New Synonymy and Useful Taxonomic Characters in *Smilax* (Smilacaceae) from the Venezuelan Guayana

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ABSTRACT. In conjunction with a treatment of *Smilax* (Smilacaceae) for the *Flora of the Venezuelan Guayana*, a number of taxonomic changes are proposed for previously described taxa from southern Venezuela. A discussion of morphological characters used in the revision and a key to the species in the Venezuelan Guayana are also presented.

Smilax is a genus of approximately 300 species of dioecious vines inhabiting tropical and temperate areas of both hemispheres, with most species concentrated in tropical Asia and the Neotropics. The genus has a well deserved reputation for being taxonomically difficult. Problems arise from the paucity of fertile collections of both sexes or even a single sex from particular localities (Huft, 1994), the use of characters that are not reliable for species delimitation (Howard, 1979), and conflicting treatment of species across flora boundaries (Sipman, 1979). For future collections of *Smilax*, collectors should strive to obtain samples from both sexes and, even more importantly, include a section or a description of the lower portion of the stem (where larger spines may be found) as well as an upper, fertile portion of the plant.

We recently completed a treatment of the Smilacaceae for the *Flora of the Venezuelan Guayana*, which includes the states of Amazonas, Bolívar, and Delta Amacuro in southeastern Venezuela. At the onset of our project, there were 37 different species names in *Smilax* that had been used to identify herbarium specimens from the flora area. Currently, we recognize only 9 species. We dealt with synonymy of names whose types are from the flora area, but we did not attempt this with species described from other countries. The next logical step in the taxonomic study of South American *Smilax* would be a comprehensive treatment which would include examination of type material and the identification of the many synonyms that undoubtedly exist across national and floristic boundaries.

The following discussion addresses our choice of characters, which should prove useful for future work in other areas. Due to the paucity of comparable fertile collections, we focused on vegetative characters more than reproductive ones. Among the type specimens examined for the nine species currently recognized in the Venezuelan Guayana, only three have flowers, and one has fruit. Also missing from these type specimens (and from most other collections in the flora area as well) is a sample of the lower stem and lower leaves of the plant, which are frequently quite different from the younger, higher stems (Killip & Morton, 1936).

Stem. The presence of stem spines can be a useful character, but young growth is often unarmed, while the base of the stem can be heavily armed. In *Smilax poeppigii* Kunth, spines may be absent on most of the stem, while the base, which may be 20 m away, has dense spines (*Berry et al. 6239*, MO). A character that is more important outside the flora area is the shape of the spines, which can range from terete and needle-like to flattened and triangular. The texture of the stem has been used in many treatments, and Steyermark and Maguire (1972) used the verruculose-tuberculate texture of the stem in *S. jauaensis* Steyermark & Maguire as virtually the sole character to differentiate it from *S. staminea* Grisebach. Stem texture has been shown to be a variable character, and verruculose-tuberculate stems also appear in occasional specimens of *S. staminea*. Another species, *S. lappacea* Humboldt & Bonpland ex Willdenow, which Steyermark and Maguire (1972) noted as having smooth stems, has some specimens with tuberculate stems, although the bumps are typically not darkened and thus not readily visible (*Huber 581*, VEN). Only in the case of *S. schomburgkiana* Kunth did we use stem texture as a diagnostic character. The stem of this species is consistently

