Examination of Species Boundaries of Solanum series Demissa and Potentially Related Species in series Acaulia and series Tuberosa (sect. Petota)

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ABSTRACT. Species boundaries were assessed by phenetic analyses of morphological data for *Solanum* sect. *Petota* series *Demissa*: *S. brachycarpum*, *S. demissum*, *S. guerreroense*, *S. hougasii*, *S. iopetalum*, and *S. schenckii*. These six hexaploid ($2n = 6x = 72$) wild potato species grow in Mexico and Guatemala and constitute all the taxa of series *Demissa* except three pentaploid hybrids involving crosses with species from other series. We also analyzed two species, *S. albicans* (series *Acaulia*) and *S. verrucosum* (series *Tuberosa*), that are morphologically very similar to some members of series *Demissa*. We chose these species because *S. verrucosum* has been hypothesized to be a progenitor in the hybrid origin of all species in series *Demissa*, and because *S. albicans* is very similar to *S. demissum*. The results show that *S. albicans*, *S. brachycarpum*, *S. demissum*, *S. schenckii*, and *S. verrucosum* are supported by multivariate analyses, but are inconclusive regarding species boundaries of the rare taxa *S. hougasii*, *S. guerreroense*, and *S. iopetalum*, and more collections are needed to resolve their taxonomic status. Extensive overlap of species-specific character states shows the difficulty of the preparation of keys, diagnosis of taxa, and cladistic analyses in this group. The results also show that *S. demissum* is phenetically more similar to *S. albicans* than to other species in series *Demissa* and that *S. verrucosum* is similar to *S. schenckii*, and they question the assignment of these species into series.

Solanum L. sect. *Petota* Dumort., the potato and its wild relatives, is distributed from the southwestern United States to southern Chile, with a concentration of diversity in the Andes. The latest comprehensive taxonomic treatment of the group (Hawkes 1990) recognizes 232 species, partitioned into 21 series, but two of these series form a separate clade and are best treated as separate sections; *Etuberosum* (Buk. and Kameraz) A. Child, *Lycopersicum* (Mill.) Wettst., and *Juglandifolium* (Rydb.) A. Child (Child 1990; Spooner et al. 1993). There are several disagreements regarding the number of species and their assignment in series throughout sect. *Petota* (Spooner and Sytsma 1992; Spooner and van den Berg 1992a).

Our study examined species boundaries of all six hexaploid taxa in *Solanum* series *Demissa* Juz. and two morphologically similar species from two other series: *S. albicans* (Ochoa) Ochoa (series *Acaulia* Juz.) and *S. verrucosum* Schltdl. [series *Tuberosa* (Rydb.) Hawkes]. We chose these species because *S. verrucosum* has been hypothesized to be a progenitor in the hybrid origin of all species in series *Demissa* (Spooner and Sytsma 1992), and because *S. albicans* is very

TABLE 1. Taxonomic rank and assignment of species to series for the hexaploid species in *Solanum* series *Demissum*, *S. verrucosum*, and *S. albicans*, according to the classification of Hawkes (1990). [a] Series abbreviations after Hawkes (1990): ACA = series *Acaulia* Juz. 1959; CON = series *Conicibaccata* Bitter 1912; DMS = series *Demissa* Buk. 1959; TUB = series *Tuberosa* (Rydb.) Hawkes 1944; VRR = series *Verrucosa* nomen nudum. Series *Acaulia* and *Tuberosa* were treated as series before their valid publication dates. [b] Originally described as *S. oxycarpum* var. *brachycarpum* (Correll 1950), Correll (1952) raised to species rank. [c] Synonymized under *S. iopetalum*. [d] Correll (1952) synonymized series *Demissa* under series *Tuberosa*. [e] Originally described as *S. verrucosum* var. *spectabilis* (Correll 1952); Correll (1958) raised to species rank; a new name was required because of the preexisting name *S. spectabile* (Stuedel 1841). [f] Originally described as *S. verrucosum* var. *iopetalum* (Bitter 1912); Hawkes (1944) raised to species rank. [g] Synonymized under *S. verrucosum*. [h] Not treated; publication apparently not seen by author. [i] Treated as *S. verrucosum* var. *iopetalum*. [j] Nomen dubium; type not seen, possibly destroyed. [k] The identity of this species was unclear until Flores Crespo (1968) relocated the species at the type locality; Hawkes (1990) designated a neotype. [l] Out of the geographical range of these treatments.

	Authors, assignment to series[a]							
Taxon, publication date of basionym	Rydberg 1924	Bukasov 1939	Hawkes 1944	Correll 1952	Correll 1962; Flores Crespo 1966	Hawkes 1963, 1966, 1978	Bukasov 1978	Hawkes 1990
S. brachycarpum, 1950[b]				CON	DMS	—[c]	DMS	DMS
S. demissum, 1848	TUB	DMS	DMS	TUB[d]	DMS	DMS	DMS	DMS
S. guerreroense, 1952				CON	DMS	DMS	DMS	DMS
S. hougasii, 1958[e]					DMS	DMS	DMS	DMS
S. iopetalum, 1912[f]	—[g]	—[h]	TUB	TUB[i]	DMS	DMS	DMS	DMS
S. schenckii, 1912[j]	—[h]	—[h]	—[k]	—[k]	CON	—[k]	—[h]	DMS
S. verrucosum, 1841	TUB	DMS	DMS	TUB	DMS	DMS	VRR	TUB
S. albicans, 1960	—[l]	ACA	ACA	—[l]	ACA	ACA	ACA	ACA

similar to *S. demissum* Lindley. We based our study entirely on the morphological criteria of prior taxonomists, and for the purposes of this study we adopt the morphological species concept.

***Classifications of Series* Demissa *and* S. verrucosum.** As circumscribed by Hawkes (1990), series *Demissa* contains six hexaploid ($2n = 6x = 72$) taxa [*S. brachycarpum* (Correll) Correll, *S. demissum* Lindley, *S. guerreroense* Correll, *S. hougasii* Correll, *S. iopetalum* (Bitter) Hawkes, *S. schenckii* Bitter], and three pentaploid ($2n = 5x = 60$) recent hybrid taxa [*S.* × *edinense* Berth. ssp. *edinense*, *S.* × *edinense* ssp. *salamanii* (Hawkes) Hawkes, and *S.* × *semidemissum* Juz.; Ugent 1967; Hawkes 1990]. Species of series *Demissa* grow from northern Mexico to central Guatemala in disturbed habitats along roadsides, in recent clearings, and among bushes, from 1,600 to 3,800 m (Hawkes 1990; Spooner et al. 1991). *Solanum demissum* grows in the highest elevations, up to 3,800 m, with the others growing to no more than 3,350 m. Species within the series differ by characters of habit, leaf shape and dissection, calyx and corolla shapes, and fruit size and surface patterns (Hawkes 1990).

Solanum series *Demissa* has been the subject of much disagreement in sect. *Petota* regarding the assignment of species to series (Spooner and Sytsma 1992). Species placed by Hawkes (1990) in series *Demissa* also have been placed in series *Conicibaccata* Bitter and series *Tuberosa* by Rydberg (1924), Hawkes (1944), Correll (1952, 1962), and Flores Crespo (1966; Table 1).

Solanum verrucosum ($2n = 2x = 24$) grows from northern Mexico to central Mexico, in habitats like those of species in series *Demissa*, from 2,400 to 3,200 m (Hawkes 1990; Spooner et al. 1991). It has been placed variously in series *Demissa*, series *Tuberosa*, and "series Verrucosa" (Table 1). Hawkes (1990) classified *S. verrucosum* in series *Tuberosa*, containing about 100 other South American species, ranging in ploidy levels from diploid to hexaploid. By morphological, distributional, crossability, and genomic evidence, *S. verrucosum* has been hypothesized to be a parent in the polyploid origin of all members of series *Demissa* (Marks 1955, 1965; Hawkes 1956, 1990).

