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Author: Ferrufino-Acosta, Lilian

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LILIAN FERRUFINO-ACOSTA¹

Taxonomic revision of the genus *Smilax* (*Smilacaceae*) in Central America and the Caribbean Islands

Abstract

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Smilax is a poorly understood genus, as the lack of agreement among the taxonomic treatments shows. Twenty-nine species of *Smilax* are recognised for Central America and the Caribbean region as the result of this study, much less than the total of c. 120 species described. Among the reasons leading to the recognition of an excessive number of species are a marked phenotypic variation, sexual dimorphism and the common occurrence of morphological intermediates. The treatment includes separate keys for the identification of flowering and fruiting material, synonymies with altogether 36 lectotypes and 5 neotypes designated here, one new combination published (*Smilax compta*), descriptions, drawings of 11 species, taxonomic notes, distribution maps and distributional data (including also the distribution area of the treated species beyond the actual study area) as well as common names and uses where known.

Additional key words: *Liliales*, taxonomy, nomenclature, Antilles, Mexico

Introduction

The family *Smilacaceae* Vent. essentially consists of the single genus *Smilax* L., comprising c. 350 species of mostly tropical and subtropical distribution. The *Smilacaceae* are included in the order *Liliales* (Takhtajan 1997; APG II 2003; Heywood & al. 2007). *Heterosmilax* Kunth, an Asiatic genus differing from *Smilax* by its connate tepals and variable number of stamens (3, 6, 9–12) with connate filaments, is sometimes recognised as distinct. However, based on molecular analyses (Cameron & Fu 2006) *Heterosmilax* is nested within *Smilax*, indicating that perianth fusion has evolved at least twice in *Smilacaceae*, perhaps in connection with a shift in pollinators. Based on morphological analyses, Chen & al. (2006b) proposed that the genus *Ripogonum* J. R. Forst. & G. Forst. (*Ripogonaceae*) is sister to *Smilacaceae*.

The genus *Smilax* produces rhizomes that are used in folk medicine and beer brewing, while the stems are used in crafts. Also, roots were exported widely from the Neotropics for use in the treatment of syphilis. Until now it was not clear which species of *Smilax* contain the active components because of phenotypic plasticity of the species in the Neotropics.

Several taxonomic studies, including various country-specific studies, have been conducted for the species of *Smilax* in Central America and the Caribbean Islands (Killip & Morton 1936; Morton 1962; Huft 1994; Grisebach 1864 for the British West Indian Islands; Standley 1937 for Costa Rica; Morton 1945 for Panama; León 1946 for Cuba; Standley & Steyermark 1952 for Guatemala; Gooding & al. 1965 for Barbados; Howard 1979 for the Lesser Antilles; Philcox 1983 for Trinidad and Tobago; Proctor 1984 for the Cayman Islands; Huft 2002 for Nicaragua) and in neighbouring regions (Sipman 1979 for Surinam; Gaskin & Berry 2005 for Venezuelan Guayana). Although diverse diagnostic characters have been used in these treatments, due to the limited geographical area covered by the authors (single islands or island groups, countries etc.) the taxonomy of the genus for the whole of Central America and the Caribbean could not be resolved.

Smilax is a taxonomically difficult genus because the plants are dioecious and show wide phenotypic variation. Furthermore, many of the specimens available for study in the herbaria lack flowers or fruits. Chen & al. (2006b)

¹ Botanischer Garten und Botanisches Museum Berlin-Dahlem, Freie Universität Berlin, Königin-Luise-Str. 6–8, 14195 Berlin, Germany; e-mail: l.ferrufino@bgbm.org

conducted a study of the pollen morphology of *Smilax* but did not find sufficient variation to discriminate between species. Ferrufino & Gómez-Laurito (2004) and Andreatta (1997) also did not find any differences in the pollen morphology of Neotropical species of *Smilax*. As a result, this study focusses on macromorphological characters.

The goals of the present revision are to clarify species circumscription, resolve synonymies and provide a means of identification.

Material and methods

The present study is based on c. 6000 specimens of herbarium material of *Smilax* from Central America, the Caribbean Islands and neighbouring areas deposited in A, B, BHUPM, BBS, BM, CAY, CR, EAP, F, FPDB, G, GH, HAC, HAJB, HBG, HULE, JE, M, MARP, MO, NY, P, SPMS, STRI, TEFH, U, UC, US and USJ (herbarium abbreviations following Thiers 2008+). Only selected collections are cited for each species. The entire list of the revised specimens is available from the author upon request.

Revision of historical specimens of B, BM and P was done with the material directly, while the revision of types and other historical collections at G and S is based on digital images. Identification of original material and the designation of type specimens were based on the respective protologues, specimen labels and annotations, identification of handwriting and the study of field books. Whenever possible, lectotypes and neotypes have been designated to clarify and stabilise nomenclature.

Field observations by the author on all Central American *Smilax* species during 2000–02 and 2007 have greatly contributed to the understanding of the morphology and plasticity of the species.

The taxonomy of *Smilax* in Central America and the Caribbean Islands provided here is based on the critical morphological analysis of the available material. It focusses on the shape of rhizomes, shape of stems (including presence and shape of prickles), leaves (including shapes of apex, base and margin, venation, petiole length and cross section shape), inflorescence type, peduncle length and colour, size of tepals, anthers and filaments, and shape, size and colour of fruits.

The species were classified in morphologically defined assemblages with the attempt to reflect natural relationships. The invalidly published sections of Killip & Morton (1936) were found to provide a suitable basis. These morphological hypotheses were tested in a molecular phylogenetic study of *Smilax* using plastid markers (*psbA-trnH* spacer, *trnL-trnF* region, *trnK-matK* region) and nr ITS (Ferrufino & al., in prep.).

Taxonomy

Smilax L., Sp. Pl.: 1028. 1753. – Lectotype (designated by Britton & Brown 1913: 527): *Smilax aspera* L.

Dioecious vines or shrubs. *Rhizomes* tuberous or elongated. *Stems* terete, quadrangular or angular, with or without prickles, terminal branches straight or zigzag (e.g. *Smilax spinosa*, *S. bona-nox*); axillary scales simple or double and overlapping on the stem. *Leaves* alternate, simple, ovate to lanceolate, cordate or pandurate (e.g. *S. bona-nox*), 5–7- or 7–9-veined, base acute or cordate (e.g. *S. subpubescens*, *S. mollis*), apex acute or acuminate, petiole terete, flattened or canaliculate with one pair of tendrils attached at the upper end of the sheathing base. *Inflorescence* a pseudumbellate cyme, solitary or aggregated in a raceme (e.g. *S. schomburgkiana*), often with brachiblasts as a replacement for scales, peduncles shorter or longer than petioles. *Flowers* actinomorphic, unisexual, trimerous, small whitish, brownish or pink. *Tepals* 6, free or connate, 1.5–2.5 mm (e.g. in *S. maypurensis* and *S. spinosa*) or 3.5–6 mm long (e.g. in *S. domingensis* and *S. febrifuga*), glabrous or pubescent or with apical hairs only (e.g. *S. mollis*), in two whorls, those of the first series ovate, of the second elliptic. *Stamina* with *anthers* dithecal, linear or elliptic in top- view, shorter or longer than filaments; *pollen* granulose, spinulose, subglobose; female flowers with staminodes. *Ovary* superior, (1–)3-merous, (1–)3-locular, styles often 3, usually free, sometimes partially united. *Berries* red to purple, reddish, orange or black, 6–12 mm in diameter. *Seeds* ovoid, reddish, orange or black.

Distribution. — A cosmopolitan genus of 200–300 species in temperate and tropical forests from sea level up to 3000 m. Twenty-nine species are recognised in Central America and the Caribbean Islands.

Phenology. — Several studies have focused on Neotropical climbers that include species of *Smilax* (Putz & Windsor 1987; Hegarty 1990; Ibarra-Manríquez & al. 1991; Morellato & Leitão-Filho 1996; Ippolito & Suárez 1998; Pérez-Salicrup & al. 2001). Ferrufino (2003) studied the phenology of five species of *Smilax*, viz. *S. domingensis*, *S. spinosa*, *S. vanilliodora*, *S. mollis* and *S. panamensis*, in three areas of Costa Rica from February 2001 to April 2002. She observed that the anthesis in male and female plants occurs between February and June but continues throughout the year. At the beginning of winter, female plants may carry fruits for 6–8 months, while male plants may have 2 or 3 flowering periods, which are very ephemeral compared to female plants. The advantage of variable flowering is the production of fruit with different maturation dates, which may increase dispersion. Ferrufino (2003) also found that the flowering times of some species overlap, which could contribute to hybridisation.

Uses. — *Smilax* is well-known for its use in folk medicine. Especially the roots, which were of great economic significance because of their use in the treatment of syphilis, were exported extensively from the Neotropics. Currently, the secondary compounds of various Neotropical *Smilax* are being studied for ethnobotanical

uses. *S. subpubescens* is used in construction and basket making.

Infrageneric relationships. – In the present work, the 29 species of the study area are classified and arranged in nine morphologically defined assemblages, which are, because of the geographically limited study area, treated for the time being as informal “species groups”. The species outside the study area belonging to these groups are included as “related species”. These species groups partly correspond to the invalidly published sections of Killip & Morton (1936) and have essentially been corroborated by the author’s molecular phylogenetic analysis of *Smilax* (Ferrufino & al., in prep.), where the infrageneric classification of *Smilax* will be dealt with in more detail.

Dichotomous keys to the species of *Smilax* in Central America and the Caribbean Islands

A. Key for flowering specimens of both sexes

1. Tepals 1.5–2 mm long 2
 - Tepals 3.5–6 mm long 15
2. Leaf margin usually spinulose, apex mucronate .. 3
 - Leaf margin entire, apex acute 11
3. Leaves lanceolate 4
 - Leaves cordate 15. *S. coriacea*
4. Stems terete 5
 - Stems angular 6
5. Leaves copper coloured. 17. *S. cuprea*
 - Leaves brownish or green 22. *S. populnea*
6. Stems glabrous 7
 - Stems muricate 9
7. Secondary venation laxly reticulate 8
 - Secondary venation tightly reticulate 14. *S. aquifolium*
8. Leaf blade often coriaceous, with (5–)7–11 robust prominent primary veins 19. *S. havanensis*
 - Leaf blade chartaceous, with 3–5(–7) thin primary veins 18. *S. gracilior*
9. Prickles blackish 16. *S. cristalensis*
 - Prickles brownish 10
10. Leaves obovate 23. *S. viscifolia*
 - Leaves lanceolate 20. *S. ilicifolia*
11. Peduncles shorter than the petiole .. 13. *S. spinosa*
 - Peduncles equal to sometimes longer than the petiole 12
12. Upper branches smooth 13
 - Upper branches muricate 14
13. Terminal branches flexuous 21. *S. oblongata*
 - Terminal branches straight 12. *S. guianensis*
14. Umbels in racemes 10. *S. schomburgkiana*
 - Umbels solitary 9. *S. compta*
15. Plants pubescent or tomentose, sometimes only when young and near petiole base; stems without prickles 16
 - Plants completely glabrous; stems armed with prickles 18

16. Branches obtusely quadrangular, sometimes pubescent at the base of the petioles ... 2. *S. subpubescens*
 - Branches terete, persistently pubescent 17
17. Adaxial leaf surface brownish or yellowish, abaxial surface tomentose-yellowish. 3. *S. velutina*
 - Adaxial leaf surface green, abaxial surface pubescent 1. *S. mollis*
18. Stems quadrangular or angled 19
 - Stems terete 21
19. Anthers shorter than the filaments .. 6. *S. officinalis*
 - Anthers longer than the filaments 20
20. Stems quadrangular; berries black ... 7. *S. regelii*
 - Stems angled; berries reddish . 11. *S. aristolochiifolia*
21. Leaves with main veins connected by parallel veins 25. *S. spissa*
 - Leaves with main veins connected by reticulate veins 22
22. Peduncles shorter than or equal to petioles 23
 - Peduncles longer than petioles 24
23. Leaves lanceolate or ovate, 5–7-veined from base 24. *S. domingensis*
 - Leaves linear or narrowly elliptic, 3-veined from base 5. *S. laurifolia*
24. Prickles acicular, blackish 8. *S. moranensis*
 - Prickles conical, greenish 25
25. Inflorescences in racemes; bracts persistent ... 26
 - Inflorescences solitary; bracts deciduous 27
26. Petioles with wings c. 2 cm long. . . 29. *S. syphilitica*
 - Petioles with wings c. 0.5 cm long .. 26. *S. febrifuga*
27. Leaf base auriculate or pandurate; berries glaucous 4. *S. auriculata*
 - Leaf base cordate or rounded; berries orange .. 28
28. Upper leaf surface shiny 28. *S. solanifolia*
 - Upper leaf surface opaque 27. *S. fluminensis*

B. Key for fruiting specimens

1. Plants pubescent, sometimes only when young and near petiole base; stems without prickles 2
 - Plants completely glabrous; stems with prickles .. 4
2. Branches obtusely quadrangular, sometimes tomentose at the petiole base 3
 - Branches terete, persistently pubescent .. 1. *S. mollis*
3. Leaf blades abaxially almost glabrous; berries orange 2. *S. subpubescens*
 - Leaf blades abaxially tomentose; berries reddish .. 3. *S. velutina*
4. Stems quadrangular, sometimes winged 5
 - Stems terete or obtusely angular, never winged .. 6
5. Berries red-orange 6. *S. officinalis*
 - Berries black 7. *S. regelii*
6. Stems obtusely angular 7
 - Stems terete 15
7. Leaves blade entire; peduncles longer than petioles; berries red 11. *S. aristolochiifolia*
 - Leaves blade dentate; peduncles shorter than petioles; berries red to black or dark purple 8
8. Stems glabrous 9

- Stems verruculose 14
- 9. Leaves blade chartaceous 10
- Leaves blade coriaceous 12
- 10. Leaf margin shallowly spinulose 11
- Leaf margin deeply spinulose .. 19. *S. havanensis*
- 11. Leaves obovate 23. *S. viscifolia*
- Leaves ovate 22. *S. populnea*
- 12. Secondary venation laxly reticulate 13
- Secondary venation tightly reticulate 14. *S. aquifolium*
- 13. Leaves cordate 15. *S. coriacea*
- Leaves obovate 18. *S. gracilior*
- 14. Prickles blackish 16. *S. cristalensis*
- Prickles brownish 20. *S. ilicifolia*
- 15. Leaves copper coloured, margin entire 17. *S. cuprea*
- Leaves brownish or green, margin spinose 16
- 16. Peduncles shorter than petioles 13. *S. spinosa*
- Peduncles equal or sometimes longer than petioles 17
- 17. Stems muricate 18
- Stems smooth 19
- 18. Inflorescences in racemes .. 10. *S. schomburgkiana*
- Inflorescences solitary 9. *S. compta*
- 19. Leaves with main veins connected by parallel veins 25. *S. spissa*
- Leaves with main veins connected by reticulate veins 20
- 20. Peduncles shorter than or equal to petioles 21
- Peduncles longer than petioles 22
- 21. Stems flexuous; berries black ... 21. *S. oblongata*
- Stems straight; berries red to black 24. *S. domingensis*
- 22. Berries glaucous 23
- Berries red to black 24
- 23. Leaves with 3(–5) principal veins; base acute 5. *S. laurifolia*
- Leaves with 5 principal veins; base auriculate 4. *S. auriculata*
- 24. Prickles acicular 8. *S. moranensis*
- Prickles conical 25
- 25. Inflorescences in racemes 27
- Inflorescences solitary 26
- 26. Bracts persistent; upper leaf surface shiny 28. *S. solanifolia*
- Bracts deciduous; upper leaf surface opaque 28
- 27. Petioles with wings c. 2 cm long ... 29. *S. siphilitica*
- Petioles with wings c. 0.5 cm long.. 26. *S. febrifuga*
- 28. Terminal branches flexuous 12. *S. guianensis*
- Terminal branches straight 27. *S. fluminensis*

I. *Mollis* group

Plants pubescent, unarmed; leaves glabrous or tomentose; inflorescences solitary; tepals c. 3.5–5 mm long with apical hairs; berries orange to red.

Includes: *Smilax mollis*, *S. subpubescens*, *S. velutina*.
Related species: *S. ecirrhata*, *S. hugeri*, *S. illinoensis*, *S.*

lasioneura, *S. pilosa*, *S. pseudochina*, *S. pulverulenta*, *S. tomentosa*.

1. *Smilax mollis* Humb. & Bonpl. ex Willd., Sp. Pl. 4: 785. 1806. – Holotype: Mexico, [“Xalapa” (according to Humboldt’s diary)], *Humboldt [& Bonpland]* 4444 (B-W 18403-1 [♀!]; isotypes: “Xalapa Nova Hispania”, P 603654 [♀!], P-Bonpl IDC 6209-1 #20 A6!).

= *Smilax triplinervia* Humb. & Bonpl. ex Willd., Sp. Pl.: 784. 1806. – Holotype: Venezuela, “rio Atabapo”, *Humboldt [& Bonpland]* (B-W 18399-1 [st.]; isotypes: P 00152434 [st.], P-Bonpl 6209-1 #20!).

= *Smilax angustiflora* A. DC. in Candolle & Candolle, Monogr. Phan. 1: 67. 1878. – Holotype: Costa Rica, “*Smilax tomentosa* H. & K., Rankend, Bl. hell-grün. Zu Korbgeflechten. Putará. Alto de la Cruz, Azarí”, 26.6.1857, *Hoffmann* 575 (B† [F, photo 10052, ♂!]; isotype: G-DC 204977-A [♂, fragm.]!).

= *Smilax candelariae* A. DC. in Candolle & Candolle, Monogr. Phan. 1: 70. 1878. – Holotype: Costa Rica, “*Smilax tomentosa* Kth., Candelaria in Costarica,” 16.6.1857, *Hoffmann* (B†; [F, photo 10054, ♀!]; isotype: G-DC 204977-B, lower half [fragm., ♀!]).

= *Smilax mollis* var. *acuminata* A. DC. in Candolle & Candolle, Monogr. Phan. 1: 68. 1878. – Lectotype (designated here): Mexico, Veracruz, “Région d’Orizaba”, 4.9.1866, *Bourgeau* 3038 (K 400952 [♀!]; isotypes: K 647277 [♀!], LE, P 647226 [♀!], US 01635980 [fragm.]!).

= *Smilax mollis* var. *pavoniana* A. DC. in Candolle & Candolle, Monogr. Phan. 1: 68. 1878 ≡ *Smilax pavoniana* (A. DC.) F. W. Apt in Repert. Spec. Nov. Regni Veg. 18: 400. 1922. – Holotype: Mexico, *Pavón* (G-BOIS).

= *Smilax pringlei* Greenm. in Proc. Amer. Acad. Arts 34: 567. 1899. – Lectotype (Killip & Morton 1936: 284): Mexico, “mountain Cañon near Cuernavaca, 6000 ft”, 20.11.1896, *Pringle* 7060 (GH 30072 [♀!]; isolectotype: MO140770 [mixed]!, US 00316793 [♀!]).

= *Smilax gymnopoda* F. W. Apt in Repert. Spec. Nov. Regni Veg. 18: 401. 1922. – Lectotype (Ferrufino & Gómez-Laurito 2004: 17): Mexico, Veracruz, “thickets near Jalapa, 4000 ft”, 14.4.1899, *Pringle* 8130 (GH 30065 [♂!]; isolectotypes: BM!, BR 6943790 [♂!], F 343671 [♂!], G 90074 [♂!], K 400950 [♂!], M 124478 [♂!], MO 140767 [♂!], P 647224 [♂!], UC 142672 [♂!], US 937826, 342784 [♂!], S 06-5851, USJ, W).

= *Smilax mollis* var. *hirsutior* Killip & C. V. Morton in Publ. Carnegie Inst. Wash. 461: 288. 1936 ≡ *Smilax hirsutior* (Killip & C. V. Morton) C. V. Morton in Brittonia 14: 307. 1962. – Holotype: Costa Rica, “Río Turrialba, Prov. Cartago, Costa Rica, 1600 pp”, 3.1894, *Smith* 4971 (US 00937827 [♂!]; isotype: GH 30069).

= *Smilax mollis* var. *congestiflora* C. V. Morton in Brittonia 14: 301. 1962. – Holotype: Mexico, “Pluma Hi-

- dalgo, Oaxaca, 1200 m”, 17.4.1917, *Reko & Conzatti 3084* (US 00892593 [♂!]).
- = *Smilax mollis* var. *villosa* C. V. Morton in *Brittonia* 14: 301. 1962. – Holotype: Mexico, “Oaxaca, Ubero, 30–90 m”, 1.4.1937, *Williams 9334* (US 01741305 [♀!]).
- = *Smilax gentlei* Lundell in *Wrightia* 3: 163. 1966. – Holotype: British Honduras, “Toledo District. Vine, berries red; in broken cohune ridge between Orange Point and Moho River”, 12.4.1952, *Gentle 7648* (TEX-LL 370271 [♀!]; isotypes: F 269898 [♀!], K 400954 [♀!], S 5803, TEX-LL 370270 [♀!]).

Rhizomes elongated. *Stems* terete, minutely pubescent or glabrous, unarmed, terminal branches straight. *Leaves* ovate to lanceolate, sometimes pubescent, membranaceous, chartaceous or rarely rugose, 9–16×4–10 cm, 7–9-veined, major veins connected by reticulate veinlets, apex acute, base cordate, margin entire; *petiole* 1–3.5 cm long, terete, pubescent. *Inflorescences* umbellate, solitary, scale single; bracts sometimes deciduous; *peduncle* 10–15 mm long, terete; *pedicels* of uniform length; tepals of male flowers 4–6 mm long, of female flowers 3.5–4.5 mm long; *anthers* linear in top-view, shorter than the filaments. *Berries* orange when ripe, not glaucous, ovoid, 8–12 mm in diameter.

Smilax mollis is characterised by a pubescent indumentum, absence of prickles, rounded stems, peduncles larger than the petioles and orange berries.

Distribution and habitat. — Mexico to Ecuador, Venezuela, Cuba (Fig. 2); montane and premontane wet areas, evergreen seasonal forest, 200–1200 m.

Variability. — This species varies widely in its vegetative and reproductive features. Several morphological characteristics were used to separate closely related species: large, tomentose flowers (e.g. *Smilax angustiflora*); longer and subappressed stem hairs (e.g. *S. gymnopoda*); peduncles shorter or longer than the petioles (e.g. *S. candelariae*, *S. angustiflora*). Although these characteristics are fairly conspicuous in some specimens, they vary widely and continuously, and thus do not merit taxonomic recognition. The same is true for species that were considered distinct simply because of their geographic distribution (e.g. *S. triplinervia* only known from the type material collected in Venezuela).

Note. — *Smilax pringlei* was described by Greenman (1899) and is characterised by glabrous leaves, staminate flowers, glabrous tepals and reddish petioles, which corresponds to *S. subpubescens*. The syntype specimens *Pringle 6843* and *7259* are indeed identified here as such. However, the lectotype *Pringle 7060* corresponds to *S. mollis* (berries), therefore, *S. pringlei* has to be treated as a synonym of *S. mollis*.

Common names. — “Zarzaparrilla cimarrona” in Cuba; “pate” in Honduras (León 1946; Nelson-Sutherland 2008).

Selected specimens examined. — BELIZE: Corozal, San Antonio, 9.1933, *Lundell & Gentle 4984* (A, NY, UC). — COLOMBIA: Choco, Riosucio, P.N. Los Catiós, 29.5.1976, *Forero & Jaramillo 1648* (MO); Valle del Cauca, Bajo Calima, Concesión Pulpapel/Buenaventura, 100 m, 3°55'N, 77°W, 26.11.1986, *Monsalve 1341* (MO). — COSTA RICA: Alajuela, San Ramón, Los Angeles, Reserva Biológica Alberto Manuel Brenes, 10°13'N, 84°37'W, 850 m, 2.2001, *Ferrufino 59* (USJ); Cartago, R. F. de Río Macho, sendero El Embalse, 9°46'35"N, 83°50'50"W, 1500 m, 3.6.1995, *Umana 692* (CR); San José, Acosta, Fila Bustamante, 9°44'22"N, 84°11'27"W, 1500–1600 m, 22.4.1995, *Morales & Urena 3997* (CR, INB). — CUBA: Pinar del Río, Guanahacabibes cercanías de la Jaula, 16.11.1976, *Bisse J. & al. 31123* (B, HAJB 33146, JE); Mariel, Tinaja, 11.6.1921, *Ekman E. L. 12890* (S). — GUATEMALA: El Progreso, Cabañas Albores, San Agustín, 14°57'N, 89°58'W, 1830 m, 17.5.2000 (F); Izabal, El Estor La Mina de Exmibal, al E del Estor, 15°31'N, 89°23'W, 50 m, 17.7.1988, *Tenorio & al. 14576* (MO). — HONDURAS: Atlántida, Esparta, 41.5 km E of Tela on the Tela-Atlántida Hwy then c. 6 km N along old timber road, 15°39'N, 87°16'W, 100–200 m, 24.4.1994, *Brant & Zúñiga 2919* (EAP); Yoro, valley of the Río Leán, Las Lomas, between San José de Texiguat and Suyapa de Leán, 15°33'N, 87°27'W, 80 m, 16.5.1991, *Davidse & al. 34452* (EAP). — MEXICO: Hidalgo, ± 14 km al SSW del Campamento El Gallo, sobre el camino a Atoyac, 17°25'N, 100°14'W, 1900 m, 26.1.1965, *Rzedowski & McVaugh 52* (MICH); Michoacán, Tancítaro, lado E-SE del Cerro La Cantera al N de Tancítaro, 19°22'40"N, 102°22'05"W, 2250 m, 6.6.1998, *Ruíz & Hernández 5208* (MICH); Veracruz, Tezonapa, a 6 km al noroeste de Motzorongo, 18°40'N, 96°40'W, 400 m, 28.2.1986, *Robles 411* (F). — NICARAGUA: Río San Juan, Castillo, refugio Bartola, parcela sobre el Río Bartola, 10°58'N, 84°40'W, 25.1.1995, *Rueda 3024* (HULE); Zelaya, along road from Siuna to El Dos, c. 1 km E of Cerro Livico; c. 13°46'N, 84°47'W, 400–600 m, 12.12.1980, *Stevens & Krukoff 18672* (NY). — PANAMA: Coclé: north of El Cope near continental divide, 8°38'N, 80°35'W c. 750 m, 8.4.1988, *McPherson 12436* (MO); Colón, road to Estación Calibrar Lluvia el Agua Clara 9°22'N, 79°42–45'W, 1300 m, 26.6.1971, *Webster & Dressler 16737* (MO); Panamá, Los Santos, above Guanico River, 7°20'N, 80°30'W, 550–650 m, 4.1.1989, *McPherson 13496* (F).

2. *Smilax subpubescens* A. DC. in Candolle & Candolle, *Monogr. Phan.* 1: 69. 1878. – Lectotype (designated here): Mexico, région d'Orizaba, St. Cristóbal, 8.7.1866, *Bourgeau 2578* (K 400524 [♀!]; isotypes: P 594653 [♀!] & 594654 [st.], US 01635979 [♀ fragm.]).

= *Smilax purpusii* Brandege in *Univ. Calif. Publ. Bot.* 6: 177. 1915. – Holotype: Mexico, Chiapas, “Cerro

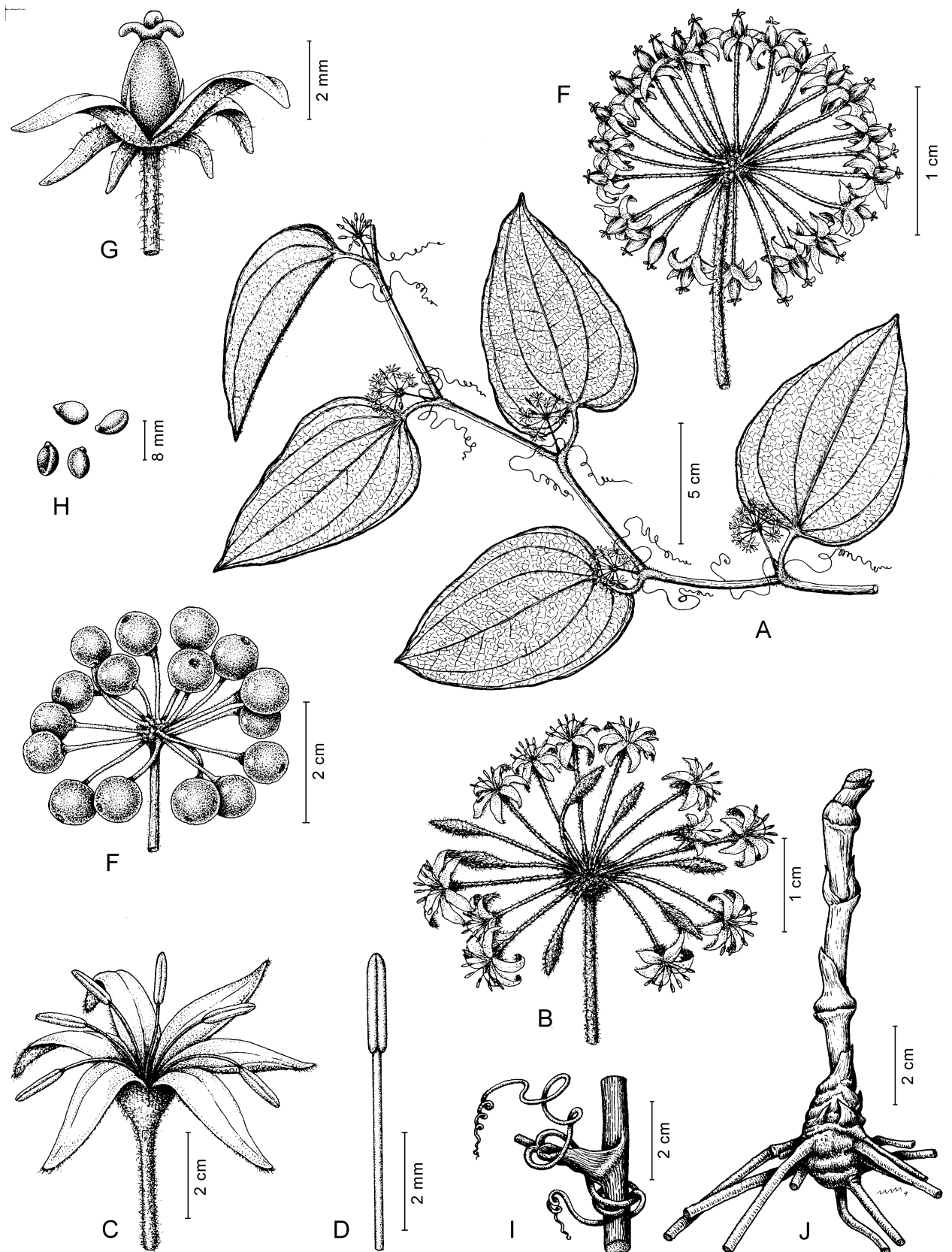


Fig. 1. *Smilax subpubescens* – A: staminate flowering branch; B: staminate inflorescence; C: staminate flower; D: stamen; E: pistillate inflorescence; F: infructescence; G: pistillate flower; H: seeds; I: stem segment; J: rhizome. – Drawn by P. Adam from *Breedlove 11114, 10938* (F), *Castillo & al. 2152* (F), *Román & Solórzano 12568* (F), *Ramírez 761* (F) and *Ferrufino & Masis 267* (B).

- del Boqueron”, 6.1914, *Purpus 7420* (UC [♀]!; isotypes: BM 796929 [♀]!, F 269945 [♀]!, G, GH 30073 [♀]!, MO 763417 [♀]!, NY 320001 [♀]!, UC 178141 [♀]!, US 00567614 [♀]!).
- = *Smilax calocardia* Standl. in Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 7. 1940. – Holotype: Panama, “Volcan de Chiriqui, Boquete District, Chiriqui Province, Republic of Panama, EL 7500 ft”, 13.7.1938, *Davidson 953* (F 343667 [♂]!; isotype: US 01791858 [♂]!).
- = *Smilax rufa* Lundell in Contr. Univ. Michigan Herb. 7: 4. 1942. – Holotype: Mexico, “Chiapas: Mt Male, near Porvenir”, 3200 m, 6.7.1941, *Matuda 4591* (MICH 1192732 [♀]!; isotype: TEX-LL 370275 [♀]!).
- = *Smilax occidentalis* C. V. Morton in Brittonia 14: 302. 1962. – Holotype: Mexico, Guerrero, “El Plato 800 m, District Galeana”, 28.6.1939, *Hinton & al. 14364* (US 01748850 [♂]!; isotypes: F 343688 [♂]!, MO 1268249 [♂]!, NY 319998 [♂]!, TEX-LL 370273, 370274 [st.]!).
- = *Smilax venosa* Lundell in Wrightia 3: 165. 1966. – Holotype: Mexico, “Chiapas: in advanced forest, Pinabeto, near Montozintla, 2585 m”, 7.5.1945, *Matuda 5426* (TEX-LL 370277 [♀]!; isotypes: F 269956 [st]!, S 7306, TEX-LL 370276 [♀]!).

