

Solanum Section *Petota* in Costa Rica: Taxonomy and Genetic Resources

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ABSTRACT

Prior to 1996, worldwide holdings of germplasm of wild potatoes from Costa Rica amounted to just two collections; this country therefore formed a priority for collecting. We mapped all localities of wild potatoes from herbarium specimen data from Costa Rica and collected throughout the country. We made 13 collections, 10 of these with botanical seeds. These collections considerably extend the numbers of accessions and geographic range of the germplasm available from Costa Rica. The taxonomic identity of the species of wild potatoes (*Solanum* sect. *Petota*) in Costa Rica was previously unresolved. Our fieldwork supports the concept that Costa Rican wild potatoes belong to a single species, *S. longiconicum*.

RESUMEN

Antes de 1996, las colecciones de germoplasma de papas silvestres de Costa Rica eran sólo dos en todo el mundo; este país, por lo tanto, estableció como una prioridad formar su colección. Con ese fin, asociamos todas las localidades de papas silvestres, tomándolas de una base de datos de muestras de herbarios de Costa Rica y las colectamos a lo largo y ancho del país. Formamos 13 colecciones, 10 de ellas con semilla botánica. Esas colecciones extendieron considerablemente el número de accesiones y rangos geográficos del germoplasma disponible de Costa Rica. La identidad taxonómica de las especies de papa silvestre (*Solanum* sect. *Petota*) de Costa Rica no había sido resuelta previamente. Nuestros trabajos de campo apoyan el concepto de que las papas silvestres de Costa Rica pertenecen a la especie singular *S. longiconicum*.

INTRODUCTION

Species of *Solanum* L. sect. *Petota* Dumort., which includes the potato and its relatives, occur from the southwestern United States to southern Chile. Section *Petota* contains seven cultivated and 225 wild species according to the latest comprehensive taxonomic treatment of Hawkes (1990). However, nine of these species lack tubers, are members of separate clades, and are alternatively treated in sect. *Etuberosum* (Buk. & Kameraz) A. Child, sect. *Lycopersicum* (Mill.) Wettst., or sect. *Juglandifolium* (Rydb.) A. Child (Child 1990; Spooner *et al.* 1993; Contreras and Spooner 1999). Costa Rica was thought to possess only two tuber-bearing species (sect. *Petota*), *S. longiconicum* Bitter and *S. woodsonii* Correll (Correll 1962; Hawkes 1990).

EXPLANATION OF ABBREVIATIONS

CGN, Centre for Genetic Resources The Netherlands
 CR, National Herbarium, Museo Nacional de Costa Rica, Apartado 749-1000, San José, Costa Rica
 F, Herbarium, Field Museum of Natural History, Chicago, IL, USA
 GH, Gray Herbarium, Harvard University, Boston, MA, USA
 INBio, Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica
 INB, Herbarium of INBio
 LL, TEX, Lundell Herbarium, and herbarium of the University of Texas, Austin, TX, USA
 MICH, Herbarium, University of Michigan, Ann Arbor, MI, USA
 MO, Missouri Botanical Garden Herbarium, St. Louis, MO, USA
 MSC, Herbarium, Botany and Plant Pathology Department, Michigan State University, East Lansing, MI, USA
 NA, Herbarium, United States National Arboretum, Washington, DC, USA
 NRSP-6, National Research Support Program-6, Sturgeon Bay, WI, USA (formerly called the Inter-Regional Potato Introduction Project [IR-1])
 NY, Herbarium, New York Botanical Garden, Bronx, NY, USA
 PTIS, Herbarium, U.S. Potato Introduction Station, Sturgeon Bay, WI, USA
 US, United States National Museum, Smithsonian Institution, Washington, DC, USA
 USJ, Herbarium, Escuela de Biología, Ciudad Universitaria Rodrigo Facio, Universidad de Costa Rica, San José, Costa Rica
 WAG, Herbarium, Wageningen Agricultural University, The Netherlands
 WIS, Herbarium, University of Wisconsin, Madison, WI, USA

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ADDITIONAL KEY WORDS: Costa Rica, genebank, germplasm, potato, *Solanum longiconicum*, *Solanum* sect. *Petota*, taxonomy.

All populations of wild potatoes in Costa Rica possess conical fruits and are members of ser. *Conicibaccata*, a group of about 40 species distributed from southern Mexico to Bolivia (Hawkes 1990; Castillo and Spooner 1997). Correll (1962) and Hawkes (1990) disagreed about the species status of *S. longiconicum* and *S. oxycarpum* Scheide in Schtdl. Correll (1962) identified all Costa Rican collections as *S. oxycarpum* and placed *S. longiconicum* in synonymy with it. Hawkes (1990) recognized *S. oxycarpum* from Mexico and *S. longiconicum* from Costa Rica, Panama, and Venezuela. In his key, Hawkes (1990) characterized *S. longiconicum* as having completely glabrous leaves, whereas those of *S. oxycarpum* were subglabrous. All of these species are tetraploid ($2n = 2x = 48$; Bamberg *et al.* 1996) providing no aid to distinguish them.

