

# New species of *Solanum* and *Capsicum* (Solanaceae) from Bolivia, with clarification of nomenclature in some Bolivian *Solanum*

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Nee, M. (The New York Botanical Garden, 200th Street & Kazimiroff Boulevard, Bronx, NY 10458-5126, U.S.A.; e-mail: mnee@nybg.org), L. Bohs (Department of Biology, 257 South 1400 East, University of Utah, Salt Lake City, UT 84112-0840, U.S.A.; e-mail: bohs@biology.utah.edu) & S. Knapp (Department of Botany, The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom; e-mail: S.Knapp@nhm.ac.uk). New species of *Solanum* and *Capsicum* (Solanaceae) from Bolivia, with clarification of nomenclature in some Bolivian *Solanum*. *Brittonia* 58: 322–356. 2006.—Nine new species of *Solanum* and two of *Capsicum* are described from Bolivia. Notes are provided on some other species, including the complex typification of *Solanum aridum*. ***Capsicum caballeroi*, *C. ceratocalyx*, *Solanum chalmersii*, *S. clandestinum*, *S. comarapanum*, *S. complectens*, *S. monantheson*, *S. moxosense*, *S. pedemontanum*, *S. saturatum*, and *S. whalenii*** are described and illustrated, and a new name, ***S. scuticum***, is proposed for the species previously known as *S. tabacifolium*.

**Key Words:** biodiversity, Bolivia, *Capsicum*, Solanaceae, *Solanum*, South America.

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Bolivian floristic diversity is high, reflecting its great topographic and habitat diversity. Habitats in Bolivia range from seasonally flooded savannas to arid Chaco and high elevation deserts to hyper-humid montane and lowland rainforests. Four areas in the country have been identified as centers of plant diversity and endemism: the Gran Chaco (SA 22 of Davis et al., 1997), southeastern Santa Cruz (SA 23 of Davis et al., 1997), the Llanos de Mojos region (SA 24 of Davis et al., 1997), and the Madidi-Apolo region (SA 36 of Davis et al., 1997). The position of Bolivia at the western edge of the Amazon basin with large areas occupied by the eastern flank of the geologically young Andes makes it a particularly rich region for Solanaceae, whose diversity is largely associated with the Andean slopes (Gentry, 1982; Knapp, 2002a). The genus *Solanum* in particular is highly diverse in the Andes, but lack of collections for Bolivia may have led to the

country's being relatively neglected as a "hot-spot" of solanaceous diversity. Recent work by a number of institutions, both Bolivian and others, has led to an explosive increase in the number of Bolivian collections available for study. This has uncovered many new, narrowly endemic taxa and has led to the re-examination and clarification of other, previously poorly understood species. Renewed impetus for the study of the Bolivian flora will undoubtedly reveal many more new taxa in the future, and the new generation of Bolivian botanists actively working on the flora will accelerate this even further.

One of the species described here, *Solanum pedemontanum*, shows how even widespread and evidently common species have remained nearly unknown until collecting in previously little-explored parts of tropical America greatly increased in the last few decades. Exploration and collecting are also essential for uncovering the existence of rare, local endemics, such as *Capsicum caballeroi* or *S. moxosense*.

The following notes and new species are

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based primarily on 15 years of botanizing in Bolivia by Nee, by a field trip by Nee and Bohs in 1998, and one by all three authors in May of 2001. This last trip was instrumental in solidifying our concepts of a number of new and critical taxa, and provided the opportunity to see them in the field and obtain material for molecular studies. The notes and new species here are in anticipation of the *Catalogue of the Vascular Plants of Bolivia* by P. Jørgensen et al. (in prep.) of the Missouri Botanical Garden and a number of Bolivian institutions, and are part of the worldwide revision of *Solanum* being undertaken by the authors in collaboration with Dr. David Spooner of the University of Wisconsin/U.S.D.A. and a host of other contributors.

This paper, and one of the most striking new species, is dedicated to the memory of Dr. Michael D. Whalen (1950–1985), the major professor of Knapp at Cornell University and colleague of Nee. Dr. Whalen was travelling in Peru and scheduled to meet with Nee on his first trip to Bolivia in late 1984. It was at this time that Dr. Whalen began to experience the visual problems which cut short his Peruvian trip and which were symptoms of the brain cancer that tragically ended his productive botanical life. He thus never had the chance to visit Bolivia and study its varied and fascinating Solanaceae. He was a professor, mentor, and friend sorely missed even still.

#### Notes on systematic characters

The species described here belong to the genera *Capsicum* and *Solanum*, both of Solanaceae subfamily Solanoideae. *Capsicum* is distinguished by its longitudinal anther dehiscence and, in at least the majority of species, its pungent fruits. In the *Capsicum* species described here, the calyx margin is truncate with five or ten appendages that emerge from below the calyx rim. Similar calyces are found in the related genus *Lycianthes* Hassl., and they have a different pattern of vasculature than is found in other Solanaceae with a more conventional calyx structure (D'Arcy, 1986).

The generic characters distinguishing *Solanum* are poricidal anther dehiscence and lack of the specialized *Lycianthes* calyx

structure described above. In many *Solanum* species, particularly in *Solanum* subgenus *Leptostemonum*, the anthers are tapered distally and the terminal pores do not enlarge as the flower ages. Other species have oblong anthers with blunt tips and the pores expand into longitudinal slits with age.

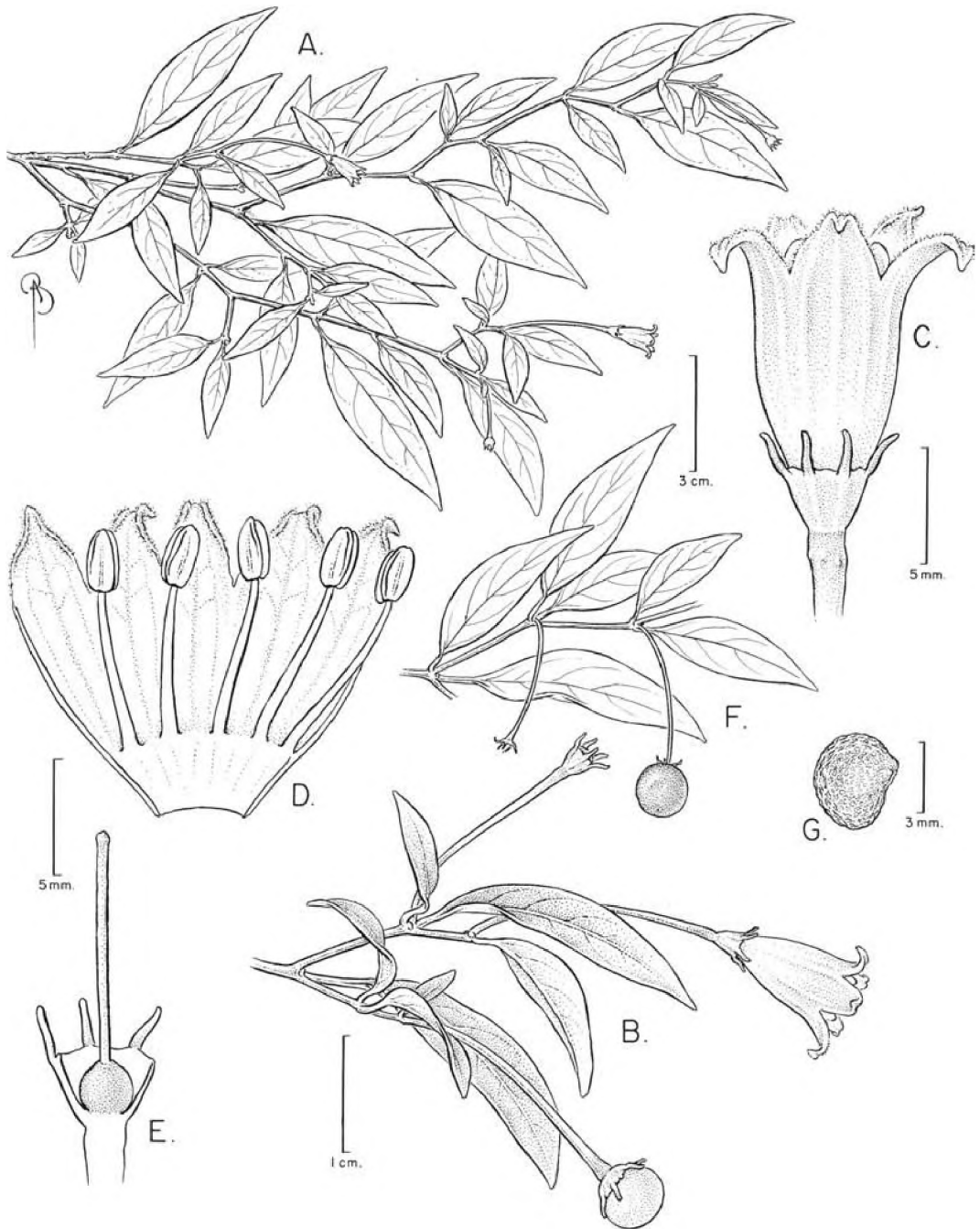
Most Solanaceae have complex branching patterns on their flowering shoots, and the details of these patterns can be taxonomically useful. Inflorescences are morphologically terminal. Further stem growth occurs by expansion of axillary shoots located below the inflorescence; these, in turn, will terminate in an inflorescence. Thus, the flowering portion of the plant is composed of a series of sympodial units, with number and arrangement of leaves in each sympodial unit of systematic importance. For instance, *Solanum* section *Geminata* takes its name from the frequent occurrence of two-leaved sympodia in which the leaves are arranged in pairs (geminate). More information on branching patterns in Solanaceae can be found in Danert (1958, 1967), Child (1979), Bohs (1989), Bell and Dines (1995), and Knapp (2002b).

#### *Capsicum* L.

Bolivia is especially rich in species of *Capsicum*; eight wild or domesticated taxa are mapped for Bolivia by Eshbaugh (1975). With the two species described below, nine native or naturalized species are now known from the country (Nee, unpubl. data), while several others are widely grown for their pungent fruits. Neither of the new species listed below appears to be close to any of the domesticated species, nor is either known to be gathered in the wild or to enter into commerce.

***Capsicum caballeroi* M. Nee, sp. nov.** TYPE: Bolivia. Santa Cruz. Prov. Caballero: Parque Nacional Amboró, Cerro Bravo, 10 km al N de Comarapa, 17°49.5'S, 64°32.5'W, 2400–2500 m, 7–10 Apr 1994 (fl, fr), *I. Vargas C. & J.M. Camacho 3118* (HOLOTYPE: USZ; ISOTYPES: CORD, MO, NY, US). (Fig. 1)

Herba vel frutex, 1–7 m altus. Inflorescentia axillaris, 1–2-flora, pedicellis per anthesin 20–25 mm longis, fructiferis 24–45 mm longis; calyx cupulatus, 2.5 mm



**FIG. 1.** *Capsicum caballeroi* M. Nee. **A.** Flowering branch. **B.** Branch with detail of flower and fruit. **C.** Flower. **D.** Corolla spread open to show stamens. **E.** Gynoecium and section of calyx. **F.** Branch with mature fruit. **G.** Seed. (A–E based on *Nee et al.* 52407, NY; F–G based on *Dorr & Barnett* 7041, NY.)

longus, appendicibus 5, per anthesin 0.8–1.8 mm longis, plerumque 5 appendicibus interpositis brevioribus; corolla angusti-campanulata, 10.5–13 × 4–6 mm, lobis 3 × 2 mm, flava; filamenta 4.5 mm longa; antherae 2–2.1 mm longae. Fructus globosus, 9–11 mm diam., vivide ruber, sapore pungenti; semina 5–17, reniformia, 3.8–4.2 × 3.2 mm.

Herb, shrub or treelet, 1–7 m tall; stems glabrous or sparsely pubescent with simple hairs. Sympodial units difoliate and geminate. Leaves 2–13 × 0.8–4.2 cm, more or less uniform in size and shape, lanceolate, glabrous adaxially and abaxially or sparsely pubescent abaxially along the midrib with simple hairs 0.3 mm long; base acute to attenuate and somewhat oblique; margin slightly revolute; apex attenuate; petioles 2–8 mm. Inflorescences axillary, 1–2-flowered; pedicels 20–25 mm in flower, 24–45 mm in fruit, terete, pendulous, slender, 0.6 mm wide at base, 1.4–1.8 mm wide distally, glabrous. Calyx cupulate, 2.5 mm long, the margin truncate, with 5 appendages 0.8–1.8 mm long in flower and with 5 intermediate, slightly shorter ones alternating with these, the appendages (1–) 3–5 mm long in fruit, sparsely pubescent with simple hairs; corolla 4–6 mm in diameter, 10.5–13 mm long, narrowly campanulate, lemon yellow, shallowly 5-lobed, the tube 3–6 mm, the lobes ca. 3 × 2 mm, narrowly triangular, acute at apices, glabrous abaxially, papillose at tips of lobes; stamens included; filaments 4.5 mm, attached ca. 1 mm above base of corolla tube, broadened at base, but without two flaps of tissue on corolla tube above site of insertion; anthers 2–2.1 × 0.8–0.9 mm, oblong, yellow, longitudinally dehiscent; ovary glabrous; style ca. 6 × 0.25 mm, cylindrical to clavate, glabrous; stigma truncate to capitate. Fruit a globose berry, 9–11 mm in diameter, pendent, glabrous, bright red, pungent (or apparently sometimes not); seeds 5–17, 3.8–4.2 × 3.2 mm, reniform, flattened, pale yellow, the surface loosely foveolate.

*Distribution and ecology.*—Known only from cloud forests (yungas) with *Podocarpus* spp., *Prumnopitys exigua* De Laub., *Weinmannia* spp., *Alnus acuminata* Kunth subsp. *acuminata*, and Myrtaceae (including *Blepharocalyx salicifolius* O. Berg) between 1880 and 2600 m elevation in Provinces of Florida and Caballero of Dept. Santa Cruz and just to the northwest in this same ecolog-

ical zone into Dept. Cochabamba, Prov. Carrasco, in the adjacent Parque Nacional Carrasco.

*Phenology.*—Found in flower in April, May, and November and in fruit in January, March, May, and November; it likely flowers and fruits all year long.

*Etymology.*—Named in honor of Bolivian botanist Israel Gerardo Vargas Caballero, whose own investigations and those of his students are making wild and domesticated plants of this part of Bolivia much better known, and incidentally (although incorrect grammatically) for the Province Manuel María Caballero, where most of the specimens have been collected.

Additional specimens examined. **BOLIVIA.** **COCHABAMBA.** Prov. Carrasco: Serranía Siberia, 20–35 km W of Comarapa, on the old Cochabamba–Santa Cruz road, ca. 2000 m, 14–15 Jan 1990 (fr), *Dorr & Barnett 7041* (NY). **SANTA CRUZ.** Prov. Caballero: Parque Nacional Amboró, Cerro Bravo, cerca Comarapa, 2600 m, 17 Jun 1995, A. Jardim et al. 1995 (MO, NY); *Nee et al. 52407* (LPB, NY, USZ); 50 km N de Mataral (en la carretera Santa Cruz–Comarapa) pasando por San Juan del Potrero y bajando a la cuenca del alto Río Ichilo, 2300–2450 m, 28 May 1989 (fl, fr), *Smith et al. 13470* (BOLIV, LPB, MO, NY); Siberia–El Empalme, 5 km entrando hacia Khara Huasi, 17°50'S, 64°43'W, 2300 m, 8–9 May 1992 (fr), *Vargas & Prado 1282* (MO, NY), *1286* (NY); San Juan del Potrero, Naranjos, 17°52'S, 64°27'W, 2150 m, 12–13 May 1992 (fr), *Vargas et al. 1343* (NY); Parque Nacional Amboró, Cerro Bravo a 10 km N de Comarapa, 17°49.41'S, 64°33.01'W, 2400–2500 m, 15 Nov 1995 (fl, fr), *Vargas et al. 4151* (NY). Prov. Florida: La Yunga, 7.5 km (línea recta) NE de Mairana, 18°05'S, 63°55'W, 1880 m, 15 Mar 1997 (fr), *Saldias 4977* (MO).

This species is characterized by its narrowly campanulate lemon yellow corollas, very long pedicels, and stamens with relatively long filaments; the fruits are pendent. The Bolivian species *C. eximium* and *C. cardenasii* also have campanulate corollas, but those of *C. caballeroi* are much larger and narrower; in addition, *C. eximium* and *C. cardenasii* have purple (or rarely whitish) corollas, in contrast to the yellow corollas of *C. caballeroi*.

The common names “ají de monte” (*Vargas & Prado 1282*) and “ulúpica de yunga” (*Vargas et al. 1343*) indicate the great similarity to other local species of *Capsicum*; in this area the cultivated peppers are called “ají” and the wild species (e.g., *C. eximium* Hunz., from which pungent fruits are col-



lected for local use and the markets) are called "ulupica." Two of the collection labels indicate that the fruits of *C. caballeroi* are pungent (Vargas & Prado 1282; Vargas *et al.* 1343), while one indicates they are not (Vargas & Prado 1286).

**Capsicum ceratocalyx** M. Nee, *sp. nov.*

TYPE: Bolivia. La Paz. Prov. Sud Yungas: 7.5 km (by road) from Huancané on road to San Isidro, moist montane forest, 16°21'S, 67°30'W, 2225 m, 10 May 2001 (buds), M. Nee, L. Bohs, S. Knapp & J.M. Mendoza F. 51778 (HOLOTYPE: LPB; ISOTYPES: MO, NY, USZ). (Fig. 2)

Frutex ad 1.5 m altus. Folia geminata, 5.5–22.5 × 2–6.5 cm, fere glabra. Inflorescentia axillaris, 6–9-flora, pedicellis per anthesin 9 mm longis, fructiferis 19–23 mm longis, alatis; calyx appendicibus 5, per anthesin 2–2.5 mm longis, curvatis; corolla flava, intus viridimaculata; antherae longitudinaliter dehiscentes. Fructus baccatus, coccineus, 1 cm diametro.

Shrub 1.5 m. tall; young stems minutely puberulent with antrorsely curved simple hairs, older stems nearly glabrous. Sympodial units difoliate and geminate. Leaves 2–22.5 × 0.6–6.5 cm, dimorphic, the minor leaves similar to the majors but about 1/3 the size, elliptic to oblanceolate, nearly glabrous adaxially and abaxially, with minute appressed hairs 0.2–0.3 mm long, mostly along the margin; base attenuate and often oblique; margin slightly revolute; apex long-attenuate; petioles to 3 cm on the largest leaves, mostly less than 8 mm in the flowering portion. Inflorescences axillary to the major leaf, evidently 6–9-flowered from the prominent corky pedicel scars, only 1–4 fruits forming per node; pedicels ca. 9 mm in flower, 19–23 mm in fruit, conspicuously ribbed and winged, erect, 1 mm in diameter at base, gradually ampliate distally to 2.2 mm in diameter, minutely puberulent. Calyx cyathiform, 5–5.5 mm long, the margin truncate to undulate, with 5 incurved appendages 2–2.5 mm long in flower and fruit, these somewhat flattened laterally, glabrous; corolla ca. 0.5 cm in diameter, ca. 6 mm long, broadly campanulate to subrotate, yellow with darker green spots within, deeply 5-lobed, the tube ca. 3 mm, the lobes 3.5 × 1.5 mm, deltate, acute at apices, glabrous except for the papillose infolded margin; stamens included; fila-

ments ca. 1 mm, inserted low within the calyx tube and apparently without two flaps of tissue on corolla tube above site of insertion; anthers ca. 1.8 × 1.5 mm, ovate, the color unknown, longitudinally dehiscent; gynoecium structure not known with certainty. Fruit a globose berry, ca. 1 cm in diameter, erect, glabrous, bright red, juicy; seeds unknown.

*Distribution and ecology.*—Known only from a few collections in the cloud forests of the Provinces of Nor Yungas and Sud Yungas in the Department of La Paz, Bolivia at 1700–2300 m elevation.

*Phenology.*—Flowering in March, May, and November, fruiting in March, May, and November.

*Etymology.*—The specific epithet refers to the horn-like protuberances on the calyx.