Rhizomes elongated. Stems terete, glabrous, unarmed, young stems sometimes reddish, terminal branches straight. *Leaves* ovate, lanceolate, glabrous or rarely pubescent, chartaceous, 7–23 × 3.5–18 cm, 7–9-veined, major veins connected by reticulated veinlets, apex acute, base cordate, margin entire, young leaves sometimes reddish; *petiole* 1.5–5 cm long, the base sparsely tomentose. *Inflorescences* umbellate, solitary, scale single; *peduncle* 15–75 mm long, terete; *pedicels* of uniform length; *tepals* of male flowers 4–6 mm long, of female flowers 3.5–5 mm long; *anthers* linear in top-view, shorter than the filaments. *Berries* orange or red-orange when ripe, not glaucous, ovoid, 7–12 mm in diameter. – Fig. 1.

Smilax subpubescens is characterised by terete, unarmed stems, glabrous or sometimes pubescent leaves, red-tomentose petioles longer than the peduncles, c. 4–6 mm long flowers and orange to red berries.

Distribution and habitat. — Mexico to Panama (Fig. 4); cloud and montane forest, pine-oak forest, 900–2500 m.

Notes. — The species was described by Candolle (1878) in his protologue as having “spines” on the stems. However, the types cited here are unarmed and all material I saw of *Smilax subpubescens* also does not have spines.

Brandege (1915) found that *Smilax purpusii* seems to be close to *S. subpubescens*, but he did not address the differences between both species. I examined the type of *S. purpusii* and included the name in the synonymy of *S. subpubescens*, because morphological differences were

not evident. My examination of the type of *S. occidentalis* yielded the same result.

A specimen (13.7.1938, *Davidson 953*, MO 1194519) is labelled to be an isotype of *Smilax calocardia*. However, this fruiting specimen does not match the collection described in the protologue by Standley (1937), because his description was based on a male plant, the specimen therefore does not represent an isotype of this name.

Common names. — “Canyugo”, “bejuco de rueda”, “bejuco canasta”, “bejuco para adorno” in Central America (Ferrufino & Gómez-Laurito 2004; MacVean 2006; Nelson-Sutherland 2008).

Selected specimens examined. — COSTA RICA: Cartago, Oreamuno, descendiendo por la falda norte del Volcán Irázú, 10°04'00"N, 83°51'00"W, 2100 m, 6.1.1995, *Cascante & al. 455* (CR); Heredia, P. N. Brualio Carrillo, Estación Barba, 10°08'00"N, 84°06'00"W, 1100 m, 20.6.1990, *Apú 68* (CR, INB); Limón, Cordillera de Talamanca, 9°00'–9°12'N, 82°58'–82°59'W, 2400–2750 m, 13.9.1984, *Davidse & al. 29069* (CR, MO); San José, Dota, Cordillera de Talamanca, La Cima de Copey de Santa María de Dota, 9°40'35"N, 83°55'00"W, 1000 m, 7.6.1989, *Chavarria 402* (CR, INB). — EL SALVADOR: Ahuachapán, Laguna de las Ninfas, 13°54'N, 89°48'W, 1830 m, 16.1.1999, *Herrera 3756* (B); Santa Ana, P. N. Montecristo, 1500 m, 29.8.2000, *Carballo 117* (B). — GUATEMALA: Alta Verapaz, Carchá, aldea Chamtacá, 15°33'N, 90°12'W, 1300 m, 27.8.2002, *Rueda 17343* (HULE); Baja Verapaz, Rabinal at summit of Sierra de Chuacus, 15°01'N, 90°29'W, 1800 m, 25.1.1987, *Croat & Hannon 63650* (MO); El Progreso, cabañas Albores, San Agustín, 14°57'N, 89°58'W, 17.5.2000, *CECON CDC 1738* (HULE). — HONDURAS: Comayagua, Cordillera de Montecillos, trail between La Danta and Cerro San Juanillo, 14°32'N, 87°52'W, 1570 m, 5.5.1991, *Davidse & Hawkins 34217* (EAP); Intibucá, La Esperanza, Cordillera de Opalaca, 25 km NE de La Esperanza, 14°36'N, 88°18'W, 2005 m, 26.7.2007, *Sandoval & al. 1267* (TEFH); La Paz, R. B. Guajiquiro, 4.5 km al Noroeste de Guajiquiro, 14°09'N, 87°53'W, 2100 m, 22.5.1993, *Mejía 421* (TEFH, EAP). — MEXICO: Chiapas, Sierra Madre de Chiapas, Huixtla-Siltepec road, 20 km W of Hwy. 211 at turnoff to Siltepec, 15°28'N, 92°18'W, 2600 m, 19.6.1985, *Luteyn & Lebrón-Luteyn 11612* (MO, NY); Mexico; along Mexican highway 153 between Temascaltepec and Toluca, 53 km SW of Toluca, at the turnoff to El Polvorín, 19°03'N, 100°02'W, c. 2000 m, 26.4.1987, *Miller & Myers 2613* (MO); Oaxaca, Miahuatlán, San Jerónimo Coatlán, 15 km al N de Piedra Larga, sobre el camino a Progreso, 16°09'00"N, 97°01'00"W, 1300 m, 16.12.1987, *Torres & Campos 10863* (MO); Veracruz, vic. “La Calavera” 10 km N of Altotonga (13 km by road), on road to Tlapacoyán, 19°51'N, 97°13'W, 1350 m, 28.1.1980, *Nee & Hansen 18647* (NY). — NICARAGUA: Jinotega, Wiwilí, Reserva Cerro Kilambé, 13°34'N, 85°41'W, 1300–1500 m, 2.9.2000, *Rueda*

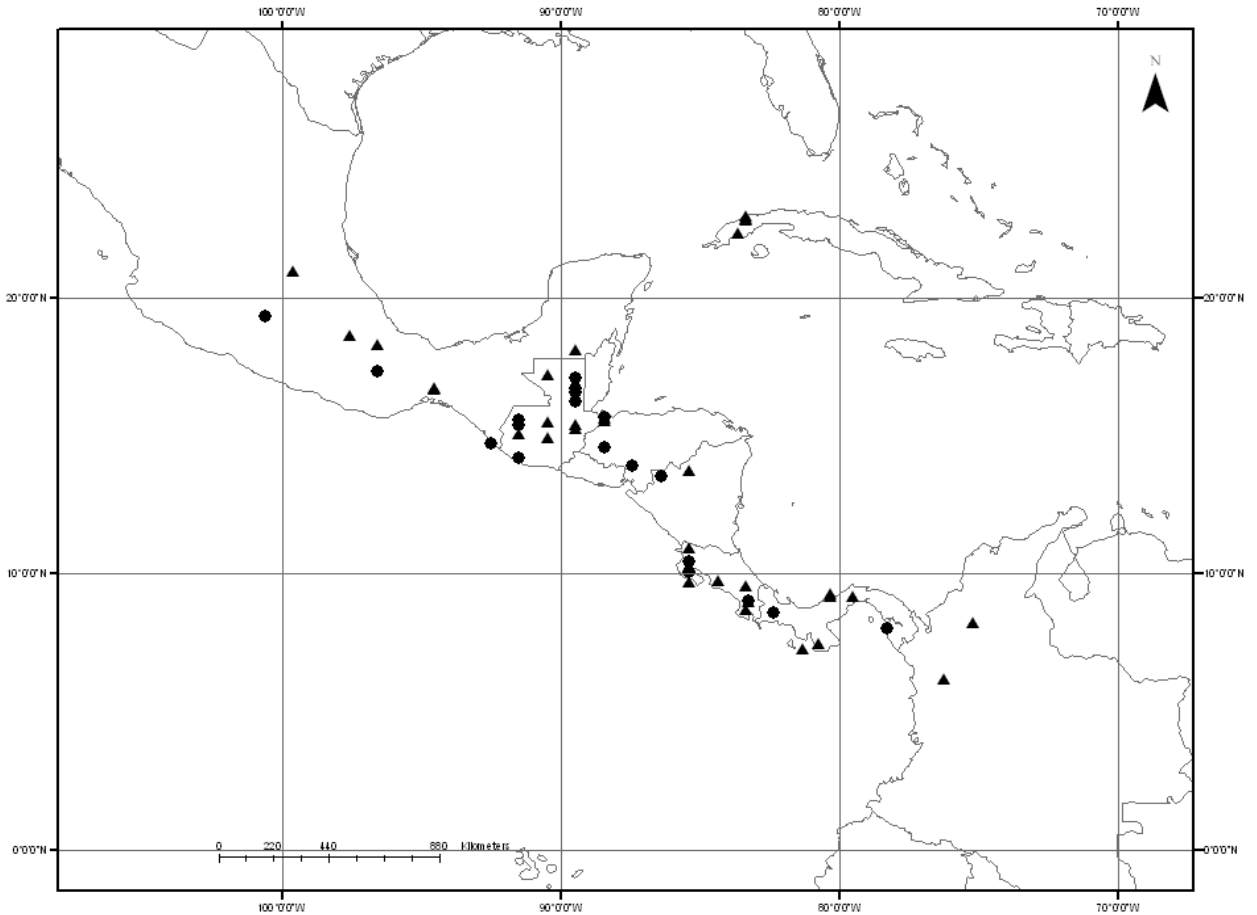


Fig. 2. Distribution of *Smilax mollis* (circles) and *S. velutina* (triangles).

14847 (HULE). — PANAMA: Bocas del Toro, Chiriquí border along ridge of Continental Divide NE of Cerro Pate Macho, above Palo Alto, 8°47'N, 82°21'W, 2200 m, 24.4.1982, Knapp & Schmalzel 4840 (MO, PMA); Chiriquí, hill E of Audubon Cabin, S of Cerro Punta, 8°52'N, 82°35'W, 1400–1800 m, 12.7.1983, Hamilton & Krager 3832 (F, G, PMA).

3. *Smilax velutina* Killip & C. V. Morton in Publ. Carnegie Inst. Wash. 461: 283. 1936. — Holotype: Mexico, Chiapas, “Finca Mexiquito”, 7.1913, Purpus 6930 (US 00567216 [♂]!; isotypes: BM 578839 [st.]!, F 269955 [st.]!, GH 30075 [♂]!, MO 741471 [♂]!, NY 320003 [♂]!, UC 173036 [♂]!).

Rhizomes elongated. *Stems* terete, pubescent, unarmed, terminal branches straight. *Leaves* ovate to lanceolate, lanate-tomentose, coriaceous, 6–16×3.5–9 cm, 7–9-veined, principal venation parallel, sometimes pubescent on the adaxial surface, connected by reticulate veinlets, apex acute, base cordate, margin entire, adaxial surface brownish, abaxial surface densely pubescent or tomentose; *petiole* 1.5–6 cm long, terete, yellowish tomentose, densely so at the base. *Inflorescences* umbellate, solitary, scale single; *peduncle* 1.5 cm long, terete, pubescent;

pedicels of uniform length, pubescent; *tepals* of male flowers 5–7 mm long, of female flowers 3.5–4 mm long, pubescent; *anthers* elliptic in top-view, shorter than the filaments. *Berries* orange or red-orange when ripe, not glaucous, ovoid, 10–15 mm in diameter.

Smilax velutina can be distinguished by the terete and pubescent stems, yellowish tomentose leaves, tepals of c. 5 mm length and reddish or orange berries. The adaxial leaf surface is glabrous and sometimes brownish in herbarium material, the abaxial surface very pubescent. This species has often been misidentified as *S. mollis* or *S. subpubescens*. It is related to *S. tomentosa*.

Distribution and habitat. — Mexico to Panama (Fig. 2); pine forest, cloud and montane forest, 2000–3300 m.

Selected specimens examined. — BELIZE: Augustine, Mountain Pine Ridge, 16°34'N, 88°54'W, 1500 ft, 6.4.1960, Hunt 436 (BM); Cayo, Chiquibul, San Pastor Pine Ridge, 16°43'N, 88°59'W, 600 m, 15.3.1997, Monro 1737 (BM, MO); Stann Creek, Sapon road, 10.10.1953, Gentle 8041 (F, MICH); Toledo, Maya mountains, directly N. of the junction of Richardson Creek and Bladen Branch, 16°33–35'N, 88°46'W, 300–620 m, 4., 6. & 8.3.1987, Dav-

idse & Brant 32113 (F, MO). — GUATEMALA: Alta Verapaz, Sierra de Chamá, Montaña Yalijux, Finca Chelemhá, Berggrat zum Mirador, 15°23'05"N, 90°04'33"W, c. 15 km Luftlinie NE von Tucurú, 2460 m, 28.3.2001, *Förther 10980* (BM, F); Chimaltenango, faldas del Volcán Acatenango, 2400 m, 27.11.1993, *Castillo & al. 2072* (F); El Progreso, Cabañas Albores, San Agustín, 14°57'N, 89°58'W, 1830 m, 17.5.2000, *CECON-CDC 10444* (F); Huehuetenango, between Ixcán and Finca San Rafael, Sierra de los Chuchumatanes, 24.7.1942, *Steyermark 49478* (F); Santa Rosa, Finca Buenos Aires, salida, Taxisco, 14°8'N, 90°18'W, 6.5.2001, *de MacVean 397* (F, HULE); Sololá, Santo Tomás Pachuj, San Lucas Toliman, 14°46'N, 91°12'W, 14.1.2001, *de MacVean 415* (HULE). — HONDURAS: Atlántida, Comarca de El Cabo, Río Leicus, 28 kms S. O. de Waspan, 66 m, 25.8.1965, *Molina 15203* (EAP); Comayagua, N of Siguatopeque, 1200 m, 17.4.1951, *Williams & Molina 18087* (EAP). — MEXICO: Chiapas, Mt Pasitar, 3–4.8.1937, *Matuda 1644* (A, MICH); Mexico, Montecristo, Chis, 1350 m, 17.6.1945, *Matuda 15943* (F); Oaxaca, Choapam, Yaveo, trail to arroyo Culebras, 480 m, 16.3.1938, *Mexia 9159* (G, GH, F, U, UC); Veracruz, entre Choapas y Chichon a unos 12 km de la primera cerca de los límites con Tabasco, 24.1.1970, *Lot 726* (GH). — NICARAGUA: Jinotega, Bocay, San Miguel de Kilambé, Reserva Natural Kilambé, 13°31'N, 85°37'W, 700–900 m, 6.1.2001, *Rueda & al. 15414* (MO); Nueva Segovia, Jalapa, subiendo por Buena Vista Chiquita, 13°58'N, 86°11'W, 23.7.2006, *Paguada 251* (HULE); Zelaya, vicinity of junction of road to Alami-kamba with road between El Empalme and Limbaika, 13°32'N, 84°30'W, 25 m, 24.2.1979, *Stevens & Krukoff 12771* (MO). — PANAMA: Bocas del Toro, ridge south of Campamiento Luchio, 9°05.052'N, 82°44.733'W, 1900 m, 20.3.2004, *Monron & Alfaro 4518* (MO); Chiriquí, near Cerro Colorado, c. 8°35'N, 81°45'W, 1500 m, 16.4.1986, *McPherson 8977* (MO, PMA); Darien, PN Darien, ridge between Rio Topalisa y Rio Pucuro c. 17 km E of Pucuro, La Laguna area, 8°03'5"N, 77°17'W, 750–850 m, 18.10.1987, *Cuadros & al. 3882* (PMA).

II. Glauca group

Plants glabrous, stems angular with flattened prickles, terminal branches zigzag; leaves membranaceous, acute, base truncate or pandurate, margin entire or dentate, sometimes glaucous; inflorescences solitary; tepals c. 4–5.5 mm long; berries purple or black and sometimes glaucous.

Includes: *S. auriculata* and *S. laurifolia*. Related species: *S. bona-nox*, *S. glauca*, *S. smallii*.

4. *Smilax auriculata* Walter, Fl. Carol.: 245. 1788. – Described from “Carolina”, no original material preserved; neotype (Ward 2008: 483): USA, South Carolina, Horry County, Myrtle Beach, 5.8.1939, *Godfrey & Tryon 1169* (GH 247991 [♀ photo]!; isoneotypes: BH, CA, CAS 292702, DUKE, F!, MO, NY, PH, US).

= *Smilax beyrichii* Kunth, Enum. Pl. 5: 207. 1850. – Holotype: USA, Carolina, *Beyrich* (B†; no isotypes found); neotype (designated here): USA, South Carolina, “Georgetown Country”, 21.11.2009, *Nelson 28065* (B 100299801 [♀]!; isoneotype: USC [♀]!).
= *Smilax lata* Small in Fl. S.E. U.S.: 284, 1329. 1903. – Holotype: USA, Florida, “Miami, Dade Co.”, 4.–7.4.1898, *Pollard & Collins 241* (NY 319988 [st.]!).

Rhizomes tuberous-elongated. *Stems* terete, glabrous, with short prickles and sometimes with blackish dots, straight, flattened, sometimes reddish, terminal branches zigzag. *Leaves* hastate, ovate, pandurate, sometimes glaucous abaxially, membranaceous, coriaceous, 2.5–8×0.7–5.5 cm, 5(–7)-veined, major veins connected by reticulate veinlets, apex acute, base hastate, acute or pandurate, margin entire, young leaves reddish; *petiole* 0.2–0.5 cm long, terete. *Inflorescences* umbellate, solitary, scale single; *peduncle* 0.5–2 cm long, flattened; *pedicels* of uniform length; *tepals* of male flowers 4–4.5 mm long, of female flowers 3.5 mm long; *anthers* linear in top-view, shorter than the filaments. *Berries* reddish (when) ripening, otherwise dark blue, purple bluish black or black, sometimes glaucous, ovoid, 9–12 mm in diameter. – Fig. 3.

Notes. — The type material of *Smilax beyrichii* at B was destroyed and isotypes could not be found. Material of *Beyrich* could also have been deposited at Schrader’s herbarium (BHUPM); however, *Beyrich*’s specimen of *Smilax* could not be located there. The specimen collected by *Nelson 28065* (B) is selected as neotype, because duplicates exist in other herbaria (e.g. USC) and it displays staminate flowers that match the original description.

Long & Lakela (1971) reported that the flowers of *Smilax auriculata* are fragrant. They considered the species to be closely related to *S. bona-nox*.

Distribution and habitat. — Louisiana, North Carolina, South Carolina, Florida, Alabama, Georgia, Missouri, West Indies (Bahamas) (Fig. 4); dunes and sandy flatwoods, open areas, 0–150 m.

Common names. — “Wild-bamboo” “dune greenbrier”, “earleaf greenbrier” in the USA (Holmes 2002); “Auricled greenbrier”, “China-brier” in the Bahamas (Britton & Millspaugh 1920).

Selected specimens examined. — BAHAMAS: Andros, Nicholl’s Town and Vicinity, 13.–15.3.1907, *Brace 6870* (F, NY); Grand Bahama, Freeport, 16.8.1974, *Correll & Kral 42922* (NY); Great Abaco, 3 miles south of Marsh Harbour airport, 1.1.1969, *Gillis 7436* (A); Nassau, 2.3.1905, *Wight 148* (F, NY); New Providence, New Providence, 18.2.1905, *Britton 3381* (F, NY). — USA: Florida, Lib-



Fig. 3. *Smilax auriculata* – A: pistillate flowering branches; B: pistillate inflorescence; C: pistillate flower; D: infructescence; E: seeds; F: staminate flowering branches; G: staminate inflorescence; H: staminate flower; I: stamen; J: stem. – Drawn by P. Adam from Curtiss 4779 (UC), Radford & Stewart 963 (UC), Demaree 10254 (UC), Small & Mosier 5812 (UC) and Nash 569 (UC).

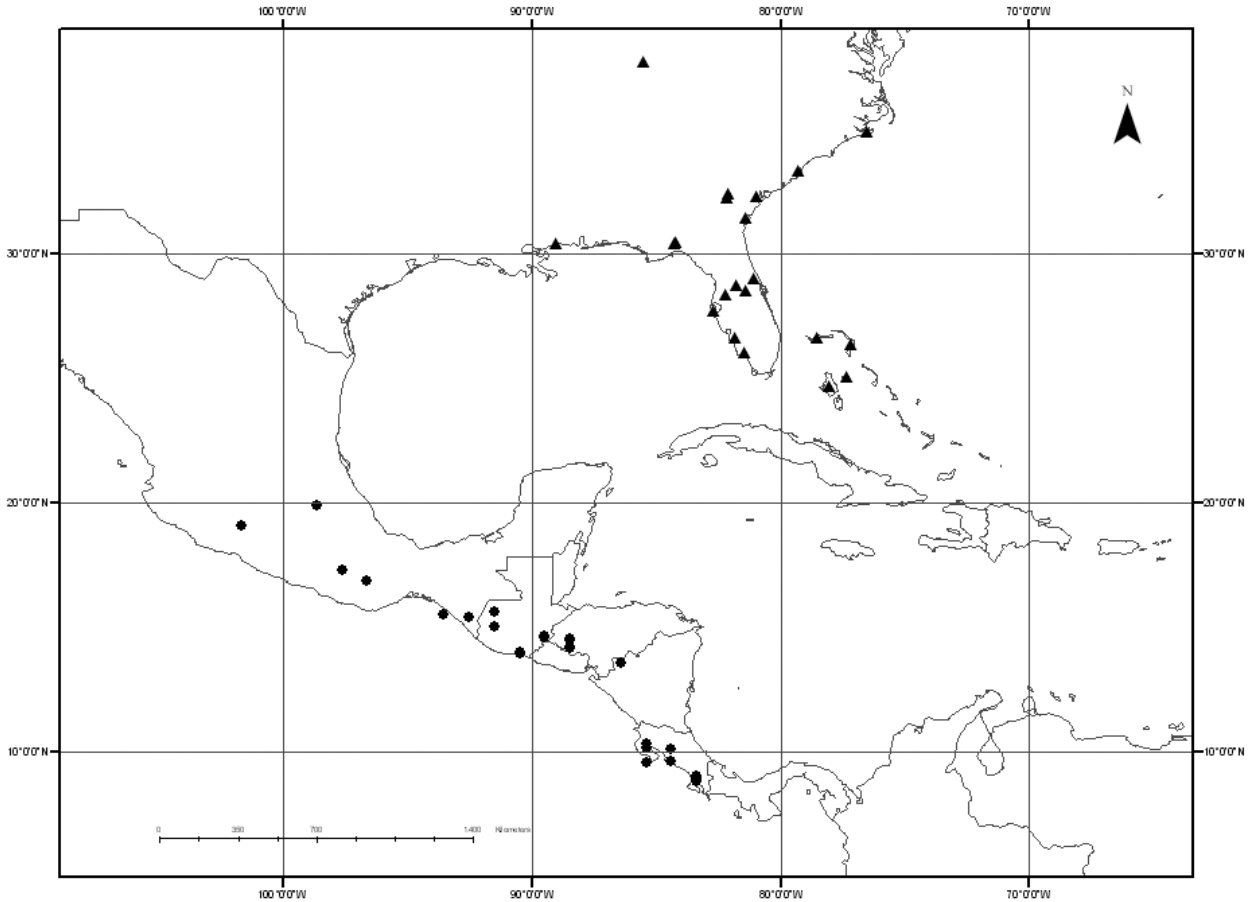


Fig. 4. Distribution of *Smilax subpubescens* (circles) and *S. auriculata* (triangles).

erty, 7.2 mi. E of Hosford on FLA 20., 30°24'N, 84°35'W, 19.5.1976, *Solomon 2077* (MO); North Carolina, Carteret county, Bogue Banks, vicinity of entrance to Ft. Macon State Park, Atlantic Beach, 17.3.1981, *Hill 9776* (NY); Mississippi, Harrison County, 6.1.1951, *Demaree 30676* (US); South Carolina, Georgetown County, 17.8.1939, *Godfrey & Tryon 1579* (NY); Georgia, Candler, SE of the town of Stillmore 3.7 km (2.3 miles) SE of the Emanuel County line on Stillmore road, 40 m, 30.5.1988, *Boufford & Wood 23884* (NY).

5. *Smilax laurifolia* L., Sp. Pl.: 1030. 1753. – Described from “Virginia, Carolina”; lectotype (Reveal in Jarvis 2007: 858): *Clayton 617* (BM 843000 [♀ photo]).

= *Smilax lanceolata* L., Sp. Pl.: 1031. 1753 ≡ *Smilax hastata* var. *lanceolata* (L.) Pursh, Fl. Amer. Sept. 1: 249. 1813. – Lectotype (Ferrufino-Acosta & Greuter 2010a: 287): “*Smilax tamnoides*”, herb. Clifford: 459, *Smilax* No. 2B (BM [st. photo 647496!]).

= *Smilax laurifolia* var. *bupleurifolia* Delile ex A. DC. in Candolle & Candolle, Monogr. Phan. 1: 99. 1878. – Holotype: “Carol. Sept. & Novemb. 1807”, *Delile* (MPU 14953 [♀!]).

= *Smilax alba* Pursh, Fl. Amer. Sept. 1: 250. 1813. – Type: USA, Carolina, June, *Walter* (possible in herb. Walter at BM).

Rhizomes tuberous. *Stems* terete, glaucous, armed with blackish flattened prickles, terminal branches straight; axillary scale single on the stem. *Leaves* ovate, lanceolate or elliptic, glaucous or minutely pubescent abaxially, coriaceous, 12×5 cm, 3(–5)-veined, major veins connected by reticulate veinlets, apex mucronate, base attenuate or rounded, margin entire, leaves turning brownish upon drying; *petiole* 0.7–1.5 cm long, terete. *Inflorescences* umbellate, scale single; *peduncle* 8–10 mm long, terete; *pedicels* of uniform length; *tepals* of male flowers 4–5 mm long, of female flowers 2.5–3 mm long; *anthers* elliptic, longer than the filaments. *Berries* black when ripe, glaucous, globose, 5–7 mm in diameter.

Note. — Fernald (1944) commented that “*Smilax laevis* Lauri folio” of Catesby was the best representation of the name *S. laurifolia*. He cited a specimen of *Clayton 617* deposited at BM and Reveal (in Jarvis 2007) designated this specimen as lectotype of *S. laurifolia*.

The drawing of *Smilax laurifolia* by Catesby does not provide extensive details; in fact, it does not even contain major features. Despite this, it gives us a good illustration of the species described by Linnaeus.

For *Smilax lanceolata*, Reveal & Jarvis (2009) designated the illustrations of Plukenet, *Phytographia*: t: 110,

f.4. 1691, as lectotype and a specimen of *L. B. Smith & A. R. Hodgson* from Virginia as epitype. The protologue of *S. lanceolata* by Linnaeus, however, does not correspond with Plukenet's illustration and Linnaeus used a question mark, revealing that he was not sure about the number of the figure. Ferrufino-Acosta & Greuter (2010a) found a mislabelled specimen in the Clifford herbarium (BM). They identified this specimen as the single extant original element on which Linnaeus based *S. lanceolata*. Therefore, they designated it as lectotype and confirmed its use as a synonym of *S. laurifolia*.

Distribution and habitat. — Bahamas, Cuba, USA (Fig. 21); swamps, bays, riparian forest, 0–80 m.

Common names. — “Raíz de China”, “laurel”, “bamboo vine”, “laurel greenbrier” in Cuba; “laurel greenbrier”, “blaspheme vine” in the USA (León 1946; Holmes 2002); “Laurel-leaved greenbrier” in the Bahamas (Britton & Millspaugh 1920).

Selected specimens examined. — BAHAMAS: Andros, Coppice, near Staniard Creek, northern section, Andros, 1.–3.2.1910, *Small & Carter 8858* (F); Grand Bahama, in freshwater sink in pinelands along Midshipman road, 11.9.1979, *Correll & Correll 50950* (MO, F); New Providence, border of swamp, 12.9.1904, *Britton & Brace 703* (F). — CUBA: La Habana, Habana, 27.6.1917, *León Hno. 7273* (GH); Matanzas, Ciénaga de Zapata, Laguna “asiento Viejo”, 22°23'06"N, 81°24'17"W, 5 m, 16.2.2002, *Greuter & al. 25865* (B). — USA: Arkansas, Ouachita, 230 ft, 7.3.1975, *Demaree 69872* (MO); Florida, Okaloosa, Eglin Air Force Base, 30°26'13"N, 86°47'19"W, 20 m, 4.6.1998, *Miller & al. 9515* (MO, B); Louisiana, Claiborne Parish, c. 7 mi. W of junction City on Stateline Road, 31.7.1991, *Holmes 5414* (F); Natchitoches, 8.10.1915, *Palmer 8906* (MO); New Jersey, Hammonton Lake, Atlantic Co., 25.10.1922, *Bassett s.n.* (NY); North Carolina, Craven, Croatan National Forest, Pocosins, 34°55'32"N, 77°04'58"W, 22.10.1998, *Stone & Bodine 1648* (MO); Mississippi, Ocean Springs, 30.7.1896, *Jackson Pollard 1137* (NY, MO, F); South Carolina, W side of S 1032, about 1 mi S of Berkeley country line, 13.8.1993, *Nelson & Horn 14703* (F); Texas, Houston, Grapeland, 26.3.1918, *Palmer 13189* (US, B); Virginia, Norfolk, 23.9.1892, *Heller 752* (MO).

III. Medica group

Plants glabrous, stems square with or without wings, with flattened prickles; inflorescence racemose; tepals c. 4–7 mm long; berries red or purple.

Includes: *Smilax officinalis* and *S. regelii*. Related species: *S. longifolia*, *S. spicata*.

6. *Smilax officinalis* Kunth in Humboldt & al., Nov. Gen. Sp. 1, ed. 4^o: 271; ed. f^o: 215. 1816. – Lectotype (designated here):

Colombia, “Sarza, *Smilax sarzaparilla*, río Magdalena, Bojorque”, 5.1801, [*Humboldt & Bonpland*] 1582 (P-Bonpl IDC 6209-1 #20 A6 [st.]; isoelectotype: P 83427 [st.]).

- = *Smilax vanilliodora* F. W. Apt in Repert. Spec. Nov. Regni Veg. 18: 416. 1922. – Lectotype (Killip & Morton 1936: 271): Costa Rica, “Hacienda El Guayabo cerca de Turrialba (Atlántico), 600–700 m, Gómez (B 100086422 [♀]; isoelectotype: US 01635984 [fragm.]).
- = *Smilax bernhardi* F. W. Apt in Repert. Spec. Nov. Regni Veg. 18: 418. 1922. – Lectotype (designated here) Costa Rica, cult. Berlin Bot. Gard. (B 100366363[♂])
- = *Smilax gilgiana* F. W. Apt in Repert. Spec. Nov. Regni Veg. 18: 417. 1922. – Holotype: Costa Rica, Desmontes de Guácimo, 120 m, 8.1901, *Tonduz 14639* (B 86421 [rootstocks only]).
- = *Smilax tonduzii* F. W. Apt in Repert. Spec. Nov. Regni Veg. 18: 414. 1922. – Holotype: Costa Rica, “au bord du Río Ciruelas, 15.3.1890, *Tonduz 2233* (B 86420 [st.]).
- = *Smilax barbilla* Cufod. in Arch. Bot. Sist. 9: 186. 1933. – Lectotype (designated here): Costa Rica, “in regione Atlantica: ‘Waldeck’ ad viam ferream, 28 milia a Puerto Limón, ad silvar. margines prope Río Barbilla, scandens, volubiois, fl. viridi-lutei”, 40 m, 12.5.1930, *Cufodontis 658* (US 1637717 [♂]; isoelectotype: F 343655 [st.]).
- = *Smilax standleyi* Killip & C. V. Morton in Publ. Carnegie Inst. Wash. 461: 280. 1936. – Holotype: Costa Rica, “Los Ayotes, near Tilarán, provincia de Guanacaste”, 600–700 m, 21.1.1926, *Standley & Valerio 45557* (US 1254174 [♀]).
- = *Smilax chiriquensis* C. V. Morton in Ann. Missouri Bot. Gard. 29: 326. 1942. – Holotype: Panama, “Provincia de Chiriquí, valley of the upper Río Chiriquí Viejo, vine on trees, 25 ft.; fls. green”, 22.3.1940, *White 348* (US 1791114 [♂]; isotypes: MO 1601950 [♂], S 5802).

Rhizomes elongated. **Stems** quadrangular, glabrous, armed with flattened prickles, terminal branches straight and often unarmed. **Leaves** ovate, lanceolate, glabrous, coriaceous or membraneous, 10–23×2–14 cm, 7–9-veined, major veins connected by reticulate veinlets, apex acuminate, base acute or rounded, margin entire; petiole 0.5–4.5 cm long, flattened. **Inflorescences** umbellate, scales paired; **peduncle** 2–8 cm long, flattened; **pedicels** of uniform length; **tepals** of male flowers 5–7 mm long, of female flowers 3.5 mm long; **anthers** linear in top-view, shorter than the filaments. **Berries** red or orange-red when ripe, not glaucous, ovoid, 10–12 mm in diameter. – Fig. 5.

Notes. — I revised the original specimens of *Smilax officinalis* and *S. longifolia* (reported from Brazil and Venezuela); both species display identical stamens and berry



Fig. 5. *Smilax officinalis* – A: fruit bearing branch; B: pistillate inflorescence; C: pistillate flower; D: infructescence; E: seeds; F: staminate inflorescence; G: staminate flower; H: stamen; I: stem; J: stem with wings. – Drawn by C. Hillmann-Huber from *Croat & Hannon 63446* (MO), *van der Werff & Herrera 7114* (MO), *de Nevers & Cavagnaro 4800* (MO), *Ferrufino & Hernández 453* (B), *Ferrufino & al. 380* (B) and *Ferrufino 421* (B).

colour. However, the stems are different. *S. longifolia* has small, recurved, evenly dispersed prickles on the stems, whereas *S. officinalis* has large, straight and scattered prickles. Both are deemed to be closely related.

The holotype of *Smilax barbillana* at W is missing; the isotype at US was selected as lectotype, because the specimen has male flowers.

Distribution and habitat. — Nicaragua, Costa Rica, Panama, Colombia (Fig. 6); humid and montane forest, open areas, roadsides, 50–900 m.

