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Authors: Tepe, Eric J., and Bohs, Lynn

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A Revision of *Solanum* Section *Herpystichum*

Eric J. Tepe[1,2,3] and Lynn Bohs[1]

[1]Department of Biology, 257 South 1400 East, University of Utah, Salt Lake City, Utah 84112, U. S. A.
[2]Department of Biological Sciences, 614 Rieveschl Hall, University of Cincinnati, Cincinnati, Ohio 45221, U. S. A.
[3]Author for correspondence: (eric.tepe@gmail.com)

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Abstract—*Solanum* section *Herpystichum* includes 10 species of ground-trailing and climbing vines that root adventitiously at the nodes. Molecular data support section *Herpystichum* as a member of the Potato clade of *Solanum*. All of the species inhabit primary and secondary rainforests and occur from southern Mexico to northern Peru. The group is defined by its vining, node-rooting habit, and by its fruit structure; several species have strongly flattened fruits that are unique in *Solanum*. Most species of sect. *Herpystichum* have narrow distributions, and four species are endemic to Ecuador and one is endemic to Colombia. Moreover, they tend to be rare in the habitats where they occur and, as a result, are poorly collected and poorly known. Also, because of their restricted distributions, small numbers of populations, and habitat destruction, seven of the 10 species are considered rare and threatened. Descriptions, distribution maps, a phylogeny, photos or illustrations, and a key to the species are presented.

Keywords—Endangered species, Neotropics, phylogeny, Solanaceae, taxonomy.

The genus *Solanum* L. is found worldwide in temperate and tropical habitats and, with ca. 1,500 species, is one of about a dozen "giant genera" with over 1,000 species (Frodin 2004). The informally named "Potato clade" is one of the largest of the 11–13 well-supported clades within *Solanum*, as revealed by molecular data (Bohs 2005; Weese and Bohs 2007). Because it contains the cultivated species potato (*S. tuberosum* L.), tomato (*S. lycopersicum* L.), and the less well-known crop pepino or pepino dulce (*S. muricatum* Aiton), the Potato clade is also one of the most intensively studied clades of *Solanum*. Despite this focus on the crop species and their close relatives, other members of the clade have received little taxonomic attention. In fact, some of the less well-known groups that make up the Potato clade, such as *Solanum* sections *Herpystichum* Bitter and *Pteroidea* Dunal, have only been recently recognized as belonging there based on morphology (Child 1990) and molecular data (Bohs 2005; Weese and Bohs 2007). Knapp and Helgason (1997) provided a taxonomic revision of sect. *Pteroidea*, but sect. *Herpystichum* has not been studied taxonomically. The present study is a revision of *Solanum* sect. *Herpystichum*.

Solanum sect. *Herpystichum* contains 10 species restricted to wet habitats, ranging from southern Mexico to northern Peru. All species of the section are ground-trailing or climbing vines that root at the nodes; pubescence, when present, is of unbranched hairs. Most species have fruits that are flattened perpendicular to the septum to varying degrees. Many species of the section have globose, apically pointed flower buds, distinctive within *Solanum*. In general, sect. *Herpystichum* has plurifoliate sympodial units and extra-axillary inflorescences. Many species of sect. *Herpystichum* are narrowly distributed, relatively inconspicuous, and tend to be rare in the habitats where they occur. Consequently, they are among the least collected species of *Solanum*.

Two distinct groups are apparent within sect. *Herpystichum*. One, the "ground-trailing" species, have herbaceous stems that creep along the ground and have either simple or compound leaves with long petioles (> 3 cm). This group includes *S. dalibardiforme*, *S. limoncochaense*, *S. pentaphyllum*, *S. phaseoloides*, and *S. trifolium* (Figs. 1A -E, 2 A-B). The other group comprises "climbing" species with herbaceous to woody stems, all with simple leaves with short petioles (< 1.5 cm), and includes *S. crassinervium*, *S. dolichorhachis*, *S. evolvulifolium*, *S. loxophyllum*, and *S. pacificum* (Figs. 1F-M, 2C).

Although we have not been able to identify an unambiguous, diagnostic morphological synapomorphy for sect. *Herpystichum*, the section can be easily distinguished from other sympatric groups of vining *Solanum* species. Three species of sect. *Pteroidea* are node-rooting vines (the other seven are free-standing herbs), but these have unifoliate sympodial units and inflorescences that are exclusively axillary in position (Child 1979; Knapp and Helgason 1997), in contrast to the mostly plurifoliate units and generally extra-axillary inflorescences of sect. *Herpystichum*. Species of sect. *Anarrhichomenum* are also node-rooting vines, but have few-flowered inflorescences on short, axillary spur shoots (Correll 1962; Child 1979) and/or pseudostipules on at least some nodes (these are not true stipules, but appear to be the first, reduced leaves on an axillary shoot; see discussion in Peralta et al. 2008). All species in sect. *Herpystichum* lack spur shoots and pseudostipules. Some species of sect. *Basarthrum* are scandent herbs or shrubs and can develop roots on parts of the stems that touch the ground, but these species can be easily distinguished by the presence of pseudostipules and the two-celled "bayonet" hairs unique to the section, whereas pubescent species of sect. *Herpystichum* have multicellular "finger" hairs (Seithe and Anderson 1982). Some species in the Dulcamaroid clade (Weese and Bohs 2007) are also vines, but do not root at the nodes, and have the characteristic sleeves or platforms at the bases of the pedicels. Finally, several groups within *Solanum* subgenus *Leptostemonum* (the "spiny solanums") include viny species, but these all have prickles on some parts of the plants, whereas sect. *Herpystichum* is unarmed.

Materials and Methods

The taxonomic conclusions in this study are based on observations of specimens in the herbarium and in the field, and are supported by molecular phylogenetic studies. We examined 574 herbarium specimens from the following 36 herbaria: AAU, B, BH, BM, BR, C, COL, CU, E, F, G, GH, GOET, K, L, LD, M, MA, MO, NY, P, QCA, QCNE, QPLS, S, SEL, TEX, U, UC, US, UT, VEN, WIS, WU, W, and Z. In addition, the first author collected six species of sect. *Herpystichum*, including three new species (Tepe and Bohs 2009), during a collecting trip to Ecuador in 2009. Details of exsiccatae are available on the Solanaceae Source webpage (www.solanaceaesource.org). Throughout this work, specimens with sheet

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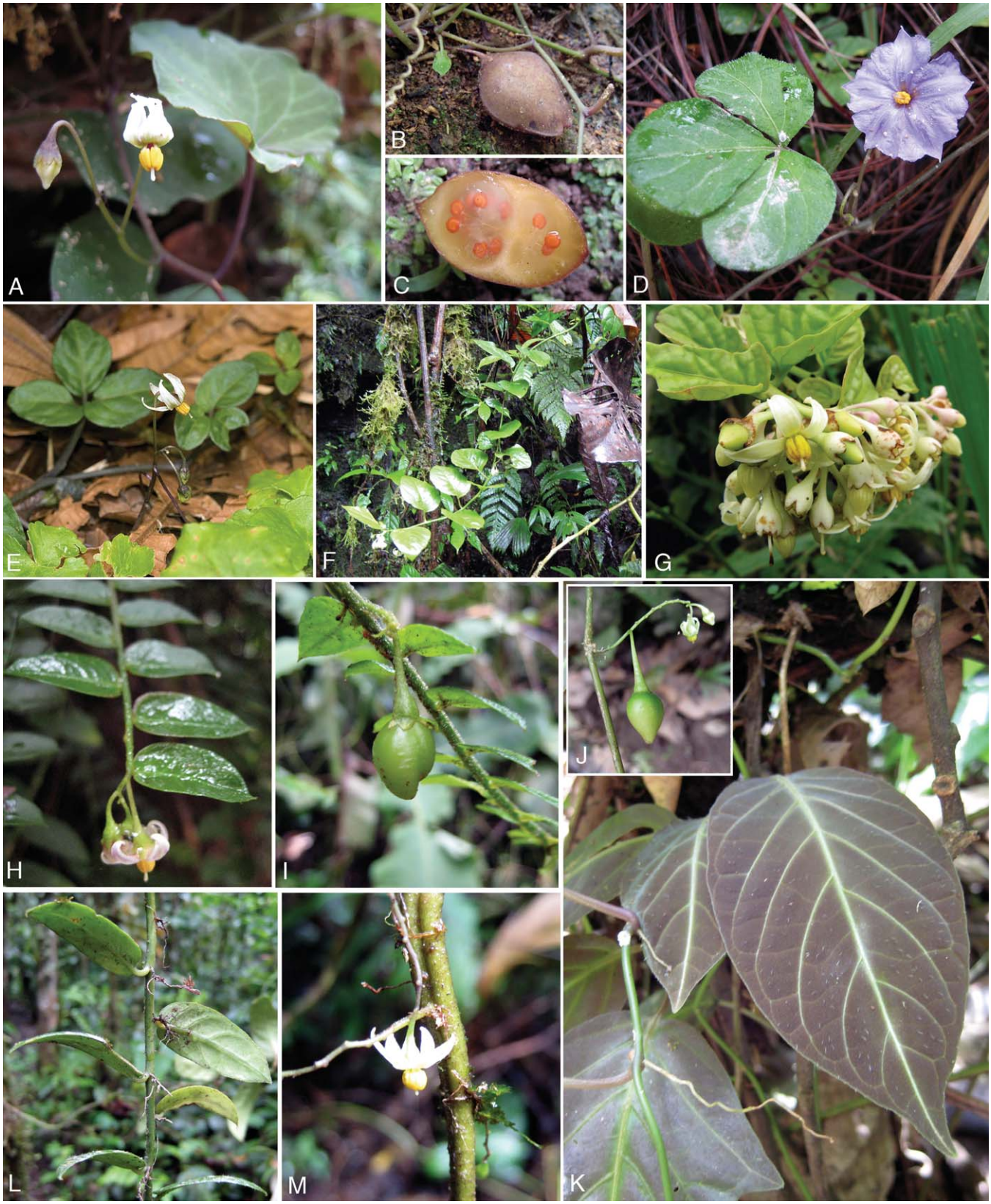


Fig. 1. Flowers fruits, and habit of *Solanum* sect. *Herpystichum*: A. *Solanum limoncochaense*, habit, flower, and bud. B. *S. limoncochaense* fruit in situ and C. in cross section (*E. J. Tepe & S. Stern 2627*, QCNE). D. *S. trifolium* flower and leaf (*E. J. Tepe & S. Stern 2682*, QCNE). E. *S. phaseoloides* habit, flower, and leaf (photo by W. H. Haber). F. *S. crassinervium* habit (*E. J. Tepe & S. Stern 2729*, QCNE), and G. flowers (*S. Stern & E. J. Tepe 400*, QCNE). H. *S. evolvulifolium* habit and flower, and I. fruit (immature) (*E. J. Tepe & S. Stern 2671*, QCNE). J. *S. pacificum* inflorescence with flowers, buds, and fruit (immature), and K. habit (*E. J. Tepe et al. 2696*, QCNE). L. *S. loxophyllum* habit, note adventitious roots at nodes, and M. older stem with inflorescences, note figure eight-shaped stem (*E. J. Tepe & S. Stern 2726*, QCNE). Inflorescences emerge from the cleft between the two lobes of the stem.

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FIG. 2. Flowers, fruits, and habit of *Solanum* sect. *Herpystichum*. A. *Solanum pentaphyllum*, habit and flower (from *O. Haught 2551*, F). B. *S. dalibardiforme*, habit and flower (from *K. von Sneidern 3121*, US). C. *S. dolichorhachis*, habit, flower, and immature fruit (from *F. H. Eggers 14641*, A).

numbers are cited with the herbarium acronym followed by the sheet number (i.e. MO–1781232), or in the case of QPLS, their generic abbreviation followed by the sheet number (i.e. QPLS–SOLA0192); barcodes are preceded by the herbarium acronym (i.e. G–G00104280, or A–GH00077619 since all herbaria incorporated into the Harvard University Herbaria are cited separately but given GH barcodes). Some specimens have both sheet numbers and barcodes and in these cases, only the barcode is listed.

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We have followed the morphological species concept or "morphological cluster" species concept (Mallet 1995) in delimiting the species recognized in this study. Individuals that clustered together based on a common set of morphological characters and that were separated from other clusters by gaps in the morphological continuum were considered species. In most cases, species that we have identified based on morphology also occupy coherent geographic ranges. Our goal was to produce a classification that both reflects the biology of the species, and that can be used by specialists and non-specialists alike to identify the taxa in the group.

The phylogeny presented here is summarized from Tepe et al. (2011) and includes DNA extracted from fresh, silica gel-dried leaf material, or herbarium specimens for 25 accessions of *Solanum*. These accessions included 19 from sect. *Herpystichum* and six were outgroups from related sections. Analyses included data from seven nuclear (ITS, GBSSI, and five COSII) and three plastid (*psbA–trnH*, *trnT–trnF*, and *trnS–trnG*) regions. Details of DNA extraction, primers, and PCR conditions are presented in Tepe et al. (2011). Phylogenetic relationships in the tree presented were estimated using Bayesian inference (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003) of a partitioned, concatenated dataset. Substitution model parameters were determined with MrModeltest 2.2 (Nylander 2004). Further details of analyses can be found in Tepe et al. (2011).

Results

***Taxonomic History*—**Michel Félix Dunal described the first species of this group, the Ecuadorean *S. trifolium*, in 1852, based on a collection from Ruiz and Pavón's exploration of Chile and "Perú" s. l. (Tafalla and Estrella 1989). He allied the species to the compound-leaved members of what we now know as *Solanum* sect. *Pteroidea*, under his *Polybotryon* group (Dunal 1852). The second species described was *S. phaseoloides*, by Hellmuth Polakowsky in 1877 from his own Costa Rican collection. Polakowsky followed Dunal's classification scheme, placing his new species in *Polybotryon*, and recognized the close relationship between his new species and *S. trifolium*. John Donnell Smith described *S. olivaeforme* (a synonym of *S. phaseoloides*) in 1889, but suggested a relationship with *S. tripartitum* Dunal, a member of the Morelloid clade (Weese and Bohs 2007), based on the fruits "among other differences." *Solanum evolvulifolium* was the first of the climbing species to be described, by Jesse Greenman in 1904, based on a Costa Rican collection, but without commentary on its relationships (Donnell Smith 1904).

Most of the remaining species were described by Georg Bitter (1912a, 1913a, b) in the early 20th century. In his description of *S. loxophyllum*, Bitter (1912a) likened it in habit and morphology to members of sects. *Anarrhichomenum* Bitter and *Polybotryon* (G. Don) Bitter (= sect. *Pteroidea* Dunal pro parte; see Knapp and Helgason 1997 for more details), but suggested that it may be distinct enough to warrant a new section of its own: sect. *Loxophylla* Bitter (ined.). Later the same year he explicitly excluded *S. loxophyllum* from sect. *Polybotryon* (Bitter 1912b), but he did not comment further on its relationships because the species was still insufficiently known. *Solanum dalibardiforme* and *S. dolichorhachis* were published simultaneously in 1913 (Bitter 1913a). Bitter mentioned a possible link between *S. dolichorhachis* and *S. loxophyllum*, but emphasized that he had not yet seen the flowers of *S. loxophyllum* nor the fruits of *S. dolichorhachis*. He also suggested an association among *S. dalibardiforme*, *S. phaseoloides*, *S. trifolium*, and *S. ionidium* Bitter. *Solanum ionidium* is a member of sect. *Anarrhichomenum* and is distinct from the other species listed here; however, the type is a rather small fragment of an herbaceous stem tip, which is not representative of the actual habit of this typically woody species. Finally, later in 1913 Bitter published *S. pentaphyllum*, suggesting a close relationship with *S. phaseoloides* (Bitter 1913b). Bitter (1921) mentioned the sectional name *Herpystichum* in reference to *S. pentaphyllum*, *S. phaseoloides*, and *S. trifolium*, which he differentiated from sect. *Polybotryon* based on the extra-axillary position of the inflorescences of the former. In this passage, Bitter cites sect. *Herpystichum* as if it had been published previously, but we have not been able to locate any previous mention of the section. This apparent reference appears to have caused some confusion, and some authors have cited several dates for the publication of sect. *Herpystichum* (see Seithe 1962). Although not a formal sectional description, the information included in the 1921 passage, however, satisfies the retroactive ICBN rules for valid publication of names (McNeill et al. 2006) and, thus, we consider *Solanum* section *Herpystichum* to have been validly published by Bitter in 1921.

Seithe (1962) grouped the ground-trailing species *S. pentaphyllum*, *S. phaseoloides*, and *S. trifolium* in her circumscription of sect. *Herpystichum*, but excluded the climbing species *S. dolichorhachis* and *S. evolvulifolium* to unspecified status within her subg. *Solanum*. Likewise, D'Arcy (1973) placed the ground-trailing species *S. phaseoloides* within sect. *Herpystichum*, but placed *S. evolvulifolium* in sect. *Anarrhichomenum*. Similarly, Child (1990), in his synopsis of D'Arcy's subg. *Potatoe* (G. Don) D'Arcy, grouped the ground-trailing species in sect. *Herpystichum*, including, as did Bitter, *S. ionidium*, and following D'Arcy, placed *S. evolvulifolium* in sect. *Anarrhichomenum*. Nevertheless, Child was the first to ally *Herpystichum* to the potatoes s. l. He did not provide explicit reasons for the relationship, but saw well-developed compound leaves, which are uncommon in *Solanum*, as a uniting feature of subg. *Potatoe* (Child 1990). Nee (1999) grouped the ground-trailing and climbing species for the first time under his circumscription of sect. *Herpystichum*, but did not state his reasons for the grouping.

The remaining three species were described by Tepe (Tepe and Bohs 2009). Many species of sect. *Herpystichum* have narrow distributions and are rare, thus we think it is likely that additional species exist in poorly collected areas, especially southern Ecuador and northern Peru.

