

Solanum sect. Petota in Guatemala; Taxonomy and Genetic Resources

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ABSTRACT

There are five wild potato species in Guatemala: *Solanum agrimonifolium*, *S. bulbocastanum*, *S. clarum*, *S. demissum*, and *S. morelliforme*. We conducted a collecting expedition there from September 11 to November 5, 1995. The goals of the expedition were to gather field data for taxonomic studies of the five species of Guatemalan wild potatoes and to collect potato germplasm. Our 43 true seed collections nearly quadruple the available wild potato germplasm for Guatemala, provide germplasm from most previously known localities, and add new ones. We provide a systematic treatment of Guatemalan wild potatoes, geographic and logistical data for collecting wild potatoes in Guatemala, statistics on human population growth and deforestation to help explain decline of wild potato populations, recommend areas for future collecting, and suggest two areas as in-situ reserves for wild potatoes.

INTRODUCTION

Solanum L. sect. *Petota* Dumort., the potato and its relatives, occurs from the southwestern United States to southern Chile. It consists of seven cultivated and 225 wild species, according to the latest comprehensive taxonomic treatment of Hawkes (1990). However, nine of these species are alternatively treated in sect. *Etuberosum* (Buk. and Kerner) A. Child, sect. *Lycopersicum* (Mill.) Wettst., and sect. *Juglandifolium* (Rydb.) A. Child (Spooner *et al.*, 1993).

Most wild potato species are distributed in the Andes, but about 30 grow in Mexico and Central America, with five in Guatemala: *Solanum agrimonifolium* Rydb., *S. bulbocastanum* Dunal, *S. clarum* Correll, *S. demissum* Lindl., and *S.*

EXPLANATION OF ABBREVIATIONS

- AGUAT, Herbarium, Universidad de San Carlos, Guatemala City, Guatemala
 BIGUA, Herbarium, Facultad de C.C.Q.Q. y Farmacia, Universidad de San Carlos, Guatemala
 BM, Herbarium, Natural History Museum, London, England
 C, Herbarium, Botanical Museum, University of Copenhagen, Copenhagen, Denmark
 ENCB, Herbarium, Departamento de Botánica, Instituto Politécnico Nacional, Mexico City, Mexico
 F, Herbarium, Field Museum of Natural History, Chicago, Illinois, USA
 G, Herbarium, Conservatoire et Jardin botaniques de la Ville de Genève, Geneva, Switzerland
 GH, Harvard University Herbaria, Cambridge, Massachusetts, USA
 K, Herbarium, Royal Botanic Gardens, Kew, England
 LL, Lundell Herbarium, Botany Department, University of Texas, Austin, Texas, USA
 MEXU, National Herbarium, Departamento de Botánico, Universidad Nacional Autónoma de México, Mexico City, Mexico
 MICH, Herbarium, University of Michigan, Ann Arbor, Michigan, USA
 MO, Herbarium, Missouri Botanical Garden, St. Louis, Missouri, USA
 MSC, Herbarium, Botany and Plant Pathology Department, Michigan State University, East Lansing, Michigan, USA
 NA, Herbarium, United States National Arboretum, Washington, D.C., USA
 NRSP-6, National Research Support Program-6, Sturgeon Bay, Wisconsin, USA (formerly called the Inter-Regional Potato Introduction Project [IR-1])
 NY, Herbarium, New York Botanical Garden, Bronx, New York, USA
 PTIS, Herbarium, United States Potato Introduction Station, Sturgeon Bay, Wisconsin, USA
 S, Herbarium, Botany Department, Swedish Museum of Natural History, Stockholm, Sweden
 TEX, Herbarium, Botany Department, University of Texas, Austin, Texas, USA
 US, United States National Herbarium, Smithsonian Institution, Washington, D.C., USA
 USCG, Herbarium, Centro de Estudios Conservacionistas, Universidad de San Carlos, Guatemala City, Guatemala
 UVAL, Herbarium, Departamento de Biología, Universidad del Valle de Guatemala, Guatemala City, Guatemala
 WAG, Herbarium, Department of Plant Taxonomy, Wageningen Agricultural University, Wageningen, The Netherlands
 WIS, Herbarium, Botany Department, University of Wisconsin, Madison, Wisconsin, USA
 Z, Herbarium, Institut für Systematische Botanik, Universität Zürich, Zurich, Switzerland

ADDITIONAL KEY WORDS: Collecting expedition, germplasm, potatoes.

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morelliforme Bitter and G. Muench (Correll, 1952, 1962; Gentry and Standley, 1974; Hawkes, 1990). These five species also grow in Mexico and reach their southern-most distribution in Guatemala, except for *S. agrimonifolium* and *S. morelliforme*, that also grow in adjacent Honduras (both in Morazán Department). The Mexican distributions of these species are: *S. agrimonifolium*, southern Mexico (States of Oaxaca and Chiapas); *S. bulbocastanum*, central to southern Mexico; *S. clarum*, southern Mexico (Chiapas); *S. demissum*, northern to southern Mexico; *S. morelliforme*, central to southern Mexico (Correll, 1952, 1962; Hawkes, 1966, 1990; Spooner *et al.*, 1991).

Central America represented a relatively under-collected region for potato germplasm, and Guatemala became a collecting priority for the Instituto de Ciencia y Tecnología Agrícolas, Guatemala (ICTA); the Centre for Genetic Resources The Netherlands (CGN); and the National Research Support Program-6, United States (NRSP-6, the United States potato genebank), that formed a joint collecting expedition to Guatemala. The goals of the expedition were to collect wild species germplasm (the cultivated species are well represented at the International Potato Center [CIP, Peru] and other national genebanks), to increase them quickly and make them freely available internationally, and to gather field data for continuing taxonomic studies.

MATERIALS AND METHODS

We collected throughout Guatemala from September 11 to November 5, 1995. Our locality data came from: 1) database files backing up germplasm records from CGN (Hoekstra and Seidewitz, 1987) and NRSP-6 (Bamberg *et al.*, 1996); 2) literature records from Correll (1962), who obtained these from herbarium material in F, G, GH, K, LL, MICH, MSC, NY, S, US, Z; 3) a database of herbarium records announced for distribution in Hawkes (1997); 4) our own inspection of herbarium specimens from AGUAT, BIGUA, BM, C, ENCB, F, GH, K, LL, MEXU, MICH, MO, MSC, NA, NY, PTIS, TEX, US, USCG, UVAL, WAG, WIS (herbarium codes follow Holmgren *et al.*, 1990).

Geographic references were found with the aid of 1) Gall (1978, 1981, 1983a,b), 2) United States Department of the Interior (1984), 3) the 1:50,000-scale topographic maps (259 sheets), and the 1:250,000-scale topographic maps (13 sheets) from the Instituto Geográfico Militar, 4) the 1:1,000,000-scale *Mapa Vial Turístico*, 1980 road map from the Instituto Geográfico Militar. These geographic resources, and comparable resources from recent expeditions to Mexico, Costa Rica, Venezuela, Colom-

bia, Ecuador, Bolivia, Argentina, and Chile, are a growing and valuable component to the Potato Introduction Station Herbarium (PTIS) library (Bamberg and Spooner, 1994).

We concentrated collecting on those areas under-represented by germplasm accessions. Local residents aided in our collections of wild potatoes, that are known locally as papa ardilla (squirrel potato), papa del monte (mountain potato), papa silvestre (wild potato), and papa del zorro (fox potato). *Solanum agrimonifolium* additionally is known as papa de marrana (pig potato) and tisbotch (Gentry and Standley, 1974). Longitude and latitude data were obtained by a global positioning system. Readings were taken as decimal fractions of minutes rather than as seconds.

Herbarium vouchers were deposited at AGUAT, PTIS, and WAG, with some at BIGUA. By written agreement with ICTA, all germplasm were exported to The Netherlands and The United States for disease screening in quarantine and later increases at CGN and NRSP-6. ICTA will obtain seeds of the first increase.

RESULTS AND DISCUSSION

Geography

Guatemala covers 108,889 km². It is divided into 22 Departments (Figure 1). The northern half of the country consists mostly of tropical lowlands below 1000 m and harbors no wild potatoes. Elevations above 1350 m (the lowest elevations for wild potatoes in Guatemala) occur only in the southern half of the country.

Guatemala has west to east and northeast running mountain chains (Figure 2), with the greatest elevations in the west. The northernmost chain is the Sierra de los Cuchumatanes, Sierra de Chamá, Sierra de Santa Cruz, and Montañas Mayas. South of these are the Sierra Madre, Sierra de Chaucús, Sierra de las Minas, Montañas del Mico, Montañas de Copán, Sierra del Meredón, and Montañas de Omoa (Gall, 1981; Piedra Santa-A., 1994). All 33 of Guatemala's volcanoes, with elevations from 1027 m to 4240 m, occur in the Sierra Madre (Figure 2). Many wild potato populations occur on these volcanoes, the five highest of which are Volcán Tajumulco (Dept. San Marcos, 4240 m), Volcán Tacaná (Dept. San Marcos, 4093 m), Volcán Acatenango (Depts. Chimaltenango, Escuintla, Sacatepéquez, 3975 m), Volcán Santa María (Dept. Quetzaltenango, 3772 m), and Volcán de Agua (Depts. Escuintla, Sacatepéquez, 3760 m).

Logistics

Figure 3 details our collection route. All potato popula-



FIGURE 1
Departments in Guatemala.

