A Revision of *Solanum* Section *Lathyrocarpum* (the Carolinense Clade, Solanaceae)

Author(s): Gregory A. Wahlert, Franco E. Chiarini, and Lynn Bohs
Source: Systematic Botany, 40(3):853-887.
Published By: The American Society of Plant Taxonomists
URL: http://www.bioone.org/doi/full/10.1600/036364415X689302

Systematic Botany (2015), 40(3): pp. 853–887

DOI 10.1600/036364415X689302
Date of publication September 22, 2015

A Revision of *Solanum* Section *Lathyrocarpum* (the Carolinense Clade, Solanaceae)

Gregory A. Wahlert,[1,3] Franco E. Chiarini,[2] and Lynn Bohs[1]

[1]Department of Biology, University of Utah, Salt Lake City, Utah 84112, U. S. A.
[2]Instituto Multidisciplinario de Biología Vegetal, Museo Botánico de Córdoba, CONICET-UNC, Córdoba, 5000 Argentina.
[3]Author for correspondence (rinorea@gmail.com)

Communicating Editor: Sven Buerki

Abstract—A new taxonomic circumscription of *Solanum* section *Lathyrocarpum* is proposed to include 11 species from North and South America. The section is placed in the cosmopolitan *S.* subgenus *Leptostemonum*, which contains 350–450 species. As defined here, *S.* sect. *Lathyrocarpum* includes all the taxa resolved in the Carolinense clade in previous molecular phylogenetic studies as well as one species not sampled in those analyses. The combination of morphological characters that define the group includes: herbaceous perennial habit with extensive root systems, often with endogenous buds that can sprout, a sparse to dense indumentum of sessile to stalked stellate hairs and tapered prickles, 2- to 3-foliate to plurifoliate sympodial units, extra-axillary inflorescences with 1–20 flowers, a weakly andromonoecious reproductive system, corollas ranging in color from white to lavender, and fruits maturing to yellow or yellowish-orange. Most species in the section have a weedy habit and grow in highly disturbed areas, but four are narrowly distributed. One species, *S. carolinense*, is a noxious invasive weed that has been inadvertently introduced to many areas around the world. There are a variety of ploidy levels represented in the group (n = 12, 18, 24, and 36). In this work, we present a new circumscription of the section and provide descriptions, distribution maps, preliminary IUCN conservation assessments, and a key to identify the 11 included species. We also designate lectotypes for nine names and select a neotype for *S. dimidiatum*.

Keywords—Invasive species, IUCN conservation assessment, polyploidy, *Solanum carolinense*, *Solanum* subgenus *Leptostemonum*, taxonomy.

The cosmopolitan genus *Solanum* L., containing ca. 1,500 species, is among the largest genera of flowering plants and includes several economically important species such as potato, tomato, and eggplant (Bohs 2005). The largest subgenus within *Solanum* is *S.* subg. *Leptostemonum* (Dunal) Bitter, consisting of 350–450 species distributed worldwide and informally known as the "spiny solanums." Species in the subgenus typically share the character combination of stellate hairs, prickles, and tapered anthers (Whalen 1984). Molecular phylogenies have shown that the majority of species in *S.* subg. *Leptostemonum* form a monophyletic group, which has been called the Leptostemonum clade in previous studies (Bohs 2005; Levin et al. 2006; Stern et al. 2011).

In his classification of *Solanum*, Don (1838) placed all prickly species known to him in *S.* sect. *Aculeata* G. Don, which he further divided into one unranked taxon and seven subsections. One of these was *Solanum* subsection *Lathyrocarpum* G. Don, which included 12 Old World species and *S. carolinense* from North America. A few years later, Walpers (1844) elevated Don's subsection to the rank of section (i.e. *S.* sect. *Lathyrocarpum* (G. Don) Walp.), but he did not provide a rationale for the new status. Walpers' circumscription included nearly all of the same species as Don, but he added one species and placed another in synonymy.

Dunal (1852) placed the spiny solanums into *Solanum* sect. *Leptostemonum* Dunal, which was further divided into three subsections, including *S.* subsect. *Asterotrichotum* Dunal (*S.* subsect. *Lathyrocarpum* was not recognized in Dunal's treatment). *Solanum* subsect. *Asterotrichotum* was partitioned into five unranked groups and included the *Solanum* Oliganthes group, which contained eight species from Don's *S.* subsect. *Lathyrocarpum* as well as an additional 83 species. The *Solanum* Oliganthes group was poorly defined morphologically and contained species of spiny solanums that were placed in different infrageneric groups in subsequent treatments. Later, Seithe (1962) proposed a taxonomy of *Solanum* based on hair types, and many of the species in the *Solanum* Oliganthes group were reassigned to *S.* sect. *Stellatipilum* (Seithe) Seithe and *S.* sect. *Simplicipilum* Bitter, but her classification was not adopted in later treatments. *Solanum* subsect. *Lathyrocarpum* did not appear in subsequent *Solanum* classifications until 1972, when D'Arcy designated *S. carolinense* as the lectotype species of the subsection.

In a taxonomic synopsis of *Solanum* subg. *Leptostemonum*, Whalen (1984) identified 33 informal species groups. He included seven species in his *S. multispinum* species group based on most of the same characters used to define *S.* sect. *Lathyrocarpum* in this study (see below). He left *S. carolinense* and *S. dimidiatum* unplaced and speculated that they may be related to the *S. torvum* species group, even though they exhibit most of the morphological characters used to delimit the *S. multispinum* group. Later, in a synoptic treatment of *S.* subg. *Leptostemonum* from the New World, Nee (1999) placed 14 described species and two undescribed species in *S.* subsect. *Lathyrocarpum*. Table 1 compares the classifications of Whalen (1984) and Nee (1999) showing those taxa recovered in the Carolinense clade in the phylogeny of Wahlert et al. (2014). Also included in Table 1 is *S. multispinum*, which was thought to belong to the group by both Whalen (1984) and Nee (1999) but was not recovered in the clade, as well as two species that were not sampled in the phylogeny (*S. chamaeacanthum* and *S. flagellare*; see Phylogenetic Relationships section). Three other species included in Nee's (1999) circumscription fell outside of the Carolinense clade and are excluded from the section (*S. euacanthum* Phil., *S. hasslerianum* Chodat, and *S. mortonii* Hunz.).

Phylogenetic studies based on DNA sequences have provided new lines of evidence to facilitate the circumscription of infrageneric taxa in *Solanum*. The phylogeny of Weese and Bohs (2007) identified 12–14 major clades in *Solanum*, including the Leptostemonum clade, which corresponds closely to *S.* subg. *Leptostemonum*. Subsequently, two densely sampled molecular phylogenetic studies within the subgenus identified up to 14 major well-supported clades, including the Carolinense clade (Levin et al. 2006; Stern et al. 2011). In the phylogeny of Stern et al. (2011), the Carolinense clade contained *S. carolinense* and four South American species: *S. aridum*, *S. comptum*, *S. juvenale*, and *S. moxosense*. The

Table 1. A list of taxa in the Carolinense clade of Wahlert et al. (2014) showing their placement in the taxonomic treatments of Whalen (1984) and Nee (1999). *Solanum chamaeacanthum* and *S. flagellare* were not sampled in the phylogeny of Wahlert et al. (2014), and *S. multispinum* was recovered outside of the Carolinense clade in a distant phylogenetic position. A dash (—) indicates a taxon that was not treated by Whalen (1984) or Nee (1999).

Carolinense clade of Wahlert et al. (2014)	Whalen (1984)	Nee (1999)
	S. multispinum species group	Series of *S.* subsect. *Lathyrocarpum*
S. aridum Morong	*S. multispinum* group (as *S. conditum* C. V. Morton)	Series 2 (as *S. conditum*)
S. carolinense L. var. *carolinense*	Incertae sedis	Series 1
S. carolinense var. *floridanum* Chapm.	Incertae sedis (as a synonym of *S. carolinense*)	—
S. chamaeacanthum Griseb.	Incertae sedis	Series 3
S. comptum C. V. Morton	S. *multispinum* group	Series 2
S. dimidiatum Raf.	Incertae sedis	Series 1
S. flagellare Sendtn.	S. *multispinum* group	Series 3
S. hieronymi Kuntze	S. *multispinum* group	Series 2
S. juvenale Thell.	S. *multispinum* group	Series 2
S. moxosense M. Nee	—	Series 3 (as *S.* sp. nov. ined, *M. Nee 34261*)
S. multispinum N. E. Br.	S. *multispinum* group	Series 2
S. perplexum Small	Incertae sedis (as a synonym of *S. dimidiatum*)	—
S. pumilum Dunal	—	Series 2
S. reineckii Briq.	S. *multispinum* group	Series 3

phylogeny of Wahlert et al. (2014), which focused on the Carolinense clade with increased taxon sampling over previous studies, recovered the same species in the clade as Stern et al. (2011), as well as four additional species (*S. dimidiatum*, *S. perplexum*, *S. pumilum*, and *S. reineckii*), giving a total of nine species in the clade. The South American species *S. hieronymi* was placed within the Carolinense clade based on plastid sequence data, but fell outside the clade in the nuclear and combined data analyses (see Phylogenetic Relationships below).

Although previous authors (e.g. D'Arcy 1972; Nee 1999) recognized the species most closely related to *Solanum carolinense* as *S.* subsect. *Lathyrocarpum*, in this study we refer to the group at the rank of section. This rank is equivalent to most of the species groups in Whalen's (1984) scheme and comparable in phylogenetic divergence to other molecular clades in *S.* subgenus *Leptostemonum* classified at the rank of section (e.g. the Torva clade; Levin et al. 2006; Stern et al. 2011).

In this work, *Solanum* sect. *Lathyrocarpum* includes 11 species: four with a native distribution in North America and seven in South America (Argentina, Bolivia, Brazil, and Paraguay). They are typically upright herbaceous perennial plants, but a few are sprawling to decumbent. Most species have an extensive root system, often growing in dense colonies and becoming invasive or noxious weeds. The roots and rhizomes of some species have endogenous buds capable of sprouting, a key feature promoting their weediness, and a few species have roots that bear starchy tuber-like swellings. All the species in the section have sparse to dense stellate pubescence on the vegetative parts, inflorescence axes, calyces and corollas and are sparsely to densely armed with yellow-brown tapered prickles. The sympodial units are 2- to 3-foliate to plurifoliate, with non-geminate leaves. The leaves are simple, petiolate, and ovate to ovate-elliptic or ovate-lanceolate with entire, sinuate, to deeply lobed margins. The inflorescences are usually extra-axillary and unbranched to several-branched with 1–20 flowers. The corolla color varies from white to light blue or deep violet to lavender. Plants are typically weakly andromonoecious, with the ratio of hermaphroditic to staminate flowers varying both among species and inflorescences on a single plant. The fruits are globose, ovoid, or depressed-globose, less than 3 cm in diameter, glabrous, and yellow to yellowish-orange with a firm or tough pericarp at maturity. Figures 1–2 show the habit, leaves, flowers, and fruit of some representative taxa in *S.* sect. *Lathyrocarpum*.

Even though we have not discovered any individual characters that define the section, the combination of characters listed above should serve to separate *Solanum* sect. *Lathyrocarpum* from other groups of spiny solanums. Table 2 shows a comparison of morphological characters to two similar groups previously identified in molecular phylogenies: the Elaeagnifolium clade and Torva clade (sensu Levin et al. 2006 and Stern et al. 2011). However, much further study is needed before a useful and comprehensive classification can be made for the spiny solanums. Future research towards this end must include identifying the species composition of clades using molecular phylogenetic approaches, revising the classification for the spiny solanums based on phylogenetic results, and a reexamination of the distribution of characters among the groups. Until then, the boundaries and circumscriptions of infrageneric taxa for many groups of spiny solanums will remain tentative.

In this work, we provide a description and new circumscription for *S.* sect. *Lathyrocarpum*, and updated nomenclatural treatments and descriptions, distribution maps, preliminary IUCN conservation assessments for the 11 species included in the group. Lectotypes for nine names are chosen, a neotype for *S. dimidiatum* is selected, and a key to identify the species is also given.

Materials and Methods

The circumscription of *Solanum* sect. *Lathyrocarpum* and the included species are based on examination of herbarium specimens and field observations, and are supported by morphological and DNA evidence. We examined 1,301 specimens from the following herbaria: BAA, BM, BRIT, C, CAS, CORD, CTES, E, FCQ, FLAS, FSU, G, GH, LIL, LP, LPB, LSU, MCNS, MO, MPU, ND, NY, P, PH, PY, S, SI, UNA, VDB, and WIS. Throughout this work, herbarium specimens with an accession number are cited with the herbarium acronym followed by the number (e.g. MO–2766698). In cases where the specimen has a bar code, the bar code number is preceded by the herbarium acronym (e.g. NY–NY00688148). When a sheet has both an accession number and a bar code, only the bar code is given, except in the case of *S. aridum*, where both numbers are presented in order to compare to previous treatments of that species. Given the large amount of herbarium material available for *S. carolinense* var. *carolinense*, we have cited only a single specimen per state in the U. S. A. The entire list of specimens examined for *S. carolinense* var.

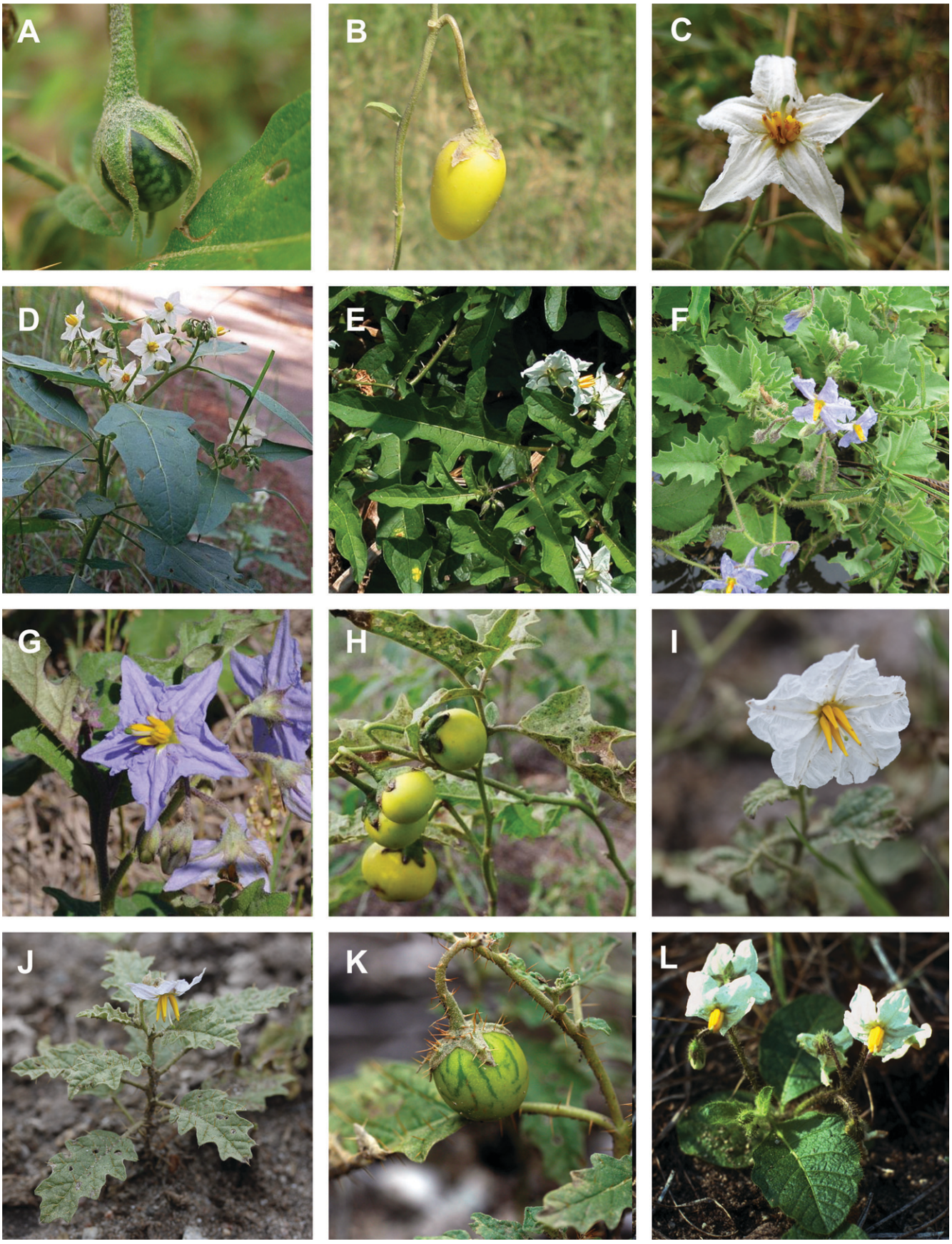

Fig. 1. Habit, flowers, and fruits of *Solanum* sect. *Lathyrocarpum*. A–C. *Solanum aridum*. A. Immature fruit. B. Mature fruit (*C. Peláez 308*). C. Flower. D. *S. carolinense* var. *carolinense*, habit and flowers. E. *S. carolinense* var. *floridanum*, habit and flowers. F. *S. comptum*, habit and flowers (*F. Chiarini & G. A. Wahlert 832*). G–H. *S. dimidiatum*. G. Flowers. H. Mature fruits. I. *S. hieronymi*, flower. J–K. *S. juvenale*. J. Habit and flower. K. Immature fruit. L. *S. pumilum*, habit and flowers. Photo credits: A–C, F, I–K, by F. Chiarini; D, G, H, by S. Hill; E, L by J. R. Allison.

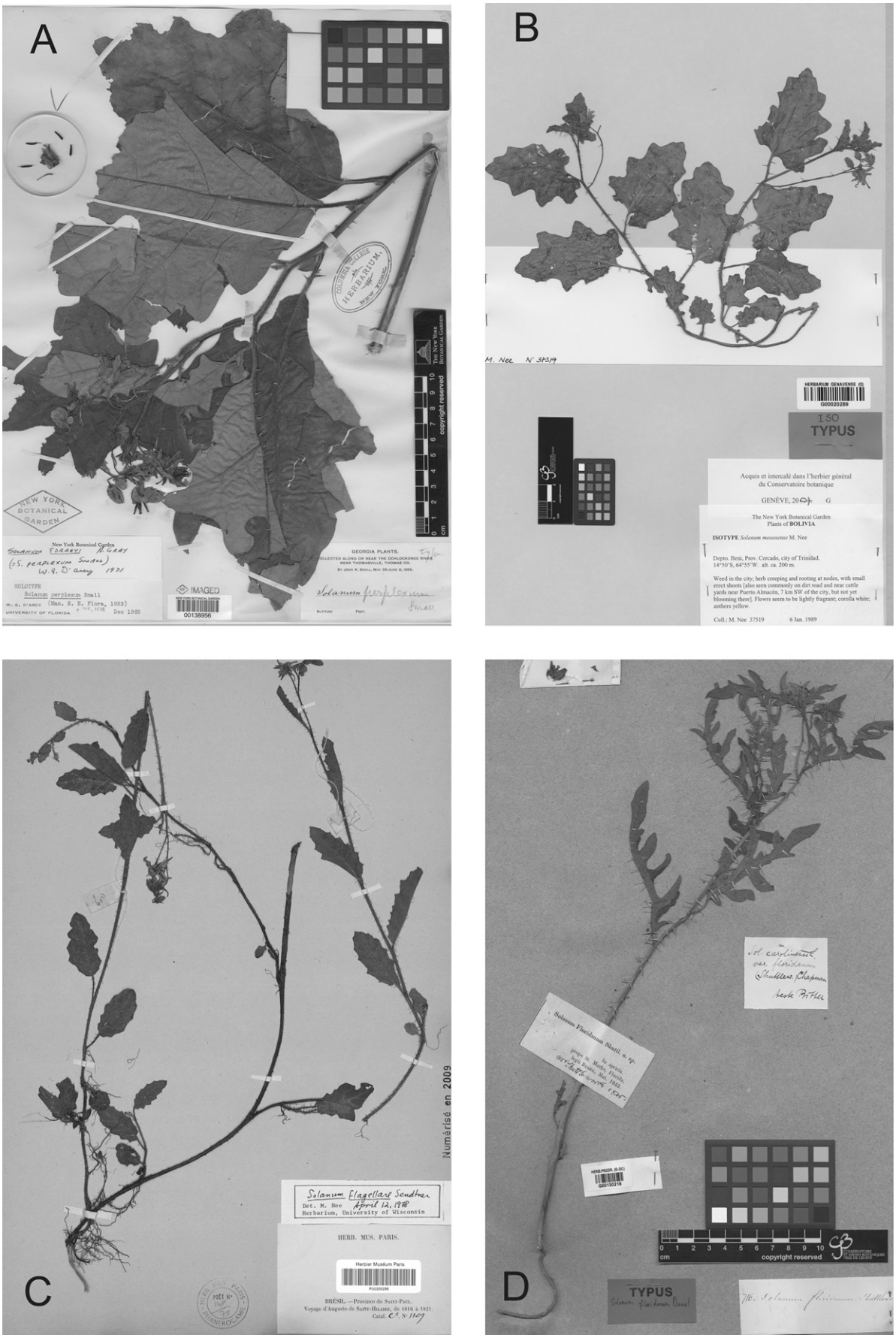

FIG. 2. Habit of some representative taxa in *Solanum* sect. *Lathyrocarpum*. A. *Solanum perplexum* (holotype, NY). B. *S. moxosense* (isotype, G). C. *S. flagellare* (*A. de Saint-Hilaire 1109*, P). D. *S. carolinense* var. *floridanum* (holotype, G).

TABLE 2. A synoptic comparison of morphological characters among *Solanum* sect. *Lathyrocarpum* as circumscribed in this study and members of the Elaeagnifolium and Torva clades as identified in Levin et al. (2006) and Stern et al. (2011).

Taxon or molecular clade	Morphological characters
Carolinense clade (*Solanum* sect. *Lathyrocarpum*)	Herbaceous perennials, usually rhizomatous or with horizontal rootstocks, the aerial stems erect to creeping, up to 1.2 m tall; prickles straight or slightly recurved; sympodial units 2- to 3-foliate to plurifoliate with non-geminate leaves; inflorescences extra-axillary, branched or unbranched, with 1–20 flowers; corollas actinomorphic, white to lavender; mature fruits indehiscent, yellow to yellowish-orange.
Elaeagnifolium clade	Herbaceous perennials, usually rhizomatous, the aerial stems erect, up to 1.5 m tall; prickles straight; sympodial units 2-foliate with non-geminate leaves; inflorescences extra-axillary, branched or unbranched, with ca. 1–6 flowers; corollas actinomorphic or zygomorphic, white to purple; mature fruits irregularly dehiscent, yellow, orange, gray-green, brown, or black.
Torva clade	Shrubs or small trees without rhizomes, the aerial stems scandent to erect, generally > 1 m tall; prickles straight or recurved; sympodial units 2-foliate, often with geminate leaves; inflorescences extra-axillary, usually branched, with 10-many flowers; corollas white to lavender; mature fruits indehiscent, green, brown, yellow, red, or yellow-red.

carolinense is available online as Supplementary Appendix S1, as is the index to numbered collections for all taxa treated in this study (Appendix S2).

Species circumscriptions were based on the morphological species concept (e.g. Cronquist 1978; Mallet 1995), whereby breaks in phenetic patterns between species are taken as evidence for reproductive isolation. Our recognition of *Solanum carolinense* var. *floridanum* Chapm. at the rank of variety was based on the infraspecific concept of Du Rietz (1930). Here, a local, distinct taxonomic entity ("local facies of a species") is distinguished by at least a few constant diagnosable morphological characters but intermediates may be found in mixed populations or at the transition areas with other varieties of the same species.

The summary phylogeny presented in Fig. 3 is based on Wahlert et al. (2014), where 17 taxa putatively belonging to the Carolinense clade were sequenced for one plastid (*trnT–trnF*) and two nuclear (ITS, *waxy*) gene regions and combined with the *Solanum* subg. *Leptostemonum* DNA matrix of Stern et al. (2011). Phylogenetic analyses of separate and combined DNA matrices were done using maximum parsimony and Bayesian methods. The simplified phylogenetic tree in Fig. 3 is based on a strict consensus of 7,819 most parsimonious trees inferred from the combined nuclear and plastid DNA matrix (results from the separate analyses of nuclear and plastid data sets are not shown). Details of taxon sampling, DNA extraction, amplification, and sequencing, and phylogenetic analyses can be found in Wahlert et al. (2014).

RESULTS

***Taxonomic History*—**The first three species to be described in *Solanum* sect. *Lathyrocarpum* are all from North America, the first being *S. carolinense* described by Linnaeus in 1753. *Solanum carolinense* has a large distribution in eastern North America, and the lectotype specimen was either collected in the southeastern U. S. A. or was from a cultivated plant grown in Europe from seed (S. Knapp, pers. comm.). Next, Thomas Nuttall described *S. hirsutum* Nutt. (= *S. pumilum* Dunal) in 1834 from Milledgeville, Georgia, U. S. A. The species was thought to be extinct but was rediscovered in Alabama in 1993 (Allison and Stevens 2001). The third species described in the section, *S. dimidiatum* from the southern United States, was published by Constantine Samuel Rafinesque in 1840 in his *Autikon Botanikon*. As is common with Rafinesque names, typification is often difficult because of inadequate descriptions and because much of his personal herbarium was discarded after his death (Merrill 1949). However, even though no type specimen has been located, the description of the species was unambiguous and the name has been in use ever since. The fourth species from North America is *Solanum perplexum*, described in 1933. Since then, it has usually been recognized as a synonym of *S. dimidiatum*, but it is reinstated in this treatment based on several morphological differences and a separate distribution.

The remaining seven species from South America were described between the period 1846–2006. *Solanum flagellare* was described in 1846 from material collected in São Paulo state, Brazil, and a similar species, *S. reineckii*, was described from Rio Grande do Sul state in 1899. *Solanum reineckii* has sometimes been treated as a synonym of *S. flagellare*, but based on consistent morphological differences as well as separate distributions, both species are recognized in this work. In 1893, Thomas Morong described *Solanum aridum* from material he had collected during an expedition to Argentina and Paraguay. The closely related *S. juvenale* was described by Albert Thellung in 1908 from a plant growing adventively near Port Juvénal, in Montpellier, France, but the species is native to Argentina. In 1893, Carl Ernst Otto Kuntze described *S. hieronymi* from Argentine material in his *Revisio Generum Plantarum*, and later, the closely related *S. comptum* was described in 1976 by Conrad V. Morton. The most recent species in the group to be described was *S. moxosense* from Bolivia by Michael Nee (Nee et al. 2006), where it is only known from the type locality.

***Morphology*—**HABIT—The species of *Solanum* sect. *Lathyrocarpum* have a stem architecture of 2- to 3-foliate to plurifoliate sympodial units with non-geminate leaves. Most members of the group are upright to spreading perennial herbs with stems that are unbranched to few-branched from a subwoody base. *Solanum flagellare*, *S. reineckii*, and *S. moxosense* have a decumbent, creeping habit and nodes that sometimes root on contact with the soil.

Most species in *Solanum* sect. *Lathyrocarpum* have an extensive root system capable of resprouting from the base of the stem after disturbance, often forming dense colonies. Such vigorous rhizomatous and vegetative growth promotes the weedy and invasive tendencies of several species in the section.

In *Solanum juvenale* and *S. hieronymi*, anatomical and morphological studies reveal that the portions of the axes nearest the soil surface are rhizomes (i.e. stem tissue) that transition to true roots that grow horizontally and then curve vertically downwards (Cosa et al. 1998; Cosa et al. 2000). Both species also have gemmiferous roots producing endogenous buds in the pericycle capable of sprouting from root cuttings. In *S. hieronymi*, the buds are produced in the stem just below the soil surface, whereas in *S. juvenale* they are produced in the deeper vertical portion of the root. The vertical roots in *S. aridum*, *S. juvenale*, and *S. hieronymi* also produce tuber-like swellings up to 2 cm long and 1 cm wide that serve as starch storage organs (Cosa et al. 1998). *Solanum carolinense*

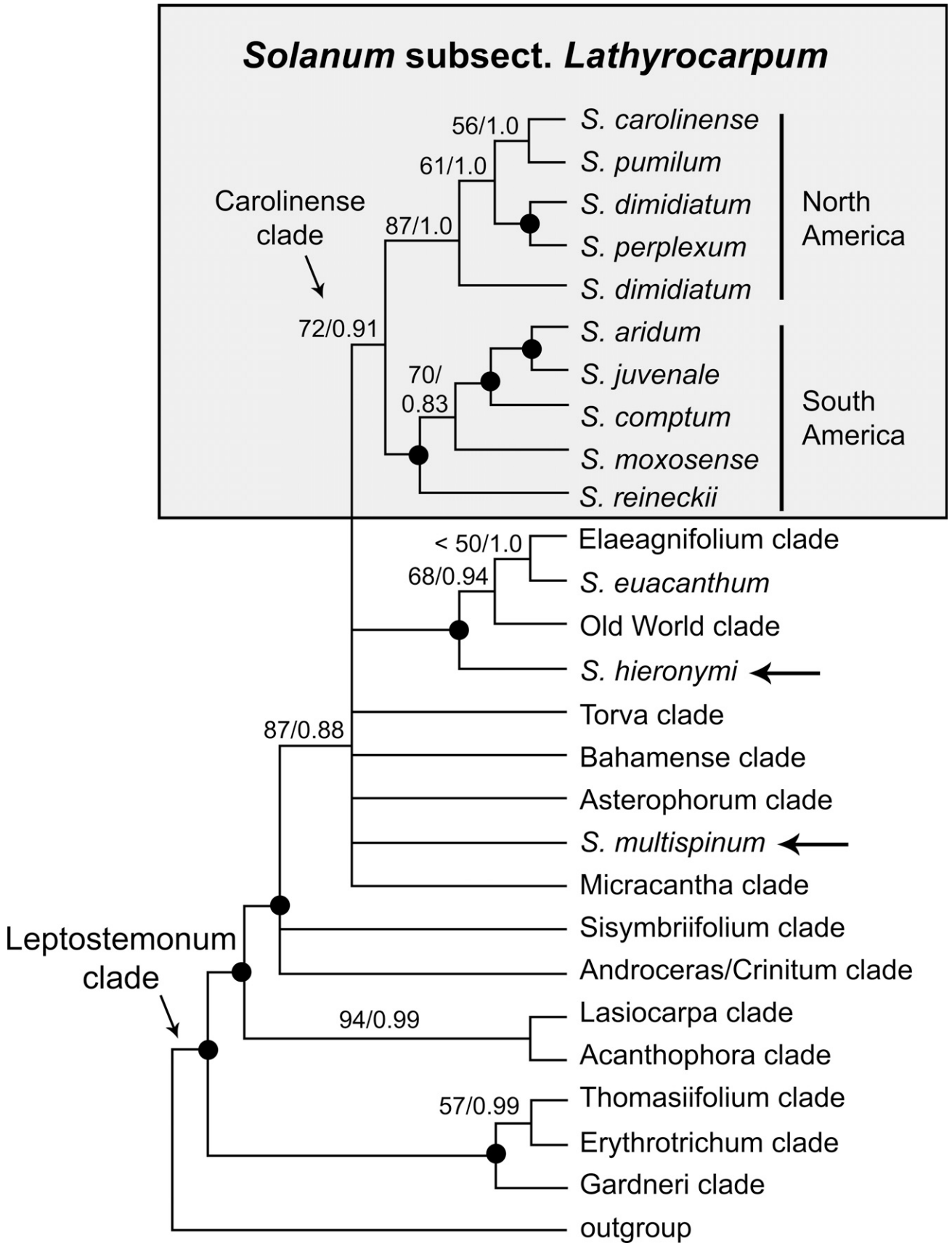

FIG. 3. Summary phylogeny of *Solanum* sect. *Lathyrocarpum* inferred from analyses of combined nuclear (ITS and *waxy*) and plastid (*trnT–trnF*) DNA sequences based on Wahlert et al. (2014). Multiple accessions of the same species have been omitted, except for *S. dimidiatum*. The cladogram is based on a strict consensus of 7,819 most parsimonious trees. Support values above the branches are given as maximum parsimony bootstrap %/ Bayesian posterior probability, and nodes with combined support values ≥ 90/0.95 are marked with a solid black circle. The arrows indicate the phylogenetic position of *S. hieronymi* and *S. multispinum* outside of the Carolinense clade in the combined DNA analysis.

and *S. dimidiatum* also have extensive root systems that are able to reproduce vegetatively from cuttings, suggesting the presence of endogenous buds in the roots (Wehtje et al. 1987; Gorrell et al. 1981). Anatomically, the below ground structures in *S. carolinense* are roots but are often incorrectly described as rhizomes (Ilnicki et al. 1962). The fleshy roots of this species contain up to ca. 50% starch. They have been reported to spread several meters vertically and horizontally and to produce shoots from deep underground, making control of this invasive pest difficult (Tisdell 1961; Gorrell et al. 1981).

Trichomes—Species are sparsely to densely stellate-pubescent with translucent, white, light brown, or golden hairs that are sessile to long-stalked with 4–10 equal or unequal lateral rays. The central ray can be absent or 1-celled and shorter than or equal to the lateral rays (*S. aridum*, *S. dimidiatum*, *S. juvenale*) or 1–5-celled and longer than the lateral rays (*S. carolinense*, *S. perplexum*, *S. pumilum*). In *S. comptum*, *S. hieronymi*, and *S. reineckii*, the stalk of the stellate hairs shows a continuum of morphology from absent to short and uniseriate, grading into a stout tapered multiseriate prickle-like stalk up to 6 mm long. *Solanum moxosense* is the only species with mainly simple hairs on the stem, and *S. hieronymi* is the only species with both stellate hairs and simple glandular hairs up to 0.3 mm long. For most, the trichome morphology is similar on all parts of the plant (e.g. stem, petiole, leaf, inflorescence axis, petiole, calyx), but in *S. carolinense*, *S. perplexum*, and *S. pumilum*, the hairs on the leaf have fewer lateral rays (4–5) and the central ray has fewer cells (1–2) than hairs of the stem.

Leaves—The leaves in *Solanum* sect. *Lathyrocarpum* are simple and petiolate, mostly ovate to elliptic in outline, but sometimes lanceolate or obovate. The leaf base varies from cuneate to attenuate, truncate, or cordate, and is typically unequal with the two sides offset by up to 1 cm. Leaf margins are usually shallowly to deeply lobed with 2–7 pairs of rounded to acute lobes or are sometimes entire, subentire, or sinuate (in *S. pumilum* and some specimens of *S. carolinense* var. *carolinense* and *S. aridum*). The margin is very deeply lobed almost to the midrib in *S. carolinense* var. *floridanum* and some plants of *S. dimidiatum* and *S. perplexum*. The leaf apex is acute, obtuse, or rounded. All species are sparsely to densely pubescent on the adaxial and abaxial surfaces, and are unarmed to moderately armed with prickles on the primary and secondary veins of both surfaces.

Inflorescences—As with other species of *Solanum*, the inflorescences in *S.* sect. *Lathyrocarpum* are developmentally terminal (Danert 1958), but have an extra-axillary position or appear axillary if they are in close proximity to the node. The inflorescences bear 1–20 flowers and develop acropetally. Inflorescences can be raceme-like and always unbranched (*S. flagellare*, *S. hieronymi*, *S. juvenale*, *S. moxosense*, *S. pumilum*, *S. reineckii*), unbranched to 1(2)-times branched (*S. aridum*, *S. carolinense*, *S. comptum*), or 2- to several-branched (*S. dimidiatum*, *S. perplexum*). The inflorescence axes and pedicels are sparsely to densely pubescent and are unarmed or sparsely to moderately armed with prickles. The pedicels of all species are weakly articulated at the base and become deflexed downward in fruit.

The species are weakly andromonoecious, with inflorescences with a variable number of hermaphroditic flowers at the proximal end and staminate flowers at the distal end (Solomon 1985, 1987; Whalen and Costich 1986; Chiarini 2007). Andromonoecy is readily detected in herbarium specimens by the hermaphroditic flowers with exserted stigmas and the staminate flowers with reduced stigmas less than or equal to the length of the anthers. In *S.* sect. *Lathyrocarpum*, the percentage of hermaphroditic flowers per inflorescence varies widely within and among species and individuals: 0–100% for *S. carolinense*, ca. 55% for *S. comptum*, and ca. 80% for *S. hieronymi* (Elle and Meagher 2000; Chiarini 2007). It has been shown that environmental factors can influence the ratio of hermaphroditic to staminate flowers in *S. carolinense*, and several hypotheses have been proposed to explain why evolutionary fitness may be conferred by andromonoecy (Solomon 1985; Whalen and Costich 1986; Wise and Cummins 2002; Vallejo-Marín and Rausher 2007 and citations therein).

Flowers—Flower buds of all species in *Solanum* sect. *Lathyrocarpum* are ovoid with a rounded apex. The flowers are pentamerous, and the corollas are actinomorphic, stellate to stellate-pentagonal, sparsely to densely stellate-pubescent abaxially, and range in color from white to light blue to light shades of violet or lavender. Herbarium specimen labels indicate that some individuals are sweetly scented at anthesis, but we could not detect a pattern among species. The anthers are yellow, equal to subequal, weakly to somewhat connivent, glabrous, and with small terminal pores directed distally. The morphology of the gynoecium is uniform across species, with an ovoid to globose ovary, an exserted style (in hermaphroditic flowers) and a clavate stigma. In some species the ovary is glandular-pubescent and may also have eglandular simple hairs (*S. carolinense*, *S. comptum*, *S. dimidiatum*, *S. perplexum*), but it is glabrous in the remaining species.