***Morphology and Natural History*—**Habit—Members of sect. *Herpystichum* are node-rooting vines. Five species trail along the ground on the forest floor or in clearings, often in dense patches, but are also weak climbers that can scramble over fallen trees. *Solanum crassinervium*, *S. evolvulifolium*, and *S. pacificum* are stronger climbers, frequently climbing understory trees, and *S. loxophyllum,* and possibly *S. dolichorhachis,* can be strong climbers. Most species are entirely herbaceous (*S. dalibardiforme*, *S. limoncochaense*, *S. pacificum*, *S. pentaphyllum*, *S. phaseoloides*, and *S. trifolium*); however, stems of some of the climbing species are strongly woody (*S. dolichorhachis*, *S. evolvulifolium*, and *loxophyllum*), but with little accumulated secondary growth. Stems of *S. crassinervium* are woody, but also somewhat fleshy, and are the thickest stems in the section. Older stems of *S. loxophyllum* are shaped like a numeral '8' in cross-section (referred to herein as "8-shaped"; Fig. 1M). Otherwise, the stems, herbaceous and woody, are terete and slender. Sympodial units are plurifoliate in most species, with considerable vegetative growth between inflorescences. The exception to this rule is *S. crassinervium* in which the sympodial units are often unifoliate.

Trichomes—Trichomes are unbranched, uniseriate, multicellular, and non-glandular. Three species, *S. pentaphyllum*, *S. phaseoloides*, and *S. trifolium* have distinctive, markedly

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tapered, uniseriate trichomes on the upper surfaces of the leaves that are 4–5 times wider at the base than the trichomes on the stems, petioles and lower leaf surfaces of the same individuals. Trichomes on other parts of those species, including the leaf veins adaxially, and on the remaining species, are slender and similar to the non-glandular, multicellular trichomes of many other *Solanum* species (e.g. Seithe and Anderson 1982). The degree of pubescence is variable among collections of *S. evolvulifolium,* which range from nearly glabrous to densely pubescent, but is relatively constant in other species. Pubescence of short hairs (mostly < 0.5 mm) on the adaxial surface of the midvein is typical in *S. dolichorhachis*, *S. evolvulifolium*, *S. loxophyllum*, and occasionally *S. crassinervium* (which is often glabrous).

Leaves—Leaves in sect. *Herpystichum* range from simple to pinnately compound. The climbing species are all simple-leaved, whereas three of the ground-trailing species have compound leaves. The compound leaves are trifoliate in two species, *S. phaseoloides* (Fig. 1E) and *S. trifolium* (Fig. 1D), and pentafoliate in *S. pentaphyllum* (Fig. 2A). Leaflet number within species appears to be constant. The margins are entire to slightly revolute, wavy, or crenate. The leaf bases of several of the climbing species are weakly to strongly oblique; this condition is especially pronounced in *S. dolichorhachis* in which the two sides of the lamina are as much 4 mm apart from each other on the petiole (Fig. 2C). Petioles of the ground-trailing species are long (i.e. > 3 cm), whereas those of the climbing species are much shorter (nearly sessile to 1.5 cm). The leaf blades, veins, and petioles of all species are more or less punctate with deposits of crystal sand, which are visible as small whitish dots (referred to herein as "sand-punctate"). These idioblasts filled with crystal sand are found in several groups within *Solanum* as well as other groups of angiosperms (Metcalfe and Chalk 1950; Whalen et al. 1986; Bohs 1990; Knapp 1992; Aliyu Aliero et al. 2006). Section *Herpystichum* lacks the pseudostipules and interjected leaflets (minute leaflets scattered among the larger leaflets, often seen on cultivated potato and tomato plants) that are present on many groups within the Potato clade (Correll 1962).

Inflorescences—Inflorescences, like those throughout *Solanum*, are morphologically terminal and the associated axillary bud continues the growth of the main stem axis (Danert 1958). In all species, most inflorescences are extra-axillary, but they can also be close enough to the node that they appear axillary or leaf-opposed. Because inflorescences in *Solanum* are terminal, the variable position with respect to the leaf axil is likely the result of concaulescence of stem, petiole, and inflorescence tissues as is the case in sect. *Pteroidea* (Danert 1967; Child 1979). Adventitious roots are frequently associated with the attachment point of the extra-axillary inflorescences in the ground-trailing species. The inflorescences are slender and unbranched in most species, but occasionally once or twice branched in *S. crassinervium*. Inflorescences in the majority of species are few-flowered (i.e. 2–10 flowers), but can have up to 50 flowers in *S. evolvulifolium* and *S. pacificum*, and > 100 in *S. dolichorhachis*. Only one or two flowers are open at one time on an inflorescence, but the total number of flowers per inflorescence can be counted by the scars left behind once the old flowers or fruits have fallen. Because the inflorescences of *S. crassinervium* can be branched, they typically have more simultaneously open flowers. The pedicels of all species are articulated at the base.

Flowers—The flower buds of sect. *Herpystichum* have a distinctive shape within *Solanum*. They are globose with an acuminately pointed apex resulting in a somewhat onion-shaped bud (see Fig. 1A). This shape is manifest in later stages of bud development, and we have seen it in all but two species (*S. dalibardiforme* and *S. trifolium*). These two species, however, are represented by few collections, and the available buds are all at early stages. Thus, it is possible that onion-shaped buds are characteristic of all species of sect. *Herpystichum*.

The flowers are pentamerous and apparently perfect in all species. They are actinomorphic, with the exception of *S. crassinervium* in which the style is deflected to one side in some flowers. The anthers are yellow and equal in length, or only slightly unequal. The filaments are glabrous and not united. The corollas are stellate in eight species (Figs. 1A, E, G, H, J, M), but there is a moderate to considerable amount of interpetalar tissue in *S. dalibardiforme* (Fig. 2B) and *S. trifolium* (Fig. 1D) resulting in rotate-stellate to pentagonal to rotate corollas. Petals of all species are ciliate, and are rarely pubescent abaxially. Flower color in most species ranges from greenish-white to white to creamy-white, but the flowers of *S. trifolium* are pure blue-violet. Flower color in *S. evolvulifolium* is variable among individuals and ranges from white to violet, with frequent mottling. Flower color may also be variable in *S. dalibardiforme* and *S. dolichorhachis*, but we have not seen these two species in the field and they are known from few specimens.

Fruits—Fruits are variable among species of sect. *Herpystichum*, and range from more or less globose to strongly flattened and arrowhead-shaped (Figs. 1B, C). All fruits, however, have a tendency toward some degree of flattening and are always flattened perpendicularly to the septum. Fruits flattened perpendicularly to the septum are rare in *Solanum* and this character, although not well developed in some species, helps to distinguish sect. *Herpystichum* from the rest of the genus.

In general, the fruits are glabrous, but those of *S. limoncochaense* may have some widely scattered hairs when young. Collections with mature fruits are rare, but green fruits probably mature to orange or red in the climbing species, whereas those of the ground-trailing species mature to yellow mottled with brown (*S. phaseoloides*), bronze-brown (*S. limoncochaense*; Fig. 1B), or blackish-purple (*S. pentaphyllum*). Little is known about seed dispersal in species of sect. *Herpystichum*, but the fruits of *S. limoncochaense,* the only species with mature fruits that we have been able to observe in the field, are strongly fragrant with a sweet, heavy scent. The color, scent, and position (i.e. lying on the ground) suggest that they are likely to be dispersed by agoutis or other terrestrial mammals (W. Haber, pers. comm.). The labels of two collections of *S. pentaphyllum* state that the fruits dig themselves into the ground as they mature; however, no other labels mention this phenomenon and we have not observed this species in the field. Additional work is necessary to determine whether *S. pentaphyllum* is, in fact, geocarpic. Stone cell aggregates, common in some groups of *Solanum* (e.g. sect. *Regmandra*; Bennett 2008) are absent from the fruits of sect. *Herpystichum*.

Habitat and Geographic Distribution—Species of sect. *Herpystichum* are native to tropical America and are found from southernmost Mexico (Chiapas), Belize, and Guatemala to northern Peru, from about 17°N to 7°S (Fig. 3). Species diversity is highest between about 5°N to 1°30″S (see individual species descriptions). In South America, they occur in

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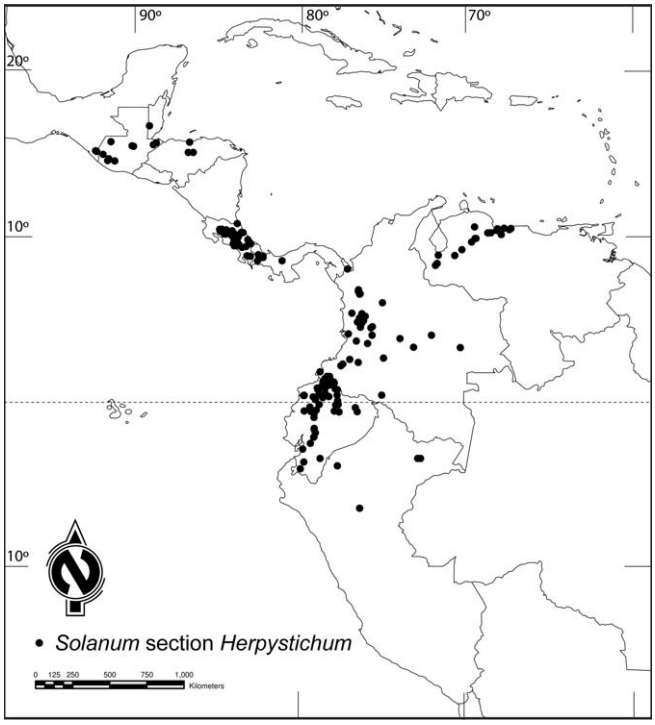


FIG. 3. Distribution of *Solanum* sect. *Herpystichum*.

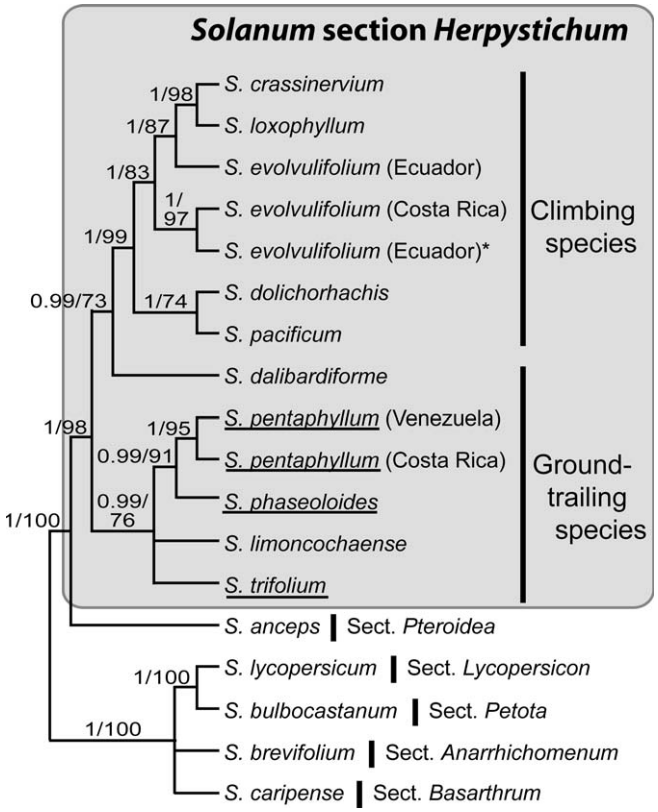


FIG. 4. Summary phylogeny of *Solanum* sect. *Herpystichum* based on based on plastid *psbA-trnH*, *trnT-trnF*, and *trnS-trnG*, and nuclear *waxy*, ITS, cos1C, cos5, cos9B, cos10B, and cos11 sequences (E. J. Tepe et al. 2011). For clarity, replicate accessions of all species except for *S. evolvulifolium* and *S. pentaphyllum* have been omitted. Provenance is indicated for species with multiple accessions, species with compound leaves are underlined, and the asterisk indicates an especially robust specimen of *S. evolvulifolium*. The topology is based on Bayesian analyses, and branch support values are Bayesian posterior probabilities/maximum parsimony bootstrap.

high- (mostly over 2,500 m) to mid-elevation (650–2,500 m) Andean forests, or occur in the lowland forests to the east and west of the Andes (sea level to mostly below 650 m). One species, *S. pentaphyllum*, extends into Venezuela along the Andes (Cordillera de Mérida) to the Cordillera de la Costa. With the exceptions of *S. evolvulifolium*, *S. pentaphyllum*, and *S. phaseoloides*, species of sect. *Herpystichum* are narrow endemics and rare (although some are locally abundant). Several species appear to be sensitive to disturbance and are not found in highly altered habitats, whereas others are frequently found on forest edges, along roadsides and trails, or in pastures and other clearings. Although several species appear to thrive in open, disturbed areas, species in this section are characteristically understory plants of humid rainforests, premontane wet forests, or cloud forests. They are absent from dry or seasonally dry habitats.

Phylogenetic Relationships—Molecular data support sect. *Herpystichum* as a member of the Potato clade (Bohs 2005; Weese and Bohs 2007). A more detailed phylogenetic study of the Potato clade is currently underway (Tepe and Bohs unpubl. data) and preliminary analyses indicate five well-supported sub-clades that correspond to the traditionally-recognized sections *Anarrhichomenum*, *Basarthrum*, *Herpystichum*, and *Pteroidea*, and a clade containing sections *Etuberosum* (Bukasov & Kameraz) A. Child, *Juglandifolia* (Rydberg) A. Child, *Lycopersicoides* (A. Child) Peralta and the economically important sections *Lycopersicon* (Miller) Wettstein and *Petota* Dumort (see Spooner et al. 1993; Peralta et al. 2008 and included references for details of relationships among these groups). Within the Potato clade, sections *Herpystichum* and *Pteroidea* are strongly supported as sister taxa (Fig. 4).

Tepe et al. (2011) provided a 10-marker phylogenetic hypothesis for all 10 species of sect. *Herpystichum* and outgroups (Fig. 4). These results support two major lineages within sect. *Herpystichum*. One clade is composed of *S. limoncochaense*, *S. pentaphyllum*, *S. phaseoloides*, and *S. trifolium*. These are all ground-trailing species and share numerous characters, including markedly flattened fruits, white stellate corollas in all species (except *S. trifolium*, which has rotate, blue-violet flowers), and wide-diameter hairs on the adaxial leaf surfaces (except for *S. limoncochaense*, which is glabrous). *Solanum dalibardiforme*, the remaining ground-trailing species, is not included in this clade, but rather is sister to the other major lineage, which is composed of all of the simple-leaved climbing species. This placement is interesting because *S. dalibardiforme* has simple leaves like the climbing species, but shares the ground-trailing habit and long petioles with the ground-trailing species. Furthermore, its corolla is rotate-stellate to pentagonal to rotate, a character shared only with *S. trifolium* within the section. The node joining *S. dalibardiforme* to the climbing species, however, has the lowest support of any node in the tree.

The simple-leaved climbing species are a strongly-supported monophyletic group. Shared characters include a climbing habit, woody stems in all species except *S. pacificum*, white to pink or violet stellate corollas, and a tendency toward oblique leaf bases. All of these species have distinctive, short trichomes on the leaf midveins adaxially (except for *S. pacificum,* which is completely glabrous). Our results indicate that *S. crassinervium* and *S. loxophyllum* have evolved

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from *S. evolvulifolium*. We fully acknowledge that *S. evolvulifolium*, as we recognize it herein, is paraphyletic; however, we believe that this circumscription of the species, a species from which another lineage has evolved, is biologically realistic and is more useful than erecting several new species that cannot be reliably differentiated based on morphology to maintain purely monophyletic species. As we have circumscribed it, *S. evolvulifolium* is a widespread, but easily recognized species and *S. crassinervium* and *S. loxophyllum* are highly differentiated, easily identifiable species.

Taxonomic Treatment

Solanum sect. *Herpystichum* Bitter, Repert. Spec. Nov. Regni Veg. 17: 331. 1921.—LECTOTYPE species: *S. trifolium* Dunal (designated by Seithe 1962).

Herbaceous to woody, ground-trailing to climbing vines, rooting at the nodes; stems and leaves glabrous to pubescent, the trichomes, if present, multicellular and unbranched. Sympodial units plurifoliate or unifoliate. Leaves simple or pinnately compound, membranous to somewhat fleshy, sand-punctate, the leaf venation palmate or pinnate, the compound leaves with 3 or 5 leaflets, with interstitial leaflets lacking; pseudostipules absent. Inflorescences usually extra-axillary, rarely axillary or leaf-opposed, usually opposed by adventitious roots in the ground-trailing species, usually unbranched, but rarely once or twice branched, ebracteate, bearing 3–116 flowers (scars), but usually fewer than 15; pedicels articulated at the base. Buds globose, rounded to pointed at apex (onion-shaped). Flowers apparently all perfect. Calyx short-lobed, the lobes membranous to fleshy; corollas stellate to pentagonal to rotate, 7–20 mm in diameter; anthers yellow, more or less equal, short and stout, oblong, not connivent, dehiscing by large apical pores, opening into introrse longitudinal slits with age, the filaments free, glabrous; ovary glabrous to minutely papillose. Fruit a berry, yellow, bronze-brown, purplish-black, to orangish-red when mature, occasionally mottled, slightly flattened and globose to conical to spindle-shaped, or strongly flattened and rhomboid to deltoid in outline, flattened perpendicular to the septum, the strongly flattened fruits with a narrow ridge around the margin. Seeds (mature) 1.5–2.5 × 1.5–2 mm, rounded, teardrop-shaped to reniform, flattened, ca. 0.5 mm thick, tan to light reddish-brown, the surface minutely rugose to granular.

