

NEW SPECIES OF *SOLANUM* SECTION *GEMINATA* (G. DON) WALP. (SOLANACEAE) FROM SOUTH AND CENTRAL AMERICA¹

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ABSTRACT

Four new species of *Solanum* section *Geminata* are described: *S. pastillum*, *S. heleonastes*, *S. dasyneuron*, and *S. aphyodendron*. Two of these are Central American, one from Guatemala and one from Costa Rica. The third is only found along the Río Paraná along the border of Argentina and Paraguay. The fourth is a widespread species that has long been confused with *S. nudum* H.B.K. ex Dunal. Nomenclature and details of natural history are discussed.

Solanum section *Geminata* (G. Don) Walp. is one of the largest sections in the genus, with approximately 70 species, all but one of which is exclusively neotropical. The section has previously been known as section *Leiodendra* Dunal (D'Arcy, 1972), but for reasons of priority (Knapp, 1983), *Geminata* (G. Don) Walp. is the correct sectional name for this species group.

Members of section *Geminata* are generally small trees or shrubs, often growing in the primary forest understory, an unusual habitat in the genus *Solanum*. Species in the section share difoliate nodes with many (but not all, see Danert, 1967; Child, 1979) other *Solanums*, which in section *Geminata*, as the name implies, are often geminate. In this situation the two leaves of the node arise from the same height on the stem due to failure of mesopodial elongation (Danert, 1958): therefore the subtending leaf of the previous shoot generation is at the same level as its daughter shoot. The leaves in a geminate cluster can be of equal size and shape or can differ in one or both of those characters. The most common situation in section *Geminata* is for the geminate cluster to be anisophyllous. The larger of the two leaves is termed the *major* leaf and the smaller the *minor* leaf. Section *Geminata* is further characterized by the leaf-opposed nature of the inflorescence, which also arises from the same level on the stem as the geminate leaves.

This "leaf-opposedness" is due to meso- and epipodial suppression and adnation of the stem and the peduncle (Danert, 1967; Child, 1979) and is not perfect in all species. Pubescence in the section is absent or consists of uniseriate trichomes ("finger hairs" sensu Seithe, 1962, 1979), but branched trichomes do occur. The flowers are small, white or greenish white, and the degree to which the petals reflex at anthesis is often a good specific character. Fruits of most species are green and remain hard until the day of maturity, when they become soft and yellowish (pers. observ.), but several species have brightly colored, presumably bird-dispersed fruits. The pedicel scars of flowers that fall off without producing fruit become corky and are prominent in later stages of inflorescence growth. The spacing and arrangement of these scars is generally an overlooked character (but see D'Arcy, 1973) and is useful in distinguishing the species of section *Geminata*.

While preparing a revision of *Solanum* section *Geminata*, I have discovered several new species, both in the herbarium and in the field. Four of these are described here. Further details of the natural history of *S. pastillum* and *S. aphyodendron* can be found in Knapp (1985).

Solanum pastillum S. Knapp, sp. nov. TYPE: Costa Rica. Puntarenas: Monteverde, Camp-

¹ I thank W. G. D'Arcy, R. L. Dressler, W. Haber, B. Hammel, W. J. Kress, J. Mallet, M. Nee, and M. D. Whalen for helpful discussions and field assistance; Carol Kalafatic for preparing the illustrations; Missy Holbrook and Jack Putz for field assistance, and W. J. Dress for help with the Latin diagnoses. I thank the curators of the following herbaria for access to their specimens: BH, CR, F, G, LL, MO, NY, P, RSA/POM, TEX, US, USM, WIS. Field work in Costa Rica was funded by an Organization for Tropical Studies Inc. Jessie Smith Noyes Fellowship and a Sigma Xi Grant-in-Aid for Research; permission to collect and work in the Monteverde Cloud Forest Reserve was kindly granted by the Tropical Science Center, San José. Field work in Panama was funded by NSF grant DEB 79-22192 to W. G. D'Arcy of the Missouri Botanical Garden. The support of these institutions is gratefully acknowledged.

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FIGURE 1. *Solanum pastillum* (from Knapp, Holbrook & Putz 6063).

bell's Woods, 1,450 m, 20 Aug. 1982, Knapp, Holbrook & Putz 6063 (holotype, BH; isotypes, CR, F, MO, US). Figure 1.

Frutex gracilis; *caules* virides petiolorum basibus leviter alati; *folia* ovata geminata utrinque glabra subtus pallide viridia, apice acuminato, basi attenuata decurrente; *inflorescentiae* foliis opposita simplices glabrae pendulae; *pedicelli* sub anthesi deflexi; *calycis* lobi orbiculati succulenti 1 mm diam.; *corolla* rotata dilute viridi-alba, lobis reflexis carinatis; *bacca* globosa flavo-viridis, pedicello lignoso infra calycis tubum expanso; *semina* ovoidea reniformia fulva, testa foveolata.

Slender arching shrubs, 1–3 m tall; stems glabrous, green, horizontally spreading, winged between the nodes with the decurrent leaf bases; bark of the older stems pale green, white-lenticellate. Leaves geminate, elliptic-ovate, widest at or just below the middle, dark green and slightly bullate above, pale sea green beneath, glabrous; major leaves 11.2–22 cm long (occasionally to 25 cm on the lower branches), 3.4–6.6 cm wide (to 11.3 cm on the lower branches), with 6–8 pairs of primary veins, raised above, paler and prominent beneath, the apex long acuminate, the base decurrent on the petiole, attenuate to cuneate; petioles 0.5–1 cm long; minor leaves dif-

fering from the major ones only in size, 2.1–6 cm long, 1.1–3.5 cm wide, the apex long acuminate, the base attenuate; petioles 3–5 mm long. Inflorescences opposite the leaves, simple, glabrous, translucent green, minutely white-lenticellate, 1.7–7 cm long, slender and pendulous, 5–50-flowered; pedicel scars irregularly spaced, 1–3 mm apart, beginning ca. 1 cm from the base of the inflorescence; pedicels at anthesis deflexed, 1.4–1.5 cm long, tapering from the calyx tube to a slender base ca. 0.5 mm diam.; buds conical, the corolla soon exerted from the globose calyx lobes, glabrous; calyx tube ca. 1.5 mm long, broadly cup-shaped, translucent green, lobes on fresh specimens consisting of 5 orbiculate projections ca. 0.5 mm diam. on the rim of the calyx tube, in dry specimens of irregularly shaped projections 0.5–1 mm long from the rim of the calyx tube, glabrous and translucent green; corolla greenish white, 1.1–1.2 cm across, lobed ca. three-fourths of the way to the base, the lobes reflexed at anthesis, the tips of the lobes carinate-hooded, minutely papillose; anthers 2.5–3.25 mm long, 1.25–1.5 mm wide, poricidal at the tips, the pores becoming slit-like upon drying; free portion of the filaments ca. 0.5 mm long, the filament tube



FIGURE 2. Distribution of *Solanum pastillum* and *Solanum dasyneuron*.

ca. 0.5 mm long; ovary glabrous; style 5–6 mm long, straight or curved in dry specimens; stigma capitate, minutely papillose. Berry globose, greenish yellow at maturity, ca. 50-seeded, 1–1.5 cm diam., usually only 1 or 2 from an inflorescence; fruiting pedicels 1.9–2.6 cm long, woody, deflexed, greatly expanded at the distal end, there ca. 4–7 mm diam., the base slender, ca. 0.5 mm diam.; seeds pale brown or tan, ovoid reniform, 3.5–4 mm long, 2–2.5 mm wide, the surfaces minutely pitted, the pits very shallow, the seeds appearing smooth. Chromosome number, $n = 12$ (Knapp, unpubl. data; voucher, Knapp et al. 6063).

