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A Revision of *Solanum* Section *Gonatotrichum*

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Abstract—*Solanum* section *Gonatotrichum* (Solanaceae) includes eight species native to North, Central, and South America. Plants of this section are herbs to woody shrubs that lack spines, are pubescent with simple or stellate hairs, and have berries that swell due to increased turgor pressure and explosively dehisce to disperse the seeds. Section *Gonatotrichum* is closely related to section *Brevantherum*, from which it differs by the presence of explosive fruit dehiscence and simple hairs in all taxa except *S. lignescens*, which has stellate pubescence. The morphology, taxonomic history, nomenclature, ecology, distribution, and reproductive biology of *Solanum* section *Gonatotrichum* are reviewed. A dichotomous key is provided for the species of the section.

Keywords—explosive fruit dehiscence, Neotropics, taxonomy.

Solanum (Solanaceae) contains approximately 1500 species and is one of the 10 largest genera of flowering plants (Frodin 2004; Bohs 2005). Due to the large size and the morphological complexity of the genus, many infrageneric groups within *Solanum* are not well defined. Recent species level taxonomy (e.g. Bennett 2008; Knapp 2008; Peralta et al. 2008; Tepe and Bohs 2011; www.solanaceaesource.org) has led to a better understanding of *Solanum* systematics and numerous molecular phylogenetic studies have helped elucidate clades within the genus (Bohs 2005; Weese and Bohs 2007). One clade that has been recognized in molecular studies is the *Gonatotrichum* clade, which corresponds to the formally named *Solanum* section *Gonatotrichum* Bitter. This contribution is a revision of that section.

Section *Gonatotrichum* includes eight species native to North, Central, and South America. They are all herbaceous or small, woody shrubs with simple hairs (except *S. lignescens* Fernald which has stellate pubescence). The fruits are unique within the genus and are a key diagnostic character for the section. They have a thin pericarp with a watery mesocarp that is held under pressure until the fruits explosively dehisce (Nee 1989). While it is unusual to witness the explosive dehiscence, the syndrome is apparent, as the fruits are white, yellow, or green and nearly transparent when mature. After dehiscence, the fruits appear deflated and shriveled. Section *Gonatotrichum* has previously been taxonomically challenging because while some species are relatively widespread in their distribution (*S. deflexum* Greenm., *S. olympicum* Hassl., and *S. turneroides* Chodat), others are narrowly distributed and relatively inconspicuous, making them among the least collected species of *Solanum*.

MATERIALS AND METHODS

The taxonomic conclusions presented are a result of extensive field and herbarium work. We examined specimens from the following herbaria: A, BH, BHC, BM, BR, CEPEC, CESJ, CORD, CTES, ESA, FUEL, G, GH, HAS, HB, HNUP, HUEFS, IAC, IAN, IBGE, ICN, INB, INPA, JPB, K, LPB, M, MBM, MBML, MEXU, MO, NY, P, PACA, PEL, QCA, QCNE, R, RB, SI, SP, SPF, SPSF, TEX, UC, UEC, UPCB, US, USZ, UT, VIC, WIS, W, WU. We also field-collected five of the eight recognized species, including two recently described species (Stern and Bohs 2009; Giacomini and Stehmann 2011). Details of exsiccatae are cited here

and are also available on the Solanaceae Source webpage (www.solanaceaesource.org). Specimens with sheet numbers are cited with the herbarium acronym followed by a dash and the sheet number (i.e. MO-1781232); barcodes are preceded by the herbarium acronym followed by a dash, then the barcode number (i.e. G-G00104280).

We have followed the morphological species concept or “morphological cluster” concept in delimiting species of sect. *Gonatotrichum* (Mallet 1995). Taxa are recognized as distinct if they possess a unique suite of characters and are separated from similar entities by morphological gaps. In nearly all cases, taxa also occupy geographically circumscribed ranges.

Measurements were made from dried herbarium material supplemented by measurements from living material. Colors of corollas, fruits, etc., are described from living material or from herbarium label data. Specimens with latitude and longitude data on the labels were mapped directly. Some species had few or no georeferenced collections; in these cases we retrospectively georeferenced the collections using available locality data. Conservation status was assessed following IUCN Red List Categories and Criteria (I. U. C. N. Standards and Petitions Subcommittee 2010).

For seed SEM studies, seed coats were digested using a 1% cellulase solution for 24 hr to remove the periclinal cell walls and expose the anticlinal cell walls. For hair SEM studies, fresh stems, when available, were mounted on a stub with double-sided tape and coated with gold-palladium. For those species where fresh material was not available, dried material from herbarium specimens was used. The material was rehydrated and postfixed in osmium tetroxide and then dehydrated in an ethanol series before being coated with gold-palladium.

Plants used in breeding studies were grown from seed in the greenhouses at the University of Utah. Voucher information and original locality data of materials used are given in Appendix 1. For plants that were not autogamous, crosses were made by shaking pollen onto a glass slide that was rubbed gently across the stigma of the pollen-receptor flower. Success or failure of the cross was monitored, as well as fruit size, shape, color, and number of seeds in successful crosses.

TAXONOMIC HISTORY

The earliest descriptions of species that would later be assigned to sect. *Gonatotrichum* were Sendtner's (1846) publication of *S. adscendens* Sendtn. and *S. hoffmanseggii* Sendtn. in his treatment of the Solanaceae in Martius' *Flora Brasiliensis*. Asa Gray described *Salpichroa wrightii* A. Gray in 1886, which would later be recognized as a synonym of *S. deflexum*. In 1897, Fernald described the Mexican species *S. lignescens*. Also in 1897, Greenman described a Central American species, *S. deflexum*. Chodat (1902) described the South American species *S. turneroides* based on material from Émile Hassler's herbarium in Geneva. In 1911,

Hassler described *S. olympicum* Hassl. from material collected in Paraguay.

In 1912, Bitter described two new species from Bolivia and Paraguay, *S. gonatotrimum* Bitter and *S. geniculatistrigosum* Bitter, both treated in this revision as synonyms of *S. turneroides*. He also formally established sect. *Gonatotrimum*, including these two species as well as *S. adscendens* and *S. deflexum*. In his concept, plants of the section were small annuals or perennials with few-celled, unbranched, often geniculate hairs, few-flowered, nearly sessile inflorescences, and glabrous filaments and styles.

One year later, Bitter (1913) described two other new species from Paraguay, *S. flavistrigosum* Bitter (here considered as another synonym of *S. turneroides*) and *S. parvistrigosum* (here considered a synonym of *S. olympicum*), and assigned *S. hoffmanseggii* to the section. Later, Bitter (1922) transferred *Bassovia setosa* Brandegee (Brandegee 1917) to *Solanum* and placed it in sect. *Gonatotrimum* (Bitter 1922). *Solanum setosum* (Brandegee) Bitter is now considered a synonym of *S. deflexum*.

Solanum sect. *Gonatotrimum* received virtually no taxonomic attention until Nee (1989) reduced the number of species in the section to two, recognizing only *S. adscendens* and *S. turneroides*; he left *S. hoffmanseggii* as a name of doubtful affinity. He reiterated the importance of hair characters in defining the section and also emphasized the explosively dehiscent fruits as a distinctive character.

Recent herbarium and field studies have resulted in the description of *S. manabiense* S.Stern from Ecuador (Stern and Bohs 2009) and *S. evolvuloides* Giacomini & Stehmann from Bahia, Brazil (Giacomini and Stehmann 2011). Concurrent phylogenetic and taxonomic work has led to the present revision as well as a published molecular phylogeny of the section (Stern and Bohs 2012; see below).

MORPHOLOGY

Habit—Members of sect. *Gonatotrimum* are small herbs, single- to few- branched from a lignescent base, with only two species, *S. lignescens* and *S. hoffmanseggii*, becoming subshrubs. Species range in height from mature individuals of *S. deflexum* that reach only 5–10 cm to the shrubby *S. lignescens* that can grow to 1 m. Some species (*S. manabiense* and *S. turneroides* and rarely *S. deflexum*) are known to produce many upright stems from underground rhizomes. The herbaceous habit of sect. *Gonatotrimum* most resembles members of sect. *Solanum* (Morelloid clade sensu Weese and Bohs 2007) but various other morphological and molecular characteristics distinguish these sections (see Bohs 2005).

Trichomes—As in some other solanums (Seithe and Anderson 1982), trichome morphology has proven to be an excellent characteristic in delimiting species within the section. Both branched and unbranched trichomes are found in sect. *Gonatotrimum* (Fig. 1). Branched, stellate hairs are found only in *S. lignescens*, which also has simple, unbranched hairs. The unbranched hairs range from one- to five-celled and can either be straight (in *S. adscendens*, *S. deflexum*, and *S. manabiense*), or bent at a 90° angle between the first and second cells (*S. olympicum* and *S. hoffmanseggii*). The trichomes of *S. turneroides* fall between these categories and vary from straight to bent at nearly a 90° angle. Glandular hairs in sect. *Gonatotrimum* appear to be confined to *S. evolvuloides* (Fig. 1F); however, SEM work has shown that very small glandular hairs not visible with light microscopy may be present in some other species (e.g. *S. turneroides*, Fig. 1B). Among the species of sect. *Gonatotrimum*, trichome density can vary from sparse to dense. Variability of trichome density changes both among and within species depending on position on the plant. For instance, the abaxial surface of the leaves is generally more pubescent than the adaxial

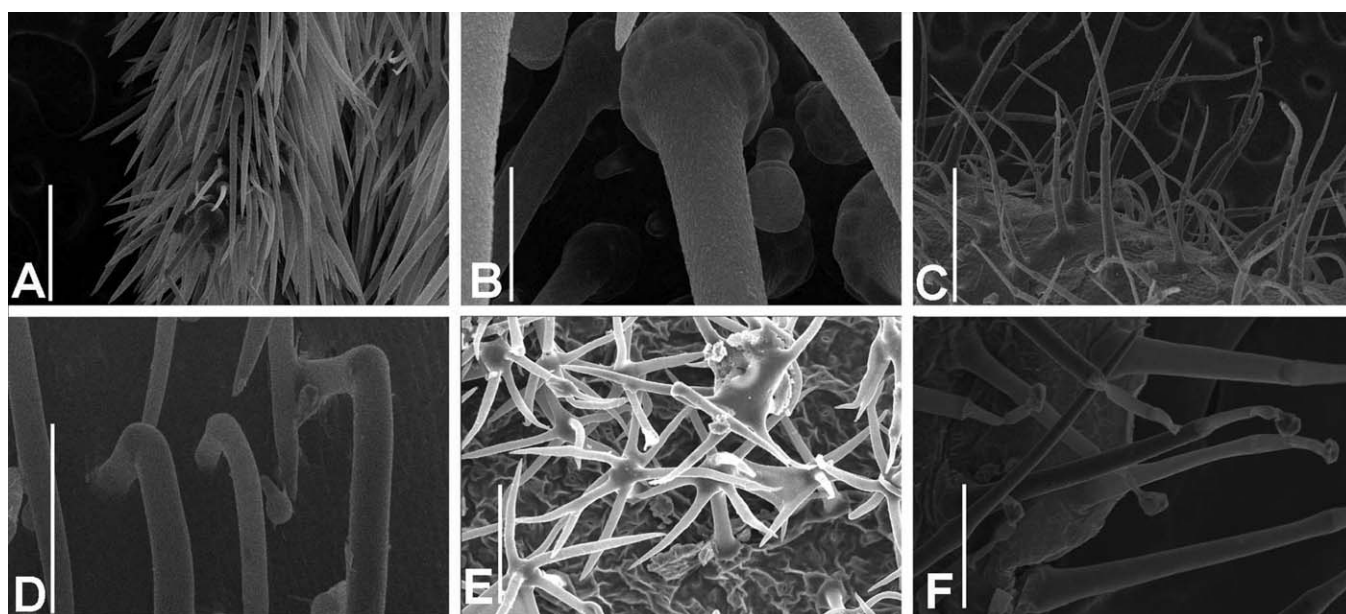


FIG. 1. Scanning electron micrographs of hairs in section *Gonatotrimum*. A. *Solanum turneroides* stem; note the hairs oriented downward at an approximately 45° angle (Bohs 2715, UT). B. Higher magnification of *S. turneroides*; note that the base of the hair is swollen with what appear to be reduced ray cells. Also note the small glandular hairs below the long, simple hairs (Bohs 2715, UT). C. Stem of *S. deflexum*; note the hairs are simple and held perpendicular to the stem (Nee 51716, UT). D. Geniculate hairs of *S. olympicum*; note the sharp 90° angle between the first and second cells (Bohs 3194, UT). E. Stellate hairs on abaxial leaf surface of *S. lignescens* (Hampshire et al. 1151, BM). F. *Solanum evolvuloides* glandular calyx hairs (Mattos Silva, s.n., CEPEC). Scale bars: A, C = 500 µm. B = 50 µm. D, E = 200 µm. F = 100 µm.

surface. Similarly, young growth is commonly densely pubescent while older growth on the same plant may be nearly glabrous.

Leaves—The leaves of sect. *Gonatotrichum* are all entire, petiolate (or nearly sessile in *S. hoffmanseggii*), and elliptic or elliptic-ovoid (except in *S. adscendens* with cordiform leaves and *S. hoffmanseggii* which can have linear leaves). The base of the leaf is somewhat decurrent into the petiole in all species except in the cordate leaves of *S. adscendens*. Leaf size is relatively uniform within the section, with the smallest leaves ca. 1 cm long and the longest ca. 7 cm long, with greater intraspecific than interspecific variation. Leaf texture is chartaceous to membranaceous. Venation is typically pinnate with one major vein from the base, except in *S. adscendens*, which has 3–5 major veins extending from the leaf base.

Inflorescences—The inflorescences in sect. *Gonatotrichum* are all sessile or nearly so, unbranched, and extra-axillary or subopposite the leaves. The inflorescences are all few-flowered, with 1–6 (12) flowers. They are typically very congested with a short to almost absent peduncle and a condensed rachis. The pedicels are all articulated at the base. The sessile inflorescence is a shared characteristic of all species of sect. *Gonatotrichum*.

Flowers—The flowers of sect. *Gonatotrichum* are all perfect, 5-merous, and white or sometimes light pink to purple in color. The flowers are small compared to many other

Solanum species, with corollas typically about 1.5 cm in diameter (to 1.8 cm in *S. lignescens*, 2.5 cm in *S. turneroides*, and 3 cm in *S. evoluloides*). The flowers of *S. adscendens*, *S. deflexum*, *S. lignescens*, and *S. manabiense* are actinomorphic. The flowers of *S. olympicum* and *S. hoffmanseggii* are very slightly heterantherous, with the lowermost anther slightly projected due to an elongated filament, although this is often so inconspicuous as to be very difficult to see on herbarium specimens. *Solanum turneroides* and *S. evoluloides* both have strongly heterantherous flowers with the lowermost filament elongating to twice the length of the others. These species also have a style that is deflected upwards at the apex. *Solanum turneroides* has flowers that are strongly fragrant, a unique trait in the section and uncommon in *Solanum* in general.

Fruits—The fruits in sect. *Gonatotrichum* are unique in the genus and are an excellent diagnostic character for the section. They are glabrous, green, white, or yellow when immature and green or green-purplish and transparent when mature. The fruits have a thin pericarp with a watery mesocarp that is held under pressure until the fruits explosively dehisce. This dehiscence can propel seeds over 15 m from a 30 cm plant in *S. turneroides*.

Seeds—The seeds of sect. *Gonatotrichum* are flattened and reniform like those of many other *Solanum* species (Fig. 2). In overall shape, *S. deflexum* is unique in that it has a swollen margin and a large notch where it connects

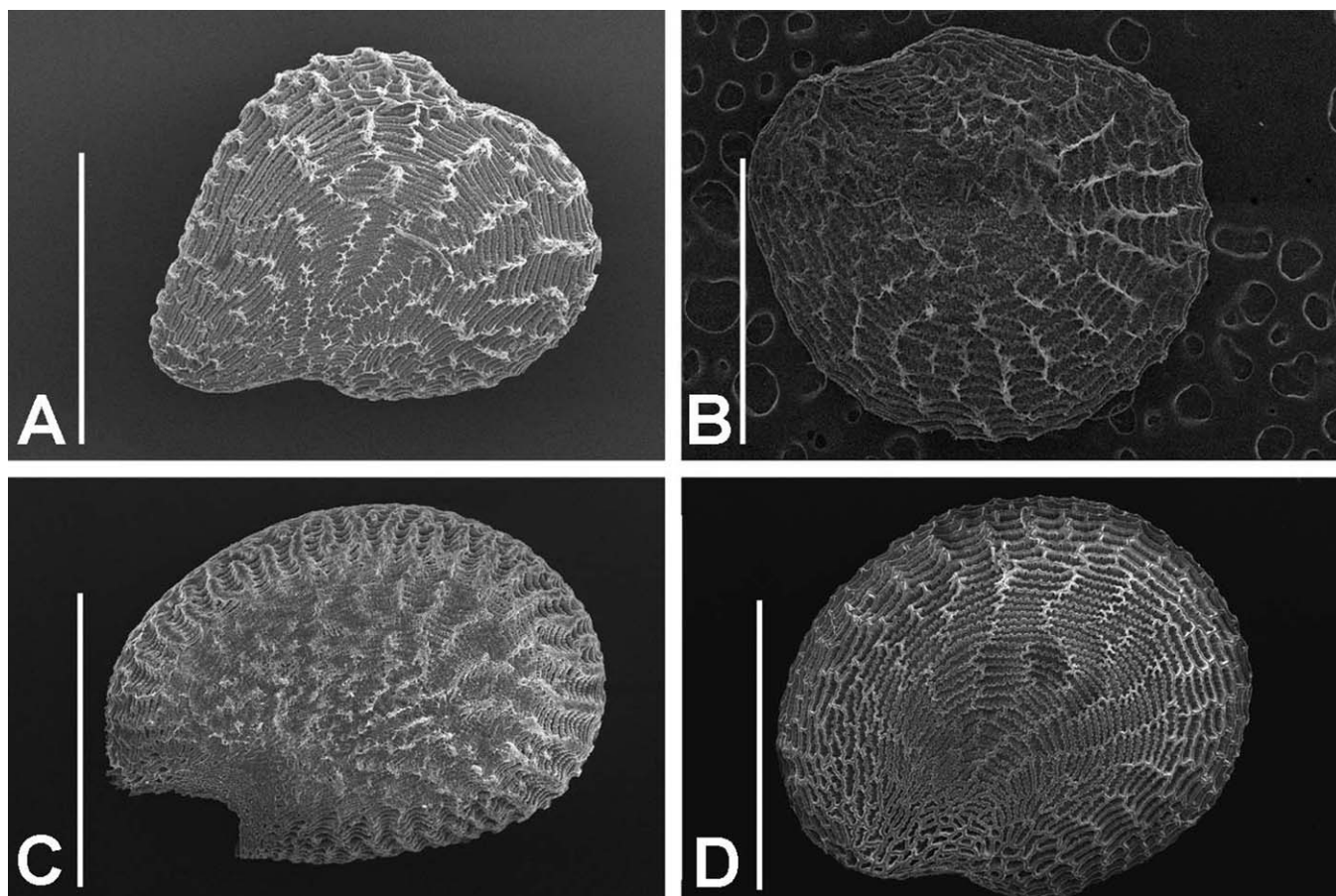


FIG. 2. Scanning electron micrographs of seeds in section *Gonatotrichum*. All seeds were treated with 1% cellulase for 24 hr and dried prior to imaging. A. *Solanum olympicum*; note the raised ridges radiating from the center to the margins (Bohs 3194, UT). B. *S. adscendens*; note the raised ridges (Leite 658, NY). C. *S. deflexum*; note the swollen margin and large notch (Nee 51716, UT). D. *Solanum turneroides* (Bohs 2715, UT). Scale bars = 2 mm.

to the placenta (Fig. 2C). In *S. turneroides* the seeds are twisted and bent, in contrast to the flat, reniform seeds of other species in the section. The arrangement of cells on the seed surface can be diagnostic. The individual cells can be seen when the periclinal cell wall is enzymatically removed and range from raised fibrils that radiate from the seed center to the margins in *S. olympicum* (Fig. 2A) to the netlike cell walls of *S. turneroides* (Fig. 2D).

BREEDING SYSTEMS

Plants of *S. deflexum*, *S. olympicum*, *S. manabiense*, and *S. turneroides* were studied in the greenhouses at the University of Utah, while those of *S. adscendens* and *S. evolvuloides* were studied at the Jardim Botânico da Fundação Zoo-Botânica, Belo Horizonte, Brazil. All species were hermaphroditic and self-compatible, and all but *S. evolvuloides* and *S. turneroides* were autogamous. Among the autogamous species, *S. adscendens*, *S. deflexum*, and *S. olympicum* were strongly autogamous, while a smaller proportion of flowers of *S. manabiense* set fruit without manipulation.

HABITATS AND GEOGRAPHIC DISTRIBUTION

Species of sect. *Gonatotrimum* are native to the southwestern United States, Mexico and Central America as far south as Costa Rica, and to coastal Ecuador, Brazil, Paraguay, Bolivia, and Argentina in South America. Species can be found from sea level to 2,700 m. Although they occupy various habitats, all seem to prefer dry sites, including dry deciduous forests, roadsides, grazed areas, and forest edges.

Some of the taxa in the section are widespread: *S. deflexum* ranges from the southwestern United States to Costa Rica, *S. lignescens* ranges from Mexico to Nicaragua, and *S. turneroides* and *S. olympicum* range throughout Bolivia and Paraguay and into southeastern Brazil and northern Argentina. Other members are restricted to much smaller regions: *S. manabiense* is only found in central coastal Ecuador in the Manabí and Guayas Provinces, *S. adscendens* is only found in Rio Grande do Sul State in Brazil and adjacent Corrientes and Misiones Provinces in Argentina, *S. hoffmanseggii* is only known from collections in Pará and Tocantins States in northern Brazil, and *S. evolvuloides* is only known from southeastern Bahia State, Brazil.

A notable aspect of the distribution of members of sect. *Gonatotrimum* is their clustering in four regions (North and Central America, coastal Ecuador, northern Brazil, and Bolivia to southeastern Brazil/northeastern Argentina) with large disjunctions between them. Bitter's (1912) description of the section noted the large geographic disjunction between the southern South American and North to Central American members of the section and predicted that a close relative of these species might be expected in the territories lying between these disjunct areas. In fact, *S. manabiense* of coastal Ecuador was found in the intervening area (Stern and Bohs 2009). *Solanum olympicum* is the only species known to span a large disjunction, being found in both the northern and southern Brazilian centers of distribution. However, specimens from the northern part of the range are somewhat aberrant in hair structure, and further collections and study may show that they are distinct from the southern populations (see taxonomic treatment below). Part of the explanation for the large disjunctions in this group may be

due to their preference for dry habitats, but even so, they are not found in all of the drier areas of the Neotropics.

PHYLOGENETIC RELATIONSHIPS

Previous authors (Sendtner 1846; Nee 1999) allied species of sect. *Gonatotrimum* with sect. *Solanum* of subg. *Solanum*. Both groups are superficially very similar in their herbaceous, often weedy habit, pubescence of unbranched hairs, usually short, unbranched, often extra-axillary inflorescences, and small white flowers. However, molecular data (Bohs 2005; Weese and Bohs 2007) showed that sect. *Gonatotrimum* is unrelated to sect. *Solanum* and instead belongs to the Brevantherum clade of *Solanum*. This clade consists of about 60 Neotropical species lacking prickles and with short, broad anthers. Most species of the Brevantherum clade have stellate or lepidote pubescence, often large, branched inflorescences, and fleshy, non-dehiscent fruits. Section *Gonatotrimum* is unusual in the Brevantherum clade because of its herbaceous habit, reduced inflorescences, simple hairs in all species except *S. lignescens*, and its explosively dehiscent fruits.