Common names. — “Zarzaparrilla”, “sarsaparrilla”, “Saskecha” (for the bribri, in Costa Rica) (Ferrufino & Gómez-Laurito 2004).

Selected specimens examined. — COLOMBIA: Antioquia, Vereda Venados, P. N. Las Orquídeas, Quebrada Las Manzanares, 3°31'N, 76°18'W, 800–1000 m, 1.1.1995, *Pipoly & al.* 18238 (MO); Chocó, area of Baudó, 8.2.1967, *Fuchs & Zanella* 21831 (U); Quindío, Salento, 2450 m, 1.7.1984, *Renteria* 3351 (MO). — COSTA RICA: Alajuela, San Carlos, Aguas Zarcas, La Gloria, Coope San Juan, 10°32'N, 84°20'W, 150 m, 23.3.2001, *Ferrufino* 50 (USJ); Guanacaste, Liberia, P. N. Guanacaste, Estación Cacao, Sendero Arenal, 10°55'4"N, 85°28'10"W, 1100 m, 9.2.1995, *Lobo* 27 (CR, INB); Heredia, P. N. Braulio Carrillo, Estación El Ceibo, 10°19'45"N, 84°04'50"W, 450–600 m, 7.10.1989, *Zumbado* 2 (CR, MO); Limón, below La Palma, along the Rio Claro (upper Rio La Hondura), 10°03'N, 83°58'W, at about 1000 m, 1.1.1967, *Burger* 4134 (NY, CR); Puntarenas, Monteverde, canyon of Rio Guacimal, 10°18'N, 84°48'W, 1350 m, 21.3.1992, *Haber* 11085 (CR, INB); San José, Mora, Finca El Rodeo, Fila Diamante, 9°54'00"N, 84°16'00"W, 800–900 m, 13.12.1993, *Cascante & al.* 88 (CR). — HONDURAS: Cortés, Rio Lindo, near El Carrizal, 550 m, 12.4.1951, *Williams & Molina* 17820 (EAP). — NICARAGUA: Río San Juan, El Castillo, refugio Bartola, 10°58'N, 84°40'W, 25.1.1995, *Rueda* 3028 (HULE); Zelaya, El Zapote, 40 km al NE de Nueva Guinea, c. 11°49'N, 84°23'W, 130–150 m, 26.2.1984, *Sandino* 4751 (NY). — PANAMA: Chiriquí, Bugaba, Santa Clara, Hartmann Finca, 8°50'N, 82°44'W, 1300 m, 26.2.1985, *van der Werff & Herrera* 7114 (MO, PMA); Comarca de San Blas, El Llano-Cartí Rd. km 19.1, 9°19'N, 78°55'W, 350 m, 10.2.1985, *de Nevers & Cavagnaro* 4800 (MO, F); Darien, Chiriquí, 9°45'N, 82°15'W, 1000–1200 m, 26.9.1976, *Correa & al.* 2919 (PMA), Panama, P. N. Altos de Campana, 8°41'N, 79°57'W, 600–700 m, 20.2.1998, *Galdames & al.* 4133 (F); Veraguas, 6.4 km outside of Santa Fe, 5.5.1977, *Folson* 2977 (MO).

7. *Smilax regelii* Killip & C. V. Morton in Publ. Carnegie Inst. Wash. 461: 272. 1936 ≡ *Smilax grandifolia* Regel, Ind. Sem. Hort. Petrop. 1856: 16. 1856 & in Ann. Sci. Nat., Bot., ser. 4, 6: 73. 1856 [non Buckley 1843]. — Described from seed sent to St Petersburg by Riedel from

Brazil; neotype (Applequist 2005: 146): “*Smilax grandifolia* Rgl. ex horto bot. Petropolitano” (GH 30064 [♂]; isoneotype: K 98398).

- = *Smilax ornata* Lem. in Ill. Hort. 12: ad t. 439. 1865. — Described from material sent by Ghiesbreght from Mexico to Gent, Belgium, and cultivated in Europe; lectotype (designated here): [icon] “*Smilax ornata*” in Ill. Hort. 12: t. 439. 1865.
- = *Smilax utilis* Hemsl. in Hooker’s Icon. Pl. 26: ad t. 2589. 1899 [non C. H. Wright 1895]. — Lectotype (designated here): “Sarsaparilla from Jamaica Botanical Dept.”, 5.1898, *Morris* (K 524863 [♀!]; isolectotype: K 524864 [st.]).
- = *Smilax regelii* var. *albida* Killip & C. V. Morton in Publ. Carnegie Inst. Wash. 461: 273. 1936. — Holotype: Honduras, “Lancetilla Valley near Tela, Department of Atlántida, ‘Zarza’, wet thicket, large woody vine. Fruit white. Frequent”, 20–600 m, 6.12.1927–20.2.1928, *Standley* 53257 (US 1407607 [♀!]; isotype: F 333657 [♀!]).

Rhizomes elongated. *Stems* quadrangular, glabrous, armed with flattened prickles, terminal branches straight, often unarmed distally. *Leaves* ovate to lanceolate, glabrous, coriaceous or membraneous, 6–32×3–24 cm, 7–9-veined, major veins connected by reticulate veinlets, apex acuminate, base cordate or rounded, margin entire; *petiole* 0.5–4 cm, flattened, sheaths spinulose. *Inflorescences* umbellate, scale single; *peduncle* 1.5–10 cm, flattened; *pedicels* of uniform length; *tepals* of male flowers 2.5–3.5 mm long, of female flowers c. 2 mm long; *anthers* ellipsoidal, longer than the filaments. *Berries* black or dark maroon when ripe, not glaucous, ovoid, 1–1.5 cm in diameter.

Affinities. — Killip & Morton (1936) stated that *Smilax regelii*, *S. aristolochiifolia* and *S. vanilliodora* (= *S. officinalis*) are, without doubt, closely related. *S. regelii* has sharply quadrangular stems and branchlets and can thus be clearly separated from *S. aristolochiifolia*, which has subterete or rounded-quadrangular stems. In the latter species, the berries are black, whereas in *S. aristolochiifolia* and *S. officinalis* they are red. In *S. aristolochiifolia*, the anthers, which are smaller than the filaments, are another useful feature to distinguish these species from each other. However, the species with (more or less) quadrangular stems offers only few diagnostic features, which is complicated by the fact that it is virtually impossible to identify sterile material accurately. Unfortunately, the majority of herbarium specimens is sterile.

Distribution and habitat. — Mexico to Honduras (Fig. 6); wet forest, premontane wet forest, pine-oak forest, 50–800 m.

Note. — Applequist (2005) concluded that no original Regel material of *Smilax grandifolia* can be located and

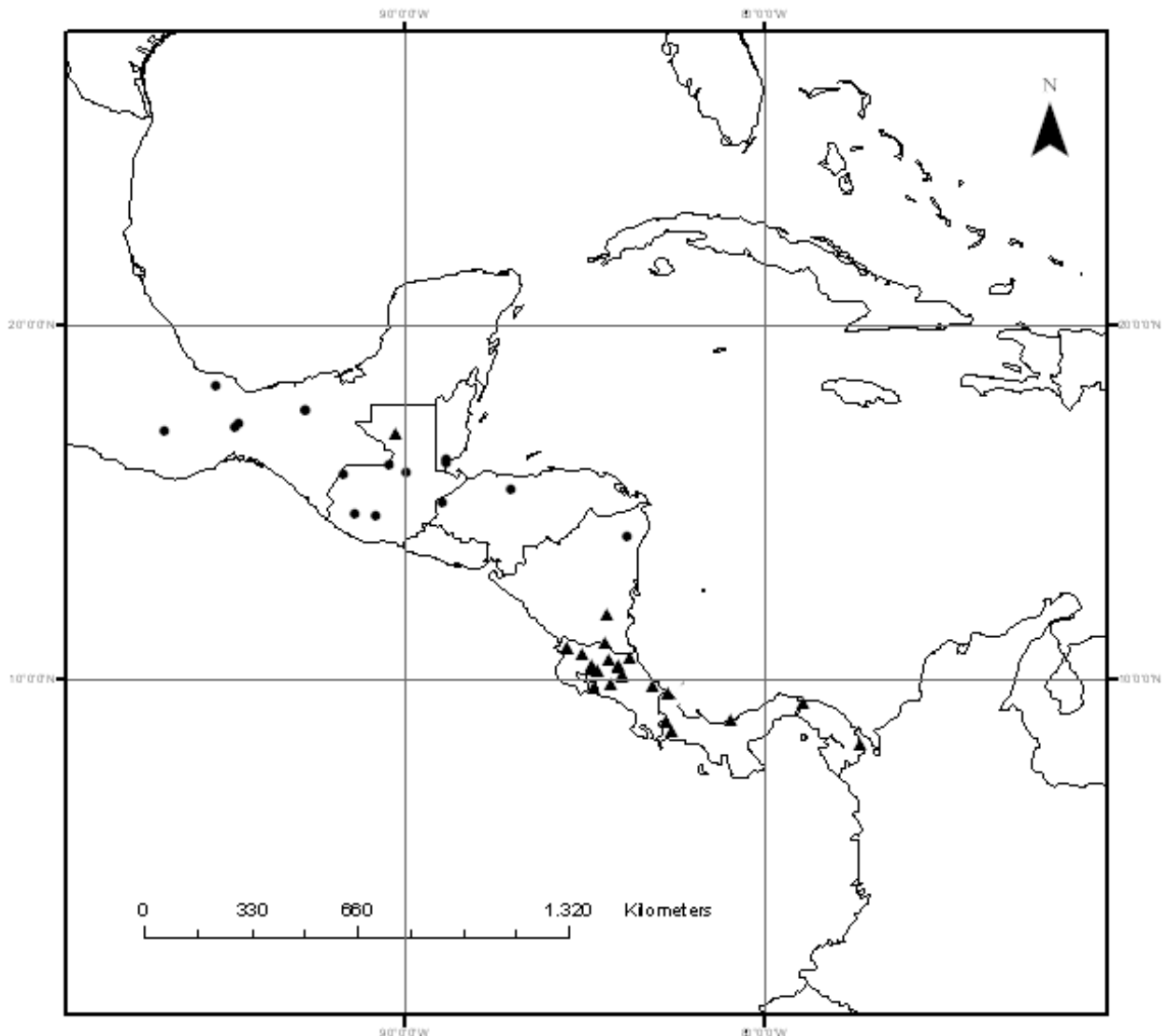


Fig. 6. Distribution of *Smilax regellii* (circles) and *S. officinalis* (triangles).

thus designated a neotype, acknowledging that the specimen had probably been seen by Regel and presumably originates from Central America.

Common names. — “Zarza”, “zarzaparilla”, “Honduras sarsaparilla”, “Jamaica sarsaparilla” (Killip & Morton 1936).

Selected specimens examined. — BELIZE: Jacinto, creek, 50 ft, 28.4.1934, *Schipp S-707* (F, G, K); Cayo, Ix Chel Farm. 17°61'N, 89°04'W, 1.12.1993, *Warrior & Romero 1864* (MO); Toledo, San Antonio-Punta Gords road, 14 miles, 7.4.1949, *Gentle 6702* (F, MICH, NY). — COSTA RICA: Cartago, Turrialba, Finca Aravar, tramo los Morados, Tayutic, 9°51'N, 83°54'W, 27.10.2000, *Masis 54* (HULE); Limón, Talamanca, Reserva Indígena kekoldi, 9°39'N, 83°6'W, 29.11.2001, *Masis 39* (HULE). — GUATEMALA: Alta Verapaz, along Río Sebol between Sebol and Carrizal, north of Sebol, 200–300 m, 18.4.1942,

Steyermark 45745 (F); Chimaltenango, Quisache, 1800 m, 5.–6.1.1939, *Standley 62025* (F); Huehuetenango, Nentón, orilla del Río Nentón, 800 m, 1.12.1996, *Castillo & al. 2804* (F); Izabal, Bay of Santo Tomás, between Escobas and Santo Tomás, 2 m, 13.4.1940, *Steyermark 39223* (F); Petén, Santa Elena, en orillando el camino para la Candelaria, a km 9, 19.10.1970, *Tún Ortíz 1382* (F, MICH, US); Sololá, Santo Tomás, 26.3.2000, *de MacVean 253* (HULE). — HONDURAS: Altántida, Tela, Lancetilla, 20–600 m, 6.12.1927–20.3.1928, *Standley 52745* (US); Colón, Trujillo, río Silin, 15°55'47"N, 85°53'29"W, 19.5.1980, *Saunders 285* (MO). — MEXICO: Chiapas, Tuxtla, Monte Grande, 7.11.1984, *Ventura & López 636* (F); Hidalgo, Jacala, near km 327 on highway between Santa Ana and Chapulhuacán, 12.7.1948, *Moore Jr 3960* (A); Oaxaca, Uxpanapa Region, 1.1 mi S of Esmeralda, 17°10'N, 94°45'W, 100 m, 19.1.1987, *Croat & Hannon 63289* (F); Tabasco, Lomas de San Sebastian, 18.3.1889, *Rovirosa 402* (NY, US); Veracruz, Jesús Car-

ranza, 17°16'N, 94°40'W, 120 m, 10.4.1982, *Vásquez & al.* V-2404 (NY); some km before Montepio, 18°38'N, 95°05'W, 2.5.1980, *Rooden 801* (U). — NICARAGUA: Río San Juan, Reserva Indio-Maíz, Municipio de el Castillo, 11°5'N, 84°15'W, 24.2.1997, *Rueda 6292* (HULE).

IV. *Hispida* group

Plants glabrous and armed with needle-like prickles; leaves glabrous, drying dark green or dark grey, margin sometimes minutely serrulate; inflorescence racemose; tepals c. 4–5.5 mm long; berries black.

Includes: *Smilax moranensis*. Related species: *S. herbacea*, *S. rotundifolia*, *S. tamnoides*.

8. *Smilax moranensis* M. Martens & Galeotti in Bull. Acad. Roy. Sci. Bruxelles 9: 389. 1842. — Lectotype (Killip & Morton 1936: 278): Mexico, Hidalgo, Morán, “Real del Monte”, 2100 m, 6.–10.1840, *Galeotti 5470* (P 603653 [st.]!; isolectotype: BR 9974630 [st.]!).

= *Smilax glaucocarpos* Schltld. in Linnaea 18: 450. 1845. — Lectotype (designated here): Mexico, “in tierra fria ad Hacienda del Carmen”, 8.1838–1840, *Ehrenberg* (HAL 63540 [♀, 2 sheets!]!).

= *Smilax acutifolia* Schltld. in Linnaea 18: 449. 1845. — Lectotype (designated here): Mexico, “prope Anganguco reg. frig.”, 11.1829, *Schiede* (HAL 71906 [♀]!).

= *Smilax jalapensis* Schltld. in Linnaea 18: 451. 1845. — Lectotype (designated here): Mexico, Veracruz, “in sylvis prope Jalapam”, 5.1829, *Schiede* (HAL 71862 [♀, 2 sheets!]!).

= *Smilax erythrocarpa* Kunth, Enum. Pl. 5: 234. 1850. — Lectotype (designated here): “Méjico, baccis rubris”, *Ehrenberg* (B† [♀, photo F 10058]!).

= *Smilax invenusta* Kunth, Enum. Pl. 5: 234. 1850. — Holotype: Mexico, “pr. el Banco”, 1.1839, *Ehrenberg 940* (B†; lectotype (designated here): HAL 71861 [♀, 2 sheets!]!).

= *Smilax schiedeana* Kunth, Enum. Pl. 5: 236. 1850 ≡ *Smilax cordifolia* var. *schiedeana* (Kunth) A. DC. in Candolle & Candolle, Monogr. Phan. 1: 84. 1878. — Holotype: Mexico, Veracruz, Jalapa?, [*Deppe & Schiede 989* (B† [st.]; lectotype (designated here): “in sylvis Xalapae altas arbores scandens.....”, HAL 101932 [st.]!).

= *Smilax sylvatica* Kunth, Enum. Pl. 5: 234. 1850. — Lectotype (Killip & Morton 1936: 279): Mexico, Veracruz, “in sylvis Papantlae” [with description, in HAL specimen], 1.1829, *Schiede 984* (B†; lectotype (designated here): HAL 101519 [♀+♂, 2 sheets!]!).

= *Smilax cordifolia* var. *papantlae* A. DC. in Candolle & Candolle, Monogr. Phan. 1: 84. 1878. — Lectotype (Killip & Morton 1936: 279): same as for *Smilax sylvatica*, above (B†).

= *Smilax botterii* A. DC. in Candolle & Candolle, Monogr. Phan. 1: 89. 1878 ≡ *Smilax jalapensis* var. *bot-*

terii (A. DC.) Killip & C. V. Morton in Publ. Carnegie Inst. Wash. 461: 280. 1936. — Lectotype (designated here): Mexico, Veracruz, Orizaba, 1857, *Botteri 467* (G 90070 [♂]!; isolectotypes: B†, BM 796925 [♂], K 400512-400511 [♂]!, P 603653 [♂]!, US 784816 [st.]!).

= *Smilax densiflora* A. DC. in Candolle & Candolle, Monogr. Phan. 1: 88. 1878. — Lectotype (Killip & Morton 1936: 277–278): Mexico, “Toluca in dit. Mexici”, *Andrieux 69* (G-DC 145867 [♀]!; isolectotypes: FI-W, K 400514-400516 [♀]!, M 124479 [♀]!) [type incorrectly cited as *Andrieux 9* in the protologue].

= *Smilax densiflora* var. *christmarensis* A. DC. in Candolle & Candolle, Monogr. Phan. 1: 89. 1878. — Holotype: Mexico, San Miguel, 1849, *Christmar* (B†; lectotype (designated here): US 1635976 [♀ fragm.]!).

= *Smilax moranensis* var. *schaffneriana* A. DC. in Candolle & Candolle, Monogr. Phan. 1: 88. 1878 ≡ *Smilax schaffneriana* (A. DC.) F. W. Apt in Repert. Spec. Nov. Regni Veg. 18: 408. 1922. — Lectotype (Killip & Morton 1936: 277): Mexico, Schaffner.

= *Smilax invenusta* var. *armata* A. DC. in Candolle & Candolle, Monogr. Phan. 1: 91. 1878. — Lectotype (Killip & Morton 1936: 279): Mexico, Veracruz, “Xalapa”, Galeotti [as “Gallotti”] (K 400953 [♂]!).

= *Smilax moranensis* var. *mexiae* Killip & C. V. Morton in Publ. Carnegie Inst. Wash. 461: 278. 1936. — Holotype: Mexico, “State of Jalisco Sierra Madre Occidental San Sebastián Arroyo de Santa Gertrudis”, 1500 m, 21.1.1927, *Mexia 1536* (US 1319300 [♀]!; isotypes: BM 885013 [♀]!, CAS 153132, F 333658 [♀]!, MICH 1145252 [♀]!, MO 970885 [♀]!, NY 319997 [♀]!, UC UC350408).

= *Smilax moranensis* f. *hispida* C. V. Morton in Brittonia 14: 306. 1962. — Holotype: Mexico, “Hidalgo; Chapulhuacan in wet Liquidamber forest”, 1300 m, 7.1937, *Lundell & Lundell 7163* (US 1688510 [♀]!).

Rhizomes elongated. *Stems* terete, obtusely angular or quadrangular, glabrous, armed with blackish, slender, acicular prickles, terminal branches straight. *Leaves* ovate, lanceolate, glabrous, membranous, 5–13×2–6 cm, 7–9-veined, major veins connected by reticulate veinlets, apex acuminate, base acute or rounded, margin entire or minutely erose-denticulate; *petiole* 0.4–1.5 cm long, flattened, purple to reddish. *Inflorescences* umbellate, solitary, scales paired; *peduncle* 0.8–3.5 cm long, flattened; *pedicels* of uniform length; *tepals* of male flowers 4–6 mm long, of female flowers 2.5–3.5 mm long; *anthers* linear in top-view, shorter than filaments. *Berries* black when ripe, not glaucous, ovoid, 6–8 mm in diameter.

Smilax moranensis can be identified by its terete stems, blackish needle-like prickles, petioles shorter than its peduncles and black berries.

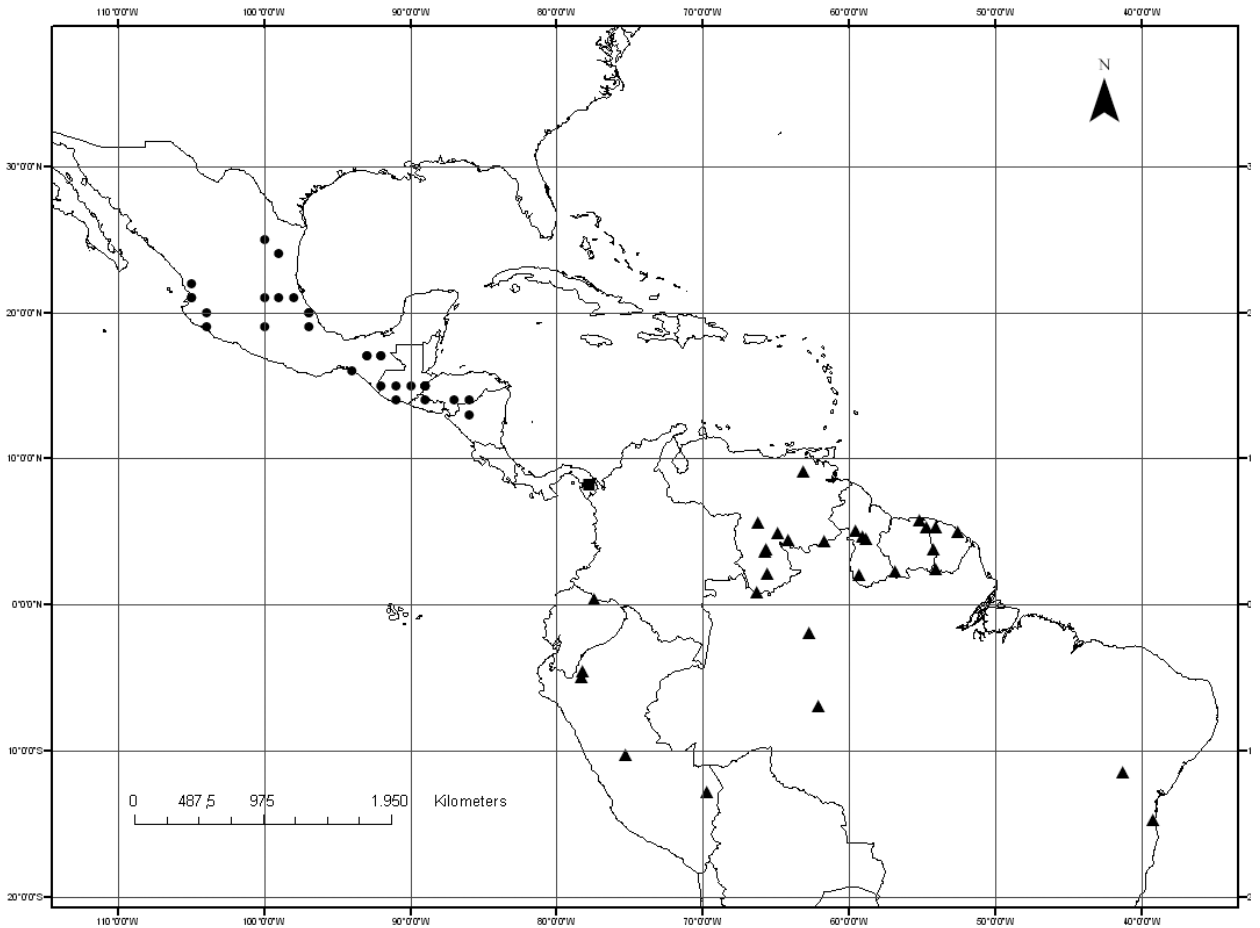


Fig. 7. Distribution of *Smilax moranensis* (circles), *S. compta* (square) and *S. schomburgkiana* (triangles).

Distribution and habitat. — Mexico to northern Nicaragua (Fig. 7); pine-oak forest, semi-evergreen seasonal forest, 800–1500 m.

Notes. — Candolle (1878), Killip & Morton (1936) and Huft (1994) noted that the examined specimens of *Smilax moranensis* are minutely erose-denticulate on the leaf margin. Killip & Morton (1936) contended that the key characteristics distinguishing *S. moranensis* from *S. jalapensis* are only minor, but even so, they believed that they could in fact be two different species. My critical analysis of the material, however, revealed, that both species cannot be distinguished. I therefore sunk *S. jalapensis* in the synonymy of *S. moranensis*.

In the protologue of *Smilax jalapensis*, Schlechtendal (1845) cites three syntypes collected in Mexico by Schiede. One of the three specimens in HAL carries fruits, the second one is sterile and the third is a seedling. The specimen with the female flowers and immature fruits was selected as lectotype.

Slechtendal (1845) described *Smilax glaucocarpos* and *S. jalapensis* and determined that they differ in that the first is armed, has terete stems, straight prickles, leaves with 5 veins and subglobose berries. The second species has few straight prickles, 7-veined leaves and obovate ber-

ries. In the protologue of *S. glaucocarpos*, two syntypes collected by Ehrenberg in Mexico are mentioned. The first is from “Tierra Fria ad hacienda del Carmen” (with fruits) and the second from “Mineral del Monte” (with flowers) (Schlechtendal 1845). In my opinion, *S. glaucocarpos* and *S. jalapensis* are not different and equally conspecific with *C. moranensis*. The fruiting specimen was selected as lectotype of the name *S. glaucocarpos* because it is more representative of the species.

The holotypes of *Smilax schiedeana* and *S. sylvatica* at B were destroyed. I have chosen a specimen referred to by Candolle (1878: 84) as lectotype of *S. schiedeana*, which is deposited at HAL (Code Art. 9.10, McNeill & al. 2006). For *S. sylvatica*, I selected a syntype as lectotype that belongs to the specimen HAL 101519 (Art. 9.12, McNeill & al. 2006). Both names are considered as synonyms of *S. moranensis*.

In the protologue of *Smilax moranensis* var. *mexiae*, Killip & Morton (1936) noted that this conspicuous variety is recognisable by its relatively broad, cordate-based leaves and slender fruiting pedicels. Here, this taxon is treated as a synonym of *S. moranensis*, because its features fall within the continuous variation of *S. moranensis*.

The type specimens of *Smilax erythrocarpa* and *S. densiflora* var. *christmarensis*, both located at B, were

destroyed. I chose the type photo at F as lectotype of *S. erythrocarpa* and the type fragment and photograph at US as lectotype for *S. densiflora* var. *christmarensis*. Both are also considered as synonyms of *S. moranensis*.

Candolle (1878) published *Smilax invenusta* var. *armata* and cited two syntypes, *Galeotii s.n.* and *Linden 48*. Killip & Morton (1936) designated *Galeotii s.n.* as lectotype. I considered the variety as a synonym of *S. moranensis*.

Both syntypes of *Smilax moranensis* var. *schaffneriana*, *Schaffner 159* (B) and *183* (B), were destroyed. Killip & Morton (1936) chose *Schaffner 159* as lectotype. A duplicate of *Schaffner 183*, located at MEXU, was established to be *Ranunculus hooheri* Schlecht. (*Ranunculaceae*).

The holotype of *Smilax invenusta* at B was destroyed. I selected an isotype deposited at HAL (Art. 9.10, McNeill & al. 2007) as lectotype.

Schlechtendal (1845) described *Smilax acutifolia* on two syntypes, *Schiede* and *Ehrenberg*, both at HAL. Here, the *Schiede* species is designated as lectotype.

Common names. — “Palo de vida”, “bejuco de la vida” in Mexico; “Kixcul”, “zarparrilla”, “corona de Cristo” in Guatemala and Honduras (Killip & Morton 1936; MacVean 2006; Nelson-Sutherland 2008).

Selected specimens examined. — EL SALVADOR: Santa Ana, Cordillera Miramundo, Mountain of Montecristo, 2000–2200 m, 27.–31.1.1966, *Molina & al. 16959* (EAP); P. N. Montecristo, 14°25'N, 89°21'W, 1900 m, 24.1.2002, *Monterrosa 191* (B). — GUATEMALA: Alta Verapaz, Coban, 4300 ft, 3.1886, *von Türckheim 890* (US); Zacapa, upper slopes along Río Repollal to summit of mountain, 2100–2400 m, 12.–13.1.1942, *Steyermark 42544* (F). — HONDURAS: Francisco Morazán, P. N. La Tigra, 22–25 km NE of Tegucigalpa, 14°12'N, 87°07'W, 1850–2125 m, 1.2.1987, *Croat & D'Arcy 64057* (EAP); Lempira, P. N. Celaque, El Súcte, 7 km al NE de San Manuel Colohete, 14°33'N, 88°42'W, 2400 m, 16.2.1993, *Mejía 270* (EAP, TEFH). — MEXICO: Villa Flores, 4.43 km al SE de Tres Picos, Reserva de la Biósfera La Sepultura, 16°12'0"N, 93°36'15"W, 1950 m, 19.4.2002, *Calónico 22821* (MO); Coahuila, about 35 miles east of Saltillo, 5–6 miles east of Los Lirios, 2300–2400 m, 27.5.1951, *McVaugh & Hoover 12332* (G); Hidalgo, Zacualtipán, Río Teponapa, 2000 m, 2.7.1947, *Moore Jr. 3237* (GH); near Trinidad Iron Works, 5800 ft, 1.5.1904, *Pringle 8898* (F, NY, U, US); Jalisco, Reserva Biosfera Sierra de Manantlan, 10.6 km N of El Terreno on the road to La Laguna, c. 35.5 km (by air) due NW of Colima, c. 38 km (air) WSW of Nevado Colima, 19°29'15"N, 103°57'53"W, 2463 m, 23.3.1989, *Wetter & al. 2053* (F, GH, UC); Nayarit, Tepic, Cerro San Juan, 21°29'N, 104°54'W, 1400 m, 17.10.1989, *Tellez & al. 12372* (MO); Nuevo León, Villa Santiago, Cañón Marisio Abajo Rancho Las Adjuntas, 27.6.1935, *Mueller 2067* (A); Morelos, near Cuernavaca, 6000 ft, 18.5.1898, *Pringle 2661* (US); Oaxaca, Puebla, Teotitlán del camino, Puerto de la Soledad por la carretera de Huautla de Jimén-

ez, 14.7.1991, *Gonzalez-Villarreal & al. 4170* (GH); Puebla, along Tehuacán-Orizaba highway on the western slopes below Puerto del Aire, 1800–2200 m, 18.7.1961, *Smith & al. 3899* (G, GH); Guanajuato, Xichú, El Puerto Chiquito, 2300 m, 23.4.1990, *Ventura & López 7905* (F); Sinaloa, Sierra Madre, 7.1897, *Rose 1636* (NY, US); Sonora, Cañón International, 23.8.1940, *White 3508* (GH); Tamaulipas, near large, loose rock formation near Rancho Gómez Farias, 4.1960, *Duke 3555* (MO); Veracruz, Huatusco, 1 km NW of Elotepec along (impasabla) road to Chichiquila, 19°12'N, 97°02'W, 1700 m, 17.1.1984, *Nee & Taylor 28895* (F). — NICARAGUA: Matagalpa, cloud forest at “Disparate de Potter” near Sta María de Ostuma, Cordillera Central de Nicaragua between Matagalpa and Jinotega, 1500 m, 20. & 24.2.1963, *Williams & al. 25066* (EAP, G); Jinotega, Wiwilí, Reserva Natural Cerro Kilambé, Comunidad Aguas Rojas, 13°33'N, 85°42'W, *Rueda 16736* (HULE).

V. *Schomburgkiana* group

Plants glabrous, stems terete or angular, muricate or verrucose; leaves glabrous; inflorescences mostly solitary, sometimes in racemes; tepals c. 2 mm long; berries red or purple.

Includes: *Smilax compta*, *S. schomburgkiana*. Related species: *S. bella*, *S. cordato-ovata*, *S. hilariana*, *S. japicanga*, *S. larvata*, *S. minarum*, *S. pilosa*, *S. stenophylla*, *S. subsessiliflora*, *S. verrucosa*.

9. *Smilax compta* (Killip & C. V. Morton) Ferrufino, **comb. & stat. nov.** ≡ *Smilax spinosa* var. *compta* Killip & C. V. Morton in Publ. Carnegie Inst. Wash. 461: 264. 1936. – Holotype: Panama, “forest on dry limestone in forests around Alhajuella, Chagres Valley”, 30–100 m, 12.–15.5.1911, *Pittier 3487* (US 678534 [♂]!); isotype: NY 320002 [♂]!).

Rhizomes unknown. **Stems** angular, verrucose, pubescent of hispid hairs, prickles fine, needle-like, terminal branches straight. **Leaves** lanceolate, glabrous, membranous, 5–20 × 1.5–5 cm, 5-veined, tertiary venation reticulate, apex acuminate, base acute or rounded, margin ciliate or entire; **petiole** 0.5–2 cm long, terete, muricate. **Inflorescences** umbellate, solitary, scale simple; **peduncle** c. 4 cm long, muricate; **pedicels** of different lengths; **tepals** of male flowers 2.5–3 mm long, of female flowers 2.5 mm long; **anthers** linear in top-view, as long as the filaments. **Berries** red to purple when ripe, not glaucous, ovoid, 0.8–10 mm in diameter.

Affinities. — *Smilax compta* is similar but not closely related to *S. spinosa*. From the latter species it can be clearly distinguished by its verruculose stems.

Distribution and habitat. — Panama (Fig. 7); wet forest, 30–1600 m.