Fruits and Seeds—Fruits range from ellipsoid, ovoid, subglobose, globose, to depressed-globose; mature fruits are not known in *S. flagellare*, *S. moxosense*, *S. pumilum*, and *S. reineckii*. Immature fruits are whitish-green to dark green and may be striped or mottled, later maturing to yellow or yellowish-orange; the rinds are always tough. The calyces are persistent in fruit and can be spreading to reflexed (*S. carolinense*, *S. dimidiatum*, *S. perplexum*), weakly accrescent and covering the proximal ⅓ to ½ of the fruit (*S. aridum*, *S. hieronymi*, *S. juvenale*), or strongly accrescent and covering the entire fruit (*S. comptum*). *Solanum aridum* and *S. juvenale* have fruits with a melon-like fragrance. Seeds are uniform among species and are flattened-reniform, lenticular, and yellow with finely foveolate surfaces. D'Arcy (1974) reports low viable seed set in fruits of *S. perplexum* (as *S. dimidiatum*) with some apparently aborted seeds being twisted-lenticular.

***Chromosome Number*—**The base chromosome number in *Solanum* subg. *Leptostemonum* is $x = 12$ (Chiarini and Bernardello 2006 and citations therein), and a first report of polyploidy in the subgenus was $n = 36$ for *S. perplexum* (as *S. dimidiatum*; D'Arcy 1969). Since then, chromosome numbers have been published for several species in *S.* sect. *Lathyrocarpum*: two are diploid ($n = 12$; *S. aridum*, *S. carolinense*), two are tetraploid ($n = 24$; *S. comptum*, *S. juvenale*), and two are hexaploid ($n = 36$; *S. dimidiatum*, *S. perplexum*); see species treatments for additional information. *Solanum hieronymi* has a variety of ploidy numbers ($n = 12$, 18, and 24). The chromosome numbers of *S. flagellare*, *S. moxosense*, *S. pumilum* and *S. reineckii* are not known. In the phylogeny of Wahlert et al. (2014), three polyploid species (*S. hieronymi*, *S. dimidiatum*, and *S. perplexum*) showed different relationships in trees derived from nuclear vs. plastid DNA sequences, a result suggestive of allopolyploidization or some other mode of reticulate evolution (see below).

Habitat and Geographic Distribution—Species of the section are native to North and South America. In North America, they primarily occur in the south-central and southeastern portions of the United States. *Solanum dimidiatum* is distributed in the southern United States (Texas, Oklahoma, Arkansas, Louisiana, Kansas, and Missouri), and the closely related *S. perplexum* is mainly distributed in the Gulf Coastal Plain areas of Alabama, Florida, and Georgia. *Solanum carolinense* var. *floridanum* is restricted to Florida and Georgia, and *S. pumilum* is a narrow endemic from central Alabama and may now be extirpated in Georgia. In striking contrast, *S. carolinense* var. *carolinense* has a very large native distribution in central and southeastern North America. In the last ca. 200 yr it has become a highly invasive weed in much of the U. S. A. and southern Canada and in several other countries around the world. With the exception of the narrow endemic *S. pumilum*, the North American species are weedy and grow in disturbed areas such as roadsides, pastures, cultivated fields, river banks, and urban waste areas, as well as in undisturbed vegetation types such as eastern deciduous forests, pine forests, prairies, and cypress swamps.

Of the seven South American species, one is limited to northern and central Argentina (*S. juvenale*), one occurs in Argentina and Paraguay (*S. comptum*), and two are more widely distributed in northern Argentina, Bolivia and Paraguay (*S. aridum* and *S. hieronymi*). *Solanum moxosense* is known only from the type locality in Beni Department in Bolivia, and *S. flagellare* and *S. reineckii* are restricted to coastal states in southern Brazil. Several of the South American species are weedy (*S. aridum*, *S. comptum*, *S. hieronymi*, and *S. juvenale*) and are commonly found in highly disturbed areas such as roadsides, cultivated fields, pastures, and urban waste areas, as well as arid chaco vegetation and other vegetation types of the paranense, páramo, and espinal biogeographic provinces.

The geographic disjunction between the North and South American species of *Solanum* sect. *Lathyrocarpum* presents a pattern of amphitropical distribution for the section. In particular, the distribution between the temperate/subtropical North American species and subtropical/subarid South American species noted here has been documented in *Solanum elaeagnifolium* Cav. and in other plant genera such as *Hoffmannseggia* Cav., *Larrea* Cav., *Menodora* Bonpl., and *Tiquilia* Pers. (see Simpson et al. 2004 for discussion). In the molecular phylogeny of Wahlert et al. (2014), the species of the Carolinense clade (i.e. *S.* sect. *Lathyrocarpum*) were recovered in either one of two subclades: one composed of the North American species and the other South American ones. It was hypothesized that, because the North American clade was nested among a much larger clade of mostly Neotropical and South American spiny solanums, the North American species originated from a South American progenitor. In addition, without any evidence for a pan-American or Caribbean distributional range for species in the section, the disjunction may have resulted from a single long-distance dispersal event. However, further study among species of *Solanum* subgenus *Leptostemonum* is needed to infer patterns of historical biogeography and likely modes of dispersal for species in the section.

Phylogenetic Relationships—Molecular phylogenetic studies inferred from nuclear and plastid DNA sequences have all recovered a well-supported Carolinense clade, but its relationship to some other clades and species within the Leptostemonum clade remain unresolved (e.g. Elaeagnifolium clade, Old World clade, Torva clade, *Solanum multispinum*; Levin et al. 2006; Stern et al. 2011; Wahlert et al. 2014). Wahlert et al. (2014) produced the most detailed phylogeny of the Carolinense clade to date and found it to be composed of nine species when the combined nuclear and plastid data set was analyzed (*S. aridum*, *S. carolinense*, *S. comptum*, *S. dimidiatum*, *S. juvenale*, *S. moxosense*, *S. perplexum*, *S. pumilum*, and *S. reineckii*; Fig. 3). Node support (reported as maximum parsimony bootstrap %/Bayesian posterior probability) for the Carolinense clade was 72/0.91 in the tree from the combined data set (Fig. 3). The clade was further divided into two subclades, with one containing the North American species and the other the South American species. We have not discovered any morphological or cytological synapomorphies that can be mapped onto the North or South American clades.

The species composition of the Carolinense clade recovered in Wahlert et al. (2014) was not entirely congruent with the species included in Whalen's (1984) *Solanum multispinum* species group nor Nee's (1999) circumscription of *S.* subsect. *Lathyrocarpum*. Of the seven species in the *S. multispinum* group, five were recovered in the Carolinense clade (Table 1, Fig. 3). *Solanum multispinum* was resolved outside the Carolinense clade and is excluded from *S.* sect. *Lathyrocarpum*. *Solanum hieronymi* was recovered in the clade only when plastid sequences were analyzed (see below), but based on its close morphological similarity to *S. comptum*, it is included in the section. Similarly, nine species from Nee's *S.* subsect. *Lathyrocarpum* were placed in the Carolinense clade, but four species fell outside the clade (*S. euacanthum*, *S. hasslerianum*, *S. mortonii*, and *S. multispinum*; Fig. 3). *Solanum chamaeacanthum* was not sampled in the phylogeny, and its phylogenetic relationships within the spiny solanums are not known. Knapp (Solanaceae Source 2014) has hypothesized a taxonomic affinity with some other endemic Caribbean species (*S. gundlachii* Urb., *S. schulzianum* Urb., and *S. selleanum* Urb. & Ekman) even though it has an unusual habit of creeping and rooting at the nodes, also seen in *S. flagellare*, *S. moxosense*, and *S. reineckii* of *S.* sect. *Lathyrocarpum*. However, it is divergent from the species included in the section by its small leaves, inflorescences with flowers crowded at the distal end, strongly reflexed corollas, and long, thin stigmas. Therefore, we have excluded *S. chamaeacanthum* from our circumscription due to a lack of both molecular phylogenetic data and morphological evidence. *Solanum flagellare* was also not sampled in the phylogeny of Wahlert et al. (2014), but we have included it in *S.* sect. *Lathyrocarpum* based on its very close morphological similarity and geographical proximity to *S. reineckii*.

In the phylogeny of the Carolinense clade (Wahlert et al. 2014), different patterns of relationships for three species were recovered depending on the analysis of nuclear (ITS and *waxy*) DNA sequences vs. plastid (*trnT–trnF*) sequences. Analysis of the nuclear data set showed *S. dimidiatum* and *S. perplexum* to be resolved within the clade, but analysis of the plastid data set placed all accessions of the two species in a well-supported (91/1.0) clade which included species from the Torva clade. Similarly, the three accessions of *S. hieronymi* were recovered in the Carolinense clade based on analysis of the plastid data set, but all three were removed to a more distant phylogenetic position outside of the clade when nuclear sequences were analyzed. The conflicting phylogenetic placement of these three species, as well as the fact that two are polyploids (*S. dimidiatum* and *S. perplexum*)

or have mixed ploidy levels (*S. hieronymi*), is consistent with a history of allopolyploidization, hybridization, or some other mechanism of reticulate evolution involving species more distantly related to the Carolinense clade.

Taxonomic Treatment

Solanum sect. Lathyrocarpum (G. Don) Walp., Repert. Bot. Syst. 3: 88. 1844.—TYPE: Based on *Solanum* subsect. *Lathyrocarpum* G. Don.

Solanum subsect. *Lathyrocarpum* G. Don, Gen. Hist. 4: 436. 1838.—LECTOTYPE SPECIES: *Solanum carolinense* L., designated by D'Arcy, Ann. Missouri Bot. Gard. 59: 270. 1972.

Solanum subsect. *Asterotrichotum* Dunal, Prodr. 13: 30, 282. 1852.—LECTOTYPE SPECIES: *Solanum carolinense* L., designated by D'Arcy, Ann. Missouri Bot. Gard. 59: 267. 1972.

Erect to decumbent or sprawling perennial herbs up to 1.2 m tall; stems unbranched or branched near the base, sometimes rooting at the nodes; roots often with a rhizomatous habit and spreading horizontally, sometimes with tuber-like swellings. Stems glabrescent to densely stellate-pubescent with translucent, white, light brown, or golden hairs, the stellae sessile to stalked, 0.2–1.8 mm in diameter, with 4–10 lateral rays, the central ray absent or 1–5-celled and up to 3 mm long, unarmed or sparsely to densely armed with straight or slightly recurved yellow-brown tapered prickles up to 7 mm long, these rarely minutely glandular-pubescent. Sympodial units 2- to 3-foliate, sometimes plurifoliate, the leaves not geminate. Leaves simple, the blades 1.8–22 × 1–18 cm, ovate, elliptic or lanceolate in outline, somewhat discolorous, sparsely to densely stellate-pubescent abaxially and adaxially, the stellae sessile to short-stalked, 0.6–1.2 mm in diameter, with 4–6 lateral rays, the central ray 1–2-celled and up to 1.7 mm long, unarmed or sparsely to moderately armed with prickles up to 9 mm long on the major veins abaxially and adaxially; base cuneate, cordate or truncate, equal to unequal; margin subentire, sinuate or lobed with 1–6 lobes per side, sometimes very deeply lobed almost to the midrib; apex acute, obtuse or rounded; petioles 0.4–7 cm, sparsely to densely stellate-pubescent with hairs like those of the stem, unarmed or sparsely to moderately armed with prickles up to 12 mm long. Inflorescences 1–15 cm long, extra-axillary, unbranched or branched, with 1–20 flowers, the plants weakly andromonoecious, the axes sparsely to densely stellate-pubescent, unarmed or sparsely armed with prickles up to 5.4 mm long; peduncle up to 8 cm long; pedicels 0.5–5.5 cm in flower, 1–5.5 cm long and curved downward in fruit, spaced 0.5–2.5 cm apart, weakly articulated at the base, sparsely to densely stellate-pubescent, unarmed or sparsely armed with prickles up to 5.5 mm long. Flowers 5-merous. Calyx 4.5–14 mm long, the tube 1–5 mm long, the lobes 2.5–10 × 1.5–5 mm, narrowly or broadly ovate-lanceolate to triangular, the apex acute to acuminate, moderately to densely stellate-pubescent abaxially, glabrous adaxially, unarmed or sparsely to densely armed with prickles up to 5.5 mm long; fruiting calyx spreading to reflexed and weakly to strongly accrescent, sometimes completely covering the fruit, 7–20 mm long, the tube 0.2–5 mm long, the lobes 4–15 × 1.5–8 mm, narrowly triangular to ovate-lanceolate, sparsely to moderately stellate-pubescent, unarmed or sparsely to moderately armed with prickles up to 5 mm long. Corollas 1.2–4.6 cm in diameter, 8–25 mm long, stellate to stellate-pentagonal or rotate-stellate, chartaceous, white, pale blue, or lavender-violet, the tube 2–15 mm long, the lobes 2–17 × 4–15 mm, deltate to triangular, the apex acute to apiculate, moderately to densely stellate-pubescent abaxially, glabrous or very sparsely stellate-pubescent adaxially. Stamens with filaments 0.6–3 × 0.15–0.6 mm; anthers 3.5–10 × 0.6–2.2 mm, narrowly lanceolate, weakly or not connivent, yellow, the pores directed distally. Ovary 1–3.2 × 0.5–2.5 mm, subglobose to ovoid, glabrous or sometimes sparsely to moderately glandular-pubescent, rarely moderately pubescent with white stellate or simple hairs; style 7–15 × 0.2–1.5 mm, cylindrical, straight, glabrous or rarely sparsely glandular-pubescent at the base, rarely moderately pubescent with stellate or simple hairs, exserted in hermaphroditic flowers; stigma capitate. Fruits 0.8–2.2 × 0.7–2.5 cm, ovoid, globose or depressed-globose, the apex rounded, light green with darker green mottling or pale greenish-white when young, yellow to yellow-orange at maturity, glabrous, the rind tough. Seeds 1.5–3.5 × 1.1–3 mm, flattened-reniform, lenticular, yellow, the surface finely foveolate.

Key to the Species of *Solanum* sect. *Lathyrocarpum*

1. Stems and petioles stellate-pubescent with the central ray 1-celled and less than or equal to the length of the lateral rays or with simple hairs in one species . . . 2
   2. Plants decumbent, creeping along the ground, sometimes rooting at the nodes . . . 3
      3. Stems glabrous or very sparsely pubescent with simple hairs and sparsely armed with prickles; Bolivia . . . 8. *S. moxosense*
      3. Stems moderately to densely pubescent with stellate hairs and moderately to densely armed with prickles; southeastern Brazil . . . 4
         4. Stems, leaves, inflorescence axes, and calyces moderately pubescent with sessile to short-stalked stellate hairs, the stalks minute, up to 0.2 mm long; calyx unarmed to sparsely armed with prickles . . . 5. *S. flagellare*
         4. Stems, leaves, inflorescence axes, and calyces moderately to densely pubescent with sessile to long-stalked stellate hairs, the stalks often stout and prickle-like, up to 2 mm long; calyx moderately to densely armed with prickles . . . 11. *S. reineckii*
   2. Plants upright, not rooting at the nodes . . . 5
      5. Leaf blades 6–15 × 3–10 cm; inflorescence 2- to several-branched, with up to ca. 20 flowers per inflorescence; North America . . . 4. *S. dimidiatum*
      5. Leaf blades 1.8–10 × 1–5 cm; inflorescence unbranched or once branched, with up to ca. 6 flowers per inflorescence; South America . . . 6
         6. Stem, petioles, leaf blades, inflorescence axes, pedicels, and calyces unarmed or sparsely armed with prickles; leaf blades 2–10 × 1–5 cm . . . 1. *S. aridum*
         6. Stem, petioles, leaf blades, inflorescence axes, pedicels, and calyces moderately to densely armed with prickles; leaf blades 1.8–5.5 × 1–2.5 cm . . . 7. *S. juvenale*
1. Stems and petioles stellate-pubescent with the central ray 1–5-celled and longer than the length of the lateral rays, simple hairs absent . . . 7

7. Calyces pubescent with few to many stellate hairs bearing stout prickle-like stalks up to 6 mm long; South America 8
8. Corollas light blue; fruits 0.8–1 × 0.7–1.3 cm, globose, completely covered by the accrescent fruiting calyx; stems, petioles, leaf blades, inflorescence axes, and pedicels sparsely to moderately armed with prickles; calyces densely armed ..... 3. *S. comptum*
8. Corollas white; fruits 1.5–2.2 × 1–2 cm, depressed globose, with only the basal portion covered by the weakly accrescent fruiting calyx; stems, petioles, leaf blades, inflorescence axes, and pedicels unarmed or rarely sparsely armed with prickles; calyces unarmed or sparsely armed ..... 6. *S. hieronymi*
7. Calyces pubescent with the stellate hairs sessile or with stalks up to 0.5 mm long; North America 9
9. Plants up to 0.2 m tall; leaf margins entire, sinuate to weakly lobed; inflorescence with up to ca. 4 flowers ..... 10. *S. pumilum*
9. Plants up to 1.2 m tall; leaf margins weakly to deeply lobed; inflorescence with up to ca. 15 flowers 10
10. Stems unarmed or sparsely armed with prickles up to 6 mm long; inflorescences unbranched or once branched; corollas 2.2–3 cm in diameter; central and southeastern U. S. A., locally naturalized worldwide ..... 2. *S. carolinense*
10. Stems sparsely to moderately armed with prickles up to 12 mm long; inflorescences 2- to several-branched; corollas 2–4.4 cm in diameter; mainly Alabama, Florida, and Georgia, rarely in Mississippi ..... 9. *S. perplexum*

1. Solanum aridum Morong, Ann. New York Acad. Sci. 7: 173. 1893.—TYPE: PARAGUAY. [Presidente Hayes?]: Falls of the Pilcomayo River, 2 May 1888–1890 (fl), *T. Morong 1007* (lectotype: US–US00027459 [US–48029]!, designated by C. V. Morton, Revis. Argentine Sp. Solanum: 229. 1976; isolectotypes: BM–BM000087516 p.p. [scan!], E–E00190949 p.p. [scan!], GH–GH00077578 p.p.!, K–K000532483 [scan!], MO–2766698!, NDG–NDG044996 [scan!], NY–NY00139054 p.p.!, PH–PH00030383 [PH–01029054] [scan!], WIS ex WELC–15091 p.p. [scan!]).

Solanum elaeagnifolium var. *ovalifolium* Kuntze, Revis. Gen. Pl. 3: 225. 1898.—TYPE: ARGENTINA. Salta: Monte Morro, Nov 1892 (fl, fr), *C. E. O. Kuntze s. n.* (lectotype, designated here: NY–NY00139143!; isolectotype: US–US00027563 [US–701686]!).

Solanum aridum var. *pusillum* Hassl., Trab. Mus. Farmacol. 21: 106. 1909.—TYPE: PARAGUAY. Presidente Hayes: Salto Palmares, Jul 1906 (fl, fr), *T. Rojas 346* (lectotype, designated here: G–G00306542!).

Solanum conditum C. V. Morton, Revis. Argentine Sp. Solanum 237. 1976.—TYPE: ARGENTINA. Santiago del Estero: Departamento C. Pellegrini, Estancia El Remate, 500 m, 22 Dec 1927 (fl), *S. Venturi 5685* (holotype: US–US00027522 [US–1548974]!; isotypes: LIL–LIL88555 [scan!], NY–NY00688148!, SI–SI065951!, SI–SI065952!).

Upright perennial herb up to 0.5 m tall; stems simple or few-branched; roots producing buds and tuber-like ellipsoid swellings ca. 1–3 × 1 cm. Stems sparsely to densely pubescent with sessile stellate hairs 0.15–0.4 mm in diameter, with 4–8 lateral rays, the central ray absent or up to 0.3 mm long, unarmed or very sparsely armed with straight tapered prickles up to 3.5 mm long. Sympodial units 2- to 3-foliate when more than one inflorescence per shoot, but often only one formed and then appearing plurifoliate, the leaves not geminate. Leaves simple, the blades 2–10 × 1–5 cm, ovate-elliptic, elliptic, or oblong in outline, discolorous, densely stellate-pubescent abaxially, less densely so adaxially with hairs like those of the stems, unarmed or sparsely armed with prickles up to 3.3(5) mm long on the major veins abaxially and adaxially; base cuneate to subtruncate; margin subentire, sinuate or shallowly lobed with 2–6 lobes per side; apex obtuse to acute; petioles 0.5–5 cm long, densely stellate-pubescent, unarmed or sparsely armed with prickles up to 4 mm long. Inflorescences 1–2.5 cm long, extra-axillary, unbranched or forked, with 1–6 flowers, weakly andromonoecious with the proximal flowers hermaphroditic and the distal flowers staminate, the axes moderately to densely stellate-pubescent, unarmed or very sparsely armed with prickles up to 3 mm long; peduncle up to 2 cm long or absent, with the lowermost flower(s) emerging directly from the node; pedicels 1–2(3) cm long in flower, 2–4 cm long and curved downward in fruit, spaced 0.5–1.5 cm apart, articulated at the base, moderately to densely stellate-pubescent, unarmed or very sparsely armed with prickles up to 1.5 mm long. Calyx 7–10 mm long, the tube 2.5–4 mm long, the lobes 4–7 × 1.8–2.5 mm, linear to lanceolate, often unequal, the apex caudate to acuminate, densely stellate-pubescent abaxially, glabrous adaxially, unarmed or very sparsely armed abaxially with prickles up to 3 mm long; fruiting calyx somewhat accrescent but not completely covering the fruit, 10–20 mm long, the tube 2–4 mm long, the lobes 6.5–15 × 2–5 mm, narrowly triangular, moderately stellate-pubescent, unarmed or very sparsely armed with prickles up to 3.5 mm long. Corollas 1.7–3.5 cm in diameter, 12–16 mm long, stellate to stellate-pentagonal or rotate-stellate, chartaceous, usually white, sometimes pale blue-violet, the tube 2–6 mm long, the lobes 5–9 × 4–8 mm, deltate to triangular, the apex acute, densely stellate-pubescent abaxially, glabrous adaxially. Stamens with filaments 0.6–1.8 × ca. 0.2 mm; anthers 7–8.5 × 1.2–2 mm, narrowly lanceolate, somewhat connivent, yellow, the pores directed distally. Ovary 1.3–2.5 × 1.2–2.5 mm, subglobose-ovoid, glabrous; style 10–12 × 1–1.5 mm, cylindrical, straight, glabrous, exserted in hermaphroditic flowers; stigma capitate. Fruits 1.2–2.2 × 1.2–1.8 cm, ellipsoid to ovoid, the apex obtuse to somewhat pointed, light green with darker green mottling when young, yellow or pale yellow to yellow-orange at maturity, glabrous, the rind tough. Seeds 1.5–2.3 × 1.1–2 mm, flattened-reniform, lenticular, yellow, the surface finely foveolate.

Distribution and Habitat—*Solanum aridum* occurs in northern and central Argentina, eastern Bolivia, and western Paraguay (Fig. 4). It typically grows in disturbed areas such as roadsides and waste areas, often in sandy or clay soils. Most specimens examined occur at elevations between 300–1,200 m, but one sheet (*C. Peláez 308*) reported an elevation of 2,025 m.

Phenology—The species flowers between September and May, and fruits between November and July.

Conservation Status—*Solanum aridum* is distributed over a large area in Argentina, Bolivia, and Paraguay with a calculated extent of occurrence of ca. 1×10^6 km^2 and an area of occupancy of 1,376 km^2. It is common throughout its range and typically grows in disturbed areas, and there is no evidence that the size of its populations or number of locations are declining. *Solanum aridum* is therefore assigned a preliminary conservation status of "least concern" (LC).

Etymology—The epithet *aridum* means dry or withered and was applied by Thomas Morong (Morong and Britton 1893) because of the perceived "parched, dried appearance" of the plant.

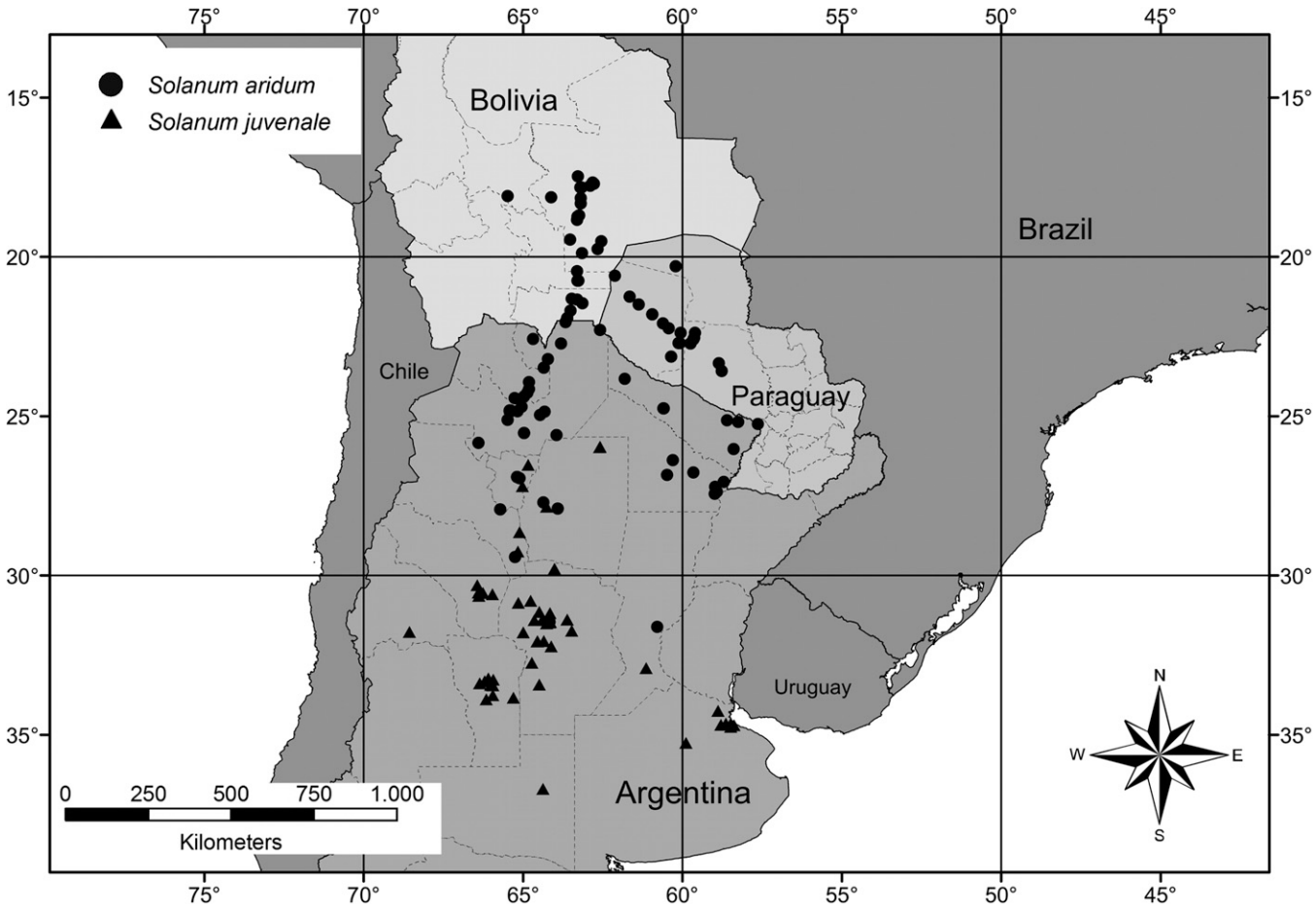

FIG. 4. Distribution of *Solanum aridum* and *S. juvenale*.

Vernacular Names and Uses—Matesevach (2002) and Barboza (2013) report several common names from Argentina: comida de víbora, meloncillo, melon del campo, and pocotillo. Two specimens from Bolivia, *G. Bourdy 2082* and *R. de Michel et al. 2539*, collected in Cordillera Province in Santa Cruz Department, recorded the names tutia and tutiami, respectively. Label information from *G. Bourdy 2082* states that the fruit was ground and used to treat scabies. The name tutia very likely refers to the ellipsoid tuber-like swellings on the roots, a name similar to tutía-tutía, which was applied to *S. hieronymi*, another species with root swellings.

Chromosome Number—Several meiotic and mitotic chromosome counts of vouchered specimens have shown *Solanum aridum* to be a diploid, with $n = 12$ (*R. Subils et al. 3566*; *G. Bernardello et al. 487*, as *S. juvenale*; *Di Fulvio 803*, as *S. juvenale*) and $2n = 24$ (*G. E. Barboza et al. 276*; *G. E. Barboza et al. 782*; *F. Chiarini 16*) (Moscone 1992; Chiarini and Bernardello 2006; Chiarini 2007).

Notes—In habit and reproductive characters, *Solanum aridum* resembles *S. juvenale*, and some intermediate forms can be found where the two species' ranges overlap (Morton 1976; Chiarini 2007). However, *S. aridum* can be separated from *S. juvenale* by the absence or very sparse density of prickles on the stem, petioles, leaf blades, inflorescence axes, pedicels, and calyces, whereas *S. juvenale* is typically moderately to densely armed with prickles, particularly on the calyces. The prickles on the leaf blades are usually much shorter in *S. aridum* (up to 3 mm long), while in *S. juvenale* they are up to 8 mm long. *Solanum aridum* also has larger leaf blades (2–10 × 1–5 cm) that are usually sinuate to shallowly lobed, compared to smaller leaf blades in *S. juvenale* (1.8–5.5 × 1–2.5 cm) that are more deeply lobed.

The ploidy level consistently differs between the two species, with *Solanum aridum* being $2n = 24$ and *S. juvenale* being $2n = 48$. Experimental studies in the greenhouse by Chiarini (2007) showed that crosses between *S. aridum* and *S. juvenale* produced triploid plants ($2n = 36$) and that ca. 90% of reciprocal crosses between the two species resulted in offspring that produced fruit with an expected amount of seeds, yet only ca. 7% of seeds were viable. *Solanum aridum* was also shown to be self-incompatible.

Of the 11 sheets of *T. Morong 1007* we examined, five are mixed collections of *Solanum aridum* and *S. multispinum* (the WIS ex WELC sheet has a specimen of *Turnera* sp.) and one sheet is composed only of *S. multispinum*. Nee et al. (2006) outlined the mixed elements of the *T. Morong 1007* collection, but here we explicitly identify the elements of each sheet. The sheets at K, MO, NDG, and PH consist solely of *S. aridum*. The BM sheet contains seven elements; six are *Solanum aridum*, but the densely prickly plant outlined in pencil with the round fruit is *S. multispinum*. The sheet at E contains three elements. The left-hand one is *S. multispinum* and the two right-hand ones are *S. aridum*; these have been annotated by M. Nee as "a." and "b." for *S. multispinum* and *S. aridum*, respectively. The GH sheet consists of five elements; the four densely prickly specimens, each with a

round fruit, are *S. multispinum*, and the central element with few prickles and buds only is *S. aridum*. The sheet at NY has five elements; the four flowering ones are *S. aridum*, and the densely prickly one with the round fruit is *S. multispinum*. The WIS ex WELC sheet contains six elements; five are *S. aridum* (four with fruit), and the other was determined by M. Nee as *Turnera* sp. and is indicated in pen on the sheet.

Finally, of the two sheets of *T. Morong 1007* at US, one sheet (US–US01014263 [US–1324449]) is composed only of *S. multispinum* while the other (US–US00027459 [US–48029]) contains only *S. aridum*. When selecting one of the two US sheets as the lectotype, Morton (1976) was unambiguous: "One of these plants [US–1324449] is the very spiny plant with stipitate-glandular stems, peduncles, and pedicels, and leaf-blades cordate at [the] base that was described a little later as *S. multispinum* N. E. Brown; the other [US–48029] is a nearly spineless plant (the few spines present being small and inconspicuous), lacking stipitate-glands, and with cuneate-based leaf-blades. I choose the latter as lectotype. . ." The sheet is also annotated as "lectotypus" in Morton's handwriting. Nee (in Nee et al. 2006) incorrectly states that the lectotype sheet is a mixture of *S. aridum* and *S. multispinum* when in fact it is composed exclusively of *S. aridum*.

In the protologue of *Solanum elaeagnifolium* var. *ovalifolium*, Kuntze (1898) cited his collection (*C. E. O. Kuntze s. n.*) from Salta Province, Argentina. Two specimens of this collection were located at NY and US. Kuntze did not indicate the location of a holotype, so we have chosen the specimen *C. E. O. Kuntze s. n.* (NY–NY00139143) as the lectotype. Both NY and US specimens are from Kuntze's herbarium and are annotated in his handwriting, but we chose the NY specimen as lectotype because it is the more complete of the two and contains several additional flowering and fruiting elements. Similarly, the collection *T. Rojas 346* from Presidente Hayes Department, Paraguay was cited in the protologue of *S. aridum* var. *pusillum*, but the herbarium where the collection was deposited was not indicated. Although the specimen now conserved at G constitutes original material, we cannot be completely certain that it was the only one used for the description, and thus we have designated the specimen *T. Rojas 346* (G–G00306542) as lectotype.

