyly of *Aristolochia* subsection *Pentandrae* (González, 1997, 1999 b; González & Stevenson, 2002; Neinhuis *et al.*, 2005; Ohi *et al.*, 2006; Wanke *et al.*, 2006; Wagner, 2010). These analyses also suggest that the subsection is sister to an informal group herein called the ‘*A. lindneri* group’, and formed by five species from central and southern South America (Bolivia to Uruguay) including *A. burelae* Herzog, *A. lindneri* A. Berger, *A. lozani* F, González, *A. stuckerti* Speg. and *A. urbaniana* Taub. (cf. González, 1999 a, 1999 b, 2001; Murata *et al.*, 2001; Sugawara *et al.*, 2001; González & Stevenson, 2002; Ohi *et al.*, 2006; Wanke *et al.*, 2006; Wagner, 2010; Figs. 1, 2 D-G). Here we describe the morphological synapomorphies that support such relationship, and the monophyly of the pentandrous species of *Aristolochia*. Furthermore, we present an updated description and report a range extension for the type species of *Aristolochia* subsect. *Pentandrae* (*A. pentandra* Jacq.), based on new stations in Guatemala and Belize and on recent collections in the Caribbean island of San Andrés (Colombia); finally, lectotypes are here designated for *A. pentandra* and one of its synonyms, *A. hastata* Kunth.

Methods

The study is based on field observations and collections made in S United States, Mexico, Guatemala, and the

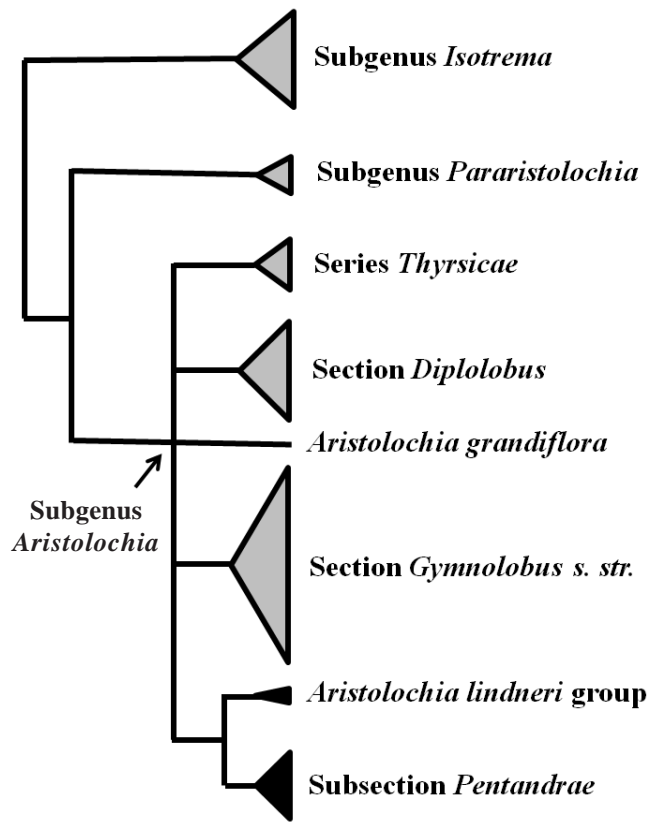


Figure 1. Summary cladogram of *Aristolochia* based on the phylogenetic analyses by González (1997, 1999 b), Murata *et al.* (2001), Sugawara *et al.* (2001), González & Stevenson (2002), Neinhuis *et al.* (2005), Ohi *et al.* (2006), Wanke *et al.* (2006), and Wagner (2010). The size of each clade indicates the relative number of species. The clades treated in this paper are shown in black.

Caribbean island of San Andrés (Colombia), and the study of numerous herbarium specimens (mainly B, BM, COL, CORD, CTES, F, FLAS, G, GH, HBG, K, L, LE, LP, LPB, LIL, LPB, MEXU, MO, NY, P, S, SI, TEX-LL, U, UC, US, and W). The detailed list of specimens examined for the present study will be included in the monograph of Aristolochiaceae for Flora Neotropica, which is underway; however, it is available upon request to FG. For scanning electron microscopy studies, floral buds and floral organs were fixed in 70% ethanol, and dissected in 95% ethanol under a Leica 7.5 stereomicroscope. All the material was dehydrated through an ethanol series and critical point dried using a Samdri 790 CPD (Rockville, MD). Material was mounted on aluminum stubs with adhesive tabs (Electron Microscopy Sciences), sputter coated with gold palladium in a Hummer 6.2 sputter coater (Anatech, Springfield, VA), and examined and photographed in a Jeol JSM-5410 LV Scanning Electron Microscope operated at 10 kV.

Results and discussion

Morphological synapomorphies. - All the phylogenetic analyses based on molecular and morphological data (González, 1999 a, 1999 b, 2001; Murata *et al.*, 2001; Sugawara *et al.*, 2001; González & Stevenson, 2002; Ohi *et al.*, 2006; Wanke *et al.*, 2006; Wagner, 2010) that have included pentandrous species of *Aristolochia* strongly suggest that the sister group of this clade is the *A. lindneri* group, an informal assemblage of five species from subtropical and temperate areas of South America, including S and SE Brazil (*A. urbaniana*), the Chaco of Bolivia, Paraguay, and Argentina (*A. burelae*; Fig. 2G), mid-elevation (<1000 m) dry interandean valleys of Bolivia and Paraguay (*A. lindneri*; Fig. 2D-E), high-elevation (c 2000 m) dry interandean valleys of Bolivia (*A. lozaniana*; Fig. 2F), and areas between Argentina and Uruguay (*A. stuckertii*). Although these species result as sister taxa of subseries *Pentandrae*, they have flowers with six stamens and six carpels, as in most of the remaining species of *Aristolochia*. Thus, the presence of five stamens and five carpels is apomorphic for subseries *Pentandrae*.