Additional specimen examined. — PANAMA (Fig. 7); Darien, Borbua, Chucunaque, Yaviza, 8°11'N, 77°42'W, 5.6.1959, Stern & al. 97 (MO).

10. *Smilax schomburgkiana* Kunth, Enum. Pl. 5: 187. 1850. – Lectotype (Andreata 1997: 109): “Guiana Angl.”, *Schomburgk* 82 (K 400607 [♂]!; isolectotype: B 100248944 [♂]!).

= *Smilax pseudosyphilitica* Kunth, Enum. Pl. 5: 188. 1850. – Lectotype (designated here): Brasilia, *Lhotzky* (B 10-247550 [♂]!).

= *Smilax pseudosyphilitica* var. *foliosa* A. DC. in Candolle & Candolle, Monogr. Phan. 1: 157. 1878. – Lectotype (Andreata 1997: 109): Brasil, “a climber, bushy places near Maçêo”, 4.1838, *Gardner 1425* (K 400985 [♂]!; isolectotype: K 400984 [♂]!).

= *Smilax schomburgkiana* var. *gracilis* A. DC. in Candolle & Candolle, Monogr. Phan. 1: 156. 1878. – Holotype: Suriname, “ad ripas fluviorum”, *Kappler 1202* (G-DC 25139 [♂]!; isotypes: M 124483 [♂]!, P ex CN).

= *Smilax latipes* Gleason in Bull. Torrey Bot. Club 56: 19. 1929. – Holotype: British Guiana, “dense upland forest, Tumatumari”, 18.6.–8.7.1921, *Gleason 294* (NY 180350 [♂]!; isotypes: K 400603 [♂]!, US 1190931 [♂]!).

= *Smilax immersa* A. C. Sm. in Bull. Torrey Bot. Club 67: 284. 1940. – Holotype: British Guiana, “liana, perianth greenish, anthers white, Membaru Creek, upper Mazaruni River”, 3.10.1938, *Pinkus 37* (NY 180353 [♂]!; isotype: US 1775925 [♂]!).

Rhizomes tuberous. *Stems* terete, verruculose, prickles straight, terminal branches straight, axillary scales double, overlapping on the stem. *Leaves* ovate, lanceolate, glabrous, membranous, 8–20×3–7.5 cm, 5–7-veined, connected by reticulate veinlets, apex acute, base acute or rounded, margin entire; *petiole* 1.8 cm long, rounded, reddish. *Inflorescences* umbellate, arranged in racemes, rarely solitary; bracts prominent, perennifolious, scales paired; *peduncle* 1–4.5 cm long, flattened, thick; *pedicels* of uniform length; *tepals* of male flowers 2.5 mm long, of female flowers 1.5–2 mm long; *anthers* linear in top-view, shorter than the filaments. *Berries* orange when ripe, not glaucous, ovoid, 8–10 mm in diameter. – Fig. 8.

Smilax schomburgkiana is characterised by verruculose stems, its racemosely composed inflorescences, c. 2 mm long tepals and orange berries.

Distribution and habitat. — Ecuador, Peru, Venezuela, Guyana, French Guiana, Suriname, Brazil (Fig. 7); roadsides, open areas, evergreen seasonal forest, lower montane forest, 50–500 m.

Notes. — Kunth (1850) described *Smilax schomburgkiana* as a glabrous, unarmed plant with straight, terete

stems and ovate-oblong, 5-veined leaves. The type specimen at B has no fruits, only peduncles and sparsely prickled branches.

Andreata (1997) proposed *Smilax schomburgkiana*, *S. syphilitica* var. *aequatorialis*, *S. pseudosyphilitica* var. *pseudosyphilitica*, *S. aequatoriales*, *S. schomburgkiana*, *S. schomburgkiana* var. *gracilis* and *S. schomburgkiana* var. *foliosa* as synonyms of *S. syphilitica*. She asserts that several authors have tried to distinguish *S. schomburgkiana* from *S. syphilitica* based on the tuberculate stems of *S. schomburgkiana*. Nevertheless, in this study *S. schomburgkiana* and *S. syphilitica* are recognised as two distinct taxa, whereas *S. pseudosyphilitica*, *S. schomburgkiana* var. *foliosa* and *S. schomburgkiana* var. *gracilis* are treated as synonyms of *S. schomburgkiana*.

Gleason (1929) suggested that the habitat of *Smilax latipes* is very similar to that of *S. schomburgkiana*. With regard to morphological features, I have found *S. latipes* to have longer flowers and broader filaments than *S. schomburgkiana*. In the type specimen, the tepals are c. 2.5 mm long, whereas in Flora of Surinam, Sipman (1979) described *S. latipes* as having tepals c. 5 mm long and orange fruits. It is therefore quite likely that the specimens examined by Sipman were confused with *S. febrifuga*. In the present study, *S. latipes* is considered a synonym of *S. floribunda*.

Smith (1940) introduced *Smilax immersa*, distinguishing it from *S. schomburgkiana* and *S. pseudosyphilitica* by the presence of immersed veinlets. I examined the type of *S. immersa* and consider the name as a synonym of *S. schomburgkiana*.

Common names. — Tu-pata-yén (Arekuna) in Venezuelan Guayana; “liane bagou” in French Guiana (Gaskin & Berry 2005; Mitchell 1997).

Selected specimens examined. — BRAZIL: Amazonas, along Rio Castanho tributary of Rio Padauri, upper Rio Negro Basin, 100–140 m, 16.–24.2.1946, *Cardona 1380* (US); Bahia, Ilhéus, Rd from Ilhéus to Serra Grande, 14°41'S, 39°09'W, 5.5.1992, *Thomas & al. 9119* (MO); Espiritu Santo, Domingos Matins, BR 262 km 35, localidade Santa Isabel, 11.5.1993, *Pirani & al. 2801* (K); Pará, Alemquer, 15.8.1943, *Baldwin Jr. 2968* (US); Rondônia, Santa Barbara, 9°10'N, 63°07'W, 26.5.1982, *Teixeira & al. 768* (MO, U). — COLOMBIA: Caucasia, Hacienda “Quintero” 8°04'N, 75°05'W, 100 m, 6.9.2000, *Fonnegra & Benavides 7234* (MO). — FRENCH GUIANA: Mont, Saint-Marcel, zone centre-est du massif, 2°23'20"N, 53°01'20"W, 500 m, 20.7.2002, *Granville & al. 15373* (B, CAY, K); Cayenne, Sainte Rupununi, Kuyuwini Landing, Kuyuwini River, 2°05'N, 59°15'W, 150–250 m, 13.10.1992, *Jansen-Jacobs & al. 2901* (B, CAY). — GUYANA: Cuyuni-Mazaruni, N side of Karawtipu, c. 470m, 19.9.1960, *Tillett & Tillett 45466* (K); Kaieteur Plateau, forest along Potaro River c. 4.5 miles above Kaieteur Falls c. 1400 ft, 9.3.1962, *Cowan & Soderstrom 2116* (K, US); Potaro-Siparuni,

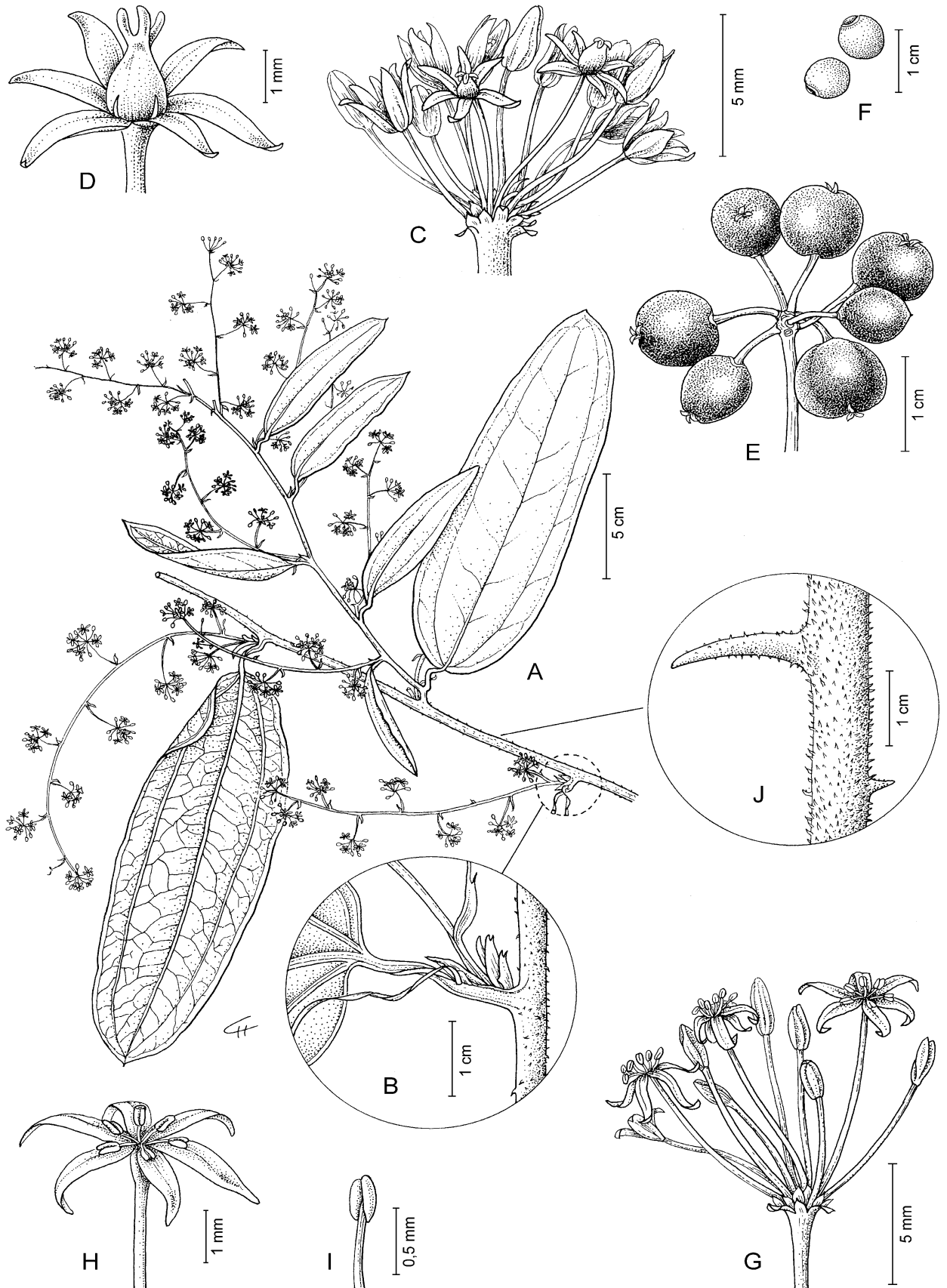


Fig. 8. *Smilax schomburgkiana* – A: flowering branches; B: inflorescence with a pair of scales; C: pistillate inflorescence; D: pistillate flower; E: infructescence; F: seeds; G: staminate inflorescence; H: staminate flower; I: stamen; J: stem. – Drawn by C. Hillmann-Huber from Skog & al. 7510 (CAY), Granville 7194 (CAY), Stege & al. 371 (CAY) and Oldeman 1999 (CAY).

Iwokrama, Siparuni R, Pakatau Falls and 2 km upstream, 4°43'N, 59°01'W, 100 m, 30.11.1994, *Mutchnick & Allcock 443* (B, US); West-Demerara, Mabura Hill, 180 km SSE of Georgetown, Kurupukari main road, near Seeballi creek, 5°20'N, 54°40'W, 0–50 m, 26.5.1988, *Steege & Dobbins 371* (CAY, B, K, U, US). — PERU: Amazonas, Bagua, Yamayakat, 4°55'S, 78°19'W, 320 m, 27.2.1996, *Jaramillo & al. 1316* (MO); Loreto, Maynas, Quistococohe, 150 m, 23.12.1988, *Ayala & Criollo 4452* (MO); Madre de Dios, Tambopata, 12°49'S, 69°43'W, 280 m, 22.7.1985, *Al Gentry & al. 51217* (MO); Pasco, Oxapampa, Palcazu valley, Cabeza de Mono, 5–6 km west of Iscosacin, 10°12'S, 75°14'W, 325 m, 13.–19.4.1983, *Smith 3739* (MO). — SURINAME: Haut Litany-Bassin du Litany, 2°31'N, 54°45'W, 170 m, 3.8.1993, *Granville & al. 12012* (US, CAY); Saramacca, Saramacca River, 16.6.1944, *Maguire 23830* (U); Sipaliwini, NW of Kwamalasamutu village, 2°22'N, 56°47'W, 50 m, 14.7.1998, *Plotkin 1299* (US). — TRINIDAD & TOBAGO: Trinidad, Arima, valley to Lalaja road, 1300 ft, 12.6.1973, *Philcox & Wood 7084* (K). — VENEZUELA: Amazonas, Rio Negro, Cerro Aratitoyope, aprox. 70 km al SSW de Ocamo, 2°10'N, 65°34'W, 990–1670 m, 24.–28.2.1984, *Steyermark & al. 130073-A* (MO); Aragua, entre La Quebrada Río Hondo al Sur de Tremaria y Choróni, 900 m, 30.4.–1.5.1972, *Steyermark & Carreña Espinoza 105867* (MO); Bolívar, 5 km S El Pauji, “El Abismo”, Rio Samay, 4°23'N, 61°38'W, 520 m, 21.10.1985, *Liesner & Holst 18896* (MO).

VI. Spinosa group

Plants armed with straight prickles, terminal branches zigzag; leaves glabrous, often with prickles on the midrib, margin entire or dentate; tepals c. 2 mm long; berries purple or black.

Includes: *Smilax aristolochiifolia*, *S. guianensis*, *S. spinosa*. Related species: *S. campestris* (= *S. assumptionis*), *S. cissoides*, *S. cognata*, *S. elastica*, *S. lappacea*, *S. maypurensis*, *S. pilcomayensis*, *S. polyantha*, *S. rufescens*, *S. spruceana*.

11. *Smilax aristolochiifolia* Mill., Gard. Dict., ed. 8, *Smilax* no. 7. 1768. — Lectotype (designated here): Mexico, *Houstoun* (BM 578842 [st.]).

= *Smilax medica* Schlttdl. & Cham. in *Linnaea* 6: 47. 1831. — Holotype: Mexico, Veracruz: “in sylvis Papantlae”, 1.1829, [*Deppe* &] *Schiede* 985 (HAL 79372 [st., 3 sheets]!); isotype: BM 796931 [♀]!).

= *Smilax medica* var. *bracteata* A. DC. in *Candolle & Candolle, Monogr. Phan.* 1: 87, 1878. — Lectotype (Killip & Morton 1936: 270): Mexico, Veracruz, “near Tantoyuca, prov. Huasteca”, 1859, *Ervendberg 336* (K 400477 [♂]!).

Rhizomes elongated. *Stems* obtusely angular, terete near the apex, glabrous, armed with flattened prickles, terminal branchlets straight, scarcely prickly. *Leaves* ovate

to lanceolate, glabrous, coriaceous or membranous, 10–22×4–12 cm, 7–9-veined, major veins connected by reticulated veinlets, with prickles on the main veins; apex acuminate, base cordate or hastate, margin of entire, petiole 1–4 cm long, flattened. *Inflorescences* umbellate, solitary, rarely to few or several in racemes, scale single; *peduncle* 2–4.5 cm, flattened; *pedicels* of uniform length; *tepals* of male flowers 3.5–4 mm long, of female flowers 3.5–4 mm long; *anthers* linear in top-view, longer than the filaments. *Berries* red when ripe, not glaucous, globose, 12–15 mm in diameter. — Fig. 9.

Notes. — Miller (1768) described *Smilax aristolochiifolia* based on sterile material. He noted that this species has terete, armed stems and ovate-lanceolate leaves. The specimen *Houstoun*, BM 678842, is selected as lectotype.

Distribution and habitat. — Mexico to Costa Rica (Fig. 10); evergreen seasonal and humid tropical forest, 100–800 m.

Variability. — The species shows features intermediate between *Smilax spinosa* and *S. officinalis*, which suggests that it is perhaps a hybrid between these two species.

Common names. — “Es ‘co’ ka” in Belize, “Cocolme-ca”, “cocomeca” in Guatemala (Killip & Morton 1936; MacVean 2006).

Selected specimens examined. — BELIZE: Toledo, upper reach of Goladen Stream, *Gentle 4515*, 9.4.1944 (MO); El Cayo, 5.–13.3.1931, *Bartlett 12010* (US). — EL SALVADOR: Santa Ana, San José Ingenio, P. N. Montecristo, 1800 m, 1.3.2002, *Martínez s.n.* (B). — GUATEMALA: Huehuetenango, trail between Catarina and San Andrés, Sierra de los Chuchumatanes, 3.9.1942, *Steyermark 51820* (F); Petén, Tikal National Park, 1.3 km. North of Tikal, on pinal trail in acahual, 6.12.1959, *Contreras 426* (F); Quezaltenango, along old road between Finca Pirineos and Patzulín, 1200–1400 m, 9.2.1941, *Standley 86922* (F); San Marcos, slopes of Tajumulco, Sierra Madre Mountains about 8–10 km, W of San Marcos, 31.12.1964–1.1.1965, *Williams & al. 26908* (F); Suchitepéquez, Mazatenango, Fac. Asturias, 1.4.2001, *MacVean & al. 309* (F). — HONDURAS: Cortés, San Pedro Sula, western edge of Sula Valley, 24.8.1951, *Kamb 2168* (A). — MEXICO: Campeche: Calakmul, 9 km al SE de Ley de Fomento Agrpecuario, camino a Dos Naciones, 17°59'52"N, 89°24'56"W, 56 m, 5.8.1997, *Martínez & al. 28062* (EAP); Chiapas, Mt Ovando, 12.1937, *Matuda 2092* (K, UC); Jalisco, Quimixt, 70 m, 29.11.1926, *Mexia 1175* (A, UC); Puebla, above Teotitlan del Camino, c. 2000–3500 m, 3.8.1961, *Smith & al. 4146* (F, G); San Luis Potosí, mountains about 10 miles northeast of Ciudad del Maíz (17 miles by road), 1400–1600 m, 7.5.1949, *McVaugh 10435* (G, NY); Tabasco, Balancan, 9.–14.5.1939, *Matuda 3015* (F); Tamaulipas, 10 km W of Encino 23°20'N, 99°10'W,

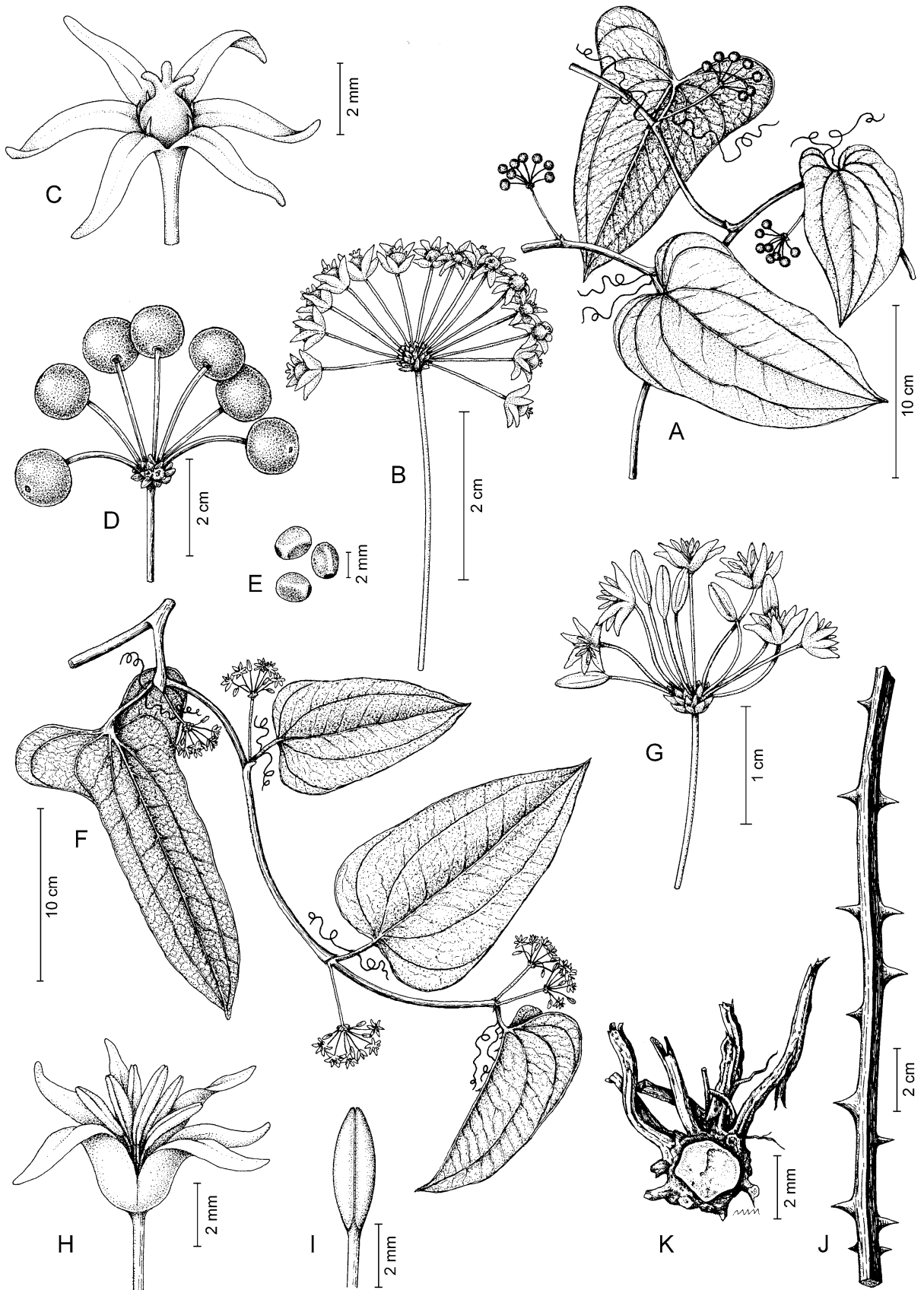


Fig. 9. *Smilax aristolochiifolia* – A: fruit bearing branches; B: pistillate inflorescence; C: pistillate flower; D: infructescence; E: seeds; F: staminate flowering branches; G: staminate inflorescence; H: staminate flower; I: stamen; J: stem; K: rhizome. – Drawn by P. Adam from Chiang 253 (F), Cook & Martin 214 (US), Contreras 426 (F), Rovirosa 402 (US), Hinton 14038 (US) and Molina 15409 (F).

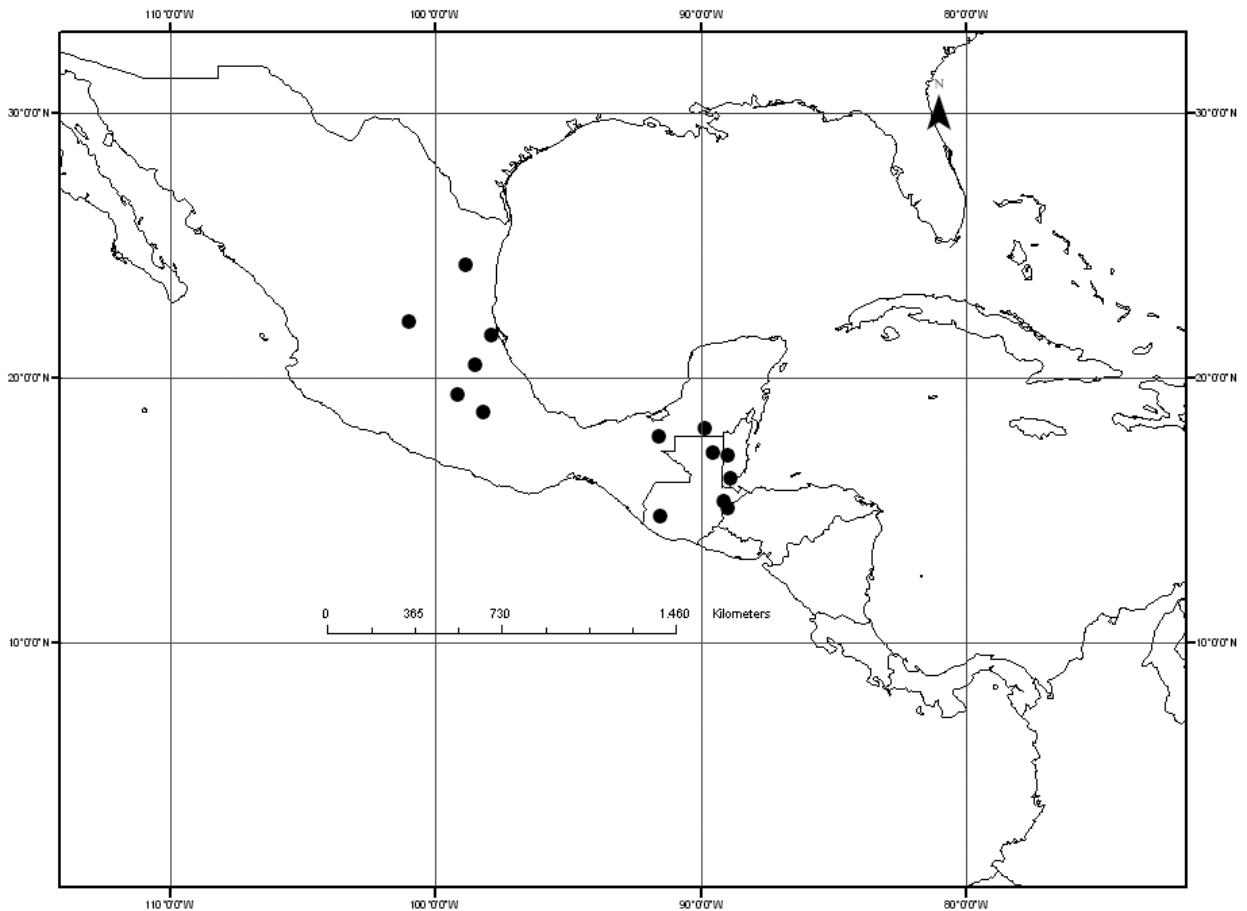


Fig. 10. Distribution of *Smilax aristolochiifolia* (circles).

100 m, 22.5.1986, *Schatz & al 1132* (MO); Veracruz, Ozuluama, Isla Juana Ramírez, 21°48'N, 97°40'W, 9 m, 5.3.1980, *Avendaño & al. 680* (F).

12. *Smilax guianensis* Vitman, *Summa Pl.* 5: 422. 1791 ≡ *Smilax macrophylla* Willd., *Sp. Pl.* 4: 786. 1806. – Holotype [icon]: “*Smilax caule inermi, foliis cordatis*” in Plumier, *Pl. Amer.*: t. 84. 1756. [♂!].

= *Smilax megalophylla* Duhamel, *Traité Arbr. Arbust.*, ed. 2, 1: 244. 1803. – Holotype: [no label data] (P-J 3022 [st.!!]).

= *Smilax guianensis* var. *subarmata* O. E. Schulz in *Urban, Symb. Antill.* 4: 149. 1903 ≡ *Smilax subarmata* (O. E. Schulz) O. E. Schulz in *Urban, Symb. Antill.* 5: 28. 1904. – Lectotype (designated here): Puerto Rico, “Prope Lares in sylvis montan. ad „Callejones?”, 13.1.1887, *Sintenis 5932* (B 100247551 [st.!!]; isolecotype: G 35823 [st.!!], HBG [st.!!]).

Rhizomes elongated. *Stems* terete, glabrous with robust, short prickles, terminal branches zigzag, angular; axillary scale single. *Leaves* ovate, cordate, 9–29 × 4–16 cm, 5–7-veined, major veins connected by reticulate veinlets, apex acute, rarely obtuse, base cordate, acute, margin entire, glabrous, coriaceous or membranaceous; *petiole*

1.2–1.5 cm long, terete. *Inflorescences* umbellate, solitary, scale single; *peduncle* 2.5 cm long, flattened; *pedicels* of different lengths; *tepals* of male flowers 2.5–3 mm long, of female flowers 2 mm long; *anthers* ellipsoidal, as long as the filaments. *Berries* black when ripe, globose, 8 mm in diameter. – Fig. 11.

Affinities. — *Smilax guianensis* has often been mistaken for *S. solanifolia* but I consider them as separate species.

Distribution and habitat. — Puerto Rico, Lesser Antilles, Guyana (Fig. 22); humid forest, 0–300 m.

Note. — Acevedo-Rodríguez (2005) stated that the syntypes of *Smilax guianensis* var. *subarmata* were destroyed at B. However, the specimens *Sintenis 4943* and *5932* are extant at B. *Sintenis 5932* is designated as lectotype and the name considered a synonym of *S. guianensis*.

Common names. — “Boyau-chat”, “liane-boyau”, “boyeau diable”, “whist”, “basket vine” in the Lesser Antilles (Howard 1979; Sastre & Breuil 2007).

Selected specimens examined. — ANTIGUA: Shambro Hills, 1849, *Wulschlägel 6* (M); Macarthy Hills, 1000',

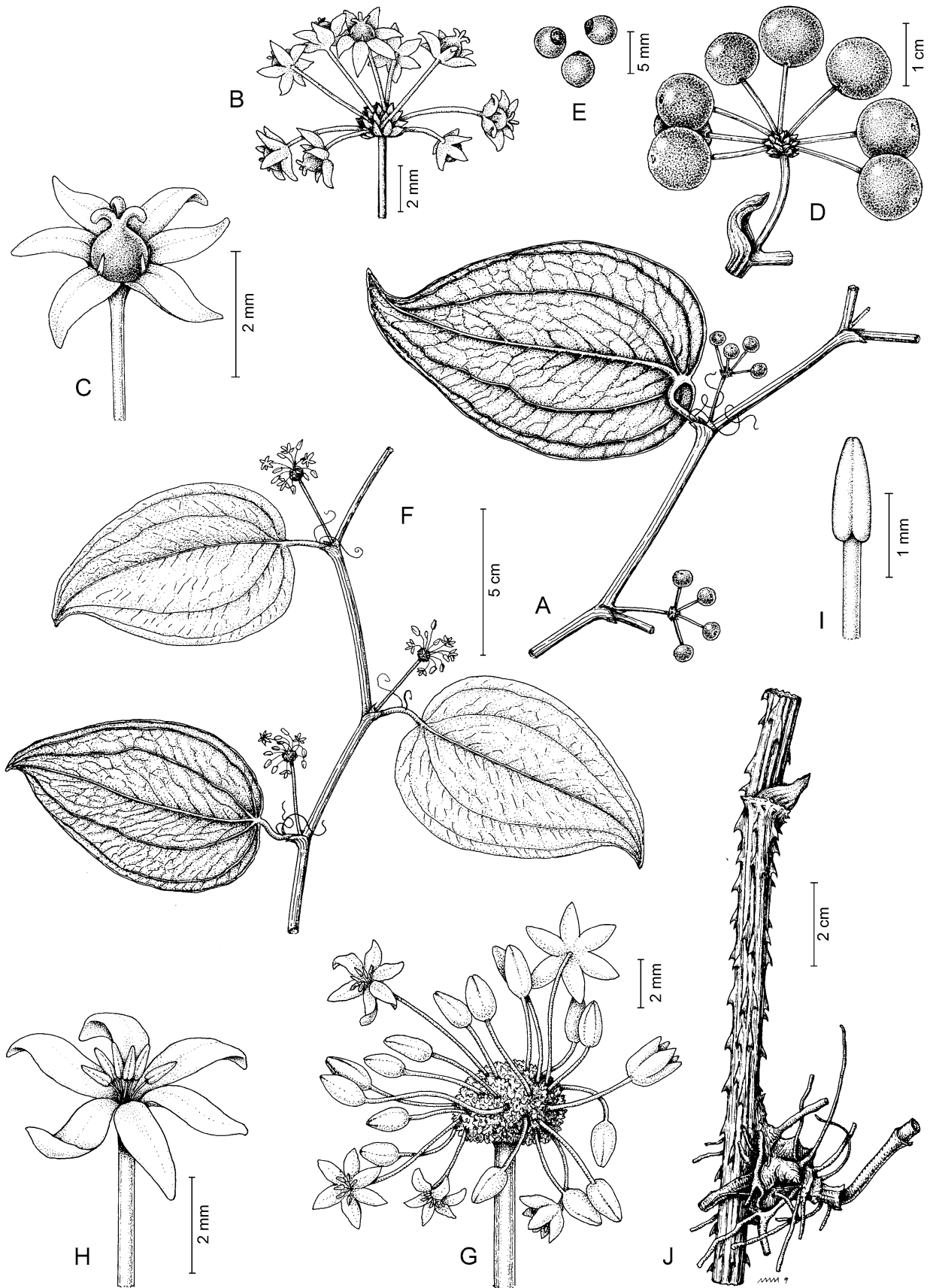


Fig. 11. *Smilax guianensis* – A: fruit bearing branches; B: pistillate inflorescence; C: pistillate flower; D: infructescence; E: seeds; F: staminate flowering branches; G: staminate inflorescence; H: staminate flower; I: stamen; J: stem and rhizome. – Drawn by P. Adam from *Duss 1047, 3864* (NY), *Hodge 331* (NY) and *Cooper III 35* (NY).

among on hillsides in the S.N. (volcanic) district Rare, 3.7.1938, *Box 1500* (A). — DOMINICA: Baiac, GR 767953, 480 m, 12.7.1989, *Pendry 71202* (K). — GUADELOUPE: Basse-terre, route menant à la crete de Village, 500 m, 18.4.1974, *Sastre & Fournet 2553* (A); 1893, *Duss 3311* (F). — MARTINIQUE: 1880, *Duss 1047* (NY). — PUERTO RICO: Maricao, Bo. Maricao Afuera, Río Maricao margins, 18°09'56"N, 66°59'17"W, 480 m, 5.2.1994, *Cedeño & Cabezudo 226* (MAPR). — SABA: Broby Hill, 12.8.1953, *Stoffers 4335* (A). — STA LUCIA: Quillesse and Morne Troumasse, 22.4.–18.5.1950, *Horward 11657* (A). — ST LUCCKE: Vicinity of south Chiltern Estate, 1300–1600 ft, 20.7.1966, *Stern & Wasshausen 2509* (B). — ST VICENT: St Patrick Parish, lower Bellewood, 22.2.1962, *Cooley 8432* (GH). — ST EUSTATIUS: Slope of the Quill near Bengalen, 20.7.1953, *Stoffers 3770* (U); top of the Quill, 1.6.1906, *Boldingh 189* (U). — TRINIDAD AND TOBAGO: Santa Cruz, 19.12.1903, *Othmer s.n.* (M); Rockly West, 5.1909, *Broadway 3083* (G, MO). — GUYANA: East coast Water Conservancy, southeast of Georgetown, sand reef at head of Hoorubia Creek, 26.11.1919, *Hitchcock 16935* (NY, US); Potaro-Siparni, Kato and vicinity, 4°40'00"N, 59°55'00"W, 750 m, 17.3.1989, *Hahn & al. 5754* (K). — SURINAME: Nickerie, c. 22 km SW of Avanavero dam site, 17.11.1976, *Heyde & Lindeman 133* (BBS).