Additional specimens examined. **BOLIVIA. LA PAZ.** Prov. Nor Yungas: 4.6 km below Yolosa, then 19.1 on road up the Río Huarinilla, 16°12'S, 67°53'W, 1700 m, 12 Nov 1982 (fl, fr), *Solomon 8844* (MO); 14.3 km SW (above) Yolosa on road to Chuspipata, 16°14'S, 67°47'W, 2000 m, 23 Mar 1984 (fr), *Solomon et al. 12086* (MO). Prov. Sud Yungas: Huancané 6.5 km hacia el Sud, 2280 m, 8 Mar 1980 (fl), *Beck 3051* (LPB), same locality, 6°20'S, 67°30'W, 2040 m, 27 May 2001 (fl, fr), *Beck et al. 28089* (LPB).

*Capsicum ceratocalyx* is characterized by its conspicuously ribbed and winged pedicels. Unfortunately the stamens and pistil of the few flowers available on the type material seem to be somewhat malformed although the plant was evidently producing fruits. One of the collections (*Beck 3051*) had been determined by A. Hunziker as *C. coccineum* (Rusby) Hunz., but this species grows at much lower altitudes in Bolivia and has a scrambling, viny habit. *Capsicum coccineum* also differs from *C. ceratocalyx* in its smaller flowers that are uniformly yellow and in its unwinged pedicels.

***Solanum* L.**

In describing these new species we have used the major clades defined by Bohs (2005), while also including the sectional designations used by both Whalen (1984) and Nee (1999) and other groups in use in recent monographic studies. As phylogenetic studies in *Solanum* become more species-rich



**FIG. 2.** *Capsicum ceratocalyx* M. Nee. **A.** Leafy branch. **B.** Pedicel scars in leaf axils. **C.** Young bud. **D.** Partially open bud. **E.** Anthers, drawn from bud. **F.** Fruiting calyx. (Based on Nee et al. 51778, NY.)

and robust, these now informal groupings will ultimately be given formal infrageneric names.

#### THE POTATO CLADE

**Solanum complectens** M. Nee & G. J. Anderson, *sp. nov.* TYPE: Bolivia. Santa Cruz. Prov. Vallegrande: 1 km by road S of Chujiillas, 18°48'S, 64°01'W, 2125 m, 26 Dec 1989 (fr), *M. Nee 38445* (HOLOTYPE: LPB; ISOTYPES: CONN, CORD, G, MO, NY, US, USZ, UT). (Fig. 3)

Herbae scandentes, fruticantes, radiculis adventitiis; rami floriferi herbacei, pubescentes, veteres ad 4 mm diametro, sulcati. Folia plerumque imparipinnata, 1–4-juga, raro simplicia; foliola elliptica vel ovata, lateralia 1.8–3.5 × 0.8–1.6 cm, terminalia ovalia, 2.8–4.1 × 1–2.5 cm; pedicelli 1–4 in apice ramulorum floriferorum; calyx dentibus 5, 2.5 × 0.8 mm; corolla stellata, lobis 4.5 × 1.5 mm; stamina 5; filamenta 0.3 mm longa, pubescentia; antherae oblongae, 1.7 × 0.8 mm; stylus 4.5 mm longus, ad basin pubescens. Bacca globosa, ca. 1 cm diametro; semina compressa, integumento pilifero.

Herbaceous vines to several meters; lower stems soft-woody, to at least 4 mm in diameter and sulcate, mostly tightly appressed to tree trunks by clusters of short, fasciculate adventitious roots at the nodes, pubescent when young with weak, simple 3–4-celled hairs 0.4–0.9 mm long, glabrescent when older, unarmed. Sympodial units 3–4- to plurifoliate, not geminate. Leaves 4–12 × 1.5–5 cm, mostly imparipinnate, more or less uniform in size and shape, generally with (3–) 7 (–9) leaflets or rarely simple grading into 3-foliolate leaves on some branches, the leaflets opposite to subopposite, membranous to slightly fleshy, sparsely pilose adaxially with 2–4-celled simple hairs ca. 0.8 mm long, the basal cell much the largest, pubescent abaxially with hairs like those of the stem; lateral leaflets 1.8–3.5 × 0.8–1.6 cm, narrowly elliptic to ovate, the bases unequal and obtuse to truncate, the margins revolute, the apices obtuse to acute, the petiolules 1–2.5 mm long; terminal leaflet 2.8–4.1 × 1–2.5 cm, always larger than the laterals and usually more broadly ovate, the base acute, the margin revolute, the apex obtuse to acute, the petiolule 9 mm long; petioles 1–4 cm, sparsely pubescent; pseudostipules 3.5–8 mm, foliaceous, cordate. Inflorescence (0–)

0.5–2 cm, borne on small axillary somewhat leafy short-shoots with bract-like leaves 1–2 mm long along the axis, unbranched, with 1–4 flowers, all flowers perfect, the axes pubescent to nearly glabrous; peduncle 0.4–2 cm; rachis 0–0.2 cm; pedicels 13–18 mm in flower, to 19 mm in fruit, spaced 0–3 mm apart, articulated at the base. Calyx ca. 3.5 mm long, the tube 1 mm long, the lobes 2.5 × 0.8 mm, lanceolate, acute at apices, pilose; fruiting calyx not accrescent, the lobes 2.5 × 0.8 mm; corolla ca. 1 cm in diameter, 5–7 mm long, stellate, white or white with blue, the tube 1–2 mm, the lobes 4.5 × 1.5 mm, lanceolate, acute at apices, glabrous abaxially at base, minutely puberulent at tips, glabrous adaxially; filaments pubescent, the free portion ca. 0.3 mm, the filament tube absent; anthers 1.7 × 0.8 mm, oblong, connivent, yellow, the pores broad, directed introrsely, often opening into longitudinal slits with age; ovary glabrous; style ca. 4.5 × 0.2–0.4 mm, cylindrical, straight, pubescent in the lower half; stigma clavate. Fruit a globose berry, ca. 1 cm in diameter, orange or red, glabrous. Seeds ca. 15 per fruit, ca. 2.5 × 2 mm, flattened, light brown, the entire surface covered by hairlike extensions of the epidermal walls.

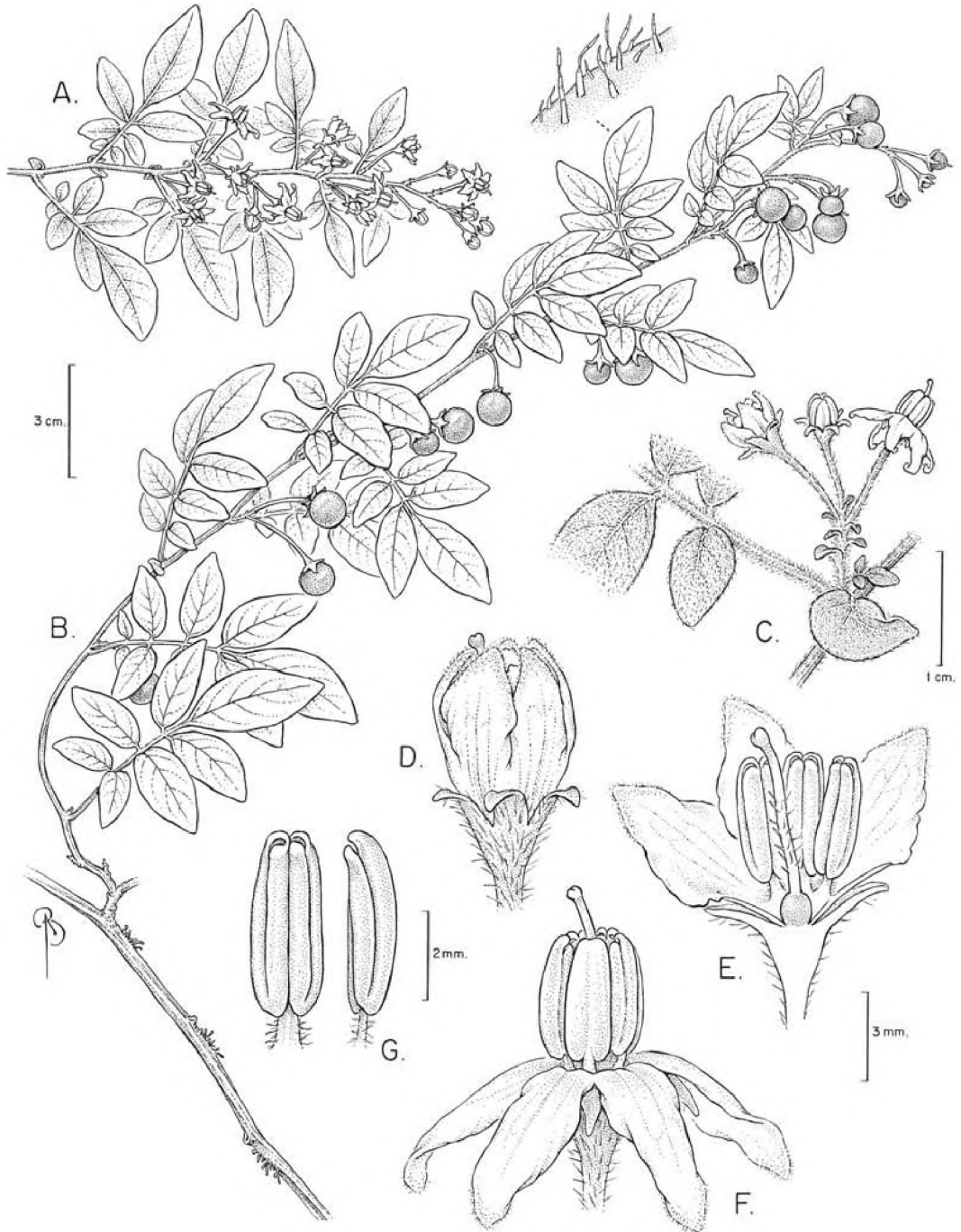
*Distribution and ecology.*—Known only from Bolivia in the Departments of Santa Cruz and southeastermost La Paz, in cloud forests along the eastern Andes, with *Podocarpus parlatorei* Pilg., *Prumnopitys exigua* De Laub. & Silba (Podocarpaceae), *Ceroxylon parvum* G. Galeano (Arecaceae), *Ternstroemia asymmetrica* Rusby (Theaceae), *Weinmannia* spp. (Cunoniaceae), *Blepharocalyx salicifolius* O. Berg (Myrtaceae), and the tree fern *Dicksonia sellowiana* (Presl) Hook. (Dicksoniaceae), from 1800 to 3330 m.

*Phenology.*—Flowering in January, May, and June and fruiting in January, June, May, and December.

*Etymology.*—The specific epithet refers to the habit of embracing or holding fast (Latin *complector*) to the supporting tree by means of its adventitious roots.

Additional specimens examined. **BOLIVIA. LA PAZ.** Prov. Inquisivi: comunidad Choquetanga–Cuchiwasí, bajando Pabellonani a 7 km NE de Choquetanga, 14°48'S, 67°17'W, 3330 m, 19 Jan 1994 (fl, fr), *Salinas 2243* (NY). **SANTA CRUZ.** Prov. Caballero: 26 km de Co-





**FIG. 3.** *Solanum complectens* M. Nee & G.J. Anderson. **A.** Flowering branch. **B.** Fruiting branch with detail of leaf pubescence. **C.** Inflorescence detail. **D.** Opening bud. **E.** Flower in longitudinal section. **F.** Flower at anthesis. **G.** Anthers. (A, C–G based on Nee & Mendoza 52538, NY; B based on Nee 38445, NY.)



marapa, carretera a Cochabamba, 17°49'10"S, 64°40'30"W, 2598 m, 13 Apr 2003 (fr), *Calzadilla et al.* 81 (NY); entre 15 y 25 km N de San Juan del Potrero hacia Cerro Bravo, 17°48'S, 64°15'W, 2000–2500 m, 6 Jun 1992 (fl, fr), *Killeen & Vargas* 4060 (NY); hwy from Epizana to Comarapa, 13 km (by road) E of El Churo, 0.4 km W of turnoff to Khara Huasi, 17°51'S, 64°42'W, 2575 m, 24 May 2001 (fr), *Nee et al.* 51858 (NY); 6 km (by air) N of Comarapa, rd to Cerro Bravo and Tinquí Laguna, 17°51.7'S, 64°31.9'W, 2325 m, 3 Aug 2003 (fl), *Nee et al.* 52447 (NY); hwy Comarapa to Cochabamba, 7.3 km (by road) and 22 km (by road) NW of bridge at Comarapa, 17°49.5'S, 64°39.1'W, 2640 m, 6 Aug 2003 (fl), *Nee & Mendoza* 52538 (LPB, NY, USZ); 50 km N de Mataral (en la carretera Santa Cruz–Comarapa), pasando por San Juan del Potrero y bajando a la cuenca del alto Río Ichilo, 2000 m, 25–26 May 1989 (fr), *Smith et al.* 13385 (MO, NY); Parque Nacional Amboró, Comarapa, 5–8 km al N por el Río Arriba hacia Verdecillo, 17°50.3'S, 64°33.5'W, 2300 m, 10 May 1993 (fl, fr), *Vargas et al.* 2400 (CONN, NY); Parque Nacional Amboró, Cerro Bravo a 10 km al N de Comarapa, 17°49.41'S, 64°33.01'W, 2400–2500 m, 12–16 Nov 1995 (fl, fr), *Vargas et al.* 4167 (NY); Siberia, 25 km desde Comarapa por la carretera Comarapa–Cochabamba, 17°49'30"S, 64°40'29"W, 2550 m, 4–6 Nov 2003 (fl), *Vargas & Jordán* 7015 (NY). Prov. Florida: Quebrada El Durazno, 7 km NE of Mairana, 18°03'50"S, 63°55'W, 2100 m, 22 Jul 1994 (ster), *Nee* 45330 (NY); Barrientos, 8 km N de Paredones (Achira Camping), 18°06'S, 63°48'W, 1800–1900 m, 25 Jun 1996 (fl, fr), *Vargas & Soliz* 4532 (NY).

*Solanum complectens* is a member of *Solanum* section *Anarrichomenum* Bitter, a small and distinctive group of herbaceous scramblers distributed from Mexico to Peru. The affinities of this section are with the potatoes, tomatoes, and relatives (Bohs, 2005). It is significant that neither this species nor any other in sect. *Anarrichomenum* has been found in Bolivia previously, especially not in the central and northern parts of the Department of La Paz whose cloud forests have been the most explored part of the entire country. This indicates a strong disjunction of this species from its relatives in northern Peru to Mexico (Correll 1962; Anderson & Jansen, 1998).

The only specimen of *Solanum complectens* with simple or 3-foliolate leaves is from the furthest northwest (*Salinas* 2243); in other respects it resembles the rest of the material available. In Correll (1962), *S. complectens* would key best to *S. chimborazense* Bitter, known only from Ecuador, but that species bears green fruits ca. 2 cm in diameter, has leaves with only three, or less commonly five, leaflets, and the filaments are united into a crown.

#### THE GEMINATA CLADE

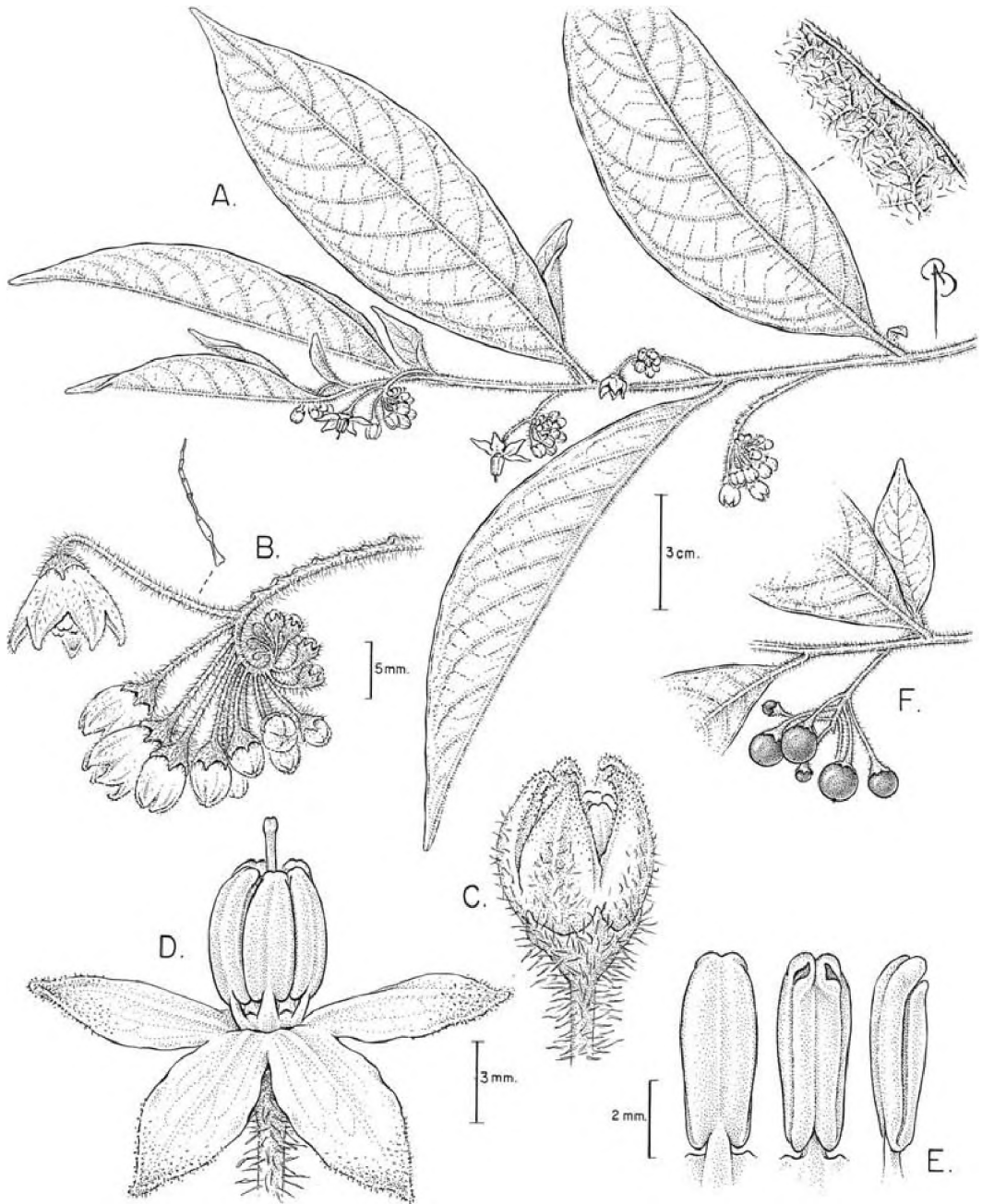
Since the publication of Knapp (2002b), new species of section *Geminata* s.l. continue to be collected throughout the neotropics. These forest plants often have narrow, endemic distributions and due to their inconspicuous nature (sparse populations of plants with small white or green flowers and green fruits) are also relatively undercollected.

#### *Solanum chalmersii* S. Knapp, sp. nov.

TYPE: Bolivia. La Paz. Prov. Sud Yungas: 7.5 km (by road) from Huancané on road to San Isidro, moist montane forest, 16°21'S, 67°30'W, 2225 m, 10 May 2001 (fl, fr), *M. Nee, L. Bohs, S. Knapp & M. Mendoza* F. 51777 (HOLOTYPE: LPB; ISOTYPES: BM, NY, USZ). (Fig. 4)

Species *Solano acuminato* Ruiz & Pavon similis, sed pubescentia pallida flavovirenti densa, foliis in stato sicco pallide viridibus, gemmis maturis obovoideis, difert.

