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A Revision of *Solanum* section *Aculeigerum* (the *Solanum wendlandii* group, Solanaceae)

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Abstract—*Solanum* section *Aculeigerum* (the *Solanum wendlandii* group, Solanaceae) comprises eight species ranging from Mexico and Central America to Ecuador and Peru with one species in southeastern Brazil, Paraguay and northern Argentina. One species, *Solanum wendlandii*, is commonly cultivated worldwide in tropical and subtropical regions, and one new species from southern Mexico, *Solanum triumfense*, is described here. Members of *Solanum* section *Aculeigerum* are differentiated from other sections of *Solanum* by a combination of plurifoliate sympodial units, branched inflorescences, presence of prickles coupled with absence of stellate trichomes, and a vine-like habit. Unlike most other prickly species of *Solanum*, which are placed into *Solanum* subgenus *Leptostemonum*, they lack stellate hairs, and phylogenetic studies suggest that the section is one of several potential sister groups for the spiny solanums. A key, descriptions, habitat and distribution data, preliminary conservation assessments, specimens examined and illustrations are provided for all species in *Solanum* section *Aculeigerum*. Lectotypes are designated for the following five names: *S. aculeolatum* M. Martens & Galeotti, *S. mazatenangense* Coult. & Donn. Sm., *S. molinarum* J. L. Gentry, *S. pachyandrum* Bitter, and *S. saganum* A. Rich., and neotypes are designated for *S. glaucescens* Zucc. and *S. wendlandii* Hook. f.

Keywords—Central America, heterandry, lianas, South America, vines.

INTRODUCTION

Solanum L. is one of the ten most species-rich genera of flowering plants (Frodin 2004) and has approximately 1,400 species (Särkinen et al. 2013) occurring on all temperate and tropical continents. The highest diversity of both groups and species is in tropical South America, concentrated in circum-Amazonia (Knapp 2002). Species of *Solanum* have usually five-merous flowers with fused sepals and petals, stellate to pentagonal corollas, stamens with short filaments, and anthers opening by terminal pores. The genus was one of Linnaeus's (1753) larger, with 23 species mostly described from European or African material. The last time *Solanum* was monographed in its entirety was in De Candolle's Prodrômus (Dunal 1852), which included 901 species (with an additional 19 listed at the end of the treatment as incompletely or poorly known). Until the 21st century, the taxonomy of *Solanum* was largely limited to rearrangements of infrageneric taxa, species-level treatments of smaller groups within the genus, and floristic works. The large size of *Solanum* and its poorly understood infrageneric structure has meant that *Solanum* taxonomy has proceeded in a piecemeal fashion until relatively recently, and the genus has acquired a reputation of being intractable. A project funded by the United States National Science Foundation's Planetary Biodiversity Inventory (PBI) program begun in 2004 has sought to accelerate species-level taxonomic work across the genus as a whole. Ongoing work by participants of the PBI *Solanum* project is resulting in a modern monographic treatment of the entire genus available online in the electronic resource Solanaceae Source (<http://www.solanaceaesource.org>). This treatment is part of that collaborative effort.

Taxonomy of *Solanum* section *Aculeigerum*—One of the principal divisions in *Solanum* is that between spiny (technically prickly) and non-spiny species. Early authors distinguished all spiny solanums as members of *Solanum* subgenus *Leptostemonum* Bitter (Dunal 1852; Bitter 1911) due to their

tapered anthers, prickles, and pubescence of stellate trichomes. Phylogenetic studies using DNA sequences confirmed the monophyly of the spiny solanums with stellate pubescence (*Solanum* subgenus *Leptostemonum* or the *Leptostemonum* clade), but the species with prickles and lacking stellate pubescence did not resolve as members of this strongly supported group (Bohs 2005; Levin et al. 2006; Weese and Bohs 2007).

Solanum section *Aculeigerum* Seithe was broadly circumscribed by Seithe (1962) and included all *Solanum* species with prickles but lacking stellate trichomes. Child (1983) segregated *Solanum* section *Nemorensis* A. Child from Seithe's *Solanum* section *Aculeigerum* and included two of her *Aculeigerum* species (*S. barbeyanum* Huber and *S. hoehnei* C. V. Morton; see Table 1) within it along with *S. coriaceum* Dunal, *S. nemorensis* Dunal, and *S. reptans* Bunbury. Child defined *Solanum* section *Nemorensis* as those species with difoliate sympodial units, scorpioid cyme inflorescences, and deeply stellate corollas up to 2 cm in diameter; he differentiated *Solanum* section *Aculeigerum* by its plurifoliate sympodial units, paniculate inflorescences, and rotate to stellate corollas up to 4 cm in diameter. Child did not consider *Solanum* section *Nemorensis* to be part of *Solanum* subgenus *Leptostemonum*, but was otherwise vague in assigning it to be closely related or affiliated with any specific section other than his large *Solanum* subgenus *Solanum*; he later included both *Solanum* sections *Nemorensis* and *Aculeigerum* in his *Solanum* subgenus *Potatoe* (G. Don) D'Arcy as "Anomalous prickly taxa" (Child 1990). Whalen (1984) recognized *Solanum* sections *Nemorensis* and *Aculeigerum* as distinct groups, the *Solanum nemorensis* and *Solanum wendlandii* species groups respectively. In contrast to Child (1983), Whalen (1984) included both these groups in *Solanum* subgenus *Leptostemonum*, but as a "phylogenetically isolated line" (Whalen 1984: 210). Nee (1999) treated these species with prickles but no stellate trichomes in *Solanum* subgenus *Leptostemonum*, with *Solanum* section

TABLE 1. Taxonomic position of species of *Solanum* section *Aculeigerum* (and other species previously considered related to them). Species treated in this revision are in bold face type.

Species	Seithe 1962	Child 1983, 1990; Child and Lester 2001	Whalen 1984	Nee 1999	Stern et al. 2011
<i>S. alternatopinnatum</i> Steud.	<i>S. sect. Aculeigerum</i> Seithe (as <i>S. juciri</i> Mart. ex Sendtn.)	<i>S. sect. Aculeigerum</i> Seithe (as <i>S. juciri</i> Mart. ex Sendtn.)	<i>Solanum wendlandii</i> group	<i>S. sect. Herposolanum</i> Bitter (series 2)	<i>S. wendlandii</i> Group
<i>S. barbeyanum</i> Huber	<i>S. sect. Aculeigerum</i> Seithe (as <i>S. megistophyllidium</i> Bitter)	<i>S. sect. Nemorensis</i> A. Child	<i>Solanum nemorensis</i> group (as <i>S. viridipes</i> Dunal)	<i>S. sect. Micracantha</i> Dunal (subsection 2)	–
<i>S. bicorne</i> Dunal	–	<i>S. sect. Aculeigerum</i> Seithe (as <i>S. refractum</i> Hook.)	<i>Solanum wendlandii</i> group (as <i>S. refractum</i> Hook. & Arn.)	–	<i>S. wendlandii</i> Group (as <i>S. refractum</i> Hook. & Arn.)
<i>S. cobanense</i> J. L. Gentry	–	<i>S. sect. Aculeigerum</i> Seithe (as <i>S. refractum</i> Hook.)	<i>Solanum wendlandii</i> group	–	–
<i>S. coriaceum</i> Dunal	–	<i>S. sect. Nemorensis</i> A. Child	–	<i>S. sect. Micracantha</i> Dunal (subsection 1, series 4)	Androceras/ Crinitum Clade
<i>S. glaucescens</i> Zucc.	<i>S. sect. Aculeigerum</i> Seithe	<i>S. sect. Aculeigerum</i> Seithe	<i>Solanum wendlandii</i> group	<i>S. sect. Herposolanum</i> Bitter (series 2)	–
<i>S. hoehnei</i> C. V. Morton	<i>S. sect. Aculeigerum</i> Seithe (as <i>S. alatum</i> Dunal)	<i>S. sect. Nemorensis</i> A. Child (Child 1983); section <i>Herposolanum</i> Bitter (Child 1990; Child and Lester 2001)	<i>Solanum nemorensis</i> group	<i>S. sect. Herposolanum</i> Bitter (series 1)	<i>S. nemorensis</i> Group
<i>S. nemorensis</i> Dunal	–	<i>S. sect. Nemorensis</i> A. Child	<i>Solanum nemorensis</i> group	<i>S. sect. Micracantha</i> Dunal (subsection 2)	<i>S. nemorensis</i> Group
<i>S. pachyandrum</i> Bitter	–	<i>S. sect. Aculeigerum</i> Seithe	<i>Solanum wendlandii</i> group	<i>S. sect. Herposolanum</i> Bitter (series 2)	–
<i>S. refractum</i> Hook. & Arn.	–	<i>S. sect. Aculeigerum</i> Seithe	<i>Solanum wendlandii</i> group	<i>S. sect. Herposolanum</i> Bitter (series 2) [as <i>S. aculeolatum</i> M. Martens & Galeotti]	–
<i>S. reptans</i> Bunbury	<i>S. sect. Herposolanum</i> Bitter	<i>S. sect. Nemorensis</i> A. Child	<i>Solanum nemorensis</i> group	<i>S. sect. Herposolanum</i> Bitter (series 1)	–
<i>S. triumfense</i> S. Knapp	–	–	–	–	–
<i>S. wendlandii</i> Hook. f.	<i>S. sect. Aculeigerum</i> Seithe	<i>S. sect. Aculeigerum</i> Seithe	<i>Solanum wendlandii</i> group	<i>S. sect. Herposolanum</i> Bitter (series 2)	<i>S. wendlandii</i> Group

Aculeigerum as “Series 2” of *Solanum* section *Herposolanum* Bitter and *S. nemorensis* Dunal + *S. barbeyanum* Huber as “Subsect. 2” of *Solanum* section *Micracantha* Dunal. He suggested the two groups were closely related, and that the lack of stellate pubescence was the result of reduction of stellate trichome complexity. See Table 1 for previous infrageneric classifications of all species treated as related to the taxa included in our current circumscription of *Solanum* section *Aculeigerum*.

Phylogenetic studies using DNA sequence data have shown that both *Solanum* sections *Aculeigerum* and *Nemorensis* do not belong to the strongly supported monophyletic *Leptostemonum* clade (*Solanum* subgenus *Leptostemonum*; Bohs 2005; Weese and Bohs 2007; Levin et al. 2006; Stern et al. 2011; Särkinen

et al. 2013). Three species of *Solanum* section *Aculeigerum* have been included in molecular phylogenetic analyses (*S. alternatopinnatum*, *S. bicorne*, and *S. wendlandii*; note that *S. bicorne* is determined as *S. refractum* in some of these publications, but all sequence data included in GenBank to date under *S. bicorne* and *S. refractum* are from *Iltis et al.* 29694, identified here as *S. bicorne*). In all of these analyses, the species of *Solanum* section *Aculeigerum* form a strongly supported clade, distinct from *Solanum* section *Nemorensis*. Within *Solanum* section *Aculeigerum* Stern et al. (2011) found *S. alternatopinnatum* resolved as sister to *S. bicorne* (as *S. refractum*) + *S. wendlandii*. In the trees resulting from some phylogenetic analyses *S. allophyllum* (Miers) Standl. is sister to *Solanum* section *Aculeigerum*, but this relationship

is poorly supported and unexpected on the basis of morphology. Resolution and support is poor in the tree backbone so that relationships among *Solanum* sections *Aculeigerum* and *Nemorense* and the Geminata, Brevantherum, Cyphomandra, and Leptostemonum clades are unclear (see Fig. 1 in Särkinen et al. 2013), but no analysis places *Solanum* section *Aculeigerum* within the well-supported Leptostemonum clade. Prickles are only found in *Solanum* sections *Aculeigerum*, *Nemorense*, and the Leptostemonum clade, while stellate hairs are found in the Leptostemonum and Brevantherum clades (see Stern et al. 2013). Thus, both prickles and stellate hairs are of ambiguous origin, depending on the sister relationships of the various groups involved. Further analyses of *Solanum* using more markers will be helpful in resolving this. It is clear, however, that the species of *Solanum* section *Aculeigerum* are not part of the core spiny solanums and their relationship to the species of *Solanum* section *Nemorense* is not well-resolved.

MATERIALS AND METHODS

The taxonomic conclusions presented here are a result of field and herbarium work and are supported by molecular phylogenetic results (Weese and Bohs 2007; Stern et al. 2011). We examined approximately 1,200 specimens representing more than 700 collections from the following herbaria (herbarium acronyms follow *Index Herbariorum*, found online at <http://sciweb.nybg.org/science2/IndexHerbariorum.asp>): AD, BH, BHC, BM, BR, C, CAS, CEPEC, CIQ, CM, CORD, CR, CUZ, DS, DUKE, E, G, GH, INB, JBSD, K, L, LE, M, MCNS, MEDEL, MEXU, MJG, MO, NY, P, PH, PMA, R, RB, SI, SP, TEX, U, UC, UPR, US, USM, WIS, XAL, and W. Images of type specimens from the web resource Global Plants (<http://plants.jstor.org>) were also used to establish the distribution of isotypes and to aid in lectotypification choices. Type specimens with sheet numbers are cited with the herbarium acronym followed by a dash and the sheet number (i.e. MO-1781232); barcodes are written as a continuous string (i.e. G00104280). We have cited geographically representative specimens for taxa where more than 100 collections are known. Identities of all numbered collections seen for this study are in the Index to numbered collections (Exsiccatae; <http://dx.doi.org/10.5519/0039503>) and full specimen details are available on the Solanaceae Source website (www.solanaceaesource.org).

Citation of literature follows BPH-2 (Bridson 2004) with alterations as implemented in IPNI (International Plant Names Index, <http://www.ipni.org>) and Harvard University Index of Botanical Publications (http://kiki.huh.harvard.edu/databases/publication_index.html). Following Knapp (2013) we have used the square bracket convention for publications in which a species is described by one author in a publication edited or compiled by another, the traditional "in" attributions such as Dunal in DC. for those taxa described by Dunal in Candolle's *Prodromus Systematis Naturalis Regni Vegetabilis*. This work is cited here as Prodr. [A. P. de Candolle] and the names are thus attributed only to Dunal. For "ex" attributions we cite only the publishing author, as suggested in the Code (McNeill et al. 2012). Standard forms of author names are according to IPNI (International Plant Names Index, <http://www.ipni.org>).

We cite page numbers for all previous lectotypifications. Where specific herbaria have not been cited in protologues we have followed McNeill (2014) and designated lectotypes rather than assuming holotypes exist.

We have followed the morphological species concept or "morphological cluster" concept (Mallet 1995) in delimiting species of *Solanum* section *Aculeigerum*. 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. Molecular evidence corroborates the delimitation of taxa using morphological methods (Stern et al. 2011).

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 retroactively georeferenced the collections using available locality data. Maps were constructed with the points in the centers of degree squares in a 1° square grid. Conservation threat status was assessed following the IUCN red list categories and criteria (IUCN 2014) using the

GIS-based method of Moat (2007) as implemented in the online assessment tools in GeoCat (<http://geocat.kew.org>). The extent of occurrence (EOO) measures the range of the species, and the area of occupancy (AOO) represents the number of occupied points within that range based on the default grid size of 2 km².

RESULTS

Morphology—**HABIT AND STEMS**—Members of *Solanum* section *Aculeigerum* are all woody or semi-woody vines with small, broad-based recurved prickles (Figs. 1A, 1B, 1D, 2C). These prickles are morphologically similar to those of the *S. lanceifolium* species group of Whalen (1984) (Micracantha clade of Stern et al. 2011) and almost certainly help the plants to clamber over and ascend vegetation. In general the prickles of *Solanum* section *Aculeigerum* are relatively widely spaced along the stems, averaging 1–5 prickles per cm of stem length, and are sometimes absent from the uppermost stems. Prickles in the spiny solanums are interpreted as being derived from stellate trichomes (Whalen 1984), and so their occurrence in members of *Solanum* section *Aculeigerum* is either convergent and follows a different developmental pathway, or stellate trichomes have been completely lost in *Solanum* section *Aculeigerum*.

Most species in *Solanum* section *Aculeigerum* can begin to flower when quite small and then they are recorded as shrubs on herbarium labels, but all species apparently grow to canopy height with long woody stems.

LEAVES—Leaves of members of *Solanum* section *Aculeigerum* vary from simple to pinnatifid, often on the same plant (e.g. *S. wendlandii*). The only species with what could be termed pinnately compound leaves with petiolulate leaflets is *S. alternatopinnatum*; others are merely very deeply pinnatifid with laminar tissue along the midrib. In common with many members of *Solanum* subgenus *Leptostemonum*, prickles can be borne on the midrib abaxially and occasionally also adaxially. The leaves of most of the species are glabrous, or occasionally with a few papillate trichomes when young; only *S. bicornis* and *S. triunfense* have multicellular trichomes on the leaf lamina. The leaves of members of *Solanum* section *Aculeigerum* often have copious crystal sand – isolated idioblasts of calcium oxalate that appear as white dots in dry specimens.

PUBESCENCE—Despite bearing prickles, members of section *Aculeigerum* do not possess the distinctive stellate trichomes of *Solanum* subgenus *Leptostemonum*. Trichomes, if present, are generally simple and uniseriate, usually composed of only a few cells. *Solanum triunfense* has a few furcate trichomes mixed with the simple uniseriate pubescence of young stems and inflorescences; these hairs have a single small branch and are not dendritic as found elsewhere in the genus (e.g. *S. aureum* Dunal, a member of the Dulcamaroid clade, see Knapp 2013). It has been suggested (Nee 1999) that the simple trichomes of *Solanum* section *Aculeigerum* are similar to those found in members of *Solanum* section *Acanthophora* Dunal or *S. leucopogon* Huber (of the Micracantha clade sensu Stern et al. 2011) and are simply stellate trichomes that have lost the lateral rays. This loss occurs in *Solanum* section *Gonatotrimum* Bitter (Stern et al. 2013) in which *S. lignescens* Fernald is stellate-pubescent and other members of the section have distinctive geniculate trichomes with one short and one long cell. The few-celled trichomes of *S. bicornis* are similar to those of *Solanum*

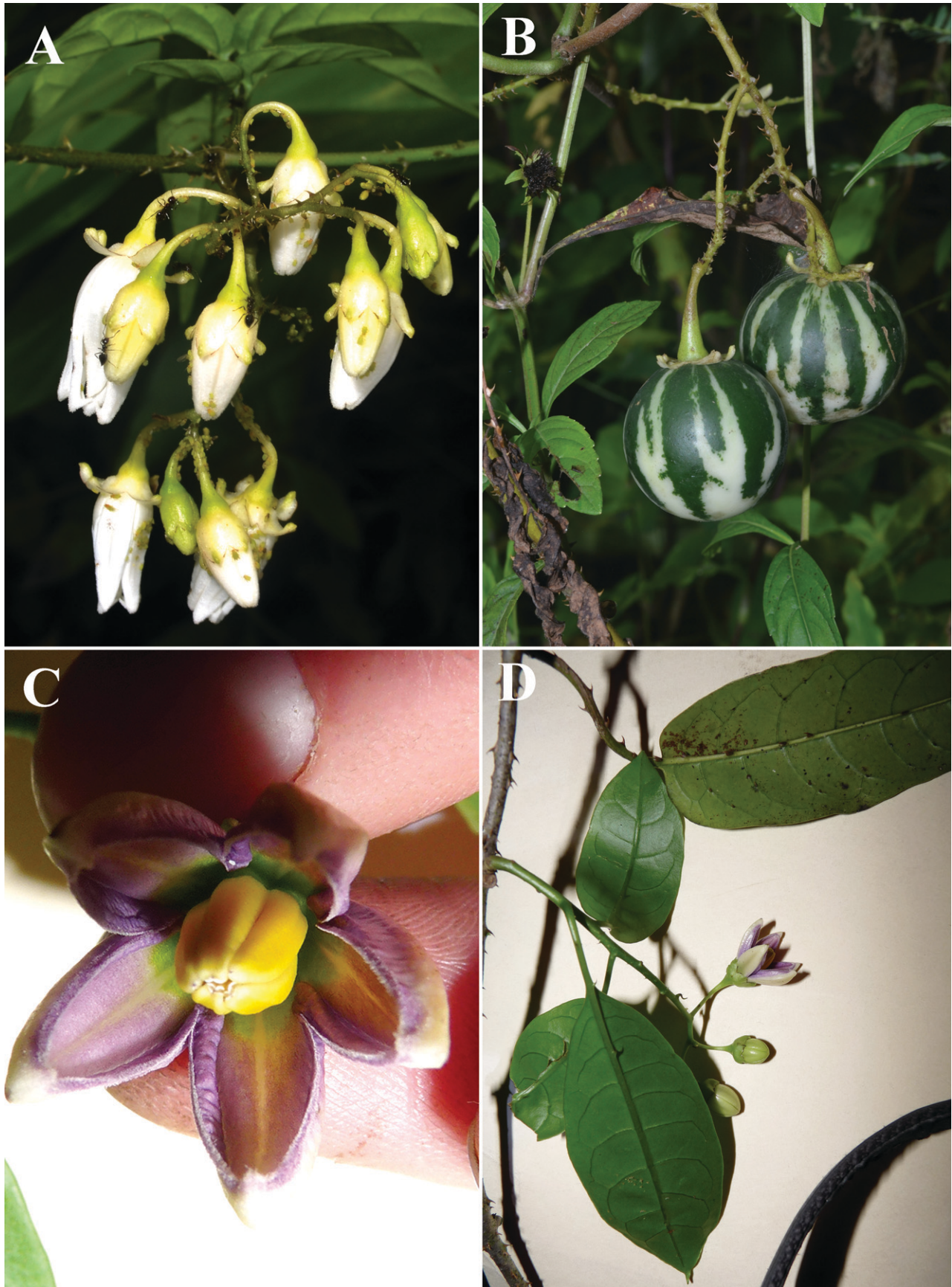


FIG. 1. Morphology of *Solanum* section *Aculeigerum*. A. *S. alternatopinnatum* inflorescence in bud (Giacomin *et al.* 1692). B. *S. alternatopinnatum* immature fruits; note the armed inflorescence rachis (Giacomin *et al.* 1692). C. Flower of *S. cobanense*; note fleshy petals and ellipsoid anthers (Christenhusz *et al.* 5584). D. *S. cobanense* inflorescence on young shoot (Christenhusz *et al.* 5584), note absence of prickles on the inflorescence rachis. Credits: A–B: L. L. Giacomin; C–D: K. Watson).

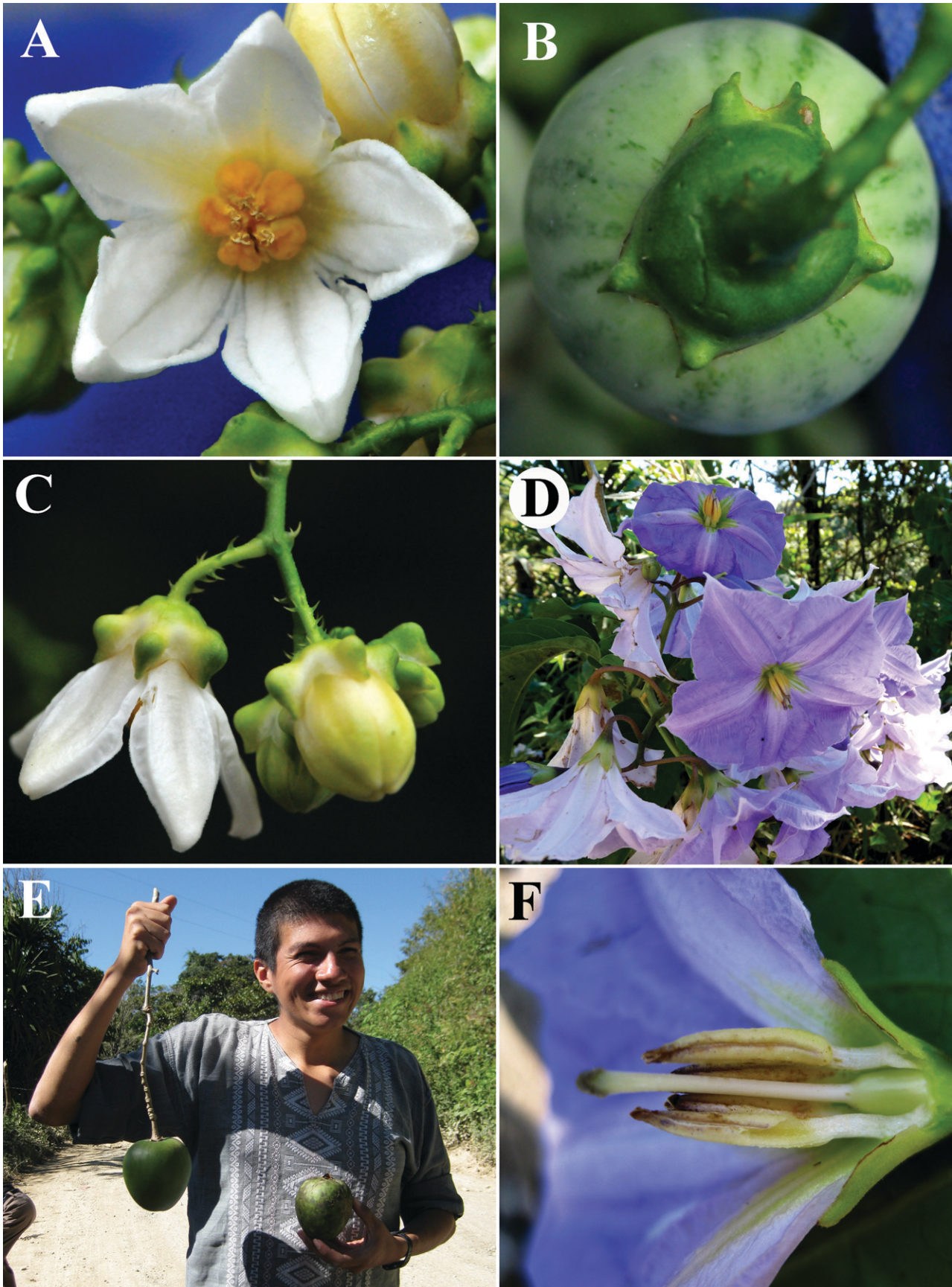


FIG. 2. Morphology of *Solanum* section *Aculeigerum*. A. *S. pachyandrum* flower; note ellipsoid anthers (Särkinen *et al.* 4546). B. *S. pachyandrum* immature fruit (Särkinen *et al.* 4546). C. *S. pachyandrum* inflorescence with buds; note the keeled calyx lobes and prickly pedicels (Särkinen *et al.* 4546). D. Inflorescence of *S. wendlandii* pistillate plant (Christenhusz *et al.* 5372). E. Immature fruit (seeds still very small and not at all well-developed) of *S. wendlandii* (Christenhusz *et al.* 5372). F. *S. wendlandii* pistillate flower (Christenhusz *et al.* 5372). Credits: A–C: T. Särkinen; D–F: M. Vorontsova.

section *Gonatotrichum*, with a long apical cell and a shorter (pustulate) basal cell (but are not geniculate). Those of *S. triumfense* are not of this morphology; they are typical simple, multicellular uniseriate trichomes like those found in major groups of non-spiny solanums (e.g. the Geminata Clade, see Knapp 2008a).