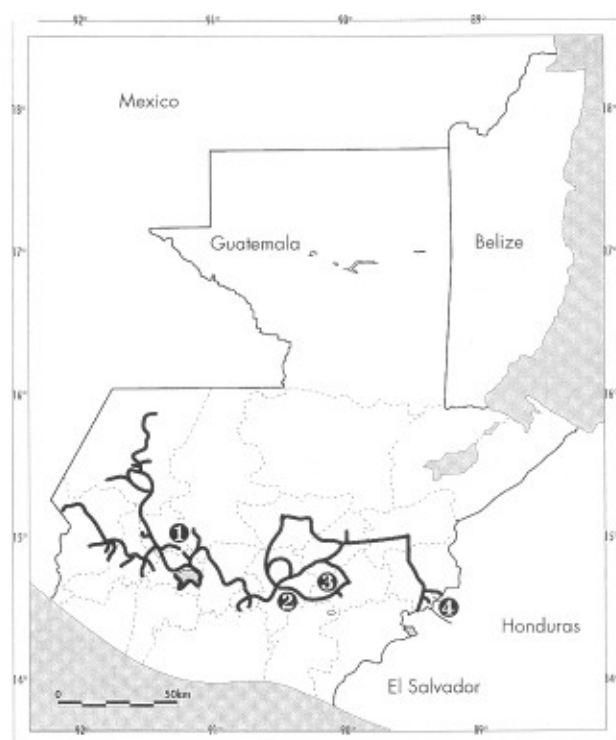


FIGURE 3
Route map for this expedition. Area 1 is the Cumbre de María Tecún (see Recommended areas for in-situ preserves for wild potatoes in Guatemala). Areas 2-4 are potential sites for wild potatoes but where they not yet been found (see Recommended areas for future collecting in Guatemala).

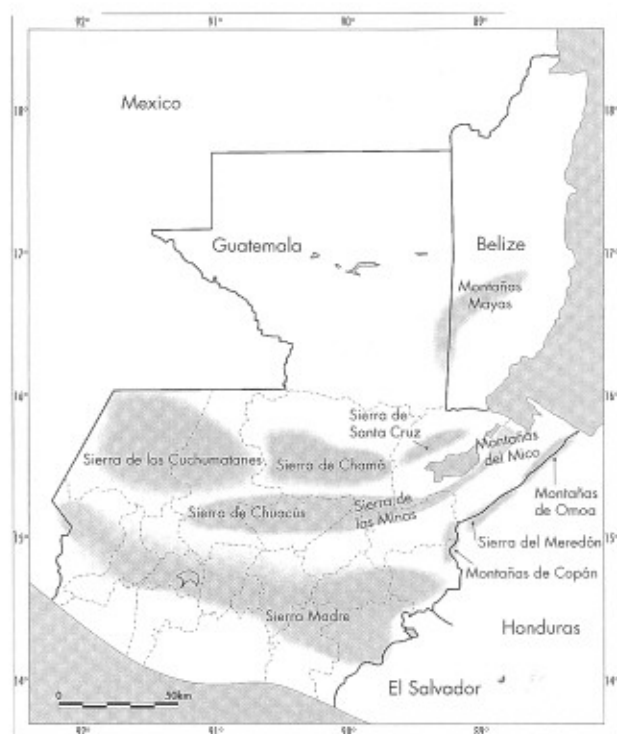


FIGURE 2
Mountain ranges in Guatemala.

tions in Guatemala can be approached within a 12 hour drive from Guatemala City, conveniently located in the center of the upland areas in southern Guatemala. Collecting at many localities, however, requires one or two days of hiking, sometimes covering a vertical distance of 1000 m or more. Many roads are not paved and are in poor condition by the end of the rainy season in mid to late October (Figure 4). A four-wheel drive vehicle is needed, and was rented in Guatemala City.

Gall (1978, 1981, 1983a,b), and United States Department of Interior (1984) provide an excellent compilation of place names. A serious problem for finding localities in the field, however, is the lack of up-to-date road and topographic maps. The most current road map is a single 1:1,000,000-scale map reprinted from one first published in 1980. There are no individual department road maps. The 1:50,000-scale and 1:250,000-scale topographic maps are based largely on 1964 data. Changes past these dates must be determined in the field, or from a knowledgeable collaborator. An additional complication is the general lack of road signs in most areas.

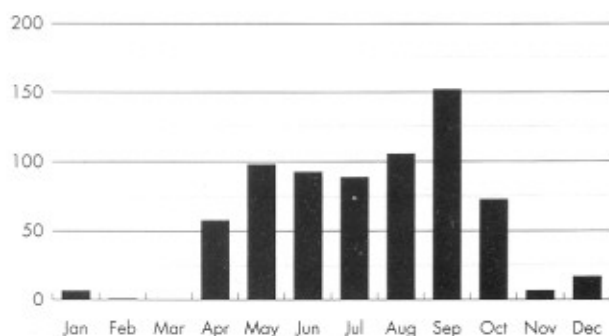


FIGURE 4
Average monthly rainfall, 1990-1994, Santa Lucia La Reforma Weather Station, Department Totonicapán, Guatemala, 1840 m, 15°07'57"W, 91°14'38"W. This station is located in western Guatemala where wild potatoes are common.

Previous Potato Collecting in Guatemala

Twenty-five individuals or teams have collected wild potatoes in Guatemala. Aguilar G., Brekon and Brekon, Baeke, Beaman, Flores C., Gibson and Laskouski, Johnston, Molina and Molina, Muench, Purpus, Rojas, Schwabe, Skutch, Smith, Standley, Stevens, Steyermark, Roe, Stevens, Veliz and Veliz, von Türckheim II, Uhde, and Williams collected wild potatoes as part of more general collecting expeditions. The most extensive of these were those of Standley and Steyermark. Their collections formed much of the material for *Flora of Guatemala*, published in serial form in *Fiediana, Botany* from 1946-1977 (*Solanum* published in Gentry and Standley, 1974).

Graham collected in Mexico and Guatemala to gain material for studies of late blight and crossability relationships of the Mexican and Central American diploid wild potatoes (Graham *et al.*, 1959; Graham and Dionne, 1961). Hawkes, Hjerting, and Lester collected in Guatemala as part of a potato collecting expedition in the southwestern United States, Mexico, Guatemala, Honduras, and Nicaragua (Hawkes, 1959). All germplasm collections in Guatemala were made by Graham, who collected 6 collections of *S. agrimonifolium*, *S. clarum*, and *S. morelliforme*; and Hawkes, who made ten collections of *S. agrimonifolium*, *S. bulbocastanum*, *S. clarum*, *S. demissum*, and *S. morelliforme*.

Phenology

Timing is one of the most important aspects of planning a germplasm collecting expedition. In Guatemala, herbarium specimens of wild potatoes were collected in all months but April and May. Most germplasm was collected during Sep-

tember to November. We collected germplasm of all five species throughout the expedition, but had to return to some populations of *S. agrimonifolium* in November to collect mature fruits (but some populations of this species had mature fruits in mid-September). We apparently were too late for ideal collecting for *S. demissum*. Considering these data, and the greater efficiency of collecting in the dry season (Figure 4), we suggest the best times to collect true seeds of wild potatoes in Guatemala would be during August to November (August for *S. demissum*).

Taxonomic treatment. Note: Germplasm collections are noted in the taxonomic treatment in "Additional collections examined" by an asterisk after herbarium codes. Our new collections should be available from NRSP-6 and CPRO-DLO, CGR in a couple of years after passage through quarantine and a first seed increase. We have examined all herbarium specimens except those listed as JGH (personal herbarium of Jack Hawkes, University of Birmingham, England). These are listed in a database of herbarium specimens announced for distribution in Hawkes (1997); these specimens are to be transferred to K but were not available for distribution during the planning of this expedition or writing this paper. Collections before Oct 13 are labeled *Spooner, Martínez and Hoekstra*, 7,004-7,053 (abbreviated *SMH* in the text), while those after Oct 17 are *Spooner, Martínez and van den Berg* 7054-7076 (abbreviated *SMV*). Our inclusion of a complete list of all known collections will greatly aid collectors and will be useful for those wishing to borrow these specimens.

Key to the Guatemalan wild species of *Solanum* sect. *Petota*

1. Leaves pinnately dissected; corolla pentagonal to rotate.
 2. Leaves with 2-4 pairs of lateral leaflets; fruits globose to ovoid *S. demissum*.
 2. Leaves with 4-7 pairs of lateral leaflets, fruits conical *S. agrimonifolium*.
1. Leaves entire; corolla stellate.
 3. Pseudostipular leaves auriculate; corollas creamy white; plants typically growing in hot and dry habitats in shallow or rocky soil *S. bulbocastanum*.
 3. Pseudostipular leaves, when present, linear to narrowly ovate; corollas pure white or pure white and purple; plants epiphytic or growing in epiphytic-like conditions in moss.
 4. Plants typically epiphytic; leaves elliptic to narrowly ovate, 1.9-3.2 times as long as wide ... *S. morelliforme*.
 4. Plants typically growing in moss in upland pine or juniper forests; leaves broadly ovate, 1.3-1.8 times as long as wide. *S. clarum*.

Solanum agrimonifolium Rydb., Bull. Torrey Bot. Club 51:

151. 1924. TYPE: MEXICO. Chiapas: Cerro del Boquerón, Sep 1913, *Purpus* 6977 (holotype: NY [2] [photos: LL, PTIS]; isotypes: BM, F [photo: PTIS], GH [photo: PTIS], MO [photo: PTIS], US 567248 [photo: PTIS]).