Shrubs or small trees 2–6 m tall; young stems densely white pubescent with simple, uniseriate trichomes ca. 1 mm long composed of 2–5 cells; older stems remaining densely white pubescent, occasionally glabrate, unarmed. Sympodial units unifoliate or difoliate and geminate. Leaves 1.5–17 × 1–6 cm, simple, dimorphic, the major leaves 9–17 × 3–6 cm, elliptic to narrowly elliptic, the minor leaves 1.5–3 × 1–2 cm, differing from major leaves only in size, but occasionally somewhat rounder in outline, thin-textured, drying pale green, evenly pubescent adaxially with simple uniseriate trichomes ca. 1 mm long, densely pubescent abaxially with white uniseriate trichomes 1–1.5 mm long, the trichomes denser on the veins; base acute; margin entire; apex acute, rounded at the very tip; petioles 0.3–0.7 cm in major leaves, ca. 0.5 cm in minor leaves, densely pubescent. Inflorescences 1.5–5 cm, opposite the leaves or occasionally somewhat internodal, unbranched, with 10–20 flowers, all flowers apparently perfect, the axes densely white-pubescent with simple uniseriate trichomes 0.5–1.5 mm; peduncle 1–3 cm; rachis 1–4.5 cm; pedicels 10–12 mm in flower, tapering from the abrupt base of the calyx tube to a slender base 0.5–0.8 mm in diameter, deflexed, 15–22 mm in fruit, 0.5–1



**FIG. 4.** *Solanum chalmersii* S. Knapp. **A.** Flowering branch, with detail of leaf pubescence. **B.** Inflorescence, with detail of a single simple, uniseriate trichome. **C.** Opening bud. **D.** Flower showing petals at anthesis. **E.** Anthers. **F.** Infructescence. (Based on Nee et al. 51777, NY.)

mm in diameter at the base, pendent, woody, closely packed, often overlapping, articulated at the base. Buds when very young appearing globose, the corolla soon exerted from the calyx lobes, the buds later becoming obovoid just before anthesis. Calyx 2–2.5 mm long, the tube 1–1.5 mm, the lobes ca.  $1 \times 1$  mm, deltate to broadly triangular, abruptly constricted to an elongate tip ca. 0.5 mm long, densely pubescent with simple, uniseriate trichomes like those of the rest of the inflorescence; fruiting calyx not accrescent, the lobes ca.  $1 \times 1$  mm, brittle and somewhat patent; corolla 1.5–2 cm in diameter, ca. 10 mm long, stellate, white or tinged purplish in some plants, the tube ca. 1 mm, the lobes ca.  $1 \times 0.5$  mm at base, ovate-lanceolate, reflexed at anthesis, acute at apices, densely and evenly pubescent abaxially with simple uniseriate trichomes ca. 0.5 mm long, glabrous adaxially except for the densely papillose margins, the tips of the lobes densely papillose and somewhat cucullate; filaments glabrous, the free portion 0.8–1 mm, the filament tube 1–2 mm, with small teeth arising from the filament tube between the anthers; anthers 4–5  $\times$  1–1.5 mm, oblong, slightly sagittate at base, connivent, yellow, the pores tear-drop shaped, opening into longitudinal slits with age; ovary glabrous; style 6–7  $\times$  ca. 0.05 mm, cylindrical, straight, glabrous; stigma capitate. Fruit a globose berry, 1–1.2 cm in diameter, green, glabrous. Seeds numerous (more than 15) per fruit, 3–3.5  $\times$  2–2.5 mm, flattened-reniform, pale yellow in dry material, the surfaces minutely pitted, the margin incrassate and darker yellow.

*Distribution and ecology*—In the understory of montane forest in northern Bolivia, on eastern Andean slopes from 1900–2200 m. Plants of *Solanum chalmersii* grow both in the forest understory and in disturbed areas along roads and streams, attaining higher population densities in open areas.

*Phenology*—Most flowering specimens have been collected in May, but if *Solanum chalmersii* is like other members of the *S. nudum* species group, it will flower and fruit year-round, but with pulses at particular seasons (see Knapp, 2002b).

*Etymology*—This species is named in honour of Sir Neil Chalmers, Warden of Wadham College, Oxford and previously Director of

the Natural History Museum in London. His support of taxonomy made the third author's collecting in Bolivia possible.

Additional specimens examined. **BOLIVIA. LA PAZ.** Prov. Sud Yungas: de Chulumani hacia el N unos 5 km hacia Irupana, entrando hacia Apa Apa, 16°21'S, 67°30'W, 2050 m, 19 Sep 1998, *Beck 24480* (NY); Sirupaya vic. de Yanacachi, 2100 m, 16 Nov 1906, *Buchtien 315* (NY); along road through primary cloud forest, 7.0–9.4 km NE of (above) Huancané, 16°20'S, 67°32'W, 17–18 May 1990, *Luteyn & Dorr 13722* (BM, LPB, NY); 5.2 km (by road) from Huancané on road to San Isidro, moist montane forest, 16°21'S, 67°30'W, 2225 m, 10 May 2001, *Nee et al. 51773* (NY, BM, LPB, USZ); road between Unduavi and Puente Villa, around hotel Castillo del Chaco and down to the Río Unduavi, humid forest on steep slopes, 16°21'S, 67°49'W, 1900–1930 m, 11 May 2001, *Nee et al. 51795* (BM, NY, LPB, USZ); Yanacachi, 3.5 km hacia Chojlla (as "Chajlla"), 4 Apr 1987, *Seidel & Richter 851* (LPB, NY); Cantón Yanacachi, Mina Chollja, camino de acceso de vehículos a Kacapi, 15°52'S, 68°07'W, 2182 m, 25 Jul 2000, *Sihani 261* (LPB); ca. 6 km along road from Huancané to San Isidro, 16°21'S, 67°31'W, 1 July 1995, *Wood 9955* (K).

*Solanum chalmersii* was mentioned as a probable new species in Knapp (2002b), but at that time material was not sufficient to distinguish it from similar species in the large *Solanum nudum* species group and good fruiting material was not available in order to place it confidently in that group. *Solanum chalmersii* possesses the flattened-reniform, pale colored seeds, simple uniseriate trichomes, and more or less closely spaced pedicel scars typical of the *S. nudum* species group. It is most similar to *S. acuminatum* Ruiz & Pav. of central Peru to Bolivia, with which it is nearly sympatric, but differs in its uniform covering of simple uniseriate trichomes (usually confined to the vein axils in *S. acuminatum*), its flowers with longer anthers with slightly sagittate bases, and in its longer fruiting pedicels. In Bolivia, *S. acuminatum* occurs at higher elevations than *S. chalmersii*.

***Solanum monantheum* S. Knapp, sp. nov.**

**TYPE:** Bolivia. Santa Cruz. Prov. Caballero: Parque Nacional Amboró, Cerro Bravo, próxima a las juntas del Río Alizar y Amparo (20 km al NW de San Juan de Potrero), 17°57'S, 64°54'W, 2000 m, 10–14 Apr 1994 (fl), *I. G. Vargas C., D. Ayala & J. Quiroga 3138* (HOLOTYPE: LPB; ISOTYPES: BM, NY, USZ). (Fig. 5)



Species *Solano symmetrico* Rusby similis, sed foliis axillaribus sparse pubescentibus, inflorescentiis unifloris, pedicellis longis differt.

Shrubs to 1.5 m tall; young stems glabrous and somewhat shiny; older stems glabrous, unarmed. Sympodial units difoliolate and geminate, the minor leaf often deciduous and so appearing unifoliolate. Leaves 2–11 × 1–4 cm, simple, dimorphic, the major leaves 7–11 × 2–4 cm, ovate to elliptic or narrowly elliptic, the minor leaves 2–5 × 1–2.7 cm, differing from the major ones only in size, thin-textured, glabrous and shiny adaxially, glabrous abaxially but with tufts of white simple uniseriate trichomes in the axils of the veins, the trichomes ca. 0.5 mm, very thin and interlaced, arising from the lamina; base acute to slightly attenuate onto the petiole; margin entire; apex acute to long-acuminate and rounded at the very tip; petioles 0.5–1 cm in major leaves, 0.5–0.7 cm in minor leaves, glabrous. Inflorescence consisting of a single flower (occasionally the scar of a second flower apparently present), opposite the leaves or occasionally somewhat internodal, all flowers perfect, the axes glabrous; peduncle and rachis absent or the pedicel appearing jointed 0.6–0.9 cm from the base; pedicels 30–35 mm in flower (to 40 mm if measured to the base of the inflorescence), deflexed, tapering from the base of the calyx tube to a slender base ca. 0.2 mm in diameter, 45–50 mm in fruit, 0.5–1 mm in diameter at the base, ca. 3 mm in diameter at the apex, pendent, slender. Buds when very young appearing globose, the corolla included within the elongate calyx lobes, the buds remaining globose until anthesis. Calyx 4–6.5 mm long, the tube 1–1.5 mm, the lobes 3–5 × ca. 0.5 mm, long-triangular, glabrous; fruiting calyx slightly accrescent, the lobes 5–6 × ca. 0.5 mm; corolla 0.8–1 cm in diameter, ca. 5 mm long, stellate, white, the tube minute, less than 0.5 mm long, the lobes ca. 0.5 × 0.3 mm at base, ovate-lanceolate, probably reflexed at anthesis, glabrous abaxially and adaxially except for the minutely papillose tips; filaments glabrous, the free portion ca. 0.5 mm, the filament tube ca. 0.5 mm; anthers 2.5–3 × ca. 1 mm, oblong, slightly sagittate at base, connivent, yellow, the pores tear-drop shaped, opening into longitudinal slits with age; ovary glabrous; style 3–4 × ca. 0.1 mm,

cylindrical, straight, glabrous; stigma capitate. Fruit a globose berry, 1–1.2 cm in diameter (immature), green, glabrous. Seeds not known from mature fruit.

*Distribution and ecology.*—Only known from two specimens collected in cloud forests in Parque Nacional Amboró and Parque Nacional Carrasco on the eastern slopes of the Andes in Bolivia at ca. 2000 m. The cloud forests where *S. monanthemum* grows have Podocarpaceae and Myrtaceae as canopy trees (fide *Vargas et al.* 3138).

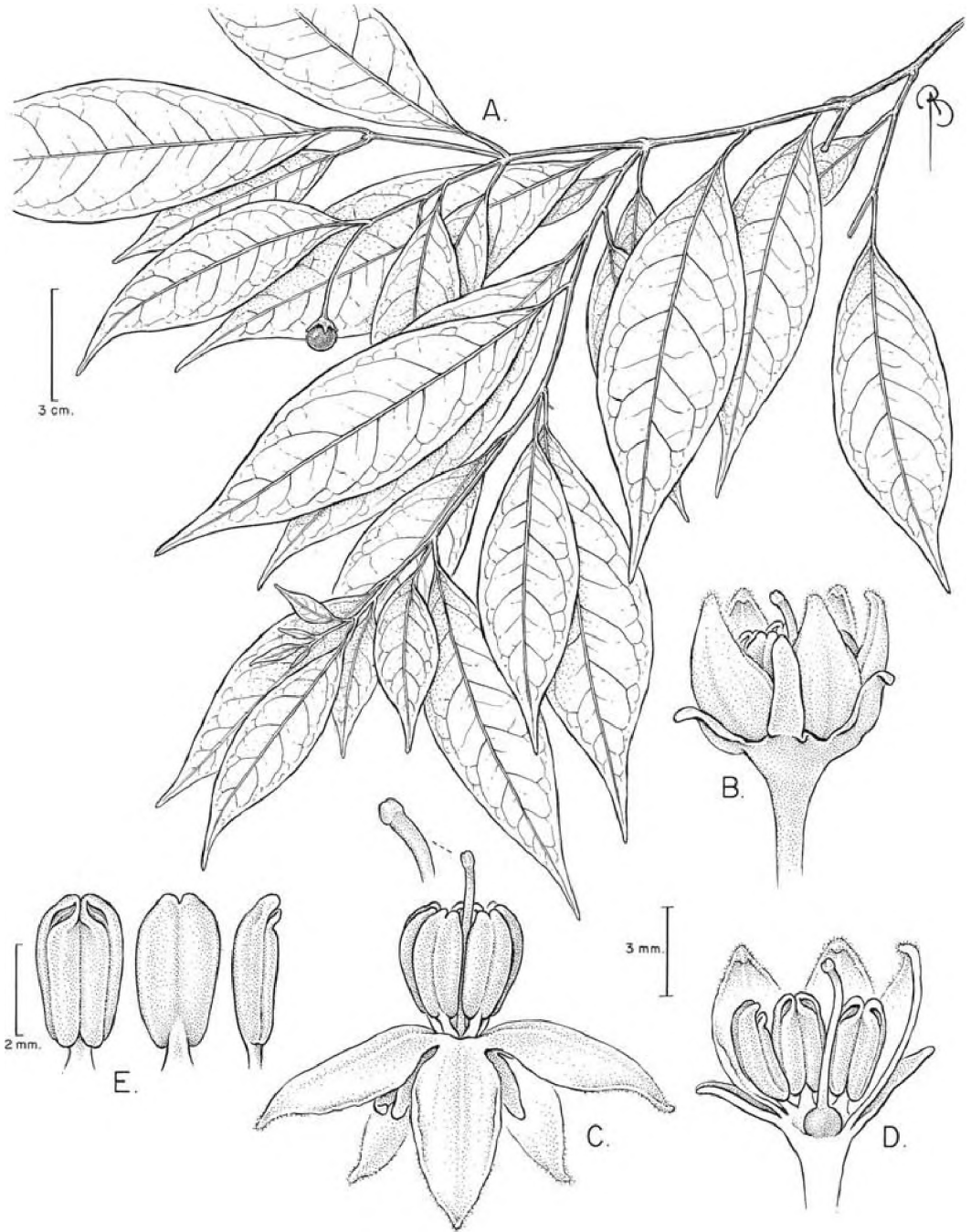
*Phenology.*—Due to the paucity of specimens, data as to flowering and fruiting are not available.

*Etymology.*—From the Greek for single (*mono-*) flower (*antheion*), referring to the unusual single-flowered inflorescences of this species.

Additional specimen examined. **BOLIVIA.** COCHABAMBA. Prov. Carrasco: Sehuencas, Río Fuerte cerca Puente, Parque Nacional Carrasco, 2150 m, 17°30'S, 65°17'W, 30 Nov 1993 (fr), P. Ibsch & C. Ibsch 93.1477 (LPB).

Specimens of *Solanum monanthemum* have occasionally been identified as the more common Bolivian species *S. trichoneuron* Lillo. It is superficially similar to that species, but differs in its dark bark and single-flowered inflorescences, which look like a single flower on an articulate pedicel arising opposite the geminate leaves. The apparent articulation is actually the joint between the inflorescence axis and the pedicel, as evidenced by some inflorescences with minute second buds that apparently abort early in inflorescence development. Many more collections of *S. monanthemum* are needed to investigate this phenomenon fully. Mature fruits of *S. monanthemum* are not known, so placement in one of the species groups of Knapp (2002b) is tentative at present. Overall morphology (i.e., tufts of hairs in the vein axils, short anthers) suggests the *S. nudum* species group, but this can be misleading (e.g., *S. smithii* S. Knapp of the *S. arenarium* species group also possesses these hair tufts; see Knapp, 2002b).

*Solanum monanthemum* can be distinguished from other species with tufts of hairs in the abaxial vein axils by its single-flowered inflorescences and its tree-like habit. It also apparently grows as isolated in-



**FIG. 5.** *Solanum monanthemon* S. Knapp. **A.** Fruiting branch. **B.** Partially open bud, showing the distinctive long-triangular calyx lobes. **C.** Flower at anthesis. **D.** Flower in longitudinal section. **E.** Anthers. (Based on Vargas *et al.* 3138, NY.)

dividuals in dense cloud forests, unlike many of the other members of the *S. nudum* species group that are plants of open areas along streams and roads.

#### THE WENDLANDII/ALLOPHYLLUM CLADE

##### *Solanum clandestinum* Bohs, sp. nov.

TYPE: Bolivia. La Paz. Prov. Nor Yungas: 2 km by road (ca. 1 km by air) NE and below Chuspipata, 16°17'30"S, 67°49'W, 2950 m, 29 Oct 1984 (fl, fr), *M. Nee & J. Solomon 30219* (HOLOTYPE: LPB; ISOTYPE: MO). (Fig. 6)

Habitu, foliis et fructibus *S. confuso* C.V. Morton similis sed pedunculis brevissimis, antheris obtusis oblongis et seminibus rotundatis differt.

Slender shrub 1–2.5 m tall; stems glabrous to densely pubescent with unbranched hairs, some with broad multiseriate bases giving the young stems a corky or roughened appearance, unarmed. Sympodial units difoliate, geminate. Leaves 3–12 × 0.5–3 cm, simple, dimorphic, the major leaves 5–12 × 1–3 cm, narrowly elliptic to lanceolate, the minor leaves 3–4 × 0.5–1 cm, differing from the major ones only in size, usually subcoriaceous, glabrous adaxially, glabrous to moderately pubescent abaxially with unbranched hairs; base cuneate to long-tapered; margin entire, glabrous to ciliate; apex acute to acuminate; petioles 0.5–2 cm, 1–2 cm in major leaves, ca. 0.5 cm in minor leaves, glabrous to moderately pubescent in adaxial channel. Inflorescence 0.5–2 cm, opposite the leaves, unbranched or rarely forked, with 1–6 flowers, all flowers perfect, the axes glabrous to sparsely pubescent; peduncle 0.2–2 cm; rachis very short, 1–4 mm; pedicels 10–20 mm in flower, 15–35 mm and slender and curved in fruit, congested and spaced up to 3 mm apart, articulated at the base. Calyx 2–3 mm long, the tube ca. 1 mm, the lobes 1–2 × 1.5–2 mm, broadly deltate, almost truncate with a small acumen at tip, glabrous at base, tomentose at tips; fruiting calyx not accrescent, the lobes 1–2 × 1.5–2 mm; corolla 1–1.5 cm in diameter, 4–7 mm long, stellate, white, the tube 1–2 mm, the lobes 3–5 × 2–2.5 mm at base, narrowly triangular to ovate, acute at apices, glabrous abaxially at base,

tomentose at tips of lobes, glabrous adaxially; filaments glabrous, the free portion 0.5–1 mm, the filament tube absent to 0.5 mm; anthers 3–4 × 1.5–2 mm, oblong, connivent, yellow, the pores broad, directed distally and adaxially, often opening into longitudinal slits with age; ovary glabrous; style 4–5 × ca. 0.5 mm, cylindrical, straight; glabrous; stigma truncate. Fruit a globose berry, 1–1.5 cm in diameter, orange when ripe, glabrous. Seeds fewer than 15 per fruit, ca. 4 × 3 mm, somewhat flattened, yellow-brown, the surfaces rugulose.

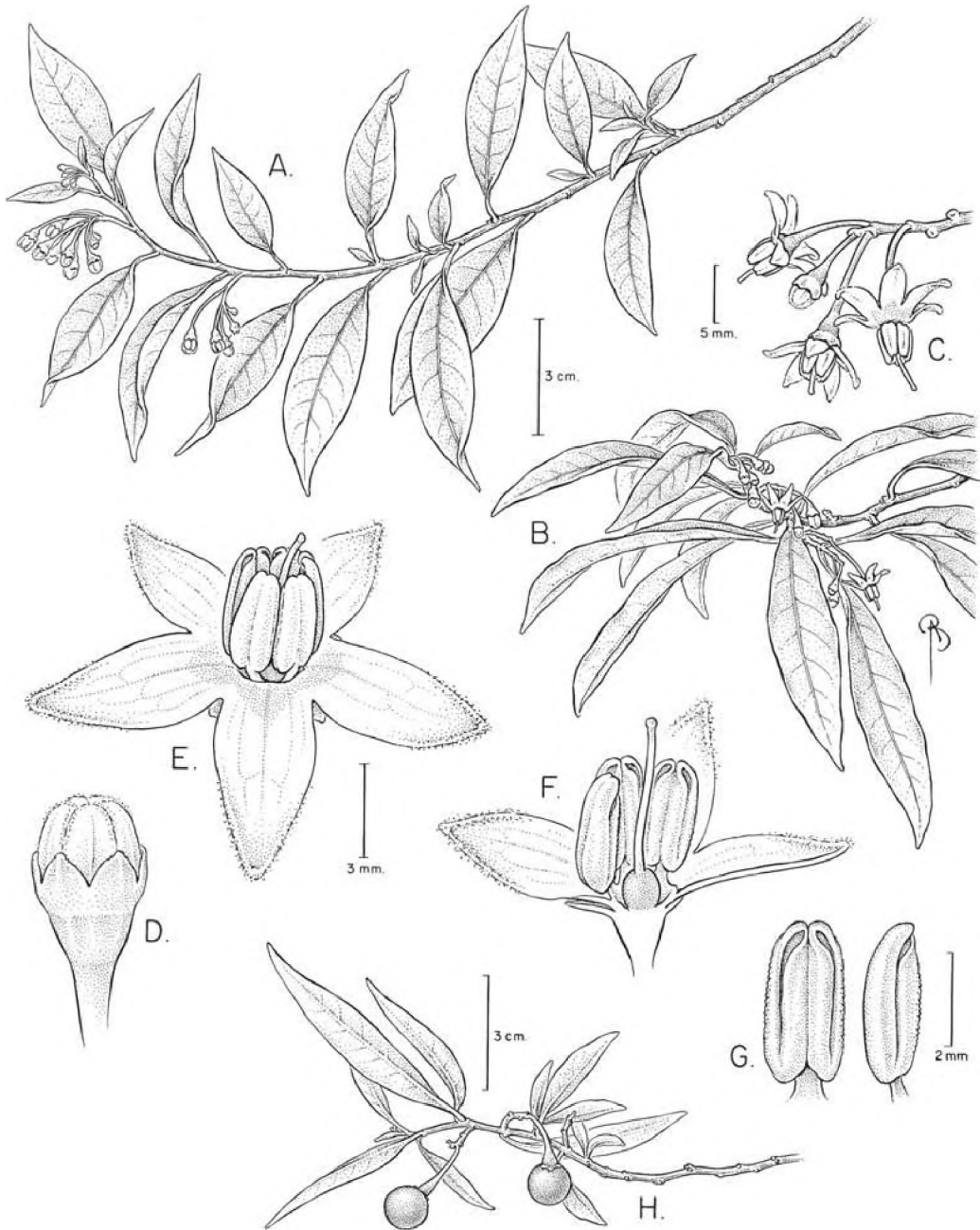
*Distribution and ecology.*—Montane rain and cloud forest, especially on slopes or in disturbed areas, of western Bolivia in Yungas de La Paz, 2200–3100 m.

