



Studies in *Aristolochia* (Aristolochiaceae) of Hispaniola

ELADIO FERNÁNDEZ¹, IRINA FERRERAS², BRIAN D. FARRELL³, BRUNO A. S. de MEDEIROS³ & GUSTAVO A. ROMERO-GONZÁLEZ^{2,4}

¹Herbario del Instituto de Investigaciones Botánicas y Zoológicas de la Universidad Autónoma de Santo Domingo, Dominican Republic.

²Harvard University Herbaria, 22 Divinity Avenue, Cambridge, Massachusetts 02138, U.S.A.

³Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts 02138, U.S.A.

⁴Corresponding author: romero@oeb.harvard.edu

Abstract

A review of the literature at large and the field photographic record of the senior author of this study indicate that there are several undescribed species of *Aristolochia* in Hispaniola (Dominican Republic and Haiti), related to *A. bilobata*. Here we show that *A. mirandae* is a synonym of *A. bilobata* and that what appears as *A. bilobata* in Marión H. (2011: 76–77) is a new species here described as *Aristolochia adiascola*. In addition, two new species, *A. bonettiana* and *A. marioniana*, also related to *A. bilobata*, are described and illustrated herein.

Key words: *Aristolochia*, Aristolochiaceae, hexandrous, West Indies

Resumen

Una revisión extensa de la literatura existente y de los registros fotográficos en campo del primer autor indican que hay varias especies no descritas de *Aristolochia* en Hispaniola (la República Dominicana y Haití). Aquí demostramos que *A. mirandae* es un sinónimo de *A. bilobata* y lo que aparece como *A. bilobata* en Marión H. (2011:76–77) es una especie nueva aquí descrita como *Aristolochia adiascola*. Otras dos especies nuevas de Hispaniola, *A. bonettiana* y *A. marioniana*, también relacionadas con *A. bilobata*, son aquí descritas e ilustradas.

Palabras clave: Antillas, *Aristolochia*, Aristolochiaceae, hexandrous, La Española

Introduction

Aristolochia Linnaeus (1753: 960) (Aristolochiaceae) is a genus of ca. 500 species (Mabberley 2017: 72), with many more species published recently. *Aristolochia* is particularly diverse in the Neotropics, where more than half of the species have been reported (González 1998, González & Pabón-Mora 2018). Plants of this genus bear perhaps the most bizarre-looking flowers found in nature, such as those in *A. glandulosa* Kickx (1839: 79), *A. ridicula* Brown (1886: 360), *A. tricaudata* Lemaire (1865: 49), and *A. grandiflora* Swartz (1788: 126), the longest flower in the world (Endress 1996: 233; Bello *et al.* 2006).

Species of *Aristolochia* exhibit a number of reproductive strategies that evolved independently in members of the monocots and eudicots (e.g., thermogenesis, resupination, and trap and deceit pollination: see comments below). The morphology of the flowers is highly complex (Fig. 1), somewhat resembling a tobacco pipe (thus one of their common generic names, “Dutchman’s pipe”), with the different parts arranged at a variety of angles. The distal portion of the flower, called the limb, is expanded and it is the showiest part of the flower, which varies tremendously within the genus: it is monosymmetric in most species and rarely approaches actinomorphy (e.g., in *A. macrophylla* Lamarck (1783: 255)). Many species bear flowers with disagreeable, fetid fragrances that attract carrion flies (personal observation by the first author, 2017; Mabberley 2017: 72), but the species we will treat here produce flowers with lemon grass, coconut, or ginger-like fragrances that attract a variety of other flies. Flowers of some species apparently exhibit thermogenesis (*vide* Mabberley 2017: 72; also present in several other families; Araceae; e.g., Seymour 2010 and references therein), supposedly to help volatilize their fragrance (e.g., Wang *et al.* 2014).

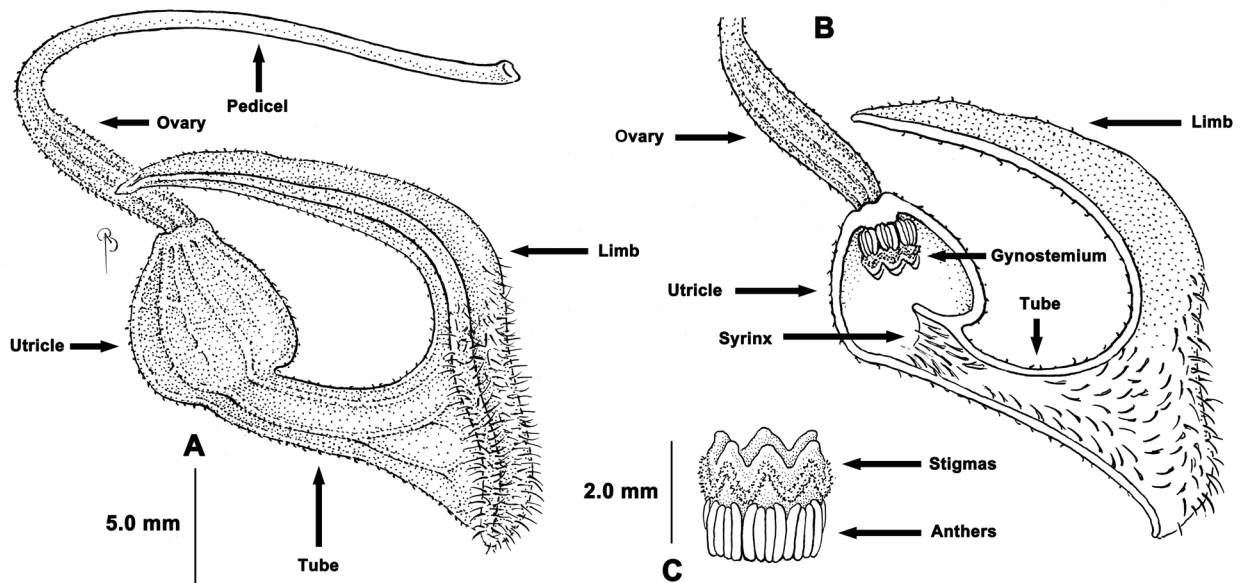


FIGURE 1. *Aristolochia adiantola* G.A. Romero & E. Fernández. **A.** Side view of flower. **B.** Longitudinal section of flower in side view. **C.** Gynostemium. Based on E. Fernández 108 (GH).

Flowers of *Aristolochia* may undergo resupination (as in Orchidaceae and Fabaceae), which, according to Pfeiffer (1966), occurs when "... the larger, median lobe of the calyx may be abaxial at anthesis (the normal state), or it may become adaxial by a 180° turn of the supporting axis. It may twist through several revolutions, making a numerical measure of the degree of resupination in the axis of the flower difficult". Flowers may also undergo subtle changes in shape as a function of their sexual status. Those of *A. adiantola*, which the senior author has been able to observe in detail, change shape from the female phase (early at anthesis), to their male phase (later the same day; see text below under *A. adiantola* G.A. Romero & E. Fernández).

The flowers of all known species of *Aristolochia* bear a gynostemium (as in Orchidaceae and Stylidiaceae; González & Stevenson 2000; Suárez-Baron *et al.* 2016). Furthermore, the flowers are protogynous: stigmas mature and wilt before anthers release pollen (Endress 1990, Judd *et al.* 2008: 347–248). The plants can be self-compatible or not, but the temporal separation of the female and male function appear to minimize self-fertilization (see data in Sakai 2002). The flowers of many species use a pollinator-trap mechanism that, again, has evolved multiple times in flowering plants (e.g., Apocynaceae: *Ceropegia* Linnaeus (1753: 211); Araceae: *Dracunculus* Miller (1754) and others; Moraceae: *Ficus* Linnaeus (1753: 1059); and Orchidaceae: Cyripedioideae). The pollinators are trapped temporarily inside using an array of trichomes that point inwards and/or "window panes" around the gynostemium (Brantjes 1980; Oelschlägel *et al.* 2009). The trichomes that trap the pollinators later wilt, after the anthers mature, and the flies can escape dusted with pollen. Not all species bear trap flowers: some lack the trichomes that trap the pollinators and in these cases the flower itself may serve as a substrate to feed the larvae of the pollinator (Sakai 2002). There is no doubt, however, that many species of *Aristolochia* employ deceit pollination (e.g., Oelschlägel *et al.* 2015), which may favor high rates of diversification (as in Orchidaceae; Cozzolino & Widmer 2005; Givnish *et al.* 2015; Bogarín *et al.* 2016). Besides the ephemeral trichomes that may line part of the limb and the entire tube, the flowers of many species in Hispaniola bear other more permanent, elaborate trichomes, especially along the margins of the limb (called, incorrectly, "fimbriae" in Pfeiffer 1966).

Fruits of *Aristolochia* produce lots of relatively small, membranous, often winged seeds that most likely are wind dispersed, although there are reports of dispersal by ants (Osorio 2010).

In the West Indies, as in the rest of the Americas, vegetative parts of *Aristolochia* serve as food plants for the larvae of species of *Battus* Scopoli (1777: 433) and *Parides* Hübner (1819; Papilionidae, Lepidoptera) (e.g., Núñez Aguila & Barro Cañamero 2011: 33 for the Cuban species). The senior author has documented larvae of *Parides gundlachianus* Felder & Felder (1864: 294) feeding on *Aristolochia lindeniana* Duchartre (1864: 453–454), in the vicinity of Moa and on *A. clementis* Alain (1948: 80), in Sardinero, near the city of Santiago. These two *Aristolochia* species are endemic to Cuba.

The papilionid genus *Battus* is represented by three species in the West Indies: *B. polydamas* Linnaeus (1758: 460), with a series of endemic island-specific subspecies; *B. devilliersii* Godart (1823: 231), from Cuba and the Bahamas; and *B. zetides* Munroe (1971: 142), endemic to Hispaniola. Marion (2011: 81) cited *Aristolochia bilabiata* Linnaeus (1763: 1361) and *A. ophioides* Marión (2000: 3–5) as food plants for *B. polydamas* subsp. *polycrates* Hopffer (1865: 24), a butterfly endemic to Hispaniola. The first author of this study has photographed larvae of the latter feeding on *A. bilobata* Linnaeus (1753: 960), *A. brachyura* Duchartre (1864: 446), *A. schotti* Marión (2000: 1), and on one of the new species described below, *A. bonettiana* E. Fernández & G.A. Romero. *Battus devilliersii* has been recorded feeding on *A. littoralis* Parodi (1878: 155) (Smith *et al.* 1994: 164).