The morphological characters that support the sister-group relationship between *Aristolochia* subsection *Pentandrae* and the *Aristolochia lindneri* group are the strong tendency to become herbaceous (Figs. 2, 4), the presence of one adaxial bract per flower (Figs. 2 A-C, F, G, 3 A, B, 4 A, D, E, G), the basipetal dehiscence of the capsule (Figs. 2E, 4G), and the triangular, flattened and smooth seeds, which are black or dark brown, have a prominulous raphe, and lack wings (Figs. 2E, 3G-I, 4G). The significance of the habit, the inflorescence and floral morphology, and the seed structure has been carefully examined by authors such as Huber (1985, 1993), González (1997, 1999a, b), González & Stevenson (2000, 2002), González & Rudall (2003), Wanke *et al.* (2006), and Wagner (2010), among others, who have recognized these characters as phylogenetically informative throughout *Aristolochia*. In turn, the monophyly of *Aristolochia* subsect. *Pentandrae* is supported by the consistent presence of two synapomorphies, the five stamens and the five carpels (Figs. 3 C-F, 4G).

Interestingly, all of the characters shared between the pentandrous species of *Aristolochia* and the *A. lindneri* group (included in the analyses by González, 1999 b, González & Stevenson, 2002, and Wanke *et al.* 2006) are also present in *A. grandiflora* Sw. (González, 1999 a, b, González & Stevenson, 2002), a species that ranges from Jamaica, Mexico and Central America to Colombia and Ecuador. Although the morphological characters support a close relationship of *A. grandiflora* with the pentandrous species