Both agreed that *S. woodsonii* was a distinct species, and distinguished it from others by a lobe at the base of the anther. Correll thought *S. woodsonii* was found only in Panama and Venezuela, while Hawkes (1990) described its distribution as including Costa Rica, Panama, and Venezuela. Hawkes (1997), in a database of identifications, cited two specimens from the same locality, Cerro de la Muerte (*Mesén* 497, 499; listed in Area 17, below).

Castillo and Spooner (1997) studied the species boundaries and interrelationships of 23 of the 40 species of ser. *Conicibaccata*, using morphology of 139 germplasm accessions planted in a common screen house environment and chloroplast DNA of 181 accessions. They showed extensive overlap of diagnostic character states in all of these 23 species and suggested that many of these 23 species needed to be relegated to synonymy. Not enough germplasm specimens of potatoes (only two) from Costa Rica were available to adequately address the distinction of *S. longiconicum* and *S. oxycarpum*, and they made no taxonomic decisions regarding these species. Therefore, in addition to collecting germplasm, we wished to resolve this disagreement in taxonomy.

There were only two collections of wild potatoes from the world's germplasm collections, and both identified as *S. longiconicum*. The low germplasm coverage stimulated collections there (Nov 24 to Dec 23 1996) by the National Research Support Program-6, United States (NRSP-6); the Centre for Genetic Resources The Netherlands (CGN); the Instituto Tecnológico de Costa Rica; and the Instituto Nacional de Biodiversidad (INBio).

MATERIALS AND METHODS

Permission to Collect

This expedition was initiated by letters to INBio and the Comisión de Recursos Fitogenéticos. With help from INBio, we obtained a general collecting permit, needed for collecting in national protected areas, and an export permit from the Ministerio del Ambiente y Energía, Dirección General de Vida Silvestre. We obtained a separate permit to collect on the privately owned Monteverde Cloud Forest Reserve. Copies of these permits are available in an unpublished collecting report deposited at NRSP-6, CGN, and INBio.

Locality Data

Prior to the expedition, we compiled locality data from (1) database files backing up germplasm records from CGN (Hoekstra 1996) and NRSP-6 (Bamberg *et al.* 1996); (2) literature records from Correll (1962), and (3) our own inspection of specimens at CR, F, GH, INB, LL, MICH, MO, MSC, NA, NY, PTIS, TEX, US, USJ, WAG, and WIS. After the expedition, the database of Hawkes (1997) became available, and we personally checked these determinations in herbaria. Herbarium codes follow Holmgren *et al.* (1990 [8th ed]). The herbaria INB and PTIS will appear in the 9th edition, but currently can be accessed at <http://www.nybg.org/bsci/ih/ih.html>.

Localities were mapped with the aid of (1) Gazetteer of Costa Rica published on the internet by the Missouri Botanical Garden at <http://www.mobot.org/MOBOT/Research/gazette2.html>; (2) Tribunal Supremo de Elecciones (1993), (3) United States Department of the Interior (1986), (4) the 1:50,000-scale topographic maps (137 sheets), and the 1:200,000-scale topographic maps (13 sheets) from the Instituto Geográfico Nacional, Costa Rica; (5) Chinchilla-V. (1987). All of these resources are available at the PTIS library in Madison, Wisconsin. Localities that were hard to find on road maps are clarified as notes in "Additional specimens examined".

Conducting the Expedition

Collections were made by the authors and occasionally with José Gonzalez and Reynaldo Aguilar (INBio). All potato populations in Costa Rica are within a 12-h drive from San José. Collecting at some localities requires two days more of hiking, covering a vertical distance of 1000 m or more. Longitude and latitude data were obtained by a global positioning system, and our readings are expressed as decimal fractions