***Additional Specimens Examined*—**ARGENTINA. Catamarca: Dpto. La Paz, km. 981, 4 Apr 1950 (fr), *J. Brizuela 1164* (C); Dpto. Santa Rosa, Bañado de Obanta, 12 Mar 1944 (fl, fr), *S. A. Pierotti s. n.* (NY); El Alto, Balcozna, 19 Jan 1928 (fl), *S. Venturi 7124* (SI). Chaco: Dpto. Resistencia, Margarita Belén, 2 Feb 1948 (fl, fr), *R. M. Aguilar 1235* (NY); Dpto. Primero de Mayo, a 6 km de Cnia. Benítez, rumbo al Río Paraná, 15 Dec 2002 (fl), *G. E. Barboza et al. 527* (CORD, MO); Dpto. Primero de Mayo, al costado de la RN11, entre Resistencia y Colonia Benítez, 27°23′57.9″S, 58°59′49.8″W, 4 Mar 2012 (fl), *F. Chiarini & G. A. Wahlert 878* (CORD, UT); Dpto. Bermejo, al costado del camino, cerca de General Vedia, 27°00′47.1″S, 58°42′08.6″W, 5 Mar 2012 (fl), *F. Chiarini & G. A. Wahlert 887* (CORD, UT); Dpto. Maipú, RP9, cerca de Tres Isletas, 26°20′20.3″S, 60°18′06.7″W, 6 Mar 2012 (fl), *F. Chiarini & G. A. Wahlert 905* (CORD, UT); Dpto. Presidencia de La Plaza, RP7, Parque Nacional Chaco, 26°43′48.1″S, 59°39′30.8″W, 7 Mar 2012 (fl), *F. Chiarini & G. A. Wahlert 907* (CORD, UT); Presidencia de la Plaza, RP 7, 26°53′47.0″S, 59°49′07.8″W, 07 Mar 2012 (fl, fr), *F. Chiarini & G. A. Wahlert 912* (CORD, UT); San Fernando, RN 11, 10 km saliendo de Resistencia hacia Formosa, 5 Jan 1985 (fl), *T. E. Di Fulvio 803* (CORD); Cmte. Fernández, Col. Rivadavia, 27 Mar 1977 (fl), *Pérez 257* (CTES). Córdoba: Capital, Barrio General Paz, 1 Dec 1998 (fl), *F. Chiarini 16* (CORD); Capital, Barrio Observatorio, 20 Nov 1950 (fl), *A. T. Hunziker 8566* (CORD). Formosa: Pilcomayo, alrededores de Laguna Blanca, 25°07′50″S, 58°15′57″W, 14 Dec 2002 (fl), *G. E. Barboza et al. 513* (CORD); Dpto. Patiño, RN81, a ± 3km de Las Lomitas, 24°42′38.5″S, 60°34′44.5″W, 5 Mar 2012 (fl, fr), *F. Chiarini & G. A. Wahlert 894* (CORD, UT); Laishi, San Francisco de Laishi, Reserva Ecológica El Bagual, 20 Dec 1998 (fr), *A. Di Giacomo 378* p.p. (CTES); Dpto. Matacos, 13 km N de Ing. G. Juárez, ruta prov. 39, 23°47′S, 61°49′W, 23 Nov 2000 (fl, fr), *R. H. Fortunato et al. 6729* (BAB-n.v., MO, NY); Dpto. Pilagá, Pilagá, 3 Oct 1945 (fl), *S. A. Pierotti 4257* (BM); Patiño, Las Lomitas, 14 Nov 1984 (fr), *A. Schinini & G. Bernardello 24108* (SI). Jujuy: San Pedro de Jujuy, 16 May 1945 (fl, fr), *J. Herrera 455* (BM); Dpto. San Pedro, Ruta Nac. 34, El Quemado, 9 Nov 1974 (fl, fr), *A. Krapovickas et al. 26695* (CTES, MO, WIS); Ledesma, entre Fraile Pintado y Ledesma, 17 Dec 1968, *P. R. Legname & A. R. Cuezzo 5975* (LIL); Dpto. San Pedro, 2 km al SW de La Mendieta, 24°19.87′S, 64°59.02′W, 800 m, 13 Apr 2000 (fl, fr), *M. H. Nee et al. 50760* (CORD, NY); Dpto. El Carmen, Perico, 936 m, 15 Feb 1937 (fl), *J. West 8355* (MO). Salta: Dpto. Chicoana, El Carril, en el pueblo, al costado del camino, rumbo a Cachi, 30 Sep 2001 (fl, fr), *G. E. Barboza et al. 276* (CORD, NY); Dpto. Capital, alrededores de la Plaza de Barrio Ceferino Velarde, 19 Jan 2002 (fr), *G. E. Barboza 331* (CORD, NY); Dpto. Anta, por ruta prov. 5, 15 km antes de Las Lajitas, 24°49′29″S, 64°19′29″W, 21 Mar 2005 (fl, fr), *G. E. Barboza et al. 1262* (CORD); Dpto. Capital, vías del ferrocarril, 20 Mar 1989 (fl), *A. Del Castillo 1138* (MCNS); Salta, pr. oppidum, 24 Sep 1901 (fl, fr), *R. E. Fries 579* (S); Dpto. Capital, Parque San Martín, 1200 m, 25 May 1978 (fl), *G. Jaime 46* (MCNS); Dpto. Anta, San Severo a San Javier, 29 Mar 1985 (fl), *F. Juárez & A. Del Castillo 1195* (MCNS); Dpto. San Martín, pasando Río Bermejo, 30 Nov 1988 (fl, fr), *F. Juárez 1737* (MCNS); Dpto. Capital, ampliación Barrio El Tribunal, calle Peñaloza, 1200 m, 19 Mar 1989 (fl, fr), *F. Juárez 1775* (MCNS); Dpto. Capital, camino a la Isla, 1200 m, 19 Mar 1989 (fl, fr), *F. Juárez 1791 & 1792* (MCNS); Dpto. Metán, El Tunal, 9 Nov 1974 (fl, fr), *A. Krapovickas et al. 26711* (MO); Orán, 5 km antes de Embarcación, 2 Jun 1963 (fl), *P. R. Legname & A. R. Cuezzo 4064* (LIL); Hwy 34 from Jujuy to Tartagal, 20.5 km SW of turnoff to San Ramón de la Nueva Orán, 23°25.95′S, 64°21.24′W, 335 m, 10 May 2005 (fl, fr), *M. H. Nee 52964* (NY); along Hwy 24 from Jujuy to Tartagal, 9.4 km SW of turnoff to General Mosconi and 15.4 km SW of Tartagal, 22°40.71′S, 63°48.83′W, 430 m, 10 May 2005 (fl), *M. H. Nee 52965* (NY); Dpto. Capital, ciudad de Salta, Parque San Martín, 1187 m, 28 Jul 1977 (fr), *L. J. Novara 416* (CORD, MCNS); Dpto. Capital, FFCC a Quijano, altura de la calle Leguizamón, 1200 m, 6 Nov 1977 (fl, fr), *L. J. Novara 539* (CORD, MCNS); Dpto. San Martín, Ruta 81, km. 14, entre Senda Hachada y Hickmann Fca. Yaveré, 1 Oct 1983 (fl), *L. J. Novara 3790* (MCNS, MO); Dpto. Capital, La Lagunilla, 5–6 km E del Cerro San Bernardo, 1,000 m, 23 Oct 1988 (fl, fr), *L. J. Novara 8150* (MCNS); Dpto. Captital, ciudad de Salta, FF.CC., 1187 m, 3 Apr 1999 (fl), *L. J. Novara 11272* (MCNS); Dpto. Capital, ciudad de Salta, 1187 m, 4 Mar 2000 (fl), *L. J. Novara 11397* (MCNS); Dpto. Metán, Metán, 30 Mar 1945 (fl), *C. A. O'Donell 2468* (NY); Dpto. Campo Santo, Güemes, 3 Apr 1945 (fl, fr), *C. A. O'Donell 2647* (NY); Dpto. Capital, ciudad de Salta, Parque San Martín, 1187 m, 21 Apr 1983 (fl, fr), *M. del C. Otero 3481* (MCNS); San Javier, 19 km al S de Joaquín V. González, 16 Dec 1987 (fl), *C. Saravia Toledo 1517* (CTES); Dpto. Capital, San Bernardo, 1800 m, 3 Dec 1946 (fl), *B. Sparre 1117* (S); Dpto. Capital, ciudad de Salta, 1187 m, 28 Aug 1978 (fl), *C. Suárez 20* (MCNS); Dpto. Capital, Cerro San Bernardo, 5 Mar 1991 (fl, fr), *J. Tolaba 98* (MCNS); Dpto. Capital, ciudad de Salta, Cementerio de la Santa Cruz, 23 Dec 1998 (fl), *J. Tolaba 1294* (MCNS); Dpto. Capital, Finca La Lagunilla, camino a Mojotoro, 4 km N de Ruta Nac. 9, km. 1585, 12 km E de la ciudad de Salta, 1100–1200 m, 29 Jan 2000 (fl), *J. Tolaba 2340* (MCNS); Dpto. General Güemes, Torzalito, Ruta 9, 9.5 km S del Río Mojotoro, 750 m, 24 Oct 1986 (fl, fr), *F. Varela 1509* (MCNS); Dpto. Capital, Parque San Martín, 1190 m, 9 Oct 1964 (fl), *L. Vargas 1005* (MCNS); same locality, 3 Mar 1965 (fl), *L. Vargas 1036* (MCNS); Dpto. Capital, ciudad de Salta, 1200 m, 25 Oct 1976 (fl), *S. Zapata 80* (MCNS). Santa Fe: without precise locality, 28 Oct 1964 (fl), *Alonso et al. 550* (CORD). Santiago del Estero: Robles, Colonia Jaime, 12 Nov 1948 (fr), *F. E. Luna 1367* (CORD); Dpto. Banda, Dique Los Quiroga, 23 Dec 1978 (fl), *R. Subils & G. Bernardello 23155* (CORD). Tucumán: Colombres, Camino a San Andrés, 4 Feb 1945, *A. R. Cuezzo 14* (LIL); without precise locality, 6 Mar 1900, *T. J. V. Stuckert 8723* (CORD); Capital, Río Salí, 4 Apr 1922 (fl), *S. Venturi 1777* (SI); Dpto. Capital, Río Sali, 450 m, Jan 1926 (fl, fr), *S. Venturi 4093* (NY).

BOLIVIA. Chuquisaca: Prov. Luis Calvo, Ñancaroinza, just E of railroad tracks of railroad from Santa Cruz to Yacuiba, 20°42′20″S, 63°17′16″W, 740 m, 19 Mar 2007 (fl, fr), *M. H. Nee & R. Flores S. 54781* (NY); Prov. Luis Calvo, El Salvador, 7 Dec 1992 (fl, fr), *J. Pensiero & D. Marino 4334* (MO); El Salvador, 18 Dec 1991 (fl), *C. Saravia Toledo & J. Joaquín 10643* (CORD). Cochabamba: Prov. Mizque, on the road Vila Vila to Station Cruz, 18°00′S, 65°30′W, 619 m, 21 Dec 1949 (fl), *W. M. A. Brooke 5901* (BM, NY); Mizque, entre la plaza y el río, saliendo hacia el sur (a dos cuadras de la plaza) 17°33′49″S, 65°12′09″W, 2025 m, 2 May 2008 (fl, fr), *C. Peláez 308* (CORD). Santa Cruz: Prov. Cordillera, around highway and railroad bridges over Río Seco on N side of settlement of Río Seco, along new highway from Santa Cruz to Abapó, 18°39′S, 63°15′W, 550 m,

24 May 1998 (fl), *L. Bohs & M. Nee 2733* (UT); Prov. Cordillera, bañados del Río Parapetí, Izozo [Izozog], 16 km al N de al comunidad Cuarirenda, 18 Sep 1998 (fl), *G. Bourdy 2082* (NY); Prov. Cordillera, Izozog, Comunidad guaraní de Ibasiriri, a 3 km de "La Brecha", en la ribera del Río Parapetí, 300 m, 18 May 1999 (fl), *R. de Michel et al. 2539* (NY); Prov. Cordillera, 20 km N de San Antonio Parapatí, 19°50′S, 63°10′W, 700 m, 20 Jun 1992 (fr), *T. Killeen et al. 4237a* (AAU-n.v., LPB, MA-n.v., MO, NY); Prov. Andrés Ibáñez, between Puerto Pailas and Monte Bello, 28 Apr 2000 (fl, fr), *N. Kuroiwa & A. Maeda 1158* (NY); Prov. Andrés Ibáñez, W side of Santa Cruz, between second and third Anillos, 17°47′S, 63°12′W, 420 m, 16 Jan 1987 (fl, fr), *M. H. Nee 33575* (CORD, LPB, NY); Prov. Andrés Ibáñez, Boyuibe, 20°26′S, 63°17′W, 810 m, 23 Jul 1987 (fr), *M. H. Nee 35329* (CORD, NY, P); Prov. Andrés Ibáñez, on E side of city of Santa Cruz, 17°47′S, 63°10′W, 420 m, 21 Nov 1988 (fl, fr), *M. H. Nee 36907* (LPB, NY); Prov. Andrés Ibáñez, 2 km NW of Puerto Pailas on road to Montero Hoyos, 17°39′S, 62°48′W, 290 m, 17 Dec 1991 (fl, fr), *M. H. Nee 42132* (LPB, MO, NY); Prov. Andrés Ibáñez, Puerto Pailas, north side of railroad bridge and edge of floodplain of the Río Grande, 17°40′S, 62°47′W, 280 m, 17 Dec 1991 (fl), *M. H. Nee 42146* (LPB, MO, NY); Prov. Andrés Ibáñez, 3 km W of Puerto Pailas, along old dirt road to Santa Cruz and railroad, 17°40′S, 62°49′W, 290 m, 11 Dec 1994 (fl), *M. H. Nee 45887* (NY); Prov. Andrés Ibáñez, old dirt road highway and railroad from Cotoca to Puerto Pailas, 2.5 km W of Río Grande bridge at Puerto Pailas, 17°40′S, 62°48′30″W, 290 m, 13 Jan 1998 (fr), *M. H. Nee 47938* (CORD, NY); Prov. Andrés Ibáñez, 3.5 km NE of Montero Hoyos on dirt road to San Antonio, 17°37′S, 62°49′W, 280 m, 24 Feb 1998 (fl), *M. H. Nee 48430* (NY); Prov. Cordillera, between new Hwy from Santa Cruz to Abapó and the railroad at turnoff to Paliza, 45 km S of turnoff from Santa Cruz–Samaipata Hwy, 18°17′S, 63°12′W, 525 m, 27 Feb 1998 (fl), *M. H. Nee 48501* (MO, NY); Prov. Cordillera, along new Hwy from Santa Cruz to Abapó, N side of settlement of Río Seco, around Hwy and bridges over Río Seco, 18°39′S, 63°15′W, 550 m, 19 Apr 1998 (fl, fr), *M. H. Nee 49091* (NY); Prov. Andrés Ibáñez, along railroad tracks in Basilio, 18°06.9′S, 63°11.7′W, 480 m, 8 Jul 2004 (fl, fr), *M. H. Nee 52657* (NY); Prov. Cordillera, 3 km NW of center of Boyuibe, along Hwy to Camiri, 20°24.99′S, 63°18.27′W, 840 m, 8 Feb 2006 (fl, fr), *M. H. Nee & I. I. Linneo F. 53978* (NY); Prov. Florida: along road between Pampa Grande and the Mairana–Mataral Hwy, 18°05′S, 64°07.25′W, 1285 m, 31 Mar 2002 (fl, fr), *M. H. Nee et al. 52086* (NY [2 sheets]); Prov. Cordillera, El Curiche, 30 Jan 1946 (fl), *Peredo s. n.* (LIL); Cabezas, 420 m, 19 Jan 1945 (fl, fr), *Peredo 7* (LIL, NY); Prov. Cordillera, 10 km by road E of Gutiérez, Laguna Caucaya, 875 m, 24 Apr 1984 (fl), *G. Schmitt & D. Schmitt 98* (LPB, MO, NY). Tarija: Prov. Gran Chaco, 15 km hacia el N de Yacuiba, 630 m, 23 Sep 1985 (fl), *S. G. Beck et al. 11524* (LPB, MO, NY); 14 km E de Villa Montes, 5 May 1983 (fl), *A. Krapovickas & A. Schinini 39193* (LPB); Yacuiba, 1977 (fl, fr), *R. Lara s. n.* (LPB); Yacuiba, pueblo El Palmar, 21°53′S, 63°37′W, 612 m, 21 Sep 2001 (fl), *M. Mendoza 126* (MO); Prov. Gran Chaco, 20 km E of Villamontes, 21°18.20′S, 63°18.26′W, 355 m, 13 May 2005 (fl, fr), *M. H. Nee & J. M. Mendoza 53004* (NY); Prov. Gran Chaco, Villa Montes, 21°15.94′S, 63°28.55′W, 385 m, 12 Feb 2006 (fl, fr), *M. H. Nee & I. I. Linneo F. 54112* (NY).

PARAGUAY. Alto Paraguay: proposed Biosphere Reserve "Gran Chaco Americano," Madrejon, 20°30′47″S, 59°52′48″W, 6 Feb 2002 (fr), *E. M. Zardini & L. Guerrero 58102* (MO, NY). Boquerón: Nueva Asunción, Ruta Transchaco km 630, 7 May 1988 (fl), *A. Charpin & L. Ramella 21372* (CORD); Filadelfia, 22°20′S, 60°05′W, 26 Nov 1982 (fl, fr), *W. Hahn 783* (MO, NY, PY); Joel Estigarribia, línea 11, 17 km W del cruce a base Pratt Gill, 16 Oct 1996 (fl), *F. Mereles 6468* (FCQ); Tyto Pozo Brillante, 15 Jul 1992 (fl, fr), *F. Mereles & R. Degen 4529* (FCQ); Area Línea 12/S, 2 Sep 1992 (fl), *F. Mereles & R. Degen 4667* (FCQ); Campo Vía, Tyto a Colonia Neuland, 22°52.05′S, 59°52.08′W, 27 May 1993 (fl, fr), *F. Mereles & R. Degen 5126* (FCQ); Picada a Mistolar, 4.2 km S de Línea 10, 21 May 1994 (fl), *F. Mereles & R. Degen 5644* (FCQ); Mayor Gardel, cercanías de la Estancia, canal de desvío del Pilcomayo, lado Paraguayo, 22 May 1994 (fl), *F. Mereles & R. Degen 5660* (FCQ); 18 km de Línea 10, Picada Estancia "Palmar Quemado", 25 May 1994 (fl, fr), *F. Mereles & R. Degen 5694* (FCQ); Camping "Flor de Chaco" a 15 km al E de Filadelfia, 25 Aug 1985 (fl, fr), *L. Molas & J. Facetti 634* (MO, PY); Ruta Trans Chaco, 8 km SE de Mcal. Estigarribia, 15 Dec 1987 (fl, fr), *A. Schinini & R. A. Palacios 25774* (FCQ); Fortín Teniente E. Ochoa, 21°43′S, 60°54′W, 21 Jan 1994 (fl, fr), *E. M. Zardini & L. Guerrero 38076* (AS-n.v., MO, NY); Fortín Teniente E. Ochoa, 21°43′S, 60°54′W, 21 Jan 1994 (fr), *E. M. Zardini & L. Guerrero 38105* (AS-n.v., MO, NY); between La Patria and Fortín Teniente Emilio Ochoa, Route 9, km 635, 21°27′S, 61°22′W, 180 m, 25 May 1994 (fl, fr), *E. M. Zardini & L. Guerrero 39281* (AS-n.v., MO, NY); Parque Nacional Teniente Agripino Enciso, 21°12′37″S, 61°39′26″W, 250 m, 14 Dec 1998 (fr), *E. M. Zardini & N. Duarte 49876* (AS-n.v., MO, NY). Presidente Hayes: Chacoí, 25°12′S, 57°38′W, 5 Dec 1989 (fl, fr), *A. Schinini 26737* (NY); Estancia Brusquetti, 29 Oct 1985 (fl, fr), *N. Soria 1116* (FCQ); Filadelfia, 13 Jun 1986 (fl), *N. Soria 1261* (FCQ); between Cruce to Loma Plata and Estancia Montiel, 2 km S of Route 9, km 413, 22°40′S, 59°45′W, 26 May 1994 (fl), *E. M. Zardini & L. Guerrero 39369* (AS-n.v., MO, NY); between Cruce to Loma Plata and Estancia Montiel, 2 km S of Route 9, km 413, 22°40′S, 59°45′W, 26 May 1994 (fl), *E. M. Zardini & L. Guerrero 39389* (AS-n.v., MO, NY); Laguna Capitán, 22°32′21″S, 59°40′31″W, 29 Jul 1997 (fl, fr), *E. M. Zardini & L. Guerrero 47077* (AS-n.v., MO, NY); Pozo Colorado–Monte Lindo, 23°32′16″S, 58°46′14″W, 30 Jul 1997 (fl, fr), *E. M. Zardini & L. Guerrero 47299* (AS-n.v., MO, NY).

2. Solanum carolinense L., Sp. Pl. 1: 187. 1753.—TYPE: *Anonymous s. n.* (lectotype: LINN 248.37 [scan!], designated by Knapp and Jarvis, Bot. J. Linn. Soc. 104: 331. 1990).

Upright perennial herb up to 1.2 m tall, unbranched or branched near the base; rhizomatous and spreading horizontally. Stems sparsely to densely pubescent with sessile to short-stalked stellate hairs 0.5–1.1 mm in diameter, with 4–5(–8) lateral rays, the central ray 1–3(–5)-celled and up to 3 mm long, sparsely to moderately armed with straight tapered prickles up to 6 mm long, rarely unarmed. Sympodial units 2- to 3-foliate, sometimes plurifoliate, the leaves not geminate. Leaves simple, the blades 2–15 × 2–10 cm, ovate, lanceolate or elliptic in outline, somewhat discolorous, moderately to densely stellate-pubescent abaxially, less so adaxially with stellate hairs 0.6–1.2 mm in diameter, with 4–5(–6) lateral rays, the central ray 1(–2)-celled and up to 1.7 mm long, unarmed or sparsely to moderately armed with prickles up to 6.5 mm long on the major veins abaxially and adaxially; base cuneate; margin subentire, sinuate, or lobed with 1–4 lobes per side, sometimes very deeply lobed almost to the midrib; apex acute to obtuse; petioles 0.4–4 cm, moderately stellate-pubescent with hairs like those of the stem, unarmed or sparsely to moderately armed with prickles up to 7 mm long. Inflorescences 2–9 cm long, extra-axillary, unbranched, or infrequently branched once, with 2–12 flowers, weakly andromonoecious, the axes sparsely to moderately stellate-pubescent, unarmed or sparsely armed with prickles up to 5 mm long; peduncle up to 4 cm long; pedicels 0.5–1 cm in flower, 1.2–1.8 cm long and curved downward in fruit, spaced 0.5–1.5 cm apart, articulated at the base, sparsely to moderately stellate-pubescent, unarmed or sparsely armed with prickles up to 1.5 mm long. Calyx 5–8 mm long, the tube 1.5–2.5 mm long, the lobes 3.2–8 × 1.5–2.5 mm, lanceolate to elliptic, the apex acuminate, moderately stellate-pubescent abaxially, glabrous adaxially, unarmed or sparsely armed with prickles up to 2.5 mm long; fruiting calyx spreading to reflexed, 8–12 mm long, the tube 0.2–2 mm long, the lobes 5–9 × 1.5–3.2 mm, narrowly triangular, moderately stellate-pubescent, unarmed or sparsely armed with prickles up to 2 mm long. Corollas 2.2–3 cm in diameter, 9–15 mm long, stellate to stellate-pentagonal or rotate-stellate, chartaceous, white to pale blue, the tube 2–6 mm long, the lobes 7–12 × 4–7 mm, deltate to triangular, the apex acute, moderately stellate-pubescent abaxially, sparsely so adaxially. Stamens with filaments 1–3 × 0.3–0.5 mm; anthers 4.5–6.5 × 1.2–1.6 mm, narrowly lanceolate, somewhat connivent, yellow, the pores directed distally. Ovary 1.2–1.5 × 0.5–1.2 mm, ovoid, glabrous or sparsely to moderately glandular-pubescent with hairs up to 0.3 mm long, rarely moderately pubescent with white stellate or simple hairs; style 8–12 × 0.2–0.5 mm, cylindrical, straight, glabrous, often sparsely glandular-pubescent at the base, rarely moderately pubescent with white stellate or simple hairs, exserted in hermaphroditic flowers; stigma

capitate. Fruits 1–2 × 1–1.8 cm, subglobose to depressed globose, the apex rounded, light green with darker green mottling or pale greenish-white when immature, bright yellow at maturity, glabrous, the rind tough. Seeds 1.7–2.4 × 1.6–1.8 mm, flattened-reniform, lenticular, yellow, the surface finely foveolate.

Key to the Varieties of *Solanum carolinense*

1. Leaf margins subentire, sinuate, or lobed; sinuses of lobes, when present, reaching less than half the distance to the midvein; apex of leaf lobes subacute to acute, sometimes rounded ..... *Solanum carolinense* var. *carolinense*
1′. Leaf margins deeply lobed to parted; sinuses of lobes reaching more than half the distance to the midvein or almost to the midvein; apex of leaf lobes typically rounded ..... *Solanum carolinense* var. *floridanum*

2a. Solanum carolinense L. var. carolinense

Solanum carolinense var. *pohlianum* Dunal, Prodr. 13(1): 305. 1852.—TYPE: BRAZIL. Without precise locality, s.d. (fr), *J. B. E. Pohl s. n.* (lectotype, designated here: M–M0171734 [scan!]).

Solanum pleei Dunal, Prodr. 13(1): 305. 1852.—TYPE: U. S. A. Am[erica] septentrionale, s.d. (fl, fr), *A. Plée 204* (holotype: P–P00325315!; isotype: MPU–MPU022909 [scan!]).

Solanum carolinense var. *albiflorum* Kuntze, Revis. Gen. Pl. 2: 454. 1891.—TYPE: U. S. A. Missouri: St. Louis, 1 Sep 1874 (fr), *C. E. O. Kuntze 2768* (lectotype, designated here: NY–NY00138948 [scan!]).

Solanum carolinense f. *albiflorum* (Kuntze) Benke, Am. Midl. Nat. 22: 213. 1939.—TYPE: Based on *Solanum carolinense* var. *albiflorum* Kuntze.

***Distribution and Habitat*—**In the protologue of *Solanum carolinense* var. *carolinense*, Linnaeus (1753) writes "*Habitat in Carolina*," but a more precise geographic origin of the lectotype specimen cannot be determined. While it is likely that it was collected in the southeastern United States in the vicinity of the Carolinas, it is possible that it was collected from a plant grown in Europe from seed collected from North America (S. Knapp, pers. comm.). Furthermore, the native distribution of *S. carolinense* var. *carolinense* prior to European settlement in North America is not known with much precision at a local scale because of its weediness and ability to disperse and colonize areas outside of its native range. Based on the location data of ca. 500 herbarium specimens examined for this work, its inferred native distribution extends from central Florida north to New York and Massachusetts and west to Texas, Oklahoma, Kansas, and Nebraska to about the 97th meridian west (Fig. 5). The species reaches Canada only in the southernmost areas

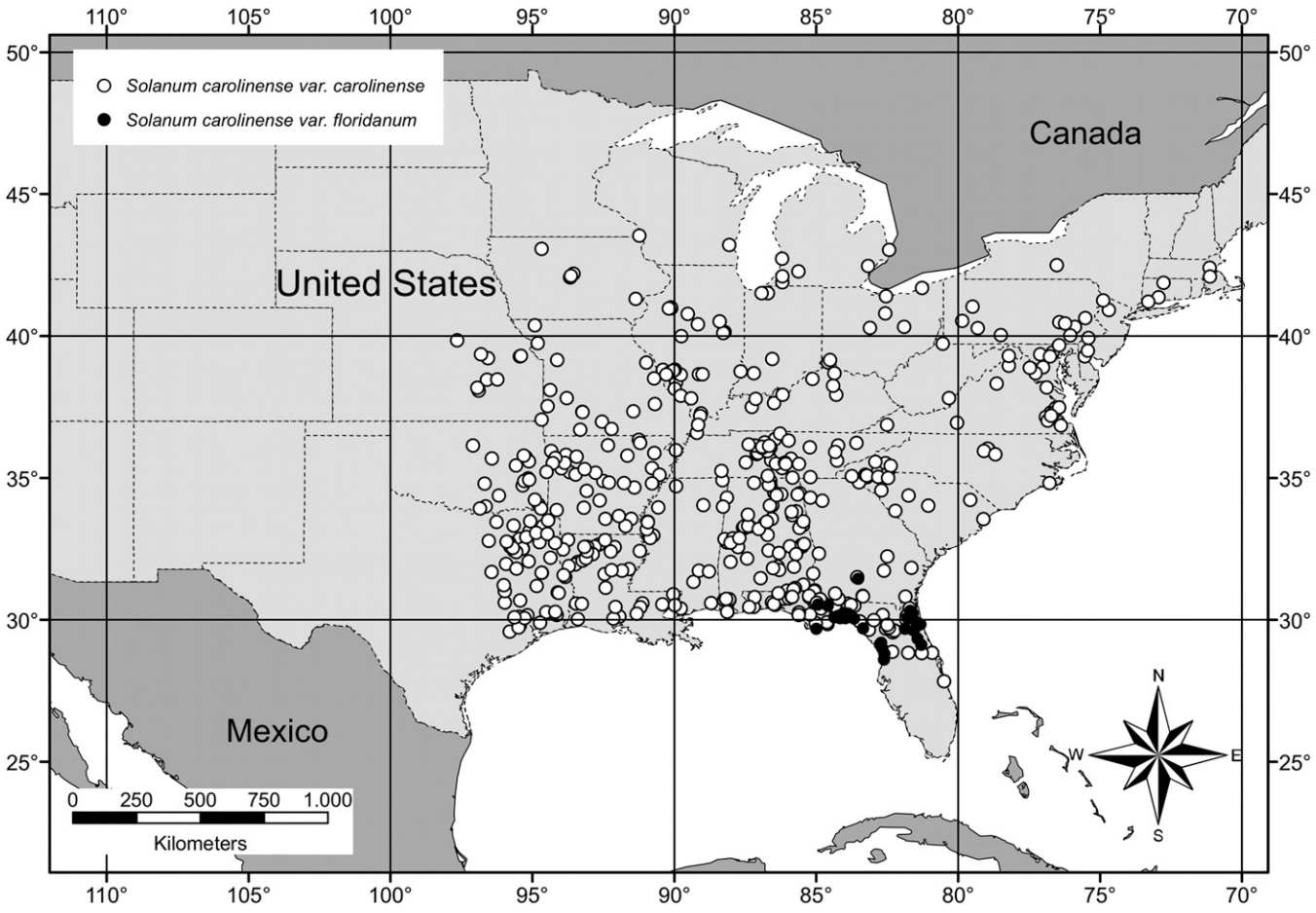

Fig. 5. Distribution of *Solanum carolinense* var. *carolinense* and *S. carolinense* var. *floridanum*.

of Ontario and Quebec Provinces (Bassett and Munro 1986; Cayouette 1972), and except for a single unverified report of the species in Mexico from the states of Sonora, Tamaulipas, and Nuevo Leon (Eberwein and Litscher 2007), we have not seen any additional evidence suggesting it occurred there as part of its native range. Recent floristic treatments and online databases record occasional occurrences in the western United States (Colorado, New Mexico, Arizona, Utah, Idaho, Washington, Oregon, and California) where some states have classified the species as a noxious weed (e.g. Arizona, California, and Nevada [USDA 2014]).

The species has been introduced in many areas around the world and has been reported from Australia, Austria, Bangladesh, Canada, China, Croatia, England, France, Georgian Republic, Germany, Haiti, India, Italy, Japan, Moldova, Nepal, the Netherlands, New Zealand, Norway, South Korea, Turkey, and Ukraine (Cayouette 1972; Trapaidze 1972; D'Arcy 1974; Gazi-Baskova and Segulja 1978; Izhevskii et al. 1981; Bassett and Munro 1986; Ouren 1987; Webb et al. 1988; Park et al. 2001; Merluzzi et al. 2003; Li et al. 2006; Imaizumi et al. 2006; Eberwein and Litscher 2007; Dirkse et al. 2007; Viggiani 2008; Yasuyuki et al. 2010; Follak and Strauss 2010; Chinnusamy et al. 2011; Klingenhagen et al. 2012; Canadensys 2014).

Solanum carolinense var. *pohlianum* was described from a Pohl collection that was likely made near the Brazilian port city of Salvador from what was an adventive population established by an accidental introduction to the area (L. Giacomin pers. comm.). There is no evidence that *S. carolinense* has been collected in Brazil since the time of Pohl's collections (Stehmann et al. 2013). In addition, we have not seen any specimens or reports of the species from other locations in Central or South America or Africa.

In some areas outside of its native range (e.g. China), *Solanum carolinense* var. *carolinense* occurs as a harmless exotic species, but in other areas the species is a serious pest (e.g. Italy, Japan). Apparently it is inadvertently dispersed by humans over long distances through shipments of soybeans or livestock fodder that are contaminated with seeds (Ouren 1987; Park et al. 2001; Follak and Strauss 2010). New introductions to temperate and subtropical regions around the world are expected to continue as long as agricultural crops are exported abroad from the eastern and southeastern United States.

Solanum carolinense var. *carolinense* grows in a wide variety of conditions, from dry, well drained soils to seasonally inundated swales, fields, and river banks, from deep shade to full sun, and in sands, clays, loams, gravels, serpentine and calcareous outcrops, and the margins of coal mine and dredge spoils. It grows in various plant communities including prairies, deciduous woodlands, swamps, and pine forests, and in disturbed areas such as roadsides, grazed and mowed pastures, ditches, cultivated fields, urban waste areas, and utility and railroad rights of way. It has been collected from cultivated fields of peanuts, wheat, maize, cotton, tomato, potato, alfalfa, green beans, and soybeans. The species grows at elevations from 0–850(–1200) m.

Phenology—In North America, the species flowers between May and October and fruits between June and November.

Conservation Status—The calculations for the extent of occurrence (ca. 3×10^6 km^2) and area of occupancy (7,328 km^2) for *Solanum carolinense* var. *carolinense* were based on its estimated native range in North America (Fig. 5). Because it is invasive and has the potential to expand its population size when introduced to suitable habitat outside of its native range, it is assigned a preliminary conservation status of "least concern" (LC).

Etymology—The specific epithet means "from the Carolinas" in the United States, the presumed type locality of the species.

Vernacular Names and Uses—*Solanum carolinense* var. *carolinense* is widely known as horsenettle or Carolina horsenettle, but several less commonly used names include ball-nettle, bull-nettle, apple-of-Sodom, and sand-brier (Alex et al. 1980, Muenscher 1951; Bassett and Munro 1986). Given its wide distribution outside of North America, vernacular names in other languages include: morelle de la Caroline (French), ortiga de caballo (Spanish), Carolinsche-Pferdenessel, Carolina-Nachtschatten, and Trostbeere (German), Paardenetel (Dutch), паслён каролинский (Russian), and waru nasubi (Japanese) (Alex et al. 1980; Eberwein and Litscher 2007).

Some accounts have reported that the dried fruits and roots have been used as a sedative, antispasmodic, diuretic, and aphrodisiac, and that poultices, ointments, and teas made from the fruits or leaves have been used for the treatment of epilepsy, sore throat, toothache, contact dermatitis, worms, and mange in dogs (Grieve 1974; Foster and Duke 1990; Yasuyuki et al. 2010). However, all parts of the plant are considered to be poisonous, and the glycoalkaloids contained in the mature fruits are known to be toxic to livestock (cattle, sheep) and humans (Muenscher 1951; Hulbert and Oehme 1963; Hardin and Arena, 1969; Hamilton 1980; Turner and Szczawinski 1991; Wink and Van Wyk 2008). Cipollini and Levey (1997) reported that mature fruits contained 10–30 mg/g dry mass of glycoalkaloids, primarily α-solasonine and α-solamargine. A case of fatal human poisoning was documented in 1963 when a 6-yr-old boy in Pennsylvania died after eating the fruit of *S. carolinense* var. *carolinense* (Kingsbury 1964).

Chromosome Number—A gametophytic chromosome number of $n = 12$ was reported by D'Arcy (1969), Hardin et al. (1972), and Bassett and Munro (1986), and a sporophytic number of $2n = 24$ was reported by Hill (1989).

Ecology—As a weedy species, *Solanum carolinense* var. *carolinense* exhibits several attributes that make it a highly competitive and invasive weed: it colonizes early successional or disturbed habitats, produces many seeds per fruit, grows rapidly, reproduces vegetatively, resists mechanical methods of control, has generalized pollinators, and can grow in a variety of biotic and abiotic conditions (e.g. Kolar and Lodge 2001). These same characteristics that contribute to the invasiveness of *S. carolinense* var. *carolinense* also make it difficult to control. Human disturbance such as plowing serve to open up new habitat for its dispersal and establishment. It is capable of producing ca. 40–170 seeds per fruit, with a single plant producing up to ca. 5,000 seeds that may be dispersed by birds and mammals (Martin et al. 1951; Gunn and Gaffney 1974; Solomon and McNaughton 1979; Cipollini and Levey 1997).

As with other weedy species, *Solanum carolinense* var. *carolinense* is pollinated by a variety of generalist insects. The flowers are odorless and without nectar, and provide pollen as a reward (Solomon 1987). In North America, the species has been observed to be buzz pollinated by a variety of non-specialist bees, including sweat bees (*Lasioglossum* spp.), bumblebees (*Bombus* spp.) carpenter bees (*Xylocopa* spp.), and mining bees (*Andrena* spp.; Hardin et al. 1972; Quesada-Aguilar et al. 2008).

In its native range and in many introduced areas, *Solanum carolinense* var. *carolinense* is extremely difficult to control in cultivated areas and pastures once established. The magnitude of the economic impact to agriculture is difficult to estimate, but given its wide distribution in the United States and locations abroad, the costs associated with control of the species, crop losses, contaminated harvests and fodder, and reduced availability of pastureland are potentially enormous (e.g. Follak and Strauss 2010). In North America, some crop yields have been decreased up to 60% by its presence, and the quality of pastures can be severely diminished (Gorrell et al. 1981; Hackett et al. 1987; Pimentel et al. 2000).

Control of the species using mechanical methods or single herbicide applications is usually not effective (Ilnicki et al. 1962; Nichols et al. 1992). Plants that are mowed during the first half of the growing season re-emerge vigorously, and tilling causes vegetative reproduction from root fragments, which often increases the severity of the infestation (Furrer and Fertig 1960; Takematsu et al. 1979; Gorrell et al. 1981; Wehtje et al. 1987). Intensive herbicide applications with certain mixtures and treatments are somewhat effective (e.g. Whaley and Vangessel 2002; Armel et al. 2003; Beeler et al. 2004), but the use of biological control agents carries considerable risk given the relatively close phylogenetic relationship to other solanaceous crops such as tomato, potato, and eggplant (Nichols et al. 1992).

In addition to being an aggressive agricultural pest, *Solanum carolinense* var. *carolinense* is a host to many insects, fungi, and viruses that can cause damage to a variety of crops, especially solanaceous ones such as potato (*Solanum tuberosum* L.), tomato (*Solanum lycopersicum* L.), tobacco (*Nicotiana tabacum* L.), pepper (*Capsicum* spp.), and eggplant (*Solanum melongena* L.). Thus, not only does var. *carolinense* need to be controlled in fields and pastures as a direct competitor, but also it needs to be managed in adjacent areas in order to limit its ability to serve as a host. Some of the important phytophagous insect pests that use it as a host include Colorado potato beetle [*Leptinotarsa decemlineata* (Say)], false Colorado potato beetle [*Leptinotarsa juncta* (Germar)], eggplant lacebug [*Gargaphia solani* (Heidemann)], potato stalk borer [*Trichobaris trinotata* (Say)], eggplant flea beetle [*Epitrix fuscula* (Crotch)], potato flea beetle [*Epitrix cucumeris* (Harris)], tobacco hornworm [*Manduca sexta* (Haworth)], pepper maggot [*Zonosemata electa* (Say)], yellowstriped armyworm [*Spodoptera ornithogalli* (Guenée)], eggplant leafminer [*Tildenia inconspicuella* (Murtfeldt)], potato tuberworm [*Phthorimaea operculella* (Zeller)], pepper weevil [*Anthonomus eugenii* (Cano)], potato psyllid *Paratrioza cacherelli* (Sulc.)], and eggplant tortoise beetle [*Gratiana pallidula* (Boheman)] (Somes 1916; Anderson and Walker 1937; Foott 1968; Bassett and Munro 1986; Hare and Kennedy 1986; Wise and Sacchi 1996; Capinera 2001; Kariyat et al. 2013). The species also acts as a host reservoir to viral and fungal pathogens, including tobacco mosaic virus, tobacco vein mottling virus, tobacco etch virus, peach rosette mosaic virus, cucumber mosaic virus, tomato leafspot fungus (*Septoria lycopersici* Speg.), and early blight of tomato [*Alternaria solani* (Ell. & G. Martin) Sor.]; Pritchard and Porte 1921; Ellis 1971; Ramsdell and Myers 1978; Natsuaki et al. 1992; Blancard 2012; Goyal et al. 2012).