Phylogenetic relationships of *Solanum* sect. *Gonatotrimum* were further examined by Stern and Bohs (2012). Molecular data indicate that sect. *Gonatotrimum* forms a monophyletic group including *S. lignescens* that is sister to all other sampled members of the Brevantherum clade (Fig. 3; Stern and Bohs 2012). Within sect. *Gonatotrimum*, phylogenetic results closely follow the geographic distribution of species in the section, with the exception of *S. adscendens*, a species from southern Brazil that does not form a clade with the other South American species, but is sister to the rest of the species in the section (Fig. 3); this relationship, however, is not well supported. The two Mexican and Central American species, *S. lignescens* and *S. deflexum*, are strongly supported as sister species. *Solanum evolvuloides*, *S. turneroides*, and *S. olympicum*, all have heteranthrous flowers (although those of *S. olympicum* are weakly so), and form a monophyletic group with *S. evolvuloides* sister to the other two species (see Fig. 3). Multiple accessions of *S. olympicum* are grouped together, with those from the northeasternmost extent of the range in Bahia, Brazil, sister to the other accessions. While these populations have some slight morphological differences, they are treated here as the same species. *Solanum hoffmanseggii* was not included in the phylogenetic study due to a lack of high quality genomic DNA.

TAXONOMIC TREATMENT

SOLANUM section *GONATOTRIMUM* Bitter, Repert. Spec. Nov. Regni Veg. 11: 230. 1912.—TYPE species: *Solanum gonatotrimum* Bitter (= *Solanum turneroides* Chodat).

Herbs or shrubs, sometimes rhizomatous, lacking prickles. Stems nearly glabrous to densely pubescent with straight or geniculate, unbranched and/or stellate hairs. Leaves simple, the blades chartaceous to membranaceous, elliptic to elliptic-ovoid to cordiform, glabrous to densely pubescent with straight or geniculate, unbranched and/or stellate hairs, the base rounded to obtuse to truncate or cordate, often decurrent into petiole, the margins entire and often ciliate, the apex acute; petioles sparsely to densely pubescent. Inflorescence nearly sessile, extra-axillary or subopposite the leaves, unbranched, with 1–6 (12) flowers, the

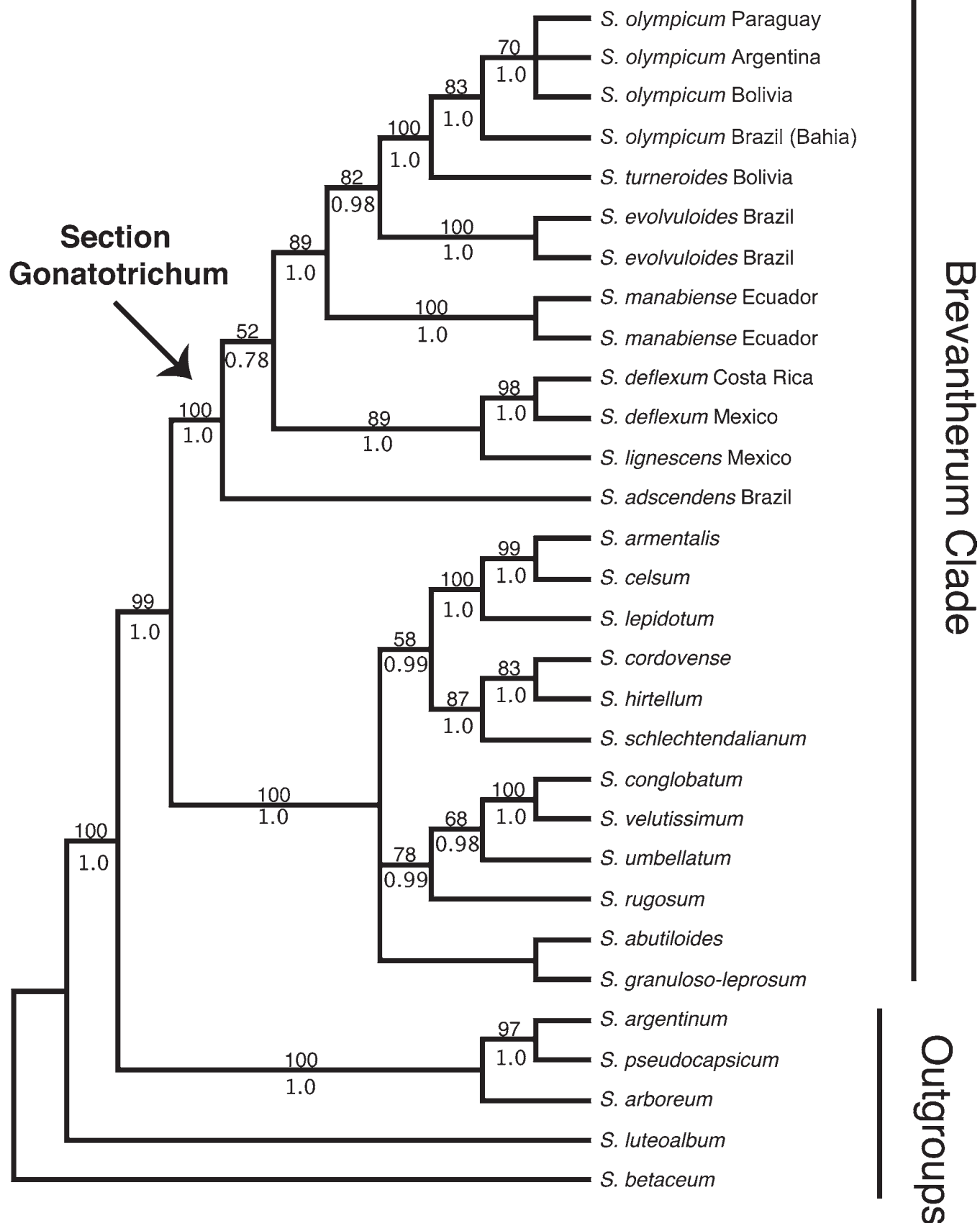


FIG. 3. Parsimony strict consensus tree of *Solanum* section *Gonatotrimum* and outgroups based on plastid *trnT-trnF* and nuclear *waxy* and ITS (from Stern and Bohs 2012).

axes sparsely to densely pubescent; pedicels articulated at the base. Flowers 5-merous, perfect, actinomorphic or zygomorphic due to heteranthery. Calyx campanulate to spreading, sparsely to densely pubescent, the lobes linear-lanceolate to broadly triangular, erect to reflexed at anthesis, not to slightly accrescent in fruit. Corolla white to pale pink or purple, membranaceous, stellate to rotate with abundant interpetalar tissue, glabrous adaxially, glabrous to sparsely pubescent abaxially, mostly on apex and main veins. Stamens equal or one stamen borne on an elongated filament to twice the length of the others, the filaments short to

greatly elongated, glabrous, inserted in corolla tube near its base; anthers connivent, yellow, sagittate at the base, poricidal at the tips, the pores directed distally, not (or rarely) opening into longitudinal slits. Ovary glabrous to sparsely pubescent; style equal to or exerted beyond stamens, cylindrical, glabrous, the stigma capitate. Fruit a globose to ovoid berry, obtuse at apex, glabrous, green to white or purplish-black when ripe, the pericarp thin, the mesocarp watery and held under pressure, dehiscing explosively at maturity. Seeds somewhat flattened, often with raised ridges on outer margin.

A KEY TO THE SPECIES OF *SOLANUM* SECTION *GONATOTRICHUM*

1. Plants usually woody (occasionally herbaceous), 0.5–1.5 m tall; hairs predominantly stellate; sympodia 3-foliate to plurifoliate; peduncle 3–8 mm 5. *S. lignescens* Fernald
- 1'. Plants herbaceous from a slightly woody base or woody in few cases (*S. hoffmanseggii*), 0.3–0.6 (0.8) m tall; hairs simple; sympodia 2-foliate; peduncle absent or nearly so 2
2. Cauline hairs exclusively geniculate (bent at a 90° angle between first and second cells), at least on the older parts of the stems, and lying flat along stems 3
3. New growth densely pubescent with simple hairs, these lying flat along stem but lacking a strong 90° bend (see Figs. 1A, B); corollas 1–2.5 cm in diameter, white to purple; flowers heterantherous with one filament longer than the rest, 2–5 mm long; mature fruits 10–20 mm in diameter, the fruit wall thickened at apex resulting in dehiscence at proximal end near calyx 8. *S. turneroides* Chodat
- 3'. Hairs strictly geniculate with a strong 90° bend; corollas 0.5–1.3 (–1.5) cm in diameter, white; flowers homantherous or very weakly heterantherous (only faintly noticeable in live plants and barely visible in dried specimens), all filaments equal or nearly so, 1–2 mm long; mature fruits up to 12 mm in diameter, the fruit wall not thickened at apex 4
4. Plants subshrubs, 50–80 cm tall; leaves lanceolate, more than three times longer than wide; plants of Amazonian Brazil (Pará and Tocantins) 4. *S. hoffmanseggii* Sendtn.
- 4'. Plants herbaceous, rarely woody, often rhizomatous, under 40 cm tall; leaves elliptic to elliptic-ovate, less than three times longer than wide; widespread species of Paraguay, Argentina, Bolivia and the xeric axis of Brazil (Bahia, Goiás and Mato Grosso do Sul) 7. *S. olympicum* Hassl.
- 2'. Cauline hairs straight, not geniculate, and not lying flat along stems 5
5. Corollas 1–2.5 cm in diameter; flowers heterantherous with one filament longer than the rest, 2–5 mm long; mature fruits 10–20 mm in diameter 6
6. Leaves typically 1.5–3.5 (4) cm long; abaxial surface of calyx and pedicels with long multicellular glandular hairs (ca. 0.5 mm long); plants of east-central Bahia, Brazil 3. *S. evoluloides* Giacomini & Stehmann
- 6'. Leaves typically 3.5–8 cm long; abaxial surface of calyx and pedicels with exclusively eglandular hairs; plants of Argentina, Bolivia, Paraguay, and Brazil (Mato Grosso do Sul and São Paulo) 8. *S. turneroides* Chodat
- 5'. Corollas 1–1.7 cm in diameter; flowers homantherous, all filaments equal, 1–2 mm long; mature fruits 5–12 mm in diameter 7
7. Plants much-branched and spreading from a slightly woody base; leaves cordate, with small glandular hairs on both sides; plants of northeastern Argentina (Provs. Misiones and Corrientes) and southern Brazil (Rio Grande do Sul) 1. *S. adscendens* Sendtn.
- 7'. Plants not or few-branched, the base typically not woody; leaves elliptic to elliptic-ovoid, the base rounded to obtuse, with exclusively eglandular hairs on both sides; plants of North and Central America and coastal Ecuador 8
8. Plants arising from a single base, rarely rhizomatous; abaxial surface of leaves densely pubescent; seeds with swollen margins and a pronounced notch where connected to placenta; plants of southwestern USA and widely distributed from Mexico through Costa Rica 2. *S. deflexum* Greenm.
- 8'. Plants always rhizomatous; abaxial surface of leaves nearly glabrous to sparsely pubescent; seeds uniformly flattened throughout without a prominent notch where connected to placenta; plants of coastal Ecuador 6. *S. manabiense* S.Stern

1. *SOLANUM ADSCENDENS* Sendtn., Fl. Bras. (Martius) 10: 17, Table 1, Figs. 9–12. 1846.—TYPE: BRAZIL. “Brasilia australiore,” (fl), *F. Sellow s.n.* (lectotype, here designated: P-P00319345!; isoelectotype: B (destroyed), photos of isoelectotype [F neg. 2798]: F!, G!, GH!).

S. amarantoides Dunal var. *hirtellum* Dunal, in DC., Prodr. 13 (1): 56. 1852.—TYPE: BRAZIL. “Province de Rio-Grande,” [“de Minas Geraes” handwritten on label], 1833 (fl), *C. Gaudichaud* 1745 (holotype: P-P00319346!).

Herb, sometimes woody at base, much-branched, the branches decumbent with apices upright, 1–3 dm tall. Stems sparsely to densely pubescent with 2–5-celled unbranched, straight hairs. Sympodia 2-foliate, the leaves solitary or geminate. Leaf blades 1.5–4 × 1–3.5 cm, cordiform, chartaceous to membranaceous, nearly glabrous to sparsely pubescent

adaxially and abaxially with 1–2 (4)-celled unbranched eglandular hairs, these 0.5–1.5 mm, erect or lying flat along blade, denser along veins, mixed with small, glandular hairs, these 0.1–0.2 mm, barely visible in dried material; base truncate to cordate, often asymmetrical, slightly decurrent into petiole; main veins 3–5, palmately leaving the leaf base; apex acuminate to acute; petioles 0.5–1.5 cm, moderately pubescent with unbranched hairs like those of stems. Inflorescences with 1–3 flowers, the axes sparsely to moderately pubescent with unbranched hairs; peduncle absent or nearly so; rachis absent; pedicels 5–15 mm in flower, 10–20 mm in fruit, pendent. Flowers with the calyx 3–10 mm long, the tube 1–3 mm, the lobes 2–7 × 0.5–1.5 mm, linear-lanceolate, moderately to densely pubescent. Corolla 0.5–1.5 cm in diameter, rotate with abundant interpetalar tissue, chartaceous to membranaceous, white, the tube

3–6 mm long, the lobes very short, $1-2 \times 0.5-1$ mm, triangular, acute at apices, glabrous abaxially and adaxially. Stamens 2–4 mm long; filaments up to 1 mm long; anthers $1.5-3 \times 0.5-1.5$ mm, oblong, the base cordate, the apex emarginate. Ovary glabrous; style 4–6 $\times$ 0.5–1 mm, equal to or exerted beyond stamens; stigma to 1 mm wide. Berries 5–12 mm in diameter, globose, white to yellow when immature, maturing semitransparent, drying brown,

glabrous, the mesocarp probably watery and held under pressure until dehiscing explosively at maturity. Seeds 10–35 per fruit, ca. 2.5×1.5 mm, with a small notch where connected to placenta, the margin not swollen, surface with fine raised ridges radiating from center to edges and shallow ridges running parallel to margin. Figure 4.

Habitat and Distribution—The majority of collections of *S. adscendens* are from Rio Grande do Sul State in Brazil

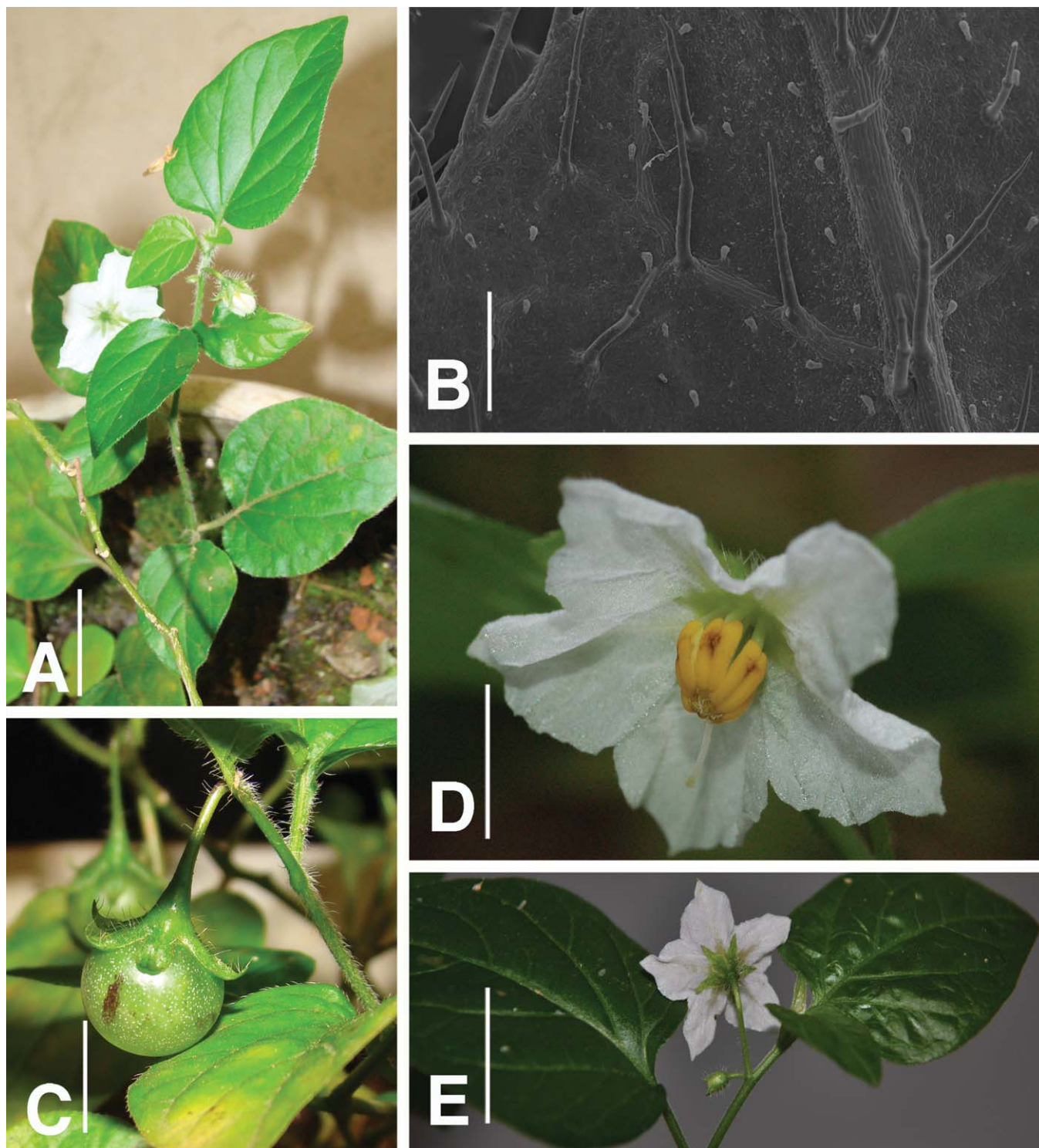


FIG. 4. *Solanum adscendens* (Stehmann 6005, BHCB). A. Habit; note the cordate leaf bases. B. SEM of the abaxial leaf surface; note the long, straight hairs and the minute glandular hairs. C. Fruit. D. Flower. E. Calyx and leaves. Scale bars: A = 2 cm. B = 200 μ m. C, E = 1 cm. D = 5 mm.

(Fig. 5). A few collections exist from Misiones and Corrientes Provinces in Argentina, but these are found near the border between the two countries. *Solanum adscendens* is a weedy species of interior forests and river banks as well as fields and roadsides (commonly ruderal) in seasonal deciduous forests at elevations from 0–600 (900) m.

Phenology—*S. adscendens* has been collected in flower and fruit in all months except January and May.

Conservation Status—While *S. adscendens* status is Least Concern because it does not meet IUCN Red List qualifications for a Threatened or even Near Threatened species, it is still of some concern due to the limited geographic distribution and rapid conversion of wildlands to grazing and farming in Rio Grande do Sul (IBGE 2010). It is advised that this species be monitored in the future.

Etymology—The epithet *adscendens* refers to the species' growth form, which begins by spreading horizontally with subsequent ascending, erect flowering stems.

Additional Specimens Examined—BRAZIL. Rio Grande do Sul: Balneário Irai, 27 Oct 1976 (fl, fr), *Arzvienco s.n.* (ICN); Derrubadas, Parque Estadual do Turvo, 31 Jan 1997 (fl, fr), *Brack 1714* (ICN); same loc., 31 Jan 1997 (fl, fr), *Brack 1807* (ICN); Montenegro, Polo Petroquímico, 28 Jun 1977 (fl), *Bueno 344* (HAS); Santo Amaro, 6 Jun 1996 (fl, fr), *Carneiro 443* (ICN); General Câmara, Santo Amaro, na quadra da igreja, 8 Oct 1995 (fl, fr), *Carneiro s.n.* (ICN); same loc., 15 Mar 1996 (fl, fr), *Carneiro s.n.* (ICN); Trindade do Sul, assentamento Trindade, 28 Feb 2008 (fl, fr), *Grings 340* (ICN); Marcelino Ramos, barranca do Rio Uruguai, 23 Sep 1987 (fl, fr), *Jarenkow 720* (ICN, MBM, PEL); Cambará do Sul, Itaimbezinho, 27 Dec 1988 (fl, fr), *Jarenkow & Bueno 1171* (ESA);

Dois Irmãos, Cascata de São Miguel, 1 Nov 1984 (fl), *Jeisen s.n.* (ICN); Vicinity of S. Leopoldo, Oct 1941 (fl, fr), *Leite 658* (NY, RB, SP, UEC); São Leopoldo, 1941 (fl, fr), *Leite 1864* (RB, SP, UEC); Nonoai, Cascata do Legeado Tigre, 2 Nov 1993 (fl, fr), *Matzenbacher s.n.* (ICN); Venâncio Aires, Vol. da Pátria, 5 Aug 1984 (fl), *Pilz s.n.* (ICN); Santa Clara, p. Lageado, 18 Nov 1940 (fl), *Rambo s.n.* (PACA); Nonoai, ad. fl. Uruguai, Mar 1954 (fl, fr), *Rambo s.n.* (PACA); Harmonia, 6 Oct 1945 (fl, fr), *Schnem 1546* (PACA, US); Veranópolis, próximo ao Rio das Antas, 2 Nov 1989 (fl, fr), *Silveira 1699* (HAS); Tenente, Parque Estadual do Turvo, na estrada para Salto de Yucumã, 11 Sep 1990 (fl, fr), *Silveira 8734* (HAS); Triunfo, Estrada para Taquari, 24 Sep 1987 (fl), *Silveira 9634* (HAS); Derrubadas, Parque Estadual do Turvo, na Estrada para Porto Garcia, 20 Jul 1995 (fl), *Sobral & Almeida 7911* (ICN); Bagé, junto ao Rio Camaquã, 26 Sep 1984 (fl, fr), *Stehmann 473* (BHCB, ICN, RB); General Câmara, Santo Amaro, Estação Ferroviária de Amarópolis, 28 Mar 2009 (fl), *Stehmann et al. 6001* (BHCB); General Câmara, Santo Amaro, Eclusa, 29°56'34.88"S, 51°53'30.51"W, 18 m, 28 Mar 2009 (fr), *Stehmann et al. 6002* (BHCB); same loc., same date (fr), *Stehmann et al. 6003* (BHCB); same loc., same date (fl), *Stehmann et al. 6004* (BHCB); same loc., same date (fr), *Stehmann et al. 6005* (BHCB); Montenegro, Arroio Bom Jardim, 30 Aug 1977 (fl, fr), *Ungaretti 549* (HAS); Triunfo, 30 Dec 1996 (fl, fr), *Ungaretti 595* (HAS); Montenegro, Polo Petroquímico, 13 Sep 1977 (fl, fr), *Ungaretti 646* (HAS); same loc., 19 Oct 1977 (fr), *Ungaretti 730* (HAS); Montenegro, 24 Jul 1979 (fl, fr), *Waechter & Zanette s.n.* (HAS).

ARGENTINA. **Corrientes:** Dept. Santo Tomé, Garruchos, Estancia San Juan Batista, 28°10'S, 55°38'51"W, 100 m, 17 Apr 2005 (fl, fr), *Barboza et al. 1494* (CORD); Garruchos, Estancia San Juan Batista, costa del Río Uruguay, 20 Sep 1974 (fl, fr), *Krapovickas et al. 25819* (CTES, MBM). **Misiones:** Concepción de la Sierra, entre Azara y Ciudad de la Sierra, 24 Aug 1978 (fl, fr), *Cabrera et al. 29445* (CTES, SI); San Pedro, Parque Provincial Moconá, 24 Oct 2006 (fl, fr), *Keller 3746* (CTES).