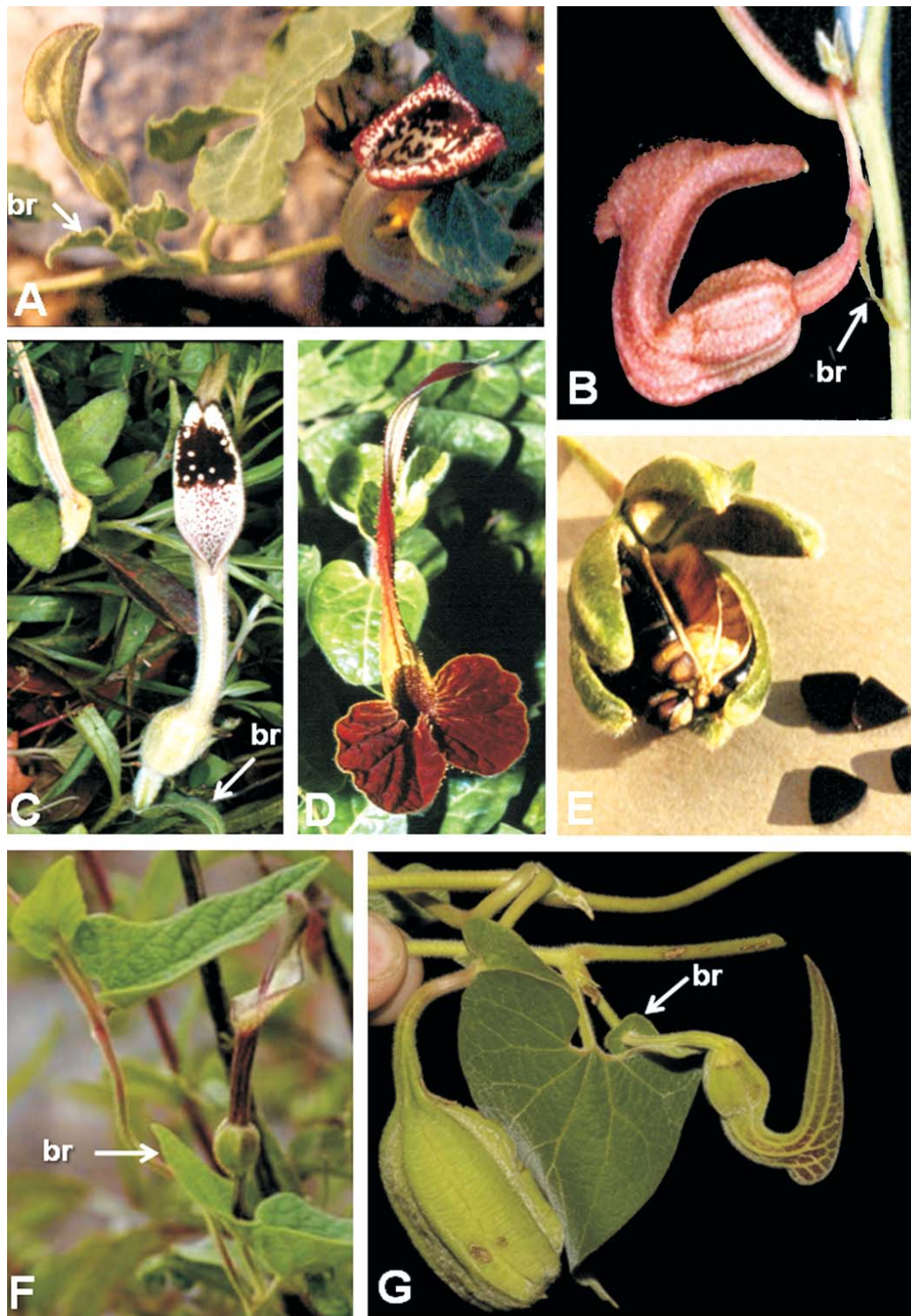


Figure 2. Representative species of the pentandrous Aristolochias (A-C) and the *Aristolochia lindneri* (D-G) clades. **A.** *Aristolochia coryi*, from Texas, USA (González 3612). **B.** *A. micrantha*, from N Mexico (González 3605). **C.** *A. erecta*, from Texas (González 3593). **D, E.** *A. lindneri*, from Bolivia (cultivated at BONN Botanical Garden). **F.** *A. lozaniata*, from Bolivia (Wanke s.n.). **G.** *A. burelae*, from Bolivia (Nee s.n.). **br**, bract. Photo credits: A-D, F. González; F: S. Wanke; G. M. Nee.

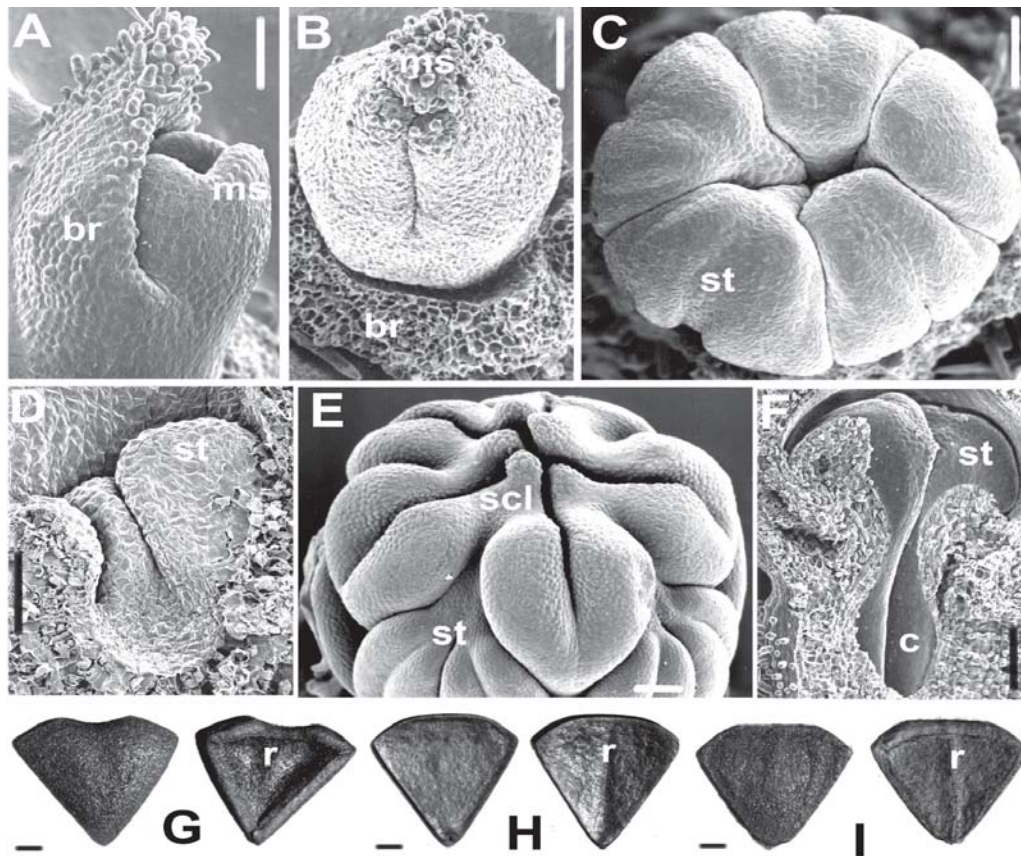


Figure 3. A-F. SEM images of floral morphology in *Aristolochia* subsection *Pentandrae* and *Aristolochia lindneri* group. **A.** Floral bud and bract of *A. pentandra* (González 3603, COL). **B.** Floral bud and bract of *A. lindneri* (González 3623, COL). **C-D.** Top view (**C**) and longitudinal section (**D**) of a young gynostemium of *A. erecta* (González 3593, COL). **E-F.** Top view (**E**) and longitudinal section (**F**) of an almost mature gynostemium of *A. pentandra* (González 3603, COL). **G-I.** Adaxial (right) and abaxial (left) views of seeds in *Aristolochia* subsection *Pentandrae* and *Aristolochia lindneri* group, under light stereomicroscopy. **G.** *A.* (subsect. *Pentandrae*) *watsoni* Wooton & Standley (Morris *et al.* 4663, NY); **H.** *A. lindneri* (Wood 17332, NY); **I.** *A. stuckerti* (Ibarrola 2503, NY). **br**, bract; **c**, carpel; **ms**, medial sepal; **r**, raphe; **scl**, stigmatic commissural lobe; **st**, stamen. Scale bars: 100 μ m in A-C, E, F; 50 μ m in D; 1 mm in G-I.

plus the *A. lindneri* group (González, 1999 b, González & Stevenson, 2002), DNA sequence-based analyses do not support such relationship (Fig. 1).

Most of the species of *Aristolochia* subsect. *Pentandrae* grow in the Sonoran province, which comprises mainly dry areas of the S United States and adjacent N Mexico (Fig. 5A). Only two species of this taxon have been reported in islands of the Pacific Ocean, both off Mexico: *A. tresmariae* Ferris, restricted to Maria Madre Island (Nayarit); and *A. islandica* Pfeifer, from the Revilla Gigedo Archipelago, at about 300 miles from Baja California. Only *Aristolochia pentandra* (out of c 40 pentandrous species) is found in the Bahamas, the West Indies, and now in the Caribbean island of San Andrés (Fig. 5B).