Reproductive Biology—*Solanum carolinense* var. *carolinense* is a weakly andromonoecious species with a system of self-incompatibility, and several studies have investigated the ecology, evolution, and biochemistry of its reproductive biology. The developmentally terminal and indeterminate inflorescence develops acropetally and produces variable numbers of hermaphroditic flowers at the proximal end and staminate flowers at the distal end. Studies of andromonoecy in the species have shown that sex expression in the inflorescence (i.e. the ratio of hermaphroditic:staminate flowers) can be influenced by various environmental and ecological factors (Solomon 1985; Steven et al. 1999; Wise and Cummins 2006; Wise et al. 2008; Wise and Hébert 2010), whereas others have found evidence that sex expression is a heritable trait (Elle 1998, 1999; Elle and Meagher 2000). Other research has shown that the androecium of both hermaphroditic and staminate flowers is fully developed and produces fertile pollen (Solomon 1985) and that the production of pollen in staminate flowers functions as a reward to attract pollinators as well as a source of pollen for other flowers (Solomon 1987; Connolly and Anderson 2003; but see Vallejo-Marín and Rausher 2007).

While *Solanum carolinense* var. *carolinense* exhibits most traits of a weedy species, a notable exception is its system of self-incompatibility (SI), which contrasts with self-compatible breeding systems in most weedy species (Travers et al. 2004). As with other species in the Solanaceae, *S. carolinense* var. *carolinense* has been shown to have a gametophytic SI system under control of the single *S*-locus gene, which regulates stigma-pollen compatibility (e.g. Richman et al. 1995; Travers et al. 2004). Studies into the SI system of *Solanum carolinense* var. *carolinense* have shown that the diversity of *S*-alleles is lower than in other SI species (Richman et al. 1995), and the SI system is plastic because of variability in the strength of SI alleles (Mena-Ali and Stephenson 2007). Even though the SI system becomes less stringent as flowers age or when there is a lack of cross pollen (Travers et al. 2004), selfed progeny do not experience the deleterious effects of inbreeding depression, which may facilitate colonization and establishment of the species (Mena-Ali et al. 2008; Kariyat et al. 2011)

Notes—*Solanum carolinense* var. *carolinense* is similar to both *S. dimidiatum* and *S. perplexum* based on habit and overall morphology, but it can be separated by its unbranched or rarely once-branched inflorescence (compared to a 1- to several-branched inflorescence in the other two species). It is further distinguished from *S. dimidiatum* by its light brown stellate hairs with 4–5(–6) lateral rays and the central ray 1(–2)-celled and longer than the lateral rays (compared to white stellate hairs with (4–)6–10 lateral rays and the central ray 1-celled and equal to or shorter than lateral rays). *Solanum carolinense* var. *carolinense* is separated from *S. perplexum* by its shorter prickles on the stems and leaves (up to 6.5 mm vs. up to 15 mm in *S. perplexum*), its smaller leaves (up to 15 × 10 cm vs. up to 22 × 18 cm), and its smaller corollas (up to 3 cm in diameter vs. up to 4.6 cm in diameter).

Solanum carolinense var. *carolinense* is a Linnean name lectotypified by Knapp and Jarvis (1990). We have placed two names, *S. carolinense* var. *pohlianum* Dunal and *S. pleei* Dunal, in synonymy under *Solanum carolinense* because their types unambiguously match the lectotype specimen of *S. carolinense* var. *carolinense*. Another name, *S. occidentale* Dunal, has been previously treated as a synonym of *S. carolinense* (e.g. D'Arcy 1974), but it is now recognized as a synonym of *S. anguivi* Lam. (Solanaceae Source 2014). Two infraspecific names have been proposed to include only white-flowered individuals of the species, and we have also placed these in synonymy under

S. carolinense var. *carolinense*. White- and blue-flowered plants are commonly found in mixed populations across the entire range of *S. carolinense*, and we do not consider corolla color to be a useful character in delimiting an infraspecific taxon. In the protologue of *S. carolinense* var. *albiflorum*, Kuntze did not cite a type specimen. We have chosen the specimen *C. E. O. Kuntze 2768* (NY) as the lectotype, which is from Kuntze's herbarium and is annotated with the name of the taxon in his handwriting. Dunal (1852) makes reference to a Pohl and Sendtner collection from Brazil in the protologue of *S. carolinense* var. *pohlianum*. We have located a single specimen collected in Brazil by Pohl, but because it is not possible to determine with certainty whether or not it was the same sheet Dunal used in his description, we have designated the specimen *J. B. E. Pohl s. n.* (M–M0171734) as a lectotype.

Selected Specimens Examined—CANADA. Ontario: Lambton County, Point Edward, 19 Aug 1902 (fl), *C. K. Dodge s. n.* (SMU); Point Edward, 14 Aug 1901 (fl), *J. Macoun 54532* (NY).

U. S. A. Alabama: Houston County, near W bank of Chattahoochee River, 2 mi. NE of Chattahoochee St. Park, 10 mi. SE of Gordon, 31°02′N, 85°01′W, 10 Jul 1988 (fr), *R. Burckhalter 1442* (UNA). Arkansas: Washington County, 4 mi. S of Prairie Grove, T14N, R32W, SWSE, S1, 30 May 1977 (fl), *D. Griffin I-8* (BRIT). Connecticut: New Haven County, Mill Rock, Hamden, 28 Jun 1955 (fl), *J. J. Neale s. n.* (FLAS). Delaware: N of Leipsic, 30 Jun 1949 (fl), *S. C. Hood 2271* (FLAS). District of Columbia: Near U. St., Washington, D.C., 3 Aug 1895 (fr), *L. H. Dewey 316* (MO). Florida: Wakulla County, St. Marks Nat'l Wildlife Refuge, Wakulla Unit, S side of Northline Rd., at second crossing, ca. 1.5 mi. WSW of Wakulla Beach Rd., 30.13884 N, 84.27885 W, 12 Jun 2007 (fl), *L. C. Anderson 23179* (FSU). Georgia: Toombs County, ca. 1 mi. E of Vidalia on US 280, 32°12′N, 82°25′W, 18 May 1976 (fl), *J. C. Solomon 5559* (MO). Idaho: Canyon County, New Plymouth, 670 m, 10 Sep 1910 (fr), *J. F. Macbride 732* (P). Illinois: Tazewell County, near 10 Mile Creek, 8 Sep 1951 (fl), *V. H. Chase 12158* (BRIT). Indiana: Porter County, US 30, ca. 4 mi. E of Valparaiso, 4 Jul 1961 (fl), *N. C. Henderson 61–543* (FSU). Iowa: Story County, just N of Iowa State University and Squaw Creek, R24W, T84N, 13 Jul 1969 (fl), *G. Davidse 1788* (MO). Kansas: Morris County, Bridwell Ranch, 8 mi. S and 1 mi. E of Council Grove, 20 Jun 1966 (fl), *D. E. Dallas 12* (VDB). Kentucky: Madison County, Fort Boonesborough State Park, SW of jct. of Ky. 627 and the Kentucky River, 25 Jun 1992 (fl, fr), *J. R. Abbott et al. 2691* (FLAS). Louisiana: Ouachita Parish, W of LA 557 between Cypress Creek and Caldwell Parish line, SW of Luna, T15N, R2E, S15, 6 May 1986 (fl), *R. D. Thomas 95925* (BRIT, FLAS, NY). Maryland: Howard County, Rt. 94, 1.5 mi. S of Lisbon, 19 Sep 1966 (fl), *C. F. Reed 80284* (MO). Massachusetts: Middlesex County, center of Cambridge, vicinity of Harvard University, 7 Jul 1975 (fl), *H. E. Ahles 80522* (SMU). Michigan: Cass County, Howard Twp., T7S, R16W, S16, 25 Jul 1950 (fl), *G. W. Parmelee 1610* (VDB). Mississippi: Washington County, NE of Stoneville, Delta Experimental Forest, T19N, R7W, S33, 29 May 1987 (fl), *C. T. Bryson 5832* (BRIT). Missouri: Lincoln County, ca. ½ mi. N of Big Creek, dirt road W of MO 61, 10 Aug 1978 (fl), *W. G. D'Arcy 1061* (FSU). New Jersey: Cumberland County, Stow Creek Twp., Gum Tree Corner, N of Gum Tree Corner Wildlife Management Area, Canton quadrangle, 4 Aug 2004 (fl), *G. Moore 6686* (VDB). New Mexico: Doña Ana County, Las Cruces, New Mexico State University, Frenger Mall between Foster Hall and Science Hall, 1219 m, 9 Oct 2002 (fl), *R. W. Spellenberg s. n.* (BRIT, NMC-n.v.). New York: Stewart Park, Ithaca, 1 Aug 1933 (fl, fr), *G. Wakeman-Bonne s. n.* (P). North Carolina: Carteret County, ca. 2 mi. NW of Beaufort, 29 Aug 1952 (fl), *H. L. Blomquist 15697* (VDB). Ohio: Delaware County, below Stratford, 15 Sep 1928 (fr), *R. Crane 3223* (FSU). Oklahoma: Creek County, Deep Fork Wildlife Management Area, T14N, R9E, S28, 23 Jun 1998 (fl), *D. Benesh et al. DFX254* (BRIT). Pennsylvania: Bedford County, 1.5 mi. E of West End, 5 Aug 1970 (fl), *H. Duppstadt & D. Duppstadt 2833* (BRIT, FLAS, NY, UNA, VDB). South Carolina: Pickens County, by US 178, 0.6 mi. N of South Carolina Hwy 11, 25 May 1972 (fl), *J. L. Collins 553* (VDB). Tennessee: Anderson County, 20,500 ft. N, 65,150 ft. E, Corp of Engineer Map, 1959, 10 Jun 1961 (fl), *W. H. Ellis 28609* (FSU). Texas: Van Zandt County, 1.5 mi. SW of Van, on Hwy. 20 frontage road at exit 450, 32°30′32″N, 95°39′18″W, 147 m, 20 May 2012 (fl), *G. A. Wahlert 144* (BRIT, MO, NY, UT). Virginia: Isle of Wight County, behind cemetery of Mill Swamp Baptist Church, St. Rts. 621 & 623, ca. 3.8 mi. N of Raynor, 8 Jun 1989 (fl) *G. M. Plunkett 295* (BRIT). West Virginia: Wetzel County, near Littleton, 26 Jul 1972 (fl), *O. E. Haught 7302* (VDB); between Hot Springs and White Sulphur Springs, 3 Jul 1938 (fl), *G. Wakeman-Bonne s. n.* (P). Wisconsin: Vernon County, Island 8, Mississippi River, mi. 688.4, T14N, R7W, S18, large island E side of main channel, 636 m, 3 Jul 1975 (fl), *S. R. Ziegler & M. F. Leykom 1581* (BRIT).

2b. Solanum carolinense var. floridanum Chapm., Fl. South. U.S. 349. 1860. TYPE: Based on *Solanum floridanum* Shuttlw. ex Dunal

Solanum floridanum Shuttlw. ex Dunal, Prodr. 13(1): 306. 1852, non Raf. (1840).—TYPE: U. S. A. Florida: Wakulla County, prope St. Marks, May 1843 (fl), *F. I. X. Rugel s. n.* (holotype: G-DC–G00130218!; isotypes: G–G00301662!, G–G00370313!, K, MO–1841550!, MPU–MPU022910 [scan!], NY–NY00138949!).

Solanum godfreyi Shinners, Sida 1: 108. 1962, nom. nov. for *Solanum floridanum* Shuttlw. ex Dunal.—TYPE: Based on *Solanum floridanum* Shuttlw. ex Dunal.

Distribution and Habitat—*Solanum carolinense* var. *floridanum* occurs primarily in Florida in the vicinity of the Suwannee, Apalachicola, and Aucilla Rivers in the Gulf Coast region and near the Atlantic coast in the northeastern part of the state. The variety is also known from several localities in the coastal plain of Georgia (Fig. 5). It often grows in moist areas and on sandy river banks, but also in slash pine–palmetto woodlands and roadsides. The variety grows at elevations from sea level to ca. 10 m.

Phenology—The variety flowers between May and September and fruits between June and November.

Conservation Status—*Solanum carolinense* var. *floridanum* is known from ca. 27 locations, several of which are situated in protected areas (Waccasassa Bay State Preserve, Chassahowitzka National Wildlife Refuge, Aucilla Wildlife Management Area, Torreya State Park, and St. Mark's National Wildlife Refuge). Because it grows in highly disturbed areas such as roadsides, cultivated fields, and grazed pastures, it is estimated that there will not be any significant reduction in population size or locations; with an extent of occurrence of ca. 35,000 km^2 and area of occupancy of 480 km^2, *S. carolinense* var. *floridanum* is assigned a preliminary conservation status of "least concern" (LC).

Etymology—The infraspecific epithet "*floridanum*" refers to the state of Florida, U. S. A. where the type locality of St. Marks is located.

Vernacular name—Commonly known as Florida horsenettle (e.g. *J. Scanlon & T. Matthews 138*).

Chromosome Number—D'Arcy (1969) reports a gametophytic chromosome number of $n = 12$ [*D'Arcy 3500* and *3501* (FLAS)].

Notes—*Solanum carolinense* var. *floridanum* has sometimes been treated as a synonym under *S. carolinense* var. *carolinense* or recognized at the rank of species (i.e. as *S. godfreyi* Shinners), but we agree with D'Arcy (1974) and others that the taxon is best maintained the rank of variety. While var. *floridanum* is very similar to var. *carolinense*, its deeply lobed leaves and rounded leaf lobes, preference for moist habitats, and mostly distinct distribution from var. *carolinense* support its continued recognition as a variety. Sometimes intermediates between var. *carolinense* and var. *floridanum* occur and a definitive determination cannot be made (e.g. *E. West & L. E. Arnold s. n.* [FLAS, GH-n.v.]; *R. L. Nichols s. n.* [MO]).

Solanum floridanum Shuttlw. ex Dunal (1852) is an illegitimate later homonym of *S. floridanum* Raf. (1840). Shinners

(1962) recognized the taxon at the rank of species and provided the replacement name *S. godfreyi* Shinners. D'Arcy (1974) mistakenly cited the specimen *R. K. Godfrey 60037* as the type of *S. godfreyi*, but under Art. 7.3 of the ICBN (McNeill et al. 2012), the type of the replacement name is typified by the type of the replaced illegitimate homonym (in this case, *F. I. X. Rugel s. n.*). According to Art. 58 of the ICBN (McNeill et al. 2012), the name *S. carolinense* var. *floridanum* Chapm. is correct when this taxon is recognized at the rank of variety. This article states that when the epithet of an illegitimate name is used in a combination at a different rank, the resulting name is treated as a nomen novem and priority does not date back to the publication of the illegitimate name.

Additional Specimens Examined—U. S. A. Florida: Citrus County, Chassahowitzka National Wildlife Refuge, 8 Jun 1969 (fr), *B. Cook s. n.* (FLAS); Hollins zone 67, monitoring transect C, T17S, R16E, SE ¼ of NE ¼ of S35, 17 Jul 2000 (fl), *J. Scanlon & T. Matthews 138* (FLAS); Clay County, Doctor's Inlet, 24 July 1968 (fl), *W. G. D'Arcy 3500* (FLAS); Doctor's Inlet, 14 Apr 1939 (fl), *W. A. Murrill s. n.* (FLAS); Duval County, Jacksonville, 23 Apr 1897 (fl), *J. H. Barnhart 2003* (NY); Apalachicola, s.d. (st), *A. W. Chapman s. n.* (MO, NY); S. Jacksonville, 18 Apr 1897 (fl), *J. R. Churchill s. n.* (MO); University and Santa Monica Blvds., So. Jacksonville, 22 Jul 1965 (fl), *D. B. Creager 476* (FLAS); [Duval County], without precise locality, 21 May 1902 (fl), *A. Fredholm 5211* (GH-n.v., NY); So. Jacksonville, May 1896 (fl), *L. H. Lighthipe s. n.* [382?] (NY); same locality, Jul 1898 (fl), *L. H. Lighthipe 631* (NY); Flagler County, Middle Haw Draw on Rt. 11, ca. 12 mi. S of Bunnell, 25 May 1981 (fl), *D. S. Correll & H. B. Correll 51902* (NY); Haw Creek, near Deanville, 25 Jun 1942 (fl, fr), *E. West & L. E. Arnold s. n.* (FLAS); Gadsden County, N. FL Experiment Station, Quincy, 8 Jun 1936 (fl), *H. Foster 25* (FLAS); Jefferson County, St. Mark's National Wildlife Refuge, 0.3 mi. E of Pinhook River bridge on Aucilla Tram Rd., 30.12968 N, 84.01426 W, 24 Jul 2007 (fl), *L. C. Anderson 23326* (FSU); Levy County, Waccasassa Bay State Preserve, T15S, R15E, S1 & S11, Fiber Factory Rd., N of Cow Creek, 9 Jul 1996 (fl), *J. R. Abbott 9234* (FLAS); US Hwy 19, 1 mi. S of Lebanon Station, 11 May 1974 (fl), *L. M. Baltzell 6245* (FLAS); between Co. Rds. 40 and 40A, 1 mi. E of Yankeetown, 21 May 1978 (fl), *L. M. Baltzell 10327* (FLAS); Post office, Yankeetown, 12 May 1948 (fl), *C. Jarrish & J. Jarrish 348* (MO); Gulf Hammock, just W of West Griffin Creek, R14E, T15S, S3 & S17, 22 May 1980 (fl), *W. S. Judd et al. 2667* (FLAS); Gulf Hammock, 18 Jun 1939 (fl), *Watson & W. A. Murrill s. n.* (MO); Liberty County, Torreya State Park, on shores of Apalachicola River, 28 Oct 1973 (fr), *R. K. Godfrey 73082* (FSU); Putnam County, Donald Gross Farm, Florahome, 28 Oct 1981 (fr), *W. T. Scudder 1468* (FLAS); E of East Palatka, 7 June 1940 (fl, fr), *E. West & L. E. Arnold s. n.* (FLAS); St. Johns County, along FL 214, 5.2 mi. E of Tocoi, T7S, R28E, S27, 16 Jul 1960 (fl), *D. B. Ward & T. Myint 2100* (FLAS); 1.8 mi. N of Switzerland, 29 Apr 1941 (fl), *Wilmot & W. A. Murrill s. n.* (FLAS); St. Augustine, May–Sep 1877 (fl), *M. C. Reynolds s. n.* (MO, NY); same locality, May 1878 (fl), *M. C. Reynolds s. n.* (FLAS, MO); same locality, 1879 (fl), *M. C. Reynolds s. n.* (NY); Taylor County, St. Mark's National Wildlife Refuge, along Mandalay Rd., 0.15 mi. N of boat landing on Aucilla River, 2.9 mi. S of Hwy 98, 30.11783 N, 83.97737 W, 12 Jul 2007 (fl), *L. C. Anderson 23263* (FSU); W of Perry, US 98, 14.6 mi. E of the Aucilla River, 22 Sep 2001 (fl), *C. Edwards & G. Ionta 77* (FLAS); ca. 5 mi. E of the Aucilla River, E of Newport, 2 Jul 1955 (fl, fr), *R. K. Godfrey 53547* (FSU, NY); vicinity of Nuttall's Rise, along the Aucilla River, 7 Jul 1960 (fr), *R. K. Godfrey 60037* (FSU); E side of Aucilla River, E of Newport, ¼ mi. off US Rt. 98, 11 Jun 1980 (fl), *R. K. Godfrey 77930* (FSU); ca. 5 mi. N of Steinhatchee, 14 May 1977 (fl), *R. Kral 60053a* (VDB); Taylor County, Aucilla [River] banks, just N of US 98, 30 Jun 1977 (fl, fr), *R. Kral & R. K. Godfrey 60548* (VDB); along dike along Hickory Mount Impoundment in the Aucilla Wildlife Management Area, western section, 5 Jul 1971 (fl), *R. L. Lazor 5581* (FSU); Aucilla Wildlife Management Area near Hwy 14, 3 May 1964 (fl), *S. McDaniel & R. K. Godfrey 4297* (FSU, UNC-n.v., VDB); Wakulla County, Hwy 98 opposite ammunition plant, 0.3 mi. W of Woodville Hwy (Rt. 363), ca. 1.2 air mi. NW of St. Marks, T3S, R1E, NW ½ of SE ¼ of S27, 11 Jun 1988 (fl), *L. C. Anderson 11452* (FSU); Newport, 3 Jun 1968 (fl), *W. G. D'Arcy 2484* (ADW-n.v., FLAS, MO); Wakulla, 21 May 1958 (fl), *R. K. Godfrey 56815* (FSU, GH-n.v.); St. Marks, 29 May 1960 (fl), *R. K. Godfrey 59554* (SMU, FSU [2 sheets]); in area between the Wakulla and St. Marks Rivers at their confluence, in town of St. Marks, 3 Nov 1993 (fr), *R. K. Godfrey 84774* (NY, VDB); Newport, 9 May 1926 (fl), *J. K. Small et al.* (NY); roadside to St. Mark's lighthouse, St. Mark's Wildlife Refuge, 25 May 1958 (fl), *L. B. Trott 179* (FSU, GH-n.v.); at bridge where Hwy 98 crosses Wakulla River, 26 May 1970 (fl), *G. S. Wilhelm 171* (FSU). Georgia: Berrien County, Alapaha Range, 11 May 1982 (fl), *Anonymous s. n.* (MO); Lowndes County, along GA 84, 2.5 mi. W of Valdosta, 25 Apr 1970 (fl), *R. Krysiak s. n.* (MO); Tift County, Experimental farm of Abraham Baldwin Agricultural College, ca. 0.5 mi. N of Davis Rd., Tifton, 7 July 1983 (fl), *C. Swann 3* (MO, VDB); Worth County, SW of Antioch Baptist Church, jct. Jewel Crowe Rd. and GA 313, Mill Cree, 14 Jun 1983 (fl), *R. L. Nichols 2* (MO).

3. Solanum comptum C. V. Morton, Revis. Argentine Sp. Solanum: 230. 1976.—TYPE: ARGENTINA. Corrientes: Departamento Mburucuyá, Establecimiento "La Yerba", 24 Nov 1944 (fl), *G. J. Schwartz 214* (holotype: NY–NY00139103!; isotypes: A, LIL–LIL001443 [scan!], NY–NY00139104!).

Erect to decumbent perennial herb up to 0.6 m tall; stems usually branched at the base, often rooting at the nodes; roots producing buds. Stems sparsely to densely pubescent with stellate hairs showing a continuum of morphology from small subsessile to short-stalked hairs (the stalks up to 0.2 mm long, 0.05–0.1 mm wide at the base, with (4)6–8 subequal lateral rays spreading 0.5–1 mm in diameter, the central ray 1-celled, up to 0.5 mm long) grading into long-stalked hairs (the stout prickle-like stalks up to 6 mm long, up to 0.4 mm wide at the base, with (4)6–8 subequal lateral rays spreading up to 2 mm in diameter, the central ray 1–3-celled, up to 3.2 mm long), sparsely to moderately armed with straight tapered prickles up to 7 mm long. Sympodial units 2- to 3-foliate, sometimes plurifoliate, the leaves not geminate. Leaves simple, the blades 5–11 × 3–10.5 cm, broadly deltoid-ovate in outline, moderately to densely stellate-pubescent abaxially and adaxially with sessile to short-stalked stellate hairs up to 1.2 mm in diameter, with (4)6–8 lateral rays, the central ray 1-celled and up to 1.0 mm long, sparsely to moderately armed with prickles up to 9 mm long on the major veins abaxially and adaxially; base cordate to cuneate, rarely truncate, equal to unequal, often with one side offset up to 1 cm from the other, often with open sinuses; margin irregularly serrate to shallowly and irregularly lobed; apex obtuse to rounded; petioles 2–7 cm long, sparsely to moderately stellate-pubescent with hairs like those of the stem, moderately armed with prickles up to 12 mm long. Inflorescence 5–15 cm long, extra-axillary, unbranched or forked, with 3–10 flowers, weakly andromonoecious with the 2–5 proximal flowers hermaphroditic and the (0)3–6 distal flowers staminate, the axes moderately stellate-pubescent, sparsely armed with prickles up to 5.4 mm long; peduncle 3–7 cm long; pedicels 1.5–3.5 cm long in flower and fruit, deflexed downward in fruit, spaced 0.5–1.5 cm apart, articulated at the base, sparsely to moderately stellate-pubescent, sparsely armed with prickles up to 5.5 mm long. Calyx 4.5–8 mm long, the tube 1–3 mm long, the lobes 2.5–6 × 2–2.5 mm, deltate-lanceolate, the apex acute-acuminate, densely pubescent with sessile stellate hairs abaxially, glabrous adaxially, sparsely to moderately armed abaxially with prickles up to 5.5 mm long; fruiting calyx strongly accrescent and completely covering the fruit, 7–15 mm long, the tube ca. 4 mm long, the lobes 5–6 × 4–5 mm, narrowly triangular, moderately stellate-pubescent, sparsely armed with prickles up to 5 mm long. Corollas 2–3 cm in diameter, 13–18 mm long, stellate to rotate-stellate, chartaceous, light blue or sky blue, the tube 5–8 mm long, the lobes 5–10 × 5–10 mm, deltate, the apex acute, moderately to densely stellate-pubescent abaxially, glabrous adaxially. Stamens with filaments

0.8–2 × 0.15–0.4 mm; anthers subequal, 3.5–10 × 0.8–2 mm, narrowly lanceolate, weakly connivent, yellow, the pores directed distally. Ovary 1–1.5 × 1–1.5 mm, subglobose, minutely glandular-puberulent at apex; style 7–12 × 0.3–1 mm, cylindrical, straight, glabrous, exserted in hermaphroditic flowers; stigma capitate. Fruits 1–1.8 × 1–2 cm, globose to subglobose, the apex obtuse, light green with darker green mottling when young, yellow at maturity, glabrous, the rind tough. Seeds ca. 3.5 × 2.5–4 mm, flattened-reniform, lenticular, yellow, the surface finely foveolate.

Distribution and Habitat—*Solanum comptum* is distributed in Chaco, Corrientes, and Formosa provinces of northeastern Argentina and in the Alto Paraguay, Boquerón, Misiones, and Ñeembucú departments of Paraguay (Fig. 6) at elevations from 30–160 m. This weedy species grows in the Chaco vegetation formation and is commonly found on roadsides and other disturbed environments. It has been reported growing in clays, sands, and in inundated areas such as river banks. Disturbance of its bud-producing roots seems to promote its propagation, and it often becomes a pest in areas such as roadsides, waste areas, and cultivated areas.

Phenology—The species flowers between October and March and fruits between October and May.

Conservation Status—*Solanum comptum* is known from ca. 21 populations in Paraguay and northern Argentina. This weedy and invasive species grows in disturbed habitats and it is doubtful that any significant reduction in population size or locations will occur. With an extent of occurrence of ca. 200,000 km^2 and area of occupancy of 464 km^2, *Solanum comptum* is assigned a preliminary conservation status of "least concern" (LC).

Etymology—The epithet *comptum* means ornamented or adorned, particularly with regard to a headdress. Morton (1976) did not explain the meaning of the name, however, it most likely refers to the stellate hairs with stout, prickle-like stalks. These hairs appear to be developmentally intermediate between stellate hairs and true prickles lacking rays at their tips. Alternatively, the name could possibly refer to the densely stellate-pubescent and armed accrescent fruiting calyces that completely cover the mature fruit.

Vernacular Names—The common name mero-rá was recorded from *L. Bernardi 18421* collected in Ñeembucú department in Paraguay. Common names recorded for *Solanum comptum* in Argentina are punguo, tutía-poñi, and melora (Matesevach 2002; Barboza 2013).

Chromosome Number—*Solanum comptum* has been shown to be a tetraploid with a sporophytic chromosome count of $2n = 48$ (*G. E. Barboza et al. 999*; *G. E. Barboza et al. 1001*; Chiarini 2007).

Notes—In habit and most vegetative and reproductive characters, *Solanum comptum* is similar to *S. hieronymi* but can be distinguished by its light blue corolla (vs. white in *S. hieronymi*), smaller (0.8–1 × 0.7–1.3 cm) globose fruits completely covered by the accrescent fruiting calyx [vs. larger (1.5–2.2 × 1–2 cm) depressed globose fruits with a weakly accrescent fruiting calyx], and small stellate hairs with central rays consisting of 1–2 cells that are shorter or equal to

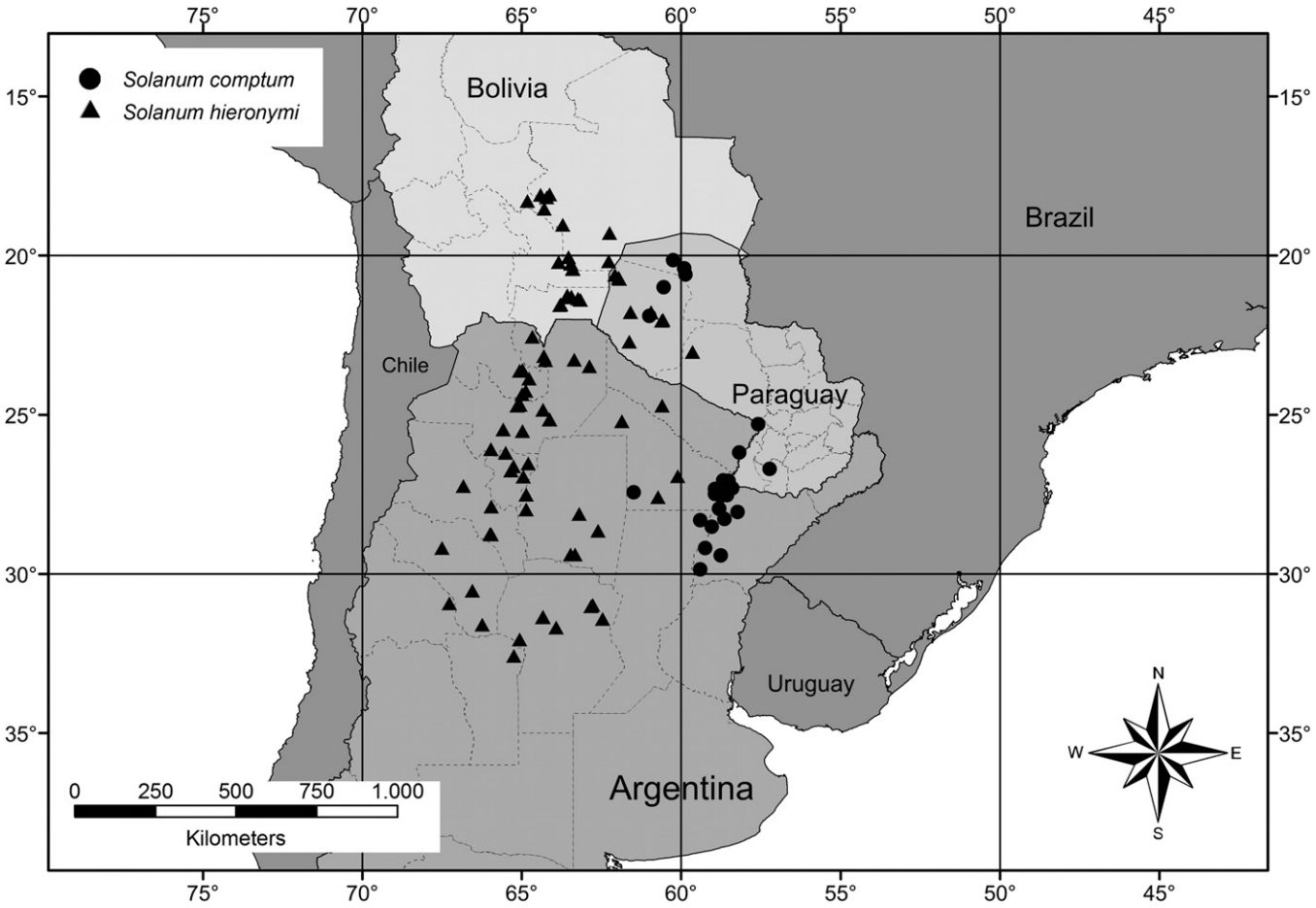

Fig. 6. Distribution of *Solanum comptum* and *S. hieronymi*.

the lateral rays (vs. central rays of 1–4 cells that are longer than the lateral rays). Another diagnostic character for *S. comptum* is the presence of large stellate hairs with stout yellow prickle-like stalks up to 6 mm long and terminated with 4–8 lateral rays and a 2-celled central ray. In *S. comptum*, these prickle-like stellae are sparsely to moderately distributed on the stem, petioles, leaf blades, inflorescence axes, and pedicels, and densely so on the calyces. In *S. hieronymi*, prickle-like stellae are absent or sometimes sparsely distributed on the petioles and calyces. Finally, *S. comptum* lacks the short (up to 0.3 mm long) unbranched glandular hairs that are moderately to densely distributed on plants of *S. hieronymi*.

***Additional Specimens Examined*—** ARGENTINA. Chaco: Resistencia, Barranquera, 10 Mar 1947 (fl, fr), *M. R. Malvárez 1153* (LIL); Río Bermejo, Las Palmas, 15 Mar 1947 (fl, fr), *M. R. Malvárez 1299* (LIL); 12 de Octubre (Campo del Cielo), General Capdevila, 14 Dec 1946 (fl), *C. Schulz 987* (LIL); Dpto. Primero de Mayo, Colonia Benítez, s.d., *A. G. Schulz 2058* (CTES, MO). Corrientes: Goya, Arroyo Guazú, 29°50′26″S, 59°24′24″W, 31 m, 3 Dec 2002 (fl), *G. E. Barboza et al. 356* (CORD); a 14 km de Corrientes, rumbo a Riachuelo, 27°33′05″S, 58°45′02″W, 4 Dec 2002 (fl), *G. E. Barboza et al. 372* (CORD); San Cosme, a 3 km de Puerto González, 5 Dec 2002 (fl, fr), *G. E. Barboza et al. 384* (CORD); Capital, Camino hacia el aeropuerto, 13 May 2004 (fr), *G. E. Barboza et al. 999* (CORD); Capital, Perichón, 29°24′34.4″S, 58°45′09.3″W, 13 May 2004 (fr), *G. E. Barboza et al. 1001* (CORD); San Cosme, desde Paso de la Patria rumbo a Puerto González, 27°18′42″S, 58°29′22″W, 13 May 2004 (fr), *G. E. Barboza et al. 1005* (CORD); Capital, Ciudad de Corrientes, parque Mitre, 14 Dec 2000 (fl), *F. Chiarini 406* (CORD); Dpto. Goya, por RN 12, en la entrada a Goya, 29°10′28.9″S, 59°14′45.5″W, 39 m, 29 Feb 2012 (fl), *F. Chiarini & G. A. Wahlert 823* (CORD, UT); Paso de La Patria, 6 Jan 1975 (fl), *A. R. Cuezzo et al. 10967* (LIL); Dpto. San Cosme, Ensenada, 27 Feb 1945 (fr), *R. Huidobro 1805* (A-n.v., LIL-n.v., NY); same locality, 28 Feb 1945 (fr), *R. Huidobro 1842* (A-n.v., LIL-n.v., NY); Dpto. San Cosme, km 10, 7 Apr 1945 (fr), *R. Huidobro 1902* (NY); Empedrado, Río Empedrado, RN 12, 29 Sep 1971 (fl), *A. Krapovickas et al. 19895* (LIL); Dpto. Capital, Corrientes, 15 Oct 1987 (fl, fr), *A. Krapovickas 41919* (FCQ, MO, NY); Dpto. Mburucuyá, Estancia "Santa Teresa", 21 Dec 1951 (fl), *T. M. Pedersen 1405* (NY, MO, P); Dpto. Empedrado, Estancia "La Yela", 8 Jan 1983 (fr), *T. M. Pedersen 13485* (NY [2 sheets], MO); orillas del Paraná, Nov 1936 (fr), *A. P. Rodrigo 903* (NY); Bella Vista, 13 Oct 1974 (fl), *A. Schinini & C. L. Cristóbal 9915* (CTES); Capital, ciudad de Corrientes, 17 Oct 1997 (fl), *A. Schinini & M. G. López 32712* (CTES, FCQ, NY); Saladas, Santo Domingo, 21 Jan 1950 (fr), *G. J. Schwarz 9292* (CORD). Formosa: Capital, en la plaza, 14 Mar 1885 (fl), *F. Kurtz 1389* (CORD).

PARAGUAY. Alto Paraguay: Palmar de las Islas, Estancia San José, 1500 m al W del casa, 7 Jan 1998 (fl, fr), *R. Insua 6* (FCQ); Ftín. Carlos A. López, Pitiantuta, 14 Oct 1992 (fl, fr), *F. Mereles & R. Degen 4719* (CTES-n.v., FCQ, MO); Parque Nacional Defensores del Chaco, 20°35′43″S, 59°51′42″W, 131 m, 13 Aug 1998 (fl), *F. Mereles et al. 7347* (FCQ); Fin de Parque Nacional, 20°30′07″S, 59°48′44″W, 25 Nov 2002 (fl), *F. Mereles et al. 8908* (FCQ); Estancia San Miguel, Palmar de las Islas, 5 Mar 1989 (fl), *L. Ramella & F. Mereles 2490* (CORD). Boquerón: 75 km al N de Tte. Montanía, Tyto. Montanía-Madrejón, a 75 km, 15 Dec 1993 (fl, fr), *R. Degen & F. Mereles 3094* (CTES-n.v., FCQ, MO); Tte. 1°A. Picco, 20°59′ S, 60°31′W, 59 m, 21 Oct 1987 (fl), *R. E. Spichiger et al. 2279* (CORD, FCQ). Chaco: Palmar de las Islas, borde de la laguna Palmar, 5 Mar 1989 (fl, fr), *F. Mereles 2705* (FCQ). Distrito Capital: city of Asunción, Villa Morra, on Dr. Quesada between Cruz del Chaco and General Gaulle, 25°17′50.9″S, 57°34′41″W, 115 m, 26 Nov 2003 (fl, fr), *L. Bohs 3193* (NY, UT). Misiones: between San Juan Bautista and road San Ignacio-Pilar, Talaty, 8 km SE of San Juan Bautista, 26°40′S, 57°14′W, 23 Feb 1994 (fr), *E. M. Zardini & T. Tilleria 38540* (AS-n.v., NY, MO). Ñeembucú: Curupayty, Humaitá, 9 Nov 1978 (fl), *L. Bernardi 18421* (NY). Presidente Hayes: along Ruta Trans-Chaco NW of Villa Hayes, near Arroyo Ka'I, 23°57′58.9″S, 58°25′40.6″W, ca. 90 m, 29 Nov 2003 (fl), *L. Bohs et al. 3203* (UT).