Key to the Species of *Solanum* Sect. *Herpystichum*

1. Leaves simple . . . 2
   2. Petioles mostly < 2 cm long; leaf venation pinnate . . . 3
      3. Leaves with 3–4 pairs of secondary veins (often obscure) . . . 4
         4. Internodes mostly < 1.5 cm long; arrangement of leaves and branches clearly distichous; branches mostly straight and arising at a near 45° angle from the main stem; leaves drying greenish to brownish, but not conspicuously blackish; inflorescences often stem-terminal or at least in the leafy part of the stem; all stems terete . . . 4. *S. evolvulifolium*
         4. Internodes mostly > 1.5 cm long; arrangement of leaves and branches variable and not regularly distichous; branches sinuous and arising at various angles from the main stem; leaves frequently drying blackish; inflorescences usually on older, leafless parts of the stem; older stems 8-shaped in cross-section . . . 6. *S. loxophyllum*
      3. Leaves with (4–)5–7 pairs of secondary veins . . . 5
         5. Plants somewhat fleshy; stems rather thick and fleshy; leaves broadly ovate to elliptic, 1–2 times as long as wide, somewhat fleshy, drying blackish; inflorescences 1–4 cm long, occasionally branched; corollas 1.5–2 cm in diameter . . . 1. *S. crassinervium*
         5. Plants herbaceous or woody, not discernibly fleshy; stems slender, herbaceous to woody; leaves lanceolate to ovate (rarely elliptic), 2–3 times as long as wide, nearly membranaceous to chartaceous, not noticeably fleshy, and drying greenish or brownish, not conspicuously blackish; inflorescences greater than 4 cm long, unbranched; corollas 0.7–1 cm in diameter . . . 6
            6. Stems wiry-woody, light brown; leaves chartaceous with asymmetrical bases, the sides of the lamina 3–4 mm distant on the petiole; petioles 0.2–0.7 cm; plants variously pubescent, especially the inflorescence . . . 3. *S. dolichorhachis*
            6. Stems herbaceous, green; leaves membranaceous with ± symmetrical bases; petioles 1–1.5 cm; plants glabrous . . . 7. *S. pacificum*
   2. Petioles mostly > 3 cm long; leaf venation palmate.....7
      7. Plants pubescent; corollas rotate-stellate (divided to about the middle); high elevations (> 2,000 m) . . . 2. *S. dalibardiforme*
      7. Plants glabrous; corollas stellate (divided nearly to the base); low elevations (< 500 m) . . . 5. *S. limoncochaense*
1. Leaves 3–5 foliate . . . 8
   8. Leaves 5-foliate, the corolla stellate . . . 8. *S. pentaphyllum*
   8. Leaves 3-foliate, the corolla stellate or rotate.....9
      9. Petiole and petiolules glabrous to sparsely pubescent; leaflets elliptical to rhomboidal to rounded with obtuse to acuminate apices (always pointed); corollas stellate, white . . . 9. *S. phaseoloides*
      9. Petiole and petiolules covered in short, dense pubescence; leaflets rounded with rounded to truncate apices, some minutely apiculate; corollas rotate, violet . . . 10. *S. trifolium*

1. Solanum crassinervium Tepe, J. Bot. Res. Inst. Texas 3: 514. 2009.—TYPE: ECUADOR. Carchi/Esmeraldas: near Lita, 600 m, wet evergreen forest, 19 May 1987 (fl, fr), *H. H. van der Werff 9496* (holotype: QCNE–8516!; isotypes: MO–4299600!, NY–NY00735823!).

Vine or scandent shrub, climbing understory trees to 4 m or more; leafy branches spreading to pendulous. Stems thickly herbaceous to weakly woody, somewhat fleshy, glabrous to sparsely pubescent and soon glabrescent. Sympodial units plurifoliate to rarely unifoliate. Leaves simple, the blades 3.5–14 × 1.5–8 cm, 1–2 times as long as wide, gradually reduced in size toward the inflorescence, ovate to elliptic, somewhat fleshy, sand-punctate, glabrous adaxially and abaxially or rarely with fine pubescence on the midvein adaxially;

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venation pinnate, with 5–7 pairs of secondary veins, these conspicuous and prominent abaxially, densely sand-punctate; base rounded to truncate to cordate, sometimes oblique; margins entire; apex shortly acuminate; petioles (0.2–)1–1.5 cm, glabrous or rarely pubescent adaxially, densely white sand-punctate. Internodes 1.5–5.5 cm. Inflorescences 1–3 cm long in flower to ca. 6 cm in fruit, unbranched to branched, stem-terminal to axillary to extra-axillary, with 2–16 flowers (scars), the axes glabrous; peduncle 0.1–0.5 cm; rachis 0.1–2 cm; pedicels 4–12 mm in flower, 9–18 mm in fruit, only slightly enlarged distally, glabrous to rarely sparsely pubescent, spaced nearly contiguously. Calyx 2.5–3.5 mm long, glabrous, the margins thickened, the tube 2.5–3 mm long, the lobes 1.5–2.5 × 1.5–2 mm, deltoid, acute to acuminate at tips, white to pale pink; fruiting calyx somewhat accrescent, the lobes 1.5–2.5 × 1.5–2.5 mm. Corolla 1.5–2 cm in diameter, 5–8 mm long, stellate, somewhat fleshy, white, the lobes 5–8 × 2.5–3 mm, planar at anthesis, acute to acuminate at apices, glabrous adaxially, sparsely pubescent near the apex abaxially, the margins densely ciliate. Stamens with filaments 1–1.5 mm long, glabrous; anthers 3–4 × 1.2–1.5 mm. Ovary glabrous; style 4–6 × ca. 0.3 mm, glabrous, cylindrical, sometimes deflected to one side of flower; stigma capitate. Fruit (immature) 0.7–1 × 0.7–0.9 cm, ovoid to nearly globose, slightly flattened, somewhat pointed at apex, green to pale orangish to brownish at maturity, glabrous. Seeds 2–2.2 × 1.8–2 mm, flattened-reniform, tan, the surface minutely reticulate-rugulose. Figure 1F–G.

Habitat and Distribution—*Solanum crassinervium* occurs west of the Andes in southwestern Colombia and northwestern Ecuador in lowland and premontane rainforest habitats, including the Mache-Chindul mountain range in northwestern Ecuador; 150–600(–1,800) m in elevation (Fig. 5).

Phenology—Flowering apparently occurs year-round; fruiting specimens have been collected from Jan.–Feb., and Sept.–Dec.

Conservation Status—According to the IUCN red list categories (IUCN 2010), *S. crassinervium* is classified as B1a+biii (endangered). This species is restricted to rainforest habitats in northwestern Ecuador and extreme southwestern Colombia, covering an area estimated to be considerably less than 5,000 km^2. This area is one of the more inaccessible parts of Ecuador, but increasing exploitation of this area continues to decrease the amount of suitable habitat for *S. crassinervium* (C. Aulestia, Bilsa Biological Station, pers. comm.).

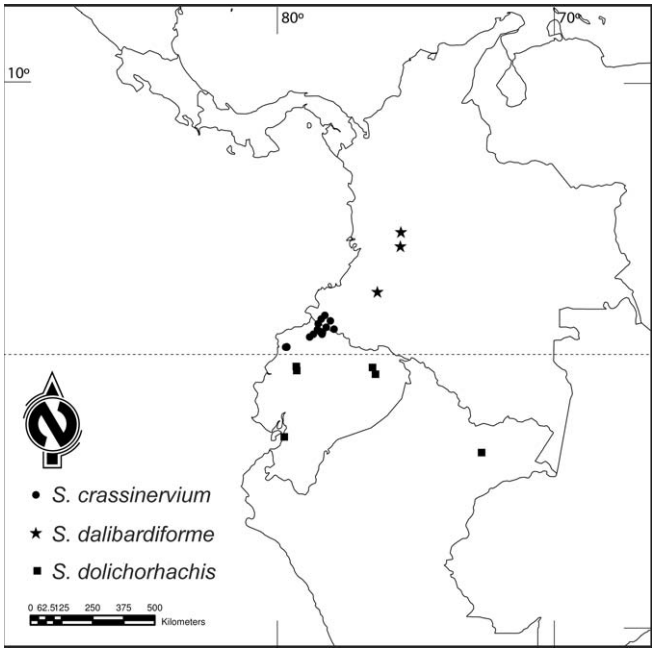


Fig. 5. Distribution of *Solanum crassinervium*, *S. dalibardiforme*, and *S. dolichorhachis*.

Etymology—The epithet *crassinervium* describes the prominent secondary veins that are useful in helping distinguish this species from its closest relatives.

Notes—*Solanum crassinervium* is one of the climbing species, and can be distinguished from the other species in the section by the somewhat fleshy texture of the stems, leaves, and flowers, its ovate to elliptical leaves with conspicuous secondary veins that are visible in fresh and dried material, and its occasionally branched inflorescences. This is the most robust species of sect. *Herpystichum*.

Solanum crassinervium is most similar to *S. evolvulifolium* and *S. loxophyllum*, but differs from both species in its robust habit, broadly ovate leaves (vs. mostly oblong), fleshy calyx and corolla, and inflorescences that may be simple and branched on the same individual. It can be easily differentiated from *S. evolvulifolium* by its much larger leaves, petioles, and internodes. The leaves of both *S. crassinervium* and *S. loxophyllum* are somewhat fleshy, and both species tend to dry dark to nearly black; however, *S. crassinervium* has more secondary veins (5–7 vs. 3–4 pairs) and these are prominent abaxially, whereas those of *S. loxophyllum* are often obscure within the fleshy leaf blade (translucent in living material and flush with the leaf surface in dried material). The often stout and branched inflorescences of *S. crassinervium* differ from those of *S. loxophyllum*, which are apparently always simple, and are slender and delicate. Furthermore, inflorescences of *S. crassinervium* are typically produced in the leafy part of the stem, as compared to those of *S. loxophyllum*, which are typically borne on older, leafless parts of the stem.

Additional Specimens Examined—COLOMBIA. Nariño**:** 1,000 m, 9 May 1939 (fl), *A. H. G. Alston 8547* (BM); Trayecto Pialapi – La Planada, 1°10′N 77°58′W, 1,300–1,700 m, 23 Jul 1988 (fr), *O. de Benavides 10150* (MO); Mpio. Barbacoas, Corregimiento Altaquer, Vereda El Barro, Reserva Natural Río Ñambí, margen derecha del Río Ñambí, 1°18′N 78°08′W, 1,325 m, 1 Dec 1993 (fl), *P. Franco et al. 4707* (COL, NY); Mpio. Tumaco, Resguardo de Albí, lado izquierdo del Río Albí, 1°22′N 78°28′W, 220–280 m, 12 Nov 1995 (fl, fr), *B. R. Ramírez et al. 8826* (NY); Mpio. Barbacoas, Resguardo Indígena de Saundé, 1°30′N, 78°20′W, 350 m, 21 Jan 1996 (fr), *B. R. Ramírez et al. 9699* (NY).

ECUADOR. Carchí: Río Blanco drainage above Chical, ca. 12 km W of Maldonado, 1,300–1,500 m, 25 Sep 1979 (fl), *A. Gentry & G. Schupp 26522* (MO); Cantón Tulcán, Parroquia Tobar Donoso, Reserva Indígena Awá, Centro El Baboso, 0°53′N 78°25′W, 1,800 m, 17–27 Aug 1992 (fr), *G. Tipaz et al. 1802* (MO); Cantón Tulcán, Parroquia Tobar Donoso, Reserva Indígena Awá, Centro El Baboso, 0°53′N 78°25′W, 1,800 m, 17–27 Aug 1992 (fr), *G. Tipaz et al. 1813* (BM, NY, QCNE); border area between Prov. Carchi and Esmeraldas, 20 km past Lita on road Lita-Alto Tambo, 550 m, 25 Jun 1991 (fl), *H. van der Werff et al. 11972* (MO, NY, QCNE). Esmeraldas: Bilsa Biological Station, Montañas de Mache, 20 km NW of Quinindé, 3 km W of Santa Isabel, 0°22′N 79°45′W, 600 m, 26 Sep 1994 (fr), *J. R. Abbott 15256* (MO, SEL); San Lorenzo, Reserva Étnica Awá, Parroquia Alto Tambo, Centro de la Union, Cañon del Río Mira, 0°52′N 78°26′W, 250 m, 22 Mar 1993 (fl), *C. Aulestia & M. Aulestia 1431* (MO, QCNE); Cantón Quinindé, Bilsa Biological Station, Montañas de Mache, 35 km W of Quinindé, 5 km W of Santa Isabel, reserve boundary N from Station road, between the Río Cube tributary and the E-bearing boundary crossing the Río Cube, 0°21′N 79°44′W, 400–600 m, 26 Sep 1994 (fr), *M. S. Bass & N. Pitman 68* (BM, NY); Bilsa Biological Station, Montañas de Mache, 35 km W of Quinindé, 5 km W of Santa Isabel, 0°21′N 79°44′W, 400–600 m, 6 Dec 1994 (fl), *M. S. Bass & N. Pitman 289* (MO); San José, km 321 along railroad from Ibarra to San Lorenzo, 1°N 78°W, 350 m, 5 May 1982 (fl), *B. M. Boom 1374* (F, NY, QCA); Cantón Quinindé, Bilsa Biological Station, Montañas de Mache,

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35 km W of Quinindé, 5 km W of Santa Isabel, Monkey Bone Trail, 0°21′N 79°44′W, 400–600 m, 15 Sep 1994 (fr), *J. L. Clark & B. Adnepos 55* (MO, QCNE); Cantón Quinindé, Bilsa Biological Station, Mache Mountains, 35 km W of Quinindé, 5 km W of Santa Isabel, 0°21′N 79°44′W, 400–600 m, 24 Jan 1995 (fl), *J. L. Clark 412* (BM, NY, QCNE); Cantón Quinindé, Bilsa Biological Station, Mache Mountains, 35 km W of Quinindé, 5 km W of Santa Isabel, 0°21′N 79°44′W, 500 m, 18 Feb 1996 (fr), *J. L. Clark 2121* (BM, NY, QCNE, US); Cantón Quinindé, Mache-Chindul Ecological Reserve, Bilsa Biological Station, Mache Mountains, 35 km W of Quinindé, 0°21′N 79°44′W, 500 m, 1–10 Jan 1997 (fr), *J. L. Clark 2993* (MO, US); Cantón Quinindé, Mache-Chindul Ecological Reserve, Bilsa Biological Station, Mache Mountains, 35 km W of Quinindé, 0°21′N 79°44′W, 500 m, 1–10 Jan 1997 (fr), *J. L. Clark et al. 3762* (MO, NY, QCNE, US); 10 km W of Lita on road to San Lorenzo, 0°55′N 78°30′W, 800 m, 12 May 1991 (fl), *A. Gentry et al. 69984* (GOET, MO, NY); Cantón San Lorenzo, Lita to El Cristal road, finca of Dr. La Lama, 13.5 km S of Lita, 0°49′N 78°26′W, 1,220–1,350 m, 2 Nov 1992 (fl, fr), *J. L. Luteyn et al. 14744* (MO, NY, QCA, US); Cantón Quinindé, carretera Herrera-El Páramo (Sta. Isabel), Estación Biológica Bilsa, 0°1′36.7″N 79°42′40.4″W, 580 m, 18 Feb-5 Mar 1995 (fr), *W. Palacios et al. 13548* (MO, NY, QCNE); Cantón Quinindé, carretera Herrera-El Páramo (Sta. Isabel), suroeste de la casa de la Estación Biológica Bilsa, 0°1′36.7″N 79°42′40.4″W, 580 m, 2–4 Mar 1995 (fl), *W. Palacios et al. 13719* (MO); Cantón Quinindé, Bilsa Biological Station, Montañas de Mache, 35 km W of Quinindé, 5 km W of Santa Isabela, Monkey Bone trail, 0°21′N 79°44′W, 400–600 m, 11 Dec 1994 (fl, fr), *N. Pitman & M. Bass 1091* (MO, NY, QCNE); San Lorenzo, Territorio Awá, centro Mataje, 1°11′44″N 78°34′29″W, 200 m, 17 Nov 2000 (fl), *W. Ramírez et al. 12* (NY), *15* (NY); Bilsa Biological Station, 5 km W of Sta. Isabel, 0°20′49″N 79°42′41″W, 540 m, 14 Feb 2009 (fl, fr), *S. Stern 400* (QCNE, UT); Bilsa Biological Station, 5 km W of Sta. Isabel, 0°20′49″N 79°42′41″W, 540 m, 13 Feb 2009 (fl, fr), *E. J. Tepe & S. Stern 2729* (BM, MU, NY, QCA, QCNE, UT); Eloy Alfaro, Reserva Ecológica Cotacachi-Cayapas, Parroquia Luis Vargas Torres, Río Santiago, Estero Angostura, 0°49′S 78°45′W, 250 m, 28 Oct 1993 (fr), *M. Tirado et al. 628* (MO); Eloy Alfaro, Reserva Ecológica Cotacachi-Cayapas, Parroquia Luis Vargas Torres, Río Santiago, Estero Angostura, 0°49′S 78°45′W, 250 m, 8–14 Dec 1993 (fr), *M. Tirado et al. 775* (MO).

2. Solanum dalibardiforme Bitter, Repert. Spec. Nov. Regni Veg. 11: 484. 1913.—TYPE: COLOMBIA. Quindío, "region froide Quindiu," Feb (fl.), *J. Goudot 19* (holotype: W–W0001345 [scan!]; photos of holotype [F neg. 33066]: F–957755!, G–G00080130!, MO–1691587!).

Herbaceous vine, terrestrial or climbing. Stems slender, herbaceous, sparsely pubescent with trichomes 0.5–1 mm long. Sympodial units plurifoliate. Leaves simple, the blades 1.5–8 × 3–5 cm, slightly longer than wide, broadly ovate, chartaceous to somewhat fleshy, sparsely pubescent adaxially, glabrous to sparsely pubescent abaxially, moderately pubescent on veins adaxially and abaxially, the trichomes on the adaxial side of the veins ca. 0.2 mm, the other leaf trichomes like those of the stems; venation palmate, with 5–7 primary veins, sparsely sand-punctate; base deeply cordate; margins minutely revolute and with small, widely spaced teeth, these often hair-tipped, often obscure; apex acuminate; petioles 2–11 cm, sparsely pubescent, sparsely sand-punctate. Internodes 5–10 cm. Inflorescences 5–13 cm long, unbranched, extra-axillary, with 3–6 flowers, the axes sparsely pubescent; peduncle 2.5–7 cm, slender; rachis 0.8–2.5 cm; pedicels 15–35 mm in flower, unknown in fruit, slender, sparsely pubescent, spaced 5–8 mm apart. Calyx 3–4.5 mm long, the tube 1–1.5 mm long, the lobes 1–3 × 1.2–1.5 mm, rounded to lanceolate, acute to acuminate at tips, sparsely pubescent abaxially with short, scattered hairs, more densely pubescent at the tips; fruiting calyx unknown. Corolla 1.5–1.8 cm in diameter, 6–10 mm long, rotate-stellate to pentagonal, membranous, white to light blue, the tube 4–9 mm, the lobes 2.3–5 × 6–7 mm, broadly deltoid, narrowly acute at tips, glabrous adaxially, sparsely pubescent abaxially, the margins ciliate apically. Stamens with filaments 0.7–1 mm, glabrous; anthers 2–2.2 × ca. 1 mm. Ovary glabrous; style 4–6 × ca. 0.2 mm, glabrous to minutely papillose in lower half, cylindrical to somewhat clavate; stigma capitate. Fruits 2–2.5 × 1.2–1.8 cm, ovoid, slightly to markedly flattened, rounded to pointed at apex, the color unknown, glabrous. Seeds unknown. Figure 2B.

