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# REVISION OF *SOLANUM* SECTION *REGMANDRA* (*SOLANACEAE*)

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*Solanum* section *Regmandra* (*Solanaceae*), a group of 11 species from the lomas of Chile and Peru, is revised. Two new species are described, *Solanum indivisum* Witasek ex J.R.Benn. and *S. coquimbense* J.R.Benn., and a new name, *S. trinominum* J.R.Benn., is proposed for *S. heterantherum* Witasek ex Reiche. Two species, *Solanum multifidum* Lam. and *S. edmonstonei* Hook.f., are endemic to Peru, seven species are endemic to Chile, and only two species are found in both countries. Descriptions, distribution maps and a key to the species are presented and several species illustrated.

*Keywords.* Chile, lomas, Peru, *Solanaceae*, *Solanum* section *Regmandra*, species delimitation, taxonomy.

## Introduction

*Solanum* L. is the largest genus in *Solanaceae* (Hunziker, 2001) and one of the largest genera of flowering plants, with an estimated 1500 species (Frodin, 2004; PBI Solanum Project, 2007). Since the last worldwide monograph by Dunal (1852), the number of described species has risen enormously, particularly of species from the Neotropics. To date, almost 6000 names have been published in *Solanum* (PBI Solanum Project, 2007), making a comprehensive worldwide revision a formidable task. Recently published revisions have therefore focused on smaller groups within *Solanum* (e.g. Bohs, 1994; Knapp, 2002a). However, the genus is currently the focus of a collaborative project to produce a comprehensive worldwide treatment (PBI Solanum Project, 2007).

Traditional infrageneric classifications of *Solanum* (e.g. Linnaeus, 1753; Dunal, 1852; Seithe, 1962) have recognised two major groups – one of species with stout, cylindrical anthers, simple or branched hairs and lacking spines, and another of species with attenuate anthers, stellate hairs and often with spines. The classification of D'Arcy (1972) is the most widely followed and divides the genus into seven subgenera (one of which, *Solanum* subgenus *Leptostemonum*, corresponds to the group of 'spiny' solanums with stellate hairs and attenuate anthers) and 52 sections, one of which is *Solanum* section *Regmandra*. Recently these morphology-based classifications have been re-evaluated using data from chloroplast and nuclear DNA

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sequences (Bohs, 2005; Weese & Bohs, 2007). These analyses show that many previously recognised infrageneric groups are not monophyletic. The non-spiny solanums comprise a grade of numerous lineages that are successively sister to a strongly supported monophyletic group corresponding to *Solanum* subgenus *Leptostemonum*, although support for the relationships between these lineages is low.

The phylogenetic analysis of Bohs (2005) provides some evidence that *Solanum* section *Regmandra* is monophyletic, although taxon sampling in this study is limited. *Solanum* section *Regmandra* is resolved as one of the earlier branching lineages within *Solanum* (Bohs, 2005; Weese & Bohs, 2007), although its relationship with other non-spiny clades, such as the potato clade and the Normania–Archaesolanum–African non-spiny clade, is unresolved (Bohs, 2005; Weese & Bohs, 2007).

The first species of what we now consider *Solanum* section *Regmandra* was described by Linnaeus (1753), probably based on an illustration in Feuillée (1725) (Knapp & Jarvis, 1990). This species, *Solanum montanum*, is common on the hillsides around Lima and northern Peru and is unique among species of *Solanum* section *Regmandra* for the development of an underground tuber-like structure. Although not homologous to the tubers of potatoes, the swollen caudex is reported to have been used as a minor food source (Hooker, 1827). Further species were subsequently described by Lamarck (Lamarck & de Monnet, 1794), Cavanilles (1791–1806) and Ruiz & Pavón (1799), based on material collected by Luis Née during the Malaspina expeditions, and by Hipólito Ruiz and José Antonio Pavón during their expedition to Peru and Chile (Ruiz, 1940; Steele, 1964). Many of these species were later transferred to *Witheringia* by Dunal (1816), although it is unclear what the criteria were for this. Three more species of *Solanum* section *Regmandra* were also described under *Witheringia* by Jules Rémy (1849), who used the form of the anther dehiscence to separate *Witheringia* from *Solanum*. Rémy (1849) distinguished between longitudinal dehiscence in *Witheringia* and poricidal dehiscence in *Solanum*, although he noted that this character alone was regarded by some taxonomists as insufficient to maintain them as separate genera. A close examination of the anther dehiscence shows that in most non-spiny species of *Solanum*, including *Solanum* section *Regmandra*, the anthers dehisce initially from an apical pore, which may then rapidly elongate longitudinally to the base of the anther. In mature anthers that have fully dehisced it is frequently difficult or impossible to see the original apical pores, and this may have been why Rémy, and perhaps also Dunal, placed several *Solanum* species in *Witheringia*.

The work of Dunal (1852) and Philippi (1860, 1873, 1895) represents a prolific increase in the number of described species of *Solanum* section *Regmandra*. In particular, Philippi described many new Chilean species from material collected during his exploration of the Atacama Desert (Philippi, 1855). However, in this current revision many of the species described by Dunal (1852) and Philippi (1860, 1873, 1895) have been reduced to synonymy, particularly the numerous infraspecific taxa described by Dunal (1852). Few species were described during the twentieth century, most of which were based on limited material (e.g. *Solanum andersonii*), or

else are varieties of the variable and widespread species *S. pinnatum*, and have been placed in synonymy in this revision.

## Morphology

### *Habit*

Species of *Solanum* section *Regmandra* are low-growing, herbaceous plants. In contrast, most *Solanum* species are woody shrubs or small trees, although species of *Solanum* section *Lycopersicon* (tomatoes) are also herbaceous and grow in the same localities in Peru and Chile as *Solanum* section *Regmandra* (Peralta *et al*., in press). Some species are erect plants with thickened stems (e.g. *Solanum multifidum* and *S. edmonstonei*), while others, such as *S. paposanum* and *S. montanum*, are often sprawling plants growing over rocks on the hillsides.

### *Leaves*

There is much variation in leaf morphology between, and sometimes within, species of *Solanum* section *Regmandra*. The leaves vary from simple leaves, with entire to strongly lobed margins, to what have been described as pinnate or bipinnately divided leaves. The leaf divisions do not fully extend to the rachis, however, and so are more accurately described as pinnatifid or bipinnatifid (the terms used in this revision). Three species have leaves that are clearly pinnatifid or bipinnatifid – *Solanum brachyantherum*, *S. multifidum* and *S. remyanum*. The lobes of the leaves of other species, such as *Solanum edmonstonei* and *S. trinominum*, are essentially simple but in some specimens there is some degree of secondary lobing. There is thus a continuum in the form of the leaf margin, from the simple, lobed leaves of *Solanum herbabona*, *S. montanum* and *S. pinnatum* to the more complex leaves of *S. brachyantherum*, *S. multifidum* and *S. remyanum*.

Leaf form is particularly variable in *Solanum montanum*. Some specimens have petiolate leaves with an entire margin, whereas others have prominently winged petioles with lobed margins. There is a range of intermediates between these two extremes, and a detailed morphometric study using extended eigenshape analysis and elliptic Fourier analysis was unable to distinguish the two leaf forms as distinct (Pickering, 2006).

The leaves of some species, such as *Solanum paposanum* and *S. trinominum*, possess a distinctive indumentum that is also useful in identifying species of *Solanum* section *Regmandra*. Leaf morphology has provided the best characters with which to delimit species of *Solanum* section *Regmandra* since the flowers and fruits are less variable between species and offer relatively few distinguishing characters. Descriptive leaf terminology follows Hickey (1979) and Jackson (1928).

### *Inflorescences*

The inflorescences of *Solanum* section *Regmandra* are terminal cymes, although these may appear axillary due to the sympodial growth form of *Solanum*. In most species of *Solanum* section *Regmandra* the sympodial units are unifoliate, with one leaf associated with each inflorescence. In some species there are several leaves between successive inflorescences (plurifoliate). Although inflorescence form is not a useful taxonomic character in *Solanum* section *Regmandra*, *Solanum paposanum* has an extremely distinctive and unusual arrangement of leaves in which a leaf arises midway up the peduncle, analogous to a bract. This is also seen in a few specimens of *Solanum montanum* in which the pedicels are prominently winged, although it is not constant in this species.

### *Flowers*

The flowers of *Solanum* section *Regmandra* are pentamerous, perfect and actinomorphic. The flowers of *Solanum brachyantherum* are amongst some of the smallest in *Solanum*, with corollas as small as 5 mm in diameter. In most species the corollas are more conspicuous, particularly in *Solanum pinnatum*, which is cultivated as an ornamental in Chile. The corollas are rotate or pentagonal and there is some variation in flower colour, sometimes within populations. Usually the corollas are white, but in some species they have been described as various shades of blue, purple, lavender or lilac.

All species of *Solanum* section *Regmandra* possess an enlarged, usually clavate, stigma, and this is the most reliable character for diagnosing the section. The stigma is exserted, and in many flowers the style hangs down out of the flower, perhaps due to the weight of the enlarged stigma.

Although there are relatively few floral characters that can be used to distinguish between species in *Solanum* section *Regmandra*, three species, *Solanum trinominum*, *S. indivisum* and *S. coquimbense*, are notable for the unequal lengths of the stamens. The two longer and three shorter stamens are composed of filaments and anthers of unequal length.

### *Fruit*

The fruits are all glabrous and mature into small, whitish, green, red or black, globose berries, 3–12 mm in diameter. There are no useful taxonomic characters in fruit morphology to distinguish between species of *Solanum* section *Regmandra*, although some species contain stone cells in their fruits. Stone cells are accretions of sclerenchyma that occur in the fleshy part of the berry (Bitter, 1911, 1914), and in some species may be numerous. Stone cells are found in some other groups of *Solanum*, such as members of *Solanum* subgenus *Archaesolanum* (Symon, 1987, 1994) and the *Cyphomandra* clade (Bohs, 1994). The phylogenetic position of these groups suggests that stone cells have been gained or lost repeatedly in *Solanum* (Knapp, 2002b).

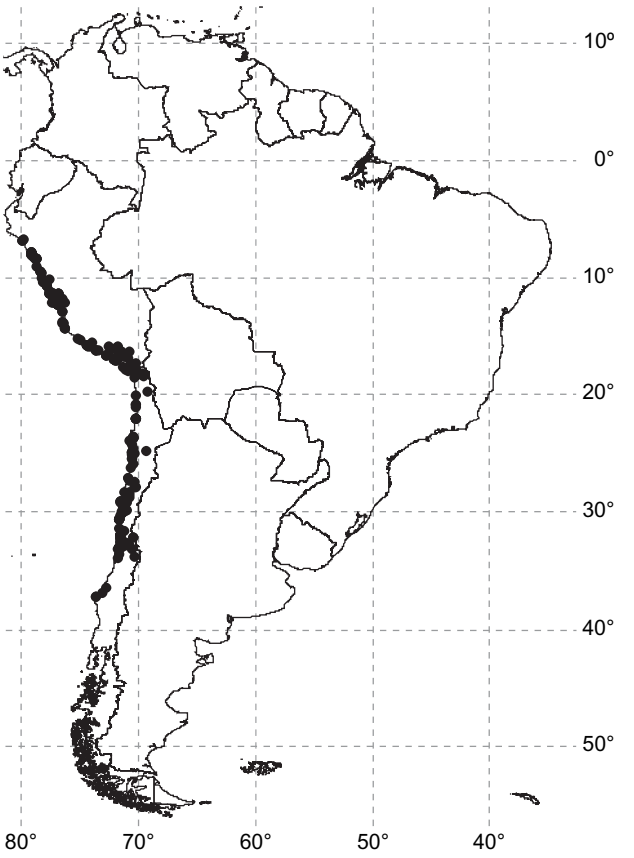


FIG. 1. Distribution map of *Solanum* section *Regmandra*, based on 409 georeferenced herbarium collections. The species are restricted to the lomas vegetation found along the coastal regions of Chile and Peru.

## ECOLOGY AND GEOGRAPHICAL DISTRIBUTION

Species of *Solanum* section *Regmandra* are found in the Peruvian and Atacama deserts between about 7° and 37°S (Table 1; Fig. 1). They are components of the lomas vegetation, a distinctive vegetation type found on small, isolated hills along the coast of Peru and Chile (Dillon, 2005). During the winter months thick stratus clouds form against the hillsides and provide sufficient moisture for vegetation to develop in an otherwise extremely arid region (Rundel *et al*., 1991). In addition, the lomas vegetation may also receive heavy rainfall during El Niño events. During these conditions the lomas experience brief periods of high rainfall and elevated temperatures that promote a great increase in plant growth (Dillon, 2005).

Lomas plant communities may form up to 1000 m altitude (Dillon, 2005), and only one species of *Solanum* section *Regmandra*, *Solanum paposanum*, extends further inland into the foothills of the western slopes of the Andes of southern Peru

TABLE 1. The geographical distribution of species of *Solanum* section *Regmandra* accepted in this treatment. Only two species are found in both Chile and Peru, and many have a restricted distribution within each country

| Species | Country | Latitudinal range (°S) |
|---|---|---|
| *Solanum brachyantherum* Phil. | Chile | 20.5–29 |
| *Solanum coquimbense* J.R.Benn. | Chile | 31.5 |
| *Solanum edmonstonei* Hook.f. | Peru | 13.5–15.2 |
| *Solanum herbabona* Reiche | Chile | 27.5–28.4 |
| *Solanum indivisum* Witasek ex J.R.Benn. | Chile | 32.5–33 |
| *Solanum montanum* L. | Chile, Peru | 6.5–30.2 |
| *Solanum multifidum* Lam. | Peru | 6.8–18 |
| *Solanum paposanum* Phil. | Chile, Peru | 11.5–31.4 |
| *Solanum pinnatum* Cav. | Peru | 18.3–37.1 |
| *Solanum remyanum* Phil. | Chile | 24.5–29.6 |
| *Solanum trinominum* J.R.Benn. | Chile | 28.2–33 |

and northern Chile, up to an altitude of 3500 m. The Peruvian off-shore islands San Lorenzo, San Gallán and Viejas are able to support limited lomas vegetation, and *Solanum multifidum* (San Lorenzo), *S. montanum* (San Gallán, San Lorenzo) and *S. edmonstonei* (San Gallán, Viejas) have been recorded from these islands.

*Solanaceae* is the second most diverse family in the lomas after the *Asteraceae*, with 18 genera and c.128 species (Dillon, 2005). The lomas plant communities are characterised by extremely high levels of endemism, and around 70% of *Solanaceae* species found in the lomas are considered endemic (Dillon, 2005). Many species of *Solanum* section *Regmandra* have a restricted distribution within Chile or Peru – only *Solanum montanum*, *S. paposanum* and *S. pinnatum* have a more widespread distribution (Table 1). Of the 11 species of *Solanum* section *Regmandra*, only two species, *Solanum montanum* and *S. paposanum*, are found in both Peru and Chile (Figs 9, 11). This phenomenon is not restricted to *Solanum* section *Regmandra*, and an analysis of the native flora of coastal Peru and Chile showed that only 93 out of c.1400 species cross the boundary between 18° and 20° (Dillon, 2005). This part of the coast between Arica and Antofagasta lacks the topography to develop lomas plant communities and is extremely arid, thus restricting plant growth (Rundel *et al*., 1991).

## MATERIALS AND METHODS

A total of 720 specimens from the following herbaria were consulted during the taxonomic revision: A, B, BM, E, F, G, GH, HAO, HUT, K, MA, MO, MOL, NY, P, SGO, SI, TCD, US, USM, W (see *Index Herbariorum* on http://sweetgum.nybg.org/ih for herbarium codes). All specimens cited have been seen by the author unless indicated otherwise. Barcode or accession numbers are provided for type specimens where available. Details of all specimens examined (including images of

some) are available on the PBI Solanum website, http://www.nhm.ac.uk/solanaceae source/. In addition, three weeks were spent in the field in Peru to examine populations of *Solanum montanum* and *S. multifidum*. Collections were made from nine populations of *Solanum montanum* and *S. multifidum* from lomas around Lima, and from two populations of *Solanum montanum* from lomas in the most northern part of its range, c.6°S.

The pattern-based species concept of Nelson & Platnick (1981: 12) has been followed in this account. The least inclusive groups of individuals that may be diagnosed by unique combinations of non-overlapping characters have been recognised at the species level; infraspecific taxa have not been used since these would merely describe non-diagnostic variation and would not represent real entities (Cracraft, 1983).

## Taxonomy

**Solanum** sect. **Regmandra** (Dunal) Ugent in D'Arcy, Ann. Missouri Bot. Gard. 59: 273 (1972). – *Solanum* [unranked] *Regmandra* Dunal in DC., Prodr. 13(1): 28, 60 (1852). – Type species: *Solanum montanum* L. (designated by Ugent in D'Arcy, 1972).

Unarmed annual or perennial herbs up to 100 cm tall. *Indumentum* of simple, uniseriate, unicellular or multicellular, eglandular (rarely glandular) hairs. *Sympodial units* usually unifoliate, in some species plurifoliate, not geminate. *Leaves* alternate, often fleshy, simple, pinnatifid, bipinnatifid or rarely tripinnatifid, the blades ovate to elliptic, often variable in size and shape within species, glandular in *Solanum brachyantherum*. *Inflorescence* terminal cymes, but usually appearing axillary, branched or unbranched, the pedicels articulated at or near the base, accrescent in fruit. *Flowers* perfect, actinomorphic, 5-merous. *Calyx* persistent, urceolate, the lobes ovate to elliptic, often accrescent in fruit. *Corolla* white, blue, purple, lavender or lilac, pentagonal or rotate, chartaceous, 5–32 mm in diameter. *Stamens* equal or unequal; filaments equal or unequal, inserted in the corolla tube near its base; anthers oblong, in two species tapering towards the apex, yellow, not connivent, poricidal at the tips, the pores opening into longitudinal slits. *Ovary* superior, glabrous. *Style* glabrous or pubescent, cylindrical, straight; stigma clavate or capitate. *Fruit* a globose berry, glabrous, whitish, green, red or black, stone cells present in most species. *Seeds* usually numerous (few in *Solanum pinnatum*), flattened, glabrous, rounded or obovate, pale to dark brown, the surface pitted. *Chromosome numbers* not known.

