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New Species of Wild Tomatoes (*Solanum* Section *Lycopersicon*: Solanaceae) from Northern Peru

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ABSTRACT. ***Solanum arcanum*** and ***S. huaylasense,*** two new wild tomato species segregated from *Solanum peruvianum* sensu lato, are described and illustrated. These two new species are placed in a key with two other segregates of *S. peruvianum* sensu lato: *S. peruvianum* sensu stricto and *S. corneliomulleri*, and the morphologically similar species *S. chilense*. We also present a list of all 13 species of wild tomatoes we recognize, and their equivalent former names in *Lycopersicon*.

Wild tomatoes (*Solanum* L. sect. *Lycopersicon* (Mill.) Wettst. are native to western South America and distributed from central Ecuador, through Peru to northern Chile, and in the Galápagos Islands, where two endemic species *S. cheesmaniae* and *S. galapagense* grow (Darwin et al. 2003) (see Table 1 for authors of species names). The putative wild ancestor of cultivated tomatoes, *S. lycopersicum*, is more widespread and most probably recently distributed into Mexico, Colombia, Bolivia, and other South American countries (Rick and Holle 1990), and from there worldwide. *Solanum peruvianum* sensu lato is the most widespread and polymorphic species in the group. It grows from northern Peru to northern Chile, in a wide diversity of habitats from near sea level along the arid Pacific coast, to mesic uplands up to 3,000 m in valleys on the western side of the Andes.

Using morphological species concepts and limited herbarium material, Müller (1940) and Luckwill (1943) produced the two most recent taxonomic monographs of wild tomatoes, and placed them in the genus *Lycopersicon*. Phylogenetically, tomatoes and their near relatives have been shown by chloroplast DNA restriction site and sequence data (Spooner et al. 1993; Bohs and Olmstead 1997, 1999; Olmstead and Palmer 1997; Olmstead et al. 1999; Bohs, in press) and by nuclear GBSSI sequence data (Peralta and Spooner 2001) to be deeply nested in *Solanum* and to form the sister clade to potatoes. Consequently, the majority of taxonomists (and recently breeders; see http://www.sgn.cornell.edu/help/about/solanum_nomenclature.html) are adopting *Solanum* as the generic name for tomatoes. We are working on a taxonomic monograph of *Solanum* sect. *Lycopersicon*. This paper publishes the final two tomato species we recognize, in order that the names become available for use in the broad tomato literature, and presents a scientific reference for currently recognized tomato names until our monograph appears (Table 1).

In recognizing species here and for our upcoming monograph, we have used an approach combining morphological, molecular, and ecological data, ultimately relying on morphological characters to provide identifications to the many specimens examined. Our decisions about recognition of species rank relied on clear morphological discontinuities to define entities; this can be difficult with widespread, polymorphic, and possibly currently evolving entities like the segregates described here. Potential reasons for variability and intergradation are recent divergence and hybridization. Despite the variability in tomato species, our decision to recognize these new taxa at the specific level is based upon a pragmatic combination of phylogeny and morphology and reflects evolving, recognizable entities within the complex.

Breeding systems have played an important role in wild tomato species evolution, and vary from allogamous self-incompatible, to facultative allogamous and self-compatible, to autogamous and self-compatible. Rick (1963, 1979, 1986), who treated tomatoes in *Lycopersicon*, recognized two species complexes based on crossing relationships: the Esculentum complex included seven intercrossable species (including the cultivated tomato), and the Peruvianum complex included two self-incompatible species, *L. chilense* and *L. peruvianum*, that intercrossed but possessed breeding barriers with the Esculentum complex.

Rick (1986) recognized 40 races in his widespread and morphologically variable *L. peruvianum*. A few of these are coastal races, but the majority are locally distributed montane races. He proposed that strict gametophytic self-incompatibility and geographic isolation drove differentiation among these *L. peruvianum* races. He recognized three groups of *L. peruvianum* races in northern Peru (the Chamaya-Cuvita group of races, the Marañón group, and Chotano-*humifusum* group), and a fourth group from south-central Peru

TABLE 1. Species list for *Solanum* section *Lycopersicon,* with equivalents in the previously recognized genus *Lycopersicon,* now part of a monophyletic genus *Solanum.*

Solanum name	*Lycopersicon* equivalent	Distribution; habitats
S. arcanum Peralta	Part of *L. peruvianum* (L.) Miller	N Peru, coastal and inland Andean valleys; lomas, dry valleys and dry rocky slopes; 100 to 2800 m.
S. cheesmaniae (L. Riley) Fosberg	≡ *L. cheesmaniae* L. Riley (incorrectly published as *cheesmanii*)	Endemic to the Galápagos Islands, Ecuador; wide variety of habitats; sea level to 500 m.
S. chilense (Dunal) Reiche	≡ *L. chilense* Dunal	S Peru (Tacna) to N Chile (Región II); in hyper-arid rocky plains and coastal deserts; sea level to 3250 m.
S. chmielewskii (C.M. Rick, Kesicki, Fobes & M. Holle) D.M. Spooner, G.J. Anderson & R.K. Jansen	≡ *L. chmeilewskii* C.M. Rick, Kesicki, Fobes & M. Holle	S Peru (Apurímac) to N Bolivia (La Paz); high dry Andean valleys; 1600–3200 m.
S. corneliomuelleri J.F. Macbr.	Part of *L. peruvianum* (L.) Miller; also known as *L. glandulosum* C.F. Mull.	Central to S. Peru, W slops of the Andes; landslides and rocky slopes; (40)200–3300 m.
S. galapagense S. Darwin & Peralta	Part of *L. cheesmaniae* L. Riley (previously known as forma or var. *minor*)	Endemic to the Galápagos Islands; mostly occurring on coastal lava to within 1 m of high tide mark within range of sea spray, but occasionally inland; sea-level to 50 m.
S. habrochaites S. Knapp & D.M Spooner	≡ *L. hirsutum* Dunal	Central Ecuador to Central Peru, on the western slopes of the Andes; in a variety of forest types from premontane forests to dry forests; (40)200–3300 m.
S. huaylasense Peralta	Part of *L. peruvianum* (L.) Miller	N Peru (Ancash); rocky slopes of the Callejón de Huaylas along the Río Santa and in the adjacent Río Fortaleza drainage; (940)1700–3000 m.
S. lycopersicum L.	≡ *L. esculentum* Miller	Known only from cultivation or escapes; world-wide in a variety of habitats, many escaped plants have smaller fruits (''cerasiforme''); sea level to 4000 m.
S. neorickii (C.M. Rick, Kesicki, Fobes & M. Holle) D.M. Spooner, G.J. Anderson & R.K. Jansen	≡ *L. parviflorum* C.M. Rick, Kesicki, Fobes & M. Holle	S Ecuador (Azuay) to S Peru (Apurímac); dry inter-Andean valleys, often found trailing over rocky banks and roadsides; (920)1950–2600 m.
Solanum pennellii Correll	≡ *Lycopersicon pennellii* (Correll) D'Arcy	N Peru (Piura) to N Chile (Tarapacá); dry rocky hillsides and sandy areas; sea level to 2300 m.
S. peruvianum L.	≡ *L. peruvianum* (L.) Miller	Central Peru (Ancash) to N Chile (Región II); coastal lomas formations and occasionally in coastal deserts, occasionally as a weed at field edges in coastal river valleys; sea level to 600 m.
S. pimpinellifolium L.	≡ *L. pimpinellifolium* (L.) Miller	Central Ecuador to central Chile; dry coastal habitats; 0–500 m, but exceptionally up to 1400 m.