- 13. *Smilax spinosa* Mill.**, Gard. Dict., ed. 8: *Smilax* No. 8. 1768. – Holotype: Mexico “*Smilax viticulis asperis, Americana*”, *Houstoun* (BM 000895887 [st. photo!]).
- = *Smilax scabriuscula* Humb. & Bonpl. ex Willd., Sp. Pl. 4: 783. 1806. – Holotype: Venezuela, [“habitat Caracas rio anavucho (according to Humboldt’s diary)”, *Humboldt 634* (B-W 18395-1 [st.]); isotypes: “Caracas Rio Anavucho” P 647213 [st.], P-Bonpl IDC 6209-1 #20, B3!).
 - = *Smilax obtusa* Benth., Bot. Voy. Sulphur: 175. 1846. – Lectotype (Killip & Morton 1936: 263): Mexico, “Manzanilla Bay”, *Beechey* (G [fragm.]; isolectotype: K 400523 [♀!]).
 - = *Smilax mexicana* Griseb. ex Kunth, Enum. Pl. 5: 167. 1850. – Holotype: Mexico, Veracruz, prope Misantla, *Schiede 986* (B†; lectotype (designated here): “*Smilax ... zarzaparrilla Papantle ... in sylvis Misantlae*”, HAL 101520 [st., 2 sheets!]; isolectotypes: K 400522 [st.], MO 2002310 [st.]).
 - = *Smilax costaricae* Vatke in Linnaea 40: 223. 1876 ≡ *Smilax mexicana* var. *costaricae* (Vatke) A. DC. in Candolle & Candolle, Monogr. Phan. 1: 117. 1878. – Lectotype (Killip & Morton 1936: 264): Costa Rica: San José, 5.1857, *Hoffmann 504* (B†; lectotype (designated here): US 1635983 [♂ fragm]).
 - = *Smilax scabriuscula* var. *fendleri* A. DC. in Candolle & Candolle, Monogr. Phan. 1: 143. 1878. – Lectotype (designated here): Venezuela, “Prope coloniam Tovar, *Fendler 1546* (G-DC 200570 [♀!]; isolectot-

types: BR 6943738 [♀!], P 603648 [♀!], US 1803259 [♀!]).

- = *Smilax wagneriana* A. DC. in Candolle & Candolle, Monogr. Phan. 1: 143. 1878. – Holotype: Panama, “*Smilax papyracea ... test Grisebach* Prov. Chiriqui in Panama”, 4.1858, *M. Wagner 630* (M 152730 [♂, photo!]).
- = *Smilax gaumeri* Millsp. in Publ. Field Columb. Mus., Bot. Ser. 1: 357. 1898. – Lectotype (Killip & Morton 1936: 263): Mexico, Yucatán, frequent on forest and brush lands about Izamal, June, *Gaumer 687* (G-Boiss [♀]; isotypes: F 343734, 343669 [♀!], MO 140758 [♀!], NY 319996 [♀!], US 571738 [♀!], S 5410).
- = *Smilax vaga* J. F. Macbr. in Publ. Field Mus. Nat. Hist., Bot. Ser. 11: 46. 1931. – Holotype: Peru, “Dept. San Martín, Alto Rio Huallaga, 360–900 m.”, 12.1929, *Williams 6757* (F 269954 [♀!]; isotype: G 98913 [♀!]).
- = *Smilax williamsi* J. F. Macbr. in Publ. Field Mus. Nat. Hist., Bot. Ser. 11: 46. 1931. – Holotype: Peru, “Dept. San Martín: Tarapoto, 750 m.”, 12.1929, *Williams 5432* (F 269957 [st.]; isotypes: B 10 0247549 [st.], G [fragm!]).
- = *Smilax lundellii* Killip & C. V. Morton in Publ. Carnegie Inst. Wash. 461: 265. 1936. – Holotype: Guatemala, Lake Petén, Sabana Cis”, 3. 5.1933, *Lundell 3190* (US 1585744 [♂!]; isotypes: MICH 1192729 [♂!], TEX-LL 370272 [♂!]).
- = *Smilax luculenta* Killip & C. V. Morton in Publ. Carnegie Inst. Wash. 461: 289. 1936. – Holotype: Honduras, [“Zarza” “Thicket near beach, vicinity of Tela, Departament of Atlantida: at see level”], 14.12.1927–15.3.1928, *Standley 54275* (US 1408214 [♀!]; isotypes: F 343682, 343686 [♀!]).
- = *Smilax munda* Killip & C. V. Morton in Publ. Carnegie Inst. Wash. 461: 265. 1936. – Holotype: Belize, “Rio Grande River, river bank, 50 ft.”, 23.7.1933, *Schipp 1181* (F 269943 [♀!]; isotypes: BM 796938 [♀!], G 35820 [♀!], K 400521 [♀!], MICH 1192730 [♀!], MO 1048251 [♀!], UC 519154 [♀!], US 1635987 [fragm!], S 06-5832).

Rhizomes elongated. *Stems* terete or angular, glabrous, prickles flattened and robust, terminal branches zigzag, often unarmed in the apical part of the branches; *axillary scale* single on the stem. *Leaves* ovate, lanceolate, glabrous, coriaceous or membranous, 7–20×3–8 cm long, 5-veined, major veins connected by reticulate veinlets, apex acute, base rounded or subcordate, margin entire, often with prickles on the midrib; *petiole* 0.6–1.5 cm long, canaliculate. *Inflorescences* umbellate, solitary, scale single; *peduncle* 3–5 mm long, flattened; *pedicels* of different lengths, long; *tepals* of male flowers 2.5 mm long, of female flowers 1.5–2 mm long; *anthers* linear, as long as the filaments. *Berries* purple to black when ripe, not glaucous, ovoid, 5–7 mm in diameter. – Fig. 12.



Fig. 12. Distribution of *Smilax spinosa* (circles).

Distribution and habitat. — Mexico to Peru, Venezuela, Guyana, French Guiana, Suriname, Trinidad and Tobago, Jamaica (Fig. 12); wet and montane forest (in Central America: mostly dry forest). 100–800 m.

Notes. — *Smilax spinosa* is a species easily recognisable by its small flowers, petioles longer than the peduncles and the zigzag terminal branches. In Central America, it is mostly found in the dry tropical and subtropical for-

ests. It is a species with a wide morphological variation and for this reason, some morphs have been described as separate species, most of them based on the size and texture of the leaves.

Macbride (1936) published *Smilax vaga* as a new species and characterised it by terete or subangular stems with short, small prickles. My examination of the type material confirmed that the terminal branches of *S. spinosa* might display prickles of the above-mentioned form;

however, I have also seen specimens in which prickles are completely absent. Therefore, *S. vaga* is treated as a synonym of *S. spinosa*.

Macbride (1936) described *Smilax williamsi* based on sterile material, considering its foliage to be entirely distinct from other species. However, I cannot see any discontinuity towards *S. spinosa* and consider both as conspecific.

The type of *Smilax mexicana* at B was destroyed in 1943, but there are isotypes at K, MO and HAL. I chose the specimen at HAL (101520, 2 sheets) as lectotype (see Art. 9.10 of the Code) because the sheets bear labels in the original handwriting of Schlechtendal. The name is considered a synonym of *S. spinosa*.

The two syntypes of *Smilax costaricae* were destroyed at B. I designate the fragments of the syntype *Hoffmann 504* at US as lectotype and the photo of the Berlin material (attached to the fragments) at US as epitype, because the lectotype is only weakly representative (Art. 9.7, McNeill & al. 2006). The name is considered a synonym of *S. spinosa*.

Common names. — “Zarzaparrilla”, “bejuco de corona”, “zarza hueca”, “espuela de gallo”, “corona de Cristo”, “madre de zarzaparrilla”, “zarzaparrilla macho”, “bejuco de la vida”, “cocolmea” in Central America; “colcomeca” in Mexico (Killip & Morton 1936; McVaugh 1989; Ferrufino & Gómez-Laurito 2004; MacVean 2006).

Selected specimens examined. — BELIZE: Corozal, 1 mi. north of Buena Vista, 100 ft, 23.6.1975, *Croat 24962* (MO); Satun Creek, Silk Grass Creek Reserve, 20.9.1939, *Gentle 3003* (F, MICH); Toledo, Rio Grande, 50 ft, 23.7.1933, *Schipp 1181* (G). — COLOMBIA: Antioquia, in the rain forest near Río León aprox. 20 to 30 km, 7°45'N, 76°50'W, 100 m, 18.3.1962, *Feddema 1946* (MICH); Santander, Barranca Bermeja, Magdalena Valley, between Sogamosos and Carare Rivers, 100–500 m, 20.11.1936, *Haught 2085* (F). — COSTA RICA: Guanacaste, P. N. Puntarenas, R. B. Carara, 9°48'N, 84°36'W, 20 m, 25.3.1987, *Grayum & al. 8220* (CR, MO); Puntarenas, Cordillera de Tilarán, San Luis, 10°16'33"N, 84°47'45"W, 1100 m, 18.4.1994, *Fuentes 729* (CR, INB). — ECUADOR: Napo, E.N.E of Cayambe Mountain, 9500 ft, 16.12.1961, *Cazalet & Pennington 5600* (B); Pichincha, Quito, Reserva Orquideológica El Pahuma, Parroquia Nono, 0°01'N, 78°37'W, 2460 m, 19.12.1996, *Freire & al. 1337* (B); Station INIAP de Payamino, 6.9.1983, *Lescure 2018* (U). — EL SALVADOR: Ahuachapán, Palo Pique, 13°55'18"N, 89°52'30"W, 600 m, 21.12.1995, *Linares & Martínez 3160* (EAP); Santa Ana, San José Ingenio, P. N. Montecristo, 14°25'N, 89°21'W, 700 m, 25.8.2001, *Martínez 194* (B). — FRENCH GUIANA: Sinnamary, Battures de Malmannoury, c. 16 km SE from Sinnamary, 5°19'N, 52°48'W, 21.11.1986, *Skog & al. 7538* (CAY, U). — GUATEMALA: Guatemala, km 33, Amatitlán, 14°28'N, 90°37'W, 18.3.2001, *de MacVean 422* (HULE); Sacatepéquez, along

Pacific escarpment, 3 km S of Alotenango on highway 14, 14°25'N, 90°45'W, 1500 m, 1.–2.8.1965, *Roe & al. 803* (G); Sololá, camino Platanares, Fca Sto Tomás, 14°63'N, 90°51'W, 1300 m, 13.3.2001, *Fahsen & Martínez 11321* (CR). — GUYANA: West Demerara, c. 7.6 km S of Timehri Airport turnoff, 6°29'55"N, 58°13'09"W, 21.5.1997, *Taylor & al. 12088* (MO). — HONDURAS: Gracias a Dios, Barra Plátano, 15°53'N, 84°42'W, 25.11.1976, *Fryxell 2839* (EAP); Intibucá, Valle de Otoro, c. 10 km W of Jesús de Otoro, Río Sirima, 14°33'N, 88°06'W, 800 m, 3.6.1991, *Davidse 34957* (TEFH, EAP); Yoro, Quebrada El Otilillo, 15 km de Yoro, 1100 m, 8.5.1956, *Molina 6831* (EAP). — MEXICO: Oaxaca, Chiltepec, 13 m, 24.4.1967, *Martínez 1376* (CR, U); Quintana Roo, Coba, in forest on bank of Lake Macanxoc, 6.–7.1938, *Lundell & Lundell 7620* (A, MICH); Yucatán, Chichen Itza, 6.–7.1938, *Lundell & Lundell 7521* (A, F, MICH). — NICARAGUA: Jinotega, Reserva Bosawas, Municipio de Bocay, Río Bocay, Salto Cayascón, 13°14'N, 86°13'W, 2.12.2001, *Rueda 16811* (HULE); Rivas, Isla de Ometepe, Municipio de Moyogalpa, Volcán Concepción, subiendo por La Concepción, 12°32'N, 85°38'W, 200–900 m, 27.10.2001, *Rueda 16712* (HULE); Zelaya, Experiment Station El Recreo on the Río Mico, 12°10'N, 84°18'W, 30 m, 1.6.1985, *Davidse & al. 30748* (CR, MO). — PANAMA: Chiriquí, mas o menos 5.4 km del Hato de Volcan en el camino a Las Lagunas, 26.4.1969, *Correa & Lazor 1466* (PMA); Panama, Barro Colorado Island, 10.4.1969, *Foster 685* (PMA); Veraguas, S of Santa Fe, c. 450 m, 17.11.1973, *Nee 8013* (PMA). — PERU: Amazonas, Chachapoyas Kuelap, Fortress, 6°25'13.5"S, 77°47'56.8"W, 3000 m, 16.5.2001, *Hemming & Schneider 252* (B); Loreto, Requena, Yarina (Rio Tapiche), 5°05'S, 73°50'W, 180 m, 11.1.1984, *Vásquez & al. 4872* (USJ); Madre de Dios, Tambopata, Santuario Nacional Pampas del Heath, Rio Heath, 12°39'23"S, 68°44'13"E, 210 m, 22.5.1996, *Aguilar & Castro 766* (USJ). — SURINAME: Sipaliwini, N of S-camp, southern Sipaliwini, 19.1.1970, *Oldenburger & al. 1031* (BBS). — TRINIDAD AND TOBAGO: Trinidad, Rockley Vale, 21.4.1910, *Broadway 3539* (BM).

VII. Havanensis group

Plants armed with straight prickles, terminal branches zigzag and angular or quadrangular; leaves glabrous, margin dentate, sometimes entire; tepals c. 2 mm long; berries purple or black.

Includes: *Smilax aquifolium*, *S. coriacea*, *S. cristalensis*, *S. cuprea*, *S. gracilior*, *S. havanensis*, *S. ilicifolia*, *S. oblongata*, *S. populnea*, *S. viscifolia*.

14. *Smilax aquifolium* Ferrufino & Greuter in Greuter & Rankin Rodríguez, Fl. Republ. Cuba, ser. A, 16(5): 12. 2010 ≡ *Smilax ilicifolia* Kunth, Enum. Pl. 5: 174. 1850 [non Desv. ex Ham. 1825]. – Holotype: Cuba, prov. Habana, “Taburete”, 28.6.1839, *Otto 339* (B 247561 [♂]); isotypes: G-DC 206588 [st.], U 0626066 [st.].

= *Smilax ilicifolia* Kunth var. *sublappacea* A. DC. in Candolle & Candolle, Monogr. Phan. 1: 125. 1878. – Holotype: Cuba, “Havane”, 1833, *Sagra 567* (G-DC 14736 [st.]).

Rhizomes unknown. *Stems* terete, glabrous, armed with small prickles. *Leaves* ovate, cordate, glabrous, coriaceous, 5–8×2–5 mm, 5–7-veined, major veins thin and connected by reticulated veinlets, prominent venation on the upper surface, apex mucronate, base rounded or cordate, margin deeply spinulose; *petiole* 0.4–1 cm long, flattened. *Inflorescences* umbellate and solitary, rarely terminal, scale single; *peduncle* 2–10 mm long, flattened; *pedicels* of uniform length; *tepals* of male flowers 2–2.5 mm long, of female flowers 1.5–2 mm long; *anthers* linear in top-view, as long as the filaments. *Berries* black or purple when ripe, not glaucous, ovoid, 5–7 mm in diameter.

Affinities. — This species is related to *Smilax havanensis*. *S. aquifolium* can be distinguished from other *Smilax* species by the secondary leaf venation being distinctly grouped and reticulate, and the leaf margins being deeply spiny.

Distribution and habitat. — Cuba, Dominican Republic (Fig. 13); semideciduous and evergreen forest, serpentine and pineland forest, 100–600 m.

Selected specimens examined. — CUBA: Habana, Taburete, 28.6.1839, *E. Otto 339* (B); Pinar del Rio, Las Terrazas, Loma Pelada de Cayajabos, 300–400 m, 18.3.1984, *Bisse & al. HFC 51949* (B, HAJB).

15. *Smilax coriacea* Spreng., Syst. Veg. 2: 103. 1825. Described from Hispaniola. – Neotype (Acevedo-Rodríguez 2005: 79): Puerto Rico, “prope Cayey ad rivulum Morrillos”, 6.10.1885, *Sintenis 2252* (US 404071 [♀]!); isoneotypes: F 79592 [♀]!, G 35817 [♀]!, HBG [♀], K, M 124506 [♀]!, P, W 34513 [♀]!).

= *Smilax havanensis* var. *portoricensis* A. DC. in Candolle & Candolle, Monogr. Phan. 1: 124. 1878. – Lectotype (designated here): Puerto Rico, “scandens in fruticeti” 4.7.1827, *Wydler 341* (FI 180288 [♂]!).

Rhizomes elongated. *Stems* terete, glabrous, armed with small, short, flattened prickles; terminal branches zigzag. *Leaves* lanceolate, cordate, glabrous, coriaceous, c. 10×2 cm, 5–7-veined, major veins connected by reticulate veinlets, apex mucronate, base rounded or cordate, margin entire, rarely spinulose; *petiole* 0.4–1 cm long, flattened. *Inflorescences* umbellate, solitary, rarely in racemes, scale single; *peduncle* 0.2–1 cm long, flattened; *pedicels* of uniform length; *tepals* of male flowers 1.5–2 mm long, of female flowers 1.5 mm long; *anthers* linear in top-view, as long as the filaments. *Berries* black or purple when ripe, not glaucous, ovoid, 4–6 mm in diameter.

Affinities. — Acevedo-Rodríguez (2005) stated that *Smilax havanensis* and *S. coriacea* are easily recognised by the venation pattern. He commented that *S. coriacea* has interprimary veins, emerging at an angle of 45° to 90° instead of 25° to 35° in *S. havanensis*. This is an interesting observation with regard to the vegetative characteristics; therefore, I have also treated it as a different species in this study.

Distribution and habitat. — Puerto Rico and Virgin Island (Fig. 13); humid forest, limestone, 0–600 m.

Note. — In the protologue of *Smilax havanensis* var. *portoricensis* (Candolle 1878), the syntypes *Wydler 341* (FI), collected in Puerto Rico, and *Schomburgk 71* (B), collected in the Dominican Republic, are given. *Wydler 341*, which has male flowers, is selected as lectotype because *Schomburgk 71* could not be located.

Common names. — “dunguey”, “dunguey blanco” in Puerto Rico (Acevedo-Rodríguez 2005).

Selected specimens examined. — PUERTO RICO: Ciales, along trail Camino de la Ceiba towards Quebrada del Pozo Azul, 15.8.2001, *Acevedo-Rodríguez & Vicens 11848* (MAPR); Isla Vieques, Lighthouse Peninsula, 11.2.1914, *Shafer 2809* (F, NY); San Juan, Rio Piedras, 15.9.1912, *Jobuston 678* (NY); Vega Baja, Bo. Algarrobo, Tortugero Lagoon Natural Reserve, 18°27'35"N, 66°25'34"W, 0 m, 20.11.2000, *Breckon 6307* (MAPR); Yauco, Susúa Alta, Susúa Forest Reserve, Quebrada Peces, north side of Quebrada Peces, 18°04'10"N, 66°54'28"W, 200 m, 27.5.2001, *Breckon & al. 6451* (MAPR). — VIRGIN ISLANDS: Virgin Gorda, *Fishlock 138*, 5.1.1919 (GH); St John, Coray Bay Quarter, 7.1.1991, *Acevedo-Rodríguez & Siaca 3818* (MO).

16. *Smilax cristalensis* Ferrufino & Greuter in Greuter & Rankin Rodríguez, Fl. Republ. Cuba, ser. A, 16(5): 9. 2010. – Holotype: Cuba, prov. Holguín / Santiago de Cuba, “mun. Sagua de Tánamo / Segundo Frente (Mayarí Arriba), Sierra del Cristal, ... entre La Zanja y el tronque de Batista y El Oro”, 2.5.1985, *Álvarez & al. HFC 57385* (HAJB [♀]!); isotypes: B, JE [♀]!).

= *Smilax populnea* var. *angustata* O. E. Schulz in Urban, Symb. Antill. 7: 492. 1913. – Holotype: Cuba, prov. Holguín, “Loma Mensura”, 680–1000 msm, *Shafer 3790* (B†). – Neotype (Ferrufino-Acosta & Greuter 2010b: 9): Cuba, prov. Santiago de Cuba, “Sierra del Cristal, camino entre El Halcón y las cabezadas del río Levisa, al sur del Pico Cristal”, 700 m, 24.4.1985, *Álvarez & al. HFC 56544* (HAJB); isoneotypes: B, JE).

Rhizomes unknown. *Stems* angular, glabrous, blackish upon drying, armed with thin and short prickles; terminal branches zigzag. *Leaves* lanceolate, cordate, glabrous,

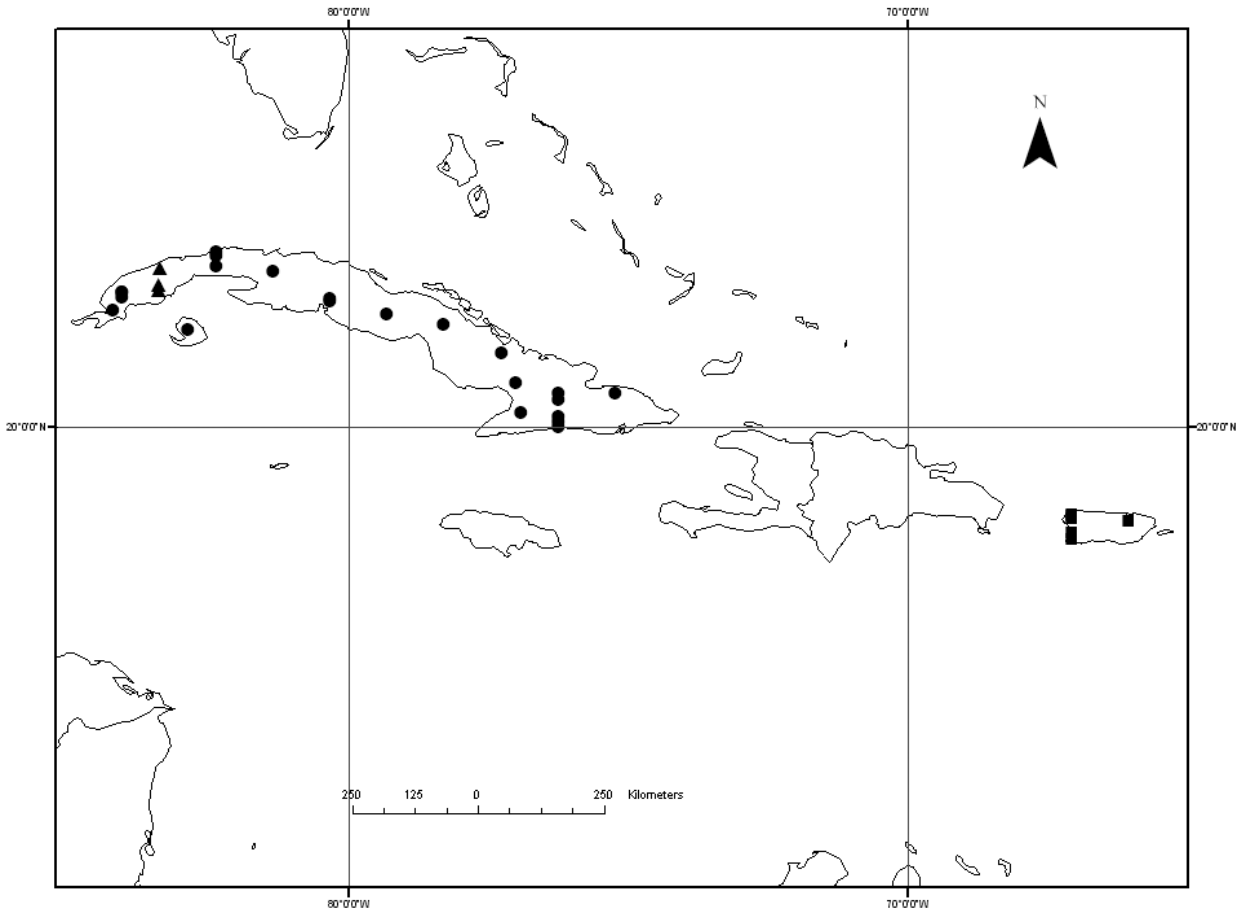


Fig. 13. Distribution of *Smilax havanensis* (circles), *S. coriacea* (square) and *S. aquifolium* (triangles).

membraneous, c. 5–14×2–9 cm, 5-veined, major veins connected by reticulate veinlets, without prominent venation on the upper surface, apex mucronate, base rounded or cordate, margin spinulose, rarely entire; *petiole* flattened, 0.3–0.6 cm long. *Inflorescences* umbellate, solitary, rarely in racemes, scale single; *peduncle* 2–10 mm long, flattened; *pedicels* of uniform length; *tepals* of male flowers 1.5–2 mm long, of female flowers 1.2–1.5 mm long; *anthers* linear in top-view, shorter than the filaments. *Berries* black or purple when ripe, not glaucous, ovoid, 4–7 mm in diameter. – Fig. 14.

Distribution and habitat. — Cuba (Fig. 15); secondary forest, pineland forest and serpentine, 0–1000 m.

Notes. — *Smilax cristalensis* is close to *S. havanensis*. It is characterised by the stems being verruculose, angular and blackish (in herbarium specimens) and zigzag terminal branches.

The holotype of *Smilax populnea* var. *angustata* at B has been destroyed. A specimen (with fruits) deposited at NY was selected as neotype.

Selected specimens examined. — CUBA: Guantánamo, Sierra de Imías, cabezadas del arroyo Los Cacaos,

600–700 m, 7.4.1984, *Bisse & al.* HFC 52432 (B, HAJB, JE); Holguín, alrededores del camino entre La Zanja y el entronque de Batista y El Oro, 2.5.1985, *Álvarez & al.* HFC 57385 (B, HAJB, JE); Santiago de Cuba, Sierra Cristal, subida entre la mina de Ocuja y el Altiplano de la Pradera 300–700 m, 6.1967, *Bisse & Rojas* HFC 04116 (B, HAJB, JE).

17. *Smilax cuprea* Ferrufino & Greuter in Greuter & Rankin Rodríguez, Fl. Republ. Cuba, ser. A, 16(5): 11. 2010. — Holotype: Cuba, prov. Holguín/ Santiago de Cuba, “mun. Mayarí / Mella [= Miranda], Pinares de Mayarí, camino entre Loma Gurugú y Loma Estrella”, 26.5.1983, *Bisse & al.* HFC 50271 (HAJB [♀]!; isotypes: B, JE [♀]!).

Rhizomes unknown. *Stems* terete, glabrous, armed with small, short and flattened prickles. *Leaves* ovate, cordate, glabrous, coriaceous, brownish or copper-coloured upon drying, 5–12×1–4 cm, 5–7-veined, major veins connected by very thin reticulate veinlets, venation on the upper surface not prominent, apex mucronate, base rounded or cordate, margin spinulose, rarely entire; *petiole* rounded, 0.7–0.9 cm long. *Inflorescences* umbellate and solitary, scale single; *peduncle* 2–10 mm long, flattened; *pedicels*



Fig. 14. Distribution of *Smilax cuprea* (triangles) and *S. cristalensis* (circles).

of uniform length; *tepals* of male and female flowers unknown; *anthers* linear in top-view, shorter than the filaments. *Berries* black or purple when ripe, not glaucous, ovoid, 6–9 mm in diameter. – Fig. 16.

Affinities. — *Smilax cuprea* is related to *S. havanensis*. This species can be distinguished from other *Smilax* species by leaves being copper-coloured upon drying.

Distribution and habitat. — Eastern Cuba (Fig. 15); secondary forest, pineland forest and serpentine, 0–800 m.

Selected specimens examined. — CUBA: Guantánamo, Báez, charrascos serpentinosos cerca del arroyo Maguana, 23.1.1977, Bisse & al. HFC 33891 (B); Holguín, Calentura del Medio, zona de Cayo Coco, 200 m, 23.4.1981, Bisse & Mory HFC 44895 (B, HAJB); Santiago de Cuba, charrascos al norte de Los Jagüeyes, 3.5.1985, Álvarez de Zayas & al. HFC 57549 (B, HAJB, JE).

18. *Smilax gracilior* Ferrufino & Greuter in Greuter & Rankin Rodríguez, Fl. Republ. Cuba, ser. A, 16(5): 16. 2010. – Holotype: Cuba, prov. Holguín, “mun. Banes, Banes, costa entre Punta Gorda y Punta Manglito, Cabo Lucrecia”, 21.10.1978, Bisse & al. HFC 38434 (HAJB [♀]!; isotypes: B 100385119 [♀, fr.]!, JE [♀]!).

Rhizomes unknown. *Stems* angular, verruculose, rarely glabrous, armed with small prickles, terminal branches

zigzag. *Leaves* ovate, lanceolate, glabrous, membranaceous, 2.5–7 × 0.7–3.5 cm, 3–5(–7)-veined, major veins thin and connected by reticulate veinlets, venation on the upper surface prominent, rarely inconspicuous, apex mucronate, base acute, margin spinulose or entire; *petioles* 0.3–0.5 cm long, rounded. *Inflorescences* solitary, terminal, scale single; *peduncle* 0.5–1.7 mm long, flattened; *pedicels* of uniform length; *tepals* of male flowers 2 mm long, of female flowers unknown; *anthers* linear in top-view, as long as the filaments. *Berries* black or purple when ripe, not glaucous, ovoid, 4–6 mm in diameter.

Affinities. — *Smilax gracilior* is a species close to *S. ehrenbergiana* and can be distinguished from other *Smilax* species by pruinose leaves and prominent secondary on the upper surface venation. Material from the Bahamas was previously identified as *S. havanensis*.

Distribution and habitat. — Endemic to central (Camaguey, Las Tunas) and eastern Cuba (Holguín, Guantánamo), Bahamas (Fig. 17); xeromorphic matorral in coastal and subcoastal areas as well as on serpentine, and in secondary forests, 0–400 m.

Common names. — “Saw-brier” in the Bahamas (information from herbarium specimen).