### *Key to species*

1a. Leaf blades highly divided; anthers equal in length ____ 2
1b. Leaf blades simple, lobed or unlobed; anthers equal or unequal in length ____ 4

2a. Segments of leaves 1 mm wide; corolla 5–7 mm in diameter; anthers less than or equal to 2 mm long; Chile ____ **1. S. brachyantherum**

2b. Segments of leaves ≥ 3 mm wide; corolla 11–22 mm in diameter; anthers greater than 3 mm long; Chile and Peru ____ 3

3a. Petioles with a prominent wing up to 6 mm wide; leaves usually glabrous, rarely sparsely to moderately pubescent; Peru ____ **2. S. multifidum**

3b. Petioles not winged or with a narrow wing up to 1 mm wide; leaves moderately to densely pubescent, never glabrous; Chile ____ **3. S. remyanum**

4a. Anthers of unequal length; leaves scabrous or densely tomentose; leaves more than twice as long as wide, corolla never rotate; Chile ____ 5

4b. Anthers of equal length; leaves subglabrous to moderately pubescent or densely velutinous; leaves less than twice as long as wide; corolla rotate or pentagonal; Chile or Peru ____ 7

5a. Leaf margin regularly lobed, the lobes with a smaller secondary lobe arising obliquely at the base; both leaf surfaces densely tomentose ____ **4. S. trinominum**

5b. Leaf margin crenate or serrate, the lobes entire; both leaf surfaces scabrous 6

6a. Leaf base cuneate, the leaves always sessile; leaf margin subentire or shallowly crenate, the teeth < 1 mm deep ____ **5. S. indivisum**

6b. Leaf base decurrent, the leaves usually petiolate; leaf margin crenate or serrate, the teeth 1–2 mm deep ____ **6. S. coquimbense**

7a. Underground base of stem swollen into a 'tuber' ____ **7. S. montanum**

7b. Underground base of stem not swollen, or underground portion of plant not known ____ 8

8a. Leaves densely velutinous ____ 9

8b. Leaves glabrous to moderately pubescent ____ 10

9a. Leaf bases decurrent on prominently winged petioles, the wing up to 10 mm wide; usually high altitude (≥ 1500 m) plants of Chile and Peru ____ **8. S. paposanum**

9b. Leaf base truncate, the leaves usually distinctly petiolate (rarely sessile), the petioles lacking a wing or occasionally with a narrow wing up to 1 mm wide; coastal plants of Chile (≤ 800 m altitude) ____ **9. S. herbabona**

10a. Corolla rotate; mature leaves usually less than 2 cm wide, twice as long as wide; leaf margins strongly lobed, the lobes usually < 3 mm long ____ **10. S. edmonstonei**

10b. Corolla pentagonal; mature leaves usually greater than 2 cm wide, usually less than twice as long as wide; leaf margin subentire or serrately lobed, the lobes > 3 mm long ____ 11

11a. Inflorescences with 4–10 flowers; leaf margin entire to serrately lobed, the lobe length less than a third of the total leaf width; Chile and Peru ____ **7. S. montanum**

11b. Inflorescences with 12–40 flowers; leaf margin serrately lobed, never entire, the lobe length a third to a half of the leaf width; Chile ____ **11. S. pinnatum**

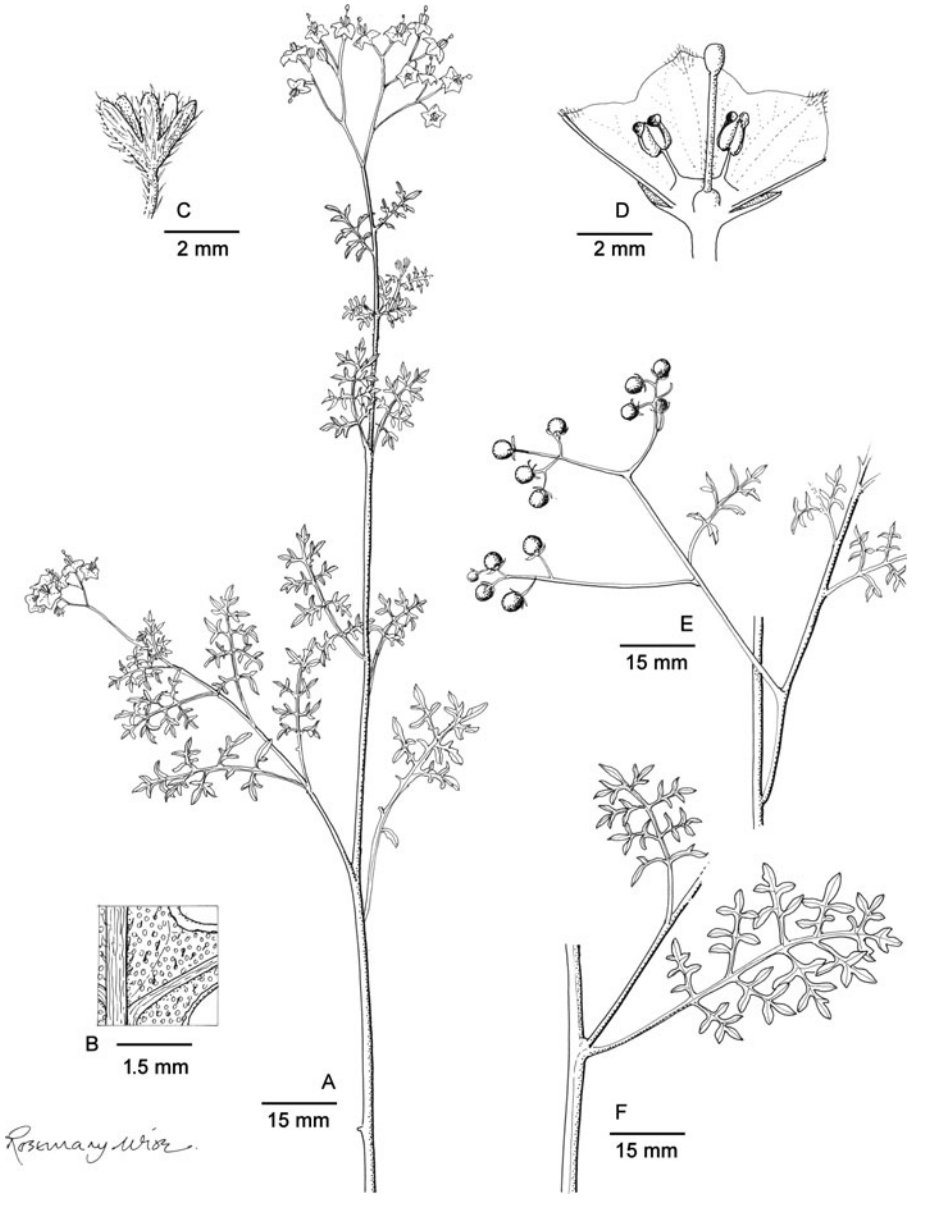


FIG. 2. *Solanum brachyantherum* Phil. A, habit; B, abaxial leaf surface; C, calyx; D, flower; E, fruiting shoot; F, leaf. A–D drawn from *Landrum et al*. 7486 (MO), E & F drawn from *Landrum et al*. 7472 (MO).

**1. Solanum brachyantherum** Phil., Anales Univ. Chile 43: 522 (1873). – Type: Chile, region III (Atacama), port of Huasco, *R.A. Philippi* s.n. (lecto SGO 42735, designated here; iso SGO 55576). **Fig. 2.**

*Solanum geissei* Phil., Anales Univ. Chile 91: 16 (1895). – Type: Chile, Isla del Morro Moreno, *M. Vidal Gormaz* s.n. (lecto SGO 55512, designated here).

Annual or perennial, erect or decumbent herb 50–100 cm tall. *Stems* woody at the base, up to 6 mm in diameter, glabrous to sparsely pubescent with uni- or multicellular hairs up to 0.5 mm long, glabrescent. *Sympodial units* unifoliate. *Leaves* pinnatifid or bipinnatifid, the blades (5–)16–80 × (5–)12–62 mm, 1–2 times as long as wide, ovate, both surfaces glabrous to sparsely pubescent, sometimes more densely so along the veins of the abaxial surface, the hairs multicellular, up to 0.25 mm long, the abaxial surface often with sessile, circular glands c.0.05 mm in diameter; lamina divided into 3–5 pairs of primary pinnae, the pinnae 5–17(–20) × c.1 mm, decreasing in length from the base to the leaf apex, with 1–3 pairs of secondary pinnae along each side, secondary pinnae 1–3(–7) mm long; apex of primary and secondary pinnae obtuse; petioles 4–22(–45) mm, occasionally with a narrow wing on either side up to 1 mm wide, the indumentum as in the blades. *Inflorescences* 3–5.1(–11) cm long, borne on axillary shoots, branched 1–3 times, with 12–30 flowers, the axes moderately to densely pubescent with appressed, uni- and multicellular hairs up to 0.4 mm long; peduncle 0.5–3.5 cm at anthesis; pedicels 1–3(–6) mm at anthesis, 4–7 mm in fruit, spaced 1–10 mm apart in fruit. *Calyx* 2–4(–4.5) mm long, the tube 0.5–2 mm, the lobes equal, 1.2–2 × 0.5–0.7(–1.2) mm at anthesis, 1.9–3 × 0.7–1.6 mm in fruit, ovate to elliptic, the apex acute, both surfaces glabrous to sparsely pubescent with multicellular hairs up to 0.4 mm long. *Corolla* 5–7 mm in diameter, pentagonal, blue, violet, pale lilac or lavender, the tube 0.75–1 mm long, the lobes 2.5–3.5 × 2.5–4 mm, moderately pubescent abaxially with multicellular hairs up to 0.2 mm long, glabrous adaxially. *Stamens* equal, filament tube 0.75–1 mm long, glabrous, filaments equal, 1.2–3.5 mm long, densely pubescent with white hairs < 0.1 mm long; anthers equal, 0.75–2 × 0.75–1 mm, oblong, yellow, the pores elliptic, rapidly opening into longitudinal slits with age. *Style* 2.8–3 × 0.1–0.3 mm, the lower half densely pubescent with white hairs < 0.1 mm long; stigma clavate, 0.6–1 × 0.5 mm. *Fruit* 4–6 mm in diameter, green-purple or black; stone cells usually present, few in number, rounded, c.0.8 × 0.6 mm. *Seeds* 1.2–1.7 × 0.8–1.2 mm, pale to dark brown, the surface shallowly pitted.

*Phenology*. Flowers from August to April.

*Distribution and habitat*. Chile [Insula San Ambrosio and regions I (Tarapacá), II (Antofagasta), III (Atacama)]. On steep, sandy or gravelly hillsides; 100–800 m. Fig. 3.

*Typification notes*. Philippi (1873) cites two Chilean specimens in the protologue of *Solanum geissei* – *Geisse* s.n. from Caldera and *Vidal Gormaz* s.n. from Isla del Morro Moreno. SGO holds several herbarium sheets labelled *Solanum geissei* which were indicated as possible types by Muñoz (1960). Two of these (SGO 42705 and SGO 42741) lack locality information. Two other sheets (SGO 72357 and SGO 71698) were collected at 'Quebrada Leones' and may have been seen by Philippi, but have no collector information. The final sheet, SGO 55512, has more precise

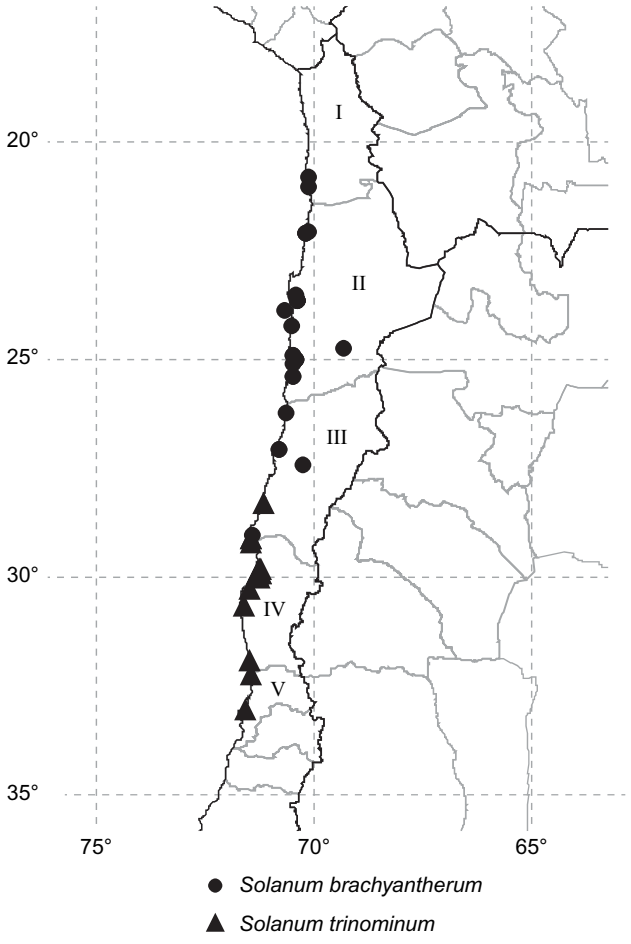


FIG. 3. Distribution map of *Solanum brachyantherum* and S. *trinominum*. Roman numerals indicate the regions of Chile (region I, Tarapacá; region II, Antofagasta; region III, Atacama; region IV, Coquimbo; region V, Valparaíso).

collector and locality information that matches perfectly the *Vidal Gormaz* collection cited by Philippi and has been selected as the lectotype.

*Etymology*. The epithet *brachyantherum* is derived from the Greek for short or small flowers that are characteristic of this species.

*Selected additional specimens examined*. CHILE. Insula San Ambrosio, 440 m, 14 xi 1960, *G. Kuschel* 14 (K, SGO). **Region I (Tarapacá)**: Punta Lobos, 1 xi 1997, *R. Pinto* s.n. (SGO); Punta Patache, 30 xi 1997, *W. Sielfeld* 22 (SGO). **Region II (Antofagasta)**: Aguada de Cardón, 30 xi 1925, *I.M. Johnston* 5273 (GH); Antofagasta, 31 x 1914, *J.N. Rose & J.N. Rose* 19419 (F, GH, NY); Cerro Perales, 550–690 m, 27 ix 1988, *M.O. Dillon & D. Dillon* 5534; Cobre, 450–460 m, 4 x 1988, *M.O. Dillon & D. Dillon* 5627 (F); La Rinconada, 200 m, 15 ix 1991, *L.R. Landrum et al.* 7472 (MO, NY); Paposo, ix 1909, *K.F. Reiche* s.n. (SGO); Paposo, 25 m, 10 xii 1997,

*M.F. Gardner & K.L. Matthews* 123 (E); Quebrada La Carmelita, 700 m, 8 xi 1969, *C. Jiles* 5339 (G); Quebrada La Chimba, 300–550 m, 17 xii 1987, *M.O. Dillon & J.T.S. Teillier* 5322 (F); Quebrada Guanillos, 610 m, 16 ix 1992, *S. Teillier et al.* 2809 (F); Taltal, 400 m, x 1925, *E. Werdermann* 841 (BM, E, G, GH, K, MO, NY, SI, US); Tocopilla, 18 x 1925, *I.M. Johnston* 3605 (GH). **Region III (Atacama)**: Chañaral, 100 m, 22 ii 1939, *A.A. Beetle* 26141 (G, GH, MO); Caldera, 1888, *W. Geisse* 9 (W); Puerto de Chañaral, 28 x 1925, *I.M. Johnston* 4813 (GH).

*Solanum brachyantherum* is easily identified by the size of the flowers which are much smaller than any of the other species of *Solanum* section *Regmandra*. The segments of the pinnatifid or bipinnatifid leaves are only about 1 mm wide, and are much narrower than those of either *Solanum remyanum* or *S. multifidum*.

**2. Solanum multifidum** Lam., Tabl. Encycl. 2: 17 (1794). – Type: Peru, sin. loc., *J. Dombey* s.n. (holo P-LA).

*Solanum pinnatifidum* Ruiz & Pav., Fl. Peruv. 2: 37 (1799). – *Witheringia pinnatifida* (Ruiz & Pav.) Dunal, Solan. Syn. 3 (1816). – Type: Peru, dept. Lima, prov. Chancay, *H. Ruiz & J.A. Pavón* s.n. (lecto MA 29725, designated here).

*Solanum multifidum* Ruiz & Pav., Fl. Peruv. 2: 37 (1799), non L. (1794). – *Witheringia multifida* (Ruiz & Pav.) Dunal, Solan. Syn. 2 (1816). – *Solanum tafallae* J.F.Macbr., Publ. Field Columbian Mus., Bot. Ser. 8: 111 (1930). – Type: Peru, dept. Arequipa, prov. Camaná, Pongo, *H. Ruiz & J.A. Pavón* s.n. (lecto MA 29724, designated here).

*Solanum senecoides* Domb. ex Dunal in DC., Prodr. 13(1): 65 (1852). *Nom. illeg. superfl.*, *Solanum multifidum* Lam. cited in synonymy.

Annual, erect or prostrate herb up to 50 cm tall. *Stems* fleshy, becoming woody, up to 12 mm in diameter at the base, glabrous or rarely sparsely pubescent with multicellular hairs up to 0.6 mm long. *Sympodial units* difoliate or rarely plurifoliate. *Leaves* pinnatifid, bipinnatifid or rarely tripinnatifid, fleshy, the blades 4–16(–19) × 1.4–7.5 cm, 1.6–2.7(–3.2) times as long as wide, usually with a narrow wing 1–6 mm wide along the midrib between the primary pinnae, both surfaces glabrous or rarely sparsely to moderately pubescent with multicellular hairs up to 1 mm long (Arequipa and Tacna specimens only); base decurrent on a winged petiole, the wing up to 10 mm wide and extending beyond the leaf node and forming a flange running parallel to the stem; margin divided into 3–6 pairs of primary pinnae, the primary pinnae 4–30(–48) × 3–22(–46) mm, usually asymmetrically arranged each side of the midrib, decreasing in size from base of leaf to the apex, the primary pinnae divided into 1–3 secondary and occasionally tertiary pinnae irregularly spaced along each side, the secondary and tertiary pinnae 2–20 × 1–8 mm; apex of all pinnae acute to obtuse; petioles indistinct, winged. *Inflorescences* 4.5–20 cm long, borne on terminal and axillary shoots, branched 1–2(–3) times, with 8–32 flowers, the axes subglabrous to moderately pubescent, the hairs often appressed, uni- or multicellular, up to 1.5 mm long; peduncle 1.7–7(–12.5) cm long; pedicels 5–11 mm at anthesis, 11–25 mm in

fruit, spaced 4–10 mm apart in fruit. *Calyx* 3.3–5.5 mm long, tube 0.6–2 mm, the lobes equal, 1.8–3.8 × 0.5–1.5 mm at anthesis, 2.2–4.2 × 1–1.8 mm in fruit, oblong, becoming ovate in fruit, the apex obtuse, both surfaces glabrous or rarely sparsely pubescent abaxially with multicellular hairs up to 0.4 mm long. *Corolla* 11–16 mm in diameter, pentagonal to rotate, white, sometimes turning light blue, purple or violet, the tube c.1 mm long, the lobes 7–10 × 5.5–8.5 mm, subglabrous to densely pubescent abaxially with white, uni- or multicellular hairs up to 1 mm long, glabrous adaxially. *Stamens* equal; filament tube c.1 mm long, glabrous; filaments equal, 1–1.5 mm long, glabrous; anthers equal, 3–4.2 × 0.6–1.2 mm, oblong, yellow, the pores tear-drop shaped, rapidly opening into longitudinal slits the entire length of the anther. *Style* 4.5–7 × 0.1 mm, glabrous; stigma clavate, 1.4–2.5 × 0.9–1 mm. *Fruit* 4–6.5(–10) mm in diameter, green, turning red when ripe, pendent; stone cells absent. *Seeds* 1–1.1 × 1.1–1.2 mm, obovate, pale brown, the surface shallowly pitted.