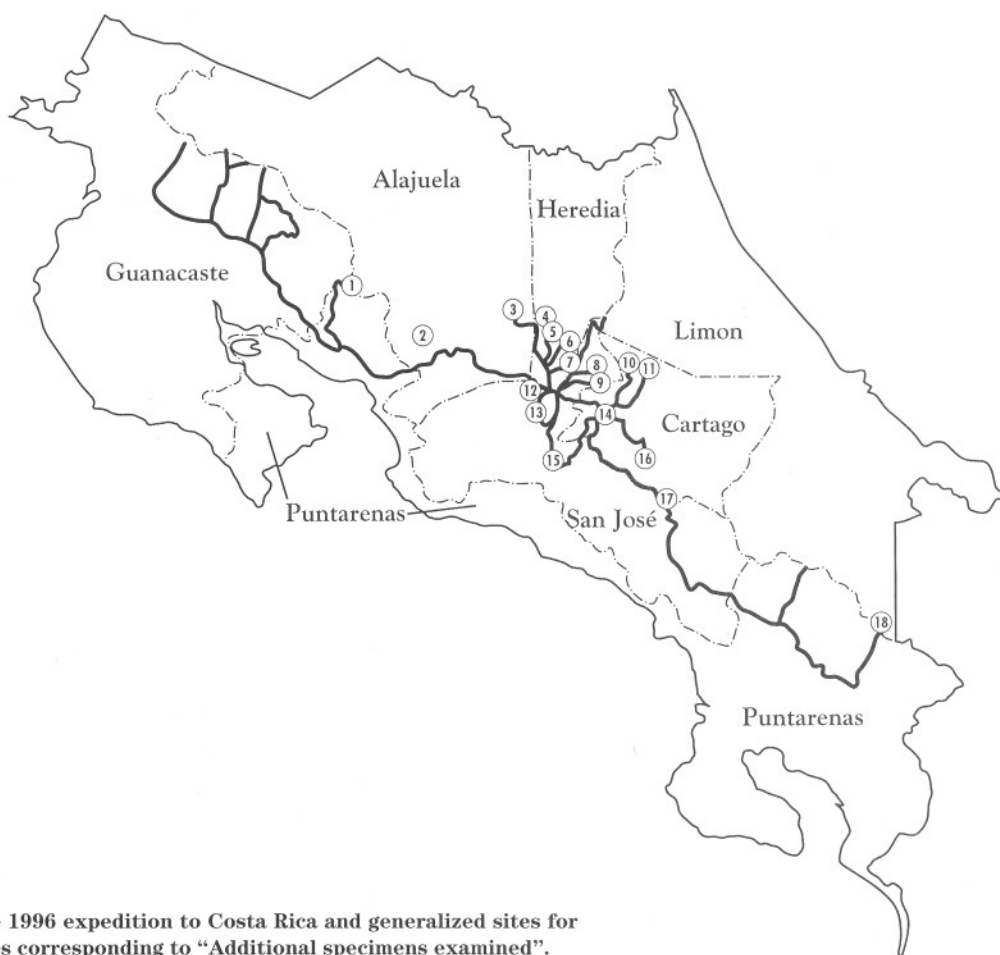


FIGURE 1
Route of the 1996 expedition to Costa Rica and generalized sites for wild potatoes corresponding to "Additional specimens examined".

of degrees rather than as minutes. We dried herbarium vouchers at INBio. A map of our collecting route with an overlay of summary localities (Figure 1) shows all known collections.

Distribution of Collections

Seed collections from the expedition were sent to NRSP-6 and CGN. There is no public genetic resources system to increase and store seeds of wild crop relatives in Costa Rica. By agreement with the government of Costa Rica, no collections were left there, but germplasm will be made freely available upon request to all parties after passage through quarantine at the USDA facility in Beltsville, Maryland (now completed), and a germplasm increase at Sturgeon Bay, Wisconsin. NRSP-6 is having difficulty producing seeds from some collections, and one of the ten germplasm collections has died. If botanical seeds cannot be produced, accessions are established in-vitro for distribution as vegetative stocks.

Herbarium specimens are deposited at CR, INB, PTIS, and WAG.

Taxonomy

We base our decision of identity of Costa Rican members of ser. *Conicibaccata* on (1) our examination of the herbarium specimens cited below, (2) field collections from throughout the range of this series in Mexico (Spooner *et al.* 1991, 2000), Guatemala (Spooner *et al.* 1998), and Costa Rica (13 new collections listed below), (3) observation of living collections in greenhouses in Madison and Sturgeon Bay, Wisconsin.

RESULTS AND DISCUSSION

Identity of Costa Rican Wild Potatoes

Our new collections and our study of herbarium speci-

mens, support Hawkes (1990) in recognizing *S. longiconicum* and *S. oxycarpum* as distinct species. Both are very similar with respect to leaf shape and numbers of lateral and interjected leaflets, and it is clear why Correll (1962) considered these species to be conspecific on the basis of herbarium material alone. They are much better distinguished in living condition, especially in the greenhouse by the glabrous to nearly glabrous and shiny leaves of *S. longiconicum*, in contrast to the slightly more pubescent and duller leaves of *S. oxycarpum*. In addition, *S. longiconicum* is distinguished by a purple seed spot, formed by a purple embryo showing through the green seed coat, that is not present on *S. oxycarpum*. A more variable character is corolla color, as *S. longiconicum* frequently has corollas white or white tinged with blue to purple, while *S. oxycarpum* almost always has purple corollas that are rarely white. In addition, *S. longiconicum* and *S. oxycarpum* are allopatric, with the latter growing in Mexico, and the former growing in Costa Rica (and possibly in Panama and Venezuela). We will determine the identity of populations from Panama and Venezuela in a later study.

Our collections from throughout the range of the species, including Cerro de la Muerte where Hawkes (1997) cited collections of *S. woodsonii*, show morphology typical of *S. longiconicum*. We will address synonymy of *S. woodsonii* in a broader treatment of Mexican and Central American members of ser. *Conicibaccata* (in preparation).

Phenology

Timing is one of the most important aspects of planning a germplasm collecting expedition. For example, germplasm collections of most populations of wild potatoes in Mexico are best made from early August to late October, in Peru from early February to late April, and in Chile from early January to late February. In Costa Rica, however, flowering specimens of *S. longiconicum* were collected in every month of the year, and fruiting plants in all months except January and March. It likely fruits year round. Our collections in November and December located some populations in full fruit, while others were immature. It is unclear if there is any ideal single time to collect germplasm of all populations from Costa Rica.