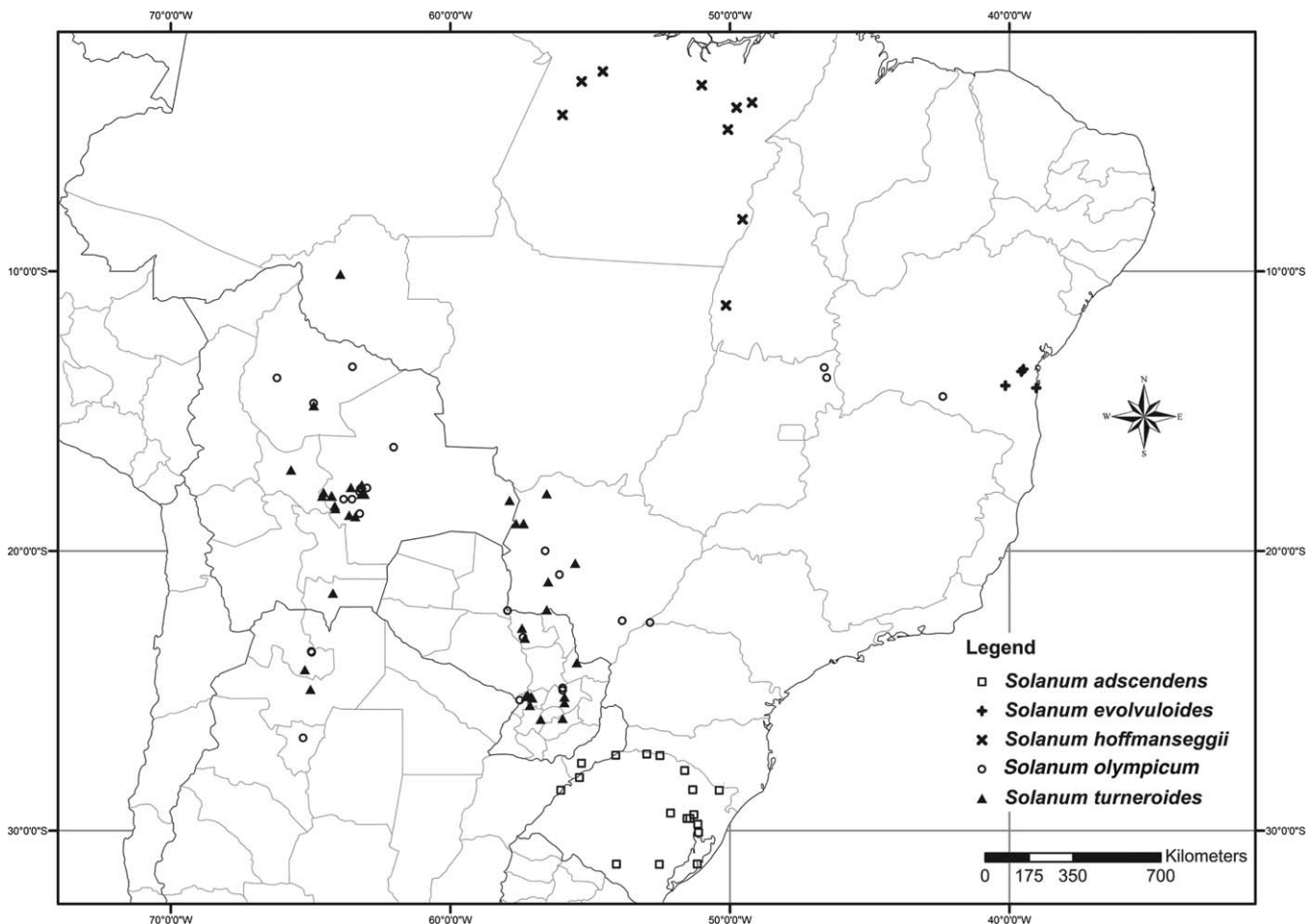


FIG. 5. Distribution of *S. adscendens*, *S. evolvuloides*, *S. hoffmanseggii*, *S. olympicum*, and *S. turneroides*.

Notes—*Solanum adscendens* is similar to *S. olympicum* and has been considered to be conspecific with it (Nee 1989). Mentz and de Oliveira (2004) also placed specimens of *S. adscendens* and *S. olympicum* together in *S. adscendens*. This placement was largely due to the absence of type material, as the presumed holotype was destroyed in Berlin and the photographs of it were not sufficient to distinguish the species. Mentz and de Oliveira's (2004) photographs of a duplicate of the type at Paris enabled us to readily distinguish *S. adscendens* from the more common and widespread *S. olympicum*. The cordate leaf bases, straight (not geniculate) hairs, glandular hairs on the abaxial leaf surface, and sprawling growth form with many branches from a single base characterize *S. adscendens* and differentiate it from *S. olympicum*, as do molecular data.

Solanum amarantoides var. *hirtellum* has not previously been considered a synonym of *S. adscendens*, but both Bitter and C.V. Morton annotated the holotype at P as "affine *S. adscendens*" and "probably = *S. adscendens*," respectively. The original printed label indicates the specimen was collected in "Province de Rio-Grande" but unidentified handwriting above this label states "de Minas Geraes." *Solanum adscendens* has its northern limit at the border of Rio Grande do Sul and Santa Catarina States, so it is unlikely that the Gaudichaud 1745 specimen was collected in Minas Gerais State.

2. *SOLANUM DEFLEXUM* Greenm., Proc. Amer. Acad. Arts 32: 301. 1897.—TYPE: MEXICO. Oaxaca: Cuicatlán, 15 Jul 1895 (fl, fr), L.C. Smith 403 (lectotype, here designated: GH-GH00295516!; possible islectotype: MEXU-00540158).

Solanum setosum (Brandege) Bitter, Repert. Spec. Nov. Regni Veg. 18: 307. 1922. *Bassovia setosa* Brandege, Univ. Cal. Publ. Bot. 6: 373. 1917.—TYPE: MEXICO. Veracruz: Zacuapan, Aug 1915 (fl, fr), C.A. Purpus 7509 (holotype: UC-178623!; isotypes: G-G00016530!, GH-GH00217435!, MO-825706!, NY-NY00138551!, US-884541!).

Salpichroa wrightii A. Gray, Syn. Fl. of N. Amer., ed. 2(1). 1: 231. 1886.—TYPE: UNITED STATES. Arizona: on the Sonoita, towards the San Pedro, 17 Sep 1851 (fr), C. Wright 1592 (erroneously as "1692" in protologue; lectotype, here designated: GH-GH00217433!; islectotypes: G-G00016521!, GH-GH00217434!, K! [2 collections, both labeled as Wright 1592, mounted on one sheet], MO-3830682!, NY-NY00138909!).

Herb, sometimes slightly woody at base, single- to few-branched, 1–3 (4) dm tall. Stems sparsely to densely pubescent with straight, one- or two-celled unbranched hairs, these denser on new growth. Sympodia 2-foliate, usually geminate. Leaf blades 1–4.5 × 0.5–2.5 cm, elliptic to elliptic-ovoid, chartaceous to membranaceous, sparsely to moderately pubescent adaxially and abaxially with 1 or 2 celled unbranched hairs, these lying flat along blade, denser along veins; base rounded to obtuse, often decurrent into petiole; apex acute; petioles 0.5–2 cm, moderately pubescent with unbranched hairs. Inflorescences with 1–5 flowers, the axes sparsely to moderately pubescent with unbranched hairs; peduncle absent or nearly so; rachis absent; pedicels 5–12 mm in flower, 10–20 mm in fruit. Flowers with the calyx 3–9 mm long, the tube 1–3 mm, the lobes 2–6 × 0.5–1.5 mm, linear-lanceolate, moderately to densely pubescent. Corolla 0.5–1 cm in diameter, rotate with abundant

interpetalar tissue, chartaceous to membranaceous, white, the tube 3–6 mm long, the lobes very short, 1–2 × 0.5–1 mm, triangular, acute at apices, glabrous abaxially and adaxially. Stamens 2–4 mm long; filaments up to 1 mm long; anthers 1.5–3 × 0.5–1.5 mm, oblong, the base cordate, the apex emarginate. Ovary glabrous; style 4–6 × 0.5–1 mm, equal to or exserted beyond stamens; stigma to 1 mm wide. Berries 5–12 mm in diameter, globose, white to yellow when immature, maturing semitransparent, drying brown, glabrous, the mesocarp watery and held under pressure until dehiscing explosively at maturity. Seeds 5–20 per fruit, ca. 2.5 × 1.5 mm, significantly notched where connected to placenta, the outer margin of seeds swollen with large raised ridges running perpendicular to margin and connected by smaller cell walls running parallel to margin, the center of seed smoother. Figure 6.

Habitat and Distribution—Weedy in grazed areas, along roadsides, and disturbed areas in dry forests from southern Arizona, U. S. A. through Mexico to Guatemala, Honduras, Nicaragua, and Costa Rica at elevations from 0–1,550 m (Fig. 7).

Phenology—Flowering specimens have been collected in all months with a peak from May through September. Fruiting specimens have been collected in all months of the year with a peak from June through October.

Conservation Status—The widespread distribution and abundant populations of *S. deflexum* give it an IUCN Red List Status of Least Concern.

Etymology—The epithet *deflexum* indicates a structure bent sharply downward but it is somewhat unclear what structure this refers to. In the description, Greenman notes that the species is well characterized by the inflorescence, calyx, and pubescence. Since only the inflorescence, specifically the pedicels, could be characterized as deflexed, it is likely that the epithet refers to this structure.

Additional Specimens Examined—UNITED STATES. **Arizona**: Fresnal Canyon, Baboquivari Mts., Pima Co., 2 Sep 1931 (fr), Gilman 80 (WIS); Baboquivari Mts., 26 Sep 1927 (fr), Harrison 4777 (US); Tumacacori, Santa Cruz Co., 29 Aug 1931 (fr), Harrison 8147 (US); Baboquivari Mts., 30 Sep 1934 (fr), Kearney & Peebles 10387 (US); near Patagonia, 18 Aug 1928 (fl, fr), Peebles et al. 5625 (US).

MEXICO. Baja California: Cape Region, Oct 12 1899 (fr), Brandege s.n. (F, NY); Corral Piedra, 10 Sep 1893 (fl), Brandege s.n. (NY, US); Corral Piedra, 9 Sep 1893 (fl, fr), Brandege s.n. (GH); Sierra San Lazaro, 11 Sep 1893 (fl, fr), Brandege s.n. (UC); San José del Cabo, 17 Sep 1890 (fl, fr), Brandege 412 (UC). **Baja California Sur**: Sierra de la Giganta, Mesa del Potrero de San Javier (northeast of Misión San Javier), ca. 25°52'N, 111°32.5'W, 800–850 m, 20 Sep 1965 (fr), Carter 4991 (NY, UC, US); Sierra de la Giganta, Cañon de Arroyo Hondo, N side of Cerro Giganta, ca. 26°8.5'N, 111°35'W, ca. 750 m, 29 Aug 1971 (fl), Carter 5621 (UC); Sierra de la Giganta, Cañada del Encinal, S side of Valle de Los Encinos (S side of Cerro Giganta), ca. 26°3.5'–4'N, 111°34'W, ca. 750 m, 1 Oct 1967 (fr), Carter & Moran 5376 (MO, TEX, UC). **Chiapas**: Mun. Cintalapa, 23 km west of Las Cruces along road to La Mina Microwave Station, 870 m, 14 Sep 1981 (fr), Breedlove 52762 (NY); Mun. Jiquipilas, a 7.5 km al ONO de Francisco Villa, 646 m, 16°24'48"N, 93°43'00"W, 11 Jul 2004 (fl, fr), Martínez & Aguilar 36935 (MO); between Topana, Oaxaca & Tonalá, 200–500 ft, 1–3 Aug 1895 (fl, fr), Nelson 2876a (GH, US). **Chihuahua**: near Rio Urique, near Urique, ca. 1700 ft, 31 Jul 1971 (fl, fr), Bye Jr. 1712 (GH). **Colima**: near km 288, ca. 20 miles ESE of Manzanillo, ca. 50 m, 23 Jul 1957 (fl, fr), McVaugh 15658 (US); along Río Cihuatlán in gorge near bridge 13 miles north of Santiago, 175 m, 27 Jul 1957 (fl, fr), McVaugh 15796 (BM, G, NY, TEX, US). **Guerrero**: Dist. Coyuca, Pungarabato, 22 Aug 1934 (fl, fr), Hinton et al. 6481 (BM, G, GH, K, K, MO, US); Dist. Mina, Placeres, 350 m, 23 Jul 1936 (fl, fr), Hinton et al. 9143 (GH, K, NY, US); Distr. Montes de Oca, Vallecitos, 7 Mar 1937 (fl), Hinton et al. 10557 (F, GH, K, NY, UC, US); along highway, 8 miles S of Mexcala, 23 Jul 1939 (fl, fr), Langman 2145

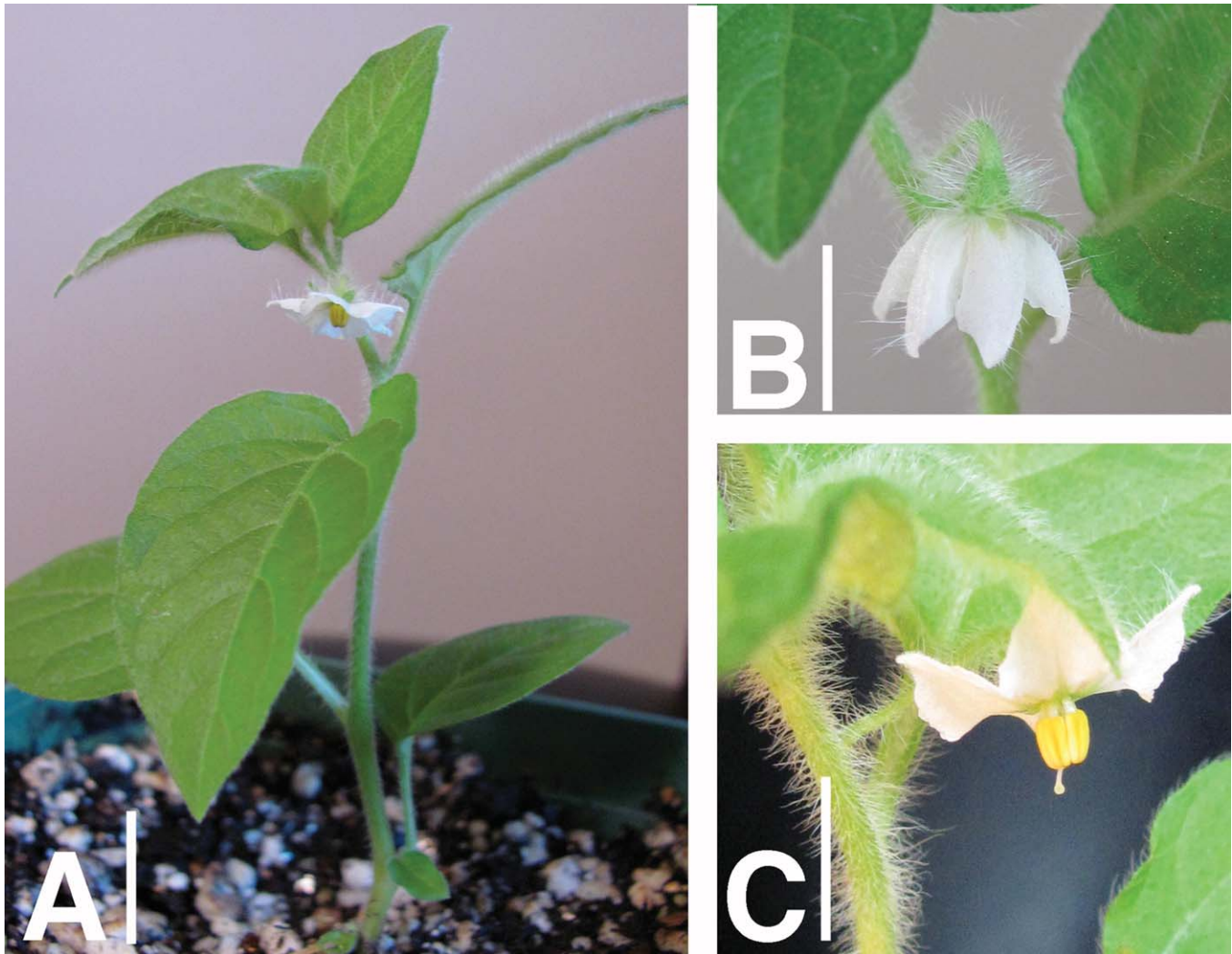


FIG. 6. *Solanum deflexum* (Bohs 2715, UT). A. Habit. B. Closed flower in the late afternoon; note straight hairs on calyx and pedicel. C. Open flower in the day; note straight hairs on stem. Scale bars: A = 1 cm. B, C = 5 mm.

(PH); Rio Balsas, 26 Aug 1910 (fl, fr), *Orcutt* 4210 (F, GH, K, MO, US); Rio Balsas, 26 Aug 1910 (fl, fr), *Orcutt* 4389 (F); Flora de la cuenca del Río Balsas, Mun. Tepecoacuilco de Trujano, Oapan, between Oapan/Ahuelicán, 17°58'53"N, 99°26'50"W 1846 ft, 2 Aug 2003 (fl, fr), *Smith & Rojas* 348 (NY); Flora de la cuenca del Río Balsas, Mun. Tepecoacuilco de Trujano, Oapan, between Oapan/Ahuelicán, 17°59'38"N, 99°26'57"W, 2018 ft, 30 Aug 2003 (fl, fr), *Smith & Rojas* 561 (NY). **Jalisco:** Mun. Huejuquilla, Rancho Los Arroyos del Agua, 15 km al NW de Huejuquilla, 1550 m, 4 Aug 1990 (fl, fr), *Flores* 2025 (WIS); near Guadalajara, 24 Aug 1901 (fl, fr), *Rose & Hay* 6288 (US). **México:** Dist. Temascaltepec, Tenayac, 1450 m, 14 Jul 1933 (fl, fr), *Hinton et al.* 4219 (BM, F, G, K, NY, US); Dist. Temascaltepec, Ixtapan, 1000 m, 2 Aug 1933 (fl), *Hinton et al.* 4470 (BM, F, G, GH, K, K, NY, US). **Michoacán:** Dist. Apatzingan, Mun. Apatzingan, 300 m, 19 Aug 1938 (fl, fr), *Hinton et al.* 12057 (K, NY, US); Mun. Apatzingan, bank of Rio Apatzingan 2 mi S of Apatzingan, 1200 ft, 5 Aug 1940 (fl), *Leavenworth* 473 (F, MO, NY); Mun. Uruapan, Tancitaro Region, 2 miles west of Uruapan, 6000 ft, 2 Aug 1941 (fl, fr), *Leavenworth & Hoogstraal* 1279 (F); Mun. Apatzingan, Tancitaro Region, La Majada, 1200 ft, 7 Aug 1941 (fr), *Leavenworth & Hoogstraal* 1344 (F, GH, MO, NY); near Morelia, ca. 2000 m, 14 Jul 1941 (fl, fr), *Schery* 107 (MO); cuenca media del Rio Balsas, en La Cuesta del Mango, 30 km al N de Huetamo, carr. A Zitácuaro, 650 m, 6 Sep 1978 (fr), *Soto Núñez* 952 (MO). **Morelos:** hillside near Cuernavaca, 5000 ft, 26 Jul 1896 (fr), *Pringle* 6400 (BR, E, G, GH, GOET, MEXU, PH, W, WU); near Yautepec, 13–13 Jul 1905 (fl, fr), *Rose et al.* 8587 (US). **Nayarit:** Cerro de la Cruz, east of Tepic, 1000 m, 17 Sep 1926 (fr), *Mexia* 673 (UC). **Oaxaca:** Dist. Tehuantepec,

Mun. Santiago Astata, Barra de la Cruz, 2 km W, por la vereda hacia Zimatán, 15°50'22"N, 95°59'4"W, 105 m, 3 Sep 1998 (fr), *Elorsa* 700 (NY); Dist. Tehuantepec, Mun. Santiago Astata, Las Tres Peladas, 3 km al SE de Barra de la Cruz cerca de la playa, 15°49'51"N, 95°57'13"W, 10 m, 15 Jun 2000 (fl, fr), *Elsora* 3117 (NY); 6 km NE of Juchitán, along the Pan-American highway (route 19), elevation less than 50 m, 9 Jul 1958 (fl, fr), *King* 446 (TEX, WIS); 11 km NW of the village of La Ventosa, along the Trans-Isthmian highway (route 185), elevation 50 m or less, 14 Jul 1958 (fl, fr), *King* 555 (TEX); 2 km NW of Juchitan, 29 Jun 1981 (fl, fr), *LaSalle et al.* 810629–2 (TEX); Mun. Salina Cruz, Dto. Tehuantepec, Carnero, 10 km al NO de Rincon Bamba, 16°05'N, 95°30'W, 8 Jul 1988 (fl, fr), *Martinez* 1461 (F, MO); near Oaxaca, 5000 ft, 5 Jul 1897 (fl, fr), *Pringle* 6729 (BH, BR, F, G, GH, K, M, MO, NY, PH, UC, US, WU); Jomillín Cañon, 6 Jul 1897 (fl, fr), *Pringle* 7508 (MO); Santa Catarina, 14 Jul 1910 (fl, fr), *Rusby* 85 (NY, US); Mun. Cuicatlán, Dist. Cuicatlán, 4 km al E de Cuicatlán, brecha a Concepción papalo, 17°41'31"N, 96°57'44"W, 925 m, 19 Jun 1993 (fl), *Salinas et al.* 7242 (NY); Almoloya, 100–250 m, Jul 1937 (fl, fr), *Williams* 9819 (F); 80 miles S of Oaxaca on Rt 190, km mark 670, 22 Jun 1966 (fl), *Winkler & Snider* 994 (MO). **Puebla:** near Oaxaca, vicinity of San Luis Tultitlanapa, Puebla, Jul 1908 (fr), *Purpus* 3563 (F, GH, MO, NY, UC, US). **Querétaro:** Mun. de Arroyo Seco, 1 km al NNW de Vegas Cuatas, 760 m, 19 Aug 1991 (fl, fr), *Carranza* 3413 (TEX); Mun. Jalpan, 4.7 mi W of Jalpan, 1260 m, 7 Jul 1985 (fr), *Cowan et al.* 5455 (MO, NY, TEX). **San Luis Potosí:** edge of hill and corn field beside Tamasopo Falls, 12 Sep 1978 (fr), *D'Arcy* 11896 (MO, TEX). **Sinaloa:** vicinity of Culiacan, Culiacan, 18 Oct 1904 (fl, fr), *Brandegge*