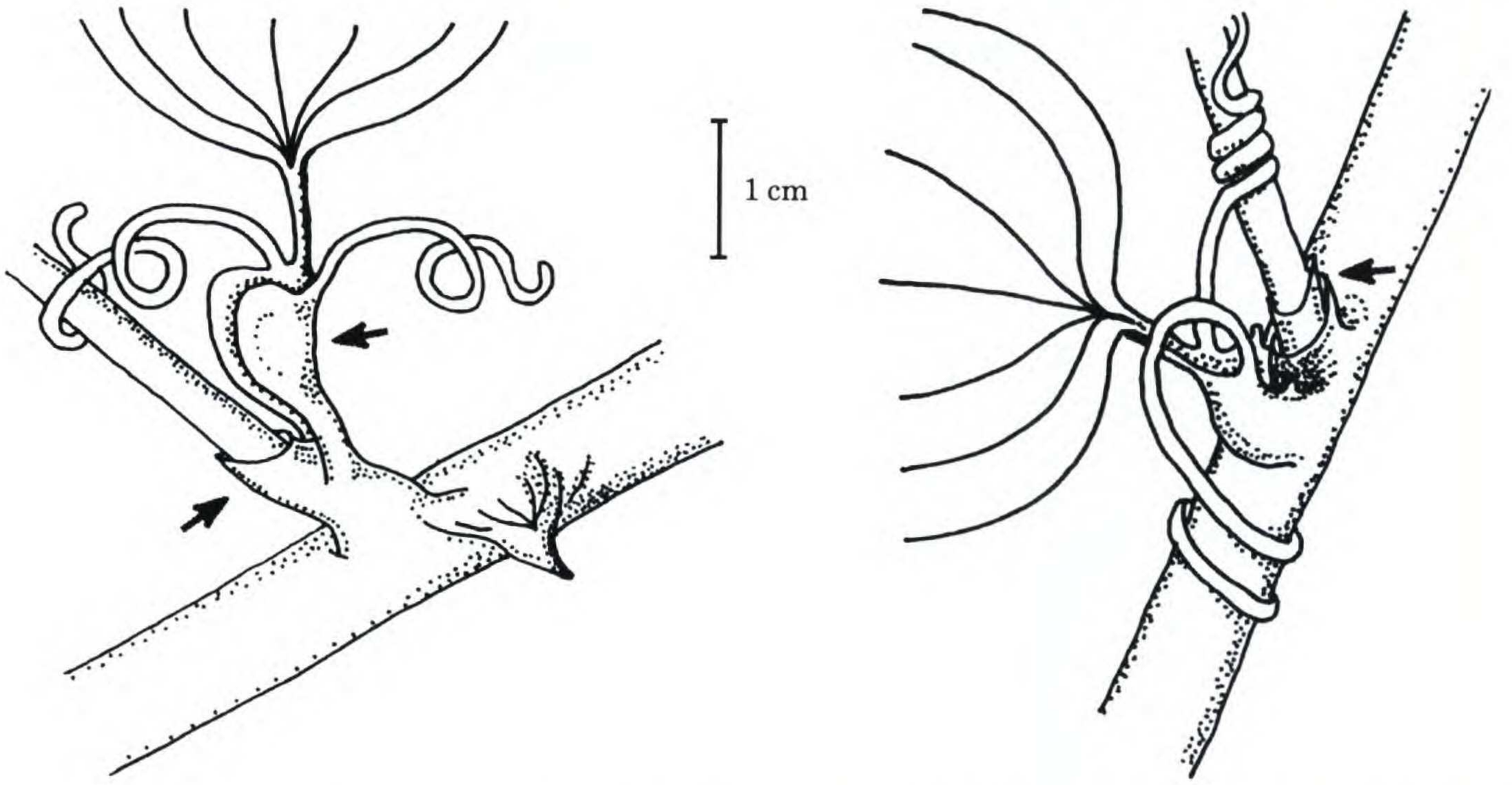

Figure 1, 2. —1 (left). *Smilax siphilitica*, showing the sheath wing on the lower part of the petiole (upper arrow) and the single adaxial scale at the lateral shoot base (lower arrow). Drawn from *Steyermark 58057*, VEN. —2 (right). *Smilax schomburgkiana*, showing two overlapping adaxial scales (arrow) at the lateral shoot base. Drawn from *Morillo & Liesner 8953*, VEN.

roughened (to the point of feeling like coarse sandpaper) on all ages of stem growth.

Stem cross-sectional shape has also been used as a character in distinguishing *Smilax* species (Andreata, 1980, 1995). In the Venezuelan Guayana, *Smilax* stems are mostly round when young, but species from adjoining countries may have quadrangular stems, as *S. longifolia* Richard, or hexagonal, as *S. spruceana* A. DC.