4. Solanum dimidiatum Raf., Autik. Bot. 8: 107. 1840.—TYPE: U. S. A. Texas: Van Zandt County, Hill Ranch, ca. 0.5 mi. N of TX State Highway 64, ca. 7.6 mi. W of Jct. of Highways 64 and 49, 32°23.952′N, 95°32.921′W, 166 m, 31 May 2014 (fl), *S. Hill 454* (neotype, designated here: BRIT!; isoneotypes: BM!, G!, MO!, NY!, P!, US!, UT [2 sheets]!).

Solanum anoplocladum Dunal, Prodr. 13(1): 346. 1852.—TYPE: MEXICO. Without precise locality, s.d. (fl), *J. M. Sessé & J. Mociño s. n.* (holotype: G–G00070145 [scan!]).

Solanum torreyi A. Gray, Proc. Amer. Acad. 6: 44. 1862.—TYPE: U. S. A. Texas: 1846 (fl), *F. J. Lindheimer 281* (lectotype: A–A00077426!, designated by W. G. D'Arcy, Ann. Missouri Bot. Gard. 61: 844. 1974; isolectotypes: BM–BM000838186 [scan!], SMU!, LL–LL00372891 [scan!], MO–3830679!, MO–3830680!, MO–3830681!, P–P00325866!, P–P00325867!, P–P00325868!, P–P00325869!, P–P00336989!, PH–PH00030492!).

Solanum torreyi f. *album* Waterf., Rhodora 51: 27. 1949.—TYPE: U. S. A. Oklahoma: Custer County, 1 mi. E of Weatherford, 3 Jul 1947 (fl), *U. T. Waterfall 7340* (holotype: OKL–OKL01–0097403 [scan!]; isotype: US–US00027827!).

Upright perennial herb up to 0.8 m tall, 1- to few-branched. Stems sparsely to densely pubescent with sessile to short-stalked stellate hairs 0.6–1 mm in diameter, with (4–)6–10 unequal lateral rays, the central ray 1-celled and up to 0.8 mm long, unarmed or sparsely armed with straight tapered prickles up to 6.5 mm long. Sympodial units 2- to 3-foliate, sometimes plurifoliate, the leaves not geminate. Leaves simple, the blades 5–16 × 2.5–10 cm, ovate in outline, moderately to densely stellate-pubescent abaxially, slightly less so adaxially with hairs like those of the stems, unarmed or sparsely armed with prickles up to 8.5 mm long on the major veins abaxially and adaxially; base truncate to cuneate, equal to unequal, often with one side offset up to 0.3–1 cm from the other; margin sinuate or shallowly to deeply lobed with 2–4 lobes per side; apex cuneate, acute or rounded; petioles 1–3 cm long, sparsely to densely stellate-pubescent, unarmed or sparsely to moderately armed with prickles up to 9 mm long. Inflorescences 6–14 cm long, extra-axillary, 1- to several-branched, with up to ca. 20 flowers, weakly andromonoecious, the axes moderately to densely stellate-pubescent, unarmed or sparsely armed with prickles up to 4 mm long; peduncle 2–7.5 cm long; pedicels 1–2.5 cm in flower, 1.5–3 cm and curved downward in fruit, weakly articulated at the base, moderately to densely stellate-pubescent, unarmed or sparsely armed with prickles up to 3 mm long. Calyx 6–14 mm long, the tube 1.5–4 mm long, the lobes 3–10 × 2–5 mm, ovate-lanceolate, the apex acuminate to caudate, densely stellate-pubescent abaxially, sparsely so towards the apex adaxially, unarmed or very sparsely armed with prickles up to 3 mm long; fruiting calyx spreading to reflexed, 9–15 mm long, the tube 0.5–3 mm long, the lobes 4–12 × 4.5–7 mm, ovate-lanceolate to triangular, sparsely to moderately stellate-pubescent, unarmed or very sparsely armed with prickles up to 2 mm long. Corollas (2–)3–4.6 cm in diameter, 8–25 mm long, stellate to stellate-pentagonal or rotate-stellate, chartaceous, lavender, pale blue or sometimes white, the tube 3–8 mm long, the lobes 5–17 × 4.5–15 mm, deltate to triangular, the apex apiculate, moderately to densely stellate-pubescent abaxially, sparsely so towards the apex adaxially. Stamens with filaments 1.2–2.5 × 0.2–0.6 mm; anthers 4.8–9 × 1.2–2.2 mm, narrowly lanceolate, weakly or not connivent, yellow, the pores directed distally. Ovary 1.3–2 × 1.5–2.5 mm, ovoid, glabrous to sparsely glandular-pubescent with hairs up to 0.3 mm long, or both glandular-pubescent and densely stellate-pubescent; style 10–15 × 0.6–1 mm, cylindrical, straight, glabrous, exserted; stigma capitate. Fruits 1.1–1.8 × 1.3–2.5 cm, subovoid to depressed globose, yellow at maturity,

glabrous, the rind tough. Seeds 1.9–3 × 1.7–2.5 mm, flattened-reniform, lenticular, yellow, the surface finely foveolate.

Distribution and Habitat—*Solanum dimidiatum* is distributed in Texas, Oklahoma, Louisiana, Arkansas, Missouri, and Kansas with a few outlier populations in Illinois, New Mexico, South Carolina, and Mexico (Fig. 7). Its native distribution prior to European settlement is not known with certainty because of its weedy, invasive nature and ability to colonize disturbed habitats. It can become a noxious weed locally and has the potential to establish reproducing populations when introduced into suitable habitats. It has been introduced in California and in Australia, but apparently has been successfully eradicated in both areas (Jepson Flora Project 2014; eFloraSA 2014). The California Department of Food and Agriculture rates *S. dimidiatum* under category A as "a pest of known . . . environmental detriment" (CDFA 2014). It grows in prairies and oak woodlands as well as disturbed areas such as roadsides, grazed and mowed pastures, ditches, cultivated and urban waste areas, and railroad rights of way in sandy soils or on a variety of other soil types at elevations from 200–600 m.

Phenology—Flowering between April and August and fruiting between July and October.

Conservation Status—The calculations of extent of occurrence (ca. 760,000 km^2) and area of occupancy (1,744 km^2) for *Solanum dimidiatum* were based on its estimated native distribution (i.e. Texas, Oklahoma, Louisiana, Arkansas, Missouri, and Kansas) and excluded the outlying occurrences in Illinois, New Mexico, South Carolina, and Mexico. Given its weedy habit and preference for disturbed habitats, *S. dimidiatum* is assigned a preliminary conservation status of "least concern" (LC).

Etymology—The specific epithet derives from the Latin word for dimidiate, meaning to be so unequally divided in halves that one half appears to be lacking. Rafinesque applied this term to describe the often unequal base of the leaf blades, with one side usually offset 0.3–1 cm from the other side.

Vernacular Names and Uses—Three common names widely used are Torrey's horsenettle, western horsenettle, and robust horsenettle. Jordan et al. (2006) report that the Plains Apache Native Americans may have utilized the fruits of *S. dimidiatum* in some aspects of their material culture; however, all parts of the plant are considered poisonous to humans and livestock. In cattle, it is known to cause "crazy cow syndrome," a debilitating disease caused by the calystegine alkaloids present in this species (Menzies et al. 1979; Anderson 2002).

Chromosome Number—Nichols and Hanna (1984) report a sporophytic chromosome number of $2n = 72$, and a gametophyic number of $n = 36$ was reported from a plant in Oklahoma (Hardin et al. 1972) and in Queensland, Australia (Symon 1981; *P. Sharp 46241* [ADW]).

Notes—In overall habit and floral and fruit morphology, *S. dimidiatum* is similar to *S. perplexum*, but it differs by the indumentum on the stems, petioles, leaves, and inflorescence axes [whitish stellate hairs with (4–)6–10 lateral rays, the

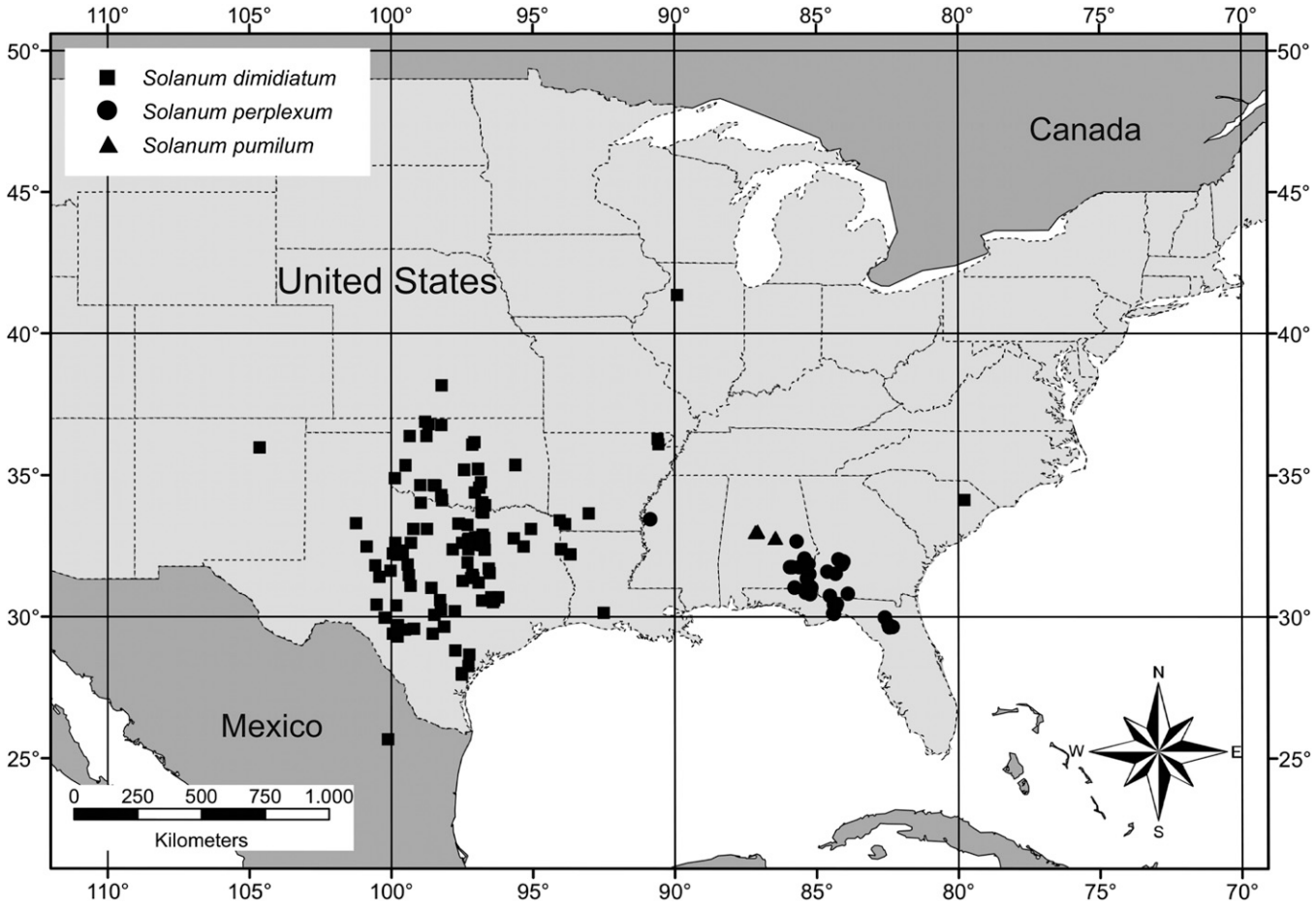

Fig. 7. Distribution of *Solanum dimidiatum*, *S. perplexum*, and *S. pumilum*.

central ray 1-celled and equal to or shorter than the lateral rays in *S. dimidiatum* vs. golden stellate hairs with (4–)6–8 lateral rays, the central ray 1–2-celled and longer than the lateral rays in *S. perplexum*]. It also differs by its smaller prickles on the stems and leaves (up to 6.5 mm vs. up to 15 mm in *S. perplexum*) and its smaller leaves (up to 16 × 10 cm vs. 22 × 18 cm). *Solanum dimidiatum* is also somewhat similar to *S. carolinense*, but can be differentiated by its larger corollas that are up to 4.6 cm in diameter (vs. corollas up to 3 cm in diameter in *S. carolinense*), its inflorescence that is branched once to several times (vs. unbranched or branched once), and its hard, somewhat dry fruit (vs. a softer, mucilaginous fruit).

Solanum dimidiatum was described by Constantine Samuel Rafinesque, and as is common with Rafinesque names, typification can be problematic because of his characteristically inadequate diagnoses or descriptions, and due to the fact that much of his personal herbarium—including many holotypes—was discarded after his death (Merrill 1949). After a thorough search of herbaria, especially of those with specimens from the Rafinesque herbarium (e.g. P, DWC), we were unable to locate any specimens that would constitute authentic material. However, Rafinesque's description was sufficiently detailed to allow us to confidently match his taxonomic concept to the species commonly identified as *S. dimidiatum*. We have designated the collection *S. Hill 454* from Van Zandt County, Texas as the neotype in order to match the name to a specimen.

***Additional Specimens Examined*—**MEXICO. Nuevo Leon: E. Monterey, 17–26 Feb 1880 (fr), *E. Palmer 933* (P).

U. S. A. Arkansas: Clay County, beside AK 90, ½ mi. SW of Knobel, 8 Jul 1968 (bud), *R. D. Thomas 10461* (SMU); Greene County, 25 May 1893 (fl), *H. K. D. Eggert s. n.* (NY); Miller County, Kiblah, 91 m, 11 May 1959 (fl), *D. Demaree 40838* (SMU); Ouachita County, beside AK 24 and railroad tracks in Chidester, 12 May 1988 (fl), *N. Taylor & C. Slaughter 104404* (MO, NY). Kansas: Barber County, vicinity of Kiowa, 9 mi. NW of town, 5 Jul 1929 (fr), *P. A. Rydberg & R. Imler 641* (NY); Rice County, 3 mi. W, 0.5 mi. S of Sterling, 10 Jul 1984 (fl, fr), *R. L. McGregor 35641* (VDB). Illinois: Henry County, Annawan, 19 Jul 1960 (fl), *V. H. Chase 16131* (VDB). Louisiana: Acadia Parish, between unpaved road and railroad S of US 90 ca. 0.5 miles east of Midland and LA 91, 20 Sep 1986 (fl), *C. M. Allen 14407* (LSU); between Southern Pacific Railroad and dirt road S of railroad, 0.1 miles west of jct. of LA 91 and US 90, 7 Aug 1987 (fl), *N. M. Gilmore 3273* (LSU); same locality and date, *N. M. Gilmore 3274* (LSU); same locality and date, *N. M. Gilmore 3275* (LSU); US 90, 1–2 miles east of Midland, 1 May 1987 (fl), *L. M. Smith 2524* (LSU); S of US 90, 1.5 mi. E of Midland, T10S, R1W, S16, 4 Oct 1986 (fr), *R. D. Thomas & C. M. Allen 98388* (BRIT); Caddo Parish, Shreveport, 10 Apr 1909 (bud), *N. F. Petersen s. n.* (LSU); I-20 W, two mi. E of US 79 and US 80 exit at Greenwood and W of Shreveport, T17N, R15W, S21, 1 Jul 1994 (st), *R. D. Thomas & K. Cascio 140253* (BRIT); I-20 W, one mi. E of US 79 and US 80 exit at Greenwood and W of Shreveport, T17N, R15W, S20, 1 Jul 1994 (fl), *R. D. Thomas & K. Cascio 140257* (BRIT, LSU, MO, NY, UNA); Desoto Parish, along Kansas City Southern Railway tracks between LA 175 and Friendship Rd. in Frierson, T15N, R13W, S34, 4 May 1984 (fl), *R. D. Thomas & D. Nixon 71240* (NY, SMU); along LA 175 in Frierson, T15N, R13W, S27 & S35, 15 May 1984 (fl), *R. D. Thomas & D. D. Taylor 88670* (FLAS, L-n.v., LSU, VDB). Missouri: Jackson County, Courtney, 25 Oct 1929 (st), *B. F. Bush 11704* (NY); Courtney, 21 Aug 1930 (st), *B. F. Bush 11941* (NY); St. Louis City, behind O'Connell's Pub, on corner of Kingshighway and Shaw Ave, 38°37′10″N, 90°16′00″W, 149 m, 8 Sep 1998 (fl), *G. Yatskievych & B. Summers 98–92* (MO [2 sheets]). New Mexico: Mora County, roadside of NM 120, 18 mi. W of Roy and 6 mi. E of Wagon Mound, T21N, R22E, S26, 3 Jul 1981 (fl), *D. Ward et al. 81–269* (NY). Oklahoma: Alfalfa County, Salt Plains National Wildlife Refuge, S of Hwy 11, 1 mi. W of refuge Rd., T27N, R9W, S20, 10 May 1963 (fl), *R. J. Baalman 292* (SMU); Cleveland County, Norman, 2 Aug 1924 (fl), *W. E. Bruner s. n.* (SMU); Comanche County, 1 mi. W of Fort Sill in Wachita Mountains [Wildlife Refuge], 15 Jul 1969 (fr), *R. L. Lazor & J. Lazor 3708* (FSU); Fort Sill, 22 May 1916 (fl), *E. J. Palmer 11764a* (NY); Geronimo Hill, Ft. Sill Reservation, 21 May 1989 (fl), *R. A. Thompson et al. S0465* (MO, SMU); Cotton County, 7 mi. E of Taylor, ¼ mi. N of jct. US 70, 4 mi. E of Jefferson County line, 34°09′36″N, 98°12′32″W, 274 m, 27 May 1996 (st), *R. Burckhalter & M. Blanchard 2721* (UNA); 4 mi. N and 1 ¾ mi. E of Temple, 8 May 1976 (fl), *B. L. Lipscomb 1547* (SMU); Craig County, Vinita, 18 Jun 1894 (fl, fr), *B. F. Bush 394* (NY); Creek County, Sapulpa, 19 Jun 1894 (fl), *B. F. Bush 395* (NY); Harmon County, breaks along Elm Creek 12–15 mi. S of Erick, 13 Jun 1973 (fl), *L. C. Higgins 7287* (NY); Jefferson County, 4.5 mi. S of Ryan on US 81, 33.938036N, 97.940835W, 11 Aug 2013 (fr), *B. L. Lipscomb 3541* (BRIT, K, MO, NY, P, US, UT); Marshall County, 2¼ mi. S of Kingston and ¼ mi. E of Co. Rd., 20 Jun 1951 (fl, fr), *V. L. Cory 58988* (SMU); Marshall County, 1 mi. W of University of Oklahoma Biological Station, Lake Texoma, 20 Jun 1952 (fl), *P. B. Riggs s. n.* (SMU); McIntosh County, Fountainhead State Park, along Eufala Lake, at campground 12 Jun 1982 (fl, fr), *M. H. Nee 24377* (NY); Murray County, 406 S. sixth St., Madill, 5 Jul 1947 (fl), *B. Duff 117* (SMU); W of Guy Campground, 26 May 1994 (fl), *F. L. Johnson et al. 112* (BRIT); Payne County, 2 mi. W of Stillwater, 5 Jun 1946 (fl), *T. R. Ferguson 4* (SMU); 6 mi. N and ½ mi. W of Stillwater, 15 Sep 1938 (fl), *W. G. Stoneman 47* (SMU); 3 mi. N of Stillwater, 11 Jun 1970 (fl), *J. S. Wright 82* (VDB); Pontotoc County, 2 mi. S and 3 mi. W of Roff, 18 Aug 1951 (fl), *D. McCoy 1675* (SMU); State Hwy 19, 7 mi. W of Ada, 18 May 1947 (fl), *G. T. Robbins 2490* (NY); Pottawatomie County, Tecumseh, 16 Jun 1937 (fl), *F. A. Barkley 1181* (SMU); Swanson County, near Mountain Park, 23 Jun 1913 (fl), *G. W. Stevens 1257½* (P); Washita County, US 40 and 66, 1 mi. E of Elk City exit, 15 Jul 1976 (fl, fr), *C. A. Bennett et al. 381* (MO, NY); Woods County, ca. 7 mi. SE of Waynoka, 2 Oct 1983 (fr), *P. Nighswonger 2091* (BRIT); Woods County, NW of Alva about 14 mi., 17 Jul 1984 (fr), *P. Nighswonger & W. Little 2165* (BRIT); Woods County, near Alva, 1 Jun 1913 (fl), *G. W. Stevens 771* (NY); Woodward County, Hal and Fern Cooper Wildlife Management Area, NW portion of S pasture, T24N, R22W, SW ¼ of S25, 25 Jul 2006 (fr), *S. Winter 1694* (BRIT). South Carolina: Florence County, Florence RR yards, 24 May 1957 (fl), *C. R. Bell 7489* (FSU). Texas: without precise locality, s.d. (fl), *T. Drummond s. n.* (P); Bandera County, Hill Country State Natural Area, N area of park, along Trail 4, 23 Apr 1994 (fl), *L. Lackey 479* (BRIT); Hill Country State Natural Area, SE area of park, along Trail 2, 7 May 1994 (fl), *L. Lackey 485* (BRIT); along the roadside of FM 470, about 1.9 road miles east of this highway's crossing over Hondo Creek; north of Tarpley, 16 Oct 1982 (fr), *A. W. Lievens 82TX35* (LSU); Bexar County, San Antonio, 5 May 1894 (fl), *A. A. Heller 1709* (NY, P [2 sheets]); Blanco County, above Blanco River ca. 6 mi. W of Blanco, 16 May 1982 (fl), *R. Kral 68513* (VDB); Johnson City unit, S maintenance area near camper sites, 30°16′N, 98°16′W, 1 May 2002 (fl), *R. W. Sanders 5132* (BRIT); Bowie County, Texarkana, 24 Jul 1896 (fr), *H. K. D. Eggert s. n.* (MO); Brazos County, Riley Rd. in E part of county, 12 May 1974 (imm. fr), *P. A. Fryxell 2391* (NY); 4.7 mi. S of the intersection of FM 2818 and FM 60 at the Texas A & M Beef Cattle Center, 20 Apr 1994 (fl), *L. A. Knox 26* (MO); College Station, railroad crossing at AAA Building, 13 Jul 1943 (fl), *J. B. Paxson 18* (BRIT); Burleson County, NW corner of Burleson County Rd. 307 and TX 36, 15 Apr 1990 (fl), *S. D. Jones & G. Jones 4434* (VDB); Burnet County, Fairland, 17 May 1920 (fl), *F. W. Pennell 10468* (NY); Callahan County, US 80, ca. 3 mi. E of the Taylor County line, 27 Apr 1963 (fl), *N. C. Henderson 63–570* (FSU, SMU, TEX-n.v.); Coke County, 8 Jun 1970 (fl, fr), *D. Demaree 62146* (SMU); Coleman County, 2 mi. N of Rockwood on Hwy 283, 24 Apr 1976 (fl), *M. R. Nixon 309* (BRIT); US Hwy 283, J. P. Miller Ranch, 5 mi. N of Coleman, 4 Nov 1965 (fr), *A. Villarreal s. n.* (SMU); Comal County, New Braunfels, May 1850 (fl), *F. J. Lindheimer 1043* (NY, P); New Braunfels, 12 May 1920 (fl), *F. W. Pennell 10424* (NY); New Braunfels, Jun 1888 (st), *F. Rautenberg 1576* (SMU); Coryell County, above Leon River just N of entrance to Mother Neff State Park, 16 May 1984 (fl), *R. Kral 71454* (VDB); Dallas County, 1½ mi. S of Cedar Hill, 500 ft. off Hwy 67, 24 May 1947 (fl), *R. E. Cotten 60* (SMU); Stults Prairie, SW corner of Coit Rd. and Belt Line Rd., 21 May 1959 (fl), *D. S. Correll 22145* (NY); same locality, 28 May 1959 (fl), *D. S. Correll & I. M. Johnston 22447* (FSU); Duncanville at Mountain View College, 9 May 1993 (fl), *E. Lehto L25575* (BRIT); E of White Rock Lake, 31 Aug 1942 (fr), *C. L. Lundell & A. A. Lundell 11709* (LL-n.v., SMU); E Dallas, East Grand Ave., 30 Jun 1947 (fl), *R. E. Niblack 49* (SMU); Lancaster, Bear Creek Park and Nature Preserve, 30 Apr 2003 (fl), *J. Quayle & J. Varnum 306* (BRIT); same locality, 17 May 2003 (fl), *J. Quayle 344* (BRIT); Dallas, 20 Aug 1901 (fr), *J. Reverchon 673* (MO [2 sheets]); S of Oak Cliff, 5 Jun 1942 (fl), *O. Sanders 165* (BRIT); beside Harry Hines Blvd. at Market Center Blvd and railroad tracks NE of I-35E in Dallas, 22 Sep 1995 (fr), *R. D. Thomas 145950* (NY, UNA); Denton County, 6 mi. NW of Denton, 18 May 1947 (fl), *V. L. Cory 53716* (NY); Edwards County, substation No. 14, 6 Oct 1946 (fl, fr), *V. L. Cory 52495* (NY, SMU); 15 mi. S of road jct. 3.5 mi. W of Rock Springs on Texas route 41, 10 May 1947 (fl), *R. McVaugh & A. M. Harvill 8262* (P, SMU); Ellis

County, near Murry Gin in Britton, near Mansfield, 24 Apr 1976 (fl), *S. Huggins s. n.* (BRIT); E of Waxahachie, 23 Jun 1939 (fl), *S. Shackelford 20* (SMU); Falls County, at crossing of Hwy 6 and Big Creek ca. 3 mi. S of Marlin, 26 Apr 1981 (fl), *P. A. Fryxell 3421* (BRIT, NY, TEX-n.v.); Garza County, Hwy 651, 7.4 air mi. NE of Post, 9 Jun 1966 (fl), *B. Hutchins 1187* (LL-n.v., SMU); Goliad County, W of Coleto Creek and N of Hwy 59, 9 May 1976 (fl), *G. Ajilvsgi 3344* (BRIT); Grayson County, Hagerman National Wildlife Refuge, ca. 16 km by air S of the Texas-Oklahoma state line, 33°44′16″N, 96°44′54″W, ca. 671 m, 1 Sep 1993 (fr), *J. Mazer & G. Diggs 5* (FLAS); Hagerman National Wildlife Refuge, Lake Texoma, 9 miles NW of center of Sherman, 1.5 miles SSE of Refuge headquarters buildings, 14.4 km SW of center of Sherman, 33°43′N, 96°45′W, 27 Sep 1993 (fr), *M. H. Nee et al. 43970* (NY); Hagerman National Wildlife Refuge, ca. 18 km by air NW of Sherman, ca. 16 km by air S of the Texas-Oklahoma state line, S of headquarters complex, near abandoned trail S of main road into Refuge, 1 Sep 1993 (fr), *J. Redmon & G. Diggs 5* (VDB); Hill County, Aquilla Creek, ca. 2 mi. SSW of Peoria, 7 Jun 1972 (fl), *G. H. Hall 71* (SMU); Hood County, near Center Mills, 14 May 1939 (fl), *C. Blackwell 37* (SMU); Johnson County, Egan, Judith Sear property, under powerline easement on E side, 32°25.991′N, 97°17.090′W, 18 Apr 2006 (fl), *J. Quayle 1005* (BRIT); Jones County, US 277, ca. 6 mi. S of Anson, 20 May 1962 (fl), *N. C. Henderson 62–475* (FSU); Karnes County, Ecleto Creek crossing, 2.5 mi. W of Runge, 24 Apr 1954 (st), *J. C. Johnson 1515* (SMU); Kimble County, South Llano River State Park, along Park Rd. 73, 0.6 mi. NW of Park headquarters, at the day use picnic area, 8 May 1996 (fl), *L. Sanchez 1308* (BRIT); Limestone County, near Tehuacana, 14 May 1939 (fl), *J. Miles 6* (SMU); Fort Parker State Park, Hwy 14 and Park Rd. 29, May 1997 (fl), *J. Singhurst et al. 1718* (BRIT); McLennan County, 1¾ mi. SSW of Robinson, 4 May 1949 (fl), *V. L. Cory 55703* (SMU); Loop 340 at Old Temple Rd., 29 Apr 1970 (fl), *M. Mauldin s. n.* (SMU); Speight and Hwy 6, 1 May 1948 (fl), *L. D. Smith 1108* (NY); Waco, vacant lot at 21st St. and Bernard Ave., 26 May 1946 (fl), *C. L. York 46113* (SMU, TEX-n.v.); McCullough County, 5 mi. N of Brady, 28 Apr 1966 (fl), *K. L. Boatman 48* (SMU, TEX-n.v.); Midland County, Midland, 9 May 1902 (fl), *S. M. Tracy 8004* (MO, NY, TEX-n.v.); Mitchell County, 7 mi. ENE of Colorado City, 17 Jun 1945 (fl, fr), *R. W. Pohl 4983* (BRIT); Rains County, 1¾ mi. NW of Alba, 7 Aug 1950 (fr), *V. L. Cory 57587* (SMU); Real County, 1 mi. N of Leakey, 488 m, 27 Jun 1971 (fl), *P. A. Fryxell 1779* (NY); along Texas farm road 337, 3 mi. W of Leakey, 29°27′N, 99°56′W, 690 m, 25 May 1990 (fl), *J. S. Miller et al. 5150* (MO); Refugio County, in Refugio city limits, 24 Mar 1955 (fl), *F. B. Jones 1002* (SMU); Robertson County, SW of Benchley, NW ¼ Bryan W Quad., Spur 231 and railroad, 15 Apr 1982 (fl), *T. Starbuck 1771* (BRIT); Runnels County, 3.2 mi. SW of Ballinger, 9 Jun 1957 (fl), *L. H. Shinners 26362* (SMU); San Patricio County, 2 mi. S of townsite of San Patricio near Nueces River, 18 Oct 1951 (st), *F. B. Jones 651* (SMU); San Patricio County, Welder Wildlife Foundation, N of Sinton, Hackberry Mott., 0.2 mi. N from place where S loop of river road bends W, ca. 6 m above and 40 m back from Aransas River, 14 m, 6 May 1959 (fl), *A. Traverse 1268* (BRIT); San Saba County, Rough Creek Rd., behind Methodist Church at Chappel, 24 Apr 1977 (fl), *B. Barnette 272* (SMU); 0.5 mi. E FM 45 on FM 500, 22 Apr 1976 (fl), *P. Burleson 256* (BRIT); Shackelford County, US 283, ca. 3 mi. S of Albany, 22 May 1963 (fl), *N. C. Henderson 63–973* (FSU, SMU, TEX-n.v.); Sutton County, without precise locality, 29 Aug 1933 (fl), *V. L. Cory s. n.* (BRIT); Tarrant County, 2 airline mi. SW of Benbrook, 8 May 1948 (fl), *V. L. Cory 54408* (SMU, LL-n.v.); above Big Fossil Creek just E of TX 183 bridge, Haltom City, N side of Ft. Worth, 26 Apr 1998 (fl), *R. Kral 87386* (VDB); by jct. Beach St. W and N Beach St., E of Belknap, 3 Jun 2001 (fl), *R. Kral 91262* (VDB); S Arlington, 18 Aug 1971 (fr), *R. L. Neill 117* (BRIT); without precise locality, 5 Aug 1921 (fl), *A. Ruth 940* (NY); E of Euless on Bear Creek, 1 mi. N of Hwy 183, 2 Jul 1946 (fl), *E. Whitehouse 16147* (NY, SMU); Taylor County, Hwy 36, 6 mi. SE of Abilene, 9 Oct 1965 (fr), *J. Davis 9* (SMU); ca. 10 mi. S of Abilene, along US 277, 30 Aug 1961 (fl), *N. C. Henderson 61–804* (FSU); along US 80 at the E edge of Abilene, 18 Apr 1963 (fl), *N. C. Henderson 63–379* (SMU, TEX-n.v.); ca. 4 mi. SW of Potosi on Arrant Ranch, 14 Oct 1962 (fl), *W. F. Mahler 3079* (SMU); near Abilene, 9 May 1943 (fl), *W. L. Tolstead 7188* (SMU); Throckmorton County, 5 km S and 6.8 km W of Throckmorton, J. A. Cornelius farm, 29 May 1980 (fl), *J. Cornelius 403* (BRIT); same locality, 22 May 1981 (fl), *J. Cornelius 838* [2 sheets] (BRIT); Titus County, 4 mi. W of Mount Pleasant, 30 Apr 1948 (fl), *A. Garcia s. n.* (SMU); Tom Green County, San Angelo, 3 Jul 1917 (fl, fr), *E. J. Palmer 12378* (MO, TEX-n.v.); Travis County, Austin, near Onion Creek near the water filtration plant settling ponds SE of Austin, 27 Apr 1975 (fl), *A. W. Lievens s. n.* (LSU); Austin, 19 Aug 1936 (fl), *W. L. McCart 482* (SMU); Austin, 8 Apr 1918 (fl), *M. S. Young 122* (MO); Co. Hwy 920, 10 mi. E of jct. with I-H 35, 20 Apr 1994 (fl), *M. F. Zermoglio 26* (VDB); Uvalde County, ca. 2 mi. S of Utopia, on banks of Sabinal River, 22 Aug 1989 (fr), *P. A. Fryxell 4990* (NY); 1¾ mi. SE of Laguna, 12 May 1938 (fl, fr), *V. L. Cory & H. B. Parks 29187* (SMU); Washington County, 1 mi. SW on Hwy 390 from its jct. with thee AT & SF Railroad in Gay Hill, 3 Apr 1990 (fl), *S. D. Jones & J. K. Wipff 4176* (VDB); Wichita County, Red River above Burkbumett, s.d. (fl), *B. C. Tharp 570* (NY); Wilbarger County, 27.1 mi. W of Electra, 6.8 mi. S of Harrold, turn W 0.6 mi. S on Hwy 25 and N at 20.9 mi., 12 May 1945 (fl), *E. Whitehouse 9863* (NY, SMU); Wise County, access road to US Hwy 287 N, 1 mi. N of Rhome, 33.086676N, 97.471717W, 10 Apr 2013 (fr), *B. L. Lipscomb 3540* (BRIT, G, K, MO, NY, P, US, UT); LBJ Grasslands Unit 23, 33°20′17.20″N, 97°37′45.34″W, 275 m, 2 May 2003 (fl), *R. J. O'Kennon & C. McLemore 18127* (BRIT); LBJ Grasslands Unit 31, 17 Jun 2004 (fl), *R. J. O'Kennon & C. McLemore 19532* (BRIT); Wood County, ca. 4 mi. E of Lindale, 7 May 1991 (fl), *R. Kral 78616* (VDB); Young County, 3 mi. S of Newcastle, near Fort Belknap, 13 Apr 1946 (st), *E. Whitehouse 15329* (SMU).

5. Solanum flagellare Sendtn., Flora Bras. 10: 68. 1846.—TYPE: BRAZIL. Without precise locality, s.d. [1836?], (fl), *F. Sellow s. n.* (lectotype, designated here: P–P00335298!; isolectotypes: B [destroyed], photo of B [F neg. 2818]!, F–621100!, P–P00335294!).

Solanum humifusum Dunal, Prodr. 13(1): 237. 1852.—TYPE: BRAZIL. San Paolo [São Paulo], 1833 (st), *C. Gaudichaud 307* (holotype: P–P00335297!).

Solanum ilicifolium Dunal, Prodr. 13(1): 190. 1852.—TYPE: BRAZIL. St. Paul [São Paulo], ad Mugi das Cruzei [Mogi das Cruzes] Nov 1833 or 1835 (bud), *P. W. Lund 794* (holotype: G-DC–G00145795 [scan]!).

Sprawling decumbent herb up to ca. 0.2 m tall. Stems sparsely to densely pubescent with sessile to short-stalked stellate hairs 0.4–0.7 mm in diameter, with 4–8 lateral rays, the central ray absent or 1-celled and up to 0.4 mm long, moderately armed with straight tapered prickles up to 5 mm long. Sympodial units 2- to plurifoliate, the leaves not geminate. Leaves simple, the blades 3–5 × 1.2–2.8 cm, elliptic to ovate, sparsely to moderately stellate-pubescent abaxially with hairs like those of the stems, slightly less so adaxially, sparsely to moderately armed with prickles up to 4 mm long on the major veins abaxially and adaxially; base rounded or truncate, often with one side offset up to 0.5 cm from the other; margin subentire to shallowly lobed with 3–6 lobes per side; apex rounded; petioles 0.5–1 cm long, moderately to densely stellate-pubescent, sparsely to moderately armed with prickles up to 5 mm long. Inflorescences up to 6 cm long, extra-axillary, unbranched, with 1–6 flowers, the axes moderately to densely stellate-pubescent, sparsely armed with prickles up to 5 mm long; peduncle up to 3.5 cm long; pedicels 0.5–1.8 cm in flower, weakly articulated at the base, moderately to densely stellate-pubescent, unarmed or sparsely armed with prickles up to 4 mm long. Calyx 4–7 mm long, the tube 1–1.3 mm long, the lobes 3–5 × 1.3–1.8 mm, triangular-lanceolate, the apex acute, moderately stellate-pubescent abaxially, glabrous adaxially, unarmed or sparsely armed with prickles up to 2.5 mm long. Corollas ca. 2 cm in diameter, ca. 10 mm long, rotate to stellate-pentagonal, chartaceous, white, the tube ca. 2.5 mm long, the lobes 8–9 × 2–4.5 mm, deltate-triangular, the apex acute, moderately stellate-pubescent abaxially, glabrous adaxially. Stamens with filaments 1.5–2 × 0.2–0.4 mm; anthers 5–6 × 0.9–1.3 mm, narrowly lanceolate, weakly or not connivent, yellow, the pores directed distally. Ovary ca. 1 × 1–1.2 mm, ovoid, glabrous; style 5–6 × ca. 0.4 mm, cylindrical, straight, glabrous, exserted; stigma capitate. Fruits unknown.

