

Revision of the *Solanum medians* Complex (*Solanum* section *Petota*)

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Abstract—*Solanum medians* is a widely distributed species of wild potato (*Solanum* sect. *Petota*), growing along the coastal lomas and up the western slopes of the Andes Mountains from central Peru and northern Chile, from 200–3800 m elevation. Fertile diploid and sterile triploid cytotypes are common, are believed to be associated with morphological variants, and are formally named as subspecies. A morphometric study based on principal components and canonical discriminant analyses of characters obtained from herbarium specimens tests the circumscription of these subspecies and other currently recognized species that are very similar to *S. medians*. The results show so much overlap of these taxa that it is impractical to use morphology to define species or to provide reliable keys or identifications. We synonymize ten names under *S. medians*: *S. medians* var. *angustifolium*, *S. medians* var. *majorifrons* subvar. *majorifrons*, *S. medians* var. *majorifrons* subvar. *protophyleucum*, *S. medians* var. *autumnale*, *S. sandemannii*, *S. tacnaense*, *S. weberbaueri* var. *decurrentialatum*, *S. tacnaense* f. *decurrentialatum*, *S. weberbaueri*, *S. weberbaueri* var. *poscoanum*. We also treat *S. neoweberbaueri* as a closely related species to *S. medians*. We consider the synonymy in *S. medians* to be part of a much larger need for reduction of names in sect. *Petota*.

Keywords—biodiversity, lomas, potato, *Solanum medians*, *Solanum* section *Petota*.

Solanum sect. *Petota*, which includes the potato and its wild relatives, is by any standard taxonomically difficult. As a widespread and economically important group, it has been the subject of various and conflicting taxonomic treatments. Taxonomy in sect. *Petota* is complicated by the weedy nature of many of its species, ease of hybridization among some morphologically distinct species, and apparent allopolyploidy (Spooner and van den Berg 1992; Spooner and Salas 2006). Hawkes (1990) recognized 21 series and 232 species in sect. *Petota*, but series *Etuberosa* Juz. and *Juglandifolia* (Rydb.) Hawkes have been placed in other sections and many names within sect. *Petota* have been reduced to synonymy (Spooner and Salas 2006).

The *Solanum medians* complex is a term used here to describe a group of species distributed along the coast and western slopes of the Andes Mountains from central Peru to northern Chile. Plants of this complex have coarse erect pubescence, articulation distal to the middle of the pedicel, and dark blue to violet corollas typically with a green central star. The relationships and difficult species boundaries of many of its members were first recognized by Correll (1962, p. 514):

“The plants described as *S. Weberbaueri*, *S. medians*, *S. neoweberbaueri*, *S. tacnaense* and *S. Sandemania* unquestionably represent “specific” separations by degrees rather than by lines of demarcation...While all the above have some common characteristics, such as high articulation of the pedicels, densely pilose calyx and rather coarse-appearing pilose-denticulate leaves, each has at least one characteristic whereby it may be distinguished from the others. It must be admitted, however, that some of these differences are somewhat recondite, and it is quite possible that these entities should be further united.” Hawkes (1990) and Ochoa (1999) likewise indicated close relationships of some of these species. Figure 1 summarizes differing taxonomic treatments of Hawkes (1990), Ochoa (1999), and our new treatment described below.

Hawkes (1990) placed *S. medians* and other species examined here in ser. *Tuberosa*, containing over 90 species. Spooner and Castillo (1997) showed *S. medians* to be a member of plastid clade 4 of sect. *Petota* that contains most of the South American species and the polyploid species from North and

Central America. Beyond these studies, the relationship of *S. medians* is unresolved, and is the subject of continuing molecular studies.

The purpose of the present study is to reevaluate the species status of members of the *S. medians* complex through examination of herbarium specimens from throughout the range of the group, as part of a comprehensive treatment of *Solanum* sect. *Petota* in “PBI *Solanum*: a worldwide treatment” (<http://www.nhm.ac.uk/research-curation/projects/solanaceasource/>).

MATERIALS AND METHODS

We collected data from 13 characters that distinguish the species of the *S. medians* complex in keys or descriptions of these taxa (Table 1) from 118 herbarium specimens from throughout the range of the group. The measured specimens are designated by an asterisk in Representative Specimens Examined (below). We used data from all of these specimens for character state distributions, but due to some missing data, we used only 104 specimens for principal components analysis (PCA) and canonical discriminant analysis (CDA). We assessed 53 specimens of *S. medians* var. *medians* for character state distributions and 49 for PCA and CDA, 34, 30 for *S. medians* var. *autumnale*, 17, 14 for *S. sandemannii*, and 12, 11 for *S. tacnaense* including its form *decurrentialatum*. We identified accessions to taxa based on identifications in Ochoa (1999), or for the few records not listed there, we identified collections based on their published ranges in Ochoa (1999). Based on Ochoa (1999) we labeled the few accessions identified as *S. weberbaueri* by Hawkes as *S. medians* var. *autumnale*. These specimens represent the entire geographic distributions of the *S. medians* complex. We also included *S. neoweberbaueri* because Correll (1962) suggested this taxon was part of this complex. Our results include observations from personal herbarium collections and field observations in Peru (Spooner et al. 1999; Salas et al. 2001).

PCA was calculated from the correlation matrix of the variance-covariance matrix. All analyses were done in SAS ver. 9.1 (SAS Institute Inc. 2004).

RESULTS

Means, ranges, and standard deviations for 12 of the 13 characters are presented in Fig. 2. For convenient space considerations we do not graph character 12 of Table 1 but it showed widely overlapping traits as described below. The characters overlapped so much with others that reliance on any of them would lead to unstable identifications of poorly defined species. PCA (Fig. 3) shows almost total intermixture of these accessions, and CDA (Fig. 4) shows only trends that

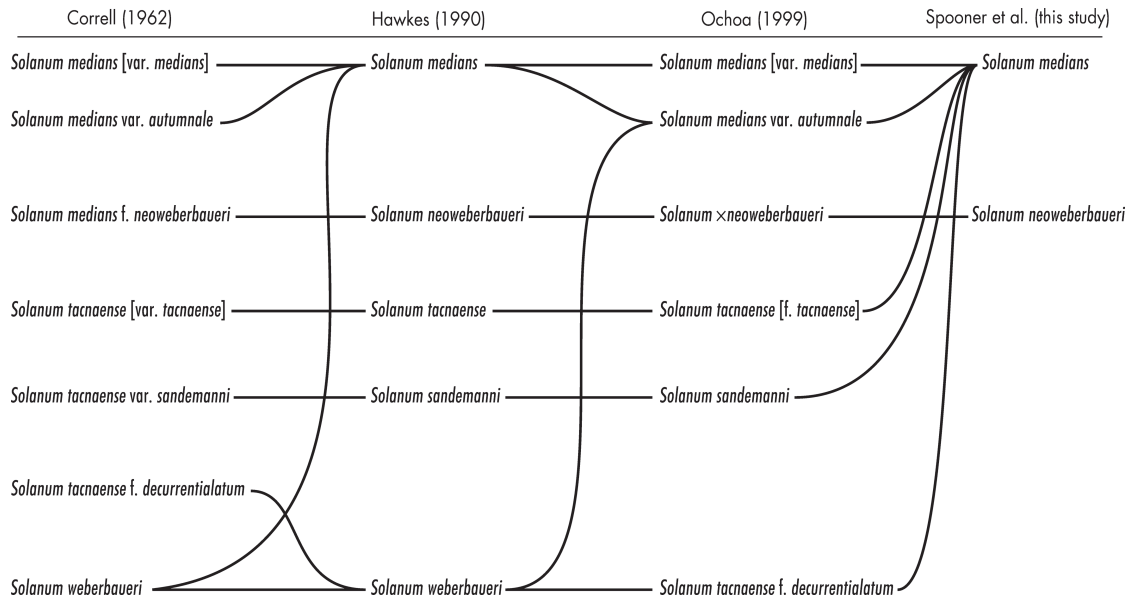


FIG. 1. Chronological flow chart of hypotheses of species boundaries of members of the *Solanum medians* complex according to Correll (1962), Hawkes (1990), Ochoa (1999), and our present study.