Taxonomic Treatment

Solanum longiconicum Bitter, Repert Spec. Nov. Regni Veg. 10: 534. 1912—SYNTYPES: COSTA RICA. Cartago: La Palma del Volcán Irazú, 1800 m, C. [Carl, or Karl] Wercklé 65 (B, destroyed, photos: F, GH, LL, NY, US).

Cartago: Irazú, massif of the Irazú, defrichements du Roble, 2000 m, 10 Jul 1891, A. Tonduz 4235 (BR, CR, G, K, LL, US, Z, K [photo: G, Z], LL [photo: Z]). A lectotype will be chosen in a later publication.

Solanum manoteranthum Bitter, Repert Spec. Nov. Regni Veg. 11: 383. 1912.—TYPE: COSTA RICA. San José: Volcán Barba, A. Roessler s. n. (holotype: M, photos: [F, LL, PTIS]).

Plants 0.2-2 m tall; stems 2-10 mm wide at base, green, simple to branched; leaves odd pinnate, glabrous or with only scattered 2-3 celled short hairs above and below, leaves shiny, blades 8-28 cm long, 5-20 cm wide, petioles 1-5 cm long; lateral leaflets (2) 3-5 (6) pairs, ovate to elliptical, apex acuminate, base oblique to cuneate, sessile or with petiolules to 1 cm long; 0 (most commonly) to 6 interjected leaflets (*Mesén 506* atypically has 6 lateral and 19 interjected leaflets); terminal leaflet ovate to elliptical, apex acute to acuminate, base attenuate; pseudostipular leaves auriculate, 2-15 mm long; inflorescence pseudoterminal and lateral with 8-16 flowers; pedicels 15-30 mm long; calyx 5-10 mm long, lobes 1-4 mm long, short and acute to long attenuate; corolla white or light to dark blue to purple, or white with mottled or striped blue to purple, rotate to rotate-pentagonal with short acumens, 2-3 cm in diameter; filaments 1.5-2 mm long, anthers 4-5.5 mm long, style exceeding stamens by 2-3 mm; fruits conical, rounded to pointed at tip, 7-29 mm wide at base, 11-39 mm long, medium to deep green; seeds green with a purple seed spot caused by the purple embryo showing through the green seed coat. Chromosome number: $2n = 4x = 48$ (Bamberg *et al.* 1996).

Distribution (Figure 1) and Ecology—*Solanum longiconicum* grows from 1400-3200 m in elevation (one record at 1050 m) from central to western Costa Rica, and likely in adjacent western Panama. It is found in a variety of moist situations in areas of cloud forests, often in organic soils, in full sun or partial shade. These include disturbed habitats such as landslides, roadcuts, moist garbage heaps, recently plowed soil in forest clearings, recently burned forests, roadside ditches, forest edges, or on rotting tree stumps. It also grows in fields that are not overgrazed, but is readily eaten by grazing animals. When growing in primary forests, it occurs near sunny openings such as paths or streambanks or treefalls.

Additional Specimens Examined—All specimens cited below are from Costa Rica. Areas 1-18 correspond to Figure 1. All records are translated to English. Details of plant habits, morphology, and habitats are excluded from individ-

ual records and summarized in the description above. Because corolla color is so variable and has been used taxonomically in ser. *Conicibaccata* (Castillo and Spooner 1997), it is documented in the individual records. Germplasm collections are followed by an asterisk. Our collections are abbreviated as combinations of A (Aguilar), G (Gonzalez), H (Hoekstra), S (Spooners), and V (Vilchez).

Area 1: Monteverde; Provinces Alajuela, Guanacaste, Puntarenas. Alajuela, Guanacaste, Puntarenas Junction:

Cerro Amigos, E side, 1750-1800 m, 25 Jan 1977, *V. T. Dryer 1150* (F, MO); high ridge N of television relay tower above Monteverde and bordering Monteverde Cloud Forest Nature Reserve, 10° 19'N, 83° 48'W, 1750-1800 m, 27 Feb 1977, bluish purple flowers, *J. L. Gentry 3819* (CR, F, MO, NY); Monteverde Biological Reserve, between La Torre and Río Negro, at the continental divide, 10° 21'N, 84° 48'W, 1600-1700 m, 21 Jan 1988, flower blue, *W. Haber & E. Bello 8029* (CR); Monteverde Cloud Forest Preserve, meeting point of the provinces of Alajuela, Guanacaste, and Puntarenas, top of Cerro Amigos, around television tower (channel 13), 10° 19.0'N, 84° 47.7'W, 1830 m, 30 Nov 1996, corolla violet, *SHG 7109* (CR, INB, PTIS, WAG)*. **Puntarenas:** ca. 2 km SE of Monteverde in the Pacific watershed, on ridge along trail, 10° 18'N, 84° 48'W, 1500 m, 18-21 Mar 1973, corolla purple, *J. L. Gentry Jr. & W. C. Burger 2712* (CR, F, MO, NY); Monteverde Biological Reserve, path to Chomogo, 9 Mar 1976, purple flowers, *J. Gómez Laurito et al. GL-1388* (USJ) [note: we found this population in a non-flowering state and made no collections].