and northern Chile. He discovered crossing barriers between the northern and southern *L. peruvianum* races, and found that some of the northern races could be crossed to a limited degree with species from both the Esculentum and Peruvianum complex. Rick (1986) hypothesized that the Río Marañón races of *L. peruvianum* were ancestral to all other wild tomatoes.

Our previous taxonomic studies of morphology (Peralta and Spooner 2005), DNA sequences (Peralta and Spooner 2001), and AFLPs (Spooner et al. 2005) all supported separate species status for the northern and southern populations of *S. peruvianum*. The present study is based on an examination of many herbarium specimens collected from the wild, and of living specimens made from seeds of living germplasm collections grown in gardens in Mendoza, Argentina and Wisconsin, USA. We recognize four species segregated from the polymorphic *Solanum peruvianum* sensu lato: *S. peruvianum* L. s.str., *S. corneliomulleri* J. F. Macbr., and two new species *S. arcanum* Peralta and *S. huaylasense* Peralta.

Materials and Methods

We obtained seeds of genebank accessions of *S. peruvianum* s.l. from the C. M. Rick Tomato Genetics Resource Center, Department of Vegetable Crops, University of California, Davis. Dr. Charles Rick, former curator of this genebank, kindly provided advice on the choice of accessions, based on geographic distribution, morphology, genetic diversity, and breeding behavior. We grew the accessions in greenhouses and experimental fields in Madison, Wisconsin, USA and the Hancock State Agricultural Experiment Station in Hancock, Wisconsin, USA (1998, 1999, 2001) and at the INTA La Consulta Experimental Station in Mendoza, Argentina (2001). Vouchers will be deposited at BM, DAV, MERL, PTIS, and WIS. We also examined herbarium specimens from wild collected plants from throughout the geographical range of each taxon. Specimens from the following herbaria were examined for this study (abbreviations follow *Index Herbariorum,* http://sciweb.nybg.org/science2/IndexHerbariorum.asp): BH, BM, CAS, E, F, G, GH, HUT, K, LL, M, LPB, MICH, MO, NY, SGO, TEX, UC, US, USM.

Taxonomic Treatment

Solanum arcanum Peralta sp. nov.–TYPE: PERU. Amazonas: western base of the Cerros Calla Calla, 9 km E of Balsas on road to Leimebamba, 1340 m, 30 May 1964, *Hutchison & Wright 5449* (holotype: USM!; isotypes: F!, K!, M!, MICH!, MO!, NY!, UC!, US!). (Fig. 1).

Lycopersicon peruvianum L. var. *humifusum* C.H. Mull., *U.S. Dept. Agric. Misc. Publ.* 382: 19. 1940; non *Solanum humifusum* Dunal in DC., Prodr. 13(1): 237. 1852. TYPE: PERU. Cajamarca: between San Juan and Magdalena, 23 Dec 1937, *Blood & Tremelling 142* (holotype: US-40370!).

Species *Solano peruviano* Linnaei affinis, sed caulibus et foliis fere glabris vel pubescentibus trichomatibus longis et patulis vel erectis, inflorescentiis simplicibus, columna staminum recta, differt.

Spreading, erect or often prostrate, perennial herbs, woody at the base, to 1 m or more in diameter and sometimes up to 1 m tall. Stem 7–12 mm diameter at base, often hollow, green, glabrous to variously pubescent with a mixture of simple uniseriate trichomes, short velvety trichomes to 0.5 mm (these eglandular or with a 1-celled head), longer patent trichomes to ca. 1 mm, from multicellular bases, short glandular trichomes with 4-celled heads, some populations (Chota valley) with very sparse short unicellular trichomes. Sympodial units 2-foliate; internodes 2–6 cm. Leaves interrupted imparipinnate, (3)5–15(25) × (1)2.5–7(10) cm, green to pale beneath, glabrous to sparsely short pubescent to densely pubescent with a mixture of simple uniseriate trichomes, some populations lacking stout patent trichomes to 1 mm on the leaves, adaxially nearly glabrous with a few scattered 1-celled trichomes to densely pubescent with short and long trichomes, abaxially the pubescence denser, with stouter trichomes to 1 mm along the veins; primary leaflets 2–4(5) pairs, the basal pair half the size of the rest, elliptic to broadly elliptic, the base acute to truncate, oblique and decurrent basiscopically, the margins almost entire (Jequetepeque) to regularly or irregularly crenate-serrate to lobed, the apex acute; terminal leaflet 1.2–5 × 0.6–2(2.5) cm, the petiolule 0.5–1 cm, the apex long-acuminate in Marañón populations; lateral leaflets 0.7–3.5(5) × 0.4–2(2.5) cm, the petiolule 0.2–1 cm; secondary leaflets occasionally present acroscopically on the larger leaflets, 0.1–0.2 × 0.1–0.2 cm, sessile; tertiary leaflets absent; interjected leaflets 0–8, 0.1–0.5 × 0.1–0.4 cm, decurrent on the leaflet rachis; petiole 0.5–2.5(3.5) cm; pseudostipules present but not developed at all nodes, 0.5–1 × 0.5–1 cm, the margin entire to irregularly crenate. Inflorescences 6–20 cm, simple, with 5–20 flowers, ebracteate or nearly all the nodes bracteate, the bracts 0.1–0.4(1) × 0.1–0.2(1) cm larger in the basal nodes; peduncle (1.5)3.5–10 cm, glabrous and minutely glandular to densely velvety pubescent with intermixed longer patent trichomes like those of the stems. Pedicels 1.1–1.7 cm, articulated at the middle or in the distal half. Buds 0.8–1 × 0.3–0.4 cm, conical, straight, approximately half way exerted from the calyx just before anthesis. Flowers with the calyx tube minute, the lobes 0.5–0.7 × 0.15–0.2 cm, lanceolate, glabrous to pubescent like those of the inflorescence; corolla 1.8–2 cm, pentagonal, yellow, the tube 0.5–0.6 cm, the lobes 0.8–1 × 0.8–1 cm, white pubescent on the tips and margins, reflexed at anthesis; staminal column 0.8–0.9 cm, straight; the filaments 0.25–0.5 mm, the anthers 0.4–0.5 cm, the sterile tip 0.1–0.25 cm; ovary globose, glabrous or with a few minute trichomes at the apex; style 0.8–1 cm, densely white pubescent in the basal half; stigma capitate, green, scarcely ex-