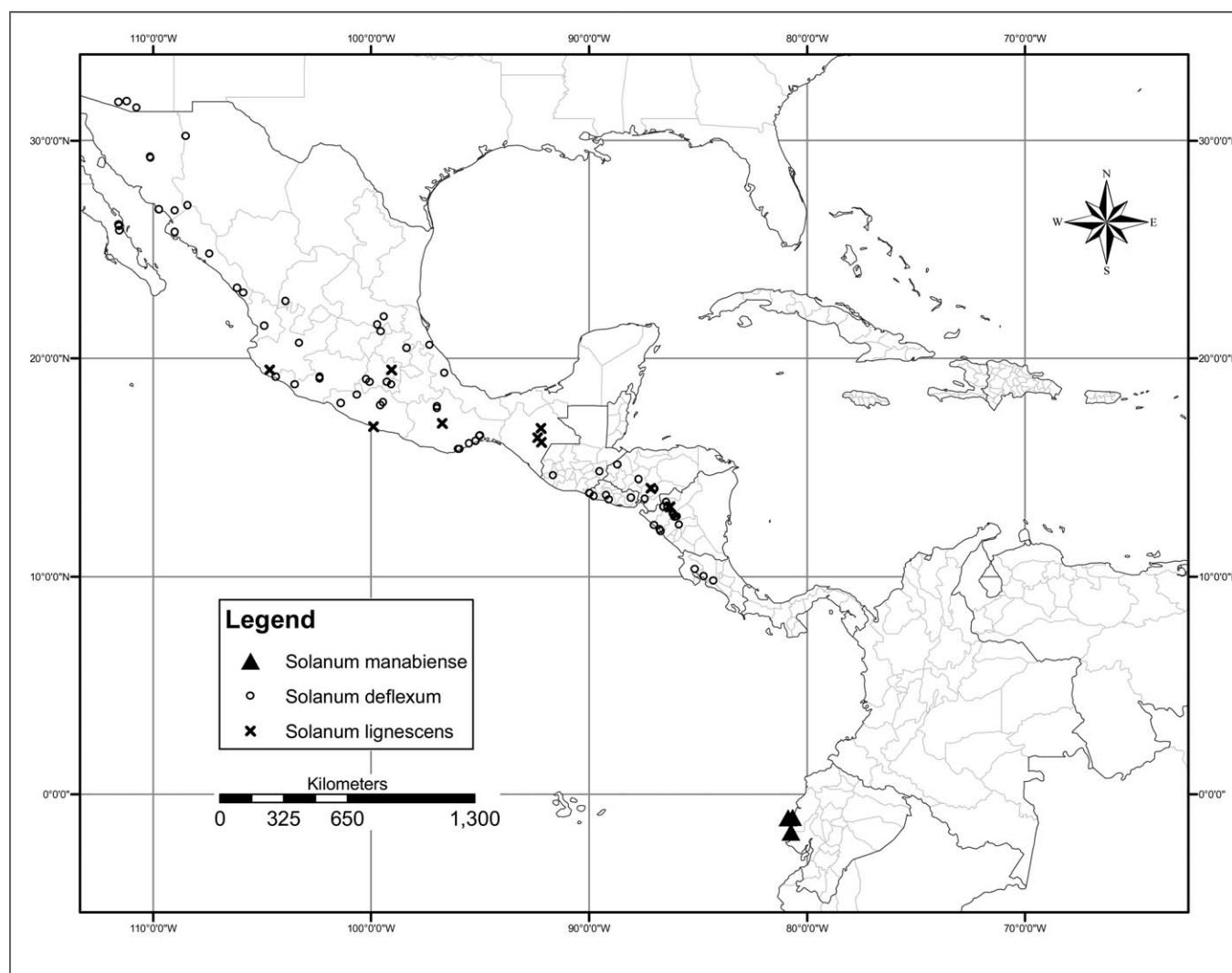


FIG. 7. Distribution of *S. deflexum*, *S. lignescens*, and *S. manabiense*.

s.n. (GH, US); vicinity of Culiacan, Culiacan, 10 Sep 1904 (fl, fr), *Brandege* *s.n.* (UC); Cerros del Fuerte, 18–24 miles north of Los Mochis, 200–1000 ft, 3–5 Oct 1954 (fr), *Gentry* 14430 (LL, US); near Rosario, on the road to Acaoponeta, 27 Jul 1897 (fl, fr), *Rose* 1852 (F, GH, K, US); E of Villa Union, on Hwy 40, near 106°08'W, 23°14'N, 200 m, 18 Aug 1988 (fl), *Sanders et al.* 8033 (NY). **Sonora:** 0.5 mi SE of Alamos at junction of Güirocoba and El Fuerte Rds., 1400 ft, 1 Sep 1973 (fr), *Fish* 73 (UC); El Naranjo, ca. 23.5 mi NE Alamos, 9 Aug 1980 (fl), *Lehto* 24716 (NY); Alamos, 4 miles N of A., 250–300 m, 3 Aug 1935 (fl), *Pennell* 19496 (PH); Mun. de Soyopa, arroyo Las Tinajas below ruins of Toledo smelter, near Loma Maderista, 3.5 km S of Tónichi, west side of Río Yaqui, 220 m, 28°34'03"N, 109°33'25"W, 17 Sep 2006 (fl, fr), *Van Devender & Reina* 2006–937 (MO); Mun. de Alamos, 1 km E of Yocogigua on road to Capitahuasa, 26°47'25"N, 109°0'55"W, 230 m, 25 Sep 1993 (fr), *Van Devender et al.* 93–1114 (MO). **Tamaulipas:** 3 miles S of Villa de Aldama, N of Tampico, 18 Jul 1971 (fl), *D. Spellman et al.* 95 (MO). **Veracruz:** La Granja Vista Hermosa, entrada a la presa de Temascal, km 25, 8 m, 20 Nov 1966 (fr), *Calderón* 1169 (BM, MO); Mun. Apazan, Baños de Carrizal, 7 km SE of Emiliano Zapata [=Carrizal], 19°19'N, 96°38'W, 250 m, 27 Jun 1980 (fr), *Hansen & Nee* 7447 (F, MO); Pte. Nacional, 3 km al E del Crucero, camino de terracería, 8 Jul 1986 (fl, fr), *Ortiz* 1029 (MO); Baños del Carrizal, Aug 1912 (fr), *Purpus* 6100 (BM, F, GH, MO, NY, UC, US); Zacuapan, Sep 1907 (fl), *Purpus* 7860 (MO, NY, UC, US); Zacuapan, 1917 (fl, fr), *Purpus* 8016 (GH, M, UC); Barranca de Panoaya, Sep 1919 (fr), *Purpus* 8498 (GH, M, MO, NY, UC, US); Rancho Tlacosinatla, Aug. 1929 (fl), *Purpus* 10771 (M, NY, PH, US); Zacuapan, Aug 1929 (fl, fr), *Purpus* 12055 (NY); Zacuapan, Aug 1929 (fl, fr), *Purpus* 13000

(A); Mun. Xalapa, Chitares, antes Arteria, cerca de San Nicolás, 640 m, 9 Jul 1971 (fl, fr), *Ventura* 3835 (CORD, F); Mun. Totutla, Encinal, 750 m, 21 Aug 1971 (fl, fr), *Ventura* 4123 (CORD, F); Mun. de Puente Nacional, Mata de Caña, 100 m, 20 Aug 1973 (fr), *Ventura* 8883 (F); La Concepción, Mun. de Jilotepec, 900 m, 7 Aug 1978 (fr), *Ventura* 11750 (F). **Zacatecas:** 5 miles NE of Mesquitula near the Río Juchilipa, 3500 ft, 11 Aug 1969 (fl, fr), *Taylor & Taylor* 6073 (NY, US). **Distrito Federal:** Vicinity of Rancho del Rosario, 10 miles N of Mexico City near Atzacapotzcolco, 7300–7500 ft, 1–15 Jul 1937 (fr), *Happ* 101 (MO). **Without State:** Mexico, (fl), *Orcutt* 5286 (MO).

GUATEMALA. **Chiquimula:** bei Chiquimula, 400 m, Jul 1881 (fl, fr), *Lehmann* 1671 (BM, G, US); near divide on road from Zacapá to Chiquimula, ca. 660 m, 9 Oct 1940 (fr), *Standley* 73719 (F); Chiquimula, transecto La Hondonada, 300–400 m, 14°51'03"N 89°31'08"W, 8 Jul 2003 (fl), *Véliz & Ramírez* 13712 (MO). **El Progreso:** San Agustín, Aldea El Rancho, 200–300 m, 14°54'42"N, 90°02'08"W 10 Jul 2003 (fr), *Cóbar & García* 520 (MO); El Jícaro, 200–300 m, 14°55'19"N, 89°52'25"W, 9 Jun 2003 (fr), *García et al.* 715 (MO); Morazán, Aldea Pasasagua, 300–400 m, 14°55'41"N, 90°03'42"W, 10 Jul 2003 (fr), *Ramírez & Véliz* 948 (MO). **Guatemala:** 15 km SE of Granados, dry hillside above Río Motagua, 15 Jul 1970 (fl, fr), *Harmon & Dwyer* 3085 (MO, WIS). **Jutiapa:** near Mongoy, 1800 m, 27 Jun 1949 (fr), *Williams & Molina* 16796 (F). **Suchitepequez:** E side of San Antonio, 30 Jul 1970 (fr), *Harmon & Dwyer* 3399 (MO). **Zacapá:** Río Hondo, 170–200 m, 15°01'32"N, 89°35'06"W, 8 Jul 2003 (fl, fr), *Cóbar & García* 385 (MO); Cabañas, 200–300 m, 14°55'54"N, 89°46'55"W, 9 Jul 2003 (fr), *Ramírez & Véliz* 813 (MO); Río Hondo, Transecto Río Hondo, 210 m, 15°01'32"N, 89°35'06"W, 8 Jul 2003 (fl, fr), *Véliz & Ramírez* 13681 (MO).

HONDURAS. **Comayagua:** vicinity of Comayagua, ca. 600 m, 12–23 Mar 1947 (fl, fr), *Standley & Chacón* 5407 (F); al Oeste de Comayagua cerca de El Taladro, 650 m, 27 Jun 1964 (fl, fr), *Standley & Molina* 14278 (F, G, NY, US). **Copán:** Mun. Nueva Arcadia, 3 mi SW of Los Tangos along Santa Rosa de Copán-San Pedro Sula highway, 15°06'25"N, 88°41'51"W, 425 m, 26 Jun 1994 (fl, fr), *Davidse et al.* 35391 (MO, NY). **Francisco Morazán:** Tegucigalpa D.C., Col. Miraflores Sur y alrededores, 900 m, 26 Jun 1978 (fr), *Díaz* 63 (MO); drainage of the Río Yeguaré, ca. 14°N, 87°W, 900 m, 2 Aug 1949 (fr), *Molina* 2535 (GH); El Zamorano, Dept. of Agronomy, common in corn field of Monte Redondo drainage of Yeguaré river, 800 m, 11 Dec 1971 (fr), *Molina* 27185 (F, US); meadows around Escuela [El Zamorano], Aug 1960 (fr), *Pfeifer* 1245 (US); Zamorano, 800 m, 21 Sep 1943 (fr), *Rodríguez* 940 (F); same loc., 24 Sep 1943 (fl, fr), *Rodríguez* 1013 (F); same loc., May 1944 (fl, fr), *Rodríguez* 2126 (F); same loc., 800 m, 7 Mar 1945 (fl, fr), *Rodríguez* 3800 (F, GH, MO, US); vicinity of El Zamorano, 780–900 m, 26 Nov 1946–9 Jan 1947 (fr), *Standley* 1654 (F); same loc. and date? (fr), *Standley* 1811 (F); same loc. (fr), *Standley* 3833 (F); same loc., 12 Oct 1948 (fl, fr), *Standley* 13024 (F); same loc. (fl), *Standley* 16093 (F); same loc., 800–850 m, 16 Jul 1949 (fl, fr), *Standley* 21306 (F); región of Río de la Orilla, southeast of El Zamorano, 900–950 m, 5 Aug 1949 (fl, fr), *Standley* 22210 (F). **Olancho:** matorrales al lado de la carretera 6 km a Juticalpa, 430 m, 18 Nov 1963 (fr), *Standley & Molina* 13233 (F, NY, US). **Valle:** Mun. Nacaome, 1 mi NE of Júcaro Galán, along main highway to Tegucigalpa, 13°32'37"N, 87°25'35"W, 80 m, 18 Jun 1994 (fl, fr), *Davidse et al.* 35103 (MO).

EL SALVADOR. **Ahuachapán:** San Francisco Menéndez, El Corozo, Mariposario, zona alta "Mariposario," 13°49'N, 89°59'W, 250 m, 25 May 2000 (fl), *Rosales* 837 (BM, MO, NY). **Cabañas:** Cinquera, zona protegida, quebrada calle antigua, 500 m, 13°51'N, 88°57'W, 13 Aug 2002 (fr), *Carballo* 371 (MO); Cinquera, zona protegida, entrada cementerio, 400 m, 13°53'N, 88°57'W, 29 Aug 2002 (fr), *Carballo & Carrillo* 433 (MO). **La Paz:** San Luis Talpa, Centro Experimental Universidad El Salvador, 29 Aug 1995 (fl, fr), *Montalvo* 6380 (MO, NY). **Morazán:** adjacent to ditch leading to reservoir, Montecristo (ca. 15 km northeast of San Miguel), 13°36'N, 88°04'W, ca. 140 m, 9 Dec 1941 (fl, fr), *Tucker* 502 (BH, F, G, GH, IAC, IAN, K, LL, NY, UC, US). **San Salvador:** vicinity of San Salvador, 650–850 m, 20 Dec 1921–4 Jan 1922 (fl, fr), *Standley* 19647 (G, GH, NY, US); vicinity of San Salvador, 650–850 m, 30 Mar–24 Apr 1922 (fl, fr), *Standley* 22678 (US). **San Vicente:** vicinity of San Vicente, 400–500 m, 7–14 Feb 1947 (fl, fr), *Standley & Padilla* 3808 (F). **Sonsonate:** vicinity of Santa Emilia, ca. 135 m, 22–25 Mar 1922 (fr), *Standley* 22063 (GH, S, US); vicinity of Santa Emilia, ca. 135 m, 22–25 Mar 1922 (fl, fr), *Standley* 22258 (GH, MO, NY, US).

NICARAGUA. **Boaco:** Km 57.5 on Hwy 7 (Carretera al Rama), ca. 5.0 km NE of Managua line, ca. 12°22'N, 85°52'W, ca. 130 m, 16 Jul 1978 (fr), *Stevens* 9363 (MO). **Chinandega:** E base of Coseguina [Coseguína] Volcano, 6 Jul 1932 (fl, fr), *Howell* 10253 (F, US); Ameyá, near sea level, 19–21 Jun 1923 (fl, fr), *Maxon et al.* 7138a (US); Ameyá, near sea level, 19–21 Jun 1923 (fl, fr), *Maxon et al.* 7191 (US); vicinity of Chichigalpa, ca. 90 m, 12–18 Jul 1947 (fr), *Standley* 11148 (F). **Chontales:** 0.9 km W of bridge at Lóvago, km 166, 95 m, ca. 12°00'N, 85°10'W, 7 Jun 1981 (fl), *Stevens & Henrich* 20473 (MO). **Estelí:** near El Dorado, 8 km N of Estelí, along the Río La Sirena, 13°09'N, 86°23'W, 800 m, 30 May 1985 (fl, fr), *Davidse et al.* 30657 (MO, NY); Mun. San Juan de Limay. Had. La Grecia "Cerro Quiniento," 13°11'N, 86°35'W, 518 m, 3 Sep 1980 (fr), *Moreno* 2157 (MO); ca. 7 km from Hwy 1 (at ca. km 193) on road to Pueblo Nuevo, from Quebrada Jamaili to near summit of Cerro El Pedrero, ca. 13°24'N, 86°27'W, 600–700 m, 3 Jul 1977 (fr), *Stevens* 2610 (BM, LL); Km 163 on Hwy 1, ca. 11.2 km N of entrance to Estelí, ca. 13°13'N, 86°23'W, ca. 920 m, 19 May 1981 (fl, fr), *Stevens & Henrich* 20185 (MO). **León:** Mun. de La Paz Centro, Miramar, nivel del mar, 12°10'N, 86°45'W, 27 Sep 1997 (fl, fr), *Rueda* 7420 (NY); Las Peñitas, al SE de Poneloya, 12°21'N, 87°01'W, 10 m, 22 Jun 1982 (fl, fr), *Sandino* 3134 (MO); slope and ridge immediately W of Quebrada Las Ruedas, N of road, NW of El Transito, ca. 12°05'N, 86°43'W, ca. 15–30 m, 16 Oct 1977 (fr), *Stevens* 4708 (MO). **Managua:** Managua, Aug 1923 (fl, fr), *Chaves* 2 (US). **Matagalpa:** 9 km south of Sebaco, collection from wet depression along road (Nic. 1), 500 m, 7 Feb 1971 (fl, fr), *Harmon & Fuentes* 6016 (MO, WIS); just W of Puente de Río Viejo, ca. 8 km SE of San Isidro, 12°53'N, 86°09'W, 460 m, 24 Jun 1982 (fl, fr), *Kral* 69080 (MO); Darío, "Cuajiniquilapa," a 4 km de la Carretera Panamericana siguiendo la carretera a Terrabona, 12°44'N, 86°04'W, 440–480 m, 18 Jun 1981 (fl, fr), *Moreno* 9222 (MO); Darío, "Las Joyas," en la quebrada a 7 km de la Carretera Panamericana, sobre el camino a Terrabona, 12°45'N, 86°01'W, 480–500 m, 18 Jun 1981 (fr), *Moreno* 9280 (MO); Darío,

"El Caracol," a 14 km de la Carretera Panamericana, 12°45'N, 85°59'W, 560–580 m, 18 Jun 1981 (fl, fr), *Moreno* 9294 (MO); Entrada Paso de Carreta, quebrada, 12°52'N, 86°08'W, 460–480 m, 24 Jun 1982 (fl, fr), *Moreno* 16703 (MO); SW slopes of Cerro El Pilón and adjacent Laguna Tecomapa, 420–540 m, 12°37'N, 86°02'W, 20 Jul 1978 (fl, fr), *Stevens* 9376 (MO). **Nueva Segovia:** above Río Dipilto 6 km N of Ocotál, 700 m, 15 Jun 1977 (fl, fr), *Neill* 2174 (MO). **Rivas:** Las Salinas, sea level, 25 Aug 1977 (fl), *Neill* 2460 (MO).

COSTA RICA. **Alajuela:** Cantón de Orotina, Valle del Tárcoles, de la carretera Orotina-Caldera, ca. 1 km S rumbo a playa Bajamar, Guacalillo, 9°53'0"N, 84°38'10"W, 100 m, 21 July 1995 (fl, fr), *Hammel & Grayum* 19933 (INB); La Balsa de Río Grande, 2 June 1911 (fl), *Pittier* 3646 (US). **Guanacaste:** Cantón de Bagaces, P.N. Palo Verde, Valle de Tempisque, A.C.T. Sector Palo Verde, sitio La Carreta, 10°22'0"N, 85°17'0"W, 10–100 m, 30 July 1996 (fl, fr), *Chavarria* 1503 (INB, MO); Cantón de Bagaces, P.N. Palo Verde, Cuenca del Tempisque, sector La Carreta, 14 m, 10°21'40"N, 85°19'20"W, 9 Oct 1997 (fr), *Chavarria* 1766 (MO); Comelco E, W of Bagaces, 2 Aug 1971 (fl, fr), *Heithaus* 274 (MO); Río Higueirón, near Taboga, 0–100 m, 10°20'N, 85°12'W, 29–30 Jun 1977 (fl, fr), *Liesner et al.* 2798 (MO); Finca La Pacífica Cañas, Secondary Plot, 100 m, 13 Jun 1972 (fl, fr), *Opler* 860 (F, UC). **Puntarenas:** vicinity of Cascajal (25 km ESE of Puntarenas), along road from Cascajal to Pigres, 30–100 m, 6 Jul 1949 (fr), *Holm & Iltis* 295 (A, G, MO); entre Mata de Limón y Cerro de las Mesas, 50 m, 1 Jun 1963 (fl, fr), *Jimenez* 721 (F); Cantón de Montes de Oro, cuenca del Aranjuez, San Isidro, Las Lomas, 2.5 km N de Cuatro Cruces, 10 m, 10°01'33"N, 84°44'12"W, 13 Aug 1998 (fr), *Rodríguez et al.* 3909 (F, MO); near junction of Hwy. 1 and road to Miramar, 50 m, 28 Aug 1966 (fl, fr), *Weston et al.* 2060 (UC).

Notes—*Solanum deflexum* and *S. lignescens* are the only two species in the section that occur in Central America. The straight, multicelled, unbranched hairs of *S. deflexum* are unlike the hairs of *S. hoffmanseggii*, *S. olympicum*, and *S. turneroides* that bend up or down the stem, and, unlike *S. lignescens*, they are not stellate. *Solanum lignescens* is sympatric with *S. deflexum*, but the latter is a diminutive non-woody plant, reaching 30 to rarely 40 cm in height. *Solanum deflexum* is frequently many-branched at the base, creating a "flat" appearance that is distinct from the upright appearance of other members of the clade. *Solanum deflexum* is also unique in that the first inflorescence often appears with the first pair of leaves after the cotyledons, giving the appearance of flowering while still a seedling (Nee 1989). Unlike other members of the clade, *S. deflexum* is rarely rhizomatous, although it does appear in patches, likely due to the explosive dehiscence of the fruits.

In the description of *S. deflexum*, Greenman lists three collections, *Nelson* 2876a, *Pringle* 6400, and *Smith* 403, but none was designated as the type. *Smith* 403 was chosen as the lectotype from among the syntypes because of the quality of the specimen, with both flowering and fruiting material. A collection bearing a label for *Smith* 403 exists at MEXU but this specimen also bears a label for *Pringle* 6400, a different syntype collection. The material is likely that of *Smith* 403 as it is both flowering and fruiting while all of the many *Pringle* 6400 collections at MEXU and other herbaria only have flower buds or fruit. *Nelson* 2876a is comprised of plants that are unusually large and are not reflective of the species as a whole.

The type of *Salpichroa wrightii* exemplifies the problems botanists have encountered with collections by Charles Wright made along the boundary with Mexico. In the protologue, Gray gives the collection locality as "Arizona on the Sonoita" and the type as *Wright* 1692. Consultation of Shaw's (1987) book about Wright's expeditions and W. T. Kittredge's label on the lectotype sheet, presumably with information taken from Wright's field notes, indicates that his field number for this collection is 549 and it was made on September 17, 1851. The specimens, all apparently belonging to the

same gathering, have been distributed with the numbers 1592 and 1692. In fact, on the lectotype sheet at GH the handwritten "1592" appears to have been changed to "1692". Because the distribution number 1692 does not exist for Wright's Solanaceae collections according to Shaw (1987), it is apparent that all the collections should bear the distribution number 1592 and the protologue contains a typographical error.

3. *SOLANUM EVOLVULOIDES* Giacomini & Stehmann, *PhytoKeys* 7: 1–9. 2011.—TYPE: BRAZIL. Bahia: Mun. Jequié, Dist. Cachoeirinhas, caatinga arbustiva em topo de morro, com lajeados graníticos, 13°54'14.4"S, 40°01'46.8"W, 299 m, 10 Jul 2009 (fr), L.L. Giacomini 974 (holotype, BHCBI; isotypes to be distributed to BM, MBM, NY, RB).

Herb, slightly woody to woody at base, few- to many-branched, 2–4 dm tall. Stems moderately to densely pubescent with multicelled unbranched erect glandular hairs, these mixed with less frequent slightly longer 1–3-celled unbranched straight hairs. Sympodia 2-foliate, solitary or more commonly geminate, unequal with the smaller leaves up to half of the size of the larger ones. Leaf blades 1–4 × 1–3 cm, elliptic-ovoid to cordiform, chartaceous to membranaceous, sparsely to moderately pubescent adaxially and abaxially with 1 or 2-celled unbranched hairs, these denser along veins; base attenuate to cordate, often decurrent into petiole; apex acute; petioles 0.5–2.2 cm, moderately pubescent with hairs like those of the stem but with fewer eglandular hairs. Inflorescences with 1–4 flowers, the axes moderately pubescent with hairs like those of the stem; peduncles absent; rachis nearly absent; pedicels 6–10 mm in flower, 7–14 mm in fruit. Flowers with the calyx 2–7 mm long, the tube 1–2 mm, the lobes 2–6 × 1–2.6 mm, ovate-elliptic, the apex acuminate, moderately pubescent abaxially with almost exclusively glandular unbranched multicellular erect hairs; fruiting calyx accrescent, the lobes up to 8 mm long, equal to or exceeding the berry at maturity. Corolla 1–3 cm in diameter, rotate with abundant interpetal tissue, membranaceous, white, the tube 4–6 mm, the lobes 2–4 × 1–3 mm, triangular, acute at apices, with a few eglandular hairs abaxially, mainly on the central part of each lobe, glabrous adaxially. Stamens 4–9.5 mm long; upper, shorter filaments 1–2 mm, the lowermost, longer filament 3–7 mm; anthers 4–6 × 1.3–2 mm, oblong, the base cordate, with a small bulge dorsally, the apex emarginate, the pores directed introrsely and subapically, not opening into longitudinal slits. Ovary glabrous; style 7–9 × 0.5–1 mm, longer than the smaller stamens, closely appressed to the larger stamen, curved near apex; stigma to 1 mm wide. Berries 8–15 mm in diameter, globose, greenish-white when immature, maturing translucent, drying brown to blackish, glabrous, the mesocarp watery and held under pressure until dehiscing explosively at maturity, normally between two calyx lobes. Seeds 10–25 per fruit, 2.5–3.6 × 1.8–2.9 mm, reniform, with a small hollow where connected to the placenta, the margin flattened, the seed surface with raised projections and grooves parallel to margin, giving a netlike impression. Figure 8.