Distribution. Found only in the cloud forests of montane central Costa Rica from 1,000 to 1,700 m. Figure 2.

Solanum pastillum is an isolated species in section *Geminata*. The most probable close relative of *S. pastillum* is *S. tuerckheimii* Greenm., also of montane central Costa Rica (but extending into Nicaragua, Guatemala, and Mexico). The two species share the understory habitat, long inflorescences of greenish white flowers with reflexed petals at anthesis, and hard green fruits which become yellow and soft upon maturity.

Solanum pastillum blooms at the beginning of the wet season at Monteverde de Puntarenas, Costa Rica, the type locality, and is pollinated primarily by bumblebees, *Bombus ephippiatus* (Knapp, 1985). The local distribution pattern of *S. pastillum* is typical of many of the forest understory species of section *Geminata*. Small clumps of three to five individuals grow at widely

spaced intervals in the understory, often at the edges of old gaps caused by fallen trees or branches. The inflorescences of *S. pastillum* are many-flowered, but only a few fruits per inflorescence develop. Whether this is due to poor pollination success or to fruit abortion is not known. The presence of a single fruit on a long inflorescence causes the effective pedicel length of the fruit to be extremely long. This may make the fruit more visible to small frugivorous bats, known to take the fruits of this and many other species of section *Geminata* in Monteverde (E. Dinerstein, pers. comm.).

The specific epithet, “pastillum” meaning small round loaf of bread, refers to the orbiculate calyx lobes, which are quite distinctive in this species.

Additional specimens examined. COSTA RICA. ALAJUELA: Llanura de San Carlos, 100 m, 21 Feb. 1966, Molina R. et al. 17659 (F); Peñas Blancas Trail, 3.5–5 km ESE of Monteverde, ca. 1,450 m, 17 Aug. 1976, Kennedy & Guindon 3713 (F); Monteverde, on road to Peñas Blancas (over Continental Divide) ca. ½ km below the Divide on Atlantic slope, 1,450 m, 10°25'N, 84°50'W, 13 Apr. 1981, Knapp & Mallet 864 (BH); Alfaro Ruíz, Guadalupe de Zarcero, 1,550 m, 1 July 1938, Smith NY810 (F, NY); Alfaro Ruíz, La Peña de Zarcero, 1,400 m, 11 July 1938, Smith NY904 (F, NY); Alfaro Ruíz, Zapate, 1,425 m, 10 May 1940, Smith P2663 (F); Alfaro Ruíz, 5 mi. S of Zarcero, 1,500 m, 17 June 1941, Smith 2789 (F). CARTAGO: El Muñeco on Río Navarro, 1,400–1,500 m, 6–7 Mar. 1926, Standley & Torres R. 51016, 51040 (US). PUNTARENAS: Sendero El Brillante, Monteverde Cloud Forest Reserve, 1,450–1,500 m, 13 May 1976, Dryer 81 (F); S of the road, Monteverde Cloud Forest Reserve, 1,520–1,580 m, 16 June 1976, Dryer 208 (F); Monteverde, near the Ventana (Continental Divide), 1,500–1,600 m, 12 July 1976, Dryer 426 (F); S of road, Monteverde Cloud Forest Reserve, 1,520–1,580 m, 28 Aug. 1976, Dryer 683, 684 (F); Monteverde Cloud Forest Reserve, ½ km from the station along the Sendero Río, 1,500 m, 10°25'N, 84°50'W, 19 Feb. 1981, Knapp 830 (BH); Monteverde Cloud Forest Reserve on Sendero Pantanoso near the Continental Divide, 1,600 m, 10°25'N, 84°50'W, 11 Mar. 1981, Knapp 840 (BH). SAN JOSÉ: Santiago de San Ramon, 1,150 m, 29 July 1937, Brenes 22615 (F); 5 mi. S of Santa María, 6,800 ft., 5 Feb. 1928, Stork 1757 (F).

***Solanum heleonastes* S. Knapp, sp. nov.** TYPE: Argentina. Corrientes: Capital, Puerto Italia en montes costeros del Río Paraná, 6 Nov. 1972, Schinini 5671 (holotype, MO; isotypes, MO, WIS). Figure 3.

Frutex vel arbor parva; caules juniores incani trichomatibus minutis uniseriatis dense pubescentes; caules veteres succulenti nitidi rubiginosi; folia ovata geminata supra glabra subtus in nervis minute papillata, nervis stramineis, apice acuto vel acuminato, basi



FIGURE 3. *Solanum heleonastes* (from Schinini 5671, fruit from Schwindt 30).

cuneata valde obliqua; *inflorescentiae* foliis opposita simplices modo caulium juniorum pubescentes; *pedicelli* sub anthesi erecti; *calycis lobi* longe acuminatae; *corolla* rotata alba, lobis planis leviter carinatis; *bacca* globosa lignosa, in specimenibus exsiccatus ochracea, pedicello lignoso erecto; *semina* fusca complanata reniformia, testa foveolata; *habitat* in paludibus fluvii Parana inter Argentina et Paraguay.

Shrubs or small trees, 1–5 m tall; young stems and leaves densely covered with appressed uniseriate papillate trichomes, 0.05–0.1 mm long, these irregular and floccose in appearance, greyish brown, the young growth with a grainy texture; bark of the older stems red-brown, shining, glabrate, minutely white-lenticellate. Leaves ovate, geminate, widest just below the middle, glabrous above, minutely papillate on the veins beneath, the veins yellowish, epidermis large-celled and appearing crystalline; major leaves

10.2–18.5 cm long, 5.8–7.9 cm wide, with 8–10 strong, evenly spaced primary veins, these yellow beneath, the secondary venation obscure, the apex acute or acuminate, the base broadly cuneate, strongly oblique; petioles 1.7–3.2 cm long, slightly winged from the decurrent leaf bases; minor leaves differing from the major ones only in size, 7–11 cm long, 3.4–5.5 cm wide, the apex acute or acuminate, the base broadly cuneate, attenuate, oblique; petioles 0.8–1.2 cm long. Inflorescences opposite the leaves, simple, 1–2 cm long, 10–30-flowered, densely covered with papillate trichomes as those of the young stems and leaves; pedicel scars closely and evenly spaced, but not overlapping; pedicels at anthesis erect, 1.1–1.4 cm long, tapering from the base of the calyx tube to a slender base ca. 0.5 mm diam., minutely white-speckled, sparsely papillate with uniseriate



FIGURE 4. *Solanum dasyneuron* (from Matuda 2849).

trichomes like those of the young stems and leaves; buds at first globose, enclosed in the urceolate calyx tube, later ovoid and exerted from the calyx tube; calyx tube 1.5–2 mm long, urceolate in bud, later cup-shaped, the lobes long triangular, 2.5–5 mm long, white-speckled, minutely papillose at the tips; corolla white (blue in *Schwarz 8182*), 1.2–1.5 cm across, lobed nearly to the base, the lobes planar at anthesis, tips of the lobes slightly carinate, minutely papillose at the tips and the margins; anthers 3.5–4 mm

long, tightly connate in young flowers, 1–1.5 mm wide, poricidal at the tips, the pores becoming slit-like upon drying; free portion of the filaments ca. 1 mm long, the filament tube ca. 0.5 mm long; ovary glabrous; style filiform, 5–7 mm long, straight; stigma minutely capitate, white-papillose. Berry globose, dry and woody with very little pulp, 1–1.2 cm diam., mustard yellow in dried specimens, the septum between the carpels dry and papery in dry specimens; fruiting pedicels erect and woody, 1.1–1.4 cm long, ca. 1 mm

