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

Author: Lilian Ferrufino-Acosta

Source: Willdenowia, 40(2) : 227-280

Published By: Botanic Garden and Botanical Museum Berlin (BGBM)

URL: https://doi.org/10.3372/wi.40.40208
LILIAN FERRUFINO-ACOSTA

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

Abstract

doi:10.3372/wi.40.40208 (available via http://dx.doi.org/)

*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 conate tepals and variable number of stamens (3, 6, 9–12) with conate 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; Godding & al. 1965 for Barbados; Howard 1979 for the Lesser Antilles; Philcox 1983 for Trinidad and Tobago; Proctor 1984 for the Cayman Islands; Huft 2001 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)

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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 Andreata (1997) also did not find any differences in the pollen morphology of Neotropical species of *Smilax*. As a result, this study focuses on macromorphological characters. The goals of the present revision are to clarify species circumscription, resolve synonyms 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 protologue, 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 pseudomubbellite cyme, solitary or aggregated in a raceme (e.g. *S. schomburgkiana*), often with brachiblasts as a replacement for scales, peduncules 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 didéal, linear or elliptic in top-view, shorter or longer than filaments; pollen granulose, spinulose, subglobosese; 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 & Windnor 1987; Hegarty 1990; Ibarra-Manríquez & al. 1991; Morelato & 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. vanillicoda*, *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”. These 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

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

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. *moranensis* |
|   | – Prickles conical, greenish | ........................................... 25 |
| 25. Inflorescences in racemes; bracts persistent | ........................................... 26 |
|   | – Inflorescences solitary; bracts deciduous | ........................................... 27 |
| 26. Petoles with wings c. 2 cm long | ........................................... 29. *S. sypiliftica* |
|   | – Petoles 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

<p>| | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Plants pubescent, sometimes only when young and near petiole base; stems without prickles</td>
<td>........................................... 2</td>
</tr>
<tr>
<td></td>
<td>– Plants completely glabrous; stems with prickles</td>
</tr>
<tr>
<td>2. Branches obtusely quadrangular, sometimes tomentose at the petiole base</td>
<td>........................................... 3</td>
</tr>
<tr>
<td></td>
<td>– Branches terete, persistently pubescent</td>
</tr>
<tr>
<td>3. Leaf blades abaxially almost glabrous; berries orange</td>
<td>........................................... 2. <em>S. subpubescens</em></td>
</tr>
<tr>
<td></td>
<td>– Leaf blades abaxially tomentose; berries reddish</td>
</tr>
<tr>
<td>4. Stems quadrangular, sometimes winged</td>
<td>........................................... 5</td>
</tr>
<tr>
<td></td>
<td>– Stems terete or obtusely angular, never winged</td>
</tr>
<tr>
<td>5. Berries red-orange</td>
<td>........................................... 6. <em>S. officinalis</em></td>
</tr>
<tr>
<td></td>
<td>– Berries black</td>
</tr>
<tr>
<td>6. Stems obtusely angular</td>
<td>........................................... 7</td>
</tr>
<tr>
<td></td>
<td>– Stems terete</td>
</tr>
<tr>
<td>7. Leaves blade entire; peduncles longer than petioles; berries red</td>
<td>........................................... 11. <em>S. aristolochiifolia</em></td>
</tr>
<tr>
<td></td>
<td>– Leaves blade dentate; peduncles shorter than petioles; berries red to black or dark purple</td>
</tr>
<tr>
<td>8. Stems glabrous</td>
<td>........................................... 9</td>
</tr>
</tbody>
</table>
– Stems verruculose ........................................ 14
– Leaves blade chartaceous .............................. 10
– Leaves blade coriaceous ............................... 12
– Leaf margin shallowly spinulose .......................... 11
– Leaf margin deeply spinulose ........................... 19. S. havanensis
11. Leaves obovate ........................................... 23. 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
– Prickles brownish ......................................... 20. S. ligulifolia
15. Leaves copper coloured, margin entire .................. 17. S. cuprea
– Leaves brownish or green, margin spinose ................. 16
– Peduncles shorter than petioles .......................... 13. S. spinosa
– Peduncles equal or sometimes longer than petioles .......... 17
– Stems muricate ........................................... 19
– Stems smooth ............................................ 18
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
– Bracts deciduous; upper leaf surface opaque .......... 28
27. Petioles with wings c. 2 cm long ...... 29. S. syphilitica
– 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*.