Plants terrestrial, to 2 m tall; stems 8-13 mm wide at base, green to purple, simple to branched; leaves odd pinnate, nearly glabrous to finely pubescent above and below, blades 13-30 cm long, 10-19 cm wide, petioles 1-5 cm long; 4-7 lateral leaflet pairs, ovate to elliptical, apex acuminate, base oblique, rounded to cuneate, sessile to subsessile; 4-14 interjected leaflets, linear to ovate, sessile; terminal leaflet ovate to elliptical, apex acute to acuminate, base attenuate; pseudostipular leaves auriculate, 2-10 cm long; inflorescence pseudoterminal and lateral, with 8-38 flowers; pedicel 15-30 mm long; calyx 5-10 mm long, lobes 3-8 mm long, long attenuate; corolla purple, rotate with short acumens, 2-3 cm in diameter; filaments 1.5-2 mm long, anthers 4-5.5 mm long, cordate at base; style exceeding stamens by 2-3 mm; fruits conical, rounded to pointed at tip, up to 5 cm long, medium to deep green. Chromosome number: $2n = 4x = 48$.

Distribution (Figure 5) and **Ecology**—*Solanum agrimonifolium* grows from 1600-3800 m, in wet and disturbed habitats, in organic soils, often in areas of cloud forests (wet upland tropical forests characterized by a profusion of epiphytes and clouds even in the dry season), in full sun to partial shade. Common habitats are recently logged or otherwise disturbed areas in valleys, streamsides, or in upland marshes.

Solanum agrimonifolium grows from southern Mexico (Oaxaca and Chiapas) south to HONDURAS. Morazán: Montaña La Tigra, 22 mi from Tegucigalpa on road to San Juancito, SW of San Juancito, 2000 m, 24 Nov 1958, *Hawkes et al.*, 2035 (C); Montaña La Tigra, between Tegucigalpa and San Juancito, SW of San Juancito, 2200 m, 29 Nov 1958, *Hawkes et al.* 2137 (C); Montaña La Tigra SW of San Juancito, 2000 m, 24 Nov 1958, *Molina* 8677 (F); above Rancho Quemado on Montaña La Tigra, 2000 m, 10 Dec 1968, *Molina* 8770 (F).

Additional specimens examined: Guatemala. **Chimaltenango**: N facing slope of Volcán Acatenango, a one-hour walk above Soledad, 1 km WSW of record 7051, 1:250,000-scale map ND 15-8, 14°31.1'N, 90°53.1'W, 2880 m, 13 Oct 1995, *SMH* 7050 (AGUAT, BIGUA, PTIS, WAG)*; N facing slope of Volcán Acatenango, a one-hour walk above Soledad, 1:250,000-scale map ND 15-8, 14°31.3'N, 90°52.7'W, 2840 m, 13 Oct 1995, *SMH* 7051 (AGUAT, WAG)*. **El Progreso**: between Finca Piamonte and top of Montaña Piamonte,

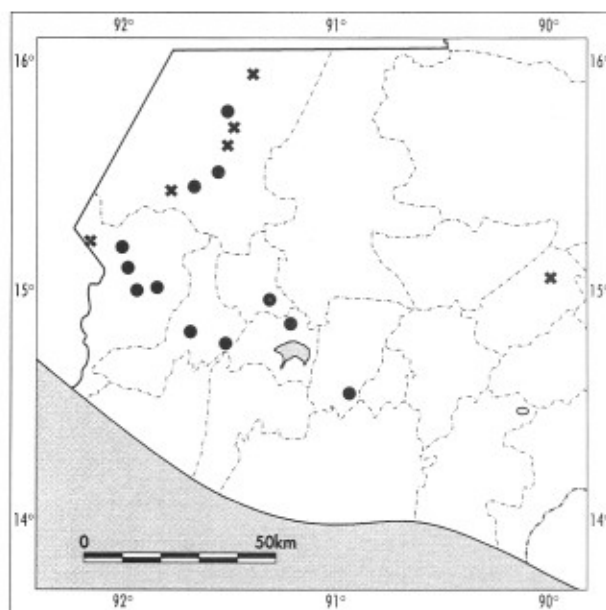


FIGURE 5

Geographic distribution of *Solanum agrimonifolium*. A circle designates an area represented by a germplasm collection; x designates an area without a germplasm collection.

along Joya Pacayal, 2500-3000 m, on summit, no date, *Steyermark* 43672 (F). **Huehuetenango**: Cuchumatane Mountains, road from Huehuetenango to Concepción, 3 km from Concepción, roadside, 2695 m, 5 Sep 1976, *Baeke* 153 (GH, MO); Chimal, 2900 m, 23 Oct 1956, *Graham* 145 (JGH, K, LL [photos BM, K], PTIS)*, 145A (PTIS)*, 145B (JGH, PTIS)*; above San Juan Ixcay, Sierra de los Cuchumatanes, 2600-2700 m, 23 Aug 1956, *Graham* 145 (K, LL [photo, K], S, US); between Xoxlac and Nucapuxlac, Sierra de los Cuchumatanes, 1650-2500 m, 17 Jul 1942, 2 km walk N of San Juan Atitán, footpath to Todos Santos, 1 km walk S of collection 7062, 1:250,000-scale map ND 15-3, 15°28.6'N, 91°37.4'W, 2730 m, 23 Oct 1995, *SMV* 7061 (AGUAT, PTIS, WAG)*; 3 km walk N of San Juan Atitán, logging path diverting from main path to Todos Santos at a point 2 km N of San Juan Atitán, 1 km NE of collection 7061 and 500 m S of collection 7063, 1:250,000-scale map ND 15-3, 15°28.7'N, 91°37.3'W, 2830 m, 23 Oct 1995, *SMV* 7062 (AGUAT, PTIS, WAG)*; 3.5 km walk N of San Juan Atitán, logging path diverting from main path from Todos Santos at a point 2 km N of San Juan Atitán, 500 m N of collection 7062, 1:250,000-scale map ND 15-3, 15°28.9'N, 91°37.3'W, 2880 m, 23 Oct 1995, *SMV* 7063 (AGUAT, PTIS, WAG)*; 24.3 km N of town square of Santa Eulalia, 5.5 km S of town square of San Mateo Ixtatán, Rt 9N, 1:250,000-scale map ND 15-4, 15°49.2'N, 91°30.5'W, 3020 m,

26 Oct 1995, *SMV 7073* (AGUAT, PTIS, WAG)*, *SMV 7074* (AGUAT)*; *Steyermark 48961* (F); top of Sierra Chemalito, Sierra de los Cuchumatanes, 3 1/2 mi W of Santa Eulalia, 3100-3150 m, 2 Aug 1942, *Steyermark 49938* (F [photos BM, K]); Cerro Pixpix, above San Ildefonso Ixtahuacan, forested summit, 1600-2800 m, 15 Aug 1942, *Steyermark 50555* (F); trail between Todos Santos and San Juan Atitán, Sierra de los Cuchumatanes, 2600-2700 m, 7 Sep 1942, *Steyermark 51942* (F). **Quezaltenango**: between San Martín Chile Verde and Mujuliá, lower slope of Volcán Lacandón, 1900 m, 18 Aug 1956, *Graham 136* (JGH, LL); road from San Martín Chile Verde to Colomba, above Majuliá, 17.5 km from San Mateo, roadside, 2100 m, 4 Nov 1958, *Hawkes et al. 1868* (C, JGH, US); Volcán Zunil, 3100-3200 m, 27 Dec 1976, *Schwabe s.n.* (MEXU); Mpio. Zunil, 2 hour walk E of Fuente de Aguas Termales Georginas (located 8 km SE of Pan-American Highway from town of Zunil), W-facing slope of Volcán Zunil, 1:250,000-scale map ND 15-8, 14°45'N, 91°25'W, 2900 m, 22 Sep 1995, *SMH 7019* (AGUAT, PTIS, WAG)*; Fuentes Georginas, western slope of Volcán de Zunil, 2850 m, 4 Mar 1939, *Standley 67499* (F); above Mujuliá between San Martín Chile Verde and Colomba, 1800 m, 1 Feb 1941, *Standley 85459* (F, US); Volcán Santo Tomás, 2500-3700 m, 22 Jan 1940, *Steyermark 34482* (F). **San Marcos**: San Luis, 4.4 mi W of Ixchiguan, road to Tacaná, 3400 m, 13 Aug 1959, *Beaman 3252* (ENCB, LL, US); Volcán Tacaná, entering Mexico from Unión de Juárez, near border with Mexico, 9 Jul 1966, *Flores-C S-950* (MEXU); outer slopes of Tajumulco volcano, Sierra Madre Mountains, ca 10 km W of San Marcos, 2400-2700, 3 Jan 1965, *Gibson and Laskowski 27192* (F); village of San Andres Chapil, 8 km on Route 12 from San Marcos to Tejutla at km 255 from Guatemala, below the cliffs, 2750 m, 3 Nov 1958, *Hawkes et al. 1851* (C, JGH, PTIS)*; 12 km from San Marcos, road to Tejutla, (entering forest from left by small bridge), 3000 m, 3 Nov 1958, *Hawkes et al. 1853* (C, JGH); 13 km from San Marcos, road to San Rafael de la Cuesta, in clearings and sides of paths, 2400 m, 3 Nov 1958, *Hawkes et al. 1854* (C, JGH, US); 12.4 km W of town square of San Marcos, road to San Rafael Pie de la Cuesta, N side of road in valley, 1:250,000-scale map ND 15-7, 14°56.8'N, 91°51.3'W, 2340 m, 23 Sep 1995, *SMH 7021* (AGUAT, PTIS, WAG)*; 1.0 km NW of town square of Ixchiguan, road to Tacaná, ca 50 m N of road, 1:250,000-scale map ND 15-3, 15°10.3'N, 91°56.8'W, 3380 m, 24 Sep 1995, *SMH 7026* (AGUAT, PTIS, WAG)*; N slope of Volcán Tajumulco, W-facing valley, a 10 minute hike S into woods from a point 2.5 km W of road from San Marcos to Tacaná to town of Tajumulco, 1:250,000-scale map ND 15-3, 15°04.6'N, 91°52.8'W, 2780 m,