TABLE 1. Characters used in the phenetic analysis of the *Solanum medians* complex. The character state distributions of these characters (except character 11) are graphed in Fig. 2.

1. Number of lateral leaflet pairs.	2. Number of interjected leaflets.	3. Second most distal lateral leaflet length (cm).	4. Second most distal lateral leaflet width (cm).	5. Second most distal lateral leaflet decurrency 3 mm down from the petiole (mm).	6. Most distal lateral leaflet length (cm).	7. Most distal lateral leaflet width (cm).	8. Most distal lateral leaflet decurrency 3 mm down from the petiole (mm).	9. Terminal leaflet length (cm).	10. Terminal leaflet width (cm).	11. Length from the widest point of the terminal leaflet to the base of its petiolule (cm).	12. Pedicel length (cm).	13. Ratio: distance from base of pedicel to the articulation (cm)/pedicel length (cm).
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support *S. sandemanii*, but again with so much overlap with other taxa that it is impractical to use morphology to define species or to provide reliable keys or identifications.

DISCUSSION

Species Boundaries—Our results provide the first morphological study of members of the *S. medians* complex. They support only a single, highly variable species, united by its coarsely pilose stems, leaves, and calyces (Fig. 5F); pedicels typically articulate distal to the middle; and pentagonal to rotate corollas colored dark blue to violet and typically with a green star above and below. We chose the name *S. medians* for this species over *S. weberbaueri*, published at the same time, as it is the more common name in the literature.

Hawkes (1990) accepted 225 wild species in sect. *Petota*, but ten new species have been described in the section since 1990, raising the total to 235 wild species. Recent morphological and molecular studies have reduced this number, and Spooner and Salas (2006) summarized this reduced list with 187 wild species. Our study synonymizes two more names from that list (*S. sandemanii* and *S. tacnaense*), and Spooner et al. (2007) synonymized two others (*S. litusinum* Ochoa and *S. tarijense* Hawkes as *S. berthaultii*), reducing the current number of wild species in sect. *Petota* to 183. We predict that continued reductions will be forthcoming in this section, as

suggested by van den Berg et al. (1998), Miller and Spooner (1999), and Spooner et al. (2005) in the *Solanum brevicaulis* complex, and Fajardo et al. (2008) for members of ser. *Conicibaccata*.

TAXONOMIC TREATMENT

SOLANUM MEDIANS Bitter, Repert. Spec. Nov. Regni Veg. 11: 366. 1912.—TYPE: PERU. Lima: hills of Mongomarca, loma formation, [Cerro de Amancaes], 500–600 m, 14 Aug 1910, A. Weberbauer 5683 (*Seler* 260) (holotype: B, destroyed, photos: F 647974! G! MO 1691266! NY! (reproduced as Fig. 123 [pg. 230] of Ochoa 1962!; lectotype, designated by Ochoa, 1999, p. 771: US 1473504!, photo of US lectotype [Correll neg. 734]: LL! NY! PTIS! UC 1152337!; isolectotypes: CUZ! F 628465! GH!, photos of F isolectotype [Correll neg. 52]: G! LL! MO 5588448! NY! PTIS! UC 1152337!, photos of GH isolectotype [Correll neg. 733]: LL! NY! UC 1152337!; drawing of GOET isolectotype: LL! MO 5588447! NY! PTIS! UC 1152337!).

Solanum weberbaueri Bitter, Repert. Spec. Nov. Regni Veg. 11: 365. 1912.—TYPE: PERU. Arequipa: Prov. Mollendo [Prov. Islay], Tambo, 500–600 m, among rocks, in loma formations, Oct 1902, A. Weberbauer 1575 (holotype: B destroyed, photo and fragment: F 647956!, photos: G! MO 1691494! NY!).

Solanum medians var. *majorifrons* subvar. *majorifrons* Bitter, Repert. Spec. Nov. Regni Veg. 12: 149. 1913.—TYPE: PERU. [Lima]: [Prov. Huarochirí]: Tambo de Viso, M. *Martinet* 232 p.p. (the bottom of two specimens on a single sheet) (holotype: P!, photo: G!).

Solanum medians var. *majorifrons* subvar. *protopoleucum* Bitter, Repert. Spec. Nov. Regni Veg. 12: 150. 1913.—TYPE: PERU. [Lima]: [Prov. Huarochirí], Tambo de Viso, M. *Martinet* 232 p.p. (the top of two specimens on a single sheet) (holotype: P!, photo: G!).

Solanum weberbaueri var. *poscoanum* Cárdenas and Hawkes, J. Linn. Soc., Bot. 53: 101, Fig. 7, 1946.—TYPE: PERU. Arequipa: Prov. Islay [Islay], Lomas de Posco, 600–900 m, in