Habitat and Distribution—An herb of the transition zone between deciduous forests and xeric formations of shrubby caatinga. It is known only from a restricted area in the southeastern part of Bahia State, Brazil at 0–275 m in elevation (Fig. 5).

Phenology—Flowering and fruiting materials were collected between February and August, with a flowering peak from February to May; fruiting specimens were collected from June to August.

Conservation Status—The IUCN Red List Status of *S. evolvuloides* is Endangered based on an area of occupancy < 5000 km², < 5 collection localities and declines in extent of occurrence, area of occupancy, quality of habitat, and number of locations. The species is known from only two localities where the landscape has been strongly modified in the last decades due to the expansion of urban centers and extensive farming. The region has been the focus of several surveys undertaken by the Centro de Pesquisas do Cacau in association with the New York Botanical Garden; despite this, just a few collections of this species have been made. Although one collection was made in a disturbed area (*Jardim 1843*), the most recent collection is from a well-preserved forest fragment, and the species was not found in surrounding areas. There are no collections from within conservation units.

Etymology—The epithet is derived from the similar leaf shape and habit shared with members of the genus *Evolvulus* L. of the Convolvulaceae.

Additional Specimens Examined—BRAZIL. Bahia: Km 7 da estrada Jequié/Ipiaú, caatinga, 10 Feb 1983 (fl), *Carvalho 1591* (CEPEC); Mun. Itacaré, Fazenda Monte Alegre, ca. 1 km a leste na rodovia para Itacaré, margem do Rio de Contas, 10 Aug 1998 (fl, fr), *Jardim 1843* (CEPEC); Mun. Jequié, Rodovia Ipiáú/Jequié, 12 May 1969 (fl, fr), *Jesus 367* (CEPEC); Mun. de Manoel Vitorino, Rod. Man. Vitorino/Caatingal, Km 4, região de caatinga, 16 February 1979 (fl, fr), *Mattos Silva s.n.* (CEPEC).

Notes—The species is closely related to *S. turneroides* and shares with it notable heteranthery, with the filament of one stamen much longer than the other four. Like *S. turneroides*, the flowers are only open in the morning and close by midday. *Solanum evolvuloides* can be easily distinguished from all other species in sect. *Gonatotrachelum* by the glandular, multicellular hairs on the stems, inflorescences, and flowers that are not found in any other species of the section.

Jardim 1843 from the banks of the Rio de Contas near the city of Itacaré might be an occasional case of water dispersal by the Contas River, which originates in a xeric environment near the center of Bahia in the caatinga biome.

4. *SOLANUM HOFFMANSEGGII* Sendtn., *Mart. Fl. Bras.* 10: 112. 1846.—TYPE: BRAZIL. "In provincia Paraensi a Siber lectum comunicavit Com. de Hoffmansegg," (fl), F.W. Sieber [as Siber] s.n. (lectotype, here designated: BR-BR000000699204!; islectotype (but see note in commentary): M-M0090348! [fragment in packet only]).

Small shrub from a thick woody taproot with the base reaching 7 mm in diameter, not appearing rhizomatous, much-branched from base, to 5–8 dm tall. Young stems moderately pubescent with two-celled unbranched hairs, these geniculate between first and second cells and pointing apically; older stems glabrescent. Sympodia appearing unifoliate but the structure is difficult to evaluate. Leaf blades 1.5–2.5 × 0.5–1 cm, linear to elliptic, chartaceous to membranaceous, nearly glabrous to moderately pubescent adaxially and abaxially with 1–2-celled unbranched hairs, these lying flat along blade; base acute, often decurrent into petiole; apex acute; petioles absent to 4 mm, moderately pubescent. Inflorescences with 1–3 flowers, the

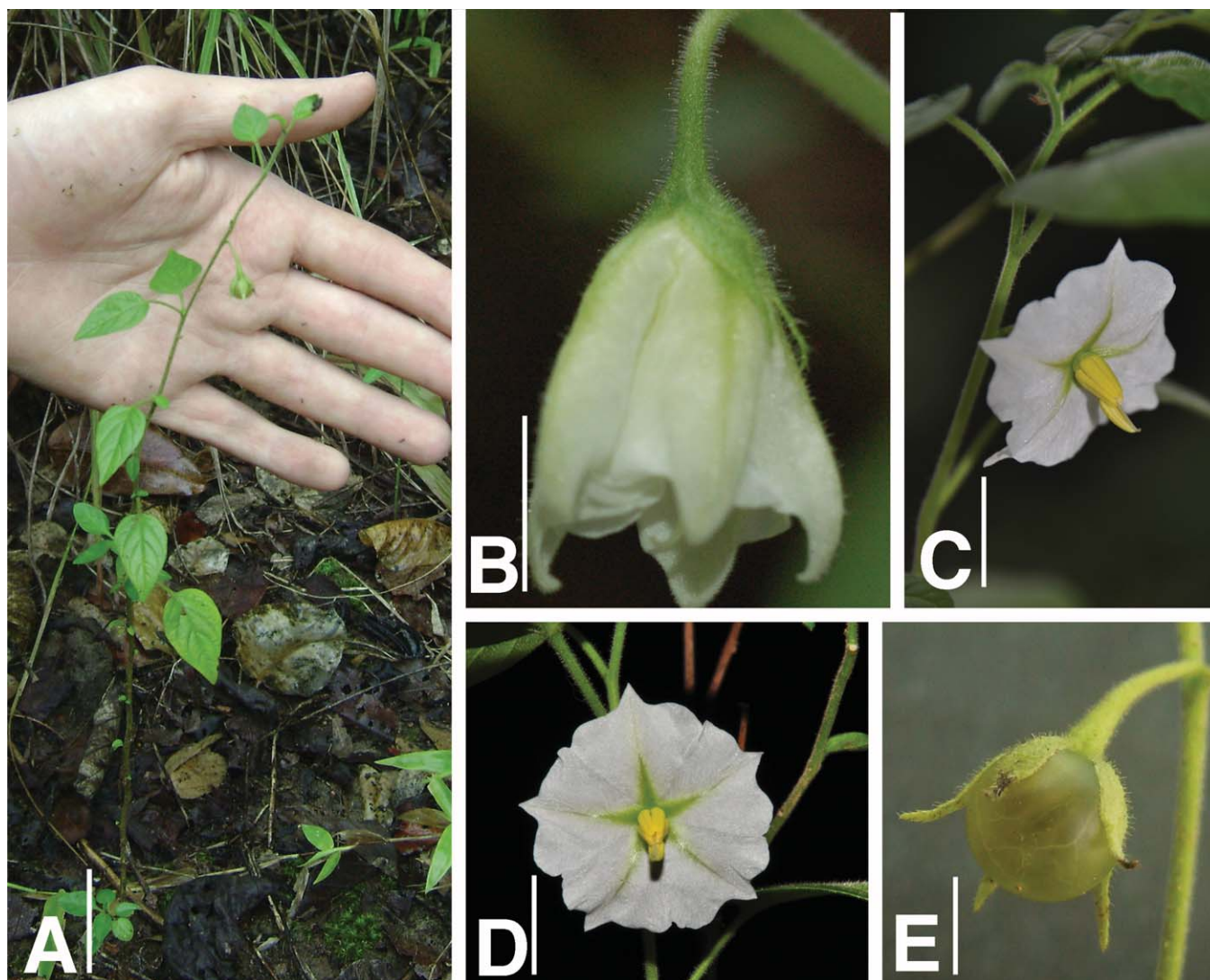


FIG. 8. Photos of type collection of *S. evoluloides* (Giacomin 974, BHCB). A. Habit. B. Flower; note glandular hairs on calyx. C. Flower; note the elongated lowermost stamen. D. Flower. E. Fruit; note the thin, nearly transparent skin. Scale bars: A = 2 cm. B = 5 mm. C, D, E = 1 cm.

axes sparsely to moderately pubescent with unbranched hairs; peduncle absent or nearly so; rachis absent; pedicels 5–10 mm in flower, 10–20 mm in fruit. Flowers with the calyx 2–4 mm long, the tube 1–2 mm, the lobes 2–3 × 0.5–1 mm, linear-lanceolate, moderately pubescent; fruiting calyx 5–8 mm in length. Corolla 8–12 mm in diameter, rotate with abundant interpetalar tissue, membranaceous, the tube 1.5–2.5 mm, the lobes 1.5–2.5 × 0.8–1.5 mm, triangular, acute at apices, moderately pubescent abaxially with hairs like those of the leaves, glabrous adaxially. Stamens 1.5–2 mm; filaments ca. 0.5 mm; anthers 1.5–2 × 0.5–1 mm, oblong, the base cordate. Ovary glabrous; style 2.5–3 × 0.2–0.4 mm, exserted beyond stamens; stigma to 0.5 mm wide. Berries 5–12 mm in diameter, globose, white to brown when dried, glabrous, appearing to be explosively dehiscent due to the presence of small tears and the wrinkled, deflated appearance of the dried fruits. Seeds 5–15 per fruit, ca. 2.5 × 1.5 mm, with a small notch where connected to placenta, the margin not swollen, the surface with fine raised ridges radiating from center to edges and shallow ridges running parallel to margin. Figure 9.

Habitat and Distribution—Known from several localities in Pará State, Brazil and one collection from Tocantins State, Brazil at elevations of 50–200 m (Fig. 5).

Phenology—Flowering materials were collected in June and October to December; fruiting specimens were collected from June to August and October through January.

Conservation Status—According to IUCN guidelines, the status of *S. hoffmanseggii* is deemed of Least Concern due to a sufficiently large number of collections over a relatively large area of occupancy. Many areas of Amazonia are under-collected, leading to difficulty in understanding the species' distribution (Milliken et al. 2011). Given this, it is highly likely that *S. hoffmanseggii* is more widespread and abundant than our data indicate.

Etymology—The epithet honors Johann Centurius Hoffmann Graf von Hoffmannsegg, a German botanist, entomologist, and ornithologist, who sent the sheet collected by F.W. Sieber (whom he employed to make entomological collections in Brazil and whose name he misspelled as Siber) to Sendtner. The specific epithet was originally published as *hoffmanseggii*, and we have

FIG. 9. Scan of lectotype of *S. hoffmanseggii* (Photo credit L. A. Mentz).

retained the original spelling (as stipulated in Art. 60 of the ICBN; McNeill et al. 2006) rather than correcting it to *hoffmanseggii*, as spelling of surnames was quite fluid in the 19th century (he was also referred to as Graf von Haffmannsegg).

Additional Specimens Examined—BRAZIL. **Pará:** Mun. Belterra, Fordlândia, Praia Tabocal, 6 Jan 1948 (fl, fr), *Black 48–2316* (IAN, SP); Rio Tocantins, nella foresta, Capuera roca presso Itacayuna, 1 Jul 1899 (fr), *Buscalioni 3656* (MG, NY); Mun. Altamira, Ilha do Inferno Verde, 28 Nov 1986 (fl, fr), *Dias 627* (MG); Mun. Marabá, Rio Tocantins, Ilha da Praia, 26 Jun 1949 (fl, fr), *Frões 24667* (IAN); Mun. Itaituba, São Luis do Tapajós, margens do Rio Tapajós, 23 Nov 1999 (fl, fr), *Lisboa 6782* (MG); Mun. Conceição do Araguaia, Rio Araguaia, Praia de Santana, 23 Sep 2000 (fl), *Lobato 2656* (MG); [Mun. Altamira] Rio Xingu, trecho compreendido entre o Rio Iriri e a cachoeira da Baleia, calha do Rio Xingu, 1 Oct, 2007 (fl, fr), *Lobato 3282* (MG); Mun. Tucuruí, BR-422, km 45, Breu Branco, margem do Rio Tocantins, 5 Nov 1983 (fl), *Ramos 1010* (INPA); Mun. Altamira, Rio Iriri, reserva indígena dos Araras, 12 Jan 1985 (fl, fr), *Rosário 713* (MG); margem esquerda do Rio Tocantins, montante da Usina Hidrelétrica de Tucuruí, meia hora de barco, acima dos canteiros da obra, 7 Dec 1979 (fl, fr), *Silva 112* (INPA, MG); Mun. Altamira, Rio Xingu, Ilha a margem direita subindo orio, em frente ao acampamento de CNEC, cachoeira do Espelho, 6 Oct 1986 (fl, fr), *da Souza et al. 223* (MG). **Tocantins:** Ilha do Bananal, foz do Rio Javaés, cerra do sujeito a inundação periódica, 20 Aug 1978 (fr), *da Silva 4868* (MG, MO, NY).

Notes—*Solanum hoffmanseggii*, although rarely collected, is morphologically and geographically distinct from the other species of sect. *Gonatotrimum*. This species is more robust than any of the other species except *S. lignescens*, which can be easily distinguished by its stellate hairs. Anomalous large plants of *S. turneroides* may reach nearly similar sizes; however, *S. turneroides* has much larger fruits and heterantherous flowers. The most similar species is *S. olympicum*, which occurs in southernmost Brazil, Bolivia, Paraguay and Argentina. The two species share distinct geniculate hairs as well as seeds with raised ridges radiating from the center to the margins. Unlike *S. hoffmanseggii*, *S. olympicum* has much broader, larger leaves and is a more diminutive plant. *Solanum hoffmanseggii* is the only member of sect. *Gonatotrimum* known from northern Brazil. The *Souza et al. 223* collection is unusual because the leaves are more ovate than other specimens of *S. hoffmanseggii* but other characteristics and its geographic location are consistent with this species. The nearest members of the section geographically are *S. evoluloides* and *S. olympicum*, which are found in the drier northeastern state of Bahia and in deciduous forest of northern Goiás respectively.

Solanum hoffmanseggii has been problematic because it is known from relatively few collections and, until recently, the only known type was a mixed collection from M. This sheet contains a sterile leafy twig bearing branched hairs and a small handwritten label with the number “787” and a packet of the same material on the lower right hand side of the sheet; this may belong to a different species of *Solanum*. Another packet contains fragments including leaves, buds, and flowers of a different plant and is labeled “echtes *S. hoffmanseggii* Sendtn.” by Bitter. However, the material in this packet does not seem to match that of the type of *S. hoffmanseggii* at BR because the leaves are larger, ovate, and more densely pubescent. This is likely material from a collection of *S. olympicum*, a species found much further south in Bolivia, Paraguay, and Argentina, that Bitter thought was *S. hoffmanseggii*. The material on the M sheet is in our view different from that of the BR collection and should be treated with some skepticism. The specimen at BR was chosen as the lectotype because it is far superior

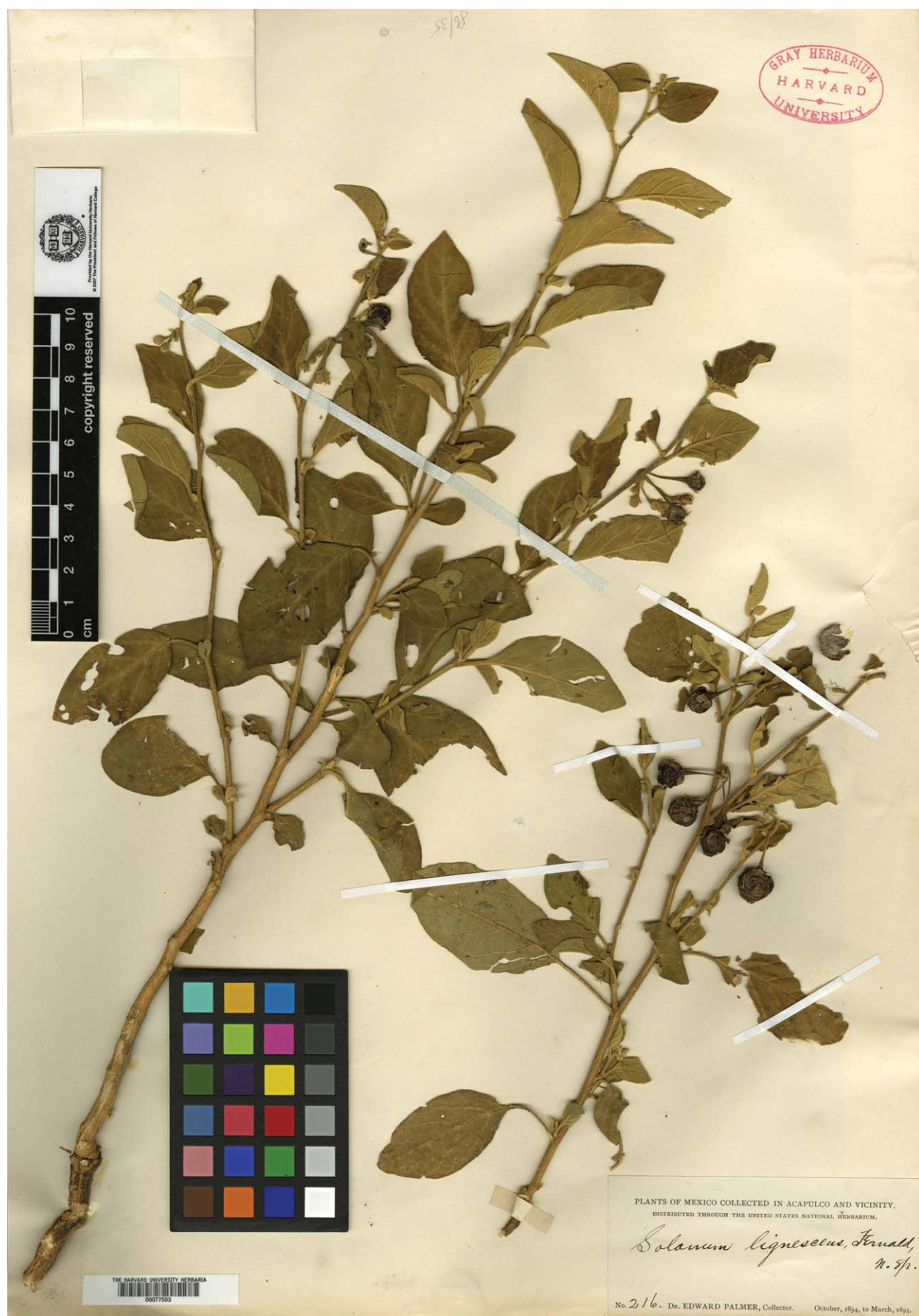
in quality and is unequivocally original material. Because of the confusion with the type material of *S. hoffmanseggii* prior to the discovery of the excellent BR collection, Stern and Bohs (2009) erroneously referred to what is now known as *S. olympicum* as *S. hoffmanseggii*. It is now clear, however, that the widespread species of Bolivia, Paraguay, Argentina and the southernmost parts of Brazil is *S. olympicum*, while this unique species of Pará, Brazil is *S. hoffmanseggii*.

5. *SOLANUM LIGNESCENS* Fernald, Proc. Amer. Acad. Arts 33: 91. 1897.—TYPE: MEXICO. Guerrero: Acapulco, Nov 1894 (fl, fr), *E. Palmer 216* (lectotype, here designated, US-259574!; isolectotypes: F-66593!, GH-GH00077503!, MO-3378770!, K!, NY-NY00139001!).

Solanum roei Ugent & Iltis, Phytologia 40: 379. 1978.—TYPE: MEXICO. Chiapas: 6 km NW of Las Rosas, in region of tropical deciduous vegetation on NE slope of Valley of Chiapas, ca. 900 m, 8 Aug 1965 (fl, fr), *K. Roe et al. 1045* (holotype: WIS).

Herb or subshrub from a lignescent base, 0.5–1 m tall. Young stems densely pubescent with pale yellow-grey, porrect-stellate hairs, the stalks nearly absent to 0.5 mm, uniseriate, 5–6 rays, 0.2–0.5 mm in length, unicellular, midpoints lacking to 0.2 mm long; older stems glabrescent with yellow-gray bark. Sympodia 3–plurifoliate. Leaf blades 2–7 × 1.5–4 cm, ovate, chartaceous to membranaceous, sparsely and uniformly pubescent adaxially with stalked stellate trichomes 0.5–1 mm, the rays often absent and the trichomes appearing simple, the base of each trichome somewhat swollen, densely pubescent abaxially with a mixture of stalked and sessile stellate trichomes 1–1.5 mm long, with 2–5 rays and midpoints small or lacking, the trichomes yellowish and almost obscuring the leaf undersides; base truncate to broadly cuneate; apex acute to more or less rounded; petioles 0.2–1 cm, densely stellate-pubescent like the leaf undersides. Inflorescences opposite the leaves or extra-axillary, with (1–) 3–6 (11) flowers, the axes densely stellate pubescent with a mixture of stalked and sessile trichomes ca. 0.5 mm, like those of the stems; peduncles 0.3–0.8 cm; rachis nearly absent; pedicels 7–12 mm in flower, 12–20 mm in fruit, expanding at the apex, spaced 1–2 mm apart. Flowers with the calyx 3–6 mm long, the tube 1–1.5 mm, the lobes 2–4 × 1–2 mm, broadly triangular, reflexed at anthesis, sparsely stellate-pubescent abaxially, glabrous adaxially with a few scattered, usually simple, trichomes along the midvein. Corolla 1.4–1.8 cm in diameter, stellate, membranaceous, white, lobed $\frac{3}{4}$ of the way to the base, the lobes 7–9.5 × 3–4 mm, planar at anthesis, sparsely stellate-pubescent abaxially, glabrous adaxially, the trichomes denser at the tips and along the lobe midveins. Stamens 3.5–5 mm; filaments to 0.5 mm; anthers 3.5–5 × 1.5–2 mm, oblong, the base sagittate, the apex emarginate. Ovary glabrous; style 7–8 × 0.5–1 mm, exerted beyond stamens; stigma 1–1.5 mm wide. Berries 10–12 mm in diameter, globose, green when immature, maturing white or purplish black, semitransparent, drying brown, glabrous, the pericarp thin, the mesocarp watery and held under pressure until dehiscing explosively at maturity; calyx lobes not expanding in fruit. Seeds 15–20 per fruit, ca. 2 × 1 mm, the surfaces minutely pitted. Figure 10.

Habitat and Distribution—An herb or subshrub of dry, deciduous forests and thickets in mountainous regions from

FIG. 10. Scan of isotype of *S. lignescens*.

the Sierra Madre Occidental in the Mexican state of Guerrero to Honduras and Nicaragua, from 1,000–1,500 m in elevation (Fig. 7).

Phenology—Flowering collections have been made in February, March, and June–October. Fruiting collections have been made in June–October.

Conservation Status—The widespread distribution and abundant populations of *S. lignescens* give it an IUCN Red List Status of Least Concern.

Etymology—The epithet *lignescens* refers to the lignescent, woody habit of the species.