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 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. congestiflora* C. V. Morton in Brittonia 14: 301. 1962. – Holotype: Mexico, “Pluma Hi-
ovate to lanceolate, sometimes pubescent, membranaceous, unarmed, terminal branches straight. Rhizomes = 7 – 9-veined, major veins connected by reticulate veinlets, apex acute, base cordate, margin entire; petiole late, solitary, scale single; bracts sometimes deciduous; flowers 3.5 – 4.5 mm long; length; tepals of male flowers 4 – 6 mm long, of female shorter than the filaments. Glaucous, ovoid, 8 – 12 mm in diameter. Common names. — “Zarzaparrilla cimarrona” in Cuba; “pate” in Honduras (León 1946; Nelson-Sutherland 2008).


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).


Selected specimens examined. — COSTA RICA: Cartago, Oreamuno, descendentiendo por la falda norte del Volcán Irazú, 10°04’00”N, 83°51’00”W, 2100 m, 6.1.1995, Cascante & al. 455 (CR); Heredia, P. N. Brulio Carrillo, Estación Barba, 10°08’00”N, 84°06’00”W, 1100 m, 20.6.1990, Apía 68 (CR, INB); Limón, Cordiller a 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, Cordiller a 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, 1300 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 Chamatáca, 15°33’N, 90°12’W, 1300 m, 27.8.2002, Rueda 17343 (HULE); Baja Verapaz, Rabinal at summit of Sierra de Chuaucus, 15°01’N, 90°29’W, 1800 m, 25.1.1987, Croat & Hannon 63650 (MO); El Progreso, cañas Albores, San Agustín, 14°57’N, 88°18’W, 2005 m, 19.6.1985, Miller & Myers 2613 (MO); Oaxaca, Sierra Madre de Chiapas, Huixla-Siutep road, 20 km W of Hwy. 211 at turnoff to Sitelpete, 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 Polvorin, 19°03’N, 100°02’W, c. 2000 m, 26.4.1987, Miller & Myers 2613 (MO); Oaxaca, Mixteca, San Jerónimo Coatlán, 15 km al N de Piedra Larga, sobre el camino a Progreso, 16°09’00”N, 97°00’10”W, 1300 m, 16.12.1987, Torres & Campos 10863 (MO); Veracruz, vic. “La Calavera” 10 km N of Atlotonga (13 km by road), on road to Tlapacoyan, 19°51’N, 97°13’W, 1350 m, 28.1.1980, Nee & Hansen 18647 (NY). — NICARAGUA: Jinotega, Wiwilí, Reserva Cero Kilambé, 13°34’N, 85°41’W, 1300–1500 m, 2.9.2000, Rueda 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 calardicaria. 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.


Distribution and habitat. — Mexico to Costa Rica: Cartago, Oreamuno, descendentiendo por la falda norte del Volcán Irazú, 10°04’00”N, 83°51’00”W, 2100 m, 6.1.1995, Cascante & al. 455 (CR); Heredia, P. N. Brulio Carrillo, Estación Barba, 10°08’00”N, 84°06’00”W, 1100 m, 20.6.1990, Apía 68 (CR, INB); Limón, 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, 1300 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 Chamatáca, 15°33’N, 90°12’W, 1300 m, 27.8.2002, Rueda 17343 (HULE); Baja Verapaz, Rabinal at summit of Sierra de Chuaucus, 15°01’N, 90°29’W, 1800 m, 25.1.1987, Croat & Hannon 63650 (MO); El Progreso, cañas Albores, San Agustín, 14°57’N, 88°18’W, 2005 m, 19.6.1985, Miller & Myers 2613 (MO); Oaxaca, Sierra Madre de Chiapas, Huixla-Siutep road, 20 km W of Hwy. 211 at turnoff to Sitelpete, 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 Polvorin, 19°03’N, 100°02’W, c. 2000 m, 26.4.1987, Miller & Myers 2613 (MO); Oaxaca, Mixteca, San Jerónimo Coatlán, 15 km al N de Piedra Larga, sobre el camino a Progreso, 16°09’00”N, 97°00’10”W, 1300 m, 16.12.1987, Torres & Campos 10863 (MO); Veracruz, vic. “La Calavera” 10 km N of Atlotonga (13 km by road), on road to Tlapacoyan, 19°51’N, 97°13’W, 1350 m, 28.1.1980, Nee & Hansen 18647 (NY). — NICARAGUA: Jinotega, Wiwilí, Reserva Cero Kilambé, 13°34’N, 85°41’W, 1300–1500 m, 2.9.2000, Rueda
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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).