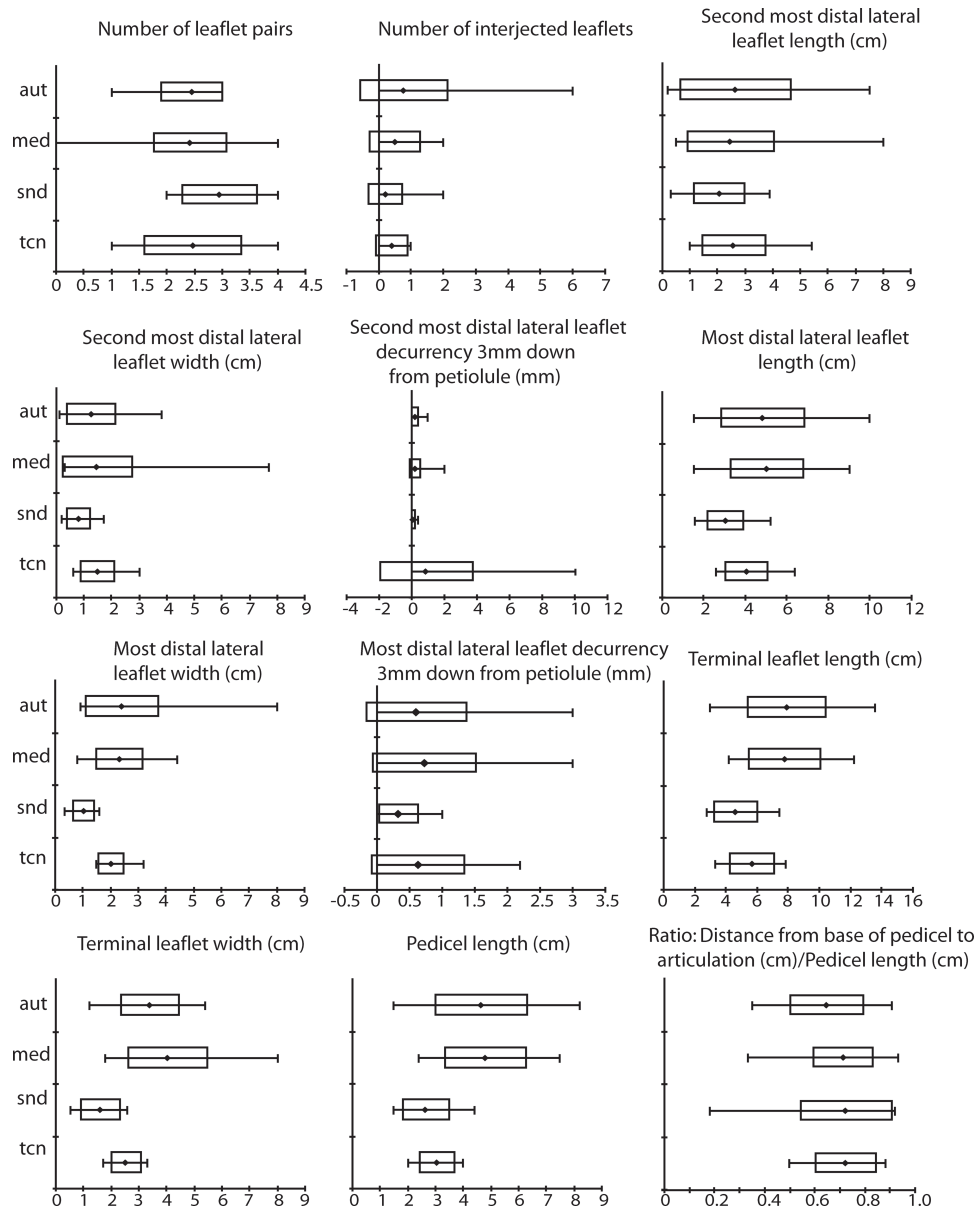


FIG. 2. Means, ranges, and one standard deviation of the mean for 12 of the 13 characters assessed in this study for *Solanum medians* var. *medians* (med), *S. medians* var. *autumnale* (aut), *S. sandemanii* (snd), and *S. tacnaense* (tcn).

sandy-rocky soils, 1 Aug 1940, C. Vargas 2019 (lectotype, here designated: K 000440664!, photos [Correll neg. 385]: F 1603661! LL! MO 5588802! UC 1152460!).

Solanum medians var. *autumnale*, Correll, *Wrightia* 2: 190. 1961.—TYPE: PERU: Lima: Prov. Huarochirí, valley of Río Rimac, near Lima-Oroya Highway at Km 70 east of Lima, 1850 m, above highway in moist cervices of rock walls, 21–26 Apr 1942, T. H. Goodspeed 33116 (holotype: GH!, photos [Correll neg. 729]: F 1603602! LL! NY! PTIS! UC 1152339!; isotypes: G!, MO 1288086! US 1834652!, photos of G isotype [Correll neg. 726]: F 1603599! LL! MO!, UC 1152339! photos of MO isotype [Correll neg. 728]: F 1603601! LL! NY! PTIS! UC 1152339!, photos of US isotype [Correll neg. 727]: LL! NY! PTIS! UC 1152339!).

Solanum tacnaense Ochoa, *Agronomía* (Lima) 18: 133, Figs. 5–6, 1953.—TYPE: PERU. Tacna: Prov. Tacna, near Minas de Toquepala, a few kilometers before reaching the radio station on the mine, 3140 m, 23 Mar 1953, C.

Ochoa 2046 (holotype: CUZ!; isotypes: GH! K [2 sheets labeled sheet 1 and sheet 2]! US 2123548!, photo of GH isotype [Correll neg. 682]: BM 000882020! F 1603639! NY! UC 1152485!, photo of US isotype [Correll neg. 152]: BM 000882021! F 1603853! MO 5609720! UC 1152485!).

Solanum sandemanii Hawkes, *Ann. Mag. Nat. Hist. Ser. 12*, 7: 709, Figs. 12, 13. 1954. *Solanum tacnaense* var. *sandemanii* (Hawkes) Correll, *Wrightia* 2: 196. 1961.—TYPE: PERU. Arequipa: rock ledges along draw above Arequipa, 2600–2700 m, 7–16 Apr 1925, F. W. Pennell 13196 p.p. (holotype: K, photo of holotype: F 1604160! MO 5594979! NY!; isotypes: F 557664! GH! PH, S 04-2978! US 1343101!; photo of F isotype [Correll neg. 680]: BM 000882019! F 1603630! PTIS!, photo of GH isotype [Correll neg. 677]: BM 000882018! F 1603633! NY! PTIS!, photos of PH isotype: [Correll neg. 679]: BM 000882017! F 1603631! NY!, photos of S isotype [Correll neg. 289]: BM 000882014! F 1604160! MO 5594979! PTIS! UC 1152418!, photo of US

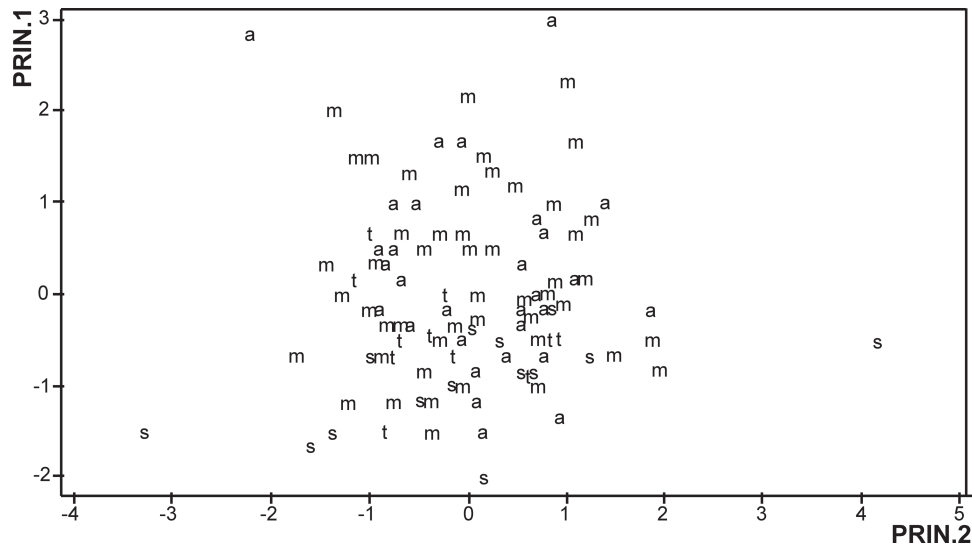


FIG. 3. Principal component analyses based on 13 morphological characters (Table 1). m = *S. medians* var. *medians*, a = *S. medians* var. *autumnale*, s = *S. sandemannii*, t = *S. tacnaense*.

isotype [Correll neg. 681]: BM 000882016! F 1603638! NY! PTIS!).