INFLORESCENCES—Members of *Solanum* section *Aculeigerum* usually have branched inflorescences; those of *S. wendlandii* can be many times branched and very large (Fig. 2D). Inflorescence branches are highly divaricate, usually spreading at ca. 90 degree angles so the structure is very open. Flowers are often clustered near the tips of the branches, but are usually evenly spaced along the inflorescence branches (0.5–1 cm apart). The rachis can be armed or unarmed; all of the pinnatifid-leaved species (*S. alternatopinnatum*, *S. pachyandrum*, *S. refractum*) have densely prickly inflorescences (Fig. 1B, 2C), while the rest of the taxa (Fig. 1D) only rarely have inflorescence prickles (*S. wendlandii* is variable in this regard).

FLOWERS—Flowers of members of *Solanum* section *Aculeigerum* are pentamerous and sympetalous, like all of *Solanum*. Flower buds are ellipsoid to tapering (turbinate), depending on the shape of the anthers (see below; Fig. 1A, C). The calyx is usually campanulate and openly spreading and the buds are usually exerted from the calyx tube when very young, long before anthesis. Most species have thickened lobes with scarious sinuses that tear early on in bud growth to leave broadly deltate regular calyx lobes. *Solanum triumfense*, however, has a calyx that completely encloses the buds until much later in growth and irregularly tears into deep uneven lobes. The calyx lobes of *S. pachyandrum* are markedly keeled (Fig. 2C). All species have copious crystal sand in the more robust tissue of the calyx lobes.

Members of *Solanum* section *Aculeigerum* have relatively large flowers; in *S. wendlandii* they can reach 6 cm in diameter (long-styled flowers, e.g. *Christenhusz et al.* 5372, see Fig. 18). Corolla shape varies from deeply stellate (*S. cobanense*; Fig. 1C, D) to almost rotate (*S. wendlandii*; Fig. 2D, F), and color varies from deep purple (*S. cobanense*, Fig. 1C) to white or greenish white (*S. alternatopinnatum*, Fig. 1A). Species that commonly have white or greenish white flowers (e.g. *S. alternatopinnatum*, *S. bicorne*, *S. refractum*) have also been recorded as having purple or lilac corollas, so it clear that polymorphism exists in corolla color as is common in other groups of solanums (e.g. Knapp 2013). Corolla color in *S. wendlandii* changes throughout anthesis (Fig. 2D); when flowers first open they are deep purple and with age they fade to pale violet (sometimes described on labels as blue) or white with a concomitant increase in size (SK, pers. obs.); this has been observed in other Solanaceae such as *Lycianthes* (Dean 2001), in some members of the Dulcamaroid clade of *Solanum* (Knapp 2013), and in *Solanum* section *Crintinum* (Whalen) A. Child in the spiny solanums (SK, pers. obs.).

ANDROECIUM—Like all species of *Solanum*, members of *Solanum* section *Aculeigerum* have poricidal anthers; the pores are directed distally and in these species usually split with age along the margins so that the anthers appear to be longitudinally dehiscent. *Solanum cobanense*, *S. pachyandrum* and *S. triumfense* have ellipsoid anthers (Figs. 1C, 2A), while the rest of the species have variously tapering anthers, from strongly tapering in *S. refractum* to only slightly tapering in *S. wendlandii* (Fig. 2F).

Many species of *Solanum* have dimorphic stamens (Anderson et al. 2006; Bohs et al. 2007; Vorontsova et al. 2013) and stamen

dimorphism occurs in almost half of the 13 major clades of the genus. It is especially diverse in *Solanum* subgenus *Leptostemonum*, with both anther (e.g. *S. rostratum* Dunal from the southwestern USA) and filament (e.g. *S. coagulans* Forssk. from Africa) dimorphism present. The dimorphic stamens of *Solanum* section *Aculeigerum* are due to differences in filament length. Four species of the group (*S. alternatopinnatum*, *S. bicorne*, *S. glaucescens*, and *S. wendlandii*) have one anther on a markedly elongate filament, while *S. cobanense*, *S. pachyandrum*, *S. refractum* and *S. triumfense* have filaments of equal size. Occasionally the anther borne on the long filament is slightly larger than the rest, but all anthers are usually of equal sizes, as are the remaining four filaments in any given flower.

Anther color in the group varies from cream to yellow or orange (*S. refractum*) to pale purplish blue (*S. wendlandii*). Label data often describes the anthers of *S. wendlandii* as yellowish at the base and blue or purple more distally (see Fig. 2F).

GYNOECIUM—The ovary and style of members of *Solanum* section *Aculeigerum* are glabrous, and the stigma is minutely papillate. Style length varies among flowers in an inflorescence, and section *Aculeigerum* has been interpreted as comprising andromonoecious plants (Whalen 1984). Short-styled flowers have styles that are included in the anther tube, while those of long-styled flowers are exerted (Fig. 2F). In *S. cobanense*, however, the stigma is held at the level of the tips of the anthers (Fig. 1C), suggesting that the expression of andromonoecy in this group may be more complex than previously described. *Solanum wendlandii* appears to have all long-styled or all short-styled flowers on any given plant; it may be dioecious, a breeding system that occurs several times in different clades of *Solanum* (Knapp et al. 1998; Martine et al. 2009), or sequentially monoecious with younger plants producing flowers with exclusively male function (see description of *S. wendlandii*). This needs further investigation of living plants in the field and greenhouse.

FRUITS AND SEEDS—Fruits of members of *Solanum* section *Aculeigerum* are bilocular berries with fleshy pulp (eaten by local people in some species; e.g. *S. pachyandrum*) and thick, leathery pericarp. The fruit surface appears rugose in dried specimens, but is smooth, glabrous and matte in fresh material (Fig. 2E). Immature fruits are often pale green or greenish white with darker markings (see Figs. 1B, 2B); mature fruit colour is quite variable. The pedicel and calyx lobes are thickened and woody in fruit, and the calyx lobes often break off in herbarium specimens. Fruiting specimens are rarely collected. Seeds are flattened-reniform, very large and many (usually > 100) per berry. The surfaces are minutely pitted with rectangular or pentagonal cells, and at least in *S. glaucescens*, the lateral testal cells walls are elongate, giving the seed a hairy appearance.

TAXONOMIC TREATMENT

SOLANUM SECTION ACULEIGERUM Seithe, Bot. Jahrb. Syst. 81: 291. 1962.—TYPE SPECIES: *S. wendlandii* Hook. f.

Solanum section *Micracantha* Dunal subsection *Juciri* Bitter ex Marzell, in Hegi, Flora von Mittel-Europa 5: 2548. 1927.—TYPE SPECIES: *S. wendlandii* Hook.f.

Perennial woody vines to canopy lianas, usually armed with recurved prickles on stems, petioles, and midveins of abaxial leaf surfaces. Stems subwoody to woody, sometimes

herbaceous, usually glabrous or puberulent with simple hairs, the prickles to 8 mm long, recurved, stout. Sympodial units usually plurifoliate, rarely difoliate, not geminate. Leaves simple and entire or pinnately lobed to compound, usually petiolate, occasionally decurrent to base. Inflorescence terminal, often appearing lateral, usually branched, with 5–35 flowers, the axes with or without prickles. Flowers 5-merous, usually long- or short-styled, the plants probably andromonoecious or in one case (*S. wendlandii*) dioecious. Calyx spreading with rounded lobes, the lobes usually equal in size but occasionally tearing and markedly unequal in size. Corolla rotate-pentagonal to stellate, purple, violet (blue), white, or greenish white. Stamens all equal or dimorphic with four filaments equal in length and one filament 2–6 times longer than the rest; anthers variously tapering, usually somewhat attenuate, ellipsoid in some species. Style cylindrical, glabrous, usually straight but sometimes slightly curved; stigma truncate or bilobed. Fruit a globose berry, ca. 2–10(–20 fide *Christenhusz et al.* 5372) cm in diameter, the surface glabrous (sometimes

rugose when dry), yellow or light green, less commonly red or orange, the mesocarp orange-red, green, or white. Seeds many per berry, strongly flattened-reniform, light brown, the surface minutely pitted, the testal cells pentagonal to rectangular in outline, the lateral testal cell walls elongate or not.

Solanum section *Aculeigerum* includes eight species: six in Mexico and Central America, one in southern Ecuador and northern Peru, and one in southeastern Brazil, northern Argentina and Paraguay (see maps of individual species). Section *Aculeigerum* is differentiated from other clades of *Solanum* by a combination of plurifoliate sympodial units, branched inflorescences, prickles with an accompanying lack of stellate trichomes, and a woody vine-like habit.

Section *Aculeigerum* is best known for the commonly cultivated species *S. wendlandii* (Figs. 2D–F). It is grown in the Americas and has also been introduced to tropical and subtropical regions of the Old World. It is also widely cultivated in greenhouses in the northern hemisphere (see description of *S. wendlandii* for more details).

KEY TO THE SPECIES OF *SOLANUM* SECTION *ACULEIGERUM*

1. Leaves simple, usually shallowly lobed, only deeply lobed on vigorous young shoots 2
2. Stem prickles all or mostly paired at base of petioles. 4. *S. glaucescens*
2. Stem prickles more or less evenly scattered, not paired at base of petioles 3
3. Leaves chartaceous, mostly clustered on short shoots, pubescent with stiff simple trichomes with long basal cells; corolla creamy white (occasionally tinged with violet). 2. *S. bicorne*
3. Leaves coriaceous, evenly distributed along the branches, glabrous or pubescent with simple uniseriate trichomes with 2–4 cells, the basal cell not markedly longer than the rest; corolla purple, blue or violet. 4
4. Flowers rotate to pentagonal; filaments unequal; usually some pinnatifid leaves present on plant 8. *S. wendlandii*
4. Flowers stellate; filaments equal; leaves never pinnatifid.
5. Leaves and stems glabrous; leaf bases truncate to acute; inflorescence axes glabrous; buds exserted from the calyx 3. *S. cobanense*
5. Leaves and stems with scattered simple uniseriate trichomes; leaf bases attenuate; inflorescence axes densely pubescent with simple 2–4-celled uniseriate trichomes; calyx completely enclosing the buds 7. *S. triumfense*
1. Leaves compound or deeply lobed with the lobe sinuses more than half the distance to the midrib, the uppermost leaves near the inflorescence sometimes only shallowly lobed or entire. 6
6. Flowers heterandrous, with one filament markedly longer than the other four.
7. Corolla light blue to purple, rotate to pentagonal; leaves highly variable in shape on the same plant, often entire near the inflorescence, generally ranging from deeply lobed to pinnately compound. 8. *S. wendlandii*
7. Corolla white or cream, stellate, lobed nearly to the base; leaves compound or deeply pinnatifid.
8. Inflorescence axis and pedicels prickly; inflorescence borne on main branches, not borne on short shoots; leaves compound with the leaflets with distinct petiolules; southern South America 1. *S. alternatopinnatum*
8. Inflorescence axis unarmed; inflorescence borne on short shoots; leaves deeply pinnatifid, the lobes with distinct wings of tissue decurrent along the main rachis, distinct petiolules absent; Mexico and Central America 2. *S. bicorne*
6. Flowers with all filaments equal in length within a flower.
7. Anthers ca. 3 mm wide; flowers white; pedicels armed with stout prickles; southwestern Ecuador and northwestern Peru. 5. *S. pachyandrum*
7. Anthers 1–1.5 mm wide; flowers greenish white; pedicels unarmed; Pacific slope, southern Mexico, Guatemala and Honduras. 6. *S. refractum*

1. *SOLANUM ALTERNATOPINNATUM* Steud., Nomencl. Bot., ed. 2: 600. 1841. Nom. nov. for *Solanum oleraceum* Vell. (1829), non *Solanum oleraceum* Dunal (1813). *Solanum oleraceum* Vell., Fl. Flumin. 89. 1829. — TYPE: BRAZIL. Rio de Janeiro (no specimens are known to exist; lectotype, designated by Knapp et al. 2015, pg. 832: original parchment plate held in Biblioteca Nacional. Rio de Janeiro [mss1198651_128]; incorrectly lectotypified by Matesevach Becerra 2013, pg. 290 on the published plate in Vellozo, Fl. Flumin. Icon. 2: Table 125. 1831).

Solanum viridipes Dunal, Prodr. [A. P. de Candolle] 13(1): 234. 1852 — TYPE: BRAZIL: Bahia, J. Guillot s. n. (holotype: P [P00384877, F neg. 39219]).

Solanum juciri Sendtn. var. *inermis* Glaz., Bull. Soc. Bot. France 58 (Mem. 3f): 497. 1911. —TYPE: BRAZIL. Rio de Janeiro: Fazenda de Boa Esperança, Chez M. Bellieni, dans les cafféiers, 22 Oct 1886, A. F. M. Glaziou 16294 (lectotype, designated here: P [P00319401]; isolectotypes: C, K [K000788574]).

Solanum juciri Sendtn. forma *paraguariense* Hassl., Repert. Spec. Nov. Regni Veg. 9: 118. 1911. *Solanum viridipes* Dunal var. *intermedium* Hassl., Repert. Spec. Nov. Regni Veg. 15: 239. 1918. —TYPE: PARAGUAY. Caaguazú [Depto. Caaguazú], Amambay [Depto. Amambay] and Paraná regions, Mar 1905, É. Hassler 9365 (lectotype, designated by Matesevach Becerra 2013, pg. 290: BM [BM000087604];

isolectotypes: G [G00443009, Morton neg. 8558; G00443010], GH [no barcode or sheet number], K [K000788653], NY [NY00172245], P [P000384878, Morton neg. 8362], W [W-1906-0001280]).

Woody or subwoody vines to 3 + m long or scandent shrubs, the stems 0.2–0.4 cm in diameter, prickly; internodes 1–5 cm long, glabrescent; prickles to 2 mm long, stout, recurved. Sympodial units usually plurifoliate, rarely difoliate, not geminate. Leaves pinnately compound, the blades in outline (5–)15–20 × (4–)6–12 cm, with 5–7 pairs of opposite to subopposite petiolulate leaflets, chartaceous, glabrous adaxially and abaxially, with calcium oxalate crystals commonly present, often armed on rachis with recurved prickles; major lateral veins 5–7 on each side, corresponding to the leaflets; petioles (1–)3–5 cm, glabrous, often armed with recurved prickles; leaflets 3–10 × 1–3 cm, oblong to elliptic, widest at the base; base cuneate and oblique; margin entire; apex acuminate; petiolules 0.3–1 cm. Inflorescences (10–)20–30 cm long and wide, terminal or appearing lateral, several times branched, with 20–35 flowers, the axes glabrous, densely prickly; peduncle (2–)5–15 cm; rachis 4–10 cm; pedicels 10–15 mm, slender at anthesis, articulated at the base; fruiting pedicels to ca. 20 × 3 mm and becoming subwoody. Flower buds ellipsoid to somewhat pointed, the corolla soon exerted from the calyx tube. Calyx campanulate, spreading, the tube 2–4 mm, the lobes ca. 3 × 2 mm, rounded, apiculate at tips, glabrous, reflexed at anthesis. Corolla 2.5–4 cm in diameter, spreading at anthesis, uniformly white or greenish white, sometimes tinged with violet (*Nee 54960*, plant cultivated in Bolivia), membranous to slightly fleshy, stellate, lobed ca. 3/4 way to the base, the lobes 1–2 × 0.3–0.5 cm, narrowly triangular, acute to acuminate at apices, glabrous abaxially and adaxially, the tips densely papillate. Stamens 5–10 mm long; filaments unequal, with four 1–1.5 mm long, the fifth 3–4 mm long, glabrous; anthers nearly equal, 5–7 × 1.5–2 mm, the one on the longer filament slightly larger, tapering at the tips, connivent, yellow or orange, poricidal at the tips, the pores lengthening to slits with age. Ovary glabrous; style in long-styled flowers ca. 10 mm long, straight, glabrous, in short-styled flowers ca. 4 mm long; stigma truncate. Fruit a globose berry, 3–4 cm in diameter, green with light green streaks when immature, yellow with white streaks when ripe, the pericarp glabrous, rugose when dry. Seeds > 20 per berry, ca. 3 × 3 mm, strongly flattened-reniform, light brown, the surface foveolate. Figs. 1A–B, 3.

Distribution and Habitat—*Solanum alternatopinnatum* (Fig. 4) occurs in Argentina (Province of Misiones), Brazil (States of Bahia, Distrito Federal, Espírito Santo, Mato Grosso, Minas Gerais, Paraná, Rio de Janeiro, São Paulo) and Paraguay (Provinces of Alto Paraná, Canindeyú, San Pedro) in the wet forests of “mata atlântica” or “Selva Paranaense” at elevations from 100–950 m.

Phenology—*Solanum alternatopinnatum* is most commonly collected in flower from November to April, and fruiting collections are most common from June to August.

Common Names—Brazil: “juciri” (*Martius s. n.*); “jiquiri” (*Warming s. n.*). Paraguay: “yuá-pará” (*Woolston 826*).

Preliminary Conservation Status (IUCN 2014)—Least Concern (LC); EOO 2,998,232 km² (LC); AOO 240 km² (EN); 75 localities. Although the AOO suggests that *S. alternatopinnatum* is of some conservation concern, the large number of localities and wide habitat preferences of this species lead us to give it the assessment of LC.

Solanum alternatopinnatum differs from other species of *Solanum* section *Aculeigerum* in its compound leaves with clearly petiolulate leaflets, heterandrous flowers, and nearly herbaceous stems. *Solanum pachyandrum* and *S. refractum* have deeply pinnatifid leaves but do not have clearly petiolulate leaflets and *S. refractum* occasionally has leaves that are very shallowly lobed. We have only seen a single specimen of *S. alternatopinnatum* (*Glaziou 16294*, one of the type collections of *S. juciri* var. *inermis*) with simple leaves. The stems of *S. alternatopinnatum* are herbaceous or rarely subwoody in contrast to the subwoody stems of *S. refractum*. These species are also completely allopatric, with *S. refractum* restricted to southern Mexico, *S. pachyandrum* found in the Huancabamba depression of northern Peru and southern Ecuador and *S. alternatopinnatum* ranging from Brazil and Paraguay to northern Argentina.

Leaves of *S. alternatopinnatum* are eaten as a vegetable in Brazil (as jiciri or juciri; Mentz and Oliveira 2004); apparently the prickles soften with cooking.

This species was known for a long time as *S. juciri* Sendtn., a name coined as a replacement for *S. oleraceum* Vell. (Vellozo 1829), a later homonym of *S. oleraceum* Dunal (Dunal 1813; a synonym of *S. americanum* Mill. of the Morelloid clade). *Solanum juciri* is an illegitimate name (McNeill et al. 2012) as *S. alternatopinnatum* was cited in synonymy, with the comment “nomen ineptissimum plantae ab auctore non visae pinni tam alternantibus quam oppositis instructe datum” (this is a silly name given to this plant by the author who did not see alternate but opposite leaflets); Sendtner (1846) recognized the existence of the name but considered it inappropriate.

In describing *S. viridipes*, Dunal (1852) cited two elements: an herbarium specimen *Guillot s.n.* from Paris, and a living plant “v.v. in hort. Monsp.” cultivated in Montpellier. Since he only cited a single herbarium specimen, this is the holotype (McNeill 2014). He also further specified and annotated material as “*S. laxiflorum* Dunal mss. in herb. Schad. nec Sendtn.” The holotype specimen in P (P00384877) has a number of annotations on it, including “*S. laxiflorum* Dun. 1842 nec Sendtn. 1848.” We suspect “in herb. Schad.” is a misprint for “in herb. Sched.” and refers to an annotation on a herbarium specimen and not to a particular herbarium.

Names coined by Glaziou (1911) in his list of plants from Central Brazil are sometimes indicated as not validly published. Here we are treating the varietal name *S. juciri* var. *inermis* as validly published as it is accompanied by a (very short) description that distinguishes it from the species. Glaziou (1911) cited only his collection number 16294 in the protologue, but a compound locality (“Fazenda de Boa Esperança, près Cantagallo et Serra da Estrella RIO-JAN”). In Paris there are two sheets of this number that are clearly collected in two places — one in Serra da Estrella (P00319400, Feb 1880, *Glaziou 16294a*) and the other from Fazenda de Boa Esperança (P00319401, 22 Oct 1886, *Glaziou 16294*). The ‘a’ has been added to the number in Glaziou’s handwriting. *Glaziou 16294a* has typical pinnately compound leaves, while the other sheet has unusual simple leaves (see above). We select P00319401 as the lectotype of this varietal name as there is a clear duplicate at Kew as evidenced by the simple leaves on the K sheet.

Hassler described *S. juciri* forma *paraguariense* using his collection *Hassler 9365* and seven years later used the same collection (together with *Fiebrig 6157*) to describe *S. viridipes* var. *intermedium* as a new name for his forma *paraguariense*

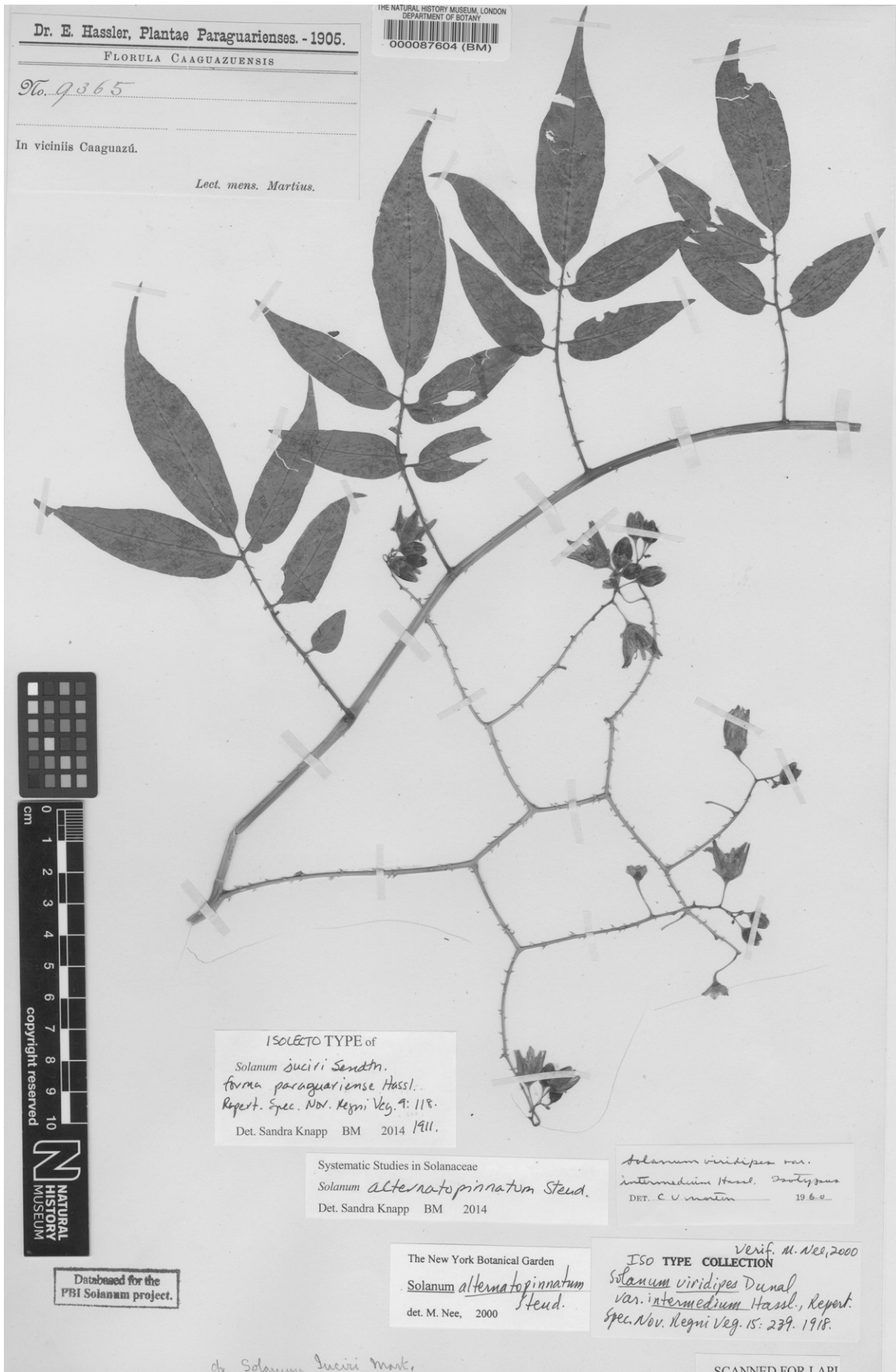


FIG. 3. *Solanum alternatopinnatum* from Paraguay (É. Hassler 9365, lectotype of *Solanum juciri* Sendtn. forma *paraguayense* Hassl., BM [incorrectly labelled isolectotype in image]). Reproduced with permission of the Natural History Museum, London.