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-

Fig. 2. Distribution of Smilax mollis (circles) and S. velutina (triangles).
idbro & 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, 1200 m, 17.4.1951, Williams & Molina 18087 (EAP). — MEXICO: Chiapas, Santa Cruz, 13°23'02"N, 92°29'02"W, 23.7.2006, Crespo & al. 3882 (PMA). — 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; pediole 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, purplish 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 stamine 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.


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).
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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 Pluket’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 & Milspaugh 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, F); Louisiana, Claiborne Parish, c. 7 mi. W of junction of City on Stateline Road, 31.7.1896, Nelson & Horn 14703 (F); 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, Grapeeland, 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*.


= *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 barbillana* 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, velubios, fl. viridi-lutei”, 40 m, 12.5.1930, Cufodontis 658 (US 1637717 [?]); isolecotype: F 343655 [st.]).


**Rhizomes** elongated. **Stems** quadrangular, glabrous, armed with flattened prickles, terminal branches straight and often unarmed. **Leaves** ovate, lanceolate, coriaceous or membranous, 10–23 cm × 2–14 cm, 7–9-veined, major veins connected by reticulate veines, 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 Manzaneras, 3°31′N, 76°18′W, 800–1000 m, 1.11.1995, Pipoly & al. 18238 (MO); Chocó, area of Baudó, 8.2.1967, Fuchs & Zanella 21831 (U); Quindio, Salento, 2450 m, 1.7.1984, Rentería 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, Zumbarbú 2 (CR, MO); Limón, below La Palma, along the Río Claro (upper Río La Honduras), 10°03′N, 83°58′W, at about 1000 m, 1.1.1967, Burger 4134 (NY, CR); Puntarenas, Monteverde, canyon of Río 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, Río LINDO, near El Carrizal, 550 m, 12.4.1991, Williams & Molina 178720 (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 Guinca, 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 Llanito-Cartí Rm. km 19.1, 9°19′N, 78°55′W, 350 m, 10.2.1985, de Nevers & Cavagnaro 4800 (MO, F); Darién, 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, Galldames & al. 4133 (F); Veraguas, 6.4 km outside of Santa Fe, 5.5.1977, Folson 2977 (MO).


≡ *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.”, 5.1899, Morris (K 524863 [Ø]!); isolecotype: K 524864 [st.]).


Rhizomes elongated. Stems quadrangular, glabrous, armed with flattened prickles, terminal branches straight, often unarumed distally. Leaves ovate to lanceolate, glabrous, coriaceous or membranous, 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 ellipsoid, 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 then 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 Regal material of *Smilax grandifolia* can be located and
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, Tamananca, 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 orilllendo 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). — MÉXICO: 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 Sebastián, 18.3.1889, Rovirosa 402 (NY, US); Veracruz, Jesús Car-

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


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

= Smilax schiedeanum Kunth, Enum. Pl. 5: 236. 1850. — Lectotype (designated here): “in sylvis de Xalapae altas arbores scandens.....”, HAL 101932 [♀]).


= Smilax cordifolia var. papapantiae A. DC. in Candolle & Candolle, Monogr. Phan. 1: 84. 1878. — Lectotype (Killip & Morton 1936: 279); same as for Smilax sylvatica, above [♀].


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


= 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 [♀!!]).


Rhizomes elongated. Stems terete, obously angular or quadrangular, glabrous, armed with blackish, slender, acicular prickles, terminal branches straight. Leaves ovate, lanceolate, glabrous, membraneous, 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.
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.

Schlechtendal (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 berries. 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, coriaceous 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. christmarenensis*. Both are also considered as synonyms of *S. moranensis*.