Additional Specimens Examined—MEXICO. **Chiapas:** Mun. Tzimol, ca. 7 km SE of Comitán, ca. 3 km SE of Tzimol, 1,350 m, 7 Jul 1990 (fl, fr), *Hampshire et al.* 1151 (BM); Mun. La Trinitaria, 4 km E of La Trinitaria along Mex. 190, 16°08'N, 92°02'W, 1480 m, 8 Jul 1990 (fl), *Hampshire et al.* 1154 (BM); same loc., 8 Jul 1990 (fl, fr), *Hampshire et al.* 1184 (BM); Las Rosas, Rancho Santa Isabel, 7 km al N de Villa Las Rosas, 16°25'00" N, 92°24'00" W, 1642 m, 9 Aug 1998 (fl), *Martínez Salas et al.* 31192 (NY); Mun. Tzimol, 5 km al SO de Tzimol, 1150 m, 14 Sep 1988 (fl), *Reyes García & Uriquijo* 794 (MEXU). **Guerrero:** Costa Verde, Acapulco, 16 Feb 1941 (fl), *Langman* 3337 (MEXU). **Jalisco:** La Huerta, arroyo Tapeixtes (La Mina), km 55 de la carretera Puerto Vallarta-Barra de Navidad, a 4 km al SE de la Estación de Biología, 19°30'00"N, 105°03'00"W, 50 m, 25 Jun 1985 (fl), *Ayala & Lott* 9 (NY); La Huerta, arroyo Maderas, antiguo camino a Nacastillo, 17.5 km de la carretera Puerto Vallarta-Barra de Navidad, 22 Aug 1985 (fl, fr), *Ayala* 136 (NY); La Huerta, Estación Biología "Chamela", estación de Investigación, Experimentación y Difusión Chamela, UNAM, 26 Jul 1982 (fl), *Magallanes* 3650 (NY); same loc., 500 m, 3 Jul 1984 (fl, fr), *Magallanes* 4230 (NY). **Oaxaca:** Mun. Pochulta, vicinity of Concordia, San Rafael, 1000 m, 2 Mar 1937 (fl), *Makrinius* 530 (US).

HONDURAS. **Francisco Morazán:** Mun. Tegucigalpa, Río Las Canoas, ca. 5 km al E de Tegucigalpa, 14°02'N, 87°10'W, 1020 m, 27 Sep 1996 (fl), *Linares* 3536 (MEXU); Támara Valley, between Amaratéca and Támara, 1,000 m, 10 Oct 1969 (fl, fr), *Molina* 24551 (BM, NY, S).

NICARAGUA. **Estelí:** Mesas Moropotenté, 12.5 km SW of Laguna Mirafior, along road to Estelí, 13°11'N, 86°17'W, ca. 1310 m, 23 Jun 1982 (fl, fr), *Stevens* 21623 (BM, NY).

Notes—The leaf upper surfaces of *S. lignescens* usually have a mixture of simple and stellate trichomes, and a given individual may have a mixture of hair types or have only simple trichomes adaxially. Due to the presence of intermediate hair types between simple and stellate, it is likely that the simple trichomes represent cases where the rays have been lost. Stellate trichomes always have a uniseriate, often unicellular stalk. The presence of these hairs and the shrubby habit make *S. lignescens* easily recognizable from the simple-haired, herbaceous species that comprise the rest of sect. *Gonatotrimum*.

The type of *S. lignescens* was not designated in the protologue. From the handwriting on the labels of the duplicates of *Palmer* 216, it appears that Fernald saw and used the specimens at GH, MO, NY, and US for the species description (the handwriting on the material at F appears to be that of someone else). The material of each of these collections is excellent; however, most collections just have buds while the US specimen has open flowers, making this our choice for the lectotype.

6. *Solanum manabiense* S.Stern, J. Bot. Res. Inst. Texas 3(2): 504. 2009.—TYPE: ECUADOR. Manabí: Pacoche Reserve, road from Manta to San Lorenzo, ~2 km W of El Aromo, 01°04'09.5"S, 80°52'32"W, 350 m, 8 Feb 2009 (fl, fr), *S. Stern & E.J. Tepe* 377 (holotype: QCNE!; isotypes: BM!, F-2295591!, QCA!, MO-6262688!, NY!, UT!).

Rhizomatous herb, sometimes slightly woody at the base, 1.5–4 dm tall. Stems sparsely to densely pubescent with two-celled, unbranched, straight hairs. Sympodial units bifoliate,

geminate. Leaf blades 1–6 × 0.5–3 cm, elliptic to elliptic-ovoid, chartaceous to membranaceous, nearly glabrous to sparsely pubescent adaxially and abaxially with one or two-celled, unbranched, straight hairs, these lying flat along the blade, denser along veins; base rounded to obtuse, often decurrent into petiole; apex acute to obtuse; petioles 0.5–1 cm, moderately pubescent with unbranched straight hairs. Inflorescence with 1–5 flowers, the axes sparsely to moderately pubescent with unbranched hairs; peduncle absent; rachis absent to ca. 1 mm; pedicels 5–15 mm in flower, 10–20 mm in fruit. Flowers with the calyx 3–10 mm long, the tube 1–3 mm, the lobes 2–7 × 0.5–1.5 mm, linear-lanceolate, moderately to densely pubescent. Corolla 0.4–1 cm in diameter, rotate with abundant interpetalar tissue, chartaceous to membranaceous, white, the tube 2–3 mm long, the lobes very short, 1–2 × 0.5–1 mm, triangular, acute at apices, sparsely to moderately pubescent abaxially and on margins with 2 or 3-celled unbranched, straight hairs, glabrous adaxially. Stamens 2–4 mm long; filaments up to 1 mm long; anthers 1.5–3 × 0.5–1.5 mm, oblong, the base cordate, the apex emarginate. Ovary glabrous; style 4–6 × 0.5–1 mm, equal to or exerted beyond stamens; stigma to 1 mm wide. Berries 5–12 mm in diameter, globose, white to yellow when immature, maturing semitransparent, drying brown, glabrous, the mesocarp watery and held under pressure until dehiscing explosively at maturity. Seeds 10–35 per fruit, ca. 2.5 × 1.5 mm, lacking an obvious notch where connected to placenta, the margin not swollen, the surface with fine raised ridges radiating from the center to the edges and shallow ridges running parallel to margin. Figure 11.

Habitat and Distribution—A species known only from the central coast of Ecuador in Provinces Manabí and Guayas from sea level to 400 m in elevation (Fig. 7).

Phenology—Flowering and fruiting specimens have been collected in February and July.

Conservation Status—Due to the very restricted geographic area in which *S. manabiense* occurs (< 5,000 km²), the small number of known populations (< 5) and the few collections (4), it is given an IUCN Red List Status of Endangered.

Etymology—The epithet *manabiense* refers to Manabí Province of Ecuador where the type was found.

Additional Specimens Examined—ECUADOR. **Guayas:** 2–4 km E from Recinto Olon, ca. 10 km N of Manglaralto, 19 Feb 1974 (fl, fr), *Gentry* 10068 (MO). **Manabí:** Montecristi, Cerro Montecristi, eastern slopes above town, 18 July 1986 (fl, fr), *Plowman & Alcorn* 14334 (F, NY); Cerro Montecristi, E slopes above town, 1°03'27"S, 80°39'58"W, 400 m, 7 Feb 2009 (fl, fr), *Stern & Tepe* 374 (QCNE, QCA, UT).

Notes—*Solanum manabiense* is unique in sect. *Gonatotrimum* due to the combination of its rhizomatous habit; bifoliate, occasionally geminate sympodia; leaves nearly glabrous on the abaxial surface; unbranched, straight (non-geniculate) hairs; small flowers with equal stamens; and seeds with unexpanded margins and no obvious notch at the attachment point to the placenta. It is apparently restricted to coastal Ecuador in the Guayas and Manabí provinces.

Solanum manabiense resembles *S. olympicum*, but the hairs of *S. olympicum* are geniculate whereas those of *S. manabiense* are straight. *Solanum manabiense* also resembles *S. turneroides*, but the latter is a more robust herb with heterantherous flowers that are much larger than those of *S. manabiense*. *Solanum manabiense* is also similar to *S. deflexum*, but the latter has leaves pubescent on both surfaces, is not rhizomatous,

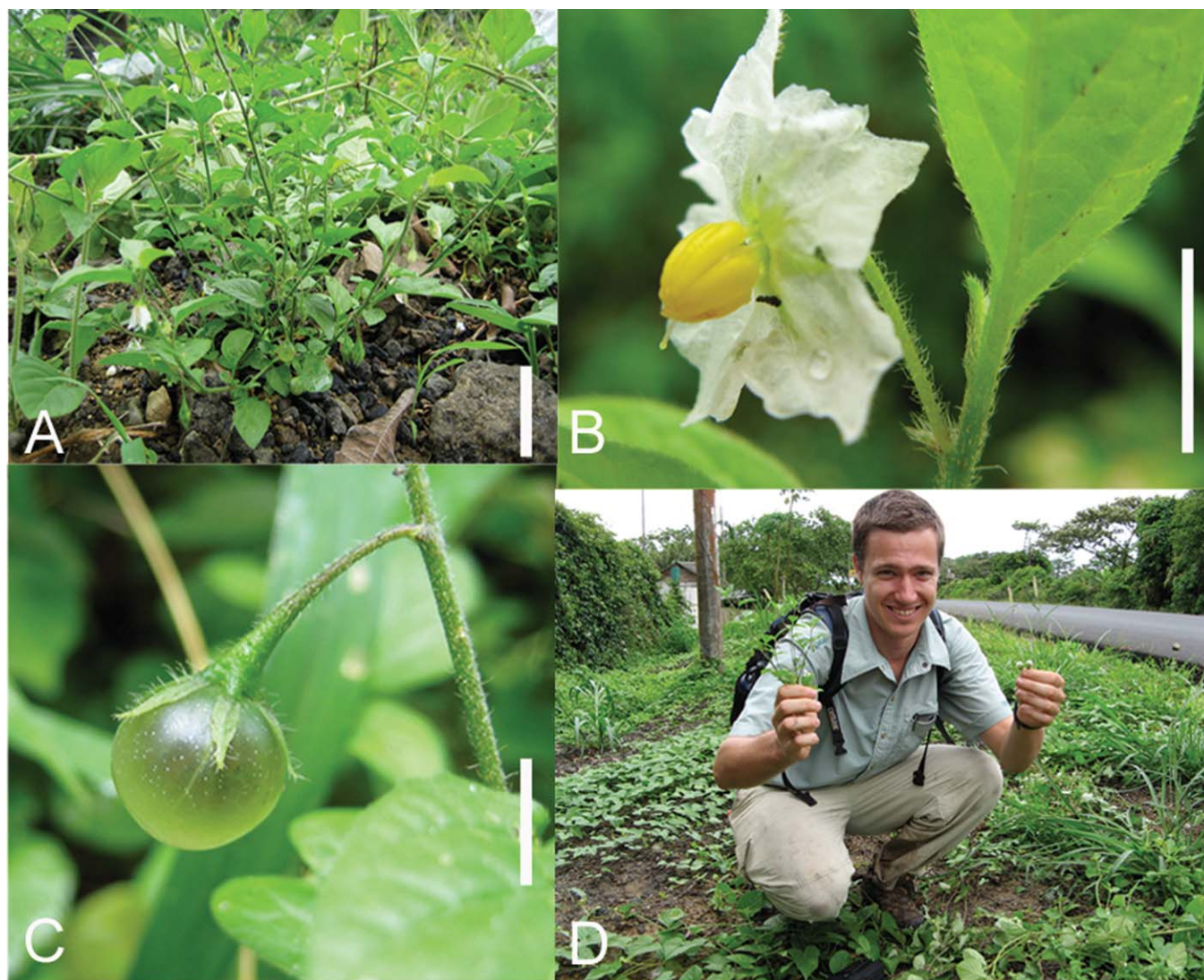


FIG. 11. Photos of type collection of *S. manabiense* (Stern & Tepe 377, QCNE). A. Habit. B. Flower; note hairs on stem and leaves. C. Fruit, with skin becoming transparent as turgor pressure increases. D. Roadside habitat in Manabí, Ecuador and author with type collection. Scale bars: A = 10 cm. B, C = 5 mm. (reprinted with permission of the Botanical Research Institute of Texas).

and has seeds with a swollen margin and pronounced notch where they connect to the placenta.

7. *SOLANUM OLYMPICUM* Hassl., Repert. Spec. Nov. Regni Veg. 9: 116. 1911.—TYPE: PARAGUAY. Alto Paraguay: Olimpo Berg [Fuerte Olimpo], Dec 1907 (fl, fr) K. Fiebrig 1392 (holotype: G-G00357994!)

Solanum paricistrigosum Bitter, Repert. Spec. Nov. Regni Veg. 12: 75. 1913.—TYPE: PARAGUAY. Estancia Sta. Maria, 18 Feb 1898 (fr), J. D. Anisits 2866 (holotype: S-04-2965!).

Herb, sometimes slightly woody at base, single- to few-branched, 1–4 dm tall. Stems sparsely to densely pubescent with two-celled unbranched hairs, these geniculate between first and second cells and pointing apically, very rarely with straight hairs. Sympodia 2-foliate, usually geminate. Leaf blades 1.5–7 × 1–3 cm, elliptic to elliptic-ovoid, chartaceous to membranaceous, sparsely to moderately pubescent adaxially and abaxially with 1 or 2-celled unbranched geniculate hairs, these lying flat along blade, denser along veins; base rounded to obtuse, often decur-

rent into petiole; apex acute; petioles 0.5–2.5 cm, moderately pubescent with unbranched geniculate hairs. Inflorescences with 1–5 flowers, the axes sparsely to moderately pubescent with unbranched hairs; peduncle absent or nearly so; rachis absent; pedicels 5–15 mm in flower, 10–20 mm in fruit. Flowers with the calyx 3–10 mm long, the tube 1–3 mm, the lobes 2–7 × 0.5–1.5 mm, linear-lanceolate, moderately to densely pubescent. Corolla 0.5–1.5 cm in diameter, rotate with abundant interpetalar tissue, chartaceous to membranaceous, white, the tube 3–6 mm long, the lobes very short, 1–2 × 0.5–1 mm, triangular, acute at apices, glabrous abaxially and adaxially. Stamens 2–4 mm; filaments up to 1 mm long, one filament 0.25–0.5 mm longer than the others; anthers 1.5–3 mm × 0.5–1.5 mm, oblong, the base cordate, the apex emarginate. Ovary glabrous; style 4–6 × 0.5–1 mm, equal to or exserted beyond stamens; stigma to 1 mm wide. Berries 5–12 mm in diameter, globose, white to yellow when immature, maturing semi-transparent, drying brown, glabrous, the mesocarp watery and held under pressure until dehiscing explosively at maturity. Seeds 10–35 per fruit, ca. 2.5 × 1.5 mm, with

a small notch where connected to placenta, the margin not swollen, the surface with fine raised ridges radiating from center to edges and shallow ridges running parallel to margin. Figure 12.

Habitat and Distribution—A weedy species of roadsides, rocky slopes, grassy areas, and forests in central southwest to eastern Brazil, eastern to central Bolivia, eastern Paraguay, and northwestern Argentina between 115–2,700 m in elevation (Fig. 5).

Phenology—Flowering specimens have been collected January through March and September through November. Fruiting specimens have been collected January through May and August through November.

Conservation Status—The widespread distribution and abundant populations of *S. olympicum* give it an IUCN Red List Status of Least Concern.

Etymology—The epithet *olympicum* refers to the type locality which was collected in the hills near Fuerte Olimpo.

Additional Specimens Examined—BRAZIL. **Bahia**: Mun. Urandi, 7 km N de Urandi, aprox. 14°48'S, 42°38'W, ca. 600 m, 20 Nov 1992 (fl, fr), *Arbo et al.* 5613 (BHC, CTES, NY, SPF). **Goiás**: Mun. Nova Roma, saída da cidade em direção a Iaciara, Fazenda Cachoeira (Proprietário Sr. Manoel R. G. de Sousa), 13°44'15"S, 46°62'11"W, 710 m, 1 Mar 2000 (fl, fr), *Alvarenga et al.* 1295 (IBGE, MO, NY, RB); Mun. Iaciara, Estrada Nova Roma-Iaciara, Fazenda Sobradinho, 7.6 km de Nova Roma, 13°47'53"S, 46°51'51"W, 466 m, 4 Nov 2003 (fl, fr), *Mello-Silva* 2286 (RB, SPF); Mun. Guarani do Goiás, fazenda Forquilha, proprietário Sr. Vigilato Francisco dos Santos, 13°48'29"S, 46°32'11"W, ca. 450 m, 6 Mar 2001 (fl, fr), *Silva et al.* 4860 (NY). **Mato Grosso do Sul**: Mun. Bonito, Fazenda Vale Verde, 13 Oct 2003 (fl, fr), *Hatschbach et al.* 76267 (MBM, NY); Mun. Miranda, Sede da Fazenda Guaicurus, Pantanal, 13 Jun 1973 (fl, fr), *Silva* 194 (SP); Mun. Taquarussu, Rio Baía, margem esquerda, 13 Dec 1992 (fl), *Souza* 2 (HNUP, RB); Mun. Jateí, Rio Ivinhema, Campinho, 11 Dec 1993 (fr), *Souza* 200 (HNUP, RB).

BOLIVIA. **Beni**: Prov. Ballivián, Espiritu en la zona de influencia del río Yacuma, 200 m, 15 Oct 1980 (fl, fr), *Beck* 5063 (MO); Prov. Iténez, palmar de Copernicia alba, 11 Nov 1993 (fl), *Moraes et al.* 1791 (NY); Prov. Cercado, a 14 km de San Javier, en la carretera a Trinidad, 14°43'14.4"S, 64°53'51.1"W, 200 m, 20 Feb 2000 (fr), *Orellana* 786 (NY). **Santa Cruz**: Prov. Ñuflo Chávez, Estancia Las Delicias, Hacienda ganadera del Vicariato Concepción, 16°29'S, 62°03'W, 400 m, 14 Nov 2000 (fl, fr), *Beck* 25662 (M); vicinity of abandoned old Jardín Botánico along Rio Pirai and roadsides on W side of Santa Cruz, 17°47'S, 63°13'W, 420 m, 28 Nov 1984 (fr), *Nee* 30473 (MO, NY); city of Santa Cruz, 17°46'S, 63°12'W, 400 m, (fl, fr), *Nee* 30494 (MO, NY); Prov. Andrés Bañez, along road from Santa Cruz to Samaipata, 1 km SW of Angostura, 18°09'S, 63°31'W, 650 m, 13 Jan 1987 (fl, fr), *Nee* 33478 (NY); Prov. Andrés Bañez, 1 km N of center of Cotoca, 17°45'S, 62°59'W, 350 m, 15 Jan 1987 (fl, fr), *Nee* 33545 (NY); Prov. Andrés Bañez, along Rio Pirai, 1 km N of La Guardia, 17°53'S, 63°15'W, 460 m, 20 Jan 1987 (fl, fr), *Nee* 33710 (MO, NY, US); Prov. Florida, valley of Río Paredones, 0.5 km N of Achiras camping resort, 18°09'S, 63°49'W, 1350 m, 8 Mar 1998 (fl, fr), *Nee* 48591 (NY); Prov. Cordillera, S side of bridge over Río Seco, 18°40.03'S, 63°14.42'W, 550 m, 1 May 2001 (fl, fr), *Nee et al.* 51724 (BM, MO, NY); Prov. Cordillera, Cabezas, 420 m, 19 Feb 1945 (fl, fr), *Pereola* 248 (A); Prov. A. Ibañez, flood plain of the Río Pirai, ca. 6 km NW of Santa Cruz, vicinity of the sewage settling ponds, 17°45'S, 63°11'W, 450 m, 22 Apr 1985 (fr), *Solomon* 13470 (MO). **Tarija**: between entre Rios and Cereré, 2700 m, Mar 1952 (fl, fr), *Cardenas* 4929 (US).

PARAGUAY. **Alto Paraguay**: Chaco, línea 3 (Oeste), km 50 [19°42'S, 61°18'W], 44 km al este de la pista de aviación de Cabrera (19°42'S, 61°19'W), 9 Nov 1992 (fl), *Ramella et al.* LR2924 (G); **Amambay**: ruta 3 y río Aquidabán, 23 Dec 1980 (fr), *Schimini & Bordas* 25042 (G). **Caaguazú**: cerca y al Norte de Yhú, 21 Feb 1982 (fl, fr), *Casas* FC6384 (G, MO); cerca y al Sur de Yhú, 24, Sep 1980 (fl), *Casas* FC3910 (NY); unos 5 km al Norte de Yhú, en una zona inundable en mayor o menor grado, 320 m, 12 Dec 1982 (fl, fr), *Casas & Schinini* 7460 (MO, NY); 15 km al N de Caaguazú, cauiuo a Yhú, 8 Feb 1966 (fl, fr), *Krapovickas et al.* 12568 (US); 10–15 km N de Caaguazú, 19 Feb 1994 (fl, fr), *Pedersen* 16075 (G); Arroyo Cambay, 22°25'S, 55°55'W, 10 Nov 1990 (fl, fr), *Zardini & Velázquez* 23807 (MO); Arroyo Yuquyry-Arroyo Taruma, 4 km N of Arroyo Yuquy ry, 25°13'S, 55°55'W, 12 Jan 1991

(sterile), *Zardini & Velázquez* 25858 (MO). **Canendiyú**: Mbaracayú Natural Reserve, administered by Fundación Moisés Bertoni, around Nandurokai, 23°59'39"S, 55°28'44"W, 27 May 1999 (fl), *Zardini & Chaparro* 50809 (NY). **Concepción**: Estancia ñu Apua, 110 km N of Concepción, a 1500 m W. de la Adm., 19 Mar 1991 (fl), *Eliceche* 44 (MO); Paso Horqueta, Río Aquidabán, 41 km N de Concepción, 140 m, 17 Dec 1983 (fl, fr), *Vanni et al.* 377 (G, NY); Estancia Bello Horizonte, Arroyo Tagatiyá-Guazú, 22°45'40"S, 57°26'15"W, 13 Oct 1994 (fr), *Zardini & Guerrero* 41286 (NY); Paso Horqueta, Río Aquidabán, 20°07'S, 57°20'W, 18 Nov 1993 (fr), *Zardini & Tilleria* 37468 (G, MO, NY). **Cordillera**: Salto Piraretá, 25°30'S, 56°55'W, 18 Oct 1994 (fl, fr), *Krapovickas et al.* 45675 (G); 4 km SE of Emboscada on road to Nueva Colombia, 25°09'S, 57°14'W, 18 Nov 1991, (fl, fr), *Zardini & T. Tilleria* 28888 (MO); Tobatí "Ybytú Silla" mesa, southern area, 25°12'S, 57°07'W, 297 m, 3 Mar 1991 (fr), *Zardini & Velázquez* 26963 (MO). **Paraguari**: National Park Ybycú, Northeastern area, 26°01'S, 56°46'W, 12 Mar 1992 (fr), *Zardini & Guerrero* 31042 (G, MO, NY); Tucangua, Cordillera de Altos, 25°31'S, 57°09'W, 9 Dec 1943, (fr), *Rojas* 10731 (MO). **Without Dept.**: N. Paraguay, zwischen Rio Apa und Rio Aquidabán, 1908/1909 (fl, fr), *Fiebrig.* 4408 = 4827 (BM, G, GH); Paraguay, 1885–1895 (fl), *Hassler* 1010 (G); in arenosis pr. Hacurubi, Dec 1885–1895 (fl), *Hassler* 1585 (G); Sapucay, Dec 1885–1895 (fl), *Hassler* 1638 (G); in silva pr. Cordillera de Altos, Jan 1885–1895 (fl), *Hassler* 1737 (G); in arenosis pr. Estero Troxler, Jan 1885–1895 (fl), *Hassler* 1793 (G); Paraguaría Centralis, in campo "Intacurabi", Jan 1900 (fl), *Hassler* 3801 (BM, G, GH, NY); Yerbales" montium "Sierra de Maracayú", in regione fluminis Tapiaguay, Aug (fl, fr), *Hassler* 4293 (G); Paraguay, (fl, fr), *Hassler* 4396 (UC); inter ad "Yerbales" montium "Sierra de Maracayú", in regione vicine "Igatimí", Oct 1898–1899 (fl, fr), *Hassler* 4841 (G); Cerros de Tobaty, (fl), *Hassler* 8069 (G, GH, MO, NY, S, UC, US); in regione lacus Ypacaray, Jan 1913 (fl, fr), *Hassler* 12141a (G); Paraguaría Centralis, in regione lacus Ypacaray, Apr 1913 (fl), *Hassler* 12441 (BM, G, GH, K, MO, NY, S, UC, US).