26 Sep 1995, *SMH 7034* (AGUAT, PTIS, WAG)*; Barranco Eminencia, above San Rafael Pie de la Cuesta, 2100-2400 m, 14 and 15 Mar 1939, *Standley 68461* (F); Barranco Eminencia, road between San Marcos and San Rafael Pie de la Cuesta, in upper part of the barranco between Finca la Lucha and Buena Vista, 2500-2700 m, 6 Feb 1941, *Standley 86448* (F); along road between San Sebastián at km 21 and km 8, 8 to 18 mi NW of San Marcos, moist thickets near waterfall, 2700-3800 m, 15 Feb 1940, *Steyermark 35728* (F); between La Vega Ridge and Río Vega and along NE slopes of Volcán Tacaná, to 3 mi from Guatemala-Mexican boundary, in vicinity of San Rafael, along stream in narrow shaded barranco, 2500-3000 m, 20 Feb 1940, *Steyermark 36178* (F); wet mountain forest near Aldea Fraternidad, between San Rafael Pie de la Cuesta and Palo Gordo, W facing slope of Sierra Madre Mountains, 1800-2400 m, 10-18 Dec 1963, *Williams et al. 25754* (US), *26292* (F). **Sololá**: between Quezaltenango and Los Encuentros, by mountain stream, 3050 m, 7 Aug 1956, *Graham 116* (LL); 17.0 km W of the intersection of the road from Nahuala to Guatemala City, and the old road W to Totonicapán, ca 20 m N of road, 1:250,000-scale map ND 15-8, 14°51.5'N, 91°11.7'W, 3000 m, 28 Sep 1995, *SMH 7036* (AGUAT, PTIS, WAG)*. **Totonicapán**: Mujuliá, 1900 m, 16 Oct 1956, *Graham 136* (PTIS)*; Cerro El Chiché, 1 mi E of Totonicapán, road to Los Encuentros [note: our field work indicated 1 mi E is a typographical error for 10 mi E], 3300 m, 5 Nov 1958, *Hawkes et al. 1889* (JGH, US); Cerro el Quiché, 1 mi E of Totonicapán, road to los Encuentros [see note above], km 163.5 from Guatemala City, by a stream on the lower side of the road, 3300 m, 5 Nov 1958, *Hawkes et al. 1891* (JGH, PTIS, US)*; Cerro el Quiché, 1 mi E of Totonicapán, road to los Encuentros, km 163.5 from Guatemala City, by a small stream, upper side of the road, 3300 m, 5 Nov 1958, *Hawkes et al. 1892* (C, JGH, US); 10.2 km E of town square of Totonicapán, 4.8 km from deviation of road to Santa Cruz del Quiché, old road to Los Encuentros, 1:250,000-scale map ND 15-8, 14°54.8'N, 91°19.1'W, 3150 m, 15 Sep 1995, *SMH 7006* (AGUAT, PTIS, WAG)*.

Solanum agrimonifolium is one of 40 species included by Hawkes (1990) in series *Conicibaccata* Bitter. According to Hawkes (1990), the other Mexican and Central American representatives of ser. *Conicibaccata* are *S. oxycarpum* Schiede [4x (2EBN)], restricted to Mexico; *S. longiconicum* Bitter [4x (2EBN)] from Costa Rica and Panama, and *S. woodsonii* Correll (ploidy and EBN unknown) from Costa Rica, Panama, and Venezuela.

Correll (1962), on the other hand, identified some Costa Rican and Panamanian collections as *S. oxycarpum*, and

considered *S. longiconicum* to be synonymous with *S. oxycarpum*. Gentry and Standley (1974) identified *Steyermark* 43672 (specimen at F) from Guatemala, Department El Progreso, as *S. oxycarpum*, a specimen collected after Correll (1962), and not commented on by Hawkes (1990). All of these taxa are morphologically very similar, and distinguished with difficulty only by reliance on apparently overlapping ranges of character states (Castillo and Spooner, 1997).

The confusion regarding identity of these collections in ser. *Conicibaccata* questions the species boundaries among *Solanum agrimonifolium*, *S. longiconicum* and *S. oxycarpum*. They are considered as distinct by number and size of lateral and interstitial leaflets and leaf pubescence (Correll, 1962; Gentry and Standley, 1974; Hawkes, 1990). We conservatively treat all our Guatemalan collections as *S. agrimonifolium* until we further study additional Mexican and Central American members of this complex.

Solanum bulbocastanum* Dunal subsp. *partitum (Correll) Hawkes, Scott. Pl. Breed. Stn. Rec. 1963: 95. 1963. *Solanum bulbocastanum* var. *partitum* Correll, Agric. Monogr. U.S.D.A. 11: 83. 1952. TYPE: GUATEMALA. Baja Verapaz: Patal, 1600 m, growing in thicket, July 1908, *H. von Türckheim* II 2316 (holotype: US 124466 [photo: PTIS]; isotypes: G [photos: NY, US], NY [photos: PTIS, US], Z [photo: NY]).

Plants terrestrial, 3-10 dm tall; stems 2-4 mm wide at base, green to brownish-purple, simple to branched; leaves simple, densely puberulent to pubescent above and below, narrow to broadly ovate to rhomboid, blades 3-10 cm long, 1.5-4 cm wide, apex acute to acuminate, base attenuate, petioles 1-4 cm long; pseudostipular leaves auriculate, to 2 cm long; inflorescence pseudoterminal and lateral, with 7-20 flowers; pedicel 10-25 mm long; calyx 3-4.5 mm long, lobes 1-2.5 mm long, acute to mucronate; corolla deeply stellate, 1-1.5 mm in diameter, creamy white; filaments 1-2 mm long, anthers 4-6 mm long, cordate at base without rounded auricle; style exceeding stamens by 1.5-2.5 mm; fruits globose, 1 cm in diameter, green. Chromosome number: $2n = 2x = 24$.

Distribution (Figure 6) and **Ecology**—*Solanum bulbocastanum* subsp. *partitum* grows from 1350-2300 m, among grasses, cacti, scrub and oak forests, often in shallow or rocky soil. It grows in drier habitats than all other wild potato species in Guatemala. It persists in grazed areas but is readily eaten by grazing animals before flowering, and it is therefore difficult to find fruiting populations. All of our fruit collections in such areas were made in areas of difficult

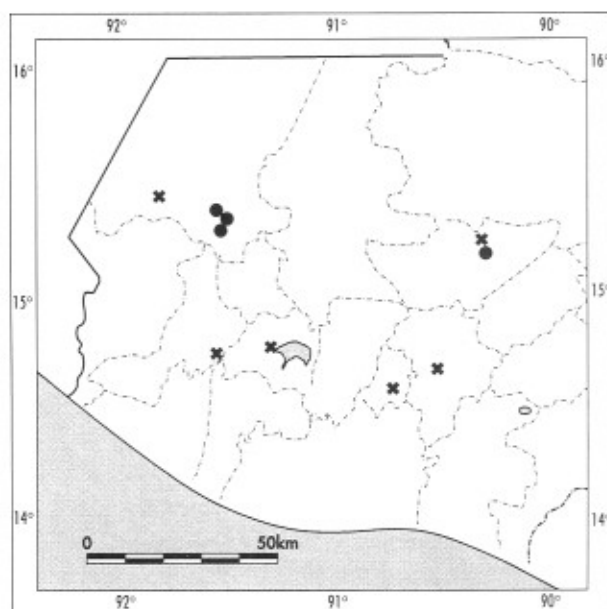


FIGURE 6
Geographic distribution of *Solanum bulbocastanum*. A circle designates an area represented by a germplasm collection; x designates an area without a germplasm collection.

access, such as steep rocky slopes, piles of stones, rock walls, or among the dense vegetation of spiny shrubs or cacti. It is an inconspicuous plant with a widely scattered distribution throughout the dry areas of Guatemala and likely is under-collected.