Candolle (1878) published *Smilax invensata var. armata* and cited two syntypes, *Galeotti s.n.* and *Linden 48*. Killip & Morton (1936) designated *Linden 48* 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 hootheri* Schlecht. (*Ranunculaceae*).

The holotype of *Smilax invensata* 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, *Schiefe and Ehrenberg*, both at HAL. Here, the *Schiefe* species is designated as lectotype.

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


The species is designated as lectotype.

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*. Related species: *S. bella*, *S. cordato-ovata*, *S. hilariana*, *S. japidanga*, *S. larvata*, *S. minarum*, *S. pilosa*, *S. phystophylla*, *S. subsessiliflora*, *S. verrucosa*.


Rhizomes unknown. Stems angular, verrucose, pubescent of hispid hairs, prickles fine, needle-like, terminal branches straight. Leaves lanceolate, glabrous, membranous, 5–20×1–5 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 is 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 Fedde, overlapping on the stem. Rhizomes long, of female flowers 1.5 – 2 mm long; tepals and orange berries. 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 specimen of S. immersa and consider the name as a synonym of S. schomburgkiana. Common names. — Tu-pata-yén (Arekuna) in Venezuela; “liane bagou” in French Guiana (Gaskin & Berry 2005; Mitchell 1997).

Selected specimens examined. — BRAZIL: Amazonas, along Rio Castanho tributary of Rio Padauiri, 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); Espírito 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 “Quinte- ría” 8°04′N, 75°05′W, 100 m, 6.9.2000, Fonnega & 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, Greville & al. 15373 (B, CAY, K); Cayenne, Sainte Rupununi, Kuyuwini Landing, Kuyuwini Creek, upper Mazaruni River, 19.9.1960, Guyana: Cuyuni-Mazaruni, N side of Karawtipu, c. 470m, 19.9.1960, Teixeira & al. 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, 1202. — Holotype: British Guiana, “dense upland forest, Tumatumari”, 18.6. – 8.7.1921, Jacob & al. 2901 (MO). — Holotype: British Guiana, “liana, bushy places near Maçeio”, 4.1838, Gardner 1425 (K); K 400985 (!); isotypes: K 400984 (!).


Rhizomes tuberous. Stems terete, verruculose, prickles straight, terminal branches straight, axillary scales double, overlapping on the stem. Leaves ovate, lanceolate, glabrous, membranous, 8 – 20 x 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 schomburgiana is characterised by verruculose stems, its racemously 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. schomburgiana, S. schomburgkiana var. gracilis and S. schomburgiana 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. schomburgiana var. foliosa and S. schomburgiana 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. schomburgiana. With regard to morphological features, I have found S. latipes to have longer flowers and broader filaments than S. schomburgiana. 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.
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).
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.


Selected specimens examined. — BELIZE: Toledo, upper reach of Golden Stream, Gentle 4515, 9.4.1944 (MO); El Cayo, 5.–13.3.1931, Bartlett 1210 (US). — EL SALVADOR: Santa Ana, San José Ingenio, P. N. Montecristo, 1800 m, 1.3.2002, Martinez 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, 24.6.1951, Kamb 2168 (A). — MEXICO: Campeche: Calakmul, 9 km al SE de Ley de Fomento Agrpecuario, camino a Dos Naciones, 17º59’S 99º10’W, 56 m, 5.8.1997, Martínez & al. 28062 (EAP); Chiapas, Mt Ovando, 12.1937, Matuda 2092 (K, UC); Jalisco, Quinixt, 70 m, 29.11.1926, Mexia 1175 (A, UC); Puebla, above Teotitlán del Camino, c. 2000–3500 m, 3.8.1961, Smith & al. 4146 (F, G); San Luis Potosí, slope of El Mastique, 1.4.2001, Mexia 1175 (A, UC); Tamaulipas, 10 km W of Encino 23º20’N, 99º10’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).
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. [σ!] = **Smilax megalophylla** Duhamel, Traité Arbr. Arbust., ed. 2, 1: 244. 1803. – Holotype: [no label data] (P-J 3022 [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 syn-types 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**.