Distribution and Habitat—*Solanum flagellare* is restricted to São Paulo state in Brazil in the coastal area near Mogi das

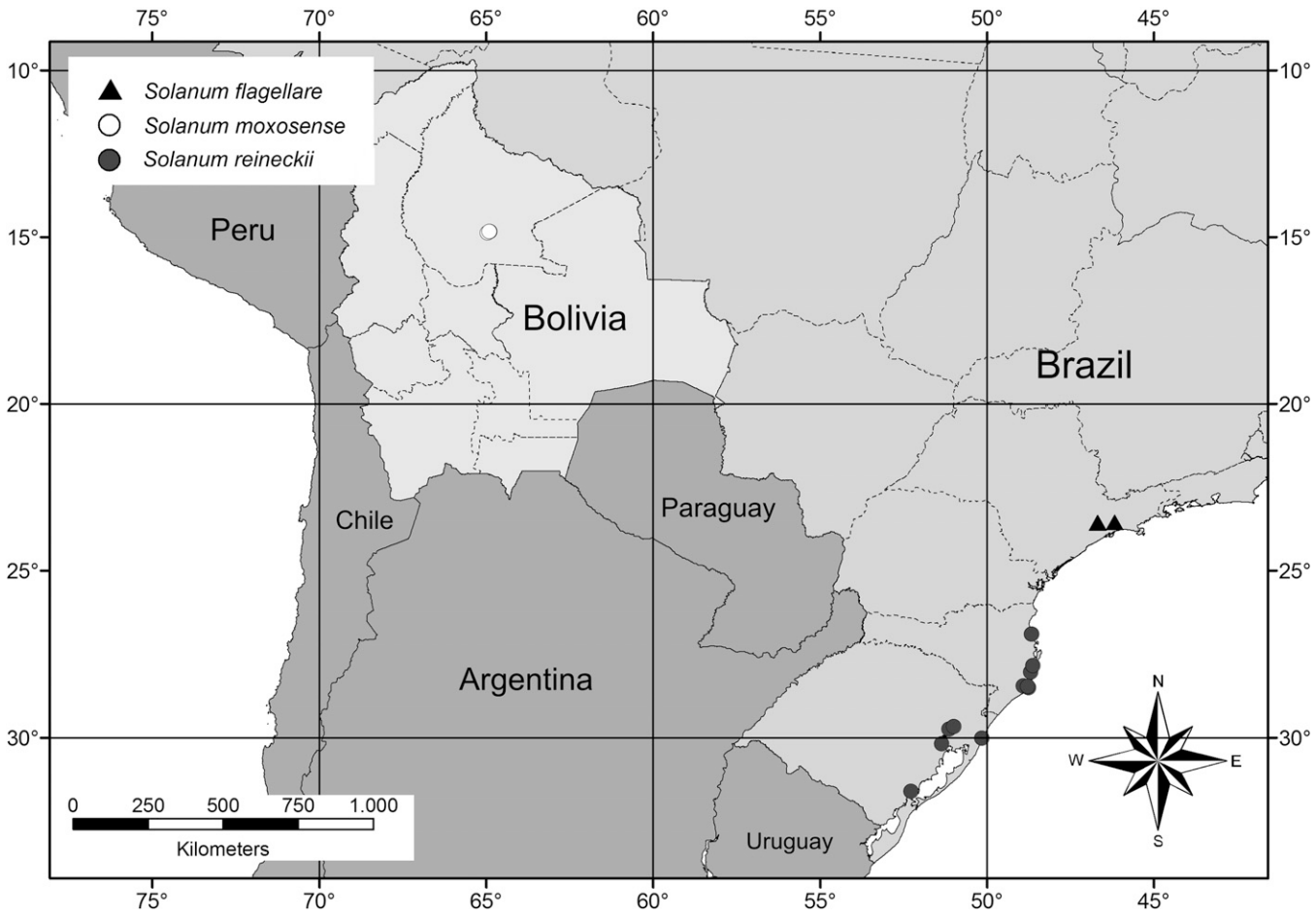

FIG. 8. Distribution of *Solanum flagellare*, *S. moxosense*, and *S. reineckii*.

Cruzes (Fig. 8). One collection (*Riedel s. n.*) records the habitat as grasslands.

Phenology—The species flowers in November.

Conservation Status—Of the five specimens of *Solanum flagellare* we examined, only one (*Riedel s. n.*) had useful locality information; it was not possible to assign post-facto distributions to the other four. The species occurs in areas of São Paulo state that have been heavily impacted by urbanization, and apparently it has not been collected in the last ca. 80 yr. A threatened IUCN status may be justified if new distribution data become available, but in the meantime we have assigned the species to the category of "data deficient" (DD).

Etymology—The epithet "*flagellare*" is the Latin word for flagellum, or whip. The name refers to the slender, whip-like shape of the stem, which has a sprawling, decumbent habit.

Vernacular Name—None recorded.

Chromosome Number—None recorded.

Notes—*Solanum flagellare* is similar to *S. reineckii* in its sprawling, decumbent habit, leaf shape, and unbranched inflorescences. It is differentiated by its stems, petioles, leaves, and inflorescence axes that are stellate-pubescent with sessile or short-stalked stellate hairs with stalks up to 0.2 mm long, and calyces that are unarmed or sparsely armed with prickles. *Solanum reineckii* has stems, petioles, leaves, and inflorescence axes that are stellate-pubescent with sessile to long-stalked hairs, the stalks often prickle-like and up to 2 mm long, and calyces that are moderately to densely armed.

In the protologue of *Solanum flagellare*, Sellow's collection at the B herbarium is cited, but it has been destroyed. Duplicates of this collection exist, one at F and two at P. Two of these consist of just a few vegetative fragments (F and P–P00335294). We have chosen the other P specimen (P–P00335298) as the lectotype because it has identical labels to the B sheet, the species name is annotated in Sendtner's handwriting, and it is the most complete specimen with several leaves and a few flowers.

Additional Specimens Examined—BRAZIL. São Paulo: without precise locality (Catalog C1), 1816–1824 (fl), *A. de Saint-Hilaire 1109* (P [4 sheets]); Mugi [Mogi das Cruzes], Nov [1933?] (fl), *Riedel s. n.* (NY [3 sheets]).

6. SOLANUM HIERONYMI Kuntze, Revis. Gen. Pl. 3: 226. 1898.—TYPE: ARGENTINA. Salta: Pasaje del Río Juramento, 21 Feb 1873 (fl), *P. G. Lorentz & G. Hieronymus 361* (lectotype, designated here: NY–NY00172025!; isolectotypes: B [destroyed], photo of B [F neg. 2778]!, BR–BR00000553968 [scan!], CORD–CORD00004225!, G–G00343447!, P–P00335881!).

Solanum pocote Hieron. ex Millán, Revista Argent. Agron. 12: 117. 1947, nom. illeg. superfl., non *S. pocote* Hieron. (1881).—TYPE: Based on *S. hieronymi* Kuntze.

Erect to decumbent perennial herb up to 0.4 m tall; stems unbranched or branched near the base; roots usually in the form of a taproot, producing buds and ellipsoid tuber-like swellings ca. 1–2 × 0.5 cm. Stems moderately to densely

pubescent with sessile to short-stalked stellate hairs 1.4–2 mm in diameter, with 4–5 lateral rays, the central ray 1–3-celled and up to 3 mm long, also moderately to densely pubescent with short unbranched glandular hairs up to 0.3 mm long, moderately armed with straight tapered prickles up to 7 mm long, these often minutely glandular-puberulent. Sympodial units 2- to 3-foliate, sometimes plurifoliate, the leaves not geminate. Leaves simple, the blades 2.5–12(21.5) × 2–7(16) cm, ovate to elliptic in outline, moderately to densely stellate-pubescent abaxially, sparsely to densely pubescent adaxially with sessile stellate hairs up to 2 mm in diameter, with 4 lateral rays, the central ray 1-celled and up to 1.4 mm long, sparsely to moderately armed with prickles up to 7.5 mm long on the major veins abaxially and adaxially; base cordate or less often truncate; margin irregularly lobed; apex obtuse; petioles 2–6 cm long, moderately to densely stellate- and glandular-pubescent with stellate hairs like those of the stem, sparsely armed with prickles up to 3.5 mm long, these rarely with 4–8 rays at the apex. Inflorescences 2–10 cm long, extra-axillary, unbranched, with 5–10 flowers, weakly andromonoecious, the axes moderately to densely stellate- and glandular-pubescent, sparsely armed with prickles up to 5 mm long; peduncle 2–8 cm long; pedicels 1–5.5 cm long in flower and fruit, strongly deflexed downward in fruit, spaced 0.5–2.5 cm apart, articulated at the base, moderately stellate- and glandular-pubescent. Calyx 5–10 mm long, the tube 1–5 mm long, the lobes 3.5–7 × 2–2.5 mm, narrowly triangular, the apex acute, moderately to densely stellate- and glandular-pubescent abaxially, rarely with stellate hairs with stout prickle-like stalks up to 3.5 mm long, glabrous adaxially, moderately to densely armed with prickles up to 4 mm long; fruiting calyx accrescent and covering the lower ⅓ to ½ of the fruit, 7–15 mm long, the tube 1–5 mm long, the lobes 5.5–12 × 5–6 mm, triangular to narrowly triangular, sparsely stellate-pubescent, moderately armed with prickles up to 4 mm long, these sometimes with 4–8 rays at the apex. Corollas 2–4 cm in diameter, 13–22 mm long, rotate to stellate-pentagonal, chartaceous, white, the tube 5–15 mm long, the lobes 2–8 × 4.5–6 mm, deltate, the apex apiculate, moderately stellate-pubescent abaxially, glabrous adaxially. Stamens with filaments 1.2–1.5 × 0.3–0.5 mm; anthers 4.2–10 × 0.6–2 mm, narrowly lanceolate, not connivent, yellow, the pores directed distally. Ovary 2.3–3.2 × 1.6–2.5 mm, subglobose to ovoid, glabrous; style 7.5–15 × 0.5–1 mm, cylindrical, straight, glabrous, exserted; stigma capitate. Fruits 1.5–2.2 × 1–2 cm, subglobose, the apex obtuse, green to whitish-green and somewhat darker green-striped at the proximal end when immature, yellow at maturity, glabrous. Seeds 1.8–2 × 2–2.2 mm, flattened-reniform, lenticular, yellow, the surface finely foveolate.

Distribution and Habitat—*Solanum hieronymi* is distributed in northern Argentina, south-central Bolivia, and northwestern Paraguay (Dept. Boquerón) (Fig. 6). It grows in disturbed areas (e.g. roadsides, borders of cultivated fields, grazed woodlands) often in sandy or clay soils and in chaco vegetation from 400–1830 m in elevation.

Phenology—Flowering between November and April and fruiting between February and June.

Conservation Status—*Solanum hieronymi* is distributed across a large area in Bolivia, Paraguay, and northern Argentina. It grows in highly disturbed habitats, and it is doubtful that there will be any significant reduction in population size or locations. With an extent of occurrence of ca. 820,000 km^2 and area of occupancy of 1,248 km^2, *Solanum hieronymi* is assigned a preliminary conservation status of "least concern" (LC).

Etymology—*Solanum hieronymi* is named after Georg Hans Emmo Wolfgang Hieronymus (1846–1921) who collected in Argentina, Bolivia, and Brazil.

Vernacular Names and Uses—From the Santa Cruz Department in Bolivia, two names recorded on herbarium sheets were papa de zorro (*I. G. Vargas C. 414*) and tutía-tutía (*A. Fuentes & C. Pítare 2400*). These common names almost certainly refer to the globose or ellipsoid swellings on the roots (the common name tutia was given to *S. aridum*, another species with swellings on the roots). Other common names in Argentina include papaquisla, pocota, pocote, and pocotillo (Matesevach 2002). Barboza (2013) reports that the tuber-like root swellings are edible.

Chromosome Number—Chromosome counts of *Solanum hieronymi* have shown it to have a variety of ploidy levels: *n* = 12 (*G. Bernardello 505; T. E. Di Fulvio 824*), *n* = 18 (*A. T. Hunziker et al. 24847*), n = 24 (*R. Subils et al. 3859; A. T. Hunziker 24846*), and 2n = 24 (*G. E. Barboza et al. 1261*) (Moscone 1992; Chiarini 2007).

Notes—In habit and most vegetative and reproductive characters, *Solanum hieronymi* is similar to *S. comptum* but can distinguished by its white corolla (vs. light blue in *S. comptum*), larger (1.5–2.2 × 1–2 cm) depressed globose fruits with a weakly accrescent fruiting calyx (vs. smaller (0.8–1 × 0.7–1.3 cm) globose fruits completely covered by the accrescent fruiting calyx), and small stellate hairs with central rays of 1–4 cells that are longer than the lateral rays (vs. central rays consisting of 1–2 cells and shorter or equal to the lateral rays). In *S. hieronymi*, large stellate hairs with stout yellow prickle-like stalks are absent or sparsely distributed on the petioles and calyces. In *S. comptum*, the same stellae are sparsely to moderately distributed on the stem, petioles, leaf blades, inflorescence axes, and pedicels, and densely so on the calyces. *Solanum hieronymi* also has short (up to 0.3 mm long) unbranched glandular hairs that are moderately to densely distributed throughout the plant, whereas *S. comptum* completely lacks glandular hairs.

Among the several duplicates of *P. G. Lorentz & G. Hieronymus 361*, the B and NY sheets were both annotated "*Solanum Hieronymi* OK" in Kuntze's hand (the B specimen was destroyed, but its image is preserved in F neg. 2778). Both the B and NY sheets likely represent original material as Kuntze is known to have worked at B, and the NY sheet was acquired from his personal herbarium. The B specimen has both a mature flower and a fruit, whereas the remaining duplicates contain only immature flowers and fruits. We have chosen the sheet NY–NY00172025 as the lectotype because it is likely to be the only other existing duplicate representing original material examined by Kuntze. Chiarini (2007) and Barboza (2013) incorrectly list the NY specimen as the holotype.

Morton (1976) discusses the convoluted case of the name *S. pocote* Hieron. Hieronymus intended to apply the name to a species of spiny *Solanum*, but cited *S. tuberiferum* var. *arenarium* Dunal in synonomy without providing any further descriptive details of the plant. This latter name is a synonym of *S. montanum* L., a non-spiny *Solanum*, and thus *S. pocote* Hiern. is also a synonym of *S. montanum* L. Millán (1947) attempted to rehabilitate the name *S. pocote*, applying it to a species of spiny *Solanum*. He cites the earlier name

S. hieronymi Kuntze in synonomy, making *S. pocote* Hiern. ex Millán a synonym of this name.

Additional Specimens Examined—ARGENTINA. Catamarca: Capayán, 26 Mar 2002 (fl), *F. Chiarini 577* (CORD); Ambato, camino entre Las Juntas y Potrerillos, 1 Mar 1998 (fl), *Gil s. n.* (CORD); Belén, Hualfín, 16 Jan 1934 (fl), *I. Peirano s. n.* (CORD, LIL); Capayán, Huillapima, Jul 1909 (fl), *P. L. Spegazzini s. n.* (SI). Chaco: Dpto. General Güemes, 2 km al SE de Fte. Esperanza en dirección a Castelli, 25°11′S, 61°49′W, 6 Mar 2000 (fl), *R. Fortunado et al. 6626* (NY); Tapenagá, Villa Angela, 7 Mar 1947, *M. R. Malvárez 1108* (LIL); Napalpí, La Clotilde, 6 Mar 1947, *M. R. Malvárez 1084* (LIL). Córdoba: San Javier, Yacanto, s.d. (fl), *M. T. Cosa 173* (CORD); entre Marull y La Para, 6 Jan 1986 (fl), *T. E. Di Fulvio 824* (CORD); Capital, cercanías de Córdoba, 5 Nov 1880 (fl), *C. Galander s. n.* (CORD); Río Segundo, s.d., *A. T. Hunziker 3674* (CORD); Colón, La Calera, 31 Dec 1902 (fl), *T. J. V. Stuckert 12422* (CORD); San Justo, Mar Chiquita, 14 Apr 1995, *C. R. Volponi 1060* (LP); San Justo, Ruta 19, Jeanmaire, 13 Feb 1991 (fl), *J. A. Zygadlo 109* (CORD). Corrientes: Dpto. Mataco, Ing. Juárez, a orillas del ferrocarril, 6 Mar 2001 (fl), *A. Schinini et al. 35282* (NY). Formosa: Patiño, 5 km antes de Las Lomitas, 18 Dec 1984 (fl), *G. Bernardello 507* p.p. (CORD); Patiño, RN81, a ± 6 km de Pozo del Tigre viniendo desde Las Lomitas, 24°51′14.5″S, 60°22′16.8″W, 6 Feb 2012 (fl, fr), *F. Chiarini & G. A. Wahlert 897* (CORD, UT). Jujuy: Santa Bárbara, Finca Franzini, Santa Clara, 23 Mar 1983, *O. Ahumada & A. Castellón 4859* (CTES); Ledesma, entre Chalicán y Ledesma, 29 May 1974, *A. R. Cuezzo et al. 10231* (LIL); Dpto. San Pedro, San Pedro de Jujuy, 12 Apr 1945 (fl, fr), *C. A. O'Donell 3059* (LIL, NY); Dpto. San Pedro, 2 km SW of La Mendieta, 24°19.87′S, 64°59.02′W, 800 m, 13 Apr 2000 (fl), *M. H. Nee et al. 50761* (NY); Dpto. Valle Grande, road from San Francisco to Valle Grande, ca. 5.5 km N of San Francisco, 23°34.661′S, 64°58.24′W, 1125 m, 21 Apr 2000 (fr), *M. H. Nee & L. Bohs 50830* (NY); Carmen, 6 leguas al S del Dpto. Carmen, Jan 1903 (st), *Peña 12287* (CORD). La Rioja: Chilecito, Puesto Las Trancas, rumbo a Mina La Mejicana, 19 Feb 2003 (fl), *G. E. Barboza et al. 569* (CORD); A. V. Peñaloza, entre Tama y Paca Tala, 28 Feb 1990 (fl), *F. N. Biurrun & E. Pagliari 3212* (CORD); Ulapes, La Dima, 3 Mar 1907 (fl), *T. J. V. Stuckert 17115* (CORD). Salta: Joaquín V. González, 25 Jan 1945 (fl), *R. M. Aguilar 287* (LIL-n.v., NY); Anta, por RP N° 5, 15.6 km antes de Las Lajitas viniendo desde Anta, 650 m, 24°49′28.9″S, 64°19′29″W, 21 Mar 2005 (fl), *G. E. Barboza et al. 1261* (CORD); Orán, alrededores de Tabacal, 10 Dec 1955 (fl), *A. E. Cocucci 92* (CORD); San Martín, La Quena, pasando Río Bermejo, 1 Jun 1974 (fl, fr), *A. R. Cuezzo et al. 10334* (LIL); Capital, Ciudad, vías del ferrocarril Mitre, 20 Mar 1989 (fl), *A. del Castillo 1142* (CORD); Campo Santo, Betania, 12 Jan 1949 (fl), *R. Filipovich 215* (CORD); La Viña, Coronel Moldes, 30 Jan 1941 (fl), *A. T. Hunziker 1014* (CORD); Dpto. Rivadavia, 30 km al E de Dragones, 8 May 1999 (fl), *A. Krapovickas & J. G. Seijo 47750* (CTES); Dpto. General Güemes, Camino de Cabeza de Buey a Río Juramento, 27 Feb 1977 (fl), *P. R. Legname et al. 5324* (LIL); Metán, El Rincón, 12 May 1949 (fl), *F. E. Luna 1472* (CORD); Dpto. Rivadavia, J. Solá (Morillos), 10 km al W del pueblo, 23°28′S, 62°53′ W, 12 Jan 1983 (fl), *A. Maranta & P. Arenas 90* (NY); Dpto. Orán, [illegible], 3 Feb 1945 (fl), *S. A. Pierotti 194* (NY); Dpto. Anta, J. V. González, Fca San Javier, 27 Jan 1949 (fl), *C. Saravia Toledo 269* (LIL); Cafayate, De Cafayate a Salta, km 77, entre Casa de Piedra y El Hongo, 19 Aug 1987 (fl, fr) *R. Subils et al. 3859* (CORD). San Juan: Valle Fértil, Ruta Provincial 511, entre Usno y Balde del Rosario, 21 Feb 1996 (fl), *F. N. Biurrun et al. 4253* (CORD). San Luis: Chacabuco, a ± 3 km al N de Concarán, 17 Feb 1989 (fl), *A. T. Hunziker 25332* (CORD). Santiago del Estero: Hill east of Sumampa, ferrocarril Central de Argentina, 31 Mar 1945 (fl), *H. H. Bartlett 19837* (GH-n.v., NY, SI-n.v., UC-n.v., US-n.v.); Sumampa, 20 Apr 1945 (fl), *P. Garcia 954* (NY); General Taboada, Tacañitas, 17 Apr 1917 (fl), *C. C. Hosseus 236* (CORD); Río Hondo, Yutuyacu, 15 Jan 1949 (fl), *P. R. Legname 51* (CORD); Matará, cerca de Yuchán, 21 Apr 1977 (fl, fr), *T. M. Pedersen 11847* (CTES); Dpto. Guasayan, El Cimbolar, 31 Mar 1944 (fr), *S. A. Pierotti s. n.* (BM); Choya, desde Punta Chiquita hacia Alto Bello, 16 Nov 1984 (fl), *R. Subils et al. 3664* (CORD). Tucumán: Trancas, Ruta 9, 5 km al N de Tapia, 27 Mar 1975 (fl, fr), *A. Krapovickas et al. 27866* (CTES); Trancas, Chulca, 5 Jan 1985, *A. T. Hunziker 24846* (CORD); Burruyacú, Cañada Alegre, 7 Feb 1907 (fl), *T. J. V. Stuckert 16955* (CORD); Tafí, Quilmes, Ruta Nac. 40, entre Amaichá del Valle y Colalao del Valle, 16 Jan 1979 (fl, fr), *R. Subils & G. Bernardello 2652* (CORD); Dept. Cruz Alta, al lado Puente del F.C.C.A., 460 m, 10 Dec 1923 (fl), *S. Venturi 2413* (BM).

BOLIVIA. Cochabamba: 18°15′35″S, 64°49′17″W, 1830 m, 13 Apr 1999 (fl), *C. Antezana 1207* (NY). Santa Cruz: Choreti, 3 mi. from Camiri, above Río Parapetí, 872 m, 16 Sep 1949 (fl), *W. M. A. Brooke 5640* (NY); Prov. Cordillera, Alto Parapetí, 850 m, 8 Jan 1982 (fl), *R. de Michel 100* (NY); Prov. Cordillera, Parque Nacional Kaa-Iya del Gran Chaco, Laguna Azul, 20°10′51″S, 62°20′23″W, 400 m, 24 May 1998 (fr), *A. Fuentes & C. Pítare 2400* (NY); Prov. Vallegrande, Pulquina, Jardín Botanico de Pulquina y sus alrededores, lado del oleoducto, 18°04.10′S, 64°24.30′W, 1557 m, 11 Jan 2004 (fl), *M. Mendoza & E. Calzadilla 765* (NY); Prov. Florida, 3.9 km S of Mataral on road to Vallegrande, 18°08′55″S, 64°12′34″W, 1420 m, 20 Jan 2006 (fl), *M. H. Nee & J. Wen 53877* (NY); Prov. Cordillera, along Hwy from Yacuiba to Camiri, 2.2 km by road SE of Salinas and turnoff to Charagua, 20°14′23″S, 63°27′19″W, 915 m, 13 Feb 2006 (fl), *M. H. Nee & I. I. Linneo F. 54151* (NY); Prov. Florida, 1.8 km SW of bridge in Los Negros, 18°04′06″S, 64°07′05″W, 1320 m, 13 Apr 2007 (fl), *M. H. Nee et al. 55073* (NY [2 sheets]); Prov. Cordillera, Las Juntas, 29 Jan 1947, *Peredo s. n.* (LIL); Prov. Cordillera, a 16.1 km al N de Boyuibe, camino a Camiri, 20°23′35″S, 63°23′53″W, 909 m,13 Jan 2005 (fl), *J. G. Seijo et al. 3426* (CORD, CTES); Prov. Vallegrande, Río Mizque, tunilla, 17 km al W de Vallegrande, 18°31′S, 64°18′W, 1200 m, 13 Feb 1990 (fl), *I. G. Vargas C. 414* (LPB-n.v., MO, NY, USZ-n.v.); Prov. Cordillera, Cerro Toborochi, 10–12 km por brecha abandonada al SE de Estancia Toborochi, 19°14′S, 62°15′W, ca. 470 m, 5–15 Jan 1993 (fl), *I. G. Vargas C. et al. 1923* (NY, USZ-n.v.). Tarija: Prov. Gran Chaco, 3 km E of center of Villa Montes on road to Paraguay, 21°16′10″S, 63°26′50″W, 391 m, 9 Feb 2006 (fl), *M. H. Nee & I. I. Linneo F. 53999* (NY); Prov. Gran Chaco, canyon of Río Pilcomayo, along road from Villa Montes to Entre Ríos and Tarija, 18.3 km (by road) W of center of Villa Montes, 12.6 km (by road) W of bridge over Río Pilcomayo, 21°13′25″S, 63°34′00″W, 471 m, 10 Feb 2006 (fl), *M. H. Nee & I. I. Linneo F. 54044* (NY); Prov. Cordillera, turnoff to Ivo from Camiri-Villa Montes Hwy, 20°23′59″S, 63°23′27″W, 910 m, 19 March 2007 (fl), *M. H. Nee & R. Flores S. 54775* (NY [2 sheets]); Prov. Gran Chaco, 33.5 km (by Hwy) and 33 km (air) SE of Villa Montes on new highway to Isibobo and Paraguay, ca. 5.5 km N or Río Pilcomayo, 21°22′07″S, 63°09′50″W, 350 m, 20 Mar 2007 (fr), *M. H. Nee & R. Flores S. 54794* (NY [2 sheets]); Prov. Gran Chaco, 24.4 km (by road) SE of Villa Montes on new Hwy to Isibobo and Paraguay, measuring from the intersection in Villa Montes of Boyuibe–Yacuiba Hwy, 21°19′49″S, 63°14′13″W, 355 m, 20 Mar 2007 (fl), *M. H. Nee & R. Flores 54810* (NY); Prov. O'Connor, 13.4 km S of Palos Blancos on road to Caraparí, then 3.8 km E, 1.2 km E of buildings at Rancho Tres Aguadas, 21°31′15″S, 63°46′40″–55″W, 850 m, 22 Mar 2007 (fl), *M. H. Nee & R. Flores 54836* (NY); Prov. Gran Chaco, 0.5 km E of Chuvere, 21°32′15″S, 63°48′10″W, 870 m, 23 Mar 2007 (fl), *M. H. Nee & R. Flores S. 54875* (NY [2 sheets]); Prov. Gran Chaco, 40 km (by road) NE of Palos Blancos, 21°17′45″S, 63°36′12″W, 1565 m, 26 Mar 2007 (fr), *M. H. Nee & R. Flores S. 54945* (CORD, NY).

PARAGUAY. Boquerón: Misión Santa Rosa, 21°45′S, 61°35′W, Nov 1981 (fl), *P. Arenas 1745* (NY); Ruta de Tte. Pico a Mcal. Estigarribia, 10 Oct 1987 (fl, fr), *I. Basualdo 845* (FCQ); circa Estancia Copagro, 586 km de Asunción, 7 Mar 1980 (fl), *L. Bernardi 20206* (NY); Fortín Nueva Asunción, bosque al termino N del aeropista militar y alrededores, 20°43′S, 61°56′W, 24 Mar 1986 (fl), *D. R. Brunner 1607* (MO, PY); Tyto. Tte. Pico-Mcal. Estigarribia, 13 km N de Mcal., 14 Dec 1993 (fl), *R. Degen & F. Mereles 3079* (FCQ); Teniente Ochoa, 21°45′S, 60°55′W, 11 Dec 1987 (st), *A. Schinini & R. A. Palacios 25570* (FCQ); 7 km NW de Nueva Asunción, 20°38′S, 62°05′W, 12 Dec 1987 (fl), *A. Schinini & R. A. Palacios 25689* (FCQ); Tte. 1° Alfredo Stroessner, asiento 7a. División Infantería (R. I. 10 Sauce), 22°41′S, 61°35′W, 200–210 m, 9 Oct 1987 (fl), *R. E. Spichiger et al. 2078* (FCQ, G-n.v.); Col. Menno, Lolita, 23°00′S, 59°35′W, 10 Nov 1990 (fl), *R. Vanni et al. 1846* (NY); Fortín Teniente E. Ochoa, 21°43′S, 60°54′W, 21 Jan 1994 (fr), *E. M. Zardini & L. Guerrero 38112* (AS-n.v., MO, NY); proposed National Park Medanos del Chaco, 20°41′03″S, 61°57′37″W, 300 m, 12 Dec 1998 (fl), *E. M. Zardini & N. Duarte 49546* (AS-n.v., MO, NY).

7. Solanum juvenale Thell., Repert. Spec. Nov. Regni. Veg. 5: 161. 1908.—TYPE: FRANCE. Herault, Port-Juvénal, près Montpellier (séchoirs à laine), Aug 1894 (fl), *J. A. Daveau s. n.* ([first-step] lectotype: designated by C. V. Morton, Revis. Argentine Sp. Solanum: 236. 1976; [second-step] lectotype, designated here: MPU–MPU022907!; isolectotypes: CAS–CAS0005763 [scan!], MPU–MPU022904!, MPU–MPU022905!).

Solanum meloncillo Parodi, Rev. Fac. Agron. Vet. Buenos Aires 7: 238. 1930.—TYPE: ARGENTINA. Buenos Aires, Azevedo, Pergamino, 1 Oct 1930 (fr), *L. R. Parodi 9288* (holotype: BAA–BAA00001177!; isotypes: GH–GH00077719!, K, US!).

Erect to decumbent perennial herb up to 0.5 m tall; stems often branched at the base; roots producing buds. Stems moderately pubescent with sessile stellate hairs 0.2–0.4 mm in diameter with 4–8 lateral rays, the central ray absent or up to 0.3 mm long, moderately to densely armed with straight tapered prickles up to 6 mm long. Sympodial units 2- to 3-foliate, sometimes plurifoliate, the leaves not geminate. Leaves simple, the blades 1.8–5.5 × 1–2.5 cm, oblong-elliptic in outline, somewhat discolorous, densely stellate-pubescent abaxially, sparsely so adaxially with hairs like those of the stems, moderately armed with prickles up to 8 mm long on the major veins abaxially and adaxially; base cuneate; margin sinuate to moderately lobed with 3–6 lobes per side; apex acute; petioles 0.5–3 cm long, moderately to densely stellate-pubescent and armed with prickles up to 7 mm long. Inflorescences ca. 1–4 cm long, extra-axillary, unbranched, with 1–3(5) flowers, the axes moderately to densely stellate-pubescent, moderately armed with prickles up to 2.5 mm long; peduncle 2–3 cm long or absent, with the lowermost flower(s) emerging directly from the node; pedicels 1–2 cm long in flower, 1–3 cm long and curved downward in fruit, articulated at the base, moderately to densely stellate-pubescent and armed with prickles up to 3.5 mm long. Calyx 7–8 mm long, the tube 2–4 mm long, the lobes 4–6 × 1.5–3 mm, narrowly deltate, the apex acute-acuminate, densely stellate-pubescent, densely armed with prickles up to 5 mm long abaxially, glabrous adaxially; fruiting calyx somewhat accrescent but not completely covering the fruit, 10–16 mm long, the tube ca. 3 mm long, the lobes 7–12 × 4–5.3 mm, narrowly triangular, moderately stellate-pubescent and armed with prickles up to 4.5 mm long. Corollas 1.2–3 cm in diameter, 15–17 mm long, stellate to stellate-pentagonal, chartaceous, white or bluish, the tube 4–8 mm long, the lobes 4–9.5 × 4–7 mm, deltate to triangular, the apex acute, densely stellate-pubescent abaxially, glabrous adaxially. Stamens with filaments 1–1.7 × 0.2–0.3 mm; anthers 5–6.5 × 1.2–1.4 mm, narrowly lanceolate, not connivent, yellow, the pores directed distally. Ovary 1.2–1.5 × 1.3–1.5 mm, subglobose, glabrous; style 7–12 × ca. 1 mm, cylindrical, straight, glabrous, exserted; stigma capitate. Fruits 1–1.9 × 0.8–1.4 cm, ellipsoid, ovoid, or globose, the apex obtuse, green with white stripes when immature, yellow at maturity, glabrous. Seeds ca. 2.4 × 1.9 mm, flattened-reniform, lenticular, yellow, the surface finely foveolate.

Distribution and Habitat—*Solanum juvenale* is restricted to the central and Pampas provinces of Argentina from 400–1,100 m in elevation (Fig. 4). It grows in disturbed areas such as roadsides, borders of cultivated fields, and waste areas, and can become a localized weed. It typically prefers relatively drier sites than the closely related *S. aridum*.

The type (*J. A. Daveau s. n.*) was collected near the old Port of Juvénal on the River Lez, near Montpellier, France. The plants were found growing in woolen waste (séchoirs à laine) which was probably imported from the Buenos Aires area. Notes on MPU specimens collected from 1868–1894 indicate that *S. juvenale* was adventive around the port or bridge at Juvénal and the customs post at Latte near Montpellier. It was growing as a weed in the Jardin des Plantes in Montpellier during 1904–1949, but L. Soudan indicates that it had disappeared from the port and garden by 1970. It was not seen in the Jardin in Montpellier during a visit by LB in 2004.

Phenology—The species flowers between October and March and fruits between November and May.

Conservation Status—While *Solanum juvenale* is restricted to central and northern Argentina, it nevertheless has a large distribution. It typically grows in highly disturbed habitats, and it is estimated that there will not be any significant reduction in population sizes or locations. With an extent of occurrence of ca. 650,000 km^2 and area of occupancy of 784 km^2, *Solanum juvenale* is assigned a preliminary conservation status of "least concern" (LC).

Etymology—The species is named for the old Port of Juvénal on the River Lez, near Montpellier, France.

Vernacular Names—Common names recorded for *Solanum juvenale* in Argentina are meloncillo de olor, meloncillo del campo, and papa de cuchi (Matesevach 2002; Barboza 2013). The name "meloncillo" refers to the melon-scented fruits.

Chromosome Number—Chromosome counts have shown *Solanum juvenale* to be a tetraploid, with a gametophytic count of $n = 24$ (*E. A. Moscone 75*; Moscone 1992) and a sporophytic count of $2n = 48$ (*F. Chiarini 503*; *F. Chiarini 504*; Chiarini 2007).

Notes—In habit and reproductive characters, *Solanum juvenale* resembles *S. aridum*, and intermediate forms can be found where the two species' ranges overlap (Morton 1976; Chiarini 2007). *Solanum juvenale* can be separated from *S. aridum* by the moderate to dense distribution of prickles on the stem, petioles, leaf blades, inflorescence axes, pedicels, and especially calyces, whereas *S. aridum* is unarmed or sparsely armed. The prickles on the leaf blades are usually much longer in *S. juvenale* (up to 8 mm long), whereas in *S. aridum* they are up to 3 mm long. *Solanum juvenale* also has smaller leaf blades (1.8–5.5 × 1–2.5 cm) that are more deeply lobed compared to the larger leaf blades of *S. aridum* (2–10 × 1–5 cm) that are shallowly lobed to sinuate. The ploidy level consistently differs between the two species, with *S. juvenale* being $2n = 48$ and *S. aridum* being $2n = 24$. Experimental crosses in the greenhouse between *S. aridum* and *S. juvenale* produced triploid plants ($2n = 36$; Chiarini 2007).

In the protologue of *Solanum juvenale* Thellung listed three syntypes. Later, Morton (1976) chose the *Daveau s. n.* collection at MPU—which consists of three specimens—as the lectotype. When a lectotype refers to a single collection or gathering, but consists of more than one specimen, Article 9.17 of the ICBN (McNeill et al. 2012) allows for a subsequent (i.e. second-step) lectotypification to narrow the designation to a single specimen. In this case, Morton (1976) designated the *Daveau s. n.* collection at MPU as the first-step lectotype, and we have further narrowed it via a second-step lectotypification to the specimen *Daveau s. n.* (MPU–MPU022907). This specimen is the most complete of the three bearing several flowers and it was also annotated as "*Solanum juvenale* n. spec." in Thellung's handwriting.