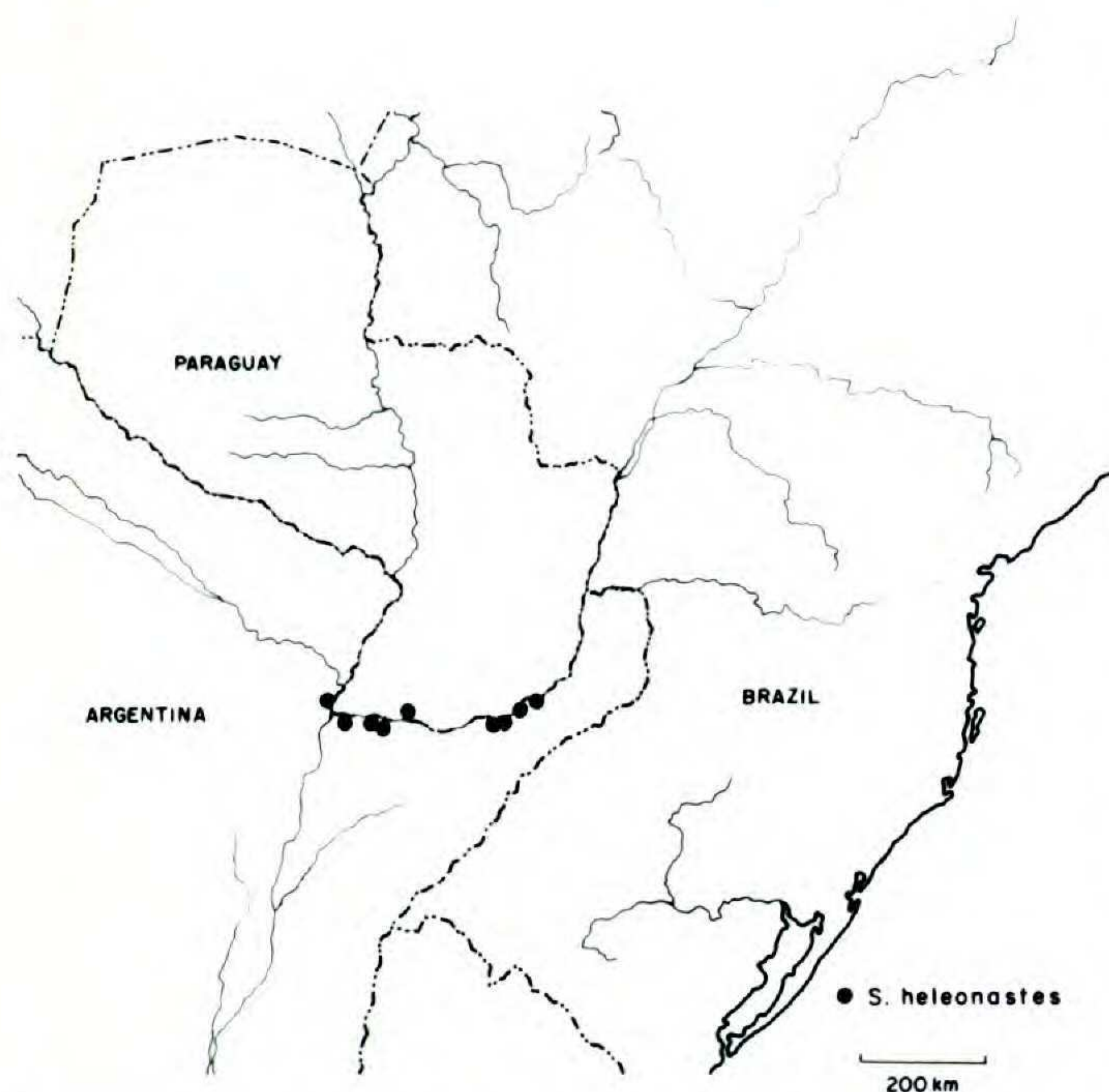


FIGURE 5. Distribution of *Solanum heleonastes*.

diam. at the base; calyx lobes becoming woody and reflexed in fruit; seeds dark brown, flattened reniform, ca. 2 mm long, 1.5 mm wide, the surfaces minutely pitted. Chromosome number, not known.

Distribution. Found only in the swampy forests on the margins and islands in the upper Rio Paraná, on the border between Argentina and Paraguay, from 100 to 200 m. Figure 5.

Solanum heleonastes is closely related to *S. robustifrons* Bitter of eastern Peru and adjacent Brazil, differing from that species in its longer calyx lobes, smaller leaves, and generally more pubescent young stems and leaves. *Solanum heleonastes* is usually a large tree, and *S. robustifrons* is a small shrub or treelet that grows in the understory of dense forests at middle elevations. *Solanum heleonastes* is one of the few species of section *Geminata* growing in swamp forest and is quite common in areas where it is found.

The specific epithet of this species, "heleo" meaning swamp and "nastes" meaning inhabitant, refers to the unusual habitat of this species.

Additional specimens examined. ARGENTINA. CHACO: 1° de Mayo, Col. Benítez, Bermejo, Isla Brasilera, 4 Oct. 1964, Schulz 9422 (F, WIS). CORRIENTES: Capital, on the Río Paraná 5 km from Corrientes, 10 Oct. 1944, Hunziker 5700 (US); Arroyo Itaimbí, 15 Dec. 1944, Sesmero 201 (NY); Capital, Puerto Italia, 27 July 1974, Schinini & Gonzalez 9502 (MO, WIS); Ituzaingó, Isla San Martín, 9 Oct. 1949, Schwarz 8182 (BH). MISIONES: Posadas, Río Alto Paraná, 18 Nov. 1907, Ekman 820 (MO); Posadas, 17 Apr. 1930, Ro-

dríguez 188 (F); Candelaria, San Juan, 216 m, 4 Jan. 1947, Schwindt 30 (RSA/POM). PARAGUAY: sin. loc., 1853–1856, Palmer s.n. (US).

***Solanum dasyneuron* S. Knapp, sp. nov.** TYPE: Mexico. Chiapas: Volcán Tacaná, Chiquihuite, 2,800 m, 27 Mar. 1939, Matuda 2849 (holotype, F; isotypes, F, NY). Figure 4.

Frutex; caules glabri in sicco nigrescentes aetate protracta albicantes; folia obovata vel anguste obovata geminata super glabra subter venis dense pubescentia, apice acuto, basi attenuata; inflorescentiae foliis opposita simplices vel interdum furcatae glabrae nitidae in sicco nigrescentes; pedicelli sub anthesi deflexi; calycis lobi succulenti deltoidei intus papilloso; corolla rotata alba succulenta, lobis planis, stigmatum capitatum; bacca immatura globosa, pedicello lignoso deflexo; habitat in sylvis nubosis Volcan Tacana insidentibus inter Mexico et Guatemala.

Shrubs 2–3 m tall; young stems and leaves glabrous or occasionally minutely rusty-papillate, drying black and shiny; bark of older stems white, exfoliating in small transverse pieces. Leaves obovate to narrowly obovate, geminate, glabrous above, the midrib depressed, the primary veins raised, densely pubescent on the primary and secondary veins beneath with uniseriate trichomes 0.25–0.5 mm long, trichomes restricted to on the veins, none on the lamina; major leaves 12.5–17.3 cm long, 5–6.5 cm wide, with 11–15 pairs of primary veins, the apex acute, the base attenuate, not decurrent on the petiole; petioles 1.5–1.9 cm long; minor leaves differing from the majors only in size, 2.2–7 cm long, 1.6–2.9 cm wide, apex acute, the base attenuate; petioles 0.6–1.1 cm long. Inflorescences opposite the leaves, simple or occasionally once furcate, 1–5 cm long, 10–20-flowered, glabrous and shining; pedicel scars closely spaced and overlapping, beginning 4–6 mm from the base of the inflorescence; pedicels at anthesis deflexed or somewhat erect, 1.1–1.5 cm long, robust and somewhat fleshy, 0.75–1 mm diam. at the base, tapering imperceptibly to the calyx lobes; buds ovoid, fleshy, pointed and constricted apically, only partially exerted from the calyx; calyx tube 1.5–2.5 mm long, conical, the lobes deltoid, apiculate, 1–2 mm long, papillose within, glabrous without, the margins of the lobes white and thickened; corolla white, thick and fleshy, ca. 1.5 cm across, lobed nearly to the base, planar at anthesis, the lobes minutely papillose on the margins and tips, tips cucullate; anthers 3.5–4 mm long, 1–1.5 mm