Additional specimens examined: GUATEMALA. **Baja Verapaz:** road from Salamá to Cobán, Patal, summit of road, 16 mi from Salamá, by roadside, 1700 m, 11 Nov 1958, *Hawkes et al. 1922* (JGH); road from Salamá to Cobán, Patal, summit of road, 15 mi from Salamá, 1650 m, 11 Nov 1958, *Hawkes et al. 1938* (JGH); road from Salamá to Cobán, Patal, summit of road, 11 mi from Salamá, 1350 m, 11 Nov 1958, *Hawkes et al. 1942* (JGH); 8.8 km N from town square of Salamá, old road to Cobán, 1:250,000-scale map ND 15-4, 15°09.3'N, 90°17.5'W, 1430 m, 5 Oct 1995, *SMH 7040* (AGUAT, PTIS, WAG)*; 11.5 km N from town square of Salamá, old road to Cobán, 50 m W of private road past power line, 1:250,000-scale map ND 15-4, 15°10.3'N, 90°17.7'W, 1640 m, 5 Oct 1995, *SMH 7042* (AGUAT)*; 18.8 km N from town square of Salamá, old road to Cobán, 1:250,000-scale map ND 15-4, 15°12.9'N, 90°17.7'W, 1420 m, 5 Oct 1995, *SMH 7043* (AGUAT, PTIS, WAG)*. **Guatemala:** Chilloni (note: no Chilloni located in references, but a Chillani in U.S. gazetteer of Guatemala at 14°43'S, 90°33'W, where we mapped this record), 1500 m, 21 Jun 1921, *Rojas 83* (US). **Huehuetenango:**

nango: between Huehuetenango and San Sebastián, junction of Huehuetenango and Pan American Highways, 1850 m, 31 Oct 1958, *Hawkes et al. 1789* (JGH, US); road from Huehuetenango to Quezaltenango, 5 km S of Malacatancito, in damp gully above the road, 1800 m, 31 Oct 1958, *Hawkes et al. 1796* (JGH, PTIS)*; between Kms 100 and 107, vicinity of Campo Bolas, way to mirador, Sierra de los Cuchumatanes, 2000 m, *Molina and Molina 26381* [note: we cannot locate this or the following record] (F); vicinity of Campo de Bolas, way to El Mirador, Sierra Cuchumatanes, 2000 m, 12 Sep 1971, *Molina and Molina 26402* (F); between Puento Negro and Los Alisos, way to Aguacatán, 1600 m, 16 Sep 1971, *Molina and Molina 26547* [note: we cannot locate Puento Negro and Los Alisos, and mapped this record with other records in Huehuetenango E of Aguacatán] (F); along 9N, at junction of entrance to Huehuetenango, 50-200 m W of road, 1:250,000-scale map ND 15-4, 15°46.0'N, 91°30.3'W, 2000 m, 18 Sep 1995, *SMH 7010* (AGUAT, BIGUA, PTIS, WAG)*; 3.1 km NW of the road entrance to Huehuetenango, Rt. CA1, 200 m uphill (SW) of road, 1:250,000-scale map ND 15-3, 15.18.8'N, 91°31.1'W, 1900 m, 18 Oct 1995, *SMV 7056* (AGUAT, PTIS, WAG)*; 7.3 km NW of entrance to Huehuetenango, Rt. CA1, 400 m uphill (SW) of road, 1:250,000-scale map ND 15-3, 15°19.3'N, 91°32.9'W, 2000 m, 19 Oct 1995, *SMV 7057* (AGUAT, BIGUA, PTIS, WAG)*; along road between Huehuetenango and San Sebastián H., 2000 m, 12 Aug 1942, *Steyermark 50404* (F); dry slopes between San Ildefonso Ixtahuacán and Cuilco, 1350-1600 m, 16 Aug 1942, *Steyermark 50687* (F). **Quezaltenango:** no exact locality, except 14°45'N, 91°31'S, *Roe et al. 685* (MICH, MO, US). **Sacatepéquez:** road between Palín and Antigua, ca 1/2 km by road S of Santa María de Jesús, 14°29'N, 90°42'S, 1900 m, 7 Jul 1976, *Breckon and Breckon 2082* (F). **Sololá:** slopes of Volcán San Pedro, 2150 m, 20 Sep 1971, *Molina and Molina 26659* (F); trail between village of San Pedro, via San Juan, San Cristóbal Buena Vista, and NW slopes of Volcán Santa Clara, 1800-2300 m, 8 Jun 1942, *Steyermark 47308* (F). **Locality not specific:** 1939, Aguilar G. 221 (F); 1938-1943, Aguilar G. 564 (F).

All of our collections have the deeply divided corolla lobes conforming to subsp. *partitum* (Correll) Hawkes (Correll, 1962; Gentry and Standley, 1974; Hawkes, 1990). Spooner and Sytsma (1992) showed the unexpected result that based on chloroplast DNA restriction site data, *S. bulbocastanum* (ser. *Bulbocastana* Rydb.) and *S. cardiophyllum* (ser. *Pinnatisecta* [Rydb.] Hawkes) were sister taxa and in a separate clade from all other Mexican and Central American diploid species, exclusive of *S. verrucosum* Schltdl. (ser. *Tuberosa* [Rydb.] Hawkes); series affiliations after Hawkes

(1990). Rodríguez and Spooner (1997) showed this result to be maintained with many additional accessions of all three subspecies of *S. bulbocastanum* and two of the three subspecies of *S. cardiophyllum* (the remaining subspecies, *S. cardiophyllum* subsp. *ehrenbergii* Bitter was in the clade of Mexican diploid species). Because chloroplast DNA is predominately maternally inherited in sect. *Petota*, the true species relationships of *S. bulbocastanum* must await data from biparentally inherited markers.

Solanum clarum Correll, Contrib. Texas Res. Found., Bot. Stud. 1: 10. 1950. TYPE: GUATEMALA. Quezaltenango: Volcán Santa María, terrestrial, 3600 m, 27 Jul 1934, *Skutch 858* (holotype: GH [photos: F, LL, NY, PTIS, US]; isotypes: F [photo: F], NY [photo: PTIS]), US 1643448 [photo: PTIS]).

Plants typically growing in moss in upland pine or juniper forests, erect, 1.5-3.5 dm tall; stems 1-3 mm wide at base, green to purple, simple to branched; leaves simple, fine pubescent above and below, elliptic to broadly ovate, blades 2-6 cm long, 1.5-4.2 cm wide, apex acute to acuminate, base attenuate to truncate to cordate, petioles 1-3 cm long; pseudostipular leaves absent or linear to narrowly ovate, to 2 cm long; inflorescence pseudoterminal and lateral, with 4-15 flowers; pedicel 10-15 mm long; calyx 1.5-2 mm long, lobes 0.7-1 mm long, acute to mucronate; corolla deeply stellate, 15-20 mm in diameter, purplish at tip, grading to white at base; filaments 1-1.5 mm long, anthers 3-5.5 mm long, cordate at base without rounded auricle; style exceeding stamens by 2-3 mm; fruits spherical, 5-8 mm in diameter, yellowish to green. Chromosome number: $2n = 2x = 24$.

Distribution (Figure 7) and **Ecology**—*Solanum clarum* grows from 2900-3800 m, in high-altitude pine and fir forests, usually in association with *Acaena elongata* L. (*SMV 7076*), *Alchemilla pectinata* HBK (*SMV 7070*), and *Pernetta ciliata* (Schlecht. and Cham.) Small (*SMV 7071*). Most populations of *S. clarum* consisted of hundreds of individuals in all stages of development from emerging plants to plants with mature fruits. However, flowers were rarely seen, and fruits generally were difficult to locate. We obtained mature fruits from all populations encountered, and we advise germplasm collectors to persevere if populations seem to lack fruits with initial inspection.

Additional specimens examined: GUATEMALA. **Huehuetenango:** Sierra de los Cuchumatanes, between Tojiah and Chemal at km 319.5, Ruta Nacional 9 N, 3380 m, 30 Jul 1960, *Beaman 3793* (LL, MSC); Sierra de los Cuchumatanes, slopes of Cerro Chemal, 28 mi from Huehuetenango, 3300 m,

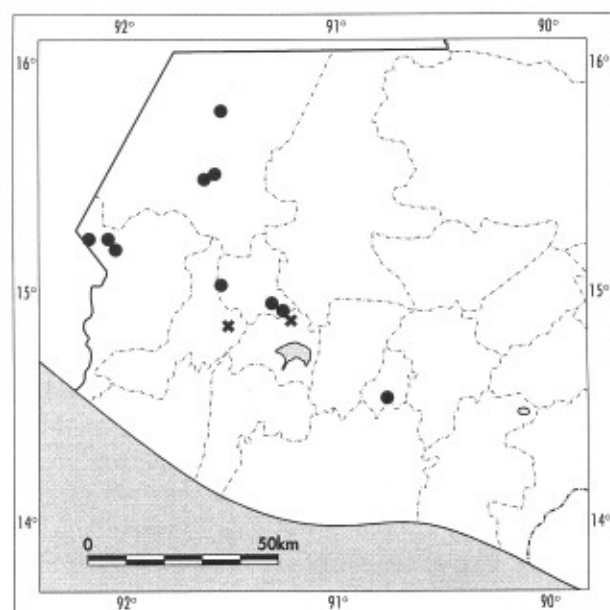


FIGURE 7

Geographic distribution of *Solanum clarum*. A circle designates an area represented by a germplasm collection; x designates an area without a germplasm collection.

30 Oct 1958, *Hawkes et al.* 1776 (JGH), 1777 (JGH), 1778 (JGH); 31 km N of town square of Huehuetenango, Rt. 9N, above Casario Chiabal, 3.5 km N of road junction to Todos Santos, ca 1 km uphill, W of road, 1:250,000-scale map ND 15-3, 15°28.5'N, 91°30.5'W, 3370 m, 16 Sep 1995, *SMH 7007* (AGUAT, PTIS, WAG)*; 4.3 km NW of road from Huehuetenango to Santa Eulalia, road to Todos Santos Cuchumatán, 100 m N of road, 1:250,000-scale map ND 15-3, 15°27.6'N, 91°31.2'W, 3280 m, 20 Oct 1995, *SMV 7059* (AGUAT, WAG)*; from Huehuetenango a point 4 km N of junction of road to Todos Santos, 1:250,000-scale map ND 15-3, 15°29.2'N, 91°30.4'W, 3430 m, 24 Oct 1995, *SMV 7064* (AGUAT, PTIS, WAG)*; 31 km N of town square of Huehuetenango, Road 9N, 3.5 km N of road junction to Casario Chiabal, 2 km uphill, W of road, 1:250,000-scale map ND 15-3, 15°29.4'N, 91°30.9'W, 3500 m, 24 Oct 1995, *SMV 7065* (AGUAT, PTIS)*; 31 km N of town square of Huehuetenango, Rt. 9N, 3.5 km N of road junction to Casario Chiabal, 2 km uphill, W of road, 1:250,000-scale map ND 15-3, 15°28.5'N, 91°30.9'W, 3500 m, 24 Oct 1995, *SMV 7066* (AGUAT)*; 6 km E of Huehuetenango-Soloma Road (9N), road past Huito to Tuinimá, 1 km E of Huito, 1:250,000-scale map ND 15-4, 15°30.1'N, 91°27.5'W, 3350 m, 25 Oct 1995, *SMV 7067* (AGUAT, PTIS, WAG)*; 24.3 km N of town square of Santa Eulalia, 5.5 km S of town square of San Mateo Ixtatán, Rt. 9N, 1:250,000-scale map ND 15-4, 15°49.2'N,

91°30.5'W, 3020 m, 26 Oct 1995, *SMV 7072* (AGUAT, PTIS, WAG)*; ca. 10.5 mi SW of San Juan Ixcay, Ruta Nacional 9N, Sierra de los Cuchumatanes, common, 18 Jul 1971, Stevens 1262 (MSC); alpine areas in vicinity of Tunimá, Sierra de los Cuchumatanes, 3400-3500 m, 7 Jul 1942, *Steyermark 48385* (F); Cerro Chermal, summit of Sierra de los Cuchumatanes, 3700-3800 m, 8 Aug 1942, *Steyermark 50294* (F, NY, US).