*Phenology.*—Flowering specimens have been collected in May, June, and August through October. Fruiting specimens have been collected in March, May, June, August, and October.

*Etymology.*—The specific epithet, meaning “hidden,” refers to the inconspicuous appearance of this species, which has probably led to it being overlooked until now. On a recent Bolivian field trip, three *Solanum* specialists ate lunch next to the plants without noticing them at first, despite the botanists’ interest in collecting this species. When one plant was finally recognized, several others were found in close proximity.

Additional specimens examined: **BOLIVIA. LA PAZ.** Prov. Nor Yungas: Guanai, 1891 (fr), *Bang s.n.* (NY); Yolosa, 23 km hacia Chuspipata, 2730 m, 16 Sept 1981 (fl), *Beck 4844* (NY); road from Coroico to divide leading to La Paz, 21 May 1980 (fl, fr), *D’Arcy & Bejarano 13875* (NY); road from Chuspipata to Yolosa, ca. 68°00'W, 16°20'S, 2000–2700 m, km 20–13, 4/11/1989 (fr), *J.F. Smith & Beck 1731* (LPB, NY); 2.2 km NE (below) Chuspipata, 16°17'S, 67°49'W, 3000 m, 24 Mar 1982 (fr), *Solomon 7296* (MO, NY); 1.6 km NW of Chuspipata, 16°18'S, 67°49'W, 3100 m, 26 Aug 1983 (fl, fr), *Solomon 10668* (MO, NY); 0.8 km SE of (below) Chuspipata on road to Chulumani, vic. Chuspipata railroad station, 16°18'S, 67°49'W, 3100 m, 7 Oct 1984 (fl), *Solomon & Escobar 12507* (MO); 1.2 km W of Chuspipata, 16°18'S, 67°49'W, 3100 m, 8 June 1985 (fr), *Solomon 13851* (MO, NY); 1.2 km E of Cotapata on road between Unduavi and Chuspipata, 16°17'S, 67°50'W, 3100 m, 26 June 1986 (fl), *Solomon 15316* (MO), (fr), *Solomon 15320* (MO); Saltos de San Juan, 10 km al NE (debajo) de Chuspipata por el camino a Yolosa, 16°16'S, 67°47'W, 2400 m, 28 May 1988 (fr), *Solomon 18499* (MO). Prov. Sud Yungas: Huancané, 7 km hacia el sur, 2400 m, 3/7/1981 (fl, fr), *Beck 4713* (NY); 7.5 km (by road) from Huancané on road to San





**FIG. 6.** *Solanum clandestinum* Bohs. **A, B.** Flowering branches. **C.** Inflorescence. **D.** Bud. **E.** Flower at anthesis. **F.** Flower in longitudinal section. **G.** Anthers. **H.** Fruiting branch. (A based on *Solomon 10668*, NY; B–C based on Bohs photos of *Nee et al. 51781*; D–G based on *Beck 4844*, NY; H based on *Nee et al. 51781*, NY.)

Isidro, 16°21'S, 67°30'W, 2225 m, 10 May 2001 (fr), *Nee et al. 51781* (LPB, NY, UT); 9 km de Huancané en la carretera hacia San Isidro, 16°21'S, 67°31'W, 2400 m, 2 May 1989 (fr), *D. N. Smith & J. F. Smith 13061* (LPB, MO, NY).

*Solanum clandestinum* is unique in its narrowly elliptic to lanceolate and usually subcoriaceous leaves, inflorescences with very short peduncles and long pedicels, white

corollas, oblong anthers, and conspicuous, orange, few-seeded fruits. It is apparently restricted to the Yungas of La Paz in northwestern Bolivia. Specimens can vary from being nearly glabrous to abundantly pubescent, especially on the young stems. The hairs are unbranched but can have wide multiseriate bases and in some specimens these give the twigs a roughened or corky aspect.

Fruiting specimens of *Solanum clandestinum* can resemble *S. confusum* C.V. Morton, another species of the Bolivian uplands. *Solanum clandestinum* is distinctive in its very short inflorescences, with the pedicels clustered and becoming long, slender, and curved in fruit. The seeds of *S. clandestinum* are not angled like those of *S. confusum*, and they always lack white pseudohairs on the surface. Flowers of *S. clandestinum* have white corollas and blunt, oblong anthers, whereas *S. confusum* flowers usually have violet corollas and tapered anthers. *Solanum confusum* lacks hairs with multiseriate bases.

Parsimony analyses of chloroplast *ndhF* sequence data place *Solanum clandestinum* in a clade with *S. mapiriense* Bitter, *S. wendlandii* Hook.f., and *S. allophyllum* (Miers) Standl. (the Wendlandii/Allophyllum clade of Bohs, 2005), but this clade is not well-supported (Bohs, unpubl. data). Nuclear ITS sequences indicate a relationship among *S. clandestinum*, *S. mapiriense*, and *S. morellifolium* Bohs, but this clade receives very little bootstrap support. Data from the nuclear *waxy* (GBSSI) gene allies *S. clandestinum* with *S. mapiriense* with 100% bootstrap support. Thus, three genes suggest an alliance between *S. clandestinum* and *S. mapiriense*, the latter another species endemic to the Bolivian Yungas that has been placed in *Solanum* section *Allophyllum* (Bohs, 1990). The elliptic leaves of *S. mapiriense* are much broader than those of *S. clandestinum* and the anthers are strongly tapered distally, in contrast to the oblong anthers of *S. clandestinum*. The fruits and seeds of *S. mapiriense* are incompletely known.

#### THE LEPTOSTEMONUM CLADE

*Typification of Solanum aridum Morong and new synonymy*— In the arid inter-Andean valleys of southern Bolivia and adjacent Chaco plains to the east grows a colonial

herbaceous species of *Solanum*. It is usually found in unshaded areas, often around temporary puddles or roadsides, on sand or more often on clay. It is also present in the Chaco of western Paraguay and adjacent areas of northwestern Argentina. The correct name for this species has long been in doubt, in part due to the paucity of collections and to the similarity of closely related species in the group. *Solanum aridum* Morong is now established as the name of this species (annotated by Nee as *S. conditum* C.V. Morton in herbaria); the lectotype and most of the isotypes are mixed collections, which has led to some confusion.

***Solanum aridum* Morong**, Ann. New York Acad. Sci. 7: 173. 1893. TYPE: Paraguay. Presidente Hayes (?): falls of the Río Pilcomayo, 2 May 1888–1890, *T. Morong 1007* (LECTOTYPE: US 48029, nonglandular, nearly unarmed plant with cuneate leaf bases, designated by Morton, 1976; ISOLECTOTYPES: BM 87516 leafy twig, E two twigs, K, MO 2766698, NDG-n.v., NY 139054 leafy twigs, PH– 2 sheets, WIS ex WELC 15091 except for plant of *Turnera*). (Fig. 7)

*Solanum elaeagnifolium* Cav. var. *ovalifolium* Kuntze, Revis. Gen. Pl. 3, 3: 225. 1898. TYPE: Argentina. Salta: Monte Morro, Nov 1892 (fl, fr), *O. Kuntze s.n.* (HOLOTYPE: NY 139143; ISOTYPE: US 701686). *S. conditum* C.V. Morton, Revis. Argent. *Solanum* 237. 1976. TYPE: Argentina. Santiago del Estero: Depto. C. Pellegrini, Estancia El Remate, 500 m, 22 Dec 1927 (fl), *S. Venturi 5685* (HOLOTYPE: US 1548974; ISOTYPES: NY, SI-2 sheets).

*Solanum aridum* is a member of a group of closely related taxa designated as the *Solanum multispinum* group by Whalen (1984) and as *Solanum* subgen. *Leptostemonum* sect. *Melongena* subsect. *Lathyrocarpum* (Dunal) G. Don by Nee (1999). The name *Solanum aridum* Morong was based on *Morong 1007*, collected along the Río Pilcomayo on the border of Paraguay and Argentina; it was considered by Morton (1976) to be a species perhaps not subsequently collected and certainly not known to him, although, in fact, in the same work he described the same species as new under the name *S. conditum* C.V. Morton. It appears under this latter name in Nee (1999).



**FIG. 7.** *Solanum aridum* Morong. Isolectotype specimen *Morong 1007* at NY (NY 139054). The majority of the stems on the sheet are *S. aridum*, but lowermost stem slightly to the left of center with a large globose fruit and cauline spines is *S. multispinum* N.E. Br. (see text).

***Solanum aridum*, Morong, n. sp.**  
 Stem shrubby, terete, 2 dm. to 1 m. in height, sparsely branched, armed with straight acicular prickles, or sometimes unarmed or armed only at the base, glabrous below and glandular downy at the summit, usually leafless below. Leaves simple, alternate, oblong or ovate-oblong, entire or with large teeth or occasionally lobed, pubescent, green above and white hairy below, most of the pubescence stellate; blade 3-5 cm. long and 1-2 cm. broad; petioles pubescent, 1-10 mm. long. Flowers solitary, axillary, on pedicels about 1½ cm. long, thickening and elongating to 4 cm. in fruit. Calyx stellately pubescent, ½ as long as corolla, the lobes nearly subulate, with longer than the tube. Corolla sulphur-yellow, pilose, deeply 5-lobed, pubescent outside, 2 cm. in diameter when expanded. Calyx and corolla usually 2-lobed, occasionally 4-lobed. Filaments very short; anthers nearly 1 cm. long, the pores minute, looking upwards. Stigma green, capitate. Ovary 2-lobed, fruit very large, glabrous, yellow, 2-lobed, globose, 1½-3 cm. in diameter.  
 The plant grows in dry or rocky places on the campo, and has a parched, dried appearance.  
 Falls of the Pilcomayo (1007). April-May.

IMAGED  
 NEW YORK BOTANICAL GARDEN  
 00139054  
 Type  
 PLANTS OF SOUTH AMERICA  
 collected by THOMAS MORONG, 1883-1890  
 Pilcomayo River, Paraguay.  
*Solanum aridum* - Morong  
 n. sp.  
 May 2  
 1007  
 70



Thomas Morong's collections from Paraguay and preserved at NY are generally good and with copious notes. *Morong 1007*, however, was a decidedly mixed collection, with at least three different species in two families represented among the various duplicates. Morong collected the plants in May (the dry season) and said in the original description that the plants "had a parched, dried appearance" (Morong & Britton, 1893). It is thus understandable that Morong would collect specimens of one species in flower and fruit (*Solanum aridum*) and a related species mostly without leaves and in fruit (*Solanum multispinum* N.E. Br.), although the addition of the flowering specimen of *Turnera* (Turneraceae) is less explicable.

*Solanum aridum* was lectotypified by C. V. Morton (1976) on the leafy and flowering part of the duplicate US 48029, although Recommendation 9A.3 of the *Code* (Greuter et al., 2000) would have recommended lectotypification on the specimen NY 139054, which is labelled "type" (Fig. 7). Morong was curator of the Columbia University Herbarium (Britton, 1894), and this herbarium subsequently became the basis of the newly formed New York Botanical Garden herbarium (NY). Morton claimed that his lectotypification was somewhat "arbitrary," but fortunately it was based on the predominant element of *Morong 1007*, and that which provides the major portion of the original description.

The full range of duplicates with their extraneous elements can be explained as follows. The lectotype sheet of *Solanum aridum*, US 48029, consists of a leafy and flowering portion of *S. aridum*, along with a very spiny plant with stipitate-glandular stems and with leaf blades cordate at the base. This latter element corresponds to *S. multispinum*, parts of which are found on other duplicates as well.

The specimens BM 87516 and NY 139054 are a mixture of *Solanum aridum*, plus leafless twigs of *S. multispinum* with globose fruits, which accounts for the description of a fruit 3 cm in diameter and of a long fruiting pedicel; *S. aridum* has an ovoid fruit 1.6–1.8 × 1.3–1.7 cm, and the fruiting pedicel is 1.8–3.1 cm long, but without the bristly hairs present on *S. multispinum*. The specimen at E

consists of two plants of *S. aridum*, one with leaves and the other with leaves and fruits; in addition there is a flowering plant of *S. multispinum*. The specimens at K, MO 2766698, and the two sheets at PH consist exclusively of *S. aridum*. The specimen WIS ex WELC 15091 has a plant with the small, ovoid fruit of *S. aridum* along with a piece of *Turnera* of the Turneraceae, which accounts for the "sulphur yellow" corolla in the original description; *S. aridum* has a white or pale blue corolla.

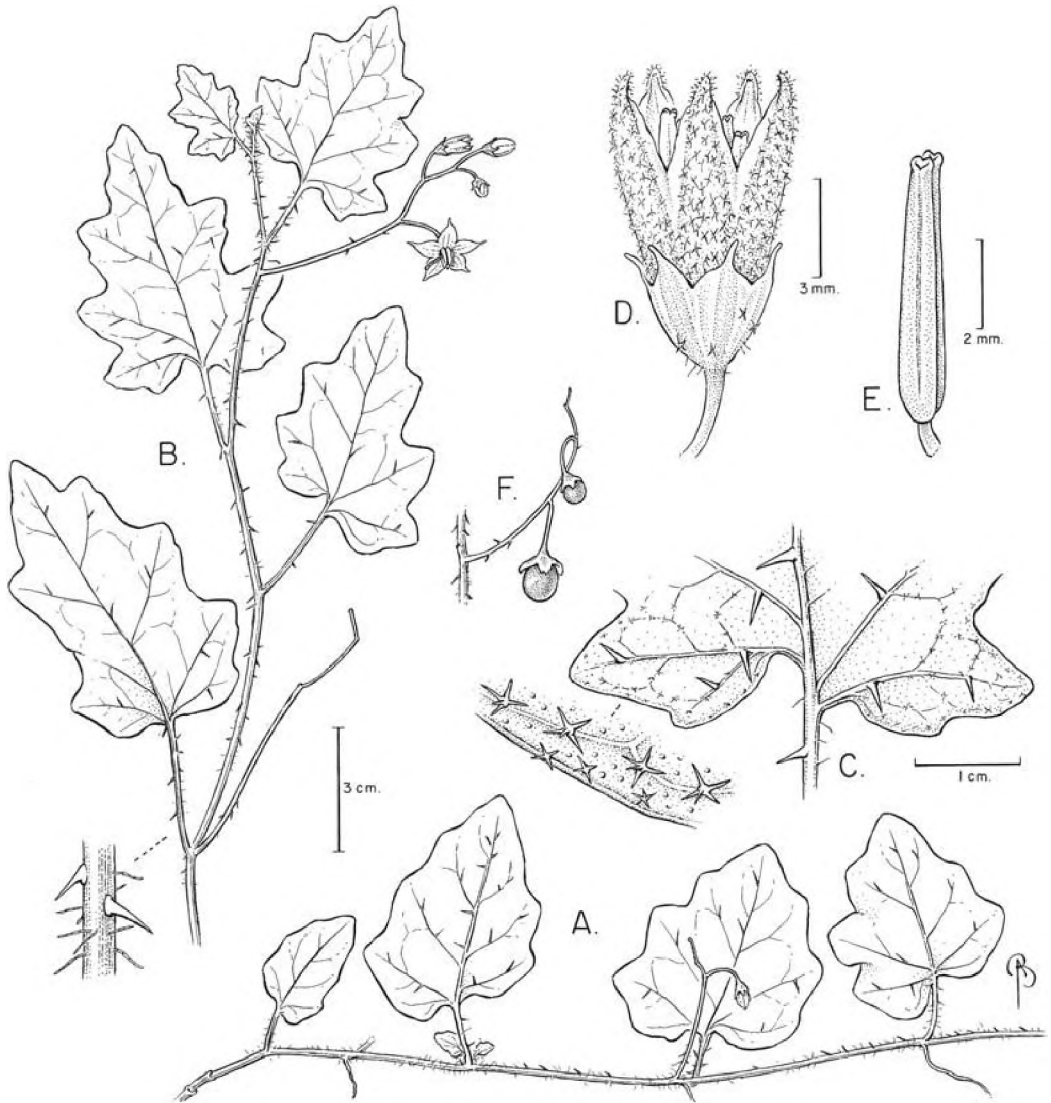
In the type region only two species of *Solanum*, *S. palinacanthum* Dunal and *S. multispinum* N.E. Br., have a fruit similar to that of the ca. 3 cm diameter fruits on *Morong 1007*. The fruiting pedicels of *S. multispinum* exactly match those on the fruiting specimen of *Morong 1007*, while the pedicels of *S. palinacanthum* are curved and generally much shorter.

During his preparation of a treatment of *Solanum* of Argentina, Morton (1976) annotated many specimens with a name transferring the epithet *ovalifolium* of *S. elaeagnifolium* Cav. var. *ovalifolium* Kuntze to a variety of *S. meloncillo* Parodi, but this transfer was never published, and instead these plants were named *S. conditum* C. V. Morton.

***Solanum moxosense* M. Nee, sp. nov.** TYPE: Bolivia. Beni. Prov. Cercado: Trinidad, 14°50'S, 64°55'W, 200 m, weed in the city, 6 Jan 1989 (fl), M. Nee 37519 (HOLOTYPE: LPB; ISOTYPES: G, MO, NY-2 sheets, USZ). (Fig. 8)

Herba repens ad nodos radicans, pilis simplicibus 2–3-cellularibus sparse pilosa, aculeis acicularibus 1.7–3.5 mm longibus sparse armata. Folia alterna, ovata, 5–7.5 × 3.5–6 cm, repanda vel non profunde lobata, subtus sparse stellato-tomentosa. Inflorescentia extra-axillaris, racemoso-cymosa, 4–5-florus; calyx inermis; corolla alba, lobis 6.5 × 3.5 mm; antherae lineari-angustatae, 5 × 1 mm; ovarium glabrum. Bacca oblongo-ovoidea, glabra.