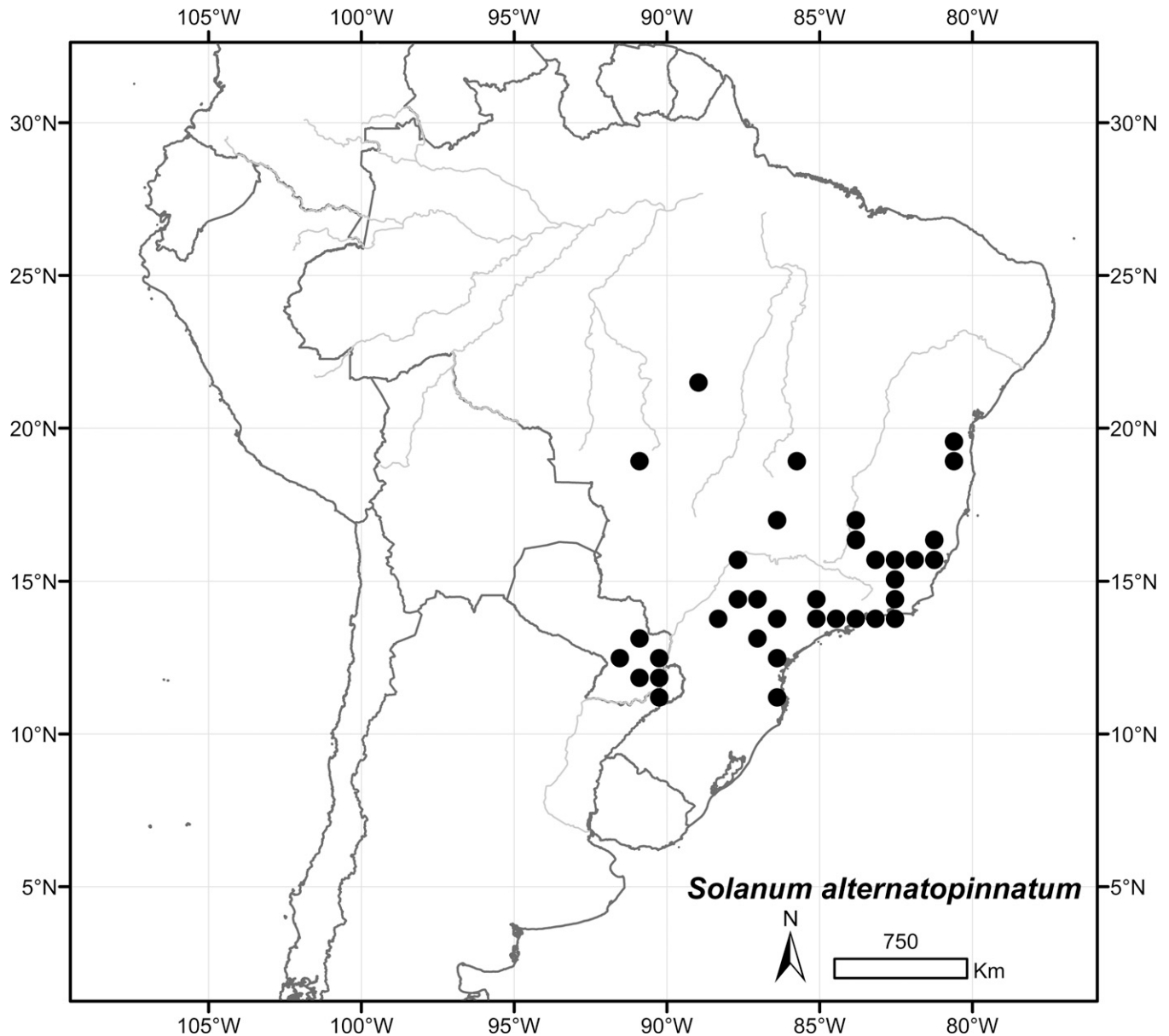


FIG. 4. Distribution of *Solanum alternatopinnatum*.

(Hassler 1911, 1918). He described var. *intermedium* in terms of his forma *paraguariense* ("Caule foliis ut in Fedde Rep. l. c. pro forma paraguariensi nob. indicatus" [stem and leaves from Fedde Rep. description of the new forma *paraguariense*]: Hassler 1918: 239). We consider that he was explicitly coining a new name using the same material to replace forma *paraguariense*, and therefore treat these two names as homotypic as did Matesevach Becerra (2013). It is unfortunate that Matesevach Becerra (2013) did not use material at G annotated by Hassler, but her lectotypification is correctly made and stands.

Representative Specimens Examined—BRAZIL. Bahia: Mun. Jussari, Palmira, entrada ca. 7.5 km de Jussari, Faz. Teimoso, RPPN Serra do Teimoso, 21 Apr 1999 (fl), *Amorim et al.* 2915 (CEPEC, MO, NY); Juçari, 27 May 1966 (fl), *Belém & Pinheiro* 2329 (US); Mun. Almadina, Faz. Beija-Flora, ramal com entrado no km 3 da Rod. Almadina/Floresta Azul, 9 Nov 1978 (fl), *dos Santos et al.* 3382 (F); Rodovia BR-330, Barragem do Funil (Rio de Contas), 33 km SE de Ipiáu, 6 Mar 1978 (fl), *Mori et al.* 9549 (MO, NY, WIS). Distrito Federal: Córrego Landim, ca. 20 km N of Brasília, 950 m, 16 Dec 1965 (fl), *Irwin et al.* 11343 (AAU, K, MO, NY,

WIS); Córrego Landim, ca. 25 km N of Brasília, 950 m, 16 Mar 1966 (fl), *Irwin et al.* 13998 (AAU, DS, K, MO, NY, WIS). Espírito Santo: Mpio. Itaguassú, Jatiboca, 28 May 1946 (fl), *Brade et al.* 18467 (K, RB); Aldeamento dos Índios, Rio Pancas, 5 Jul 1942 (fl), *Bueno & Emygdio* 208 (R); Fazenda Salvador, Rio Doce, 17 Jul 1942 (fl), *Bueno & Emygdio* 209 (R); Reserva Florestal de Linhares, 31 Oct 1995, *Folli* 2668 (RB). Mato Grosso: Mun. Chapada dos Guimarães, rodovia Chapada dos Guimarães-Campo Verde, km 10, 11 Aug 1997 (fl), *Hatschbach et al.* 66672 (BHCB); Vale do Caxipó, 28 May 1983 (fl), *Guilherme* 8 (R). Minas Gerais: Parque Estadual do Rio Doce, Marliéria, 15 Jun 1995 (fl), *Lombardi & Temponi* 784 (F); Mun. Belo Horizonte, Serra do Taquaril, 31 Apr 1933 (fl), *Mello Barreto* 7826 (F); Fazenda de Aguada, 19 Sep 1930 (fl), *Mexia* 5066a (US); Paraopeba, 31 Mar 1957 (fl), *Pereira & Pabst* 2731 (RB, US, WIS); Mun. Juiz de Fora, Morro do Imperador, 8 May 2003 (fl, fr), *Pifano et al.* 511 (BHCB); Belo Horizonte, Sep 1988 (fl), *Requens* s.n. (BHCB); Caratinga, Aug 1991 (fl), *Stehmann* 19535 (RB); Mun. Caratinga, Fazenda Macadonea/Cenibra-Ipaba, 22 Aug 1992 (fl), *Stehmann & Soares* s.n. (BHCB). Paraná: Foz do Iguaçu, Parque Nacional, 20 Feb 1963 (fl), *Hatschbach* 9749 (US); Mun. Cerro Azul, Cab. Rib. do Tigre, 24 April 1987 (fl) *Hatschbach & Cervi* 51229 (MO, US); Porto de Cima, 24 Jun 1914 (fl), *Jönsson* 585a (GH, NY); Jaguarihyva, 25 Oct 1910 (fl), *Dusén* 16559 (GH, NY). Rio de Janeiro: Tres Fomosos, *Alampaio* 3181A (US);

Itaipuaçu, Pico Alto Moirão 14 Apr 1982 (fr), *Andreata* 413 (RB); Mangaratiba, Reserva Ecológica do Rio das Pedras, trilha do Cambucá, 17 Aug 1996 (fr), *Bovini* et al. 1011 (RB); Guaratiba, May 1929, *Brade* 10516 (US); Paraíba do Sul, Mar 1954 (fl), *Duarte & Ahumada* 3691 (RB); Barra da Tijuca, 15 Oct 1961 (fl), *Duarte* 9880 (RB); Corcovado, Rio de Janeiro, 20 Apr 1922 (fl), *Ducke & Kuhlmann* 396 (RB); Rio de Janeiro, 1867 (fl), *Glaziou* 1333 (BR); mata do Horto Florestal, Rio de Janeiro, 14 May 1929 (fl), *Kuhlmann* 1117 (RB); Vista Chinesa, 20 May 1958 (fl), *Liene* et al. 3793 (RB); Morro do Pão de Açúcar, 17 Oct 1977 (fl), *H. C. de Lima* 117 (RB); Serra dos Órgãos, 22 Oct (fl), *Riedel* s.n. (NY); Rio Janeiro, May 1832 (fr), *Riedel* s.n. (NY); Niterói, Córrego dos Colibris, 30 Jun 1998 (fl,fr), *Santos* et al. 168 (RB); Tejuco, *Schott* 5447 (F, W); Serra do Mendanha, 450 m, 27 Nov 1969 (fl), *Sucre* et al. 6395 (RB); Rio Janeiro, 18 Jan 1864 (fl), *Warming* s.n. (C). Santa Catarina: Tapura, Tibeirão, 19 Jun 1968 (fl), *Klein* et al. 7961 (US). São Paulo: Serra do Mar above Ubatuba, 100–200 m, 21 Aug 1976 (fl), *Davis* et al. 59838 (E); Barreiro, Expedição do Rio Feio, *Edwall* 15378 (US); Mun. Iepe, Fazenda C.A.P.I. 4 km N of Rio Parapanema & 6 km E of Porto Alvorada, 22°44' S, 57°70' W, 9 Feb 1965 (fl), *Eiten* et al. 5956 (US); Ubatuba, Parque Estadual da Serra do Mar, Núcleo Picinguaba, trilha saindo da Base Cambucá para a sede da fazenda (Base de Pesquisa), 3 m, 23°19'39" S, 44°56'21" W 26 Jan 2012, *Giacomin & Almeida* 1692 (BHCB); Campinas, 8 Jan 1905 (fl), *Heiner* 377 (MO); Serra de Caraguatatuba, 15 May 1938 (fl), *Kuhlmann & Gehrt* s.n. (F, NY, SP); Mun. Aguas de Prata, Rod. Governador Adhemar P. Barros, ca. 1 km do centro Aguas de Prata, 21 Mar 1994 (fl), *Martins* et al. 31435 (BHCB); Guaratinguetá, *Martius* s.n. (M); Ilha Seca, 1940 (fl), *Santos* s.n. (R); Mun. Campinas, Fazenda Santa Elisa, Feb 1996 (fl), *Vasconcellos-Neto* s.n. (BHCB); Reserva Municipal da Santa Genebra, near Campinas, 750 m, 1 Feb–21 Mar 1987 (fl), *Vogel* 59 (MJG).

PARAGUAY: in regione fluminis Alto Paraná, 1909–1910 (fl), *Fiebrig* 6157 (BM, E, GH, K, L, US). Alto Paraná: Reserva Limoy, 10 Nov 1981 (fl), *Binacional* 896 (MO); Centro Forestal Alto Paraná, 12 km W del Puerto Presidente Stroessner, 25°28'S, 54°42'W, 16 Apr 1986 (fl), *Brunner* 1816 (PY). Canindeyú: Jejui-mí, 23 km NE de Ygatimí, 24 Apr 1996 (fl), *Jiménez* et al. 1212 (BM, MO, PY). Caazapá: National Park Caaguazú, 26°05'52" S, 55°26'35" W, 24 Nov 1997 (fl), *Zardini & Benítez* 47379 (NY). San Pedro: Alto Paraguayo, Primavera, Rozados, 8 Jun 1957 (fl), *Woolston* 826 (C, K, NY, US); Yaguareté forest (Sustainable Forest Systems Site), 23°46'16" S, 55°59'37" W, 20 Jun 1995(fr), *Zardini & Balbuena* 42892 (NY).

ARGENTINA. Misiones: Dto. Cainguaés, Capiovysño, 6 Apr 1949 (fl), *Schwarz* 7674 (CORD); ruta 7, 5 km W de acceso a Aristóbulo del Valle, 30 Jul 1987 (fr), *Vanni* et al. 886 (GH).

2. *Solanum bicorne* Dunal, Prodr. [A. P. de Candolle] 13: 232. 1852.—TYPE: MEXICO, "*Pavón* s. n." [a collection made by M. Sessé and J. Mociño and distributed from Pavon's herbarium, see Knapp 2008b] (holotype: G [G000343458, F neg. 34109]).

Solanum bicorne Dunal var. *angustifolium* Dunal, Prodr. [A. P. de Candolle] 13(1): 233. 1852.—TYPE: MEXICO, "*Pavón* s. n." [a collection made by M. Sessé and J. Mociño and distributed from Pavon's herbarium, see Knapp 2008b] (holotype: G [G000343452, F neg. 34110]; isotype: F [F-846743]).

Solanum dichotomum Sessé & Moc., Pl. Nov. Hisp. 35. 1888.—TYPE: MEXICO. Guerrero: Mazatlán, *M. Sessé & J. Mociño* 5348 (lectotype, designated by Knapp 2008b, pg. 11: MA [MA-604601, F neg. 48342]; isolectotypes: F [F-845066, fragment], MA [MA-604599, F neg. 48341; MA-604600]).

Solanum guamuchilense Cast.-Campos, Acta Bot. Mex. 27: 34, Fig. 1. 1994.—TYPE: MEXICO. Nayarit: Mpio. Bahía de Banderas, El Guamúchil, between Bucerías and Sayulita, ejido of Punta Mita, 300 m, 10 Oct 1990, *G. Castillo Campos* 6103 (holotype: XAL [XAL0106656]; isotype: XAL [XAL0106655]).

Woody vine to 15 + m long, the stems 0.25–0.9 cm in diameter; internodes 5–10 cm long on main stems, 0.5–1 cm long on short shoots, glabrous or puberulent with simple hairs to 0.5 mm long with enlarged pustulate bases; prickles

2–5 mm long, stout, recurved, occasionally very sparse on long internodes. Sympodial units plurifoliate, not geminate, the leaves clustered on short shoots to 5 cm long. Leaves usually simple (one specimen seen with deeply pinnatifid juvenile leaves on vigorous shoots), the blades 10–28 × 5–10 cm, oblanceolate to lance-elliptic, chartaceous, puberulent adaxially and abaxially with simple 2–4-celled hairs 1–1.5 mm long with an elongate basal cell, often armed abaxially on midrib with recurved prickles; major lateral veins 3–5 on each side; base long-attenuate; margin usually entire, occasionally sinuate with 2–3 pairs of shallow lobes ca. 3 × 2.5 cm (leaves on very young shoots possibly more deeply lobed); apex acute to acuminate; petioles broadly winged to base and nearly sessile. Inflorescences ca. 30 × 20 cm, terminal or lateral on young growth of short shoots, many times branched, with 20–55 flowers, the axes glabrous or occasionally minutely puberulent with simple 1–2-celled trichomes to 0.5 mm long, not prickly, or sometimes with a few prickles at the base (*Soto* N. 10188); peduncle 6–15 cm; rachis (5–)15–20 cm; pedicels 10–15 mm and slender at anthesis, elongating in fruit to 2–2.5 × ca. 1 cm and becoming subwoody, terminally clustered, articulated at the base. Flower buds narrowly ellipsoid to pointed, the corolla early exerted from the calyx tube. Calyx campanulate, spreading, the tube 2–4 mm, the lobes ca. 1.5 × 2 mm, rounded, apiculate at tips, glabrous. Corolla 2.5–4 cm in diameter, spreading at anthesis, creamy white, membranous, deeply stellate, lobed nearly to the base, the lobes 1–2 × 0.3–0.5 cm, narrowly deltate to triangular, acute to acuminate, glabrous abaxially and adaxially, densely short white pubescent at the hooked cucullate tips. Stamens 5–10 mm long; filaments unequal, with four ca. 1 mm long, and one ca. 5–6 mm long (at approximately the same height as the tips of the other four anthers), glabrous; anthers nearly equal, 4–6 × 1.5–2 mm, the one on the longer filament slightly larger, usually somewhat tapering, connivent, yellow or orange, poricidal at the tips, the pores lengthening to slits with age. Ovary glabrous; style in long-styled flowers ca. 10 mm long, approximately equal in height to the long stamen, straight, glabrous, in short-styled flowers ca. 5 mm long; stigma capitate. Fruit a globose berry, ca. 5.5 cm in diameter, globose, red or orange, the pericarp glabrous, rugose when dry. Seeds > 50 per berry, ca. 5 × 5.5 mm, strongly flattened-reniform, brown, the surfaces minutely pitted. Fig. 5.

Distribution and Habitat (Fig. 6)—*Solanum bicorne* is endemic to Mexico (States of Colima, Durango, Guanajuato, Guerrero, Jalisco, Michoacán, Morelos, Nayarit, Sinaloa, and Zacatecas), in deciduous forests, grasslands, and humid montane forests at elevations from sea level to 2,000 m.

Phenology—*Solanum bicorne* appears to flower and fruit throughout the year, but more fruiting specimens have been collected from November to April (e.g. *Gentry* 5248).

Uses—Mexico: "The fruits are red when ripe in March and April and eaten by birds" (*Gentry* 5248).

Common Names—Mexico. Guerrero: "chilacayote" (*Halbinger* s.n.); "tomate de chicalaca" (*Halbinger* s.n.); Sinaloa: "toronjo" (*Montes & Salazar* 591 and *Ortega* 4021).

Preliminary Conservation Status (IUCN 2014)—Least Concern (LC); EOO 545,195 km² (LC); AOO 404 km² (EN); 126 localities. *Solanum bicorne* is a commonly collected and apparently relatively common species where it occurs.

This species is easily differentiated from others in section *Aculeigerum* by the presence of clustered leaves on short shoots

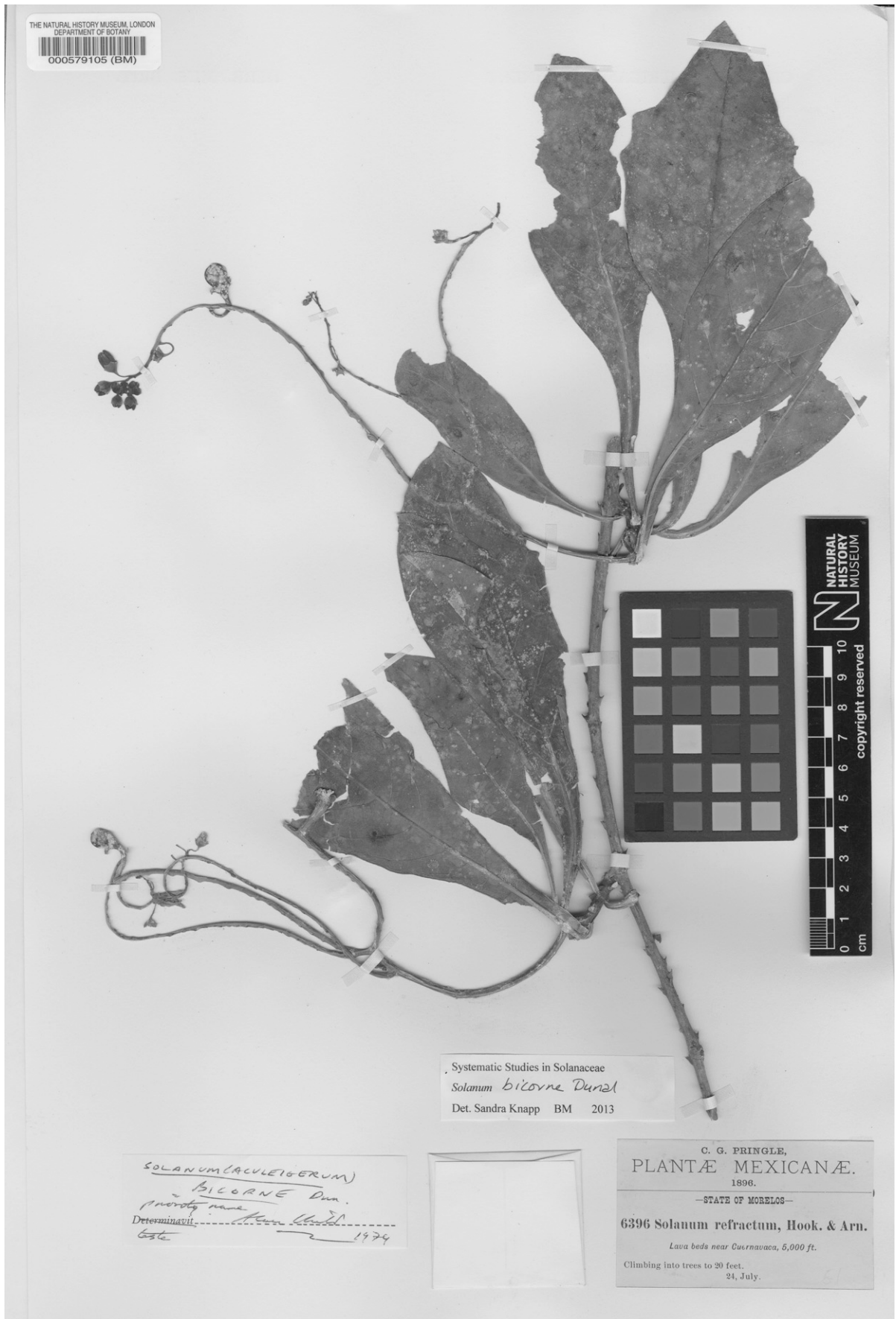


FIG. 5. Representative specimen of *Solanum bicorne* from Mexico (C. Pringle 6396, BM). Reproduced with permission of the Natural History Museum, London.

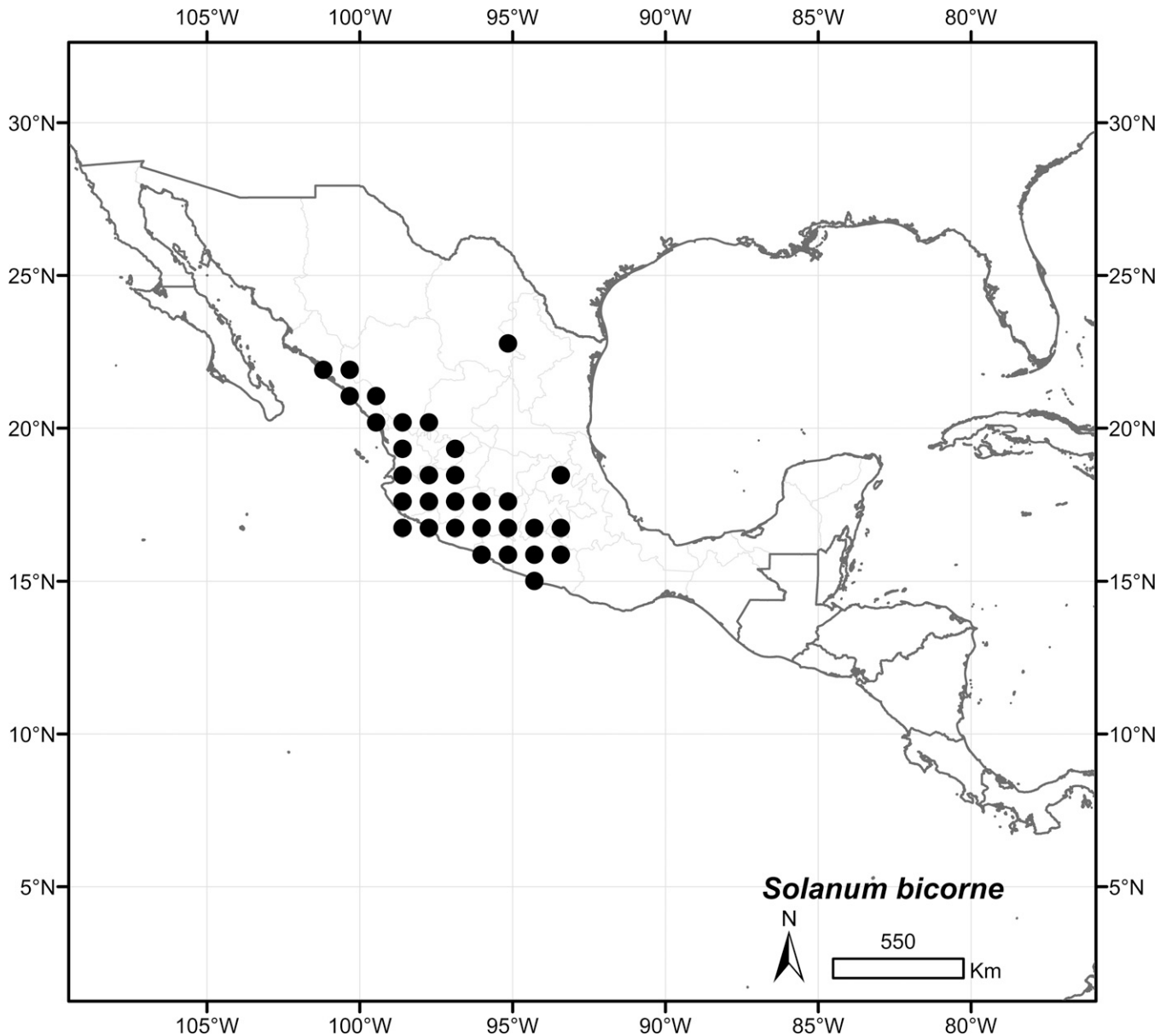


FIG. 6. Distribution of *Solanum bicorne*.