Area 2: Socorro; Province Alajuela.

Between Socorro and San Ramón, path to San Antonio, 25 Aug 1926, *A. M. Brenes s. n.* (CR).

Area 3: Volcán Poás; Province Alajuela.

Volcán Poás, 2678 m, 30 Jan 1922, *J. M. Greenman & M. T. Greenman 5374* (GH, MO); Volcán Poás, on SE shoulder of volcano, 2135 m, 26 Mar 1947, *C. Horn 1* (GH, LL, NA); road between large meadow of Volcán Poás and Poasito, at edge of road, 19 Aug 1961, white flowers, *A. Jiménez M. 174* (F); Volcán Poás, 8.5 km from Poasito, 400 m before large meadow in the National Park, 10° 10.7'N, 84° 14.3'W, 2560 m, 9 Dec 1996, corolla blue or white, *SHV 7122* (CR, INB, PTIS, WAG)*; Volcán Poás, Clairieres de l'Achiote, 2200 m, Nov 1896, *A. Tonduz 10801* (US); Volcán Poás National Park at main entrance, 400 m S of main road, 2500 m, 1 May 1993, flowers white, *M. Valerio 657* (CR).

Area 4: Vara Blanca; Provinces Alajuela, Heredia.

Alajuela: Isla Bonita [note: Isla Bonita is located on

the road N of Vara Blanca, at 10° 14'N, 84° 10'W, on 1:50,000-scale topographic map 3346-I, at about 1,050 m] no date, *C. Hope, s. n.* (K, PTIS)*; **Heredia:** between Los Cartagos and Vara Blanca, 1830 m, 22 Jun 1963, purple flowers, *A. Jiménez M. 762* (CR, F, NY, US); between Poás and Barba volcanoes, Vara Blanca, 1600-1700 m, 22 Jul 1923, *W. R. Maxon & A. D. Harvey 8274* (BM, US); Central Cordillera, N slope, between Poás and Barba volcanoes, Vara Blanca de Sarapiquí, 1920 m, Feb 1938, *A. F. Skutch 3580* (F, GH, K, MO, NY, S, US).

Area 5: Volcán Barva (Barba is a variant spelling); Province Heredia.

Volcán Barba, E slopes, between Río Nuevo (upper Río Patria), 10° 06'N, 84° 03'W, 2000 m, 25 Oct 1975, white flowers, *W. C. Burger & R. Baker 9486* (F); Volcán Barva, SW slopes, above Sacramento, 10° 07'N, 84° 07'W, 2200-2300 m (record also lists 10° 08'N, 84° 08'W), 3 Feb 1982, flowers blue-purple, *W. C. Burger et al. 11432* (F); Volcán Barba, E slope, Río Uvertas (upper Río Patria) near the continental divide, 10° 06'N, 84° 04'W, 2000 m, 22-24 Nov 1969, petals white, *W. C. Burger & R. L. Liesner 6419* (F, MO); Río Uvertas (upper Río Patria) on the E slope of Volcán Barba at the Caribbean side of the Continental divide, 10° 06'N, 84° 04'W, 1900 m, 1 & 3 Apr 1973, corolla white, *J. L. Gentry Jr. & W. C. Burger 2869* (F, MO); around lake of Volcán Barva, 2900 m, 25 Jan 1979, white flowers, *J. Gómez Laurito GL-4387* (USJ); slopes and ridges above Laguna del Barva and summit of Volcán Barva, 10° 08'N, 84° 06.30'W, 2840-2900 m, 27 Apr 1986, *Grayum & Quesada 7425* (MO); Finca la Selva, San Rafael de Vara Blanca, slopes N of Volcán Barba, 1700 m, 23 Jun 1963, purple flowers, *A. Jiménez 801* (CR, F, NY); Volcán Barba, 2900 m, edge of path, 17 Feb 1962, white flowers, *R. L. Rodríguez C. 839* (CR); Volcán Barva, 500 m after entrance of park, 100 m NW towards viewpoint, 10° 07.2'N, 84° 07.5'W, 2570 m, 29 Nov 1996, corolla white, *SHV 7105* (CR, INB, PTIS, WAG)*; Volcán Barva, above Laguna Barva on the path to Laguna Copey, 10° 08'N, 84° 06.5'W, 2780 m, 29 Nov 1996, corolla light blue, *SHV 7107* (INB, PTIS, WAG); Volcán Barva, along path above Laguna Copey, 10° 09'N, 84° 06'W, 2780 m, along path in cloud forest, 29 Nov 1996, corolla white to light blue, *SHV 7108* (INB, PTIS, WAG)*; Rancho Flores (on Volcán Barva according to INBio gazetteer), 2043 m, forest, 22 Feb 1890, *A. Tonduz 2181* (BR); Cerro Gallito [note: the village of Gallito is at ca. 2100 m, on the lower S-facing slopes of Volcán Barva, as seen on the 1:50,000-scale 3346 II topographic map (Barba is at 10° 06'N, 84° 06'W; but Correll [1962] lists this record in San José Province), 2000 m,

3 Feb 1935, *J. Valerio 1048* (F); Braulio Carillo National Park, Estación Barva, 10° 07'2"N, 84° 07'2"W, 2500 m, 30 Jun 1990, flower violet, *G. Varela 83* (INB).