Quezaltenango: (see locality of type, above). **Sacatepéquez:** above Santa Maria de Jesús, N facing slope of Volcán de Agua, in the long grass by the trail, 2900 m, 8 Nov 1958, *Hawkes et al.* 1909 (JGH, PTIS, US)*. **San Marcos:** 1.0 km NW of town square of Ixchiguan, road to Tacaná, ca 50 m N of road, 1:250,000-scale map ND 15-3, 15°10.3'N, 91°56.8'W, 3380 m, 24 Sep 1995, *SMH 7027* (AGUAT, PTIS, WAG)*; 7.2 km NW of town square of Ixchiguan, 20 m S of road, 1:250,000-scale map ND 15-3, 15°10.3'N, 91°58.4'W, 3360 m, 24 Sep 1995, *SMH 7028* (AGUAT, PTIS, WAG)*; 2.5 hours hike SW of town of Tacaná, towards village of San Rafael, at area of village of Chemealón, 1:250,000-scale map ND 15-3, 15°11'N, 92°04'W, 3260 m, 25 Sep 1995, *SMH 7029* (AGUAT, PTIS, WAG)*. **Sololá:** km 152 between Quezaltenango and Los Encuentros, 3100 m, 7 Oct 1956, Graham 118 (LL); road from Totonicapán to Los Encuentros, km 143 from Guatemala City, 3200 m, 5 Nov 1958, *Hawkes et al.* 1895 (JGH). **Totonicapán:** near margin of small stream in semi-open meadow, near Cerro Quiché, Tecum Uman Ridge at km 154, Ruta Nacional No. 1, 20 km E of Totonicapán, 3340 m, 14 Aug 1960, *Beaman 4176* (LL, MSC, US); between Totonicapán and los Encuentros, 19 Oct 1956, 3000 m, Graham 138 (JGH, PTIS)*; near the Quezaltenango border, 22 mi N of Quezaltenango, Cerro Calel, 3100 m, 2 Nov 1958, *Hawkes et al.* 1813, 1824, 1827 (same, but 3200 m in shade of *Abies*), 1839* (same, but 3250 m), 1849 (same, but 3200 m as epiphyte on *Abies*) (all JGH, US); 22 mi N of Quezaltenango, near the Guatemalan border, 3250 m, 2 Nov 1958, *Hawkes et al.* 1833 (JGH, PTIS)*; Cerro El Chiché, 1 mi E of Totonicapán, road to Los Encuentros, just below the summit on NW side, rare, 3400 m, 5 Nov 1958, *Hawkes et al.* 1884 (JGH); 20 km from Totonicapán, road to Los Encuentros, Cerro Quiché, 3400 m, 5 Nov 1958, *Hawkes et al.* 1894 (JGH, PTIS)*; 4.1 km E of town square of Calel, road to the Pan-American Highway which begins at Puente Pologua, 1:250,000-scale map ND 15-3, 15°04.3'N, 91°33.5'W, 3020 m, 20 Sep 1995, *SMH 7011* (AGUAT, PTIS, WAG)*; along old road N of Quezaltenango, going through Buenabaj to Calel, 1 km S of intersection of this road from Calel to Pan-American Highway, ca 4 km E of Calel, 1:250,000-scale map ND 15-3, 15°03.8'N, 91°33.9'W, 3010 m, 20 Sep 1995, *SMH 7014* (AGUAT, PTIS)*; along old

road from Los Encuentros to Totonicapán, 2 km W from border of Departments Sololá/Totonicapán, 1:250,000-scale map ND 15-8, 14°51.6'N, 91°13.7'W, 3260 m, 12 Oct 1995, *SMH 7046* (AGUAT, PTIS, WAG)*; along old road from Los Encuentros to Totonicapán, 4 km W of border of Departments Sololá/Totonicapán, 1:250,000-scale map ND 15-8, 14°52.6'N, 91°13.7'W, 3220 m, 12 Oct 1995, *SMH 7048* (AGUAT, PTIS, WAG)*; along old road from Los Encuentros to Totonicapán, 7.5 km W of border of Departments Sololá/Totonicapán, 1:250,000-scale map ND 15-8, 14°52.9'N, 91°14.8'W, 3220 m, 12 Oct 1995, *SMH 7049* (AGUAT)*; 7.3 km E of town square of Totonicapán, 4.8 km from old road to Santa Cruz del Quiché, old road to los Encuentros, ca 200 m uphill (S) of road, 1:250,000-scale map ND 15-8, 14°54.8'N, 91°19.1'W, 3180 m, 17 Oct 1995, *SMV 7055* (AGUAT, PTIS, WAG)*; 12.4 km E of Totonicapán, 9.9 km E from deviation of road to Santa Cruz del Quiché, old road to Los Encuentros, 1:250,000-scale map ND 15-8, 14°54.4'N, 91°17.7'W, 3150 m, 27 Oct 1995, *SMV 7075* (AGUAT, PTIS)*.

Solanum clarum and *S. morelliforme* were classified by Hawkes (1990) in the ser. *Bulbocastana* (also containing *S. bulbocastanum*) and the monotypic ser. *Morelliformia* Hawkes, based on floral, reproductive, serological, and ecological differences (ser. *Bulbocastana* terrestrial, ser. *Morelliformia* epiphytic). Our collections showed *S. clarum* to most commonly grow on the ground in moss, in shaded epiphytic like conditions, and occasionally as an epiphyte. Based on chloroplast DNA data, *S. clarum* and *S. morelliforme* are united as sister taxa, and *S. bulbocastanum* and *S. clarum* divided into distinct clades (Spooner and Sytsma, 1992). Other reproductive and cytological characters supporting *S. clarum* and *S. morelliforme* as sister taxa are summarized in Spooner and Sytsma (1992).

Solanum demissum Lindl., J. Hort. Soc. London 3: 68. 1848.

TYPE: cultivated in the gardens of the Royal Horticultural Society from tubers sent by C. A. Uhde from MEXICO, location unknown, 8000-9000 ft, ca. 1846-1847, C. A. Uhde 5 p. p. (holotype: CGE [photos: LL, NY, US]; isotype: MPU).

Solanum alpicum Standl. and Steyerl., Field Mus. Nat. Hist., Bot. Ser. 23: 232. 1947. TYPE: GUATEMALA. Huehuetenango: Cerro Chimal, summit of Sierra de los Cuchumatanes, 3700-3800 m, 8 Aug 1942, *Steyermark 50303* (holotype: F [photo: LL, PTIS]).

Plants terrestrial, a basal rosette when growing in open rocky grazed areas, to erect to 6 dm tall when growing in pro-

tected or shady conditions; stems 1-3 mm wide at base, green to purple, simple to branched; leaves odd pinnate, nearly glabrous to finely pubescent above and below, blades 2.5-15 cm long, 1.5-10 cm wide, petioles 1-5 cm long; 2-4 lateral leaflet pairs, ovate to elliptical, apex obtuse to acute, base rounded to cuneate, sessile to subsessile; 0-10 interjected leaflets, ovate, sessile to subsessile; terminal leaflet larger than the laterals, ovate to elliptical, apex acute to obtuse, base rounded to cuneate; pseudostipular leaves auriculate, 1-5 cm long; inflorescence pseudoterminal and lateral, with 5-10 flowers; pedicel 3-15 mm long; calyx 4-8 mm long, lobes 3-5 mm long, acute; corolla white to purple, or white above and purple below, rotate with short acumens, 1.5-1.3 cm in diameter; filaments 1-1.5 mm long, anthers 2-4.5 mm long, cordate at base; style equaling or exceeding stamens by 2 mm; fruits globose to ovoid, rounded at tip, 1-2.5 cm in diameter, medium to deep green. Chromosome number: $2n = 6x = 72$.

Distribution (Figure 8) and **Ecology**—*Solanum demissum* grows from 2250-3800 m in pine or juniper forests, or in rocky open pastures. It varies tremendously in size and habit, with plants growing in open grazed areas smaller.