**Selected specimens examined.** — **ANTIGUA**: Shambro Hills, 1849, **Wallschlägel** 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)*.
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 forests. 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 Hoffman 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”, “bejucu de corona”, “zarza hueca”, “espuela de gallo”, “corona de Cristo”, “madre de zarzaparrilla”, “zarzaparrilla macho”, “bejucu de la vida”, “cocolmeca” in Central America; “colcolmeca” in Mexico (Killip & Morton 1936; McVaugh 1989). “Zarzaparrilla”, “bejucu de corona”, “zarzaparrilla de mala”, “zarzaparrilla macho”, “bejucu de la vida”, “cocolmeca” in Central America; “colcolmeca” in Mexico (Killip & Morton 1936; McVaugh 1989). — **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, Schipp 1181 (G). — **COLOMBIA:** Antioquia, in the rain forest near Rio León approx. 20 to 30 km, 7°45′N, 76′50″W, 100 m, 18.3.1962, Feddeuma 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, Cordilleria de Tilarán, San Luis, 10°16′33″N, 84°47′45″W, 1100 m, 8.5.1956, Molina 6831 (EAP); 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 Rio Mico, 12°10′N, 84°18′W, 30 m, 1.6.1985, Davide & al. 30748 (CR, MO). — **CHINA:** Chiriquí, mas o menos 5.4 km del Hato de Volcan en el camino a Las Lagunas , 26.4.1969, Corea & Lazor 1466 (PMA); Panama, Barro Colorado Island, 10.4.1969, Foster 685 (PMA); Veraguas, S. of Santa Fe, c. 450 m, 17.11.1973, Neen 8013 (PMA). — **PERU:** Amazonas, Chachapoyas Kuelap, Fortress, 6′25″13.5′′S, 77°47′56.8′′W, 3000 m, 16.5.2001, Hennes & 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). — **SWEDEN:** Sipaliwini, N of S-camp, southern Sipaliwini, 19.1.1970, Oldenburger & al. 103 (BBS). — **TRINIDAD & 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. vixcifolia*.

= 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 veins, 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 group and reticulate, and the leaf margins being deeply spiny.

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).


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 veins, apex mucronate, base rounded or cordate, margin entire, rarely spiny; 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.


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, Fishkill 138, 5.1.1919 (GH); St John, Coray Bay Quarter, 7.1.1991, Acevedo-Rodríguez & Siaca 3818 (MO).


Rhizomes unknown. Stems angular, glabrous, blackish upon drying, armed with thin and short prickles; terminal branches zigzag. Leaves lanceolate, cordate, glabrous,
membraneous, c. 5–14 × 2–9 cm, 5-veined, major veins connected by reticulate veinlets, without prominent ve- 
nation on the upper surface, apex mucronate, base round- 
ed or cordate, margin spinulose, rarely entire; petiole 
flattened, 0.3–0.6 cm long. Inflorescences umbellate, sol- 
itary, 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 fila-
ments. 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 termin-
al 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, Si-
erra Cristal, subida entre la mina de Ocujal 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 & 
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 [G]!; iso-
types: B, JE [G]!).

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 connect-
ed 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
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).

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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; pedicels 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 venation on the upper surface. Material from the Bahamas was previously identified as S. havanensis.

**Distribution and habitat.** — Endemic to central (Camagüey, 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: infrutescence; F: seeds. – Drawn by C. Hillmann-Huber from HFC 12002, 18052, 35985, 50271, JE.
26.6.1890, Northrop & Northrop 663 (F, GH); 18.8.–10.9.1906, Brace 5089 (F); Ben Rolle, 1.1976, Nickerson s.n. (GH); 18.8.–10.9.1906, Brace 5089 (F); Ben Rolle, 1.1976, Nickerson s.n. (GH); 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, 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).


= Smilax havanensis f. inermis O. E. Schulz in Urban, Symb. Antill. 5: 41. 1903. – Holotype: Cuba, Sagra (B†).

Rhizomes elongated. Stems terete or angulate 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; pedicel 2–10 mm long, flattened; pedicels of uniform length; tepals of male flowers 1.5–2 mm long, of female

Fig. 17. Distribution of S. gracilior (circles) and Smilax ilicifolia (square).
flowers 1.5 mm long; anthers linear in top-view, as long as the filaments. Berries black or purple when ripe, very often angulate due to the presence of three seeds, red-dish, 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 Americanam”, 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 lectotyped with Jacquin’s illustration.