Area 6: Cerro Chompipe; Province Heredia.

Heredia, Alto de Roblé, 2000 m, May 1888, *H. F. Pittier 18* (G, photos at K, F; US; GH, photo Z; TEX), *34* (G), *215* (BR); Braulio Carillo National Park, sector Cerro Chompipe, 6.3 km N of San Rafael, along recently cleared path to the top for new road, 10° 05.1'N, 84° 04.4'W, 2200 m, 10 Dec 1996, corolla white or light blue, *SHV 7123* (CR, INB, PTIS, WAG)*; Cerro Chompipe, San Rafael, 10° 05'13"N, 84° 05'23"W, 2100 m, 16 Dec 1993, white flowers, *G. Vargas et al. 1617a* (CR).

Area 7: Cerro Zurqui; Provinces Heredia, San José.

Heredia: along the Río Vara Blanca (Pacific drainage), Cerros Zurqui, 10° 03'N, 84° 01'W, 1600-1800 m, 7 Feb 1977, corolla lobes white, *J. Gentry s. n.* (CR); forest at base of Cerro Zurqui, 10° 03'N, 84° 02'W, 1650 m, 8 Jul 1973, flowers white, *R. W. Lent 3569* (CR, F); NE of San Isidro, Yerba Buena [note: Yerba Buena is located at 10° 02'N, 84° 00'W, according to the U.S. gazetteer], 2000 m, Feb 22-28, 1926, *P. C. Standley & J. Valerio 49948* (US), *49973* (US), *49982* (US); Cerro de Las Lajas, N of San Isidro, 2000-2400 m, Mar 7, 1926, *P. C. Standley & J. Valerio 51583* (F, US); **San José:** high above Río Hondura, 10° 03'N, 83° 59'W, 1400 m, roadside, 10 Mar 1973, light violet flowers, *R. W. Lent 3227* (F).

Area 8: Las Nubes; Province San José.

Las Nubes, 1500-1900 m, 20-22 Mar 1924, *P. C. Standley 38614* (US), *38666* (US), *38756* (US), *38818* (US).

Area 9: Rancho Redondo; Province San José.

Potreros of Rancho Redondo, 2220-2600 m, 9-18 Oct 1929, *C. W. Dodge & W. S. Thomas 4926* (F, MO).

Area 10: Volcán Irazú; Provinces Cartago, San José.

Cartago: Volcán Irazú, 1948, *E. G. Casseres 1* (CR); on the road from Cartago to Volcán Irazú, 23 Aug 1940, *M. A. Chrysler 5552* (F); Irazú, 2500 m, 6 Sep 1953, *C. Heiser 3486* (US); road up Volcán Irazú, near bridge over Río Birrís, 2900 m, 24 Feb 1965, white flowers but veins of petal green inside and purple outside, *R. W. Lent 387* (F); Volcán Irazú, Hacienda Chicua, 3000 m, 29 Apr 1948, *J. M. Orozco 525* (K); Volcán Irazú, slopes, 2745 m, bank of a stream, 28 Jun 1920, *W. Pope-noe 1015* (NA, NY, US); Volcán Irazú, 2.9 km N of Potrero Cerrado, at Km 25, under bridge over Río Birrís, 09° 57.6'N, 83° 50.5'W, 2900 m, 13 Dec 1996, corolla purple, *SHV 7136* (INB, PTIS, WAG); Volcán Irazú, S slope, Río Birrís, wet thicket, 23 Feb 1924, *P. C. Standley 35400* (US); N of Irazú, 3050 m, 28 Mar 1928, *H. E. Stork 1281* (F). **San José:** Cartago or San José: Valley of Archangeles, massif of the

Irazú, 24 May 1888, *H. F. Pittier 260 p. p.*, *261 p. p.* (BR); Irazú on road to El Roble, 3050 m, 16 May 1928, *H. E. Stork 1999* (F).

Area 11: Volcán Turrialba; Province Cartago.

Road to crater of Volcán Turrialba, 17 Jun 1976, *J. Gómez Laurito GL-1680* (USJ); between milk factory and base of Volcán Turrialba, 3000 m, 1 Nov 1948, *Oviedo* (K), *522* (K), *523* (K), *524* (K); Volcán Turrialba, 9.5 km on road towards volcano, 10° 00.7'N, 83° 45.4'W, 2910 m, along road at base of steep mountainside, 12 Dec 1996, corolla white or white with violet nerves, *SHV 7133* (CR, INB, PTIS, WAG)*; Volcán Turrialba, S slope, near the Finca del Volcán Turrialba, 2000-2400 m, 22 Feb 1924, *P. C. Standley 34993* (US).