(Fig. 5). Dunal, in describing *Solanum bicorne*, mistook the clustered stem leaves as being the rosette of a possibly acaulescent herb (Dunal 1852: 232) when in fact the plant is a high-climbing, robust, woody vine. This species is similar to *S. glaucescens*, especially with respect to the white, stellate flowers with dimorphic stamens, but differs by its leaves that are narrowed to the base with definite wings on the petiole and short shoots with densely crowded leaves. A pair of prickles at the base of the petiole is present in *S. glaucescens* but absent in *S. bicorne*.

A single specimen identified here as *S. bicorne* from Sinaloa (Sanders *et al.* 4576, MO-3279500) has quite deeply lobed leaves that resemble those of *S. refractum*, but these seem to be from a very young shoot and have fewer lobes than typical specimens of *S. refractum*. The non-prickly inflorescence rachis arising from a short shoot and distribution suggest this specimen is *S. bicorne* with juvenile foliage. Other *Solanum* species have pinnatifid juvenile foliage (e.g. members of the Dulcamaroid clade such as *S. dulcamaroides* Poir., see Knapp

2013) that is rarely collected; this needs further investigation in the case of *S. bicorne* and other members of this group of woody vines.

In his description of *S. bicorne* Dunal (1852) cited a specimen from “Nova Hispania (Pavon in hb. Boiss. sub nom. *S. bicorne*)”; he used the name on the specimen that almost certainly came from the original collection made in Mexico by Martin Sessé and José Mociño. A single specimen from the Boissier herbarium (now part of the general collections at G) is therefore the holotype for this name. The complex typification of names for this species based on the Mexican and Central American collections of Martin Sessé and José Mociño is discussed in detail in Knapp (2008b).

Representative specimens examined—MEXICO. Colima: 14 mi WNW of Santiago, road to Cihuatlán, Jalisco, 5 m, 25 Jul 1957 (fl), *McVaugh 15741* (MEXU); Mpio. Comala, Rancho El Jabalí, 22 km NNW of Colima, 19°27'N, 103°41'W, 1,325 m, 10 Jul 1991 (fl), *Vázquez V. & Phillips 822* (K, MEXU). Durango: Tamazula [westernmost point, almost in Sinaloa], 1,000 ft, 16 Dec 1939 (fr), *Gentry 5248* (DS, F, GH, MO, NY). Guanajuato: Mpio. Acámbaro, 3 km NW de Irámucio, 1,950 m, 15 Aug 1993 (fl),

Rzedowski 52029 (MEXU). Guerrero: 36 km by road N of coast road (Hwy 200) on road to Ciudad Altamirano, 600 m, 26 Sep 1983 (fl), *Anderson* 12827 (CAS, MEXU, MO); Mpio. José Azueta, 1.8 km SO del caserío La Vainilla, 17°42'N, 101°31'W, 350 m, 26 Oct 1989 (fl), *Gallardo Hernández et al.* 162 (MEXU); Mochitlán al E de Chilpancingo, Aug 1962 (fl, fr), *Halbinger s.n.* (MEXU); Cruz de Ocote, adelante de Filo de Caballo, 1,800 m, Apr 1975 (fr), *Halbinger s.n.* (MEXU). Jalisco: 5–10 km SW of Talpa de Allende on road toward Tomatlán, 23 Sep 1983 (fl, fr), *Anderson* 12773 (NY); La Manzanilla, 4.5 km E de la carretera Barra de Navidad–Puerto Vallarta, 17 Jan 1986 (fr), *Ayala & Bullock* 531 (MEXU); 16 km N de Garita, 8 Jul 1967 (fl), *Cedillo Trigos* 31 (MEXU); below SE edge of Cerro Toxín in bottom of Arroyo Pitahayas, 1 km NE of Toxín, barely N of Puerto de Toxín–La Loma crossroads, along El Sauz–San Pedro Toxín road, 19°30'N, 104°00'W, 1,180 m, 13 Jan 1990 (fr), *Cochrane et al.* 12266 (WIS-2 sheets); Reserva Biósfera Sierra de Manantlán, E end of the Sierra de Manantlán in the pass between Cerro Grande and Cerro en Medio, midway between Puerto de Toxín and Piedras Cuatas, 19°33'N, 103°59'W, 1,260–1,290 m, 14 Jan 1990 (fr), *Cochrane et al.* 12279 (WIS); S of Sayola, 304–914 m, Sep 1961, *Faberge s.n.* (TEX); Mpio. Jocotepec, 5 km S de Huejotitlán, entre Huejotitlán y San Marcos, 1,500 m, 15 Oct 1989 (fr), *Flores M. et al.* 1718 (MEXU); Mpio. Zapotitlán, 82 km de Cd. Guzmán, carr. a San Antonio (pasando por Quesería), a 8 km de San Antonio por brecha a Zapotitlán, 12 Jun 1988, *Gaona P.* 418 (NY); 18–20 miles SW of Autlán, 23 Jul 1951, *Gentry* 10953 (LL); west of Magdalena, 25 May 1849 (fl, fr), *Gregg* 880 (MO); Cerro Viejo, above Zapotitlán de Hidalgo, about 25 mi S of Guadalajara, 1,800 m, 17 Jun 1956 (fl, fr), *Gregory & Eiten* 229 (MO); Mpio. Talpa de Allende, 15 km S de Talpa de Allende, 1,300–1,400 m, 4 Oct 1982 (fr), *Hernández M. et al.* 9058 (MEXU, NY); between Nacastillo and Chamela, 13 Jan 1979 (fr), *Illis & Nee* 1567 (WIS); 1 km S of N end of Tecopatán valley, 4.5 km SSE of El Chante on road to Manantlán, 19°41'N, 104°11'W, 1,200 m, 11 Jan 1980 (fr), *Illis & Schatz* 2548 (WIS-2 sheets); Reserva Biósfera Sierra de Manantlán, path to La Lima from El Rodeo, 19°33'N, 104°03'W, 1,350 m, 15 Oct 1982 (fr), *Illis et al.* 28923 (WIS-2 sheets); Mpio. Venustiano Carranza, 4 km N de V. Carranza, camino a Tapalpa, puente sobre el Río Jiquilpan, 30 Jun 1981 (fl), *Lott et al.* 428 (MEXU); Mpio. La Huerta, Rancho Cuixmala, Cumbres 1, E of Puerto Vallarta–Barra de Navidad hwy, 19°31'N, 104°56'W, 14 Jan 1991 (fr), *Lott et al.* 3261 (MEXU); Mpio. La Huerta, Estación Biología “Chamela”, 4 Sep 1982 (fl), *Magallanes* 3674 (MEXU, NY); 11 mi N of bridge of Río Cihuatlán on road from Santiago, Colima, to Durazno, Jalisco, 500–550 m, 1 Aug 1957 (fl, fr), *McVaugh* 15968 (MEXU, US); hills 2–3 miles E of La Manzanilla, settlement on the SE shore of Bahía Tenacatita, 150–200 m, 11 Nov 1960 (fr), *McVaugh* 20967 (NY-2 sheets, US); Mpio. Zapopan, “La Piedrera”, 10 km NW de Tesisán, 1,700 m, 9 Oct 1980 (fl), *Nieves Hernández* 53 (F); Barranca, near Guadalajara, Jun 1886 (fl), *Palmer* 108 (BM, GH-2 sheets, NY-2 sheets, P, U); Tequila, 6 Jul 1893 (fl), *Pringle* 7918A (E, F, MO, NY); as 2918A in F, US); Mpio. Cuautitlán, al NE de Ayotitlán, 950 m, 10 Aug 1986 (fl), *Ramírez D. & Rodríguez C.* 430 (WIS); Mpio. Tala, a lo largo del Arroyo Caliente y Los Laderos, Bosque Escuela, La Primavera, 1,450 m, 13 Aug 1988 (fl), *Rodríguez C. & Reynoso D.* 1432 (MEXU, NY); Mpio. Zapotitlán, La Joya area of Rancho El Jabali, 22 km NNW of the city of Colima, 19°27'30" N, 103°40' W, 24 Sep 1988, *Sanders et al.* 8236 (CAS, MO, NY, TEX); Mpio. Autlán, 14–16 km NE de Casimiro Castillo, 2 km NE de Ahuacapan, 19°14'N, 104°19'W, 5 Aug 1988 (fl), *Santana M. & Lorente* 3732 (MEXU, WIS); 15 km al SW de Autlán, Barranca del Tecolote, 5–8 km al NE de Casimiro Castillo, 19°37'N, 104°23'W, 800–900 m, 22 Jul 1987 (fl), *Vázquez* 4510 (WIS); Mpio. Tamazula, 16 km al SE de Tamazula, brecha a Uña de Gato, 1,500 m, 14 Dec 1989, *Villa C. & Chávez L.* 452 (NY). México: 3 km NW de Los Pinzanes, Tejuipilco, 29 Jan 1973 (fr), *González-Medrano* 5498 (MEXU); Mpio. Temascaltepec, Salitre Cañitas, 12 Jul 1933, *Hinton* 4312 (BM, K, UC, US); Mpio. Temascaltepec, Luvianos, 14 Jul 1933 (fl), *Hinton* 4320 (K, GH, MO). Michoacán: Santa Ana Maya, Sep 1955 (fl), *Castillo* 2735 (MEXU); lower north-facing slopes of Cerro Santa María, 8–10 km SW of Jiquilpán and 5 km NE of Quitupán, 2,000 m, 5–7 Aug 1959 (fr), *Feddema* 102 (TEX); Villa Victoria, District Coalcomán, 700 m, 11 Jul 1939, *Hinton* 13906 (GH, LL, US, W); “El Salto”, E of Morelia on road to Ciudad Hidalgo, 2,250 m, ca. 19°14'N [sic], 100°50'W, 11 Aug 1960 (fl), *Illis et al.* 839 (WIS); Mpio. Hidalgo, 2 km S de Mil Cumbres, camino a San Antonio Villalongín, 2,500 m, May 1985 (fl), *Soto N. et al.* 8494 (MEXU, US); Mpio. Aguililla, 11 km NO de Aguililla, 1180 m, 11 Jul 1985 (fl), *Soto N. et al.* 9250 (MEXU, TEX); Mpio. Lázaro Cárdenas, 10 km N de Playa Azul, carretera a Nueva Italia, 250 m, 22 Aug 1985 (fl), *Soto N. & Román G.* 10188 (MEXU). Morelos: Cuernavaca, 5,000 ft, 24 Jul 1896 (fl), *Pringle* 6396 (BM, CM, E, F, GH, K, MO, NY, P-3 sheets, PH, UC, US-2 sheets, W); near Cuernavaca, 10 Sep 1903, *Rose* 6947 (US).

Nayarit: San Blas, 2 Oct 1925 (fr), *Ferris* 5341 (DS, GH, US); Mpio. Nayar, 10 km NE de La Guerra, camino La Guerra–Huejuquilla, 22°15'N, 104°15'W, 1,300 m, 10 Nov 1990 (fr), *Flores F. & Ramírez R.* 2388 (MEXU); Mpio. Ahuacatlán, 8 km W de Jala, camino a la estación de Microondas, Volcán El Cebruco, 21°05'N, 104°30'W, 1,700 m, 18 Mar 1991 (fr), *Flores F. & Ramírez R.* 2596 (MEXU); Mpio. Xalisco, 1 km SW de Palapitas, 21°25'N, 105°03'W, 790 m, 16 Sep 1994 (fr), *Flores-Franco et al.* 3830 (MEXU); Tres Mariás Islands, María Madre, 24 Jul 1932 (fl, fr), *Howell* 10440 (CAS); Tepic, 14 Feb 1927 (fr), *Jones* 22925 (F, UC); Tres Mariás Islands, María Madre, 17 May 1925 (fr), *Mason* 1732 (CAS, K); road from Tepic to Calixcillo, 1,000 m, 13 Sep 1926 (fl, fr), *Mexia* 588 (CAS, F, GH, MO, UC, US); Barranca, SE of Trapichillo, 650–700 m, 19 Aug 1935 (fl), *Pennell* 19826 (PH); Acaponeta, 11 Apr 1910 (fl), *Rose et al.* 14372 (NY, US); Mpio. Compostela, 20–25 km S de Tepic, carr. a Compostela, 21°20'N, 104°51'W, 31 Jul 1990 (fl), *Téllez V.* 12766 (K, MEXU, MO, NY). Sinaloa: Mpio. Concordia, 3 km above El Coco on Mex. Hwy. 40, 1,020 m, 6 Aug 1980 (fl), *Breedlove & Almeda* 45058 (CAS, MEXU, MO); Labradas, 22 Sep 1925 (fl, fr), *Ferris & Mexia* 5246 (DS-2 sheets, GH); Mpio. Mazatlán, Rancho de Los Cannobio, Juantillos, comunidad San Marcos, Sindicatura de la Noria, 10 Apr 1994 (fr), *Guizar Nolasco* 3150 (MEXU); Mpio. Escuinapa, La Campana, 100 m, 30 Aug 1990 (fr), *Hernández A. et al.* 930 (MEXU); Rancho de Campanillas, San Ignacio, 13 Sep 1918, *Montes & Salazar* 591 (US); San Agustina, *Ortega* 4021 (US); Culiacán, 27 Aug–15 Sep 1891 (fl, fr), *Palmer* 1534 (F, GH, NY, UC); Rosario, 22 Jul 1897, *Rose* 1819 (GH, US); vicinity of Villa Union, 2 Apr 1910, *Rose et al.* 13909 (US); Mpio. Concordia, along Hwy. 40, 0.6 mi. above Cantil and 21 mi. NE of Concordia, ca. 600 m, 31 Dec 1983, *Sanders et al.* 4576 (MO); Mpio. Culiacán, Sanalona a 30 km E de Culiacán, 200 m, 13 Nov 1989 (fr), *Vega A. & Hernández* 3586 (MEXU); rd. between El Salto and Concordia, 10.5 mi by road N of Chupaderos, 23°30'N, 105°50'W, 3500 ft, 1 Jul 1969 (fl), *Webster & Breckon* 15545 (GH, MEXU, MO, TEX). Zacatecas: Mpio. Moyahua, 3 km W de Las Palmas, 3 Sep 1992 (fl), *Enríquez E.* 201 (MEXU).

3. *SOLANUM COBANENSE* J. L. Gentry, *Phytologia* 26(4): 276. 1973.—TYPE: Nom. nov. for *Cyphomandra aculeata* Donn. Sm. (1914), non *Solanum aculeatum* (Jacq.) O. E. Schulz.

Cyphomandra aculeata Donn. Sm., *Bot. Gaz.* 57: 423. 1914.—TYPE: GUATEMALA. Alta Verapaz: Cobán, Apr 1882, *F. Lehmann* 1334 (holotype: US [US-1324994, barcode US00036715]; isotypes: BM [BM000514914], G [G00442620]).

Robust woody vine or canopy liana to 18 m long, the stems 0.3–0.8 cm in diameter, prickly, sometimes densely so; internodes 3–10 cm long, completely glabrous; prickles to 3 mm long, stout, recurved. Sympodial units plurifoliate, not geminate. Leaves simple, the blades (6–)12–17 × 3–5(–9) cm, ca. 3 times as long as wide, oblong or elliptic to narrowly elliptic, widest at the middle, coriaceous, glabrous on both surfaces, armed abaxially on midrib with recurved prickles; major lateral veins 6–9 on each side; base truncate to acute; margin entire; apex acuminate to acute; petioles (1–)3–7 cm, glabrous, armed with recurved prickles. Inflorescences 10–15 cm long and wide, terminal, few-branched, the axes glabrous, not prickly; peduncle 3–5 cm; rachis (3–)5–10 cm; pedicels (10–)25–50 mm and slender at anthesis, elongating in fruit to ca. 50 × 6 mm and becoming woody, articulated at the base. Flower buds ellipsoid, the corolla strongly exerted from the calyx when very young. Calyx campanulate, spreading, the tube 5–7 mm, the lobes ca. 2 × 4 mm, rounded, the tips apiculate, minutely papillate on the thickened margins. Corolla 4–6 cm in diameter, spreading at anthesis, thick and fleshy, blue to violet, deeply stellate, lobed ca. 3/4 of the way to the base, the lobes 1.2–2 × 0.3–0.6 cm, deltate to triangular, glabrous adaxially, mostly glabrous abaxially, the tips deeply cucullate, minutely papillate at the tips and margins. Stamens equal, to 12 mm long; filaments ca. 2 mm long, glabrous; anthers ca. 10 × 1 mm, ellipsoid, yellow, poricidal at the tips, the pores lengthening to slits with age. Ovary glabrous;



FIG. 7. Representative specimen of *Solanum cobanense* from Guatemala (Förther et al. 10950, BM). Reproduced with permission of the Natural History Museum, London.

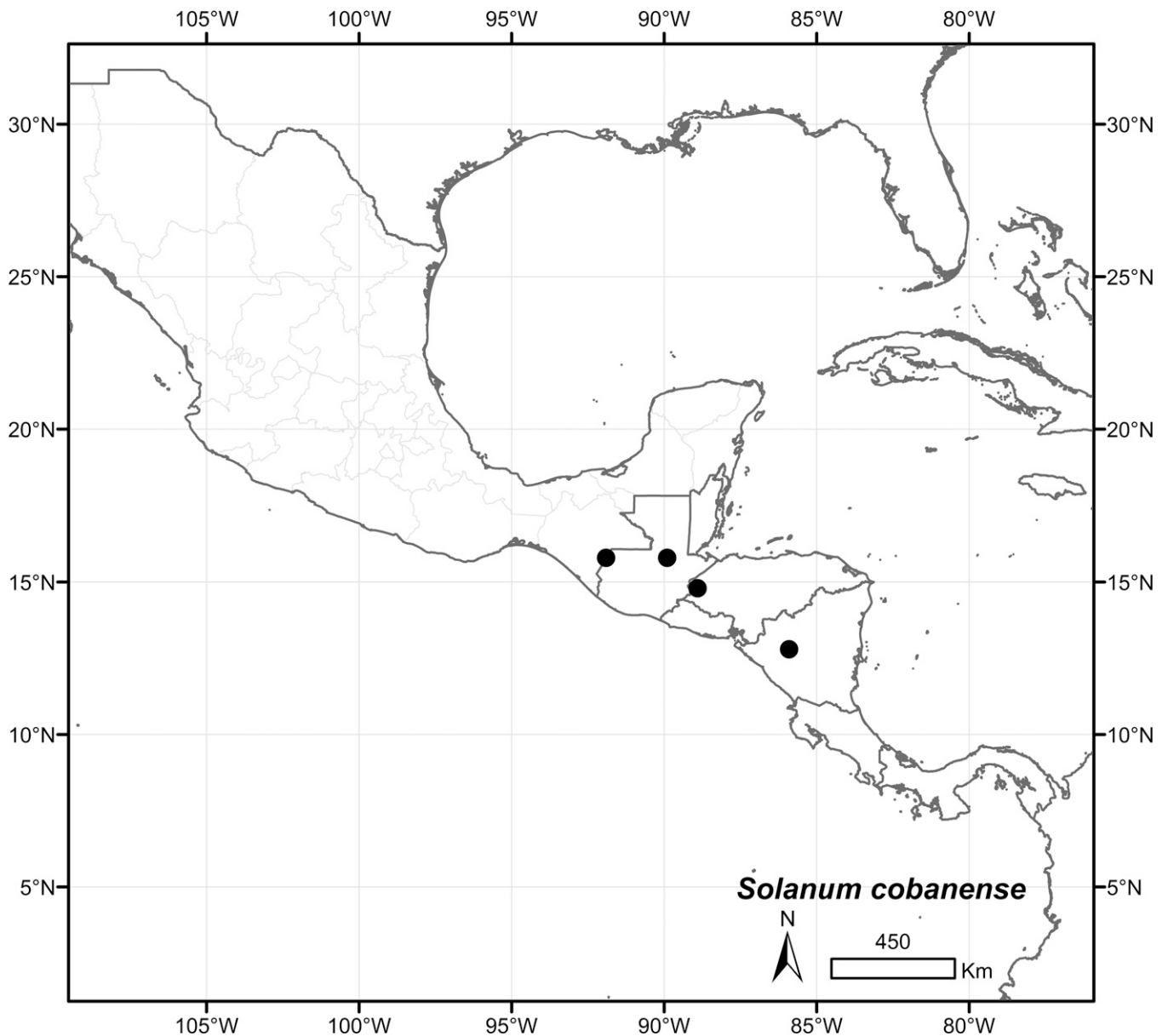


FIG. 8. Distribution of *Solanum cobanense*.

style in long-styled (?) flowers ca. 6 mm long; stigma clavate and somewhat bilobed. Fruit a globose or apically pointed ("turnip-shaped" fide Steyermark 42873) berry ca. 3.5 × 4 cm, green, glabrous with rugose surface when dry, the flesh white. Seeds < 30 per berry, ca. 4 × 5 mm, strongly flattened, light brown, the surface foveolate. Figs. 1C–D, 7.

Distribution and Habitat—*Solanum cobanense* (Fig. 8) occurs in the cloud forests of Honduras (Depts. of Lempira, Comayagua), Nicaragua (Dept. of Estelí), and Guatemala (Depts. of Alta Verapaz, Huehuetenango) at elevations from 900–2,550 m.

Phenology—*Solanum cobanense* is most commonly collected in flower from March to May, and fruiting specimens have been collected from October to January.

Preliminary Conservation Status (IUCN 2014)—Vulnerable (VU); EOO 6,668 km² (LC); AOO 28 km² (EN); 8 localities. *Solanum cobanense* would merit a status of endangered based on the AOO, but given that it is a canopy liana, it is likely that it is overlooked by many general collectors.

Solanum cobanense differs from all species of *Solanum* section *Aculeigerum* except *S. triunfense* by its woody canopy liana habit, coriaceous leaves, and large, fleshy flowers (4–6 cm in diameter) with stamens and anthers of equal size (Fig. 1C). Some specimens of *S. wendlandii* have simple leaves and might be confused with *S. cobanense*, but the rotate flowers of *S. wendlandii* with unequal anthers are distinctive.

Solanum cobanense differs from *S. triunfense*, with which it is nearly sympatric, in its regular calyx lobes that do not completely enclose the bud at late stages, the completely glabrous stems and new growth, and the acute, rather than attenuate, leaf bases. The flowers of *S. cobanense* are more deeply stellate than those of *S. triunfense*, but this character can be difficult to assess in herbarium sheets where flowers are collected at different stages of development.

Specimens examined—GUATEMALA. Alta Verapaz: Sierra de Chamá, Montaña Yalijux, Finca Chelem-há, Aufsteig vom Tal des Riachuelo Yalijux [15°23'09"N - 90°03'45"W] zum nördlichen Bergkamm [15°23'32"N - 90°04'12"W], ca. 15 km Luftlinie NE von Tucurú, 27 Mar 2001 (fl), Förther

et al. 10950 (BM); Pansamala, May 1887 (fl), *von Türckheim 746* (US). Huehuetenango: Nentón, Nuevo San José Frontera, along trail to Laguna Yolnojal (=Laguna Brava), 16°03'N, 91°33'W, 900–1,100 m, 6 Mar 2009 (fl), *Christenhusz et al.* 5584 (BM, NY). Zacapa: Sierra de Las Minas, between Cerro de Monos and upper slopes of Monte Virgen, 6,562–8530 ft., 17 Jan 1932 (fr), *Steyermark 42873* (F, NY).

HONDURAS. Comayagua: Campo Naranja, trail from Gracias “El Mahon,” 10 km SW of Gracias, 13°32'N, 88°39'W, 2,550 m, 13 May 1992 (fl), *D’Arcy 17923* (MO). Lempira: Quebrada Naranjo, W of Campo Don Tomás, 10 km SW of Gracias, Parque Nacional de Celaque, 14°33'N, 88°40'W, 1,950 m, 29 Jan 1992 (fr), *Hawkins et al.* 140 (MO); Río Naranjo, Parque Nacional de Celaque, 14°33'N, 88°40'W, 2,100 m, 24 May 1991 (fl), *House & Andino 968* (MO); W of Campo Don Tomás, 10 km SW of Gracias, Parque Nacional de Celaque, 14°32'N, 88°40'W, 2,200 m, 11 Feb 1993 (fr), *Mejia 252* (MO).