Stem pubescence is a character employed in many regional floras (Huft, 1994; Morton, 1945, 1962; Wallace, 1983). In the Venezuelan Guayana, the only obviously pubescent species is *S. triplinervia* Humboldt & Bonpland ex Willdenow, which is only known from the type specimen.

Lateral shoot bases. The lateral shoots of all *Smilax* species in the Venezuelan Guayana have either a single adaxial (sometimes bifid) scale at the base, or else two closely spaced overlapping scales. The scale closer to the base is a prophyll; when it is followed by a reduced internode, it overlaps a second scale, which is actually a reduced leaf or cataphyll (Sipman, 1979; Guaglianone & Gattuso, 1991); see Figures 1 and 2. Species are very consistent in having either one or two scales, and this character has been underutilized in most other floristic treatments of *Smilax*. The lateral shoots should not be confused with the petioles, which can also have a scale near their junction with the stem and may sometimes appear quite similar to the shoot bases.

For species with a single scale at the base of the lateral shoot, the length of the basal internode compared to the more distal internodes is another useful character (Sipman, 1979). *Smilax staminea* always has the basal internode longer than the more distal ones, and this character has been employed to redetermine many specimens (see Fig. 3).

Sheath wing. If a section of the sheath, proximal to the tendrils, is elongated 5–15 mm perpendicular to the petiole axis, it is called a sheath wing (Sipman, 1979; Mitchell, 1997); see Figure 1. Sheath wing presence or absence is easily determined, but the wings of older herbarium specimens can be broken off and make them appear wingless. In the Venezuelan Guayana, we encountered a problematic group of specimens that had previously been determined as either *S. siphilitica* Humboldt & Bonpland ex Willdenow, *S. pseudosyphilitica* Kunth, *S. aequatorialis* (Grisebach) A. DC., or *S. febrifuga* Kunth, in which we were unable to find any consistent characters to support the four different taxa. Within this complex, we currently view the presence or absence of sheath wings and their size as variable, so while we did not go so far as to synonymize all of the above names (and only the type of *S. siphilitica* was from the flora area), we determined all specimens from this group as *S. si-*

Figure 3. *Smilax staminea*, showing a lateral shoot with the basal internode longer than the more distal ones (upper arrow). Note also the short pedicels (insert), single adaxial scale at base of the lateral shoot (lower arrow), and 5-veined leaf blades. Drawn from *Steyermark 123975*, MO (inset), and *Steyermark et al. 109801*, NY.

philitica due to their other morphological similarities: two lateral shoot base scales, similar petiole length and width, smooth stem texture, glabrous foliage, and common leaf morphology and similar range of reproductive characters. Recently, in a revision of the Brazilian species of *Smilax*, Andreata (1995) did propose placing *S. pseudosyphilitica* and *S. aequatorialis* in synonymy with *S. siphilitica*.

Petiole articulation and length. The point at which a petiole breaks naturally, and the relative length of the section of petiole remaining on the plant when the leaf abscises, were used as important characters by both de Candolle (1878) and Koyama (1960). However, these characters vary in both *Smilax pittieriana* Steyermark and *S. cumanensis* Humboldt & Bonpland ex Willdenow. It is not always clear on herbarium specimens whether the leaf has abscised naturally from the point of articulation, or whether the petiole has broken artificially upon drying.

In material from the Venezuelan Guayana, mature petioles range in length from 5 to 60 mm. When comparing mature leaves, *Smilax poeppigii* has a consistently lower ratio of blade to petiole length (approximately 3:2) than other *Smilax* species from the flora area (usually around 10:1).

Leaf morphology. Leaf shape is generally a poor character in *Smilax* (Howard, 1979; Andreata, 1995), since a species or even a single plant can show a wide degree of variability in leaf shape depending on the position of the shoot (basal stem vs. distal shoots reaching the canopy), age or degree of maturity of the leaf, fertile vs. sterile branch systems, and locally varying environmental factors such as soil type or shade cover. When used carefully, however, such as comparing only fully expanded leaves on lateral shoots, leaf shape can be characteristic of certain species. For example, *Smilax poeppigii* has broadly ovate leaves with cordate bases, and *S. staminea* has ovate-lanceolate leaves with acuminate tips.