***Classifications of* S. albicans.** *Solanum albicans* ($2n = 6x = 72$), and *S. acaule* Bitter ($2n = 4x = 48$) were placed by Hawkes (1990) as the only representatives of series *Acaulia* (except for two locally-distributed named hybrids). *Sola-*

TABLE 2. Genome designations for *S. acaule*, *S. albicans*, *S. verrucosum*, series *Longipedicellata*, and series *Demissa*. [1] Hawkes (1966, 1978, 1990) designated series *Demissa* as A_1A_4(B,C,D,etc.), slightly modified from his earlier designation as $A_1A_4B_{(1-4)}$. [2] Modified from his earlier designations for series *Demissa* as D_1D_2V, with V homologous to *S. verrucosum* (Kawakami and Matsubayashi 1957), AC_1C_2 (Matsubayashi 1981), and $A^dC_1C_2$ (Matsubayashi 1984).

Author	*S. acaule*	*S. albicans*	*S. verrucosum*	series *Longipedicellata*	series *Demissa*
Marks 1955			A		$ABB^{(1-4)}$
Hawkes 1990[1]	A_2A_3		A_1	A_4B	A_1A_4(B,C,D,etc.)
Irikura 1976	AB^a		A	AB^s	AB^sB^d
Ramanna and Hermsen 1979			A_1		A_1A_4B
Matsubayashi 1991[2]	AA^a	AA^aX	A	AB	$ADD^{(bdgs)}$

num albicans grows from central Ecuador to central Peru, from 3,000 to 4,750 m (Ochoa 1962, 1990; Hawkes 1990; Spooner et al. 1991), while *S. acaule* grows from central Peru to northwestern Argentina, from 2,950 to 4,650 m (Ochoa 1962; Hawkes 1990). A report of *S. acaule* from central Ecuador (Spooner et al. 1992b) may be *S. albicans*. The somatic chromosome number obtained from root tips grown from seeds of this collection (*Spooner, Castillo, and López 5070* = PI 561642) is here first reported as $2n = 72$, typical of *S. albicans*, not *S. acaule*. Unlike the extensive disagreement regarding assignment of *S. brachycarpum*, *S. demissum*, *S. guerreroense*, *S. iopetalum*, *S. schenckii*, and *S. verrucosum* to series (Table 1), all workers (e.g., Correll 1962; Bukasov 1978; Ugent 1981; Gorbatenko 1989; Hawkes 1990) have placed *S. acaule* and *S. albicans* in series *Acaulia*.

***Morphological Criteria Used to Define Series* Acaulia, *Series* Demissa, *and Series* Tuberosa.** These three series are not clearly distinct. Bukasov and Kameraz (1959) distinguished series *Acaulia* from *Demissa* by its obtuse vs. acuminate leaf apices, shorter peduncles, indistinct articulation, and smaller corollas, and placed *S. verrucosum* in series *Demissa*. Correll (1962) followed Bukasov and Kameraz (1959), but he added new characters on position of the articulation of the pedicels and corolla shapes: series *Acaulia* with high articulation and series *Demissa* with medial to above medial articulation; series *Acaulia* with rotate corollas and series *Demissa* with rotate-pentagonal to rotate-stellate corollas. Hawkes (1990) placed *S. verrucosum* in series *Tuberosa*. He distinguished series *Acaulia* from *Demissa* by its higher pedicel articulation (when present), and series *Tuberosa* from both series by corollas with larger acumens.

***Biological Criteria Used to Define Series* Acaulia, *Series* Demissa, *and Series* Tuberosa.** Most interspecific crosses within series *Demissa* exhibit greatly reduced pollen fertility, lowered chiasmata frequencies, or meiotic pairing frequencies approaching 24 bivalents and 24 univalents, in contrast to the 36 bivalents of the parents (Swaminathan and Hougas 1954; Marks 1955, 1965; Hawkes 1956). These results have been interpreted as the presence of two genomes in common, one different. Hawkes (1956, 1966) and Marks (1965) used these data to speculate that members of series *Demissa* are of hybrid origin between *S. verrucosum* and Mexican and Central American tetraploids in series *Conicibaccata* or series *Longipedicellata* Juz., and that the species are isolated by crossing barriers (Table 2). An exception to the above type of pairing resulted from a cross between *S. guerreroense* and *S. iopetalum*. The F_1 showed a high frequency of bivalents and was interpreted to suggest synonymy between these taxa (Marks 1965). These studies, however, lacked intraspecific crossing controls and replications and should be interpreted with caution.

Hawkes postulated two divergent A genomes for *S. acaule* relative to series *Demissa*, while Irikura (1976) and Matsubayashi (1991) postulated homology of only one genome of *S. acaule* to series *Demissa*. The only genome designation for *S. albicans* was presented by Matsubayashi (1991) who postulated its origin from hybridization of *S. acaule* and an unknown species (Table 2). There are no published results for meiotic analyses of a cross between *S. albicans* and *S. demissum*.

Purpose of the Present Study. This study is an outgrowth of previous field collections in Mexico where problems were encountered in identification of specimens in series *Demissa*

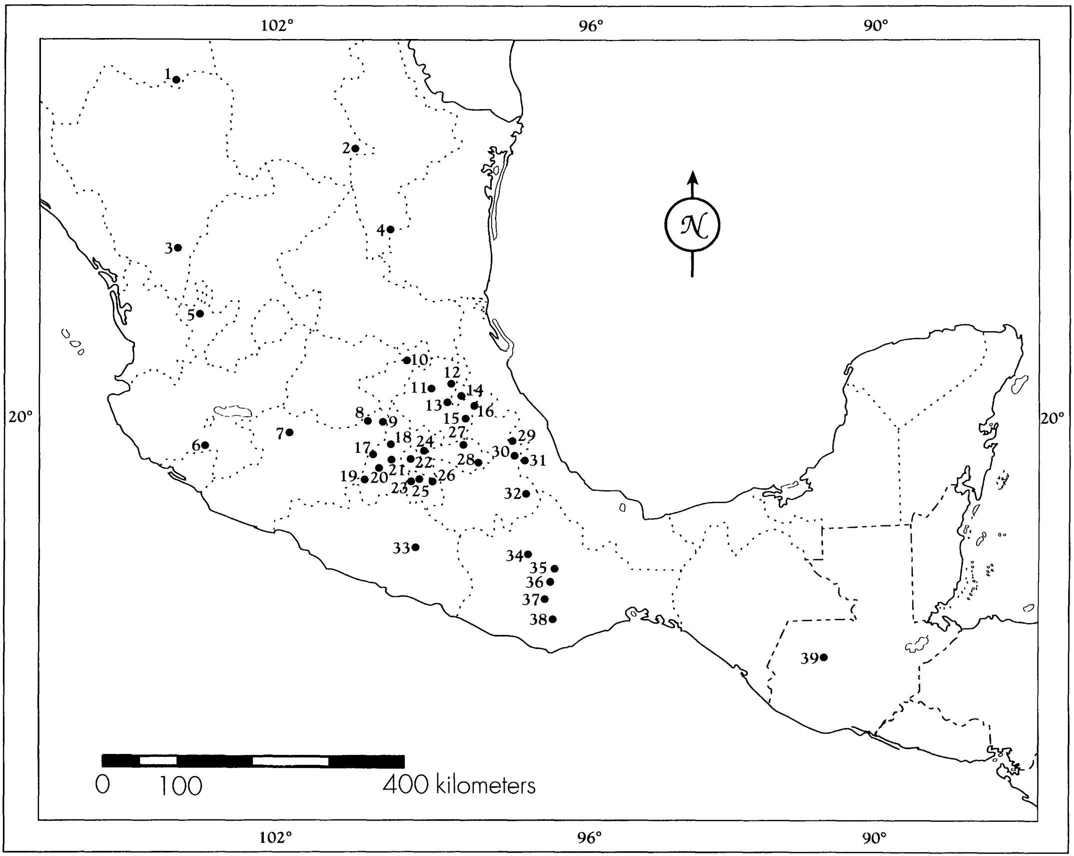


FIG. 1. Map showing the 39 generalized areas of the accessions of *Solanum brachycarpum, S. demissum, S. guerreroense, S. hougasii, S. iopetalum, S. schenckii,* and *S. verrucosum* examined in this study. Six accessions of *S. albicans* from Peru also were included. Numbers are cited as generalized map areas in Table 3 and as map locations in Fig. 3.