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 & Millsbaugh 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); North Bimini, in coppice on white-stone, 0–800 m.

Selected specimens examined. — DOMINICAN REPUBLIC: Azua, the 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); Barahona, trail between Pdernales and Aetácil, 3800′, 8–12.8.1946, Howard & Howard 8230 (GH); Duarte, Loma Quita Esquila, 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’W, 25.11.1985, García & al. 657 (JBSD); Pedernales, 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).
Rhizomes unknown. Stems terete, angular, armed with short prickles; terminal branches zigzag. Leaves lanceolate, ovate, glabrous, membrane, 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 5–1 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 Prodrumus (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.


= 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, membranous 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 color of its berries.

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

Selected specimens examined. — DOMINICAN REPUBLIC: Altagracia, La Altogracia, Llanó 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, Managuas, Sierra Ríeta, 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, Sosú, 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, Velo & al. 302 (JBSD); Samaná, Playa El Rincón 0–50 m, 28.5.1980, Mejía & Zanoni 6555 (JBSD). — HAITI: Massif du nord, Nord-Ouest, 3.1 km al este de Anse-a-foleure en la carretera a Le Borgne, 19°53’N 72°35’W, 20–30 m, 7.6.1985, Zanoni & al. 34889 (JBSD).


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

= Smilax ehrenbergiana Kunth, Enum. Pl. 5: 174. 1850.

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

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 (Poirier herbarium). Previous publications (Kunth 1850; Candolle 1878; Schulz 1904) mentioned that a possible type of Smilax viscifolia = Smilax subaculeata a Bertero specimen representing 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.

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 & Schaab 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. 24200 (JBSD). — JAMAICA: Haycock hill, near Balcarres, slope on foothill S of the mountain, 18°10’N, 71°35’W, 520 m, 16.7.2003, lic.


c. 3.5 – 5.5 mm long; berries red to purple or black.

reddish when young; inflorescences solitary; tepals reddish; leaves membraneous or coriaceous, sometimes


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


≡ Smilax staminea Griseb. in Martius, Fl. Bras. 3(1): 11. 1842. – Lectotype (Andreatta 1997: 150); Brazil, “Brasilia”, Sello (G 39933 [!]!); isolecotypes: 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.].


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

≡ Smilax eucalyptofolia Kunth. Enum. Pl. 5: 230. 1850. – Holotype: Peru, 1778–1788 (B†); neotype (designated here): “Peru”, Ruiz (B 100277645 [!]!).


≡ Smilax domingensis var. sagraeana A. DC. in Candolle & Candolle, Monogr. Phan. 1: 101. 1878. – Lectotype (Ferrufino-Acosta & Greuter, 2010a: 8); Cuba, “La Havanne”, 1829, Sagre 237 (G 206590 [!]!).

≡ 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 [!]!); isolecotypes: G 39926 [!]!, P 594655 [!]!, 39926 [!]!, K 400509 [!]!, MICH 1192733 [!]!, US 1635975 [!]!, BR 6943424 [st.].


VIII. Domingensis group

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


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 eucalytiftolia* at B was destroyed. Two specimens were identified as *S. eucalytiftolia* 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 Desvaux’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 & Galeotti (1842) published the name *Smilax multiflora* based on an unarmred 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*.