Only two species in the flora area typically have leaf spines. *Smilax lappacea* Humboldt & Bonpland ex Willdenow consistently has spines on the leaf margin and lower side of the primary veins. *Smilax maypurensis* Humboldt & Bonpland ex Willdenow varies from having spines on the leaf margin and lower side of the midvein to totally lacking spines on the leaf blade.

The number of primary leaf veins was used as a diagnostic character by de Candolle (1878) and Huft (1994). We found this character to be consistent in some species (*S. schomburgkiana* and *S. triplinervia*, each with 3 primary veins), while other species have a consistent range of primary veins (large mature leaves of *S. pittieriana* are 5-veined, while smaller mature leaves on the same specimen are 3-veined). Mature leaves of *S. poeppigii* have 5 or 7 primary veins. The primary veins closest to the margin can be conspicuous or else so close to the margin that they are barely distinguishable, so we did not resort to using this as a key character in the flora area.

De Candolle (1878) and Morton (1962) relied upon the character of how the primary veins are attached to the main nerve, with character states of triplinerved (the two closest primary veins attached to the main nerve above the base of the leaf) or trinerved (the two closest primary veins attached to the main nerve at the base of the leaf). On the isotype specimen of *S. triplinervia* (*Humboldt & Bonpland s.n.*, photo of B at NY), we found it difficult to detect more than a subtle triplinerved state. Some specimens of *S. schomburgkiana* (which was described as triplinerved by de Candolle) from the flora area have trinerved leaves (*Steyermark 107478*, NY; *Steyermark 87263*, NY). Leaves that are supposed to be trinerved often appear triplinerved when they have dried and folded together near the apex of the petiole.

Mitchell (1997) described a new species (*Smilax saülensis* J. D. Mitchell) from French Guiana based mainly on having the higher-order venation branched inward toward the primary veins (admedially ramified). We found no species with this character state in the Venezuelan Guayana, but it may be of value in other areas.

Inconspicuous higher-order venation was used as a character in the flora area by Steyermark (1951) to distinguish *S. pittieriana*, which has an upper leaf blade surface that is lustrous and almost perfectly flat, with no evident higher-order veins. Huft (1994) also used this same character state to distinguish *S. luculenta* Killip & C. V. Morton. Although secondary veins can be distinguished on some specimens of *S. pittieriana*, they are much less obvious than in most other species.

Inflorescence. Inflorescence type in *Smilax*, i.e., either a simple umbel or raceme, has been used by de Candolle (1878), Koyama (1960), Steyermark (1966), and Mitchell (1997). This character can be useful, though sometimes misleading. Even in de Candolle's fine work there was a category of species in which he was unable to distinguish a raceme from a branch of simple umbels (de Candolle, 1878: 146). One often finds that the peduncle is subtended by a normal leaf, but that leaf falls off, and the remainder of the petiole looks like a bract.

There are also specimens of some species that are characterized by racemosely arranged umbels in which the peduncles are subtended by both fully developed leaves on one part of the plant, and bracts or small leaflets on other parts (*S. schomburgkiana*: *Steyermark 107478*, NY, and *S. pittieriana: Steyermark 90823*, US).

Receptacle and pedicel length. The shape of the inflorescence receptacle can be either globular or reniform (Sipman, 1979), with reniform receptacles generally associated with flattened peduncles. In the Venezuelan Guayana, we found that the peduncles of all species were somewhat flattened, although the thinner ones appear more terete, so that receptacle morphology appears to be largely a function of the thickness of the peduncle. Sipman (1979) indicated that each receptacle morphology has its own type of bract, the globular receptacles with acute, stiff bracts, and the reniform receptacles with obtuse, soft bracts.

We used the ratio of pedicel length to peduncle length as a fairly consistent character to differentiate *Smilax cumanensis* from *S. lappacea* and *S. maypurensis*. In most species, however, peduncle length is too variable to use as a consistent character, or else pedicels are lacking on many herbarium specimens.