Solanum weberbaueri var. *decurrentialatum* Ochoa, *Agronomía* (Lima) 26: 219, Figs. A, B on pg. 220. 1959. *Solanum tacnaense* f. *decurrentialatum* (Ochoa) Correll, *Wrightia* 2: 197. 1961.—TYPE: PERU. Tacna: Prov. Tarata, rocky hills near Tarata, Cerro Ticalaco, 3200 m, 22 Mar 1953, C. Ochoa 2040 (holotype: personal herbarium of C. Ochoa, photo: Ochoa, 1999, pg. 911!).

Solanum medians var. *angustifoliolum* Ochoa, *Los Solanum Tuberíferos Silvestres del Perú*, 242. 1962.—TYPE: PERU. Lima: Prov. Cajatambo, San José, 2700 m, near Churín, 6 Apr 1961, C. Ochoa 2352 (holotype: personal herbarium of C. Ochoa; photo: Ochoa, 1962, pg. 243!; isotype: CUZ[2]!, photos: PTIS!).

Plants 0.2–0.6 m tall, herbaceous, terrestrial, erect. Stems 3–5 mm in diameter at base of plant, coarsely pilose with typically whitish non-glandular erect trichomes, dark green

and sometimes tinged with purple. Pseudostipules minute to 12 mm long, lunate. Leaves 8–15 cm long, 5–15 cm wide, odd-pinnate, pubescent (like the stems), medium to dark green and sometimes tinged with purple underneath; petioles 0.7–3.0 cm long; lateral leaflet pairs 1–4, greatly subequal and rapidly decreasing in size to the base; most distal lateral leaflets (1.5-) 2.0–8.0 (-10) cm long, (0.4-) 1–4 (-8) cm wide, narrowly to broadly ovate to more rarely orbicular, the apex typically acute to acuminate to more rarely rounded and apiculate, the base typically sessile and short to widely decurrent on the basisopic side to more rarely short petiolulate; terminal leaflet 3–11 (-14) cm long, 1–6 (-8) cm wide, narrowly to broadly ovate to more rarely orbicular, the apex typically acute to acuminate to more rarely rounded and apiculate, the base attenuate; interjected leaflets 0–2 (-7), sessile to short petiolulate, ovate to orbicular. Inflorescences generally in distal half of plant; peduncle 1.3–8.0 cm long. Flowers 5–15; pedicels (1.5-) 2–6 (-8) mm long, articulate typically

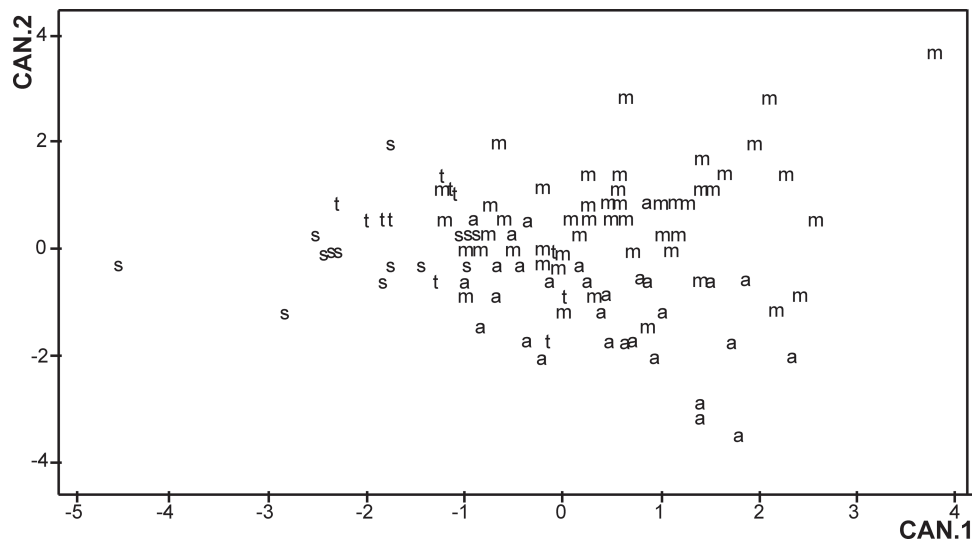


FIG. 4. Canonical discriminant analysis based on 13 morphological characters (Table 1). The accessions examined and taxon codes are the same as in Fig. 3.