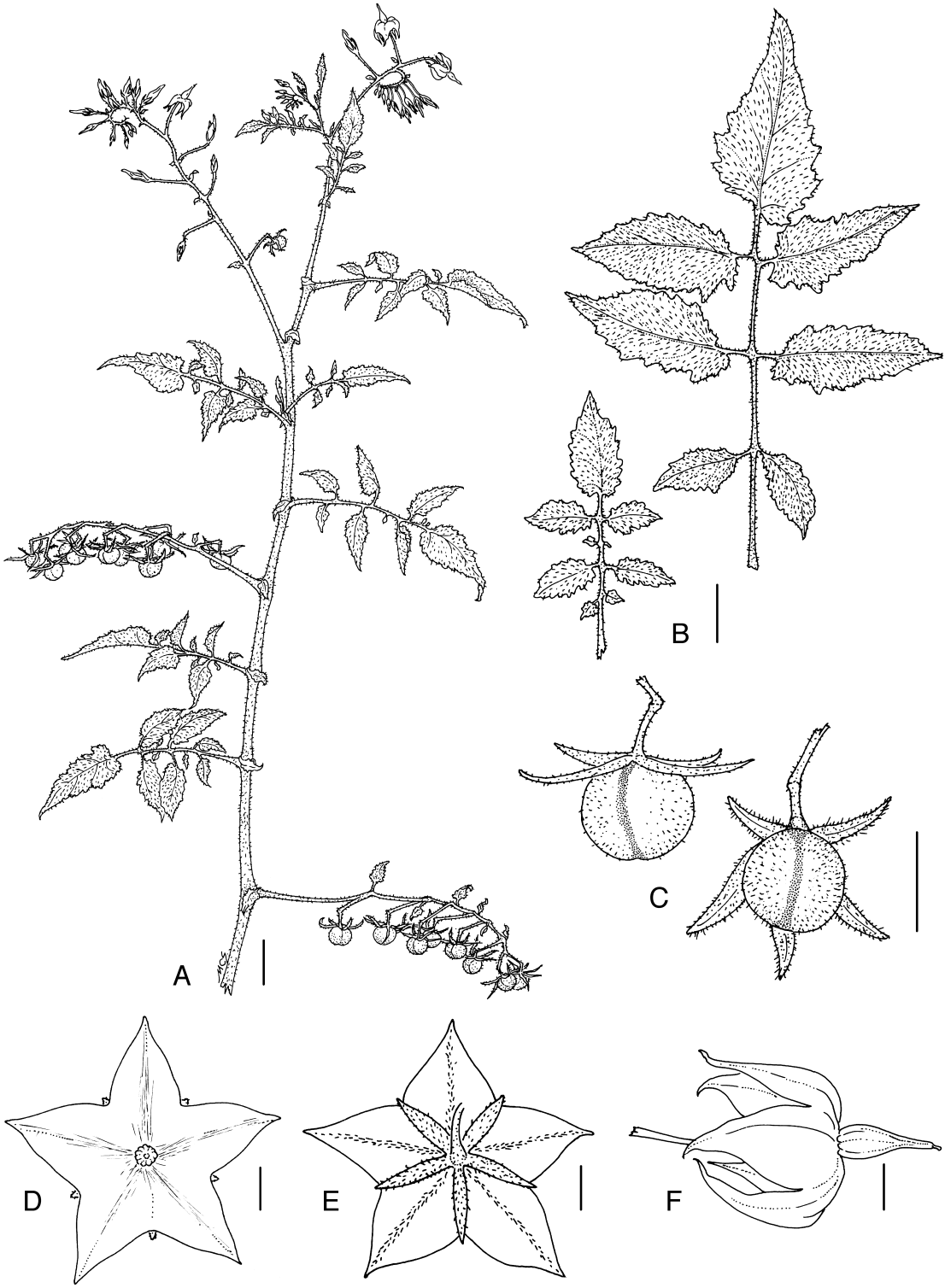

FIG. 1. *Solanum arcanum*. A. Habit (scale = 2 cm). B. Leaves (scale = 1 cm). C. Fruits (scale = 1 cm). D, E, F. Flowers (scale = 0.5 cm). Illustrations from cultivated specimens (accession LA1396 from the C. M. Rick Tomato Genetic Resources Stock Center; a plant of the ''Marañón'' geographical race).

erted to exerted ca. 0.5 mm from the staminal column. Fruit 1–1.4 cm in diameter, globose, 2-locular, green with a dark green stripe around it that may change to purple at maturity, glabrous to more or less densely pubescent with weak-walled simple uniseriate trichomes less than 0.5 mm long; fruiting pedicels 1.5–2.3 cm, angled towards the inflorescence axis, occasionally straight; calyx lobes in fruit 0.9–1 × 0.2–0.25 cm, spreading to loosely investing the berry. Seeds 2.2–3.2 mm × 1.2–1.6 mm × 0.5–0.6 mm, obovate, narrowly winged at the apex and acute at the base, pale brown, pubescent with hair-like outgrowths of the tegument cell radial walls, which give a silky appearance to the surface. Chromosome number: $n = 12$ (voucher LA 1396 (BM), see Table 2).

Distribution (Fig. 2). Coastal and inland Andean valleys in N Peru; in lomas, dry valleys and dry rocky slopes; 100 to 2500 m.