Additional specimens examined: GUATEMALA. **Huehuetenango**: Sierra de los Cuchumatanes, at edge of Llano de Tierra Blanca, near trail to Todos Santos from Llanos de San Miguel near Chimal, 5 km W of km 311, Ruta Nacional 9 N, 3595 m, 5 Aug 1959, *Beaman 3100* (LL, MSC); Sierra de los Cuchumatanes, slopes of Cerro Chimal, 28 mi from Huehuetenango, 3500 m, 30 Oct 1958, *Hawkes et al. 1779* (JGH); summit of Cerro Chimal, 28 mi from Huehuetenango, 3450 m, 30 Oct 1958, *Hawkes et al. 1780, 1781* (JGH); Sierra de los Cuchumatanes, slopes of Cerro Chimal, open place, 28 mi from Huehuetenango, 3500 m, 30 Oct 1958, *Hawkes et al. 1782* (JGH, PTIS)*; near Chimal, Sierra de los Cuchumatanes, 15 Sep 1941, *Johnston 1969* (F); between Yac and Todos Santos Cuchumatán, Todos Santos, 3660 m, 7 Aug 1977, *Smith 628* (F); 49 km N of town square of Huehuetenango, road diverting W of 9N to Chanchoc, 1:250,000-scale map ND 15-3, 15°33'N, 91°31'W, 3400 m, 16 Sep 1995, *SMH 7008* (AGUAT, PTIS, WAG)*; alpine areas in vicinity of Tunimá, Sierra de los Cuchumatanes, 3400-3500 m, 7 Jul 1942, *Steyermark 48369* (F); vicinity of Chimal, summit of Sierra de los Cuchumatanes, rocky limestone outcrops around entrance to cave, in shade, 3700-3750 m, 8 Aug 1942, *Steyermark 50247* (F, NY, US); Todos Santos, 3000 m, 8 Jun 1995, *Veliz and Veliz 95.4962* (BIGUA). **Sacatepéquez**: slopes of Volcán de Agua, above Santa María de Jesús, in trail, 2250-3000 m, 11 Feb 1939, *Standley 65276* (F). **Totonicapán**: Cerro El Chiché, 1 mi E of Totonicapán, road to Los

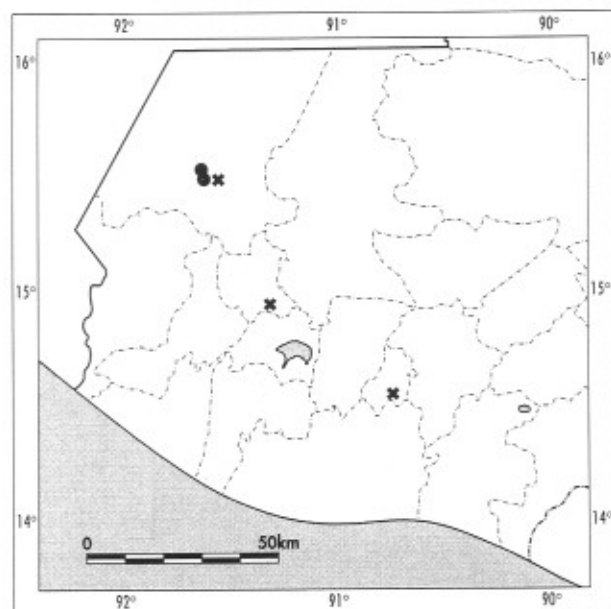


FIGURE 8

Geographic distribution of *Solanum demissum*. A circle designates an area represented by a germplasm collection; x designates an area without a germplasm collection.

Encuentros, shade of small cave, base of cliff, NW facing slope, 3350 m [note: our field work indicated 1 mi E is a typographical error for 10 mi E], 5 Nov 1958, *Hawkes et al.* 1887 (JGH, as note only [in database announced in Hawkes, 1997], no specimen); 7.3 km E of town square of Totonicapán, 4.8 km E from deviation of road to Santa Cruz del Quiché, old road to los Encuentros, 200 m uphill (S) of road, 1:250,000-scale map ND 15-8, 14°54.8'N, 91°19.1'W, 3180 m, 17 Oct 1995, SMV 7054 (AGUAT, PTIS, WAG).

This self-pollinated species readily sets fruit in nature and is one of the most common wild potato species in genebanks. All of these collections were from northern to southern Mexico, where the species is widespread, and there was only a single germplasm collection from Guatemala. It has been recorded from three general areas in the Departments of Huehuetenango, Sacatepéquez, and Totonicapán. We found it in Huehuetenango (SMH 7008) and Totonicapán (SMV 7054). The former was found only as an isolated and persistent fruit, but seeds from these led to a germplasm increase; the latter lacked flowers and fruits and the tubers we collected died before being increased.

Hawkes (1990) included *Solanum demissum* in series *Demissa* Buk., containing five other hexaploid species from Mexico. The morphological characters defining this series are unclear. Spooner *et al.* (1995) showed that on the basis of

morphology, the species is more similar to *S. albicans* (ser. *Acaulia* Juz.) from South America than to any other species in ser. *Demissa*.

Solanum morelliforme Bitter and G. Muench, Feddes Rept. Spec. Nov. Regni Veg. 12: 154. 1913. TYPE: MEXICO. Chiapas: Gueytepec [in a knothole], Feb 1912, G. Muench s. n. (holotype: not seen; this specimen cited in database backing up in Hawkes [1997] at GOET).

Plants typically epiphytic in pine or oak trees, rarely growing in rotting wood or moss at base of trees, erect to ascending, 1-6 dm tall; stems 2-3 mm wide at base, green to purple, simple to branched; leaves simple, finely pubescent above and below, elliptic to narrowly ovate, blades 3-14 cm long, 1.5-4.4 cm wide, apex acute to acuminate, base attenuate, petioles 1-4 cm long; pseudostipular leaves absent or linear to narrowly ovate, to 2 cm long; inflorescence pseudoterminal and lateral, with 7-15 flowers; pedicel 10-15 mm long; calyx 1.5-2 mm long, lobes 0.7-1 mm long, acute to mucronate; corolla deeply stellate, 15-20 mm in diameter, white to white tinged with purple; filaments 1-1.5 mm long, anthers 4-5.5 mm long, with basal rounded auricle; style about equaling stamens; fruits spherical, 5-8 mm in diameter, yellowish to green. Chromosome number: $2n = 2x = 24$.

Distribution (Figure 9) and **Ecology**—*Solanum morelliforme* grows from 1600-3000 m, almost exclusively as an epiphyte on horizontal branches of mature elm, pine, or oak trees. Occasionally, the species is found on the ground in the woods, in rotting wood of fallen trees, or in moss, both epiphytic-like conditions (see *S. clarum*, above). We were unable to locate the species at some previously documented localities that have been logged and reforested. Because the fruits and seeds of all members of sect. *Petota* are not wind borne, the species probably is distributed in the droppings of birds or tree-dwelling animals.

A collection first reported here extends the known distribution of *S. morelliforme* south to HONDURAS. Morazán: at Lapaterique river bank thicket, epiphyte on oak tree, 1600 m, 11 Aug 1961, *Molina and Molina* 26100 (F).

Additional specimens examined: GUATEMALA. **Chimaltenango:** above Tecpán, 2400 m, 10 Oct 1956, *Graham* 120 (LL, PTIS)*; above Tecpán, 2500 m, 11 Oct 1956, *Graham* 122 (LL); above Tecpán, 2400 m, Oct 1965, *Graham* S-743 (ENCB); Santa Elena (note: we cannot find this locality on map), 2400-2700 m, 18 Jul 1933, *Skutch* 441 (F); plains, 2200 m, near Tecpán, 3 Aug 1933, *Skutch* 525 (MICH, US). **Huehuetenango:** 11.8 km N of town square of Santa Eulalia, road to San Mateo Ixtatán, Road 9N, 50-250 m W of

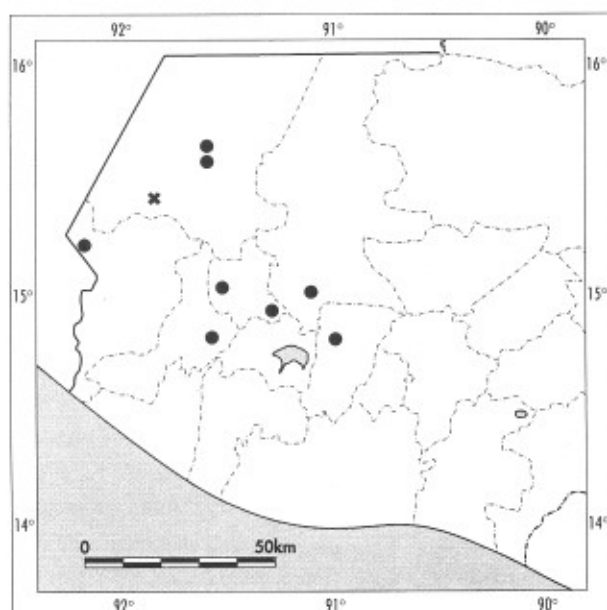


FIGURE 9
Geographic distribution of *Solanum morelliforme*. A circle designates an area represented by a germplasm collection; x designates an area without a germplasm collection.