Herb or vine, creeping and rooting at the nodes, or some stems erect, to 20 cm tall; stems slender, to ca. 2.5 mm in diameter, nearly glabrous to sparsely pilose with simple, 2–3-celled hairs, sparsely armed with prickles 1.7–3.5 mm long, slightly reflexed, nearly straight or slightly curved. Sympodial units 2- to 3-foliolate, not geminate. Leaves 5–7.5 × 3.5–6 cm, simple, more or less uniform



**FIG. 8.** *Solanum moxosense* M. Nee. **A.** Habit. **B.** Leafy branch with inflorescence and detail of prickles. **C.** Close-up of leaf base with detail of stellate hairs. **D.** Partially open flower. **E.** Anther. **F.** Fruits. (A–E based on Nee 37519, NY; F based on Nee 34261, NY.)

in size and shape, ovate, thin-textured, glabrous adaxially, very sparsely pubescent abaxially with sessile 4-rayed stellae 0.7–1 mm wide, the midpoints shorter than the lateral rays, sparsely armed above and below with straight acicular prickles 1–3.5 mm long on the major veins; base truncate to subcordate, nearly equal to very unequal and with one side offset by up to 1 cm from the other; margin repand to shallowly lobed with 3–4

rounded to obtuse lobes per side; apex obtuse; petioles 0.7–3 cm, with hairs and prickles like those of the stems. Inflorescence 5–6 cm, extra-axillary or opposite the leaves, unbranched, with 4–5 flowers, the plants probably andromonecious and only the lowest one or two flowers fertile, the axes nearly glabrous to sparsely pilose with simple or stellate hairs and with 1 or 2 acicular prickles ca. 2 mm long; peduncle 3–4 cm; rachis ca. 2

cm; pedicels 9–11 mm in flower, to 15 mm and somewhat thickened in fruit, expanded distally to 1.5 mm in diameter, recurved, widely spaced, 7–14 mm apart, articulated at the base. Calyx 6–7 mm long, the tube 2–3 mm, the lobes in anthesis to  $4 \times 1.4$  mm including the ca. 1 mm long caudate tip, oblong-ovate, with a few sessile stellate hairs, unarmed; fruiting calyx somewhat accrescent, the lobes to ca.  $6.5 \times 3.2$  mm; corolla ca. 1.3 cm in diameter, 12 mm long, stellate to stellate-pentagonal, white, lobed about half way, the tube 6 mm, the lobes ca.  $6.5 \times 3.5$  mm, triangular, tomentose abaxially with small sessile stellae, glabrous adaxially; filaments glabrous, the free portion ca. 2 mm, the filament tube absent; anthers ca.  $5 \times 1$  mm, linear-tapered, not connivent, yellow, the pores minute and directed distally, not opening into longitudinal slits with age; ovary glabrous; style ca.  $8 \times 0.5$  mm, cylindrical, straight, glabrous; stigma capitate. Fruit (immature) an oblong-ovoid berry, ca. 1 cm in diameter, the color when ripe unknown, glabrous. Seeds unknown.

*Distribution and ecology.*—The few collections to date show *Solanum moxosense* is adapted to weedy or disturbed areas around cattle pens, but the original adaptation is probably to natural disturbances of the seasonally inundated savanna in which Trinidad is situated. So far this species is only known from the immediate vicinity of the city at ca. 200 m in elevation. It is a weed in the city of Trinidad and was also seen commonly on dirt roads and near cattle yards near Puerto Almacén, 7 km SW of the city, but not yet blooming there, so no specimens were collected. No collections have been seen from the Estación Biológica del Beni, ca. 150 km to the west, one of the few areas of the Beni plains that has been thoroughly explored botanically.

*Phenology.*—Flowering in January and August.

*Etymology.*—The name refers to the Llanos de Moxos, one of the largest seasonally flooded savannas in the world. This part of Bolivia is a perfectly flat alluvial plain between the pre-Cambrian shield of crystalline rocks to the east and the Andes to the west, which provide the recent sediments from their numerous rivers flowing northwards to

the Madeira and then the Amazon. The region has been identified as a center of diversity and endemism and a priority for conservation (Beck & Moraes-R., 1997).

Additional specimens examined. **BOLIVIA. BENI.** Prov. Cercado: Trinidad, on savanna, 200 m, Aug 1944 (fl), *Cárdenas* 3525 (MO, US); Trinidad,  $14^{\circ}50'S$ ,  $64^{\circ}55'W$ , 150 m, weedy areas in the town, 25 Feb 1987 (fl, fr), *Nee* 34261 (MO, NY).

*Solanum moxosense* is a much more nearly glabrous plant than related species in the *Solanum multispinum* species group (sensu Whalen, 1984) or sect. *Melongenina* subsect. *Lathyrocarpum* G. Don (sensu Nee, 1999), most of which are found further south in southern Bolivia (from about Santa Cruz de la Sierra south) into northern Argentina and especially Paraguay. It appears most similar to species such as *S. hieronymi* Kuntze from dry areas of southern Bolivia, northwestern Argentina and Paraguay, or *S. comptum* C. V. Morton of eastern Paraguay and northeastern Argentina, but these species are more robust in all respects, more densely stellate-tomentose, and display the very spiny fruiting calyx typical of the group.

In habit, *Solanum moxosense* resembles the Cuban endemic *Solanum chamaeacanthum* Griseb., but that species appears not to root along the nodes, the leaves are fleshier, smaller ( $1.5\text{--}4 \times 1.2\text{--}2$  cm), with more regular and more acute lobes, and the plant is more densely armed with longer prickles (to 6.5 mm long). *Solanum moxosense* is also similar to the creeping species *S. flagellare* Sendtn. and *S. reineckii* Briquet of coastal southeastern Brazil, but differs again by more profuse rooting at the nodes and a suite of other characters.

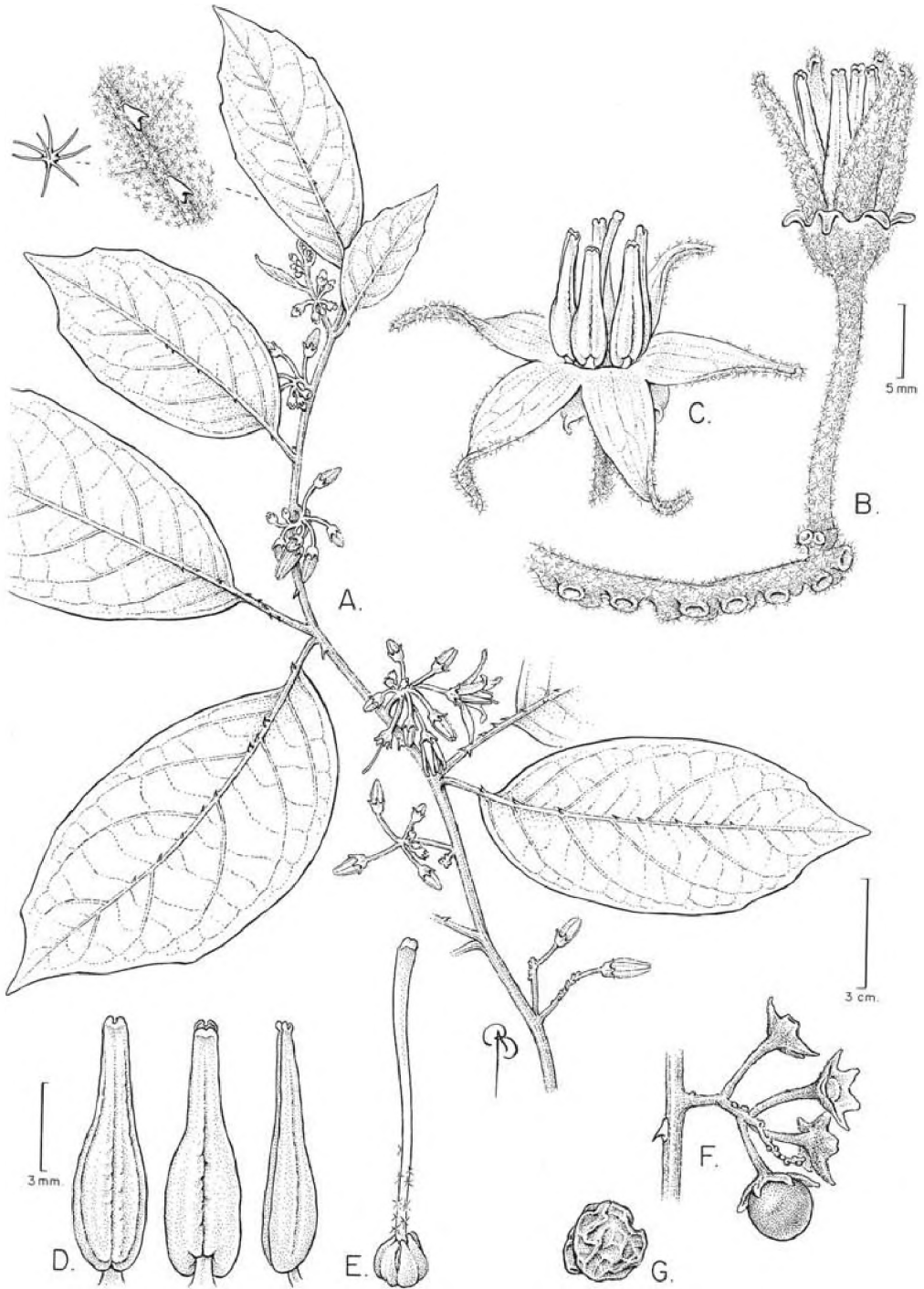
### ***Solanum pedemontanum* M. Nee, sp. nov.**

TYPE: Ecuador. Napo: Añangu, Parque Nacional Yasuní,  $0^{\circ}31\text{--}32'S$ ,  $76^{\circ}23'W$ , 30 May–21 Jun 1982 (fr), *B. Øllgaard et al.* 39285 (HOLOTYPE: QCA; ISOTYPE: NY).

Fig. 9

Liana lignosa, aculeis solum recurvis 1.5–3 mm longis armata. Folia plerumque geminata, altero minore, folia longiora anguste elliptica, 10–18  $\times$  2.5–6.5 cm, integra vel angulati-lobata, supra inermia, subtus costa aculeis recurvis armata. Inflorescentiae extra-axillares, in-





**FIG. 9.** *Solanum pedemontanum* M. Nee. **A.** Flowering branch with detail of adaxial leaf surface with prickles and hairs. **B.** Inflorescence and flower. **C.** Flower at anthesis. **D.** Anthers. **E.** Gynoecium. **F.** Infructescence. **G.** Dry fruit. (A, B, D-G based on *Balslev & Balseca 4721*, NY; C based on *Skutch 4545*, NY.)

ermes, racemosae; calyx 3 mm longus, fere truncatus; corolla eburnea, profunde lobata, lobis linearilanceolatis, 12–20 × 2–2.5 mm; antherae attenuatae, 11–12 × 1.5 mm, vel nonnunquam 6–7.5 mm longae. Baccae nitidae, aurantiacae vel rubrae, 1.5–2 cm diametro; semina complanata, reniformia, 3.4–3.7 × 2.8–3.2 mm.

Scrambling vine; stem closely tomentose with ferruginous sessile (or nearly) 7–8-rayed stellae, 0.4 mm wide, with obsolete midpoints, eventually glabrescent, armed with uniform small recurved prickles 1.5–3 mm long from enlarged flattened bases. Sympodial units unifoliate or usually difoliate, rarely 3-foliate, geminate. Leaves 5–18 × 1.3–6.5 cm, simple, dimorphic or not, the major leaves 10–18 × 2.5–6.5 cm, narrowly elliptic, the minor leaves 5–18 × 1.3–6.5 cm, differing from the major ones only in size, thin-textured, sparsely to densely tomentose adaxially with sessile 4–8-rayed stellae 0.3–0.5 mm wide, the midpoints absent to 1.5 mm long, the trichomes not obscuring the surface, tomentose abaxially with sessile or very short-stipitate stellae 0.6–0.7 mm wide, somewhat larger than those above but with obsolete midpoints, the surface visible, the leaf undersides with recurved prickles on the midrib similar to those of the stem; base unequal (oblique); margin entire or very shallowly angulate-lobed; apex acute to attenuate; petioles 0.8–2.5 cm, armed with hairs and recurved prickles like those of the stem. Inflorescence 3–5.5 cm, extra-axillary, unbranched, with 5–15 flowers, all flowers apparently perfect, the axes stellate-tomentose, unarmed; peduncle 0.8–1.1 cm; rachis 2.5–4.5 cm; pedicels 8–9 mm in flower, 16–20 mm in fruit, thick and enlarged at the apex, slightly curved, spaced 1–1.5 mm apart, articulated at the base. Calyx ca. 3 mm long, the tube ca. 2.5–3 mm, the margin almost truncate and lobes nearly absent, with an apicular extension of the midrib up to 1 mm long, stellate-tomentose abaxially, glabrous adaxially; fruiting calyx accrescent, to ca. 6 mm long, splitting nearly to the base, eventually breaking off irregularly, the remaining calyx tube flattened and somewhat woody; corolla 2.5–5 cm in diameter, 18–20 mm long, stellate, attenuate and slightly curved in bud, creamy white, the tube 2 mm, the lobes 12–20 × 2–2.5 mm, linear-lanceolate, tomentose abaxially with weak whitish stellae,

glabrous adaxially; filaments obsolete; anthers (6–) 11–12 × 1.5 mm, very slender, attenuate, not connivent, yellow, the pores minute and directed distally, not opening into longitudinal slits with age; ovary sparsely tomentose at apex, glabrescent; style ca. 12 × 0.3–0.4 mm, exceeding the anthers by about 1.5 mm, clavate, straight to slightly curved, stellate-tomentose near the base; stigma truncate to capitate. Fruit a globose berry, 1.5–2 cm in diameter, shiny bright orange or red, glabrous. Seeds numerous (more than 15 per fruit), 3.4–3.7 × 2.8–3.2 mm, flattened, reniform, light brown or yellowish, the surfaces minutely pitted.

*Distribution and ecology.*—Humid evergreen forests of the Amazon basin near the eastern base of the Andes from Colombia to the southern limit of the tropical forest just northwest of the city of Santa Cruz, Bolivia, also more rarely on the western Andean slopes in Ecuador, at 90–1800 m elevation.

*Phenology.*—Flowering and fruiting all year.

*Etymology.*—The epithet reflects the distribution along the piedmont, the lower eastern slopes of the Andes and immediately adjacent Amazon lowlands, and the western Andean slopes in Ecuador.

*Common names.*—Ecuador: “cocona del monte” (*Lawesson et al. 39532B*); Peru: “ayac mulláca” (bitter fruit, *Mexia 6485*), “chirapahuasca” (*Schunke 77*).

*Uses.*—The seeds are said to be used for “skin spots; caustic” (*Mexia 6485*).

Additional specimens examined. **COLOMBIA.** **AMAZONAS:** Municipio Leticia, Parque Nacional Natural Amacayacu, sector de Mata-matá, a la orilla de la quebrada Bacaba, 3°47'S, 70°15'W, 100 m, 16 Apr 1992 (fr), *Rudas & Prieto 4278* (BM); Municipio Leticia, brazo del Río Amazonas, lado de la estación principal del Parque Nacional Natural Amacayacu, 14 Jun 1992 (fl), *Rueda 556* (BM); Loretoyacu River, 100 m, Mar 1946 (fr), *Schultes 7130* (GH).

**ECUADOR.** **ESMERALDAS:** San José, km. 321 along railroad from Ibarra to San Lorenzo, 1°N, 78°W, 350 m, 4 May 1982 (fr), *Boom 1364* (MO); Cantón San Lorenzo, Reserva Indígena Awá, Cañon del Río Mira, 10 km W de Alto Tambo, Comunidad “La Unión”, 1°02'N, 78°26'W, 250 m, 16–26 Mar 1991 (fr), *Rubio et al. 1112* (NY). **MORONA-SANTIAGO:** Pozo petrolero “Garza” de TENNECO, 35 km NE de Montalvo, 1°49'S, 76°42'W, 260 m, 2–12 Jul 1989 (fr), *Zak & Espinoza 4376* (MO, NY), 4448 (BM, MO, NY). **NAPO:** Yasuní Forest Reserve, 1–3 km E of Pontificia Universidad Católica de Ecuador Science Station, by Tiputini River, 0°40.8'S,

76°23.7'W, 240 m, 16 Jun 1995 (fr), *Acevedo-Rodríguez & Cedeño 7339* (MO); Cantón Archidona, S del Volcán Sumaco, carretera Hollín-Loreto, km. 31, Comuna Chalu Yacu, 0°43'S, 77°36'W, 15–17 Nov 1988 (fr), *A. Alvarado 53* (NY); Orellana Cantón, Parque Nacional Yasuní, carretera y oleoducto de Maxus en construcción, km. 54–58, 00°48'S, 76°30'W, 250 m, 26–30 Sep 1993 (fl, fr), *Aulestia & Andi 760* (BM, MO, QCNE); Aguarico, Reserva Étnica Huorani, carretera y oleoducto de Maxus en construcción, km 61, S del río Tivacuno, 0°48'S, 76°23'W, 250 m, 26–30 Oct 1993 (fr), *Aulestia et al. 1041* (MO, NY); Río Wai si ayá, 1 km upstream from the outlet in Río Aguarico, 1°15'S, 76°21'W, 6 Aug 1981 (fr), *Brandbyge et al. 33229* (NY, QCA); road between Baeza and Lago Agria, 72.5 km W of Lago Agria, 1166 m, 19 Dec 1979 (fr), *Croat 49532* (MO, NY); Cantón La Joya de los Sachas, Parque Nacional Yasuní, carretera de Maxus, km. 45, 0°45'S, 76°28'W, 230 m, 8–15 Aug 1993 (fr), *Dik 96* (QCNE); Orellana, Parque Nacional Yasuní, carretera y oleoducto de Maxus en construcción, 13–16 Sep 1993 (fl), *Dik 449* (BM); Aguarico, Reserva Étnica Huorani, carretera Maxus, km. 72–75, 0°50'S, 76°21'W, 270 m, 23–31 Jan 199–(fr), *Dik & Andi 931* (MO, QCNE); Cantón Aguarico, Reserva Étnica Huorani, carr. Maxus, km 77–78, 0°49'S, 76°19'W, 250 m, 24–28 Feb 1994 (fr), *Dik & Enomenga 1089* (MO, QCNE); 3.5–4.8 km E of Río Conejo on rd to Lago Agrio (7.8–9.1 km W of Lago Agrio), 1 Apr 1972 (fr), *Dwyer & Macbryde 9811* (MO); 17 km W of Lumbaque (70 km W of Lago Agrio), 1130 m, 6 Nov 1974 (fl, fr), *Gentry 12573* (MO); Cantón Orellana, Sector Huashito, 20 km N de Coca, propiedad de PALMORIENTE, 0°20'S, 77°05'W, 250 m, 3–21 Nov 1989 (fr), *Gudiño 150* (MO, NY); road Lago Agrio–El Conejo, between El Conejo and Proyecto San Miguel, 380 m, 15 Feb 1980 (fl, fr), *Harling & Andersson 16534* (MO); road Coca–Aucca oilfields, 3 km along the road to Yocca, 0°28'S, 76°55'W, 400 m, 20 Aug 1979 (fl), *Holm-Nielsen et al. 19635* (AAU); Río Aguarico, Tangoy, 1 hour upstream from Zancudo, 0°34'S, 75°27'W, 300 m, 29 Aug 1979 (fr), *Holm-Nielsen 20092* (AAU, BM); 3 km E de Caserío de Huamani, N de la carretera Hollín-Loreto, 0°43'S, 77°36'W, 1200 m, 17 Sep 1988 (fr), *Hurtado & Alvarado 310* (MO, NY); vfa Lago Agrio–Río San Miguel (frontera con Colombia), 0°10'N, 76°42'W, 700 m, 11 Feb 1980 (fr), *Jaramillo 2232* (MO, QCA); Coca–Río Payamino–Cooperativa de la Comuna, Río Payamino, 23 Feb 1981 (fr), *Jaramillo & Coello 4141* (QCA, QCNE); Parque Nacional Yasuní, Bloque 16, CONOCO, localidad Daimi 1, 0°59'S, 76°12'E, 14 Sep 1989 (fr), *Jaramillo et al. 10941* (NY, QCA); Añangu, Río Napo, 0°31–32'S, 76°23'W, 28 Apr–6 May 1983 (fr), *Lawesson et al. 39532B* (AAU, QCA); Coca, 7 Sep 1983 (fl, fr), *Lescuré 2029* (NY, QCA); 4.2–7.5 km W of Lago Agrio (5–8.2 km E of Río Conejo) near Lago Agrio–Baeza road, 340 m, 31 Mar 1972 (fr), *MacBryde & Dwyer 1366* (MO); carretera Hollín-Loreto, km 32, 8 km W de Guamani, arriba del Río Guamani, 0°43'S, 77°38'W, 1200 m, 20 Sep 1988 (fl), *Neill et al. 8609* (MO, NY); Prov. Orellana, Yasuní National Park, Maxus road and pipeline construction project, km 21, 0°33'S, 76°31'W, 250 m, 24 Jul 1994 (fl, fr), *Pitman 644* (BM, MO, QCNE). **NAPO-PASTAZA:** vic. Puyo, 750–1000 m, Sep 1939 (fl), *Skutch 4545* (MO). **PASTAZA:** Lorocachi, 5 km upriver Río Curaray from the military camp,

1°38'S, 75°58'W, 200 m, 30 May 1980 (fr), *Brandbyge & Asanza 31260* (AAU, BM); Pastaza Cantón, pozo petrolero “Moretecocha” de ARCO, 75 km E de Puyo, 1°34'S, 77°25'W, 580 m, 4–21 Oct 1990 (fl), *Gudiño et al. 854* (BM, MO, NY); Río Papayacu at Río Curaray, 1°29'S, 76°42'W, 235 m, 23 Mar 1980 (fl), *Holm-Nielsen et al. 22639* (AAU); Montalvo, Río Bobonaza, 29 Dec 1976 (fl, fr), *McElroy 251* (CM, QCA). **PICHINCHA:** Carretera Quito–Puerto Quito, km. 113, 10 km al N de la carretera principal, 0°05'N, 79°02'W, 27–29 Dec 1983 (fl, fr), *Balslev & Balseca 4721* (NY, QCA); Reserva Forestal ENDESA, Río Silanche, Corp. Forestal Juan Manuel Durini, km 113 de la carretera Quito–Puerto Quito, 10 km N de la carretera principal, 00°05'N, 79°02'W, 650–700 m, 18 Feb 1984 (fl), *Jaramillo 6360* (MO). **SUCUMBIOS:** Reserva Faunística Cuyabeno, Laguna Grande, 0°00'S, 76°10'W, 265 m, 11 Mar 1990 (fr), *Balslev et al. 97395* (QCNE); Cantón Gonzalo Pizarro, Parroquia El Reventador, 2 km SO del caserío El Reventador, 0°03'S, 77°38'W, 1800 m, 31 Jul 1991 (fr), *Yáñez & Bonilla 339* (QCA).