Representative Specimens Examined. **PERU. Amazonas**: Prov. Bagua, km 248 between Milagro and Amojao, near Pongo de Retema, 380–400 m, 27 Jun 1959, *Ferrerya 13674* (USM); Prov. Bongará, Pedro Ruiz-Chachapoyas, km 35, Oct 1990, *Kahn & Moussa 2882* (USM). **Ancash**: Prov. Huaráz, just above Pariacoto, 1400 m, 28 Mar 1960, *Correll & Smith P943* (LL, NY); Prov. Huaráz, just above Pariacoto, 1550 m, 28 Mar 1960, *Correll & Smith P945* (F, LL, NY); Prov. Casma, near Yaután, 28.1 miles E de Casma, 750 m, 9 Dec 1970, *Rick SAL-442* (USM); Prov. Huaráz, below Callán, between La Punta and Casma, 2800 m, 23 Oct 1972, *Ferrerya et al. 16510* (USM); hacienda 24 miles W of Huaráz, Chacchan, ca 2800 m, 8 Oct 1922, *Macbride & Featherstone 2554* (F, G); Chacchan, hacienda 24 miles W of Huaráz, ca 2800 m, 8 Oct 1922, *Macbride 2553* (F); Prov. Caraz (Carhuaz), Distrito Pamparomas, road from Moro to Pamparomas, 2000 m, 25 Oct 2000, *Weigend et al. 2000/692* (BM). **Cajamarca**: between San Juan and Magdalena, 23 Dec 1937, *Blood & Tremelling 142* (US); Prov. San Ignacio, San Martín del Chinchipe, 5°19′16″S, 78°41′05″W, 1000 m, 15 Sep 1999, *Flores et al. 161* (NY); near Magdalena between Chilete and pass on road to Cajamarca, 1400 m, 24 Mar 1960, *Correll & Smith P834* (F, LL, NY); 34 km from Cajamarca on road to Chilete, 2450 m, 24 Mar 1960, *Correll & Smith P845* (F, LL, NY); 34 km from Cajamarca on road to Chilete, 2450 m, 24 Mar 1960, *Correll & Smith P846* (LL, NY); between San Marcos and Cajabamba, 2150 m, 26 Mar 1960, *Correll & Smith P904* (LL, NY); between San Marcos and Cajabamba, 2150 m, 26 Mar 1960, *Correll & Smith P905* (LL, NY); between San Marcos and Cajabamba, 2150 m, 26 Mar 1960, *Correll & Smith P907* (LL); Prov. Cajamarca, near Choropampa, ca 11 km W of San Juan and 48 km SW of Cajamarca on road to San Pedro de Lloc, ca 1840 m, 20 Oct 1984, *Dillon & Whalen 4081* (BH, F, USM); above Chilete, ca 15 km from Chilete road to Cajamarca, 1 Apr 1948, *Ferrerya 3336* (USM); about 2 km W of Cajamarca, 2800 m, 3 Dec 1974, *Hudson 1096* (NY); Prov. Contumazá, San Antonio-Portachuelo (road from Ascope to San Benito), 350 m, 13 May 1972, *López & Sagástegui 7922* (NY); Prov. Contumazá, San Antonio-Portachuelo (road from Ascope to San Benito), 350 m, 13 May 1972, *López 7931* (F, MO); Prov. Contumazá, El Balcón (Algarrobal-San Benito), 1820 m, 20 Aug 1977, *López & Sagástegui 8432* (HUT, NY); Prov. Contumazá, above Rupe (Chilete-Contumazá), 1350 m, 25 Jun 1983, *López et al. 9224* (BM, F, HUT, MO, NY); Prov. Contumazá, San Antonio-Portachuelo (road from Ascope to San Benito), 350 m, 22 Apr 1993, *López & Sagástegui 9731* (F, MO); Prov. San Pablo, Distr. San Pablo, Cunish, 26.1 km NE along road from Chilete, 7°06′17″S 78°51′28″W, 2000 m, 23 Aug 1994, *Merello et al. 1088* (CAS); Chiquiden, from San Juan to Cajamarca, 2800 m, 17 May 1953, *Ochoa 1976* (F); Prov. Contumazá, in area of Sascas, 28 Aug 1956, *Rick 126* (USM); along Río Jequetepeque, road to Cajamarca, 31 Aug 1956, *Rick 132* (USM); Magdalena, road to Cajamarca, 2 Sep 1956, *Rick 139* (USM); Rope, 9.2 miles S of Chilete, 2000 m, 6 Dec 1970, *Rick SAL-435* (USM); Prov. Contumazá, El Portachuelo (Ascope to San Benito), 900 m, 17 May 1979, *Sagástegui et al. 9228* (F, MO, NY); Prov. Contumazá, Rupe to Contumazá, 2100 m, 24 May 1981, *Sagástegui et al. 9814* (BM, MO, NY); Prov. Contumazá, El Platanar, above Cascas, 1250 m, 27 Jun 1992, *Sagástegui & Leiva 14625* (F); Prov. Contumazá, El Platanar, above Cascas, 1200 m, 11 Oct 1992, *Sagástegui & Leiva 14795* (BM, F, HUT, NY); Prov. Contumazá, area about Guzmango, 2500 m, 18 Dec 1994, *Sagástegui et al. 15473* (F); Prov. Chota, Yamaluc-Huambos, 1880 m, 19 May 1997, *Sagástegui et al. 16013* (NY); Prov. Contumazá, 5 km W of Chilete, 884 m, 9 Jun 1963, *Ugent & Ugent 5523* (F, MO, US, WIS); Prov. Cajamarca, 50 km SW of Cajamarca, between Magdalena and San Juan, 1840 m, 5 Jun 1963, *Ugent & Ugent 5388* (US, WIS); Prov. Santa Cruz, 9 km from Santa Cruz on road to Catache (FO1), 4 May 2003, *Weigend et al. 7541* (BM); 10 km W of San Juan on road to Chilete, Río Jequetepeque valley, 2550 m, 20 Oct 1984, *Whalen & Dillon 896* (BH, MO, NY, USM). **La Libertad**: Prov. Trujillo, Cerro Prieto, 250 m, 14 Aug 1949, *Ángulo 1018* (F); Prov. Trujillo, Cerro Campana, 460 m, 8 Jun 1950, *Ángulo 1236* (F); Prov. Trujillo, near Trujillo, 100 ft., 15 Dec 1937, *Blood & Tremelling 97* (GH); near Trujillo, 6000 ft, 17 Dec 1937, *Blood & Tremelling 111* (UC); Prov. Trujillo, Cerro Campana, 850 m, 21 May 1977, *Boeke 1754* (MO, NY); Prov. Otuzco, Plaza to Pampa, 1800 m, 26 Jul 1953, *de Cevasco s.n.* (USM); Prov. Trujillo, E side of Cerro Campana, ca 15 km N of Trujillo, 150–600 m, 4 Jan 1983, *Dillon et al. 2703* (F, MO, NY, TEX, US, USM); Prov. Trujillo, Cerro Campana, 400–500 m, 18 Aug 1952, *Ferrerya 8610* (USM); Prov. Otuzco, above Samme, between Trujillo and Otuzco, 1500–1600 m, 28 May 1960, *Ferrerya 14088* (USM); Prov. Tru-

TABLE 2. Tomato Genetics Resource Center accession numbers (LA numbers) previously identified as *Lycopersicon peruvianum* referable to *Solanum arcanum* and *Solanum huaylasense*. Voucher specimens for these genebank accessions are held in BML and MERL.