ARGENTINA. **Jujuy**: Dept. Valle Grande, ca. 10 km N from San Francisco on road to Valle Grande, 23°35.713'S, 64°58.396'W, 1230 m, 17 Apr 2000 (fr), *Nee & Bohs* 50808 (NY); Dept. Valle Grande, along gravel and sandbars of Río Valle Grande, directly below (W of) San Francisco, 23°37.5'S, 64°57.5'W, 915 m, 20 Apr 2000 (fr), *Nee & Bohs* 50825 (NY). **Salta**: Hill San Bernardo just outside city of Salta, shady woods among rocks, 5 Mar 1983 (fr), *Bohs* 2109 (GH); Dept. Orán, a orillas del río Colorado, 30 Jan 1945 (fl), *Krapovickas* 1565 (US). **Tucumán**: Dept. Capital, El Cadillal, Jardín de las Americas, 27 Mar 1975 (fr), *Krapovickas et al.* 27853 (MO, WIS).

Notes—*Solanum olympicum* is the one of the two members of sect. *Gonatotrimum*, along with *S. hoffmanseggii*, with characteristic geniculate hairs. These hairs always bend between the first and second cells and point upwards. This trait is absent in some specimens from the northern extent of the species' range in Bahia and Goiás, Brazil (including *Arbo et al.* 5613, *Alvarenga et al.* 1295, *Mello-Silva* 2286, and *Silva et al.* 4860). These specimens are disjunct in their distribution and have a mixture of hairs that are held perpendicular to the stem (similar in orientation but shorter than those of *S. deflexum*; see Fig. 1) and hairs that are adpressed and lie flat along the stem. However, other morphological characteristics of these specimens correspond to the concept of *S. olympicum*, and molecular phylogenies place one of these Bahian specimens as sister to the other populations of *S. olympicum*. One specimen from Mato Grosso do Sul, *Hatschbach et al.* 76267, has a shrubby habit with a mixture of geniculate and glandular hairs. This might represent a new species or simply a shrubby example of *S. olympicum*; however, since this form is only represented by one specimen we have included the collection within *S. olympicum*.

Solanum olympicum is similar to *S. hoffmanseggii*, but these species can be distinguished by the narrow, lanceolate leaves and shrubby habit of *S. hoffmanseggii* compared with the elliptic to elliptic-ovoid leaves and herbaceous habit of *S. olympicum*. The flowers of *S. olympicum* are weakly heterantherous with one filament slightly elongated (Fig. 12),

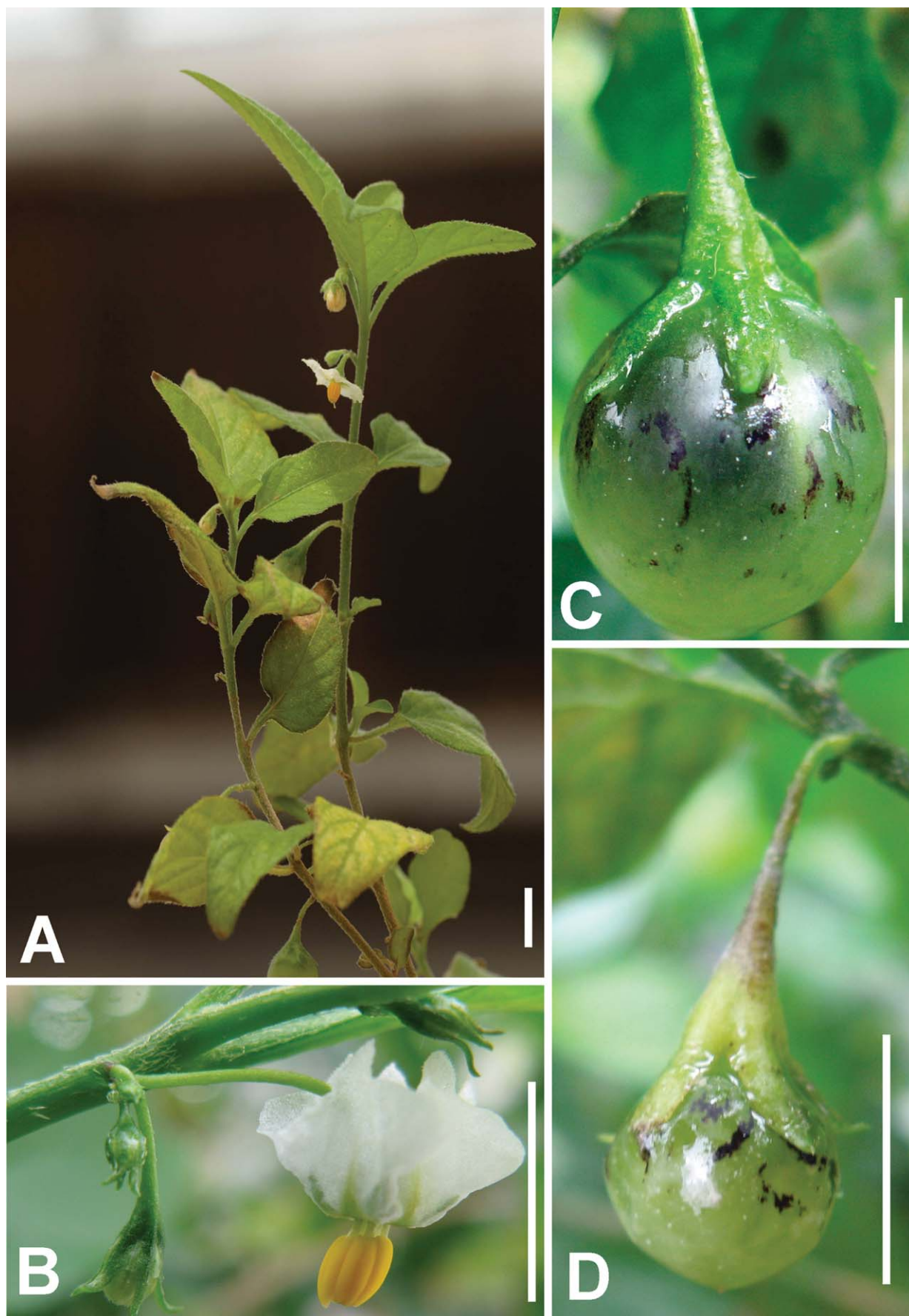


FIG. 12. *Solanum olympicum* (Bohs 3194, UT). A. Habit. B. Inflorescence with flower buds; note adpressed, geniculate hairs on stem. C. Mature fruit prior to dehiscence; note the skin becoming transparent as turgor pressure increases. D. Fruit after explosive dehiscence. Scale bars = 1 cm.

which is typically only visible in living plants and differentiates it from the larger, strongly heterantherous flowers of *S. turneroides* and *S. evoluloides*. *Solanum olympicum* also resembles *S. adscendens*, but the latter species has cordate leaves, a more branched, spreading growth form, and is restricted to Rio Grande do Sul in Brazil and neighboring parts of Argentina. The Bahian collections of *S. olympicum* lack glandular hairs on the stems and calyx, unlike the Bahian species *S. evoluloides*, which has abundant glandular pubescence.

The protologue describing *S. olympicum* placed it in sect. *Morella* Dumort. (now sect. *Solanum*) and until this revision the name *S. olympicum* has not been associated with sect. *Gonatotrimum*. All specimens of *S. olympicum* cited in this revision have been recently annotated as "*S. parctrigiosum*," which was the accepted name until the earlier *S. olympicum* was discovered. The protologue describing *S. olympicum* clearly indicates that the specimen in the Hassler Herbarium in Geneva is the holotype. Bitter's description of *S. parctrigiosum* cited only one specimen at the Stockholm herbarium, making this the holotype.

8. *SOLANUM TURNEROIDES* Chodat, Bull. Herb. Boissier sér. 2, 2: 814. 1902.—TYPE: PARAGUAY. In campis arenosis pr. fl. Capibary, 5 Sep 1898–1899 (fl), *E. Hassler* 4396 (lectotype, here designated, G-G00076272!; isolectotypes, BM-BM000074102!, NY-NY00172221!, UC-944864!).

Solanum gonatotrimum Bitter, Repert. Spec. Nov. Regni Veg. 11: 230. 1912.—TYPE: BOLIVIA. Tarija: Chiquiacá, in silva, 1000 m, 8 Mar 1904 (fl), *K. Fiebrig* 2732 (lectotype, here designated, M-M0090347!, photo of lectotype [Morton neg. 8692]: F!, GH!, UC!; isolectotypes: B (destroyed), CORD!, SI!, W-W1922–0001732!, photo of B isolectotype [F neg. 2713]: GH!).

Solanum geniculatrigrisum Bitter, Repert. Spec. Nov. Regni Veg. 11: 232. 1912.—TYPE: PARAGUAY. Yaguaron, en los campos, 1 Dec 1879 (fl), *R. Balansa* 3132 (holotype: B (destroyed); photos of holotype [F neg 2751]: F!, G!, GH!, WIS!; lectotype, here designated, BM-BM000087589!; isolectotypes: LE!, P-P00384651!).

Solanum flavistrigiosum Bitter, Repert. Spec. Nov. Regni Veg. 12: 74. 1913.—TYPE: PARAGUAY. Campo cerrado, Estancia Sta. Maria, 2 Jan 1897 (flower bud), *J. D. Anisits* 2018 (holotype: S-05–10!).

Herb, sometimes slightly woody, few- to many-branched, 2–7 dm tall. Stems sparsely to densely pubescent with straight one-celled or geniculate two-celled hairs, the straight hairs common on older growth, the geniculate hairs dense on new growth. Sympodia 2-foliate, usually geminate. Leaf blades 1–7 × 0.75–3 cm, elliptic to elliptic-ovoid, chartaceous to membranaceous, sparsely to moderately pubescent adaxially and abaxially with 1- or 2-celled unbranched hairs, these lying flat along blade, denser along veins; base rounded to obtuse, often decurrent into petiole; apex acute; petioles 0.5–2.5 cm, moderately pubescent with unbranched hairs. Inflorescences with 1–5 flowers, the axes sparsely to moderately pubescent with unbranched hairs; peduncle absent or nearly so; rachis absent; pedicels 5–15 mm in flower, 12–20 mm in fruit. Flowers with the calyx 3–6 mm long, the tube 1–3 mm, the lobes 2–4 × 0.5–1.5 mm, linear-lanceolate, moderately to densely pubescent. Corolla 1–2.5 cm in diameter, rotate with abundant interpetalar tissue, chartaceous to

membranaceous, white to purple, the tube 4–10 mm, the lobes 2–4 × 1–2 mm, triangular, acute at apices, glabrous abaxially and adaxially. Stamens 3–6 mm; upper, shorter filaments 1–2 mm, the lowermost, longer filament 3–7 mm, glabrous or pubescent; anthers 4–6 × 1–2 mm, oblong, the base cordate, the apex emarginate. Ovary glabrous; style 7–10 × 0.5–1 mm, longer than the smaller stamens, closely appressed to larger stamen, curved near the apex; stigma to 1 mm wide. Berries 10–20 mm in diameter, globose, white to yellow when immature, maturing semitransparent, drying brown, glabrous, the mesocarp watery and held under pressure until dehiscing explosively at maturity. Seeds 10–35 per fruit, ca. 2.5 × 1.5 mm, the entire seed twisted, not flattened, with a small notch where connected to placenta, the surface with raised cell walls forming netlike projections. Figure 13.

Habitat and Distribution—A weedy species of roadsides, grassy pastures, gallery forest, alluvial flats, forest edges, and open shrubby vegetation that occurs from central Bolivia to eastern Paraguay and the Brazilian state of Mato Grosso do Sul and south into northwestern Argentina between 300–1,950 m in elevation (Fig. 5).

Phenology—Flowering specimens have been collected in all months except August with a peak from October through February. Fruiting specimens have been collected in January through May and September through December.

Conservation Status—The widespread distribution and abundant populations of *S. turneroides* give it an IUCN Red List Status of Least Concern.

Etymology—The epithet *turneroides* presumably refers to a resemblance to the genus *Turnera* (Turneraceae), possibly due to the five-parted flowers that usually open in the morning and last for only a few hours. In the description, Chodat mistakenly likens the habit of *S. turneroides* to that of *S. caripense* Dunal, a viny member of *Solanum* sect. *Basarthurum*.

Additional Specimens Examined—BRAZIL. **Mato Grosso do Sul:** Mun. Corumbá, Morro Bocaina, 18 Oct 1991 (fl), *Damasceno* 178 (COR, UEC); Bairro Aeroporto, morro defronte ao aeroporto, rua Alan Kardec, 19°01'S, 57°39'W, 220 m, 25 Jan 2001 (fl) *Gomes* 39 (SPF); Mun. Bela Vista, 10 km W, 17 Mar 1985 (fl), *Hatschbach & Zelma* 49158 (MBM, NY); Mun. Aquidauana, Piraputanga, 4 Jun 1994 (fl), *Hatschbach et al.* 60696 (MBM, NY); Mun. Porto Murtinho, rodovia Bonito-Campo do Índios, Fazenda Água Doce, 10 Nov 2002 (fl, fr), *Hatschbach* 74004 (MBM); Mun. Bonito, Fazenda Nossa Senhora do Perpétuo Socorro, 12 Oct 2003 (fl, fr), *G. Hatschbach et al.* 76260 (CTES, MBM, NY); Mun. Porto Murtinho, rodovia Jadim-Porto Murtinho, BR-267, próximo do Rio Perdido, 250 m, 15 Mar 2004 (fl), *Hatschbach* 77410 (MBM); Mun. Corumbá, Jul 1911 (fl), *Hoehne* 3749 (R, US); Estrada para a Chácara São Marcos, Bairro entre Cristo Redentor e Cravo Vermelho, 19°02'16.8"S, 57°37'41.7"W, 29 Nov 2000 (fl, fr) *Moraes* 554 (UEC); Corumbá, Fazenda do Dr. Romeu, 19°01'S, 57°39'W, 20 Nov 1987 (fl), *Ratter et al.* 6043 (MO); 15 km from Corumbá, 29 Jan 1991 (fl) *Ratter* 6513 (CPAP, MBM); Mun. Corumbá, Morro de Azeite, 10 Apr 1992 (fr), *Resente* 667 (BHCB, CGMS); Corumbá, 18 Dec 1902 (fl, fr), *Robert* 721 (BM); Mun. Miranda, Salobra, Dec 1941 (fl) *Santos s.n.* (R 79588); Mun. Bela Vista, Rio Guaviral, 12 Nov 2006 (fl, fr), *Silva et al.* 5266 (MBM).

BOLIVIA. **Beni:** Prov. Cercado, campus of the Universidad Tecnica del Beni, 2.5 km N of center of Trinidad, 14°48'S, 64°53'W, 200 m, 13 Dec 1988 (fl, fr), *Nee* 37160 (NY). **Chuquisaca:** Oropeza, ca. 5 km below Chuquichuqui in Río Chaco Valley, 1800 m, 19 Jan 1997 (fl, fr), *Wood* 11679 (K, LPB). **Cochabamba:** Río Caine, 1,180 m, Jan 1949 (fl, fr), *Cárdenas* 4098 (US). **Santa Cruz:** Prov. Nuflo de Chavez, Concepción, 500 m, 18 Feb 1995 (fr), *Abbot* 16233 (WU); Santa Cruz, 1200 ft, 23 Sep 1964 (fl, fr), *Badcock* 416 (K); Prov. A. Ibañez, ca. 15 km hacia el N de Santa Cruz, por el Nuevo aeropuerto Viru Viru, 420 m, 19 Mar 1981 (fl, fr), *Beck* 6666 (M); Prov. Cordillera, Alto Parapetí, 800 m, 16 Jan 1980 (fl), *de Michel* 44 (NY); Prov. Caballero, Estancia Lanza-Lanza, 2 km del Río Comarapa sobre ladera con 30° de inclinación exposición W, 18°02'04"S, 64°35'00"W, 1600 m, 22 Jan 1995 (fl, fr), *Gutiérrez et al.* 1521 (NY); Prov. Andrés Bbañez, 1 km N from Pedro Lorenzo, 20 km along

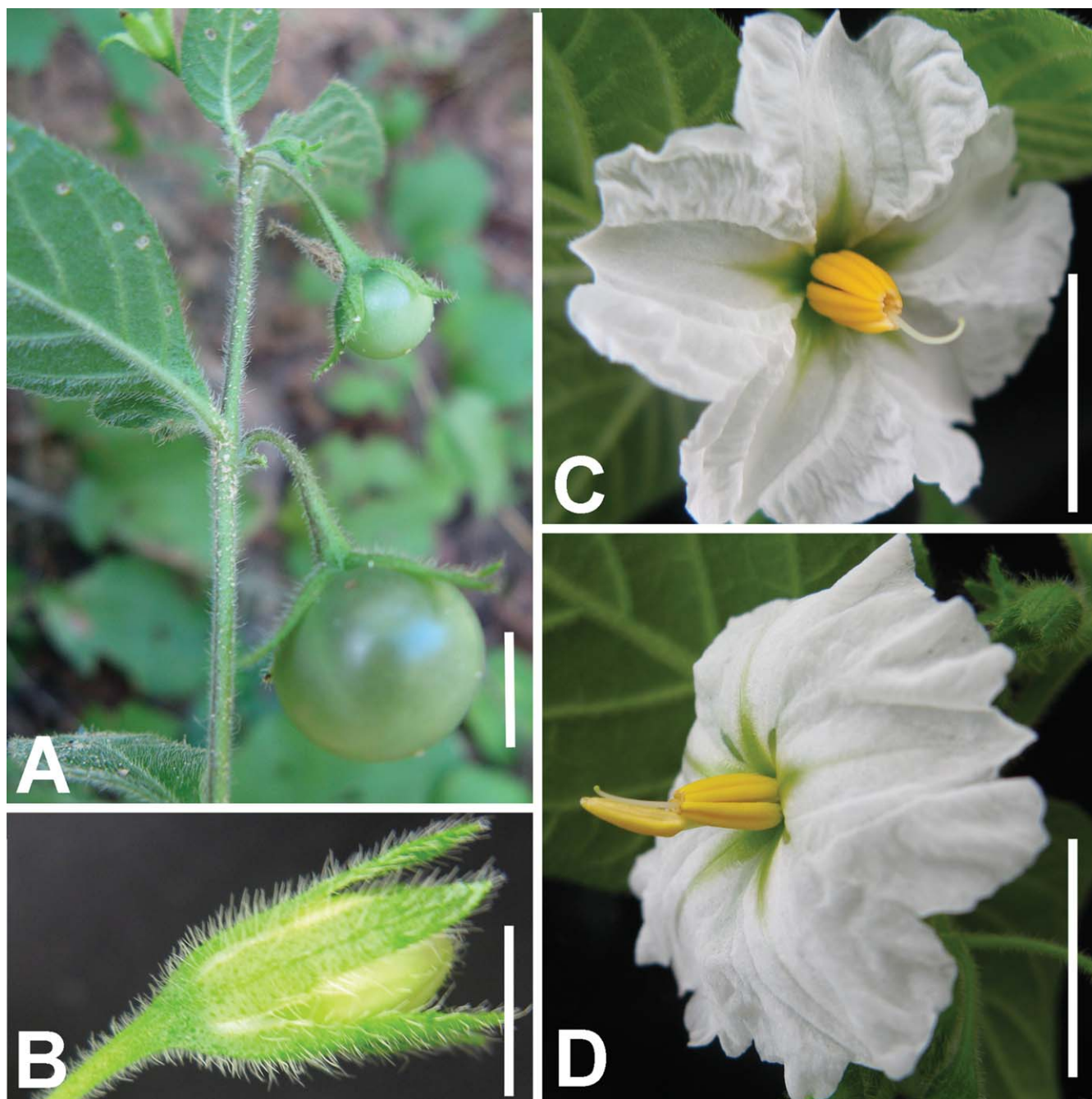


FIG. 13. *Solanum turneroides* (Bohs 2715, UT). A. Stem with nearly mature fruits. B. Flower bud; note densely pubescent calyx and long calyx lobes. C. Flower on first day of opening; note that lowermost filament has not expanded. D. Flower after first day; note that the filament of the lowermost anther is now greatly elongated. Scale bars: A, C, D = 1 cm. B = 5 mm.

the Camiri highway, 9 May 2000 (fr), Kuroiwa & Maeda 1596 (NY); Alto Parapetí, 850 m, 8 Jan 1982 (fl), Michel 98 (LPB); Prov. Andrés Ibáñez, along Río Pantano [=Río Chore-Chore], 7 km SE of Palmar del Oratorio and 18 km SE of center of Santa Cruz, 17°56'S, 63°06'W, 380 m, 9 Dec 1988 (fl, fr), Nee 37085 (LPB, TEX, NY, WIS); Prov. Andrés Ibáñez, 13 km SE of Palmar del Oratorio and 6 km SE of Río Chore-Chore [= Río Pantano] 17°58'S, 63°04'W, 375m, 22 Jan 1989 (fl, fr), Nee 37668 (G, MO, NY); Prov. Andrés Ibáñez, NW side of "Valle Sanchez," 4 km W of Aeropuerto Internacional Viru-Viru, 15 km N of Santa Cruz, 17°38'S, 63°10'W, 375 m, 26 Jan 1989 (fl, fr), Nee 37741 (NY); Prov. Caballero, W side of Río Comarapa, 0.5 km W of center of Comarapa, 17°54'S, 64°32'W, 1825 m, 12 Dec 1992 (fl), Nee 43093 (NY); Prov. Andrés Ibáñez, along highway from Santa Cruz to Abapó, 3 km S of crossing of railroad and 2 km S of bridge over Quebrada Peji, 17°58'S, 63°11'W 450 m, 25 Apr 1998 (fl, fr), Nee 49117

(CORD, G, NY); Prov. Vallegrande, 4 km SW of El Trigal on road to San Juan del Chaco, S side of Río Ariruma, 19 km (by air) NNW of Vallegrande, 18°29'S, 64°07'W, 1950 m, 31 Jan 1987 (fl), Nee & Coimbra 33932 (NY); Prov. Vallegrande, 10 km (by air) NNW of Vallegrande, 18°23'S, 64°08'W, 1850 m, 1 Feb 1987 (fl, fr), Nee & Coimbra 33944 (G, NY, US); Prov. Florida, 7 km (by air), 10.2 km (by road) NNW of Mataral on road to San Juan del Potrero, 18°02'45"S, 64°14'25"W, 1475 m, 30 Jan 1994 (fl, fr), Nee & Vargas 44789 (NY); Prov. Andrés Ibáñez, along highway from Santa Cruz to Abapó, 3 km S of crossing of railroad and 2 km S of bridge over Quebrada Peji, 17°58'S, 63°11'W, 450 m, 27 Feb 1998 (fr, fl), Nee et al. 48485 (NY); Prov. Andrés Ibáñez, along highway from Santa Cruz to Abapó, 3 km S of crossing of railroad and 2 km S of bridge over Quebrada Peji, 17°58'S, 63°11'W, 450 m, 1 May 2001 (fl), Nee et al. 51716 (NY); Prov. Florida, 3 km (by air), 7 km (by road) NE of Mairana on road to Parque Nacional

Amoró camp "Yunga de Mairana," 18°06'S, 63°56'W, 1850 m, 28 Mar 2002 (fl, fr), *Nee et al.* 52003 (NY); Prov. Cordillera, Cabezas, 420 m, 19 Feb 1945 (fl), *Pareolo* 253 (A, NY); Prov. Cordillera, Cabezas, 420 m, 18 Mar 1945 (fl, fr), *Pareolo* 444 (NY); Serranías de Chiquitos, camino a Tucavaca 2 Feb 2005 (bs), *Solis Neffa* 1790 (BHCB, CTES); Prov. Sara, "Arenales del Gwendá" [sandy areas in savanna of Río Guendá, now forming border of Prov. Ichilo and Prov. Andrés Báñez, M. Nee 2001] 450 m, 8 May 1921 (fl, fr), *Steinbach* 5625 (GH, NY); Prov. Sara, Arenales, Río Perdix, 400 m, 23 Oct 1924 (fl), *Steinbach* 6627 (G, GH, K); Prov. Sara, Río Perdix, 400 m, 29 Dec 1925 (fl), *Steinbach* 7367 (F, G, GH, MO); Prov. Chiquitos, Cerro Mutún, 7 km al NE de la pista de aterrizaje del campamento minero (25 km al S de Puerto Suárez), 18°11.3'S, 57°52.7'W, 750 m, 17–20 Oct 1994 (fl), *Vargas et al.* 3328 (CTES, NY, USZ); ca. 4 km E of San Isidro (Palizada) on road to Mataral, 18°2'S, 64°25'W, 1400 m, 3 Jan 2000 (fl), *Wood* 15770 (LPB). **Tarija:** Prov. Gran Chaco, 5–5.7 km W of the center of Villa Montes on road to Entre Ríos and Tarija (not the new segment under construction now), 0–0.7 km toward Villa Montes from the highway bridge over the Río Pilcomayo, 21°15'28"S, 63°30'40"W, 400 m, 9 Feb 2006 (fr), *Nee & Linneo* 54034 (G); Gran Chaco, San Francisco de Inti, camino de Yacuiba a Villa Montes, a 22 km N de la rotonda de Yacuiba, 21°48'56"S, 63°35'05"W, 586 m, 16 Jan 2004 (fl), *Neffa et al.* 989 (CTES, G); Prov. O'Connor, hills north of Entre Ríos, 1400 m, 6 Feb 1937 (fl, fr), *West* 8254 (GH, MO, UC).