road, 1:250,000-scale map ND 15-4, 15°46.0'N, 91°30.3'W, 3050 m, 17 Sep 1995, *SMH 7009* (AGUAT, PTIS, WAG)*; 9 km W of town square of Santa Eulalia, and 2 km S of junction of road to San Mateo Ixtatán and road to San Sebastián Coatán, walk 500 m up to near top of Cerro Chemalito, W-facing side, Rt 9N, 1:250,000-scale map ND 15-3, 15°43.9'N, 91°30.2'W, 2930 m, 26 Oct 1995, *SMV 7069* (AGUAT, PTIS, WAG)*; Cerro Pixpax, above San Ildefonso Ixtahuacán, forested summit, 1600-2800 m, 15 Aug 1942, *Steiermark 50558* (F [photos: F, GH, LL, NY, US], NY, US). **Quezaltenango:** above Quezaltenango to south off road to Retalhuleu, 2500 m, 6 Oct 1956, *Graham 111* (LL, US); 5 km SW of Quezaltenango, lower slopes of Volcán Santa María, Bajo, 2550 m, 1 Nov 1958, *Hawkes et al. 1805* (JGH, PTIS, US)*, *1809* (C, JGH, PTIS, US)*. **Quiché:** 5 mi S of Chichicastenango, Rt 15, 2300 m, 29 Oct 1958, *Hawkes et al. 1731* (JGH, PTIS, US)*. **San Marcos:** 4 hours hike SW of town of Tacaná, towards village of San Rafael, SW slope descending to San Rafael, 1:250,000-scale map ND 15-3, 15°08'N, 92°07'W, 2900 m, 25 Sep 1995, *SMH 7030* (AGUAT, PTIS, WAG)*; **Totonicapán:** 48 km on road from Quezaltenango to Huehuetenango, 3000 m, 31 Oct 1958, *Hawkes et al. 1802* (C, JGH); 7.3 km E of town square of Totonicapán, 1.9 km from deviation of road to Santa Cruz del Quiché, old road to

Los Encuentros, 1:250,000-scale map ND 15-8, 14°55.3'N, 91°19.9'W, 2960 m, 15 Sep 1995, *SMH 7005* (AGUAT, PTIS, WAG)*; along old road N of Quezaltenango, going through Buenebaj to Cael, 1 km S of intersection of this road and new road from Cael to Pan-American Highway, ca 4 km E of Cael, 1:250,000-scale map ND 15-3, 15°03.8'N, 91°33.9'W, 3010 m, 20 Sep 1995 *SMH 7013* (AGUAT, PTIS, WAG)*; 6.5 km E of town square of Totonicapán, along road to Santa Cruz del Quiché, ca 100 m E of junction of road to Santa María Chiquimula, ca 100 m N of road, 1:250,000-scale map ND 15-8, 14°55.6'N, 91°20.3'W, 2810 m, 15 Sep 1995, *SMH 7004* (AGUAT, BIGUA, F, PTIS, WAG)*.

Habitat Destruction and its Effect on Wild Potato Populations in Guatemala

Guatemala has changed considerably since the many collections of wild potatoes in the 1940's and 1950's. Our expedition searched most of the known populations. Many populations now apparently are extirpated due to habitat destruction. Much of the primary forest is being cut for firewood, structural timbers, and clearing for agriculture, and logging is a common practice in almost all of the primary forests we visited. In many areas, forests harboring wild potatoes are now reduced to small isolated stands, surrounded by cleared and grazed areas.

Population has nearly doubled in Guatemala from 4.3 million persons in 1964 (Dirección General de Estadística, 1971), to an official count of 8.3 million in 1994 (Instituto Nacional de Estadística, 1995), or a more realistic estimate of slightly over 10 million in 1994 (UNICEF, 1994). The median number of children each Guatemalan woman is projected to have during the years 1995-2000 is 4.9, resulting in an estimated population by the year 2000 of 12 million (UNICEF, 1994). Sixty-two percent of Guatemala's population is rural, and 76% of the population live below the poverty line (UNICEF, 1994), placing growing needs on the use of Guatemala's remaining primary forests that harbor wild potatoes.

Deforestation has accelerated rapidly in Guatemala. In 1978-1988, the average deforestation was 60,000 hectares per year (Ministerio de Agricultura, Ganadería y Alimentación, Dirección General de Bosques y Vida Silvestre, 1994). Sixty-two percent of this wood is lost to forest fires, 35% is used for domestic firewood, and 2% is used for industrial purposes, including domestic house construction and export. Twenty-three percent of deforestation occurs in coniferous forests (Ministerio de Agricultura, Ganadería y Alimentación,

Dirección General de Bosques y Vida Silvestre, 1994), concentrated in the uplands of western Guatemala where wild potatoes grow. Another growing cause of deforestation in Guatemala is attack by a bark boring beetle *Dendroctonus* spp. that is killing entire stands of pine forests, especially the upland pine *Pinus rudis*. The most severe attacks are in the upland western Departments of Huehuetenango, Totonicapán, Quetzaltenango, Sololá, and San Marcos (Instituto Nacional Forestal, 1982).

Any prediction of the survival of Guatemalan wild potatoes can only be a rough guess, based on observation of areas where potatoes now grow, their disappearance in recently disturbed areas, and a guess of how many natural areas will remain in the future. *Solanum morelliforme* usually grows in large trees, and is probably the most susceptible to disappearance by logging. *Solanum clarum* usually grows only in the shade of large trees among moss or pine needles, and is readily eaten by grazing animals. *Solanum agrimonifolium* grows in much more disturbed habitats, but almost always in areas of recently cleared primary forests in deep, moist, organic soils, and it also is readily eaten by grazing animals. *Solanum bulbocastanum* grows among shrubs of dry grazed areas, and is probably the least susceptible to elimination. Natural areas are disappearing rapidly, and some of our collections will be the last available for some areas.

Recommended Areas for Future Collecting in Guatemala

We focused collecting in areas where potatoes previously have been collected but that lacked germplasm collections. We additionally searched areas with appropriate elevations for wild potatoes but without any records for them. These included three mountains in the Departments of Guatemala, Jalapa, and Chimaltenango with elevations from 2000-3000 m (labeled on Figure 3 as areas 2-4), but we found no wild potatoes there. These three localities had some mesic and relatively undisturbed sites with much epiphytic vegetation apparently ideal for the growth of *S. agrimonifolium* and *S. morelliforme*. Because we devoted only one day each to these areas, it is possible we overlooked wild potatoes there.

Our 43 new collections, and the 16 prior collections of Graham and Hawkes (Table 1), provide good germplasm representation for all the species in Guatemala regarding numbers of populations and geographic coverage (Figs. 5-9, Table 1). Consequently, future potato germplasm collecting in Central America should be conducted in less collected countries,

such as Costa Rica (conducted in 1996, paper in progress), Honduras, and Panama.

If wild potato collecting is done again in Guatemala, we suggest the following areas that we did not explore to expand geographic coverage:

1. Political instability prevented us from exploring the three volcanoes south of Lago Atitlán in the Department of Sololá with elevations from 2995-3537 m (Volcán Atitlán, Volcán San Pedro, Volcán Tolimán). There are no records there, but these may be rich areas for any of the five species known for Guatemala.

2. Political instability also prevented us from exploring the far eastern part of the Sierra de los Cuchumatanes, in the Department of El Quiché, north of the road from Río Blanco to Uspatán, with some elevations over 2700 m.

3. The mountains in the extreme southwestern portion of the Sierra de los Cuchumatanes, in the Department of Huehuetenango, north of Cuilco.

4. The extreme northern portion of the Sierra de los Cuchumatanes, in the Department of Huehuetenango, north of San Mateo Ixtatán.

5. The Sierra de las Minas in the eastern part of the Department of El Progreso, and the western part of the Department of Zacapa, where the sierra is highest. We spent two days searching unsuccessfully for *S. agrimonifolium* (Steyermark 43672) north of the town of Jute de La Cobana (see above), and there were many appropriate habitats for this species there.

6. *Solanum bulbocastanum* grows in much drier sites than the other Guatemalan species, and our collecting experience shows it to persist in some grazed areas. The species probably is under-collected because it is inconspicuous. In Guatemala, the species occurs from 1350-2300 m (Table 1), and it may occur in dry regions at these elevations, present in many places in southern Guatemala.

Recommended Areas for In-situ Preserves for Wild Potatoes in Guatemala

Two areas are notable for the concentration of wild potatoes and some remaining natural areas: 1) The Cumbre de María Tecún in the Department of Totonicapán (Figure 3), and 2) scattered areas in the Sierra de los Cuchumatanes (Figure 2). Both harbor populations of all of Guatemala's wild potato species except *S. bulbocastanum*. Both areas are listed in Guatemala's protected areas law (Ley de Areas Protegidas, Decreto 4-89) to have official protection under this law but lacking practical enforcement until it is formally studied, and given a push for protection.

TABLE 1.—Numbers and distribution of germplasm of the five species of wild potatoes from Guatemala.

Species	Accessions from Mexico before the expedition	Accessions from Guatemala before the expedition: (division by Department) ¹	Total current Guatemalan accessions (division by Department) ¹	Elevations of occurrence in Guatemala
<i>Solanum agrimonifolium</i>	3	6: 3 (H), 1 (SM), 1 (T), 1 (Qe)	19: 2 (C), 8 (H), 2 (Qe), 4 (SM), 1 (So), 2 (T)	1600-3800 m
<i>S. bulbocastanum</i>	40 ²	1 (H)	7: 3(B), 4 (H)	1350-2300 m
<i>S. clarum</i>	1	4: 1 (So), 3 (T)	21: 7 (H), 3 (SM), 1 (So), 10 (T)	2900-3800 m
<i>S. demissum</i>	140	1 (H)	2 (H)	2250-3800 m
<i>S. morelliforme</i>	8	4: 1 (C), 2 (Qe), 1 (Qi)	10: 1 (C), 2 (Qe), 2 (H), 1 (Qi), 1 (SM), 3 (T)	1600-3050m

¹Department abbreviations are: Baja Verapaz (B), Chimaltenango (C), Guatemala (G), Huehuetenango (H), El Progreso (P), Quezaltenango (Qe), Quiché (Qi), San Marcos (SM), Sacatepéquez (Sa), Sololá (So), Totonicapán (T).

²Does not include the nine accessions collected in Mexico by Rodríguez *et al.* (1995) that are still in U.S. quarantine.

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