NICARAGUA. Estelí: Salto de Estancuela, Río Estancuela, ca. 6 km S of Estelí, 13°01' N, 86°20'W, 920–1,020 m, 1 Oct 1979 (fr), *Stevens et al.* 14381 (MO).

4. *Solanum glaucescens* Zucc., *Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss.* 2: 325. 1837.—TYPE: Grown in the Munich Botanical Garden by Zuccarini from seeds collected in Mexico by Karwinsky [Wilhelm Friedrich Karwinsky von Karwin], 1835, *Anonymous s.n.* (neotype, designated here: M [M0124264, Morton neg. 8691]; isoneotype: BR [BR0000008366221]).

Solanum hamatile Brandegee, *Univ. Calif. Publ. Bot.* 6: 192. 1915.—TYPE: MEXICO. Oaxaca: Río San Gerónimo, Jul 1914, *C. Purpus 7164* [“6164” in the protologue] (holotype: UC [UC175042]; isotypes: BM [BM000514922], F [F-424575], MO [MO-555119], NY [NY00138991], US [US-467485]).

Solanum oaxacanum Dunal, *Prodr.* [A. P. de Candolle] 13(1): 204. 1852.—TYPE: MEXICO. Oaxaca: Tehuantepec, Aug, *G. Andrieux 189* (holotype: G-DC [G00154874, F neg. 6832, IDC microfiche 800–61.2078:I.6]; isotypes: K [K000063703, K000195650], W [W0003308]).

Solanum sagraanum A. Rich., *Hist. Fis. Cuba* 11: 124. 1850, as “*sagraeanum*”. *Solanum lanceifolium* Jacq. var. *sagraanum* (A. Rich.) M. Gómez, *Anal. Hist. Nat. Madrid* 23: 268. 1894, as “*sagraeanum*”—TYPE: CUBA. Sin. loc., *R. De la Sagra s.n.* (lectotype: designated here: P [P00370903]; isolectotypes: F, K [K000449492], P [P00371124, P00371122, P00371123, P00445150], W).

Woody vine or scandent shrub 2–5 m long, the stems 0.25–0.6 cm in diameter, usually very sparsely prickly; internodes 1–5 cm long, glabrous, with paired prickles at base of each petiole, these 2–8 mm long, stout, recurved. Sympodial units plurifoliate, not geminate. Leaves deciduous in the dry season, simple, the blades 3.5–9 × 1.5–5.5 cm, 1.6–2.3 times as long as wide, narrowly oblong to ovate, chartaceous, glabrous adaxially and abaxially, often armed abaxially on midrib with recurved prickles; major lateral veins 3–6 on each side; base cuneate to decurrent; margin entire; apex acuminate; petioles 1–4 cm, glabrous, often prickly. Inflorescences 7–10 × 15–20 cm, terminal or lateral, unbranched or few-branched, with 5–12 flowers, the axes glabrous, not prickly; peduncle 1–2 cm; rachis 2–7 cm; pedicels 5–10 mm and slender at anthesis, articulated at the base; fruiting pedicels elongating to 3–4 cm and becoming woody. Flower buds ellipsoid, the corolla exerted from the calyx tube long before anthesis. Calyx campanulate, spreading, the tube 2–4 mm, nearly entire with five shallowly subcaudate, broadly deltate, acuminate lobes, glabrous except for the

puberulent tips. Corolla 2–4 cm in diameter, spreading at anthesis, pale yellow to yellow-green, membranous, deeply stellate, lobed nearly to the base, the lobes ca. 1.5 × 0.5 cm, lanceolate to broadly deltate, acute at apices, glabrous abaxially, glabrous adaxially except puberulent at tips. Stamens 10–15 mm long; filaments unequal, with four 1.5–2 mm long, the fifth 3.5–4.5 mm long, glabrous; anthers nearly equal, 6–9 × 1.5–2 mm, the one on the longer filament slightly larger, slightly tapering, connivent, white to yellowish-orange, poricidal at the tips, the pores lengthening to slits with age. Ovary glabrous; style in long-styled flowers ca. 15 mm long, straight, glabrous in short-styled flowers ca. 2 mm long; stigma truncate. Fruit a globose berry, ca. 3.5 cm in diameter, mottled dark green and light green when immature, turning orange when mature with orange-red pulp, the pericarp glabrous, rugose when dry. Seeds > 50 per berry, 4–5 × 3–5 mm, flattened-reniform to somewhat ovoid, light brown, the surfaces minutely pitted, the testal cells pentagonal in shape, the lateral cell walls elongate and the seed appearing hairy when outer testal walls break down. Fig. 9.

Distribution and Habitat (Fig. 10)—Endemic to southern Mexico (States of Chiapas, Guerrero, Oaxaca, and Puebla) in deciduous and semi-deciduous forests; 10–1,400 m.

Phenology—*Solanum glaucescens* appears to flower and fruit at the same time; flowering specimens are most commonly collected from April to July and fruiting specimens from July to January.

Common names—Mexico. Puebla: “cuatomate” (*Huerta Z. & Huerta Z. 1*); Oaxaca: “zarza” (*Elorsa 301*).

Preliminary Conservation Status (IUCN 2014)—Least Concern (LC); EOO 221,062 km² (LC); AOO 324 km² (EN); 95 localities. *Solanum glaucescens* is known from a large range, and is relatively commonly collected within it.

Solanum glaucescens differs from other members of section *Aculeigerum* by the presence of paired recurved prickles flanking the petiole base (Fig. 9). These appear stipular, but stipules are absent in the Solanaceae, and these are prickles like those found on the rest of the plant. The similar situation occurs in the unrelated spiny solanum species *S. microphyllum* (Lam.) Dunal of the West Indies (Knapp 2009). *Solanum glaucescens* differs from *S. bicornis*, with which it is partly sympatric, in its widely spaced leaves (not clustered as in *S. bicornis*), smaller yellowish green rather than white flowers, and in its glabrous leaf undersides. *Solanum glaucescens* is usually a more delicate plant than *S. bicornis*. Trichomes, if present, on all parts of *S. glaucescens* are small and unicellular, not the uniseriate trichomes with elongate basal cells of *S. bicornis*.

Zuccarini (1837) mentions no herbarium specimens in the protologue of *S. glaucescens*, and states only “Crescit in imperio mexicano, unde semina misit clar. de Karwinski. Floret nobis caldariis Augusto, Septembri (v.v.)”, although the herbarium of the Munich garden is mentioned in the title of his article. The indication “(v.v.)” indicates he saw a living plant, from which the extant herbarium specimens were presumably made. We therefore designate the sheet in the Munich herbarium (M0124264) taken from plants cultivated there in 1835 as the neotype of *S. glaucescens*; the sheet in BR labelled as coming from “h. Mon.” (garden [hort.] or herbarium [herb.] of Munich) with no date is a probably an isoneotype.

The epithet *sagraanum* honoring Ramón De la Sagra was originally spelled *sagraeanum*, a correctable orthographic error following Art. 60 Rec. 60C.1of the *Code* (McNeill et al. 2012).

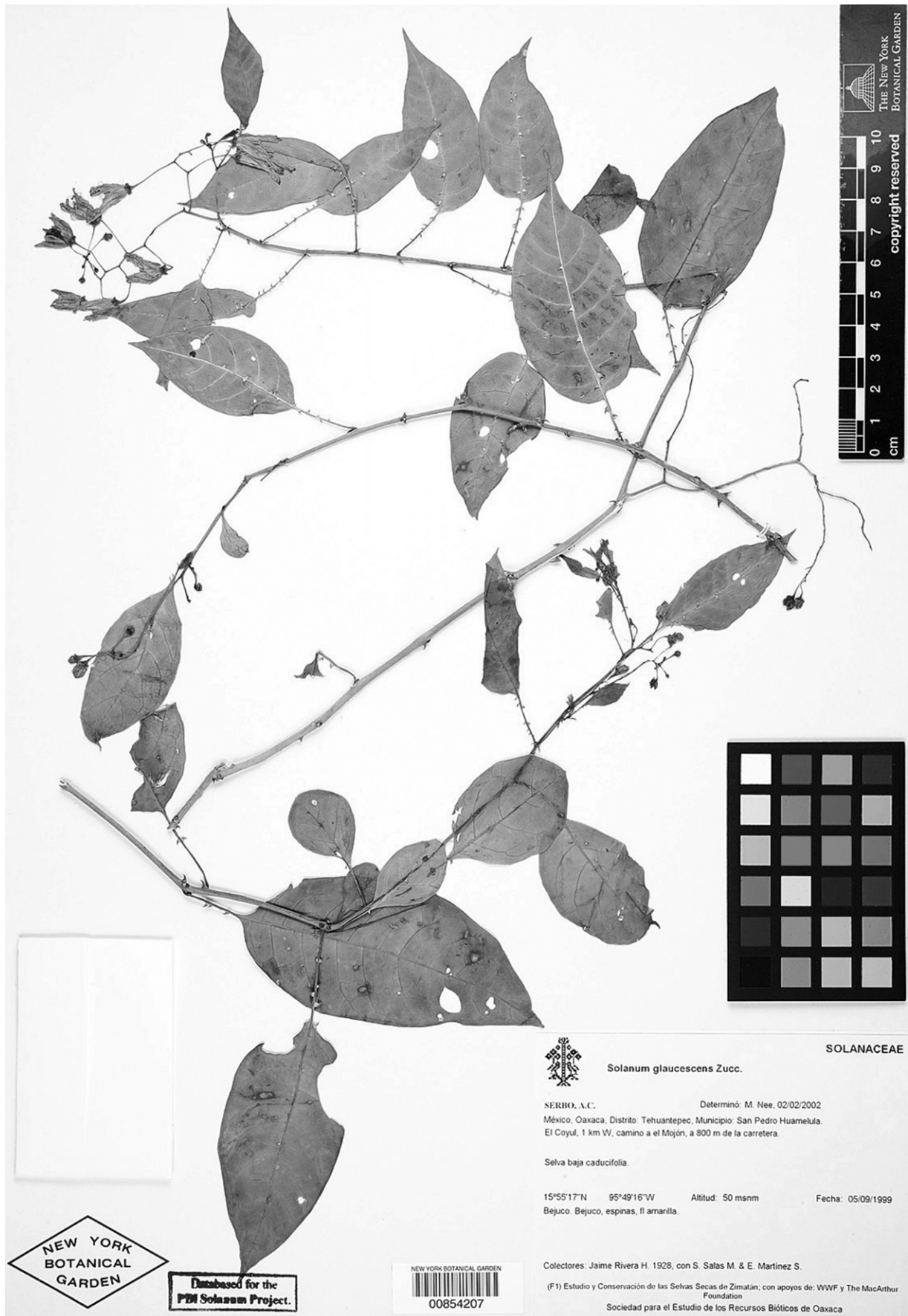


FIG. 9. Representative specimen of *Solanum glaucescens* from Mexico (J. Rivera H. et al. 1928, NY). Reproduced with permission of the New York Botanical Garden, Bronx, NY.

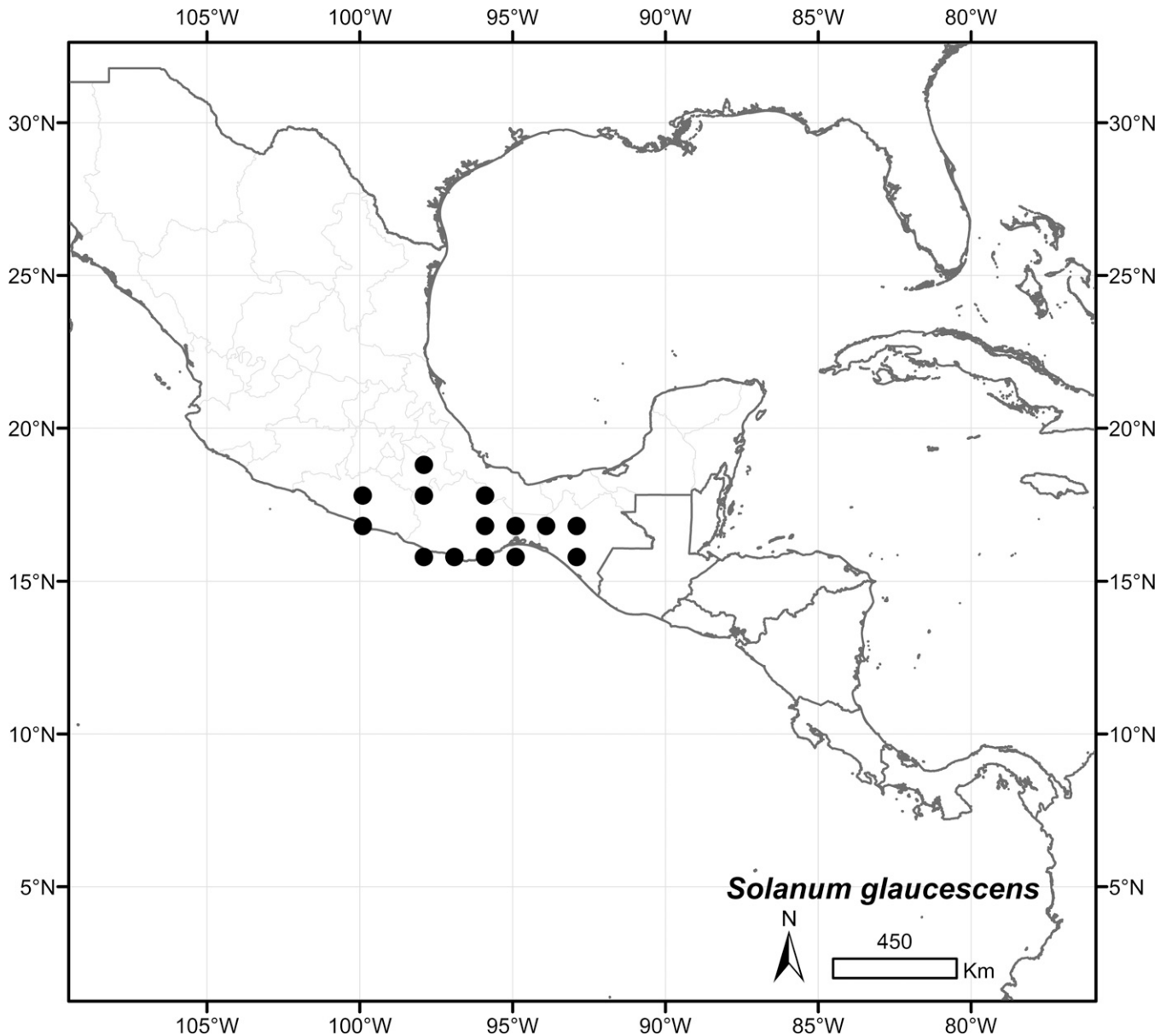


FIG. 10. Distribution of *Solanum glaucescens*.

The illustration of *Solanum sagranum* in the plates (De la Sagra 1855: pl. 62) accompanying the botany volumes of De la Sagra's *Historia física, política y natural de la isla de Cuba* published five years after the protologue (Richard 1850) is clearly *S. glaucescens*. The paired recurved prickles at the base of the petioles are distinctly shown, but the heterandrous flowers clearly described in the protologue ("Uno de sus estambres es constantemente mayor que los otros cuatro." [One of the stamens is always longer than the other four]; Richard 1850: 124) are not; specimens at P and K collected by De la Sagra (see below) have heterandrous flowers and paired prickles. No other collections of *S. glaucescens* from Cuba have been seen, and its occurrence on Cuba has not been reconfirmed. The type of *Solanum sagranum* may represent a cultivated collection and/or a mis-labeling of the collecting locality. Several duplicates of a collection attributed to Ramón De la Sagra exist in the Paris herbarium. We have selected that labeled as "Herbarium Richard" and "*Solanum punctulatum* nob.

Sagræanum nob." (P00370903) as the lectotype as it was clearly part of A. Richard's herbarium and is indicated as a new species on the sheet ([*Solanum punctulatum* new *Sagræanum* new]; Richard clearly changed his mind about the name for this taxon and crossed his original epithet, *punctulatum*, out). Other sheets attributed to De la Sagra (see synonymy) appear to be duplicates and are here recognized as isoelectotypes.

Representative Specimens Examined—MEXICO. Chiapas: Mpio. Jiquipilas, 8 miles E of Cintalapa, along hwy. 190, 2,200 ft, 12 Jun 1965 (fl), *Breedlove* 10304 (F, US), 10317 (F, TEX, US); Mpio. Chiapa de Corzo, at the Río Grijalva, 10 km W of Chiapa de Corzo, Mex. Hwy. 190, 500 m, 22 Jul 1972 (fl), *Breedlove* 26219 (CAS, MEXU, MO); Mpio. Villa Corzo, 56 km S of Mex. Hwy. 190 near junction to Jérico on road to Nueva Concordia, 700 m, 10 Sep 1974 (fl), *Breedlove* 37464 (MEXU, MO); Mpio. Cintalapa, NW of Cintalapa along road to Colonia Francisco I. Madero, 560 m, 30 Dec 1980 (fr), *Breedlove* 48993 (MEXU); Mpio. Acala, along Río Grijalva, 20 km N of Acala, 550 m, 30 Jul 1981 (fl), *Breedlove* 51893 (CAS, DUKE, MEXU, MO, TEX); Mpio. Jiquipila, Cerro San Lorenzo o La Chumpa, 580 m, 8 Jul 1998 (fl), *Farrera* S. 1004

(MEXU; Mpio. Venustiano Carranza, along the road from Acala to Venustiano Carranza 15 km SE of Acala, 3 May 1966, *Laughlin 860* (US); San Nicolás, cerca de Cupia, SE de Tuxtla Gutiérrez, 500 m, 19 Feb 1950 (fl,fr), *Miranda 6061* (MEXU-3 sheets); Mpio. Chiapa de Corzo, carretera a La Concordia, cerca del Rancho Chuquiyá, 23 Oct 1991 (fl), *Palacios E. 2004* (MEXU). Guerrero: 3 km NW of Zumpango, 1,000 m, 25 May 1973 (fl), *Hansen et al. 1503* (MEXU, US, WIS); 2.5 km W de Puerto Márquez, 10 Aug 1977 (fl,fr), *López F. 467* (MEXU, TEX); Mpio. Chiapilla, Vicente Guerrero, 6 km NW of Flores Magón, 16°25' N, 92°43' W, 475 m, 21 Dec 1985 (fr), *Nee 32311* (CORD, MO, NY, P, XAL). Oaxaca: Dto. Tlacolula, Mpio. San Pedro Totolapan, 5 km NW de Las Margaritas, 17 Jul 1987 (fl), *Aguilar S. 249* (MEXU, NY); Itepec, 11 Jan 1945 (fl), *Alexander 326* (NY); Puerto Ángel, 25 Dec 1974 (fr), *Boege 3317* (MEXU); Mpio. San Miguel Soyaltepec, Presa Miguel Alemán, Temascal, 350 m, 20 May 1987 (fl), *Calzada 9250* (MEXU); Mpio. Tehuantepec, recorrido a Cerro El Arenal, NO de Buenos Aires, 16°19'N, 95°32'W, 950 m, 28 Jun 1991 (fl), *Campos V. 3700* (MEXU); Mpio. Huatulco, camino a Barra de Boca Vieja, bajos de Coyula, 15°04'N, 96°18'W, 5 m, 31 Oct 1992 (fl), *Castillo Campos et al. 9208* (MEXU); Mpio. Huatulco, NE de playa de Cacaluta, 15°45'N, 96°10'W, 20 m, 3 Nov 1992 (fr), *Castillo Campos et al. 9352* (MEXU); Distr. Pochutla, 1 km S de la desviación a la Bahía de Santa Cruz Huatulco, 27 Jun 1982 (fl), *Cedillo Trigos & Torres 1558* (MEXU, MO); Distrito Tuquila, Chacahua, 5 m, 17 Dec 1921 (fr), *Conzatti 4486* (MEXU, US); Mex. 190, 8 mi E of Gramal, 17 Sep 1978 (fl), *D'Arcy 11993* (MEXU, MO); Mpio. Santiago Astat, Dto. Tehuantepec, Zimatán, 4.5 km S del puente, playa El Mojón, 15°48'44" N, 95°59'18" W, 21 Jun 1998 (fl), *Elorsa C. 301* (NY); Mpio. San Miguel del Puerto, Dto. Pochutla, Petatengo, 3.5 km S, Rancho Zimatán, 15°56'23" N, 96°01'33" W, 30 Jun 1998 (fl), *Elorsa C. 319* (NY); Dto. Tehuantepec, Mpio. Santiago Astat, Campamento Tortuguero, 4 km SE de Barra de la Cruz, 15°50'70" N, 95°56'55" W, 10 Oct 2000 (fr), *Elorsa C. 3699* (NY); Dto. Tehuantepec, Mpio. San Pedro Huamelula, Carretera vieja a Mazcalaco, 3 km NE de Playa Grande, 15°51'24" N, 95°53'39" W, 10 Aug 2000(fr), *Elorsa C. 3374* (NY); Dto. Juchitán, Mpio. Asunción Ixtaltepec, 1 km N de Nizanda, 16°40'N, 95°02'W, 200 m, 2 Jun 1996 (fl), *Gallardo H. & Reyes D. 1149* (MEXU); Mpio. Asunción Ixtaltepec, 2.2 km SO de Nizanda, 16°38'N, 95°00'W, 200 m, 9 Jul 1995 (fl), *Gallardo H. & Pérez-García 1464* (MEXU); Dto. Juchitán, Mpio. Asunción Ixtaltepec, bosque riparia hacia el "Agua Tibia", 500 m al N de Nizanda, 16°40'N, 95°00'W, 115 m, 1 Aug 1995 (fl,fr), *Gallardo H. & Pérez-García 1562* (MEXU); Dto. Juchitán, Mpio. Asunción Ixtaltepec, camino hacia el cerro de la "Piedra Azul", cercano a Nizanda, 16°39'N, 95°00'W, 180 m, 22 Jul 1996 (fl,fr), *Gallardo H. & Pérez-García 1876* (MEXU, MO); Agua Blanco, 21 mi S of Mitla road junction along hwy, 16°45'N, 96°22'W, 3,400 ft, 21 Oct 1967 (fl), *Gentry 21361C* (A, MEXU); Mpio. San Pedro Pochutla, 15 km E de San Pedro Pochutla, 5 Oct 1980 (fl), *González O. 595* (MEXU); 0.5 km E of Tehuantepec, 50 m or less, 30 Jun 1958 (fl), *King 279* (MEXU, TEX, WIS); La Ventosa, 7 km E of Salina Cruz, 50 m or less, 3 Jul 1959 (fl), *King 1277* (NY, TEX, UC, US); 3–4 km W of Ixtaltepec, ca. 50 m, 10 Jul 1959 (fl), *King 1519* (NY, TEX, UC, US); Mpio. Huatulco, Dto. Pochutla, Bahía de Tangolunda, 11 Oct 1984 (fr), *López G. 156* (NY); Tehuantepec, 15 Oct 1953 (fl), *MacDougall s.n.* (MEXU); Mpio. Tehuantepec, Dto. Tehuantepec, El Limón—El Milagrito, El Limón está a 17 km al O de Tehuantepec entrando por Hierba Santa, 8 Jul 1985 (fl), *Martínez R. 23* (MEXU); Dto. Tehuantepec, Mpio. Salina Cruz, Carnero, entrando por Rincón Bamba, carr. a Pochutla, O de Salina Cruz, 23 Jun 1986 (fl), *Martínez R. 584* (MEXU); Dto. Yautepec, Mpio. Santa María Ecatepec, 15 km SO de La Reforma camino a Santa María Ecatepec, 16°20'N, 95°50'W, 15 Jul 1988 (fl), *Martínez R. 1470* (MEXU, MO); Distr. Tehuantepec, Mpio. San Pedro Huamelula, 2 km N de Sta. María Huamelula, 15°59'N, 95°42'W, 15 Aug 1988 (fl), *Martínez R. 1714* (MEXU, MO); Mpio. Asunción Ixtaltepec, Dto. Juchitán, alrededores del vía del tren Transistmico, Nizanda, 16°40'N, 95°01'W, 110 m, 15 Sep 1995 (fr), *Meave del Castillo & Pérez-García 1925* (MEXU); Dto. Juchitán, Mpio. Asunción Ixtaltepec, camino hacia el EVX 1, cercano a Nizanda, 16°39'N, 95°00'W, 180 m, 16 Sep 1995 (fr), *Meave del Castillo & Pérez-García 1945* (MEXU); Dist. Yautepec, Mpio. Nejapa, vic. Camarón, 13 km NW of San Juan la Jarcia, along hwy. Mex. 190, 16°34' N, 96°02' W, 700 m, 19 Dec 1985 (fr), *Nee & Andres 32280* (G, K, MO, NY, TEX, XAL); Dto. Pochutla, Mpio. San Miguel del Puerto, Zimatán, 3 km LR N del puente, por el Chorro, 15°52'31" N, 96°00'17" W, 27 Aug 1999, *Rivera H. et al. 1818* (NY); 70 km (by road) SE of Pinotepa Nacional on road to Puerto Escondido, 16°10'N, 97°40'W, 150 m, 23 Jul 1965 (fl), *Roe et al. 523* (WIS); Dto. Tehuantepec, Mpio. San Pedro Huamelula, Mascalco, N de la laguna, 2.5 km S de la carretera costera, 15°52'20" N, 95°52'22" W, 24 Jul 1998 (fr), *Salas M. et al. 1896* (NY); Dto. Tehuantepec, Mpio. Santiago Astat, Barra de la Cruz, 4 km NE LR, ladera arriba del puente del Curuelo, 15°52' N, 95°57'15" W, 15 Sep 1999 (fr), *Salas M. et al. 2321* (NY); 1.2 km S de la

desviación a Bahía de Santa Cruz, la desviación a 15.2 km SW de Copalita, 150 m, 30 Jul 1984 (fl), *Torres C. & Martínez 5763* (MEXU); Distr. Tehuantepec, Arroyo de las Minas, W de El Limón, entrando por la desv. a Buenos Aires, 17 Jun 1985 (fl), *Torres C. & García M. 6849* (MEXU); Distr. Yautepec, 5.5 km SW de la entrada a Santa María Ecatepec, SW de la Reforma, 19 Jun 1985 (fl), *Torres C. & M. Laubin 6888* (MEXU, MO, NY); Distr. Pochutla, Mpio. Santa Cruz Huatulco, 6 km hacia el E de Bahía de Santa Cruz, hacia Chahue, 30 m, 15 Jun 1986 (fl), *Torres C. & O. Téllez 8405* (MEXU). Puebla: Mpio. Izúcar de Matamoros, Paraje La Poza de Malpaso, Los Amates, 1,240 m, 18 Jun 1998 (fl), *Gútzar Nolasco & Herrera 4023* (MEXU); Mpio. Tocomatlán, Tezoquipán, 1,000 m, Aug 1988 (fl, fr), *Huerta Z. & Huerta Z. 1* (MEXU); 12 miles E of jct. of hwy. 190 and 160 out of Izúcar Matamoros, 3400 ft, 2 Aug 1975 (imm fr), *Torke et al. 364* (MO).