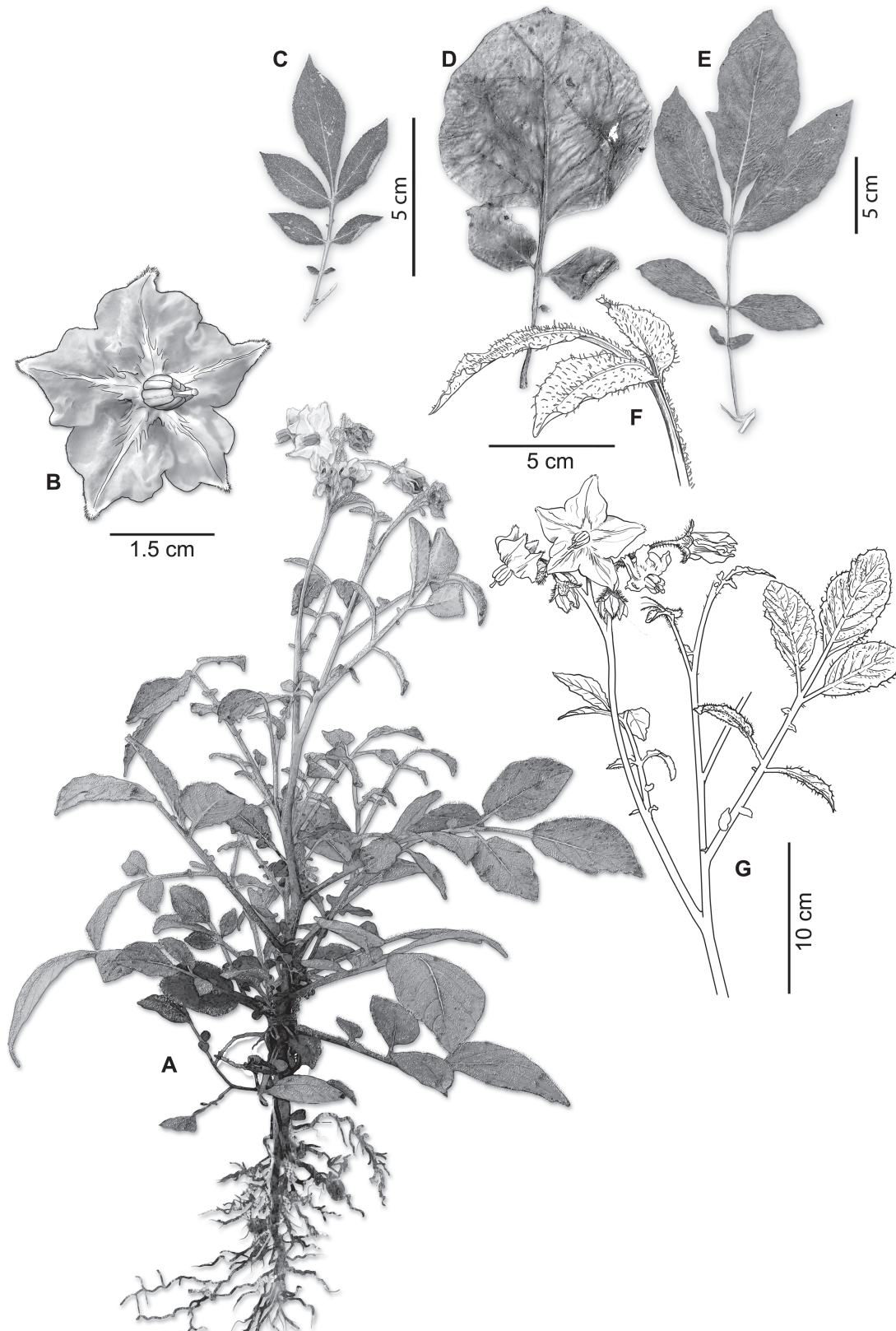


FIG. 5. *Solanum medians*. A. Habit. B. Flower. C-E. Adaxial surface of leaf showing differences in leaflet shape with C typical of the narrow-leaflet morphotype characteristic of *S. sandemannii*, D a rarer type with orbicular leaflets, and E the more common morphotype. F. Oblique view of adaxial surface of leaf showing trichomes typical of stems, leaves, and calyces. G. Upper part of plant including inflorescence. (Based on A, B, F, G, *Salas et al.* 7314, from a living plant vouchered at CIP and PTIS; C, *Ochoa* 5057, US; D, *Ferreya* 17742, USM; E, *Ochoa and Salas* 14900 US).

above the middle; calyx 6–11 mm long, the lobes linear to long-attenuate, the acumens 2–4 mm long; corolla 2.8–3.5 cm in diameter, pentagonal to rotate, the acumens 1.0–1.5 mm long, edges of corolla flat, not folded dorsally, dark blue to violet and typically with a green star above and below; anthers 4–7 mm long, connate; style 8–9 mm long, exceeding stamens by 2–4 mm, straight, stigma clavate to capitate. Fruits 1.5 cm long, globose to slightly ovoid, medium to deep green, often with scattered white dots. Seeds from living specimens green-white throughout. Chromosome number and EBN $2n = 2x = 24$ (2EBN) and $2n = 3x = 36$ (Spooner & Salas 2006; Hijmans et al. 2007). Figure 5.

Phenology—Flowering and fruiting along the coast from May to October, and in the higher Andes from November to April.

Distribution (Fig. 6)—Central Peru (Department of Ancash) south to northern Chile in Regions I (Tarapacá) and II (Antofagasta), along the western slopes of the Andes; growing in a variety of sunny habitats along the dry coastal lomas to high frigid areas near snow fields and among *Stipa ichu* grasses in the puna. The most frequently mentioned habitat characteristics are apparently poor soils in rocky and sandy areas, but it has been collected along field margins and streambanks; 200–3800 m.

Representative Specimens Examined—Note: an asterisk designates

specimens measured for the phenetic study. Additional specimens examined are listed in <http://www.nhm.ac.uk/research-curation/projects/solanaceaesource/>

CHILE. Antofagasta: Salar de Atacama, Peine, Jul 1949, *Gonzalez & Bohme s.n.* (SGO). Tarapacá: camino de Arica al Portezuelo de Chapiquiña, Cuesta de Chapiquiña, 3250 m, 25 Mar 1961, *Ricardi et al. 133* (CONC, MA); camino a Chusmisa, 9 Apr 2002, 3600 m, *P. Riedemann s.n.* (SGO).

PERU. Ancash: Aija, Succha, Casablanca, arriba de Huayán, 7 Apr 1970, 3100 m, *C. M. Ochoa 2722* (CIP*); Bolognesi, frente a Timpo, 14 Apr 1963, 2900 m, *C. M. Ochoa 2488* (CUZ, F, GH, MOL*, USM); Aija, al terminar la cuesta del Mellizo subiendo hacia Aija, 25 Apr 1983, 3400 m, *C. M. Ochoa 15188* (CIP*, CUZ, GH). Arequipa: Arequipa, Baños de Jesús, east of Arequipa, 1 km on road from Baños de Jesús towards Puno, 4 Mar 1974, 2500 m, *J. G. Hawkes et al. 5405* (K*); Arequipa, Baños de Jesús, east of Arequipa, on hill slope about 1 km of Baños de Jesús, 4 Mar 1974, 2500 m, *J. G. Hawkes et al. 5407* (K*); Arequipa, Yura, entre Huasaloma y Candamo, arriba de Jesús, 27 Mar 1974, 2940 m, *C. M. Ochoa 5047* (CIP*); Arequipa, Cuesta de Liquirca, subiendo de Yura a Huanca, 28 Mar 1974, 3260 m, *C. M. Ochoa 5061* (CIP*); Arequipa, Yura, de Liquirca a cumbre de Pampacolco, 28 Mar 1974, 3410 m, *C. M. Ochoa 5081* (CIP*); Caravelí, Lomas de Atiquipa, Infiernillo, Dec 1982, 600 m, *C. M. Ochoa & A. Salas 14900* (CIP*, F, GH, GOET, MO, MOL, NY, US, USM, WIS); Arequipa, Yura, entre Huasaloma y Candamo, arriba de Jesús, 27 Mar 1974, 2940 m, *C. M. Ochoa 5046* (CIP*, US); Arequipa, Yura, entre Huasaloma y Candamo, arriba de Jesús, 27 Mar 1974, 2940 m, *C. M. Ochoa 5057* (CIP*, GH, US); Arequipa, cuesta de Liquirca, subiendo de Yura a Huanca, 28 Mar 1974, 3260 m, *C. M. Ochoa 5070* (CIP*, US); Arequipa, cuesta de Liquirca, subiendo de Yura a Huanca, 28 Mar 1974, 3260 m, *C. M. Ochoa 5071* (CIP*, GH); Chihuata, 17 Mar 1953, *C. M. Ochoa 2033* (K*); Chihuata, 17 Mar



FIG. 6. Map of *S. medians* (including its synonyms as detailed in taxonomic treatment).