*Phenology*. Flowers July to March.

*Distribution and habitat*. Coastal Peru in the departments of Ancash, Arequipa, Ica, La Libertad, Lima, Moquegua and Tacna. On arid sandy soil and dunes, rocky and gravelly hillsides; 0–1200 m. Fig. 4.

*Etymology*. The epithet *multifidum* describes the multiple divisions of the pinnatifid or bipinnatifid leaves.

*Selected additional specimens examined*. PERU. **La Libertad**: Cerro Cabezón, 500 m, 10 iii 1998, *S. Leiva et al*. 2173 (F, HAO, HUT, MO); Cerro Cabras, 150 m, 6 viii 1949, *N. Angulo* 1211 (F, HUT, NY); Cerro Campana, 550 m, 3 x 1997, *S. Leiva & V. Quipuscoa* 2074 (F, HAO, MO, NY); Lomas de Cerro Combo, 400–500 m, 9 vii 1983, *R. Ferreyra* 19896 (USM); Quebrada de San Idelfonso, 100–300 m, 13 iv 1998, *E. Rodríguez & T. Aguilar* 2083 (HAO, HUT); Cerro Reque, 437 m, 1 xi 2005, *M. Nee et al*. 53561 (BM, HUT, NY). **Ancash**: Lomas de Lupín, 360 m, 23 ix 1952, *R. Ferreyra* 8644 (USM); Cerro Chimbote, 620 m, 26 ix 1986, *J. Mostacero & C. Mejía* 1470 (HUT); Lomas de Mongon, 450 m, 17 ix 1938, *H.E. Stork et al*. 9182 (G, GH, K). **Lima**: Pachacámac, 440 m, 29 x 2005, *J. Bennett et al*. 105 (BM, NY, USM); La Ramas, 1876, *L. Savatier* 1572 (K); Lomas de Cerro Negro, 2 x 1966, *S.S. Tillett* 6610 (GH); Novia Solar, 200 m, viii 1910, *A. Weberbauer* 5691 (GH); San Agustín, 27 ix 1940, *E. Asplund* 13790 (G); Isla San Lorenzo, viii 1913, *N. Esposto* s.n. (K); Lomas de Chancay, 28 x 1998, *L. Bohs* 2863 (NY); Lomas de Lachay, 300 m, 13 x 1945, *R. Ferreyra* 203 (USM); Lomas de San Jerónimo, 250–300 m, 1 xi 1965, *R. Ferreyra & E. Cerrate* 16541 (USM); Pasamayo, 404 m, 28 x 2005, *J. Bennett et al*. 103 (BM, NY, USM); 400 m, 4 x 1938, *H.E. Stork & C. Vargas* 9343 (G, GH, K, MO, SI); Amancaes valley, 243 m, ix 1943, *C. Lauderman* 4351 (K); Lomas de Quebrada Verde, 320 m, 7 viii 1948, *R. Ferreyra* 3919 (USM); Lomas del Cerro Paredes, 300 m, 8 viii 1998, *J. Roque* 691 (USM); Lomas del Manzano, 150–180 m, 10 ix 1989, *R. Ferreyra* 20994 (USM); Lomas de Quilmana, 320 m, 8 x 2002, *M. Weigend et al*. 7328 (BM, F, NY, USM). **Ica**: Lomas de Marcona, 740 m, 17 xi 1994, *A. Cano et al*. 6125 (USM). **Arequipa**: Lomas de Atico, 150–200 m, 13 xi 1949, *R. Ferreyra* 6459 (MOL, USM); Lomas de Capacc, 200 m, 14 ix 1957, *P.C. Hutchinson* 1294 (K, NY, USM); Lomas de Cachendo, 900 m, 9 ii 1983, *M.O. Dillon et al*. 3294 (F, HUT, MO, US); Lomas of Mollendo, 50 m, 20 xi 1983, *M.O. Dillon & D. Dillon* 3906 (F, HUT, MO, USM); Quebrada Fiscal, 700–750 m, 5 ii 1998, *Anon*. 1040 (HAO, NY). **Tacna**: Lomas de Sama, 500–600 m, 1 xii 1955, *R. Ferreyra* 11647 (USM); Lomas de Sama Grande, 500–600 m, 4 x 1957, *R. Ferreyra* 12508 (USM); Lomas of

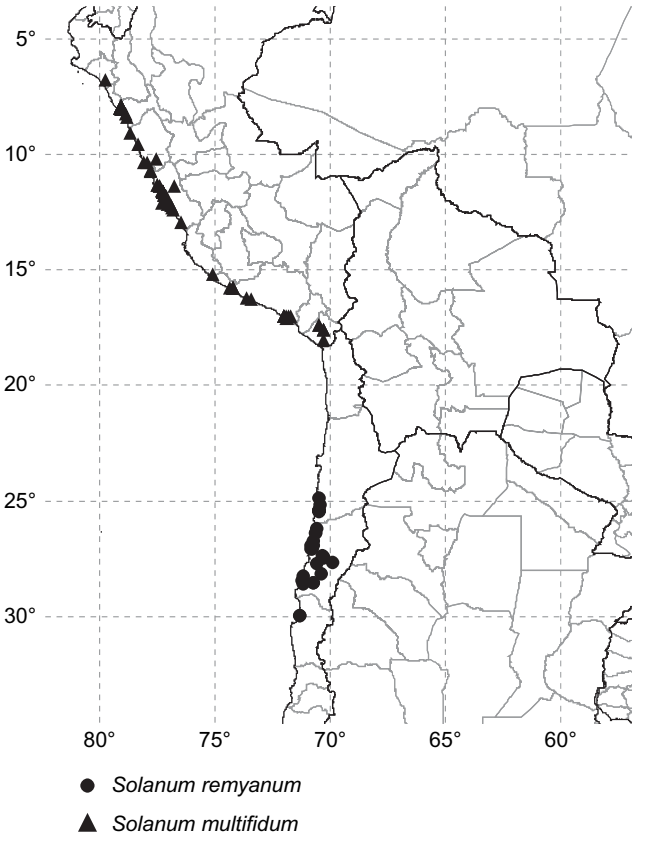


FIG. 4. Distribution map of *Solanum remyanum* and *S. multifidum*.

Tacna, 530–620 m, 20 x 1983, *M.O. Dillon & D. Dillon* 3678 (F, USM); Puerto Grau, 50 m, 22 vi 1998, *A. Cano et al*. 8459 (USM).

*Solanum multifidum* is most similar to the Chilean species *S. remyanum*, but is restricted to Peru. It may be distinguished by the usually glabrous leaves and the winged leaf bases that extend beyond the leaf node, which in some cases may form a broad, conspicuous flap of tissue. There are a small number of specimens collected from the southernmost part of its range in the departments of Arequipa and Tacna that are intermediate between the typical forms of *Solanum remyanum* and *S. multifidum*. Compared with specimens of *Solanum multifidum* from the northern part of its range the leaf bases of these specimens are less prominently winged (although not distinctly petiolate as specimens of *S. remyanum*), the pinnae are narrower, and the leaves are not entirely glabrous. However, the indumentum is not as dense as that found on specimens of *Solanum remyanum*. I have maintained these as two separate species as there is usually no difficulty in assigning the majority of specimens to one or the other species based on the indumentum and form of the petiole, and there is no geographic continuity between the two species. A similar

trend in increasing indumentum density with increasing latitude can be seen in *Solanum montanum* and *S. paposanum*.

**3. Solanum remyanum** Phil., Anales Univ. Chile 91: 17 (1895). – *Witheringia flexuosa* J.Rémy in Gay, Fl. Chil. 5: 70 (1849). – *Solanum flexuosum* (J.Rémy) F.Phil., Cat. Pl. Vasc. Chile 228 (1881), *nom. illeg*., non *Solanum flexuosum* Vahl (1796) nec *Solanum flexuosum* Willd. (1819), *nom. illeg*. – Type: Chile, region III (Atacama), Copiapo, *C. Gay* s.n. (lecto P 335300, designated here). **Fig. 5.**

Woody shrub 20–100 cm high. *Stems* green when young, becoming brown and woody, subglabrous to densely pubescent, the hairs erect, uni- or occasionally multicellular, up to 0.2 mm long. *Sympodial units* plurifoliate. *Leaves* pinnatifid or bipinnatifid, fleshy, the blades 3.3–8.5 × 0.8–5.5 cm, 0.95–2 times as long as wide, sometimes with a narrow wing 2–3 mm wide along the midrib between the primary pinnae, green or greyish, both surfaces moderately to densely tomentose, the hairs denser abaxially along the midvein, erect, uni- or multicellular, up to 0.3 mm long; margin divided into 4–5 pairs of primary pinnae, 5–30 × 3–19 mm, decreasing in size from base of leaf to the apex, with (0–)2–4 irregular secondary pinnae along each side, the secondary pinnae (0.5–)1–5(–8) × (0.5–)1–3(–4.5) mm; apex of primary and secondary pinnae acute to rounded; petioles 5–32 mm, occasionally with a narrow wing up to 1 mm wide, with indumentum as on the stems. *Inflorescences* 4–14 cm long, borne on leafy axillary shoots, leaf-opposed, branched 1–2(–3) times, with 6–22 flowers, the axes densely pubescent with multicellular hairs up to 0.4 mm long; peduncle 3.3–5.5 cm long; pedicels 7–10 mm long, not accrescent in fruit, spaced 5–15 mm apart in fruit. *Calyx* 2.9–4.5(–5) mm long, the tube 1–2(–2.5) mm long, the lobes 1–3(–3.4) × 0.7–1.4 mm at anthesis, 3–5 × 1.1–2 mm in fruit, elliptic to oblong, glabrous to sparsely pubescent adaxially, moderately to densely pubescent abaxially, especially in the lower half, the hairs unicellular, up to 0.3 mm long, the apex acute to obtuse. *Corolla* 1.1–2.2 cm in diameter, pentagonal, blue or violet, the tube 1–1.5 mm long, the lobes 6–10 × 7–11 mm, sometimes reflexed at anthesis, densely pubescent abaxially with white, unicellular hairs up to 0.2 mm long, glabrous adaxially. *Stamens* equal; filament tube 1–1.5 mm long, glabrous; filaments equal, 0.6–1 mm long, glabrous; anthers equal, 3.5–4.6 × 1–1.5 mm, oblong to elliptic, yellow, the pores tear-drop shaped, tardily opening into longitudinal slits with age. *Style* 8–10 × 0.2–0.3 mm, densely pubescent with white multicellular hairs up to 0.2 mm long, rarely glabrous; stigma clavate, 1–1.5 × 0.5–0.8 mm. *Fruit* 4–7 mm in diameter, colour unknown; stone cells absent. *Seeds* 1.5–1.9 × 1.2–1.5 mm, pale to dark brown, shiny, surface shallowly pitted.

*Phenology*. Flowers August to January.

*Distribution and habitat*. Endemic to Chile [regions II (Antofagasta), III (Atacama) and IV (Coquimbo)]. Arid, rocky or gravelly slopes, quebradas and coastal lomas formations; 20–2200 m. Fig. 4.

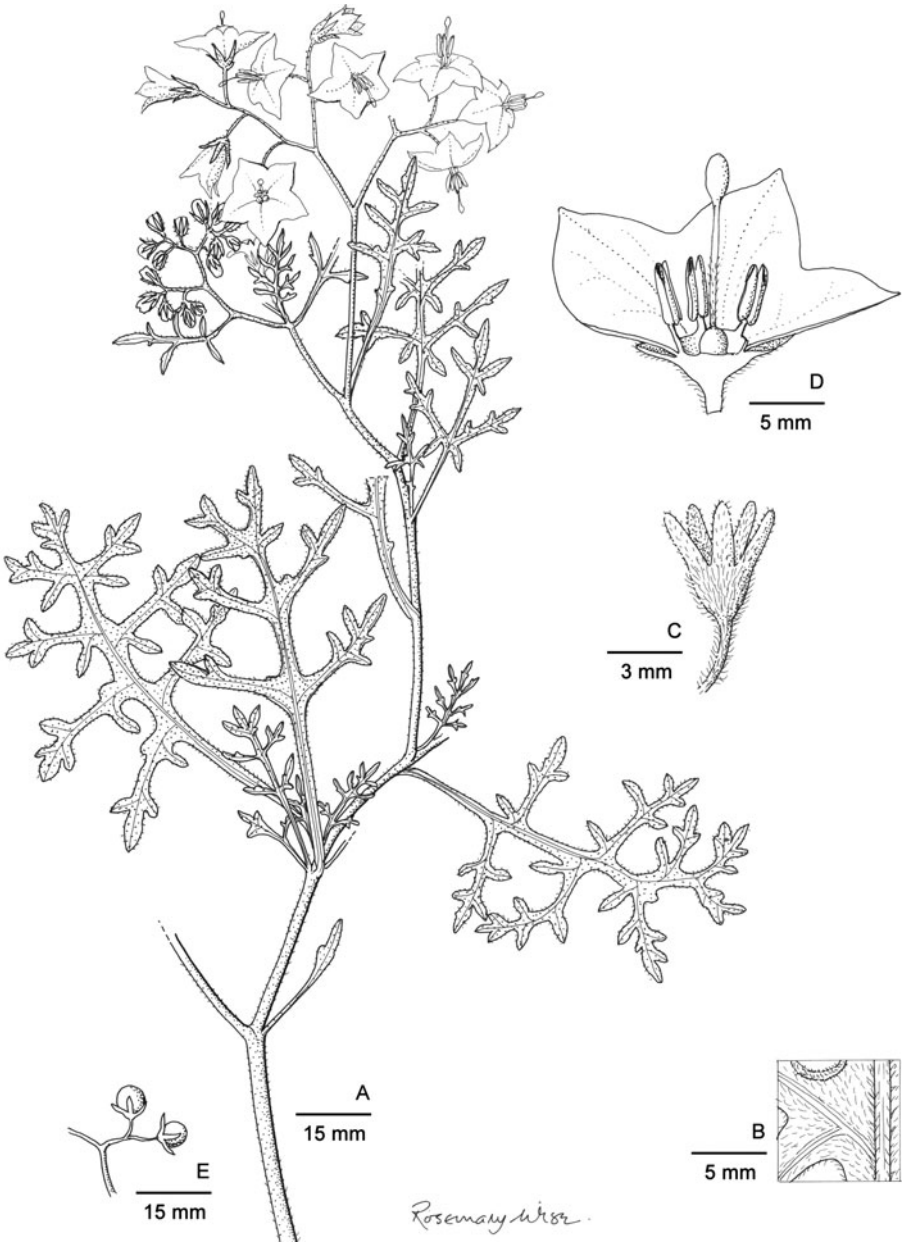


FIG. 5. *Solanum remyanum* Phil. A, habit; B, abaxial leaf surface; C, calyx; D, flower; E, fruits. A–D drawn from *Muñoz* 3081 (SGO), E drawn from *Worth & Morrison* 15806 (K).

*Etymology*. Named in honour of the French botanist Jules Rémy (1826–1893), who wrote the *Solanaceae* account for *Historia física y política de Chile* (Rémy, 1849).

*Selected additional specimens examined*. CHILE. **Region II (Antofagasta)**: Aguada de Cachinalcito, 29 xi 1925, *I.M. Johnston* 5193 (GH); 10.5 km N of Paposo, 200 m, 15 ix 1991, *L.R. Landrum et al*. 7473 (MO, NY); Paposo, 25 m, 10 xii 1997, *M.F. Gardner & K.L. Matthews* 133 (E); Puerto de Chañaral, 28 x 1925, *I.M. Johnston* 4766 (GH); Quebrada de Taltal, 12 x 1938, *C.R. Worth & J.L. Morrison* 15806 (GH, K, MO, NY); hills southeast of Taltal, 25 xi 1925, *I.M. Johnston* 5068 (GH); Taltal, 200 m, x 1925, *E. Werdermann* 836 (BM, E, G, GH, K, NY, SI, US). **Region III (Atacama)**: Atacama desert, ix 1890, *T. Morong* 1132 (GH, K, MO, NY); Bandurias, 1885, *G. Geisse* s.n. (GH); Barquito harbor, 50 m, 18 xi 1935, *J. West* 3866 (GH); Caldera, 50 m, ix 1924, *E. Werdermann* 986 (E); Caldera Morro, 500 m, ix 1924, *E. Werdermann* 386 (BM, GH, K, MO, SI); entre Caldera y Obispito, 4 x 1991, *C. von Bohlen* 1214 (SGO); Chañaral, 6 x 1987, *S. Teillier* 798 (SGO); Huasco, x 1940, *C. Grandjot & G. Grandjot* 4309 (SGO); Morro de Copiapo, 100 m, 21 x 1938, *C.R. Worth & J.L. Morrison* 16168 (GH, K); Quebrada de Algarrobal, 7 x 1987, *S. Teillier* 902 (NY); Quebrada Cerro Castillo, 13 x 1992, *M. Muñoz* 3081 (SGO); Quebrada de Chanchoquin, ix 1885, *E.E. Gigoux* s.n. (GH); Quebrada Conchas, 2200 m, 10 xi 1925, *I.M. Johnston* 4952 (GH); Quebrada de los Infieles, 10 m, 29 ix 1995, *M.F. Gardner & S.G. Knees* 5852 (E); Quebrada de los Infieles, 10 m, 4 iii 1996, *P. Brownless et al*. 532 & 535 (E); Quebrada del Leon, 150 m, 20 x 1938, *C.R. Worth & J.L. Morrison* 16146 (GH, K); Quebrada Paipote, i 1885, *F. Philippi* s.n. (SGO); Tierra Amarilla, 700 m, ix 1924, *E. Werdermann* 401 (BM, E, GH, K, MO, NY, SI); Vallenar, 16 x 1992, *M. Muñoz* 3120 (SGO); 15 km in the north of Vallenar, 12 x 1987, *O. Zöllner* 15064 (MO). **Region IV (Coquimbo)**: Coquimbo, *F. Philippi* s.n. (K).

*Solanum remyanum* is restricted to Chile and is distinguished from *S. brachyantherum*, the other Chilean species of *Solanum* section *Regmandra* with highly divided pinnatifid leaves, by the larger size of the pinnae, the corolla and the anthers. The pinnae of *Solanum remyanum* are broader than those of *S. brachyantherum* and the anthers of *S. remyanum* are c.3 mm long compared with c.1 mm long in *S. brachyantherum*. *Solanum multifidum* from Peru has a similar leaf morphology, but the leaves of *S. multifidum* are glabrous and the petiole and internodes more prominently winged; the leaves of *S. remyanum* are always pubescent and the petioles are usually distinct or with only a narrow wing (up to 1 mm wide).