Despite the high diversification of the pentandrous species of *Aristolochia* in the continental Sonoran province (sensu Bray, 1898), the first pentandrous *Aristolochia*, *A. pentandra*, was described by Jacquin (1760, 1763; Fig. 4A), from “sylvis circa Havanam”, Cuba (Jacquin 1763: 234). *A. pentandra* is the type species of *Aristolochia* subsect. *Pentandrae*. This species is also the most widely distributed species of this subsection, as it reaches the Bahamas, the West Indies, and two small islands off the Caribbean coasts of Central America (Swan Island and the first records from San Andrés Island reported here; see below; Fig. 5B). A second Cuban species of *Aristolochia* with five stamens, *A. clementis*, has been described (Alain, 1948). However, flowers of this Cuban endemic can have five to six stamens and five to six carpels (Rankin

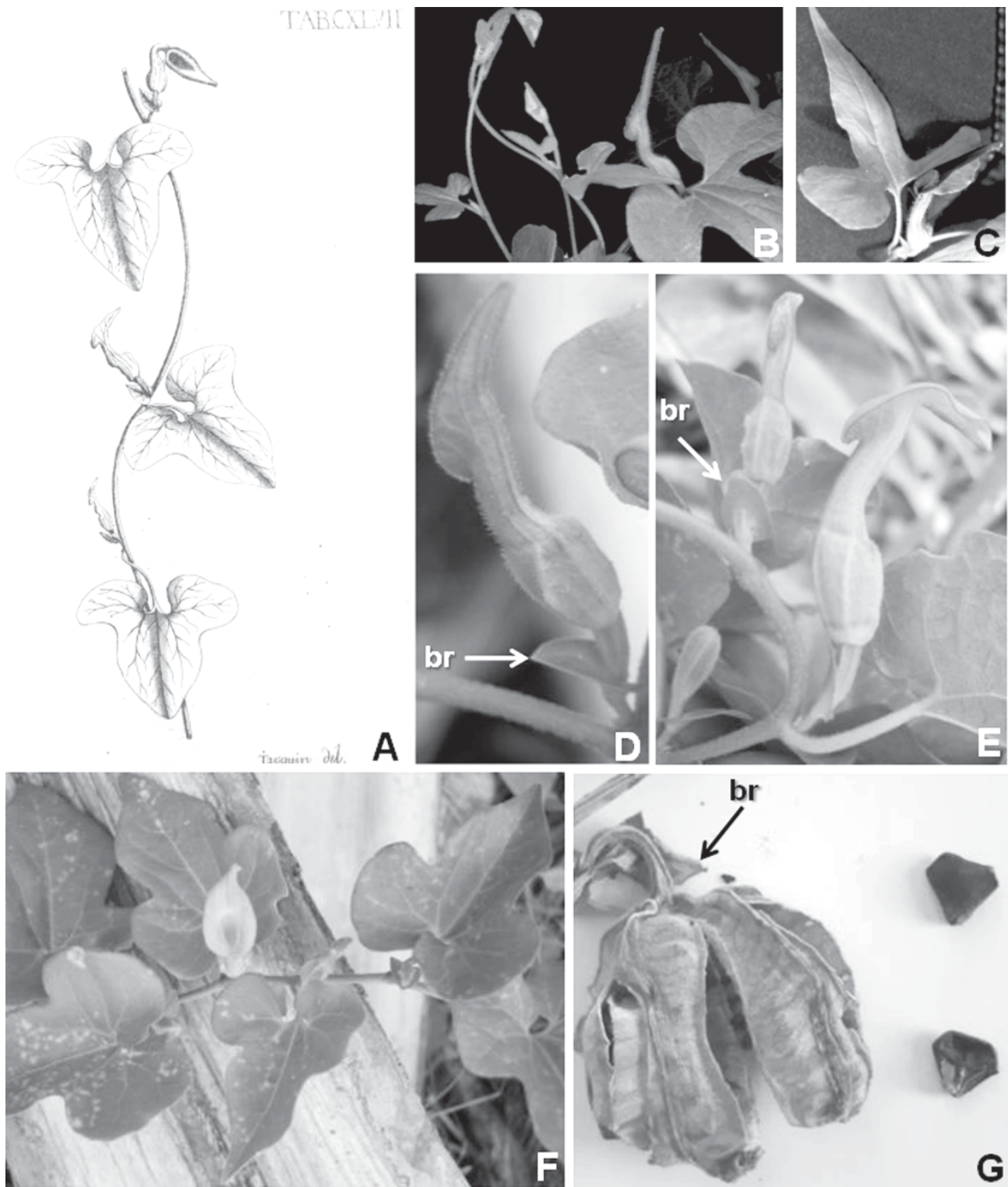


Figure 4. A. *Aristolochia pentandra*, lectotype (Jacquin, 1763, Table 147). B, C. Floral buds and flowers in anthesis of *A. pentandra* cultivated in Texas (González 3603, COL), seeds from Mexico. D-G. *A. pentandra* from San Andrés Island, Colombia. D-F. Floral buds and flowers in anthesis (Pabón-Mora & al. 232, NY). G. Capsule and seeds (Murcia 100, TOL1). br, bract. Photo credits: B-C, G: F. González; D-F: N. Pabón-Mora.