(Spooner et al. 1991) and understanding the cladistic relationships with chloroplast DNA data of series *Demissa* and other Mexican and Central American members of sect. *Petota* (Spooner and Sytsma 1992). We pose the following question in this study: What is the pattern of character state variation, and does this provide morphological support for the six hexaploid species of series *Demissa* and the morphologically similar species *S. albicans* (series *Acaulia*) and *S. verrucosum* (series *Tuberosa*)?

MATERIALS AND METHODS

Species. We analyzed a total of 98 accessions of *S. albicans* (6), *S. brachycarpum* (30), *S. demissum* (26), *S. guerreroense* (2), *S. hougasii* (4), *S. iopetalum* (2), *S. schenckii* (12), *S. verrucosum* (16; Table 3). All accessions were from the National Research Support Program-6 (NRSP-6; formerly the Inter-Regional Potato Introduction Project, IR-1). The examined accessions represent the maximum geographic distribution available from the NRSP-6 collection (Fig. 1). These accessions represent nearly the entire geographic ranges for these species as last mapped by Hawkes (1966), and sometimes even exceed these distributions. The low numbers of accessions examined of *S. guerreroense, S. hougasii,* and *S. iopetalum* indicate the rarity of these species (Hawkes 1966). Vouchers are deposited at the NRSP-6 herbarium in Sturgeon Bay, Wisconsin (PTIS, to appear in Edition 9 *Index Herbariorum*).

Identifications of these accessions have been provided in past years by visiting taxonomists during on-site visits to NRSP-6 to inspect living representatives in field plots (Hanneman 1989).

TABLE 3. Accessions examined. Vouchers are deposited at the herbarium of the National Research Support Program-6, Sturgeon Bay, Wisconsin. [1] alb = *S. albicans*, bcp = *S. brachycarpum*, dms = *S. demissum*, grr = *S. guerreroense*, hou = *S. hougasii*, iop = *S. iopetalum*, snk = *S. schenckii*, ver = *S. verrucosum*. [2] Generalized map areas (Fig. 1). [3] United States Department of Agriculture Plant Introduction Numbers. [4] Collector unknown; accession from the Instituto Nacional de Investigaciones Forestales y Agropecuarias, México. [5] Collector unknown; accession from the Commonwealth Potato Collection, Scotland.

Accession number and taxon[1]	Area[2]	PI[3]	Collector	Locality
1 bcp	6	275179	*Hawkes 1547*	Mexico. Jalisco: Nevado de Colima, W side of Tranquitas; 3200 m.
2 bcp	6	558426	*Spooner et al. 4133*	Mexico. Jalisco: on microwave tower road E of Sayulapa, on Alista-La Mesa and El Fresnito Road; 3.3 km from top of microwave tower of Víboras; 2700 m, 19°37'N, 103°35'W.
3 bcp	8	558419	*Spooner et al. 4060*	Mexico. Michoacán: 20 km N of road from Rt. 15, just W of Cd. Hidalgo, N past San Pedro Jacuaro to Ucareo-Quérendaro Rd., by Los Tejamaniles; 2700 m; 19°48'N, 100°39'W.
4 bcp	8	558420	*Spooner et al. 4065*	Mexico. Michoacán: 1 km N of Laguna Larga, on rd. N of Rt. 15, diverting just E of Cd. Hidalgo, past San Pedro Jacuaro, 17 km S of Ucareo-Quérendaro Rd.; 2750 m; 19°50'N, 100°40'W.
5 bcp	9	230459	*Hawkes 1043*	Mexico. Michoacán: near Zitácuaro, km 147 from México to Morelia; 2920 m.
6 bcp	9	558414	*Spooner et al. 4040*	Mexico. Michoacán: on slope on N side of Rt. 15, 11 km E of Macho de Agua (E of Zitácuaro), 0.3 km W of México-Michoacán border; 2820 m; 10°27'N, 100°12'W.
7 bcp	9	558415	*Spooner et al. 4260*	Mexico. Michoacán: on slope on N side of Rt. 15, 11 km E of Macho de Agua (E of Zitácuaro), 0.3 km W of México-Michoacán border; 2820 m; 10°27'N, 100°12'W.
8 bcp	9	558416	*Spooner et al. 4049*	Mexico. Michoacán: ca. 2 km S of Rt. 15, on gravel road beginning just E of Macho de Agua; 2850 m; 19°25'N, 100°13'W.
9 bcp	9	558417	*Spooner et al. 4050*	Mexico. Michoacán: SE side of Cerro El Cacique, ca. 6.5 km E of main road S from Zitácuaro; 2300 m; 19°23'N, 100°18'W.
10 bcp	9	558418	*Spooner et al. 4052*	Mexico. Michoacán: SE side of Cerro El Cacique, ca. 7 km E of main road S from Zitácuaro; 2350 m; 19°23'N, 100°18'W.
11 bcp	11	498022	*Tarn et al. 58*	Mexico. Hidalgo: N of Ixmiquilpan, 18 km N of Nequeteje, between El Defay and Agua Florida; 2630 m.
12 bcp	12	498020	*Tarn et al. 53*	Mexico. Hidalgo: from Hwy. 105, Pachuca to Zacualtipán, 5.5 km along the track towards Huayacocotla; 1950 m.
13 bcp	14	498021	*Tarn et al. 55*	Mexico. Veracruz: ca. 2.2 km S of Huayacocotla on the road to Tulancingo; 2300 m.
14 bcp	15	243344	*Graham 93*	Mexico. Hidalgo: San Mateo, 20 km E of Tulancingo.
15 bcp	20	545769	*Tarn et al. 206*	Mexico. México: from Toluca-Temascaltepec, Hwy. 130, along Rt. 130 at ca. 30 km, immediately before Paredones; 2880 m; 19°02'N, 99°53'W.

TABLE 3. Continued.

Accession number and taxon[1]	Area[2]	PI[3]	Collector	Locality
16 bcp	20	545771	*Tarn et al. 295*	Mexico. México: from Toluca–Temascaltepec Hwy. 130 along Rt. 3 at ca. km 30, immediately before Paredones (ca. 0.5 km NE of Paredones; 2900 m; 19°02'N, 99°53'W.
17 bcp	20	545772	*Tarn et al. 296*	Mexico. México: road from Toluca to Sultapec, ca. 5 km from Paredones towards Tequisquiapan; 2730 m; 19°02'N, 99°55'W.
18 bcp	20	558409	*Spooner et al. 4021*	Mexico. Jalisco: near microwave tower road to top of Nevado de Colima, 16 km from beginning of this road which begins ca. 0.5 km SE of La Mesa y el Fresnito; 2710 m; 19°35'N, 103°34'W.
19 bcp	20	558412	*Spooner et al. 4026*	Mexico. México: ca. 200 m N of road from Rt. 130 (134) to Valle de Bravo, 2 km E of San Ramón; 2450 m; 19°10'N, 100°01'W.
20 bcp	20	558413	*Spooner et al. 4255*	Mexico. México: ca. 200 m N of road from Rt. 130 (134) to Valle de Bravo, 2 km E of San Ramón; 2450 m; 19°10'N, 100°01'W.
21 bcp	20	558436	*Spooner et al. 4024b*	Mexico. México: on S side of road from Rt. 130 (134) to Valle de Bravo, 2 km E of San Ramón; 2450 m; 19°10'N, 100°01'W.
22 bcp	32	498025	*Tarn et al. 181*	Mexico. Puebla: road from Tehuacán to Oaxaca turning off at Coxcatlán towards Zoquitlán, 22 km along this road, 1 km past La Griega towards Coyomeapa; 2640 m.
23 bcp	32	545716	*Tarn et al. 183*	Mexico. Puebla: road from Tehuacán to Oaxaca, turning off at Coxcatlán, 24 km towards Zoquitlán, ca. 3 km past La Griega towards Coyomea; 2640 m.
24 bcp	37	558430	*Spooner et al. 4192*	Mexico. Oaxaca: 22.5 km (by posted km signs) W of main road in Zaachila, on dirt road toward Santa Inés del Monte; 2600 m; 16°57'N, 96°51'W.
25 bcp	38	498024	*Tarn et al. 170*	Mexico. Oaxaca: El Manzanal, km 144 from Oaxaca towards Puerto Angel, Rt. 175; 2780 m.
26 bcp	38	498251	*Ochoa 14146*	Mexico. Oaxaca: Manzanal; 2250 m.
27 bcp	38	545770	*Tarn et al. 275*	Mexico. Oaxaca: road from Oaxaca to Puerto Angel, Hwy. 175 at Puerto Angel, km 144; 2710 m; 16°08'N, 96°30'W.
28 bcp	38	558427	*Spooner et al. 4166*	Mexico. Oaxaca: along W side of Rt. 175, S of Miahuatlán de Porfirio Díaz, 10 km S of S end of San Miguel Suchixtepec; 2250 m; 16°04'N, 96°30'W.
29 bcp	38	558428	*Spooner et al. 4167*	Mexico. Oaxaca: along E side of Rt. 175, S of Miahuatlán de Porfirio Díaz, 2.8 km S of S end of San Miguel Suchixtepec; 2260 m; 16°05'N, 96°27'W.
30 bcp	38	558429	*Spooner et al. 4172*	Mexico. Oaxaca: along E side of Rt. 175, S of Miahuatlán de Porfirio Díaz, ca. 20