TGRC LA#	Species	Locality
LA2185	*S. arcanum*	Amazonas: Pongo de Rentema, in the gap of the Marañón, E of Coral Quemado; 400 m, 5°26′S, 79°39′W.
LA1396	*S. arcanum*	Amazonas: Balsas, 4°25′S, 80°17′W.
LA2326	*S. arcanum*	Amazonas: Balsas, 1500–1800 m, 4°25′S, 80°17′W.
LA1031	*S. arcanum*	Amazonas: Balsas.
LA1394	*S. arcanum*	Amazonas: Balsas, Río Utcabamba.
LA1395	*S. arcanum*	Amazonas: Chachapoyas; 1000 m.
LA2172	*S. arcanum*	Cajamarca: Cuyca; 161 km from Olmos junction with the Panamerican Hwy, 11°31′S, 75°07′W.
LA1708	*S. arcanum*	Cajamarca: between Chamaya and Jaén; 700 m.
LA2157	*S. arcanum*	Cajamarca: Tunel Chotano, 23 km N of Chota; 1600 m.
LA2163	*S. arcanum*	Cajamarca: between Cochabamba and Yamaluc, 2–5 km N of Cochabamba; 1800–1900 m.
LA2164	*S. arcanum*	Cajamarca: Yamaluc, 12–14 km N of Cochabamba, very dry slopes; 2000 m.
LA392	*S. arcanum*	Cajamarca: Llallan, 78 km from Car. Panamericana, 12 km W of Chilete; 900 m.
LA1351	*S. arcanum*	Cajamarca: Rupe; 1800–2100 m.
LA2152	*S. arcanum*	Cajamarca: Río Jequetepeque, 140 km from Panamerican Hwy, 2 km W of San Juan; 2150 m; 7°17′S, 78°29′W.
LA2334	*S. arcanum*	Cajamarca: San Juan, Río Jequetepeque.
LA385	*S. arcanum*	Cajamarca: San Juan, drainage of Río Jequetepeque, mountainside 140 km from Car. Panamericana; 2500 m.
LA389	*S. arcanum*	Cajamarca: Abra Gavilán, between Abra Gavilán and San Juan, 10 km from Abra Gavilán, roadbank and up slope; 2700 m.
LA2548	*S. arcanum*	Cajamarca: La Muyuna, Río Jequetepeque; 870 m.
LA2553	*S. arcanum*	Cajamarca: Balconcillo-San Marcos; 2650 m; 7°20′S, 78°11′W.
LA378	*S. arcanum*	Cajamarca: Cascas, 1200 m; 7°29′S, 78°49′W.
LA1027	*S. arcanum*	Cajamarca.
LA2327	*S. arcanum*	Cajamarca: Aguas Calientes, immediately S of Aguas Calientes in cultivated area; 2400 m.
LA2388	*S. arcanum*	Cajamarca: Cochabamba-Huambos; 1700 m.
LA441	*S. arcanum*	La Libertad: Cerro Campana, W of Panamerican Hwy N of Trujillo; 350 m; 5°05′S, 79°17′W.
LA1984	*S. arcanum*	La Libertad: Otuzco (Río Moche), 2 km on side road E of Otuzco; 2800 m; 7°54′S, 78°35′W.
LA2328	*S. arcanum*	La Libertad: Aricapampa; 2300–2500 m; 7°48′S, 77°43′W.
LA2330	*S. arcanum*	La Libertad: Chagual, 3 km above the Chagual bridge across Río Marañón, about 12 km below LA2328, steep roadbank, very dry situation; 1700 m.
LA1032	*S. arcanum*	La Libertad, Aricapampa.
LA2331	*S. arcanum*	La Libertad, Agallapampa, on steep slopes; 2500 m.
LA2555	*S. arcanum*	La Libertad: Mariscal Castilla (Moche); 2620 m.
LA1985	*S. arcanum*	La Libertad: Casmiche, (Río Moche), 68 km E of Trujillo, steep road bank; 1900 m.
LA1626	*S. arcanum*	Ancash: mouth of Río Rupac; 1700 m.
LA1981	*S. huaylasense*	Ancash, Vocatoma, (Río Santa), roadside extending about 1 km; 1600 m.
LA1982	*S. huaylasense*	Peru. Ancash: Huallanca, Río Santa, near the hydroelectric plant, about 4 km beyond LA1981; 1400 m; 8°49′S, 77°52′W.
LA1983	*S. huaylasense*	Ancash, Río Manta, (Río Santa), 30 km W of collection LA1982, very dry spot on a steep gravel slope; 940 m.
LA2561	*S. huaylasense*	Ancash, Huallanca (Santa); 1580 m.
LA2562	*S. huaylasense*	Ancash, Huallanca (Santa), Canyon del Pato; 1650 m.
LA2808	*S. huaylasense*	Ancash: Huaylas.
LA2809	*S. huaylasense*	Ancash: Huaylas.
LA1364	*S. huaylasense*	Ancash, Alta Fortaleza, moderately moist slopes, not near Río Fortaleza; 2920 m.

jillo, SE side of Cerro Campana, 750 m, 24 Sep 1957, *Hutchison 1356* (UC); Prov. Huamachuco, Río Marañón canyon, 1 km below Aricapampa, 2600 m, 8 Aug 1964, *Hutchison et al. 6203* (E, F, GH, K, M, MO, NY, SGO, UC, US, USM); Prov. Otuzco, below José Balta (near Agallpampa), 2000 m, 30 Oct 1993, *Leiva 952* (F, HUT, NY); Prov. Otuzco, below José Balta (road to Agallpampa), 2600 m, 3 Feb 1994, *Leiva 1015* (F); Prov. Otuzco, about El Platanar (W of Salpo), 1310 m, 19 Mar 1994, *Leiva 1019* (F, NY); Prov. Otuzco, below José Balta (road to Agallpampa), 2540 m, 9 Jun 1994, *Leiva 1137* (F, NY); area around Huangabal (Simbal to La Cuesta),

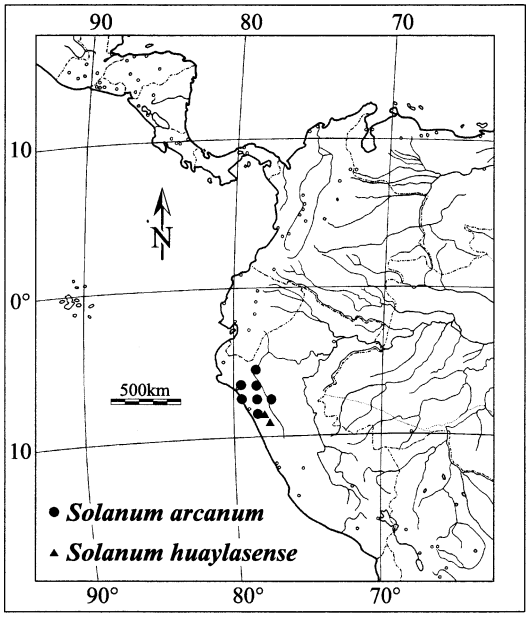

FIG. 2. Distribution of *Solanum arcanum* and *Solanum huaylasense*.