5. *SOLANUM PACHYANDRUM* Bitter, Repert. Spec. Nov. Regni Veg. 13: 88. 1914.—TYPE: ECUADOR. Manabí: El Recreo ["El Keereo"], 200 m, 6 Mar 1897, *H. von Eggers 15730* (lectotype, designated here: US [US-1324689, barcode US00027720]; isolectotypes: B, †destroyed [F neg. 2672], F [F-143295], K [K000788525], L [L-897313–55], LE, M [M0124267], P [P00367219]).

Woody vine to 5 + m long, the stems 0.4–0.7 cm in diameter, densely prickly; internodes (2–)4–9 cm long, glabrous; prickles 0.5–1.2 mm long, stout, recurved. Sympodial units plurifoliate, not geminate. Leaves pinnatifid to deeply pinnatifid with 4–6 pairs of lobes, the blades in outline 12–19(–27) × 5–10(–17) cm, oblong, chartaceous, glabrous on both surfaces, the midrib with recurved prickles abaxially; major lateral veins 4–6 on each side, corresponding to the lobes; petioles 2–3 cm, glabrous, often armed with recurved prickles; leaflets 2–4 × ca. 1 cm, widest at the middle or in the basal third, basally decurrent on the midrib and with a wing of tissue to 3 mm wide connecting all leaflets to some degree, not petiolulate; base rounded to acute; margins deeply pinnatifid, entire, the terminal leaflet confluent with lateral leaflets; apex acuminate to rounded. Inflorescences 12–20 cm long and wide, lateral or terminal, several times branched, with 5–20 flowers, the axes glabrous or minutely papillate, densely prickly; peduncle 5–8 cm; rachis 4–8 cm; pedicels 4–5 mm, prickly, slender at anthesis, elongating in fruit to ca. 2.5 × 0.2 cm and becoming subwoody, articulated at the base. Flower buds ellipsoid to oblong, the corolla soon exerted from the calyx tube. Calyx campanulate, spreading, the tube 1–2 mm, the lobes ca. 3 × 2 mm, deltate, glabrous, the central part a protruding green knob, this more prominent in fresh plants. Corolla to 3.5 cm in diameter, spreading at anthesis, white, fleshy, stellate, lobed 1/2–2/3 of the way to the base, the lobes 1–1.2 × 0.5–0.6 cm, narrowly triangular, acute to acuminate at apices, glabrous on both surfaces, minutely papillate at the tips. Stamens equal in size, 6–8 mm long; filaments ca. 2 mm long, glabrous; anthers 5–6 × 2.5–3 mm, ellipsoid, connivent, yellow, poricidal at the tips, the pores lengthening to slits with age. Ovary glabrous; style in long-styled flowers ca. 10 mm long, straight, glabrous, in short-styled flowers ca. 5 mm long; stigma truncate. Fruit a globose berry, 3–5 cm in diameter, purple when immature and yellow when mature (*Rodríguez et al. 1607*), the pericarp glabrous. Seeds ca. 100 per berry, ca. 2 × 4 mm, strongly flattened, light brown, the surfaces minutely pitted, the testal cells rectangular. Figs. 2A–C, 11.

Distribution and Habitat (Fig. 12)—*Solanum pachyandrum* occurs on the western slopes of the Andes and in the Huancabamba Depression of Ecuador (Prov. Manabí) and Peru (Depts. of Cajamarca, La Libertad, and Tumbes) in moist forests on slopes; 200–1,000 m. The Ecuadorian type collection is somewhat disjunct from the rest of the species distribution.

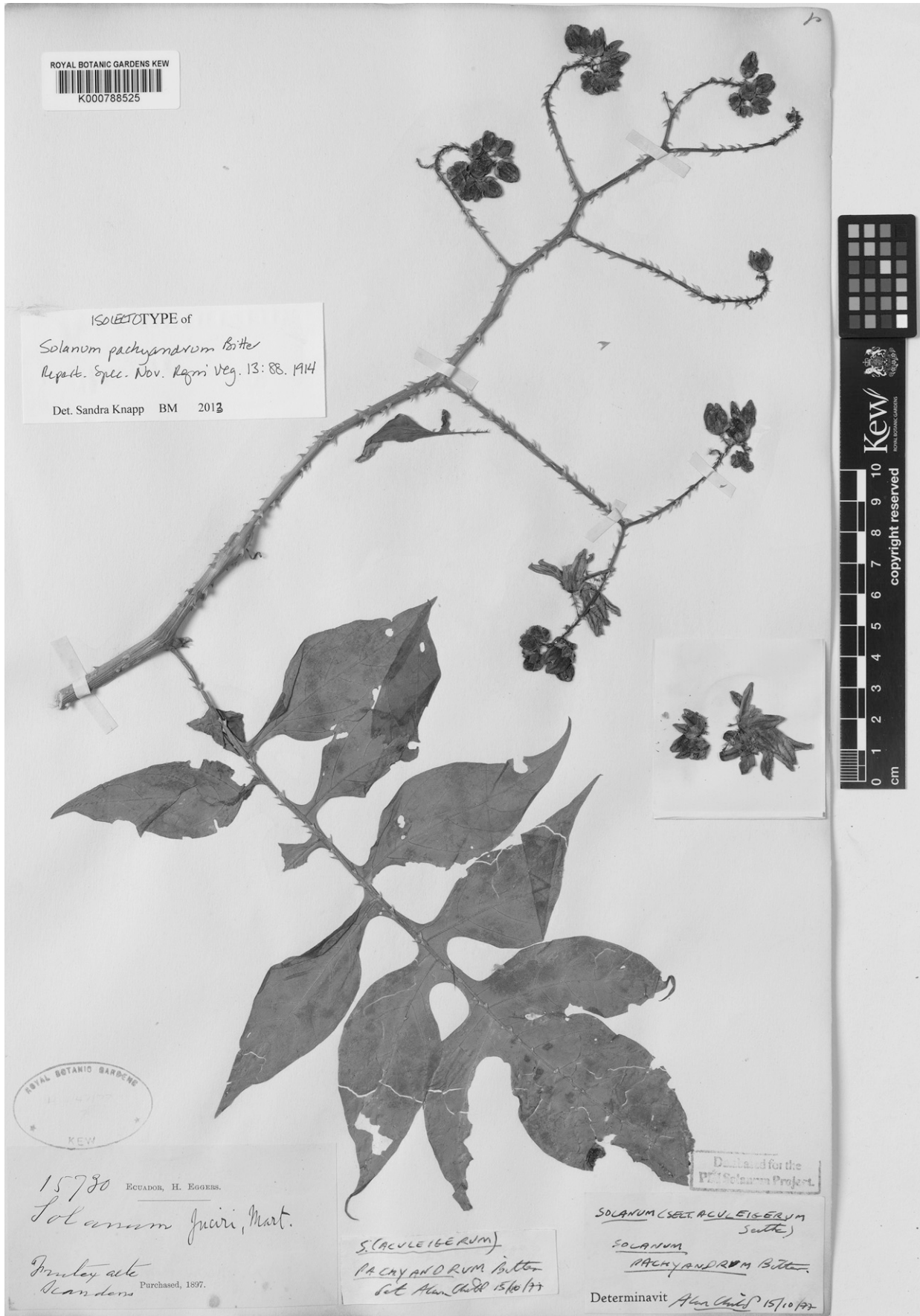


FIG. 11. Isolectotype specimen of *Solanum pachyandrum* from Ecuador (H. Eggers 15730, K). © Trustees of the Royal Botanic Gardens, Kew. Reproduced with permission of the Royal Botanic Gardens, Kew.

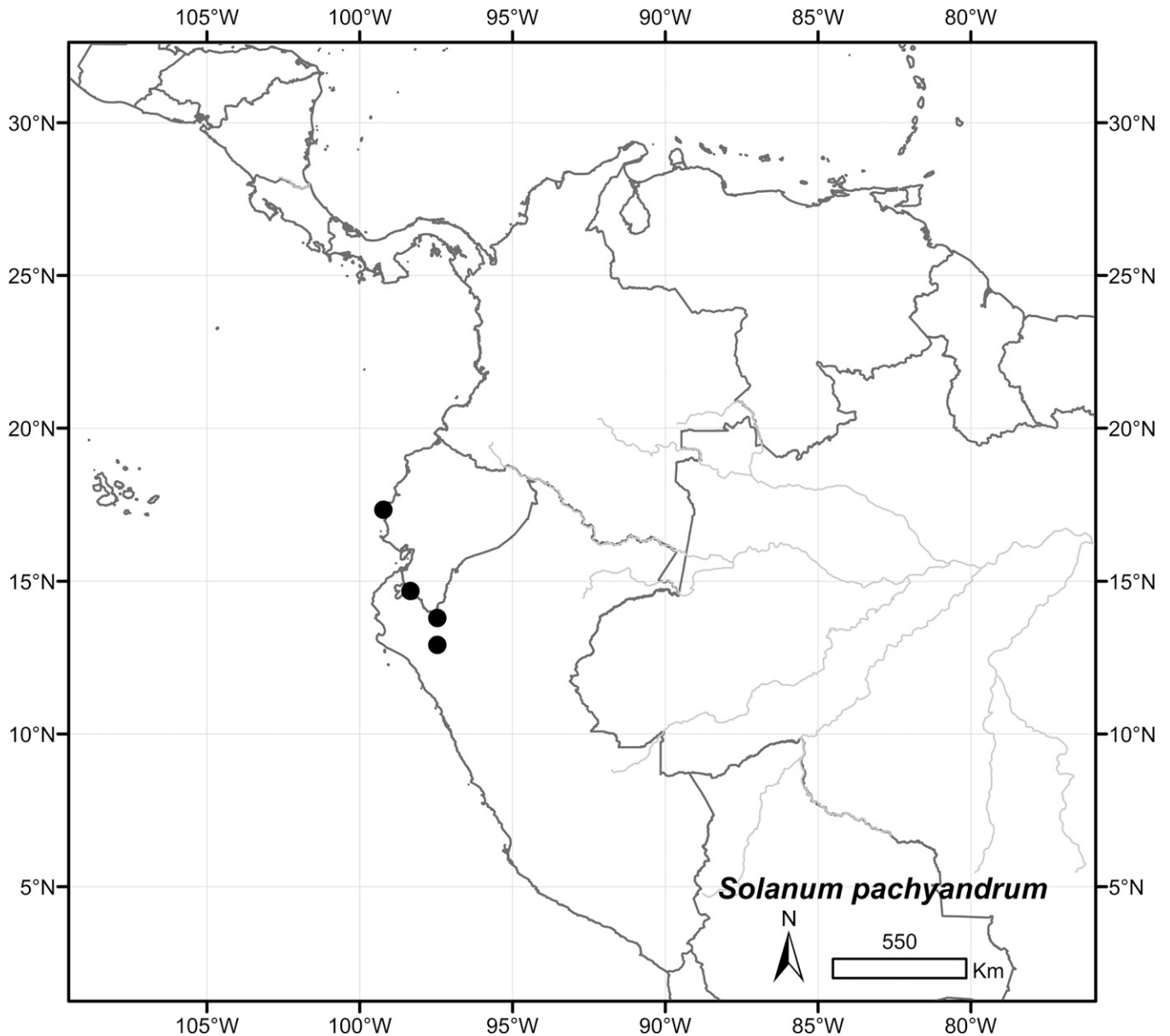


FIG. 12. Distribution of *Solanum pachyandrum*.

Phenology—*Solanum pachyandrum* appears to flower and fruit at the same time; flowering and fruiting specimens have been collected from April to September.

Common Names—Peru. Cajamarca: “bombona” (Rodríguez *et al.* 1607).

Preliminary Conservation Status (IUCN 2014)—Near Threatened (NT); EOO 30,173 km² (LC); AOO 24 km² (EN); 7 localities. Although the EOO would not place *S. pachyandrum* into one of the threatened categories (CR, EN or VU) the single point that expands the range is derived from the type collection. *Solanum pachyandrum* has not been collected again in coastal Ecuador since. If that point is removed from the analysis the threat status is EN. Searches for *S. pachyandrum* in southern Ecuador are a priority.

Solanum pachyandrum differs from all other species in section *Aculeigerum* by the presence of stout armed prickles on its pedicels and non-tapering (ellipsoid) anthers. Additionally, *S. pachyandrum* is restricted to the western lowlands of

Ecuador and northwestern Peru. This species is geographically isolated from all other members of the section. The large juicy fruits are eaten by local people and are considered a great treat by children (J. Campos, pers. comm.).

No herbarium was cited in the protologue of *S. pachyandrum*. We have therefore chosen the best preserved of the duplicates of Eggers 15730 as the lectotype (US00027720). It is often assumed that when Bitter cited no herbarium he was citing a specimen in Berlin; no internal evidence to that effect is to be found in the publication, so we are including a reference to the B sheet photographed by MacBride among the isolectotypes.

Specimens Examined—PERU. Cajamarca: Prov. San Ignacio, Distrito Huarango, San Martín, 5°16′S, 78°43′W, 900 m, 18 May 1996 (fl,fr), Campos *et al.* 2806 (MO, MOL, NY, USM); Prov. San Ignacio, San Martín del Chinchipe, 5°19′16″S, 78°41′05″W, 1,000 m, 15 Sep 1999 (fr), Flores *et al.* 160 (BM, NY, USM-2 sheets); Prov. Jaén, Huayhuaya–Peña Blanca (Tamborapa–Tabaconas), 890 m, 1 Aug 1994 (fr), Leiva G. *et al.* 1231 (HAO+[destroyed], NY); Prov. San Ignacio, distrito Namballe, Namballe, arriba del margen derecho del Río Namballe, 4°58′S, 79°10′W, 760–800 m, 6 Jul 1997 (fl,fr), Rodríguez *et al.* 1607 (HAO+[destroyed], HUT, MO, NY,

USM); Prov. Cutervo, on road from La Capilla to Jaen, in Laguna, km 1575, 1,126 m, 9°09'57.77"S, 78°51'14"W, 14 Apr 2013 (fl, fr), *Särkinen et al.* 4546 (BM, E, USM). Tumbes: Prov. Zarumilla, entre puesto de vigilancia El Caucho–Campoverde, 700 m, 9 Jul 1992 (fr), *Díaz et al.* 4739 (HUT, MO, USM).

6. *Solanum refractum* Hook. & Arn., Bot. Beechey Voy. 304. 1838.—TYPE: MEXICO. Nayarit: Tepic, *F. Beechey s.n.* (holotype: K [K000195651, MICH neg. 751]).

Solanum aculeolatum M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 12: 143. 1845.—TYPE: MEXICO. Oaxaca: “Près la Mer Pacifique”, 1840, *H. G. Galeotti 1170* (lectotype, designated here: BR [BR0000005538768, BH neg. 2394]; isolectotype: P [P00445058]).

Solanum molinarum J. L. Gentry, Phytologia 26: 276. 1973.—TYPE: HONDURAS. Comayagua: edge of Humuya River bank, vicinity El Edén, Comayagua Valley, 500 m, 28 Sep 1969, *A. Molina R. & A. R. Molina 24532* (lectotype, designated here: F [F-1724479]; isolectotypes: EAP [EAP70442], F [F-1964597, F-1724480, F-1964595], NY [NY00139010]).

Woody or subwoody vine to 15 m long, the stems 0.2–0.3 cm in diameter, prickly; internodes (2–)4–10 cm long, glabrous or puberulent with simple hairs ca. 0.2 mm long; prickles 0.5–1.5 mm long, stout, recurved. Sympodial units plurifoliate, not geminate. Leaves pinnatifid to deeply pinnatifid, the blades in outline 6–12(–16) × 3–10(–16) cm usually ovate (rarely elliptic), widest at the base, chartaceous, glabrous adaxially and abaxially, or rarely both surfaces puberulent with minute simple papillae, often armed abaxially on midrib with recurved prickles; major lateral veins 3–5 on each side, corresponding to lobes; petioles 1–2.5(–5) cm, glabrous, often armed with recurved prickles; lobes (1.5–)3–6 × (1–)1.5–3 cm, widest at the middle of in the basal 1/3, confluent with the midrib and with a wing of tissue to 1 cm wide connecting all leaflets; base acute; margin deeply pinnatifid with 3–4 pairs of lobes, the terminal and adjacent lateral lobes broadly confluent; apex acuminate to rounded; petiolules absent, the lobes confluent with the midrib. Inflorescences 10–15 cm long and wide, terminal, several times branched, with 20–40 flowers, the axes glabrous or puberulent with minute papillae, moderately to densely prickly, occasionally with very few prickles only at the base (type specimen); peduncle 3–5(–10) cm; rachis 3–10 cm; pedicels 3–5 mm and slender at anthesis, articulated at the base; fruiting pedicels elongating to ca. 2.5 × 0.4 cm and becoming woody. Flower buds sharply pointed (turbinate), the corolla strongly exerted from the calyx tube before anthesis. Calyx campanulate, spreading, the tube 1–3 mm, the lobes ca. 1 × 1.5 mm, broadly rounded and the calyx almost truncate, glabrous, the lobe tips somewhat rounded and swollen. Corolla to 2.5 cm in diameter, spreading at anthesis, green or yellowish green, sometimes tinged with purple (*Hinton 10967* “flowers purple and yellow”), membranous, stellate, lobed to the base, the lobes 0.9–1.5 × 0.2–0.3 cm, narrowly triangular to lanceolate, acute to acuminate at apices, glabrous abaxially and adaxially. Stamens equal in size, 7–9 mm long; filaments ca. 0.5 mm long, glabrous; anthers 6–8 × 0.75–1 mm, strongly tapering, connivent, yellow, poricidal at the tips, the pores only somewhat lengthening to slits with age. Ovary glabrous; style in long-styled flowers 12–13 mm long, straight, glabrous, in short-styled flowers ca. 6 mm long; stigma truncate. Fruit a globose berry, ca. 3–5 cm in diameter, light green, the pericarp glabrous, rugose surface dry. Seeds 20–50 per

berry, ca. 3 × 5 mm, strongly flattened-reniform, light brown, the surfaces minutely pitted. Fig. 13.

Distribution and Habitat (Fig. 14)—*Solanum refractum* occurs in Mexico (States of Chiapas, Guerrero, Oaxaca), Guatemala (Depts. of Chiquimula, Zacapa, Jalapa), and Honduras (Depts. of Comayagua, La Paz) in deciduous and semi-deciduous forests at elevations from sea level to 1,100 m.

Phenology—*Solanum refractum* appears to flower and fruit at the same time throughout the year, with a small peak in flowering specimens from June to August (but this is possibly a collecting artefact) and in fruiting specimens from September to November.

Preliminary Conservation Status (IUCN 2014)—Least Concern (LC); EOO 133,321 km² (LC); AOO 112 km² (EN); 31 localities. *Solanum refractum* is widespread in the habitats where it occurs.

Solanum refractum is similar to *S. alternatopinnatum* of southeastern Brazil, Paraguay, and northern Argentina but the terminal leaflets in the latter are usually petiolulate and not broadly confluent with the uppermost pair of lateral leaflets. The leaves of *S. refractum* are occasionally puberulent with unbranched papillae on both surfaces in contrast to the consistently glabrous leaves of *S. alternatopinnatum*. The inflorescence structure, flowers, and fruits, are very similar in *S. alternatopinnatum* and *S. refractum*. *Solanum pachyandrum* of Ecuador and Peru shares consistently pinnatifid or deeply pinnatifid leaves with *S. refractum*, but differs from it in its white flowers with ellipsoid anthers; the yellow-green flowers of *S. refractum* are more delicate than those of *S. pachyandrum* and have strongly tapered rather than ellipsoid anthers. *Solanum alternatopinnatum*, *S. pachyandrum* and *S. refractum* all share a prickly inflorescence rachis, a character that can be used to differentiate these species from cultivated *S. wendlandii* with pinnately compound leaves.

Confusion over the application of the names *S. refractum* and *S. bicornis* has resulted in many specimens of *S. bicornis* being annotated in herbaria as *S. refractum* (in these cases the name *S. aculeolatum* was used for the plants here recognized as *S. refractum*). Considerable care must be exercised in using pre-2005 annotations on specimens not re-annotated for this monograph.

The type locality for *Solanum refractum* is given by Hooker and Arnott (1838: 275) on the page at the beginning of their Mexico section in the account of the Beechey voyage as: “When no habitat is mentioned, the specimens are understood to have been collected at Tepic.”

Martens and Galeotti (1845) mentioned no specific herbarium in the protologue of *S. aculeolatum*. We have selected the specimen at BR (BR0000005538768) as the lectotype because it has more copious inflorescence and leaf material than the duplicate of *Galeotti 1170* at P (P00445058); both are relatively scrappy specimens.

We have selected F-1724479 from among the many duplicates of *Molina R. & Molina 24532* as the lectotype of *S. molinarum* because it is annotated as “holotype” in J. L. Gentry’s hand, and the species name is also written by Gentry on the sheet. The other duplicate labelled “holotype” (F-1964595) has a typed species name on the label.

Representative Specimens Examined—MEXICO. Chiapas: Cintalapa de Figueroa, km 22 de la carretera Tapanatepec–Tuxtla Gutiérrez, 16°27'N, 94°05'W, 700 m, 4 Jun 1995 (fl), *Panero et al.* 5750 (NY). Guerrero: Atoyac, Distr. Galeano, 40 m, 25 Nov 1937 (fl), *Hinton et al.* 10967 (GH, K, LL, MEXU, NY, U, US); Mpio. Petatlán, 22 km NW de Petatlán, camino a El Camalote, 180 m, 23 Oct 1983 (fr), *Martínez S. et al.* 5116 (MEXU, NY);



FIG. 13. Holotype specimen of *Solanum refractum* from Mexico (Beechey s.n., K). © Trustees of the Royal Botanic Gardens, Kew. Reproduced with permission of the Royal Botanic Gardens, Kew.

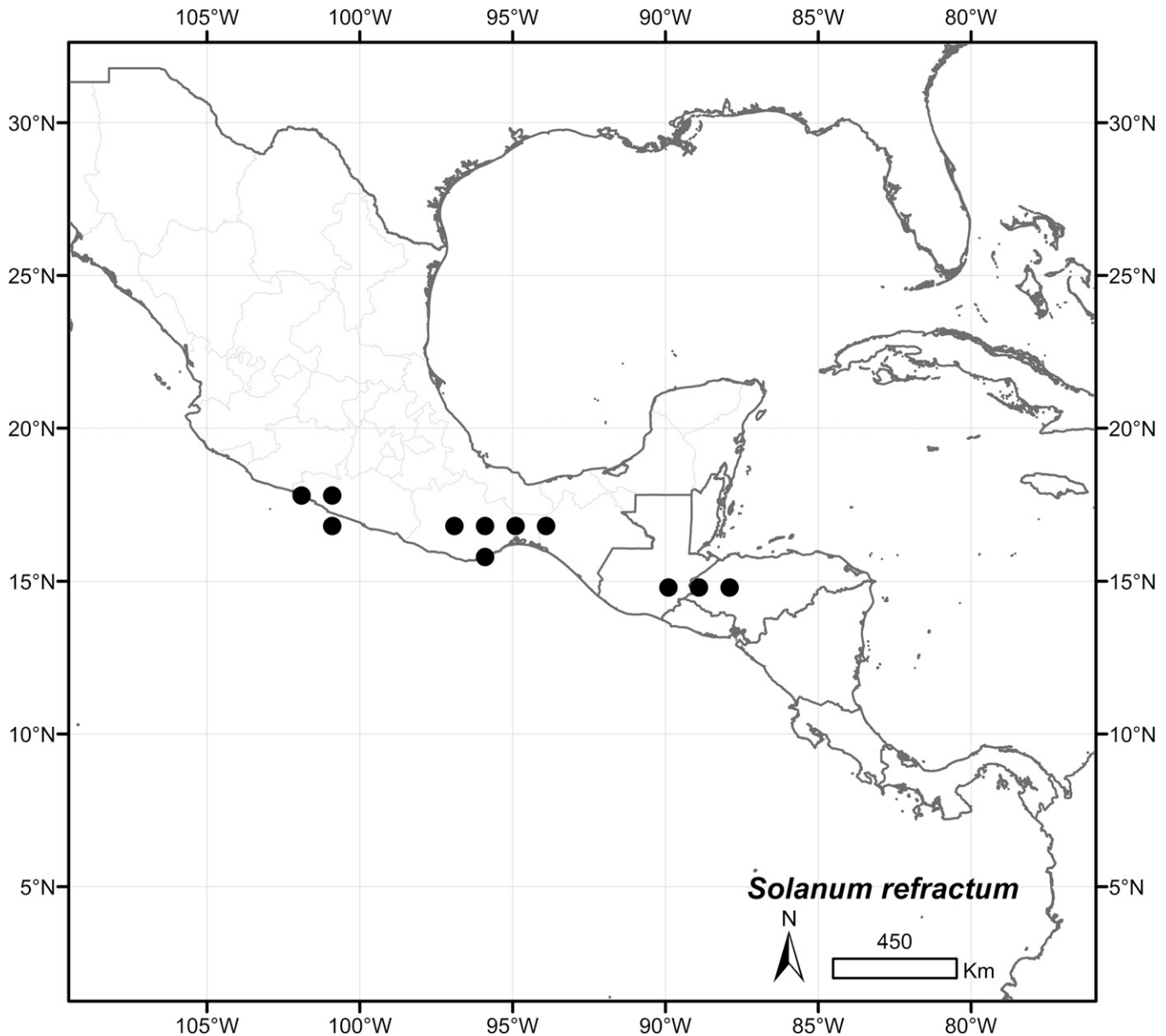


FIG. 14. Distribution of *Solanum refractum*.