FIGURE 6. *Solanum aphyodendron* (from Knapp, Kress & Hammel 4136).

wide, poricidal at the tips, the pores becoming slit-like upon drying; free portion of the filaments ca. 0.25 mm long, the filament tube ca. 0.5 mm long, drying black; ovary glabrous; style ca. 7 mm long, straight; stigma large and capitate, ca. 1 mm diam., minutely papillose. Berry globose, 8 mm diam. (immature), green; fruiting pedicels deflexed, woody, 1–1.5 mm diam. at the base; calyx lobes enlarging and becoming woody in fruit, ca. 4 mm long; seeds unknown. Chromosome number, not known.

Distribution. Endemic to the upper slopes of Volcan Tacana, on the border of Mexico and Guatemala, in wet forest from 2,500 to 3,000 m. Figure 2.

Solanum dasyneuron is closely related to *S. narcoticosmum* Bitter and *S. vacciniiflorum* Standley & Williams, both of montane Central America. *Solanum dasyneuron* differs from both of those species in its large fleshy flowers, thick pedicels, its tendency to dry blackish, and by the dense pubescence on the veins on the undersides of the leaves.

The species epithet, “dasy” meaning hairy and “neuron” meaning nerve, refers to the distinctive pubescence on the veins of the leaf undersides.

Additional specimen examined. GUATEMALA. SAN MARCOS: between La Vega ridge along Río Vega and NE slopes of Volcán Tacaná, to 3 mi. from Guatemala–Mexico border, in vicinity of San Rafael, 2,500–3,000 m, 20 Feb. 1940, Steyermark 36198 (F, 2 sheets).

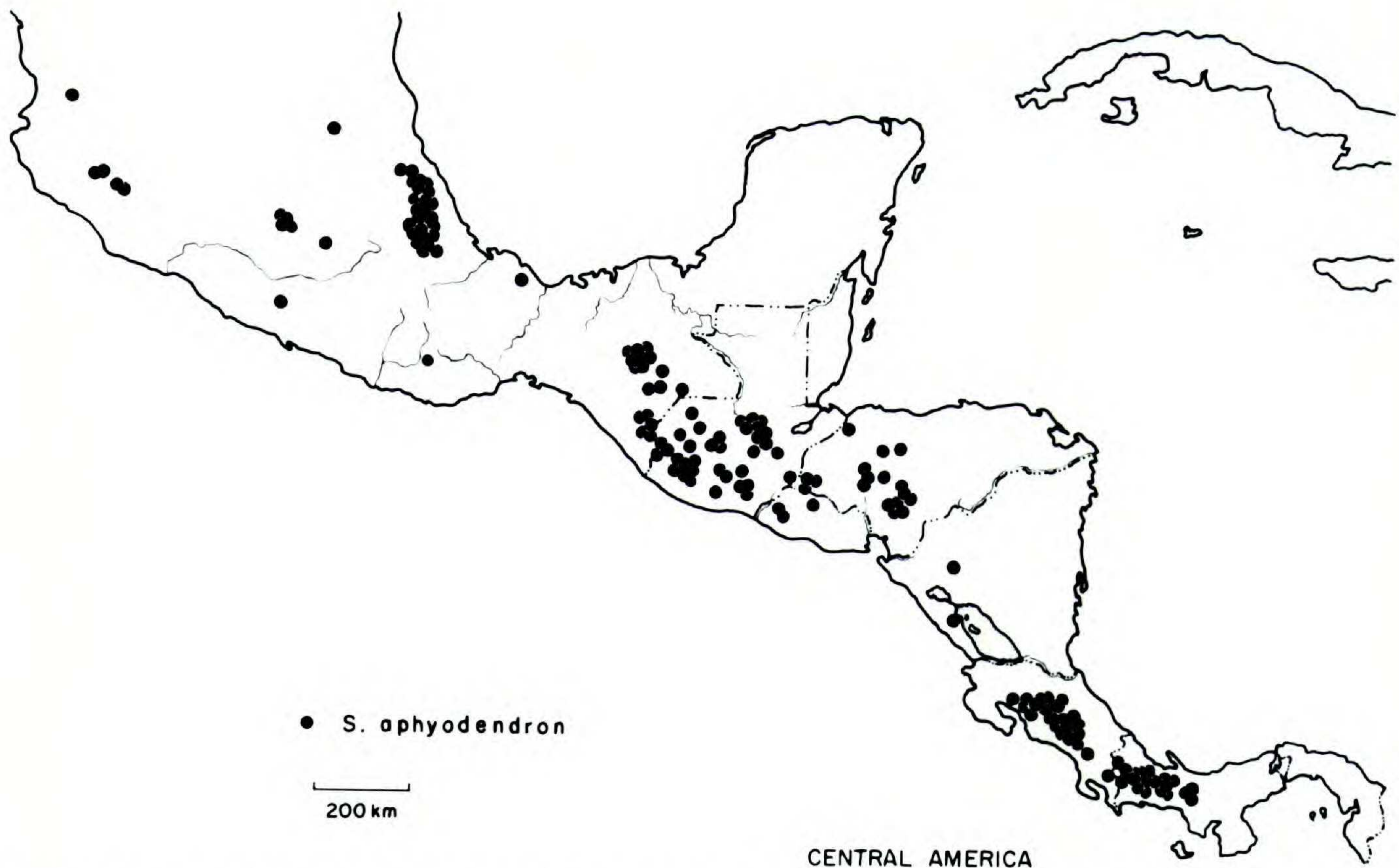


FIGURE 7. Distribution of *Solanum aphyodendron* in Central America and Mexico.

Solanum aphyodendron S. Knapp, sp. nov. TYPE: Panama. Chiriquí: along Quebrada Alemán, 8 mi. N of Los Planes de Hornito, IRHE Fortuna Hydroelectric Project, 1,200 m, 8°45'N, 82°12'W, 13 Mar. 1982, Knapp, Kress & Hammell 4136 (holotype, BH; isotypes, MO, others to be distributed). Figure 6.

Bassovia foliosa Brandege, Univ. Calif. Publ. Bot. 6: 373. 1917 non *Solanum foliosum* Link in Buch. TYPE: Mexico. Veracruz: Zacuapan, Dec. 1915, Purpus 7565 (CAL, isotype, MO!).

Solanum nudum auct. non H.B.K. ex Dunal, Solan. Syn. 20. 1816.

Solanum parcebarbatum Morton & Standley, Publ. Field Mus. Nat. Hist. Bot. Ser. 18: 1088. 1938 pro parte, non Bitter.

Frutex vel arbor parva locos apertos habitantes; *caules* teretes virides glabri albescentes in sicco nigrescentes; *folia* anguste ovata geminata in sicco pallide viridia supra glabra subtus caespitibus trichomatibus uniseriatarum in axillis nervorum pubescentia, viridi-albis, apice acuto vel acuminato, basi cuneata vel leviter attenuata et decurrento; *inflorescentiae* foliis oppositae simplices glabrae; *gemmae* globosae; *pedicelli* sub anthesi deflexi; *calycis lobi* deltoidei trichomatibus uniseriatis pubescentes 1 mm longi; *corolla* rotata alba lobis sub anthesi reflexis; *bacca* globosa flavo-viridis, pedicello lignoso; *semina* fulva complanata reniformia, testa foveolata, marginibus incrassata.