Habitat and Distribution—*Solanum dalibardiforme* is apparently endemic to Colombia (Depts. Cauca, Quindío, and Tolima); 2,400–3,500 m in elevation (Fig. 5).

Phenology—Flowering specimens have been collected in Apr.–Aug., and Nov. The single fruiting specimen seen was collected in July.

Conservation Status—According to the IUCN red list categories (IUCN 2010), *S. dalibardiforme* is classified as D2 (vulnerable). This species occupies a restricted area in the Cordillera Central in Colombia and is only known from three locations. Furthermore, *S. dalibardiforme* is only known from nine collections, suggesting that it is rare.

Etymology—The epithet *dalibardiforme* refers to the superficial similarity of the leaves and habit of this species to the genus *Dalibarda* (Rosaceae).

Notes—*Solanum dalibardiforme* is one of the ground-trailing species, and is one of the most distinctive species of the section. It can be distinguished from the rest of the species in this group by its simple leaves and rotate-stellate to pentagonal corollas. It is most similar to the Ecuadorean *S. limoncochaense*, but has pubescent vegetative parts, pentagonal corollas, and occurs in high elevation habitats. *Solanum trifolium* is the only other member of sect. *Herpystichum* with considerable interpetalar tissue, resulting in pentagonal or rotate corollas, but is easily distinguished by its 3-foliate compound leaves. We have seen only one scan of a fruiting specimen of this species (*L. Reyes 119*, COL), and the fruits appear to be elliptical and pointed apically, but without the distinctive arrowhead shape of *S. limoncochaense*, *S. phaseoloides*, *S. pentaphyllum*, and *S. trifolium*. It is not possible to determine the cross sectional shape of the fruit from the pressed specimens available, and it is not clear whether this species has flattened fruits like the rest of the ground-trailing species.

Additional Specimens Examined—COLOMBIA. Cauca: Puracé, Parque Nacional Puracé, 15 Jun 1974 (fl, fr), *L. Reyes 119* (COL). Tolima: La Suiza, Cordillera Central, 2,600 m, 11 May 1932 (fl), *J. Cuatrecasas 3355* (MA); Quebrada Cajamarca to "Mermillon", New Quindio Trail, Cordillera Central, 14 Aug 1922 (fl), *E. P. Killip 9753* (NY); Along Quindo highway, between Cajamarca and summit of Divide, 2,400 m, 27 Mar 1939 (fl), *E. P. Killip & G. Varela 34519* (COL, US); Roncesvalles, Vereda de San Marcos, Finca el Corazón, 5 Nov 2003 (fl), *J. Mora & J. Palma 743* (COL); Roncesvalles, Vereda de San Marcos, Finca el Orinoco, 5 Nov 2003 (st), *J. Mora & J. Palma 924* (COL); Toche, 2,500 m, 25 May 1942 (fl), *K. Von Sneidern 3121* (NY, S); Toche, 2,500 m, 25 Apr 1942 (fl), *K. Von Sneidern 3121bis* (LL, US).

3. Solanum dolichorhachis Bitter, Repert. Spec. Nov. Regni Veg. 11: 490. 1913.—TYPE: ECUADOR. Guayas: Balao, "in silvestris, rarium," May 1892 (fl, fr), *H. Eggers 14641* (holotype: M–M0111203!; isotypes: A–GH00077619!, B [destroyed], L–L0403275!, LE [photo!], US–1324515!, WU!; photo of B isotype [F neg. 2658]: G–G00080131!).

Scandent shrub or liana, climbing to 8 m or more. Stems slender, wiry-woody, glabrous to moderately pubescent with trichomes 0.1–0.2 mm long, these frequently in distinct lines along stem. Sympodial units plurifoliate. Leaves simple, the arrangement distichous, the blades 4.4–11 × 1.3–4.5 cm, 2–3 times as long as wide, ovate to elliptical, chartaceous to coriaceous to somewhat fleshy, glabrous to moderately pubescent on the midvein adaxially, glabrous abaxially; venation pinnate, with ca. 5 pairs of secondary veins, the veins

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sand-punctate; base oblique, sides of the lamina 3–4 mm distant on the petiole, the two sides rounded to truncate to somewhat cordate; margins entire; apex acuminate; petioles 0.2–0.6 cm, moderately pubescent adaxially, sand-punctate. Internodes 0.7–2.8 cm. Inflorescences 3–55 cm long, unbranched, terminal to extra-axillary to nearly leaf-opposed, with 14–116 flowers (scars), the axes slender, densely pubescent; peduncle 2–5 cm; rachis 2–49 cm; pedicels 5–6 mm in flower, slender, 13–14 mm in fruit, glabrous to minutely pubescent, spaced 1.5–8 mm apart. Calyx 1.5–2 mm long, membranous, sparsely pubescent, sand-punctate, the tube ca. 1 mm long, the lobes 0.5–1 × ca. 2 mm, broadly rounded, rounded to shortly acuminate at tips; fruiting calyx not accrescent. Corolla 0.7–1 cm in diameter, 3–5 mm long, stellate, membranous, white to greenish-white, the lobes 3–4.5 × 1.5–2 mm, lanceolate, acute at tips, reflexed at maturity, glabrous adaxially, pubescent along center of petal abaxially, the margins ciliate. Stamens with filaments 0.5–1 mm long, glabrous; anthers ca. 2.5 × 1 mm. Ovary glabrous; style 3–4 × ca. 0.3 mm, clavate, glabrous; stigma capitate. Fruits (immature) 9–18 × 4–6 cm, 2–3 times as long as wide, spindle-shaped to possibly cordate, pointed at apex, the color unknown, glabrous. Seeds unknown. Figure 2C.

Habitat and Distribution*—Solanum dolichorhachis* occurs in the Pacific and Amazonian lowlands of Ecuador and in the Amazonian lowlands of Peru; 50–350 m in elevation. (Fig. 5)

***Phenology*—**Flowering specimens have been collected in Apr. and Dec.; fruits have been collected in Apr.

***Conservation Status*—**According to the IUCN red list categories (IUCN 2010), *S. dolichorhachis* is classified as B1a+biii (critically endangered). This species is only known from five widely scattered locations, two of which are in western Ecuador, an area that continues to experience extreme habitat degradation (Dodson and Gentry 1991). The location at Limoncocha is in the center of an oil field, continued development of which is encroaching on all sides of the 4,600 ha Reserva Biológica Limoncocha (E. J. Tepe, pers. obs.). Despite its broad distribution, only five collections of this species are known, suggesting that it occurs at low densities, and appears to have been rare even at the time of collection. The label on the type specimen notes *in silvestris, rarium* (and *in silvis rarissimum* on some of the isotypes). *Solanum dolichorhachis* was collected near the Laguna de Limoncocha near the Río Napo in 1974 (*B. A. Drummond III 7329*, MO); however, EJT was unable to relocate this species during a five day visit to the Reserva Biológica Limoncocha in 2009.

Montúfar (2000) listed *S. dolichorhachis* as a critically endangered species endemic to Ecuador. If the Peruvian collection is, in fact, a population of *S. dolichorhachis* (see below), then the species is more widespread than previously believed. Nevertheless, based on the number of collections available for this species, we believe that it is critically endangered, especially in western Ecuador where the type was collected and which has experienced tremendous habitat destruction.

***Etymology*—**The epithet *dolichorhachis* refers to the long, slender inflorescences of this species.

Notes*—Solanum dolichorhachis* is a climbing species recognizable by the long and slender inflorescences, small stellate flowers, spindle-shaped fruits, and the simple, usually large leaves with distinctly oblique bases. This species is most similar to *S. pacificum*, but the wiry-woody stems, densely short-pubescent inflorescences and young stems, and oblique leaf bases set this species apart.

The label from the type collection describes the fruits as cordate (*fructu cordato*). It is difficult to know what Eggers saw in three dimensions based on the single fruit on the isotype at A, but Egger's notes suggest that the fruits may have been flattened and, therefore, possibly somewhat like those of the ground-trailing species in shape (i.e. Figs. 1B–C).

The collections of this species from eastern Ecuador differ somewhat from the type in that they have longer pubescence, darker stems that are densely sand-punctate (vs. light tan, non-punctate stems), inflorescences with less dense and coarser pubescence, and non-punctate calyces. The Peruvian collection is closer to the type in leaf shape than collections from eastern Ecuador, but the plant appears to be rather fleshy. It is possible that the two variants from the regions east of the Andes merit recognition at the species level; however, they have no unambiguous, qualitative differences and, since this species has been collected few times, there is currently insufficient material upon which to base further taxonomic decisions.

***Additional Specimens Examined*—**ECUADOR. Los Ríos: Near Quevedo, Canton Vinces, Hacienda San José, 0°30′S 79°21′W, 50 m, 28 Oct 1934 (fl), *Y. Mexia 6617* (UC, US). Sucumbíos: Limoncocha on Río Napo, 0°23′15″S 76°36′35″W, 300 m, 1 Oct 1974 (fr), *B. A. Drummond III* (MO). Orellana: Parque Nacional Yasuni, Río Tiputini, al noroeste de al confluencia con el Río Tivacuno, 0°38′ S 76°30′ W, 200–300 m, 25 Apr 2002 (fl), *G. Villa et al. 1461* (BM, F).

PERU. Loreto: Maynas, Indiana, Reserva Explorama, 3°28′S 72°50′W, 106 m, 9 May 1990 (fl), *R. Vásquez & N. Jaramillo 13680* (MO, NY).

4. Solanum evolvulifolium Greenm., Bot. Gaz. 37: 211. 1904.—TYPE: COSTA RICA. San José: La Palma, 1,460 m, Sep 1898 (fl, fr), *A. Tonduz 12615* (lectotype, here designated: GH–GH00077489!; possible isolectotypes: CR–12615, K–K000449423!, K–K000449424!, M–M0111204!, NY–NY00138984!, US–US00027570!).

Vine, sometimes shrubby, climbing tree trunks or other vegetation. Stems slender, woody, glabrous to densely pubescent, the trichomes typically ca. 1 mm or longer, occasionally in distinct lines along stem. Sympodial units plurifoliate. Leaves simple, the arrangement distinctly distichous, the blades 0.5–5 × 0.3–3 cm, 1–3 times as long as wide, ovate to oblong-ovate, chartaceous to coriaceous, sand-punctate, glabrous to densely pubescent on the leaf blade adaxially and abaxially, pubescent on midvein adaxially with hairs 0.2–0.5 mm, discolored, occasionally reddish below; venation pinnate, with 3–4 pairs of secondary veins, the veins densely sand-punctate; base truncate to cordate, often oblique; margins entire to undulate, revolute; apex rounded and apiculate to acute, sometimes acuminate; petioles nearly absent to 0.5 cm, glabrous to densely pubescent, densely sand-punctate. Internodes 0.5–1.5(–3.5) cm. Inflorescences 1–15 cm long, unbranched, nearly leaf-opposed to extra-axillary, with 2–80 flowers (scars), the axes glabrous to pubescent with simple, uniseriate, curled hairs; peduncle 0.6–1.5 cm; rachis 1–14 cm; pedicels 4–10 mm in flower, green to pink, 10–15 mm in fruit, glabrous to densely pubescent, spaced nearly contiguously to 8 mm apart. Calyx 1.5–3 mm long, conical, the tube 1–2.5 mm long, the lobes 0.5–1.5 × 0.8–1.5 mm, deltate, rounded and minutely apiculate at tips to acute, the margins somewhat thickened, glabrous to sparsely pubescent along margins, more dense at tips of the lobes, pale green to pink; fruiting calyx minutely accrescent. Corolla 1–2 cm in diameter, 5–8 mm long, stellate, membranous, greenish, white, pink, to bluish-purple, sometimes mottled, the lobes 5–11 × 2–3 mm, lanceolate, acute at apices, glabrous adaxially and abaxially, the margins

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ciliate. Stamens with filaments ca. 1 mm long, glabrous; anthers 2–3 × 0.8–1.5 mm. Ovary glabrous; style 4–6 × ca. 0.25 mm, cylindrical to somewhat clavate, minutely papillose in lower 2/3; stigma truncate to somewhat capitate. Fruit 0.6–1.5 × 0.6–1 cm, globose to ovoid, slightly flattened, rounded to acute at apex, glabrous, red to reddish-brown when ripe. Seeds 1.5–2 mm in diameter, rounded, tan, the surface rugulose. Figure 1H–I.

Habitat and Distribution—*Solanum evolvulifolium* occurs in Costa Rica, Panama, Colombia, Venezuela, Ecuador, and Peru as an epiphyte on tree trunks in rain and cloud forest habitats; (200–)800–2,600 m in elevation (Fig. 6).

Phenology—Flowering and fruiting apparently occurs year-round.

Etymology—The epithet *evolvulifolium* refers to the similarity of the leaves of this species to some species of *Evolvulus* (Convolvulaceae).

Notes—*Solanum evolvulifolium*, a climbing species, is recognizable by its characteristic distichous leaf arrangement (Fig. 1H) and branching pattern. The main stem of this species is most often encountered climbing on tree trunks, attached with adventitious roots at the nodes; secondary branches extend away from the main stem. Higher order branches are typically distichous and arise at ca. 45° angles, often giving the plant a characteristic, flattened appearance. The leaves often diminish in size along a branch, occasionally to a branching point or inflorescence, and then increase in size again. The pedicels, calyx and corolla are frequently pinkish-white to greenish-pink. This species can be distinguished from other simple leaved, viny members of sect. *Herpystichum* by the uniformly short internodes, somewhat coriaceous leaves (instead of chartaceous or somewhat fleshy), and the flattened aspect of the branches that results from the distichous leaves branches.

South American collections are more variable than those from Central America in leaf shape and, especially, the degree of pubescence. The calyx lobes of Central American collections are broadly ovate and rounded apically, whereas the lobes of most South American collections are deltoid in shape and acute apically. These calyx characters, however, are not sufficiently uniform, nor are they correlated with other characters that might justify segregation of *S. evolvulifolium* into one or more additional species. Several extreme forms from South America are included here, and these include especially robust forms from Colombia and Ecuador and an especially pubescent form from Ecuador. It is possible that the differences merit specific status, but both forms are represented by only a few collections and are thus included within a broadly defined and variable, yet easily identifiable *S. evolvulifolium*. Furthermore, the three sequenced accessions of *S. evolvulifolium*, including one accession of the robust form and two of the standard form, form a monophyletic group together with *S. crassinervium* and *S. loxophyllum* (Fig. 4). The robust form of *S. evolvulifolium* is strongly supported as sister to Central American accessions of *S. evolvulifolium* lending support for its inclusion in a morphologically variable, yet easily recognizeable *S. evolvulifolium*.

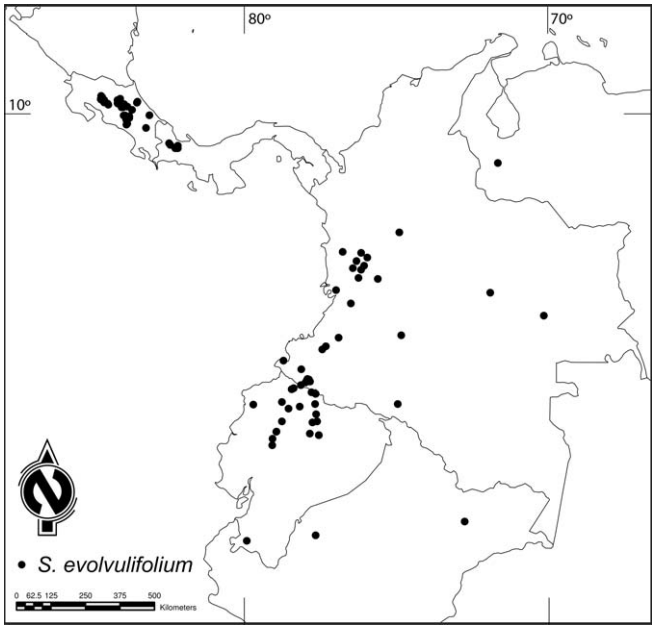


Fig. 6. Distribution of *Solanum evolvulifolium*.

There is some confusion about the numbering and collector of the lectotype collection of *S. evolvulifolium*. Greenman's protologue states that the collector and number is *Pittier 7413*. However, the handwritten labels on the K specimens give the collector as Tonduz. They do not have a collector number, but they do have a "herb. nat. Cost. number 12615 (Herbario del Museo Nacional de Costa Rica). Nevertheless, there is sufficient overlap of label information on different specimens to determine that they are all clearly part of the same collection. All labels list Tonduz' name and the herb. nat. Cost. number. Furthermore, it seems that Tonduz was the actual collector, but that Pittier distributed the specimens under his own set of numbers (Dauphin López 2009; B. Hammel, pers. comm.). For these reasons, we refer to the collection as *Tonduz 12615*.

Greenman cited two syntypes, *Tonduz 12615* (as *Pittier 7413*) and *Wercklé 11599*, in his original description of *S. evolvulifolium*. *Tonduz 12615* is chosen as the lectotype because this collection has many duplicates, whereas only a single specimen is known of the Wercklé collection. The GH specimen of *Tonduz 12615* is chosen as the lectotype because Greenman was at GH in 1904 and this is likely the specimen that he used in his description of *S. evolvulifolium*. Furthermore, the GH specimen gives the altitude as 1460 m, the altitude stated in the protologue. The rest of the *Tonduz 12615* collections report an altitude of 1,542 m and therefore they are listed above as possible isolectotypes.