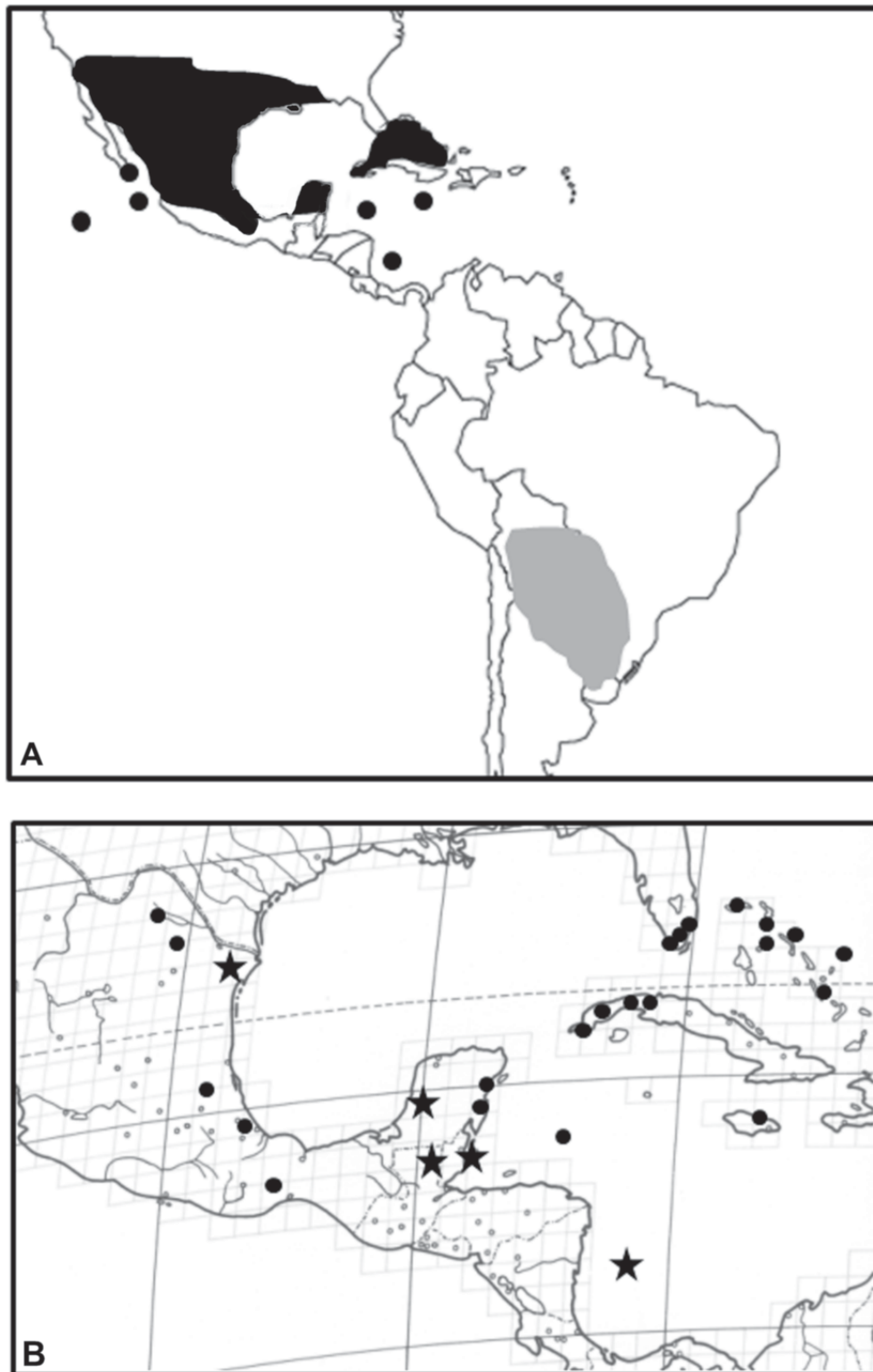


Figure 5. A. Disjunct distribution of the pentandrous species of *Aristolochia* (black area and black dots) and its sister group in South America (grey area). B. Map of distribution of *Aristolochia pentandra*. Locations newly reported here are labeled with a star.

Rodríguez, 1998); such intraspecific variation, along with the absence of the typical adaxial bract characteristic of all the species of *Aristolochia* subsect. *Pentandrae*, strongly suggests that this species does not belong to this subsection.

The distribution of the pentandrous species of *Aristolochia* and the five species of the *A. lindneri* group (Fig. 5 A) constitutes an additional example of the so-called (Johnston, 1940; Solbrig, 1972) the temperate South America-Temperate North America disjunction. This disjunction, often found in plants from semi-desertic or dry habitats, has been a matter of interest since Gray and Hooker's times (Bray, 1898; Campbell, 1944), and was considered by Solbrig (1972) to be the most puzzling intercontinental disjunction. Similar biogeographic disjunctions have been reported in members of the Hydrophyllaceae (Heckard, 1963), the two species of the family Koeberliniaceae (Takhtajan, 1997; Heywood *et al.*, 2007; Holmes *et al.*, 2008), and even at the population level in species of Apiaceae (Constance, 1963). A more detailed list of taxa showing such disjunction was given by Johnston (1940) and Solbrig (1972).

At least two competing scenarios have been proposed to explain such disjunct distributions. First, Johnston (1940) postulated the presence of an ancient distribution of desert/dry flora in the New World, and the connections between the deserts/dry floras of North- and Central America and those of South America. The second scenario is based on the long-distance dispersal and further *in situ* diversification of such taxa (Raven, 1963). However, more data are needed in order to explore which is the more acceptable explanation.