Number of flowers per receptacle. This character is variable in most species from the flora area, though the species we treat as *Smilax poeppigii* often has 30–70 flowers per receptacle, which is unusually high compared to other flora-area species. Koyama (1960) used flower number to separate sections within *Smilax*. This character has been reported to vary with the sex of the plant as well as on different parts of the plant (Howard, 1979), and thus may not be reliable except in extreme contrasts.

Floral characters. According to Howard (1979), perianth color can vary even within a single plant. Notations on specimen sheets from the Venezuelan Guayana show fairly consistent color within some species (*S. lappacea* and *S. pittieriana*, with green flowers), and a range of colors in other species (*S. maypurensis*, *S. siphilitica*, and *S. staminea*, with white to green flowers). When dried, however, flowers of all species eventually turn a similar brownish red.

Perianth length may vary between the two sexes of the same species, with the staminate perianth parts up to 50% longer than those of pistillate plants (Howard, 1979). Although perianth length has been used in many treatments (de Candolle, 1878; Morton, 1945; Huft, 1994; Killip & Morton, 1936), we did not use it as a key character due to its wide variability and the lack of flowers on numerous herbarium specimens. For the same reason, we did not use the presence or number of staminodes as a character, despite its prior use in various *Smilax* treatments (Koyama, 1960; Morton, 1962). Howard (1979) found that the number of staminodes in pistillate flowers of some species varies widely even within a single inflorescence.

Certain species have mature fruits of a consistent color (*Smilax cumanensis* and *S. maypurensis* with blue to black fruits; *S. pittieriana* and *S. schomburgkiana* with orange fruits), but *S. siphilitica* has fruits that vary from orange to blue-gray. These distinctions are lost upon drying, however, and all fruits from the flora area dry a similar blackish color.

Key to the Species of *Smilax* in the Venezuelan Guayana

1. Lateral shoots (not individual petioles) with 1 scale (sometimes bifid) at the base on the adaxial side (see Fig. 1) 2
1. Lateral shoots with 2 closely placed, overlapping scales at the base on the adaxial side (see Fig. 2) 5
2(1). Basal internode of branches 2–16 cm long, longer than the more distal internodes; peduncle shorter or equal to the petiole length; 1200–2300 m elevation . . . . . *S. staminea*
2. Basal internode of branches 0.5–3 cm long, shorter than the more distal internodes; peduncle usually longer than the petiole, sometimes shorter; 0–1300(–1650) m elevation 3
3(2). Pedicels longer than the peduncle; leaf without spines, blade ovate to elliptic, often drying green, apex acute; Delta Amacuro and Bolívar states, rarely in northern Amazonas . . . . . *S. cumanensis*
3. Pedicels shorter than the peduncle; leaf usually with spines, blade lanceolate to ovate, drying reddish or green, apex mucronate or acute; Amazonas state and rarely in southeastern Bolívar state 4
4(3). Leaf blade lanceolate; apex mucronate or acute, not oblique, drying reddish or green; lower midvein, primary veins, and margin with spines . . . . . *S. lappacea*
4. Leaf blade ovate to rarely lanceolate; apex acute, often oblique, drying reddish; lower midvein and margin often with spines, lower primary veins without spines . . . . . *S. maypurensis*
5(1). Upper branches very scabrous, without spines . . . . . *S. schomburgkiana*
5. Upper branches not scabrous, with or without spines 6
6(5). Stem and midvein pubescent on lower side of leaf . . . . . *S. triplinervia*
6. Stem and lower side of leaf glabrous 7
7(6). Mature leaf blade strongly cordate, 5–20 cm

long, 8–20 cm wide; receptacle usually with many flowers (30–70) . . . . . *S. poeppigii*

7. Mature leaf blade oblong to ovate, 8–35 cm long and 4–10 cm wide; receptacle with < 30 flowers 8

8(7). Mature leaf blade 15–35 cm long, membranous to subcoriaceous, upper surface dull to sublustrous; lower-order venation evident; with or without spines on stem . . . . . *S. siphilitica*

8. Mature leaf blade 8–15 cm long, coriaceous, upper surface lustrous and plane; lower-order venation inconspicuous; stem spineless . . . . . *S. pittieriana*

New Synonymy

Smilax pittieriana Steyermark, Fieldiana, Bot. 28: 155. 1951. TYPE: Venezuela. Bolívar: mesa between Ptari-tepui and Sororopán-tepui, 1615 m, 15–17 Nov. 1944, [staminate], *Steyermark 60251* (holotype, F; photo, NY).