Representative Specimens Examined—COSTA RICA. La Palma, 1,500 m, Nov 1897 (fr), *K. Wercklé 11599* (GH). Alajuela: Reserva Biológica Monteverde, 10°19′N 84°43′W, 820 m, 22 Oct 1988 (fl), *E. Bello 468* (F, MO); Reserva Forestal de Arenal, 10°18′N 84°42′W, 850–900 m, 28 Feb 1990 (fl), *E. Bello 1961* (MO); San Carlos, La Forma, Finca El Jilguero, 10°25′25″N 84°42′05″W, 800 m, 22 Nov 1992 (fl), *G. Herrera 5696* (MO); 12 km NNW of San Ramón by road on way to San Lorenzo, 1 km S of Balsa, 10°10′N 84°29′W, 1,100 m, 25 Apr 1983 (fl), *R. L. Liesner & E. Judziewicz 14936* (MO, WIS). Cartago: Beside Río Villegas, valley of Río Grande de Orosi, 9°42′N 83°47′W, 1,620 m, 11 Jan 1970 (fl), *R. W. Lent 1849* (F, MO, U); Monumento Nacional Guayabo, 9°58′N 83°41′W, 26 Jan 1993 (fl), *G. Rivera 2054* (F, K); growing in dense upland rain forest about 5 km SW of Tapanti, 9°47′N 83°55′W, 1,500 m, 17 Aug 1967 (fr), *J. Taylor & C. Taylor 4472* (MO, NY). Heredia: Vicinity of Colonia Virgen del Socorro, 10°17′N 84°10′W, 900 m, 10 Aug 1975, (fl), *J. Utley & K. Utley 2824* (F); Parque Nacional Braulio Carrillo, 10°15′50″N 84°05′W, 1,200–1,400 m, 13 Nov 1986 (fl), *M. Grayum & G. Herrera 7881* (MO). Limon: Guápiles, Los Angeles, San Miguel, 10°04′20″N 83°50′40″W, 1,300 m, 21 Feb 1990 (fl), *A. Chacón et al. 744* (MO); Parque Nacional Cordillera de Talamanca, 9°22′30″N 83°14′10″W, 1,700 m, 24 Mar 1993 (fl), *A. Fernández 818* (BM, MO); El Progreso, 9°47′20″N, 83°07′30″W, 1,600 m, 24 Apr 1989 (fl), *G. Herrera & A. Chacón 2771* (F, MO, NY); San Jose: road between Alto La Palma and Bajo La Hondura, 1,400 m, 24 Feb 1978 (fl), *F. Almeda & K Nakai 3913* (MO); Pérez Zeledón,

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Savegre, 9°31′N 83°51′W, 1,900 m, 3 Aug 1994 (fl, fr), *G. Herrera et al. 7253* (K); woods near Quebrada Vargus, Alto La Palma, 10°04′N 83°59′W, 1,400 m, 31 Mar 1974 (fl), *R. W. Lent 3852* (AAU, F, MO).

PANAMA. Bocas del Toro: N slope of Cerro Horqueta, 8°49′24″N 82°26′54″W, 6,000–7,000 ft, 5 Aug 1947 (fr), *P. H. Allen 4995* (F, G, U); along road from Fortuna Dam, towards Chiriquí Grande, 2.2 miles N of the continental divide, 8°45′N 82°15′W, 800 m, 12 Mar 1985 (fl), *G. McPherson 6815* (MO, WIS). Chiriqui: Boquete, Bajo Chorro, 8°50′N 82°29′W, 6,000 ft, 12 Jan 1938 (fl) *M. E. Davidson 112* (GH, F, US). Chiriquí/Bocas del Toro: Zona Protectora Palo Seco, along continental divide, 8°47′N 82°13′W, 1,100–1,300 m, 11 Aug 2000 (fl), *S. Knapp & J. Mallet 9178* (BR, MO).

COLOMBIA. Antioquia: Río Caldera, 5°58′N, 74°58′W, Jan 1953 (fl), *Bro. Daniel 4498* (US). Caldas: La Finca, Quindío, 4°27′N 75°40′W, 3,200 m, Feb 1937 (st), *E. Dryander 2136* (US); Santa Cecelia, Cordillera occidental,vertiente occidental, 5°18′N 76°13′W, 800 m, 29 Dec 1945 (fl), *K. von Sneidern 5524* (F). Cauca: El Tambo, Parque Nacional Munchique, 2°36′40″N 74°54′10″W, 2,570 m, 20 Jul 1993 (fl, fr), *G. Lozano et al. 6961* (COL, MA); El Cairo, Cerro del Inglés, Cordillera Occidental, 4°45′N 76°13′W, 2,260 m, 5 Jan 1987 (fl), *F. A. Silverstone Sopkin et al. 2967* (NY); El Tambo, La Costa, 4°4′N 77°1′W, 1,500 m, 25 Mar 1938 (infl), *K. von Sneidern 1663* (F, G, S, US). Chocó: San Jose del Palmar, Hoya del Rio Torito, Finca Los Guaduales, 5°02′N 76°22′W, 630 m, 6 Mar 1980 (fl), *E. Forero et al. 6793* (COL, MO); 6 km E of Río Pato, ca. 48 km W of Las Animas on the Pan American Highway, 5°20N 76°49′W, 250 m, 11 Jan 1979 (fl, fr), *A. H. Gentry & A. Renteria 24016* (AAU, MO). Nariño: Cordillera Occidental, Finca La Planada, near Chucunes, 1°11′N 77°58′W, 1,950 m, 13 Jan 1981 (fr), *A. H. Gentry et al. 30549* (COL, MO, NY); Junin-Barbacoas road, 2–10 km. N of Junin, 1°30′N 78°10′W, 900 m, 26 Jul 1986, (st), *A. H. Gentry et al. 55333* (MO). Putumayo: Villagarzón, Carretera a Pto. Asis, 4 May 1994 (st), *J. L. Fernández 11431* (COL); Punto de Buenos Aires, Cerro Portachuelo, 0°22′N 75°01′W, 2,080 m, 27 Jul 1964 (fl), *D. D. Soejarto 1139* (GH). Risaralda: Apía, Vereda La Cumbre, 5°8′42N 76°0′46″W, 2,285 m, 24 Feb 1983 (fl), *J. H. Torres 2216* (COL); Pereira, La Pastora, 2,500 m, 20 Jan 1998 (fl), *G. Vargas 4472* (COL). Valle: Cordillera occidental, Hoya del Río Digua, La Elsa, 3°15′N 70°51′W, 1,000–1,200 m, 9 Nov 1943 (fl, fr), *J. Cuatrecasas 15313* (F, US).

VENEZUELA. Mérida: Rivas Dávila, 22–27 km S of Tovar along rd. to Canaguá, 8°14′N 71°45′W, 2,100–2,256 m, 16 Apr 1984 (fl, fr), *J. L. Luteyn et al. 9960* (NY).

ECUADOR. Carchi: Mira, Norte del Carmen, Camino a Chical, 0°17′N 78°13′W, 2,000 m, 10 Feb 1992 (fl), *W. A. Palacios et al. 9753* (MO); Tulcan, Reserva Indígena Awá, 0°53′N 78°25′W, 1,800 m, 17 Aug 1992 (fr), *G. Tipaz et al. 1923* (MO). Carchi/Esmeraldas: Near Lita, 0°52′N 78°27′W, 600 m, 19 May 1987 (fl). *H. Van der Werff et al. 9493* (MO). Cotopaxi: Sigchos, Triunfo Grande, 0°32′22″S 78°58′59″W, 2,349 m, 6 Aug 2003 (fl, fr), *J. E. Ramos Perez et al. 7061* (NY); Pujilí, Reserva Biológica Los Ilinizas, 0°58′45″S 79°06′53″W, 1,725 m, 10 Aug 2003 (st), *F. A. Silverstone Sopkin et al. 10027* (MO, NY). Esmeraldas: Road Lita-Alto Tambo, ca. km 17.8, 0°51′N 78°29′W, 850 m, 28 Sep 1991 (fl), *B. Ollgaard 99154* (AAU). Loja: Cerro de Celica, Celica - Guachanamá, km 2.7, 4°05′46″S 79°56′45″W, 2,250 m, 12 Apr 1994 (fl, fr), *P. M. Jorgensen et al. 93* (NY). Napo: Parque Nacional Sumaco y Comunidad de Pacto Sumaco, 0°38′56″S 77°35′49″W, 1,550–1,700 m, 26 Apr 1997 (fr), *A. Alvarez et al. 2017* (MO); Quijos, Cosanga, Yanayacu Biological Station and Center for Creative Studies, 0°35′55″S 77°53′22″W, 2,200 m, 18 Aug 2005 (fl), *J. L. Clark et al. 9438* (BM, NY, US); Km 2, carretera nueva Cotundo – Coca, 0°42′N 77°42′W, 1,130 m, 5 Aug 1984 (fl), *C. H. Dodson et al. 15031* (NY, MO). Pichincha: Reserva ecológica Río Guajalito, km 59 de la carretera antigua Quito-St. Domingo de los Colorados, 0°13′53″S 74°48′10″W, 1,800–2,000 m, 4 May 2000 (fl, fr), *I. Tapia 1254* (SEL). Sucumbios: El Reventador, colecciones en ámbas márgenes del Rio Reventador, 0°02′N 77°41′W, 1,850 m, 6 Oct 1990 (st), *J. Jaramillo & E. Grijalva 12933* (AAU, NY).

PERU. Amazonas: Monte Virgen, 50 m frente la comunidad de Caterpiza, 3°55′S 77°42′W, 200 m, 30 Aug 1979, (fl, fr), *V. Huashikat 268* (MO).

5. Solanum limoncochaense Tepe, J. Bot. Res. Inst. Texas 3: 516. 2009.—TYPE: ECUADOR. Sucumbíos: Limoncocha, Reserva Biológica Limoncocha, in wet primary forest near NW corner of lake, 250 m, 22 Jan 2009 (fl, fr), *E. J. Tepe & S. Stern 2627* (holotype: QCA!; isotypes: BM!, MO!, MU–272379!, NY–NY01163478!, QCNE!, US!, UT!).

Herbaceous vine, terrestrial or climbing to ca. 1 m from ground. Stems slender, glabrous. Sympodial units plurifoliate. Leaves simple, the blades 3.5–7 × 3.5–8 cm, slightly wider than long, rounded, somewhat fleshy, moderately sand-punctate, glabrous; venation palmate with 5(–7) primary veins, these sparsely sand-punctate; base cordate; margins entire, slightly revolute on some leaves; apex rounded to obtuse to shortly acuminate; petioles 3–16 cm, moderately sand-punctate, glabrous. Internodes 2.5–20 cm. Inflorescences 4–8 cm long, unbranched, extra-axillary, with 2–3 flowers, the axes glabrous; peduncle 1.3–4.5 cm, slender; rachis 0.9–1.5 cm; pedicels 15–25 mm in flower, 25–30 mm in fruit, slender, glabrous, spaced ca. 15 mm apart. Calyx 2.5–4.2 mm long, the tube 1–1.5 mm long, the lobes 1.5–2 × ca. 1.2 mm, rounded, acuminate at tips, glabrous to sparsely pubescent abaxially, densely pubescent adaxially, purplish; fruiting calyx slightly accrescent, the lobes 1–1.2 × 1.5–2 mm, truncate-acuminate. Corolla 1–1.6 cm in diameter, 5–8 mm long, stellate, membranous, white, the tube 1.5–2 mm, the lobes 6–10 × 1.5–3 mm, lanceolate, narrowly acute at tips, the apex papillose adaxially and abaxially, the margins ciliate apically. Stamens with filaments ca. 1 mm, glabrous; anthers 2–2.5 × ca. 1 mm. Ovary sparsely papillose; style 2–2.5 × ca. 0.3 mm, straight, cylindrical, stout, sparsely papillose in lower half; stigma capitate, somewhat 2-lobed. Fruits 1–3 × 0.6–3.2 cm, ovoid-rhomboid, flattened, the apex truncate to emarginate, greenish-brown to purplish near apex when immature, bronze-brown when mature, sparsely pubescent with hairs < 0.1 mm to glabrous when mature, strongly fragrant with a sweet, heavy scent, juicy, the flavor sweet. Seeds 2–2.5 mm in diameter, lenticular, light reddish-brown, the surface minutely rugose. Figure 1A–C.

Habitat and Distribution—This species appears to be endemic to Sucumbíos Province (historically part of Napo Province), Ecuador, near the Laguna de Limoncocha, where it grows in terra firme primary forests and clearings; 240–300 m (Fig. 7).

Phenology—Flowering specimens have been collected in Jan., June, Sept., and Oct.; fruiting specimens have been collected in Jan and Jun.

Conservation Status—According to the IUCN red list categories (IUCN 2010), *S. limoncochaense* is classified as B1a+ biii (critically endangered) and D2 (vulnerable because of restricted area of occupancy). This species is only known from the terra firme forest near the northwest part of the Laguna de Limoncocha in western Ecuador. The four known collections of this species are all from this area, where it is common, but exploration of much of the Reserva Biológica Limoncocha

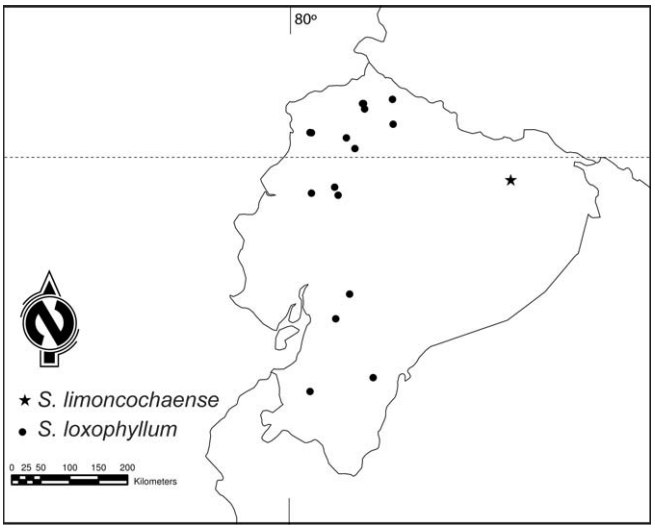


Fig. 7. Distribution of *Solanum limoncochaense* and *S. loxophyllum*.

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did not reveal any additional populations (E. J. Tepe, pers. obs.). There is also a continuing decline in suitable habitats in the area due to deforestation for additional oil exploration, and an increase in the local population resulting from oil-associated jobs (H. Moya, Reserva Biológica Limoncocha, pers. comm.).

Etymology—*Solanum limoncochaense* is named for the Laguna de Limoncocha in western Ecuador, the only known collection locality of this species.

Notes—*Solanum limoncochaense* is one of the ground-trailing species and can easily be recognized by its simple, palmately veined leaves, glabrous vegetative parts, and stellate flowers. It is most similar to the Colombian *S. dalibardiforme*, which is pubescent throughout, has rotate-stellate corollas, and appears to be a strictly high-elevation species.

This species grows in dense patches on the rainforest floor and over fallen trees. It is a weak climber, and plants in the field were encountered climbing tree trunks up to ca. 1 m from the ground (E. J. Tepe and S. Stern, pers. obs.).

Additional Specimens Examined—ECUADOR. Sucumbíos: Limoncocha on Río Napo, 300 m, 18 Oct 1974 (fl), *B. A. Drummond 7350* (MO); environs of Limoncocha, 240 m, 16 Jun 1978 (fl, fr), *M. T. Madison et al. 5327* (AAU, F, K, MO, NY, QCA, SEL); near northwest corner of lake, Limoncocha, Sep 1969 (fl), *R. N. Mowbray 699104* (MO).

6. Solanum loxophyllum Bitter, Repert. Spec. Nov. Regni Veg. 11: 14. 1912.—TYPE: ECUADOR. Chimborazo/Guayas: "In silvis tropicalibus prope Puente de Chimbo," Sep 1891 (fr), *L. Sodiro 114/20* (holotype: B, [destroyed]; photos of holotype [F neg. 2668]: G–G00080136!, NY!, NY!; isotype: QPLS–SOLA0192!).

Vine, woody, climbing understory vegetation and canopy trees to 15 m or more. Stems slender, strong and wiry, the older stems 8-shaped in cross section, reaching ca. 3 × 6 mm in cross section or larger, glabrous to sparsely pubescent, the trichomes slender, 0.8–1.5 mm long. Sympodial units plurifoliate. Leaves simple, the blades 2.5–8 × 0.8–3.5 cm, 2–3 times as long as wide, ovate to elliptical, somewhat fleshy, moderately sand-punctate, pubescent on the midvein adaxially with small trichomes 0.3–0.5 mm long, more rarely glabrous or pubescent across the leaf surface, glabrous to pubescent on the veins or the entire leaf surface abaxially; venation pinnate, with 3–4 pairs of secondary veins, these translucent in living material, inconspicuous and flush with the leaf surface on dried specimens, moderately sand-punctate; base rounded to truncate, oblique, the sides of the lamina 1–2 mm distant on the petiole; margins entire; apex acute; petioles 1–5 mm, moderately sand-punctate, pubescent adaxially. Internodes 1.5–2.2 cm. Inflorescences 1–11 cm long, simple or rarely once branched, extra-axillary to nearly leaf opposed, with 3–50 flowers (scars), the axes glabrous, slender and delicate; peduncle 0.3–0.5 cm, slender; rachis 2–10 cm; pedicels 3–10 mm in flower, slender, 9–12 mm and slightly enlarged in fruit, 9–12 mm, somewhat thickened apically, glabrous, spaced 1–6 mm apart. Calyx 2.5–5 mm long, glabrous except for the margins which are sparsely ciliate apically, the tube 1–1.5 mm long, the lobes ca. 1.5 × 1.5 mm, rounded-deltoid, shortly apiculate at the tips, pale pinkish-white; fruiting calyx only slightly accrescent, the lobes 1.5–2 × ca. 1.5 mm. Corolla 0.8–1 cm in diameter, 3–5 mm long, stellate, membranaceous, white, the tube ca. 1 mm, the lobes 7–8 × 2–2.5 mm, lanceolate, attenuate at tips, glabrous adaxially and abaxially, the margins minutely ciliate apically. Stamens with filaments 0.8–1 mm, glabrous; anthers 2.5–3 × 1.2–1.5 mm. Ovary glabrous; style ca. 5 × 0.3 mm, cylindrical, glabrous; stigma capitate. Fruits 1–1.5 × 0.5–1.1 cm, ellipsoidal to conical, the apex somewhat pointed, glabrous. Seeds ca. 2 × 1.5 mm, ca. 0.5 mm thick, flattened, teardrop-shaped, light tan in color, the surface minutely rugose. Figure 1L–M.

Habitat and Distribution—*Solanum loxophyllum* is apparently endemic to the Pacific lowlands and low mountains of western Ecuador; 100–600(–850) m in elevation (Fig. 7).

Phenology—Flowering and fruiting apparently occur throughout the year.

Etymology—The epithet *loxophyllum* (loxo = oblique in Greek) makes reference to the oblique leaf bases found in this species. The leaf bases of *S. dolichorhachis*, however, are much more markedly oblique than they are in *S. loxophyllum*.