TABLE 3. Continued.

Accession number and taxon[1]	Area[2]	PI[3]	Collector	Locality
				km N of San Miguel Suchixtepec, at km 131.1 (by posted road signs); 2390 m; 16°13′N, 96°32′W.
31 dms	1	275207	*Hawkes 1296*	Mexico. Chihuahua: Municipio Balleza, near Vergel, by the side of a small lake, not far from the fire tower; 2600 m.
32 dms	3	498012	*Tarn et al. 123*	Mexico. Durango: S of Durango, 72 km along the track from La Ferreria, just before La Flor; 2800 m.
33 dms	8	558392	*Spooner et al. 4064*	Mexico. Michoacán: 21 km N of Rt. 15, at jct of road N of Rt. 15 just W of Cd. Hidalgo, past San Pedro Jacuaro and road to steam wells at Los Azufres; 2750 m; 19°49′N, 100°39′W.
34 dms	9	558390	*Spooner et al. 4045*	Mexico. México: at Rancho La Piedra, at top of microwave tower rd, N of Rt. 15, just E of México-Michoacán border; 3000 m; 19°29′N, 100°12′W.
35 dms	9	558391	*Spooner et al. 4062*	Mexico. Michoacán: 20 km N of rd from Rt. 15 just W of Cd. Hidalgo, N past San Pedro Jacuaro to Ucareo-Queréndaro Rd., by Los Tejamanilles; 2700 m; 19°48′N, 100°39′W.
36 dms	12	498014	*Tarn et al. 167*	Mexico. México: road between Santa Marta and Huitzilac, near Lagunas de Zempoala, ca. 13 km from Tres Marias; 2900 m.
37 dms	13	161168	*Correll 14243*	Mexico. Hidalgo: Real del Monte.
38 dms	17	338618	*Rowe 1*	Mexico. México/Michoacán: Mexico City-Morelia road, on the border of México and Michoacán states; 2800 m.
39 dms	18	498016	*Tarn et al. 192*	Mexico. México: Cerro Jocotitlán between Toluca and San Juan del Río, road up to the microwave station, 4 km N above the village of Jocotitlán; 2960 m.
40 dms	19	275208	*Hawkes 1601*	Mexico. México: 32.5 km from the main Toluca-Morelia road, towards Valle de Bravo from Toluca; 2900 m.
41 dms	20	558386	*Spooner et al. 4010*	Mexico. México: near junction of road S of Rt. 130 and spur road that goes directly to the top of Nevado de Toluca; 3465 m; 19°09′N, 99°48′W.
42 dms	20	558387	*Spooner et al. 4017*	Mexico. México: on road on top of Nevado de Toluca, E of Rt. 3, S of Rt. 120; 3800 m; 19°08′N, 99°47′W.
43 dms	20	558388	*Spooner et al. 4041*	Mexico. Michoacán: on slope on N side of Rt. 15, 11 km E of Macho de Agua (E of Zitácuaro), 0.3 km W of México-Michoacán border; 2820 m; 19°27′N, 100°12′W.
44 dms	20	558482	*Spooner et al. 4019*	Mexico. México: along roadside, near jct. of road S of Rt. 130 and spur road that goes directly to the top of Nevado de Toluca; 3465 m; 19°09′N, 99°48′W.
45 dms	21	545767	*Tarn et al. 304*	Mexico. México: 44 km along the road

TABLE 3. Continued.

Accession number and taxon[1]	Area[2]	PI[3]	Collector	Locality
				from Ixtlahuaca to Mexico City, slope of Cerro Cañada Honda; 3370 m; 19°31'N, 99°29'W.
46 dms	22	186551	*Hawkes 1077*	Mexico. Distrito Federal: Ajusco, between the railway station and the village; 2825 m.
47 dms	23	161366	*Correll 14283*	Mexico. Morelos: in the mountains above Tres Cumbres.
48 dms	23	160229	*Correll 14219*	Mexico. Distrito Federal: upper slopes of Mt. Ajusco.
49 dms	24	161151	*Correll 14209b*	Mexico. México: Molina de Flores.
50 dms	26	160208	*Correll 14212*	Mexico. México: volcanoes road above Amecameca, slope of Mt. Popocatapetl.
51 dms	27	161686	*Correll 14435*	Mexico. Tlaxcala: above San Agustín Tlaxco, Mt. Cuyaguen.
52 dms	28	275206	*Hawkes 1295*	Mexico. Chihuahua: Municipio Balleza, near Vergel, by the side of a small lake, not far from the fire tower; 2850 m.
53 dms	29	545764	*Tarn et al. 289*	Mexico. Veracruz: Perote, grounds of Perote Experimental Station; 2400 m; 19°34'N, 97°15'W.
54 dms	31	161367	*Correll 14286*	Mexico. Puebla: above Tesmalaquilla, on the upper slopes of Pico de Orizaba.
55 dms	35	545763	*Tarn et al. 271*	Mexico. Oaxaca: 21.8 km N of Ixtlán de Juárez on Hwy. 175 to Tuxtepec; 2870 m; 17°28'N, 96°30'W.
56 dms	39	275211	*Hawkes 1782*	Guatemala. Huehuetanango: Sierra de los Cuchumatanes, 28 mi from Huehuetenango; 3500 m.
57 grr	6	161727	*Correll 14324a*	Mexico. Jalisco: near Sayulapa, slopes of Volcán Nevado.
58 grr	33	161730	*Correll 14410a*	Mexico. Guerrero: mountains N of Chilpancingo.
59 hou	6	161174	*Correll 14253*	Mexico. Michoacán: 7 mi above Opopeo.
60 hou	6	161726	*Correll 14340*	Mexico. Jalisco: near El Isote, upper slopes of Volcán Nevado.
61 hou	6	558402	*Spooner et al. 4124*	Mexico. Jalisco: near microwave tower road to top of Nevado de Colima, 24 km from beginning of this road which begins 0.5 km SE of La Mesa y el Fresnito; 3135 m; 19°34'N, 103°35'W.
62 hou	10	558422	*Spooner et al. 4116*	Mexico. Jalisco: At San Isidro, on road from Llanitos to Cruz de Garibay, S of Cd. Guzmán, 7.4 km N of Alotitlán, on W side of road by streamside; 1870 m; 19°19'N, 103°17'W.
63 iop	16	275181	*Hawkes 1654*	Mexico. Puebla: 2–3 km from Honey, on the path N to Tehuatlán; 1950 m.
64 iop	16	275182	*Hawkes 1655*	Mexico. Puebla: 2–3 km from Honey, on the path N to Tehuatlán; 1950 m.
65 snk	38	498250	*Ochoa 14140*	Mexico. Oaxaca: between La Cumbre and Yavila; 2750 m.
66 snk	10	498041	*Tarn et al. 107*	Mexico. Querétaro: Hwy. 120, Jalpan to San Juan del Río, just beyond Madroño,

TABLE 3. Continued.