Area 12: Escazú City; Province San José.

Interamerican Highway, Km 29, section 4, Jaboncillos [note: Jaboncillo is a small village just W of Escazú, just W of San José, at 9° 56'N, 84° 09'W, on map 3345-1], 2900 m, Jun 1944, *R. Mesén 501* (K); Km 29 + 700, section 4, Jaboncillos, 2950 m, 16 Jan 1948, *R. Mesén 513* (K).

Area 13: Cerro Escazú; Province San José.

Cantón de Aserri, Cerros de Escazú Protected Area, Cerros Escazú, La Carputera, El Cedral, Alto Hierbabuena, high oak woods to the NE, 10° 09.3'N, 84° 06.4'W, 2150 m, 6 Nov 1993, corolla light violet, *J. F. Morales 1964* (INB). [note: Spooner and Hoekstra looked for potatoes at Cerros de Escazú Protected Area without success, but later spoke with Morales at INBio, and he indicated the plant was collected on the road there, but outside of the protected area proper. The correct latitude and longitude is approximately 9° 50.16'N, 84° 07.4'W].

Area 14: Cartago; Province Cartago.

Cartago, 1400 m, Sep 1908, *C. Wercklé 17296* (GH).

Area 15: Cristóbal; Province San José.

San Cristóbal Road, 2440 m, 27 May 1928, *H. E. Stork 2213* (F); San Cristóbal, *C. Wercklé s. n.* (US).

Area 16, Tapantí; Province Cartago.

S of Tapantí along the new road on the E slope above the Río Grande de Orosi, 09° 42'N, 83° 47'W, 1400-1600 m, 10-24 Jun 1968, white flowers marked with lavender, *W. C. Burger & R. G. Stolze 5723* (CR, F, MO, NY); ca. 15 km S of Tapantí along the new road on E slope above Río Grande de Orosi near the concrete bridge, 09° 42'N, 83° 47'W, 1500 m, on steep bank above road, 13-14 Apr 1973, corolla white, *J. L. Gentry Jr. & W. C. Burger 2935* (F, MO); Tapantí Nacional Park, 9.2 km from entrance of park, from concrete bridge until the end of the road at electricity station, 09° 41.2'N, 83° 45.5'W, 1740 m, along road on wet mountain slopes, 11 Dec 1996, corolla white or light violet with white nerves, *SHV 7129* (CR, INB, PTIS, WAG).

Area 17: Cerro de la Muerte; Provinces Cartago, San José.

Cartago: SE slope of Cerro de la Muerte, Talamanca Cordillera, along Interamerican Highway, 2700 m, 23 May 1976, *T. Croat 35386* (M); Cerro Buena Vista (Cerro de la Muerte), Panamerican Hwy, Cordillera de Talamanca, 9° 33'N, 83° 45'W, 20 Apr 1947, *Fosberg 27307* (WIS), 10 km SE of Empalme along Interamerican Highway, 2000 m, 8 Feb 1971, pale violet flowers, *W. T. Gillis & T. C. Plowman 10037* (F); Tres de Junio Biological Reserve, 21 Aug 1975, purple flowers, *J. Gómez Laurito et al. GL-1200* (USJ); Panamerican Highway, 50 km from Cartago, 2700 m, 7 Nov 1949, *J. G. Hawkes 1127* (K); Interamerican Highway, 52 km S of Cartago, 2850 m, 7 Nov 1949, *J. G. Hawkes 1128* (K); Interamerican Highway, 65 km S of Cartago, 2970 m, 7 Nov 1949, *J. G. Hawkes 1129* (K); Interamerican Highway, 60 km S of Cartago, 2850 m, 7 Nov 1949, *J. G. Hawkes 1130* (K, PTIS)*; Interamerican Highway, 35 km S of Cartago, 2520 m, 7 Nov 1949, *J. G. Hawkes & R. Mesén 1126* (K); 9 km from Millsville to Cartago, 3000 m, 22 Jul 1949, *R. W. Holm & H. H. Iltis 517* (G, MO); Dos Amigos [note: Dos Amigos at 09° 37.4'N, 83° 50.7'W on 1:50,000-scale topographic map 3444 IV], southern Pan American Highway, 3000 m, Sep 1943, *O. Jiménez 5* (CR, US); La Trinidad, SE of Empalme, 2500 m, no date, white flowers with pale tinted violet, *A. Jiménez M. 2197* (F); Interamerican Highway, Cerro de la Muerte, 2526-3150 m, Jun 1944, *R. Mesén 496* (K), *497* (K), *498* (K), *499* (K), *500* (K); same, between Empalme and Cañon, Jun 1944, *R. Mesén 503* (K); section 4, 3000 m, Jun 1944, *R. Mesén 504* (K); Pan American Highway, Km 11, section 4, between Madreselva and Cañon, 2510 m, Jun 1944, *R. Mesén 505* (K); Interamerican Highway, Km 21, section 4, near Río Humo [note: Río Humo is N of Tres de Junio at 9° 41'N, 83° 50'W], 2790-2860 m, Jun 1944, *R. Mesén 506* (K), *508* (K); section 4, 3150 m, Jun 1944, *R. Mesén 511* (K); Interamerican Highway, sect. 4, Km 34 + 900, 3150 m, 16 Jan 1948, *R. Mesén 515* (K); Km 22 + 900, 2860-2880 m, 16 Jan 1948, *R. Mesén 516* (K), *521* (K); Km 21, between Madreselva and Cañon, 2570 m, 16 Jan 1948, *R. Mesén 517* (K); Interamerican Highway, section 4, Río Humo, Km 22 + 400, 2860 m, 16 Jan 1948, *R. Mesén 519* (K); Interamerican Highway, Sect. 4, Río Humo, 2860 m, 16 Jan 1948, *R. Mesén 520* (K); Cordillera de Talamanca, Cerro de la Muerte, Interamerican Highway between Km 60 & 77, La Trinidad, 3140 m, cloud forest, 26 Feb 1966, flowers lavender, *A. Molina R. et al. 17888* (F); 28 km S of Empalme, Jan 11, 1975, *R. A. Ocampo & C. Otorola 960* (CR); 9.3 km S of Empalme at Km 66 of the Interamerican Highway, 09° 40.2'N, 83° 51.8'W, 2500