Conservation Status—According to the IUCN red list categories (IUCN 2010), *S. loxophyllum* is classified as B1a+biii (endangered). Although this species is common in the habitats where it occurs, deep shade of low to midelevation rainforests in western Ecuador, less than 1,500 km^2 of these habitats remain, and they continue to be converted to agricultural lands (Dodson and Gentry 1991; C. Aulestia, Bilsa Biological Station, pers. comm.).

Common Names—Ecuador: Chinba chuba tape (Cayapa; *Kvist 40522*, AAU, QCA), chiro nairamo tape (Cayapa; *Kvist 40437*, AAU, BM), quinfo aran sili (Colorado; *Kvist 40691*, AAU, BM).

Uses—Ecuador: the leaves are used for pain relief and for healing of open wounds at joints. Leaves are applied to the affected joint (*Kvist 40437*). The flowers are crushed and rubbed on the body as a perfume (*Kvist 40522*). The plant is used for a bath (baño de caliente) when feeling cold (*Kvist 40691*).

Notes—*Solanum loxophyllum* is a climbing species closely allied to *S. evolvulifolium*, with which it has frequently been synonymized. It differs from *S. evolvulifolium* in its thin, but distinctly fleshy, larger leaves, less regular branching, sinuous rather than more or less straight branches, older stems that are 8-shaped in cross section, a tendency toward cauliflory, its high-climbing habit (individuals have been seen to climb to 12 m or more; E. J. Tepe, pers. obs.), and distribution under 850 m (*S. evolvulifolium* has occasionally been collected as low as 250 m, but is most frequently encountered above 1,000 m).

Solanum loxophyllum can be distinguished from other species of sect. *Herpystichum* by its fleshy leaves with inconspicuous veins (translucent in fresh material), cauliflorous inflorescences, and the distinctive older stems that are 8-shaped in cross section. The slender, delicate inflorescences emerge from the cleft between the two halves of the 8-shaped stems. Several collections from the area around Zapallo Grande and the Colorado community, Congoma Grande, are more robust and are more densely pubescent than collections from other areas. Herbarium specimens of *S. loxophyllum* typically dry dark to nearly black, a character shared with *S. crassinervium*.

The provenance of the type collection is rather vague, given that the town of Puente de Chimbo is no longer extant. One references states, however, that Puente de Chimbo was located at the end of the Chimbo valley, where the Chimbo river leaves the mountains and enters the plains, and turns from a south-flowing to a west-flowing river (Wolf 1892, p. 132). This would place Puente de Chimbo near the current town of Bucay (Bromley and Bromley 1975), and the locality falls well within the geographic and altitudinal range of other collections of *S. loxophyllum*.

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Based on recent fieldwork, it appears that *S. loxophyllum* is widespread and common in the Pacific lowlands of Ecuador. It seems to be tolerant of intermediate levels of disturbance, and is abundant along trails and in secondary, but shady habitats. Flowering is apparently rather rare, and the flowers are inconspicuous and few in number. Consequently, *S. loxophyllum* is underrepresented in herbarium collections.

Additional Specimens Examined—ECUADOR. Azuay/Cañar: Manta Real, Río Patul, Sur de la Carretera La Troncal-Zhud, 2°33′S 79°20′W, 450–800 m, 13 Jul 1991 (fr), *R. B. Foster & B. Mitsui 13542* (F, QCA). El Oro: Hcda. Daucay, Limón – Playa, 3°28′S 78°45′W, 500 m, 22 Apr 1994 (st), *X. Cornejo & C. Bonifaz 2478* (NY); 11 km W of Pinas on new road to Sta. Rosa, 850 m, 8 Oct 1979 (fl), *C. H. Dodson et al. 9049* (MO, SEL). Esmeraldas: Mache-Chindul Ecological Reserve, Bilsa Biological Station, Mache Mountains, 35 km W of Quinindé, 5 km W of Sta. Isabel, 0°21′N 79°44′W, 500 m, 17 Feb 1996 (fl), *J. L. Clark et al. 2054* (BM, MO, NY); Reserva Cotacachi-Cayapas, La Aguita, 0°28′48″N 78°26′24″W, 150 m, 26 Jun 1998 (infl), *X. Cornejo & C. Bonifaz 6389* (NY); Río Cayapa, Zapallo Grande, 1 km upriver Río Zapallo Grande, 0°48′N 78°54′W, 100 m, 29 Jun 1982 (infl), *L. P. Kvist 40437* (AAU, BM); Río Cayapa, Zapallo Grande, 1 km upriver Río Zapallo Grande, 0°48′N 78°55′W, 100 m, 3 Jul 1982 (st), *L. P. Kvist 40522* (AAU, QCA); environs of Lita, on the Ibarra-San Lorenzo RR, 550–650 m, 10 Jun 1978 (fl), *M. T. Madison et al. 5154* (F, QCA); Mache-Chindul Ecological Reserve, Bilsa Biological Station, Mache Mountains, 35 km W of Quinindé, 5 km W of Sta. Isabel, 0°21′N 79°44′W, 500 m, 13 Feb 2009 (fl), *E. J. Tepe & S. Stern 2726* (QCNE, UT); Reserva Ecológica Cotacachi-Cayapa, Charco Vicente, Río San Miguel, 0°43′N 78°53′W, 200 m, 20–31 Sep 1993 (fr), *M. Tirado et al. 391* (MO, QCNE). Los Ríos: Río Palenque Biological Station, km 56 on the Quevedo-Santo Domingo Rd, 0°30′S 79°21′W, 150–220, 8 Jun 1974 (fl, fr), *C. H. Dodson 5543* (SEL, US); Río Palenque Biological Station, km 56 on the Quevedo-Santo Domingo Rd, 0°30′S 79°21′W, 150–220 m, 29 Mar 1980 (fr), *C. H. Dodson & A. Gentry 10040* (MO, SEL); Río Palenque Biological Station, km 56 on the Quevedo-Santo Domingo Rd, 0°30′S 79°21′W, 150–220 m, 5 Feb 2009 (st), *E. J. Tepe et al. 2698* (QCNE, UT). Los Ríos or Pichincha: El Centinela at crest of Montañas Ila on road from Patricia Pilar to 24 de Mayo, 0°37′33″S 79°17′46″W, 600 m, 6 Feb 1979 (fl), *C. H. Dodson 7389* (MO, SEL); El Centinela at crest of Montañas Ila on road from Patricia Pilar to 24 de Mayo, 0°37′33″S 79°17′46″W, 600 m, 20 Jul 1979 (fr), *C. H. Dodson et al. 8626* (MO, SEL). Pichincha: Santo Domingo bypass ca. 3 km S of Santo Domingo, 530 m, 8 Apr 1980 (fl), *C. H. Dodson & A. Gentry 10359* (F, MO, SEL); Reserva Forestal ENDESA, Río Silanche, 0°06′N 79°02′W, 650–700 m, 9 Jun 1984 (fl, fr), *J. Jaramillo* (AAU, MO, QCNE); in the Colorado community "congoma grande" at km 23 on the Santo Domingo - Puerto Limon road, 0°21′S 79°22′W, 100 m, 21 Jul 1982 (st), *L. P. Kvist 40691* (AAU, BM).

7. Solanum pacificum Tepe, J. Bot. Res. Inst. Texas 3: 512. 2009.—TYPE: ECUADOR. Los Ríos: Centro Científico Río Palenque, in secondary forest, 215 m, 5 Feb 2009 (fl, fr), *E. J. Tepe et al. 2696* (holotype: QCNE!; isotypes: BM!, MO!, NY–NY01163476!, QCA!, UT!).

Herbaceous vine, climbing secondary vegetation in gaps. Stems slender, weakly herbaceous, glabrous; fertile branch tips pendent. Sympodial units plurifoliate. Leaves simple, the blades 14–19 × 4.5–8 cm, 2–3 times as long as wide, lanceolate to ovate, membranaceous to thinly chartaceous, moderately to densely sand-punctate, glabrous adaxially and abaxially; venation pinnate, with 4–7 pairs of secondary veins, these densely sand-punctate; base rounded to obtuse, more or less symmetrical; margins entire; apex acuminate; petioles 1–1.5 cm, densely sand-punctate, glabrous. Internodes 1.5–7 cm. Inflorescences 4–10 cm long, slender, unbranched, extra-axillary, with 17–58 flowers (scars), the axes glabrous, slender; peduncle 2–4.5 cm; rachis ca. 6 cm; pedicels 8–10 mm in flower, slender, 15–20 mm in fruit, enlarged apically, glabrous, spaced nearly contiguously to 12 mm apart. Calyx 1–1.2 mm long, glabrous to minutely and sparsely ciliate along margins, the tube 0.5–0.7 mm long, the lobes 0.5–0.6 × 0.8–1 mm, rounded, rounded to weakly acuminate at tips; fruiting calyx somewhat accrescent, the lobes 0.6–0.8 × ca. 1 mm. Corolla 0.8–1 cm in diameter, ca. 5 mm long, stellate, membranous, green to white near the margins of the petals, the lobes 4–5 × 1.2–2.5 mm, ovate, reflexed at maturity, acute at apices, glabrous adaxially and abaxially, the margins ciliate. Stamens subequal, with filaments ca. 0.8 mm long, glabrous; anthers 1.5–2 × 0.7–1.2 mm. Ovary glabrous; style 4–4.5 × 0.1–0.2 mm, glabrous, slightly clavate; stigma truncate. Fruit (immature) ca. 0.9 × 0.6 cm, ovoid, somewhat flattened, pointed at apex, green, glabrous. Seeds unknown. Figure 1J–K.

Habitat and Distribution—*Solanum pacificum* occurs in primary and secondary rainforest habitats in the Pacific lowlands of Ecuador; 50–380 m in elevation (Fig. 8).

Phenology—Flowering specimens have been collected from Feb.–Aug.; the type collection, collected in Feb., is the only fruiting specimen seen. It is likely that fruiting is more frequent than the collection record indicates.

Conservation Status—According to the IUCN red list categories (IUCN 2010), *S. pacificum* is classified as B1a+3iii (critically endangered) and D2 (vulnerable because of restricted area of occupancy). This species is restricted to lowland rainforest habitats of western Ecuador. This habitat type has suffered extreme degradation, and has been reduced from an estimated 32,000 km² to ca. 1,500 km² (Dodson and Gentry 1991). The six known collections of *S. pacificum* are from a small portion of this area, and because of the extensive habitat destruction, it is possible that this species survives only within the 0.87 km² Centro Científico Río Palenque.

Etymology—*Solanum pacificum* is named after the Pacific lowlands of Ecuador where it is endemic, and for María Paz Moreno, the first author's wife and frequent field companion. "Pax," Latin for peace, is the root of both "Pacific" and "Paz."

Notes—*Solanum pacificum* is a climbing species recognizable by its completely glabrous vegetative parts; slender, weakly herbaceous stems; small, greenish flowers; and large, thin leaves. The leaves of *S. pacificum* are deep purplish-green above with whitish veins, and are weakly to intensely purple below. The upper surfaces of fresh leaves have a distinctly velvety luster.

Within sect. *Herpystichum*, this species is most similar to *S. dolichorhachis*, but differs in having leaves with ± symmetrical vs. distinctly oblique leaf bases and green, herbaceous vs. tan, woody stems. It can be distinguished from other climbing species by the texture, shape, and size of the leaves. *Solanum*

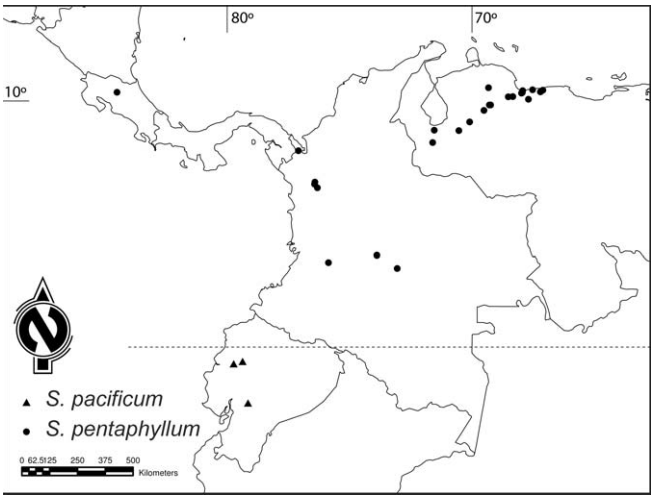


Fig. 8. Distribution of *Solanum pacificum* and *S. pentaphyllum*.

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pacificum is also similar to the sympatric *S. leptorhachis* Bitter [sect. *Geminata* (G. Don) Walp.] in the size and shape of the leaves, the long, slender inflorescences, and small, greenish-white, stellate flowers; however, *S. leptorhachis* is an upright, woody shrub with unifoliate sympodial units on flowering stems and geminate leaves at nonflowering nodes. In contract, *S. pacificum* has plurifoliate sympodial units and always has only one leaf per node (i.e. not geminate).

Additional Specimens Examined—ECUADOR. Junction of the provinces Bolivar, Cañar, Chimborazo, and Guayas: Foothills of the western cordillera near the village of Bucay, 1,000–1,250 ft, 8–15 Jun 1945 (st), *W. H. Camp E-3782* (MO). Los Ríos: Cantón Quevedo, Centro Científico Río Palenque, along road between Santo Domingo de los Colorados and Quevedo at km 47, 1.7 km S of Patricia Pilar, 0°35′S 79°21′W, 220 m, 9 Apr 1992 (st), *T. B. Croat 73807* (MO); Río Palenque Biological Station, km 56 Rd. Quevedo-Santo Domingo, 150–220 m, 26 Oct 1974 (st), *C. H. Dodson 5663* (SEL); Río Palenque Biological Station, km 56 Rd. Quevedo-Santo Domingo, 150–220 m, 7 Aug 1975 (fl), *C. H. Dodson 5933* (AAU, MO, QCA, SEL); Río Palenque Field Station, half way between Quevedo and Santo Domingo de los Colorados, 200 m, 22 Feb 1974 (fl), *A. Gentry 10109* (MO).

8. Solanum pentaphyllum Bitter, Repert. Spec. Nov. Regni Veg. 12: 70. 1913. *Bassovia pentaphylla* (Bitter) Pittier, Cat. Fl. Venez. 2: 356. 1947.—TYPE: COLOMBIA. Tolima: Ibagué, 1845 (fr), *J. Goudot s. n.* (holotype: G–G00104280 [scan!]; photos of holotype [Morton neg. 8546]: F–1589922!, MO–1781232!, NY!; isotype: G–G00096093 [scan!]; photos of isotype [F neg. 23140]: F–758058!, MO–1691340!, NY!).

Solanum pentaphyllum Bitter var. *caraboboanum* Bitter, Repert. Spec. Nov. Regni Veg. 12: 70. 1913. *Bassovia pentaphylla* (Bitter) Pittier var. *caraboboana* (Bitter) Pittier, Cat. Fl. Venez. 2: 356. 1947.—TYPE. VENEZUELA. Carabobo: Valencia, Oct 1843 (fl), *N. Funck 791* (holotype: G–G00104281 [scan!]; possible isotypes: BR–BR00000988419!, P–P00578798 [scan!]).

Herbaceous vine, terrestrial, trailing over ground or fallen logs. Stems slender, herbaceous, sparsely to densely pubescent, the trichomes 1–2 mm long. Sympodial units plurifoliate. Leaves 5-pinnate, the blades 1.2–7 × 1.5–8 cm, about as long as wide, membranaceous to chartaceous, sparsely sand-punctate, sparsely pubescent adaxially with widely scattered, short, wide-diameter trichomes 0.3–1.5 × 0.1–0.2 mm, with thinner trichomes occasionally present on midvein adaxially, glabrous to pubescent only on the veins abaxially, the margins entire, the rachis sparsely to densely pubescent with hairs like those of the stem, the pubescence especially dense in the adaxial groove; lateral leaflets (the most distal pair) 0.8–4 × 0.4–2 cm, oblique, elliptical on lower side, obovate on upper side giving the leaflets a falcate appearance, the base oblique, acute to obtuse to slightly cordate on the proximal side, the apex obtuse to rounded to minutely acuminate, the basal pair slightly smaller than the upper pair, the upper pair more strongly oblique, the petiolules 0.5–2 mm on upper pair of leaflets, 1.5–6 mm on lower pair, glabrous to densely pubescent, especially in the adaxial groove; apical leaflet 0.8–4.5 × 0.6–2.4 cm, obovate, rhomboid, the base acute to cuneate, the apex obtuse to shortly acuminate, sessile to shortly petiolulate, the petiolule 0.5–2.5 mm, glabrous to densely pubescent, especially along adaxial groove; petioles 1.5–5.5 cm, sparsely sand-punctate, sparsely to densely pubescent, especially in adaxial groove. Internodes 2.5–9 cm. Inflorescences 3–7 cm long, unbranched, extra-axillary, with 1–3 flowers, the axes sparsely pubescent; peduncle 2–6 cm, slender; rachis 0.5–1 cm; pedicels 5–10 mm in flower, 15–22 mm in fruit, slender, sparsely pubescent, spaced 2–10 mm apart. Calyx 1.5–2 mm long, the tube 0.5–1 mm long, the lobes 0.5–0.8 × 1–1.2 mm, deltoid, acute to acuminate and slightly thickened at tips, sparsely pubescent with short trichomes (< 0.1 mm), the margins ciliate; fruiting calyx slightly accrescent, the lobes 1.5–3 × ca. 1.5–1.8 mm. Corolla 1–1.5 cm in diameter, ca. 0.5 mm long, stellate, membranous, white, the tube 1–3 mm, the lobes 3–5 × 1.5–2 mm, lanceolate, acute at tips, glabrous abaxially and adaxially, the margins ciliate. Stamens with filaments 0.6–1 mm, glabrous; anthers 2–2.5 × 0.8–1.2 mm. Ovary glabrous; style 3–5 × ca. 0.2 mm, clavate, papillose in lower half; stigma capitate. Fruits 2.2–3 × 1–2.5 cm, ovoid-rhomboid, flattened, the apex acute, green to purplish brown, glabrous. Seeds 2.2–2.5 × 1.8–2 mm, ca. 0.5 mm thick, lenticular, orangish tan in color, the surface sparsely granular. Figure 2A.

Habitat and Distribution—*Solanum pentaphyllum* occurs in Colombia and Venezuela. Two collections are also known from Costa Rica. It is usually terrestrial, but occasionally grows over fallen logs; 600–1,700 m in elevation (Fig. 8).

Phenology—Flowering specimens have been collected year round; fruiting specimens have been collected from Feb. to Apr., and in Aug.