Selected specimens examined. — BAHAMAS: Abaco, 8.12.1904, Brace 1581 (F); Andros, Andros, deep creek,

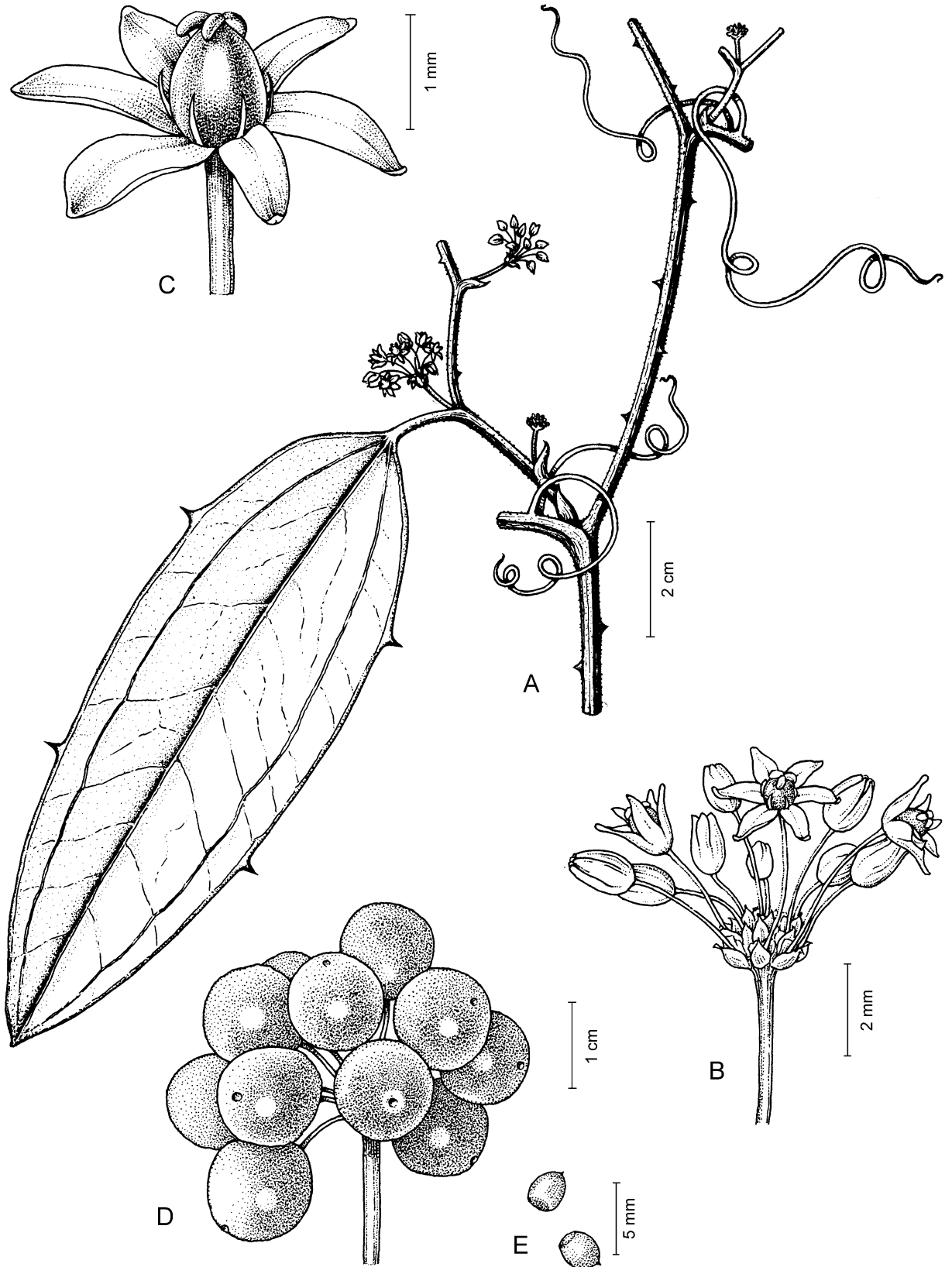


Fig. 15. *Smilax cristalensis* – A: pistillate flowering branches; B: pistillate inflorescence; C: pistillate flower; D: infructescence; E: seeds. – Reprinted with permission from Ferrufino-Acosta & Greuter (2010a).

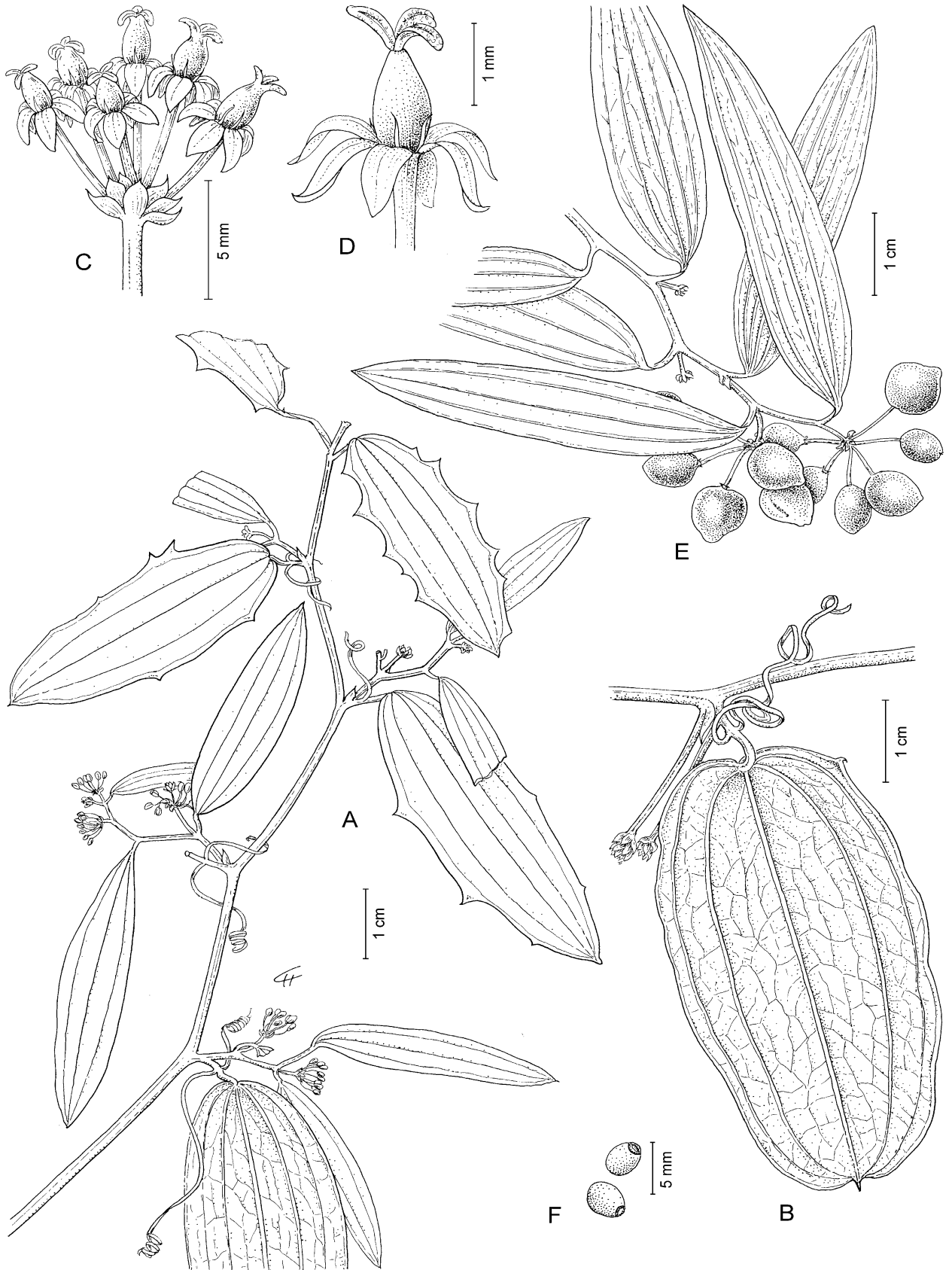


Fig. 16. *Smilax cuprea* – A: flowering branches; B: leaf; C: pistillate inflorescence; D: pistillate flower; E: infructescence; F: seeds. – Drawn by C. Hillmann-Huber from HFC 12002, 18052, 35985, 50271, JE.



Fig. 17. Distribution of *S. gracilior* (circles) and *Smilax ilicifolia* (square).

26.6.1890, *Northrop & Northrop* 663 (F, GH); 18.8.–10.9.1906, *Brace* 5089 (F); Ben Rolle, 1.1976, *Nickerson s.n.* (GH); Cat Island, 20.5.1968, *Byrne* 492 (A); the Bight and vicinity, 1.–6.3.1907, *Britton & Millspaugh* 5866 (F); Eleuthera, Glass Window to Gregora Town, 18.2.1907, *Britton & Millspaugh* 5424 (F); Great Guana Cay, Exuma Chain, 21.–22.2.1905, *Britton & Millspaugh* 2889 (F); Hummingbird, behind sunover beach, 16.1.1969, *Nickerson & Semple* 2974 (A); Inagua, 0.6 miles SSW of Devils Point, in rocky thickets near the sea, 3.6.1974, *Proctor & Gillis* 33907 (A); Long Island, North End, 21.3.1907, *Britton & Millspaugh* 6366 (F); Nassau, 9.1.1890, *Northrop & Northrop* 59 (F, G, GH); North Caico, Kew, 1.7.1954, *Proctor* 9082 (A); Parrot Cay, 3.3.1911, *Millspaugh & Millspaugh* 9201 (F, GH, NY); South Bimini, coastal coppice along west end, 18.1.1975, *Correll* 44187 (NY). — CUBA: Camaguey, Cayo Paloma, Camaguey, 12.10.1909, *Shafer J. A.* 2570 (F, NY); Guantánamo, entre la Tinta y Jauco, 2.6.1982, *Bisse & al.* HFC 47406 (B, HAJB, JE); Holguin, costa entre Punta Gorda y Punta Manglito, Cabo Lucrecia, 21.10.1978, *Bisse & al.* HFC 38434 (B, HAJB, JE); Las Tunas, maniguas cerca de Playa Herradura, 22.4.1987, *Arias & al.* HFC 61688 (B, HAJB, JE).

19. *Smilax havanensis* Jacq., Enum. Syst. Pl.: 33. 1760. — Neotype (Ferrufino-Acosta & Greuter 2010b: 13): [icon] Jacquin, *Select. Stirp. Amer. Hist.*: t. 179, f. 102. 1763 [st.!).

- = *Smilax dentata* Humb. & Bonpl. ex Willd., *Sp. Pl.* 4: 774. 1806 ≡ *Smilax ilicifolia* subvar. *dentata* (Willd.) A. DC. in Candolle & Candolle, *Monogr. Phan.* 1: 123. 1878 ≡ *Smilax havanensis* subvar. *dentata* (Humb. & Bonpl. ex Willd.) A. DC. in Candolle & Candolle, *Monogr. Phan.* 1: 123 (1878). — Holotype: Cuba, [“inter Havanam & Guana(ba)coa” (according to Humboldt’s diary)], *Humboldt [& Bonpland]* 1321 (B-W 18378-01!; isotypes: “Havana” P 647206-647207 [st.], P-Bonpl 6209-1 #20, A3!).
- = *Smilax havanensis* var. *armata* O. E. Schulz in Urban, *Symb. Antill.* 5: 41. 1904. — Holotype: Cuba, prov. Ciudad de La Habana, “Vedado”, *Torrallas* 79 (B†).
- = *Smilax havanensis* f. *inermis* O. E. Schulz in Urban, *Symb. Antill.* 5: 41. 1903. — Holotype: Cuba, *Sagra* (B†).

Rhizomes elongated. *Stems* terete or angulose at the apical branches, glabrous, sometimes verrucose, armed with small, short, flattened prickles; terminal branches zigzag. *Leaves* variable, oblong, elliptic, ovate to lanceolate, glabrous, coriaceous, c. 10×2 cm, (5–)7–11-veined, major veins strong, connected by reticulate veinlets, apex mucronate, base rounded or cordate, margin deeply spinulose or entire; *petiole* flattened, 0.4–1 cm long. *Inflorescences* umbellate, solitary, rarely in racemes, scale single; *peduncle* 2–10 mm long, flattened; *pedicels* of uniform length; *tepals* of male flowers 1.5–2 mm long, of female

flowers 1.5 mm long; *anthers* linear in top-view, as long as the filaments. *Berries* black or purple when ripe, very often angulose due to the presence of three seeds, reddish, not glaucous, ovoid, 4–6 mm in diameter. – Fig. 18.

Affinities. — *Smilax havanensis* can be distinguished from other *Smilax* species by its prickly stems, zigzag angular branches, the often spinulose leaf margin, tepals of c. 1.5–2 mm and black berries.

Distribution and habitat. — USA (southern Florida), Bahamas, Cayman Islands (Fig. 13); humid forests, limestone, 0–800 m.

Variability. — *Smilax havanensis* has a wide phenotypic plasticity, particularly regarding the leaves. Various leaf characteristics (e.g. shape, size) may respond to environmental conditions.

Note. — In his “Selectarum Stirpium Americanum”, Jacquin pointed out that *Smilax havanensis* was originally found in Havana. Jacquin’s drawing of this species is based on a simple, 7-veined, ovate leaf with spinulose margins. As D’Arcy (1970) stated, there is no “Jacquin Herbarium” and his specimens can be found at W, LINN or in other European herbaria. The type of *Smilax havanensis*, however, could not be located. Because no original material of *Smilax havanensis* could be found, this name is lectotypified with Jacquin’s illustration.

Common names. — “Alambrillo”, “bejuco de ñame”, “bejuco de china” in Cuba; “china-brier” in the Bahamas; “tsiguina”, “tsiguna” in Haiti; “wire wiss” in the Cayman Islands; “liane-bamboche”, “boyau-chat”, “liane-noyau”, “salsepareille bâtard” in Martinique (León 1946; Proctor 1984).

Selected specimens examined. — BAHAMAS: Abaco, 17.12.1904, *Brace 1741* (NY); Andros, Island, Big Wood Cay, N.E. tip, 3.1966, *Dawson 267036* (US); Cat Island, the Bight and vicinity, 1.–6.3.1907, *Britton & Millspaugh 5866* (F); Mariguana Islands, Abraham Bay and vicinity, 6.–7.12.1907, *Wilson 7504* (F, NY); New Providence, coastal thicket, Ft. Montague, 23.8.1904, *Britton & Brace 177* (F, NY); Noth Bimini, in coppice on white-lands, Easter Key, 17.4.1974, *Correll 42119* (NY); North Caicos, Bellemont and vicinity, 2.3.1911, *Millspaugh & Millspaugh 9191* (F). — CAYMAN ISLANDS: Grand Cayman, 11.1890, *Hitchcock s.n.* (MO). — CUBA: Camaguey, Vilató, entre el pueblo y Ocuja, 100 m, 25.4.1984, *Bisse & al. HFC 53853* (B, JE); Cienfuegos, orillas del río Jabacoa al oeste del pueblo [se extrajo muestra para ADN], 21.2.2009, *Greuter & al.* (B, herb. Greuter); Santa Clara, Soledad, Potrero, *Howard R. A. 6576*, 8.1941 (GH, NY); Holguin, charrascos entre El Oro y los Güiros, 26.4.1985, *Álvarez de Zayas & al. HFC 56731* (JE); Pinar del Río, Sumidero, mogotes de Si-

erra de Sumidero, 13.12.1978, *Bisse & al. HFC 38599* (B, JE); Sanctis Spiritus, Santa Clara, Banao, 5.1920, *Luna A. 637* (NY); Santiago de Cuba, charrascos de Saca la Lengua, 25.4.1985, *Álvarez de Zayas & al. HFC 56650* (JE); Villa Clara, lomas de Agabama, cerca de la Presa Agabama, 30.10.1986, *Arias & al. HFC 60005* (JE). — USA: Florida, Grassy Key, 24.4.1896, *Curtiss 5636* (F, G, MO, NY, US).

20. *Smilax ilicifolia* Desv. ex Ham., Prodr. Pl. Ind. Occid.: 58. 1825 ≡ *Smilax coriacea* var. *ilicifolia* (Desv. ex Ham.) O. E. Schulz in Urban, Symb. Antill. 4: 150. 1903. — Lectotype (designated here): Antilles “Habitat in ind. Occ.”, *Desvaux* (P 686923 [♂]).

Rhizomes unknown. *Stems* angular, verruculose, armed with thin and short prickles; terminal branches zigzag. *Leaves* lanceolate, cordate, glabrous, coriaceous, brownish, c. 5–14×2–9 cm, 5-veined, major veins connected by reticulate veinlets, venation on the upper surfaces not prominent, apex mucronate, base rounded, margin with straight, blackish spines, deeply spinose; *petiole* flattened, 0.3–0.6 cm long. *Inflorescences* umbellate, solitary, scale single; *peduncle* 2–8 mm long; flattened; *pedicels* of uniform length; *tepals* of male flowers 1.5–2 mm long, of female flowers 1.2–1.5 mm long; *anthers* linear in top-view, shorter than the filaments. *Berries* black or purple when ripe, not glaucous, ovoid, 4–6 mm in diameter.

Affinities. — *Smilax ilicifolia* is close to *S. havanensis* and *S. cristalensis*.

Distribution and habitat. — Haiti, Dominican Republic (Fig. 17); secondary forest, pineland forest, 0–500 m.

Nomenclature — The *Desvaux* specimen P 686923 is a mixture of two elements, male and female flowers. The male specimen is selected as lectotype.

Selected specimens examined. — DOMINICAN REPUBLIC: Azua, el poblado rural Pocilga, c. 1.5 km N de Sabana de San José, 18°39'N, 70°44'W, 4000–4400 pies, 27.7.1982, *Zanoni & Pimentel 22060* (JBSD, U); Barahona, trail between Pdernales and Aceitil, 3800', 8.–12.8.1946, *Howard & Howard 8230* (GH); Duarte, Loma Quita Espuela, 19°21'N, 70°09'W, 300–800 m, 6.5.1993, *Bastardo & al. 9* (JBSD, MO); Espailat, 8.5 km E de Gaspar Hernández, 19°38'N, 70°13'W, 170–200 m, 13.2.1990, *García & Jiménez 2788-C* (JBSD); Independencia, Sierra de Bahoruco, 18°12'N, 71°31'W, 1700–1800 m, 7.5.1985, *Zanoni & al. 34410* (GH); La Vega, Constanza, al SO del poblado El Río, Loma La Calentura, 18°55'56"N, 70°35'06"W, 1498 m, 20.5.2004, *Veloz & Townsend 3243* (JBSD); Monte Plata, P. N: Los Haitises, 18°53'N, 69°35'W, 25.11.1985, *García & al. 657* (JBSD); Peder-nales, Sierra de Bahoruco, Aceitillar, Hoyo de Pelempito,



Fig. 18. *Smilax havanensis* – A: staminate flowering branches; B: staminate inflorescence; C: staminate flower; D: stamen. Reprinted with permission from Ferrufino-Acosta & Greuter (2010a).

18°02'N, 71°39'W, 400–600 m, 24.6.2005, *Clase & al.* 4004 (JBSD); Peravia, 14.2 km N del Parque Central de San José de Ocoa, y 4.1 km desde el Cruce Los Arroyos, 18°37'N, 70°31'W, 4200 pies, 7.4.1982, *Zanoni & al.* 19839 (JBSD); Samaná, Península of Samaná, near Los Banaderas Prietas, 450 m, 4.6.1930, *Ekman* 15215 (GH); Salcedo, carretera Tenares-Gaspar Hernández, 19°31'N, 70°21'W, 700–760 m, 25.11.1992, *García & Jiménez* 4231 (JBSD); San Cristóbal, Loma Humeadora, Ladera Este, 18°38.5'N, 70°15'W, 1100 m, 21.4.1994, *Jiménez & al.* 1390 (JBSD); San Juan, Sierra de Neiba, al sur de Vallejuelo, 18°37.5'N, 71°23'W, 1800 m, 5.3.1994, *García* 5434 (JBSD); Santiago, Franco Bidó, Parajo Sierra Prieto, P. N. Armando Hernández, 1450 m, 20.2.1999, *Clase & Peguero* 642 (JBSD). — HAITI: Massif de la Hotte, Grand

Ansesud limite, 13.6 km Norte de Camp Perrin, 18°23'N, 73°53'W, 720 m, 15.11.1982, *Zanoni & al.* 24301 (JBSD); Massif de la Selle, Quest, Morne Cadet, una loma, 4 a 5 km al E de Fermathe, 18°28'N, 72°14'W, 1100–1200, 3.6.1985, *Zanoni & al.* 34747 (JBSD); Nord, Marmelade, 800 m, 19.12.1925, *Leonard* 8213 (UC).

21. *Smilax oblongata* Sw., Prodr.: 59. 1788. – Lectotype (designated here): “India occid.” (S 86232 [♀]!).

= *Smilax cumanensis* Humb. & Bonpl. ex Willd., Sp. Pl. 4: 783. 1806. – Holotype: Venezuela, [“Bordones in umbrosis semel invenimus” (according to Humboldt’s diary), *Humboldt* [& *Bonpland*] 285 (B-W [♀ 18396-1!]); isotype: “Bordones” P 0647205 [st.]!, P-Bonpl IDC 6209-1 #20, B4!).

Rhizomes unknown. *Stems* terete, angular, armed with short prickles; terminal branches zigzag. *Leaves* lanceolate, ovate, glabrous, membranous, c. 10×2 cm, 5-veined, major veins connected by reticulate veinlets, apex acute, base acute or rounded, margin entire; *petiole* 0.5–1 cm long, rounded. *Inflorescences* umbellate, solitary, scale single; *peduncle* 5–7 mm long, flattened; *pedicels* of different lengths; *tepals* of male flowers 1.5–2 mm long, of female flowers 1.5 mm long; *anthers* linear in top-view, as long as the filaments. *Berries* black or purple when ripe, not glaucous, ovoid, 6–8 mm in diameter.

Affinities. — In certain cases, it is difficult to differentiate this species from *Smilax spinosa* due to similarities in leaf morphology.

Distribution and habitat. — Lesser Antilles, Venezuela, Brazil (Fig. 19).

Notes. — In the protologue of *Smilax oblongata*, Swartz did not mention any type. In the herbariums of BM and S, there are two specimens that could be possible matches. Howard (1979) contended that the Anderson specimen from St Vincent deposited at BM is the lectotype, but that the specimen deposited at S is probably not a corresponding type. He also claimed that the *S. oblongata* specimen at S does not bear Swartz's writing. Despite this, I chose the specimen deposited at S as a lectotype, because Swartz brought his collection to London in 1786 and returned to Sweden in autumn 1787. One year later, he published his *Nova Genera & Species Plantarum seu Prodrum* (Stearn 1965).

The type specimen of *Smilax cumanensis* is sterile; there are only remains of the inflorescence. In his protologue, Willdenow (1806) noted obtusely angular, unarmed stems and ovate-oblongate, triplinerviate leaves. Howard (1979) mentioned that all the *S. cumanensis* material from the Lesser Antilles is moderately spinulose on the stem and on the midrib (lower leaf surface). He referred to this material as *S. oblongata*. He also examined material from Trinidad and Tobago as well as northern South America and noted that all specimens had unarmed stems. Sipman (1979) described this species as having angular branches, 2–2.5 mm long tepals, blue or black berries and occasional prickles. I examined the type *S. cumanensis* and also consider this name as a synonym of *S. oblongata*.

Common names. — “Bejuco de corona”, “Bejuco de corona e cristo”, “Cajiro”, “Hala por detras”, “Këmëhkë tuku'ya këmën” (Panare) in Venezuelan Guayana (Gaskin & Berry 2005).

Selected specimens examined. — GRENADA: Carriacou Island, 7.–25.3.1950, Howard 10856 (GH); Tempés St. Georges, 21.9.1905, Broadway s.n. (A, GH). — GUADELOUPE: Basse-Terre, Côte sous le Vent, Crête de Vil-

lage, 500 m, 11.2.1976, Sastre & Fournet 4265 (A). — FRENCH GUIANA: Sinnamary, Battures de Malmanoury, end of Rte. D7, c. 16 km SE from Sinnamary, 5°19'N, 52°48'W, 21.11.1986, Skog & al. 7538 (CAY). — GUYANA: “Heatrov”, 4.1886, Jenman 2145 (K); Barima-Waini, Morawhana, Barima River, 8°15'N, 59°45'W, 14.1.1920, Hitchcock 17504 (GH); Cuyuni-Mazaruni, foot of Mt. Waleliwatipu, 5°51'N, 61°03'W, 680–790 m, 29.5.1990, McDowell & Hughes 2939 (U); Rupununi, Basin of Rupununi River, near mouth of Charwair Creek, 2°35'N, 1.–4.11.1937, Smith 2333 (A, F, G, U); U. Takutu, along Essequibo River between Cashew Falls and Apoteri, 4°15'0"N, 58°35'0"W, 25.9.1990, McDowell 3383 (US); West Demerara, 1837, Schomburg 353 (K). — MARTINIQUE: Camp Balata, 8.3.1978, Howard 18317 (A). — ST. LUCIA: Dense woodland, 800 ft, 5.1968, Sturrock 539 (A). — ST. VICENTS: 9.1889, Smith & al. 233 (GH). — SURINAME: Tumuc Humac Mts., second peak S of Talouakem, 2°27'N, 54°48'W, 550 m, 20.8.1993, Acevedo-Rodríguez & al. 6106 (CAY, K, US); Saramacca, Saramacca River, Saron Creek, 13.6.1944, Maguire 23772 (A, U); Paramaribo, Kwatta-weg, 4.6.1913, Soeprato 36 A (U). — TRINIDAD AND TOBAGO: Trinidad, San Fernando Hills, 25.3.1908, Broadway 2202 (F); Tobago, Bacolet, 100 ft, 8.8.1958, Purseglove 6227 (K). — VENEZUELA: Amazonas, Atures, Raudales de Atures, 10 km south of Puerto Ayacucho, downstream along Río Orinoco, 5°35'N, 67°34'W, 280 m, 6.9.1985, Steyermark & al. 131472 (MO); Carabobo, Bárbula, on the road from Valencia to Puerto Cabello, along river, 380m, 6.7.1920, Pittier 8939 (NY); Distrito Capital, Caracas, Jardín Botánico, c. 500 m, 24.6.1978, Liesner 5349 (MO); Delta Amacuro, Antonio Díaz, upper reaches of riverine forest of Caño Atoiba tributary of Boca Araguao, 9°15'–17'N, 60°57'W, 50 m, 19.10.1977, Steyermark & al. 114956 (MO, NY); Guárico, Estación Biológica de los Llanos de la Sociedad Venezolana de Ciencias Naturales, a 12 km SE de Calabozo, 8°56'N, 67°25'W, 75 m, Ramírez 3300 (MO); Orinoco, Lower Orinoco, Sacupana, 4.1896, Rusby & Squires 86 (F, G, MO, NY); Portuguesa, 45 kms al NE por la autopista Guanare-Ospino, en el sitio Las Marías, al Este de Guanare, 9°19'N, 69°41'30"W, 400 m, 3.11.1982, Steyermark & al. 127232 (F, MO); Sucre, Península de Paria, 10°43'30"N, 62°48'49"W, 2.12.1979, Steyermark & Liesner 120975 (MO); Zulia, Mara, Cuenca del Río Guasare, entre el Pozo de la Danta y el Destacamento, o sea entre km 34–52 al suroeste del Embalse, 150–250 m, 17.11.1982, Bunting & al. 12441 (MO).

22. *Smilax populnea* Kunth, Enum. Pl. 5: 192. 1850. — Lectotype (designated here): Dominican Republic, “*Smilax cordato-ovata* S. Dom (Balbis)”, Bertero (B 10247558 [♂, specimen]!; isolectotype: B 10247559 [st.]!). = *Smilax populnea* var. *horrida* O. E. Schulz in Urban, Symb. Antill. 5: 44. 1904. — Holotype: Santo Domingo, “Hab. in Sto Domingo prope Altamira in sylvis, 325 m, in alabastris”, Eggers 2419 (P).

Rhizomes elongated. *Stems* terete, glabrous, armed; terminal branches zigzag. *Leaves* lanceolate, cordate, glabrous, membranaceous or coriaceous, c. 10×2 cm, 5–7-veined, major veins connected by reticulate veinlets, apex acute or acuminate, base cordate or rounded, margin spinulose, rarely entire; *petiole* flattened, 0.4–1 cm long. *Inflorescences* umbellate, solitary, or rarely in racemes, scale single; *peduncle* 2–10 mm long, flattened; *pedicels* of uniform different length; *tepals* of male flowers 1.5–2 mm long, of female flowers 1.5 mm long; *anthers* linear in top-view, as long as the filaments. *Berries* black or purple when ripe, not glaucous, ovoid, 5–7 mm in diameter.

Affinities. — *Smilax populnea* is close to *S. guianensis*, but differs by its short pedicels, its tepal size and the colour of its berries.

Distribution and habitat. — Dominican Republic (Fig. 19).

Selected specimens examined. — DOMINICAN REPUBLIC: Altagracia, La Altagracia, Llano costero, Bavaro, 27 km al sur del poblado de El Macao, 18°40'N 68°23'W, 0–5 m, 30.1.1986, *Zanoni & al. 36042* (JBSD); Azua, Azua, Sierra Martín García, 18°19'N 70°56'W, 300 m, 13.11.1985, *Pimentel & al. 339* (JBSD); Barahona, Sierra de Baoruco, 17°58'N 71°13'W, 650 m, 16.1.1985, *Zanoni & al. 33075* (JBSD); Dajabón, 14.7 km desde el Parque Central al pueblo de Loma de Cabrera, 19°23'N 70°41'W, 1600 pies, 11.11.1981, *Zanoni & Mejía 12986-A* (JBSD); La Romana, SW of the Preea Chavón, 18°25'N, 68°54'W, 50–60m, 17.11.1980, *Mejía & Zanoni 9175* (JBSD); La Vega, La vega, East of Bonao, on Loma El Caribe, 18°58'N, 70°24'W, 400 m, 30.7.1981, *Zanoni & al. 15778* (JBSD); Maimón, Maniaguas, Sierra Rieta, Villa Malla, 200 m, 26.5.1973, *Alain & Liogier 19281* (JBSD); Pedernales, Sierra de Baoruco, 26 km norte desde el Puerto de Cabo Rojo, 18°06'N, 71°36'W, 2000 pies, 16.2.1982, *Zanoni & al. 19061* (JBSD); Puerto Plata, Sosús, P.N. El Choco, 19°34'N, 70°28'W, 200–300 m, 19.1.1999, *Clase & al. 362* (JBSD); San Cristobal, 2 km al N de Cambita Garabito, 19°27'N, 70°10'W, 225 m, 6.11.1994, *García & al. 5655* (JBSD); Santiago Rodríguez, La Leonor, 15 km al N de Monción, 18°19'N, 71°14'W, 650 m, 30.5.1992, *González & al. 228* (JBSD). Santo Domingo, Sierra Prieta, al Noreste de Villa Mella, camino a Yamasá, 18°19'N, 69°58'W, 190 m, 9.9.1995, *Veloz & al. 302* (JBSD); Samaná, Playa El Rincón 0–50 m, 28.5.1980, *Mejía & Zanoni 6555* (JBSD). — HAITI: Massif du nord, Nord-Quest, 3.1 km al este de Anse-a-foleur en la carretera a Le Borgne, 19°53'N 72°35'W, 20–30 m, 7.6.1985, *Zanoni & al. 34889* (JBSD).

23. *Smilax viscifolia* Duhamel, *Traité Arbr. Arbust.*, ed. 2, 1: 243. 1803 ≡ *Smilax oblongata* var. *viscifolia* (Duhamel) O. E. Schulz in *Urban, Symb. Antill.* 5: 43. 1904.

– Holotype: Hispaniola, “e Domingo”, *Lamarck 163* (P-LA liasse 81: 108 [♂ part A!]; isotype: “*Smilax viscifolia*. *Encycl. Herb. Poiret*” P 647222 [part B]).

= *Smilax subaculeata* Spreng., *Syst. Veg.* 2: 102. 1825. – Neotype (designated here): Jamaica, “e Jamaica *D. Bertero*” (TO-Balbis 7357 [♀!]).

= *Smilax ehrenbergiana* Kunth, *Enum. Pl.* 5: 174. 1850. – Holotype: Haiti, *Ehrenberg* (B†; lectotype (designated here): “S. Domingo”, 1828–31, HAL 076915 [♀, specimen]!; isolectotype: HAL 101732 [♀!]).

= *Smilax celastroides* Kunth, *Enum. Pl.* 5: 184 (1850). – Lectotype (designated here): Jamaica “*Smilax cumanensis* W. e Jamaica, *D. Bertero*”, 1821 (TO-Balbis 7357 [♀!]).

Rhizomes unknown. *Stems* angular, glabrous, armed with small prickles; terminal branches zigzag. *Leaves* lanceolate, ovate, glabrous, membranaceous, 10×2 cm, 5-veined, major veins connected by reticulate veinlets, apex acute, base rounded or acute, margin entire; *petiole* 0.6–1 cm long, rounded. *Inflorescences* umbellate, solitary, scale single; *peduncle* 2–4 mm long, flattened; *pedicels* of different length; *tepals* of male flowers 1.5–2 mm long, of female flowers 1.5 mm long; *anthers* linear in top-view, as long as the filaments. *Berries* black when ripe, not glaucous, ovoid, 5–7 mm in diameter.

Affinities. — *Smilax viscifolia* is related to *S. spinosa* and *S. cumanensis* but has frequently been misidentified as *S. havanensis*. From the latter species it is distinguished by its obovate leaves with rarely spinose margin and black, shiny berries.

Distribution and habitat. — Bahamas, Jamaica, Haiti, Dominican Republic (Fig. 19); 100 m.

Notes. — *Smilax ehrenbergiana* was described by Kunth (1850) based on a specimen at B collected by Ehrenberg, which was destroyed. A duplicate, however, is extant at HAL, which also matches Kunth’s original description. I have selected this as lectotype.

Duhamel (1801–03) described *Smilax viscifolia* based on the material present in Lamarck’s herbarium at P. A fragment removed from this specimen was deposited at the general herbarium at P (Poiret herbarium). Previous publications (Kunth 1850; Candolle 1878; Schulz 1904) mentioned that a possible type of *S. viscifolia* is deposited at the Balbis Herbarium in Jamaica (TO). Here, for *S. subaculeata* a Bertero specimen representing *S. viscifolia* from the Balbis herbarium is designated as neotype, because the original material has seemingly been lost. Consequently, *S. subaculeata* is treated as a synonym of *S. viscifolia*.

In the Balbis Herbarium at TO, there are two syntypes of *Smilax celastroides*. I have chosen as lectotype TO 7357 because it is more representative, better preserved and also a better match of the description by Kunth.

Common names. — “Briar Withe”, “Chainy Root” or “China Root” in Jamaica (Adams 1972).