m, 28 Nov 1996, corolla white to light blue, *SHV 7101* (CR, INB, PTIS, WAG)*; 13.5 km S of Empalme at the Interamerican Highway, 09° 37.9'N, 83° 50.4'W, 2770 m, along the road, 28 Nov 1996, corolla light blue to dark blue, *SHV 7103* (INB, PTIS, WAG)*; 20.3 km S of Empalme along Interamerican Highway, 09° 36.4'N, 83° 45.8'W, 3020 m, along the road, 28 Nov 1996, corolla light blue with white nerves, *SHV 7104* (CR, INB, PTIS, WAG)*. **Cartago and San José border:** near Division, Cerro de la Muerte, 3000 m, 6 Oct 1978, petal lavender, *T. Antonio 667* (CR, F); 22 km SE of Empalme, along Interamerican Highway, 2500-2600 m, 9 Aug 1971, flower pale lavender, *W. C. Burger 7961* (F); Interamerican Highway near Trinidad and Km 72, ca 20 km SE of Empalme, 09° 40'N, 83° 53'W, 2600-2800 m, 5 Feb 1982, *W. C. Burger & K. Barringer 11479* (CR, F); 22 km SE of Empalme, along Interamerican Highway, 09° 40'N, 83° 50'W, 2500-2600 m, 27 Nov 1969, corolla lavender, *W. C. Burger & R. L. Liesner 6466* (CR, F, MO); Interamerican Highway, 22 km SE of Empalme, 09° 40'N, 83° 50'W, 9 Aug 1971, *W. C. Burger 7969* (F, MO); 20 km SE from Empalme along Interamerican Highway, Km 72, El Trinidad, 09° 40'N, 83° 53'W, 2600 m, 25 May & 19 Jun 1968, *W. C. Burger & R. G. Stolze 5262* (F); Interamerican Highway, Km 37, section 4, Cerro de la Muerte, 3150 m, Jun 1944, *R. Mesén 509* (K); Km 34 + 900, 16 Jan 1948, *515* (K); Cordillera de Talamanca, near and below Cerro de la Muerte, 3200 m, 26 Jan 1965, lilac flowers, *L. O. Williams et al. 28304* (F); **San José:** Angostura, 3080 m, Jul 1944, flowers violet, *R. Mesén 502* (K); Cordillera de Talamanca, Pacific slope near Chirripó massif, 2700-3000 m, *G. Davidse & R. Pohl 1638* (MO); Cerro de Las Vueltas [note: Cerro de Las Vueltas at 09° 37.4'N, 83° 51.5'W on 1:50,000-scale topographic map 3444 IV] 2700-3000 m, 29 Dec - 1 Jan 1925/6, *P. C. Standley & J. Valerio 43591* (GH, US), *43661* (GH, US), *43759* (GH, US), *43913* (GH, US) *49931* (GH, US); new road from La Estrella to Copey, 2450 m, 15 Feb 1935, *J. Valerio 1050* (F).

Area 18: Valle Silencio; Province Limón.

Cordillera de Talamanca, Atlantic slope, Valle de Silencio, area just N of Cerro Hoffman, 4 1/2 airborne km W of the Panama border, 09° 08'N, 82° 58'W, 2350-2450 m, 8 Sep 1984, corolla violet, *G. Davidse et al. 28690* (CR); Cordillera de la Talamanca, Parque Internacional de la Amistad, N of Cerro Hoffman, along trail which begins at park station Altamira, 09° 06.5'N, 82° 57.7'W, 2320 m, 5 Dec 1996, corolla white, *SHVA 7116* (INB, PTIS, WAG).

Localities unknown

Monté Sin fé, 6 Feb 1967, *L. D. Gómez 27* (CR); Cerro del Fugles, 24 Dec 1931, *W. Kupper 173* (M); Ferralos?, or Feualos?, 23 Jan 1913, *J. León 1115* (CR).

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