1953, C. M. Ochoa 2034 (K*); Arequipa, 5 km de Chiguata hacia Arequipa, Río Grande, 12 Mar 1953, 2900 m, E. Petersen & J. P. Hjerting 1108 (C, CUZ, K*); Arequipa, 5 km de Chiguata hacia Arequipa, Río Grande, 12 Mar 1953, 2900 m, E. Petersen & J. P. Hjerting 1112 (K*); Arequipa, Arequipa, at base of small cliff on E side of Quebrada Honda, about 25 m from base of quebrada, about 100 m upstream, (N) from Arequipa to Chiguata road, at a point 59.8 km ENE of Pan American Highway (by posted road signs), 2750 m, A. Salas & D. Spooner 7250 (CIP*, PTIS); Arequipa, 1.1 km N of Arequipa to Chiguata Road, from a point 61.4 km ENE of Pan American Highway (by posted road signs), departing the road at bridge over Río Agua Salada, 9 May 1998, 2770 m, A. Salas & D. Spooner 7251 (CIP*); Arequipa, Arequipa, 18 km N of main town square (Plaza de Armas) of Arequipa on road to Cabrera (just S of this locality), then 100–150 m W or road, 2600 m, A. Salas & D. Spooner 7252 (PTIS*); Arequipa, Baños de Jesús, 2 Feb 1943, 2850 m, C. Sandeman 3812 (CUZ, K*, OXF); Arequipa, Quebrada de Crontay, 31 Mar 1949, 2850 m, C. Vargas 8086 (CUZ, K*); Ayacucho: about 45 km from Nazca on road to Puquio, 14 Feb 1958, 2200 m, D. S. Correll & E. E. Smith P148 (CUZ, LL). Huancavelica: Tayacaja, arriba de Marcavalle, distrito de Huachocolpa, 21 Apr 1964, 3100 m, O. Tovar 4776 (WIS). Lima: Huarochirí, above San Mateo, near Chicla Vilaver, 21 Apr 1882, 1200–1300 m, J. Ball s.n. (USM*); Chancay, Naupay, 22 Mar 1975, 2400 m, M. Cerrate et al. 257 (USM*); 80 km below Canta on road to Lima, 7 Mar 1958, 2200 m, D. S. Correll et al. P282 (CUZ, F, LL, U, UC, US, USM*); Yauyos, Huancracha, arriba de Tupe, 15 Jan 1952, 3300 m, E. Cerrate 1170 p.p. (USM*); Lima, La Molina, cerca a Lima, 30 Oct 1952, R. Ferreyra 3 (USM*); Canta, alrededores de Canta, 16 Mar 1950, 2900–2950 m, R. Ferreyra 6915 (CUZ, USM*); Canta, alrededores de Canta, 16 Mar 1950, 2900–2950 m, R. Ferreyra 6918 (CUZ, K, USM*); Canta, entre Canta y Yangas, 16 Mar 1950, 2300–2400 m, R. Ferreyra 6932 (CUZ, K, USM*); Huarochirí, cerca a San Mateo, carretera Lima-Huancayo, 25 Mar 1950, 2800–2900 m, R. Ferreyra 6961 (CUZ, K, LL, MOL*, USM*); Canta, cerca a Canta, 2 Apr 1953, 2600 m, R. Ferreyra 9000 (CUZ, K, LL, USM*); Canta, entre Canta y Yaso, 2 Apr 1953, 1800–2000 m, R. Ferreyra 9022 (K, USM*); Lima, Lomas de Lurín, cerca a Lurín, 18 Aug 1953, 200–250 m, R. Ferreyra 9527 (USM*); Canta, cerca de Canta, 7 Mar 1958, 2700–2800 m, R. Ferreyra et al. 12948 (CUZ, LL, USM*); Lima, Lomas de Lurín, 8 Aug 1971, 250–260 m, R. Ferreyra 17742 (G, USM*); Canta, Cerro Canta, 28 Apr 1974, 2700–2800 m, R. Ferreyra & J. P. Hjerting 18346 (MO, USM*); Canta, Obrajillo, 2 Mar 1974, 2600–2700 m, R. Ferreyra 18323 (MO, USM*); Cajatambo, arriba de Churín, 25 Mar 1976, 2500–2600 m, R. Ferreyra & J. P. Hjerting 18698 (MO, USM*); Santa Eulalia road, NE of Huinca, 7 Mar 1982, 2350–2450 m, A. Gentry & D. Smith 36121 (MO, USM*); Canta, near Canta, J. G. Hawkes 2491 (CUZ, MOL*); Huarochirí, San Mateo, km 99 carretera central, 14 Apr 1972, 3400 m, Z. Huamán et al. 306 (CIP*, USM); Huarochirí, Huinco, Quebrada del Río Santa Eulalia subiendo por Chosica, 28 Apr 1972, 3000 m, Z. Huamán 291 (CIP*); Huarochirí, entre Huinco y Agropica, Quebrada de Santa Eulalia subiendo por Chosica, 3 Apr 1973, 2700 m, Z. Huamán 357 (CIP*); Huarochirí, Autisha, Casta 2 km mas alla en el valle, km 25 del Valle de Santa Eulalia, 7 Mar 1975, 3500 m, H. Kang & M. Jackson 1 (CIP*); San Mateo, J. McLean, s.n. (GH*); Canta, Colca (alrededores de Canta), 13 Apr 1964, 2700 m, I. Merza 230 (USM*); Canta, Valle de Río Chancay, above Tingo, Jan 1972, 2900 m, G. Miller & al. 1232A (USM*); Lima, Pachacamac, 1 km E de Atocongo, 21 Aug 1971, 350 m, C. M. Ochoa 3036 (CIP*, CUZ, USM); Huarochirí, San Bartolomé, Bosque Zárate, subiendo por ruta pedestre, Mar 1975, 2200–2500 m, C. M. Ochoa 7413 (CIP*, CUZ); Lima, San Bartolo, km 55 Panamerica Sur, cerca de las Lomas de Pucusana, 21 Oct 1975, 250 m, C. M. Ochoa 11249 (CIP*, CUZ); Huarochirí, San Pedro Casta, cerca Huinco, subiendo de Chosica por la Quebrada de Santa Eulalia, 21 Feb 1978, 2200 m, C. M. Ochoa 11878 (CIP*, CUZ); Huarochirí, San Pedro Casta, Represa de Seque, Sta. Eulalia-Huinco, 21 Feb 1975, 3000–3100 m, C. M. Ochoa 11882 (CIP*, CUZ); Huarochirí, San Pedro Casta, Represa de Seque, Sta. Eulalia-Huinco, 21 Feb 1975, 3000–3100 m, C. M. Ochoa 11884 (CIP*, CUZ, MOL, USM); Huarochirí, Surco, alrededores de Surco, 10 Apr 1978, 2240–2280 m, C. M. Ochoa 12047 (CIP*, CUZ, MOL); Huarochirí, Antioquia, Saquinanga, arriba de Antioquia, en ruta Langa-Huarochirí, Apr 1978, 2000 m, C. M. Ochoa 12533 (CIP*, CUZ, MOL); Lima, San Bartolo, Lomas Caringa, 9 km E San Bartolo, Sep 1978, 300–350 m, C. M. Ochoa 13035 (CIP*, CUZ, MOL); Canta, 6 Apr 1979, 2700 m, C. M. Ochoa 13261 (CIP*, CUZ, MOL); Huarochirí, San Pedro Casta, Autisha, por quebrada Sta Eulalia-Seque, 11 Apr 1979, 2325–2700 m, C. M. Ochoa 13270 (CIP*, CUZ, MOL); Huarochirí, San Mateo, carretera central Lima-La Oroya, 3 May 1983, 3200 m, C. M. Ochoa 15209 (CIP*, CUZ); Cañete, Quilmaná, Lomas de Quilmana, 15 km N Cañete, 25 Oct 1975, 350 m, C. M. Ochoa & A. Salas 11253 (CIP*, CUZ); Oyón, Naván, 3200 m, C. M. Ochoa & A. Salas 12500 (CUZ, MOL*, USM); Oyón, Andajes, Tunaspatá, near Churín, Apr 1978, 3280 m, C. M. Ochoa & A. Salas 12573 (CIP*, CUZ,