Range extension of *Aristolochia pentandra* (Fig. 4). According to Pfeifer (1970), this species grows in Florida and Texas (United States), Bahama Islands, western Cuba, Jamaica, Swan Islands (Honduras) and Mexico. While working on the monograph of Aristolochiaceae for Flora Neotropica, one of the authors (FG) found specimens of *A. pentandra* from Guatemala and Belize (Fig. 5 B). The specimens from the latter two countries, along with the specimens previously found in the Swan Islands (Honduras) remained as the southernmost stations for the species until recently, when two of us (GAM and NPM, Fig. 4 D-G) independently found it in the Caribbean island of San Andrés (Colombia), at approximately 12°35'16" N latitude. These findings now become the southernmost station of *A. pentandra*, and by extension, of the whole subsection *Pentandrae*. The station reported here is located about 5°S and 3°E of the closest locality in the Swan Islands (Honduras; Fig. 5 B).

Aristolochia pentandra Jacq., Enum. Syst. Pl. 30. 1760; Select. Stirp. Amer. Hist. 233-234, t. 147. 1763. **Lectotype, here designated:** Jacquin, Select. Stirp. Amer. Hist., 233-234, t. 147. 1763. *Einomeia pentandra* (Jacq.) Raf., Med. Fl. 1:62. 1828; Klotzsch in Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859:605. 1859.

A. conferta Miller, Gard. Dict. Ed. 8.n.11. 1768. (*ex char.*).

A. hastata Kunth, Nov. Gen. Sp. Pl. 2: 148, t. 116. 1817, *non* Nutt. (1818), *nec* Jack (1822), *nec* Jacq. (*sphalm.* = Jack.) *ex* Klotzsch (1859). *Einomeia hastata* (Kunth) Klotzsch, Monatsb. Acad. Berlin 1859: 625, t. 2. 1859. *Aristolochia pentandra* Jacq. var. *hastata* (Kunth) Duchartre in DC. Prodr. 15(1): 440. 1864. **Lectotype, here designated:** Cuba: "Havana", s.f. (fl), *A. Bonpland 1342* (P).

Einomeia bracteata Raf., Fl. Tellur. 4: 98. 1836. (*ex char.*).

A. racemosa Brandg., Univ. Calif. Publ. Bot. 6: 363. 1917. Type: Mexico: Veracruz, Zacuapan, Feb 1911 (fl fr), C. A. Purpus 5333 (Holotype UC; isotypes BM, F, GH, MO, NY, US).

A. marshii Standl., Publ. Field Mus. Nat. Hist. Chicago. Bot. Ser. 17: 238. 1937. Type: Mexico: Coahuila, Muzquiz, E. G. Marsh 10 (Holotype F).

Procumbent to twining, scarcely puberulous perennial herbs (Fig. 4 A, B, F). Rhizome cylindrical, to 8 x 1.5 cm. Petiole (1-)2-4.3 cm long, glabrescent; blade shape variable, usually ovate, sagittate, subhastate or slightly to deeply trilobed, lobes ascending to descending, (2.5-)5-9(-13.2) x (0.8-)1.4-7.5(13) cm, membranous, base cordate-lobed (cuneate), sinus 6-20(-25) mm in depth, glabrescent to scarcely puberulous above especially along the veins, glabrescent to minutely puberulous below, apex of the central and the lateral lobes usually acute. Bracts at about 1/10-1/2 from the length of the peduncle, sessile, ovate, 4-10(-20) x 2-6(-10) mm. Peduncle plus ovary c 1-2 cm long. Perianth puberulous on the outside, rectilinear to slightly bent; utricle obovoid, 7-10 x 4-5 mm, syrinx eccentric, c 1.5 mm long; tube slightly bent, 7-12 mm long, forming an angle of about 140-180° with the utricle; limb ovate and bright yellow in the West Indian and the San Andrés collections (Fig. 4 A, D-F), narrowly-ovate and reddish or pink except for the whitish fauces in the continental collections (Fig. 4 B, C), 17-26 x 7-11 mm, forming an angle of about 140-180° with the tube, acute at the apex; gynostemium about 3.5 x 1.5 mm. Capsule subglobose, 1-2.3 x 1-2 cm, glabrescent, dehiscent from the top to the bottom; seeds triangular, black to dark brown, 4-6 x 4-6 mm, about 1 mm thick, flattened, wingless, raphe prominent and with membranose extensions as large as the seed itself (Fig. 4 G).

Distribution (Fig. 5B). - South Florida (United States), Bahama Islands, Mexico, Cuba, Jamaica, Swan Islands (Honduras), Guatemala, Belize, and San Andrés Island (Colombia). It grows in a variety of habitats, such as dry thickets or deciduous forests, or in beach communities in rocky, limestone or sandy shores; occasionally, it also grows in “milpas” (Mexico). In the island of San Andrés only one small population has been detected, near disturbed sandy shores, along with *Ipomoea pes-caprae* (Convolvulaceae), *Morinda roioc* (Rubiaceae), *Sphagneticola trilobata* (Asteraceae), and *Stachytarpheta jamaicensis* (Verbenaceae).