15 km N de La Unión, camino a Coahuayutla, 150 m, 24 Oct 1983 (fl), *Soto N. et al.* 6026 (MEXU); Mpio. La Unión, 2 km N de La Unión, 150 m, 22 Oct 1985 (fr), *Soto N. et al.* 11284 (MEXU). Oaxaca: Mpio. Santa María Huatulco, Dto. Pochutla, 5 km al E de Santa Cruz Huatulco, 15°46' N, 96°07' W, 15 Aug 1988 (fl), *Campos V. & Cortes* 2288 (NY); Mpio. Sto Domingo Tehuantepec, Dto. Tehuantepec, Cerro El Arenal, 17°19' N, 95°30' W, 3 Sep 1991 (fr), *Campos V.* 3954 (NY); Mpio. Huatulco, NE de la playa de Cacaluta, 15°45' N, 96°10' W, 20 m, 3 Nov 1992 (fr), *Castillo Campos et al.* 9347 (MEXU); Mpio. Santiago Astata, Dto. Tehuantepec, Barra de la Cruz, 2.5 km S LR, vereda hacia la Mareña al E de la bocana del Río Zimatán, 15°49'10" N, 95°58'24" W, 17 Sep 1998 (fl), *Elorsa C.* 737 (NY); Mpio. Chivela, Dto. Juchitán, Nizanda entrando por La Pedrera rumbo a Chivela, 15 km NE de La Ventosa, 16°37' N, 95°00' W, 18 Jul 1988 (fl), *Martínez R.* 1540 (MEXU, NY); Mpio. Sta. María Ecatepec, Dto. Yautepec, Cerro San Lorenzo, 15 km O de La Reforma, 16°20' N, 95°50' W, 3 Oct 1988 (fl), *Martínez Calderón* 1900 (MEXU); Mpio. Santiago Astata, Dto. Tehuantepec, Puente Zimatán, 26 Aug 1999 (fl, fr), *Martínez S.* 32499 (NY); Mpio. San Pedro Huamelula, Dto. Tehuantepec, Tapanalá, 1.5 km NNE, 15°58'23" N, 95°43'33" W, 28 Jul 1999 (fl), *Rivera H. et al.* 1642 (NY).

GUATEMALA. Chiquimula: between Ramírez and Cumbre de Chiquimula, road between Chiquimula and Zacapa, 400–600 m, 15 Oct 1940 (fr), *Standley* 74557 (F, US). Jalapa: Jalapa, 4,450 ft, 7 Jan 1908 (fr),

Kellerman 7052 (F). Zacapa: road between Agua Blanca and Cumbre de Chiquimula, 350–500 m, 15 Oct 1940 (ster), *Standley* 74426 (F).

HONDURAS. Comayagua: Comayagua, Comayagua valley, Río Humuya, El Edén, 28 Sep 1969, *Molina R.* 24532 (NY); NW of Comayagua, 2,100 ft, 1 Aug 1962 (fl), *Webster et al.* 12723 (WIS). La Paz: 4 km O de la ciudad de La Paz, 700 m, 2 Sep 1979 (fr), *Soto Valerio* 81A (MEXU, MO). Lempira: Gualan, along Honduras Road, 20 Jun 1909 (fl), *Deam* 6375 (GH, MO, US).

7. *SOLANUM TRIUNFENSE* S. Knapp, sp. nov.—TYPE: MEXICO. Chiapas: Mpio. Jaltenango/Mapastapec, Reserva El Triunfo (Campamento/HQ 15°39' N, 92°48' W), path to Palo Gordo, 1,900 m, May 1989 (fl), *M. Heath & A. Long* MA129 (holotype: MEXU [MEXU-877597]; isotype: BM [BM001118119]).

Diagnosis—Like *S. cobanense* J. L. Gentry but differing in densely puberulent new growth and buds, long-attenuate leaf bases, calyces completely enclosing the buds until just before anthesis and tearing into irregular lobes at flowering.

Woody vine or scandent shrub to 3 + m long, the stems 0.2–0.7 cm in diameter; internodes (2–)4–10 cm long, puberulent with 0.2 mm long simple uniseriate few-celled trichomes, these occasionally furcate; prickles 0.5–1.5 mm long, stout, recurved, sometimes absent on young shoots near the inflorescence. Sympodial units plurifoliate, not geminate. Leaves simple, the blades 6–15 × 2.5–6.5 cm, elliptic, widest at the middle, chartaceous, both surfaces minutely puberulent with simple or occasionally furcate uniseriate 2–5-celled trichomes ca. 0.5 mm long, often armed abaxially on midrib with recurved prickles; major lateral veins 6–9 on each side; base acute; margin entire; apex acute; petioles 0.5–3 cm, minutely puberulent with simple uniseriate trichomes like those of the leaf surfaces, sometimes armed with recurved prickles. Inflorescences 5–10 cm long and wide, terminal, few-branched, with 10–15 flowers, the axes puberulent with simple or furcate uniseriate 2–7-celled trichomes, not prickly; peduncle 1–3 cm; rachis 1–3 cm; pedicels 17–35 mm, articulated at the base, evenly spaced 2–5 mm apart; fruiting pedicels not known. Flower buds ellipsoid, the corolla completely enclosed in the calyx until shortly before anthesis. Calyx campanulate, spreading, tearing into irregular lobes, the tube 1–3 mm, the lobes 5–8 × 4–6 mm, pubescent with simple or occasionally furcate uniseriate 2–4-celled trichomes; fruiting calyx not known. Corolla to 4.5 cm in diameter, spreading at anthesis, purple or violet, membranous or slightly fleshy, stellate, lobed 1/2 way to the base, the lobes 1–1.5 × 0.6–1 cm, broadly deltate, glabrous on both surfaces, the tips cucullate and minutely papillate abaxially. Stamens equal in size, 8–11 mm long; filaments 1–2 mm long, glabrous; anthers 7–10 × 1–1.5 mm, ellipsoid, connivent, yellow, poricidal at the tips, the pores lengthening to slits with age. Ovary glabrous; style in long-styled flowers ca. 13 mm long, straight, glabrous, in short-styled flowers ca. 3 mm long; stigma capitate. Fruit and seeds not known. Fig. 15.

Distribution and Habitat (Fig. 16)—*Solanum triumfense* is endemic to the Sierra Madre Occidental in the State of Chiapas, Mexico, in evergreen humid forests at elevations from 1,800–1,900 m. Most collections are from the El Triunfo Biosphere Reserve.

Phenology—*Solanum triumfense* has been collected in flower from February to June; fruiting specimens are not known.

Common Names—Mexico. Chiapas: “quistan” (Heath & Long MA129).

Preliminary Conservation Status (IUCN 2014)—Endangered (EN) B1,2a,b iii; EOO 493 km² (EN); AOO 16 km² (EN); 4 locations. *Solanum triumfense* is assessed as endangered based on the low extent of occurrence and area of occupancy and the threats to the habitat in the region where it occurs. It does occur in a protected area (Reserva El Triunfo, a UNESCO Biosphere Reserve) so is afforded some protection there.

Solanum triumfense is very similar to *S. cobanense*, and has also been identified in herbaria as *S. wendlandii*. It differs from *S. cobanense* in its buds that are completely enclosed in the calyx until just before anthesis (Fig. 15), the pubescence of simple uniseriate and sometimes furcate trichomes on the new growth, and in the attenuate leaf bases. The flowers of *S. triumfense* are stellate, as opposed to the rotate to pentagonal flowers of *S. wendlandii*. Plants of *S. wendlandii* collected at very early anthesis could be mistaken for *S. triumfense*, but lack the pubescence on the new growth that is characteristic of this new species.

Specimens Examined—MEXICO. Chiapas: SW side of Cerro Mozotal, 11 km NW of the junction of the road to Montozintla along the road to El Porvenir and Siltepec, 25 Jun 1972 (fl), *Breedlove 25708* (DS, MEXU, MO); Mpio. La Concordia, El Triunfo Reserve, trail WSW from Palo Gordo towards Finca Catarina, 15°40'N, 92°51'W, 1850 m, 25 Feb 1990 (fl), *Hampshire et al. 694* (BM); El Triunfo, S edge, 29 Apr–1 May 1960 (fl), *MacDougall s.n.* (MEXU); Mpio. Escuintla, Santa Rosa, Ojo de Agua, 2 Jun 1948 (fl), *Matuda 17838* (DS, F).

8. *SOLANUM WENDLANDII* Hook. f., Bot. Mag. 113: pl. 6914. 1887.—TYPE: Cultivated at Kew in the Water Lily House, 28 Jul 1886, *Anonymous s.n.* (neotype, designated here: K [K000195647]; isoneotype: K [K000195646]).

Solanum mazatenangense Coult. & Donn. Sm., Bot. Gaz. 37: 421. 1904.—TYPE: GUATEMALA. Retalhuleu: San Felipe, 2050 ft, Apr 1892, *J. Donnell Smith 2669* (lectotype, designated here: US [US-1324650, barcode US00840548]; isolectotypes: F [F-267128], GH [GH0077513], K [K000195648, K000195649], NY [NY00139006], US [US-1324649, US-258628]).

Solanum tlacotalpense Sessé & Moc., Fl. Mexic., ed. 2. 1894.—TYPE: MEXICO. Veracruz: “ad fluviorum Tuxtentium” [on the banks of Río Tuxtla, presumably near San Andrés Tuxtla], *M. Sessé & J. Mociño s.n.* (lectotype, designated by Knapp 2008b, pg. 20: MA [MA-604681, F neg. 48334]; isolectotypes: MA [MA-604680, F neg. 483333, MA-604682, F neg. 48335]).

Solanum unguis-cati Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 320. 1929.—TYPE: HONDURAS. Atlántida: Lancetilla Valley, near Tela, 50 m [“20–600” on label], 9 Mar 1928 [“Dec. 6, 1927–Mar. 20, 1928” on label], *P. Standley 56726* (holotype: F [F-581029]).

Woody (sometimes herbaceous) vine or canopy liana to 20 + m long, the stems 0.25–0.8 cm in diameter, prickly, the prickles often lacking on herbarium collections of flowering material; internodes 1–10 cm long, glabrous; prickles to 1 mm long, stout, recurved, sometimes absent on terminal shoots near the inflorescence. Sympodial units plurifoliate, not geminate. Leaves highly variable in shape on the same plant, ranging from simple (usually near the inflorescences) to pinnately compound, the blades 10–20 × 8–15 cm, usually ovate (rarely elliptic), widest at the base, chartaceous, glabrous adaxially and abaxially, or occasionally the abaxial surface puberulent with unbranched hairs, often armed abaxially on midrib with curved prickles; major lateral veins 5–8 on each side; base rounded to acute; margin entire or pinnatifid or pinnate with 3–7 lobes or leaflets, the terminal and adjacent lateral leaflets broadly confluent; apex acuminate to rounded; petioles 1.5–7 cm, glabrous, often armed with curved prickles. Inflorescences 10–20 cm long and wide, terminal, many times branched (rarely unbranched), with 20–30 flowers, with either staminate or pistillate flowers on a single individual, glabrous, not prickly, or occasionally with a few prickles at the very base; peduncle 5–10 cm; rachis 5–20 cm; pedicels 15–20 mm and slender at anthesis, articulated at the base; fruiting pedicels elongating to 3–5 × 0.3 cm and becoming woody. Flower buds narrowly ellipsoid, the corolla long exerted from the calyx tube, the calyx tube in bud unlobed with deep papery sinuses regularly tearing before anthesis. Calyx campanulate, spreading, the tube 2–9 mm, the lobes ca. 3 × 2 mm, rounded or quadrate with a distinct apiculate tip, glabrous to puberulent on the tips. Corolla 2.5–6(–9) cm in diameter, spreading at anthesis, pale lavender to deep

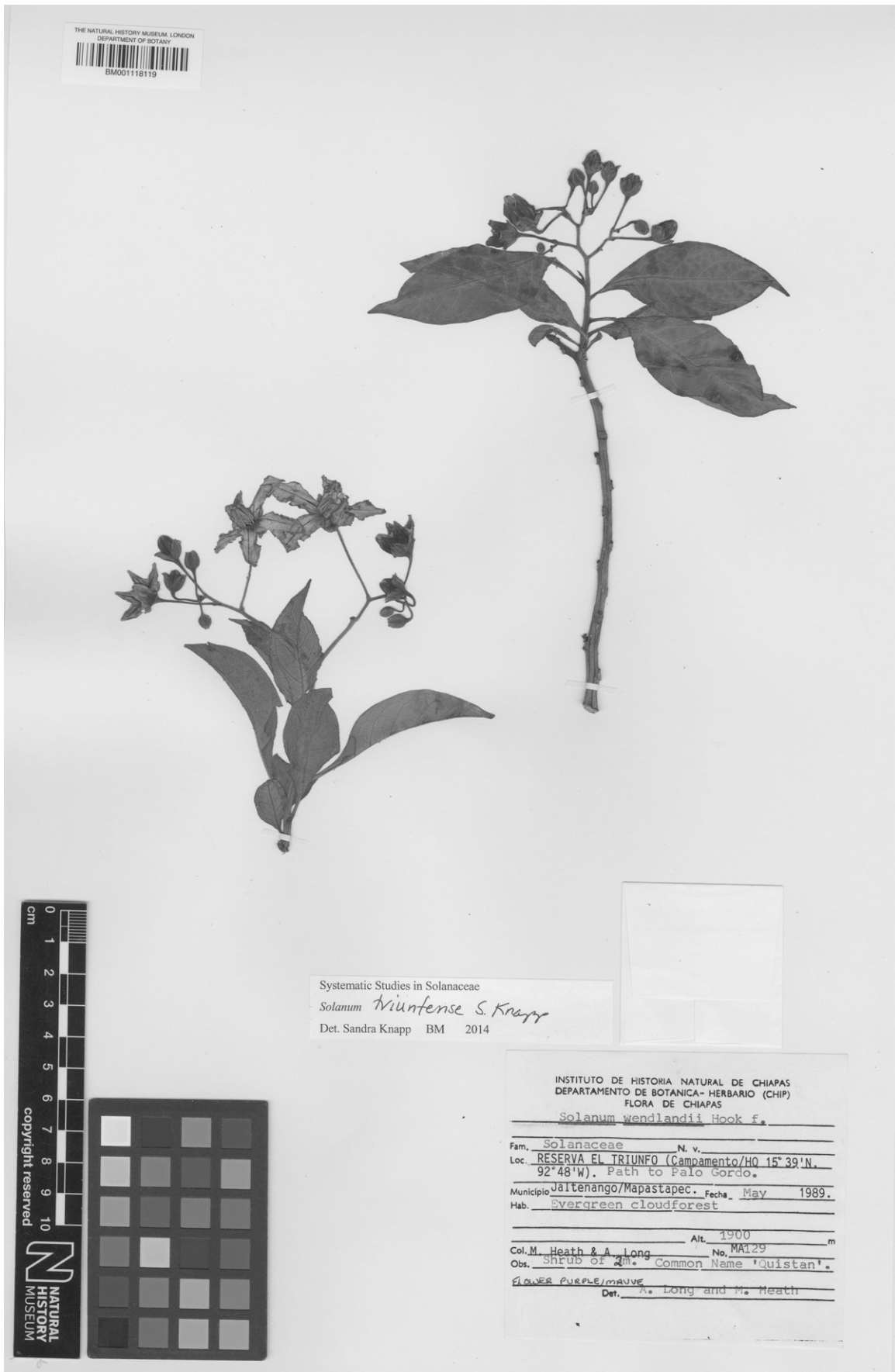


FIG. 15. Isotype specimen of *Solanum triunfense* from Mexico (M. Heath & A. Long MA129, BM). Reproduced with permission of the Natural History Museum, London.

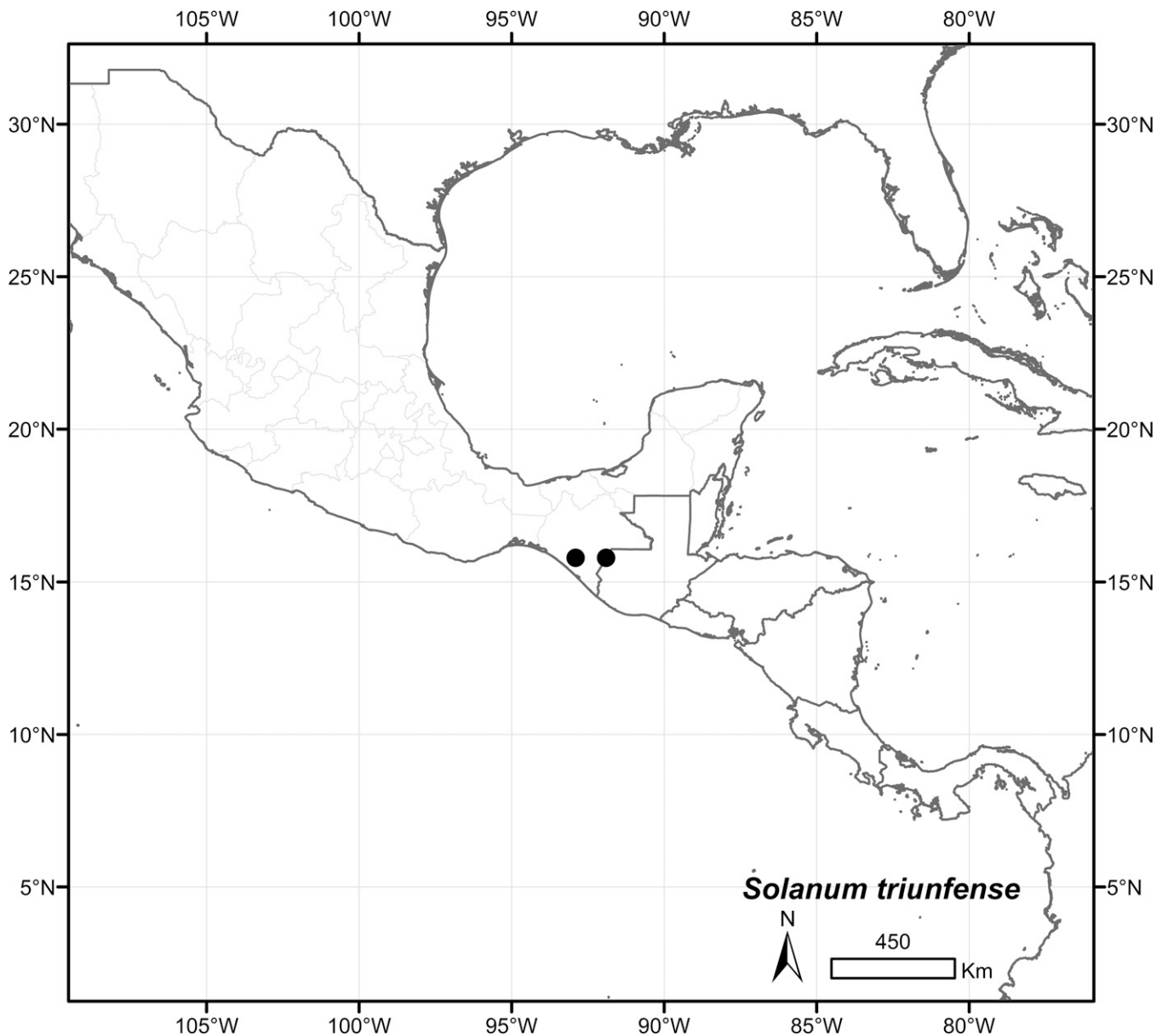


FIG. 16. Distribution of *Solanum triunfense*.

purple, membranous, rotate-pentagonal, lobed ca. 1/4–1/3 of the way to the base, the lobes $0.7\text{--}1.2 \times 1.2\text{--}1.7$ mm, broadly deltate, acuminate at the tips, glabrous abaxially and adaxially. Stamens 5–10 mm long; filaments unequal, with four 1–1.5 mm long, the fifth 2.5–4 mm long, glabrous; anthers nearly equal, $4\text{--}10 \times 1.5\text{--}2$ mm, the one on the longer filament slightly larger, somewhat to strongly tapering, connivent, cream or pale purplish blue, sometimes yellowish cream at base and pale purple distally, poricidal at the tips, the pores lengthening to slits with age. Ovary glabrous; style in long-styled flowers ca. 12 mm long, straight, glabrous, in short-styled flowers 2–4 mm long; stigma truncate. Fruit a globose berry, 4.5–10 cm (dry, to 20 cm in diameter when fresh fide Christenhusz et al. 5372) in diameter, globose, green with green to white pulp, the pericarp glabrous, rugose when dry. Seeds 50–100 per berry, $4\text{--}5 \times 6\text{--}8$ mm, strongly flattened-reniform, light reddish brown, the surfaces minutely pitted, the testal cells pentagonal. Chromosome number: $n = 12$ (Fedorov 1974). Figs. 2D–F, 17–19.

Distribution and Habitat—*Solanum wendlandii* is probably native from southern Mexico to Panama in wet and semi-deciduous forests at elevations from 400–2,200 m. It is a commonly cultivated and sometimes naturalized vine in tropical and subtropical areas worldwide. Most cultivated plants apparently never bear female-fertile (long-styled) flowers and are possibly clones of plants with only staminate flowers (see below).

Phenology—*Solanum wendlandii* flowers throughout the year; fruiting specimens have been collected in its putative native range in January and February.

Common Names—Mexico. Chiapas: “kishtan” (Matuda 17481); Tabasco: “cola de gato” (Roviroso 885); Guatemala. Retalhuleu: “kishtan” (Cosminsky 112 and 128).

Preliminary Conservation Status (IUCN 2014)—Least Concern (LC). We have not evaluated *S. wendlandii* using GeoCat due to the large number of cultivated and/or naturalized specimens whose status is not clear from collecting information. We do consider it of some conservation

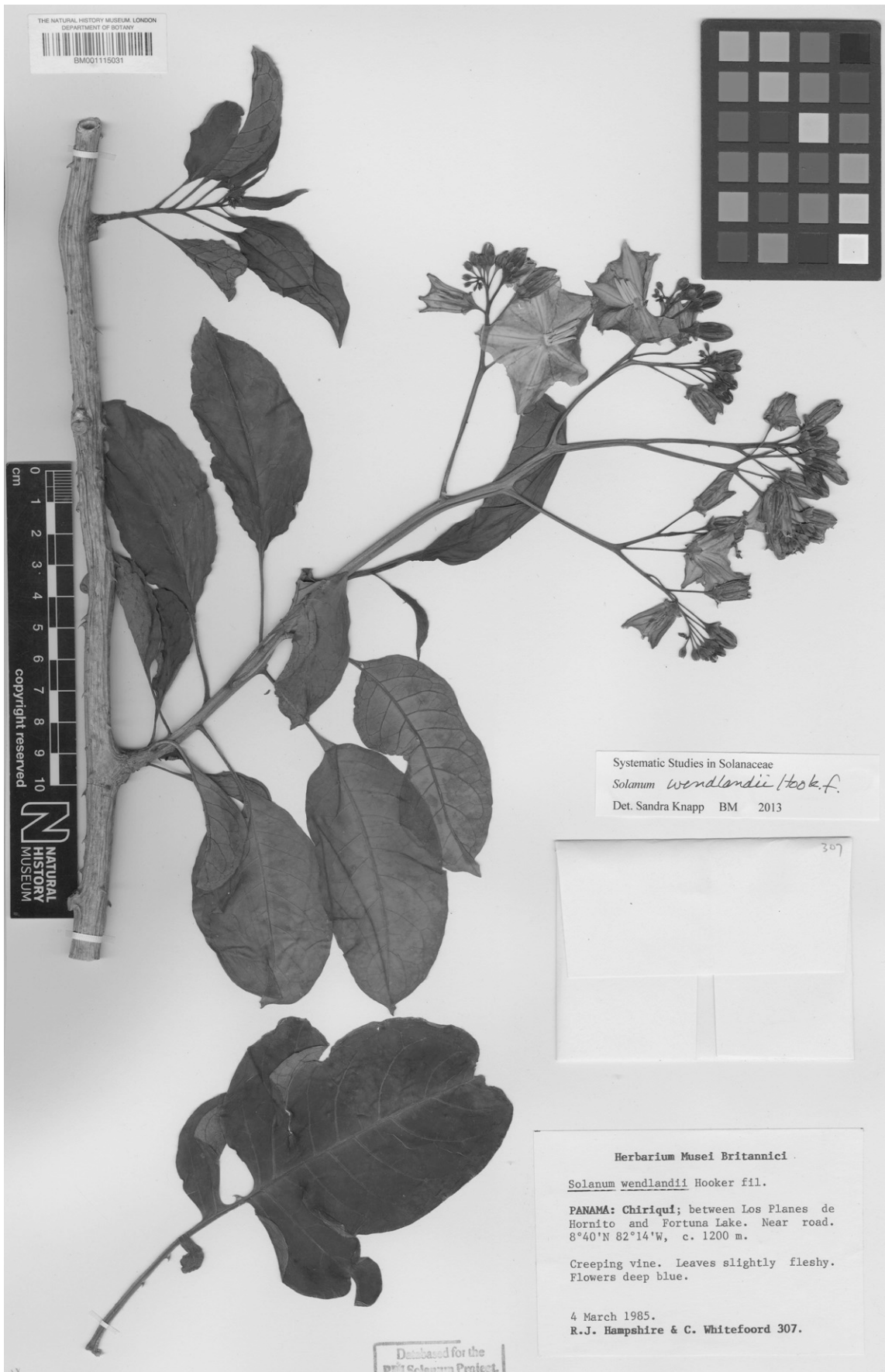


FIG. 17. Staminate-flowered specimen of *Solanum wendlandii* from Panama (R. Hampshire & C. Whitefoord 307, BM). Reproduced with permission of the Natural History Museum, London.