Etymology—This species takes its name, *pentaphyllum*, from its 5-foliate compound leaves.

Notes—*Solanum pentaphyllum* is one of the ground-trailing species, and can easily be differentiated from the others based on its 5-foliate leaves. The leaves from several populations in Antioquia, Colombia are smaller than the average and are reddish below. The two collections known from Costa Rica are indistinguishable from South American collections. We obtained *trnT–trnF* and *trnS–trnG* sequences from one of the Costa Rican collections (*Haber & Zuchowski 9863*, NY), and it was well supported as sister to the South American collection of *S. pentaphyllum* rather than to Costa Rican *S. phaseoloides* (Fig. 4). Based on available collections, *S. pentaphyllum* is apparently absent from Panama, thus the Costa Rican collections represent a significant disjunction from the species' primary range in Colombia and Venezuela. The labels of two collections state that the deep green to purplish-brown fruits dig themselves into the ground during development (*Pittier 8031*, GH; *Tamayo 2224*, G). From these labels, it is unclear whether the fruits are actively pressed in to the ground by the plant and are truly geocarpic (this seems unlikely because the infructescences of this species are thin) or if they become buried during development as they lie on the ground. This intriguing phenomenon merits further research.

The protologue of *S. pentaphyllum* var. *caraboboanum* states that this variety differs from variety *pentaphyllum* in that it is smaller and less pubescent than var. *pentaphyllum*, and has a distribution in northern Venezuela. These morphological characters hold true for some specimens, but the same variation can be found among specimens throughout the range of the species. We were unable to identify any consistent morphological character to reliably identify variety *caraboboanum*, and could not separate the varieties unless their provenance was known. As a result, *S. pentaphyllum* var. *caraboboanum* is not recognized in this treatment.

The holotype of *S. pentaphyllum* at G is clearly identifiable because the locality information on Goudot's label matches the protologue. An isotype is also housed at G. Several of the photos of this specimen indicate Brazil as the country of origin; however, the locality on Goudot's label, Ibagué, is unequivocally Colombian. Furthermore, Goudot lived in Colombia and most of his collections are from there (Palmer

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1918). He also collected in northern Venezuela from the upper Orinoco to Puerto Cabello on the Caribbean coast, but he does not seem to have collected in Brazil.

The holotype of *S. pentaphyllum* var. *caraboboanum* is also at G. Possible isotypes, held at BR and P, are also labeled *Funck 791*, but the localities of these two specimens differ from the holotype.

Additional Specimens Examined—COSTA RICA. Alajuela: Cantón de San Ramón, Cordillera de Tilarán, Bajo Los Rodríguez, Río La Esperanza, Quebrada Mirasol, Finca Araya, 10°18′30″N 84°35′0″W, 500–600 m, 10 Mar 1993 (fl), *Bello et al. 4862* (INB); Reserva Biológica Monteverde, Finca Villalobos, 8 km S of Volcán Arenal, 10°23′N 84°43′W, 1,000–1,200 m, 21 Apr 1990 (fl), *W. Haber & W. Zuckowski 9863* (INB, NY).

COLOMBIA. Antioquia: Frontino, Corregimiento Nutibara, Región Murí, camino hacia La Blanquita, 6°45′N 76°25′W, 1,440 m, 10 Jul 1986 (fl), *P. Acevedo-Rodríguez et al. 1203* (NY); Frontino, Corregimiento La Blanquita, región de Murrí, vía Nutibarra-La Blanquita, 6°45′N 76°25′W, 1,350–1,450 m, 10 Jun 1988 (fl) *R. Callejas Posada et al. 6525* (MO, NY); Frontino, Region of Murrí, road between Nutibara and La Blanquita, 06°40′N 76°26′W, 1,460 m, 10 Feb 1989 (fl, fr), *J. M. MacDougal et al. 3876* (NY); Parque Nacional Natural Las Orquideas, Sector de Calles, Río Calles, 6°31′N 76°19′W, 1,300–1,320 m, 29 Mar 1991 (fl), *J. G. Ramírez & E. Muñoz 4062* (MO). Chocó: Slopes of Serranía del Darién E of Ungía, 8°01′N 77°05′W, 300–1,300 m, 19 Jun 1976 (st), *A. Gentry et al. 16770* (MO). El Valle: Río Dagua Valley, La Margarita, 3°30′N 75°52′W, 760 m, 4 Apr 1939 (fl, fr), *E. P. Killip 34895* (COL, F, GH, NY, US). Los Llanos: Intendencia, El Meta, near Villavicencio, 3°16′N 73°05′W, 600 m, 20 Jan 1939 (fl), *O. Haught 2551* (COL, F, MA, US). Meta: Trayecto desde la Vereda Aguas Claras (escuela) hasta el puente colgante del Río Ariari, 760–800 m, 25 Oct 1995 (fl), *J. L. Fernández 12883* (COL); Cubarral, Vda. Aguas Claras alrededores de la escuela Aguas Claras, 3°47′42″N 73°54′37″W, 855 m, 19 Nov 1995 (fl), *M. E. Morales 590* (COL).

VENEZUELA. Aragua: Colonia Tovar, between Maracai and Chorona, 10°24′N 67°17′W, 5,500 ft, 1856 (fl, fr), *A. Fendler 2092* (GH, GOET); between Portachuelo and Ocumare, 10°34′N 69°23′W, 20 Jan 1924 (fl), *H. Pittier 11379* (G, NY, US); Toma de Rancho Grande, 10°27′N 68°0′W (fl), *H. Pittier 15311* (US); Alto de Choroni, 10°29′N 67°36′W, 1,600 m, 16 Apr 1967 (fl), *B. Trujillo 7632* (WIS). Barinas: Bolivar, Altimira, La Gallineta Caserío El Celoso near feldspar mine, 8°50′N 70°35′W, 1,500–1,700 m, 6 Jun 1988 (fr), *L. J. Dorr et al. 5444* (MO, NY); Bolivar, near feldspar mine, between La Soledad and Santo Domingo, 8°51′N 71°35′W, 1,300 m, 24 Nov 1984 (fl, fr), *H. Van der Werff & F. Ortega 6142* (MO, NY). Carabobo: Montagne La Soledad, 2,000 ft, Dec 1840(?) (st), *J. Linden 1599* (G); Hacienda de Cura, near San Joaquín, 10°06′N 67°46′W, 1,300 m, 15 Aug 1918 (fl, fr), *H. Pittier 8031* (GH, US); Soto de la selva pluvial de Borburrata, 10°21′N 68°03′W, 600 m, Feb 1942 (fl, fr), *F. Tamayo 2224* (G, US). Distrito Capital: Along old road between Portachuelo and Peñita (Petaquire) and Carayaca, between Colonia Tovar-Junquito road and Hacienda El Limon, 10°28′N 67°11′W, 25 May 1963 (fl), *J. A. Steyermark 91446* (F, NY, US, VEN). Lara: Jiménez, Between Alto del Viento to Cerro Pando, 09°39′N 69°34′W, 1,400 m, 26 Oct 1982 (fl), *G. Davidse & A. C. González 21180* (NY); Iribarren, Vecinidades de la Laguna Negra, Loma de Los Naranjos, Montaña de Macanillal y Fila de San Estaban, 9°52′N 69°18′W, 1,300–1,500 m, 24 Mar 1975 (infl), *J. A. Steyermark et al. 111628* (VEN); Jiménez, Montaña Oscura, en La Briza, 9°52′N 69°21′W, 1,630 m, 8 Aug 1970 (fl, fr) *J. A. Steyermark et al. 103578* (M, US, VEN). Trujillo: 13 km ESE of Bocono, 1 km W of Guarameca, 9°11′N 70°09′W, 1,600 m, 16 Mar 1982 (infl), *R. L. Liesner et al. 12907* (MO, NY). Yaracuy: El Amparo camino abierto hasta la fila, 8°21′N 71°39′W, 1,300 m, 19 Mar 1973 (fl), *E. Diederichs 108* (MO); Cerro la Chapa, 10°12′N 68°24′W, 1,250 m, 12 Apr 1999 (fl), *J. R. Grant et al. 99–03335* (US); Nirgua, Serranía Santa María - Cerro la Chapa, 10°12′N 68°35′W, 1,200–1,350 m, 31 Apr 1994 (fl), *W. Meier et al. 3919* (MO).

9. Solanum phaseoloides Pol., Linnaea 41: 585. 1877.—TYPE: COSTA RICA. Alajuela: Desengaño, Jun 1875 (fl), *H. Polakowsky 147* (lectotype, here designated: BM–BM000579755!; isolectotype: B [destroyed]).

Solanum olivaeforme Donn.Sm., Bot. Gaz. (Crawfordsville) 14: 28. 1889.—TYPE: GUATEMALA. Alta Verapáz: Pansamalá, 3,800 ft, May 1887 (fl), *H. von Tuerckheim 1226* (lectotype, here designated: US–US00027712!; isolectotypes: GH–GH00077524!, K–K000449425!, NY–NY00169750!).

Herbaceous vine, terrestrial. Stems slender, glabrous or rarely pubescent with slender trichomes 0.8–1.5 m long. Sympodial units plurifoliate. Leaves 3-pinnate, the blades 1.5–7.5 × 1–7 cm, about as long as wide, membranous to chartaceous, glabrous adaxially or with widely scattered to dense, wide-diameter trichomes, 0.3–1.2 × 0.1–0.2 mm on the leaf blade, with trichomes like those of the stem more abundant along veins, glabrous abaxially, the margins entire to undulate, minutely revolute on some leaves, the rachis glabrous; lateral leaflets 0.5–5 × 1–5.5 cm, elliptical to rounded, the base oblique, cuneate to cordate on the proximal side, the apex obtuse to acuminate, the petiolules 0.5–3 mm, glabrous; apical leaflet 0.8–4 × 1–6 cm, broadly elliptical to rhomboid, the base cuneate, the apex obtuse to acute, apiculate, the petiolule 1–5 mm, glabrous; petioles 1.5–13 cm, sparsely sand-punctate, glabrous or rarely pubescent. Internodes 3–12 cm. Inflorescences 3–12 cm long, unbranched, extra-axillary, with (2–)3(–7) flowers, the axes glabrous; peduncle 1.5–5 cm, slender; rachis 1–6.5 cm; pedicels 10–25 mm in flower and fruit, slender, glabrous, spaced 4–8 mm apart. Calyx 1.5–2 mm long, the tube 1–1.5 mm long, the lobes 0.5–1 × ca. 1.5 mm, deltoid to truncate, acute to acuminate at tips, glabrous; fruiting calyx slightly accrescent, the lobes 1–1.2 × 1.5–2 mm, truncate-acuminate. Corolla 1–1.5 cm in diameter, ca. 5 mm long, stellate, white, the tube 1–3 mm, the lobes 6–7 × 1.2–3 mm, lanceolate, acute at the tips, glabrous adaxially and abaxially, the margins ciliate. Stamens with filaments 1–1.5 mm, glabrous; anthers 2–2.5 × ca. 1 mm. Ovary glabrous; style 4–5 × ca. 0.2 mm, cylindrical, glabrous; stigma capitate. Fruits 2–4 × 1–2.5 cm, ovoid-rhomboid, flattened, pointed at apex, greenish to yellowish, often mottled, glabrous. Seeds ca. 2 × 1.5 mm in diameter, lenticular, light brown, the surface smooth. Figure 1E.

Habitat and Distribution—*Solanum phaseoloides* occurs in the understory of wet forests and in clearings from southern Mexico (Chiapas), Guatemala, Belize, Honduras, Costa Rica, to Panama. It is usually terrestrial, but occasionally grows on fallen logs or as an epiphyte; 500–2,900 m in elevation. A single collection is known from Peru (Fig. 9).

Phenology—Flowering and fruiting occur throughout the year.

Etymology—The name, *phaseoloides*, refers to the similar leaves and viny habit of the genus *Phaseolus* L. (Fabaceae).

Notes—*Solanum phaseoloides* is a ground-trailing species characterized by 3-foliate leaves and stellate flowers. It is most similar to *S. pentaphyllum* from which it differs by its 3-foliate vs. 5-foliate leaves. It also resembles *S. trifolium*, but can be differentiated by its white, stellate flowers and pointed leaf apices vs. blue-violet, rotate flowers and rounded leaf apices. Vegetative parts of most collections are glabrous; however, plants with pubescent stems and petioles appear to be localized in the Cordillera de Talamanca in Costa Rica at 1,700–3,200 m. A single collection of *S. phaseoloides* is known from north-central Peru. The leaves of this collection are somewhat fleshier than typical plants from Central America, but it corresponds to them in other characters. If this specimen truly represents a population of *S. phaseoloides*, then it is a remarkable disjunction from the species' native range in Central America. Alternatively, it is possible that this collection represents an additional species of sect. *Herpystichum*; however, we must reserve judgment until additional collections are available. We have been unable to successfully obtain a DNA sequence from this Peruvian collection. Finally, we have not seen collections of *S. phaseoloides* from Nicaragua; however, its

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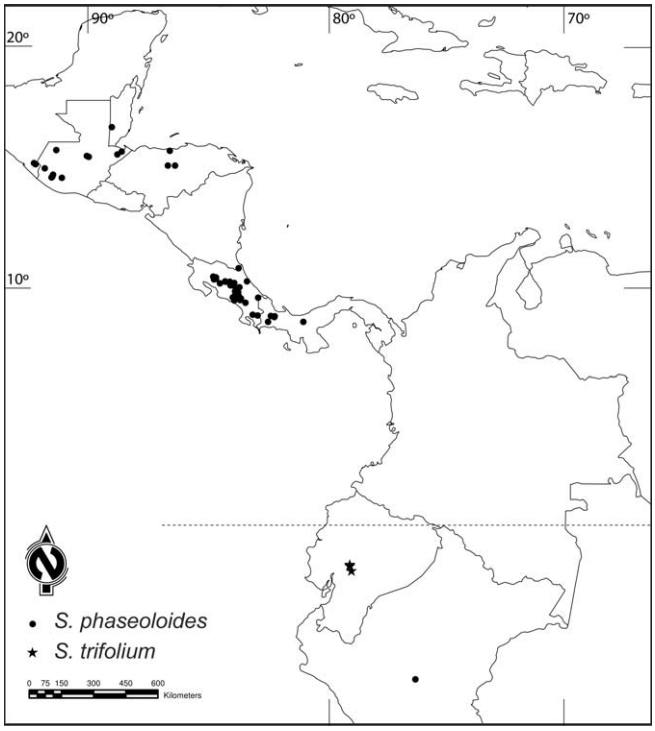


Fig. 9. Distribution of *Solanum phaseoloides* and *S. trifolium*.

presence there is expected based on the overall distribution of this species.

The location Polakowsky's holotype is not explicitly stated in the protologue; the existence of a specimen at B is implied, but it has almost certainly been destroyed and no photos of the specimen are known to exist. A duplicate of this collection exists at BM and this specimen (BM000579755) has been chosen as the lectotype.

Donnell Smith did not designate a single sheet of *Tuerckheim 1226* as the holotype of *S. olivaeforme* in his 1889 protologue. The specimen from US (US00027712) is here chosen as the lectotype. Donnell Smith's herbarium is now held at US and this specimen has the original label written in Donnell Smith's hand.

Representative Specimens Examined—MEXICO. Chiapas: Finca Irelanda, Jun 1914 (fl), *C. A. Purpus 7310* (BM, F, GH, NY, UC); Finca Mexiquito, Jun 1913 (fl), *C. A. Purpus 7460* (UC).

GUATEMALA. Alta Verapaz: Barranca de Rubelcruz, 15°29′N 90°08′W, 2,500 ft, Apr 1889 (fr), *J. Donnell Smith 1785* (G, GH, M, US); Vicinity of Laguna Sapalá (Chajvuvuch), 280 m, 11 Mar 1942 (fl), *J. A. Steyermark 44895* (F, UC). Izabal: Montañas del Mico, 7–8 km W of Santo Tomás de Castilla on road to microwave tower, 15°40′N 88°40′W, 600–650 m, 19 Aug 1988 (fl, fr), *W. D. Stevens et al. 25577* (NY). Peten: La Cumbre, Pusila road, in high forest, 17 Aug 1976 (fl), *C. L. Lundell & E. Contreras 20189* (F, LL). Quetzaltenango: Finca Pirineos, lower south-facing slopes of Volcán Santa María, between Santa María de Jesús and Calahuaché, 1,300–1,500 m, 31 Dec 1939 (infl), *J. A. Steyermark 33254* (F). Retalhuleu: Barranca de Salamá, 1,700 ft, Apr 1892 (fl, fr), *J. Donnell Smith 2673* (F, GH, K, M, MO, NY, US, WU); Near Chivolandia (Dept. Quezaltenango), along road to San Felipe, 650 m, 15 Feb 1941 (infl), *P. C. Standley 87182* (F). San Marcos: Finca El Porvenir, along Río Chopal, south-facing slopes of Volcán Tajumulco, 1,300–1,500 m, 11 Mar 1940 (fl), *J. A. Steyermark 37528* (F). Suchitepéquez: Southern lower slopes of Volcán Zunil, vicinity of Finca Las Nubes, along Quebrada Chita, E of Pueblo Nuevo, 500–800 m, 2 Feb 1940 (fl), *J. A. Steyermark 35395* (F).

BELIZE. Esperanza Rd, 2600 ft, 2 Jul 1934 (fl), *W. A. Schipp 727* (F). Cayo: Chiquibul, Ceibo Grande to Main Divide track, 16°31′49″N 89°05′06″W, 500 m, 26 Aug 1998 (fl), *A. K. Monro & S. Cafferty 2689* (BM, MO). Toledo: in high ridge, on hill slope, Edwards road beyond Columbia, 16°14′N 88°14′W, 18 Feb 1948 (fl), *P. H. Gentle 6417* (LL).

HONDURAS. La Muralla visitors center and environs, 8 km NNW of La Union, 15°05′N 86°44′W, 1,415–1,580 m, 4 Jun 1992 (fl), *W. G. D'Arcy 18123* (MO, NY). Yoro: Ca. 16 km from Yarucha on Quebrada de Oro to Cerro Bufalo, 900–950 m, 16 Aug 1982 (fl, fr), *W. C. Holmes 4407* (NY).