Shrubs or small trees, 3–15 m tall; young stems and leaves glabrous or with a few scattered uni-

seriate trichomes, drying blackish; bark of older stems greenish white and rough; stems slightly winged from the decurrent petiole bases. Leaves narrowly ovate, geminate, widest at or just below the middle, drying pale greyish green, glabrous above and below, except for tufts of uniseriate trichomes in the axils of the primary veins beneath, the trichomes ca. 1 mm long, white; major leaves 8.5–15 cm long, 3–6.1 cm wide, with 8–10 pairs of primary veins, these depressed above, raised and pale greenish white beneath, the apex acute or acuminate, the base cuneate or slightly attenuate, with a small wing on the petiole; petioles 0.6–1.7 cm long; minor leaves differing from the major ones only in size, 3.2–8.6 cm long, 1–4 cm wide, the apex acute or acuminate, the base cuneate; petioles 4–8 mm long. Inflorescences opposite the leaves, simple, 1–2.6 cm long, 20–30-flowered, glabrous or occasionally with a few scattered uniseriate trichomes distally; pedicel scars closely spaced, occasionally overlapping, beginning ca. 1 cm from the base of the inflorescence; pedicels at anthesis deflexed, 0.7–1.1 cm long, tapering from the calyx tube to a slender base ca. 0.5 mm diam.; buds globose, the corolla soon exerted from the calyx, pubescent with uniseriate trichomes 0.1–1 mm long; calyx tube ca. 1 mm long, crateriform, the lobes broadly triangular, 0.5–1 mm long, densely to sparsely

pubescent with uniseriate trichomes 0.1–1 mm long, the margins of the lobes white and scarious; corolla white, often drying with a lavender tinge, 1–1.2 cm across, lobed nearly to the base, the lobes slightly reflexed at anthesis, tips and margins of the lobes minutely papillose; anthers 2.5–3 mm long, 1–1.5 mm wide, poricidal at the tips, the pores becoming slit-like upon drying; free portion of the filaments ca. 0.25 mm long, the filament tube ca. 0.5 mm long; ovary glabrous; style 5–7 mm long, straight; stigma not distinct from the body of the style, minutely papillose. Berry globose, bright green, ripening yellow-green, 1–1.2 cm diam., remaining hard until maturity, then softening overnight; fruiting pedicels deflexed, woody, 1.5–2.3 cm long, ca. 1 mm diam. at the base; seeds tan, flattened reniform, 2.5–3 mm long, 1.5–2 mm wide, the surfaces minutely pitted, margins incrassate, pitting of margins larger than that of the body. Chromosome number, $n = 12$ (Knapp, unpubl. data; voucher, Knapp *et al.* 4136).

Vernacular names. “Capulin de pajaró,” “yerba de zopilote,” Mexico; “zorrillo,” Las Cruces, Puntarenas, Costa Rica; “kaqi sakyol,” Quecchi language, Alta Verapaz, Guatemala; “huele de noche,” Chiquimula, Guatemala; “hedionilla,” Quezaltenango, Guatemala; “hiede hiede,” Cerro Punta, Chiriqui, Panama.

Distribution. Widely distributed in second growth at middle to high elevations (800–2,500 m) from Mexico to Bolivia. Figures 7 and 8.

Solanum aphyodendron is a common species of roadsides throughout Central America and northern South America, and it often forms large monospecific stands in open areas. Material from Central America, Colombia, and Venezuela is quite uniform. Variability in pubescence increases in Peruvian and Bolivian specimens, with some specimens having shorter trichomes on the calyx lobes and denser trichomes in the vein axils.

In Monteverde de Puntarenas, Costa Rica, *Solanum aphyodendron* blooms at irregular intervals throughout the year (Knapp, 1985). Data from herbarium specimens and observations of this species in Panama indicate that its flowering behavior is very much the same throughout its range. At Monteverde, *S. aphyodendron* is pollinated by Meliponine bees, primarily by *Melipona fasciata* (Knapp, 1985). The occurrence of large monospecific stands of *S. aphyodendron*

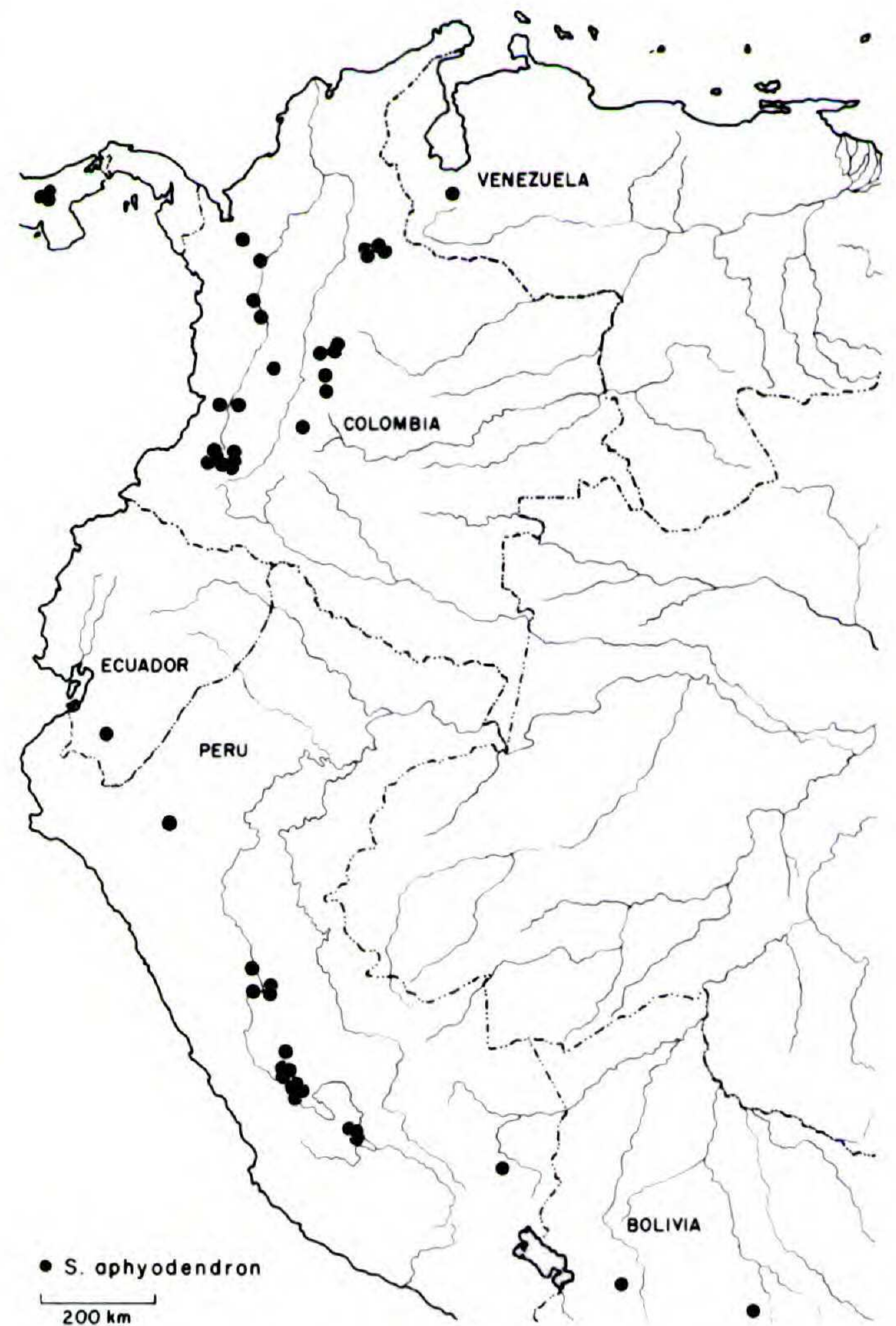


FIGURE 8. Distribution of *Solanum aphyodendron* in South America.

combined with the foraging behavior of *Melipona* produces high fruit set in this species. The ripe fruits are eaten by small frugivorous bats and disappear soon after they become ripe (E. Dinerstein, pers. comm.).