**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, Sibir River, 4.2.1931, Bartlett 11359 (UC). — BOLIVIA: La Paz, Larecaja, Cobacabana, 8.10.–15.11.1939, Krakoff 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-Bage, 3–4 km, 7°35'N, 75°16'W, 16.5.1987, Callejas & al. 3576 (K, MO, U); Quindío, Salento, Reserva del Alto Quindío Acaina, 4°37'N, 75°32'W, 3070 m, 12.6.1990, Ranjifo 129 (MO). — COSTA RICA: Alajuela, San Ramón, Los Ángeles, 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: Matanza, 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: Monsenor Novel, 3 km al sur de Maimón, Loma mala, Río Maimón, 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, Valеur 899 (F, GH, K, MO). — GUATEMALA: Alta Verapaz, Chichu’chab 8 km al SW de Cobán, 15°26'N, 90°27'W, 400 m, 22.7.1988, Tenorio & al. 14717 (MO); Suchitepéquez, Samayac, Canton Chiquise, Finca El Caotal, 14°7'N, 91°28'W, 450 m, Rueda 17340 (HULE). — GUIANA: Potaro-Siparuni, Iwokrama Rainforest reserve, 4°20'N, 58°50'W, 600–800 m, 22.11.1995, Clarke & Hoffman 380 (K, U). — HAITI: Massif de la Hotte, Grand’Ansesud limite: 13.6 km N de Camp Perrin en la cerrereta a Roseaux y Jérémie, 18°23'N, 73°53'W, 720 m, 15.11.1982, Zanoni & al. 24323 (MO); Massif du Nord, Chaine Bonnet Levique, 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 Jilinco, 20 km al O. de San Pedro Sula, 15°30'N, 88°14'W, 2120 m,
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. 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).
**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.

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


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, membraneous, 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 perennifoliolous, 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 & Záñiga 761* (USJ); San José, Montana Jamaíca, c. 3 km NE of Bijagual de Turribues, R. B. Carara, 9°45.5’N, 84°33’3W, 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); Colé, PN G.D. Omar Torrijos Herrera, camino a Coclesito, 8°40’10’’N, 80°35’34’’W, 900 m, 18.11.2003, *Aizpría & Flores B3887* (PMA); Darien, to the Serranía 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 membraneous; inflorescences composed in a raceme with a terminal or determinate inflorescence or often with bracts, very prominent and perennifoliolous; tepals c. 3.5–5 mm long; berries orange.

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


= *Smilax febrifuga* var. *aecuatoris* A. DC. in Candolle & Candolle, Monogr. Phan. 1: 159. 1878. — Holotype: Ecuador, “ad radices m. Chimborazo, secus rivulum Chasuan frequens”, 8.1860 (K 201314 [σ†]).


Rhizomes tuberous, white. Stems terete, glabrous, armed with straight prickles. Leaves ovate to lanceolate, glabrous, membraneous, 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.
ripe, not glaucous, ovoid, 6–12 mm in diameter. 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 sytypes 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 in the zona de influencia del rio Yacuma, al borde de la “Isla” (II), 28.9.1979, Beck 2536 (NY); Santa Cruz, Ichilo, Parque Nacional Amorbo, Río Saguayo near mouth of Quebrada Yaporé, 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 Pu- rus, 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, 1220 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 (Rio 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 form road Bogotá to La Mesa, 2056–2100 m, 29.11.1990, Wijninga 596 (MO, U); Huília, Río Caqueta, Aracuara, 13.12.1990, van Dalmen 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 Frío, 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 Ángeles, Reserva Biológica Alberto Manuel Brenes, 10°13', 84°37'W, 850 m, 9.3.2002, Ferrufino 229 (USJ); Limón, Matina, Baltimore, 4°34'20''N, 82°39'50''W, 100–150 m, 7.A.2001, Ferrufino 62 (USJ); Puntarenas, Buenos Aires, P. N. La Amistad, Cuenca Táraba-Sierra, 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). — GUAYANA: Rupununi, along trail from Morris Mines (on Ireng River) to Karasabai Village,
4°00'N, 59°21'W, 300-400 m, 7.1.1982, Knapp & Mallet

— Honduras: Atlántida, J. B. Lancetilla, entrada principal, 15°08'N, 88°05'W, 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°31'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, 26.2.1985; Veraguas, Montijo, Cerro Hoya, suiviendo por Cobachón, 7°18'45''N, 80°40'23''W, 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 & Dadivise 116945 (MO).


Rhizomes tuberous. Stems terete, glabrous with robust prickles. Leaves ovate, lanceolate, cordate, glabrous, coriaceous or membraneous, 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 pinnatifid; 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 misidentified as Smilax panamensis. In Costa Rica, this species spreads to the southern part of the country.
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.