Additional Specimens Examined—ARGENTINA. Buenos Aires: Hurlingham F. C. P., 16 Mar 1945 (fl, fr), *R. Alvarez 632* (NY); Paternal, Nov 1930 (fl), *A. E. Burkart 3370* (CORD); alrededores de La Plata, Facultad de Agronomía, 27 Dec 1932 (fl, fr), *A. L. Cabrera 2666* (NY [2 sheets]); Moreno, Oct 1946 (fl), *A. Castellanos 808* (CORD); La Plata Bosque, 14 Jan 1939 (fl, fr), *A. Chichi 18* (NY); same locality, 23 Jan 1939, *A. Chichi 21* (NY); Campana, 14 Oct 1945, *A. Krapovickas 2591* and *2592* (LIL); La Plata, Feb 1945, *P. Boffa 127* (LIL); Barracas Sud, 20 Feb 1902 (fl, fr), *S. Venturi 35* (CORD). Catamarca: La Paz, La Brea, 14 Jan 1950 (fl), *J. Brizuela 472* (CORD). Córdoba: Río Cuarto, Río Cuarto, verano 1891 (fr), *L. Anetto 7702* (CORD); Colón, Sierra Chica, Agua de Oro, 3 Feb 1955 (fl), *A. Castellanos 3194* (CORD); Capital, Barrio Carola Lorenzini, calle Sol de Mayo al 1500, casi ruta 20, 8 Dec 2001 (fl, fr), *F. Chiarini 504* (CORD); Barrio Carola Lorenzini, calle Sol de Mayo al 1400, 11 Dec 2001 (fl, fr), *F. Chiarini 510* (CORD); Sobremonte, cerca de

San Francisco del Chañar, 29°45′52″S, 64°00′02″W, 29 Nov 2001 (fl), *F. Chiarini et al. 503* (CORD); Sobremonte, cerca de San Francisco del Chañar, 29°45′16″S, 64°00′04″W, 28 Feb 2002 (fl, fr), *F. Chiarini et al. 553* (CORD); El Durazno, finca "Tío Rubio", 1100 m, 5 Nov 1984 (fl), *A. A. Cocucci 89* (CORD); Capital, en las cercanías de Córdoba, 5 Nov 1880 (fl), *C. Galander s. n.* (CORD); Colón, Casa Bamba, 27 Oct 1946 (fl), *A. T. Hunziker 7056* (CORD); San Martín, Cárcano, 14 Nov 1950 (fl), *A. Krapovickas 7358* (CORD); Capital, San Vicente, 23 Feb 1885 (fl), *F. Kurtz 899* (CORD); Río Primero, entre Estancia Tomás García y Punta del Arroyo, 21 Feb 1887 (fl, fr), *F. Kurtz 4686* (CORD); Capital, Ciudad, Ciudad Universitaria, Facultad de Ingeniería, 12 Dec 1984 (fr), *E. A. Moscone 72* (CORD); Río Cuarto, Alpa Corral, 21 Jan 1985 (fl), *E. A. Moscone 75* (CORD); Falda del Sauce, ruta 36, 5 km antes de Villa General Belgrano, 800 m, 10 Nov 1985 (fl), *E. A. Moscone 110* (CORD); Falda del Sauce, 2 Feb 1986 (fr), *E. A. Moscone 114* (CORD); Calamuchita, Falda del Sauce, 14 Jan 1990 (fr), *E. A. Moscone 190* (CORD); Cruz del Eje, Dique de Cruz del Eje, 19 Jan 1947, *C. A. O'Donell 4413* (LIL); San Alberto, entre Mina Clavero y Nono, 22 Mar 1944 (fl, fr), *C. A. O'Donell & J. M. Rodriguéz 701* (CORD); Río Tercero, 26 Mar 1897, *T. J. V. Stuckert 2399* (CORD); Capital, Alto Sur, 15 Dec 1899 (fl), *T. J. V. Stuckert 8096* (CORD); Río Primero, San Teodoro, 16 Jun 1905 (fr), *T. J. V. Stuckert 13173* (CORD); Punilla, La Falda, 30 Dec 1900 (fl), *T. J. V. Stuckert 16612* (CORD); Río Segundo, 8 Mar 1917 (fl), *T. J. V. Stuckert 23358* (CORD); Capital, 13 Oct 1931 (fl), *T. J. V. Stuckert 23745* (CORD); Calamuchita, próximo a Villa General Belgrano, al sur del dique Los Molinos, 15 Mar 1990 (fr), *J. A. Zygadlo 42* (CORD); Cruz del Eje, Pichanas, entre Tuclame y Villa de Soto, en el dique Compensador, 25 Apr 1991 (fr), *J. A. Zygadlo 97* (CORD). La Pampa: Toay, a 3 km hacia el noroeste de la intersección de Avda. Pato Argentino y Avda. Perón (ca. 4 km de Toay), 36°38′51.3″S, 64°22′42.3″W, 19 Feb 2005 (fl, fr), *G. E. Barboza et al. 1173* (CORD); Lihuel Calel, Sierra del Lihuel Calel, 400 m, 30 Dec 1959 (fl), *A. E. Burkart s. n.* (SI). La Rioja: Ruta Nac. 38, entre Chamical y Chañar, campo experimental Las Vizcacheras, 9 Feb 1990 (fl), *F. N. Biurrun & D. Leguiza 3073* (CORD); Chamical, RN 79, entre Chamical y Olta, 9 Apr 1988 (fr), *F. N. Biurrun & E. Pagliari 2353* (CORD); Sierra de Los Quinteros, entre Casas Viejas y El Chilcal, paraje La Laguna, 26 Nov 1989 (fl, fr), *F. N. Biurrun & E. Pagliari 2655* (CORD); Sierra de Los Quinteros, El Toro Muerto, rumbo a Las Barrancas, 26 Nov 1989 (fl, fr), *F. N. Biurrun & E. Pagliari 2666* (CTES, CORD); General Belgrano, entre Chañar y Olta, a 15 km del primero, 20 Jan 1997 (fl, fr), *F. N. Biurrun & E. Pagliari 4618* (CORD); Gordillo Polco, finca Francisco Díaz, 10 Mar 1977 (fr), *F. N. Biurrun et al. 696* (CORD); Sierra de Los Llanos, 10 km al SW de Chamical, entre la represa de La Aguadita y las piletas de Obras Sanitarias, 19 Jan 1990 (fl), *F. N. Biurrun et al. 3028* (CORD); Las Huertas, a lo largo del río, ± 1100 m, 2 Dec 1984 (fl), *R. Subils & F. N. Biurrun 3759* (CORD). San Juan: Pocito, La Rinconada, Dec 1876 (fl, fr), *D. S. Echegaray s. n.* (CORD). San Luis: Pedernera, Estancia Don Roberto, 42 km al S de Villa Mercedes, 17 Nov 1970 (fl), *D. L. Anderson 1816* (CORD); Estancia Las Tres Marías, 30 km al S de San Luis, 21 Mar 1979 (fr), *D. L. Anderson et al. 3642* (CORD); Pedernera, Estancia La Moneda, al N de Chalanta, 685 m, 7 Jan 1981 (fl), *D. L. Anderson et al. 3786* (CORD); Coronel Pringles, Saladillo, 9 Nov 1940, *A. E. Burkart 12118* (SI); La Capital, Paseo Thays, 3 Apr 1989 (fr), *L. A. Del Vitto & E. M. Petenatti 3161*, (CORD); La Capital, entre el Chorrillo y Cruz de Piedra, ruta 20, 2 Dec 1988 (fl), *L. A. Del Vitto & E. M. Petenatti 3559* (CORD); La Capital, Cruz de Piedra, entre el vertedero y ruta 20, 21 May 1972 (fr), *Giordano & Guerreiro 21* (CORD); Ruta 7, salida de San Luis, rumbo a Villa Mercedes, 14 Nov 1956 (fl), *A. T. Hunziker 13094* (CORD); San Martín, entre el Alto Grande y San Martín, camino que viene de Concarán, 16 Jan 1960 (fl, fr), *A. T. Hunziker & A. E. Cocucci 14690* (CORD); Eleodoro Lobos, ruta 7, 17 Jan 1969 (fl, fr), *A. Krapovickas & C. L. Cristóbal 14640* (CORD); San José del Morro, 3 Jan 1892 (fl), *C. E. O. Kuntze s. n.* (NY). Santa Fé: San Lorenzo, Carcarañá, Estancia La Carolina, 1886–1887 (fl), *Berndt 5256* (CORD). Santiago del Estero: Capital, Mar 1914 (fl), *Castañeda Vega 66* p.p. (SI); Copo, Obraje Los Tigres, 20 Sep 1971, *T. Meyer & Vaca 23275* (LIL); Los Tigres, 7 Dec 1979 (fl, fr), *A. Schinini 19493* (CTES); Choya, RN 157, alrededores de Frías, 1 Jun 1990 (st), *R. Subils et al. 4412* (CORD). Tucumán: Burruyacú, Cañada Alegre, Feb 1907 (fl, fr), *T. J. V. Stuckert 16954* (CORD); Burruyacú, 31 Dec 1908 (fl, fr), *T. J. V. Stuckert 19727* (CORD); Leales, Chañar Pozo, Oct 1919 (fl), *S. Venturi 476* (SI).

FRANCE. Languedoc-Roussillon: Hérault, Montpellier, au Pont-Juvénal, 30 Jul 1868 (fl), *André s. n.* (MPU-scan); près Montpellier, May 1870 (fl), *André s. n.* (MPU-scan); Hérault, séchoir sur la route au le Pont Juvénal, Montpellier, 26 May 1870 (fl), *André s. n.* (MPU-scan); adventice au Jardin [Montpellier], Oct 1904 (st), *L. Soudan s. n.* (MPU-scan).

8. Solanum moxosense M. Nee, Brittonia 58: 339. 2006.—TYPE: BOLIVIA. Beni: Prov. Cercado, Trinidad, 14°50′S, 64°55′W, 200 m, 6 Jan 1989 (fl), *M. H. Nee 37519* (holotype: LPB; isotypes: G–G00020289 [2 sheets]!, MO, NY–NY00745813!, NY–NY00745839!, USZ–26728 [scan!], USZ [scan!]).

Creeping to erect herb up to 0.2 m tall, usually rooting at the nodes. Stems glabrous or very sparsely pubescent with simple (1)2–4-celled hairs up to 2 mm long, sparsely armed with straight or slightly curved tapered prickles up to 3.5 mm long. Sympodial units 2- to 3-foliate, sometimes plurifoliate, the leaves not geminate. Leaves simple, the blades 5–7.5 × 3.5–6 cm, ovate in outline, very sparsely pubescent abaxially with sessile stellate hairs 0.7–1 mm in diameter, with 4(5) lateral rays, the central ray absent or 1-celled and up to 0.5 mm long, glabrous adaxially, sparsely armed with prickles up to 5 mm long on the major veins abaxially and adaxially; base truncate to cordate, equal to very unequal, often with one side offset up to 1 cm from the other; margin repand to shallowly lobed with 3–4 rounded to obtuse lobes per side; apex obtuse to subacute; petioles 0.7–3 cm long, sparsely pubescent with simple and stellate hairs like those of the stems, sparsely armed with prickles up to 5 mm long. Inflorescence 5–6 cm long, extra-axillary or subopposite the leaves, unbranched, with 4–5 flowers, probably andromonecious with the proximal one or two flowers hermaphroditic, the axes nearly glabrous to sparsely pubescent with simple and stellate hairs, sparsely armed with prickles up to 2 mm long; peduncle 3–4.5 cm long; pedicels 0.9–1.1 cm long in flower, glabrous or sparsely pubescent with simple hairs, unarmed, up to 1.5 cm long and somewhat thickened and curved downward in fruit, spaced 7–14 mm apart, articulated at the base. Calyx 3–7 mm long, the tube 1.5–3 mm long, the lobes 1.5–4 × 1–1.5 mm, oblong-ovate, the apex acuminate, very sparsely pubescent with simple and stellate hairs, the stellae with the central ray longer than the lateral rays, unarmed; fruiting calyx somewhat accrescent but not completely covering the fruit, ca. 5–8 mm long, the tube ca. 1.5–2 mm long, the lobes ca. 2–6.5 × 2–4.5 mm. Corollas 1.3–2 cm in diameter, 7–12 mm long, stellate to stellate-pentagonal, chartaceous, white, the tube ca. 6 mm long, the lobes ca. 6.5 × 3.5 mm, triangular, the apex acute, moderately to densely pubescent abaxially with sessile stellate hairs, glabrous adaxially. Stamens with filaments 1.5–2 mm long, glabrous; anthers 4–5 × 0.6–1 mm, linear-tapered, not connivent, yellow, the pores directed distally. Ovary ca. 0.7 × 0.7 mm, glabrous; style ca. 8 × 0.5 mm, cylindrical, straight, glabrous, exserted; stigma capitate. Fruits (immature) ca. 1 × 0.8 cm, oblong-ovoid, the apex rounded, the color when ripe unknown, glabrous. Seeds unknown.

Distribution and Habitat—*Solanum moxosense* is only known from the area near the town of Trinidad in the Department of Beni, Bolivia (Fig. 8). It has a weedy habit and grows in disturbed and grazed areas at elevations from 150–200 m.

Phenology—The few known specimens of *Solanum moxosense* have been collected in flower in August and January and with immature fruit in February.

Conservation Status—*Solanum moxosense* is known from five collections, three of which have geographical coordinates. All were made in or very near the town of Trinidad, and none are from protected areas. Thus, all of the material

known for the species likely represents a single location and population with a highly restricted extent of occurrence of 4.5 km^2 and area of occupancy of 12 km^2. *Solanum moxosense* is assigned a preliminary conservation status of "critically endangered" [CR B1ab(i,ii,iii,v)].

Etymology—*Solanum moxosense* is named for the Llanos de Moxos, a seasonally flooded savanna in the Department of Beni in the northern part of Bolivia.

Vernacular Names—None recorded.

Chromosome Number—None recorded.

Notes—*Solanum moxosense* is similar to *S. flagellare* and *S. reineckii* in its unbranched inflorescences and decumbent, creeping habit, but differs by its stems that are glabrous to sparsely pubescent with simple (1)2–4-celled hairs compared to the sparsely to densely stellate-pubescent stems of *S. flagellare* and *S. reineckii*.

Additional Specimens Examined—BOLIVIA. Beni: Prov. Cercado, Trinidad, 200 m, Aug 1944 (fl), *M. Cárdenas 3525* (MO, US-n.v.); Trinidad, 14°50.159′S, 64°54.034′W, 197 m, 9 May 2007, *D. McClelland & S. Stern 408* (NY-n.v., USZ-n.v.); Puerto Almacén, 9.3 km SW of center of Trinidad, main road to Baradora, ca. 100 m E of bridge over Río Ibare, 14°52.065′S, 64°58.130′W, 10 May 2007, *D. McClelland & S. Stern 419* (NY-n.v., USZ-n.v.); Trinidad, 14°50′S, 64°55′W, 150 m, 25 Feb 1987 (fl, fr), *M. H. Nee 34261* (MO, NY).

9. Solanum perplexum Small, Man. S. E. Fl. [Small]: 1115, 1508. 1933.—TYPE: U. S. A. Georgia: Thomas County, along or near the Ochlockonee River near Thomasville, 28 May–6 Jun 1895 (fl), *J. K. Small s. n.* (holotype: NY–NY00138956!).

Upright perennial herb up to 1 m tall, 1- to few-branched. Stems glabrous or sparsely to densely pubescent with sessile to short-stalked stellate hairs 0.5–1.2 mm in diameter, with (4–)6–8 lateral rays, the central ray 1–2-celled and up to 1.4 mm long, unarmed or sparsely to moderately armed with tapered prickles up to 12 mm long. Sympodial units 2- to 3-foliate, sometimes plurifoliate, the leaves not geminate. Leaves simple, the blades 7–22 × 8–18 cm, broadly ovate in outline, sparsely to densely stellate-pubescent abaxially, slightly less so adaxially with hairs like those of the stem, sparsely to moderately armed with prickles up to 15 mm long on the major veins abaxially and adaxially; base truncate to cuneate, equal to unequal, often with one side offset up to ca. 1.2 cm from the other; margin shallowly to deeply lobed with 2–5 lobes per side; apex acute or rounded; petioles 1–6 cm long, sparsely to densely stellate-pubescent with hairs like those of the stem, sparsely to densely armed with prickles up to 12 mm long. Inflorescences 7–15 cm long, extra-axillary, 1- to several-branched, with up to ca. 15 flowers, weakly andromonoecious, the axes moderately to densely stellate-pubescent, sparsely armed with prickles up to 8 mm long; peduncle 4–7 cm long; pedicels 1–2 cm in flower, up to ca. 2.4 cm and curved downward in fruit, weakly articulated at the base, moderately to densely stellate-pubescent, unarmed or sparsely armed with prickles up to 5 mm long. Calyx 7–13 mm long, the tube 1–4 mm long, the lobes 4–10 × 2–5 mm, ovate-lanceolate, the apex acute to shortly acuminate, densely stellate-pubescent abaxially, glabrous adaxially, unarmed or sparsely armed with prickles up to 1.3 mm long; calyx of immature fruit spreading to reflexed, weakly accrescent, 10–12 mm long, the tube 0.5–2 mm long, the lobes 4–10 × 4–8 mm, ovate-lanceolate to triangular, sparsely to moderately stellate-pubescent, very sparsely armed with prickles up to 4 mm long. Corollas 2–4.4 cm in diameter, 10–20 mm long, stellate to stellate-pentagonal or rotate-stellate, chartaceous, lavender, the tube 2–9 mm long, the lobes 4–17 × 4–15 mm, deltate to triangular, the apex acute, moderately stellate-pubescent abaxially, glabrous adaxially. Stamens with filaments 1–2.5 × 0.25–0.7 mm; anthers 4–10 × 1.2–2.4 mm, narrowly lanceolate, weakly or not connivent, yellow, the pores directed distally. Ovary ca. 2.5 × 2–2.5 mm, ovoid, glabrous or sparsely pubescent with simple white hairs up to 0.5 mm long and glandular hairs up to 0.2 mm long; style 10–13 × 0.4–1 mm, cylindrical, straight, glabrous or sparsely pubescent at base, exserted; stigma capitate. Fruits ca. 1.8 × 2 cm, subglobose, the color unknown at maturity, glabrous, the rind tough. Seeds ca. 2 × 2.5 mm, flattened-reniform, often twisted, lenticular, yellow, the surface finely foveolate.

Distribution and Habitat—*Solanum perplexum* occurs in southeastern Alabama, southwestern Georgia and northern Florida, with a single collection from western Mississippi (Fig. 7). It grows sandy and clay soils in disturbed areas such as cultivated fields (e.g. peanut, cotton), roadsides, grazed pastures, forest edges, and urban waste areas at elevations from near sea level to ca. 120 m.

Phenology—Flowering between May and August; fruiting between September and November.

Conservation Status—*Solanum perplexum* is distributed mainly in the region where the borders of Alabama, Georgia, and Florida meet, with a single outlying population in western Mississippi. Excluding the single collection from Mississippi, the species has an extent of occurrence of 53,000 km^2 and area of occupancy 132 km^2. *Solanum perplexum* is a weed and often grows in disturbed habitats. It is doubtful that there will be a significant reduction in the population size or number of locations, and the species is assigned a preliminary conservation status of "least concern" (LC).

Etymology—Small (1933) did not provide any clues about his use of the word "*perplexum*." However, because of the reported polyploidy in *Solanum perplexum* and its morphological intermediacy between *S. carolinense* and *S. dimidiatum*, "*perplexum*" seems a fitting epithet.

Vernacular Names—None recorded.

Chromosome Number—D'Arcy reported a gametophyic chromosome number for *Solanum perplexum* (as *S. dimidiatum*) of $n = 36 \pm 1$ (D'Arcy, 1969).

Notes—Many herbarium specimens have been annotated by W. G. D'Arcy as *Solanum perplexum*, but he placed the species in synonymy under *S. dimidiatum* in his treatment of *Solanum* in Florida (D'Arcy 1974). Examination of both *S. perplexum* and *S. dimidiatum* for this revision revealed several consistent, non-overlapping morphological differences between the two species, as well as separate geographical ranges (Fig. 7), and we consider *S. perplexum* to be worthy of taxonomic recognition at the rank of species. In floral and fruit morphology, *S. perplexum* is similar to *S. dimidiatum*, but it differs by the indumentum of golden stellate hairs with (4–)6–8 lateral rays with the central ray 1–2-celled and longer than lateral rays (vs. whitish stellate hairs with (4–)6–10 lateral rays with the central ray 1-celled and equal to or shorter than lateral rays in *S. dimidiatum*), the larger prickles on the stems and leaves (up to 15 mm long vs. up to 6.5 mm long), and the larger leaves (up to 22 × 18 cm vs. up to 16 × 10 cm).

The protologue of *Solanum perplexum* is divided over two non-consecutive pages, with a description in English on page 1115 and the citation of a type on page 1508, which

reads: "Type, near Thomasville, Ga., Small, May 28–June 6, 1895, in herb. C. U." The abbreviation "herb. C. U." refers to the herbarium at Columbia University, which was transferred to The New York Botanical Garden in 1898, and the collection information unambiguously refers to the specimen *J. K. Small s. n.* (NY–NY00138956!). Because a single herbarium was indicated for the type in the protologue, and due to the fact that there is no evidence of duplicates deposited elsewhere, we interpret the *J. K. Small s. n.* specimen at NY as the holotype.

Additional Specimens Examined—U. S. A. Alabama: Barbour County, Barbour Co. Hwy 5, 1.3 mi. N of AL Hwy 10, T9N, R24E, S30, 2 Jun 2002 (fl), *A. R. Diamond 13245* (VDB); roadside of Hwy 30 at 4.9 mi. W of jct. with Hwy 431 in Eufala, 12 May 1997 (fl), *J. R. MacDonald 10468* (VDB); vicinity of Comer, roadside of Silo Rd. at 2.1 mi. N of jct. with Hwy 82, 9 May 1998 (fl), *J. R. MacDonald 11155* (VDB); Geneva County, Geneva Co. Hwy 6, 1.5 mi. W of Geneva Co. Hwy 55, T1N, R23E, S19, 16 May 2002 (fl), *A. R. Diamond 13182* (UNA, VDB); Geneva, farm of Charles Turner on Co. Rd. 6 at 3 mi. E of jct. with Co. Hwy 4, 28 Apr 1999 (fl), *J. R. MacDonald 12745* (VDB); Gilchrist County, ca. 1½ mi. N of Lovedale community center on W side of Timerlane Rd., 17 Jun 1993 (fl), *A. M. Andreasen s.n.* (FLAS); Henry County, Trawich Farm, 18 Aug 1982 (fl), *R. L. Nichols s. n.* (FLAS); 4–5 mi. SE of Headland, Hemp City, 18 Aug 1982 (fl), *R. L. Nichols s. n.* (MO); Houston County, above Cowart's Creek, SW Cottonwood, 20 Jun 1978 (st), *R. Kral 62097* (VDB); ca. 2.2 mi. NE of Grangeburg, on Bazemores Rd. at 0.6 mi. E of jct. with Houston Co. Hwy 81, T1N, R10W, NW ¼ of NE ¼ of S25, 8 Jun 1996 (fl), *J. R. MacDonald 9538* (NY, VDB); 4 mi. S of Ashford, on Houston Co. Rd. 55, 25 May 1971 (fl), *H. D. Moore 1163* (VDB); Lee County, ca. 1.5 mi. W of Roxana, toward Notasulga, 25 May 1987 (fl), *J. D. Freeman s. n.* (VDB); Pike County, Pike Co. Hwy 25 at S side of Good Hope Church, T10N, R20E, S28, 8 Jul 2000 (fl), *A. R. Diamond 11780* (VDB); ca. 1 mi. N of Brundidge, on Co. Hwy 26 at 0.5 mi. W of jct. with State Hwy 93, 6 May 1995 (fl), *J. R. MacDonald 8599* (MO, VDB). Florida: Alachua County, Old Rocky Point Rd., near Gainesville, 21 Jun 1937 (fl), *L. E. Arnold & E. West s. n.* (DUKE-n.v., FLAS); between FL 24 & 26, 1 mi. W of US 75, 12 May 1967 (fl), *W. G. D'Arcy 1587* (FLAS, MO); NW of Gainesville, S of SR 232, T9S, R18E, S13, 14 Jul 1978 (fl), *W. J. Dunn 1* (FLAS); 2 mi. S of Gainesville, 3 May 1933 (fl), *J. W. Kea s. n.* (FLAS); Paynes Prairie, Gainesville, 28 Apr 1935 (fl), *G. F. Weber s. n.* (FLAS [2 sheets]); Columbia County, Lake City off October Rd., 20 Jul 2004 (st), *P. Tomlinson s. n.* (FLAS); Gilchrist County, ca. 2 mi. W of Bell, along FL Hwy 341, 17 May 1968 (fl), *W. G. D'Arcy 2477* (FLAS, MO); Jackson County, bordering Rt. 167 just N of jct. with Rt. 1656c, ca. 4 air mi. SW of Marianna, 12 May 2006 (fl), *L. C. Anderson 21774* (FSU); [Jackson County], without precise locality, s.d. (fl), *A. W. Chapman s. n.* (NY); 0.5 mi. W of intersection of Gulf Power Rd and Douglas Rd., T4N, R7W, NE corner of S11, 10 Jun 2005 (fl), *S. Halpern s. n.* (FSU); Jefferson County, along Lake Miccosukee, 22 Apr 1924 (fl), *J. K. Small et al. 11201* (NY); Waukeenah, 11 Jul 1940 (fl), *W. A. Murrill s. n.* (FLAS); Monticello, 14 May 1928 (fl), *R. E. Nolen s. n.* (FLAS [2 sheets]); Leon County, N Monroe St. across from Tallahassee Mall in front of Capitol Cinemas, 17 Nov 1984 (fr), *L. C. Anderson 7800* (FSU); near Tallahassee, s.d. (fl), *N. K. Berg s. n.* (NY); Tallahassee, 2 May 1955 (fl), *R. K. Godfrey 53226* (DUKE-n.v., FSU, GA-n.v., NY, SMU-n.v., UNA); West Tallahassee, 15 May 1951 (fl), *C. Jackson 533* (FSU); Tallahassee, 7 May 1961 (fl), *R. K. Godfrey 60805* (FSU); ca. 1 mi. W of Tallahassee, 23 May 1926 (fl, fr) *H. Kurz s. n.* (NY); Apalachicola National Forest 10 mi. S of Tallahassee, 13 May 1955 (st), *P. L. Redfearn 350–2-55* (FSU); Wakulla County, 3 mi. S of Crawfordsville, by US Rt. 319, 13 May 1978 (fl), *R. K. Godfrey 76461* (FSU); 3 mi. S of Crawfordsville, 6 May 1957 (fl), *R. Kral 4711* (FSU, VDB); prope St. Marks, May 1843 (fl), *F. I. X. Rugel s. n.* (NY); 1.6 mi. N of Medart on US 319, 30 Apr 1982 (fl), *R. P. Wunderlin & J. Beckner 9285* (FLAS). Georgia: Calhoun County, 5 mi. NE of Morgan off Rt. 41N, 13 Sep 1982 (st), *R. L. Nichols s. n.* (FLAS, MO); Decatur County, ca. 1 mi. W of Attapulgus along road to Faceville, 4 Jun 1982 (fl), *L. C. Anderson 5959* (FSU); Dougherty County, 1 mi. N of Pretoria, 17 May 1947 (fl), *R. F. Thorne 4010* (NY); Lee County, 5.4 mi. SSW of Leslie, 23 Aug 1977 (fl), *R. Kral 60931* (MO, VDB [2 sheets]); Sumter County, off Rte. 280 E, 13 Sep 1982 (fl, fr), *R. L. Nichols s. n.* (FLAS); just W of South Lee St. (GA 377) and S of Mill Creek, ca. 2.4 mi. S, and slightly E of downtown Americus, ca. 100 m, 16 May 1997 (fl), *R. A. Norris 6846* (VDB); Thomas County, US-84, 6.3 mi. E of Thomasville, 4 June 1970 (fl), *W. R. Faircloth 6723* (MO). Mississippi: Washington County, ca. 3 mi. NE of Stoneville, 13 May 1997 (fl), *C. T. Bryson 15820* (VDB).

10. Solanum pumilum Dunal, Prodr. 13: 287. 1852, nom. nov. for *Solanum hirsutum* Nutt.—TYPE: Based on *Solanum hirsutum* Nutt.

Solanum hirsutum Nutt., J. Acad. Nat. Sci. Philadelphia 7: 109. 1834, non Dunal (1813), nec Roxb. (1814).—TYPE: U. S. A. Georgia. Without precise locality, s.d. (fl), *S. Boykin s. n.* (lectotype, designated here: PH–PH00030417!).

Solanum carolinense var. *hirsutum* A. Gray, Syn. Fl. N. Amer. 2: 230. 1878.—TYPE: Based on *Solanum hirsutum* Nutt.

Solanum carolinense var. *hirsutum* D'Arcy, Ann. Missouri Bot. Gard. 61: 840. 1974.—TYPE: Based on *Solanum hirsutum* Nutt.

Upright perennial herb up to 0.2 m tall. Stems moderately to densely pubescent with sessile stellate hairs 0.4–0.8 mm in diameter, with 4–8 lateral rays, the central ray (1)2–5-celled and up to 3 mm long, unarmed or sparsely armed with tapered prickles up to 2 mm long. Sympodial units 2- to 3-foliate, sometimes plurifoliate, the leaves not geminate. Leaves simple, the blades 2.2–8.6 × 1.1–5.1 cm, elliptic to obovate, somewhat discolorous, sparsely to densely stellate-pubescent abaxially, slightly less so adaxially with sessile stellate hairs 0.4–0.8 mm in diameter, with 4–5 lateral rays, the central ray 1–2-celled and up to 1.5 mm long, sparsely armed with prickles up to 3.4 mm long on the major veins abaxially and adaxially; base cuneate to attenuate; margin entire, sinuate or shallowly lobed with 2–6 lobes per side; apex obtuse to rounded; petioles 0.2–1 cm long, moderately to densely stellate-pubescent with hairs like those of the stem, unarmed or sparsely armed with prickles up to 2 mm long. Inflorescences 3–7 cm long, extra-axillary, unbranched, with 1–4 flowers, the axes moderately stellate-pubescent with hairs like those of the stem, unarmed or sparsely armed with prickles up to 2 mm long; peduncle up to 4 cm long; pedicels 1–3.5 cm in flower, weakly articulated at the base, moderately to densely stellate-pubescent, unarmed or sparsely armed with prickles up to 1 mm long. Calyx 6–7 mm long, the tube 3–4 mm, the lobes 1.8–2.2 × 1.2–2 mm, deltate-triangular, the apex acuminate, densely stellate-pubescent abaxially, glabrous adaxially, unarmed or sparsely armed with prickles up to 1 mm long; fruiting calyx unknown. Corollas 1.8–3 cm in diameter, 10–16 mm long, stellate to stellate-pentagonal, chartaceous, white, the tube 1.3–1.8 mm, the lobes 4–8 × 5–7 mm, triangular, the apex acute, sparsely to moderately stellate-pubescent abaxially, glabrous adaxially. Stamens with filaments 1–1.5 × ca. 0.2 mm; anthers 6–7 × 1–2 mm, narrowly lanceolate, somewhat connivent, yellow, the pores directed distally. Ovary 1.2–2 × 1.1–1.8 mm, subglobose-ovoid, glabrous; style 9–12 × 0.5–1 mm, cylindrical, straight, glabrous, exserted; stigma capitate. Fruits unknown.

Distribution and Habitat—*Solanum pumilum* is a narrowly distributed endemic currently found on the Ketona dolomite outcroppings near the Little Cahaba River in Bibb County, Alabama and on amphibolite outcroppings near the Coosa River in Coosa and Chilton Counties, Alabama (Fig. 7). The type locality of the species is in Georgia, but it has not been found there since it was described in 1834. In 1980, Kral collected it in Bibb County, Alabama, but was unaware of the significance of his finding (*R. Kral 65126* [VDB]). In 1993, Allison and Stevens made many new collections of the species in Alabama and confirmed its rediscovery (Allison and Stevens 2001).

Phenology—Flowering between April and May.

Conservation Status—The four known specimens of *Solanum pumilum* from Georgia do not have useful locality data and were not used in the conservation assessment. In contrast, the 13 collections from Alabama have precise location information on the specimen labels, allowing for high-confidence post-facto assignment of coordinates. These represent five locations and populations with a restricted extent of occurrence of 22.5 km^2 and area of occupancy of 16 km^2. None of the specimens used to derive occurrence data were found in nearby protected areas, such the Cahaba River National Wildlife Refuge and the Nature Conservancy's Kathy Stiles Freeland Bibb County Glades Preserve, although the species has been reported from the latter (Nature Conservancy 2014). Threats to the populations come from forestry operations and perhaps fire, although fire is needed to maintain the open glade habitat of *Solanum pumilum*. Given that the species is only known from vouchered specimens outside of protected areas and that its habitat is threatened by human activity, *Solanum pumilum* is assigned a preliminary conservation status of "critically endangered" [CR B1abc(i,ii,iii,v)].

Etymology—The specific epithet "*pumilum*" derives from the Latin word meaning dwarf or pygmy and refers to the short stature of *Solanum pumilum*.

Vernacular Name—*Solanum pumilum* is commonly known as dwarf horsenettle (also spelled with a hyphen: dwarf horse-nettle).

Chromosome Number—None recorded.

Notes—In general habit and vegetative morphology, *Solanum pumilum* is somewhat similar to *S. carolinense*, but can be differentiated by its small stature (up to 0.2 m vs. up to 1.2 m in *S. carolinense*), its smaller (2.2–8.6 × 1.1–5.1 cm) obovate to elliptic leaf blades (vs. larger (2–15 × 2–10) ovate, lanceolate, or elliptic leaf blades), its inflorescence with 2–4 flowers (vs. 2–12), and its strictly white corollas (vs. blue to white). The leaf margins of *S. pumilum* are most often entire to sinuate, but can be shallowly lobed, and while *S. carolinense* also can have entire to shallowly lobed margins, they are usually moderately to deeply lobed. Ecological traits differing between *S. pumilum* and *S. carolinense* include flowers that are sweetly fragrant (vs. usually odorless in *S. carolinense* [Allison and Stevens 2001]), small populations with well spaced individuals (compared to the invasive habit and dense colonies of *S. carolinense*), and the restricted distribution on undisturbed dolomite and amphibolite substrates (vs. disturbed substrates and waste areas).

The name *Solanum hirsutum* Nutt. (1834) is an illegitimate later homonym of *S. hirsutum* Dunal (1813) and *S. hirsutum* Roxb. (1814). Dunal (1852) corrected this by providing the replacement name *Solanum pumilum* Dunal. Later, both Gray (1878) and D'Arcy (1974) recognized *Solanum hirsutum* Nutt. as a variety of *S. carolinense* and separately published new combinations. Under Art. 58 of the ICBN (McNeill et al. 2012), when an illegitimate name is used at a different rank, its priority does not date back to the publication of the illegitimate name.

In the protologue of *Solanum hirsutum*, Nuttall (1834) writes "discovered by Dr. [Samuel] Boykin, in the vicinity of Milledgeville in Georgia." Among the three known Boykin collections of this species (PH–PH00030417, NY–NY00821153, and E–E00190703), only the PH specimen is annotated in Nuttall's handwriting and is from the Academy of Natural Sciences in Philadelphia, where he worked from 1836 until 1841, and is chosen here as the lectotype. The NY specimen was collected in Columbus, Georgia and the E specimen has no locality data, and thus we interpret these two Boykin collections to be paratypes and not duplicates of the PH sheet, which was presumably collected near Milledgeville, Georgia.

Additional Specimens Examined—U. S. A. Alabama: Bibb County, ca. 8.6 mi. NE of Centreville, ca. 0.2 mi. N of the mouth of Six Mile Creek, "Nightshade Glade", Ketona Dolomite outcrop ca. 0.15 mi. E of the Little Cahaba River, 26 Apr 1993 (fl), *J. R. Allison & T. Stevens 7557* (NY-photocopy); ca. 8.6 mi. NE of Centreville, ca. 0.25 mi. N of the mouth of Six Mile Creek, "Double Glade North", Ketona Dolomite outcrop ca. 0.1 mi. E of the Little Cahaba River, 26 Apr 1993 (fl), *J. R. Allison & T. Stevens 7563* (NY-photocopy, US); ca. 7.9 mi. NNE of Centreville, ca. 0.25 mi. E of the mouth of Pratt Creek, perhaps 0.3 mi. to E of "Eastside Glade", Ketona Dolomite outcrop ca. 0.2 mi. E of the Cahaba River, 2 May 1993 (fl), *J. R. Allison & T. Stevens 7590* (NY-photocopy, UNA); ca. 5.6 mi. NNW of Centreville, "Hwy 5 Glade East", Ketona Dolomite outcrop just E of AL Hwy 219, 16 May 1993 (fl), *J. R. Allison & T. Stevens 7642* (NY-photocopy); ca. 5.5 mi. NNW of Centreville, ca. 0.1 mi. S of the intersection of AL Hwys. 5 and 219, "Hwy 219 Glade", Ketona Dolomite outcrop, E side of AL Hwy 219, 16 May 1993 (fl), *J. R. Allison & T. Stevens 7644* (UNA); same locality and date (fl), *J. R. Allison & T. Stevens 7645* (NY-photocopy); ca. 5.5 mi. N of Centreville, ca. 0.4 mi. ESE of the intersection of AL Hwys. 5 and 219, "Tread-softly Glade", ca. 100 ft. S of the road one would take from AL Hwy 219 to Schultz Creek Church, 16 May 1993 (fl), *J. R. Allison & T. Stevens 7649* (MO, NY-photocopy); same locality and date (fl), *J. R. Allison & T. Stevens 7650* (NY-photocopy); ca. 8.6 mi. NE of Centreville, ca. 0.25 mi. N of the mouth of Six Mile Creek, "Double Glade North", Ketona Dolomite outcrop ca. 0.1 mi. E of the Little Cahaba River, 5 Sep 1993 (fr), *J. R. Allison & T. Stevens 7959* (NY-photocopy); ca. 9.8 mi. NE of Centreville, ca. 0.4 mi. NW of Bulldog Bend Bridge, W of "Bulldog Glade", ca. 0.35 mi. N of the Little Cahaba River, 14 Oct 1993 (imm. fr), *J. R. Allison et al. 8044* (NY-photocopy); bluffs above Cahaba River ca. 0.5 mi. S of Pratts Ferry bridge, 17 May 1980 (st), *R. Kral 65126* (VDB); Chilton County, N of AL Hwy 22, W of the Coosa River, 1 May 1994 (fl), *J. R. Allison & T. Stevens 8239* (MO, NY, VDB-n.v.); Coosa County, N of AL Hwy 22, E of the Coosa River, 1 May 1994 (fl), *J. R. Allison & T. Stevens 8241* (UNA). Georgia: Without precise locality, s.d. (fl), *S. Boykin s. n.* (E-scan); without precise locality, s.d. (fl), *Ellis s. n.* (NY-photocopy of WIS); Muscogee County, Columbus, s.d. (fl), *S. Boykin s. n.* (NY-scan).