**PERU. HUÁNUCO:** Pachitea, Codo de Pozuzo, Río Pozuzo, 9°40'N, 75°25'W, 450 m, 18 Oct 1982 (fl, fr), *Foster 9259* (BM, MO); Huánuco to Pamayacu, 13 Jan 1927 (fr), *Kanehira 189* (F). **LORETO:** Prov. Alto Amazonas, Dtto. Pastaza, Río Pastaza, Andoas, Capahuari Norte, 12 Nov 1979 (fr), *Ayala 2252* (NY); Maynas, Dtto. Iquitos, Río Mamon, tributary of Río Nanay, 150 m, 10 Dec 1976 (fl), *Davidson & Revilla 5376* (F, MO, NY); Prov. Maynas, Río Itaya, 10 minutos arriba de San Juan de Munches, 3°58'S, 73°25'W, 130 m, 21 Nov 1978 (fr), *Díaz et al. 644* (MO, NY); Prov. Alto Amazonas, Quebrada Nucuray (tributary del Río Marañón), a media hora arriba de la quebrada, 4°59'S, 75°35'W, 23 Jan 1979 (fr), *Díaz & Ruiz 897* (MO, NY); Prov. Alto Amazonas, Río Pastaza, una hora arriba de la boca del Lago Rimachi, 4°20'S, 76°35'W, 200 m, 25 Jan 1979 (fr), *Díaz & Ruiz 918* (MO, NY); Prov. Alto Amazonas, orillas del Río Pastaza, entre Rimachi y Río Witoyacu, 4°15'S, 76°35'W, 31 Jul 1979 (fr), *Díaz et al. 1298* (MO, NY); Maynas, mouth of Río Nanay below Iquitos, 120 m, 18 Mar 1979 (fl, fr), *Gentry et al. 25818* (MO, NY); Prov. Alto Amazonas, Capihuari, 5 km NE of Andoas on Río Capihuari, near Ecuador border, 240 m, 17 Nov 1979 (fl, fr), *Gentry & Díaz S. 28184* (MO, NY); Prov. Alto Amazonas, Andoas, Río Pastaza near Ecuador border, 2°48'S, 76°28'W, 14 Aug 1980 (fr), *Gentry et al. 29691* (MO, NY); Prov. Maynas, Explorama Camp, Quebrada Sucusari, Río Napo, 3°15'S, 72°55'W, 130 m, 30 May 1991 (fl), *Gentry 74303* (BM, MO, NY); lower Río Momón, tributary of Río Nanay, near Iquitos, 8 Dec 1979 (fl), *Jones & Davidson 9718* (NY); along Río Marañón, near mouth of Río Tigre, 115 m, 19 Aug 1929 (fr), *Killip & Smith 27519* (NY); Puerto Arturo, lower Río Huallaga below Yurimaguas, 135 m, 24–25 Aug 1929 (fl, fr), *Killip & Smith 27753* (NY, US); Río Itaya, above Iquitos, 110 m, 17–22 Sep 1929 (fl), *Killip & Smith 29389* (NY); Mishuyacu, near Iquitos, 100 m, Feb–Mar 1930 (fl), *Klug 910* (F, NY, US); Maynas, Dtto. Iquitos, Río Itaya, barrera de Peña Negra, 110 m, 6 Mar 1973 (fl, fr), *McDaniel 16879* (MO); Maynas, Dtto. Punchana, Río Momón, mouth to Porvenir, 90 m, 10 Jan 1994 (fl, fr), *McDaniel & Rimachi Y. 32105* (MO); Distrito Iquitos, Creek Itaya, 100 m, 6 Feb 1932 (fl), *Mexia 6485* (F, MO, NY, PH, UC); Río Javari, below mouth of



Rio Curaça, 27 Oct 1976 (fr), *Prance et al. 24160* (MO, NY); Gamitanacocha, Río Mazán, 100–125 m, 18 Jan 1935 (fl), *Schunke 77* (F, NY, UC); Maynas Prov., Las Amazonas, rivera de la Quebrada Sucusari, Explor Napo Camp, 3°20'S, 72°55'W, 140 m, 18 Apr 1991 (fr), *Vásquez & Jaramillo 16131* (MO); Caballo-Cocha on the Amazon River, 14 Aug 1929 (fl), *Ll. Williams 2479* (F); Alto Río Itaya, 145 m, 10 Sep 1929 (fl), *Ll. Williams 3448* (F). **PASCO:** Prov. Oxapampa, Palcazu valley, Cabeza de Mono, 5–6 km W of Iscosacin, 10°12'S, 75°14'W, 325 m, 17–20 Apr 1983 (fr), *D. N. Smith 3825* (NY).

**BRAZIL. ACRE:** Município Rio Branco, estrada Rio Branco/Puerto Acre km 33, a 2 km da margem, 12 Oct 1980 (fr), *Cid & Nelson 2883* (NY); Município Bujari, basin of Rio Purus, Rio Antimari, Floresta Estadual do Antimari, 9°24'S, 68°07'W, 8 Mar 1997 (fl, fr), *Daly et al. 9352* (MO); Boca do Acre–Rio Branco road, 14 km from Rio Branco, 27 Sep 1980 (fr), *Lowrie et al. 228* (R); Proj. RADAM, sub-base de Cruzeiro do Sul, Ponto 2, SB-18-ZB, 16 Feb 1976 (fl, fr), *Marinho 206* (NY); Município Sena Madureira, Fazenda Nova Olinda, 10°07'S, 69°13'W, 8 Sep 1995 (fr), *Oliveira et al. 644* (NY); Mun. Bujari, Riozinho do Andirá, 24 Mar 1995 (fl, fr), *M. de Pardo et al. 60* (MO); Maitá, Rio Moa, 26 Oct 1966 (fl, fr), *Prance et al. 2893* (NY, WIS); Mun. Sena Madureira, bacia do Rio Purus, Faz. Nova Olinda, Rio Iaco, Carreador do São Bento II, ca. 10 km da Sede, 10°07'S, 69°13'W, 29 Oct 1993 (fr), *Silveira et al. 686* (MO, NY); RBO-AC, F.E.A., Rio Antimari, 26 Feb 1992 (fr), *Sothers & Santos 83* (MO, NY). **AMAZONAS:** Mun. São Paulo de Olivença, Palmares, 11 Sep–Oct 1936 (fl), *Krukoff 8421* (F).

**BOLIVIA. COCHABAMBA.** Prov. Carrasco: Puerto Villarroel, 16°49'S, 64°48'W, 200 m, 8 Jun 2000 (fr), *Villavicencio et al. 1780* (NY). **LA PAZ.** Prov. Iturrealde: Luisita, W del Río Beni, zona inundada del Río Muquí, 13°05'S, 67°15'W, 180 m, 29 Feb 1984 (fl, fr), *Beck & Haase 10142* (MO). **SANTA CRUZ.** Prov. Ichilo: [Río] Yapacaní, 400 m, Jun 1892 (fl), *Kuntze s.n.* (NY); Parque Nacional Amboró, Río Saguayo, 17°40'S, 63°44'W, 500 m, 19 Jan 1988 (fr), *Nee 35991* (NY, USZ); La Víbora, ca. al puente sobre el Río Chore, 17°20'S, 63°55'W, 275 m, 9 Nov 1990 (fr), *Saldias et al. 1274* (MO, NY).

*Solanum pedemontanum* belongs to a closely related assemblage of woody vines that scramble by means of recurved prickles. Four species are found in Mexico and Central America (Nee, 1993), but many more are found in South America, including this surprisingly widespread species that has not yet received a name. The group has been called the *Solanum lanceifolium* group by Whalen (1984) and section *Micracantha* Dunal by Nee (1999).

Evidently some flowers are functionally male, as heterostyly is common in all collections seen. However, a study of the living plants is needed to fully understand the sexual expression of the flowers.

The young parts are ferruginous-tomentose, but the general aspect is much paler and more yellowish than in *Solanum aturense* Dunal, which is partly sympatric in the northern part of the range of *S. pedemontanum*. The underside of the leaf, in particular, has both pale stellate hairs and a partially visible pale surface. The very close tomentum of this species is a good visual character. A few of the specimens resemble *S. leucopogon* Huber with very short trichome midpoints instead of the long midpoints that gives a very pilose appearance to the latter species.

Part of this material was reported for Peru by Macbride (1962) as *Solanum heterophyllum* Lam., a synonym of *S. subinermis* Jacq., which differs by being an upright shrub with violet corollas and decidedly curved anthers. *Solanum pedemontanum* resembles the description of *S. ternifolium* Werderm., a species described in the mid-20th century (Werdermann, 1940) from a single Ecuadorian specimen collected at Mera (*Shulze-Rhnhöf 2858*) and lost from the Berlin herbarium during the Second World War. The description of *S. ternifolium* is detailed but not quite definitive; the name is much more likely a synonym of *S. aturense* Dunal. Only the local phase of *S. aturense*, but not *S. pedemontanum*, would be described as having “pedunculo . . . stellato-piloso,” “calyx stellato-pilosus,” and “corolla . . . extus dense stellato-pilosis.”

***Solanum comarapanum* M. Nee, sp. nov.**

**TYPE:** Bolivia. Santa Cruz. Prov. Caballero: Abra Catalina, along hwy. from Comarapa to Cochabamba, 8 km W of Comarapa, 17°54'S, 64°36'W, 2425 m, 10 Mar 1988 (fl, fr), *M. Nee & J. Solomon 36599* (HOLOTYPE: LPB; ISOTYPES: AD, BH, CORD, K, MO, NY, USZ, WIS).

(Fig. 10)

Frutex 1.5–3 m altus; rami juniores aculeis rectis vel parum recurvatis ad 8 mm longis armati, vetustiores saepe inermes; caules dense stellato-tomentosi; folia ramorum floriferorum plerumque inermia, ovata, 7–20 × 3–10 cm, ambitu variabilia, integra, repanda vel lobulata. Inflorescentiae 2–4-ramosae; calyx tubo 2 mm longo, lobis lanceolatis ad fere linearibus; corolla rotato-quinquangula, 2–2.5 cm lata; antherae 4.5–5 mm longae, fere lineares; ovarium dense stellato-tomentosum. Baccae dense stellato-tomentosae, 1.9 cm



**FIG. 10.** *Solanum comarapanum* M. Nee. **A.** Juvenile leaf. **B.** Branch with flowers and fruits. **C.** Flower at anthesis, abaxial and adaxial views. **D.** Anthers. **E.** Gynoecium. **F.** Infructescence. (A, C–E based on Nee & Solomon 34035, NY; B based on Nee *et al.* 37413, NY; F based on Nee & Solomon 36599, NY.)

diametro; semina complanata, reniformia,  $3.6 \times 2.9$  mm.

Shrubs 1.5–3 m tall; stems densely stellate-tomentose, ferruginous when young, paler when mature, with 6–9-rayed stellae ca. 0.6 mm broad, the midpoints ca. 0.2 mm long, young plants and sprouts normally armed with broad-based prickles to 8 mm long, these mostly straight, some slightly reflexed or recurved, the base usually densely tomentose, older stems mostly unarmed. Sympodial units difoliate, not geminate. Leaves 7–20  $\times$  3–10 cm, simple, more or less uniform in size and shape on flowering branches, but those of young plants or sprouts much larger (to 35  $\times$  23 cm), ovate, thin-textured, pubescent adaxially with stipitate stellae 0.3–0.6 mm broad, the rays 6–8, the midpoints ca. 1 mm long, the stipes variable in length, up to 0.2 mm long, more densely stellate-tomentose abaxially and with the stellae lighter in color, unarmed except rarely with a few stout prickles on major veins on undersides of sprout leaves; base truncate to rounded, oblique; margin highly variable in outline, with leaves of flowering stems often entire or irregularly repand or lobed near the base, the juvenile leaves with three lobes per side, the sinuses to reaching within 2 cm of the midrib and the lobes again pinnately lobed, the lobes rounded to rarely acute; apex attenuate to sometimes rounded; petioles to 5 cm, densely stellate-tomentose, unarmed except on sprouts, then with prickles 1.5–2.5 (–4) cm long like those of the stem. Inflorescences 4–8 cm, extra-axillary, 2–4 branched, with few to 26 flowers, all flowers evidently perfect, the axes densely stellate-tomentose with hairs like those of the stem, unarmed; peduncle 1–2 cm; rachis 2–6 cm; pedicels ca. 10 mm in flower, 17–19 mm in fruit, sulcate and slightly clavate, spaced 2–4 mm apart, articulated at the base; calyx 3–7 mm long, the tube ca. 2 mm, the lobes 4.5–8  $\times$  ca. 1.5 mm, lanceolate to nearly linear, densely stellate-tomentose abaxially; fruiting calyx not accrescent, the lobes 4.5–8  $\times$  ca. 1.5 mm; corolla 2–2.5 cm in diameter, 8–11 (–16) mm long, rotate-pentagonal, white, the tube 1 mm, the lobes 7.5–11 (–15)  $\times$  2.5–5 mm, deltate, with ample interpetalar tissue, densely stellate-tomentose abaxially on the

midribs with slightly smaller and finer stellae than on the stems, glabrous adaxially; filaments glabrous, the free part ca. 1.5 mm, the filament tube absent; anthers 4.5–5  $\times$  1–1.3 mm, nearly linear, connivent, yellow, the pores minute and directed distally, not opening into longitudinal slits with age; ovary densely stellate-tomentose; style ca. 7  $\times$  0.4–0.5 mm, cylindrical, straight or slightly curved, with a few stellae in the basal third; stigma capitate. Fruit a globose berry, to 1.9 cm in diameter, shiny, green when immature, the color when mature not known, densely stellate-tomentose with sessile stellae, tardily glabrescent. Seeds ca. 25 per berry, ca. 3.6  $\times$  2.9 mm, flattened, reniform, yellowish tan, the surfaces minutely foveolate.

*Distribution and ecology.*—Known only from a small area of the mountains at the border of the Departments of Cochabamba and Santa Cruz at (1300–)2100–2800 m elevation. It apparently also occurs in the Department of Tarija, but the identification of the single collection is still somewhat doubtful. It occurs in weedy disturbed areas such as along roadsides in the dry forests just below the cloud forest zone but does not descend into the semi-arid valleys, which are dominated by cacti and *Schinopsis haenkeana* Engl. (Anacardiaceae). Many of the collections are from the highway to Cochabamba between Comarapa and the cloud forest area known as “Siberia.”

*Phenology.*—Flowering in March, June, and December; fruiting in February, March, June, and December.

*Etymology.*—The species is named after the town of Comarapa, the site of many collections of this species.

Additional specimens examined. **BOLIVIA. COCHABAMBA.** Prov. Carrasco: Siberia, 2800 m, Dec 1959 (fl, fr), *M. Cárdenas* 5779 (K). **SANTA CRUZ.** Prov. Caballero: 12.5 km by road NW of Comarapa on road to Cochabamba, near Torrecillas, 2450 m, 10 Feb 1987 (fr), *Nee & Solomon* 34035 (LPB, NY); along road from Comarapa to Cochabamba, 15 km NW of Comarapa, 6.5 km NW of Torrecillas, 2600 m, 10 Mar 1988 (fr), *Nee & Solomon* 36605 (LPB, NY); hwy. from Comarapa to Cochabamba, 4 km (by air) NW of Comarapa, 17°54'S, 64°34'W, 2100 m, 11 Dec 1992 (fl), *Nee* 43056 (LPB, NY, USZ). Prov. Florida: Hierba Buena, 1300 m, 8 Jun 1966 (fl, fr), *R. F. Steinbach* 271 (F, GH, MO, NY, UC, WIS). Prov. Vallegrande: 6 km E of Guadalupe, 2450 m, 5 Feb 1988 (fr), *Nee & Saldias* P. 36242 (LPB, NY); between Mataralcito and El Palmar on road from Valle-



grande to Tierras Nuevas, 17 km ESE of Vallegrande, 2150 m, 29 Dec 1988 (fl, fr), *Nee et al. 37413* (LPB, NY). **TARIJA.** Prov. O'Connor: camino de Junacas a Narváez, 1950 m, 8 Nov 1974 (fl), *Türpe et al. 5047* (W).

Most species of spiny solanums, and perhaps most especially those of this group (the *Solanum torvum* group of Whalen, 1984 or section *Torva* Nees of Nee, 1999), are characterized by the leaves becoming progressively smaller and less lobed as the plant matures. Saplings and sprouts have deeply lobed, spiny leaves and often the flowering branches of older plants have much smaller, entire, and unarmed leaves, sometimes being easy to confuse with the unarmed subgenus *Solanum*. However, each species has a particular range of variation of leaf lobing. *Solanum comarapanum* has very tomentose and unusually prominently lobed leaves except on the oldest or least vigorously growing material, and at least some of the lobes tend to be undulate. The herbarium specimens available have a widely divergent aspect because of this leaf lobing, but observations in the field and collections from individual plants demonstrate that they all belong to a single species. The very pubescent fruits are useful for identification, but apparently this is variable, as some collections, noticeably *Nee & Saldias 36242* and *Nee et al. 37413*, have glabrescent fruits; fully mature fruits of this species are not yet known. The ferruginous color of the young growth, partly maintained in older plants, is obscured on many of the specimens as they were collected at the edge of the gravel highway and the dense tomentum has become covered with road dust.

***Solanum saturatum* M. Nee, sp. nov.** TYPE:

Bolivia. Santa Cruz. Prov. Caballero: 1.5 km down from El Empalme (on Comarapa–Cochabamba hwy) on road to Khara Huasi, 17°50.4'S, 64°42.2'W, 2475 m, 2 Aug 2003 (fl), *M. Nee et al. 52413* (HOLOTYPE: USZ; ISOTYPES: LPB, NY).

(Fig. 11)

Frutex 1–4 m altus; caulis ad 4 cm diametro; rami juniores aculeis parum recurvatis ad 7 mm longis armati, vetustiores fere semper inermes; caules dense stellato-tomentosi; folia ramorum floriferorum inermia, ovato-lanceolata, 7–15 × 3–10 cm, integra vel lobata. Inflorescentiae simplices vel 2-ramosae; calyx lobis triangulariter apiculatis; corolla rotato-quinquangula, 4–

4.5 cm lata; antherae 9–11 × 2 mm, attenuatae; ovarium glabrum. Baccae glabrae, 1.2–1.4 cm diametro; semina complanata, reniformia, 2.5 × 2 mm.