Smilax auraimensis Steyermark, Bol. Soc. Venez. Ci. Nat. 26: 472. 1966. Syn. nov. TYPE: Venezuela. Bolívar: Sierra Auraima, en la parte terminal norte sobre el margen oeste del Río Paragua, en la zona del raudal de El Perro, 6°32′N, 63°33′W, 400 m, 16 Jan. 1962, *Steyermark 90823* (holotype, VEN; isotypes, NY, US).

Smilax chimantensis Steyermark & Maguire, Mem. New York Bot. Gard. 17(1): 440. 1967. Syn. nov. TYPE: Venezuela. Bolívar: along Río Apacará, Apacará-tepui, Chimantá Massif, 400 m, 25 Mar. 1953, [staminate], *Steyermark 74652* (holotype, NY; isotype, F).

Steyermark's differentiation among *Smilax pittieriana*, *S. auraimensis*, and *S. chimantensis* stems from his confusing designation of a "type" (= holotype) and "co-type" of *S. pittieriana*. The holotype has racemose male inflorescences, two axillary scales at the base of the branches, and ovate, coriaceous leaves with a rounded base and a plane, glossy upper surface. The "co-type," *Steyermark 60251a* (F), has no nomenclatural significance. It has remnants of simple umbellate inflorescences, a single axillary scale at the base of the branches, and narrowly elliptic, membranous leaves with an acute base, a prominently reticulate venation, and a matte upper surface; as such, it corresponds to what we here recognize as *S. staminea*.

Steyermark (1966) differentiated *Smilax auraimensis* and *S. chimantensis* from *S. pittieriana* by their compound inflorescences instead of a simple umbel. In this, he must have been referring to the "co-type" of *S. pittieriana* (actually *S. staminea*), which has remnants of simple umbels. The holotype of *S. pittieriana*, however, has compound inflorescences and cannot be differentiated from the types of *S. auraimensis* or *S. chimantensis* in terms of inflorescence morphology. Steyermark also differentiated *S. chimantensis* from *S. pittieriana* by the following character states: (1) shorter staminate pedicels (6–7 vs. 9–12 mm, but we measured Steyermark's type specimen of *S. pittieriana* and found no pedicel longer than 9 mm); (2) shorter and narrower perianth segments (4–4.5 × 0.6–0.9 vs. 5.2–5.3 × 1.2–1.4 mm, but we measured Steyermark's type specimen of *S. pittieriana* and found the perianth segments to be 4.0–4.5 × 1.0–1.1 mm); (3) immersed vs. non-immersed nerves on the upper surface of the leaf blades; and (4) rounded to slightly cordate instead of subacute to obtuse leaf bases. The differences in leaf morphology are again due to Steyermark's deriving some of the *S. pittieriana* character states from the "co-type" specimen representing *S. staminea*.

Some specimens of *Smilax pittieriana* from the flora area were previously determined as *S. guianensis* Vitman. However, this is a species of uncertain affinity that was based on an illustration by Charles Plumier (1756: tab. 84) of a plant from Martinique; Vitman apparently thought that Plumier's drawing represented the same species as material he examined for his treatment of *Smilax* from French Guiana, explaining his choice of the specific epithet (Vitman, 1791: 422).

Smilax siphilitica Humboldt & Bonpland ex Willdenow, Sp. Pl. 4(2): 780. 1806. TYPE: Venezuela. Amazonas: Río Casiquiare, 1800, *Humboldt & Bonpland 1147* (photo of B holotype at US).