Solanum aphyodendron has long been confused with *S. nudum* H.B.K. ex Dunal, to which it is extremely closely related, but differs in habitat, flower size, pubescence of flower parts, and in the color and texture of the bark of older stems. *Solanum nudum* occurs in low elevation thickets, sometimes on beach strands, and has dark brown bark and glabrous, globose buds. The type specimen of *S. nudum* in the H.B.K. herbarium at Paris clearly belonged to the lowland, glabrous budded taxon, which left the pubescent, middle to high elevation taxon without a name. Brandegee's (1917) epithet “*foliosa*” unfortunately cannot be used, as an earlier homonym exists (*Solanum foliosum* Link in C. L. Buch, 1825). An unpublished name, *S. chamaecerasus* Bitter, has been applied to this species in a few herbaria,

but I have chosen not to use it, as inappropriate to the characteristics of the species.

This species is named for its distinctive whitish bark, "aphyo" meaning becoming white and "dendron" meaning tree.

Representative specimens examined. MEXICO. CHIAPAS: Tenejapa, paraje of Koltol Te', 4,750 ft., 10 July 1964, *Breedlove 6121* (US); Unión Juárez, Bosque de Pino, 1,360 m, 18 Nov. 1977, *Calzada et al. 3711* (F); along Mexican Hwy. 195, 2 mi. N of Colonia San José, 8 mi. S of Layón, 1,500 m, 3–4 June 1973, *Hansen et al. 1689* (BH, US, WIS); Mt. Tacaná, 1,000–2,000 m, Aug. 1938, *Matuda 2466* (F, US); Mt. Pastal, 12 Apr. 1948, *Matuda 17683* (F); near Finca El Suspiro, 11 Jan. 1953, *Miranda 7654* (US); near Tumbala, 4,000–5,500 ft., 20 Oct. 1895, *Nelson 3332* (US); Finca Mexiquito, July 1913, *Purpus 6980* (F, US); Cerro del Boquerón, June 1914, *Purpus 7318* [F (mixed collection with *S. narcoticosmum* Bitter), MO]; Tenejapa, paraje Balum K'aual, 8,400 ft., 13 Apr. 1966, *Shilom Ton 811* (F, LL, NY). GUERRERO: 5 km E of Omiltemi, Chilpancingo, 2,300 m, 1 Sept. 1962, *Rzedowski 16019* (US). HIDALGO: Chapulhuacan, 1,300 m, 12 July 1937, *Lundell & Lundell 7192* (LL, NY). JALISCO: SW foothills of the Nevado de Colima, ca. 10 mi. SW of Atenquique on the Tonila road, 1,600 m, 5 Apr. 1951, *McVaugh 11801* (NY, US); above Ahuacapán, road to Corralitos 10–12 mi. SSE of Autlán, 1,500–1,800 m, 29 Sept. 1960, *McVaugh 19586* (US); 12 mi. SW of Chante along road to Sierra Manantlan, 5,500 ft., 4 Feb. 1975, *Gentry & Gentry 23510* (US). MEXICO: Temascaltepec, Tejupilco, 1,340 m, 9 Apr. 1934, *Hinton et al. 5753* (LL, NY, US). MORELOS: Sierra de Ocuila, 18 Sept. 1941, *Lyonnet 3329* (US). NAYARIT: along Hwy. 28, between Tepic & Jalcatlán (Rt. 66 on some maps) at Km 14–16, 950–1,050 m, 8 Jan. 1979, *Croat 45256* (MO). OAXACA: 10 mi. S of Sola de Vega along road to Puerto Escondido, 7,000 ft., 8 May 1965, *Breedlove 9855* (US). VERACRUZ: Huatusco, road to Tepampa 4 km from the hwy. between Huatusco & Coscomatepec, 1,580 m, 14°10'N, 97°00'W, 10 Aug. 1979, *Avendaño & Calzada 411* (F); environs of Orizaba, *Bottieri & Sumichrast 1857* (P); Jalapa, 6 Sept. 1936, *MacDaniels 934* (BH, F); Xico, 6 km NE of Xico, 1,500 m, 19°27'N, 97°01'W, 12 May 1973, *Marquez & Gandara 101* (F); near La Calavera, 10 km N of Altotonga (13 km by road) on road to Tlapacoyan, 1,350 m, 19°51'N, 97°13'W, 28 June 1980, *Nee & Hansen 18643* (BH, F); 2.5 km (by road) E of Ayahualulco & 1.6 km (by road) W of Ixhuacán de los Reyes, 1,900 m, 19°2'N, 97°08'W, 7 Nov. 1981, *Nee 22959* (F); Jilotepec "El Esquilón," 1,390 m, 7 Jan. 1976, *Ortega et al. 104* (F, MO); Cerro de la Martinica, NE of Banderilla, 1,680 m, 10 Feb. 1976, *Ortega et al. 152* (F, MO); Los Reyes, 1,600 m, 22 Mar. 1976, *Vasquez S. 311* (F, NY); Tlazololapan, Tequila, 1,170 m, 29 Mar. 1976, *Vasquez T. 358* (F, NY); Yecuatla, Lomas de Santa Rita, 1,350 m, 3 June 1971, *Ventura A. 3268* (F); Atzalán, La Florida, 1,600 m, 20 Mar. 1978, *Ventura A. 15102* (F). GUATEMALA. ALTA VERAPAZ: near Cobán, 1,260–1,440 m, 26 Mar.–15 Apr. 1939, *Standley 69240* (F, US); 3 km W of San Julián, Tactic, 1,600 m, 15°20'N, 90°15'W, 1 Feb. 1969, *Williams et al. 40415* (F). BAJA VERAPAZ: below Patal, 1,550 m, 4