In Cuba, the senior author documented adults of *Battus devilliersii* and *B. polydamas* subsp. *cubensis* Dufrane (1946: 102) simultaneously laying eggs on *A. glandulosa* near Bermejas, Ciénaga de Zapata. Both butterflies were reported feeding on *A. passiflorifolia* Richard (1850: 195) near Holguín (F. Bermúdez Hernández, personal communication 2016).

Historically, *Aristolochia* has played an important role in ethnobotany. The generic name is derived from the Greek *aristos* (ἀριστος), “best”, and *locheia* (λοχεία), “delivery”, in reference to its known ancient use in childbirth. Heinrich *et al.* (2009) summarized an extensive list of references providing an account of the use of *Aristolochia* plant parts for medicinal uses, some of which are, when used without supervision, reportedly highly deleterious to human health (see also Dauncey & Larsson 2018: 168–169). According to an ancient manuscript of uses of *Aristolochia* in Peru (Ruiz 1805: 52), the stems, after removing the bark, were used by the native Indians to make thick ropes employed as suspension and handrails in bridges, as well as to tie poles in house construction. Other authors cite the medicinal use of the root (Pittier 357–358, as “Raíz de mato”, for the treatment of “... snake bites and tetanum”; Schnee 1973: 339–340, “Guaco”, as “medicinal”; see also Otero *et al.* 2000; Giovannini & Howes 2017).

This is the first of a series of articles describing the diversity of *Aristolochia* in Hispaniola based largely on the fieldwork of the senior author. His extensive photographic record has been particularly useful. After examining this evidence, depicting flowers of *Aristolochia* of Hispaniola and neighboring islands, it appears that there is either a large range of intraspecific variation and/or many undescribed species. Another possible explanation is natural hybridization: some of the variation could be typical representatives of hybrid swarms. The senior author recently detected a population found between the geographical ranges of two of the species described here (*Aristolochia adiantola* G.A. Romero & E. Fernández and *A. marioniana* E. Fernández & G.A. Romero), the plants of which produce flowers somewhat intermediate between these two species (Fig. 2). However, this possible case of introgressive hybridization seems to be an isolated event, and all sampled populations of these two species, away from this confluence zone, are fairly homogeneous, showing no apparent morphological evidence of gene exchange. In addition, a collaborator of the senior author (Martin Reith) found recently, this time in Haiti, what appears to be a hybrid population that suggests *Aristolochia punctata* Lamarck (1783: 253) and *A. ehrenbergiana* Chamisso (1832: 210) as the putative parents, as plants of both were found mixed with the hybrids.

We continue exploring ways to explain such wide variation. Two of the authors (E. Fernández and B. D. Farrell) currently conduct studies on the role of plant parts of *Aristolochia* as substrates for different insects. Another group (B. A. S. de Medeiros *et al.*) has focused on reconstructing a molecular phylogeny of all the species of *Aristolochia* in Hispaniola and possibly other islands in the Greater Antilles, the results of which will be published separately; preliminary results are presented solely in the context of the species described here (see concluding remarks).

Marión (2011) has been the most recent reference for species of *Aristolochia* of Hispaniola. A review of this work and the literature at large, and, again, the photographic record of the senior author, indicates that *A. mirandae* Marión (2002: 18–21) is a synonym of *A. bilobata* and that what appears as *A. bilobata* in Marión H. (2011: 76–77) is an undescribed species, which we describe and illustrate next. Here we report the results of studying photographic and herbarium material previously associated or closely related to with *A. bilobata*, and we describe three new species.

Taxonomic treatment

Aristolochia adiantola G.A. Romero & E. Fernández, *sp. nov.* (Figs. 3, 4)

Aristolochia adiantola differs from *A. bilobata* by the absence of a constriction between the limb and the tube, the color of the limb (purple to brown with white spots in the new species versus greenish to yellowish with purple veins in *A. bilobata*), the orientation of the flowers, and their allopatric distribution.



FIGURE 2. Possible natural hybrids between *Aristolochia adiantola* G.A. Romero & E. Fernández and *A. marioniana* E. Fernández & G.A. Romero. Two flowers (Figs. A, B) were found in the eastern-most range of the hybrid population; they present an orientation similar to *A. marioniana*, as well as the typical radiated dark pattern on white, whereas the apex of the limb is erect and apiculate as in *A. adiantola*. In one case, medium-length trichomes are also present at the central limb margins (fig. 2A), whereas in the other (Fig. 2B) there are fewer withered trichomes typical of second to third day flowers that are in the process of senescence. They retain the shape and posture of *A. adiantola*, while exhibiting the radiated dark pattern on white of *A. marioniana*. The flowers shown in 2C and 2D also exhibit medium length conical trichomes along the side central margins of the limb, as in *A. marioniana*, which has long feather-like trichomes along its central limb margins.

≡ *Aristolochia bilobata* auct. non Linnaeus, Marión (2011: 76–77).

Type:—DOMINICAN REPUBLIC. Peravia province: Loma Tibisi, Arroyo Salado, about 5 miles N of Bani on El Recodo Road, limestone hills, 200–300 m; vine, about 5 m long, calyx brown with white stripes radiating from throat, in dense thickets on hillside, quite common, 22 June 1968, *A.H. Liogier 11774* (holotype NY-01507932!; isotypes: GH-00556739!, US-00855830!).

Glabrous lianas to 4 m long. Stem thin and woody at the base to ca. 12.4 mm in diameter; branches green to ca. 1.3 mm in diameter. Petioles 17–21 mm long, with a basal abscission zone; leaf 25–50 × 23–51 mm, membranaceous, glabrous above, glabrescent below, base rounded, obtuse or cuneate; blade bilobate, albeit variable, lobes recurved, convergent, to linear, widely divergent, 25–49 × 23–51 mm; venation acrodromous, basal, primary veins 2. Flowers axillary, solitary; peduncle plus ovary 30–32 mm long; perianth to 20.11–31.70 mm long, slightly curved between the utricle and the tube, greenish to maroon, external surface puberulous when young and at anthesis, ephemeral later; utricle obovoid, 8.3–10.0 mm long, 6.6–6.6 mm in diameter; syrinx present, oblique, 1.7–1.8 mm long; tube narrowly funnelliform, slightly bent, 11.6–21.6 mm long, to 2.4 mm proximal diam. and 6.8 mm distal diameter, forming an angle of ca. 45° with the utricle; limb 1-lobed, ovate to narrowly ovate, 26.4–31.9 mm, forming an angle of ca. 90° with the tube, apex acute to acuminate, smooth inside. Gynostemium sessile, to 3 mm long; anthers 1.6 mm long. Ovary 11.8–15.1 mm long, costate, twisted or not. Capsule broadly oblong, to ca. 25.1 mm long and 16.6 mm diameter, acute, each locule with 35–50 seeds. Seeds many, subtriangular, winged, to ca. 5.5 mm high and 4.5 mm wide.

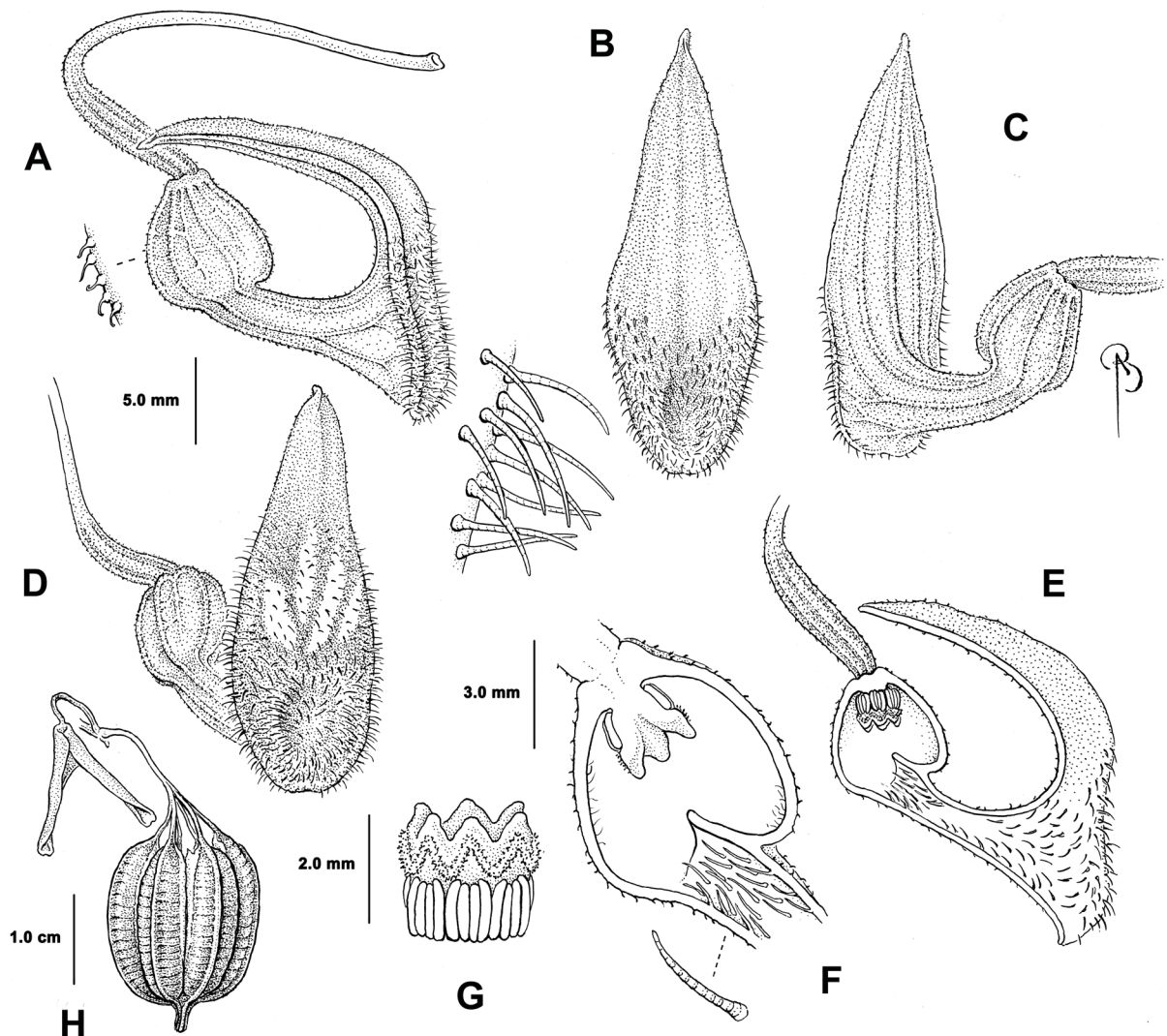


FIGURE 3. *Aristolochia adiantola* G.A. Romero & E. Fernández. Lateral (A), frontal (B), back (C) and oblique (D) views of flower. Views of the flower. E. Longitudinal section of flower. F. Cross section of utricle. G. Gynostemium. H. Capsule. Illustration by B. Angell based on *E. Fernández 108* (GH).