**4. Solanum trinominum** J.R.Benn., **nom. nov.** – *Witheringia tomentosa* J.Rémy in Gay, Fl. Chil. 5: 71 (1849). – *Solanum tomentosum* (J.Rémy) F.Phil., Cat. Pl. Vasc. Chil. 229 (1881), non L. (1753), *nom. illeg*. – *Solanum heterantherum* Witasek ex Reiche, Anales Univ. Chile 124: 446 (1909), *nom. illeg*., non *Solanum heteranthera* Willd. (1819). – Type: Chile, region IV (Coquimbo), Coquimbo, *C. Gay* s.n. (lecto K, designated here). **Fig. 6.**

*Solanum gaudichaudii* Dunal var. *canescens* Dunal in DC., Prodr. 13(1): 60 (1852). – Type: Chile, region IV (Coquimbo), Coquimbo, *C. Gay* 835 (lecto G-DC, designated here).

Perennial, probably erect, shrub up to 60 cm tall. *Stems* pale brown, woody, densely pubescent, the hairs uni- or multicellular, up to 0.5 mm long, glabrescent. *Sympodial units* unifoliate. *Leaves* simple, the blades 2–4.5(–5.5) × 0.4–2.3 cm, 2–4.2(–5) times as long as wide, ovate to oblong, grey-green, both surfaces densely tomentose with erect, uni- or multicellular hairs up to 0.5 mm long; base cuneate; margin regularly lobed with 3–5(–7) pairs of lobes, usually with a smaller secondary lobe arising

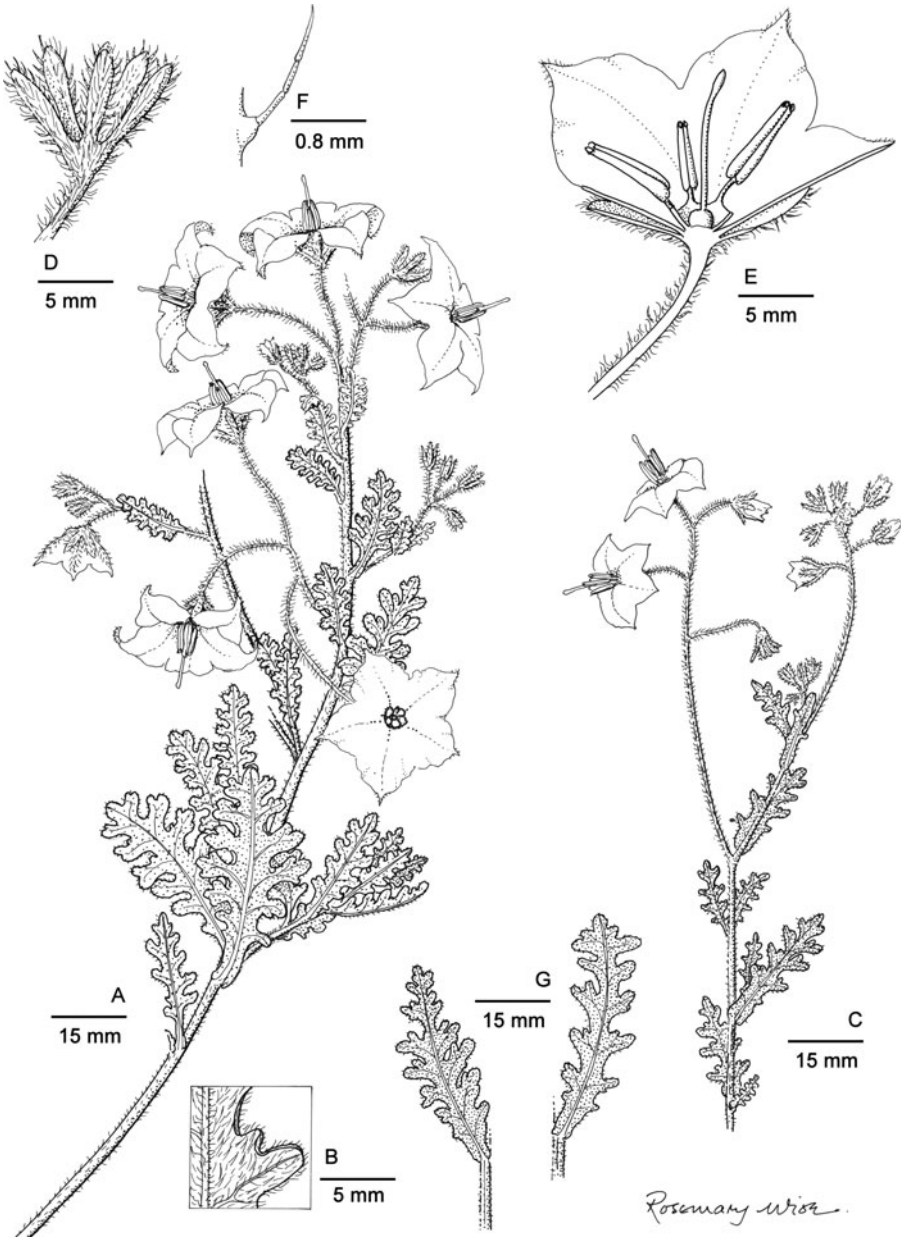


FIG. 6. *Solanum trinominum* J.R.Benn. A, habit; B, abaxial leaf surface; C, flowering shoot; D, calyx; E, flower; F, hair; G, leaves. A–F drawn from *Muñoz* 4253 (SGO), G drawn from *Cassells* s.n. (SGO).

obliquely at the base of the apical side of the primary lobe, primary lobes 2–10 × 0.5–3 mm, the basal and apical sides of lobes straight or concave, the primary lobe apex obtuse to rounded; petioles absent. *Inflorescences* 4–10 cm long, leaf-opposed, branched 2–3 times, with (1–)4–7 flowers, the axes moderately to densely pubescent with multicellular hairs up to 1 mm long; peduncle 1.3–9 cm; pedicels 8–17(–25) mm at anthesis, not accrescent in fruit, spaced 6–8 mm apart in fruit, articulated at the base. *Calyx* 5–6 mm long, the tube 1–1.5 mm, the lobes equal, 3.5–6.9(–10) × 1.2–3(–5) mm, not accrescent in fruit, ovate to oblong, the apex rounded to obtuse, both surfaces moderately to densely pubescent with uni- or multicellular hairs up to 1 mm long. *Corolla* 2.8–3.1 cm in diameter, pentagonal, white, blue or purple, the tube 1–1.5 mm long, the lobes 7–15 × 8–23 mm, moderately pubescent abaxially, densely so towards apices with white, uni- or multicellular hairs up to 1 mm long, glabrous adaxially. *Stamens* unequal with two longer and three shorter; filament tube 1–2 mm, glabrous; filaments unequal, the longer pair 3–3.5 mm, the shorter 1–1.5 mm; anthers unequal, the longer pair 6.5–8.5 × 1.5 mm, the shorter 5–5.8 × 1.5–1.7 mm, narrowly ovate to lanceolate, strongly tapering in width towards the apex, yellow, usually with purple longitudinal markings, the pores directed laterally and opening into longitudinal slits with age. *Style* 8.5–9.5 × 0.2–0.4 mm, the lower half pubescent with unicellular hairs up to 0.2 mm long; stigma globose, 0.8–0.9 mm in diameter. *Fruit* 6–9 mm in diameter, colour unknown; stone cells absent. *Seeds* 1.4–2 × 1–1.8 mm, shiny, dark brown to black, the surface deeply pitted.

*Phenology*. Flowers August to January.

*Distribution and habitat*. Endemic to Chile [regions III (Atacama), IV (Coquimbo) and V (Valparaíso)]. On dunes and sandy lomas; 10–120 m. Fig. 3.

*Typification notes. Solanum gaudichaudii* Dunal was originally described with two varieties, var. *viride* and var. *canescens*. Neither has previously been chosen to lectotypify the species. Three specimens are cited under *Solanum gaudichaudii* var. *canescens*: *Gay* 835 (G-DC) and *Gay* 99 (P), both from Chile, and *Krauss* s.n. (G-DC) from Guadalupe. The *Krauss* specimen is not a species of *Solanum* section *Regmandra*, and *Gay* 99 was not located at Paris and so its correct identity has not been verified. *Gay* 835 is a specimen of *Solanum trinominum* and I have chosen it as the lectotype of *S. gaudichaudii* var. *canescens*. The specimens cited by Dunal (1852) of *Solanum gaudichaudii* var. *viride* are specimens of *S. pinnatum* (see discussion under that species). The name *Solanum gaudichaudii*, although not widely used, has always been used for specimens of *S. pinnatum* and not *S. trinominum*. I have therefore chosen not to typify *Solanum gaudichaudii* on var. *canescens* (which would provide the earliest name for *S. trinominum*) but on *Solanum gaudichaudii* var. *viride*.

*Etymology*. The epithet *trinominum* refers to the three names that have been applied to this plant since its first description, namely *tomentosum*, *heterantherum* and *trinominum*.

*Selected additional specimens examined*. CHILE. **Region III (Atacama)**: Dunas al norte de Huasco, 20 m, 8 ix 1991, *C. von Bohlen* 1340 (SGO); Playa Carrizalillo, 9 x 2002, *A. Moreira* 712 & 713 (SGO); Copiapo, *Bridges* 1320 (E). **Region IV (Coquimbo)**: 15 km de Coquimbo al Sur, 20 m, 12 viii 1993, *M. Hermann & A. Contreras* 1255 (SGO); Coquimbo, 10 m, xi 1923, *E. Werdermann* 127 (BM, G, GH); entre Coquimbo y Tongoy, 15 ix 1957, *C. Muñoz* 4253 (SGO); Fray Jorge, 26 ix 1935, *C. Muñoz* 201 (GH, SGO); Playa de la Herradura, 20–50 m, 14 ix 1941, *C. Muñoz & G.T. Jones* 1848 (SGO); Herradura, 27 ix 1917, *C. Skottsberg & I. Skottsberg* 1050 (NY); Punta Choros, 9 x 2002, *A. Moreira* 701 (SGO); 10 km south of Serena, road to Ovalle, 50 m, 14 ix 1940, *R. Wagenknecht* 18570 (B, G, GH); entre La Serena y Punta Teatinos, 15 x 1940, *G. Looser* 4450 (GH); La Serena, 120 m, 12 x 1965, *C. Muñoz* 43 (SGO); Los Vilos, 8 i 1976, *B. Holto* 6 (SGO). **Region V (Valparaíso)**: Los Molles, xi 1862, *R.A. Philippi* s.n. (W); Valparaíso, *A. Calvert* s.n. (BM).

*Solanum trinominum* is most similar to *S. edmonstonei*, but may be distinguished by the unequal lengths of the stamens. From other Chilean species of *Solanum* section *Regmandra* that have stamens of unequal length it may be distinguished by the distinctive oblique, secondary lobes of the leaves. From the Chilean *Solanum pinnatum* it may be distinguished by the unequal length of the stamens and the densely tomentose leaves, often greyish in appearance, which are usually much smaller than those of *S. pinnatum*.

**5. Solanum indivisum** Witasek ex J.R.Benn., **sp. nov.**
Staminibus inaequalibus *Solano trinomini* et *S. coquimbensi* similis sed a *S. trinomine* foliorum marginibus subintegris vel leniter dentatis distinguenda; a *S. coquimbense* foliis sessilibus, foliorum basibus cuneatibus, corollis pentagonis differt. – Type: Chile, region V (Valparaíso), Valparaíso, Concón, viii 1827, *E.F. Poeppig* s.n. (holo W 3645). **Fig. 7.**

Annual or perennial, erect herb, c.30–40 cm tall. *Stems* woody at the base, sparsely to moderately pubescent with multicellular hairs up to 1 mm long. *Sympodial units* unifoliate. *Leaves* simple, the blades 2.4–5.3 × 0.6–1.8 cm, 2.7–4.3 times as long as wide, elliptic, both surfaces scabrous, the hairs multicellular, up to 0.6 mm long, the base cuneate, margin irregularly and shallowly crenate, the teeth < 1 mm long, occasionally subentire, the apex acute to obtuse; petioles absent. *Inflorescences* 1.8–2.4 cm long, borne towards the tips of short axillary branches, unbranched or branched once, with c.2–4 flowers, the axes densely pubescent with multicellular hairs up to 0.6 mm long; pedicels c.4 mm at anthesis. *Calyx* c.6.5 mm long, the tube c.1 mm, lobes equal, c.5.5 × 2.3–2.5 mm, elliptic, the apex obtuse to rounded, both surfaces densely pubescent with multicellular hairs up to 0.8 mm long. *Corolla* c.16 mm in diameter, pentagonal, colour unknown, the tube c.2 mm long, lobes c.8 × 8 mm, moderately pubescent abaxially with multicellular hairs up to 0.6 mm long, glabrous adaxially. *Stamens* strongly unequal with two longer and three shorter; filament tube c.2 mm, glabrous; filaments unequal, the longer pair c.4.5 mm, the shorter c.2–2.5 mm; anthers unequal, the longer pair c.5.8 × 1 mm, the shorter 4 × 1 mm, tapering in width towards the apex, colour unknown, the pores directed laterally and opening into longitudinal slits with age. *Style* c.7 × 0.2 mm, pubescent

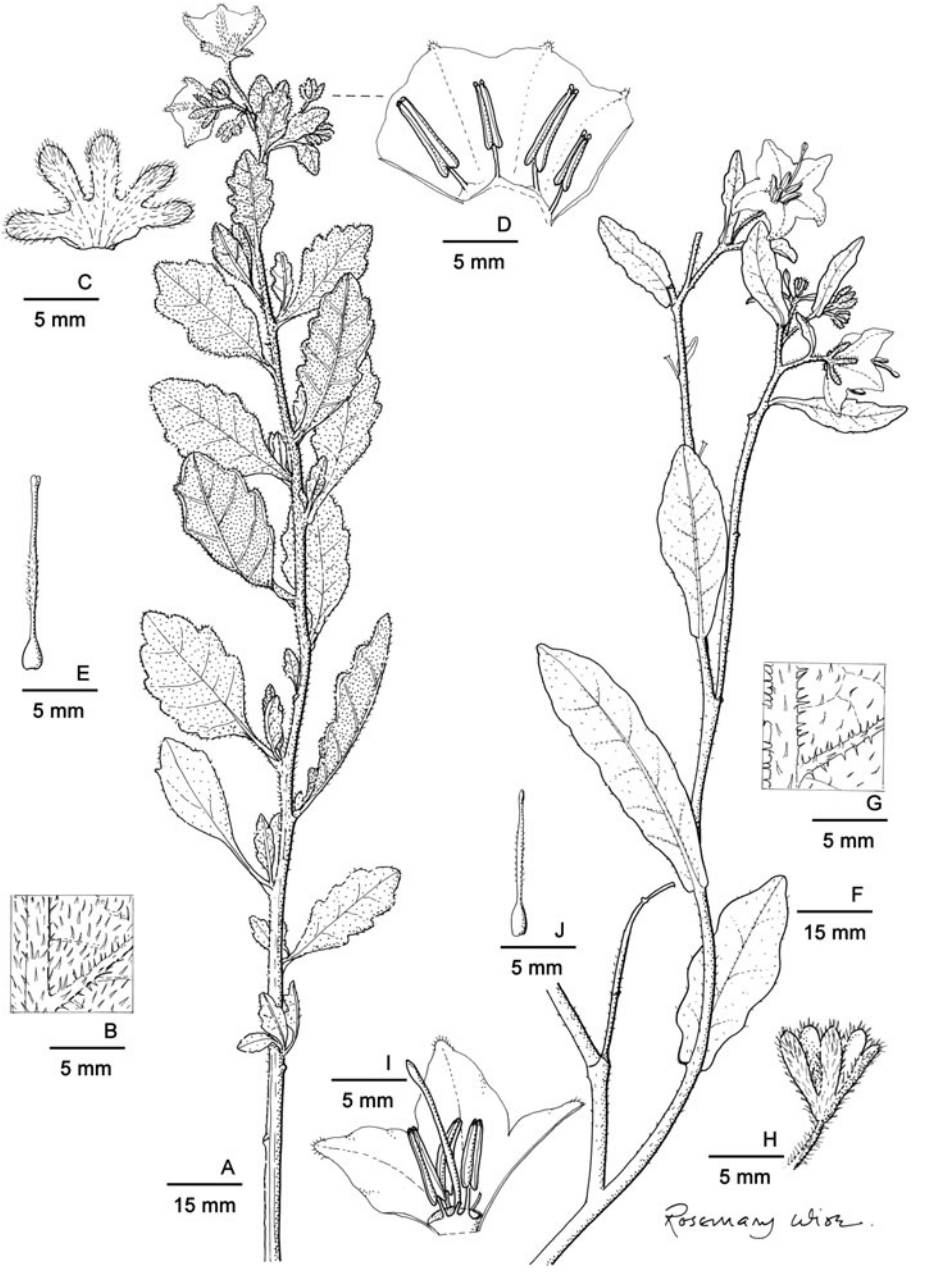


FIG. 7. *Solanum coquimbense* J.R.Benn. A, habit; B, abaxial leaf surface; C, calyx; D, flower; E, gynoecium. Drawn from *Cassells* s.n. (SGO). *Solanum indivisum* Witasek ex J.R.Benn. F, habit; G, abaxial leaf surface; H, calyx; I, flower; J, gynoecium. Drawn from *Poeppig* s.n. (W).

with fine, white, uniseriate hairs up to 0.2 mm long; stigma clavate, 0.3 × 0.2 mm. *Fruits and seeds* not known.

*Phenology*. Flowers August.

*Distribution and habitat*. Endemic to region V (Valparaíso) of Chile. Fig. 8.

*Etymology*. The epithet *indivisum* refers to the leaves which, in contrast to many species of *Solanum* section *Regmandra*, are not strongly divided but have only a weakly dentate or almost entire margin.

*Additional specimen examined*. CHILE. Sin. loc., *Endlicher* s.n. (W [2 sheets]).