MOL, USM); Cajatambo, Cajatambo, Oshacoto, 2 km NE de Cajatambo, 31 Jan 1979, 3600 m, C. M. Ochoa & A. Salas 13140 (CIP*, CUZ); Huarochirí, San Bartolomé, Monte Zárate, al norte de Lucmani, subiendo a pie desde San Bartolome, distrit. Santiago de Tuna, 17 Mar 1983, 3000 m, C. M. Ochoa & A. Salas 15099 (CIP*, CUZ, MOL); Huarochirí, alrededores de Matucana, km 76 del camino Lima a Oroya, 9 Mar 1949, 2200 m, C. M. Ochoa 691 (CUZ, GH, MOL*, US, USM); Huarochirí, ruta de Huinco, Mar 1975, 2200 m, C. M. Ochoa 7406 (CIP*, CUZ, GH); Huarochirí, entre San Bartolomé y Zárate, Mar 1975, C. M. Ochoa 7411 (CIP*, CUZ, F, MOL); Canta, Chuquitama, near Obrajillo, in the vicinity of Canta, 10 Mar 1977, 2700 m, C. M. Ochoa 11302 (CIP*, CUZ, F, GH, MOL, NY); Cajatambo, Huaylancaña, 3 km E Cajatambo, 31 Jan 1979, 3600 m, C. M. Ochoa 13141 (CUZ, F, GH, MOL*); Huarochirí, Autisha, 11 Apr 1979, 2500 m, C. M. Ochoa 13268 (CIP*, CUZ, F, GH, MOL, USM); Canta, Dist. Acos, Tambobamba, encima de Tambo, margen izquierda Río Chancay, 2200 m, C. M. Ochoa 14629 (CUZ, F*); Cajatambo, Cruzcirca, en ruta Cajatambo-Cajamarquilla, 13 Apr 1982, 3400 m, C. M. Ochoa 14672 (CUZ, F*, US); Cajatambo, Dist. Canjul, Mancocona, 16 Apr 1982, 3400 m, C. M. Ochoa 14684 (CIP*, CUZ, F, US); Lima, San Juan Lurigancho, Lomas Mangomarca, Zárate-Canto Grande, cerca de Amancaes, 13 Feb 1983, 400–500 m, C. M. Ochoa 14908 (USM*); Canta, colectado a la altura del km 89 de la carretera Lima-Canta, 8 Apr 1983, 2800 m, C. M. Ochoa & A. Salas 15148 (CIP*, F, US); Canta, on the Lima to Canta road, on the side of the road and about 200–300 m SW from the bridge called Puente Verde, located 9.2 km SW of the town of Canta, 7 Apr 1999, 2310 m, A. Salas et al. 7361 (CIP*); Canta, growing at a local place named Pallacusco, located 4 km walk E of Arahuy on a footpath to Cerro Putaca, 8 Apr 1999, 2895 m, A. Salas et al. 7369 (CIP*); Canta, growing at Huaytana, located ac 5 km walk NE of town of Canta on the path to Antura, 8 Apr 1999, 2775 m, A. Salas et al. 7371 (CIP*); Huaral, collected on the NW side of the road, 14 km NE of Acos, on the road to Pacaraos, about 50 m NE of the small bridge crossing over the road of Río Chancay, 10 Apr 1999, 2075 m, A. Salas et al. 7379 (CIP*); Huarochirí, collected on roadside, 32.3 km NE of Santa Eulalia, on the road to Millo, 12 Apr 1999, 3065 m, A. Salas et al. 7383 (CIP*); Yauyos, 1 km E of Villa Franca, located on the road from Catahuasi to Lincha, 8 Mar 1999, 2200 m, A. Salas et al. 7300 (CIP*); Yauyos, growing at a local place called Arpayo, about a 5 km walk from Villa Franca, which is located on the road from Catahuasi to Lincha, 9 Mar 1999, 2620 m, A. Salas et al. 7301 (CIP*); Yauyos, about a 1 km NE of Caca on the footpath to Hongos, 9 Mar 1999, 2880 m, A. Salas et al. 7302 (CIP*); Yauyos, about 3 km NW of Hongos, about 1 km N (uphill) of path from Caca to Hongos, 9 Mar 1999, 3290 m, A. Salas et al. 7303 (CIP*); Yauyos, growing at a local place called Nuñe, about 2 km SW of San Jose, near Villa Franca, 9 Mar 1999, 3200 m, A. Salas et al. 7304 (CIP*); Huarochirí, Bosque de Zárate, 3 Mar 1976, 3090–3150 m, N. Valencia 47 (USM*); Canta, Carhua, 8 km arriba del Puente a San Jose, 16 Apr 1974, 2700 m, G. Vilcapoma 199–2 (CIP*); Canta, San Buenaventura, 15 Mar 1974, 2700–2800 m, G. Vilcapoma 200 (USM*); Canta, San Buenaventura, margen derecha del Río Chillón, 15 Mar 1974, 2800 m, G. Vilcapoma 201 (CIP*, G, USM); Canta, San Buenaventura, 15 Mar 1974, 2800–2850 m, G. Vilcapoma 202–1 (CIP*), 202–3 (CIP*); Canta, Carhua (Chiringano), 15 Mar 1974, 2800 m, G. Vilcapoma 203 (CIP*), Canta, San Miguel, 2800–2950 m, G. Vilcapoma 211 (CIP*[3 measurements from 3 plants], PTIS); Canta, San Miguel, cerca de Canta, 12 Apr 1974, 2800–2950 m, G. Vilcapoma 212–2 (CIP*); Canta, alrededores de Canta, ruta a Pariamarca, 13 Apr 1974, 3000 m, G. Vilcapoma 213 (USM*), 213–2 (CIP*); 214–1 (CIP*); Canta, en ruta hacia Pariamarca, Apr? 1974, 3100 m, G. Vilcapoma s.n. (CIP*, MOL, USM); Canta, Huayllahuasi, G. Vilcapoma 885 (MOL*); Canta, en ruta hacia Pariamarca, Apr? 1974, 3100 m, G. Vilcapoma 218 (CIP*). Moquegua: Ilo, Lomas de La Buitrera, 25 km SSE Ilo y a unos 2 km al N del Cerro Huaca de La Luna, 29 Oct 1976, 350–400 m, C. M. Ochoa 11269 (CIP*, CUZ, US); Mariscal Nieto, arriba del Hospital de Cuajone, unos 15 km (en línea recta) al NNE de Torata, 2 Apr 1977, 3100 m, C. M. Ochoa 11611 (CIP*, CUZ, GH); Mariscal Nieto, arriba del Hospital de Cuajone, unos 15 km (en línea recta) al NNE de Torata, 2 Apr 1977, 3100 m, C. M. Ochoa 11612 (CIP*, CUZ, GH, US); Mariscal Nieto, 15 km NW of El Cruce on road to Carumas (33 km between these places), 6 Apr 1998, 3660 m, A. Salas & D. Spooner 7246 (CIP*); Moquegua, Lomas de Ilo, 11 Aug 1957, 350 m, O. Velarde 6157 (MOL*, US, USM); Moquegua, Carumas, 21 Mar 1925, 2600 m, A. Weberbauer 7276 (F*). Tacna: Tacna, cerca parque público de Toquepala, 2 Apr 1977, 3000 m, C. M. Ochoa 11610 (CIP*, CUZ); Candarave, Huanuara, Cerro Antavilca, cerca a Huanuara, a unos 10 km en línea recta, al sur-suroeste de Candarave, 4 Mar 1981, 3450 m, C. M. Ochoa 14261 (CUZ*); Tacna, vecindades de la Mina Toquepala, 4 Mar 1981, 3200 m, C. M. Ochoa 14262 (CIP*, CUZ); Tacna, vecindades de la Mina Toquepala, 4 Mar 1981, 3200 m, C. M. Ochoa 14263 (CIP*, CUZ); Tacna, Ilabaya, cerca Planta Concentradora Toque-

pala, 2 Apr 1977, 3100 m, C. M. Ochoa 11609 (CIP*, CUZ, GH); Tarata, niveles inferiores del Cerro Antavilca, cerca de Huanuara, a unos 10 km (en línea recta) al SSO de Candarave, 4 Mar 1981, 3450 m, C. M. Ochoa 14260 (CIP*, CUZ, US); Tacna, Morro de Sama, O. Velarde 6187 (MOL*); Candarave, 11 Mar 1925, 2900–3000 m, A. Weberbauer 7379 (CUZ, F*, US).