FIGURE 4. *Aristolochia adiastrum* G.A. Romero & E. Fernández. A. Bani, Peravia province, Dominican Republic. B. Jardín Botánico Nacional, Santo Domingo, Dominican Republic. C. Jardín Botánico Nacional, Santo Domingo. D. Balneario Mucha Agua. Photographs by E. Fernández. No vouchers were prepared.

Etymology:—From the Greek *ἀδιαστολή*, *adiastolos*, “not separated, confused” (Brown 1954: 228). An examination of herbarium specimens from A, GH, JBSD, NY, US, and USD (herbarium acronyms cited according to Thiers, continuously updated), filed under *Aristolochia bilobata*, as well as a search of images on the Internet under “*Aristolochia bilobata*”, revealed a mixture of *A. adiantola*, *A. bilobata*, and several undescribed species. This confusion can be traced back to the fact that *A. bilobata* was thought not to have any close relatives (Rankin and Greuter 1999) and that “while this species was frequently collected without flowers or fruits, it could be readily identified by the curious bilobate leaves” (Pfeifer 1966). Following these criteria, all plants from Hispaniola bearing bilobate leaves were at first identified, albeit often incorrectly, as *A. bilobata*.

As pointed out above, *in vivo*, *Aristolochia adiantola* can be easily distinguished from *A. bilobata* based on the color and orientation of the flowers (Fig. 4). Regarding orientation, the utricle is always pendant and the tube horizontal to pendant in *A. adiantola*; the former is always horizontal, and the latter erect in *A. bilobata*. Flower buds of *A. adiantola* start with the largest medial lobe abaxial (“1” in Pfeifer 1966: figure 2 therein; “a” in González 1999: 54, figure 12 therein); a flexure downward and a twist in the peduncle make the ovary and utricle pendant, and a slight bending upward of the tube relative to the utricle makes the tube horizontal to pendant and the medial lobe of the calyx adaxial and vertical (Figs. 3, 4). It is not clear whether the “twist” mentioned above always occurs in the peduncle: it is sometimes evident in the ovary (Fig. 4B, C).

Flowers of his species change shape in function of their development. At anthesis, early in the day, the edges of the limb are not revolute (Fig. 4B); by noon the edges are conspicuously revolute (Fig. 4A, B, C; in the afternoon, the edges of the limb bent forward, as the flower becomes senescent.

The white spots on the limb of flowers of the new species vary from inconspicuous, small, to conspicuous, horizontal to transversal, white spots. Likewise, the density and length of the multicellular trichomes along the basal margin of the limb also vary considerably (Fig. 3). A collaborator of the senior author recently found a population of *A. adiantola* the plants of which bore totally green flowers, with subtle lighter green spots at the base of the limb (Fig. 4D).

The specimen collected by O. P. Swartz at SBT (11433, *Ex Ind. Occident.*, as “*Aristolochia bilobata* Linn.” [image seen]) has two deteriorated flowers that yet show somewhat the limb shape of *A. adiantola* but, according to the senior author of this contribution, it may be referable to an undescribed species from Haiti. Two other specimens attributed to Swartz and identified as *A. bilobata*, one at B (B-W 17050-01 0 [image seen]), with one deteriorated, undeterminable flower and a fragment of another one in the convolute, based on its size possibly belonging to another species, and one at S (08-1029 [image seen]) bears leaves only; another one at S [08-1032 [image seen]) bears only leaves and a fruit (with seeds in the packet).

Field and herbarium diagnostic characters:—*In vivo*, at anthesis, utricle pendant, tube horizontal to pendant, limb erect, purple to brownish red with white spots of variable size, without a constriction, the margins revolute at late anthesis. Flowers in herbarium specimens may conserve the original color, or the flower color may be cited in the label and, if mature flowers are present, the limb without constriction is easily discernable. Ultimately, herbarium specimens of the new species with accurate locality can be easily distinguished from *A. bilobata* because of the strictly allopatric distribution of these two species (Fig. 5).

Iconography:—Marión (2011: 76–77, as *A. bilobata*); Watts (2017: 59, as *A. bilobata*, flower shown upside down).

Additional specimens examined:—DOMINICAN REPUBLIC. Peravia Province: Las Caobas, on the road to San José de Ocoa, 430 m; trailing, 1 m long; flowers atropurpureous, with white stripes, rare; 13 April 1963, *J. de J. Jiménez* 4735 (US 855819). Hainas, scrubby woods, April 1921, *J.A. Faris* 179 (US 855823). Haina, rocky hilltop, July 1921, *J.A. Faris* 291 (US 855824); 8 km N of Galeón (La Ciénaga) on road to Matadero, between Honduras and Matadero, low muddy place in canyon, 18°24'N, 70°26'W, 1150 ft, 7 May 1981, *M. Mejía et al.* 13272 (NY 1507923; US 00855819). La Romana province: Farallón de Cumayasa, en Manigua sobre rocas calcáreas, 50 m, trepadora de 2–3 m de largo; flores pardo-rojizo, 14 November 1975, *A.H. Liogier & N. Melo* 24215 (JBSD). San Cristobal Province: Haina, scrubby woods, April 1921, *J. A. Farris* 179 (US 855823); Haina, rocky hilltops, July 1921, *J. A. Farris* 291 (US 855824); parte este de la carretera, frente al balneario Mucha Agua, 100 metros antes del primer portón de seguridad de la hidroeléctrica, 21 November 2018, *M. Rodríguez Bobadilla s.n.* (UASD). Distrito Nacional: Santo Domingo, Jardín Botánico Nacional, en bosque, trepadora de 3–4 m de largo; flores pardo obscuro, 27 October 1976, *A.H. Liogier* 25756 (JBSD); same locality, 25 May 2017, *E. Fernández* 108 (GH, in spirits).

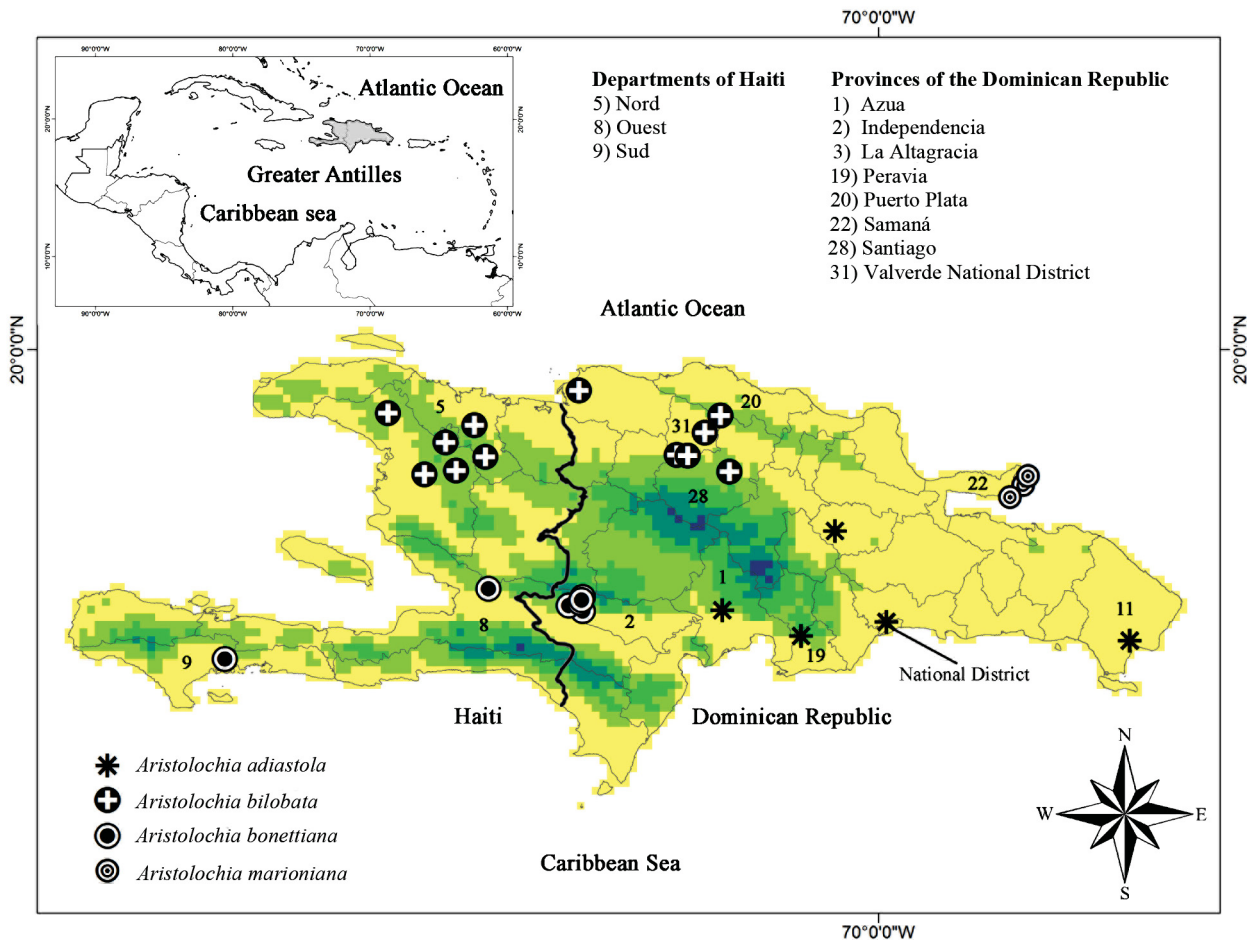


FIGURE 5. Distribution map of four species of *Aristolochia* in Hispaniola. [□] *A. adiastrala* G.A. Romero & E. Fernández; [+]
A. bilobata L.; [•] *A. bonnettiana* E. Fernández & G.A. Romero; [⊙] *A. marioniana* E. Fernández & G.A. Romero. Map prepared by W. Cetzal Ix based on geographical data provided by the authors.

***Aristolochya bilobata* Linnaeus (1753: 960) (Figs. 6, 7)**

≡ *Tropexa biloba* Rafinesque (1838: 98).

≡ *Howardia bilobata* (Linnaeus) Klotzsch (1859: 619).

Type:—"*Aristolochia longa, scandens, foliis, ferri equini effigie*" in Plumier, Descr. P1. Amer.: t. 106. 1693 (lectotype, designated by Rankin and Greuter (1999); epitype, designated by Rankin and Greuter (1999). HAITI. Vicinity of St Raphael, Département du Nord, flowers purple veined on whitish, vining on shrubs, arid foot hills, ca. 350 m, 3 December 1925, *E. C. Leonard 7686* (epitype GH 00273119!; isoepitype NY 00335793!).