Shrubs or treelets, 1–4 m tall; stems sparsely tomentose with sessile or stipitate 7–8-rayed stellate hairs 0.7–0.8 mm wide, the midpoints absent, grading into small prickles to at least 2 mm long with a stellate hair on the tip, fertile branches densely stellate-tomentose with sessile or short-stalked stellae, the younger parts ferruginous-tomentose, the lower part of the main stem and sprouts heavily armed with thick-based, slightly recurved prickles to 7 × 3 mm at the base, with sessile stellae on the bottom 1/3; fertile branches unarmed, or only rarely with a few short prickles. Sympodial units unifoliate or the uppermost ones bifoliate and geminate. Leaves 7–15 × 3–10 cm, more or less uniform in size and shape, but younger plants or sprouts with much larger leaves (to 22 × 16 cm), ovate-lanceolate, thin-textured, ferruginous-tomentose on both sides with sessile or short-stalked stellae, scabrous adaxially with sessile 5–7-rayed stellae 0.5–0.6 mm wide, the midpoint nearly obsolete to 0.3 mm long, the leaf surface partially visible, more densely and loosely tomentose abaxially with lighter colored short-stalked stellae obscuring the leaf surface, unarmed even on vigorous sprout leaves (except on very young plants or sprouts); base truncate to cuneate; margins of blades on fertile branches usually entire, or sometimes with 2 shallow lobes per side; apex acute; petioles 1–2.5 (–5.5) cm, densely stellate-tomentose, unarmed. Inflorescence 2–5.5 cm, extra-axillary, usually appearing terminal, eventually overtopped and lateral, unbranched or forked, with 3–10 flowers, often with one flower at the base and the rest more clustered toward the tip, all flowers perfect, the axes ferruginous-tomentose with stellate hairs, unarmed; peduncle 0–0.8 cm; rachis 2–3.5 cm; pedicels 13–15 mm in flower, up to 20 mm in fruit, spaced 3–8 mm apart, articulated at the base. Flowers with a thick sweet fragrance, the calyx ca. 5 mm long, the lobes ca. 3 × 2.5 mm, triangular, apiculate at tips, densely stellate-tomentose; fruiting calyx not accrescent, the lobes ca. 3 × 2.5 mm; corolla 4–4.5 cm in diameter, 25 mm long, rotate-stellate, pentagonal in bud, white, the tube 6 mm, the

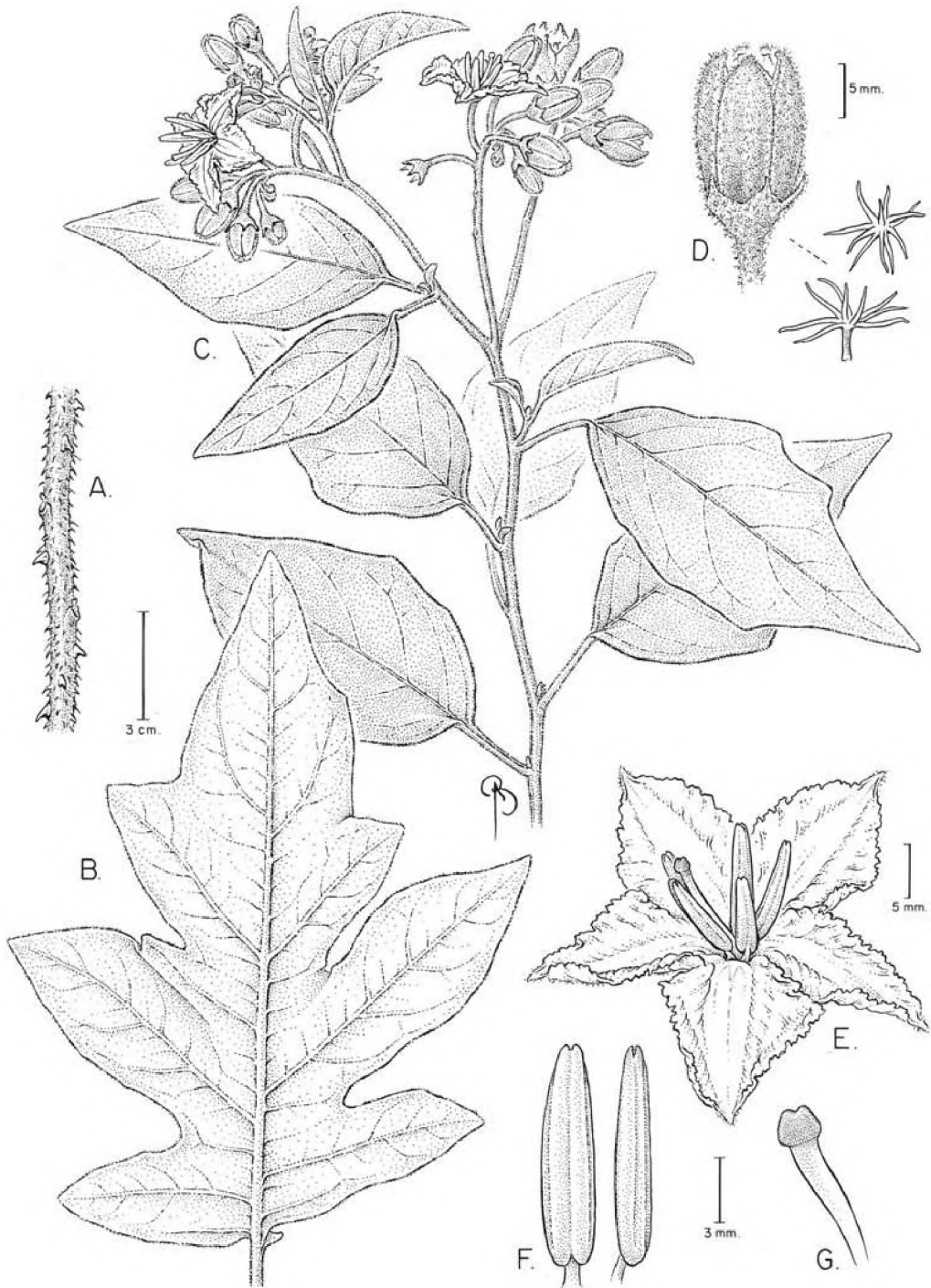


FIG. 11. *Solanum saturatum* M. Nee. A. Stem detail. B. Juvenile leaf. C. Flowering branch. D. Bud with detail of stellate hairs. E. Flower at anthesis. F. Anthers. G. Style and stigma. (A based on Steinbach 8343, NY; B-G based on Nee et al. 52413, NY.)

lobes ca. 10 × 15 mm, ovate-lanceolate, with ample glabrous interpetalar tissue, acute at apices, abaxially pubescent with brownish hairs on the midrib, glabrous adaxially; filaments glabrous, the free part 2–3 mm, the filament tube absent; anthers 9–11 × ca. 2 mm, tapered, not connivent, yellow, the pores small and directed distally, not opening into longitudinal slits with age; ovary glabrous; style ca. 11 × 0.5 mm, cylindrical, straight or slightly curved, glabrous; stigma capitate. Fruit a globose berry, 1.2–1.4 cm in diameter, green (perhaps not fully ripe?), glabrous. Seeds numerous (one count of 17), ca. 2.5 × 2 mm, flattened-reniform, yellow, minutely foveolate.

*Distribution and ecology.*—Found in the cloud forest along the “old” highway from Santa Cruz to Cochabamba, in the Departments of Cochabamba and Santa Cruz, Bolivia at 2200–3000 m elevation.

*Phenology.*—Flowering in February, May, June, August, September, and October, and fruiting in February, August, and October. It will probably be found to flower and fruit throughout the year.

*Etymology.*—The epithet *saturatum* refers to the thick sweet fragrance of the flowers, an odor rare elsewhere in *Solanum*, but also found in related species of the *S. torvum* group from Department La Paz, Bolivia into Peru.

Additional specimens examined. **BOLIVIA. COCHABAMBA OR SANTA CRUZ:** hwy. Cochabamba–Santa Cruz, km. 205, 9000 ft, 18 Sep 1964 (fl), *Badcock 381* (K, NY). **COCHABAMBA.** Prov. Carrasco: Siberia Este, Monte Hotel, 17°47'19"S, 64°47'18"W, 2700 m, 22 Sep 2003 (fl), *Duran et al. 92* (MO); hwy. Epizana–Comarapa, 15 km (by road) E of highway bridge near Pojo, 9 km W of El Churo, 17°47'S, 64°48'W, 2675 m, 24 May 2001 (fl), *Nee et al. 51856* (NY); road from Comarapa to Cochabamba, 4 km W of border with Depto. Santa Cruz, 20 km (by air) and 28 km (by road) NW of Comarapa, 17°49'S, 64°41'W, 2525 m, 10 Feb 1987 (fr), *Nee & Solomon 34054* (LPB, NY). **SANTA CRUZ.** Prov. Caballero: S of Ambaró National Park, Cerro Bravo area, 4–10 km N of Comarapa, 17°51'S, 64°32'W, 2300–3000 m, 23 Jun 1995 (fl), *Abbott & Jardim 17206* (NY); Siberia Sud, Astilleros, 17°50'37'S, 64°42'10"W, 2850 m, 20 Sep 2003 (fl), *E. Fernández et al. 31* (MO); Astillero, 17°49'26"S, 64°41'22"W, 2550 m, 13 Aug 2003 (fl, fr), *E. Fernández et al. 2002* (MO); between Capilla and Siberia on the old Cochabamba hwy, 17°50'S, 64°42'W, 2500 m, 18 Aug 2000 (fl), *Kuroiwa & Maeda 2205* (NY); 6.5 km (by air) N of Comarapa, Cerro Bravo area, 17°51.6'S, 64°32.1'W, 2380 m, 3 Aug 2003 (fl), *Nee et al. 52442* (NY); Empalme, 17°49'13'S,

64°36'37"W, 2600 m, 6 Feb 2004 (fl, fr), *Rivera et al. 52* (MO); Bergwald von Comarapa, 2800 m, 20 Oct 1928 (fl, fr), *J. Steinbach 8343* (BM, E, F, GH, MO, NY, PH). Prov. Florida: 7 km (by air) NE of Mairana, 18°04'S, 63°55'W, 2200 m, 2 Jun 1991 (fl), *Nee 40657* (NY).

*Solanum saturatum* is a member of Whalen's (1984) *Solanum torvum* group and Nee's (1999) section *Torva*. Before more material became available and fieldwork demonstrated the difference of the two species, *Nee & Solomon 34054* and *J. Steinbach 8343* were considered to belong to *S. comarapanum*. The two are nearly sympatric, but *S. saturatum* grows in clearings in cloud forest, whereas *S. comarapanum* is more likely to be found on shrubby roadsides in drier woodland just below this cloud forest zone. The leaves of *S. saturatum* never develop the complex lobing found in *S. comarapanum*.

*Solanum saturatum* is morphologically somewhat similar to the local expression of *S. asperolanatum* Ruiz & Pav. (often annotated as its synonym *Solanum hispidum* Pers.), but this species in the Siberia area has long-stipitate stellate hairs giving it a distinctly bristly appearance, and its inflorescence does not begin branching near the base, but instead in the more distal half of the inflorescence.

***Solanum scuticum* M. Nee, nom. nov.** Replaced name: *Solanum tabacifolium* Dunal, in A. DC., Prodr. 13(1): 261. 1852. nom. illeg. TYPE: Brazil, Bahia, 1830, *Salzman 389* (HOLOTYPE: G–DC [F neg. 6808, photos: BH, F, MO, NY, US]; probable isotypes (without number but “nov. sp.”): K-2 sheets, W). Non *S. tabacifolium* Vell., 1825. (Fig. 12)

Shrubs 1.5–3 (–4) m tall; flowering stems densely ferruginous-tomentose with 7–8-rayed stellae 0.4–0.8 mm broad, with stipes of various lengths, to 1 mm long, tardily and irregularly glabrescent, unarmed or often with a few broad-based prickles to 4 mm long. Sympodial units difoliate, geminate. Leaves simple, dimorphic, the major leaves 15–23 × 7–12 cm, ovate, the minor leaves 8.5–14 × 5–9.5 cm, about the same shape as the majors, thin-textured, moderately and evenly ferruginous-tomentose adaxially with 4–8-rayed stellae 0.3–0.5 mm wide, the hairs



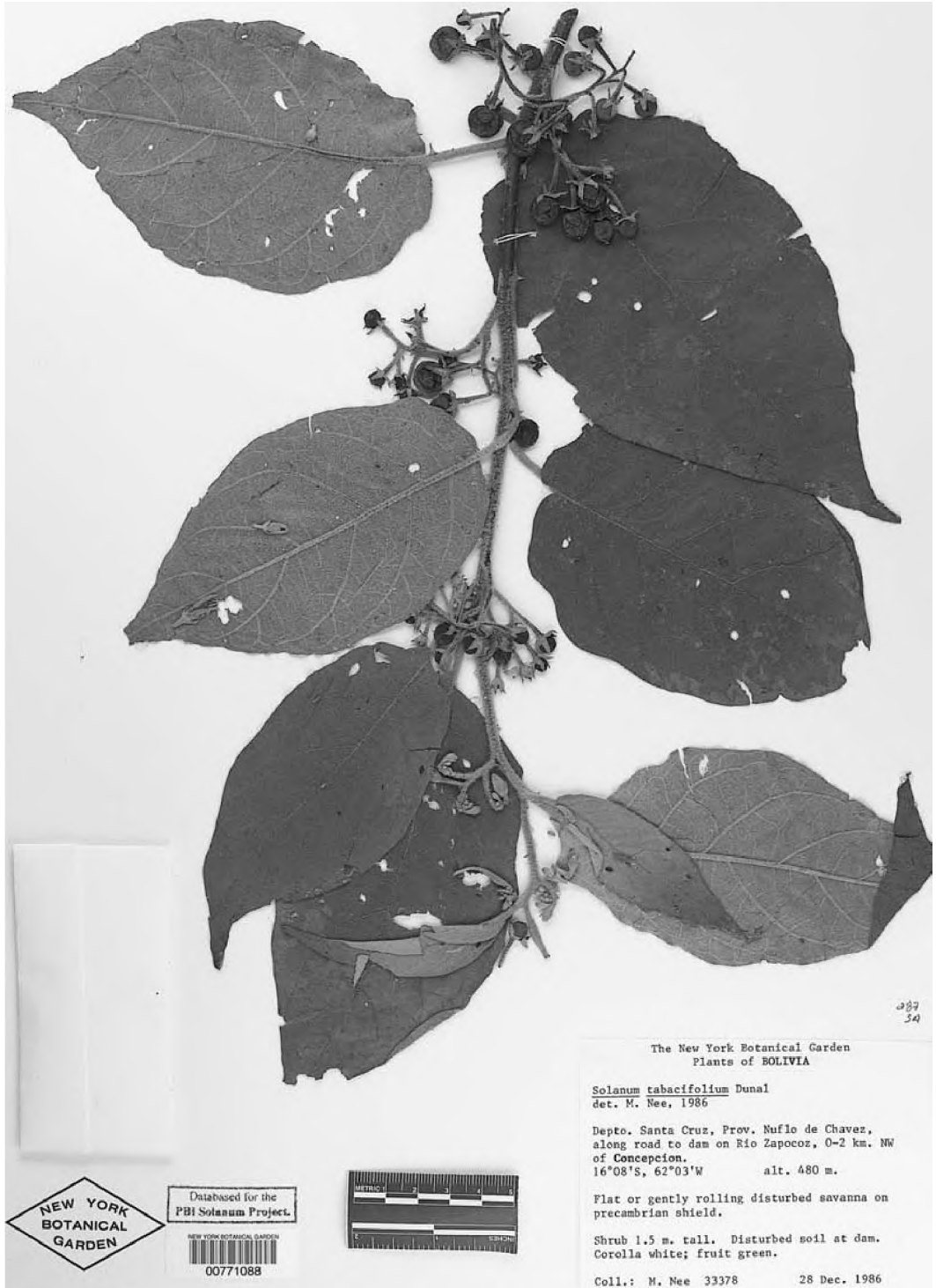


FIG. 12. Representative specimen of *Solanum scuticum* M. Nee (Nee 33378, NY).

mostly sessile and not overlapping, but with denser and more stipitate hairs on the major veins, densely pale stellate-tomentose abaxially with mixed sessile and stipitate stellae forming several layers, the stipitate stellae like those of the stem, usually unarmed abaxially or with a few acicular prickles up to 9 mm long on the major veins beneath; base acute to truncate or subcordate, unequal; margin usually entire, but often irregularly repand to undulate or with 1–3 shallow lobes per side; apex acute to attenuate; petioles 1–1.5 (–3.5) cm, stellate-tomentose like the stem, unarmed or rarely with a few prickles like those of the leaf underside. Inflorescence 0.5–3 cm, opposite the leaves, branched, many- (more than 10-) flowered, all flowers perfect, the axes densely ferruginous-tomentose, the stellae 6–8-rayed, the midpoints slightly shorter than the rays, the stipes of various lengths, to 0.6 mm long; peduncle 0–0.7 cm; rachis 1.5–4.5 cm; pedicels ca. 8 mm in flower, to 11–20 mm long in fruit, spaced 1–2 mm apart, articulated at the base. Calyx 3 mm long, the tube 2 mm, the lobes ca. 1 × 1.5–2.5 mm, triangular, attenuate-apiculate at tips, densely stellate-tomentose abaxially; fruiting calyx not accrescent, the lobes ca. 1 × 1.5–2.5 mm; corolla ca. 2 cm in diameter, 14–16 mm long, stellate-pentagonal, white, the tube 2–3 mm, the lobes 9 × 4.5 mm, deltate, with ample interpetalar tissue, acute at apices, closely and finely stellate-tomentose abaxially on the midrib with stellae smaller than on the rest of the inflorescence, glabrous adaxially; filaments glabrous, the free part ca. 1 mm, the filament tube absent; anthers 6–7.5 × 1 mm, tapered, free, yellow, the pores minute and directed distally, not opening into longitudinal slits with age; ovary densely stellate, glabrescent; style of hermaphrodite flowers ca. 8 × 0.3–0.5 mm, cylindrical, straight, stellate in the lower part; stigma capitate. Fruit a globose berry, 0–1.4 cm in diameter, green, turning yellow-orange, glabrous. Seeds numerous, 90–265 per fruit, 1.6–2.5 mm, flattened-reniform, yellow, the surface minutely foveolate.

*Distribution and ecology.*—Only the Bolivian and Paraguayan collections are listed here; there are very numerous collections from Brazil from the states of Acre, Bahia,

Distrito Federal, Espírito Santo, Goiás, Mato Grosso, Minas Gerais, Paraná, Rio de Janeiro, Rondônia, Santa Catarina and São Paulo, where it is a common, somewhat weedy species of open areas and forest edges. The distribution nearly coincides with the geological formation of pre-Cambrian crystalline rocks, known as the Brazilian shield. In Bolivia the known distribution is also confined to the pre-Cambrian shield area of eastern Department Santa Cruz.

*Etymology.*—The epithet *scuticum* is derived from the Latin *scutum*, a shield, in figurative reference to the geological Brazilian shield.

Additional specimens examined (outside Brazil). **BOLIVIA. SANTA CRUZ.** Prov. Ñuño de Chávez: E of San Javier on road to Concepción, 16°17'S, 62°21'W, 450 m, 22 Feb 1995 (fl, fr), *Abbott 16345* (SI); road to dam on Río Zapocoz, 0–2 km NW of Concepción, 480 m, 28 Dec 1986 (fl, fr), *Nee 33378* (LPB, NY); 6 km E of San Javier on road to Concepción, 16°16'S, 62°27'W, 540 m, 1 Dec 1990 (fr), *Nee 40142* (LPB, MO, NY).

**PARAGUAY. AMAMBAY:** Upper Río Apa, Jan 1912–13 (fl), *Hassler 11252* (BM, GH, K, MO, S, UC, W).

This common species, a member of section *Torva* sensu Nee (1999) or the *Solanum torvum* group sensu Whalen (1984), is here documented from Bolivia; it has long needed a name, but none has been found among the several thousand epithets that have been proposed in *Solanum*. The species was known to Sendtner (1846) who treated it under a very heterogeneous concept of *Solanum torvum* Sw., in which he included several other species from Mexico to Brazil in a complicated hierarchy of infraspecific taxa at indeterminate ranks, rendering all his infraspecific epithets invalid. These names will be treated in more detail in a revision of section *Torva* (Whalen & Nee, in prep.). The similar *S. torvum*, found sparingly along coastal eastern Brazil from Bahia to São Paulo and now spread throughout the tropics as an abundant weed, differs most obviously by its sparsely glandular-tomentose pedicels; *Solanum scuticum* lacks glandular hairs on the pedicels.