Selected specimens examined. — DOMINICAN REPUBLIC: Dajabón, paraje Santiago de la Cruz, 19°27'N, 71°35'W, 520 m, 16.7.2003, *Clase & al. 3573* (JBSD); Independencia, Sierra de Neiba, 18°36'N, 71°47'W, 600 m, 1.8.1990, *Santana & Schaub 589-A* (JBSD); Monte Cristí, en la Costa del Océano Atlántico, aprox. 9 km al N de los Uberos, 19°52'N, 71°24'W, 18.4.1984, *Zanoni & Pimintel 29595* (JBSD); Santiago Rodríguez, Los Quemados, cruce de carretera Santiago Rodríguez, 19°22'N, 71°71'W, 100 m, 3.12.1997, *González & León 1080* (JBSD). — HAITI: Centre, Montagnes Noires, 20 km desde Mirebalais, en la carretera a Croix-des-Bouquets, 18°44'N, 72°10'W, 600 m, 11.11.1982, *Zanoni & al. 24020* (JBSD). — JAMAICA: Haycock hill, near Balcarres, slope on foothill S of the mountain, 18°10'N, 76°42'W, 600 m, 14.1.2004, *Christenhusz & al. 3044* (K); Saint Ann, Albir Peu, 12.5.1915, *Harris 12017* (K).

VIII. Domingensis group

Plants glabrous, stems terete with prickles, sometimes reddish; leaves membranous or coriaceous, sometimes reddish when young; inflorescences solitary; tepals c. 3.5–5.5 mm long; berries red to purple or black.

Includes: *Smilax domingensis*, *S. spissa*. Related species: *S. quinquenervia*, *S. walteri*.

24. *Smilax domingensis* Willd., Sp. Pl. 4: 783. 1806. — Holotype: Santo Domingo, “S. Domingo & Porto-rico” *Richard* (B-W 18397-1 [♀]!).

= *Smilax berteroi* Spreng., Syst. Veg. 2: 102. 1825. — Lectotype (designated here): La Hispanola, *Bertero* (TO-Balbis?).

= *Smilax reticulata* Desv. ex Ham., Prodr. Pl. Ind. Occid.: 58. 1825. — Lectotype (Ferrufino-Acosta & Greuter 2010b: 8): In India Occidentali, “*Smilax domingensis* Willd. *Smilax reticulata* Desv. In Ham. St. Thomas”, ex herb. Desvaux (P 647212 [♂]!).

= *Smilax multiflora* M. Martens & Galeotti in Bull. Acad. Roy. Sci. Bruxelles 9(2): 390. 1842. — Lectotype (designated here): “Mexico, Oaxaca, cordillera, Lalana (Chinantla)”, 3000 ft, 6.11.1840, *Galeotti 5475* (BR 6943455 [♀]!).

= *Smilax staminea* Griseb. in Martius, Fl. Bras. 3(1): 11. 1842. — Lectotype (Andreato 1997: 150): Brazil, “Brasilia”, *Sello* (G 39933 [♂]!); isolectotypes: K 400505 [♂]!, G 39932 [st.]!, P).

= *Smilax balbisiana* Kunth, Enum. Pl. 5: 183. 1850. — Holotype: Jamaica, *Bertero* (B†; neotype (designated here): “as Pseudochina”, TO 7357 [st.]!).

= *Smilax floribunda* Kunth, Enum. Pl. 5: 229. 1850 [non Desv. ex Ham. 1825] ≡ *Smilax kunthii* Killip & C. V. Morton in Publ. Carnegie Inst. Wash. 461: 269.

1936. — Holotype: Peru, *Hartweg 856* (B†); lectotype (designated here): P 647208 [♂]!; isolectotypes: BR 6944032 [♂]!, K 400479 [♂]!, P 647209 [♂]!).

= *Smilax eucalyptifolia* Kunth, Enum. Pl. 5: 230. 1850. — Holotype: Peru, 1778–1788 (B†); neotype (designated here): “Peru”, *Ruiz* (B 1001277645 [♀]!).

= *Smilax schlechtendalii* Kunth, Enum. Pl. 5: 224. 1850. — Lectotype (Killip & Morton 1936: 268): Mexico, in sylvis Misantlae “*Smilax domingensis*”, *Schiede & Deppe 987* (B 100277098 [♀]!); isolectotypes: HAL 101920 [♀]!, K 400510 [♀]!, MO 2095842 [♀]!, US 1635977 [♀ fragm.]!).

= *Smilax domingensis* var. *sagraeana* A. DC. in Candolle & Candolle, Monogr. Phan. 1: 101. 1878. — Lectotype (Ferrufino-Acosta & Greuter, 2010a: 8): Cuba, “La Havanne”, 1829, *Sagra 237* (G 206590 [♀]!); isolectotype: “Cuba” FI-W 180249 [st.]!).

= *Smilax schlechtendalii* var. *lindenii* A. DC. in Candolle & Candolle, Monogr. Phan. 1: 102. 1878. — Lectotype (Killip & Morton 1936: 268): Mexico, “Miradores”, 5.1839, *Linden 50* (G 90069 [♀]!); isolectotypes: G 39926 [♀]!, P 594655 [♀]!, 39926 [♀]!, K 400509 [♀]!, MICH 1192733 [♀]!, US 1635975 [♀]!, BR 6943424 [st.]!).

= *Smilax canaliculata* F. W. Apt in Repert. Spec. Nov. Regni Veg. 18: 406. 1922. — Holotype: Costa Rica, Las Vueltas, Tucurrique, 700–800 m, *Tonduz 13303* (B†; lectotype (designated here): K 400946 [♀]!); isolectotypes: BM, G 98906 [st.]!, US 937816 [♀]!).

= *Smilax engleriana* F. W. Apt in Repert. Spec. Nov. Regni Veg. 18: 407. 1922. — Lectotype (Killip & Morton 1936: 266): Costa Rica, “Lisieie de la forêt à Santa Rosa du Copey”, 1100 m, 4.1898, *Tonduz 11732* (B 100247562 [♂]!); isolectotypes: BM 578841 [♂]!, BR 6943752 [♂]!, CR!, GH 30063 [♂]!, K 400947 [♂]!, NY 319995 [♂]!, US 937821 [♂]!).

= *Smilax colubrina* J. F. Macbr. in Publ. Field Mus. Nat. Hist., Bot. Ser. 11: 44. 1931. — Holotype: Peru, “Dept. Loreto: Mishuyacu near Iquitos”, 100 m, 5–6.1930, *Klug 1327* (F 269895 [♂]!); isotypes: NY 320006 [♂]!, US 1456440 [♂]!).

= *Smilax gilva* J. F. Macbr. in Publ. Field Mus. Nat. Hist., Bot. Ser. 11: 45. 1931. — Holotype: Peru, “Dept. Loreto: Mishuyacu near Iquitos”, 100 m, 2–3.1930, *Klug 874* (F 269899 [♂]!); isotypes: G 98908 [♂, fragm.]!, NY 320008 [♂]!, US 937821 [♂]!).

= *Smilax domingensis* var. *microscola* B. L. Rob. in Proc. Amer. Acad. Arts 35: 323, 1900 ≡ *Smilax microscola* (B. L. Rob.) Killip & C. V. Morton in Publ. Carnegie Inst. Wash. 461: 267. 1936. — Lectotype (Killip & Morton 1936: 267): Mexico, Chiapas, “between Tumbala & El Salto”, 466–1400 m, 29.10.1895, *Nelson 3392* (GH 30062 [♂]!); isotype: US 233326 [♂]!).

= *Smilax krukovii* A. C. Sm. in J. Arnold Arbor. 20: 290. 1939. — Holotype: Brazil, “Basin of Rio Solimoes, State of Amazonas: Municipality São Paulo de Olivença: basin of Creek Belem”, 10–12.1936, *Krukoff*

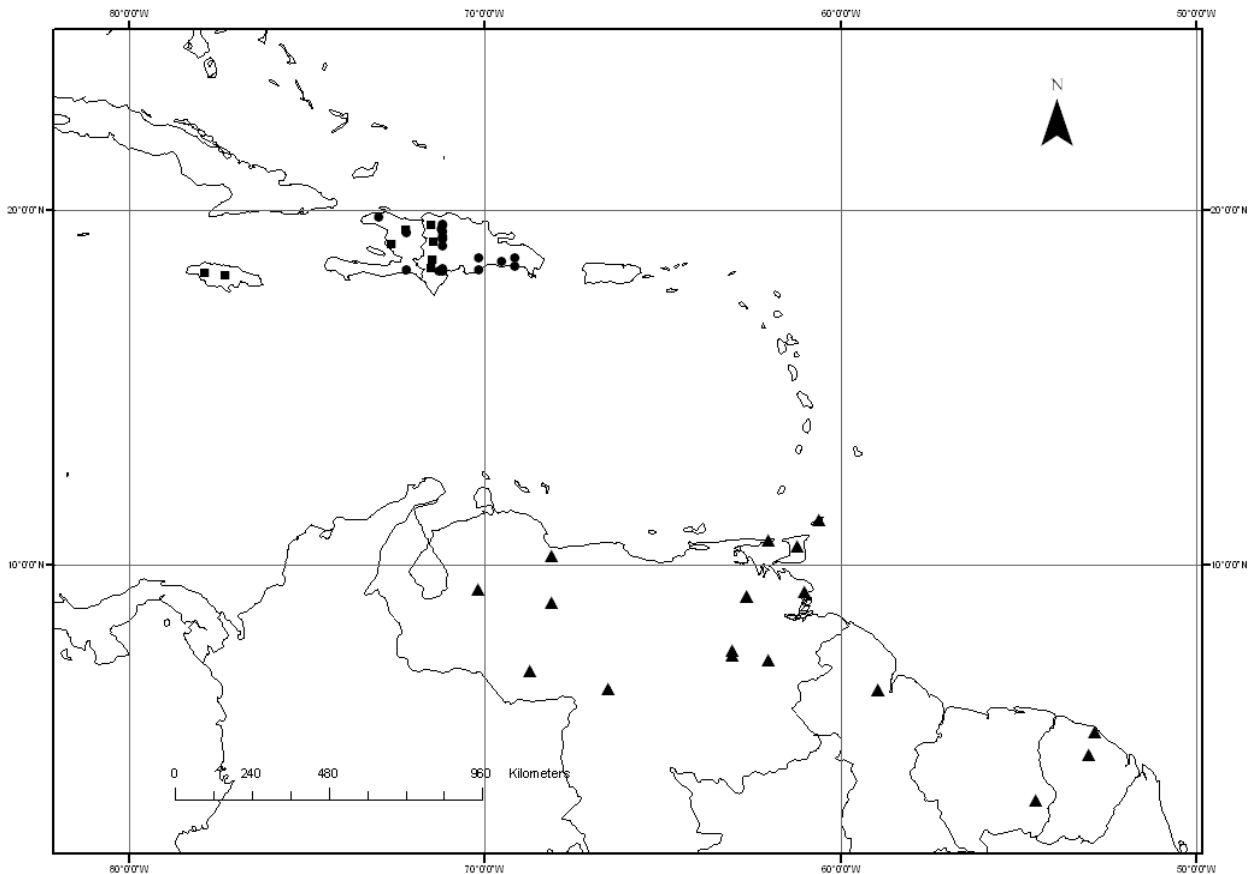


Fig. 19. Distribution of *Smilax populnea* (circles), *S. ehrenbergiana* (square) and *S. oblongata* (triangles).

- 8964 (NY 180356 [♂!]; isotypes: BM 896133 [st.], F 333656 [st.], BR 6944124 [st.], G 90071 [st.], GH 30076 [st.], K 400488 [st.], MICH 1187391 [♂!], MO 1254884 [♂!], P, S 5805, US 1741960, 2250432 [st.]).
- = *Smilax chiapensis* Lundell in Contr. Univ. Michigan Herb. 7: 3. 1942. – Holotype: Mexico, Chiapas, “Mt Ovando CHI8”, 1000 m, 14–18.11.1939, *Matuda* 3988 (MICH 1192727 [♂!]; isotypes: MO 1195502 [♂!], GH 30061 [♂!], TEX-LL 370268, 370269 [♂!]).
- = *Smilax staminea* f. *obtusata* Steyerem. in Fieldiana, Bot. 28 (1): 156. 1951. – Holotype: Venezuela, “State of Bolivar: Ptari-tepuí, forested sandstone south-facing slopes between plateau portion and “Cave Camp”, 1700–1800 m, 1.11. 1944, *Steyermark* 59695 (F 330732 [♀!]; isotype: NY 180349 [♀!]).
- = *Smilax caudata* Lundell in Wrightia 3: 162. 1966. – Holotype: Guatemala, “Alta Verapaz. On Coban road, between Chiracte and Chapultepec Farm, km 285/286, in high forest”, 24.5.1964, *Contreras* 4783 (TEX-LL 370267 [♀!]; isotype: 370266 TEX-LL [♀!]).

Rhizomes tuberous, red with perennial and coriaceous scales. *Stems* terete, glabrous, armed with recurved prickles, often unarmed apically, terminal branches straight and reddish; *axillary scale* single on the stem. *Leaves* ovate to lanceolate, glabrous, coriaceous or membranous, 7–15 × 2.5–5 cm, 5–7-veined, major veins connected

by reticulate veinlets, apex acuminate, base acute, margin entire, young leaves sometimes reddish; *petiole* 1–1.5 cm long, terete. *Inflorescences* umbellate, solitary, scale single; *peduncle* 0.2–0.7 mm long, terete; *pedicels* of uniform length; *tepals* of male flowers 4–7 mm long, of female flowers 3.5–4.5 mm long; *anthers* linear in top-view, shorter than the filaments. *Berries* red to purple when ripe, not glaucous, globose, 7–10 mm in diameter. – Fig. 20.

Distribution and habitat. — Honduras to Peru, Venezuela, Brazil, Greater Antilles (Fig. 21); open areas, lower montane wet forest, humid forest, 100–1000 m.

Notes. — *Smilax domingensis* is a species with a wide distribution and morphological variation. Lundell (1942) described *S. chiapensis* based on a specimen previously determined to be *S. lanceolata*, although he stated that *S. chiapensis* was closer to *S. kunthii*. He distinguished *S. chiapensis* from other species through the size of tepals, peduncles, anthers and filaments (Gaskin & Berry 2005; Andreata 1997), despite species like *S. domingensis* ranging widely in phenotypic variation and the size of tepals, measuring between 4 and 7 mm. Therefore, in this study, *S. chiapensis* is treated as a synonym of *S. domingensis*.

Smilax staminea is distinguished from *S. domingensis* and *S. kunthii* based on its unarmed stems and peduncle length. All of them, however, display tepals either 3.5 mm

(in pistillate flowers) or 4–5 mm long (in staminate flowers) as well as red to black fruits when ripe. During field observations, stems were observed to be armed toward the base and unarmed toward the upper part. Therefore, it seems possible that the herbarium material was only collected from the upper part of the plant, because the majority was found not to display prickles. During the examination of *S. staminea* the aspects relating to the morphological variation of *S. domingensis* were verified, concluding that *S. staminea* can be considered conspecific with *S. domingensis*.

The holotype of *Smilax eucalytifolia* at B was destroyed. Two specimens were identified as *S. eucalytifolia* by G. M. Schulze. The specimen B 1001277645 is selected as neotype.

Macbride (1931) stated that *Smilax gilva* is a species very similar to *S. floribunda* and *S. staminea*. He distinguished it from other *Smilax* species by its small flowers, subopaque leaves, longer petioles, shorter-vaginate and broader perianth segments. The tepals of all three species measure c. 4 mm; therefore, *S. floribunda*, *S. gilva* and *S. staminea* are considered synonyms of *S. domingensis*.

Since the type specimen of *Smilax canaliculata* at B was destroyed during the Second World War, the isotype (with fruits) deposited at K is selected as lectotype. This species is considered a synonym of *S. domingensis* (Art. 9.10, McNeill & al. 2006).

The type material of *Smilax reticulata* consists of only one specimen at Paris (P 647212), which corroborates Desvieux's annotation. This taxon is considered a synonym of *S. domingensis*.

The syntype of *Smilax kunthii* collected by Ruiz & Pavón in Peru was destroyed at B. The specimen *Hartweg 896* with male flowers at P is selected as lectotype and the name regarded a synonym of *S. domingensis*.

I have not seen the type specimen of *Smilax balbisiana* personally. However, Kunth (1850) cited a specimen annotated with the unpublished name *S. pseudochina* Bertero at TO, which I presume to be the type specimen of *S. balbisiana*. However, Candolle (1878) remarked that the type specimen is not present at B and also did not examine any other material. The specimen deposited at TO is selected as neotype, because both *S. balbisiana* and an anonymous specimen found at the Balbis herbarium were considered conspecific with *S. domingensis* (Art. 9.14, McNeill & al. 2006).

Martens & Galeotii (1842) published the name *Smilax multiflora* based on an unarmed specimen with female flowers (tepals c. 3.5 mm). For the most part, the specimens of *S. domingensis* do not have prickles on the apical or terminal branches. Sometimes, the female plants may have racemose inflorescences. Therefore, *S. multiflora* is also regarded a synonym of *S. domingensis*.

The flower size is said to distinguish *Smilax colubrina* from other species. León (2006) and Macbride (1931) reported that *S. colubrina* is endemic to the Loreto region, N Peru, although this species is only known from

the type specimen. While Macbride (1931) described the male tepals of *S. colubrina* to be 2–2.5 mm long, I have found that they measure c. 4 mm in length. Therefore, *S. colubrina* is considered a synonym of *S. domingensis*.

Common names. — “ñame de China”, “Raíz de China” in Cuba; “cuculmecca”, “cuculmecca roja”, “cuculmecca morada”, “diente de perro”, “curlo” in Central America; “cocolmeco”, “bejuco de uva”, “popo medicinal” in Mexico; “bejuco chino” in Venezuela; “bejuco de riñón” in the Dominican Republic (León 1946; Hernández Cano & Volpato 2004; Ferrufino & Gómez-Laurito 2004; MacVean 2006).

Selected specimens examined. — BELIZE: Cayo, Ceibo Grande to main divide track by old repeater, 16°32'26"N, 89°05'43"W, 740 m, 8.3.2000, *Monro & al. 3226* (MO); Belize, Cohune ridge, Sibur River, 4.2.1931, *Bartlett 11359* (UC). — BOLIVIA: La Paz, Larecaja, Copacabana, 8.10.–15.11.1939, *Krukoff 11129* (U). — BRAZIL: Acre, Cruzeiro do Sul, km 6 of Cruzeiro do Sul-Boa Fé road, 7°28'22"S, 72°49'17"W, 16.10.2001, *Maas & al. 8972* (MO); São Paulo, São Vicente, 20.3.1955, *Hoehne 3933* (F); Rio de Janeiro, 1876, *Glaziou 8502* (G). — COLOMBIA: Antioquia, Cáceres, Troncal de la Paz, Cáceres-Bagre, 3–4 km, 7°35'N, 75°16'W, 16.5.1987, *Callejas & al. 3576* (K, MO, U); Quindío, Salento, Reserva del Alto Quindío Acaime, 4°37'N, 75°32'W, 3070 m, 12.6.1990, *Ranjifo 129* (MO). — COSTA RICA: Alajuela, San Ramón, Los Angeles, Reserva Biológica Alberto Manuel Brenes, 10°13'N, 84°37'W, 850 m, 16.2.2001, *Ferrufino 35* (USJ); San José, Dota, Cordillera de Talamanca, Madreselva, 9°40'05"N, 83°57'22"W, 2500–2600 m, 24.8.1996, *Gómez-Laurito & al. 12877* (USJ). — CUBA: Matanzas, lomas al oeste de Las Tres Ceibas, 80–100 m, 23°06'–07'N, 81°39'W, *Greuter & al. 25034* (B); Sanctus Spiritus, Finca Cuba, alrededores de Mogote Caburni, 650 m, 13.4.1994, *Acevedo-Rodríguez & al. 6465* (US). — DOMINICAN REPUBLIC: Monseñor Novel, 3 km al sur de Maimón, Loma mala, Río Maimon, 18°53'N, 70°18'W, 110 m, 26.6.1994, *Jiménez & Veloz 1611* (F, MO); Santiago, San José de las Matas, 700–800 m, 2.6.1930, *Valeur 899* (F, GH, K, MO). — GUATEMALA: Alta Verapaz, Cobán Chicu'sha'b 8 km al SW de Cobán, 15°26'N, 90°27'W, 400 m, 22.7.1988, *Tenorio & al. 14717* (MO); Suchitepéquez, Samayac, Canton Chiguaste, Finca El Cacaotal, 14°7'N, 91°28'W, 450 m, *Rueda 17340* (HULE). — GUYANA: Potaro-Siparuni, Iwokrama Rainforest reserve, 4°20'N, 58°50'W, 600–800 m, 22.11.1995, *Clarke & Hoffman 580* (K, U). — HAITI: Massif de la Hotte, Grand'Ansesud limite: 13.6 km N de Camp Perrin en la cerretera a Roseaux y Jérémie, 18°23'N, 73°53'W, 720 m, 15.11.1982, *Zanoni & al. 24323* (MO); Massif du Nord, Chaîne Bonnet Leveque, 19°35'N, 72°14'W, 700–750 m, 25.10.1985, *Mejía 35770* (U). — HONDURAS: Cortés, P. N. Cusuco, Filo entre Cerro Cantiles y Cerro Jilincó, 20 km al O. de San Pedro Sula, 15°30'N, 88°14'W, 2120 m,



Fig. 20. *Smilax domingensis* – A: pistillate flowering branches; B: infructescence; C: seeds; D: staminate flower; E: staminate inflorescence; F: stamen. – Reprinted with permission from Ferrufino-Acosta & Greuter (2010a).

20.3.1993, *Mejia 348* (TEFH, EAP); Yoro, along Quebrada El Aguacatal and in ravines that enter into el Rio Guan Guan, 15°31'N, 87°28'W, 100–300 m, 19.4.1994, *Hazlett & Brant 8084* (EAP). — JAMAICA: Saint Andrew, Grand Ridge of the Blue Mountains between Morce's Gap and John Peak, 18°05'N, 76°40'W, c. 1620 m, 18.4.1990,

Bellingham 1170 (BM). — MEXICO: Oaxaca, San Miguel Chimalapa, Cima del Cerro Salomón al No de Benito Juárez, c. 44 km en línea recta al N de San Pedro Tapanatepec, 16°46'15"N, 94°11'45"W, 1770 m, 7.4.1986, *Ishiki 1443* (MO); Veracruz, Jesús Carranza, Loma al S de Poblado 2, 17°12'N, 94°38'W, 200 m, *Wendt & al. 5774* (MO). —



Fig. 21. Distribution of *Smilax domingensis* (circles) and *S. laurifolia* (triangles).

PANAMA: Chiriquí, Fortuna Dam, along trail across valley south of lake 9°45'04"N, 82°15'04"W, 1300–1400 m, 7.1.1987, *McPherson 10392* (PMA); Panama, Cerro Jefe region, 9°15'N, 79°30'W, 600 m, 2.5.1987, *McPherson & Stockwell 10893* (PMA). — PERU: Amazonas, Bagua, Imaza, Tayu Mujaji, 5°15'56"S, 78°22'07"W, 900–1030 m,

17.2.2002, *Vásquez 27594* (USJ); Cajamarca, San Ignacio, San José de Lourdes, Estrella del Oriente, 4°46'00"S, 78°59'00"W, 1600–1700 m, 6.9.1997, *Campos & Díaz 4420* (USJ). — PUERTO RICO: Ciales, along trail Camino de la Ceiba towards Quebrada del Pozo Azul, 15.8.2001, *Acevedo-Rodríguez & Vicens 11835* (US); Luquillo,

Sierra de Luquillo, Monte Jimenez, 5.1885, *Sintesis 1417* (F, G, MO, U, US); Naguabo, Sierra de Naguabo, Loma Icacó, 210–675 m, 24.7.1914, *Shafer 3449* (F, K, US). — SURINAME: Jodensavanne, Mapane creek are, 13.12.1954, *Mennega 568* (U). — VENEZUELA: Amazonas, Atures, 9 km NW of settlement of Yutaje, 4 km W of Rio Coro-Coro, W of Serrania de Yutaje, 5°41'N, 65°10'W, 1400–1760 m, 6.3.1987, *Liesner & Holst 21702* (MO); Bolivar, Meseta del Jaua, Cerro Jaua, 4°48'50"N, 64°34'10"W, 1850–1920 m, 4.3.1974, Sucre, Pensinsula de Paria, 10°42'N, 62°37'W, 730–1050 m, 1.12.1979, *Steyermark & Liesner 120931* (MO).

25. *Smilax spissa* Killip & C. V. Morton in Publ. Carnegie Inst. Wash. 461: 273. 1936. — Holotype: Costa Rica, “Entre la Muerte & la Division dans les forêst”, 19.1.1891, *Pittier 3470* (US 1080290 [♂]!); isotype: BR 6944100 [♂]!. — Fig. 22.

Rhizomes tuberous. *Stems* terete, glabrous, armed with flattened prickles, terminal branches straight, scarcely prickly at apex; *axillary scale* single on the stem. *Leaves* ovate, lanceolate, glabrous, membranous, 9–22×3–10 cm, 5-veined, major veins connected by parallel venation, apex acuminate, base acute, margin entire; *petiole* 1–2 cm long, terete. *Inflorescences* umbellate, glomerulate, solitary, scale single; *bracts* perennifolious, *peduncle* 1.5–5 cm long, flattened; *pedicels* of uniform length; *tepals* of male flowers 4–5 mm long, of female flowers 3.5 mm long; *anthers* oblong in top-view, longer than the filaments. *Berries* red when ripe, not glaucous, ovoid, 8–10 mm in diameter.

Affinities. — *Smilax spissa* can be distinguished from other *Smilax* species by its muricate stems, the parallel secondary venation, c. 4–5 mm long tepals and red berries.

In many herbaria, this species has been mistaken for *Smilax panamensis* and *S. subpubescens*. While *S. spissa* is close to *S. syringoides*, it differs by its long pedicels, spread umbells and the colour of its berries (see also diagnostic key below).

Distribution and habitat. — Panama and southern Costa Rica (Fig. 22); lowland forest, wet forest, 300–800 m.

Selected specimens examined. — COSTA RICA: Puntarenas, Puntarenas, R. B. Carara Lomas Pizote, Sendero a Bijagual, 9°47'10"N, 84°35'10"W, 300 m, 8.12.1989, *Jiménez & Zúniga 761* (USJ); San José, Montana Jamaica, c. 3 km NE of Bijagual de Turrubares, R. B. Carara, 9°45.5'N, 84°33'W, 500–600 m, 7.8.1985, *Grayum & al. 5843* (CR, MO). — PANAMA: Comarca de San Blas, El Llano-Carti road, 9°20'N, 79°00'W, 300–400 m, 28.8.1982, *Hamilton & Stockwell 1049* (F, PMA); Coclé, PN G.D. Omar Torrijos Herrera, camino a Coclesito, 8°40'10"N, 80°35'34"W, 900 m, 18.11.2003, *Aizprúa*

& *Flores B3887* (PMA); Darien, to the Serrania del Darien, Colombia Frontier, top of Cerro Mali, c. 1400 m, 17.1.1975, *Gentry & Mori 13675* (PMA); Panama, Canal Zone, Barro Colorado Island, S of Armour 14, 24.5.1969, *Foster 872* (MO, PMA).

IX. Panamensis group

Plants glabrous, stems terete, armed with straight prickles; leaves membranous; inflorescences composed in a raceme with a terminal or determinate inflorescence or often with bracts, very prominent and perennifolious; tepals c. 3.5–5 mm long; berries orange.

Includes: *Smilax febrifuga*, *S. fluminensis*, *S. solanifolia*, *S. syphilitica*. Related species: *S. santaremensis*.

- 26. *Smilax febrifuga*** Kunth, Enum. Pl. 5: 201. 1850. — Lectotype (designated here): Peru, “Smilax China Peruviana Smilax Purhampui & Santopalo in Peruviae Andúm Montibus memorosis”, Ruíz (B 10127767 [st.!]!).
- = *Smilax insignis* Kunth, Enum. Pl. 5: 200. 1850. — Holotype: Peru, “*Smilax lanceolata* in Peruvia”, 1778–1788, Ruíz (B 100127766 [st.!]!).
 - = *Smilax poeppigii* Kunth, Enum. Pl. 5: 192. 1850. — Holotype: Peru, “Maynas alto”, *Poeppig 1916* (B 100127763 [st.!]!) [incorrectly cited as *Poeppig 1960* in the protologue].
 - = *Smilax febrifuga* var. *aequatoris* A. DC. in Candolle & Candolle, Monogr. Phan. 1: 159. 1878. — Holotype: Ecuador, “ad radices m. Chimborazo, secus rivulum Chasuan frequens”, 8.1860 (K 201314 [♂]!).
 - = *Smilax panamensis* Morong in Bull. Torrey Bot. Club 21: 441. 1894. — Lectotype (Killip & Morton 1936: 275): Panama, “Borders of the Garden of Gatun Sta. P. R. R.”, *Hayes 63* (NY 319999, 320000 [♂]!); isolecotypes: NY 320000 [♂]!, USJ!).
 - = *Smilax ramonensis* F. W. Apt in Repert. Spec. Nov. Regni Veg. 18: 405. 1922. — Lectotype (Killip & Morton 1936: 274): Costa Rica, “n v. Zarza, Bois de San Pedro, près San Ramon”, 1400–1600 m, *Tonduz 17723* (B†; lectotype (designated here): BM 796927 [♂]!; Isolectotypes: BR, CR, G 90075-90076, 39975 [♂]!, M 124481 [♂]!, S 5806, US 1635981 [fragm.!]!).
 - = *Smilax graciliflora* A. C. Sm. in J. Arnold Arbor. 20: 291. 1939. — Holotype: Brazil, “Basin of Rio Solimoes, State of Amazonas: Municipality São Paulo de Olivença: basin of Creek Belem”, 26.10.–11.12.1936, *Krukoff 8806* (NY 180354 [♂ specimen]!); isotypes: F 335997 [♂]!, S 5804).

Rhizomes tuberous, white. *Stems* terete, glabrous, armed with straight prickles. *Leaves* ovate to lanceolate, glabrous, membranous, 8–25×5–18 cm, 5–7-veined, submarginal veins connected by reticulate veinlets, apex acuminate, base acute, margin entire; *petiole* 1–1.7 cm long, terete, sheath winged. *Inflorescences* umbellate, in racemes; *scales* paired, bracts conspicuous, brownish

c. 0.5–1 cm long; *peduncle* 10–35 mm, flattened; *pedicels* of uniform length; *tepals* of male flowers 5–6 mm, of female flowers 3.5–5 mm long; *anthers* linear in top-view, longer than the filaments. *Berries* orange when ripe, not glaucous, ovoid, 6–12 mm in diameter.

Affinities. — The most representative features of *Smilax febrifuga* are its tuberous, white rhizomes, the terete and armed stems, the inflorescences composed in racemes with prominent bracts, tepals of c. 4–5 mm length and its orange berries.

Distribution and habitat. — Honduras to Peru, Bolivia, Venezuela, Brazil, French Guiana (Fig. 23); evergreen seasonal forest, riparian forests, humid forests, montane rain forests, 0–800 m.

Note. — Two syntypes of *Smilax febrifuga*, collected by Ruiz, exist at B. One of these was chosen as lectotype (B 10127767) because it is the more representative and better preserved specimen, and also because it better matches Kunth's description of the species.

In his protologue, Morong (1894) noted that *Smilax panamensis* has unarmed, slightly pubescent stems, almost glabrous peduncles and tendrils as well as black berries with a reddish tinge in dried specimens. Killip & Morton (1936) suggested that there is confusion regarding this species, dating back to the original publication by Morong, because the specimens collected by Hayes belong to different taxa. The lectotype *Hayes 63* represents *S. panamensis*, whereas *Hayes 209* matches representative specimens of *S. mollis*. Also, Killip & Morton (1936) mentioned that several specimens of *S. spissa* were mistaken for *S. panamensis*. However, both species are growing in association, but differ in some important characteristics, such as venation, type of inflorescence and berry colour. The taxon so far known from Honduras to Panama by the name of "*S. panamensis*" is the same taxon known as *S. febrifuga*, which is currently reported for Ecuador, Peru and Bolivia, with the particularity that plants occurring in South America have bigger leaves than those growing in Central America. The lectotype of *S. panamensis* was studied by the author and found to represent *S. febrifuga*.

The lectotype of *Smilax ramonensis* designated by Killip & Morton (1936) was destroyed at B. An isolecotype deposited at BM is selected as lectotype. McBride (1936) suggested that *S. ruiziana* is a species close to *S. febrifuga* and described it as having peduncles of 8–20 mm and bracts of 5–7 mm length. The type collection deposited at B and cited by Kunth (1850) has flower buds of c. 5 mm, but in his protologue, Kunth mentioned tepals of c. 2.5 mm; here, *S. ruiziana* is proposed as a new synonym of *S. febrifuga*.

The name *Smilax poeppigii* was originally published by Kunth in 1850 and, according to the protologue, based on *Poeppig 1960*, collected in Huallaga, Peru, and deposited at B. However, the corresponding specimen

with Kunth's handwriting at B has the collection number "1916". Apparently the collection number "1960" in the protologue is a typographical error.

Smilax insignis described by Kunth (1850) was based on sterile material. In his protologue, Kunth described it as a glabrous and unarmed plant. Although the specimen collected by Ruiz & Pavón in Peru holds only remains of a raceme and displays verruculose peduncles of c. 0.75 cm length, these features are evident in the type specimen. I consider *S. insignis* as conspecific with *S. febrifuga*.

Common names. — "Zarsa Masha" in Peru; "cuculmeca blanca" in Central America (Ferrufino & Gómez-Laurito 2004).