Apr. 1941, *Standley 90958* (F). CHIMALTENANGO: road to Iximche Ruins, Tecpán, 2,500 m, 12–23 Jan. 1966, *Molina R. et al. 16128* (F, NY). CHIQUIMULA: Cerro Brujo, vicinity of Río Negro, below Montaña Montenegro, near village of Brujo, 1,500–2,000 m, 1 Nov. 1939, *Steiermark 30939* (F, US). EL PROGRESO: Sierra de las Minas, between El Jute de Cobara & Finca Piamontes, 1,400–2,400 m, 3 Feb. 1942, *Steiermark 43381* (F, NY). ESCUINTLA: between Santa María de Jesús & Palin, 1,800 m, 29 Dec. 1938, *Standley 61307* (F, US). GUATEMALA: Km 28 F.D.R. between San Lucas & Guatemala City, 2,000 m, *Molina R. et al. 16657* (F, TEX). HUEHUETENANGO: 3 mi. NW of Santa Cruz Barillas along road to San Mateo Ixtatlán, 6,000 ft., 7 Aug. 1965, *Breedlove 11651* (F); Chiantla, 6,700 ft., 15 Dec. 1934, *Skutch 1949* (F, NY, US); 13 km W of Huehuetenango near Puente de Xinaxó, 1,800 m, 30 Dec. 1940, *Standley 81575* (F, US); spring of Río San Juan near Aguacatán, 1,800 m, 6 Dec. 1962, *Williams et al. 22501* (F, NY, US, WIS). QUEZALTENANGO: Los Positos SW of San Martín Chile Verde, 1,500 m, 8 Mar. 1939, *Standley 67901* (F, US); vicinity of Fuentes Georginas, slopes of Volcán de Zunil, 2,300–2,500 m, 3 Feb. 1941, *Standley 85865* (F, US); W slopes of Volcán de Zunil, opposite Santa María de Jesús, 1,500 m, 21 Jan. 1940, *Steiermark 35124* (F). SACATEPEQUEZ: near Pastores, 1,560–1,650 m, 14 Dec. 1938, *Standley 59937* (US). SAN MARCOS: Finca Vogel, near Rodéo, 900 m, 15 Mar. 1939, *Standley 68906* (F); barranco of Río (Tonana) Suchatí between Canjulá & La Unión Juárez, near SE portion of Volcán Tacaná, 2,000–3,000 m, 2 Feb. 1940, *Steiermark 36278* (F). SANTA ROSA: Jumaytepeque, 6,000 ft., Aug. 1892, *Heyde & Lux 4105* (F, MO, NY, US); near El Molino, 600 m, 26 Nov. 1940, *Standley 78379* (US); Volcán Tecuamburro, along trail to San Francisco Tecuamburro on summit of volcano, N of Chiquimulilla, 250–2,000 m, 20 Dec. 1939, *Steiermark 33149* (F). SUCHITEPEQUEZ: SW lower slopes of Volcán de Zunil between Finca des Asturias & Finca Alto Mira, NE of Pueblo Nuevo, 1,000–2,000 m, 1 Feb. 1940, *Steiermark 35349* (F). HONDURAS. COMAYAGUA: Montaña Le Choca, Cordillera Comayagua, near Coyocutena, 1,200 m, 22 May 1956, *Molina R. 7113* (F); Montaña El Cedral, Cordillera Montecillos, 1,600 m, 24 May 1956, *Molina R. 7194* (F, US); El Rincón, ca. 10 mi. W of Siguatepeque, 1,400–1,500 m, June–Aug. 1936, *Yuncker et al. 6050* (F, MO). CORTES: near Corinto, border with Guatemala 55 km W of Puerto Cortés, 9–11 Aug. 1975, *Nelson et al. 2936* (MO). MORAZÁN: Mt. San Juancito, 7,000 ft., 19 June 1948, *Glassman 1666* (F, NY, TEX, WIS); Cerro de Uyuca, 1,600–2,000 m, 10–20 Mar. 1951, *Morton 7167* (US). OCOTEPEQUE: around Belen Gualcho, 40 km E of Nueva Ocotepeque, 1,500–2,000 m, 29 June–3 July 1976, *Nelson et al. 3817* (MO). YORO: El Portillo Grande, 4,000 ft., July 1937, *van Hagen & van Hagen 1006* (F, NY); Quebrada Olotillo, 15 km from Yoro, 1,100 m, 8 May 1956, *Molina R. 6829* (US). EL SALVADOR. CHALATENANGO: E slope of Los Esemiles, 2,100–2,300 m, 14°21'N, 89°09'W, 1 Apr. 1942, *Tucker 1186* (F, LL). SANTA ANA: along road to Cerro Monte Cristo at Los Planes at Km 22, 1,800 m, 31 July 1977, *Croat 42332* (MO). SONSONATE: Cerro Verde, 1,800 m, 25 Feb. 1968, *Molina R. & Montalvo 21726* (F, NY). NICARAGUA. GRANADA: Mombacho Volcano, 960 m, 5 July 1923, *Maxon et al. 7781* (F, US). JINOTEGA: along