≡ *Aristolochia mirandae* L. Marión (2003: 18).

Type:—DOMINICAN REPUBLIC. Santiago Rodríguez province: km 7 de la carretera Santiago-Jánico, bosque de transición, de seco a húmedo, a 150 m de la Cafetería El Príncipe, a mano izq. de terraplén. Traída y cultivada por el Dr. R. M. Miranda Matos el 2 de junio del 2001. Colectada bajo cultivo, 31 December 2001 (fl., fr.), *F. Jiménez & A. Velóz 3382A* (holotype JBSD 102656!; isotype B, not seen), **syn. nov.**

Field and herbarium diagnostic characters:—*In vivo*, at anthesis, utricle slightly erect to slightly pendant, mostly horizontal, tube always erect, limb erect, spatulate, acute, apiculate, to slightly emarginate, greenish to yellowish with or without brownish veins, with a constriction between the tube and the limb, the margin along the constriction strongly revolute, with translucent cells at the base. Flowers in herbarium specimens may conserve remains of the original color, or the flower color may be cited in the label; if mature flowers were pressed the constriction between the tube and the limb and the bent ovary should be easily discernable (see note below). Regardless, and as pointed out above, herbarium specimens of *A. bilobata* can be easily distinguished from those of *A. adiastrala* based on their strictly allopatric distribution (Fig. 4).

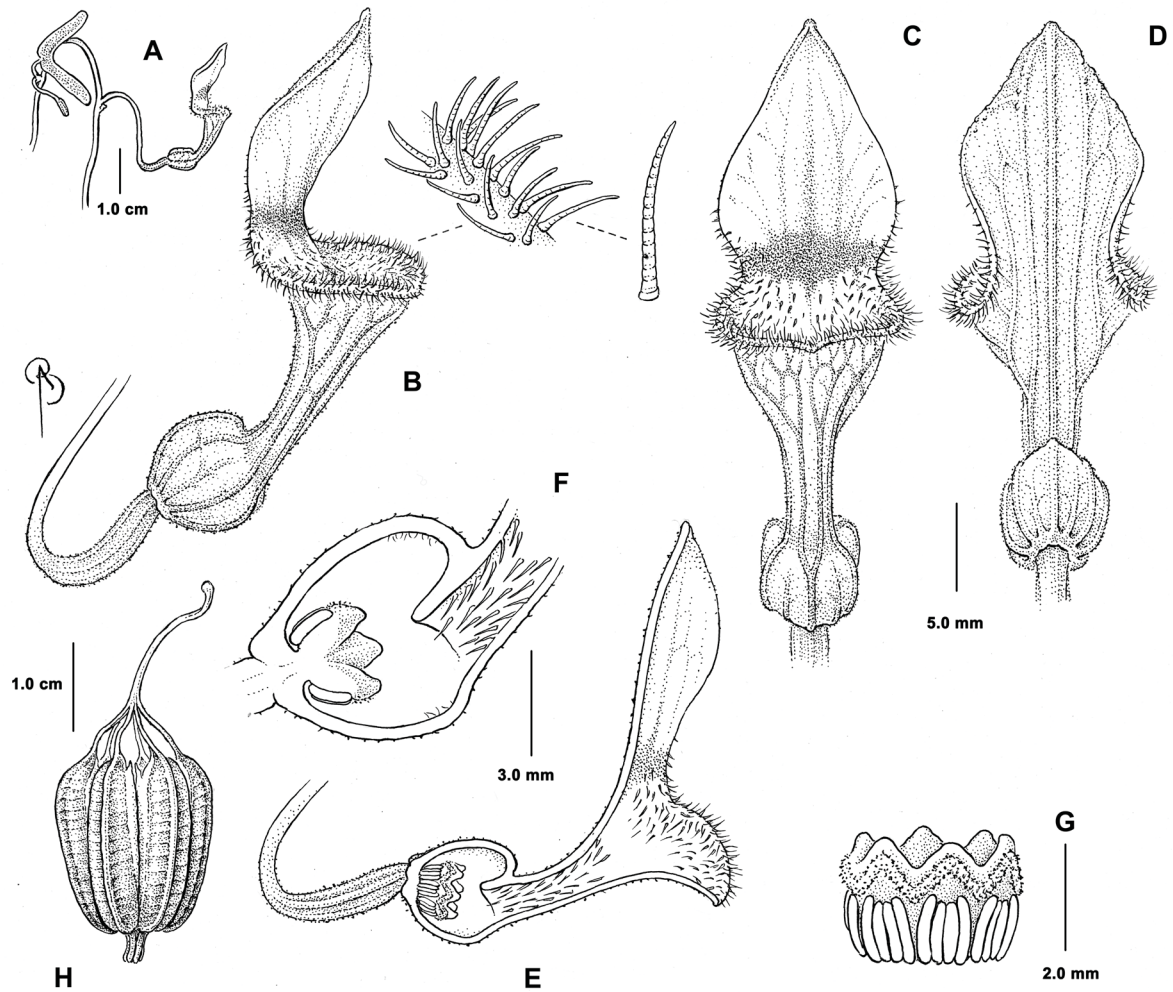


FIGURE 6. *Aristolochya bilobata* L. A. Leaf and resupinated flower. Lateral (B), Frontal (C), and back (D) view of flower. E. Longitudinal section of flower. F. Cross section of utricle. G. Gynostemium. H. Capsule. Illustration by B. Angell based on *E. Fernández 109* (GH).

Iconography:—Plumier (1693: tab. 106); Rankin and Greuter (1999); Marión (2003, as *A. mirandae*); Marión (2011: 79, as *A. mirandae*); Watts (2017: 25, mature flower shown upside down; 169, flower upside down; 187, image to be turned 90° counterclockwise).

Additional specimens examined:—DOMINICAN REPUBLIC. Barahona province: El Peñón, above Las Lavas, about 25 km NW of Santiago, dry hillside on limestone, 600 m, vine, forming tangles, 2--3 m high, flowers brown with whitish and yellow spots, 7 May 1968, *A. H. Liogier 11144* (GH, NY 1507946). Monte Cristi Province: Cordillera Central, Monción, at Arroyo Bulla, dry hillside thickets, 200m, 3 July 1929, *E. L. Ekman H13082* (US 855822). Santiago Rodríguez province: Jaiquí Picado, 20 miles W of Santiago, dry hills, on roadside, vine 3 m long or longer, flowers brown, 4 May 1968, *A. H. Liogier 11089* (GH, NY 1507934, US 855826); about 20 miles E of Santiago Rodríguez, in tickets on limestone rocks, 100 m, vine about 2 m long, flowers brown with whitish spots, 24 October 1968, *A. H. Liogier 13278* (GH, NY 1507927); Jaiquí Picado, 20 miles W of Santiago, in thickets on limestone hills, 300–400 m, vine on shrubs, about 2–3 m long, flowers pale brown without, dark brown with lighter areas within, 9 May 1969, *A.H. Liogier 15151* (NY 01507930, US 855828); same locality and altitude, in thickets on plateau, vine, 2–3 m long, flowers creamy white, 6 June 1969, *A.H. Liogier 15586* (NY 01507929; US 855829). Monción, 18 March 2017, *E. Fernández 109* (GH, in spirit). HAITI. Dépt. du Nord, Vicinity of St. Michel de l'Atayale, NE of U. West Indies Co. plantation, arid plain, 350 m, 17 November 1925, *E. C. Leonard 7106* (US 855856); Vicinity of St. Michel de l'Atayale, north slope of mt. La Cidre, 350 m, on shrub, flower dark purple lines with greenish, 23 November 1925, *E. C. Leonard 7493* (US 855857); vicinity of St. Raphael, on arid foot hills E of village, 350 m, on shrub, flowers purple veined on whitish, 3 December 1925, *E. C. Leonard 7686* (US 855858); Milot, on road between Sans Souci and Citadelle fort, on west side of cobble stone road, on cliff of limestone rock, 19°59'84"N, 72°22'63"W, 418 m,

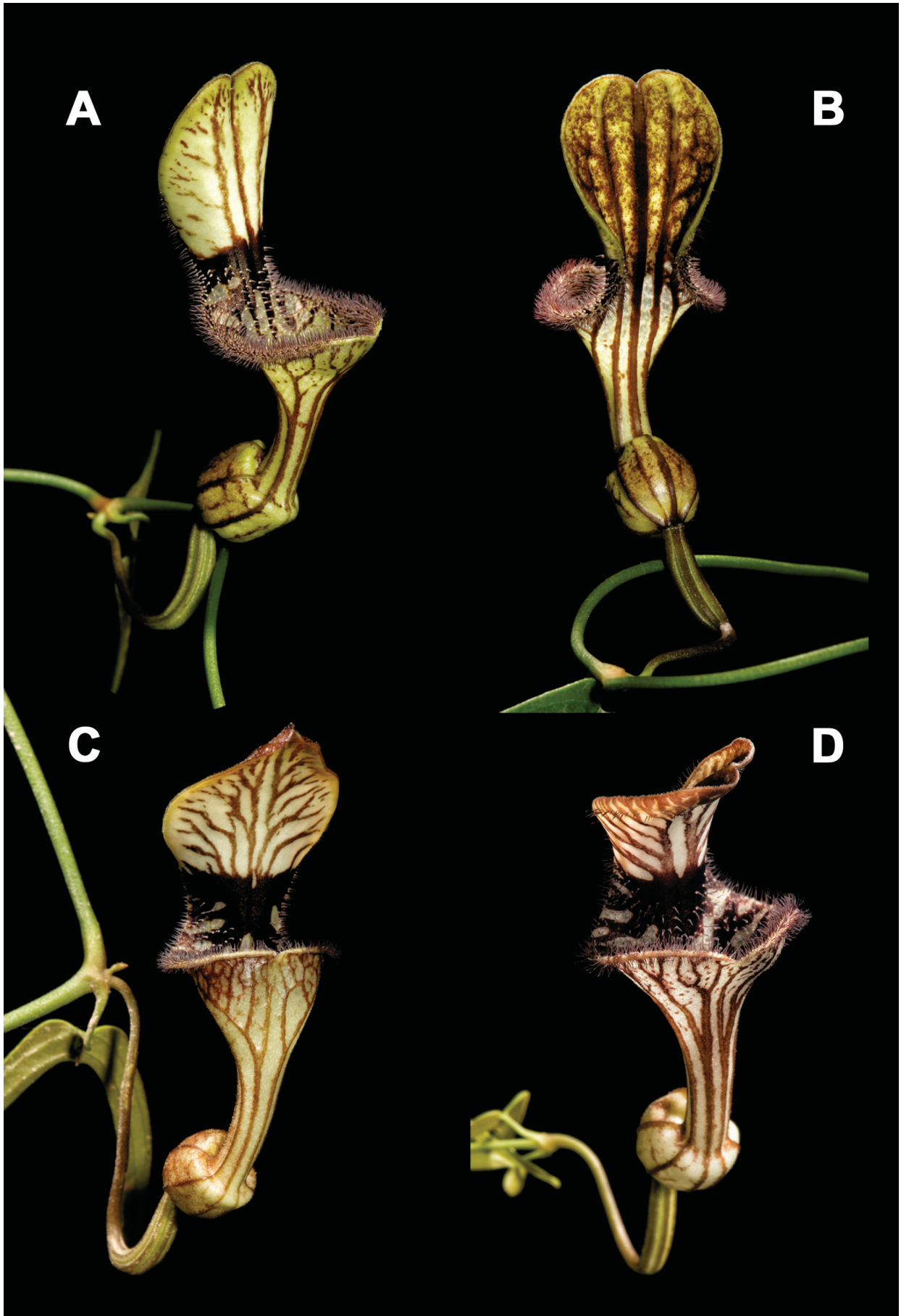


FIGURE 7. *Aristolochya bilobata* L. Specimens from Santiago Rodríguez province, Monción, Dominican Republic (A, B), Milot, Haiti (C), and Santiago Province, Jánico (D). Photographs by E. Fernández. No vouchers were prepared.