Smilax duidae Steyermark, Fieldiana, Bot. 28: 154. 1951. Syn. nov. TYPE: Venezuela. Amazonas: Cerro Duida, SE-facing slopes along Caño Negro, 260–610 m, 26 Aug. 1944, *Steyermark 58057* (holotype, F; photo, NY).

We cannot find any evidence that Steyermark ever dealt with the name *Smilax siphilitica*, even though the type specimen was collected in southern Venezuela. However, he did contrast *S. duidae*, whose type is also from Amazonas state in Venezuela, with *S. pseudosyphilitica* (type from Prov. Rio de Janeiro, Brazil). In his protologue of *S. duidae*, Steyermark stated that the plants are unarmed, though we found small axillary spines (similar to the spines described in the protologue of *S. siphilitica*) on the type specimen. The type of *S. duidae* is also similar to that of *S. siphilitica* in the coriaceous, oblong, mucronate leaf morphology and the long sheath wings, a character employed by Sipman (1979).

Specimens of *Smilax siphilitica* from the flora area have also been determined as *S. aequatorialis* (type from Prov. Pará, Brazil, and originally de-

scribed as a variety of *S. siphilitica*), *S. febrifuga* (type from Peru), or *S. pseudosyphilitica*. In her recent revision of Brazilian *Smilax*, Andreata (1995) placed both *S. aequatorialis* and *S. pseudosyphilitica* in synonymy under *S. siphilitica*.

Smilax staminea Grisebach, in Martius, Fl. Bras. 3(1): 11. 1842. TYPE: Brazil. "In Brasilia meridionali," *Sello s.n.* (lectotype, G; isolectotypes, K, P not seen). This lectotypification follows Andreata (1995).

Smilax lasseriana Steyermark, Fieldiana, Bot. 28: 154. 1951. Syn. nov. TYPE: Venezuela. Bolívar: Sororopán-tepui, 2255 m, 14 Nov. 1944, *Steyermark 60121* (holotype, F; isotypes, NY, US).

Smilax jauaensis Steyermark & Maguire, Mem. New York Bot. Gard. 23: 854. 1972. Syn. nov. TYPE: Venezuela. Bolívar: Cerro Jaua, 4°45′N, 64°26′W, 1922–2100 m, 22–27 Mar. 1967, *Steyermark 98073* (holotype, VEN).

Smilax staminea forma *obtusata* Steyermark, Fieldiana, Bot. 28: 156. 1951. TYPE: Venezuela. Bolívar: Ptaritepui, 1700–1800 m, 1 Nov. 1945, *Steyermark 59695* (holotype, F; isotype, NY).

The types of *Smilax staminea* and the other two names listed above in synonymy all have a single scale at the lateral shoot base, the basal internode of the lateral shoots longer than the more distal internodes, and similar petiole length and width. Steyermark differentiated *Smilax jauaensis* and *S. lasseriana* from *S. staminea* as having verruculose-tuberculate vs. smooth stems, and he further differentiated *S. lasseriana* from *S. staminea* by its leaf shape (ovate-oblong vs. ovate-lanceolate). Verruculose-tuberculate-stemmed specimens (*Steyermark 98073*, VEN) and smooth-stemmed ones (*Steyermark et al. 109771*, VEN) with otherwise similar inflorescence and vegetative morphology are found together on Cerro Jaua, Bolívar, Venezuela. Leaf morphology and stem texture, as discussed earlier in this paper, are unreliable characters to differentiate species in this complex.

Some specimens of *Smilax staminea* from the flora area have previously been determined as *S. nitida* Grisebach (type from southern Brazil), but Andreata (1995) now regards *S. nitida* as a synonym of *S. rufescens* Grisebach. Outside the flora area, but within Venezuela, specimens that may be referable to *S. staminea* have been collected in the Andes and in the coastal ranges of Distrito Federal and Estado Sucre. This material has mostly been determined as *S. kunthii* Killip & C. V. Morton (= *S. floribunda* Kunth, nom. illegit., type from Ecuador), but a broader examination of specimens will be necessary to determine if this name should also be treated as a synonym of *S. staminea*.

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