- Hwy. 3 from Jinotega to Metagalpa, 5–8 mi. SW of Jinotega, 1,500 m, 7 Aug. 1976, *Croat 43055* (MO).
- COSTA RICA. ALAJUELA: Finca de los Ensayos ca. 11 mi. NW of Zarcero, 850 m, 15 Aug. 1977, *Croat 43541* (MO); along Río Alajuela, Alajuela–Carrizal road 5 km S of Carrizal, 1,200 m, 24 Mar. 1974, *Hartshorn 1423* (F, MO); Monteverde, road to Peñas Blancas (over Continental Divide) ca. 1 km below the Divide, Atlantic slope, 1,400 m, 10°25'N, 84°50'W, 13 Apr. 1981, *Knapp & Mallet 865* (BH, CR, to be distributed); Santa María National Park, Caribbean slope, 600 m, 10°27'N, 85°17'W, 7 Feb. 1978, *Leisner 5139* (MO); Zarcero, Palmiras, 6,000 ft., 16 Aug. 1937, *Smith A152* (F, MO, US); San Carlos, Sucre, 1,025 m, 2 Mar. 1939, *Smith H1638* (F, US); Naranjo, 5,600 ft., 5 Apr. 1928, *Stork 1852* (F).
- CARTAGO: Cartago, 1,650 m, Dec. 1887, *Cooper 5868* (F, US); overlooking Río Grande de Orosí, ca. 3 km SE of Tapantí, 1,350 m, 16 Apr. 1967, *Lent 832* (F, WIS); 5 km SW of Tobosí, 1,900 m, 9°50'N, 84°01'W, *Lent 3160* (F, MO); El Muñeco on the Río Navarro, 1,400–1,500 m, 6–7 Mar. 1926, *Standley & Torres R. 50939* (US); near La Sierra ca. 25 km S of Cartago, Cordillera de Tamanca, 2,000 m, 23 Jan. 1965, *Williams et al. 28048* (F).
- GUANACASTE: along road between Santa Elena & Monteverde, ca. 2 mi. from Santa Elena–Monteverde junction, 1,350 m, 7 Feb. 1979, *Croat 47100* (BH, MO).
- HEREDIA: vicinity of Alto la Palma between Paracito & Bajo La Hondura, 1,500 m, 14 Jan. 1978, *Croat 44484* (MO); Vara Blanca de Sarapiquí, N slope of Central Cordillera, 1,500–1,750 m, July–Sept. 1937, *Skutch 3286* (MO, NY, US).
- PUNTARENAS: Monteverde, pasture edges in village, 1,400–1,500 m, 15 Aug. 1976, *Dryer 566* (CR, F); Finca Las Cruces, 3 km S of San Vito de Java, 4,000 ft., 11 Feb. 1971, *Gillis & Plowman 10129* (F, TEX).
- SAN JOSE: Los Angeles de San Ramón, 1,075 m, 20 Nov. 1923, *Brenes 3947* (CR, F); La Palma, 1,250 m, 10 Sept. 1924, *Brenes 4063* (CR, F); near Quebrada Grande, 3 km NW of Cascajal, 1,750 m, 12 Dec. 1971, *Lent 2295* (F, MO); hills above Aserri, 14 June 1955, *Schubert & Rogerson 701* (US); vicinity of El General, 1,430 m, Dec. 1936, *Skutch 2987* (MO, NY, US); Río Segundo, 2,000 m, 10 May 1840, *Tonduz 1795* (US); Río Candelaria, 1,215 m, Apr. 1893, *Tonduz 7892* (US).
- PANAMÁ. CHIRIQUÍ: trail from Paso Ancho to Monte Lirio, upper valley of the Río Chiriquí Viejo, 1,500–3,000 m, 16 Jan. 1939, *Allen 1492* (F, MO, NY, US); Cerro Colorado, 1,500 m, 26 July 1976, *Antonio 1502* (MO); above Boquete, 4,500 ft., 12 May 1971, *D'Arcy 5443* (F, MO, P); roadside between Nueva California & Río Chiriquí Viejo, 7 Aug. 1972, *D'Arcy & D'Arcy 6492* (F, MO, NY, P, RSA/POM, WIS); Cerro Hornito, 4,500 ft., 8 May 1978, *Hammel 3028* (MO).
- VERAGUAS: Cerro Tute, E slopes, 1 km beyond Escuela Agrícola Alto Piedra above Santa Fé, 900–1,200 m, 14 May 1981, *Sytsma & Andersson 4644* (MO).
- VENEZUELA. MERIDA: Quebrada El Oso, Palmira, Justo Briceno, 1,600 m, 3–11 Oct. 1973, *López-Palacios & Bautista-Bautista 3481* (MO).
- COLOMBIA. ANTIOQUIA: between Río Guapa & Río León, 1,000 m, 18 Mar. 1948, *Ruíz Landa et al. 118* (US); 4 km from Palmitas, 1,700 m, 5 Mar. 1949, *Skolnik et al. 19An168* (F, US); road between Yarumal & Valdívía, region of Ventanas, (*Gutierrez et al.*) *Valdivia 5* (US); road between Curamonta & Valparaíso, (*Travedo & Gouzy*) *Valparaíso 3* (US).
- CAUCA: Popayán, Timbio in Hato-Viejo, 1,800 m, 14 July 1939, *Cuatrecasas & Pérez-Arbeláez 6070* (F, US); Cordillera Occidental, E slope, Cuchilla de Tambo, 1,750 m, 23 Aug. 1949, *Idrobo & Fernandez 246* (US); “La Gallera” Micay valley, near Río Joaquín, Cordillera Occidental, 1,400–1,500 m, 29–30 June 1922, *Killip 7846* (NY); Popayán, 1,500–2,000 m, Jan.–Mar., *Lehmann 4770* (F, US) (type of *S. chamaecerasus*).
- CUNDINAMARCA: Anolaima, 14 Jan. 1954, *David 4852* (US); Santana station, above Sasaima, 160–1,700 m, 25–29 July 1945, *Dugand & Jaramillo 3877* (US); Cordillera Oriental, Finca, “Alto Oscar” 11 km S of La Palma, 5,600 ft., 10 Mar. 1944, *Little 7388* (NY, US).
- HUILA: Finca Cedral, Quebrada Urraca, Río Fortalecillas above Vega Larga, 30 km E of Neiva, 1,300 m, 2°58'N, 74°58'W, 18 Jan. 1943, *Fosberg 19765* (NY, US).
- SANTANDER: Río Suratá valley above Suratá, 2,000–2,500 m, 5–6 Jan. 1927, *Killip & Smith 16531* (NY, US); vicinity of Charta, 2,000–2,600 m, 1–11 Feb. 1927, *Killip & Smith 19089* (NY, US); vicinity of Tona, 1,900–2,100 m, 17 Feb. 1927, *Killip & Smith 19505* (NY, US).
- TOLIMA: El Líbano above San José, 1,580–1,620 m, 19 July 1947, *García-Barriga 12239* (US).
- VALLE DE CAUCA: Cordillera Occidental, E slope between Bitaco & Yumbo, 1,700 m, 5 Apr. 1979, *Cuatrecasas & Cuadros 28837* (US); Río Nima above Tenjo, 1,850 m, 2 Oct. 1974, *Maas & Plowman 1827* (MO).
- ECUADOR. LOJA: Km 25, Loja to San Lucas, 2,200 m, 15 Sept. 1961, *Dodson & Thien 635* (MO, US).
- PERU. sin. loc. 1840, *Mathews 3249* (NY).
- AMAZONAS: Bongará, Jalca zone 3 km S of Pomacocha, E of Shipasbamba trail, 2,400 m, 20 June 1962, *Wurdack 997* (US).
- AYACUCHO: La Mar, ca. 25 km walking distance SW of Hacienda Luisana & Río Apurímac, ca. 12 km from Hacienda Santa Rosa, ca. 25 km from Tambo, E massif of Cordillera Central, 1,570 m, 12°43'S, 73°50'W, 20 Aug. 1968, *Dudley 11879* (F); Ccarrapa between Huanta & Río Apurímac, 2,200 m, 5, 6, 17 May 1929, *Killip & Smith 2306* (NY); La Mar, just below Huanhuachayo on the Caprichio–Puncu trail, W slope of Río Apurímac valley, 1,590 m, 12°43'S, 73°47'W, 15 July 1970, *Madison 10265–70* (F).
- CUZCO: “Pillahuata” Cerro de Cusilluyoc, 2,400–2,500 m, 3–6 May 1925, *Pennell 13951* (F, NY).
- HUÁNUCO: Pachitea, Panao, 2,700–2,900 m, 3 Mar. 1947, *Ferreyra 1766* (US, USM); Huacachi, station near Muña, 6,500 ft., 20 May–1 June 1923, *Macbride 4155* (F); road from Huánuco to Tingo María N of Carpish Pass, 54 km NE of Huanuco, 2,310 m, 6 Dec. 1981, *Plowman & Rury 11164A* (F).
- JUNÍN: Tarma, at little bridge on Tarma–San Ramon road, 1 km above Matichacra, just below Carpuata, E side of Río Tarma valley opposite mouth of Río Huasihuasi, 11 km NNE of Palca, 2,000 m, 4 Dec. 1962, *Iltis et al. 322* (US, WIS); Pichis trail, between Yapas & Eneñas, 1,800 m, 28 June–8 July 1929, *Killip & Smith 25618* (US); Schunke hacienda above San Ramón, 1,300–1,700 m, Aug.–Oct. 1923, *Schunke A101* (US); Chancamayo valley, 1,500 m, Nov. 1925–1927, *Schunke 258* (F).
- PUNO: Sandía, Santo Domingo, 1,550 m, 4 Nov. 1939, *McCarroll 52* (NY).
- BOLIVIA. LA PAZ: S Yungas, basin of Río Bopi, San Bartolome (near Calisaya), 750–900 m, 1–22 July 1939, *Kruckoff 10452* (F, MO, NY, US).
- SANTA CRUZ: Río Piraymiri, Valle Grande, 2,900 m, Feb. 1956, *Cardenas 5118* (US).

LITERATURE CITED

- BRANDEGEE, T. S. 1917. *Plantae Mexicanae Purpusianae VIII*. Univ. Calif. Publ. Bot. 6: 373.
- BUCH, C. L. VON. 1825. *Physicalische Beschreibung der Canarischen Inseln*. Berlin.
- CHILD, A. 1979. A review of branching patterns in the Solanaceae. Pp. 345–356 in J. G. Hawkes, R. N. Lester & A. D. Skelding (editors), *The Biology and Taxonomy of the Solanaceae*. Linnaean Society, London.
- DANERT, S. 1958. Der Verzweigung der Solanaceen in reproduktiven Bereich. *Abh. Deutsch. Akad. Wiss. Berlin (K1. 1957)* 6: 1–183.
- . 1967. Die Verzweigung als infragenerisches Gruppenmerkmal in der Gattung *Solanum* L. *Kulturpflanze* 15: 275–292.
- D'ARCY, W. G. 1972. Solanaceae studies II: typification of the sections of *Solanum*. *Ann. Missouri Bot. Gard.* 59: 262–278.
- . 1973. Solanaceae. In R. E. Woodson & R. S. Schery (editors), *Flora of Panama*. *Ann. Missouri Bot. Gard.* 60: 573–780.
- KNAPP, S. 1983. Sectional nomenclature in *Solanum* (Solanaceae). *Taxon* 32: 635–636.
- . 1985. Reproductive biology of *Solanum* section *Geminata* (= *Leiodendron*) in a Costa Rican cloud forest. In W. G. D'Arcy (editor), *Solanaceae: Systematics and Biology*. Columbia Univ. Press, New York.
- SEITHE, A. 1962. Die Haararten der Gattung *Solanum* L. und ihre taxonomische Verwertung. *Bot. Jahrb. Syst.* 81: 261–336.
- . 1979. Hair types as taxonomic characters in *Solanum*. Pp. 307–319 in J. G. Hawkes, R. N. Lester & A. D. Skelding (editors), *The Biology and Taxonomy of the Solanaceae*. Linnaean Society, London.