11. Solanum reineckii Briq., Annuaire Conserv. Jard. Bot. Genève 3: 167. 1899.—TYPE: BRAZIL. Rio Grande do Sul: entre Navegantes et São João, 25 Sep 1897 (fl), *E. M. Reineck & J. Czermak 45* (lectotype, designated here: G–G00070158 [scan]!; isolectotypes: FR–FR0031973 [scan]!, JE–JE00004771 [scan!]).

Sprawling decumbent herb up to ca. 0.7 m tall. Stems moderately to densely pubescent with sessile to long-stalked stellate hairs 0.4–0.8 mm in diameter, with 4–8 lateral rays, the central ray absent or 1-celled and up to 0.4 mm long, the stalks up to 2 mm long, moderately to densely armed with straight tapered prickles up to 6 mm long. Sympodial units 2- to plurifoliate, the leaves not geminate. Leaves simple, the blades 3–11 × 1.2–6.5 cm, narrowly ovate to oblong, moderately to densely stellate-pubescent abaxially and adaxially with hairs like those of the stems, moderately to densely armed with prickles up to 5 mm long on the major veins abaxially and adaxially; base rounded or truncate, often with one side offset up to 0.8 cm from the other; margin lobed to irregularly serrate; apex rounded; petioles 1–2.4 cm long, moderately to densely stellate-pubescent, moderately to densely armed with prickles up to 5 mm long. Inflorescences up to 12 cm long, extra-axillary, unbranched, with up to 10 flowers, the axes moderately to densely stellate-pubescent, moderately armed with prickles up to 5 mm long; peduncle up to 6 cm long; pedicels 0.5–2 cm in flower, weakly articulated at the

base, moderately to densely stellate-pubescent, moderately to densely armed with prickles up to 4 mm long. Calyx 4–8 mm long, the tube 1–1.4 mm long, the lobes 3–5 × 1.2–1.8 mm, triangular-lanceolate, the apex acute, moderately to densely stellate-pubescent abaxially, glabrous adaxially, moderately to densely armed with prickles up to 3.5 mm long; calyx of immature fruit spreading to reflexed, ca. 7 mm long, the tube ca. 1 mm long, the lobes ca. 6 × 2 mm, narrowly triangular, moderately stellate-pubescent, moderately to densely armed with prickles up to 3.5 mm long. Corollas up to 2.4 cm in diameter, ca. 13 mm long, rotate to stellate-pentagonal, chartaceous, white to rose, the tube ca. 2.5 mm long, the lobes 8–10 × 2–5 mm, deltate-triangular, the apex acute, moderately stellate-pubescent abaxially, glabrous adaxially. Stamens with filaments 1.5–2 × 0.2–0.4 mm; anthers 5–6 × 1–1.3 mm, narrowly lanceolate, weakly or not connivent, yellow, the pores directed distally. Ovary ca. 1 × 1–1.2 mm, ovoid to globose, glabrous; style 5–7 × ca. 0.4 mm, cylindrical, straight, glabrous, exserted; stigma capitate. Immature fruits ca. 1 × 0.8 cm, subglobose to ovoid, the color when ripe unknown, glabrous. Seeds unknown.

Distribution and Habitat—*Solanum reineckii* occurs in Rio Grande do Sul and Santa Catarina states in southernmost Brazil. It grows in grasslands and restinga vegetation near the coast at elevations of ca. 0–5 m (Fig. 8).

Phenology—The species flowers between September and January; a single specimen had an immature fruit in October.

Conservation Status—*Solanum reineckii* has been documented at 10 localities in the coastal areas of Rio Grande do Sul and Santa Catarina states in Brazil. With none of the documented localities currently protected and a historical range size comprising an extent of occurrence of 11,134 km^2, *S. reineckii* can be assigned a preliminary conservation status of vulnerable: VU B1ab(iii).

Etymology—The species is named after Eduard Martin Reineck (1869–1931) who collected the lectotype specimens.

Vernacular Name—Smith and Downs (1966) report joá-chicote as a common name.

Chromosome Number—None recorded.

Notes—*Solanum reineckii* is most similar to *S. flagellare* in its decumbent habit, leaf shape, and unbranched inflorescences. It differs by its stellate-pubescent stems, petioles, leaves, and inflorescence axes with sessile to long-stalked hairs, the stalks often prickle-like and up to 2 mm long, and calyces that are moderately to densely armed with prickles. *Solanum flagellare* has stems, petioles, leaves, and inflorescence axes that are stellate-pubescent with sessile or short-stalked stellate hairs, the stalks up to 0.2 mm long, and calyces that are unarmed or sparsely armed with prickles. The two species are also disjunctly distributed, with *Solanum reineckii* occurring in Rio Grande do Sul and Santa Catarina states whereas *S. flagellare* is restricted to São Paulo state.

In the protologue of *Solanum reineckii*, Briquet cited *E. M. Reineck & J. Czermak 45* as the type, but did not indicate an herbarium. We have chosen the sheet at G (G–G00070158) as the lectotype from among the known duplicates at G, FR, and JE. Even though the sheet at G was not annotated by Briquet, it likely represents the sheet from which he described the species because the G was his home institution; the G sheet is also the most complete specimen. The duplicates of *E. M. Reineck & J. Czermak 87* at B [F neg. 2847], GOET, and S are incorrectly annotated as type material.

Additional Specimens Examined—BRAZIL. Rio Grande do Sul: Pelotas, 27 Feb 1958 (st), *J. da Costa Sacco 925* (F, PACA-n.v., PEL-n.v.); entre Navegantes et São João, 25 Sep 1897 (fl), *E. M. Reineck & J. Czermak 87* (B [F neg. 2847], GOET [scan], K [scan], P [2 sheets], S [scan]); São Leopoldo, 10 Nov 1946 (bud), *E. Henz 35492* (MO, NY, PACA-n.v.); Garopaba, Perto da Cidade, 5 m, 31 Oct 1970 (fl, imm. fr), *R. M. Klein & A. Bresolin 8837* (FLOR-n.v., HBR-n.v., US); vicinity of São Leopoldo, Oct 1946 (fl), *E. Leite 657* (NY); Guaíba, Fazenda São Maximiano, 4 Nov 2013 (fl), *N. I. Matzenbacher s. n.* (NY, UT); Navegantes, prope Porto Alegre, 11 Nov 1949 (fl), *B. Rambo 44355* (P); estero prope São Leopoldo, 20 Nov 1950 (fl), *B. Rambo 49167* (ICN-n.v., US); ao norte da lagoa de Tramandaí, 15 Nov 1983 (fl), *J. R. Stehmann 193* (BHCB, ICN-n.v.). Santa Catarina: Laguna Mar Grosso, 24 Jan 1994 (fl), *M. T. Cosa 153* (CORD); Cabo Santa Marta, Mun. Laguna, 3–5 m, 14 Nov 2001 (fl), *G. G. Hatschbach et al. 72691* (NY); Laguna, Morro do Farol de Santa Marta, 14 Jan 1996 (fl), *L. A. Mentz 228* (ICN-n.v., NY); Laguna, 22 Dec 1951 (bud), *P. R. Reitz & R. M. Klein 167* (HBR-n.v., US); Massiambú, Palhoça, 5 m, 5 Nov 1953 (fl), *P. R. Reitz & R. M. Klein 1318* (HBR-n.v., US).

Doubtful and Excluded Names—

Solanum multispinum N. E. Br., Trans. & Proc. Bot. Soc. Edinburgh. 20: 65. 1894.—TYPE: ARGENTINA. Prov. Formosa, Río Pilcomayo, cerca del Fortín Page, 1890–1891 (fl), *J. G. Kerr s. n.* (holotype: K–K000590012 [scan!]).

In his synopsis of *Solanum* subgenus *Leptostemonum*, Whalen's (1984) informal *S. multispinum* group included *S. multispinum* as well as five other species treated in this work (*S. aridum* [as *S. conditum*], *S. flagellare*, *S. hieronymi*, *S. juvenale*, and *S. reineckii*). Nee (1999) also included *S. multispinum* in his circumscription of *S.* subsect. *Lathyrocarpum*. However, the species differs morphologically from the others in the section by its dense indumentum of minute simple glandular hairs and stellate hairs often with a glandular central ray (*S. hieronymi* has simple glandular hairs, but none of the species treated here have glandular stellate hairs). In addition, it has large globose fruits up to 3.2 cm in diameter, whereas species in section *Lathyrocarpum* have ellipsoid, ovoid, subglobose, or globose fruits up to 2.5 cm in diameter. Also, *S. multispinum* is excluded from *S.* sect. *Lathyrocarpum* based on molecular phylogenetic evidence. The three accessions of *S. multispinum* sampled in Wahlert et al. (2014) were recovered as a clade in an unresolved position outside of the Carolinense clade (Fig. 3).

Acknowledgments. LB and GAW would like to dedicate this work to the memory of our late friend Ann Kelsey (1948–2013), collections manager at the Garrett Herbarium (UT) at the Natural History Museum of Utah for 23 years. We thank the many curators and collections managers that helped us with loans and access to collections, particularly BRIT, FLAS, FSU, G, GH, MO, NY, P, PH, UNA, and US. Sonnia Hill generously collected and provided us with several duplicates of the neotype of *S. dimidiatum*, as well as several images of *Solanum*, from Van Zandt County, Texas. We would also like to thank Barbara J. Hellenthal (NDG) for images of a *Solanum aridum* isotype, Sharon Bartholomew-Began (DWC) for searching the Rafinesque herbarium for specimens of *S. dimidiatum*, Wayne J. Elisens (OKL) for images of the holotype of *S. torreyi* f. *album*, and Marc Jeanson (MPU) for sending several high resolution images of type specimens. Barney Lipscomb (BRIT) provided images and collections of *S. dimidiatum* from Texas and Oklahoma. LB thanks her brother Larry for searching for *S. carolinense* in North Carolina. We are grateful to Lilian A. Mentz (ICN) who provided us with leaf tissue and recent collections of *S. reineckii* from Brazil. Leandro Giacomin (BHCB) provided many helpful comments on the Brazilian taxa. Loran C. Anderson (FSU) shared with us his field observations of *Solanum carolinense* var. *floridanum*. Sandra Knapp (BM) provided background information on the lectotypification of *S. carolinense* and other names and assisted with databasing specimens for the Solanaceae Source website. James Allison (Georgia, U. S. A.) kindly provided information and field photographs of several southeastern taxa, especially *S. pumilum*. CONICET-UNC (Córdoba, Argentina) provided logistical support for collecting plants in Argentina. This work was supported by the NSF through the PBI *Solanum* grant to LB (DEB-0316614).

Literature Cited

Alex, J. F., R. Cayouette, and G. A. Mulligan. 1980. Common and botanical names of weeds in Canada/Noms populaire et scientifiques des plantes nuisibles du Canada. Publication 1397. Ottawa, Ontario: Canadian Department of Agriculture.

Allison, J. R. and T. E. Stevens. 2001. Vascular flora of Ketona Dolomite outcrops in Bibb County, Alabama. *Castanea* 66: 154–205.

Anderson, H. C. 2002. *Calystegine alkaloids in Solanaceous food plants*. Copenhagen: Nordic Council.

Anderson, L. D. and H. G. Walker. 1937. Control of the potato flea beetle, *Epitrix cucumeris* Harris on the eastern shore of Virginia. *American Potato Journal* 14: 319–325.

Armel, G. R., H. P. Wilson, R. J. Richardson, and T. E. Hines. 2003. Mesotrione combinations for postemergence control of horsenettle (*Solanum carolinense*) in corn (*Zea mays*). *Weed Technology* 17: 65–72.

Barboza, G. E. 2013. Solanaceae. Pp. 1–350 in *Flora vascular de la República Argentina*, Vol. 13, eds. A. M. Anton and F. O. Zuloaga. San Isidro, Argentina: Instituto de Botánica Darwinion, Instituto Multidisciplinario de Biología Vegetal.

Bassett, I. J. and D. B. Munro. 1986. The biology of Canadian weeds: 78. *Solanum carolinense* L. and *Solanum rostratum* Dunal. *Canadian Journal of Plant Science* 66: 977–991.

Beeler, J. E., G. N. Rhodes, G. E. Bates, C. L. Main, and T. C. Mueller. 2004. Horsenettle (*Solanum carolinense*) control in tall fescue (*Festuca arundinacea*) and clover (*Trifolium* sp.) pastures with mixtures of 2,4-D and picloram. *Weed Technology* 18: 1091–1095.

Blancard, D. 2012. *Tomato diseases: Identification, biology and control*, 2nd edition. London: Manson Publishing.

Bohs, L. 2005. Major clades in *Solanum* based on *ndhF* sequence data. Pp. 27–49 in *A festschrift for William G. D'Arcy: The legacy of a taxonomist*, eds. R. C. Keating, V. C. Hollowell, and T. B. Croat. St. Louis: Missouri Botanical Garden Press.

Canadensys. 2014. Available online at website http://www.canadensys.net.

Capinera, J. L. 2001. *Handbook of vegetable pests*. New York: Academic Press.

Cayouette, R. 1972. Additions to the adventitious flora of Quebec. *Naturaliste Canadien* 99: 135–136.

CDFA. 2014. California Department of Food and Agriculture. http://www.cdfa.ca.gov.

Chiarini, F. E. 2007. Estudios multidisciplinarios en las especies de Solanum *subgen*. Leptostemonum *de Argentina y regions limítrofes, con especial referencia a su taxonomía*. Ph.D. Dissertation. Córdoba, Argentina: Universidad Nacional de Córdoba.

Chiarini, F. and G. Bernardello. 2006. Karyotypic studies in South American species of *Solanum* subgen. *Leptostemonum* (Solanaceae). *Plant Biology* 8: 486–493.

Chinnusamy, C., M. R. Nandhakumar, K. Govindarajan, and P. Muthukrishnan. 2011. Incidence of quarantine invasive weed *Solanum carolinense* L. in different ecosystems of Tamil Nadu. Proceedings of the 23rd Asian-Pacific Weed Science Society Conference, Vol. 2: Weed management in a changing world, Cairns, Queensland, Australia, 26–29 September 2011.

Cipollini, M. L. and D. J. Levey. 1997. Why are some fruits toxic? Glycoalkaloids in *Solanum* and fruit choice by vertebrates. *Ecology* 78: 782–798.

Connolly, B. A. and G. J. Anderson. 2003. Functional significance of the androecium in staminate and hermaphroditic flowers of *Solanum carolinense* (Solanaceae). *Plant Systematics and Evolution* 240: 235–243.

Cosa, M. T., G. Bruno, and N. Dottori. 1998. Anatomía de los órganos vegetativos en *Solanum juvenale* y su comparación con *S. elaeagnifolium* (Solanaceae). *Anales del Instituto de Biología de la Universidad Nacional Autónoma de México. Ser. Bot* 69: 9–22.

Cosa, M. T., N. Dottori, and G. Bruno. 2000. Propagación y anatomía de órganos vegetativos en *Solanum hieronymi* (Solanaceae). *Kurtziana* 28: 211–220.

Cronquist, A. 1978. Once again, what is a species? Pp. 3–20 in *Biosystematics in agriculture*, ed. J. A. Romberger. Montclair, New Jersey: Allanheld and Osmun.

Danert, S. 1958. Die Verzweigung der Solanaceen im reproduktiven Bereich. *Abhandlungen der Deutschen Akademie der Wissenschaften zu Berlin, Klasse für Chemie, Geologie und Biologie* 6: 253–297.

D'Arcy, W. G. 1969. Chromosome numbers of phanerogams 3. *Annals of the Missouri Botanical Garden* 56: 471–475.

D'Arcy, W. G. 1972. Solanaceae studies II: Typification of subdivisions of *Solanum*. *Annals of the Missouri Botanical Garden* 59: 262–278.

D'Arcy, W. G. 1974. *Solanum* and its close relatives in Florida. *Annals of the Missouri Botanical Garden* 61: 819–867.

Dirkse, G., W. Holverda, S. Hochstenbach, and F. Reijerse. 2007. *Solanum carolinense* L. and *Pimpinella peregrina* L. in The Netherlands. *Gorteria* 33: 21–27.

Don, G. 1838. *A general history of the dichlamydeous plants* vol. 4. London: Gilbert and Rivington.

Dunal, F. 1852. Solanaceae. Pp. 1–690 in *Prodromus systematis naturalis regni vegetabilis* vol. 13, ed. A. P. De Candolle. Paris: Victoris Masson.

Du Rietz, G. E. 1930. The fundamental units of biological taxonomy. *Svensk Botanisk Tidskrift* 24: 332–428.

Eberwein, R. K. and T. Litscher. 2007. *Solanum carolinense* L. (Solanaceae), ein gefährlicher Neubürger in Österreich. *Rudolfinum–Jahrbuch des Landesmuseums für Kärnten* 2005: 325–330.

eFloraSA. 2014. Electronic Flora of South Australia. http://www.flora.sa.gov.au.

Elle, E. 1998. The quantitative genetics of sex allocation in the andromonoecious perennial, *Solanum carolinense* (L.). *Heredity* 80: 481–488.

Elle, E. 1999. Sex allocation and reproductive success in the andromonoecious perennial *Solanum carolinense* (Solanaceae). I. Female success. *American Journal of Botany* 86: 278–286.

Elle, E. and T. R. Meagher. 2000. Sex allocation and reproductive success in the andromonoecious perennial *Solanum carolinense* (Solanaceae). II. Paternity and functional gender. *American Naturalist* 156: 622–636.

Ellis, M. B. 1971. *Dematiaceous hyphomycetes*. Kew: Commonwealth Mycological Institute.

Follak, S. and G. Strauss. 2010. Potential distribution and management of the invasive weed *Solanum carolinense* in Central Europe. *Weed Research* 50: 544–552.

Foott, W. H. 1968. The importance of *Solanum carolinense* L. as a host of the pepper maggot, *Zonosemata electa* (Say), (Diptera: Trypetidae) in southwestern Ontario. *Proceedings of the Entomological Society of Ontario* 98: 16–17.

Foster, S. and J. A. Duke. 1990. *A field guide to medicinal plants*: Eastern and central North America. Boston: Houghton Mifflin.

Furrer, A. H. and S. N. Fertig. 1960. Life history studies of horse-nettle (*Solanum carolinense*). *Proceedings of the Northeastern Weed Control Conference* 14: 336–342.

Gazi-Baskova, V. and N. Segulja. 1978. The appearance of dangerous weeds of the genus *Solanum* on the Kvarner Island of Plavnik [English title]. *Fragmenta Herbologica Jugoslavica* 6: 55–59.

Gorrell, R. M., S. W. Bingham, and C. L. Foy. 1981. Control of horsenettle (*Solanum carolinense*) fleshy roots in pastures. *Weed Science* 29: 586–589.

Goyal, G., H. K. Gill, and R. McSorley. 2012. *Common weed hosts of insect-transmitted viruses of Florida vegetable crops*. Gainesville: University of Florida Institute of Food and Agricultural Services, No. ENY-863.

Gray, A. 1878. *Synoptical flora of North America.* New York: Ivison, Blakeman, Taylor, and Company.

Grieve, M. 1974. *A modern herbal*. New York: Hafner Press.

Gunn, G. R. and F. B. Gaffney. 1974. Seed characteristics of 42 economically important species of Solanaceae in the United States. *United States Department of Agriculture Technical Bulletin 1471*. Washington D. C.: U. S. Department of Agriculture.

Hackett, N. M., D. S. Murray, and D. L. Weeks. 1987. Interference of horsenettle (*Solanum carolinense*) with peanuts (*Arachis hypogaea*). *Weed Science* 35: 780–784.

Hamilton, M. W. 1980. Potentially poisonous or otherwise harmful higher plants of Oklahoma. *Proceedings of the Oklahoma Academy of Science* 60: 54–62.

Hardin, J. W. and J. M. Arena. 1969. *Human poisoning from native and cultivated plants*. Durham, North Carolina: Duke University Press.

Hardin, J. W., G. Doerksen, D. Herndon, M. Hobson, and F. Thomas. 1972. Pollination ecology and floral biology of four weedy genera in southern Oklahoma. *The Southwestern Naturalist* 16: 403–412.

Hare, J. D. and G. G. Kennedy. 1986. Genetic variation in plant-insect associations: Survival of *Leptinotarsa decemlineata* populations on *Solanum carolinense*. *Evolution* 40: 1031–1043.

Hill, L. M. 1989. IOPB chromosome data 1. *International Organization of Plant Biosystematists Newsletter* 13: 17–19.

Hulbert, L. C. and F. W. Oehme. 1963. *Plants poisonous to livestock in the United States and Canada,* 2nd ed. Manhattan, Kansas: Kansas State University Press.

Ilnicki, R. D., T. F. Tisdell, S. N. Fertig, and A. H. Furrer. 1962. Life history studies as related to weed control in the Northeast. 3–Horsenettle. *Rhode Island Agricultural Experiment Station Bulletin* 368: 1–54.

Imaizumi, T., S. Kurokawa, M. Ito, B. Auld, and G. X. Wang. 2006. Population structure of *Solanum carolinense* along the Takano River in Kyoto, Japan as determined by amplified fragment length polymorphism analysis. *Weed Research* 46: 219–225.

Izhevskii, S. S., A. E. Livshits, G. E. Murusidze, and G. G. Gogoladze. 1981. Prospects of using alke-strain in integrated control of *Solanum carolinense* in tea plantations [English title]. *Subtropicheskie Kul'tury* 4: 60–65.

Jepson Flora Project. 2014. Baldwin, B. D., D. J. Keil, S. Markos, B. D. Mishler, R. Patterson, T. J. Rosatti, and D. H. Wilken, eds. http://ucjeps.berkeley.edu/IJM.html.

Jordan, J., W. Elisens, and R. Thomas. 2006. Vascular plants utilized by the Plains Apache in southwestern Oklahoma. *Publications of the Oklahoma Biological Survey, 2nd Series* 7: 24–33.

Kariyat, R. R., S. R. Scanlon, M. C. Mescher, C. M. De Moraes, and A. G. Stephenson. 2011. Inbreeding depression in *Solanum carolinense* (Solanaceae) under field conditions and implications for mating system evolution. *PLoS One* 6: e28459.

Kariyat, R. R., K. E. Mauck, C. M. Balogh, A. G. Stephenson, M. C. Mescher, and C. M. De Moraes. 2013. Inbreeding in horsenettle (*Solanum carolinense*) alters night-time volatile emissions that guide oviposition by *Manduca sexta* moths. *Proceedings. Biological Sciences* 280: 20130020.

Kingsbury, J. M. 1964. *Poisonous plants of the United States and Canada*. Englewood Cliffs, New Jersey: Prentice-Hall.

Klingenhagen, G., M. Wirth, B. Wiesmann, and H. Ahaus. 2012. Occurrence of horse nettle (*Solanum carolinense* L.) in North Rhine-Westphalia. 25. Deutsche Arbeitsbesprechung über Fragen der Unkrautbiologie und –bekämpfung, March 13–15, 2012, Braunschweig, Germany.

Kolar, C. S. and D. M. Lodge. 2001. Progress in invasion biology: Predicting invaders. *Trends in Ecology & Evolution* 16: 199–204.

Knapp, S. and C. E. Jarvis. 1990. The typification of the names of New World *Solanum* species described by Linnaeus. *Journal of the Linnean Society. Bot* 104: 325–367.

Kuntze, O. 1898. *Revisio Generum Plantarum*, vol. 3. Leipzig: Arthur Felix.

Levin, R. A., N. R. Myers, and L. Bohs. 2006. Phylogenetic relationships among the "spiny solanums" (*Solanum* subgenus *Leptostemonum*, Solanaceae). *American Journal of Botany* 93: 157–169.

Li, G.-Y., S.-H. Jin, and J.-G. Ai. 2006. Species, characteristics and control measures of injurious plants in Zhejiang Province. *Journal of Zhejiang Forestry College* 23: 614–624.

Linnaeus, C. 1753. *Species plantarum*. Stockholm: L. Salvius.

Mallet, J. 1995. A species definition for the modern synthesis. *Trends in Ecology & Evolution* 10: 294–299.

Martin, A. C., H. S. Zim, and A. L. Nelson. 1951. *American wildlife and plants*. New York: Dover.

Matesevach, M. 2002. Solanaceae, parte 12. *Solanum* subgen. *Leptostemonum. Flora Fanerogámica Argentina* 79: 1–35.

McNeill, J., F. R. Barrie, W. R. Buck, V. Demoulin, W. Greuter, D. L. Hawksworth, P. S. Herendeen, S. Knapp, K. Marhold, J. Prado, W. F. Prud'homme van Reine, G. F. Smith, J. H. Wiersema, and N. J. Turland. 2012. *International Code of Nomenclature for algae, fungi, and plants (Melbourne Code): adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011*. Koenigstein: Koeltz Scientific Books.

Mena-Ali, J. I. and A. G. Stephenson. 2007. Segregation analyses of partial self-incompatibility in self and cross progeny of *Solanum carolinense* reveal a leaky *S*-allele. *Genetics* 177: 501–510.

Mena-Ali, J. I., L. Kesser, and A. G. Stephenson. 2008. Inbreeding depression in *Solanum carolinense* (Solanaceae), a species with a plastic self-incompatibility response. *BMC Evolutionary Biology* 8: 10.

Menzies, J. S., C. H. Bridges, and E. M. Bailey. 1979. A neurological disease of cattle associated with *Solanum dimidiatum. The Southwestern Veterinarian* 32: 45–49.

Merluzzi, P., G. Oriolo, M. Tomasella, S. Costalonga, F. Martini, M. Buccheri, and P. Sergo. 2003. Segnalazioni floristiche dalla regione Friuli Venezia Giulia. XI-XIII. *Gortania* 25: 187–206.

Merrill, E. D. 1949. *Index rafinesquianus*. Jamaica Plain, Massachussetts: The Arnold Arboretum of Harvard University.

Millán, R. 1947. Nota taxonómica de *Solanum pocote. Revista Argentina de Agronomía* 12: 116–118.

Morong, T. and N. L. Britton. 1893. An enumeration of the plants collected by Dr. Thomas Morong in Paraguay, 1888–1890. *Annals of the New York Academy of Sciences* 7: 45–280.

Morton, C. V. 1976. *A revision of the Argentine species of Solanum*. Córdoba: Academia Nacional de Ciencias.

Moscone, E. A. 1992. Estudios de cromosomas meióticos en Solanaceae de Argentina. *Darwiniana* 31: 261–297.

Muenscher, W. C. 1951. *Poisonous plants of the United States*. New York: Macmillan Co.

Nature Conservancy. 2014. Available online at website http://www.nature.org/ourinitiatives/regions/northamerica/unitedstates/alabama/placesweprotect/kathy-stiles-freeland-bibb-county-glades-preserve.xml.

Nee, M. 1999. Synopsis of *Solanum* in the New World. Pp. 285–333 in *Solanaceae IV: Advances in biology and utilization*, eds. M. Nee, D. E. Symon, R. N. Lester, and J. P. Jessop. Richmond, U. K.: Royal Botanic Gardens, Kew.

Nee, M., S. Knapp, and L. Bohs. 2006. New species of *Solanum* and *Capsicum* (Solanaceae) from Bolivia, with clarification of nomenclature in some Bolivian *Solanum*. *Brittonia* 58: 322–356.

Nichols, R. L. and W. W. Hanna. 1984. Irregular meiosis in *Solanum dimidiatum. Solanaceae Newsletter* 2: 15.

Nichols, R. L., J. Cardina, R. L. Lynch, N. A. Minton, and H. D. Wells. 1992. Insects, nematodes, and pathogens associated with horsenettle (*Solanum carolinense*) in bermudagrass (*Cynodon dactylon*) pastures. *Weed Science* 40: 320–325.

Nuttall, T. 1834. A description of some of the rarer or little known plants indigenous to the United States, from the dried specimens in the herbarium of the Academy of Natural Sciences in Philadelphia. *Journal of the Academy of Natural Sciences of Philadelphia* 7: 61–115.

Ouren, T. 1987. Soyabønne-adventiver i Norge. *Blyttia* 45: 175–185.

Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. *Bioscience* 50: 53–64.

Park, G.-J., S.-H. Yoon, J.-K. Lee, and Y.-J. Kim. 2001. Studies on ecological characteristics and control of exotic weeds. 1. Distribution and ecological characteristics of exotic weeds in forage crop field. *Journal of the Korean Society of Grassland Science* 21: 97–102.

Pritchard, F. J. and W. S. Porte. 1921. Relation of horse nettle (*Solanum carolinense*) to leafspot of tomato (*Septoria lycopersici*). *Journal of Agricultural Research* 21: 501–507.

Quesada-Aguilar, A., S. Kalisz, and T.-L. Ashman. 2008. Flower morphology and pollinator dynamics in *Solanum carolinense* (Solanaceae): Implications for the evolution of andromonoecy. *American Journal of Botany* 95: 974–984.

Ramsdell, D. C. and R. L. Myers. 1978. Epidemiology of peach rosette mosaic virus in a Concord grape vineyard. *Ecology and Epidemiology* 68: 447–450.

Richman, A. D., T.-H. Kao, S. W. Schaeffer, and M. K. Uyenoyama. 1995. *S*-allele sequence diversity in natural populations of *Solanum carolinense* (Horesenettle). *Heredity* 75: 405–415.

Seithe, A. 1962. Die Haararten der Gattung *Solanum* L. und ihre taxonomische Verwertung. *Botanische Jahrbücher für Systematik* 81: 261–336.

Shinners, L. H. 1962. *Solanum godfreyi* Shinners, nom. nov. (Solanaceae). *Sida* 1: 108.

Simpson, B. B., J. A. Tate, and A. Weeks. 2004. The biogeography of *Hoffmannseggia* (Leguminosae, Caesalpinioideae, Caesalpinieae): a tale of many travels. *Journal of Biogeography* 32: 15–27.

Small, J. K. 1933. *Manual of the southeastern flora*. New York: published by the author.

Smith, L. B. and R. J. Downs. 1966. Solanáceas. Pp. 1–321 in *Flora Ilustrada Catarinense*, ed. P. R. Reitz. Itajaí, Brazil.

Solanaceae Source. 2014. Available online at website http://solanaceae.myspecies.info/.

Solomon, B. P. 1985. Environmentally influenced changes in sex expression in an andromonoecious plant. *Ecology* 66: 1321–1332.

Solomon, B. P. 1987. The role of male flowers in *Solanum carolinense*: Pollen donor or pollinator attractors? *Evolutionary Trends in Plants* 1: 89–93.

Solomon, B. P. and S. J. McNaughton. 1979. Numerical and temporal relationships in a three-level food chain. *Oecologia* 42: 47–56.

Somes, M. P. 1916. Some insects of *Solanum carolinense* L., and their economic relations. *Journal of Economic Entomology* 9: 39–44.

Stehmann, J. R., L. A. Mentz, M. F. Agra, and M. Vignoli-Silva. M., and L. Giacomin. 2013. *Solanaceae* in Lista de espécies da flora do Brasil. Jardim Botânico do Rio de Janeiro. Available at: http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/. Accessed on: 18 November 2013.

Stern, S., M. F. Agra, and L. Bohs. 2011. Molecular delimitation of clades within New World species of the "spiny solanums" (*Solanum* subg. *Leptostemonum*). *Taxon* 60: 1429–1441.

Steven, J. C., P. A. Peroni, and E. Rowell. 1999. The effects of pollen addition on fruit set and sex expression in the andromonoecious herb horsenettle (*Solanum carolinense*). *American Midland Naturalist* 141: 247–252.

Symon, D. E. 1981. A revision of the genus *Solanum* in Australia. *Journal of the Adelaide Botanical Garden* 4: 1–367.

Takematsu, T., M. Konnai, Y. Takeuchi, and N. Ichizen. 1979. Study on the ecological properties and control of perennial weed horsenettle. *Bulletin of the College of Agriculture. Utsunomiya University* 10: 93–102.

Tisdell, T. F. 1961. *A life cycle study of horsenettle (*Solanum carolinense). Doctoral thesis. New Brunswick, New Jersey: Rutgers University.

Trapaidze, A. S. 1972. Horsenettle in western Georgia and ways of controlling it [English title]. *Subtropicheskie Kul'tury* 4: 119–123.

Travers, S. E., J. Mena-Ali, and A. G. Stephenson. 2004. Plasticity in the self-incompatibility system of *Solanum carolinense*. *Plant Species Biology* 19: 127–135.

Turner, N. J. and A. F. Szczawinski. 1991. *Common poisonous plants and mushrooms of North America*. Portland, Oregon: Timber Press.

USDA. 2014. United States Department of Agriculture, Natural Resources Conservation Service, PLANTS Database, National Plant Data Team, Greensboro, NC 27401–4901 USA. Available online at website http://plants.usda.gov.

Vallejo-Marín, M. and M. D. Rausher. 2007. The role of male flowers in andromonoecious species: Energetic costs and siring success in *Solanum carolinense* L. *Evolution* 61: 404–412.

Viggiani, P. 2008. Come cambiano le infestanti del mais. *Informatore Agrario* 64: 55–59.

Wahlert, G. A., F. Chiarini, and L. Bohs. 2014. Phylogeny of the Carolinense clade of *Solanum* (Solanaceae) inferred from nuclear and plastid DNA sequences. *Systematic Botany* 39: 1208–1216.

Walpers, W. G. 1844. *Repertorium botanices systematicae* vol. 3. Leipzig: Friderici Hofmeister.

Webb, C. J., W. R. Sykes, and P. J. Garnock-Jones. 1988. *Flora of New Zealand. Vol. IV. Naturalised pteridophytes, gymnosperms, dicotyledons*. Christchurch: Botany Division, D. S. I. R.

Weese, T. L. and L. Bohs. 2007. A three-gene phylogeny of the genus *Solanum* (Solanaceae). *Systematic Botany* 32: 445–463.

Wehtje, G., J. W. Wilcut, T. V. Hicks, and G. R. Sims. 1987. Reproductive biology and control of *Solanum dimidiatum* and *Solanum carolinense*. *Weed Science* 35: 356–359.

Whalen, M. D. 1984. Conspectus of species groups in *Solanum* subgenus *Leptostemonum*. *Gentes Herbarum* 12: 179–282.

Whalen, M. D. and D. E. Costich. 1986. Andromonoecy in *Solanum*. Pp. 284–302 in *Solanaceae biology and systematics*, ed. W. G. D'Arcy. New York: Columbia University Press.

Whaley, C. M. and M. J. Vangessel. 2002. Horsenettle (*Solanum carolinense*) control with a field corn (*Zea mays*) weed management program. *Weed Technology* 16: 293–300.

Wink, M. and B.-E. Van Wyk. 2008. *Poisonous plants of the World*. Portland, Oregon: Timber Press.

Wise, M. J. and C. F. Sacchi. 1996. Impact of two specialist insect herbivores on reproduction of horse nettle, *Solanum carolinense*. *Oecologia* 108: 328–337.

Wise, M. J. and J. J. Cummins. 2002. Nonfruiting hermaphroditic flowers as reserve ovaries in *Solanum carolinense*. *American Midland Naturalist* 148: 236–245.

Wise, M. J. and J. J. Cummins. 2006. Strategies of *Solanum carolinense* for regulating maternal investment in response to foliar and floral herbivory. *Journal of Ecology* 94: 629–636.

Wise, M. J. and J. B. Hébert. 2010. Herbivores affect natural selection for floral-sex ratio in a field population of horsenettle, *Solanum carolinense*. *Ecology* 91: 937–943.

Wise, M. J., J. J. Cummins, and C. De Young. 2008. Compensation for floral herbivory in *Solanum carolinense*: Identifying mechanisms of tolerance. *Evolutionary Ecology* 22: 19–37.

Yasuyuki, K., S. Bhaskar, T. Mingki, H. Tag, T. Riba, and K. Ando. 2010. Roadside distribution patterns of invasive alien plants along an altitudinal gradient in Arunachal Himalaya, India. *Mountain Research and Development* 30: 252–258.