PARAGUAY. **Alto Paraguay:** Chaco, línea 3 (Oeste), km 50 [19°42'S, 61°18'W], 44 km al E de la pista de aviación de Cabrera (19°42'S, 61°19'W), 9 Nov 1992 (fl), *Ramella et al.* LR2924 (G). **Amambay:** Ruta 3 y Río Aquidabán, 23 Dec 1980 (fr), *Schinini & Bordas* 25042 (G). **Caaguazú:** cerca y al N de Yhú, 21 Feb 1982 (fl, fr), *Fernández Casas* FC6384 (G, MO); cerca y al S de Yhú, 24, Sep 1980 (fl), *Fernández Casas* FC3910 (NY); unos 5 km al N de Yhú, en una zona inundable en mayor o menor grado, 320 m, 12 Dec 1982 (fl, fr), *Fernández Casas & Schinini* 7460 (MO, NY); 15 km al N de Caaguazú, camino a Yhú, 8 Feb 1966 (fl, fr), *Krapovickas et al.* 12568 (US); 10–15 km N de Caaguazú, 19 Feb 1994 (fl, fr), *Pedersen* 16075 (G); Arroyo Cambay, 22°25'S, 55°55'W, 10 Nov 1990 (fl, fr), *Zardini & Velázquez* 23807 (MO); Arroyo Yuquyry-Arroyo Taruma, 4 km N of Arroyo Yuquyry, 25°13'S, 55°55'W, 12 Jan 1991 (sterile), *Zardini & Velázquez* 25858 (MO). **Canendiyú:** Nandurocai, Reserva Natural de Bosque Mbaracayú, 13 km S de Ipé-hú, 3 Dec 1997 (fl, fr), *Schinini* 33262 (CTES); Mbaracayú Natural Reserve, administered by Fundación Moisés Bertoni, around Nandurokai, 23°59'39"S, 55°28'44"W, 27 May 1999 (fl), *Zardini & Chaparro* 50809 (NY). **Concepción:** Estancia Ñu Apua, 110 km N of Concepción, a 1500 m W de la Adm., 19 Mar 1991 (fl), *Eliceche* 44 (MO); Paso Horqueta, Río Aquidabán, 41 km N de Concepción, 140 m, 17 Dec 1983 (fl, fr), *Vanni et al.* 377 (G, NY); Estancia Bello Horizonte, Arroyo Tagatiyá-Guazú, 22°45'40"S, 57°26'15"W, 13 Oct 1994 (fr), *Zardini & Guerrero* 41286 (NY); Paso Horqueta, Río Aquidabán, 20°07'S, 57°20'W, 18 Nov 1993 (fr), *Zardini & Tilleria* 37468 (G, MO, NY). **Cordillera:** Salto Piraretá, 25°30'S, 56°55'W, 18 Oct 1994 (fl, fr), *Krapovickas et al.* 45675 (G); 4 km SE of Emboscada on road to Nueva Colombia, 25°09'S, 57°14'W, 18 Nov 1991, (fl, fr), *Zardini & Tilleria* 28888 (MO); Tobatí "Ybytú Silla" mesa, southern area, 25°12'S, 57°07'W, 297 m, 3 Mar 1991 (fr), *Zardini & Velázquez* 26963 (MO). **Paraguari:** Piraretá, 14 Nov 1969 (fl, fr), *Pedersen s.n.* (CTES 315405); National Park Ybycu'í, Northeastern area, 26°01'S, 56°46'W, 12 Mar 1992 (fr), *Zardini & Guerrero* 31042 (G, MO, NY); Tucangua, Cordillera de Altos, 25°31'S, 57°09'W, 9 Dec 1943, (fr), *Rojas* 10731 (MO). **Without Dept.:** N Paraguay, zwischen Rio Apa und Rio Aquidaban, 1908/1909 (fl, fr), *Fiebrig* 4408 = 4827 (BM, G, GH); Paraguay, 1885–1895 (fl), *Hassler* 1585 (G); Sapucay, Dec 1885–1895 (fl), *Hassler* 1638 (G); in silva pr. Cordillera de Altos, Jan 1885–1895 (fl), *Hassler* 1737 (G); in arenosis pr. Estero Troxler, Jan 1885–1895 (fl), *Hassler* 1793 (G); Paraguaria Centralis, in campo "Intacurabi," Jan 1900 (fl), *Hassler* 3801 (BM, G, GH, NY); "Yerbales" montium "Sierra de Maracayú," in regione fluminis Tapiraguay, Aug (fl, fr), *Hassler* 4293 (G); Paraguay, (fl, fr), *Hassler* 4396 (UC); Inter ad "Yerbales" montium "Sierra de Maracayú," in regione vicine "Igatimi," Oct 1898–1899 (fl, fr), *Hassler* 4841 (G); Cerros de Tobaty, (fl), *Hassler* 8069 (G, GH, MO, NY, S, UC, US); in regione lacus Ypacaray, Jan 1913 (fl, fr), *Hassler* 12141a (G); Paraguaria Centralis, in regione lacus Ypacaray, Apr 1913 (fl), *Hassler* 12441 (BM, G, GH, K, MO, NY, S, UC, US).

ARGENTINA. **Jujuy:** Dept. Capital, Alto La Viña, ruta 56, 4 km al NE de Jujuy, 1250–1300 m, 29 Dec 1989 (fr), *Novara* 9287 (G). **Salta:** Dept. Capital, Chachapoyas, Sierra de Vélez, cerros al E de la Univers. Católica, 1200 m, 30 Jan 1987 (fl), *Novara* 5884 (G); same locality and date, *Novara* 5919 (G).

Notes—Strongly heterantherous flowers are only found in two members of the section, *S. turneroides* and *S. evolvuloides*. *Solanum turneroides* can be distinguished from *S. evolvuloides* by its lack of glandular hairs, its larger flowers, and its more widespread South American distribution. As noted by Nee (1989), the flowers of *S. turneroides* are not open in the heat of the day, as is also the case for *S. evolvuloides* (L. Giacomini, pers. obs.). When grown in the greenhouse at UT the flowers were open and very fragrant during the night and early morning. As the day gets warmer the flowers take on a wilted appearance. The pollinators of these flowers are unclear. Fragrance is unusual in the genus and is commonly only found in *S. sect. Pachyphylla* (Bohs 1994). The floral development is also of interest, with the stamens of equal length on the first day the flower is open and then the filament of the lowermost anther doubling in length the following day (Figs. 13C, D).

Although herbarium sheets rarely display the feature, *S. turneroides* seems to spread rhizomatously. The hairs of *S. turneroides* are also unique in the section. While they superficially appear to be geniculate, like those of *S. olympicum* and *S. hoffmanseggii*, closer inspection shows that the hairs are simply bent downward on the stem and lack the 90° elbow bend that characterizes the hairs of the latter two species. Using scanning electron microscopy, the base of these hairs appears to have a ring of small lateral cells, hinting that perhaps these hairs are reduced stellate hairs. If so, it may suggest that the simple hairs found in this and other species of sect. *Gonatotrimum* may represent evolutionary reductions from stellate hairs.

The protologue of *S. turneroides* cites many Hassler specimens as syntypes, all from Paraguay, but gives no herbarium locations. *Hassler* 4396 has been chosen from among the many syntypes cited because of the quality of the collection and its wide distribution in herbaria. The sheet from the Hassler herbarium at G is chosen as the lectotype.

Bitter cited four syntypes in his protologue for *S. gonatotrimum*, including *Fiebrig* 2732 and three un-numbered specimens collected in Salta, Argentina by *Hieronymus & Lorentz*, all from Berlin and destroyed. A duplicate specimen of the only numbered syntype, *Fiebrig* 2732, is at Munich and we have designated this as the lectotype because of the quality of the material and widespread photographs of the specimen.

Bitter's protologue of *S. geniculatistrigosum* cited only a single specimen from B, the holotype, which was destroyed in 1942. Photos of this sheet remain at F, G, GH and WIS; a duplicate at BM has been designated the lectotype and isolectotypes have been seen at LE and P.

Bitter also cited only one specimen of *S. flavistrigosum* at S, making it the holotype. The only unusual aspect of this is that Bitter describes the flowers in detail, but the specimen only has buds.

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LITERATURE CITED

- Bennett, J. L. 2008. A revision of *Solanum* section *Regmandra*. *Edinburgh Journal of Botany* 65: 69–112.
- Bitter, G. 1912. Solana nova vel minus cognita III: X. Sectio: *Gonatotrimum* Bitter, nov. section *Repertorium Specierum Novarum Regni Vegetabilis* 11: 230–234.
- Bitter, G. 1913. Solana nova vel minus cognita. X. XXVI. Ergänzungen zur Sektion *Gonatotrimum*. *Repertorium Specierum Novarum Regni Vegetabilis* 12: 73–75.
- Bitter, G. 1922. Solana nova vel minus cognita. XXI. *Repertorium Specierum Novarum Regni Vegetabilis* 18: 301–309.
- Bohs, L. 1994. *Cyphomandra* (Solanaceae). *Flora Neotropica Monographs* 63: 1–175.
- Bohs, L. 2005. Major clades in *Solanum* based on *ndhF* sequence data. Pp. 27–49 in *A Festschrift for William G. D'Arcy: the legacy of a taxonomist*, eds. R. C. Keating, V. C. Hollowell, and T. B. Croat. St. Louis: Missouri Botanical Garden Press.
- Brandege, T. S. 1917. *Plantae Mexicanae Purpusianae* VIII. *University of California Publications in Botany* 6: 363–375.
- Chodat, R. H. 1902. *Plantae Hasslerianae*. *Bulletin de l'Herbier Boissier* 2: 811–824.
- Frodin, D. G. 2004. History and concepts of big plant genera. *Taxon* 53: 753–776.
- Giacomin, L. and J. Stehmann. 2011. A new heterandrous species of *Solanum* section *Gonatotrimum* Bitter (Solanaceae) from Bahia, Brazil. *Phytokeys* 7: 1–9, doi: 10.3897/phytokeys.7.1855.
- IBGE. 2010. Projeto levantamento e classificação do uso da terra: Uso da terra no Estado do Rio Grande do Sul. http://geoftp.ibge.gov.br/documentos/recursosnaturais/usodaterra/usoterra_RS.pdf.
- I. U. C. N. Standards and Petitions Subcommittee. 2010. Guidelines for Using the IUCN Red List Categories and Criteria. Version 8.0. Prepared by the Standards and Petitions Subcommittee in March 2010. Downloadable from <http://intranet.iucn.org/webfiles/doc/SSC/RedList/RedListGuidelines.pdf>.
- Knapp, S. 2008. A revision of the *Solanum havanense* species group and new taxonomic additions to the Geminata clade (Solanaceae). *Annals of the Missouri Botanical Garden* 95: 405–458.
- Mallet, J. 1995. A species definition for the modern synthesis. *Trends in Ecology & Evolution* 10: 294–299.
- McNeill, J., F. R. Baeme, H. M. Burdet, V. Demoulin, D. L. Hawksworth, K. Marhold, D. H. Nicolson, J. Prado, P. C. Silva, J. E. Skog, J. H. Wiersema, and N. J. Turland. 2006. International Code of Botanical Nomenclature (Vienna Code). *Regnum Vegetabile* 146. Liechtenstein: A.R.G. Gartner Verlag KG.
- Mentz, L. A. and P. L. de Oliveira. 2004. *Solanum* (Solanaceae) no região sul do Brasil. *Pesquisas* 54: 1–327.
- Milliken, W., D. Zappi, D. Sasaki, M. Hopkins and R. T. Pennington. 2011. Amazon vegetation: how much don't we know and how much does it matter? *Kew Bulletin* 65: 691–709.
- Nee, M. 1989. Notes on *Solanum* section *Gonatotrimum*. *Solanaceae Newsletter* 3: 80–82.
- Nee, M. 1999. Synopsis of *Solanum* in the New World. Pp. 285–333 in *Solanaceae IV: advances in biology and utilization*, eds. M. Nee, D. E. Symon, R. N. Lester, and J. P. Jessop. London: Royal Botanic Gardens Kew.
- Peralta, I. E., D. M. Spooner, and S. Knapp. 2008. Taxonomy of wild tomatoes and their relatives (*Solanum* sect. *Lycopersicoides*, sect. *Juglandifolia*, sect. *Lycopersicon*; Solanaceae). *Systematic Botany Monographs* 84: 1–186.
- Sendtner, O. 1846. Solanaceae. Pp. 1–227 in *Flora Brasiliensis* vol. 10, ed. K. F. P. Martius. Munich and Leipzig: P. Fleischer.
- Shaw, E. A. 1987. Charles Wright on the Boundary 1849–1852, or *Plantae Wrightianae Revisited*. Westport: Meckler Publishing Corp.
- Seithe, A. and G. J. Anderson. 1982. Hair morphology and the systematics of *Solanum* section *Basarthurum*. *Plant Systematics and Evolution* 139: 229–256.
- Stern, S. and L. Bohs. 2009. Two new species of *Solanum* from Ecuador and new combinations in *Solanum* section *Pachyphylla* (Solanaceae). *Journal of the Botanical Research Institute of Texas* 3: 503–510.
- Stern, S. and L. Bohs. 2012. An explosive innovation: phylogenetic relationships of *Solanum* section *Gonatotrimum* (Solanaceae). *PhytoKeys* 8: 83–98.
- Tepe, E. J. and L. Bohs. 2011. A revision of *Solanum* section *Herpystichum*. *Systematic Botany* 36: 1068–1087.
- Weese, T. L. and L. Bohs. 2007. A three-gene phylogeny of the genus *Solanum* (Solanaceae). *Systematic Botany* 32: 445–463.

APPENDIX 1. Herbarium vouchers and seed provenances for breeding studies.

S. adscendens, BRAZIL: Est. Rio Grande do Sul, Stehmann 6003 (BHCB); *S. deflexum*, COSTA RICA: Prov. Guanacaste, Bohs 2715 (UT); *S. evoluloides*, BRAZIL: Est. Bahia, Giacomin 974 (BHCB); *S. manabiense*, ECUADOR: Prov. Manabí, Stern & Tepe 374 (UT) & 379 (UT); *S. olympicum*, BOLIVIA: Dept. Santa Cruz, Bohs 2738 (UT); *S. turneroides*, BOLIVIA: Dept. Santa Cruz, Nee et al. 51716 (UT);

Numerical List of Species—1. *S. adscendens* Sendtn.; 2. *S. deflexum* Greenm.; 3. *S. evoluloides* Giacomin & Stehmann; 4. *S. hoffmanseggii* Sendtn.; 5. *S. lignescens* Fernald; 6. *S. manabiense* S.Stern; 7. *S. olympicum* Hassl. 8. *S. turneroides* Chodat

Index to Numbered Collections—The numbers in parenthesis refer to the corresponding species in the text and in the Numerical List of Species presented above. Abbot, J. R. 16233 (8), Alvarenga, D. et al. 1295 (7), Anisits, J. D. 2018 (8), 2866 (7), Arbo, M. M. et al. 5613 (7), Ayala, M. G. 136 (5), Ayala, M. G. & Lott, E. J. 9 (5), Badcock, W. J. 416 (8), Balansa, B. 3132 (8), Barboza, G. et al. 1494 (1), Beck, S. G. 5063 (7), 6666 (8), 25662 (7), Black, G. A. 48-2316 (4), Bohs, L. 2109 (7), 3194 (7), Brack, P. 1714 (1), Brandege, T. S. 412 (2), Breedlove, D. 52762 (2), Bueno, O. L. 344 (1), Buscalioni, L. 3656 (4), Bye Jr., R. 171 (2), Cabrera, A. et al. 29445 (1), Calderón, S. 1169 (2), Carballo, R. A. 371 (2), Carballo, R. A. & Carrillo, M. 433 (2), Cardenas, M. 4098 (8), 4929 (7), Carneiro, A. 443 (1), Carranza, E. 3413 (2), Carter, A. 4991 (2), 5621 (2), Carter, A. & Moran, R. 5376 (2), Carvalho, A. M. de 1591 (3), Chavarria, U. 1503 (2), 1766 (2), Chaves, D. 2 (2), Côbar & García 385 (2), 520 (2), Cowan, C. C. et al. 5455 (2), da Souza, M. C. et al. 223 (4), D'Arcy, W. G. 11896 (2), Damasceno, G. 178 (8), Davidse, G. et al. 30657 (2), 35391 (2), 35103 (2), Dias, A. T. G. 627 (4), Díaz, A. L. 63 (2), Elicheche, A. 44 (8), Elorsa, C. M. 700 (2), 3117 (2), Fernández Casas, J. FC3910 (8), FC6384 (8), Fernández Casas, J. & Molero, J. F. C. 6384 (7), Fernández Casas, J. & Schinini, A. A. 7460 (8), Fiebrig, K. 2732 (8), 4408=4827 (8), Fish, J. 73 (2), Flores M. A. 2025 (2), Fróes, R. L. 24667 (4), García et al. 715 (2), Gentry, A. H. 10068 (6), 14430 (2), Giacomin, L. L. 974 (3), Gilman, M. F. 80 (2), Gomes, C. G. 39 (8), Grings, M. 340 (1), Gutierrez, E. et al. 1521 (8), Hammel, B. & Grayum, M. 19933 (2), Hampshire, R. J. et al. 1151 (5), 1154 (5), 1184 (5), Hansen, B. F. & Nee, M. 7447 (2), Happ, G. B. 101 (2), Harmon, W. E. & Dwyer, J. D. 3085 (2), 3399 (2), Harmon, W. E. & Fuentes, J. A. 6016 (2), Harrison, G. J. 4777 (2), 8147 (2), Hassler, E. 1010 (8), 1585 (8), 1638 (8), 1737 (8), 1793 (8), 3801 (8), 4293 (8), 4396 (8), 4841 (8), 8069 (8), 12141a (8), 12441 (8), Hatschbach, G. 74004 (8), 77140 (8), Hatschbach, G. & Zelma 49158 (8), Hatschbach, G. et al. 60696 (8), 76260 (8), 76267 (7), Heithaus, E. R. 274 (2), Hinton, G. B. et al. 4219 (2), 4470 (2), 6481 (2), 9143 (2), 10557 (2), 12057 (2), Hoehne, F. C. 3749 (8), Holm, R. & Iltis, H. H. 295 (2), Howell, J. T. 10253 (2), Jardim, J. 1843 (3), Jarenkow, J. A. 720 (1), Jarenkow, J. A. & Bueno, O. L. 1171 (1), Jesus, J. A. 367 (3), Jiménez, A. 721 (2), Kearney, T. H. & Peebles, R. H. 10387 (2), Keller, H. A. 3746 (1), King, G. 446 (2), 555 (2), Kral, R. L. 69080 (2), Krapovickas, A. 1565 (7), Krapovickas, A. et al. 12568 (8), 25819 (1), 27853 (7), 45675 (8), Kuroiwa, N. & Maeda, N. 1596 (8), Langman, I. K. 2145 (2), 3337 (5), LaSalle, J. et al. 810629-2 (2), Leavenworth, W. C. 473 (2), Leavenworth, W. C. & Hoogstraal, H. 1279 (2), 1344 (2), Lehmann, F. C. 1671 (2), Lehto, E. 24716 (2), Leite, J. E. 658 (1), 1864 (1), Liesner, R. et al. 2798 (2), Linares, J. L. 3536 (5), Lisboa, R. 6782 (4), Lobato, L. C. B. 2656 (4), 3282 (4), Magallanes, A. S. 3650 (5), 4230 (5), Makrinius, E. 530 (5), Martínez, C. R. 1461 (2), Martínez, C. R. & Aguilar 36935 (2), Martínez Salas, E. M. et al. 31192 (5), Maxon, W. R. et al. 7138a (2), 7191 (2), McVaugh, R. 15658 (2), 15796 (2), Mexia, Y. 673 (2), Michel, R. 44 (8), 98 (8), Molina, A. R. 2535 (2), 24551 (5), 27185 (2), Montalvo, A. M. 6380 (2), Moraes, M. 554 (8), Moraes, M. et al. 1791 (7), Moreno, P. P. 2157 (2), 9222 (2), 9280 (2), 9294 (2), 16703 (2), Nee, M. 30473 (7), 30494 (7), 33478 (7), 33545 (7), 33710 (7), 37085 (8), 37160 (8), 37668 (8), 37741 (8), 43093 (8), 48591 (7), 49117 (8), Nee, M. & Bohs, L. 50808 (7), 50825 (7), Nee, M. & Coimbra, S. 33932 (8), 33944 (8), Nee, M. & Linneo, I. I. 54034 (8), Nee, M. & Vargas, I. 44789 (8), Nee, M. et al. 48485 (8), 51716 (8), 51724 (7), 52003 (8), Neffa, V. et al. 989 (8), Nelson, E. W. 2876a (2), Neill, D. A. 2174 (2), 2460 (2), Novara, B. 5884 (8), 5919 (8), 9287 (8), Opler, P. 860 (2), Orcutt, C. R. 4210 (2), 4389 (2), 5286 (2), Orellana, R. 786 (7), Ortiz, J. J. 1029 (2), Palmer,

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