Accession number and taxon[1]	Area[2]	PI[3]	Collector	Locality
				ca. 4 km NW along the track to the microwave tower; 2850 m.
67 snk	10	498049	*Tarn et al. 104*	Mexico. Querétaro: from Hwy. 120, Jalpan to San Juan del Río, beyond Madroño; 2900 m.
68 snk	30	545733	*Tarn et al. 185*	Mexico. Puebla: on road from Orizaba to Puebla, km 107.8 from Puebla, ca. 40 km from Orizaba; 2600 m.
69 snk	30	545790	*Tarn et al. 283*	Mexico. Puebla: ca. km 228 on road from Mexico City to Orizaba, 5–6 km after the Esperanza railway station; 2470 m; 18°51'N, 97°21'W.
70 snk	30	545791	*Tarn et al. 290*	Mexico. Puebla: Esperanza, going 9 km SE, ca. 2–3 km past Boca del Monte station on the road to Cumbre de Aguila; 2470 m; 18°50'N, 97°20'W.
71 snk	32	498042	*Tarn et al. 179*	Mexico. Puebla: Tehuacán–Oaxaca Rd., turning at Coxcatlán towards Zoquitlán, 21 km along this road, La Griega, to where the road divides to Zoquitlán and Coyomeapa; 2660 m.
72 snk	34	498280	*Ochoa 14137*	Mexico. Oaxaca: vicinity of Tlaxiaco; 2750 m.
73 snk	35	275261	*Hawkes 1724*	Mexico. Oaxaca: Sierra de Juárez, 14 mi on the Oaxaca–Ixtlán road past the divergence from the Oaxaca Tehuantepec Hwy.; 2700 m.
74 snk	35	558457	*Spooner et al. 4199*	Mexico. Oaxaca: along E side of Rt. 175, 17.9 km N of entrance to Ixtlán de Juárez, ca. 0.5 km S of posted km 137 sign; 2720 m; 17°27'N, 96°30'W.
75 snk	36	558456	*Spooner et al. 4194*	Mexico. Oaxaca: in clearing in shrubs around microwave tower, 1.9 km SE of Rt. 175 N of Oaxaca City, on road to Yuvilla, ca. 16 km (by air) NNE of outskirts of Oaxaca City; 2690 m; 17°09'N, 96°36'W.
76 snk	?	498410	*INIFAP[4] 790*	No locality data provided.
77 ver	2	498061	*Tarn et al. 161*	Mexico. Coahuila: road from Saltillo towards E, between Jame and Cienega de La Purísima, at the highest part of the road; 2720 m.
78 ver	4	498060	*Tarn et al. 94*	Mexico. Nuevo León: from Doctor Arroyo to Galeana road, 39 km NE along the track to Zaragoza; 2620 m.
79 ver	4	545745	*Tarn et al. 93*	Mexico. Nuevo León: from Doctor Arroyo to Galeana road, 35 km NE along the track to Zaragoza, just beyond Puerto El Pino; 2620 m.
80 ver	4	545746	*Tarn et al. 96*	Mexico. Nuevo León: from Doctor Arroyo to Galeana road, 60 km NE, just beyond La Encantada, on the track to Zaragoza; 2160 m.
81 ver	5	558483	*Spooner et al. 4100*	Mexico. Jalisco: along Volcán Tequila mi-

TABLE 3. Continued.

Accession number and taxon[1]	Area[2]	PI[3]	Collector	Locality
				crowave tower Rd., S of town of Tequila, 17.3 km S of railroad tracks at base of Volcán Tequila; 2600 m; 20°48'N, 103°50'W.
82 ver	5	558484	*Spooner et al. 4102*	Mexico. Jalisco: along Volcán Tequila microwave tower Rd., S of town of Tequila, on top of the highermost of the two microwave tower roads on the top of Volcán Tequila; 2700 m; 20°48'N, 103°51'W.
83 ver	6	558485	*Spooner et al. 4122*	Mexico. Jalisco: new microwave tower road to the top of Nevado de Colima, 16.5 km from the beginning of this road which begins 0.5 km SE of La Mesa y el Fresnito, near waterfall; 2725 m; 19°35'N, 103°34'W.
84 ver	6	558487	*Spooner et al. 4125*	Mexico. Jalisco: near microwave tower road to top of Nevado de Colima, 24 km from beginning of this road which begins 0.5 km SE of La Mesa y El Fresnito; 3475 m; 19°34'N, 103°35'W.
85 ver	6	558488	*Spooner et al. 4127*	Mexico. Jalisco: near microwave tower road to top of Nevado de Colima, 24 km from beginning of this road which begins 0.5 km SE of La Mesa y El Fresnito; 1.5 km W of Estación de Vigilancia; 3410 m; 19°34'N, 31°35'W.
86 ver	13	275260	*Hawkes 1658*	Mexico. Hidalgo: Pachuca, Real del Monte, in the woods above the town; 2700 m.
87 ver	18	498062	*Tarn et al. 193*	Mexico. México: Cerro Jocotitlán, road up to the microwave station, 6 km above the village of Jocotitlán; 3060 m.
88 ver	18	545747	*Tarn et al. 197*	Mexico. México: Cerro Jocotitlán, road up to the microwave station, 8 km above the village of Jocotitlán; 3200 m.
89 ver	20	545810	*Tarn et al. 199*	Mexico. México: from Toluca–Temascaltepec, Hwy. 130, along Rt. 3 from La Puerta towards Sultepec at km 14, just W of the road; 3440 m; 19°07'N, 99°49'W.
90 ver	25	545811	*Tarn et al. 251*	Mexico. México: along Hwy. 142 from Oaxtepec to Xochimilco, 6.1 km N of Morelos–México state boundary, 3 km W towards CICITEC and 1 km along track; 2930 m; 19°06'N, 98°57'W.
91 ver	26	310966	*Ugent 1289*	Mexico. Puebla: Popocatepetl; 2338 m.
92 ver	28	195170	*CPC[5] 54.3*	Mexico. Tlaxcala: Mt. Malinche, San Diego de Pinar.
93 alb	P[3]	266381	*Correll P863*	Peru. Cajamarca: 3.5 mi from the entrance to Hacienda Porcón; 3300 m.
94 alb	P	365306	*Ochoa S-21*	Peru. Lima: Pomaca, between Oyón and Catatambo; 3650 m.
95 alb	P	365376	*Ochoa 2713*	Peru. La Libertad: Santiago de Cucho, San José farm.
96 alb	P	498203	*Ochoa 13014*	Peru. Ancash: Recuay, between Ticapampa and Conococha; 4100 m.

TABLE 3. Continued.

Accession number and taxon[1]	Area[2]	PI[3]	Collector	Locality
97 alb	P	310986	*Hawkes 2427*	Peru.
98 alb	P	365305	*Ochoa S-17*	Peru. Apurimac: Purguania road from Coinora to Huanipaca; 3400 m.

Some taxa here determined as *S. brachycarpum* appear in the inventory of tuber-bearing *Solanum* species (Bamberg and Martin 1993) under *S. iopetalum.*

Seeds were planted in a greenhouse in early May, seedlings were transferred to peat pots in late May, and six individuals per accession were transplanted together in rows in a field plot at Sturgeon Bay in early June. Hand pollinations were done in the field to ensure fruit set for all species except *S. albicans* and *S. demissum,* which set abundant fruit without such treatment.