FIG. 18. Pistillate-flowered specimen of *Solanum wendlandii* from Guatemala (M.J.M. Christenhusz et al. 5372, BM). Reproduced with permission of the Natural History Museum, London.



FIG. 19. Lithograph of *Solanum wendlandii* illustrating the plant from which the neotype specimen was probably taken (*Curtis's Botanical Magazine* 113: pl. 6914. 1887). Reproduced with permission of the Library of the Natural History Museum, London.

concern, however, in its presumed area of native distribution, given the few fruiting specimens (and thus contributors to future native populations) we have seen.

Solanum wendlandii is quite variable in appearance. Most herbarium specimens, collected from flowering twigs, have only simple, entire leaves while much of the rest of the vine has pinnatifid to pinnate leaves. Simple-leaved collections of *S. wendlandii* can be confused with *S. cobanense*, but the leaves of the latter are more coriaceous and the flowers are stellate and very fleshy rather than pentagonal in outline with thin petal tissue like those of *S. wendlandii*. Non-flowering pinnately-leaved specimens of *S. wendlandii* can be very similar to *S. refractum*, but lack the densely prickly inflorescence of that species.

Flower size in *S. wendlandii* is extremely variable, but this is in part due to flower growth throughout anthesis. Flowers of this species last approximately three days (Shelly et al. 2000), and on the first day they are both darker purple and smaller than on subsequent flowering days (see Figs. 2D, 19). Plants with small-flowered inflorescences (young ones with flowers only one day old) can be confused with *S. triumfense* and *S. bicorne*, but both of these species have stamens of equal size.

The breeding system of this species has not been closely investigated. Nearly, if not all, cultivated material seems to bear only staminate flowers with vestigial styles and fruit from cultivated collections is almost never seen (although immature fruits are described in the protologue; Hooker 1887). Fruiting material is seldom collected from the wild, perhaps because the plants only produce their large fruit upon reaching the canopy. The species is possibly dioecious, this may in part account for the paucity of fruiting collections.

Solanum wendlandii is apparently native from southern Mexico to western Panama in wet forests of the Atlantic Coast, but the exact range is difficult to discern since it is seldom collected in the wild, is widely planted for the showy panicles of large flowers, and label data usually do not specify whether the plants were cultivated or truly wild. Collections outside this range seem to be either escapes from cultivation or merely cultivated plants, although this is not always stated clearly on herbarium labels. We have not cited these numerous collections here, but full details can be found on the Solanaceae Source website (www.solanaceaesource.org). We have seen cultivated or perhaps naturalized material from the following countries outside its native range: Argentina, Australia, Bermuda, Brazil, Cameroon, China, Colombia, Cuba, Dominican Republic, Ecuador, Egypt, Haiti, India, Jamaica, Kenya, Malawi, Paraguay, Peru, Philippines, Puerto Rico, Singapore, Sri Lanka, Tanzania, United Kingdom, United States of America, Venezuela, and Zimbabwe.

Solanum wendlandii is reportedly used in cooking in Guatemala ("Leaves and flowers cooked" fide *Cosminsky 112* and *128*) and the plants are reported in the Flora of Guatemala to be edible (Gentry and Standley 1974). In at least one collection (*Nee & Taylor 28770*) from Veracruz, Mexico, however, it was noted that the fruits are not eaten. In this location, where the plants seem to be native, the green fruits were pecked open by birds, which remove the seeds and green pulp, leaving only an empty shell (*Nee & Taylor 29770*).

No herbarium specimens were cited in the protologue of *S. wendlandii* (Hooker 1887). The neotype collection was made by an unknown collector from a cultivated plant

grown in England at the Royal Botanic Gardens, Kew (see Fig. 19). The species was described from living plants by Hooker (1887) as "Living plants of this beautiful *Solanum* were sent to the Royal Gardens [Kew] in 1882 by Dr. Wendland, Director of the Royal Gardens at Herrenhausen, Hanover, with the information that it is a native of the cold regions of Costa Rica, where it climbs trees. This habit it has retained at Kew, where it ascends to the rafters of the Water Lily House, and flowers profusely."

Two specimens at Kew are labeled "Type specimen of Bot. Mag. t. 6914!" and dated 28 July 1886 in an unknown handwriting (not Joseph Dalton Hooker's); one (K000695647) has stem, leaves and one opened out flower, while the other (K000695646) has only stem and leaves. We select the more complete K000195647 as the neotype for *S. wendlandii*. Another specimen collected from the Water Lily House in 1892 (K000195646) may have come from the same plant, but is not type material. Edmonds (2012) incorrectly cited a Kew holotype for *S. wendlandii*, and did not effectively typify the name.

Six Guatemalan collections were cited in the protologue of *S. mazatenangense*: *Shannon 618*, *Shannon 624*, *Heyde & Lux 4735*, *Heyde & Lux 3442*, *Donnell Smith 2263* and *Donnell Smith 2669*. We have chosen the US duplicate (US-1324650) of *Donnell Smith 2669* as the lectotype of this species, as it is the best preserved and most widely distributed of the collections cited. It is likely that Donnell Smith used the US sheet in his description of the material annotated by Coulter as this species.

Representative Specimens Examined—(putative native range only; cultivated and naturalized specimens outside this range can be viewed in Solanaceae Source, <http://www.solanaceaesource.org>) — MEXICO. Chiapas: Mpio. Unión Juárez, Rancho La Libertad, km. 22 carr. á Unión Juárez, 25 Mar 1992 (fl), *Aquino V. 110AA* (MEXU); Mpio. Tuxtla Gutiérrez, El Sumidero, 22 km N of Tuxtla Gutiérrez, 4,500 ft, 9 Apr 1965 (fl), *Breedlove 9613* (F, US); Mpio. Ocozacoautla, Curva de la Gringa, 2 km adelante de Ocozacoautla, carretera Ocozacoautla-Tuxtla Gutiérrez, 600 m, 10 May 1983 (fl), *Calzada et al. 10125* (MEXU); Mpio. Tapachula, 7.5 km de Tapachula, carretera Costera, 14°55'N, 92°29'W, 160 m, 17 Jul 1986 (fl), *Cigarroa MA2* (MEXU); Mpio. Unión Juárez, volcán Tacaná, camino de Talquián a la cima del volcán, 2,200–2,400 m, 6 Feb 1987 (fr), *Martínez S. et al. 19677* (MEXU); Trapichito, Comitán, 1,350 m, 2 Jun 1945 (fl), *Matuda 15671* (F, MEXU, MO); Mpio. Tenejapa, río de "Cruz Pital", 900 m, 1 May 1982 (fl), *Shilom Ton 4230* (MEXU, NY); Mpio. Tapachula, Cantón El Tesoro, 250 m, 17 Apr 1985 (fl), *Ventura & López 1527* (MEXU); Mpio. Tuxtla Chico, Ejido Francisco Villa, 4 Apr 1986 (fl), *Ventura & López 3421* (MEXU). Oaxaca: Dto. Miahuatlán, Mpio. San Jerónimo Coatlán, Espuelas de San Antonio, 13.5 km SW de San Jerónimo Coatlán, 16°12'N, 96°57'W, 1,950 m, 17 May 1988 (fl), *Campos V. 1824* (MEXU); Distr. Ixtlán, 4 km N de Vista Hermosa entre Metates y Vista Hermosa, 1,340 m, 17 Apr 1982 (fl), *Cedilla T. et al. 1241* (MEXU); carretera Oaxaca–Puerto Escondido, km. 183, 16 Apr 1963 (fl), *MacDougall s.n.* (MEXU); carretera Oaxaca a Tuxtepec, km. 100, 21 Apr 1963 (fl), *MacDougall 512* (MEXU); Mpio. Comaltepec, Vista Hermosa, km. 131 carr. Tuxtepec–Oaxaca, 1,700 m, 24 May 1966 (fl), *Martínez C. 838* (MEXU); Mpio. San Jerónimo Coatlán, Dto. Miahuatlán, Espuelas de San Antonio, 13.5 km SW de San Jerónimo Coatlán, brecha a Piedra Larga, 2,050 m, 27 Jun 1990 (fl), *Toriz & Campos 936* (MEXU); Cerro Espino, Finca Montecristo entrando por Chacalapa 5 km N de Pochutla carr. a Oaxaca, 31 May 1984 (fl), *Torres C. et al. 5239* (MEXU); Mpio. Santiago Lachiguirí, Dto. Tehuantepec, E de cruceo Guadalupe, 12.5 km NE de Santiago Lachiguirí, 16°43'N, 95°30'W, 1,400–1,700 m, 9 May 1991 (fl), *Torres C. 13967* (MEXU). Puebla: Bosque Ajenibre, May 1952 (fl), *Matuda 1* (MEXU). Quintana Roo: Mpio. F. Carillo Puerto, F. Carillo Puerto, 8 Jun 1989 (fl), cult., *Cabrera 16494* (CIQ, MEXU). San Luis Potosí: Mpio. Aquismón, Tampaxal, 1 Aug 1979 (fl), *Alcorn CO1* (MEXU). Tabasco: Mpio. Tacotalpa, 3.5 km adelante de la panga de Oxolotan camino hacia Oxolotan, 22 May 1983 (fl), *Cowan et al. 3994* (MEXU, NY); Cerro de Coconá, 19 Jul 1890, *Rovirosa 885* (K). Veracruz: Mpio. San Andrés Tuxtla, Cerro Mastagaga, ca. 13 km NE de San Andrés Tuxtla, 18°35'N, 95°09'W, 1,200 m, 1 Mar 1972 (fl), *Beaman 5818* (F, XAL); Mpio. Hidalgotitlán, brecha Hnos. Cedillo–La Escuadra, 17°16'N, 94°37'W, 152 m, 6 May 1974 (fl), *Brigada Vázquez 583*

(MEXU, MO, XAL); Mpio. Hidalgotitlán, km. 1–6 camino Cedillo–La Laguna, 140 m, 17°17'N, 94°30'W, 12 Jun 1974 (fl), *Dorantes* 3193 (F), Basurars, km. 18 Catemaco–Las Palmas, *González Leija & Garza* 3126 (MEXU); Mpio. San Andrés Tuxtla, Est. Biol, 95°04'–09'W, 150 m, 8 Aug 1968 (fl), *Martínez Calderón* 1740 (F, GH, INIF, MEXU, NY, XAL); Mpio. Naolinco, 3 km. W of San Antonio Paso del Toro, 19°35'N, 96°52'W, 850 m, 14 Jan 1984 (fr), *Nee & Taylor* 28770 (CORD, F, G, MO, NY, XAL); Mpio. Hidalgotitlán, Campamento La Laguna, 100 m, 17°17'N, 94°30'W, 1 Mar 1984 (ster), *Nee* 29728 (F, NY, XAL); Mpio. Xico, San Marcos de León, 19°26'N, 96°57'W, *Ortega O.* 2311 (XAL); 1 km S of Monte Pío, 18°38'N, 95°05'W, 10 Jul 1978 (fl), *Poole et al.* 1433 (MEXU); Mpio. San Andrés Tuxtla, Cd. Madero, carretera a San Martín, 24 Apr 1983 (fl), *Ramamoorthy* 3552 (MEXU); Mpio. Uxpanapa, Esfuerzo Nuevo, 17°10'N, 94°21'W, 230 m, 2 May 1996 (fl), *Rivera H. & Escobedo* 66 (MEXU); Mpio. Santiago Tuxtla, Loma Quemada, 350 m, 11 May 1977 (fl), *Ventura A.* 14022 (F, MEXU), Mpio. Naolinco, Almolonga, 700 m, 15 Dec 1981 (fr), *Ventura A.* 19238 (MEXU, XAL), Mpio. Tlapacoyan, El Embarcadero, 150 m, 9 Jun 1983 (fl), *Ventura A.* 20274 (MEXU, XAL); Cerro de Tuxpango Ixtaczoitlán, 10 km SE of Orizaba, 29 May 1944 (fl), *Vera S.* 2968 (MEXU). Yucatán: 6 km antes de Oxholom Samahil, 20°40'N, 89°W, 17 Mar 1987 (fl), *Góngora* 377 (CIQ, MEXU).

GUATEMALA. Alta Verapaz: near Tactic, above bridge across Río Frío, 1400–1500 m, 30 Mar 1941 (ster), *Standley* 90308 (F). Guatemala: Arrazola, 1600 m, May 1892 (fl), *Heyde & Lux* 3442 (F, US); Guatemala City, 1,530 m, 3 May 1970 (fl), *Harmon* 2280 (MO); Calderas, 5 Jul 1941 (fl), *Johnston* 1896 (F). Escuintla: Escuintla, 1,100 ft, Apr 1890 (fl), *Donnell Smith* 2263 (BM, US). Huehuetenango: Barillas, along the road between Barillas and Malpais, 1,554 m, 28 Feb 2009 (fl, fr), *Christenhusz et al.* 5372 (BM, NY); between Xoxlad and Nucapuxlac, Sierra de los Cuchumatanes, 1,650–2,500 m, 17 Jul 1942 (ster), *Steyermark* 48926 (F). Jutiapa: Cuesta de la Conora, between San José Acatempa and Río de los Esclavos, 900–1,200 m, 21 Dec 1938 (ster), *Standley* 60614 (F). Petén: Chichí, 9 Apr 1933 (fl), *Lundell* 2751 (F); La Libertad, 23 Apr 1933 (fl), *Lundell* 2984 (F, GH). Quetzaltenango: Fuentes Georginas, W slope of Volcán de Zunil, 2,850 m, 4 Mar 1939 (ster), *Standley* 67476 (F); Los Positos, SW of San Martín Chile Verde, 1,500 m, 8 Mar 1939 (ster), *Standley* 67932 (F); above Mujulia, between San Martín Chile Verde and Colomba, 1,800 m, 1 Feb 1941 (ster), *Standley* 85541 (F); Finca Pirineos, between Santa María de Jesús and Calahuache, 1,300 m, 20 Jan 1940 (fl), *Steyermark* 34499 (F). Quiché: Chichicastenango, 8 Apr 1949 (fl), *Beer s.n.* (CM). Retalhuleu: Finca San Luis, Dec 1974 (fl), *Cosminsky* 112 (F); Finca San Luis, San Sebastián, 1,000–1,500 ft, Jan 1976 (ster), *Cosminsky* 128 (F); Las Delicias, S of Retalhuleu, 200 m, 22 Feb 1941 (fl), *Standley* 88039 (F). Sacatepéquez: 5 km E of Antigua, 1700 m, 24 May 1970, *Harmon* 2358 (MO); Embaulada, 5,500 ft, Nov 1891 (fl), *Heyde & Lux* 4735 (F-2 sheets, US); Las Lajas, 1,200 m, 28 Nov 1938 (ster), *Standley* 58087 (F). San Marcos: between Canjula and La Unión Juárez, SE portion of Volcán Tacana, 2,000–3,000 m, 22 Feb 1940 (fl), *Steyermark* 36504 (F, US); between Tajumulco and Tecutla, 9 miles S and W of Tajumulco, NW slopes of Volcán Tajumulco, 1,800–2,500 m, 27 Feb 1940 (ster), *Steyermark* 36751 (F); Aldea Fraternidad, between San Rafael Pie de la Cuesta and Palo Gordo, 1,800–2,400 m, 10–18 Dec 1963 (fl), *Williams et al.* 25977 (F); Tajumulco Volcano, 8–10 km W of San Marcos, 2,300 m, 31 Dec 1964–1 Jan 1965 (fl), *Williams* 26935 (F). Santa Rosa: Cuilapa, 895 m, 20–27 Nov 1940 (fr), *Standley* 78130 (F). Sololá: Santa Bárbara, 410 m, Aug 1891, *Shannon* 618 (US). Suchitepéquez: Las Animas, 200 m, Sep 1891, *Shannon* 624 (US); SW slopes of Volcán Zunil, Finca Montecristo, SE of Santa María de Jesús, 1,200–1,300 m, 31 Jan 1940 (ster), *Steyermark* 35231 (F). Zacapa: Zacapa, 225 m, 23 Apr 1939 (ster), *Standley* 71996 (F); Quebrada Alejandria, summit of Sierra de las Minas, Finca Alejandria, 2,500 m, 13 Oct 1939 (ster), *Steyermark* 29864 (F).

HONDURAS. Atlántida: Lancetilla Valley, near Tela, 20–600 m, 6 Dec 1927–20 Mar 1928 (ster), *Standley* 53328 (F, GH, US). Comayagua: Comayagua Valley, 22 Sep 1973 (fl), *Hazlett* 853 (MO); Río Selguapa, El Taladro, 650 m, 27 Jun 1964 (fl), *Molina R.* 14320 (F, NY); Valle Comayagua entre Las Mercedes y Villa de Flores, 650 m, 28 Jun 1964 (fl), *Molina R.* 14367 (F, NY); Comayagua Valley between Comayagua and Villa San Antonio, 570 m, 1 May 1947 (fl), *Williams & Molina R.* 12610 (F). Morazán: drainage of the Río Yeguare, entre San Antonio del Mico y La Estancia, camino Río Cobre, 1,600 m, 29 Sep 1948 (fl), *Molina R.* 1152 (F); Suyapa, 1,100–1,200 m, 1 Aug 1950 (ster), *Standley* 22266 (F). Yoro: entre Yoro y Morazán, 700 m, 11 May 1956 (fl), *Molina R.* 6924 (F); Coyoles, 30 Jun 1938, *Yuncker et al.* 8160 (F, NY).

EL SALVADOR. Ahuachapán: P. N. El Imposible, camino al cerro Dávila, 13°49'N, 89°56'W, 26 Sep 1991 (fr), *Morales et al.* 1284 (MEXU). La Libertad: Mpio. Antiguo Cuscatlán, Laderas de la Laguna, 13°40'N, 89°15'W, 830 m, 18 May 1989 (fl), *Cruz* 195 (MEXU). San Salvador: San

Salvador, 650–850 m, 30 Mar–24 Apr 1922 (fl), *Standley* 22402 (GH, NY). Santa Ana: Cerro Las Mesas, 10 km NO de la ciudad de Santa Ana, 14°02'N, 89°36'W, 850 m, cult., *Linares & Martínez* 2623 (MEXU).

NICARAGUA. Estelí: road to Laguna de Miraflores, 8 Jun 1975 (fl), *Atwood* 320 (NY). Jinotega: Sierra W of Jinotega, along trail to Cerro de la Cruz, 1,050–1,350 m, 27 Jun 1947 (fl), *Standley* 10277 (F); La Montanita and Las Mesitas, W of Jinotega, 1,100–1,400 m, 29 Jun 1947 (fl), *Standley* 10416 (F). Madriz: Cerro Quisuca, 13°31'N, 86°31'W, 1,100–1,250 m, *Stevens & Montiel* 17336 (MEXU). Managua: Reparto Belmonte, NO de la ciudad de Managua, 49 m, 10 Aug 1979 (fl), *Araquistain* 6 (MEXU); Casa Colorada near El Crucero, summit of Sierra de Managua, 800–900 m, 14–25 May 1947 (fl), *Standley* 8664 (F). Matagalpa: Finca La Castilla, 23 km NE de Matagalpa, carretera al Tuma, 6 May 1982 (fl), cult., *Sandino* 2810 (MEXU).

COSTA RICA. Alajuela: R.B. Monteverde, Río Peñas Blancas, 10°19'N, 84°43'W, 700 m, 27 Mar 1988 (fl), *Haber & Bello* 8350 (CR); Cantón de San Ramón, Cordillera de Tilarán, Monteverde, San Gerardo Biological Station, Sendero Congo, 1 km W of station, 10°22'0" N, 84°48'0" W, 1,200–1,300 m, 14 Mar 1995 (fl), *Pennys* 249 (CR, INB, MO); Arenal Volcano, S slope of Cerro Chato, trail to summit, 25 Feb 1989 (fl), *Russell et al.* 988 (CR, US). Guanacaste: El Dos de Tilarán, 54 km N, Cerro La Chirripa, Atlantic slope rain forest, 10°25'N, 84°50'W, 1,000 m, 12 Apr 1986 (fl), *Haber et al.* 4422 (MO); Río Chiquito de Tilarán, 10 km N Monteverde, 12 Nov 1986 (fl), *Haber & Bello* 6366 (CR). Heredia: Cantón de Santo Domingo, town of Santo Domingo, 9°59' N, 84°06'W, 1,150 m, 2 Sept 1990 (fl), *Solomon* 19142 (CR, INB, MO). Limón: near Rangalle, Telire River watershed, 400–900 m, 25–29 Mar 1983 (ster), *Hazlett* 5211 (MO); Telire, Talamanca, 24–28 Mar 1983 (ster), *Ocampo* 4011 (CR). Puntarenas: Zarcero de Alvaro Ruiz, 1,550 m, 21 Dec 1924 (fl), *Brenes* 4157 (F); Cantón de Coto Brus, P. I. La Amistad, Cordillera de Talamanca, Estación Pittier, 9°01'30"N, 82°57'40"W, 1,680 m, 28 Jan 1995 (fl), *Donzo et al.* 3 (CR, INB, MO); Zarcero, 5300 ft, 7 Sep 1937 (fl), *Smith* 319 (F). San José: Sabanilla de Montes de Oca, Residencias Palas Atena, S side of Rte. 202, ca. 0.5 km W of Cristo, 9°57'N, 84°02'W, 1,310 m, 16 Jan 1987 (fl), *Grayum* 7967 (CR, MO); San Ignacio de Acosta, Carretera 4, km 27–28, cult., 1100 m, 17 Jan 1984 (fl), *Khan et al.* 292 (BM, CR); Cerro Pico Blanco, 4 km S of Escazu, 2,000 m, 12 Dec 1976 (fr), *Lent* 3987 (CR, F, MO, NY); Cantón de Aserri, Z. P. Cerros de Escazu, Cuenca del Río Poás, Mesón, en la cuenca media del Río Lajas, 4 km aguas arriba, 9°52'15"N, 84°05'50"W, 1,500 m, 30 Jan 1994 (fl), *Morales et al.* 2312 (INB, MO).

PANAMA. Bocas del Toro: Caribbean slopes of Cerro Fabrega at foot of 'Falso Fabrega' in Palo Seco Reserve, second N-most tributary (on map) of Río Culebre, Pavón Camp, 9°09'51"N, 82°39'41"W, 1,300 m, 20 Mar 2005 (fl), *Monro & Cafferty* 4802 (BM, INB, MEXU, MO, PMA). Chiriquí: Palo Santo, 3 miles N of Volcán, 14 Feb 1971 (fl), *Croat* 13547 (F, MO); between Los Planes de Hornito and Fortuna Lake, 8°40'N, 82°14'W, 1,200 m, 4 Mar 1985 (fl), *Hampshire & Whiteford* 307 (BM, MEXU).

NAMES NOT VALIDLY PUBLISHED

Solanum dichotomum Pav. ex Dunal, Prodr. [A. P. de Candolle] 13(1): 233. 1852. Nom. nud. pro syn. *S. bicornne* Dunal var. *angustifolium* Dunal.

Solanum juciri Mart. ex Sendtn., Fl. Bras. [Martius] 10: 110. 1846. Nom. illegit. superfl. with *S. alternatopinnatum* Steud. (1841), in synonymy.

Solanum laxiflorum Dunal, Prodr. [A. P. de Candolle] 13(1): 234. 1852. Nom. nud. pro syn. *S. viridipes* Dunal.

Solanum shannoni Coult., nom. nud. in sched. (*Heyde & Lux* 4735). This collection is a syntype for *S. mazatenangense* Coult. & Donn. Sm. and the epithet also appeared as a name only in the original description of *S. unguis-cati* (Standley 1929), but with no description it does not meet the requirements for valid publication.

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