climbing on dead *Leucaena leucocephala* with *Chrysopogon zizanioides*, *Miconia angustilamina*, *Catalpa longissima*, *Simarouba glauca*, *Roystonea borinquena*, *Panicum maximum*, vine scrambling over shrubs with occasional flowers and seed pods, bilobed leaves, 22 August 2016, J. Timyan & E. Fernández H011 (JBSD 127698). Dept. L'Artibonite: San Michel [de L'Atalaye], 500 m, vine, 5 August 1905, G. V. Nash & N. Taylor 1394 (NY 01507925, US 855836); San Michel [de L'Atalaye] to Marmelade, 530 m, vine, flowers purple, 6 August 1905, G. V. Nash & N. Taylor 1451 (NY 01507926); NE of Gros Morne, 350 m, in dry thicket, on shrubs, flower purple, 17 February 1926, E. C. Leonard 9781 (US 855851); NE of Gros Morne, 235 m, on shrub, 17 February 1926, E. C. Leonard 8937 (US 855852); dry region SE of Gros Morne, 235 m, flowers purple, 18 February 1926, E. C. Leonard 9956 (US 855853).

According to Marión (2003), *Aristolochia mirandae* was similar to *A. bilobata* but it differed in its slightly cordate leaves (“escotadas en la base”) versus truncate in *A. bilobata*, and also because the enlarged floral limb was truncate, versus emarginate in *A. bilobata*. The examination of much live and herbarium material shows that leaf differences are not consistent (Fig. 8) and that the flowers shown in the lectotype and epitype proposed for *A. bilobata* (cited above; Rankin and Greuter 1999) have an acute limb. Flowers of *A. bilobata* also can have a slightly emarginate limb.

Aristolochia bilobata apparently undergoes the same perianth elongation of *A. adiantola*. However, before anthesis, it is evident that the ovary at some point bends upwards, and at anthesis the tube is erect, whereas the limb is suberect.

According to Rankin and Greuter (1999) and Marión (2011: 77), this species can be found in St. Thomas, Virgin Islands, yet it was not cited by Acevedo (2005), who has not encountered any specimens of this species from the Virgin Islands (Personal communication to GAR-G, 2017).

The following two new species were detected by the senior author during his photographic expeditions in Hispaniola. They appear to be related to *A. bilobata*, as their plants bear relatively small, bilobate leaves. It is entirely possible that specimens of these two new taxa are represented in herbaria, again, erroneously referred to *A. bilobata*.

Aristolochia bonettiana E. Fernández & G.A. Romero, *sp. nov.* (Figs. 9, 10)

Aristolochia bonettiana differs from *A. bilobata* by the absence of a constriction between the limb and the tube, the color of the limb (brown at the terminal end and greenish yellow at the base with central whitish patch at base versus greenish to yellowish with purple veins in *A. bilobata*), and their allopatric distribution.

Type:—DOMINICAN REPUBLIC. Independencia province: Postrer Río, 1.3 kms on road Postrer Río-Los Bolos, west side of the road growing on barb wire and *Prosopis* sp.; Vine about 1 meter long, calyx brown and greenish yellow, 04 April 2017, E. Fernández 0102 (holotype: UASD; isotypes: GH, K, NY).

Glabrous lianas to 4 m long. Stem thin and woody at the base to ca. 4.5 mm in diameter; branches green to ca. 0.8 mm in diameter. Petioles 12.2–5.6 mm long, with a basal abscission zone. Leaf 19.7–37.8 × 16.0–46.7 mm, membranaceous, glabrous above, glabrescent below, base rounded, obtuse or cuneate; blade bilobate, albeit variable, lobes recurved, convergent, to linear, widely divergent; venation acrodromous, basal, primary veins 2. Flowers axillary, solitary; peduncle plus ovary 23.4–30.0 mm long; perianth to 21.2–24.7 mm long, slightly curved between the utricle and the tube, greenish yellow to brown, external surface puberulous when young and at anthesis, ephemeral later; utricle obovoid, 6.4–9.0 mm long, 5.4–5.7 mm in diameter; syrinx present, oblique, 2.3–2.7 mm long; tube narrowly funnellform, slightly bent, 13.2–15.7 mm long, to 3.0 mm proximal diameter and 5.7 mm distal diameter, forming an angle of ca. 45° with the utricle; limb 1-lobed, widely to narrowly spatulate, 24.0–35.7 mm, forming an angle of ca. 90° with the tube, apex acute, smooth inside, margins revolute at late anthesis. Gynostemium sessile, to 2.8 mm long; anthers 1.68 mm long. Ovary 9.7–11.7 mm long, costate, twisted or not. Capsule broadly oblong, to ca. 19.0–26.8 mm long and 15.0–15.2 mm diameter, acute, each locule with ca. 65 seeds. Seeds many, subtriangular, winged, to ca. 0.4 mm high and 6.3 mm wide.

Etymology:—In honor of Rosa Margarita Bonetti, president of Fundación Propa-gas and a sponsor of *Aristolochia* research in the Dominican Republic.

Field and herbarium diagnostic characters:—*In vivo*, at anthesis, utricle pendant, tube horizontal to pendant, limb erect, brown at the terminal end and greenish yellow at the base with a whitish central patch, without a constriction, the margins revolute at late anthesis. Some individuals manifest an absence of brown at the terminal end of the limb (Fig. 10B). At anthesis, the flowers present a strong scent of lemongrass. Flowers in herbarium specimens may not conserve the original color, but the flower color may be cited in the label and, if mature flowers are present, the limb without constriction is easily discernable. Ultimately, herbarium specimens of the new species with accurate locality can be easily distinguished from *A. bilobata* because of the strictly allopatric distribution of these two species (Fig. 5).

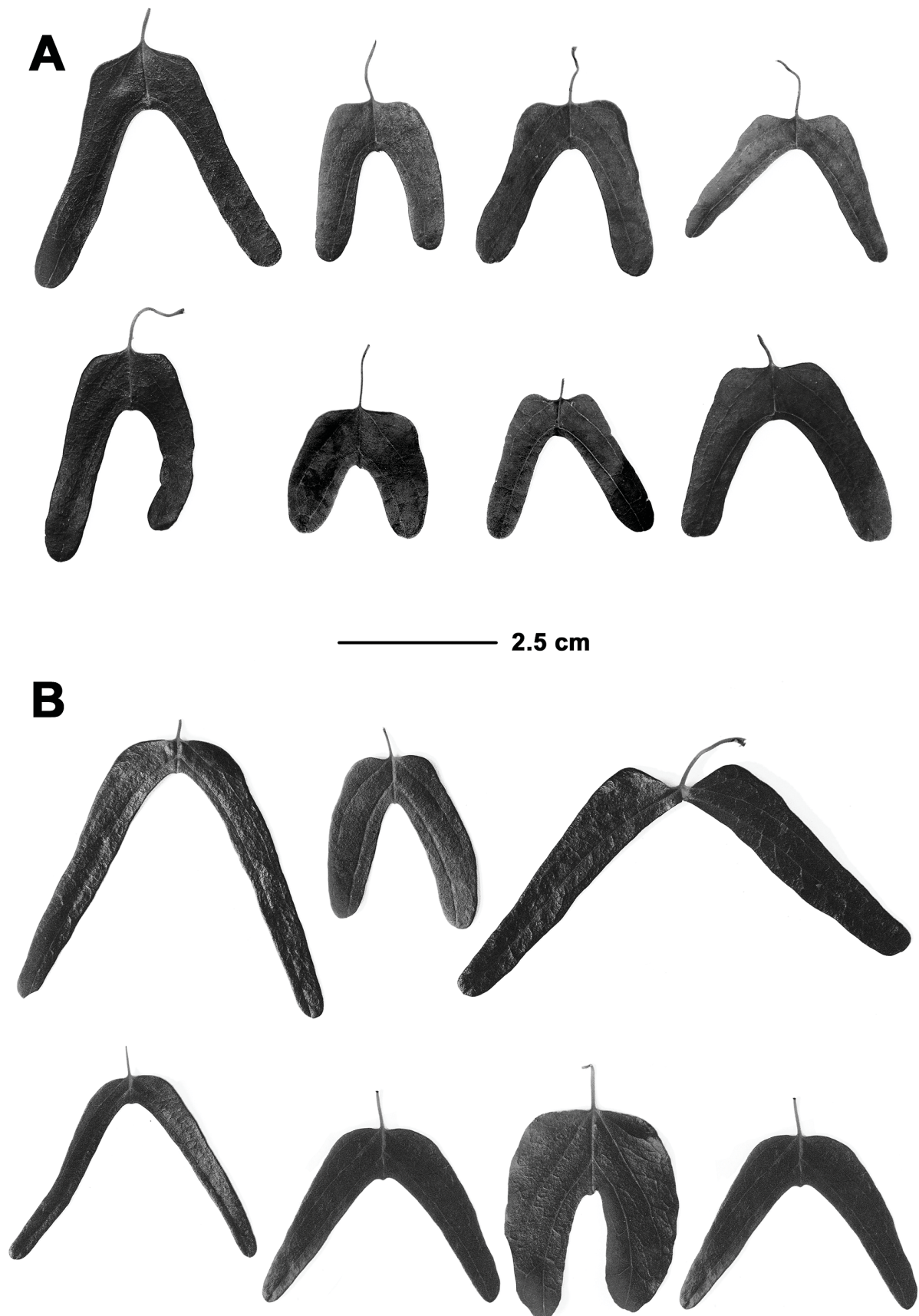


FIGURE 8. Leaf variation of *Aristolochia* species. A. *Aristolochia adiastrum* G. A. Romero & E. Fernández. B. *Aristolochia bilobata* L. No vouchers were prepared.