**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, Rio Abuna, 3 km above confluence of Rio 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); Paraíba, Mata de Pau Ferro, 6°58′12″S, 35°42′15″W, 600 m, 24.9.1980, Fevereiro & al. M41 (K); Puraná, Quatro Barras, Morro Mái Catira, 24.7.1987, Cordeiro & Silva 440 (MO). — COLOMBIA: Antioquia, San Luis, Cañón del Río Clarro, 5°53′N, 74°39′W, 330 – 350 m, 30.5.1984, Cogollo 1713 (MO); Caldas, Río Navarro, Salento, 1400 – 1700 m, 31.7.1922, Pennell 9083 (K, NY); Cauca, Valle del Cauca, Queremal, vereda La Victoria, 340 m, 28.3.1972, Davidse 24516 (A, BM). — COSTA RICA: Puntarenas, Cordillera de talamanca, Coto Brus, 8°59′N 82°46′W, 1800 – 1900 m, 10.9.1987, MO); Coclé, between Río Blanco and Caña Susio, 8°38′N, 1300 m, 26.2.1985, van der Werff & Herrera 7073 (F, US); Bangalore, 5°03′N, 55°08′W, 150 m, 10.7.1982, Prance & al. 6865 (MO). — PANAMA: Chiriquí, Bugaba, Santa Clara, 8°50′N 82°44′W, 1300 m, 26.2.1985, van der Werff & Herrera 7073 (F, US); Cocle, between Rio Blanco and Cañca Susío, 8°38′N, 80°36′W, 13.12.1980, Sysmá & Hahn 2459 (MO); Panama, Canal Zone, near Vigia and San Juan on R. Pequeno, 66 m, 27.11.1934, Dodge & al. 16594 (G, MO). — PARAGUAY: Amambay, Estancia 5 Hermanos, camino a Piria, 9.6.1996, Soria 7645 (MO); Concepción, Estancia 3 Hermanas, Potrocerro Aquidjdan, 22.10.1991, Basualdo 3960 (MO). — PERU: Cajamarca, San Ignacio Province, Ricardo Palma, 5°07′29″S, 79°05′16″W, 1720 m, 19.5.1998, Campos & López 4903 (B, MO); Loreto, Maynas, Pucacuro, Rio 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, 240 m, 15.9.1996, Aguilar & Castro 1037 (MO). — SURINAME: Brokopondo, along road between Berg en Dal and Brownsweig, 5°53′N, 55′08′W, 150 m, 10.7.1982, Croat 53858 (MO). — VENEZUELA: Bolivar, 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 [!]!).


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, axillary 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 specimens 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).


*Rhizomes* tuberous. *Stems* terete, glabrous, prickles straight, terminal branches straigth. *Leaves* lanceolate, glabrous, membraneous or coriaceous, 12– 30×3.5–14 cm, 7–9-veined, connected by reticulate veinlets, apex acuminate, base acute or rounded, margin entire; *pediole* 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. 24. Distribution of *Smilax solanifolia* (triangles) and *S. syphilitica* (circles).
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).
antlers 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 guayaca” 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, Marumbaba, 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, Hartschbach & Silva 61413 (B). — **French Guiana:** Cayenne, Commune de Régina-Bassini de l’Approuague, 52°7’N, 35°7’W, 30 m, 6.12.1994, Bordenave 1327 (U); Mont Bakra, Région des Emérrilons, 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). — **Guyana:** 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, Bordenave 1327 (U); Mont Bakra, Région des Emérrilons, 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). — **Surinam:** 10.9.2001, Polak 207 (U); S Rupununi, S Rupununi Savanna, Wakadananawa 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, 9.10.1977, Lindeman & al. 775 (K). — **Trinidad and Tobago:** Aura?, 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 Leoni, al SW de Urumán, 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 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. — Neo-type (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.: 581825. — 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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I am grateful to the German Academic Exchange Service (DAAD) for financial support, which allowed me to pursue my Ph.D. The project was also financially supported by the Botanic Garden and Botanical Museum Berlin-Dahlem and by OTS (Organization for Tropical Studies). I am grateful to the curators of the following herbaria: 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 for processing my loan requests or assisting me during my visit. I would like to give particular thanks to Peter Adam, Christine Hillmann-Huber and Gisela Jahrmärker for providing the line drawings, to Prof. emer. Dr Werner Greuter (Berlin) and Dr Hermann Manitz (Jena) for their advice and helpful discussions, to two reviewers and the editor for their valuable comments on and improvements of a previous version of this paper.

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