Solanum medians is morphologically very similar to some populations of *S. oplocense* Hawkes, an inland species ranging from central Bolivia to northern Argentina. Correll (1962, pg. 512) identified some collections from Bolivia as *S. tacnaense* var. *sandemanii* that we examined and identify as *S. oplocense*. Both species share similar pubescence, leaf shape, and corolla

morphology. *Solanum oplocense*, however, generally has pedicel articulation at or below the middle, and *S. medians* is distinct based on AFLP data (Spooner et al. 2005).

No herbarium was designated for the type of *S. weberbaueri* var. *poscoanum*. The label states *Herbarium Vargasianum, Universidad del Cuzco*, and Correll's labels distributed with his photos of these plants state the specimen was at herbarium CUZ, but the only specimen we found was at K. Ochoa (1999) lists specimens in CPC (Commonwealth Potato Collection at Dundee Scotland) and his personal herbarium. The CPC has



FIG. 7. *Solanum neoweberbaueri*. (Based on Ochoa 14860, US).

distributed all of its specimens, and Ochoa has distributed his herbarium widely, but mostly to CUZ. We found no isolecotype at CUZ on our visits in 2006 and 2007.

Hawkes (1954) designated *F. W. Pennell 13196* at K as holotype for *S. sandemanii*. We have not located this specimen but have seen photos of it as listed above. Ochoa (1999) invalidly designated a specimen of *F. W. Pennell 13196* at F as lectotype of *S. sandemanii*.

SOLANUM NEOWEBERBAUERII Wittm., Bot. Jahrb. Syst. 50 (Suppl.) 540, Figs. 1–2. 1914. *Solanum medians* f. *neoweberbaueri* (Wittm.) Correll, Wrightia 2: 191. 1961.—TYPE: PERU. Lima: Morro Salar, near Chorrillos, 250 m, in rocky places in a formation called loma, 21 Aug 1910, *Weberbauer 5689* (holotype: B, destroyed, photo and fragment, Fl, photos of B holotype: G! MO! NY!; lectotype, designated by Ochoa, 1999, pg. 840: F!, photos [Correll neg. 724]: LL! NY! UC!, isolecotypes: GH! US 144889! US 1444890!, photo of GH isolecotype [Correll neg. 725]: F! GH! MO! NY! UC!, photo of US 1444889 isolecotype [Correll neg. 723]: LL! MO! NY! UC!, photo of US 1444890 isolecotype [Correll neg. 721]: LL! NY! PTIS! UC!).

Plants 0.2–0.5 m tall, herbaceous, terrestrial, erect. Stems 2–6 mm in diameter at base of plant, subglabrous to sparsely pubescent, light to dark green and rarely tinged with purple. Pseudostipules minute to 12 mm long, lunate. Leaves 7–16.6 cm long, 4–10 cm wide, odd-pinnate, pubescent as the stems, light green; petioles 1.0–3.0 cm long; lateral leaflet pairs 1–3, slightly to greatly subequal and decreasing in size to the base; most distal lateral leaflets 1.8–6.5 cm long, 0.5–2.8 cm wide, narrowly to broadly ovate, the apex acute to acuminate, the base typically sessile and short decurrent on the basiscopic side to more rarely short petiolulate; terminal leaflet 1.7–8.5 cm long, 0.8–3.5 cm wide, narrowly to broadly ovate, the apex typically acute to acuminate, the base attenuate; interjected leaflets 0–2, sessile to short petiolulate, ovate to orbicular. Inflorescences generally in distal half of plant; peduncle 3–8.5 cm long. Flowers 2–25; pedicels 2–6.5 mm long, articulate typically above the middle; calyx 6–7 mm long, the lobes linear to long-attenuate, the acumens 2–3 mm long; corolla 2.7–4.7 cm in diameter, pentagonal to rotate, the acumens 1.5–2.0 mm long, edges of corolla flat, not folded dorsally, white to blue to lilac with a white star or white and blue mottled above and below; anthers 5–7 mm long, connate; style 8–9 mm long, exceeding stamens by 3–5 mm, straight, stigma clavate to capitate. Ovaries not maturing to fruits. Chromosome number $2n = 3x = 36$ (Spooner & Salas 2006; Hijmans et al. 2007). Figure 7.

Phenology—Flowering and fruiting along the coast in October.

Distribution (Fig. 6)—Central Peru (Department of Lima) in the coastal lomas, growing among rocks, often on slopes, in sandy or rocky soils, 200–750 m. elevation.

Specimens Examined—PERU. Lima: Lomas Manzano, cerca pueblo Pachacamac, al SSE de Lima, 25 Oct 1958, 200–300 m, *C. M. Ochoa 1807* (GH, US); *1808* (GH, US); *2163* (K, US); Lima, Lomas de Atosisa, unos 35 km al SSE de Lima y al E del pueblo de Pachacamac, 21 Jul 1971, 300 m, *C. M. Ochoa 3035* (US); Lima, San Bartolo, lomas al E de San Bartolo, entrando por el km 58 de la carretera Panamericana Sur, 21 Oct 1976, 350 m, *C. M. Ochoa 11248* (GH, US, USM); Cañete, Quilmaná, Lomas de Quilmaná, 10 km al N de Cañete, 26 Oct 1976, 350 m, *C. M. Ochoa & A. Salas 11252* (GH, US, USM); Cañete, lomas, cerca de la Mina Condestable, unos 5 km al E de Bujama Baja, entre Mala y Asia, al S de Lima, Oct 1976,

600 m, *C. M. Ochoa 11272* (MOL, US); Cañete, lomas, cerca de la Mina Condestable, unos 5 km al E de Bujama Baja, entre Mala y Asia, Oct 1976, 600 m, *C. M. Ochoa 11273* (F, GH, MOL, NY, US, USM); Huarochiri, lomas, cerca de la Mina Huarochiri, unos 5 km entrando al pueblo de Lurín, hacia el E, al S de Lima, 22 Oct 1982, 750 m, *C. M. Ochoa 14860* (US).

Solanum neoweberbaueri is similar to *S. medians*, but it differs by its subglabrous to sparsely pubescent leaves and calyx; the pedicels, which are typically articulate in the middle or slightly below the middle; and the corollas, which are pure white to white and mottled blue or blue to purple with a white star. All populations are sterile. Ochoa (1999) postulated that *S. neoweberbaueri* is a sterile triploid nothospecies resulting from hybridization of *S. medians* and *S. chancayense*. Ochoa, a sympatric white-flowered species. *Solanum chancayense* is unrelated to *S. medians* as it is a member of plastid clade 3, not clade 4 of Spooner and Castillo (1997). Ochoa (1999) may be correct in the hybrid origin of *S. neoweberbaueri* but we consider its hybrid origin speculative at present and do not designate it as a nothospecies.

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