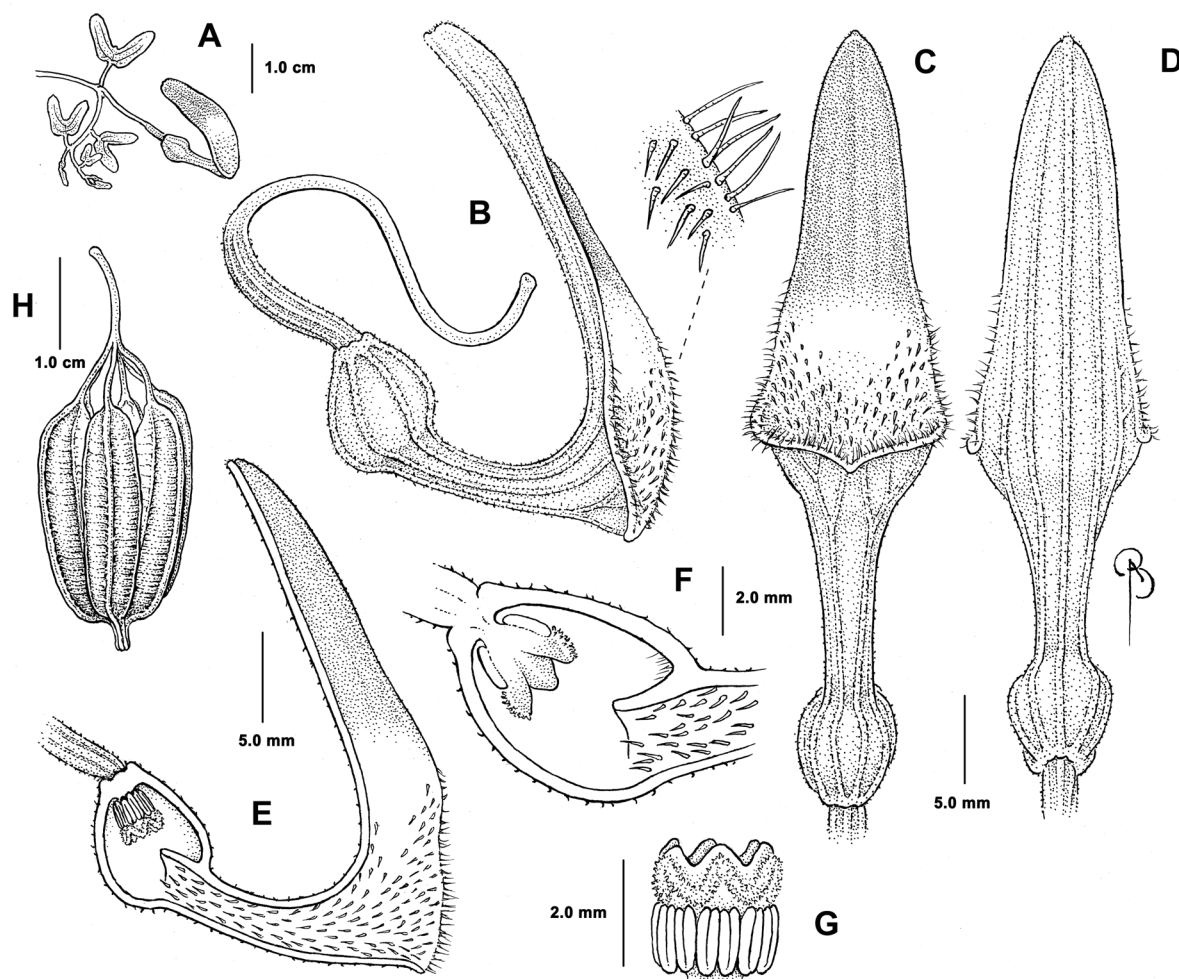


FIGURE 9. *Aristolochia bonettiana* E. Fernández & G.A. Romero. A. Habit. B, C, D. Views of flower. E. Cross section of flower. F. Cross section of utricle. G. Gynostemium. H. Fruit. Illustration by B. Angell based on E. Fernández 110 (GH).

As pointed out above, *in vivo*, *Aristolochia bonettiana* can be easily distinguished from *A. bilobata* based on the color of the flowers (Fig. 10 versus Fig. 4) and the shape of the limb (spatulate versus ovate; Figs. versus 9, 10 versus 3, 4). Flower buds of *A. bonettiana* start with the largest medial lobe abaxial (“1” in Pfeifer 1966: Fig. 2 therein; “a” in González 1999” 54, Fig. 12 therein); after a flexure downward and a twist in the peduncle, the ovary and utricle become pendant, and a slight bending upward of the tube relative to the utricle makes the tube horizontal to pendant and the medial lobe of the calyx adaxial and vertical (Figs. 9, 10).

The terminal brown patch and the yellow with central whitish patch at the base of the limb of the flowers of the new species remain very constant in the populations examined by the senior author. However, the density and length of the trichomes along the basal margin of the limb vary considerably (Fig. 10). The senior author did find a rare morph totally devoid of dark pigments, yet showing the central lighter portion of the limb (Fig. 10B).

Iconography:—Apparently never illustrated in the literature.

Additional specimens examined:—DOMINICAN REPUBLIC. Independencia province: Postrer Río, 25 May 2017, E. Fernández 110 (GH, in spirits); Sierra de Neiba, en la ladera de la cañada de Maniel, entre los Pinos de Eden y Angel Felix, bosque algo seco, 800 m, liana, 16 July 1987, T. Zanoni *et al.* 40121 (NY 1507921).



FIGURE 10. *Aristolochia bonettiana* E. Fernández & G.A. Romero. Flowers (A, B, C) and capsule (D). Photographed along the road between Postrer Rio and Los Bolos (southern slope of Sierra de Neiba), Dominican Republic. Photographs by E. Fernández. No vouchers were prepared.

Aristolochia marioniana E. Fernández & G.A. Romero, *sp. nov.* (Figs. 11, 12)

Aristolochia marioniana differs from *A. bilobata* by the absence of a constriction between the limb and the tube, the color of the limb (thick red-violet veins on white and greenish to brown sagittate patch at the terminal portion of the limb versus greenish to yellowish with slender red-violet veins in *A. bilobata*), the barbate trichomes around the edge of the tube and limb (the “fauce” or “throat”; F. González, personal communication, 2019; absent in *A. bilobata*), and their allopatric distribution.

Type:—DOMINICAN REPUBLIC. Samaná province: Villa Gran Bahía, Punta de Chinguela, north of the road between Samaná and Las Galeras, limestone marine terrace; vine about 2 m long, calyx brownish yellow with barbate trichomes and red-violet veins radiating from throat, on fern thicket growing on karst, 16 April 2017, *E. Fernández 0100* (holotype: UASD; isotypes: GH, K, NY).

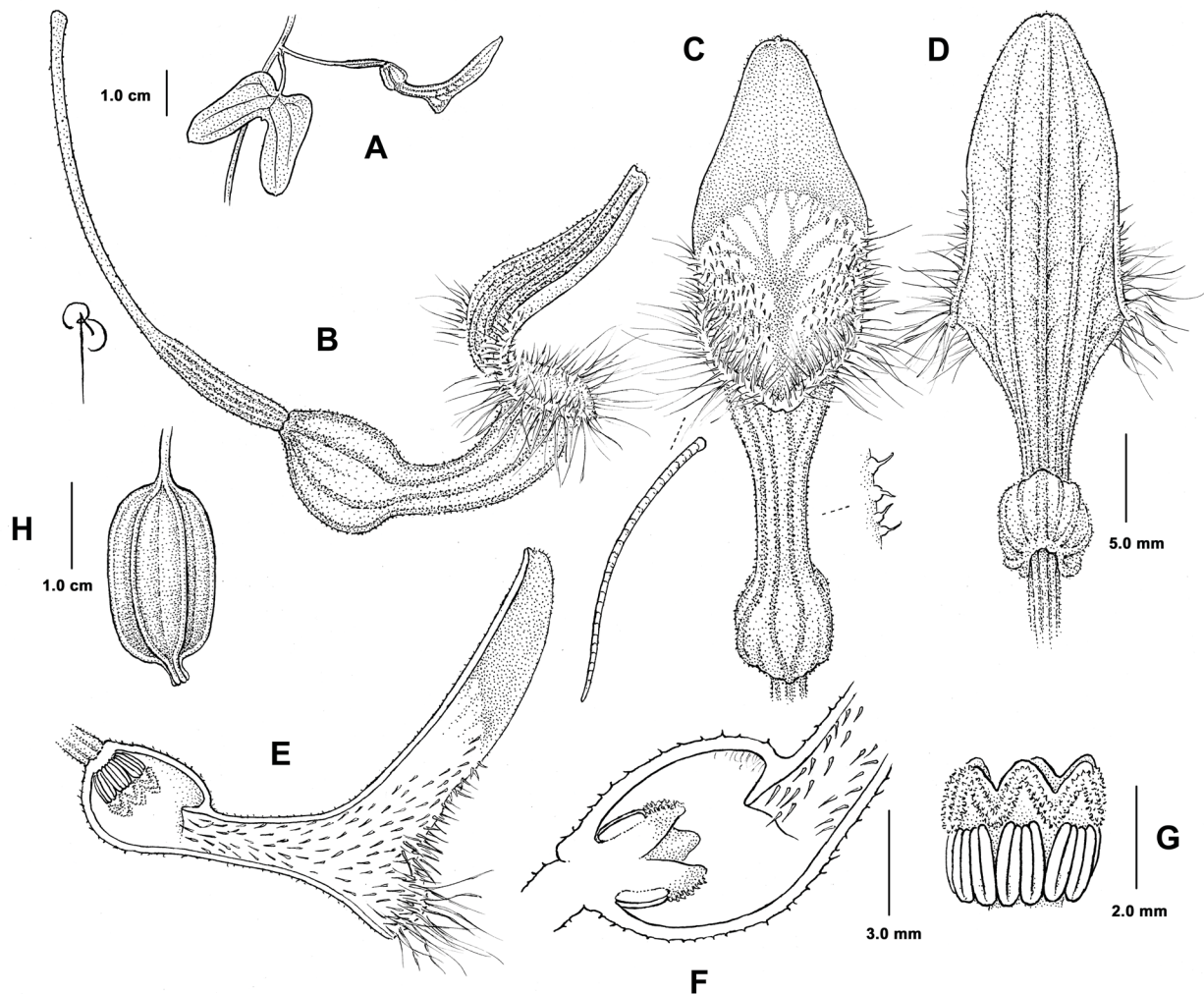


FIGURE 11. *Aristolochia marioniana* E. Fernández & G.A. Romero. A. Leaf and resupinated flower. Lateral (B), frontal (C), and back (D) views of flower. E. Longitudinal section of flower. F. Longitudinal section of utricle. G. Gynostemium. H. Capsule. Illustration by B. Angell based on *E. Fernández III* (GH).