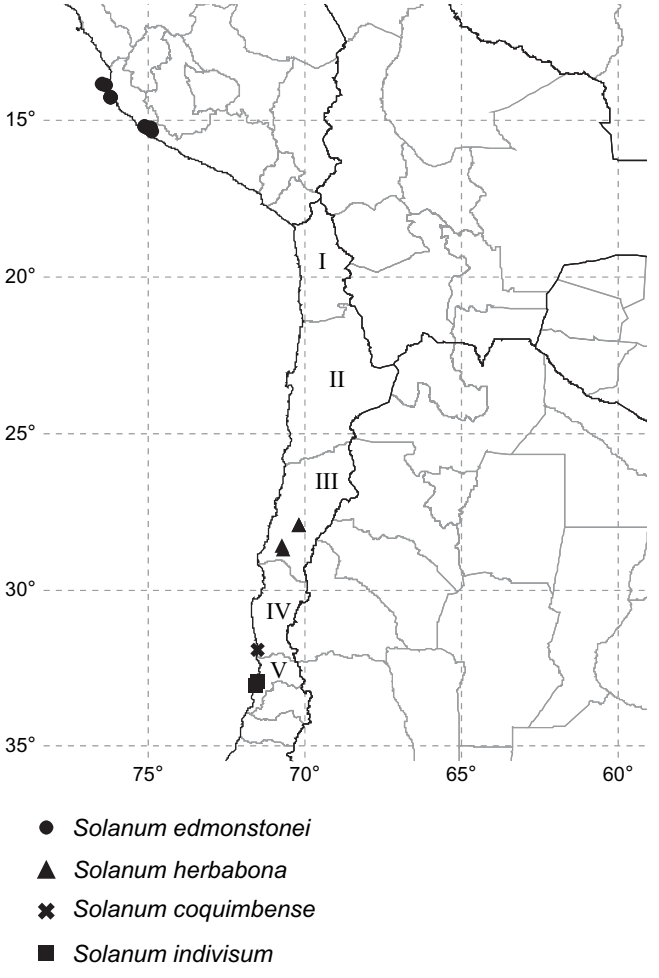


FIG. 8. Distribution map of *Solanum edmonstonei*, *S. herbabona*, *S. coquimbense* and *S. indivisum*. Roman numerals indicate the regions of Chile (region I, Tarapacá; region II, Antofagasta; region III, Atacama; region IV, Coquimbo; region V, Valparaíso).

*Solanum indivisum* is known from only three sheets, all collected in Chile in the nineteenth century. It is similar to *Solanum trinominum* and *S. coquimbense* in the strongly unequal length of the stamens. However, the long, narrow, sessile leaves of *Solanum indivisum* have a weakly dentate or subentire margin, in contrast to the strongly lobed leaves of *S. trinominum* and *S. coquimbense*. The pentagonal corolla, cuneate leaf bases, sessile leaves, and longer internodes are points of difference from *Solanum coquimbense*. No fruiting material is known and further collections are required.

**6. Solanum coquimbense** J.R.Benn., **sp. nov.**

Staminibus inaequalibus *Solano trinomi* et *S. indiviso* similis sed a *S. indiviso* foliorum marginibus valde dentatis, corollis rotatis, basibus foliorum attenuatis, foliorum petiolatis distinguenda. – Type: Chile, region IV (Coquimbo), Los Vilos, 20 ix 1974, *B. Cassells* s.n. (holo SGO). **Fig. 7.**

Probably an erect, woody perennial herb up to c.30 cm tall. *Stems* green, becoming woody at the base, scabrous, the hairs multicellular, up to 0.5 mm long. *Sympodial units* unifoliate. *Leaves* simple, the blades 2.9–4 × 1.2–1.9 cm, 1.6–3.2 times as long as wide, olive green, elliptic, both surfaces densely scabrous, the hairs simple, uniseriate, multicellular, up to 0.5 mm long; base decurrent; margin crenate, 4–5 pairs of lobes each side, the lobes rounded, 1–2 × 3–5 mm, the apex obtuse; petioles 0–10 mm, usually indistinct and the leaves subsessile. *Inflorescences* 2.5–3 cm long, leaf-opposed, unbranched, with c.5 flowers, the axes densely scabrous with hairs like those of the leaves; peduncle c.8 mm; pedicels 3–8 mm at anthesis, spaced 2–3 mm apart at anthesis. *Calyx* c.8 mm long, tube c.2.5 mm, the lobes equal, c.5.5 × 3 mm, elliptic to weakly spathulate, the apex obtuse to rounded, both surfaces densely pubescent with hairs like those of the leaves. *Corolla* c.17 mm in diameter, rotate, colour unknown, the tube c.1.5 mm long, the lobes c.10 × 11 mm, moderately pubescent abaxially with multicellular hairs up to 0.3 mm long, glabrous adaxially. *Stamens* 5, unequal, with two longer and three shorter; filament tube c.1 mm, glabrous; filaments unequal, glabrous, the longer pair c.2.5 mm, the shorter 1.5–2 mm; anthers unequal, the longer pair c.7 × 1.6 mm, the shorter 5.2–5.8 × 1.8 mm, narrowly ovate to lanceolate, strongly tapering in width towards the apex, yellow, the pores tear-drop shaped and opening into longitudinal slits with age. *Style* c.10 × 0.1 mm, the lower half pubescent with unicellular hairs up to 0.2 mm long; stigma clavate, 0.8 × 0.5 mm. *Fruits and seeds* not known.

*Phenology*. Flowers September.

*Distribution and habitat*. Coastal areas of region IV (Coquimbo) of Chile. Fig. 8.

*Etymology. Solanum coquimbense* is named after Coquimbo, the region of Chile where the type specimen was collected.

*Solanum coquimbense* is one of three species from Chile that have stamens of unequal length. Each may be distinguished by the form of the leaves, particularly the leaf margin. The margin of *Solanum coquimbense* is dentate, the lobes rounded and

deeper than those of *S. indivisum*. The leaf bases of *Solanum indivisum* are cuneate and the leaves never petiolate, whereas those of *S. coquimbense* are attenuate and sometimes shortly petiolate. The leaves of *Solanum trinominum* may be readily distinguished from those of both *S. indivisum* and *S. coquimbense* by the secondary lobes arising at the base of the primary lobes. Additionally, the internodes are shorter (c.1.5–2.5 cm) than those of *Solanum indivisum* (c.3–4 cm). Although there are few flowers on the specimens of *Solanum indivisum* and *S. coquimbense* available for study, it appears that the corolla of *S. coquimbense* is rotate, whereas that of *S. indivisum* is pentagonal.

*Solanum coquimbense* is known only from the type specimen, collected at Los Vilos, Coquimbo. Further collections of both this species and *Solanum indivisum* are required. Few details of the habit and habitat of these species are known.

**7. Solanum montanum** L., Sp. Pl. 1: 186 (1753). – *Witheringia montana* (L.) Dunal, Solan. Syn. 2 (1816). – Type: Peru, probably dept. Moquegua, Ilo, illustration in Feuillée (1725, vol. 3: 65, pl. 45) (lecto designated by Knapp & Jarvis, 1990).

*Solanum phyllanthum* Cav., Icones 4: 35 (1797). – *Witheringia phyllantha* (Cav.) Dunal, Solan. Syn. 2 (1816). – Type: Peru, La Madalena, *L. Née* s.n. (lecto MA 476360, designated by Knapp (2007); iso MA 476357, 476358, 476359).

*Witheringia purpurea* Lodd., Bot. Cab. 1892 (1832). – *Solanum purpureum* (Lodd.) Dunal in DC., Prodr. 13(1): 372 (1852). – Type: cultivated in London, no specimens exist (lecto pl. 1892, Loddiges (1832), designated here).

*Solanum tuberiferum* Dunal in DC., Prodr. 13(1): 63 (1852). – Type: Peru, cultivated at Chelsea, England from Mexico, *W. Anderson* s.n. (lecto G-DC, designated here).

*Solanum tuberiferum* var. *arenarium* Dunal in DC., Prodr. 13(1): 63 (1852). – *Solanum pocote* Hieron., Bol. Acad. Cienc. Córdoba 4: 384 (1882). – Type: Peru, sin. loc., *J. Dombey* s.n. (lecto P 384600, designated here; iso P 384601).

Perennial herb, often scandent or prostrate, 10–30(–50) cm tall, sometimes arising from a subterranean spheroidal swollen caudex 10–30(–40) mm in diameter, occasionally elongate and up to 75 mm long. *Stems* slender, glabrous to sparsely pubescent or rarely moderately pubescent, the hairs uni- or multicellular, up to 0.5 mm long. *Sympodial units* unifoliate. *Leaves* simple, the blades (1.1–)1.7–8.5(–13.5) × (0.8–)1–6(–11) cm, 0.8–2.2 times as long as wide, ovate to elliptic, succulent or semi-succulent, both surfaces glabrous to sparsely pubescent, rarely moderately to densely pubescent, particularly along the veins, the hairs multicellular, up to 0.5 mm long; base decurrent; margin subentire to deeply lobed with 2–3 pairs of lobes, the lobes 0.3–2(–4) × 0.4–1(–2.2) cm, the lobe apex acute; leaf apex acute; petioles 0–1.5(–4.5) cm, sometimes indistinct and with a wing up to 5 mm wide each side, pubescent with hairs like those of the leaf lamina. *Inflorescences* 2–11.5(–19) cm, sometimes arising midway along the petiole or midrib of the associated leaf, unbranched or branching once, with 4–8(–10) flowers, the axes moderately pubescent, the pedicels more densely so, the hairs appressed, multicellular, sometimes purple, up to 2 mm long;

peduncle (1.5–)3–8(–11.5) cm; pedicels 0.5–1.4(–2) cm at anthesis, 11–25 mm in fruit, spaced 5–10(–15) mm apart in fruit, articulated at the base. *Calyx* 5.5–9.5 mm long, the tube 1–3.5 mm, the lobes equal, 4.5–6 × 1–2 mm at anthesis, 3.5–5 × 2–2.2 mm in fruit, ovate to elliptic, the apex acute to obtuse, moderately to densely pubescent abaxially with uni- or multicellular hairs, these sometimes purple, up to 1 mm long, glabrous to sparsely pubescent adaxially. *Corolla* 1.5–2.6 cm in diameter, pentagonal, white, lilac, purple or violet, often with purplish markings along the abaxial surface, the tube 1–1.5 mm long, the lobes 7.5–13 × 6–13 mm, glabrous to densely pubescent abaxially, especially along the midveins, with multicellular hairs, these sometimes purple, up to 0.5 mm long, glabrous adaxially. *Stamens* equal; filament tube 1–1.5 mm long, glabrous; filaments equal, 1.2–2.5 mm long, glabrous; anthers equal, 2.7–3.5(–5.2) × 0.9–1.2(–1.4) mm, oblong, yellow, the pores tear-drop shaped, rapidly opening into longitudinal slits with age. *Style* c.5.5 × 0.2 mm, glabrous; stigma clavate, 0.8–1.5 × 0.5–0.7 mm. *Fruit* 0.6–1.1 cm in diameter, pale green to whitish, sometimes with white markings; stone cells absent or a few present, angular, c.1 × 0.7 mm. *Seeds* 1.2–1.4 × 0.8–1 mm, glabrous, pale to dark brown or black, the surface deeply pitted.

*Phenology*. Flowers all year round, but predominantly August and September.

*Distribution and habitat*. Region I (Tarapacá) of northern Chile and the departments of Ancash, Arequipa, Lima, Ica, La Libertad, Lambayeque, Moquegua and Tacna of Peru. On sandy or rocky lomas; 5–1000 m. Fig. 9.

*Etymology*. The epithet *montanum* refers to the 'mountains' or more specifically, to the lomas hillsides of Peru where this plant is common.

*Additional specimens examined*. PERU. **Lambayeque**: Cerro Reque, 580 m, 21 xi 1982, *S. Llatas* 941 (HUT). **La Libertad**: Cerro Cabras, 20 m, 6 viii 1949, *N. Angulo* 1203 (F, HUT, NY); Cerro Campana, 600 m, 30 x 1985, *A. Sagástegui et al*. 12955 (F, HUT, MO, NY); 585 m, 3 xi 2005, *M. Nee et al*. 53564 (BM, HUT, NY); Lomas of Cerro Chiputur, 200–500 m, 14 x 1986, *M.O. Dillon et al*. 4685 (F, HUT, MO, USM); Lomas de Virú, 450 m, 30 ix 1976, *A. López et al*. 8415 (F, HUT, MO, NY); Cerro Reque, 437 m, 1 xi 2005, *M. Nee et al*. 53560 (BM, HUT, NY). **Ancash**: Huarmey, 330 m, 10 x 2000, *M. Weigend et al*. 661 (BM, HUT, USM); Lomas de Casma, 250–300 m, 9 ix 1950, *R. Ferreyra* 8037 (MOL, USM); Lomas de Lupín, 330 m, 1 xi 1986, *M.O. Dillon & J. Santisteban* 4702 (BM, F, MO, USM); Lomas de Mongon, 400 m, 17 ix 1938, *H.E. Stork et al*. 9165 (GH). **Lima**: 5 km north of Barranca, 80 m, 5 ix 1938, *J.L. Morrison & A.A. Beetle* 9100 (GH); Chorillos, 152 m, 15 ix 1923, *J.F. Macbride* 5860 (F, G); Cerro Agustino, 250 m, 9 viii 1952, *C.M. Ochoa* 4815 (HUT); Cerro Chosica, 1000–1100 m, 13 iv 1946, *R. Ferreyra* 736 (MOL); Isla San Lorenzo, 1852, *N.J. Anderson* s.n. (MO); Lomas de Amancaes, 556 m, 22 x 2005, *J. Bennett et al*. 93 (BM, USM), 94 (BM, NY, USM), 95 (BM, NY, USM), 96 (USM), 97 (BM, USM), 98 (BM, NY, USM), 99 (BM, USM), 100 (BM, NY, USM), 101 (BM, NY, USM), 102 (BM, NY, USM); 300 m, 12 viii 1948, *C.M. Ochoa* 565 (F, GH, MOL, NY); Lomas de Atocongo, 300–350 m, 24 ix 1974, *G.S. Vilacapoma* 250 (G); Lomas de Carabayllo, 450–850 m, 17 ix 2001, *A. Cano et al*. 10944 (USM); Lomas de Caracoles, 250–300 m, 31 viii 1949, *R. Ferreyra* 6293 (MOL, USM); Lomas de Chancay, 460–550 m, 14 vii 1948, *C.M. Ochoa* 2100 (MOL); Lomas de Cerro Paredes, 300 m, 8 viii 1998, *J. Roque* 675 (USM); Lomas de Iguanil, 2 xi 1986, *C. del Carpio* 64 (USM); Lomas of Lachay,

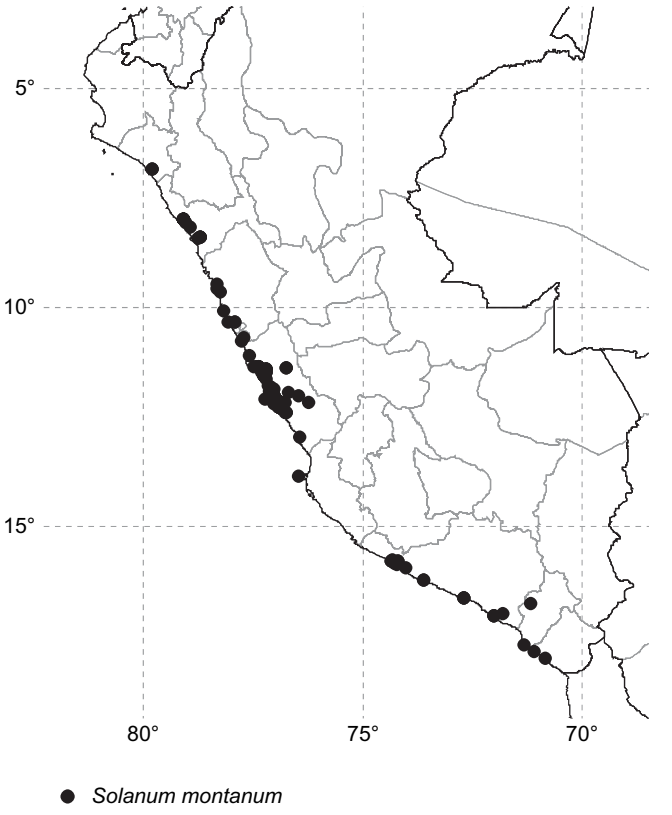


FIG. 9. Distribution map of *Solanum montanum*.

300–500 m, 15 x 1983, *M.O. Dillon et al*. 3636 (F, HUT, MO); Lomas de Lurín, 250–260 m, 8 viii 1971, *R. Ferreyra* 17739 (USM); Lomas de Pachacamac, 100 m, 4 vii 1976, *A. Lourteig* 3120 (USM); Lomas de Pacta, 300 m, ix 2001, *M.I. La Torre et al*. 3155 (USM); Lomas de Pucará, 200–300 m, 9 ix 1992, *R. Ferreyra* 21066 (USM); Morro Solar, 200–250 m, viii 1910, *A. Weberbauer* 5687 (GH); San Agustín, 27 ix 1940, *E. Asplund* 13782 (G, US); San Bartolo, 10 xii 1987, *D. Zerpa* s.n. (USM); Quebrada Verde, 250–350 m, 27 ix 1997, *M. Weigend & H. Förther* 547 (F, HUT, USM). **Arequipa**: 8 km north of Atiquipa, 100 m, 20 ix 1938, *C.R. Worth & J.L. Morrison* 15674 (GH); entre Camaná y Arequipa, 400–500 m, 10 xi 1947, *R. Ferreyra* 2565 (USM); Cachendo, 914 m, 1 xi 1937, *D. Stafford* 1026 (BM, K); 10 km east of Chala, 50–100 m, 19 ix 1938, *C.R. Worth & J.L. Morrison* 15609 (GH); Lomas de Atiquipa, 150–750 m, 17 x 1997, *M. Weigend & H. Förther* 924 (F, HUT, USM); Lomas de Camaná, 20 xi 1961, *O. Tovar* 3442 (USM); lomas cerca a Chala, 100–150 m, 20 viii 1946, *R. Ferreyra* 1492 (USM); Lomas de Capacc, 400 m, 18 x 1946, *R. Ferreyra* 1410 (USM); Lomas de Chamas, 1 x 1976, *A. Salas* 17254 (MOL); Lomas de Cháparra, 400–500 m, 10 x 1955, *R. Ferreyra* 11438 (USM); 6 km northeast of Mollendo, 400 m, 29 ix 1938, *C.R. Worth & J.L. Morrison* 15750 (GH). **Moquegua**: Lomas de la Huitrera, 16 v 1980, *C.M. Ochoa & A. Salas* 11255 (US); Lomas de Tacahuay, 400–700 m, 3 xii 1997, *Anon*. 394 (NY). **Tacna**: Morro Sama, 600–700 m, 7 x 1957, *R. Ferreyra* 12650 (USM).

CHILE. **Region I (Tarapacá)**: Punta Patache, 8 xi 1997, *W. Sielfeld* 38 (SGO).