Data Measurement. We measured 32 quantitative and five qualitative characters (Table 4) when the plants were in full bloom in August, or in September for fruits. The first four plants per row were measured for all characters, and means of the four plants were used as representative of each accession (thus the accession is the Operational Taxonomic Unit, OTU). Measurements of leaves were made on the largest leaf per plant. Corolla colors were measured with the aid of the R.H.S. Colour Charts (Royal Horticultural Society 1986), based on recommendations of Tucker et al. (1991), and scored as 1–10 from white (color 155D), to violet-blues (colors 92D, 92C, 92B, 92A), to violets (colors 84A, 83D, 83C, 83B, 83A). When there was variation in colors (e.g., stripes, mottling), we scored the predominant color. Verrucose (raised dot) fruit surfaces have been used to distinguish *S. verrucosum* (Correll 1962) and *S. schenckii* and *S. verrucosum* (Hawkes 1990). These and other species examined sometimes had white verrucose dots on a green background, but these more commonly graded into flat white dots on a green background. We scored all gradations of raised to flat white dots equally to assess this character.

Data Analysis. Each character was analyzed for its mean, range, standard deviation, and significance (within species) by one-way ANOVA in Minitab (Ryan et al. 1985), using the means of four individuals per accession. Dendrograms including all accessions were produced by NTSYS-pc®, version 1.70 (Rohlf 1992). Averages for each character were standardized (STAND) and similarity matrices (in SIMINT), using average taxonomic distance (DIST), Euclidean distance (EUCLID), Manhattan distance (MANHAT), and product-moment correlation (CORR) were generated. Clustering was performed using the unweighted pair-group method (UPGMA) in SAHN. Cophenetic correlation coefficients (COPH, in MXCOMP) were used to measure distortion between the similarity matrices and the resultant four phenograms (Rohlf and Sokal 1981; Sokal 1986). Principal components analysis (PCA), canonical discriminate analysis (CDA), and stepwise discriminate analysis (SDA) were performed by SAS Version 6 (SAS Institute Inc. 1989) using PRINCOMP, CANDISC, and STEPDISC, using the means of four individuals per accession.

RESULTS

Character State Variation. One-way ANOVA demonstrated that all characters examined (Table 4) differed significantly (at least 0.05 level) between one or more species (Fig. 2). There was much variation in ranges of character states among series *Demissa, S. albicans,* and *S. verrucosum.* Because of the low numbers of available accessions for *S. guerreroense, S. hougasii,* and *S. iopetalum,* conclusions regarding these species are tentative.

There were few absolute species-specific ranges of character state variation, with exceptions or near exceptions for the following (Table 4; Fig. 2): *Solanum albicans* had the highest leaf length/width ratios (character 3). *Solanum hougasii* had the longest peduncles (19) and lightest corollas (31). *Solanum iopetalum* had the darkest adaxial surfaces of the corollas (31). Almost all, but not all, accessions of *S. verrucosum* had the margins of the corollas rolled (30).

However, trends in species-specific character states were more common. *Solanum albicans* gen-

TABLE 4. Characters used in the phenetic analysis of *Solanum* series *Demissa*, *S. verrucosum*, and *S. albicans*. All measurements for the quantitative characters are in mm. Character numbers correspond to those in Fig. 2.

Leaf characters

1. Leaf length. 2. Ratio: length from the widest point of the leaf to the leaf apex/length of leaf. 3. Ratio: leaf length/width. 4. Number of lateral leaflets. 5. Number of interjected leaflets. 6. Length of terminal leaflet petiolule. 7. Length of terminal leaflet lamina. 8. Ratio: length of terminal leaflet lamina from its widest point to apex/length of lamina. 9. Ratio: length of terminal leaflet lamina/lamina width. 10. Width of terminal leaflet from a point 5 mm below apex. 11. Length of most distal lateral leaflet petiolule. 12. Length of most distal lateral leaflet lamina. 13. Ratio: length from the widest point of the most distal lateral leaflet to the apex/length of lamina. 14. Ratio: most distal lateral leaflet length/width. 15. Width of most distal lateral leaflet from a point 5 mm below apex. 16. Width of basiscopic decurrent tissue of most distal lateral leaflet from a point on the petiole 5 mm basiscopic to the junction of the petiolule and petiole. 17. Ratio: length of most distal lateral leaflet/length of second-most distal lateral leaflet. 18. Ratio: second-most distal lateral leaflet length/width.

Floral characters (see Spooner and van den Berg 1992b) for illustrations of characters 26, 28, and 29.

19. Peduncle length. 20. Pedicel length. 21. Ratio: length of pedicel/length from base of pedicel to articulation. 22. Number of flowers per inflorescence. 23. Length of calyx lobe. 24. Width of calyx lobe. 25. Length of calyx acumen. 26. Radius of corolla. 27. Interpetalar tissue: entire (1), erose (2). 28. Ratio: radius of petal/radius to junction of petal lobes. 29. Ratio: width of petal lobe/length of petal lobe. 30. Margins or corolla: flat (1), rolled on top (adaxial) edges (2). 31. Adaxial corolla color (1 = white, through 10 = dark violet; see Materials and Methods). 32. Adaxial corolla color code (see 31) minus abaxial corolla code. 33. Length of stamen. 34. Length of style.

Fruit characters

35. Fruit surface pattern: green throughout (1), with white unconnected dots (2), with white dots, occasionally contiguous (3). 36. Ratio: length of fruit/width of fruit at its wider dimension. 37. Ratio: length of fruit/length of fruit from its widest point to the distal end of the fruit.

erally was distinguished by larger numbers of lateral leaflets (character 4), shorter terminal leaflet laminas (7), shorter distal lateral leaflet petiolules (11), longer pedicels (20), and narrower calyx lobes (24); *S. guerreroense* by more interjected leaflets (5) and more flowers per inflorescence (22); *S. hougasii* by less rotate corollas (29); and *S. schenckii* by fewer lateral (4) and interjected (5) leaflets, longer (23) and wider (24) calyx lobes, greater difference between adaxial and abaxial corolla colors (32), and more white dots on the fruits (35). *Solanum albicans* and *S. demissum* shared similar ranges of character states of more obtuse leaf apices (10), higher pedicel articulation (21), smaller corollas (26), shorter stamens (33), and shorter styles (34) (Table 4; Fig. 2).

Species Boundaries. Some, but not all, of the character states provided in the keys and species descriptions of taxonomists (Table 1) to distinguish taxa within series *Demissa* are supported by our data. Obtuse leaf apices (10) generally distinguish *S. demissum*, but with considerable overlap with *S. brachycarpum*. Decurrent lateral leaflets (16) distinguish *S. schenckii*, but do sometimes occur in other species. White corollas (31) help distinguish *S. hougasii*. Deep purple corollas (31) generally distinguish *S. iopetalum*.

Other characters used in the keys and species descriptions do not separate the taxa. "Verrucose" fruits (35) occur in all of the species and fail to distinguish consistently *S. schenckii* and *S. verrucosum*. There is no significant difference between the length of the first and second most distal lateral leaflets (17) used to distinguish *S. brachycarpum* from *S. iopetalum*. Although conical fruits (37) generally are present in *S. brachycarpum* and *S. iopetalum*, they often are ovoid, not conical, in *S. guerreroense* and *S. schenckii*.

Despite lack of specific individual characters to distinguish each species, phenetic analyses generally distinguish the taxa. The phenogram produced by CORR (Fig. 3) had the highest cophenetic correlation coefficient (0.82), only slightly higher than those produced by the other similarity (or dissimilarity) algorithms: DIST and EUCLID, 0.78; and MANHAT, 0.71. Rohlf (1992) stated that cophenetic correlations between 0.8 and 0.9 can be interpreted subjectively as good fits to the cluster analysis, and those between 0.7 and 0.8 as poor fits.