The island of San Andrés is an oceanic island formed by coral reef deposits during the Pliocene, which are on top of the Nicaragua/Hondura volcanic basement plate formed during the Miocene; however, there is no evidence of land connection between the island deposits and Central American mainland (**Barriga et al.**, 1969). The flora of the Archipelago of San Andrés and Providencia has been relatively well studied, and at least two major expeditions have included these islands, the “Fifth George Vanderbilt Expedition” in 1941, and the “Catherwood Chaplin West Indies Expedition” from the Academy of Sciences of Philadelphia in 1948, of which only the Pteridophytes were published (**Proctor**, 1950). Although extensive floristic and ethnobotanic work in the Archipelago has been published by **Toro** (1929), **Barriga et al.** (1969), **González et al.** (1995) and **Cabrera** (2005), *Aristolochia* was not recorded in any of these studies. Thus, this new record, along with the site in which *A. pentandra* grows in this island (extremely disturbed areas close to the beach, and near the local airport and some major harbours along the N end of the island) could well be a recent introduction from Jamaica, Swan Islands or Central America.

Additional specimens seen (new records are indicated by an asterisk*). - **UNITED STATES. FLORIDA**: Dade Co., 19-57-42, Biscayne National Monument, Elliott Key, 16 Feb 1978 (fl), *Avery 1823* (FLAS); Soldiers Key, 30 Nov 1904 (fl fr), *Britton 335* (F); south Florida, 1936 (fl), *Chapman 33* (US); south Florida, s.f. (fl), *Herb. Chapman 146* (F, FLAS); Dade Co., Elliott Key, 19 Jan 1966 (fr), *Craighead s.n.* (FLAS); Elliotts Key, 3 Oct 1939 (fl), *Fennell 1046* (UC); Miami, Mar-May 1877 (fl), *Garber s.n.* (F, FLAS, US); Hammocks, Soldier Key, 6 Jan 1909 (fl, fr), *Small & Carter s.n.* (FLAS, US); Hammocks, Pumpkin Key, Monroe Co., 9 Mar 1915 (fl fr), *Small & Carter 5674* (MO).

BAHAMA ISLANDS: Abaco, Old Kerris Point, 2 Jan 1905 (fl), *Brace 2000* (F, NY); Great Bahama, West End, 16 Apr-8 May 1905 (fl fr), *Brace 3534* (F, NY, US); Andros, road to Morgan’s Bluff, 4 Mar 1907 (fl), *Brace 6697* (F,

NY); Andros, Nicholl’s town and vic., road to Morgan’s Bluff, 5-6 Mar 1907 (fl fr), *Brace 6740* (F, NY); Great Bahama, Luland, Pinder’s Point, 5-13 Feb 1905 (fl fr), *Britton & Millspaugh 2500* (F, NY, US); Watlings Island, 15 Mar 1907 (fl fr), *Britton & Millspaugh 6214* (F, NY, US); Long Island, Clarence Town and vicinity, 16-19 Mar 1907 (fl fr), *Britton & Millspaugh 6257* (F, NY, US); Eleuthera, Harbour Island, 18 Feb-4 Mar 1907 (fl fr), *Britton 6391* (F, GH, NY, US); North Eleuthera, Ca. Ridley Head, 8 Jan 1874 (fl fr), *Correll 41020* (FTG, NY); Ridley Head Beach area, (fl fr), *Correll 41198* (FTG); Great Exuma, SE end of Orion Road, 9 Jan 1975 (fr), *Correll 44072* (FTG, NY); Little Abaco, W of Cedar Harbour, 17 Mar 1975 (fl fr), *Correll & Meyer 44731* (F, FTG, NY); Grand Bahama, Pinder’s Point, 25 Jan 1976 (fl fr), *Correll & Popenoe 46685* (F, FTG, GH, NY); Great Abaco, Green Turtle Cay, in vacant lot in New Plymouth, 27 Nov 1976 (fl fr), *Correll & Correll 47689* (F, FTG, NY); Long Island, ca. Clarence Town, 14 Mar 1977 (fl fr), *Correll 48149* (FTG, NY); Little Exuma, high coastal ridge NW of Williams Town, 4 Mar 1980 (fl fr), *Correll & Wasshausen 51204* (FTG, NY, US); Mayaguana, beach E of Abrahams Bay, 10 Feb 1973 (fl fr), *Gillis & Proctor 11634* (A, B); between Harbor Store and Post Office, Clarence Town, Long Island, 15 Jun 1974 (fl), *Hill 2155* (FTG, NY); North Bimini Island, May 1948 (fl fr), *Howard & Howard 10034* (A, FTG, GH, NY, S, UC, US); Nicols Town, Andros, 26 Mar 1890 (fl fr), *Nortrop & Nortrop 385* (F, GH, K, NY); San Salvador, near Graham’s Harbor, 13 Dec 1976 (fl), *Smith & Bacharach 216* (FTG); New Providence, along road near Sea House, 8 Jun 1909 (fl fr), *Wilson 8434* (F, K, NY).

CUBA. LA HABANA: Estación Central Agronómica, La Habana, 20 Sep 1904 (fl), *Baker 1815* (NY); prope Morro ad terram, 27 May 1914 (fl), *Ekman 1161* (G, NY, S); playa de Cajimar, 15-20 Mar 1906 (fl fr), *Hitchcock s.n.* (F); playa de Marianao, 24 Feb 1914 (fl), *Bro. León 4210* (NY); playa de Santafé, near sea shore, 7 Oct 1915 (fl fr), *Bro. León 5660* (NY); ca. Habana, 6 Sep 1923 (fl), *Bro. León 11518* (NY); Habana del Este, Cojimar, frente al paradero del ómnibus, 4 Ene 1992 (fr), *Rankin Rodríguez & Silva 69992* (K); Habana, 1864 (fl fr), *Schott 127* (BM). **PINAR DEL RÍO**: 10-12 Mar 1911 (fr), *Britton & Cowell 9908* (NY, US). **WITHOUT FURTHER DATA**: “Guio iter Cubense? *Malaspina? Nee?*, s.f. (fl), *Boldo s.n.* (MA)”; “in rupibus maritimis Cubae ad Matanzas” (fl), *Poeppig s.n.* (BR, LE); s.f. (fr), *de la Sagra 178* (G); (fl), *de la Sagra s.n.* (P); Nov 1822 (fl), *Herb. Shuttleworth s.n.* (BM); 1 May 1860-1864 (fl fr), *Wright 2610* (BM, G, GH, K, MA, NY, P).