*Solanum tabacifolium* Dunal is a later homonym of *S. tabaccifolium* Vell. and thus illegitimate (Greuter et al., 2000; Article 53.1.). *Solanum tabaccifolium* Vell. is probably a synonym of *S. mauritianum* Scop., a

widespread member of the *Brevantherum* clade sensu Bohs (2005).

A Brazilian specimen, *Lhotsky s.n.* (G-DC), was one of the three syntypes of *S. daturifolium* Dunal; it belongs to *Solanum scuticum*. However, from among the syntypes, Schulz (1909) chose *Sieber 67* (G) from Martinique as the lectotype for *S. daturifolium* Dunal. *Sieber 67* belongs to the widespread species *S. torvum* Sw., making the name *S. daturifolium* a synonym of *S. torvum*.

*Solanum scuticum* is similar to *S. rudepannum* Dunal from Mexico, Central America, Colombia, and Ecuador in having very ferruginous inflorescences, stems, and leaves. However, in *S. scuticum* the calyx in bud stage is much shorter than that of *S. rudepannum* and the lobes are very shallow. In late bud stage and especially by the time the plant is in fruit, the calyx lobes split apart and become oblong, often with an acuminate tip. Many herbarium specimens of *S. scuticum* had been previously identified as *S. asperolanatum* Ruiz & Pav., but this is a very different, more robust species from mid-elevations in the Andes from Bolivia to Venezuela, with a larger inflorescence which normally has a peduncle several cm long.

***Solanum whalenii* M. Nee, sp. nov.** TYPE:

Bolivia. La Paz. Prov. Nor Yungas: 3.2 km S of and below Chuspipata on road to Chulumani, 16°18'S, 67°49'W, 2900–3000 m, 28 Sep 1985 (fl), M. Nee & J. Solomon 31958 (HOLOTYPE: LPB; ISOTYPES: AD, BH, CORD, G, K, MO, NY, P, US, WIS).

(Fig. 13)

Frutex vel arbor parva, 2–8 m altus; caules aculeis muniti. Folia ovata, integra vel leviter lobata, (12–) 18–40 × (6–) 10–20 cm, valde bicoloria, super glabrescentia viridiaque, inferne dense et persistenter albidotomentosa. Inflorescentia extra-axillaris, dense albidotomentosa, (7–) 10–25 cm, 2–9-ramosa, pedunculo 1.5–3.5 cm longo; pedicelli floriferi 2–2.5 cm longi, fructiferi 2.4–3.1 cm longi, 5-angulati; corolla alba, 4 cm diametro, profunde 5-lobata; antherae 8.5 × 2.5 mm. Fructus glaber, 1.2–1.5 diametro, viridis; semina plurima, 2 × 1.6 mm. *Solano albido* Dunal valde simile sed robustius.

Shrub or tree, 2–8 m tall; stems densely appressed-tomentose with sessile, multi-rayed stellae so dense as to be individually difficult to distinguish, flowering stems usually unarmed but the lower stem with stout prickles, younger stems conspicuously striate

when dry. Sympodial units difoliate, geminate. Leaves (12–) 18–40 × (6–) 10–20 cm, simple, more or less uniform in size and shape, ovate on flowering stems, strongly bicolorous, thin-textured, initially pubescent adaxially with sessile whitish stellae 0.4 mm broad and with ca. 16 rays, the midpoints very short or obsolete, soon glabrate-green, densely white-tomentose abaxially with sessile and short-stipitate stellae in interwoven layers, with about 16 rays, the midpoints obsolete, unarmed; base asymmetrically obtuse to sub-cordate, rarely acute; margin entire or obscurely sinuate-repand; apex acuminate; petioles of major leaves 4–5 cm, strongly striate or canaliculate when dry, this striation continuing onto the lower part of the midvein and onto the stem, densely whitish tomentose like the stem, unarmed. Inflorescence (7–) 10–25 cm, up to ca. 30 cm in fruit, extra-axillary, 2–9-branched, with many (up to more than 100) flowers, all flowers apparently perfect, the axes densely stellate-tomentose; peduncle 1.5–3.5 cm; rachis 4–16 cm, up to 26 cm in fruit; pedicels 20–25 mm in flower, to 24–31 mm in fruit, spaced 3–5 mm apart, straight, relatively stout, gradually enlarged toward apex, 5-angled; calyx 6–10 mm long, the tube ca. 2 mm long, 5-costate, the lobes ca. 2 × 4 mm, deltoid, apiculate at tips, densely stellate-tomentose abaxially; fruiting calyx somewhat accrescent, often splitting in the sinuses and the lobes then appearing longer, the lobes 6–7 × 3–4 mm; corolla ca. 4 cm in diameter, 21–25 mm long, rotate-stellate, white, the tube 1.5–2 mm, the lobes 19–23 × 5–6 mm, ovate-lanceolate, with ample glabrous interpetalar tissue, acute at apices, densely stellate-tomentose abaxially with stellae like those of the inflorescence, glabrous adaxially except for a few stellate hairs distally along the midrib; filaments glabrous, the free part ca. 2 mm, the filament tube absent; anthers 8.5 × 2.5 mm, slightly tapered, not connivent, yellow, the pores small, directed distally, not opening into longitudinal slits with age; ovary glabrous or minutely stipitate-glandular at apex; style 11–13 × 0.8–0.9 mm and well-exserted, cylindrical, straight or somewhat curved, glabrous or minutely stipitate-glandular at base; stigma capitate. Fruit a globose berry, 1.2–1.5 cm in diameter, dark



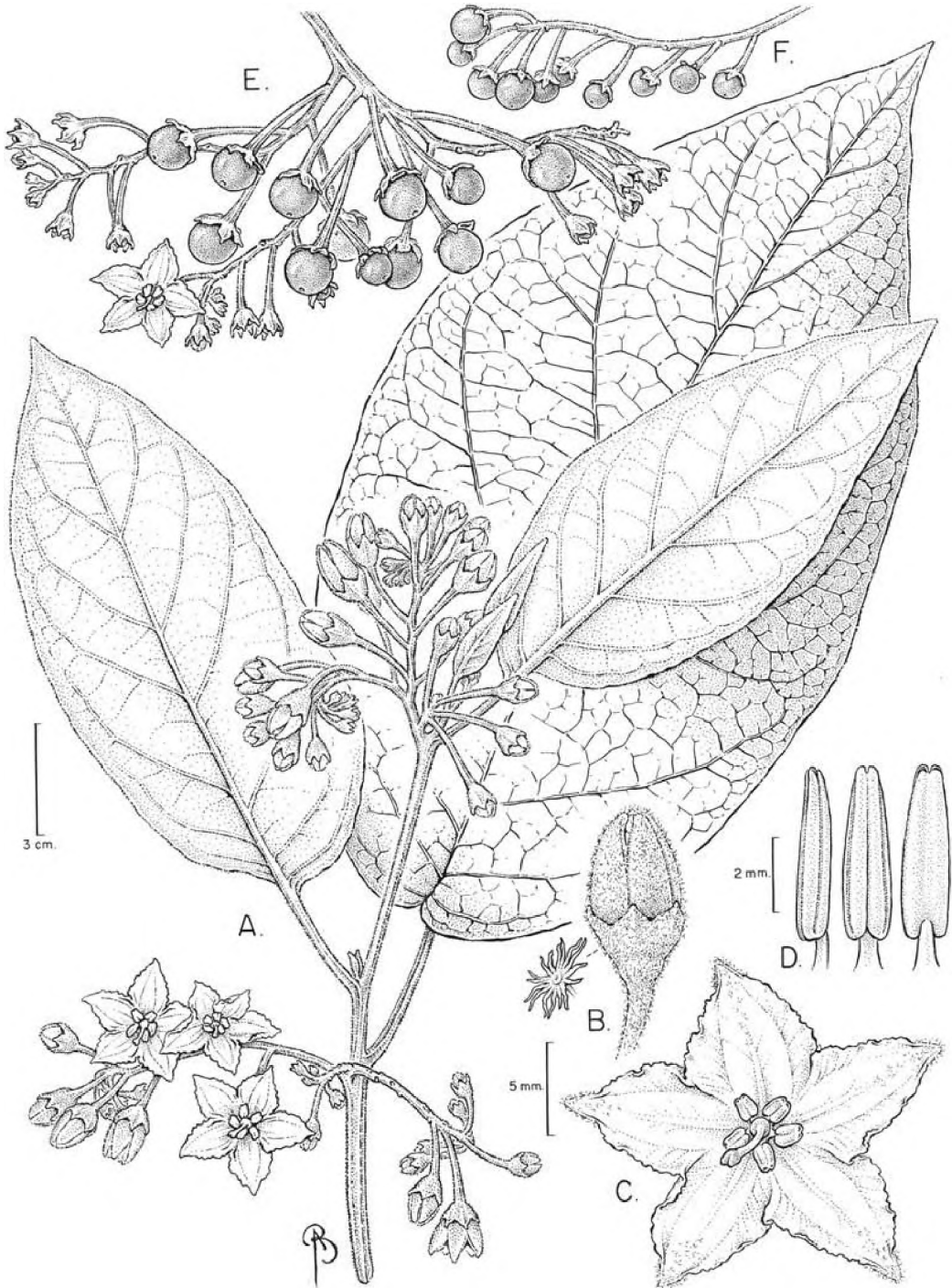


FIG. 13. *Solanum whalenii* M. Nee. **A.** Leafy branch with inflorescences. **B.** Bud with detail of inflorescence trichomes. **C.** Open flower. **D.** Anthers. **E.** Inflorescence with immature berries. (**A** based on Nee *et al.* 51765; **B**–**E** based on Nee *et al.* 51806). **F.** Inflorescence of *Solanum albidum* Dunal for comparison (based on Nee 36826, NY).

green when immature, the color when fully ripe unknown, glabrous. Seeds numerous (ca. 120 per fruit), ca.  $2 \times 1.6$  mm, flattened-reniform, yellow-brown, the surface minutely foveolate.

*Distribution*.—Andean slopes in western and central Bolivia in Departments of Cochabamba and La Paz at 1800–3000 m elevation.

*Phenology*.—Flowering in May, September, and October, and fruiting in January, March, May, and October. Further collecting will show whether flowering is confined to the dry season.

*Etymology*.—The epithet honors Michael Dennis Whalen, an expert on the Solanaceae, whose work on *Solanum* was cut short much too soon.

Additional specimens examined. **BOLIVIA. COCHABAMBA.** Prov. Carrasco: Sehuencas, después pasar el Río Fuerte,  $17^{\circ}30'S$ ,  $65^{\circ}17'W$ , 2100 m, 1 May 1993 (fl, fr), *P. Ibsch & C. Ibsch 194* (LPB); narrow canyon of Río Monte Puncu, 5 km NE of Monte Puncu, 10 km (by air) NW of Epizana,  $17^{\circ}33'S$ ,  $65^{\circ}16'W$ , 2700–2750 m, 10 Mar 1988 (fr), *Nee & Solomon 36625* (MO), *36634* (MO). Prov. Chapare: camino de Cochabamba a Villa Tunari, Villa Tunari, 23 Sep 1982 (fl), *Cabrera & Gutiérrez 33722* (LPB, SI); Incacorral, 1900 m, Mar 1941, *Cárdenas 2246* (US); km. 120, Cochabamba to Chapare, 1800 m, Apr 1961, *Cárdenas 5974* (K, US); 23.8 km N of Colomi (junction of the road to Candelaria) on road to the Chapare, then 5 km NW (left) on side road, upper Río Cayani,  $17^{\circ}10'S$ ,  $65^{\circ}33'W$ , 2600 m, 19 Oct 1985 (fl), *Solomon 14404* (MO); Incachaca, 2500 m, 16 Sep 1921 (fl), *J. Steinbach 5786* (SI); Nordosthänge der Sierra de Cochabamba, Umgebung von Incachaca, 2500 m, Jul 1926, *Werdermann 2063* (MO); Incacorral, forest opening, 2400 m, 10 Jun 1929, *J. Steinbach 9820* (BM, E, F, MO, NY, PH, US). Prov. Mizque: Mizque, 2000 m, Jun 1940, *Cárdenas 2133 & 2134* (US). **LA PAZ.** Prov. Larecaja: Quiabaya, Sorata, *Mandon 425* (G–DC [F photo 23130; a specimen of this number at G seems to be *S. albidum*]). Prov. Murillo: Valle de Zongo, vic. Escuela Cambaya, 28.3 km N of (below) La Cumbre, along Río Zongo,  $16^{\circ}07'S$ ,  $68^{\circ}05'W$ , 2560–2800 m, 10 May 1990 (fl), *Luteyn & Dorr 13616* (MO); Río Zongo valley, 22.5 km below dam at Lago Zongo,  $16^{\circ}09'S$ ,  $68^{\circ}07'W$ , 3000 m, 9 Oct 1982 (fl, fr), *Solomon 8432* (MO); Zongo valley, 25.2 km below the dam at Lago Zongo,  $16^{\circ}08'S$ ,  $68^{\circ}07'W$ , 2700 m, 19 Jan 1985 (fr), *Solomon 13102* (MO). Prov. Nor Yungas: road from La Paz to Coroico, S of divide, ca. 20 km from La Paz, 4000–4700 m, 21 May 1980 (fl), *D'Arcy & Bejarano 13833* (MO, NY); 9 km by road (ca. 4 km by air) down from and NE of Chuspipata,  $16^{\circ}16'S$ ,  $67^{\circ}47'W$ , 2450 m, 29 Oct 1984 (fl, fr), *Nee & Solomon 30227* (NY). Prov. Sud Yungas: Chuspipata 6.5 km hacia Chulumani, 2570 m, 13 Sep 1981 (fl), *Beck 4780* (LPB).

This species is similar to the more widespread *Solanum albidum*, but is more robust in nearly every part and is usually found at higher altitudes. It is more restricted ecologically; in the area where they are sympatric in Bolivia, *S. albidum* grows from 270 to 2600 m, but is generally found below 2000 m, whereas *S. whalenii* is restricted to 1800–3000 m. The color of the fully mature fruits is not known; they are held erect on erect inflorescences and if they remain dark green, it may indicate that they are dispersed by bats.

*Solanum whalenii* is one of the most spectacular species of section *Torva* (*Solanum torvum* group sensu Whalen, 1984). A photograph of the flower appears on the cover of a theme issue of the *Philosophical Transactions of the Royal Society, Biological Sciences* dedicated to “Taxonomy for the twenty-first century” (Godfray & Knapp, 2004).

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### Literature Cited

- Anderson, G.J. & R.K. Jansen. 1998. Biosystematic and molecular systematic studies of *Solanum* section *Basarthrum* and the origin and relationships of the pepino dulce (*S. muricaum*). Monographs in Systematic Botany from the Missouri Botanical Garden 68: 17–32.
- Beck, S.G. & M. Moraes-R. 1997. Interior dry and mesic forests: CPD site SA24: Llanos de Mojos region. Pp. 421–425. In: S.D. Davis, V.H. Heywood, O. Herrera-MacBryde, J. Villa-Lobos & A.C. Hamilton (eds.), Centres of plant diversity: a guide and strategy for their conservation. Vol. 3. The Americas. IUCN Publications Unit, Cambridge, UK.

- Bell, A.D. & T.D. Dines.** 1995. Branching patterns in the Solanaceae. Pp. 157–172. *In*: P.C. Hoch & A.G. Stephenson (eds.), Experimental and molecular approaches to plant systematics. Missouri Botanical Garden Press, St. Louis, Missouri.
- Bohs, L.** 1989. *Solanum allophyllum* (Miers) Standl. and the generic delimitation of *Cyphomandra* and *Solanum* (Solanaceae). *Annals of the Missouri Botanical Garden* 76: 1129–1140.
- . 1990. The systematics of *Solanum* section *Allophyllum* (Solanaceae). *Annals of the Missouri Botanical Garden* 77: 398–409.
- . 2005. Major clades in *Solanum* based on *ndhF* sequence data. Pp. 27–49. *In*: R.C. Keating, V.C. Hollowell & T.B. Croat (eds.), A festschrift for William G. D'Arcy: the legacy of a taxonomist. *Monographs in Systematic Botany from the Missouri Botanical Garden*, Vol. 104. Missouri Botanical Garden Press, St. Louis, Missouri.
- Britton, N.L.** 1894. Thomas Morong. *Bulletin of the Torrey Botanical Club* 21: 239–244.
- Child, A.** 1979. A review of branching patterns in the Solanaceae. Pp. 345–356. *In*: J.G. Hawkes, R.N. Lester & A.G. Skelding (eds.), *The biology and taxonomy of the Solanaceae*. Academic Press, London, UK.
- Correll, D.S.** 1962. The potato and its wild relatives: section *Tuberarium* of the genus *Solanum*. Texas Research Foundation, Renner, Texas.
- Danert, S.** 1958. Die Verzweigung der Solanaceen im reproduktiven Bereich. *Abhandlungen der Deutschen Akademie der Wissenschaften zu Berlin, Klasse für Chemie, Geologie und Biologie* 6:1–183.
- . 1967. Die Verzweigung als infragenerisches Gruppenmerkmal in der Gattung *Solanum* L. *Kulturpflanze* 15: 275–292.
- D'Arcy, W.G.** 1986. The calyx in *Lycianthes* in some other genera. *Annals of the Missouri Botanical Garden* 73: 117–127.
- Davis, S.D., V.H. Heywood, O. Herrera-MacBryde, J. Villa-Lobos & A.C. Hamilton.** 1997. Centres of plant diversity: a guide and strategy for their conservation. Vol. 3. *The Americas*. IUCN Publications Unit, Cambridge, UK.
- Eshbaugh, W.H.** 1975. Genetic and biochemical systematic studies of chili peppers (*Capsicum*—Solanaceae). *Bulletin of the Torrey Botanical Club* 102: 396–403.
- Gentry, A.H.** 1982. Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Annals of the Missouri Botanical Garden* 69: 557–593.
- Godfray, H.C.J. & S. Knapp.** 2004. Taxonomy for the twenty-first century. *Philosophical Transactions of the Royal Society, Biological Sciences* 359: 557–739.
- Greuter, W., J. McNeill, F.R. Barrie, H.M. Burdet, V. Demoulin, T.S. Filgueiras, D.H. Nicolson, P.C. Silva, J.E. Skog, P. Trehane, N.J. Turland, and D.L. Hawksworth.** 2000. International code of botanical nomenclature (Saint Louis Code). Koeltz Scientific Books, Königstein, Germany.
- Knapp, S.** 2002a. Assessing patterns of plant endemism in Neotropical uplands. *Botanical Review* 68(1): 22–37.
- . 2002b. *Solanum* section *Geminata*. *Flora Neotropica Monograph* 84: 1–495.
- Macbride, J.F.** 1962. Solanaceae. *In*: *Flora of Peru*, Field Museum of Natural History, Botanical Series 13 (V-B,1): 1–267.
- Morong, T. & N.L. Britton.** 1893. An enumeration of the plants collected by Dr. Thomas Morong in Paraguay, 1888–1890. *Annals of the New York Academy of Sciences* 7: 45–280.
- Morton, C.V.** 1976. A revision of the Argentine species of *Solanum*. *Academia Nacional de Ciencias, Córdoba, Argentina*.
- Nee, M.** 1993. Solanaceae II. *Flora de Veracruz* 72: 1–158. Instituto de Ecología, Xalapa, Veracruz.
- . 1999. Synopsis of *Solanum* in the New World. Pp. 285–333. *In*: M. Nee, D.E. Symon, R.N. Lester & J.P. Jessop (eds.), *Solanaceae IV: Advances in biology and utilization*. Royal Botanic Gardens, Kew.
- Schulz, O.E.** 1909. Solanacearum genera nonnulla. Pp. 140–279. *In*: I. Urban (ed.), *Symbolae Antillanae*. Fratres Borntraeger, Leipzig.
- Sendtner, O.** 1846. Solanaceae. *In*: C. Martius (ed.), *Flora Brasiliensis* 10: 5–338.
- Werdermann, E.** 1940. Neue Arten aus Ecuador III. (ed. L. Diels): Solanaceae. *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem* 15: 53–58.
- Whalen, M.D.** 1984. Conspectus of species groups in *Solanum* subgenus *Leptostemonum*. *Gentes Herbarum* 12 (4): 179–282.