*Solanum montanum* is a common plant of the lomas of coastal Peru. Some specimens are notable for the swelling of the subterranean caudex which forms a small 'tuber-like' structure. Although this is not homologous to the true tubers of potato (*Solanum tuberosum* L.), this feature has given rise to its common name '*papa de loma*'. Field investigations of populations of *Solanum montanum* have shown that this character is not constant (pers. obs.) and may perhaps be related to environmental conditions (e.g. rainfall). In general, plants that develop a swollen caudex have a small, compact habit, with leaves that are to some degree petiolate with a subentire margin (similar to the type illustration of *Solanum montanum*). In contrast, other specimens (similar to the type specimen of *Solanum phyllanthum*) have a more robust and spreading habit, with leaves that are strongly decurrent on a winged petiole and have a lobed margin. In this respect they are similar to *Solanum paposanum* from high altitude regions of Chile, with which they share the unusual arrangement of the inflorescence in which the peduncle arises some way along the midrib of a bract-like leaf. However, the leaves of *Solanum paposanum* are always densely velutinous whereas those of *S. montanum* are subglabrous. A whole range of intermediate forms can be found and *Solanum phyllanthum* Cav. is here reduced to synonymy with *S. montanum*.

**8. Solanum paposanum** Phil., Fl. Atac. 42 (1860). – Type: Chile, region II (Antofagasta), Paposo, *R.A. Philippi* s.n. (lecto SGO 55605, designated here; iso SGO 42759). **Fig. 10.**

*Solanum crassipes* Phil., Anales Univ. Chile 91: 14 (1895). – *Solanum phyllanthum* Cav. var. *crassipes* (Phil.) Witasek ex Reiche, Anales Univ. Chile 124: 443 (1909). – Type: Chile, region III (Atacama), Bandurrias, Quebrada del Molle, *G. Geisse* s.n. (lecto SGO 55610, designated here; iso SGO 42744, 71699, 72365).

*Solanum aberrans* Phil., Anales Univ. Chile 91: 15 (1895). – *Solanum phyllanthum* Cav. var. *aberrans* (Phil.) Witasek ex Reiche, Anales Univ. Chile 124: 443 (1909). – Type: Chile, region IV (Coquimbo), Andes de Llapel, Las Mollacas, i 1888, *R.A. Philippi* s.n. (lecto SGO 55609, designated here; iso SGO 42768).

Perennial, erect or procumbent shrub up to 60 cm tall. *Stems* woody, sparsely pubescent with uni- or multicellular hairs up to 0.5 mm long, glabrescent; internodes with a wing up to 3 mm wide, sparsely to moderately pubescent adaxially, velutinous abaxially. *Sympodial units* apparently difoliate, the two leaves oppositely arranged, strongly anisophyllous, the smaller leaf sessile and appearing bract-like, adnate to and arising (0–)0.8–3 cm along the peduncle. *Leaves* simple, the blades 2.4–6 × 4.8–11.5 cm, 1.4–2.8 times as long as wide, ovate to oblong, sparsely to moderately pubescent adaxially, velutinous abaxially with multicellular hairs to 0.5 mm long, olive green above, paler below; base decurrent on the winged petiole; margin deeply incised with (2–)4–5 pairs of regularly spaced lobes, the lobes serrate, up to 15 mm long, decreasing in size from the leaf base to the apex, the basal side of lobes concave, the apical side convex; lobe apices acute; petioles indistinct, winged from the decurrent leaf bases, the wings up to 10 mm wide on each side. *Inflorescences* (5–)7–11 cm long,

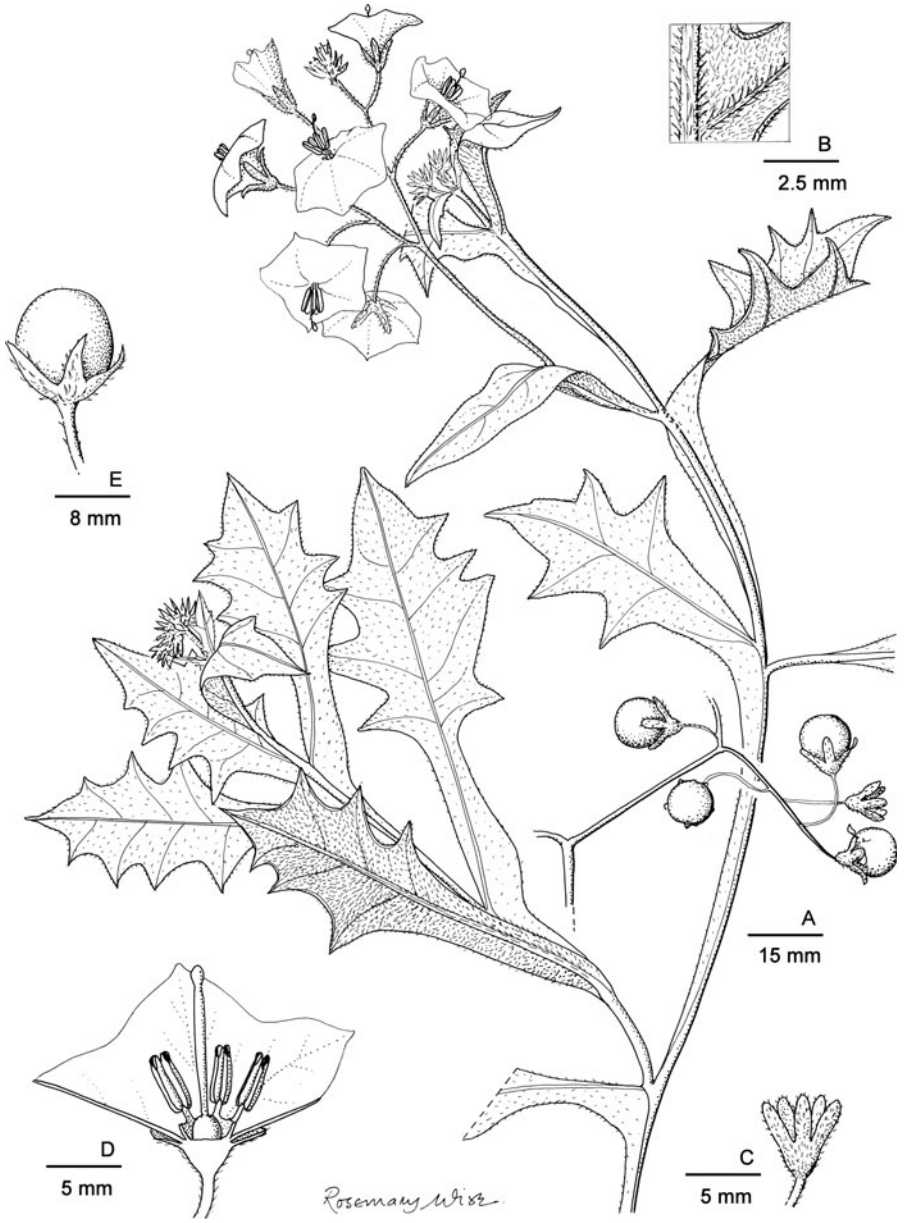


FIG. 10. *Solanum paposanum* Phil. A, habit; B, abaxial leaf surface; C, calyx; D, flower; E, fruit and calyx. Drawn from *Weigend & Weigend* 2000/13 (F).

leaf-opposed, branched up to 3 times, with 6–8 flowers, the axes densely pubescent with uni- or multicellular hairs up to 0.5 mm long; peduncle 4–7(–9.5) cm; pedicels 0.2–2.3 cm at anthesis, (0.5–)1–2.2 cm in fruit, spaced 6–10 mm apart in fruit. *Calyx* 5–8 mm long, the tube 2–4.5 mm long, the lobes equal, 2–5.5(–7) × 1–2(–3) mm at

anthesis, 4–7 × 1.3–2.9 mm in fruit, lanceolate or elliptic, green with red-purple stripes, moderately pubescent adaxially, densely so abaxially with multicellular, white or purple hairs up to 0.5 mm long, the apex acute. *Corolla* (1.6–)2–3.2 cm in diameter, pentagonal, blue, lilac or purple, the tube 2–2.5 mm long, the lobes (6–)9–12 × 8–18 mm, moderately to densely pubescent abaxially with multicellular hairs up to 0.5 mm long, glabrous adaxially. *Stamens* equal; filament tube 2–3 mm long, glabrous; filaments equal, 2–2.5 mm long, glabrous; anthers equal, 4.5–5.5 × 1–1.2 mm, oblong, the apex rounded, yellow, the pores directed distally, rapidly opening into longitudinal slits with age. *Style* 9–10 × 0.1–0.3 mm, glabrous; stigma 0.4–1 × 1–2.5 mm, clavate. *Fruits* 0.7–1.1 cm in diameter, green with black markings; stone cells present, few in number, rounded, 1–1.5 mm in diameter. *Seeds* c.2 × 1.5 mm, pale brown, the surface shallowly pitted.

*Phenology*. Flowers January to November.

*Distribution and habitat*. Chile [regions I (Tarapacá), II (Antofagasta), III (Atacama), IV (Coquimbo)] and Peru (departments Arequipa, Ica, Lima, Moquegua, Tacna); 200–3500 m. Fig. 11.

*Etymology*. Named after Paposo in Chile where the type was collected.

*Selected additional specimens examined*. PERU. **Lima**: Lurínta1 bei Pachacamac, 29 vii 1985, *G.K. Müller & G. Krebs* 12201 (B); Matucana, 2300 m, 12 iv 1922, *J.F. Macbride & W. Featherstone* 331 (G); valley of Rio Rimac, 1900 m, 21 iv 1942, *T.H. Goodspeed* 33111 (A, G, MO); Viso, 23 iv 1939, *T.H. Goodspeed et al*. 11522 (G, GH). **Ica**: Km 37 on road Nazca-Puquio, 2200 m, 2 x 1997, *M. Weigend & H. Förther* 659 (HUT, USM). **Arequipa**: Arequipa-Yura, 2500 m, 23 iii 1970, *A. López* 7373 (GH, HUT, MO); Baños de Jesús, 2600 m, 16 xi 1957, *A. Sagástegui & H. Aguado* 2602 (HUT); Chachani mountain, 2439 m, iii 1920, *F.E. Hinkley* 9 (GH, NY); road from Juliaca to Arequipa, 3100 m, 28 ix 2002, *M. Ackermann* 415 (BM, F, USM); Quiscos, 3052 m, 26 i 1937, *J. West* 8214 (GH, MO); Quebrada Huayrondo, Cerro Verde, 2300–2600 m, 6 ii 1995, *A. Cano* 6449 (USM); Torrentera, 2800 m, 7 iv 1973, *G. Arenas* 94 (USM). **Moquegua**: cerca a Toquepala, 3400–3500 m, 29 iv 1963, *R. Ferreyra & Smith* 14867 (USM); c.41 km NE of Moquegua, 2550 m, 15 xi 1986, *M.O. Dillon et al*. 4814 (BM, F, HUT, USM); Torata, 3000–3130 m, 5 ix 1997, *J. Albán & N. Malca* 10241 (USM). **Tacna**: Candarave, 3000 m, 15 iv 1942, *R.D. Metcalf* 30372 (A, G, MO); Camino a Caro, 3070–3480 m, 5 xii 1997, *M.I. La Torre* 1835 & 1843 (USM).

CHILE. **Region I (Tarapacá)**: Usmagama, 15 ii 1885, *C.F. Rahmer* s.n. (SGO); Pampa de Zapahuira, 3400 m, 13 iv 1994, *W.A. Smith* 6 (MO); Putre-Zapahuira, 3430 m, 5 xi 1991, *F. Billiet & B. Jadin* 5462 (BM, MO). **Region II (Antofagasta)**: Quebrada Rinconada, 550 m, 12 xi 1991, *F. Billiet & B. Jadin* 5516 (MO); Aguada de Miguel Díaz, 1 xii 1925, *I.M. Johnston* 5381 (GH); Cerro de la Cachina, 14 xii 1925, *I.M. Johnston* 5693 (GH); Tocopilla, 18 x 1925, *I.M. Johnston* 3607 (GH). **Region III (Atacama)**: Cuesta Pajonales, 10 x 1987, *S. Teillier* 1028 (NY, SGO). **Region IV (Coquimbo)**: Coquimbo, ix 1897, *Soehrens* s.n. (SGO); Quebrada Potrerillos, 500 m, 5 xii 1940, *R. Wagenknecht* 18113 (GH).

*Solanum paposanum* is most similar to *S. montanum*, particularly to the larger and more branched specimens formerly considered *S. phyllanthum*. However, *Solanum paposanum* may be distinguished by the dense, velvety indumentum of the leaves, especially of the lower surface, in contrast to the glabrous to moderately pubescent

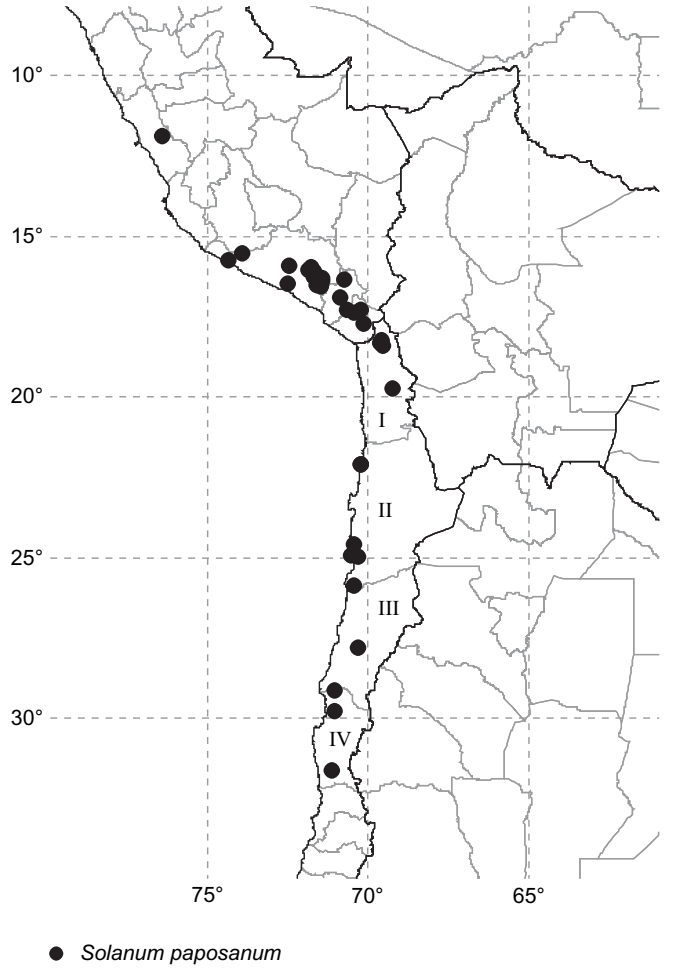


FIG. 11. Distribution map of *Solanum paposanum*. Roman numerals indicate the regions of Chile (region I, Tarapacá; region II, Antofagasta; region III, Atacama; region IV, Coquimbo).

leaves of *S. montanum*. *Solanum paposanum* is found almost exclusively at higher altitudes, usually between 1500 and 3400 m; only three specimens have a recorded altitude of less than 1000 m (*Hjerting* 1141, *Ferreyra* 4039 and *Anon*. 2199). *Solanum paposanum* and *S. montanum* have broadly non-overlapping distributions, with almost all collections of *Solanum paposanum* being from southern Peru and northern Chile. It is one of the few species of *Solanum* section *Regmandra* that occurs in both Chile and Peru.

The inflorescences of *Solanum paposanum* are unusual for the presence of a small 'bract-like' leaf adnate to, and in some cases arising some way up, the peduncle. This leaf is usually smaller and narrower than normal leaves. The peduncle arises opposite an additional, normal-sized leaf. Thus, the sympodial structure may be described as

difoliate, with the two leaves separating successive inflorescences, or unifoliate if the smaller bract-like organ is not regarded as a true leaf.

Two species described by Rodolfo Philippi from Chile, *Solanum aberrans* and *S. crassipes*, are placed in synonymy. The type material of *Solanum aberrans* is of poor quality, but the leaves are described as pilose-muricate with a sinuate-dentate margin and the species is most probably *S. paposanum*.

**9. Solanum herbabona** Reiche, Anales Univ. Chile 124: 443 (1909). – Type: Chile, region III (Atacama), Hierba Buena, *K.F. Reiche* s.n. (lecto SGO 55606, designated here).

Annual or perennial herb up to 40 cm tall. *Stems* green, slender, becoming woody, the young stems densely pubescent, the hairs erect, glandular or eglandular, uni- or multicellular, up to 0.5 mm long. *Sympodial units* plurifoliate. *Leaves* simple, the blades (1.6–)2–5 × (1–)1.5–4 cm, 1–1.6 times as long as wide, ovate, probably not fleshy, densely velutinous adaxially and along the midvein, moderately velutinous abaxially with multicellular hairs up to 0.5 mm long; base truncate; margin regularly lobed, with 3–4 pairs of lobes, the lobes serrate, the apical side of lobes straight or convex, the basal side convex, lobe apex acute to obtuse; leaf apex acute; petioles (0–)1–2.5(–3) cm, absent on smaller leaves, occasionally narrowly winged, the wings densely pubescent with hairs like those of the lamina. *Inflorescences* up to 5 cm long, leaf-opposed, unbranched or branching once, with 2–4 flowers, the axes densely pubescent with uni- or multicellular hairs up to 0.5 mm long; peduncle 1–2 cm; pedicels 8–15 mm at anthesis, 2–2.5 cm in fruit, spaced 5–7 mm apart in fruit, articulated at the base. *Calyx* 5.5–10.5 mm long, the tube 2–2.5 mm, the lobes 3.4–5 × 1.4–1.5 mm at anthesis, 6.5–8.5 × 2.1–3.5 mm in fruit, lanceolate, the apex acute, both surfaces moderately to densely pubescent with multicellular hairs up to 0.5 mm long. *Corolla* c.1.2 cm in diameter, pentagonal, blue, the tube c.2 mm long, the lobes c.8 × 10 mm, densely pubescent abaxially with white, uni- or multicellular hairs up to 0.2 mm long, glabrous adaxially. *Stamens* equal; filament tube c.2 mm long, glabrous to sparsely pubescent with white, unicellular hairs up to 0.1 mm long; filaments equal, c.0.8 mm long, with indumentum as the filament tube; anthers 5–5.5 × c.1.5 mm, oblong, colour unknown, the pores tear-drop shaped, directed distally, tardily opening into longitudinal slits with age. *Style* c.10 × 0.2 mm, glabrous to densely pubescent in lower 2/3 with white, unicellular hairs to 0.1 mm long; stigma capitate to clavate, c.0.6 × 0.5 mm. *Fruit* 6–12 mm in diameter, colour unknown, stone cells few, c.0.8–1 mm long. *Seeds* 3–4 × 3 mm, pale brown, shiny, the surface shallowly pitted.

*Phenology*. Flowers October to November.

*Distribution and habitat*. Endemic to region III (Atacama) of Chile; c.800 m. Fig. 8.