1250 m, 18 Feb 1996, *Leiva & Salinas 1785* (F, M, NY); Prov. Trujillo, Cerro Campana, 550 m, 3 Oct 1997, *Leiva & Quipuscoa 2077* (F, NY); Prov. Trujillo, km 580 Cerro Cabezón, N of Trujillo, 280 m, 10 Feb 1998, *Leiva et al. 2157* (NY); Prov. Trujillo, km 580 Cerro Cabezón, N of Trujillo, 330 m, 10 Feb 1998, *Leiva et al. 2159* (F); Prov. Trujillo, Lomas de Virú, 450 m, 30 Oct 1976, *López & Sagástegui 8418* (NY); Prov. Trujillo, Lomas de Virú, 300 m, 5 Sep 1986, *Mostacero 678* (BM, HUT, MO); Prov. Trujillo, Lomas de Virú, 550 m, 15 Sep 1986, *Mostacero et al. 1451* (F); Prov. Otuzco, area about Otuzco, Cerro Chologday, 2550 m, 4 Jul 1993, *Mostacero & Quipuscoa 3163* (HUT); Prov. Bolívar, between Pusac and Longotea, 1750 m, 20 Jun 1995, *Mostacero et al. 3566* (HUT); Prov. Trujillo, Lomas de Cerro Campana, 30 Aug 1956, *Rick 128* (USM); Prov. Trujillo, Cerro Campana, 23 Oct 1974, *Sagástegui 7821* (MO, NY); Prov. Trujillo, Cerro Campana, 600 m, 6 Oct 1982, *Sagástegui & López 10414* (F, G, MO, NY); Prov. Trujillo, Cerro Campana, 500 m, 25 Oct 1983, *Sagástegui 10939* (F); Prov. Trujillo, Cerro Cabezón, ca 650 m, 4 Nov 1983, *Sagástegui & López 11017* (F); Prov. Trujillo, Cerro Chiputur, 400 m, 11 Nov 1983, *Sagástegui & Mostacero 11035* (F); Prov. Trujillo, Lomas de Virú, 500 m, 20 Jan 1984, *Sagástegui & Mostacero 11380* (BM, MO, NY); Prov. Trujillo, Cerro Cabezón, 600 m, 20 Feb 1983, *Sagástegui & Mostacero 203441* (NY); Prov. Trujillo, Cerro Cabezón, near Trujillo, 5000 m, 11 Aug 1939, *Weberbauer s.n.* (USM); Prov. Trujillo, Lomas de Virú, Cerro de las Lomas, 8°22′43″S 78°46′13″W, 200–500 m, 12 Oct 2000, *Weigend et al. 2000/696* (BM, MO). **Piura**: Prov. Talara, 10 miles E of Talara, 26 Dec 1928, *Haught 2* (USM).

Observations of Cultivated Plants. Accessions of *Solanum arcanum* grew well under cultivation and completed their life cycle, producing numerous flowers and fruits until the first frost. Cultivated specimens tend to produce vigorous plants, with larger stems, internodes, leaves, inflorescences, flowers, and fruits, but they are similar to wild specimens collected in similar geographic areas, and the cultivated accessions generally can also be assigned to the four groups mentioned below.

Etymology. The specific epithet (*arcanum* = hidden) refers to the cryptic nature of this species, remaining hidden in the extremely variable *Solanum peruvianum* s.l.

Intraspecific Variation. *Solanum arcanum* is an extremely variable species, consisting of four weakly defined morphotypes (''groups'') with discrete geographic ranges. The complex overlapping variability, especially in leaf morphology, makes the consistent assignment of any given specimen to a species group difficult in the absence of geographical data, so we do not recognize them as formal taxa.

A. ''MARAÑÓN'' GROUP. Robust erect plants, sometimes up to 1 m tall, later decumbent; little to no velvety pubescence, dense long patent trichomes, leaflets dentate or more deeply incised; growing in the Río Marañón Valley (includes the type of *Solanum arcanum*). Our new species includes the Chamaya-Cuvita and the Marañón group of races that Rick (1986) recognized as closely related to each other based on crossability.

B. ''HUMIFUSUM'' GROUP. Prostrate plants; with velvety pubescence; leaflets entire or with only a few marginal teeth, velvety pubescent on the abaxial side, and dark green; inflorescence unbranched; growing in the Pacific drainages. The type of *Lycopersicon peruvianum* var. *humifusum* C.H. Mull. comes from among these populations.

C. ''CHOTANO'' GROUP. Prostrate plants; almost completely glabrous; with deeply lobed lateral leaflets; growing in the Río Chota valley near Yamaluc in the Department of Cajamarca. The ''Humifusum'' and ''Chotano'' groups have also a close relationship according to crossability (Rick 1986), and molecular data (Peralta and Spooner 2001), and differ mainly by pubescence.

D. ''LOMAS'' GROUP. Prostrate to semi-erect plants; velvety pubescence; leaflets dentate or almost entire; inflorescences simple or sometimes branched; growing at the Lomas of Cerro Campana and Lomas de Virú. These populations are incredibly variable from year to year, specimens collected in El Niño years have very large leaves, while those collected in drier seasons have smaller, more pubescent leaves with fewer leaflets and less lobed margins. The northern ''Lomas'' populations are quite variable in morphological characters

like the inflorescence branching pattern, and seem to represent transition forms towards southern populations of *S. peruvianum* s.str.

Relationships. Based on morphological and molecular data *Solanum arcanum* is closely related to the self-compatible species *S. neorickii* and *S. chmielewskii* (Peralta and Spooner 2001, in press; Spooner et al. 2005).

Solanum huaylasense Peralta, sp. nov.–TYPE: PERU. Ancash: trail to cave across Río Santa from Mancos, 9 Apr 1970, *Smith & Blas 4889* (holotype: USM!; isotypes: F!, US!). (Fig. 3).

Species *Solano chilense* Dunalii similis, sed caulibus et foliis et baccis viridibus sparse pubescentibus, floribus plerumque minoribus, columna staminum recta vel curva, baccis uniformiter viridibus, differt.