COSTA RICA. Rampante - Forets de la Palma, Sep 1898, *A. Tonduz 12611* (US). Alajuela: Primary forest on ridge top between Río Gorrión and Río Toro, 10°12′N 84°19′W, 1,700 m, 7 Oct 1972 (fl), *R. Lent 2998* (F). Cartago: Paraíso, P. N. Tapantí-Macizo de La Muerte, Cuenca del Reventazón, 9°45′20″N 83°47′00″W, 1,250 m, 15 Mar 2000 (fl, fr), *L. Acosta & V. Ramirez 646* (NY); El Muñeco, S of Cartago and Navarro Valley, near boundary of San José and Cartago provinces, 4,500 ft, 19 Jun 1928 (fr), *H.E. Stork 2659* (F, UC). Heredia: Braulio Carrillo Park, 1,700–2,000 m, Mar 1983 (st), *L. D. Gómez 20200* (MO, NY); Vara Blanca de Sarapiquí, North slope of Central Cordillera, 1,500–1,750 m, Jul 1937 (fl, fr), *A. F. Skutch 3177* (K, MO, NY, US). Puntarenas: Ca. 2 km SE of Monteverde, 10°18′N 84°48′W, 1,500–1,550 m, 18 Mar 1973 (fl, fr), *J. L. Gentry & W. C. Burger 2696* (AAU, F, MO); Cantón de Osa, Fila Costeña, Fila Cruces, cabeceras del Río Piedras Blancas, Cerro Anguciana, faldas al Oeste, 8°48′56″N 83°10′37″W, 1,400–1,600 m, 10 Dec 1993, *B. Hammel 19293* (MO); Fila las Cruces near San Vito de Java, 1,400 m, 22 Aug 1974 (fl, fr), *P. J. Maas & B. McAlpin 1400* (F, GH, U). San José: Cordillera Talamanca, mountain of Cerro de la Muerte, Panamerican highway between San Isidro El General and Division, 1,900 m, 4 Mar 1966 (fl), *A. Molina Rositto et al. 18354* (BM, F, GH, NY); San José, slopes of Cordillera de Talamanca N of San Isidro El General, 1,750–2,000 m, 5 Feb 1963 (fl), *L. O. Williams et al. 24342* (F, G, GH, NY).

PANAMA. Chiriqui: Vicinity of Fortuna Dam, S of lake on E side of river valley across river, 1,400 m, 7 Feb 1987 (fl, fr), *L. Bohs & G. McPherson 2311* (GH); 3.5 mi NE of Boquete, end of road along Río Palo Alto, 17 Nov 1978 (fr), *B. Hammel 5679* (MO); Vicinity of Fortuna Dam, 8°45′04″N 82°15′04″W, 1,300–1,400 m, 7 Feb 1987 (fr), *G. McPherson 10387* (MO). Veraguas: 5 mi W of Santa Fe on road past Escuela Agrícola Alto Piedra on Pacific side of divide, 800–1,200 m, 18 Mar 1973 (fl), *R. L. Liesner 948* (C, F, L, LL, NY).

PERU. San Martín: Cataratas de Ahuashiyacu, km 15 Tarapoto-Yurimaguas Road, 6°29′S 76°21′W, 700 m, 10 Jun 1986 (fl), *S. Knapp & P. Alcorn 7791* (MO).

10. Solanum trifolium Dunal in DC. Prodr. 13(1): 68. 1852.—TYPE: ECUADOR. "In Peruviæ provinciâ Huyaquil," 1804 (fl), *H. Ruiz & J. Pavón s. n.* (holotype: G–G00080145 [scan!]; photos of holotype [F neg. 8591]: F–651206!, MO–1691471!, NY!; isotypes: MA–747193!; possible isotype: G-DC–G00144594 [scan!]).

Herbaceous vine, terrestrial. Stems slender, sparsely pubescent with trichomes 0.2–0.5 mm long. Sympodial units plurifoliate. Leaves 3-pinnate, the blades 1–5 × 1–6.5 cm, chartaceous to slightly fleshy, pubescent adaxially with widely scattered, wide-diameter trichomes ca. 1 mm long, the pubescence on veins adaxially of slender trichomes like those of the stem, the pubescence more dense abaxially and of slender (typical) trichomes, the margins entire, ciliate with short, fine hairs, the rachis with short, dense pubescence with trichomes like those of the stems; lateral leaflets 0.4–3 × 0.4–3 cm, rounded, the base oblique, rounded to cuneate, the apex rounded to truncate, minutely apiculate, the petiolules 2–3 mm, with short, dense pubescence; apical leaflet 0.6–3.5 × 0.6–4 cm, rounded, the base cuneate, the apex rounded to truncate to emarginate, minutely apiculate, the petiolule 1–3 mm, with short, dense pubescence; petioles 0.5–13.5 cm, sparsely to moderately sand-punctate, with short, dense pubescence. Internodes 1.5–10 cm. Inflorescences 2.5–6 cm long, unbranched, extra-axillary, with 2–3 flowers, the axes sparsely pubescent; peduncle 1–2 cm, slender; rachis 0.5–4 cm; pedicels 15–60 mm in fruit and flower, slender, sparsely pubescent, spaced 5–15 mm apart. Calyx 1.5–2.5 mm, the tube 1.2–1.5 mm long, the lobes 1–1.2 × ca. 1 mm, deltoid, acute at tips, sparsely pubescent abaxially with short, slender hairs, more densely pubescent adaxially; fruiting calyx slightly accrescent, the lobes ca. 2 × 2 mm. Corolla ca. 1.5 cm in diameter, 7.5–8 mm long, rotate, violet, the tube 5–9 mm, the lobes ca. 2.5 × 1.5 mm,

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acuminate at tips, glabrous abaxially, pubescent adaxially near the tips, the margins ciliate near the tips. Stamens with filaments 1–1.2 mm, glabrous; anthers 1–1.8 × ca. 1.2 mm. Ovary glabrous; style 3–3.5 × ca. 0.25 mm, clavate, papillose in middle; stigma capitate. Fruits 0.8–1 × 0.7–0.8 cm, ovoid-deltoid, flattened, pointed at apex, the color unknown, glabrous. Seeds ca. 2 mm in diameter, lenticular, the color and surface unknown. Figure 1D.

Habitat and Distribution*—Solanum trifolium* is endemic to Ecuador and is only known from the western slopes of the Andes in Bolívar Province; 2,600–3,000 m in elevation (Fig. 9).

***Phenology*—**Flowering specimens have been collected in Feb., May, and Sept. to Nov. Fruiting specimens have been collected in Feb.

***Conservation Status*—**According to the IUCN red list categories (IUCN 2010), *S. trifolium* is classified as D2 (vulnerable). The nine known collections of this species are from two to three closely clustered localities within a narrow elevational band (2,500–3,000 m) between San José de Chimbo and Chillanes, Bolívar Province, Ecuador. *Solanum trifolium* appears to be well suited to the disturbed habitats in the area, and has been collected in disturbed forest fragments, along roadsides, and in cow pastures. Nevertheless, it seems prudent to list it as vulnerable, because of the extremely narrow distribution of this species.

***Etymology*—**The epithet *trifolium* refers to the 3-foliate compound leaves, and their striking similarity in size and shape to the leaves of some species in the genus *Trifolium* L. (Fabaceae).

Notes*—Solanum trifolium*, a ground-trailing species, is the only species in sect. *Herpystichum* with compound leaves and rotate flowers. The other two species with compound leaves, *S. pentaphyllum* and *S. phaseoloides*, both have stellate flowers, and the only other species with rotate or rotate-stellate flowers is *S. dalibardiforme*, which has simple leaves.

Dunal's (1852) protologue lists a specimen in "h. Lambert et Boiss.", and the Boissier herbarium is now held at G. A specimen at G-BOIS is labeled "*Solanum trifolium* Dun.! in DC Prodr." in Dunal's hand, and this is interpreted as the holotype. A presumed duplicate of this collection exists at MA, but does not have Dunal's annotation. It is interpreted as an isotype. Both specimens have "Fl. H. no. 449" on the labels, which has been interpreted by some as a collection number; however, the number refers to description No. 449 in a manuscript by J. A. Manzanilla (of *S. ternatum*, the original determination of Ruiz and Pavón's collection), which has only recently been published in Tafalla's *Flora Huayaquilensis* (Tafalla and Estrella 1989). Another possible isotype exists at G. This sterile specimen was found in the DC herbarium, but with no associated collection information.

***Additional Specimens Examined*—**ECUADOR. Bolívar: Chillanes, Urcu-corral, 2,600–3,000 m, 3 Nov 1943 (fl), *M. Acosta Solís 6594* (F); Road Chimbo-Babahoyo, 12 km from Chimbo, 1°43′S 79°06′W, 2,800 m, 3 Nov 1983 (fl), *B. Boysen Larsen 45527* (AAU); Chillanes, Crecit in lugares sombríos silvestres interandinos pueblo Atenas et Chillanes, Sep 1881 (infl), *L. Sodiro /121* (QPLS); Crecit in silvis inter Atenas et Chillanes, Prov. Riobamba, 1881 (infl), *L. Sodiro* 336*/11* (QPLS); in Quebrada Lanszi, ca. 1 km E of rd from La Magdalena to Balsapamba, 01°39′S 79°06′W, 2,820 m, 12 May 1991 (fl), *D. M. Spooner et al. 5073* (NY); in Andibus, 1857 (fl, fr), *R. Spruce 5535* (C, E, G, GH, GOET, P, NY, S, W); Magdalena-Balzapamba road, ca. 5 km W of Magdalena, 1°40′36″S 79°06′15″W, 2,800 m, 2 Feb 2009 (fl, fr), *E. J. Tepe & S. Stern 2684* (MU, QCNE, UT); Rivulet NE of Chillanes, 2,500, Sep-Oct 1995 (fl), *M. Weigend & S. Horn 3820* (QCA).

***Doubtful and Excluded Names*—**

Solanum ionidium Bitter, Repert. Spec. Nov. Regni Veg. 11: 484–485, 1913.—TYPE: MEXICO. Veracruz or Puebla: Volcán de Orizaba, Ahuayeca, 7,500–8,000 ft., *C. B. Heller 205* (holotype: W-0001947 [scan!]).

Bitter (1912b, 1913a) and later authors (Child 1990) include this species, implicitly, in sect. *Herpystichum*, allying it closely to *S. dalibardiforme*, but its thickly coriaceous leaves and pseudostipules do not fit the concept of sect. *Herpystichum* presented here. Instead, based on morphological and molecular data (E. J. Tepe and L. Bohs, unpubl. data), it is a member of sect. *Anarrhichomenum*.

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Numerical List of Species 1. *S. crassinervium,* 2. *S. dalibardiforme,* 3. *S. dolichorhachis,* 4. *S. evolvulifolium,* 5. *S. limoncochaense,* 6. *S. loxophyllum,* 7. *S. pacificum,* 8. *S. pentaphyllum,* 9. *S. phaseoloides,* 10. *S. trifolium,*

Exsiccatae Abbott, J. R. 15256 (1), Acevedo Rodríguez, P. et al. 1203 (8), Acosta Solis, M. 6594 (10), Acosta, L. & Ramírez, V. 646 (9), Alfaro, E. & Castro, J. 2819 (9), Alfaro, E. & Monro, A. K. 5289 (4), 5399 (4), 5600 (4), Allen, P. H. 508 (9), 4995 (4), Almeda, F. & Nakai, K. 3913 (4), Alston, A. H. G. 8547 (1), Alvarez, A. et al. 1903 (4), 2017 (4), Aulestia, C. & Aulestia, M. 1431 (1), Barfod, A. et al. 48160 (6), Barringer, K. & Gómez Laurito, J. 2584 (4), Bass, M. & Pitman, N. 289 (1), Bello, E. 468 (4), 1961 (4), Bello, E. et al. 4862 (8), Benavides, O. de 8849 (4), 9238 (4), 10150 (1), Bernoulli, K. G. 633 (9), Betancur, J. C. et al. 2586 (4), Bittner, J. 430 (4), 755 (4), 864 (4), 962 (4), Bohs, L. & McPherson, G. 2311 (9), Boom, B. M. 1301 (1), 1374 (1), Boysen Larsen, B. et al. 45527 (10), Brade, C. 2163 (9), Brenes, A. M. 3757 (9), 3970 (9), 13613 (4), Callejas Posada, R. et al. 6525 (8), Camp, W. H. 3782 (7), Chacón, A. & Corrales, E. 645 (4), Chacón, A. et al. 744 (4), Chacón, A. 2346 (4), Chacón, A. & Herrera, G. 1727 (4), Churchill, H. W. et al. 4500 (4), Churchill, H. W. 5864 (4), Clark, J. L. & Adnepos, B. 55 (1), Clark, J. L. 412 (1), 2121 (1), Clark, J. L. et al. 2054 (6), 2993 (1), 3762 (1), 9438 (4), Core, E. L. 1323 (4), Cornejo, X. & Bonifaz, C. 2478 (6), 6389 (6), Croat, T. B. 33278 (9), 71302 (4), 73807 (7), 79008 (4), 93047 (4), Croat, T. B. & Grayum, M. 59989 (4), Cuatrecasas, J. 3355 (2), 15313 (4), D'Arcy, W. G. 16340 (4), 16360 (9), 18123 (4), Daniel, B. 4498 (4), Davidse, G. & González, A. C. 21180 (8), Davidson, M. E. 112 (4), Diederichs, E. 108 (8), Dodson, C. H. 5543 (6), 5663 (7), 5933 (7), 7389 (6), Dodson, C. H. & Gentry, A. 10040 (6), 10359 (6), Dodson, C. H. et al. 8626 (6), 9049 (6), 15031 (4), Donnell Smith, J. 1785 (9), 2673 (9), Dorr, L. J. et al. 5444 (8), Drummond, B. A., III 7329 (3), Dryander, E. 2136 (4), Dryer, V. J. 1608 (9), Eggers, F. H. 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A. & Zuchowski, W. 9863 (8), Hammel, B. 2258 (4), 5679 (9), 19293 (9), Hammel, B. & Grayum, M. 16606 (4), Harling, G. & Andersson, L. 16365 (4), Herrera, G. 5696 (4), Herrera, G. & Chacón, A. 2771 (4), Herrera, G. et al. 2753 (4), Holmes, W. C. 4407 (9), Holmgren, I. 845 (4), Haught, O. 2551 (8), Huashikat, V. 268 (4), Jaramillo, J. 276 (4), 6767 (6), 8256 (4), Jaramillo, J. & Grijalva, E. 12933 (4), Jiménez M., A. 1222 (9), 3858 (9), Jorgensen, P. M. et al. 93 (4), Kennedy, H. 560 (9), Khan, R. et al. 1303 (9), Killip, E. P. 9753 (2), 34895 (8), Killip, E. P. & Varela, G. 34519 (2), Knapp, S. 877b (9), 5032 (4), Knapp, S. & Vodica, M. 5647 (4), Knapp, S. & Alcorn, P. 7791 (9), Knapp, S. & Mallet, J. 9178 (4), Krukoff, B. A. s. n. (9), Kvist, L. P. 40437 (6), 40522 (6), 40691 (6), Lehmann, B. T. 858 (4), Lent, R. 989 (4), 1313 (9), 1849 (4), 2998 (9), 3023 (9), 3104 (4), 3562 (9)3790 (4), 3811 (9), 3852 (4), Libenson, S. et al. 30549 (4), Liesner, R. L. 948 (9), Liesner, R. L. & Judziewicz, E. 14936 (4), Liesner, R. L. et al. 12907 (8), Linden, J. 1599 (8), López Figueiras, M. 8259 (4), Lozano, G. et al. 6531 (4), 6961 (4), Lundell, C. L. & Contreras, E. 20189 (9), Luteyn, J. L. & Lebrón-Luteyn, M. 99600 (4), Luteyn, J. L. & Sylva, S. 13900 (4), Luteyn, J. L. et al. 4522 (4), 7515 (4), 14744 (1), Maas, P. J. M. & McAlpin, B. 1400 (9), MacDougal, J. M. et al. 3876 (8), Madison, M. T. et al. 4751 (1), 5154 (6), 5327 (5), McPherson, G. 6815 (4), 10387 (9), Meier, W. et al. 3919 (8), Mexia, Y. 6617 (3), Molina Rositto, A. et al. 18354 (9), Monro, A. K. & Alfaro, E. 4482 (4), Monro, A. K. & Cafferty, S. 2689 (9), 4722 (4), Mora, J. & Palma, J. 743 (2), 924 (2), Mowbray, R. N. 699104 (5), Ollgaard, B. 99154 (4), Orozco, J. M. 396 (9), Palacios, W. 5399 (4), Palacios, W. et al. 9753 (4), 9754 (4), 13548 (1), 13719 (1), Pennell, F. W. 5714 (4), Pérez Arbeláez, E. and Cuatrecasas, J. 6231 (4), Pittier, H. 683 (9), 8031 (8), 11379 (8), 15311 (8), Pitman, N. & Bass, M. 1091 (1), Polakowsky, H. 147 (9), Purpus, C. A. 7310 (9), 7460 (9), Ramírez, H., et al. 12 (1), 15 (1), Ramírez, B. R. et al. 8826 (1), 9699 (1), Ramírez, J. G. & Muñoz, E. 4062 (8), Ramos Perez, J. E. 1804 (4), Ramos Perez, J. E. et al. 7061 (4), 7084 (4), Restrepo, C. CR555 (9), Rivera, G. 2954 (4), Romero C., R. 2645 (4), Rossbach, G. B. 3239 (9), Ruiz, H. & Pavón, J. s. n. (10), Ruiz, N. 202 (4), Schipp, W. A. 727 (9), Silverstone Sopkin, F. A. et al. 1670 (4), 2967 (4), 9658 (4), 10027 (4), Skutch, A. F. 3123 (4), 3177 (9), Smith, A. 22 (9), 96 (9), 1342 (9), Sneidern, K. von 1663 (4), 3121 (2), 3121bis (2), 5524 (4), Sodiro, L. 114/20 (6), 336/11 (10), /121 (10), Soejarto, D. D. 1139 (4), Spooner, D. M. et al. 5073 (10), Spruce, R. 553 (10), Standley, P. C. 33101 (9), 33555 (9), 37741 (9), 38132 (9), 39226 (9), Standley, P. C. & Valerio, J. 43316 (9), 49125 (9), 52062 (9), Standley, P. C. & Torres, R. 47849 (9), 51012 (9), Stern, S. R. 400 (1), Stevens, W. D. et al. 25577 (9), Steyermark, J. A. 33254 (9), 35395 (9), 37528 (9), 41997 (9), 44895 (9), 91446 (8),

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