*Etymology*. Named after Hierba Buena [ = Yerba Buena] in Chile where the type specimen was collected.

*Additional specimens examined*. CHILE. **Region III (Atacama)**: Vallenar, 800 m, xi 1923, *E. Werdermann* 170 (BM, GH); Vallenar, 16 x 1992, *M. Muñoz* 3121 (SGO); Yerba Buena, 29 ix 1885, *A. Borchers & R.A. Philippi* s.n. (BM); Yerba Buena, *E.C. Reed* s.n. (BM).

Known from only six collections (including the type), *Solanum herbabona* is restricted to the region around Vallenar in Atacama, extending south near to the border with Coquimbo. The species is easily recognised by the leaves which are usually petiolate with truncate bases. No details are known of its habitat, and further collections are required.

**10. Solanum edmonstonei** Hook.f., Trans. Linn. Soc. 20: 201 (1847). – Type: Protologue and specimen label states 'Charles Island, Galapagos', but probably collected along the coast of Chile or Peru, *T. Edmonston* s.n. (lecto K 5299, designated here; iso CGE n.v., TCD).

*Solanum murphyi* I.M.Johnst., Contrib. Gray Herb. 95: 34 (1931). – Type: Peru, Viejas Island, *R.C. Murphy* 3219 (holo BKL 4336).

*Solanum ferreyrae* Ugent, Phytologia 31: 18 (1975) [as *ferreyrii*]. – Type: Peru, dept. Arequipa, between Nazca and Chala, *R. Ferreyra* 1523 (holo US US1998785; iso MO, MOL).

*Solanum andersonii* Ochoa, Phytologia 46: 225 (1980). – Type: Peru, dept. Ica, Marcona, *C.M. Ochoa* 13026 (holo herb. Ochoa n.v.; iso MOL, US).

Perennial, erect shrub 60–100 cm tall, sometimes arising from a thickened woody rootstock up to 12 mm thick. *Stems* pale brown, woody, glabrous to sparsely pubescent with multicellular hairs up to 0.6 mm long, glabrescent. *Sympodial units* plurifoliate. *Leaves* simple, the blades 1.2–4(–5.5) × 0.3–2(–2.7) cm, 1.9–2.7(–4) times as long as wide, ovate or oblong, probably fleshy, both surfaces glabrous to moderately pubescent with multicellular hairs up to 0.5 mm long; base decurrent; margin regularly or occasionally irregularly lobed with (2–)3–5 pairs of primary lobes, the lobes (2–)4–9 × 1–3(–5.5) mm, serrate, the basal side of lobes concave or straight, the apical side convex, the margin entire or erose, sometimes with smaller secondary lobes arising from the apical side, the lobe apex obtuse to acute; petioles 0–1.4 cm, glabrous. *Inflorescences* 4–9 cm, often borne on leafy axillary shoots, leaf-opposed, unbranched or branching once, with 1–11 flowers, the axes glabrous to densely pubescent with multicellular hairs up to 0.5 mm long; peduncle 2.5–4(–6) cm; pedicels 2–10 mm at anthesis, 8–16(–19) mm in fruit, spaced 3–12 mm apart in fruit. *Calyx* (5–)7–8(–9) mm long, the tube 1–3 mm, the lobes equal, 2.5–7 × 1–2.5 mm, not accrescent, narrowly elliptic to lanceolate, the apex acute, both surfaces glabrous or sparsely pubescent abaxially towards apex and along margins with unicellular hairs up to 0.2 mm long. *Corolla* 1.5–2.5(–3.2) cm in diameter, rotate to campanulate, pale blue, violet or lilac, the tube c.2 mm long, the lobes 1.6–2.4 × 0.6–1 cm, sparsely pubescent abaxially with uni- or multicellular white hairs up to 0.5 mm long, glabrous adaxially. *Stamens* equal; filament tube 2.5 mm long, glabrous; filaments equal, c.2 mm long, glabrous; anthers equal, 2.5–5.5 × 1–1.5 mm, oblong, yellow,

the pores directed distally, opening into longitudinal slits with age. *Style* c.9 × 0.2–0.3 mm, glabrous; stigma clavate, 1–2 × 0.7 mm. *Fruit* 6–9 mm in diameter, colour unknown; stone cells absent. *Seeds* 1.5–1.6 × 1–1.1 mm, dark brown, the surface deeply pitted.

*Phenology*. Flowers May to November.

*Distribution and habitat*. Peru (departments of Arequipa and Ica). On sandy or rocky coastal lomas; 300–1080 m. Fig. 8.

*Etymology*. Named in honour of its collector, Thomas Edmonston (1825–1846), a young Scottish botanist who was the naturalist aboard the frigate HMS *Herald*. After sailing around Cape Horn and visiting the Galapagos Islands, the ship stopped at several localities along the coast of Peru; on 24 January 1846, whilst Edmonston was re-embarking at Sua Bay, a rifle was accidentally fired and Edmonston was instantly killed (Allen, 2004).

*Additional specimens examined*. PERU. **Ica**: San Gallán Island, 330–440 m, 27 xi 1919, *R.C. Murphy* 3479 (BKL); Viejas Island, 17 xi 1919, *R.C. Murphy* 3222 (GH); Viejas Island, 17 xi 1919, *R.C. Murphy* 3220 (GH); c.47 km S of Nasca, 620–700 m, 20 ii 1998, *M.O. Dillon et al.* 8186 (HAO); San Juan de Marcona, 810 m, 19 xi 1994, *A. Cano et al.* 6160 (USM); lomas de los alrededores de las minas de Marcona, 800 m, 22 ix 1958, *R. Ferreyra* 13369 (MO, USM); Lomas de Marcona, 840 m, 17 xi 1994, *A. Cano et al.* 6127 (USM); Cerro Lechuza, Paracas, 10 x 1978, *E. Peralta & S. Garcia* s.n. (USM). **Arequipa**: Lomas de Jahuay, 300–400 m, 3 x 1957, *R. Ferreyra* 12487 (G). **Moquegua**: Pampa de Marcona, 700 m, 12 x 1978, *C. Ochoa* 13026 (MOL).

*Solanum edmonstonei* is known from relatively few collections and is restricted to the coastal area around Ica and the nearby islands of Viejas and San Gallán. This species resembles *Solanum trinominum*, but has stamens of equal lengths, rotate or campanulate corollas and the plant is usually glabrous or only moderately pubescent. The lack of recent good quality specimens makes delimitation problematic, and without adequate knowledge of the infraspecific variation it is difficult to accept the three species listed here in synonymy as distinct species. The leaves of the type material of *Solanum andersonii* at MOL (although not those of the rather poor quality duplicate held at US) are larger than those of the other specimens. However, their shape is consistent with other typical specimens of *Solanum edmonstonei* such as *Ferreyra* 13369. There is some similarity in this respect with the variation in leaf size in natural populations of *Solanum multifidum*, which highlights the need for further field studies of *S. edmonstonei*.

The protologue of *Solanum edmonstonei* states that the plant was collected from Charles Island of the Galapagos by Thomas Edmonston. No further specimens of *Solanum edmonstonei* have ever been collected from the Galapagos, and it is likely that Edmonston's collection was mislabelled. The account of the voyage of HMS *Herald* (Seemann, 1853) indicates that the ship docked periodically along the coast of Peru, and it is likely that the collection was made during one of these stops, probably in the department of Ica.

**11. Solanum pinnatum** Cav., Icon. 5: 23 (1799). – *Witheringia pinnata* (Cav.) J.Rémy in Gay, Fl. Chil. 5: 72 (1849). – Type: Chile, region IV (Coquimbo), Coquimbo, *L. Née* s.n. (lecto MA 656494, left hand specimen, designated by Knapp (2007)). **Fig. 12.**

*Solanum runcinatum* Ruiz & Pav., Fl. Peruv. 2: 36 (1799). – Type: Chile, sin. loc., *H. Ruiz & J. Pavón* s.n. (lecto OXF, designated here; iso B† [F negative 2738]).

*Solanum maritimum* Meyen ex Nees, Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur., Suppl. 19: 384 (1843). – *Witheringia maritima* (Meyen) J.Rémy in Gay, Fl. Chil. 5: 72 (1849). – Type: Chile, region III (Atacama), Copiapo, *F.J.F. Meyen* s.n. (lecto K, designated here; iso B† [F negative 2735]).

*Witheringia gaudichaudiana* J.Rémy in Gay, Fl. Chil. 5: 71 (1849). – *Solanum gaudichaudiana* (J.Rémy) F.Phil., Cat. Pl. Vasc. Chile 228 (1881). – Type: Chile, region IV (Coquimbo), Coquimbo, *M. Gaudichaud* 61 (lecto P 335385, designated here; iso P 335386, P 335387).

*Solanum novemlobum* Dunal in DC., Prodr. 13(1): 70 (1852). – Type: Chile, region V (Valparaíso), Quillotae, *C.G.L. Bertero* 1326 (lecto G-DC, designated here; iso BM, F, MO, NY).

*Solanum novemlobum* Dunal var. *pauciflorum* Dunal in DC., Prodr. 13(1): 71 (1852). – Type: Chile, sin. loc., *C. Gay* 429 (holo P 366870).

*Solanum gaudichaudii* Dunal in DC., Prodr. 13(1): 60 (1852). – *Solanum gaudichaudii* Dunal var. *viride* Dunal in DC., Prodr. 13(1): 60 (1852). – Type: Chile, region IV (Coquimbo), Coquimbo, 1838, *C. Gay* s.n. (lecto P 335384, designated here).

*Solanum cavanillesii* Dunal in DC., Prodr. 13(1): 61 (1852), *nom. illeg. superfl.*, *Solanum pinnatum* Cav. listed in synonymy.

*Solanum cavanillesii* Dunal var. *subintegrifolium* Dunal in DC., Prodr. 13(1): 61 (1852). – *Solanum pinnatum* Cav. var. *subintegrifolium* (Dunal) Reiche, Anales Univ. Chile 124: 450 (1909). – Types: Chile, sin. loc., *C. Gay* 95 (P n.v.); Chile, sin. loc., *C. Gay* 17 (MPU n.v.).

*Solanum feuillei* Dunal in DC., Prodr. 13(1): 70 (1852). – Type: Chile, region V (Valparaíso), Valparaíso, *L.E. Feuillée* s.n. (G-BOIS n.v. [F photo 8584!]).

*Solanum albiflorum* Phil., Linnaea 33: 202 (1864–1865). – Type: Chile, region IV (Coquimbo), Coquimbo, Illapel, *C.L. Landbeck* s.n. (lecto SGO 42712, designated here).

*Solanum septemlobum* Phil., Anales Univ. Chile 91: 10 (1895). – Type: Chile, region IV (Coquimbo), Aconcagua, Pichidangui, *M. Vidal Gormaz* s.n. (lecto SGO 55538, designated here).

*Solanum pinnatum* Cav. var. *tomentosum* Reiche, Anales Univ. Chile 124: 450 (1909). – Type: Chile, region IV (Coquimbo), Coquimbo, Frai Jorj, *K.F. Reiche* s.n. (lecto SGO 55581, designated here).

Perennial, erect shrub 30–200 cm tall. *Stems* pale brown, brittle, woody, glabrous to moderately pubescent with multicellular hairs up to 0.25 mm long. *Sympodial units* unifoliate, not geminate. *Leaves* simple, fleshy, the blades 1.3–8 × 0.8–5.6 cm, 1.2–2(–2.7) times as long as wide, both surfaces subglabrous to moderately or occasionally densely pubescent, the hairs multicellular, up to 0.5 mm long; base

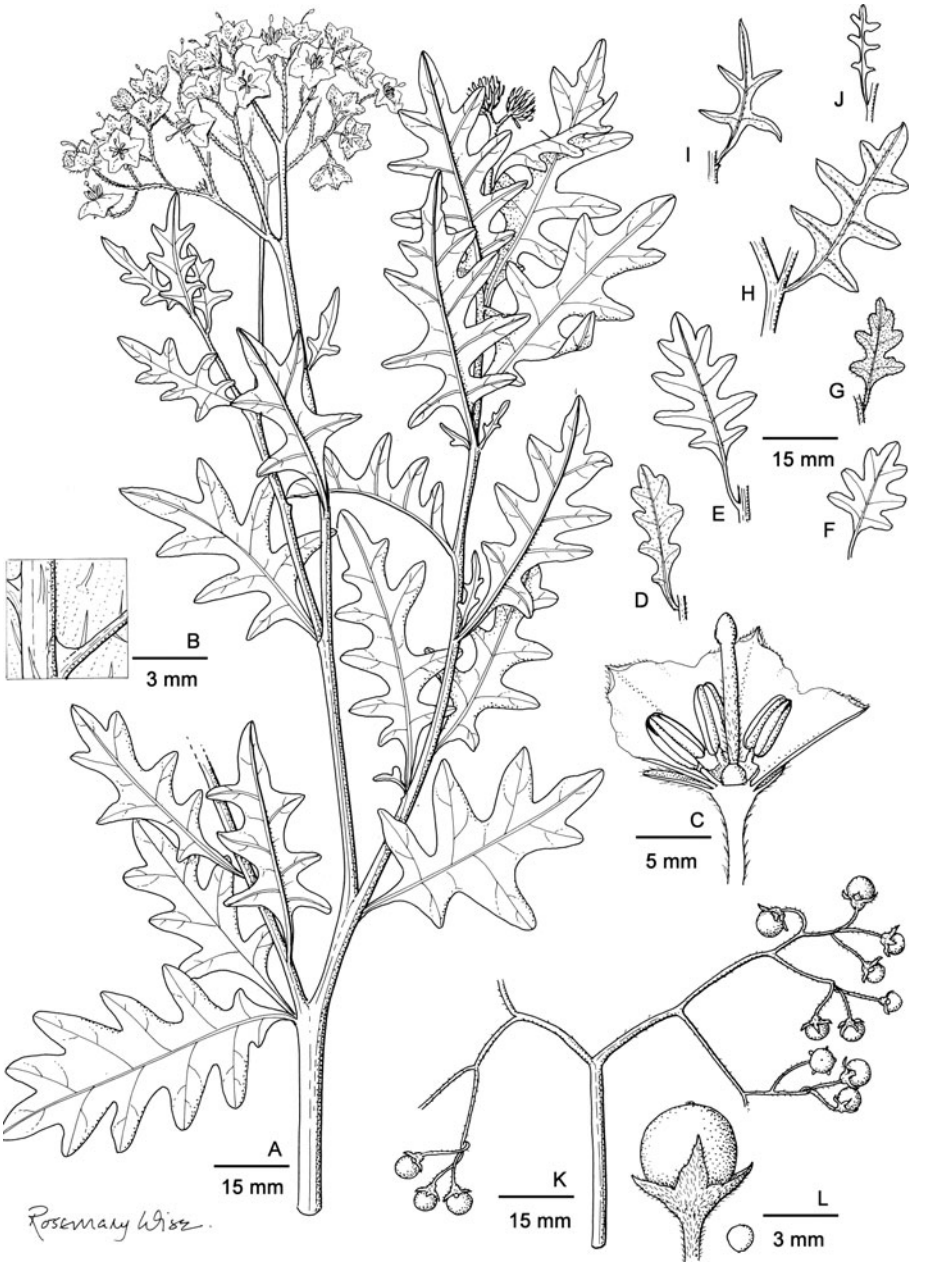


FIG. 12. *Solanum pinnatum* Cav. A, habit; B, abaxial leaf surface; C, flower; D–J, variation in leaf form; K, infructescence; L, fruit and seed. A–C drawn from *Bertero* 1326 (BM), D drawn from *Anon.* s.n. (SGO), E drawn from *Skottsberg* 1045 (NY), F drawn from *Lammers* 7907 (F), G drawn from *Werdermann* 898 (BM), H drawn from *Cabrera* 11409 (SGO), I drawn from *Landrum* 5664 (NY), J drawn from *Meza* 1196 (SGO), K & L drawn from *Lauderman* 220 (BM).

decurrent; margin regularly lobed with 3–5 pairs of lobes, the lobes 3–24 × 1–9 mm, 1.8–5 times as long as wide, dentate or serrate, elliptic to ovate, the basal and apical sides of lobes convex; lobe apex acute to rounded; petioles 0–20 mm, with indumentum like that of leaf blades. *Inflorescences* 3–17 cm long, borne on terminal and axillary shoots, branched 2–3 times, with 12–30(–40) flowers, the axes subglabrous to densely pubescent with appressed, multicellular hairs up to 0.6 mm long; peduncle 0.5–12 cm; pedicels 3–8 mm at anthesis, 5–10 mm in fruit, spaced 3–5 mm apart in fruit, articulated at the base. *Calyx* 3–5 mm long, the tube 0.8–3 mm, the lobes equal, 2–4.2 × 0.6–1 mm at anthesis, 2–3 × 1.5–1.7 mm in fruit, elliptic to ovate, the apex acute to rounded, subglabrous to densely pubescent adaxially and abaxially with multicellular hairs up to 0.3 mm long. *Corolla* 12–20 mm in diameter, pentagonal, chartaceous, white, violet, purple or blue, the tube 1–3 mm long, the lobes 6–10 × 5.5–12 mm, moderately to densely pubescent abaxially, especially in bud and towards the lobe apices, the hairs simple, uniseriate, multicellular, up to 0.4 mm long, glabrous adaxially. *Stamens* 5, equal; filament tube 1–1.2 mm, glabrous; filaments equal, 1–2 mm long, glabrous; anthers equal, 3–4.5 × 1–1.5 mm, oblong, yellow, poricidal at the tips, the pores tear-drop shaped and opening into longitudinal slits with age. *Style* 5–6 × c.0.2 mm, glabrous to densely pubescent in lower 2/3 with white, unicellular hairs to 0.1 mm long; stigma capitate or clavate, 0.9–1 × 0.6–0.8 mm. *Fruit* 3–4 mm in diameter, globose, glabrous, green, few-seeded; stones cells present, abundant, rounded, c.0.5 mm in diameter. *Seeds* 1.4–1.5 × 1.6–1.8 mm, pale brown, the surface shallowly pitted.

*Phenology*. Flowers April to February.

*Distribution and habitat*. Endemic to Chile [regions I (Tarapacá), II (Antofagasta), III (Atacama), IV (Coquimbo), V (Valparaíso), VI (Libertador General Bernardo O'Higgins), VIII (Bío-Bío), Metropolitana]. On dry, sandy or rocky coastal slopes and dunes; 0–2300 m. Fig. 13.

*Typification notes*. The specimens listed under the two varieties of *Solanum gaudichaudii* Dunal belong to three different species. The two Chilean collections listed under *Solanum gaudichaudii* var. *viride*, *Gaudichaud* 61 (G-DC) and *Gay* s.n. (P), are both specimens of *S. pinnatum* as delimited in this revision. The Paris specimen (P 335384) has been chosen as a lectotype of *Solanum gaudichaudii* var. *viride* and also of *S. gaudichaudii*. For further discussion on the typification of *Solanum gaudichaudii* var. *canescens*, see under *S. trinominum*.