Sprawling perennial herbs, woody at the base, to 1 m in diameter, ca. 1 m tall. Stem basal diameter 7–10 mm at base, not hollow in age, green, minutely puberulent with simple, uniseriate, stiff 1–2-celled trichomes mixed with scattered simple uniseriate glandular trichomes with 4-celled heads, glabrescent in age, all trichomes less than 0.5 mm long. Sympodial units 2-foliate (sometimes 3-foliate); internodes 2–6 cm. Leaves interrupted imparipinnate, 3.5–13 × 1–6 cm, bright green, minutely pubescent with stiff simple uniseriate trichomes like those of the stems, pubescence denser abaxially, especially along the veins; primary leaflets 3–7 pairs, gradually becoming smaller towards the base of the leaf, subopposite to alternate, narrowly elliptic, the base truncate, more or less oblique basiscopically, the margins deeply and irregularly lobed to occasionally almost entire in some leaflets, the apex acute to acuminate; terminal leaflet 1.2–2.5 × 0.4–1.5 cm, the petiolule 0.2–0.5(1) cm; lateral leaflets 0.7–2.5 × 0.3–1.2 cm, the petiolule 0–0.5(1) cm, usually decurrent on the rachis basiscopically; secondary leaflets occasionally present in some leaflets, especially acroscopically, 0.3–0.5 × 0.25–0.4 cm, sessile and decurrent on the leaflet rachis; tertiary leaflets absent; interjected leaflets (0)3–12 (20), 0.2–0.5 × 0.1–0.4 cm, sessile and decurrent on the main leaf rachis, often 2 sets of unpaired interjected leaflets between each set of primary lateral leaflets; petiole 1–4(6) cm; pseudostipules present or absent, if present then present on most nodes, 0.3–0.4 × 0.2–0.3 cm. Inflorescences (6)12–30 cm, once branched, usually regularly bifurcate, with 8–30 flowers, ebracteate or bracteate on most nodes from the base, the bracts 0.2–0.6 × 0.1–0.4 cm, the largest bract at the bifurcation and first nodes, peduncle 5–15 cm, overtopping the new vegetative shoots, minutely pubescent like the stems, with more prominent and numerous glandular trichomes especially at the apex. Pedicels 0.8–1.6 cm, articulated in the upper half. Buds 1–1.2 × 0.4–0.5 cm, narrowly conical, straight or curved at the very tip, more than half exerted from the calyx just before anthesis. Flowers with the calyx tube minute, ca. 0.5–1 mm, the sinuses often hyaline, the calyx lobes 2.5–5 × 1–1.5 mm, lanceolate or in some populations (Fortaleza) the tips rounded, minutely pubescent like the rest of the inflorescence with short, simple uniseriate 1–2-celled white trichomes; corolla 1.8–2.5 cm, stellate, yellow, the tube 0.2–0.5 cm, the lobes 1–1.5 × 0.3–0.4 cm, uniformly and sparsely pubescent abaxially with 1-celled uniseriate trichomes, these not denser along the midveins, the lobe tips elongate and acuminate, reflexed at anthesis; staminal column 1–1.2 cm, straight or curved, the filaments less than 0.5 mm, united into a tube, the anthers 0.4–0.6 cm, the sterile tip 0.15–0.4 cm; ovary conical to globose, minutely and sparsely pubescent with simple trichomes at the apex; style 0.8–1.2 cm, sparsely pubescent in the basal half; stigma capitate, exerted 0.05–0.1(0.17) cm from the staminal column, green. Fruit 1–1.4 cm in diameter, globose, 2-locular, green when ripe, sparsely pubescent with weak-walled simple uniseriate trichomes to 0.5 mm long and occasionally also with minute glandular trichomes with 4-celled heads; fruiting pedicels 1–2 cm, straight or slightly incurved towards the inflorescence axis; calyx lobes in fruit 1.1–1.6 × 0.15–0.2 cm, spreading, in some populations (Fortaleza) the lobe tips recurved. Seeds 2.4–3 mm × 1.1–1.5 mm × 0.5–0.6 mm, obovate, narrowly winged at the apex and acute at the base, pale brown, pubescent with hair-like outgrowths of the tegument cell radial walls, which give a silky appearance to the surface. Chromosome number: $n = 12$ (voucher LA1982 (BM, MERL), see Table 2).

Distribution. On rocky slopes around Callejón de Huaylas along the Río Santa in the Department of Ancash, Peru, and in the adjacent Río Fortaleza drainage; 940–3000 m. (Fig. 2).

Representative Specimens Examined. **PERU. Ancash**: Prov. Huari, 11 km N of Pariashpampa, 3200 m, 19 Dec 1979, *Aronson 1005* (NY); Huallanca, 5 km towards Caraz, Callejón de Patos, 1700 m, 9 Mar 1983, *Beck 7906* (F, LPB, NY); near km 290, on road from Conococha to coast, 3000 m, 31 Mar 1960, *Correll & Smith P977* (F, LL); road from Pativilca to Conococha, ca 2800 m, 11 Jul 1982, *Gentry et al. 37473* (MO, NY, USM); roadside at Punto Huarto, on main tarmac road from Lima to Huaráz, 2500 m, 19 Jun 1979, *Gibby & Barrett 6* (BM); Prov. Recuay, Dist. Marca (Marahuay), 2400 m, 13 Aug 1964, *Gómez 134* (USM); Prov. Bolognesi, Valle de Fortaleza, 2100–2300 m, 28 Jun 1966, *Ferrerya 16885* (USM); Prov. Corongo, Tres Cruces, deviation on road from La Pampa to Sihuas, 1820 m, 6 Aug 1993, *Leiva et al. 843* (F, NY); Prov. Huaylas, near Shupluy, road to Cueva Guitarrero, 9°11′32″S 77°42′20″W, 2530 m, 27 May 2001, *León et al. 4874* (BM, USM); Prov. Corongo, road from Huallanca to