MEXICO. CAMPECHE: Escarcega, margen oriental de la laguna de Silvituk, Silvituk, 1-2 km S de la carretera Escarcega-Xpujil, 18°37’50” N, 90°16’20” W, 21 Sep 1999

(fl fr), *Carnevali et al.* 5745 (F, MO)*. COAHUILA: Muzquiz, Apr 1938 (fl), *Marsh 1143* (F, TEX). NUEVO LEÓN: SE Monterrey on MEX 85, ½ m W on road to El Barreal, Jul-Aug 1971 (fl), 12 m, *Parker 473* (TEX); near Monterrey, 7 Sep 1902 (fl fr), *Pringle s.n.* (US); valley near Monterrey, 1600 ft, 22 Jul 1906 (fl fr), *Pringle 13804* (GH, L, S); valley near Monterrey, 1600 ft, 22 Jul 1906 (fl fr), *Pringle 13805* (GH, US); Sabinas Hidalgo, along the main highway in to Monterrey, 0.7 mi N of the bridge over the rio Sabinas, 300 m, 26°30' N, 100°12' W, 18 May 1995 (fl), *Westlund 5-18-88.1* (TEX). OAXACA: Tehuantepec, Jul 1936 (fl), *Matuda 585* (US). QUINTANA ROO: Coba, Jun-Jul 1938 (fl), *Lundell & Lundell 7753* (US). TAMAULIPAS: Cd. Victoria, hotel San Antonio, Av. Tijerino, Blvd. Tamaulipas, 18 Mar 1991 (fl), *Vincent & Lammers 4523* (UC)*. VERACRUZ: Pr. Mirador, 3000-3800', s.f. (fl), "*Sartorius Pl. Mexicanae, Ed. Hohenacker*" (G); Tomata, Atzalan, 550 m, 25 Feb 1970 (fl fr), *Ventura 592* (CONN, NY, US). YUCATÁN: Opichen, alrededores de las grutas de Calcehtok, 20°33'00" N, 89°54'27" W, 20 Nov 1997 (fl), *Carnevali et al.* 4716 (FLAS, MO, NY, TEX)*; entrance to grotto above Calcehtok near Opichen, 5 Jan 1982 (fl), *Darwin et al.* 2142 (S); above Calcehtok near Opichen, 5 Jan 1982 (fr), *Darwin et al.* 2146 (S); 1895 (fl fr), *Gaumer 441* (BM, K, NY, P, S); Opichen, 1-2 km S del pueblo de Calcehtok, aprox. 20°33'00" N, 89°54'27" W, 30-100 m, 24 Feb 1999 (fl fr), *May & Chi 1416* (MO)*; "Yucatán", 31 Mar 1866 (fl), *Schott 839* (BM). WITHOUT FURTHER DATA: Apr-May 1921 (fl fr), *Rutten & Rutten-Pekelharig 684* (U).

JAMAICA: Sandiger Küstenstreifen bei Silver Sands/Trelawny, ca. 1 m ub. NN, 17 Sep 1985 (fl), *Heckel 2248* (B); parish St. Ann, Dunns river beach, 16 Jan 1958 (fl), *Howard & Proctor 15058* (A); parish St. Ann, Casa Nina, 1 mi ENE of Ocho Ríos, 210 ft, Dec 1954 (fl), *Proctor 9561* (A, U).

BELIZE: Half Moon Caye, Lighthouse Reef, 17°12'16" N, 87°32'13" W, 21 Oct 1995 (fl), *Meerman s.n.* (NY)*.

GUATEMALA: PETÉN: Westufer des Lago Petén Itzá: im Anwesen von Don Gabriel Uliva-Estrada (SW an den Chakmamantok-Felsen angrenzend), das ist 0.5 km NE Zentrum von San José, 115 msm, 16°59'8" N, 89°53'54" W, 29 Ago 1993 (fl fr), *Wallnöfer 6086* (MO, NY)*.

HONDURAS. SWAN ISLANDS: Larger Island, 9 Apr 1913 (fl fr), *Nelson 18* (GH); ibid, 7 Apr 1913 (fl), *Nelson 39* (GH, US); Great Swan, 17°25' N, 83°56' W, 15-24 Aug 1971 (fl fr), *Proctor 32493* (BM, F, GH, TEX-LL).

COLOMBIA: SAN ANDRÉS Y PROVIDENCIA: San Andrés, Spratt Bight, 12° 35' 16.7" N, 81°41' 58.6", 1 msnm,

01 Nov 2009, *Murcia 100* (COL, TOLI)*; Isla de San Andrés, Spratt Bight, 12° 35' 16.7" N, 81° 41' 58.6", 1 msnm, 04 Nov 2009, *Murcia 141* (COL, TOLI)*; Isla de San Andrés, Spratt Bight, matorrales cerca del camino peatonal sobre la bahía, a 50 m al occidente de la casa de la Defensa Civil, 01 Abr 2010 (fl), *Pabón-Mora et al.* 232 (COL, NY, TOLI)*.

Vernacular names – Camote, camotillo, guaco (Mexico).

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