Glabrous lianas ca. 2 m long. Stem thin and woody at the base to ca. 1.96 mm in diameter; branches green to ca. 0.89–0.91 mm in diameter. Petioles 14.8–18.7 mm long, with a basal abscission zone. Leaf 21–36 × 18–34 mm, membranaceous, glabrous above, glabrescent below, base rounded or obtuse; blade bilobate, albeit variable, lobes recurved, convergent, to linear, widely divergent, 21–36 × 6–10 mm; venation acrodromous, basal, primary veins 2. Flowers axillary, solitary; peduncle plus ovary 26–31 mm long; perianth to 37–48 mm long, slightly curved between the utricle and the tube, with brown veins on a yellow background, external surface puberulous when young and at anthesis, ephemeral later; utricle obovoid, 8.4–8.5 mm long, 4.6–6.9 mm in diameter; syrinx present, oblique, 1.8 mm long; tube narrowly funnelliform, slightly bent, 14.5–14.6 mm long, proximal diameter 2.7–3.3 mm and distal diameter 6.1–6.9 mm, forming an angle of ca. 45° with the utricle; limb 1-lobed, ovate to narrowly ovate, 13.4–24.7 mm, forming an angle of ca. 45° with the tube, apex acute to acuminate, slightly puberulous, margins with barbate trichomes



FIGURE 12. *Aristolochia marioniana* E. Fernández & G.A. Romero. Flowers (A, B, C, D) from a population in Villa Gran Bahía, Samaná (Dominican Republic). Photographs by E. Fernández. No vouchers were prepared.

at the base, decreasing in size toward the apex, the apical margin puberulous. Gynostemium sessile, to 3 mm long; anthers 1.6 mm long. Ovary 10.8–11.8 mm long, costate, twisted or not. Capsule broadly oblong, to ca. 17.6–20.8 mm long and 11.0–13.9 mm diameter, acute. Seeds many, subtriangular, winged, to ca. 0.20 mm high and 4.8 mm wide.

Etymology:—In honor of Dr. Luis Marión Heredia, psychiatrist, naturalist, former director of the *Museo de Historia Natural “Dr. Eugenio de Jesús Marcano”*, co-founder of the *Sociedad de Orquídeas de República Dominicana*, founding member of the *Academia de Ciencias de la República Dominicana* and author of *Las Aristolochias de la Isla La Española*.

Field and herbarium diagnostic characters:—*In vivo*, at anthesis, utricle slightly erect to slightly pendant, mostly horizontal, tube horizontal to slightly erect, limb erect at ca. 45° angle relative to the tube, spatulate, acute, apiculate, without a constriction between the tube and the limb, greenish to red-violet sagittate terminal patch, red-violet veins on white translucent cells at the base of the limb, long barbate trichomes extend from the revolute margins around the opening of the tube up (on each side) to the sagittate terminal patch. Flowers in herbarium specimens may conserve the original color, or the flower color may be cited in the label and, if mature flowers are present, the limb without constriction is easily discernable and some barbate trichomes may be present. Ultimately, herbarium specimens of the *A. marioniana* with accurate locality can be easily distinguished from *A. bilobata* and other species with plants bearing bilobate leaves because of the strictly allopatric distribution of the four species treated here (Fig. 4; *A. marioniana* is restricted to the Samaná Peninsula).

As pointed out above, *in vivo*, *Aristolochia marioniana* can be easily distinguished from *A. bilobata* based on the color of the flowers and the barbate trichomes that cover the base of the limb (Fig. 6 *versus* 11). Flower buds of *A. marioniana* start with the largest medial lobe abaxial (“1” in Pfeifer 1966: figure 2 therein; “a” in González 1999: 54, figure 12 therein).

In the populations of *Aristolochia marioniana* examined by the senior author, the patterns of red-violet veins on white at the base of the limb remain constant as does the greenish to red-violet sagittate patch on the apex. However, the density and length of the barbate, multicellular trichomes along the basal margin of the limb vary slightly (Fig. 12).

Iconography:—Apparently never illustrated before in the literature.

Additional specimens examined:—DOMINICAN REPUBLIC. Samaná province: Villa Adriana, La Guazuma, Las Galeras, growing on an ornamental specimen of the family Euphorbiaceae that grew on the sides of a walkway between the houses on the property, growing on a limestone marine terrace, several plants present both on the Euphorbiaceae and on nearby fern thickets, 16 April 2017, *E. Fernández 0101* (UASD). Villa Gran Bahía, 19 May 2017, *E. Fernández 111* (GH, in spirits).

Discussion

Preliminary results of a phylogenetic reconstruction based on genomic data including nearly all the species of *Aristolochia* found in Hispaniola and thousands of genetic markers by one of the authors (B. A. S. de Medeiros *et al.*, in preparation) indicate that species that bear bilobate leaves do not form a monophyletic group. *Aristolochia bilobata* and the three species described herein, the plants of which all bear bilobate leaves, are part of a clade with 100% bootstrap support that includes *A. samanensis* O.C. Schmidt (1935: 393), plants of which bear small oblong leaves. A separate and equally well-supported clade (i.e., 100% bootstrap support) includes *A. ekmanii* O.C. Schmidt (1927: 1) and *A. chasmema* Pfeifer (1966: 168), the plants of which bear small oblong leaves, but also an apparently undescribed species with bilobate leaves. These results indicate multiple transitions between leaf shape states in Hispaniola, which will be thoroughly discussed in the upcoming publication.

The present study is an example of the discoveries yet to be made in Hispaniola, and that unsuspected diversity may be revealed even in such showy, familiar plant genera as *Aristolochia*.

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References

- Acevedo-Rodríguez, P. (2005) Vines and climbing plants of Puerto Rico and the Virgin Islands. *Contributions from the United States National Herbarium* 51: 1–483.
- Alain, Hno. (1948) *Aristolochia clementis*. In: León, Hno. & Alain, Hno. (Eds.) Novedades de la flora cubana. *Revista de la Sociedad Cubana de Botánica* 5: 75–81.
- Bello, M.A., Valois-Cuesta, H. & González, F. (2006) *Aristolochia grandiflora* Sw. (Aristolochiaceae): desarrollo y morfología de la flor más larga del mundo. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 30 (115): 181–194.
- Bogarín, D., Pupulin, F., Smets, E. & Gravendeel, B. (2016) Evolutionary diversification and historical biogeography of the Orchidaceae in Central America with emphasis on Costa Rica and Panama. *Lankesteriana* 16: 189–200.
<https://doi.org/10.15517/lank.v16i2.26005>
- Brantjes, N.B.M. (1980) Flower morphology of *Aristolochia* species and the consequences for pollination. *Acta botanica Neerlandica* 29: 212–213.
- Brown, N.E. (1886) *Aristolochia ridicula* n. sp. *The Gardeners' Chronicle* N.S., 26: 360.
- Brown, R.W. (1954) *Composition of Scientific Words—A Manual of Methods and a Lexicon of Materials for the Practice of Logotechnics*. Published by the author, Baltimore, 883 pp.
- Chamisso, A. de (1832) De plantis in expeditione Romanzoffiana—Aristolochieae. *Linnaea* 7: 207–212.
- Cozzolino, S. & Widmer, A. (2005) Orchid diversity: an evolutionary consequence of deception? *Trends in Ecology and Evolution* 20: 487–494.
<https://doi.org/10.1016/j.tree.2005.06.004>
- Dauncey, E.A. & Larsson, S. (2018) *Plants that Kill—A Natural History of the World's Most Poisonous Plants*. Princeton University Press, Princeton, 223 pp.
- Duchartre, P.E.S. (1864) Aristolochiaceae. In: de Candolle, A. (Ed.) *Prodromus Systematis Naturalis Regni Vegetabilis* 15, Sect. 1. Victoris Masson et Filii, Parisiis, pp. 431–498.
- Dufrane, A. (1946) Papilionidae. *Bulletin et Annales de la Societe Entomologique de Belgique* 82: 101–122.
- Endress, P.K. (1990) Evolution of reproductive structures and functions in primitive angiosperms (Magnoliidae). *Memoirs of the New York Botanical Garden* 55: 5–34.
- Endress, P.K. (1996) *Diversity and Evolutionary Biology of Tropical Flowers*. Cambridge University Press, Cambridge, 511 pp.
- Felder, C. & Felder, R. (1864) Species lepidopterorum hucusque descriptae vel iconibus expressae. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* 14: 289–378.
- Giovannini, P. & Howes, M.R. (2017) Medicinal plants used to treat snakebite in Central America: Review and assessment of scientific evidence. *Journal of Ethnopharmacology* 199: 240–256.
<https://doi.org/10.1016/j.jep.2017.02.011>
- Givnish, T.J., Spalink, D., Ames, M., Lyon, S.P., Hunter, S.J., Zuluaga, A., Iles, W.J.D., Clements, M.A., Arroyo, M.T.K., Leebens-Mack, J., Endara, L., Kriebel, R., Neubig, K.M., Whitten, W.M., Williams, N.H. & Cameron, K.M. (2015) Orchid phylogenomics and multiple drivers of their extraordinary diversification. *Proceedings of the Royal Society B: Biological Sciences* 282: 1–10.
<https://doi.org/10.1098/rspb.2015.1553>
- Godart, J.B. (1823) Description de quelques espèces nouvelles de lépidoptères diurnes. *Mémoires de la Société Linnéenne de Paris* 2: 226–243.
- González, F. (1998) Two new species of *Aristolochia* (Aristolochiaceae) from Brazil and Peru. *Brittonia* 50: 5–10.
<https://doi.org/10.2307/2807710>
- González, F. (1999) *A phylogenetic analysis of the Aristolochioideae (Aristolochiaceae)*. Doctoral Dissertation, City University of New York, New York, 352 pp.