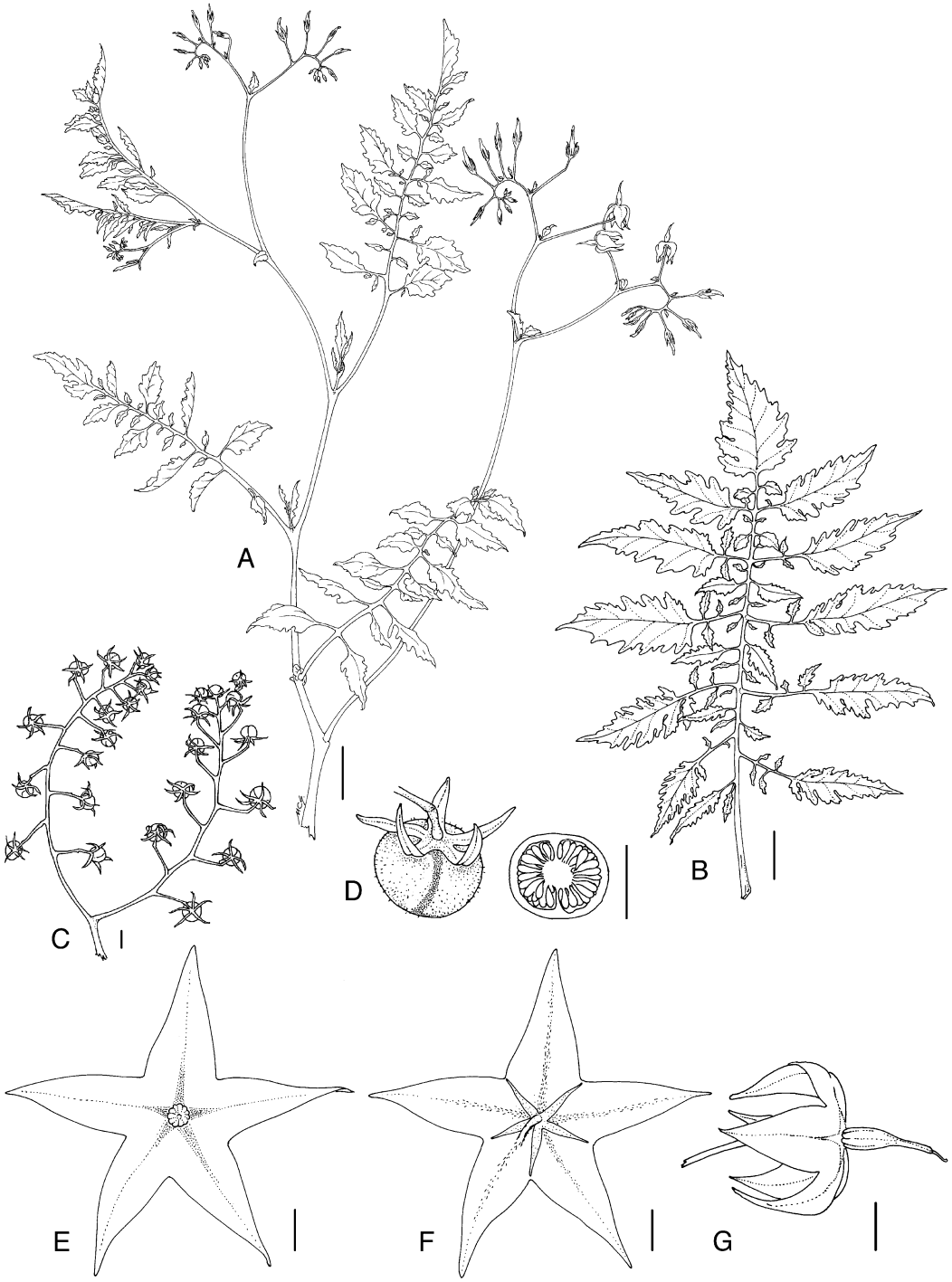

FIG. 3. *Solanum huaylasense*. A. plant (scale = 2 cm); B. leaf (scale = 1 cm); C. inflorescence (scale = 1cm); D. fruits (scale = 1 cm); E, F, G. flowers (scale = 0.5 cm). Illustrations from cultivated specimens (accession LA2561, from the C. M. Rick Tomato Genetic Resources Stock Center).

Yanac, near Yanac, ca 2800 m, 7 Mar 2001, *Weigend et al. 5018* (BM).

Observations from Cultivated Plants. Cultivated specimens of *Solanum huaylasense* grew well and completed their life cycle, producing flowers and fruits until the first frost in the fall. They were robust and erect plants at the beginning and later decumbent, with highly dissected leaves, very long peduncles, inflorescences always two-branched but often three-branched. Stems, internodes, leaves, inflorescences, flowers, and fruits were usually larger than those on herbarium specimens, but maintain similar character proportions to those collected in the wild.

Etymology. The specific epithet (*huaylasense* = growing in Huaylas) refers to the Callejón de Huaylas in the Department of Ancash, Peru, in the region where this species is endemic.

Intraspecific Variation. The plants from Río Fortaleza (high up in the Callejón de Huaylas) are slightly more pubescent than the others, and have curved buds and recurved calyx lobe tips in fruit.

Relationships. We consider *S. huaylasense* to be most closely related to *S. chilense*, *S. habrochaites*, *S. corneliomulleri*, and *S. peruvianum* s.str. based on morphological similarity and data from GBSSI sequence data (Peralta and Spooner 2002) and AFLP data (Spooner et al. 2005).

Key to the Four Segregates of *Solanum peruvianum* S.L. and the Sympatric and Morphologically Similar *S. chilense* (for a key to all other tomato species see Rick et al. 1990)

1. Inflorescence unbranched.
   2. Anther cone straight in bud. Stem, leaves and inflorescences glabrous or with sparse short unicellular trichomes to variously pubescent, with a mixture of trichome types, short velvety trichomes to longer trichomes with multicellular bases, and short glandular trichomes . . . . . *Solanum arcanum*
   2. Anther cone curved in bud. Stem, leaves and inflorescences velvety pubescent. . . . . *Solanum peruvianum*
1. Inflorescence branched.
   3. Anther cone strongly curved, especially visible in bud.
      4. Pubescence of a mixture of trichome types, at least some longer than the rest and glandular. Fruits densely pilose at maturity. . . . . *Solanum corneliomulleri*
      4. Pubescence uniform of soft short, white trichomes. Fruits puberulent
         5. Inflorescence with large bracts, usually to 1 cm; leaves grayish due to dense velvety pubescence, pinnate, leaflet margin entire or slightly dentate or crenate. . . . . *Solanum peruvianum* (some populations in central Peru)
         5. Inflorescence with the bracts always less than 1 cm; leaves greenish, pubescence sparse, leaves pinnate or bipinnatisect, leaflet margin dentate, usually deeply divided and lobulate . . . . . *Solanum huaylasense* (Río Fortaleza populations)
   3. Anther cone straight.
      6. Inflorescence peduncle equal to or shorter than the branches, and the inflorescence length is shorter than the apical growing shoot . . . . . *Solanum arcanum* (some populations in lomas of N Peru)
      6. Inflorescence peduncle longer than the inflorescence branches, and the inflorescence length is larger than the apical growing shoot.
         7. Stem and leaves densely white pubescent; typically green-grey canescent; petals with a medial darker stripe; coastal S Peru and N Chile . . . . . *Solanum chilense*
         7. Stem and leaves sparsely pubescent, bright green; petals uniformly yellow; Callejón de Huaylas, Ancash, Peru. . . . . *Solanum huaylasense*

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