Dunal lists two specimens of *Solanum cavanillesii* Dunal var. *subintegrifolium* Dunal collected by Claudio Gay in Chile. A search of the Paris herbarium failed to locate *Gay* 95, and *Gay* 17 is presumed to be at MPU, but has not been seen. As I have not been able to see either of these specimens I am unable to designate a lectotype.

*Etymology*. The epithet *pinnatum* means with feather-like divisions and refers to the strongly lobed leaves. However, the leaves of *Solanum pinnatum* are not strictly pinnate since the lamina is not divided completely to the rachis.

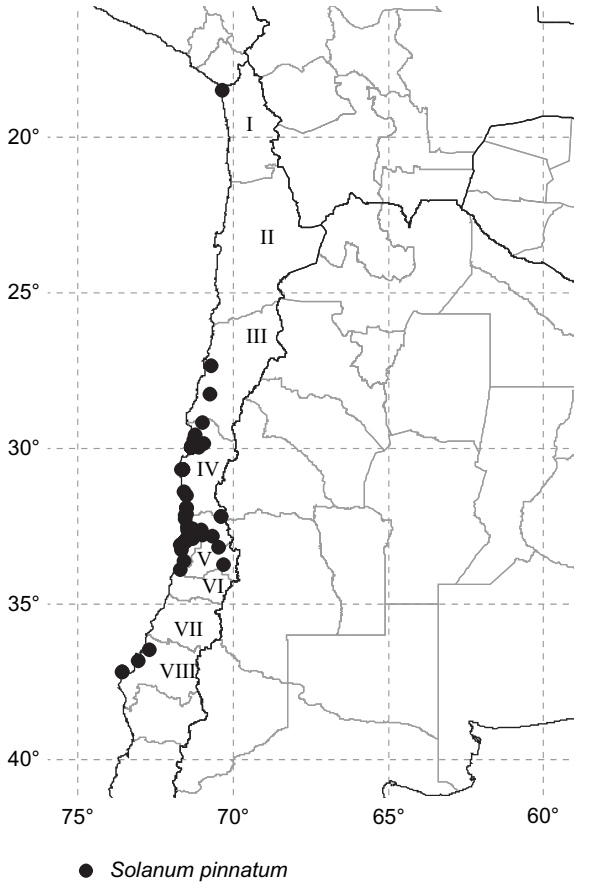


FIG. 13. Distribution map of *Solanum pinnatum*. Roman numerals indicate the regions of Chile (region I, Tarapacá; region II, Antofagasta; region III, Atacama; region IV, Coquimbo; region V, Valparaíso; region VI (Libertador General Bernardo O'Higgins); region VII, Maule; region VIII, Bío-Bío).

*Additional specimens examined*. CHILE. **Region I (Tarapacá)**: Arica, ix 1926, *F. Jaffuel* 20 (GH); Punta Lobos, 1 xi 1997, *R. Pinto* s.n. (SGO). **Region III (Atacama)**: Monte Amargo, *F. Philippi & A. Borchers* s.n. (BM). **Region IV (Coquimbo)**: Choapa, 8.9 km north of Los Vilos, 100 m, 28 x 1990, *T.G. Lammers et al*. 7531 (F); Coquimbo, 100 m, xi 1923, *E. Werdermann* 108 (BM, E, G, GH, MO, SI); Cuesta Porotos, c.30 km N of La Serena, 50 m, 3 xii 1987, *S.S. Landrum & L.R. Landrum* 5664 (NY); La Higuera, 20 m, 8 xii 1997, *M.F. Gardner & K.L. Matthews* 86 (E); Lagunillas, 11 x 1987, *O. Zöllner* 15076 (MO); Fray Jorge, 500 m, xi 1925, *E. Werdermann* 898 (B, BM, E, G, GH, K, MO, NY, SI, US); Fray Jorge National Park, 632 m, 4 xii 2004, *P. Baxter et al*. DCI1825 (CONC, E, SGO); Limari, between Guanaqueros and Route 5, 20 m, 27 ii 1993, *M.F. Gardner & S.G. Knees* 5650 (E); Los Vilos, 20 m, 8 x 1965, *G. Montero* 7212 (G); Orillas de la Pampila, 70 m, 29 xi 2004, *P. Baxter et al*. DCI1728 (CONC, E, SGO); Quilimarí, 26 x 1985, *O. Zöllner* 12516 (MO); Cuesta de Pajonales, 10 i 1973, *C. Marticorena et al*. 619 (B); Punto Tortuga, 25 m, 31 x 1990, *T.G. Lammers et al*. 7642 (F); Totoralillo, 79 m, 29 xi 2004, *P. Baxter et al*. DCI1719 (CONC, E, SGO); c.53 km north of Vallenar, 100 m,

1 xi 1938, *C.R. Worth & J.L. Morrison* 16324 (G, GH, K, MO). **Region Metropolitana**: San Antonio, 35 m, 12 i 1936, *G. Montero* 2671 (GH); Santo Domingo, 7 xii 1930, *G. Looser* 1454 (GH). **Region V (Valparaíso)**: Bucalemu, i 1878, *Sanfurgo* s.n. (SGO); Chagres, 13 ix 1975, *O. Zöllner* 8284 (MO); Concón, *J. Miers* 62 (BM); Laguna Virde, 7 x 1930, *A. Garaventa* 2125 (GH); Papudo, 18 ix 1919, *E.W.D. Holway & M.M. Holway* 38 (GH, NY); Quebrada El Lúcamo, 98 m, 21 xi 2004, *P. Baxter et al.* DCI1554 (CONC, E, SGO); Reñaca, 5 m, 10 xii 1938, *J.L. Morrison* 16851 (GH, K); Tunquén, 5 xi 1995, *H. Niemeyer & C. Fernández* 9595 (SGO); Valparaíso, 1832, *H. Cuming* 424 (BM, E, GH, K); Viña del Mar, 26 ii 1952, *O. Boelcke* 6463 (MO); Zapallar, ix 1920, *F. Jaffuel* 746 (GH); Zapallar, 50 m, 7 ii 1992, *M.F. Gardner & C.N. Page* 5094 (E). **Region VI (Libertador General Bernardo O'Higgins)**: Pichilemu, 6 m, 5 ii 2004, *P. Brownless et al.* P1234 (BM, E). **Region VIII (Bío-Bío)**: Concepción, *A. Caldcleugh* s.n. (K); Llico, xii 1861, *R.A. Philippi* s.n. (W).

*Solanum pinnatum* is a morphologically variable species from Chile. The leaf shape and indumentum are particularly variable, ranging from small, narrowly dissected leaves with the lobes almost needle-like (such as those of the type of *Solanum maritimum*) to much larger and more rounded lobes (such as those of the type of *S. novemlobum*). An examination of a large number of specimens has shown that the shape and size of the leaves vary continuously and cannot be divided into discrete taxa. Consequently, a large number of previously described taxa are here placed in synonymy.

The species can be recognised by the singly lobed leaves and usually dense, many-flowered inflorescences. The calyx and filaments are shorter than those of another Chilean species with lobed leaves, *Solanum paposanum*. *Solanum paposanum* also differs from *S. pinnatum* in the densely velutinous indumentum, which is subglabrous to moderately pubescent in *S. pinnatum*, and the more narrowly acute apices to the leaf lobes in *S. paposanum*. The fruits of *Solanum pinnatum* are unusual among species of *Solanum* section *Regmandra* because they contain a very small number of seeds – the majority of the fruit contents consists of stone cells. The low seed set ($< 5$ seeds per fruit) is particularly intriguing given how widespread this species is in Chile, particularly around Coquimbo and Valparaíso.

## Doubtful and Excluded Names and Names not Validly Published

*Solanum laurentii* S.Mitch., Bot. Mag. 54(1): 2768 (1827), *nomen nudum*.

*Solanum montanum* Ruiz & Pavón, Fl. Peruv. 2: 32 (1799).
This is not a new name since Ruiz and Pavón refer to *Solanum montanum* L.

*Solanum montanum* var. *arenarium* Dunal, Hist. Nat. Solanum 146 (1813).
Although Dunal (1852) referred to this name as if it were a validly published taxon, there is nothing in the publication of 1813 to indicate that this was to be regarded as a new infraspecific taxon.

*Solanum phyllanthum* Cav. var. *minus* Nees, Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur., Suppl. 19: 387 (1843).

*Solanum phyllanthum* Cav. var. *majus* Nees, Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur., Suppl. 19: 387 (1843).

These two names are accompanied by minimal descriptive information and no type material is indicated. They are here interpreted as simply a list of the variation in *Solanum phyllanthum*, which in this treatment is considered a synonym of *S. montanum*, rather than as new taxa.

*Solanum quercifolium* Poepp. ex Dunal in DC., Prodr. 13(1): 70 (1852), *nomen nudum*, in synonymy of *Solanum runcinatum* Ruiz & Pavón (= *S. pinnatum* Cav.).

*Solanum rhopalostigma* Bitter, Abh. Naturwiss. Vereine Bremen 23: 148 (1914), *nomen nudum*.

*Solanum vidali* R.Phil., Verh. Deutsch. Wiss. Verein, Santiago de Chile 2: 108 (1890), *nomen nudum*.

This is probably *Solanum geissei* Phil. (= *S. brachyantherum* Phil.).

*Witheringia montana* (L.) Dunal var. $\beta$, Solan. Syn. 2 (1816). Name invalidly published with no epithet.

*Lycopersicon procumbens* Mill., Gard. Dict. ed. 8 (1768), *nomen dubium*.

This is possibly *Solanum montanum* L.

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## ENUMERATION OF ACCEPTED NAMES AND SYNONYMS

*Solanum aberrans* Phil. = *Solanum paposanum* Phil.
*Solanum albiflorum* Phil. = *Solanum pinnatum* Cav.
*Solanum andersonii* Ochoa = *Solanum edmonstonei* Hook.f.
**Solanum brachyantherum** Phil.
*Solanum cavanillesii* Dunal = *Solanum pinnatum* Cav.
*Solanum cavanillesii* Dunal var. *subintegrifolium* Dunal = *Solanum pinnatum* Cav.
**Solanum coquimbense** J.R.Benn.
*Solanum crassipes* Phil. = *Solanum paposanum* Phil.
**Solanum edmonstonei** Hook.f.
*Solanum ferreyrae* Ugent = *Solanum edmonstonei* Hook.f.
*Solanum feuillei* Dunal = *Solanum pinnatum* Cav.
*Solanum flexuosum* (J.Rémy) F.Phil. = *Solanum remyanum* Phil.
*Solanum gaudichaudiana* (J.Rémy) F.Phil. = *Solanum pinnatum* Cav.
*Solanum gaudichaudii* Dunal = *Solanum pinnatum* Cav.
*Solanum gaudichaudii* Dunal var. *canescens* Dunal = *Solanum trinominum* J.R.Benn.
*Solanum gaudichaudii* Dunal var. *viride* Dunal = *Solanum pinnatum* Cav.
*Solanum geissei* Phil. = *Solanum brachyantherum* Phil.
**Solanum herbabona** Reiche
*Solanum heterantherum* Witasek ex Reiche = *Solanum trinominum* J.R.Benn.

**Solanum indivisum** Witasek ex J.R.Benn.
*Solanum laurentii* S.Mitch. = *Solanum montanum* L.
*Solanum maritimum* Meyen ex Nees = *Solanum pinnatum* Cav.
**Solanum montanum** L.
**Solanum multifidum** Lam.
*Solanum multifidum* Ruiz & Pav. = *Solanum multifidum* Lam.
*Solanum murphyi* I.M.Johnst. = *Solanum edmonstonei* Hook.f.
*Solanum novemlobum* Dunal = *Solanum pinnatum* Cav.
*Solanum novemlobum* Dunal var. *pauciflorum* Dunal = *Solanum pinnatum* Cav.
**Solanum paposanum** Phil.
*Solanum phyllanthum* Cav. = *Solanum montanum* L.
*Solanum phyllanthum* Cav. var. *aberrans* (Phil.) Witasek ex Reiche = *Solanum paposanum* Phil.
*Solanum phyllanthum* Cav. var. *crassipes* (Phil.) Witasek ex Reiche = *Solanum paposanum* Phil.
*Solanum pinnatifidum* Ruiz & Pav. = *Solanum multifidum* Lam.
**Solanum pinnatum** Cav.
*Solanum pinnatum* Cav. var. *subintegrifolium* (Dunal) Reiche = *Solanum pinnatum* Cav.
*Solanum pinnatum* Cav. var. *tomentosum* Reiche = *Solanum pinnatum* Cav.
*Solanum pocote* Hieron. = *Solanum montanum* L.
*Solanum purpureum* (Lodd.) Dunal = *Solanum montanum* L.
**Solanum remyanum** Phil.
*Solanum runcinatum* Ruiz & Pav. = *Solanum pinnatum* Cav.
*Solanum senecoides* Domb. ex Dunal = *Solanum multifidum* Lam.
*Solanum septemlobum* Phil. = *Solanum pinnatum* Cav.
*Solanum tafallae* J.F.Macbr. = *Solanum multifidum* Lam.
*Solanum tomentosum* (J.Rémy) F.Phil. = *Solanum trinominum* J.R.Benn.
**Solanum trinominum** J.R.Benn.
*Solanum tuberiferum* Dunal = *Solanum montanum* L.
*Solanum tuberiferum* Dunal var. *arenarium* Dunal = *Solanum montanum* L.
*Witheringia flexuosa* J.Rémy = *Solanum remyanum* Phil.
*Witheringia gaudichaudiana* J.Rémy = *Solanum pinnatum* Cav.
*Witheringia maritima* (Meyen) J.Rémy = *Solanum pinnatum* Cav.
*Witheringia montana* (L.) Dunal = *Solanum montanum* L.
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*Witheringia pinnatifida* (Ruiz & Pav.) Dunal = *Solanum multifidum* Lam.
*Witheringia purpurea* Lodd. = *Solanum montanum* L.
*Witheringia tomentosa* J.Rémy = *Solanum trinominum* J.R.Benn.

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*Macbride, J.F.* 5860 (7). *Macbride, J.F. & Featherstone, W.* 331 (8). *Marticorena, C. et al.* 619 (11). *Mathews, A.* 210 (11). *Matthews, B.* 443, 846 (7); 994 (2). *Metcalf, R.D.* 30372 (8). *Mexia, Y.* 04013, 04054, 8099a (7). *Meza, I. & Villagrén, C.* 966, 1028, 1196 (11). *Miers, J.* 62, 6643 (11); 6764 (4). *Montero O., G.* 2671 (11); 2891 (3); 2903 (1); 7212 (11). *Moreira, A.* 701, 712, 713 (4). *Morong, T.* 32 (3); 134 (4); 1132, 1289 (3). *Morrison, J.L. & Beetle, A.A.* 9098, 9100 (7); 16851 (11). *Mostacero L., J. & Mejía F., C.* 1470 (2). *Mostacero L., J. et al.* 805, 1061 (7); 1063 (2); 1424, 3307 (7). *Müller, G.K. & Krebs, G.* 12181 (2); 12185 (7); 12201a (8). *Muñoz S., C.* 43 (4). *Muñoz S., M.* 924 (11); 3003, 3081, 3120 (3); 3121 (9). *Muñoz S., M. et al.* 2617 (11). *Muñoz, P., C.* B-201 (4); B-219 (11); 3632 (1); 4159 (11); 4253 (4). *Muñoz, P., C. & Coronel, A.* 1353 (11). *Muñoz, P., C. & Jones, G.T.* 1848 (4). *Murphy, R.C.* 3219, 3220, 3222 (10); 3470 (7); 3479 (10).

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*Ochoa, C.M.* 565, 576 (7); 600 (2); 1816 (7); 2036 (8); 2100, 2101, 4815 (7); 5040 (8); 5082, 8622, 8687 (7); 13068 (11); 14897 (7). *Ochoa, C.M. & Salas, A.* 11254, 11255 (7).

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*Sagástegui A., A. & Aguado, H.* 2602 (8). *Sagástegui A., A. & López S., M.* 10993 (2). *Sagástegui A., A. & Mostacero, J.* 10479 (2). *Sagástegui A., A. et al.* 12955 (7). *Sánchez, H. & Montes, G.* 3 (11). *Saunders, S.G.E.* 195 (2); 347 (8). *Savatier, L.* 1572 (2); 1574 (7). *Shepard, R.S.* 249 (8). *Sielfeld, W.* 22 (1); 38 (7). *Skottsberg, C. & Skottsberg, I.* 760, 1045 (11); 1050 (4). *Smith, W.A.* 6 (8). *Solbrig, O.T.* 3065 (1). *Solomon, J.C. & Solomon, A.* 4234 (11). *Soukup, J.* 1851 (2); 1852 (7); 3526 (2). *Stafford, D.* K30 (2); K31, 905, 1026 (7). *Stork, H.E. & Vargas, C.* 9343 (2). *Stork, H.E. et al.* 9165, 9166 (7); 9182 (2); 9238 (7). *Straw, R.M.* 2342 (8).

*Taylor, C.M. & Pool, A.* 11631 (3). *Teillier, S.* 798, 902 (3); 1028 (9); 5741 (1). *Tillett, S.S.* 669-3, 6610-6 (2). *Torre, M.I. La* 1835, 1843 (8). *Torre, M.I. La & Cano, A.* L3095 (7). *Torre, M.I. La et al.* 3125, 3129, 3155, 3156, 3160, 3165 (7). *Tovar, O.* 1761 (7); 2692 (2); 3442 (7). *Tryon, R.M. & Tryon, A.F.* 6569 (2); 6572 (7).

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*Wagenknecht, R.* 18113 (8); 18570 (4). *Wawra, H.* 2601 (7); 2804 (11). *Weberbauer, A.* 1577, 5224 (7); 5239 (2); 5687 (7); 5691 (2). *Weigend, M. & Förther, N.* 97/547 (7); 97/659, 97/735 (2); 97/762 (8); 97/924 (7). *Weigend, M. & Weigend, K.* 2000/13 (8). *Weigend, M. et al.* 2000/652 (2); 2000/661 (7); 7328 (2); 7332 (7); 7365 (2). *Werdermann, E.* 108 (11); 127 (4); 170 (9); 386, 401 (3); 724 (2); 836 (3); 841 (1); 898 (11); 986 (2). *Werff, H. van der et al.* 14454 (7); 14460 (2). *West, J.* 3866 (3); 3930, 3955 (11); 8214 (8). *Worth, C.R. & Morrison, J.L.* 15609, 15674 (7); 15731 (2); 15750 (7); 15753 (2); 15806, 16146, 16168 (3); 16324 (11).

*Zöllner, O.* 15064 (3); 15076 (11); 8005, 8284, 12516 (11).