- González, F. & Stevenson, D.W. (2000) Gynostemium development in *Aristolochia* (Aristolochiaceae). *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 122: 249–291.
- González, F. & Pabón-Mora, N. (2015) Trickery flowers: The extraordinary chemical mimicry of *Aristolochia* to accomplish deception to its pollinators. *New Phytologist* 206: 10–13.
<https://doi.org/10.1111/nph.13328>
- González, F. & Pabón-Mora, N. (2018) Sinopsis actualizada de *Aristolochia* (Aristolochiaceae, Piperales) en Panamá. *Acta Botanica Mexicana* 122: 109–140.
<https://doi.org/10.21829/abm122.2018.1249>
- Heinrich, M., Chan, J., Wanke, S., Neinhuis, C. & Simmonds, M.S.J. (2009) Local uses of *Aristolochia* species and content of aristolochic acid 1 and 2—a global assessment based on bibliographic sources. *Journal of Ethnopharmacology* 125: 108–44.
<https://doi.org/10.1016/j.jep.2009.05.028>
- Hopffer, C. (1866) Neue Arten der Gattung *Papilio* im Berliner Museum. *Entomologische Zeitung* 27: 22–32.
- Hübner, J. (1816–1826) *Verzeichniss bekannter Schmettlinge*. Published by the author, Augsburg, 431 pp.
<https://doi.org/10.5962/bhl.title.48607>
- Jacquin, N.J. (1797) *Plantarum rariorum horti caesarei schoenbrunensis descriptions et icons*. C. V. Wappler, Wien, London & Leiden.
<https://doi.org/10.5962/bhl.title.332>
- Judd, W.S., Campbell, C.S., Kellogg, E.A., Stevens, P.F. & Donoghue, M.J. (2008) *Plant Systematics, A Phylogenetic Approach* Ed. 3. Sinauer Associates Inc., Sunderland, Massachusetts, 611 pp.
- Kickx, J. (1839) Sur le genre *Aristolochie*, et description d'une espèce inédite. *Bulletin de l'Académie Royale des Sciences et Belles-lettres de Bruxelles* 6, 2^{me} partie, No. 11: 450–455.
- Lamarck, J.B.A.P. de M. de. (1873) *Encyclopédie Méthodique, Botanique* 1. Panckoucke, Paris, 752 pp.
- Linnaeus, C. von. (1753) *Species Plantarum* 2. Laurentii Salvii, Holmiæ, 1200 pp.
- Linnaeus, C. von. (1763) *Species Plantarum*, Ed. 2, 2. Laurentii Salvii, Holmiæ, 1684 pp.
- Linnaeus, C. von. (1758) *Systema Naturae* Ed. 10, 1. Laurentii Salvii, Holmiæ, 824 pp.
- Mabberley, D.J. (2017) *Mabberley's Plant-Book*, ed. 4. Cambridge University Press, Cambridge, 1102 pp.
<https://doi.org/10.1017/9781316335581>
- Marión H., L. (2000) Dos especies de *Aristolochia* (Aristolochiaceae) nuevas para la ciencia. *Moscoso* 11: 1–6.
- Marión H., L. (2011) *Aristolochias de la Isla Española*. Jardín Botánico Nacional Dr. Rafael M. Moscoso and Academia de Ciencias de la República Dominicana, Santo Domingo, 108 pp.
- Marión, H.L. (2003) Una especie de *Aristolochia* (Aristolochiaceae) nueva para la ciencia. *Moscoso* 13: 18–21.
- Miller, P. (1754) *The Gardeners Dictionary [...] Abridged from the last folio edition, Ed. 4, 1*. Printed for the author, London, without pagination.
- Munroe, E.G. (1971) A new name for *Papilio zetes* (Westwood, 1847), nec Linnaeus, 1758 (Papilionidae). *Journal of the Lepidopterists' Society* (Los Angeles): 25: 142.
- Núñez Aguila, R. & Barro Cañamero, A. (2011) Los lepidópteros y su relación con otros organismos. In: Barro, A. & Núñez, R. (Eds.) *Lepidópteros de Cuba*. Spartacus Foundation y la Sociedad Cubana de Zoología, Santiago de Cuba, pp. 32–43.
- Oelschlägel, B., Gorb, S., Wanke, S. & Neinhuis, C. (2009) Structure and biomechanics of trapping flower trichomes and their role in the pollination biology of *Aristolochia* plants (Aristolochiaceae). *The New Phytologist* 184: 988–1002.
<https://doi.org/10.1111/j.1469-8137.2009.03013.x>
- Oelschlägel, B., Nuss, M., Tschirnhaus, M. von, Pätzold, C., Neinhuis, C., Dötterl, S. & Wanke, S. (2015) The betrayed thief—the extraordinary strategy of *Aristolochia rotunda* to deceive its pollinators. *The New Phytologist* 206: 342–351.
<https://doi.org/10.1111/nph.13210>
- Osorio, R. (2010) Ant dispersal in *Aristolochia serpentaria* (Virginia snakeroot). Available from: <http://rufino-osorio.blogspot.mx/2010/08/ant-dispersal-in-aristlochia.html> (accessed 10 December 2017)
- Otero, R., Nunez, V., Barona, J., Fonnegra, R., Jimenez, S.L., Osorio, R.G., Saldarriaga, M. & Diaz, A. (2000) Snakebites and ethnobotany in the northwest region of Colombia Part III: Neutralization of the haemorrhagic effect of *Bothrops atrox* venom. *Journal of Ethnopharmacology* 73: 233–241.
[https://doi.org/10.1016/S0378-8741\(00\)00321-4](https://doi.org/10.1016/S0378-8741(00)00321-4)
- Parodi, D. (1878) Contribuciones á la flora del Paraguay. *Anales de la Sociedad Científica Argentina* 5: 153–162.
- Pfeifer, H.W. (1966) Revision of the North and Central American hexandrous species of *Aristolochia* (Aristolochiaceae). *Annals of the Missouri Botanical Garden* 53: 115–196.
<https://doi.org/10.2307/2394940>
- Pfeifer, H.W. (1970) *A revision of the pentandrous species of Aristolochia*. The University of Connecticut Publication Series, Storrs, Connecticut, 134 pp.

- Pittier, H. (1926) *Plantas usuales de Venezuela*. Litografía del Comercio, Caracas, 458 pp.
- Plumier, C. (1693) *Description des plantes de L'Amérique [avec leurs Figures]*. L'Imprimerie Royale, Paris, 334 pp.
<https://doi.org/10.5962/bhl.title.119945>
- Rankin Rodríguez, R. & Greuter, W. (1999) Charles Plumier's drawings of American plants and the nomenclature of early Caribbean *Aristolochia* species (Aristolochiaceae). *Taxon* 48: 677–688.
<https://doi.org/10.2307/1223639>
- Rankin Rodríguez, R. (1998) Aristolochiaceae. In: Manitz, H. (Ed.) *Flora de la República de Cuba* 1 (2). Koeltz Scientific Books, Königstein, pp. 9–39
- Richard, A. (1850) Aristolochiaceae. In: de la Sagra, D.R. (Ed.) *Historia Física Política y Natural de la Isla de Cuba*, Botánica 11. Arthus Bertrand, Paris, pp. 194–195.
- Ruiz, H. (1805) *Memoria sobre las virtudes y usos de las planta llamada en el Perú bejuco de la estrella*. Imprenta de D. José del Collado, Madrid, 58 pp.
- Sakai, S. (2002) *Aristolochia* spp. (Aristolochiaceae) pollinated by flies breeding on decomposing flowers in Panama. *American Journal of Botany* 89: 527–534.
<https://doi.org/10.3732/ajb.89.3.527>
- Schnee, L. (1973) *Plantas comunes de Venezuela*. Universidad Central de Venezuela, Facultad de Agronomía, Aragua, 822 pp.
- Schmidt, O.C. (1927) *Aristolochia ekmanii*. In: Urban, I. (Ed.) *Plantae Haitiensis novae vel rariores IV a cl. E. L. Ekman 1924-26 lectae*. *Arkiv för Botanik* 21A (5): 1–2.
- Schmidt, O.C. (1935) *Beiträge zur Kenntnis der Aristolochiaceen V*. Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 12: 389–394.
<https://doi.org/10.2307/3994900>
- Scopece, G., Cozzolino, S., Johnson, S.D. & Schiestl, F.P. (2009) Pollination efficiency and the evolution of specialized deceptive pollination systems. *The American Naturalist* 175: 98–105.
<https://doi.org/10.1086/648555>
- Scopoli, G.A. (1777) *Introductio ad historiam naturalem, sistens genera lapidum, plantarum et animalium hactenus detecta, caracteribus essentialibus donata, in tribus divisa, subinde ad leges naturae*. Wolfgangum Gerle, Prague, 540 pp.
<https://doi.org/10.5962/bhl.title.10827>
- Seymour, R.S. (2010) Scaling of heat production by thermogenic flowers: limits to floral size and maximum rate of respiration. *Plant, Cell & Environment* 33: 1474–1485.
<https://doi.org/10.1111/j.1365-3040.2010.02190.x>
- Smith, D.E., Miller, L.D. & Miller, J.E. (1994) *The butterflies of the West Indies and South Florida*. Oxford University Press, Oxford, 264 pp.
- Stevens, P.F. (2001 onwards) Angiosperm Phylogeny Website. Version 12, July 2012 [and more or less continuously updated since] Available from: <http://www.mobot.org/MOBOT/research/APweb/> (accessed 10 December 2017)
- Suárez-Baron, H., Pérez-Mesa, P., Ambrose, B.A., González, F. & Pabón-Mora, N. (2016) Deep into the *Aristolochia* flower: expression of C, D, and E-class genes in *Aristolochia fimbriata* (Aristolochiaceae). *Journal of Experimental Zoology, B, Molecular and Developmental Evolution* 328: 55–71.
<https://doi.org/10.1002/jez.b.22686>
- Swartz, O. (1788) *Nova Genera et Species Plantarum seu Prodrromus*. Bibliopoliis Acad. M. Swederi, Holmiæ, Upsaliæ, & aboæ, 152 pp.
- Thiers, B. (2017 [continuously updated]) *Index Herbariorum: A global directory of public herbaria and associated staff*. New York Botanical Garden's Virtual Herbarium. Available from: <http://sweetgum.nybg.org/ih/> (accessed 10 December 2017)
- Wang, R., Xu, S., Liu, X., Zhang, Y., Wang, J. & Zhang, Z. (2014) Thermogenesis, flowering and the association with variation in floral odour attractants in *Magnolia sprengeri* (Magnoliaceae). *PLOS ONE* 9: e99356.
<https://doi.org/10.1371/journal.pone.0099356>
- Watts, B. (2017) *The field photographs of Alain H. Liogier: Plants of Hispaniola*. The New York Botanical Garden, Bronx, New York, 264 pp.