All phenograms produce similar results, but the CORR phenogram is presented and discussed because of its greatest cophenetic correlation coefficient. It separates most accessions of *S. brachycarpum*, *S. schenckii*, *S. verrucosum*, *S. albicans* with *S. demissum*, and *S. guerreroense* with *S. hougasii* (but with two accessions of *S. brachy-*

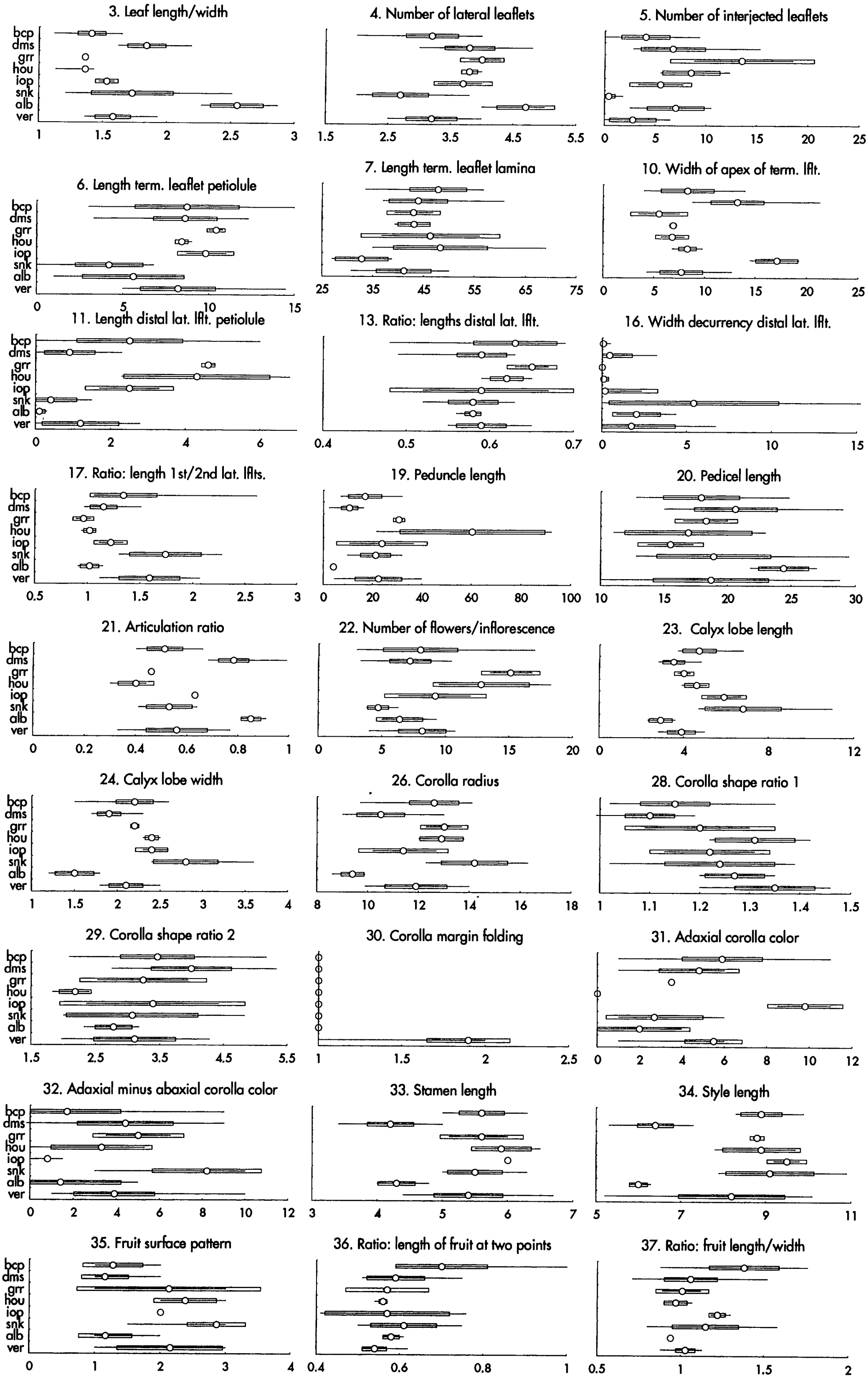

3. Leaf length/width
4. Number of lateral leaflets
5. Number of interjected leaflets
6. Length term. leaflet petiolule
7. Length term. leaflet lamina
10. Width of apex of term. lflt.
11. Length distal lat. lflt. petiolule
13. Ratio: lengths distal lat. lflt.
16. Width decurrency distal lat. lflt.
17. Ratio: length 1st/2nd lat. lflts.
19. Peduncle length
20. Pedicel length
21. Articulation ratio
22. Number of flowers/inflorescence
23. Calyx lobe length
24. Calyx lobe width
26. Corolla radius
28. Corolla shape ratio 1
29. Corolla shape ratio 2
30. Corolla margin folding
31. Adaxial corolla color
32. Adaxial minus abaxial corolla color
33. Stamen length
34. Style length
35. Fruit surface pattern
36. Ratio: length of fruit at two points
37. Ratio: fruit length/width

FIG. 2. Means, ranges, and one standard deviation of the mean for 27 of the 37 characters examined in this study showing the greatest differences between taxa. *Solanum albicans* = alb; bcp = *S. brachycarpum;* dms = *S. demissum;* grr = *S. guerreroense;* hou = *S. hougasii;* iop = *S. iopetalum;* snk = *S. schenckii;* ver = *S. verrucosum.*

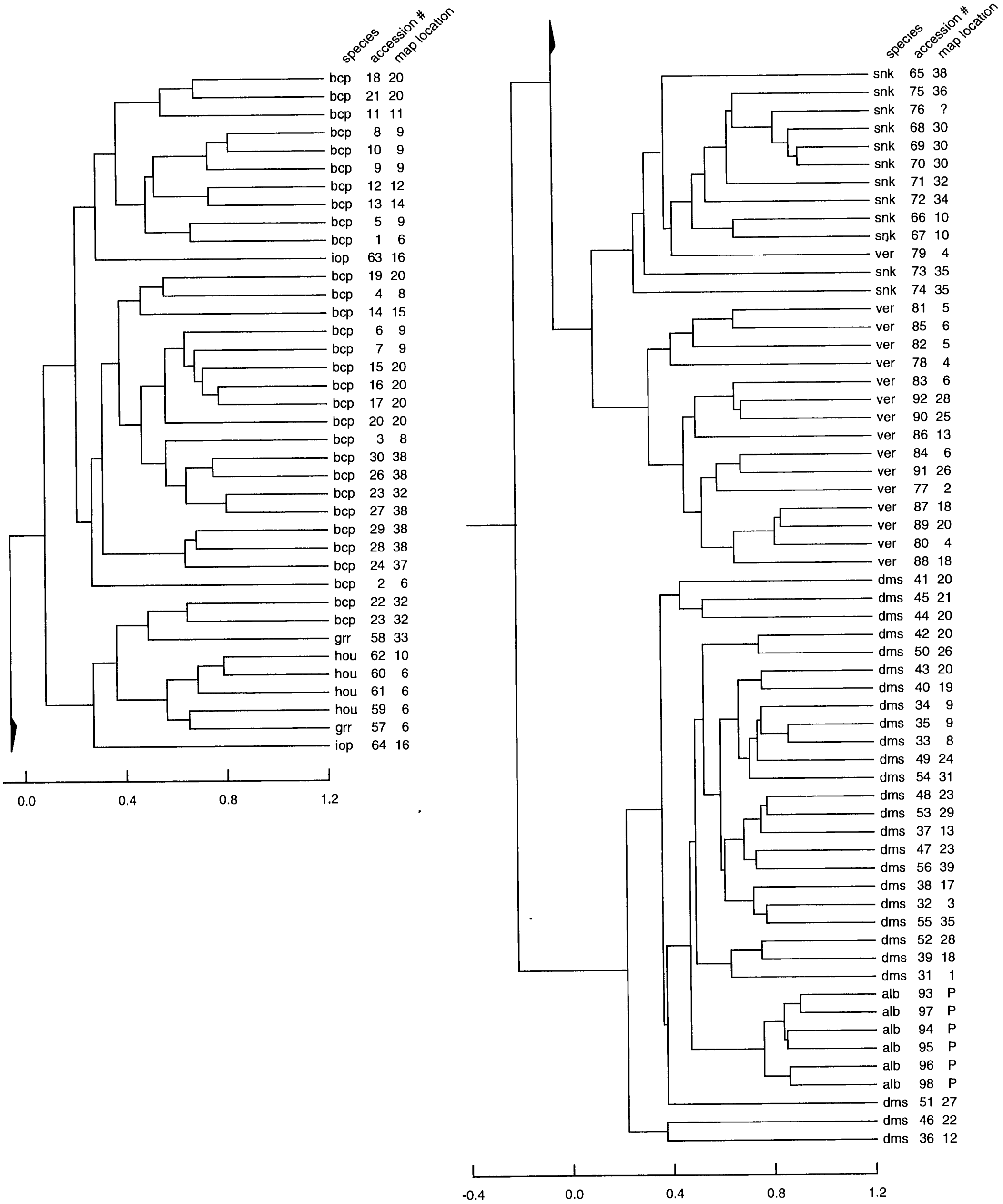


FIG. 3. UPGMA phenogram (CORR similarity option) based on 37 morphological characters (Table 4). P = Peru, unmapped in Fig. 1. Species codes as in Fig. 2, accession numbers as in Table 3.