Selected specimens examined. — BOLIVIA: Beni, Ballivian, Espiritu en la zona de influencia del río Yacuma, al borde de la "Isla" (II2), 28.9.1979, *Beck 2536* (NY); Santa Cruz, Ichilo, Parque Nacional Amboró, Río Saguyayo near mouth of Quebrada Yapojé, 17°34'S, 63°44'W, 350 m, 11.6.1991, *Nee 40900* (NY). — BRAZIL: Acre, Sena Madureira, trail from W bank of Rio Iaco to Rio Purus, 5.10.1968, *Prance & al. 7877* (F, MO). — COLOMBIA: Amazonas, Misión, Río Mavaca, 2°26'N, 65°07'W, 185 m, 31.1.1991 (MO); Antioquia, Jardín, 2 km N de Jardín, vía a Morro Amarillo, Alto de las Flores, 5°40'N, 75°48'W, 2220 m, 10.6.1987, *Callejas & al. 3990* (MO, NY, US); Boyaca, El Humbo, 3000 ft, 4.4.1933, *Lawrence 738* (A, G, F, K, MO, UC); Caquetá, Sierra de Chiribiquete, 1°05'N, 72°40'W, 26.8.1992, *Palacios & al. 2695* (MO); Chocó, 3 km W of Istmo de San Pablo (Río Quito), c. 15 km W of Las Minas on new Pan American Highway, 80 m, 10.1.1979, *Gentry & Renteria 23948* (NY); Cundinamarca, Laguna de Pedro Palo, 4 km from road Bogotá to La Mesa, 2056–2100 m, 29.11.1990, *Wijninga 596* (MO, U); Huilía, Río Caqueta, Araracuara, 13.12.1990, *van Dulmen 62A* (U); Putumayo, Mocoa, corregimiento San Antonio, vereda Alto Campucana, finca La Mariposa, 1°12'N, 76°38'W, 1400 m, 20.4.–1.5.1994, *Betancour & Marín 5168* (MO); Santander, N slope of Mesa de los Santos, 100–1500 m, 11.–15.12.1926, *Killip & Smith 15380* (A); Valle del Cauca, Río Frio, vereda La Trinidad, Finca El Provenir, 4°10'N, 76°13'W, 1200 m, 5.4.1986, *Al Gentry 54040* (MO) — COSTA RICA: Alajuela, San Ramón, Los Angeles, Reserva Biológica Alberto Manuel Brenes, 10°13'N, 84°37'W, 850 m, 9.3.2002, *Ferrufino 229* (USJ); Limón, Matina, Baltimore, 9°34'20"N, 82°39'50"W, 100–150 m, 7.4.2001, *Ferrufino 62* (USJ); Puntarenas, Buenos Aires, P. N. La Amistad, Cuenca Térraba-Sierpe, 9°02'11"N, 83°01'21"W, 1350 m, 22.4.1999, *Castro & al. 311* (CR, INB). — ECUADOR: Napo, Estación Biológica Jatun Sacha, 8 km al este de Misahualli, 1°04'S, 77°36'W, 450 m, *Palacios & al. 10488* (MO); Pastaza, 1 km al E de Topo por carretera entre Banos y Mera, 1°21'N, 78°10'W, 1300 m, 18.3.1985, *Palacios & al. 185* (MO). — GUYANA: Rupununi, along trail from Morris Mines (on Ireng River) to Karasabai Village,



Fig. 22. Distribution of *Smilax spissa* (circles) and *S. guianensis* (triangles).

4°00'N, 59°21'W, 300–400 m, 7.1.1982, *Knapp & Mallet* 2880 (MO). — HONDURAS: Atlántida, J. B. Lancetilla, entrada principal, 15°08'N, 88°05'W, 0–500 m, 7.4.1994, *Nelson & Andino 18018* (TEFH). — NICARAGUA: Río San Juan, Reserva Indio-Maíz, Municipio de El Castillo, A lo largo del Caño Chontaleño, 11°9'N, 84°11'W, 22.2.1997, *Rueda 6284* (HULE); *Zelaya*, Camino a lo largo del Río Punta Gorda, entre la Corriente la Guitarrona y San José, 11°31'N, 84°14'W, 26.2.1994, *Rueda 3600* (HULE). — PANAMA: Chiriquí, Bugaba, Santa Clara, Hartmann Finca, 8°50'N, 82°44'W, 1300 m, 26.2.1985, *van der Werff & Herrera 7073* (PMA); Veraguas, Montijo, Cerro Hoya, subiendo por Cobachón, 7°18'45"N, 80°40'23"W, 5.2.1997, *Deago & al. 263* (PMA). — PERU: Cajamarca, San Ignacio, Huarango, Nuevo Mundo, Quebrada Santa Rosa, 5°10'05"S, 68°32'00"W, 1700 m, 10.11.1997, *Campos & Nunez 4585* (B, MO, USJ); Cusco, Quispicanchis, Hills around Río Araza between Pande Azucar and Quince Mil Airport, 13°13'S, 70°45'W, 543 m, 10.8.1991, *Nunez 13991* (USJ); Loreto, Río Samiria, c. 5°2'S, 74°30'W, 140–160 m, 4.8.1982, *Gentry & al. 38056* (USJ); Madre de Dios, Tambopata, Las Piedras, Cusco Amazónico, 12°29'S, 69°03'W, 200 m, 13.11.1991, *Timaná & Jaramillo 3184* (B, MICH, MO, USJ); San Martín, Rioja, Pedro Ruíz-Moyobamba road, km 390, 5°50'S, 77°45'W, 1750 m, 29.7.1983, *Smith 4442* (USJ). — VENEZUELA: Amazonas, Cano de Cholo, 16 km NE of San Carlos de Río Negro, 4 km SW of Solano, 1°56'N, 66°58'W, 120 m, 2.2.1980, *Liesner 8985* (MO, NY); Miranda, Cerros del Bachiller, above Quebrada Corozal, south of Santa

Cruz, 10 km (by air) west of Cúpira, 10°09'N, 65°48'W, 20–700 m, 22.–23. & 25.–26.3.1978, *Steyermark & Dadvise 116945* (MO).

27. *Smilax fluminensis* Steud., *Nomencl. Bot.*, ed. 2, 2: 598. 1841 ≡ *Smilax china* Vell., *Fl. Flumin. Icon.* 10: t. 105, 106. 1831 ["1827"] [non *Smilax china* L. 1753] ≡ *Smilax syringoides* Griseb. in *Martius, Fl. Bras.* 3(1): 11. 1842. – Lectotype (Guaglianone & Gattuso 1991: 112): *Smilax china* in Vellozo, *Fl. Flumin. Icon.* 10: t. 105. 1831 [♂]!

Rhizomes tuberous. *Stems* terete, glabrous with robust prickles. *Leaves* ovate, lanceolate, cordate, glabrous, coriaceous or membranous, 9–21 × 6–17 cm, 5–7-veined, major veins connected by reticulate veinlets, apex acute, acuminate, rarely obtuse, bases cordate, acute or rounded, margin entire; *petiole* 3–4 cm long, flattened. *Inflorescences* umbellate, arranged in racemes, scale single, bracts perennifolious; *peduncle* 3–3.5 cm long, flattened; *pedicels* of uniform length; *tepals* of male flowers 3–5 mm long, of female flowers 3–3.5 mm long; *anthers* ellipsoidal, longer than the filaments. *Berries* yellow to orange when ripe, not glaucous, globose, 8–10 mm in diameter.

Notes. — This taxon is here newly reported for Costa Rica and Panama. Some specimens had been misdetermined as *Smilax panamensis*. In Costa Rica, this species spreads to the southern part of the country.

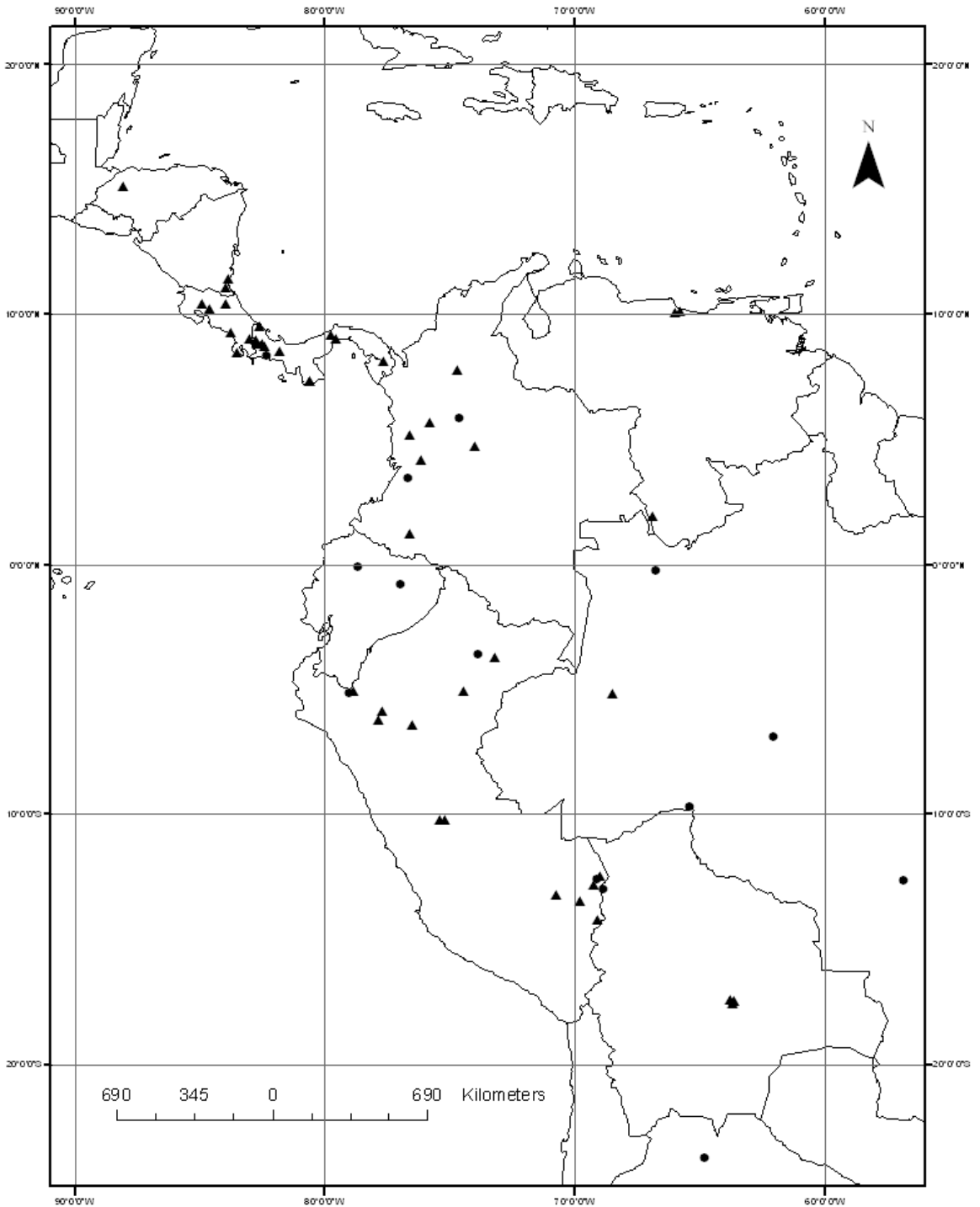


Fig. 23. Distribution of *Smilax fluminensis* (circles) and *S. febrifuga* (triangles).

In 1841 Steudel published *Smilax fluminensis* as a new name. The images of individual flowers (t. 105 and 106) with its corresponding analysis for Vellozo's illegitimate name constitute valid publication of the name (see Art. 42.3, McNeill & al. 2006).

Distribution and habitat. — Costa Rica, Panama, Colombia, Peru, Ecuador, Venezuela, Brazil, Peru, Bolivia, Argentina (Fig. 23); riparian forests, 150–1800 m.

Common names. — “Japicanga”, “Yuapecá guasu”, “Salsa”, “Salshina”, “zarzaparrilla”, “ijuapecá guasu” in Brazil; “Zarzaparrilla” in Bolivia; “Vena China” in Ecuador (Andreata 1997; Guaglianone & Gattuso 1991).

Selected specimens examined. — ARGENTINA: Misiones, Ledesma, P. N. Calilegua, 23°44'S, 64°50'W, 720 m, 27.2.1997, Zuloaga & al. 6323 (MO). — BOLIVIA: Pando, Río Abuna, 3 km above confluence of Río Negro south

bank, 16.11.1968, *Prance & al.* 8529 (F); Santa Cruz, 18°06'30"S, 63°57'00"W, 315 m, *Nee 39394* (NY); Sara, Buenavista, 450 m, 10.1925, *Steinbach 7287* (U). — BRAZIL: Amazonas, Rio Curicuriari, 1.1948, *Schultes & López 9705* (US); Matto Grosso, Cuyaba, 23.9.1943, *Baldwin 3001* (US); Paraiba, Mata de Pau Ferro, 6°58'12"S, 35°42'15"W, 600 m, 24.9.1980, *Fevereiro & al.* M41 (K); Paraná, Quatro Barras, Morro Mãe Catira, 24.7.1987, *Cordeiro & Silva 440* (MO). — COLOMBIA: Antioquia, San Luís, Cañón del Río Claro, 5°53'N, 74°39'W, 330–350 m, 30.5.1984, *Cogollo 1713* (MO); Caldas, Rio Navarco, Salento, 1400–1700 m, 31.7.1922, *Pennell 9083* (K, NY); Cauca, Valle del Cauca, Queremal, vereda La Victoria, 3°31'N, 76°42'W, 1480 m, 27.7.1997, *Croat & Gaskin 80430* (MO). — COSTA RICA: Puntarenas, Cordillera de talamanca, Coto Brus, 8°59'N 82°46'W, 1800–1900 m, 3.9.1983, *Davidse 24516* (U). — ECUADOR: Bolívar, carretera Chillanes–Bucay, 1°55'N, 79°05'W, 2100 m, 10.9.1987, *Zak & Jaramillo 2866* (F); Pichincha, Quito, Parroquia Nanegalito, 0°05'S, 78°40'W, 1200 m, 14.6.1989, *Cerón & al.* 6865 (MO); Napo, Santa Cecilia, 340 m, 28.3.1972, *MacBryde & Dwyer 1314* (MO). — PANAMA: Chiriquí, Bugaba, Santa Clara, 8°50'N 82°44'W, 1300 m, 26.2.1985, *van der Werff & Herrera 7073* (F, MO); Coclé, between Río Blanco and Caña Susio, 8°38'N, 80°36'W, 13.12.1980, *Systema & Hahn 2459* (MO); Panama, Canal Zone, near Vigía and San Juan on R. Pequení, 66 m, 27.11.1934, *Dodge & al.* 16594 (G, MO). — PARAGUAY: Amambay, Estancia 5 Hermanos, camino a Pirity, 9.6.1996, *Soria 7645* (MO); Concepción, Estancia 3 Hermanas, Potrero Aquidqdan, 22.10.1991, *Basualdo 3600* (MO). — PERU: Cajamarca, San Ignacio Province, Ricardo Palma, 5°07'29"S, 79°03'16"W, 1720 m, 19.5.1998, *Campos & López 4903* (B, MO); Loreto, Maynas, Pucacuro, Río Chambira, 3°35'S, 73°54'W, 160 m, 20.4.1986, *Vásquez & al.* 7447 (B, MO); Madre de Dios, Tambopata, pto. San Antonio, 12°57'12"S, 68°52'60"W, 210 m, 15.9.1996, *Aguilar & Castro 1037* (MO). — SURINAME: Brokopondo, along road between Berg en Dal and Brownsweg, 5°03'N, 55°08'W, 150 m, 10.7.1982, *Croat 53858* (MO). — VENEZUELA: Bolívar, between Hato de Nuria and camp., 23.1.1961, *Steyermark 88738* (F).

28. *Smilax solanifolia* A. DC. in Candolle & Candolle, Monogr. Phan. 1: 161. 1878. – Lectotype (designated here): “St. Lucia” *Anderson* (K 400486 [♂]!).

= *Smilax pittieriana* Steyer. in *Fieldiana*, Bot. 28: 155. 1951. – Holotype: Venezuela, “State of Bolívar: vicinity of “Misia Kathy camp” on mesa between Ptari-tepuí and Sororopán-tepuí, altitude 1615 meters”. 15–17.11.1944, *Steyermark 60251* (F 331436 [♂]!).

= *Smilax auraimensis* Steyer. in *Bol. Soc. Venez. Ci. Nat.* 26: 472. 1966. – Holotype: Venezuela, Bolívar, “Sierra Auraima: en la parte terminal norte sobre el margen oeste del río Paragua, en la zona del raudal de El Perro; bosque achaparrado sobre piedras areniscas, Lat. 6°32'; Long. 63°33'. altura 400 metros”,

16.1.1962, *Steyermark 90823* (VEN 90823 [♂]!; iso-types: NY 180347 [♂]!, US 2486806 [♂]!).

= *Smilax chimantensis* Steyer. & Maguire in *Mem. New York Bot. Gard.* 17(1): 440. 1967. – Holotype: Venezuela, Bolívar, “Chimantá Massif, rainforest along Río Apacará, Apacará-tepuí atitudo 400 meter”, 25.3.1953, *Steyermark 74652* (NY 180348 [st.]!).

Rhizomes unknown. *Stems* terete, glabrous, prickly. *Leaves* ovate, lanceolate, membranous, 8–20 × 3–7.5 cm, 3–5-veined, upper surface shiny, venation on both surfaces prominent, connected by reticulate veinlets, apex acute or mucronate, base acute or rounded, margin entire, glabrous; *petiole* 1–1.8 cm long, rounded, with a simple adaxial scale at the lateral shoot base. *Inflorescences*, umbellate, usually arranged in racemes, rarely solitary, scale single; *peduncle* 1.2–2 cm long, flattened, thick; *tepals* of male flowers 4–4.5 mm long, of female flowers 3.5 mm long; *anthers* shorter than the filaments. *Berries* orange when ripe, ovoid, 8–10 mm in diameter.

Distribution and habitat. — Venezuela, French Guiana, Suriname, Guyanas, Lesser Antilles (Fig. 24); 50–700 m.

Notes. — *Smilax solanifolia* was described by Candolle (1878) as a plant with angular branches, prickles, ovate-acute leaves, 5–7 veins, axillar racemes, lanceolate bracts and flower buds c. 5–6 mm long. Howard (1979) claimed that *S. solanifolia* was a synonym of *S. guianensis*. Nevertheless, the drawing of *S. guianensis* (Plumier Pl. Amer. t. 84. 1756) differs from the type specimen of *S. solanifolia* deposited at K in the inflorescence and tepal size. In the protologue of *S. solanifolia* (Candolle 1878), two syntypes collected by *Anderson* (K, photo) are mentioned, one of them from the island of St Lucia (flowering) and the other one from the island of Trinidad (sterile). The flowering specimen is selected as lectotype.

Steyermark's protologue (1951) of *Smilax pittieriana* cited two specimen as types (*Steyermark 60251* and *60251a*). Nevertheless, as has been stated by Gaskin & Berry (2005) and is confirmed here, these specimens represent different species: *Steyermark 60251* is the type of *S. pittieriana*, but *Steyermark 60251a* represents *S. domingensis*. Steyermark & Maguire (1967), about 15 years after the publication of *S. pittieriana*, described *S. chimantensis*, stating several characteristics that separate this new species from *S. pittieriana*. However, these differences were based on the alleged “cotype” *Steyermark 60251a* representing *S. staminea* (= *S. domingensis*).

Selected specimens examined. — BARBADOS: 19.2.1924, *Miller 64* (US). — DOMINICA: *Do Imray 285* (K). — FRENCH GUIANA: Piste de Saint-Elie- interefluve Sinnamary/Counamama, 5°20'N, 53°00'W, 6.6.1995, *Prévost 3152* (B, U). — GRENADA: Forest trail from Grand Etang to Morne Quaqua, 4.–10.3.1979, *Howard & Howard 18756* (A, BM). — GUADELOUPE: Basse Terre, Haut de



Fig. 24. Distribution of *Smilax solanifolia* (triangles) and *S. syphilitica* (circles).

Sofaía, près d' une petite rivière, 26.4.1974, *Sastre & Clairon* 2733 (GH). — GUYANA: near Mabura Hill sawmill, 5°19'N, 58°38'W, 29.10.1982 (U); Cuyuni-Mazaruni, Essequibo River, Butakari, 5°46'N, 58°44'W, 9.6.1995, *Chanderbali & Gopaul* 64 (U); Rupununi, Shea Rock, 25.8.1995, *Jansen-Jacobs & al.* 4853 (U); U. Takutu-U. Essequibo, SE Kanuku Mts near upper part of Tulukwau, 3°02'N, 59°26'W, 28.6.1989, *Gillespie & al.* 1930 (U). — ST LUCIA: Fonds St Jacques, 23.3.1889, *Wif & pl committee Rec* (K). — ST VINCENT: Charlotte Parish, upper valley of the Grand Sable River, 13.3.1962, *Cooley* 8497 (SPMS). — TRINIDAD AND TOBAGO: Aurora?, forest, via Sangre Grande, 9.4.1926, *Broadway* 6092 (BM). — VENEZUELA: Amazonas, Territorio Federal Amazonas, Atures, Caño Yutaje at S base of serranía de Yutaje, 5°38'N, 66°06'W, 110–200 m, 17.2.1987, *Liesner & Holst* 21200 (MO); Bolivar, between camp and Agua Linda, 7 km E of Hato de Nuria, E of Miamo Altiplanicie de Nuria, 400 m, 14.1.1961, *Steyermark* 88428 (GH); Piar, Guayaraca, between escarpment and Rio Guayaraca southern base of Auyan-tepui, 5°44'N, 62°32'W, 950 m, 25.–27.11.1982, *Davidse & Huber* 22673 (MO); Miranda, Paez, drainage of the Rio Guapo, Cerro Riberon between Rio Guapo and Rio Chiquito, 44.5 km directly (in a straight line) SE of Caucagua, 10°05'N, 66°01'W, 200–400 m, 1.–2.6.1977, *Davidse & González* 13627 (MO); Trujillo, Selva Virgen, arriba de Escuque, en-

tre Escuque y La Mesa de San Pedro, 1300–1650 m, 20.–23.2.1971, *Steyermark* 104614 (G).

29. *Smilax syphilitica* Humb. & Bonpl. ex Willd., Sp. Pl. 4: 780. 1806. — Holotype: Venezuela, [“Cassiquiare habit prairial an 8” [20.5.–18.6.] (according to Humboldt’s diary)], *Humboldt [& Bonpland]* 1147 (B-W 18387-1 [st.]); isotype: “rio cassiquiare” P-Bopl 6209-1 #20, A7 [st.], “rio Casiquiare prairial an 8 envocu.” P 83424 [st.],).

= *Smilax duidae* Steyerm. in *Fieldiana*, Bot. 28(1): 154. 1951. — Holotype: Venezuela, “Territorio Federal Amazonas: Cerro Duida southeastern-facing forested sandstone slope along Caño Negro (tributary of Caño Negro)”, 260–610 m, 26.8.1944, *Steyermark* 58057 (F 330735 [♂ specimen]!).

Rhizomes tuberous. *Stems* terete, glabrous, prickles straight, terminal branches straight. *Leaves* lanceolate, glabrous, membranous or coriaceous, 12–30×3.5–14 cm, 7–9-veined, connected by reticulate veinlets, apex acuminate, base acute or rounded, margin entire; *petiole* 2–3 cm long, rounded with very prominent wings, c. 0.5–2 cm long. *Inflorescences* umbellate, in racemes, rarely solitary, scales paired; *receptacle* reniform; bracts brownish, very conspicuous; *peduncle* 3–5 cm long, flattened and thick; *pedicels* of uniform length; *tepals* of male flowers 2.5 mm long, of female flowers 1.5–2 mm long;

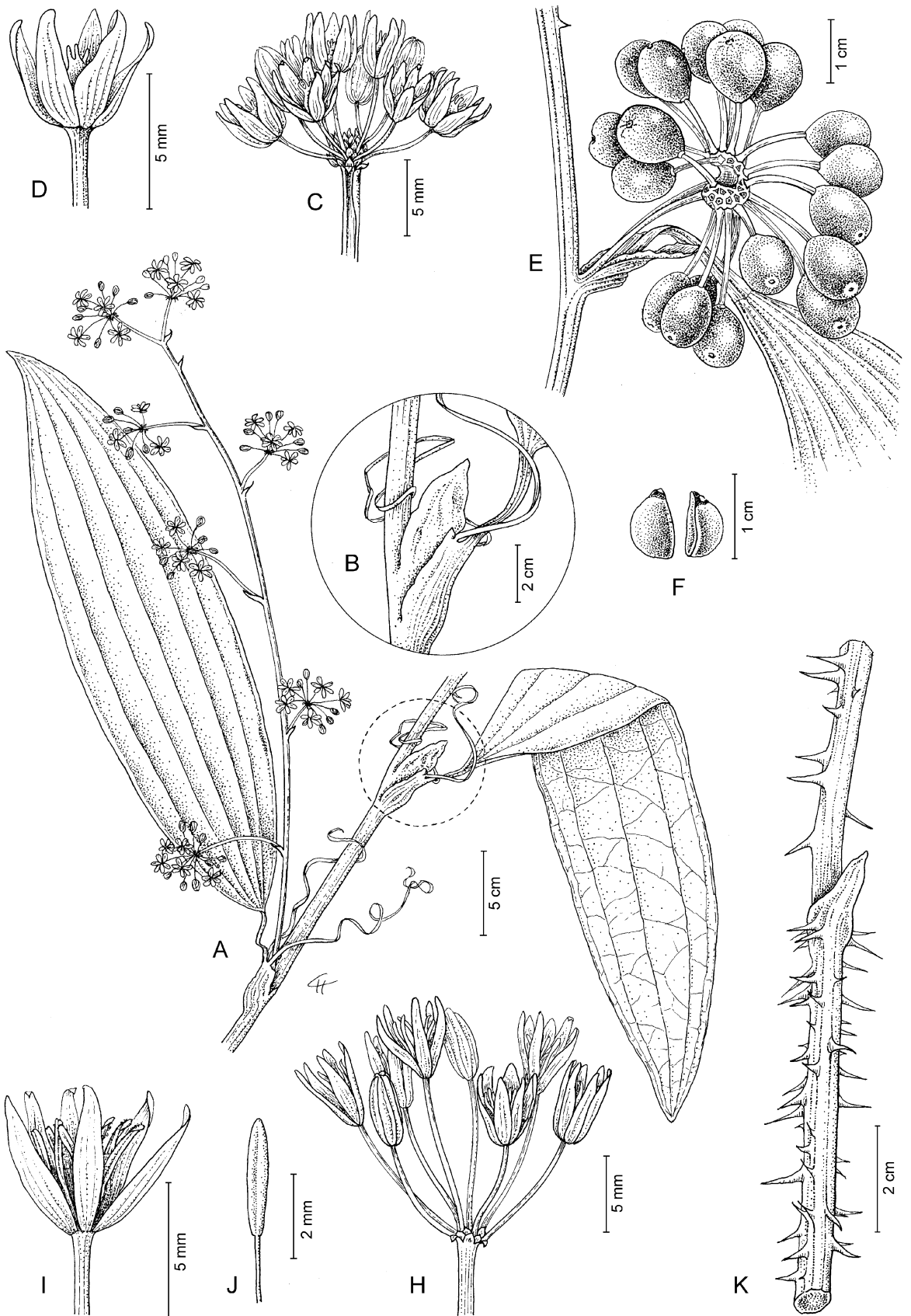


Fig. 25. *Smilax syphilitica* – A: flowering branches; B: inflorescence with a pair of scales; C: pistillate inflorescence; D: pistillate flower; E: infructescence; F: seeds; G: staminate inflorescence; H: staminate flower; I: stamen; J: stem. – Drawn by C. Hillmann-Huber from Grenand 646 (CAY), Larpin 320 (CAY), Cremers 13076 (CAY), Granville 8101, 5122 (CAY) and Prévost 286 (CAY).

anthers ellipsoidal, longer than the filaments. *Berries* orange when ripe, not glaucous, ovoid, 8–15 mm in diameter. – Fig. 25.

Notes. — *Smilax syphilitica* was described by Willdenow (1806) based on two different specimens with the same collector number, which belong to different species. The sterile specimen is designated as lectotype of *Smilax syphilitica*, because this conserves the current use of the name and is more in accordance with the original description.

Gaskin & Berry (2005) treated *Smilax duidae* as a synonym of *S. syphilitica*. My examination confirms this synonymy.

Distribution and habitat. — Colombia, Ecuador, Venezuela, Brazil, French Guiana, Guyana, Suriname, Lesser Antilles (Fig. 24); riparian and secondary forests, 100–1000 m.

Common names. — “Corona guaica” in Venezuelan Guayana (Gaskin & Berry 2005); “Durrakwarra pimpla” in Guyana.

Selected specimens examined. — BARBADOS: 19.2.1924, *Miller 64* (US). — BRAZIL: Acre, Sena Madureira, Estrada de Bonsucesso km 7, mata da margem esquerda do rio Caeté, 1.10.1980, *Cid & Nelson 2663* (K); Bahia, Itacaré, Marambaja, 6 km W of Itacaré, 14°20'S, 39°05'W, 16.5.1992, *Thomas & al. 9403* (MO); Espírito Santo, São Bento de Urânia, 14.1.1995, *Hatschbach & Silva 61413* (B). — FRENCH GUYANA: Cayenne, Commune de Régina-Bassin de l'Approuague, 52°7'N, 18°57'W, 30 m, 6.12.1994, *Bordenave 1327* (U); Mont Bakra, Région des Emérillons, 3°18'N, 52°57'W, 550 m, 14.4.1993, *Cremers 13076* (U); Pic Matécho, versant sud, 3°44'N, 53°02'W, 500 m, 19.9.2000, *Granville & al. 14266* (U). — GRENADA: 22.11.1895, *Broadway 770* (F). — GUADELOUPE: 1904, *Duss 4191* (MO, NY, US); 1899, *Duss 3864* (NY); 1904, *Duss 4191* (F). — GUYANA: Kamo River, Clarence Hill, 21.9.1989, *Jansen-Jacobs & al. 1727* (U); Demerara-Mahaica, Yarowkabra settlement and Forest Station, 6°25'00"N, 58°10'0"W, 0–10 m, 25.5.1986, *Pipoly & Godfrey 7441* (K); Cuyuni-Mazaruni, Mazaruni Station, 6.5.1943, *Forest Depto 4009* (K); E. Berbice-Corentyne, Baba-Grant Sawmill, ± 5 mi. above Cow Falls, 5°00'N, 57°42'W, 13.4.1990, *McDowell & Gopaul 2239* (U); Mabura, near township of Mabura, 5°15'N, 58°45'W, 0–100 m, 17.12.1990, *Polak 207* (U); S Rupununi, S Rupununi Savanna, Wakadanawa Savanna, 1°60'N, 59°34'W, 290 m, 14.9.1997, *Jansen-Jacobs & al. 5518* (U); Wets Pibiri, Estación de Tropenbos; Mabura Hill, a unos 15 km del Pueblo de Mabura, 5°01'N, 58°37'W, 10.9.2001, *Díaz & Mitro 5368* (MO). — SURINAMA: SW plateaus covered by ferrobauxite between 550 and 710 m, 4.10.1975, *Lindeman & al. 775* (K). — TRINIDAD AND TOBAGO: Aurora?, forest, via Sangre Grande, 9.4.1926, *Broadway 6092* (BM); St George, Maracas, Trail to El

Tucuche, 14.7.1987, *Johnson & al. 140* (BM). — VENEZUELA: Amazonas, Atures, Río Coro-Coro, 6 km N of settlement of Yutaje, 5°44'N, 66°07'W, 320 m, 22.2.1987, *Liesner & Holst 21314* (MO); Bolívar, Raul Leóni, al SW de Uriman, 4°55'N, 62°49'W, 410 m, 9.1986, *Fernández 3326* (MO); Territorio Delta Amacuro, Tucupita, 9°35'N, 61°55'W, 9.10.1977, *Steyermark & al. 114420* (MO).

Taxa excluded

Smilax acuminata Willd., Sp. Pl. 4: 779. 1806 ≡ *Sarsaparilla acuminata* (Willd.) Kuntze, Revis. Gen. Pl. 2: 713 (1891). – Lectotype (designated here): [illustration] “*Smilax caule aculeato, foliis ovatis*” in Plumier, *Burm. Amer.*: t. 83. 1755. [st!], based on material from the West Indies. – This is not *Smilax* but represents a species of *Dioscorea*.

Smilax elliptica Desv. ex Ham., Prodr. Pl. Ind. Occid.: 58. 1825. – According to Candolle (1878: 190) the type, originally in the Desvaux herbarium (now P), does not come from the West Indies but from India as stated by Hamilton (1825). It is conspecific with *Smilax zeylanica* L.

Smilax hastata Jacq., Enum. Syst. Pl.: 33. 1760. – Neotype (designated here): [illustration] “*Smilax hastata*” in Jacquin, *Select. Stirp. Amer. Hist.*: t. 179, f. 103. 1763, based on material from Hispaniola. – This is not a *Smilax* but belongs to *Dioscoreaceae* and is probably conspecific with the polymorphic *Rajania hastata* L.

Smilax sagittata Desv. in Hamilton, Prodr. Pl. Ind. Occid.: 58. 1825. – Holotype: “India Occidentali”. – According to Candolle (1878: 165) the type, originally in the Desvaux herbarium (now P), does not come from the West Indies as stated by Hamilton but possibly from the Mediterranean. It is conspecific with *Smilax aspera* L.

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