carpum). The *S. albicans* with *S. demissum* cluster is on a separate branch from the rest of series *Demissa* with *S. verrucosum*. All accessions of *S. albicans* cluster together, but are embedded within the *S. demissum* cluster of the CORR phenogram (Fig. 3). However, *S. albicans* and *S. demissum* cluster separately, but on adjacent branches on the DIST and EUCLID phenograms (not shown). The two accessions of *S. iopetalum* do not cluster together, but instead are separated on the *S. brachycarpum* cluster and the *S. guerreroense* with *S. hougasii* cluster.

The results of the PCA are presented in Fig. 4. Principal components 1 and 2 account for 25.4% and 14.8% of the variation, respectively, for a total of 40.2%. The third principal component raised the total to 48.0% but did not change the overall pattern and is not presented. Principal component 1 is most highly influenced by the width of the terminal leaflet apex (character 10), position of pedicel articulation (21), radius of corolla (26), length of stamen (33), and length of style (34), and principal component 2 by number of interjected leaflets (5), length of petiolule of most distal lateral leaflet (11), length of most distal lateral leaflet lamina (12), width of decurrency of most distal lateral leaflet (16), and fruit surface pattern (35). The results of the PCA are similar to that of the CORR phenogram (Fig. 3) in showing *S. albicans* and *S. demissum* to be more similar to each other than to the other species examined, *S. verrucosum* and *S. schenckii* to cluster, and for *S. guerreroense, S. hougasii* and *S. iopetalum* to be similar to *S. brachycarpum.*

The CDA (Fig. 5) better separates taxa, and like both the CORR phenogram and PCA, clusters *S. albicans* closer to *S. demissum,* and clusters *S. brachycarpum* with *S. guerreroense* with *S. hougasii* with *S. iopetalum.* Unlike the CORR phenogram and PCA, *S. verrucosum* clusters separately. The following five most important characters in distinguishing species in the SDA, ranked from the most important first are: posture of margin of corolla (30), leaf length/width (3), width of calyx lobe (24), length of stamen (33), and length of peduncle (19). However, nearly all accessions of *S. verrucosum* have inrolled margins of the corolla, in contrast to all other accessions of all other species having flat (unrolled) margins. When character 30 is removed from the CDA analysis, the CDA analysis is similar to the results of the CORR phenogram and PCA.

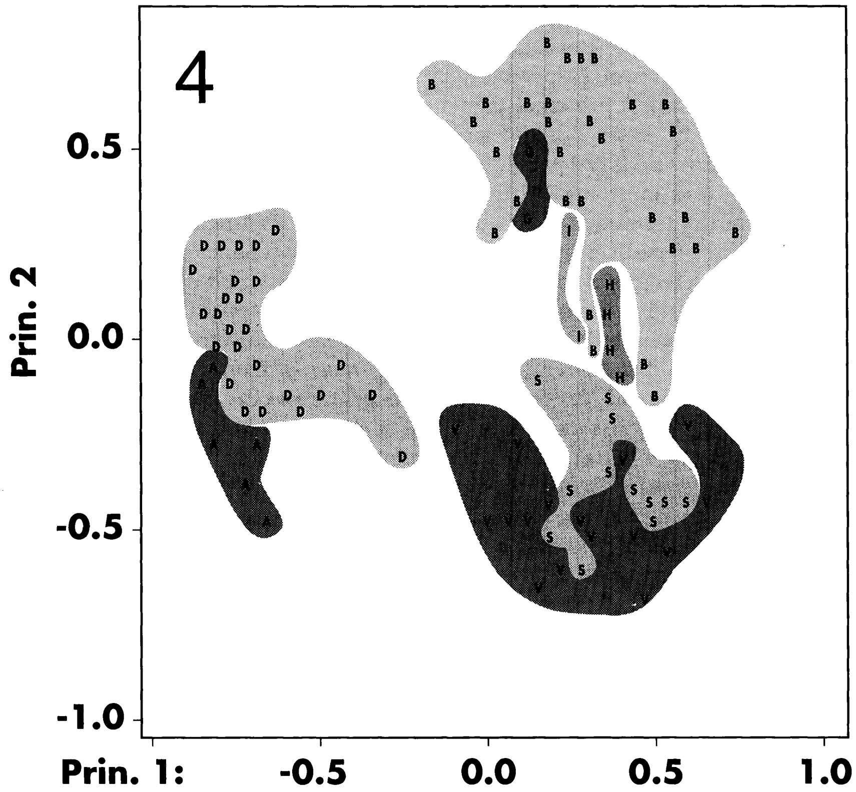
The data do not provide differences of character states to clearly distinguish members of series *Demissa* from *S. albicans* (series *Acaulia*) and *S. verrucosum* (series *Tuberosa*). The only characters Hawkes (1990) used to separate series *Tuberosa* from series *Acaulia* and series *Demissa* are longer corolla lobes and corolla acumens of series *Tuberosa.* Characters 28 and 29 provide independent measures of corolla shapes. *Solanum verrucosum* (series *Tuberosa*) is significantly different (p = 0.001) in character 28 from all other examined taxa. However, the values of *S. albicans* (series *Acaulia*) and *S. hougasii* (series *Demissa*) approach those of *S. verrucosum* (Fig. 2) more than do the other species. When *S. albicans, S. hougasii,* and *S. verrucosum* are compared to the remaining species, these two groups are similarly significantly different (p = 0.001). There is no significant difference in lengths of corolla lobes (character 29) of *S. verrucosum* from all other examined species. Therefore, corolla shapes do not separate all species of series *Demissa* from *S. albicans.* The CDA (Fig. 5) separates *S. verrucosum* from all other species. However, the posture of the corolla margin (character 30) is almost always inrolled in *S. verrucosum* and never inrolled in other species (Fig. 2). Character 30 most highly influences the CDA, suggesting that the phenetic separation of *S. verrucosum,* seen in the CDA, but not the CORR phenogram and PCA, is an artifact of this single character.

All keys and descriptions distinguish series *Acaulia* from series *Demissa* by the higher pedicel articulation of the former. *Solanum albicans* does have significantly higher pedicel articulation than any species of series *Demissa* (p = 0.001). However, *S. albicans* and *S. demissum* (series *Demissa*) are more similar to each other with regard to pedicel articulation than to all other members of series *Demissa* (p = 0.001), so pedicel articulation does not separate series *Demissa* from *S. albicans.*

DISCUSSION

Species Boundaries. Our results provide the first objective analyses of morphological differences of the constituent species of series *Demissa* and the morphologically similar taxa *S. albicans* and *S. verrucosum.* The combined phenetic results provide good support (but with much overlap of putative species-specific character states) for the separate recognition of *S. albicans, S. brachycarpum, S. demissum, S. schenckii,* and *S. verrucosum. Solanum verrucosum* clusters with *S. schenckii* and with all species of series *Demissa* except *S. demissum* on the CORR phenogram and the PCA, but separate from all other species on the CDA, based on the single character of the posture of the margin of the corolla. Otherwise, all phenetic results are concordant.

Because accessions of *S. guerreroense* and *S. iopetalum* are not clearly separated in any anal-



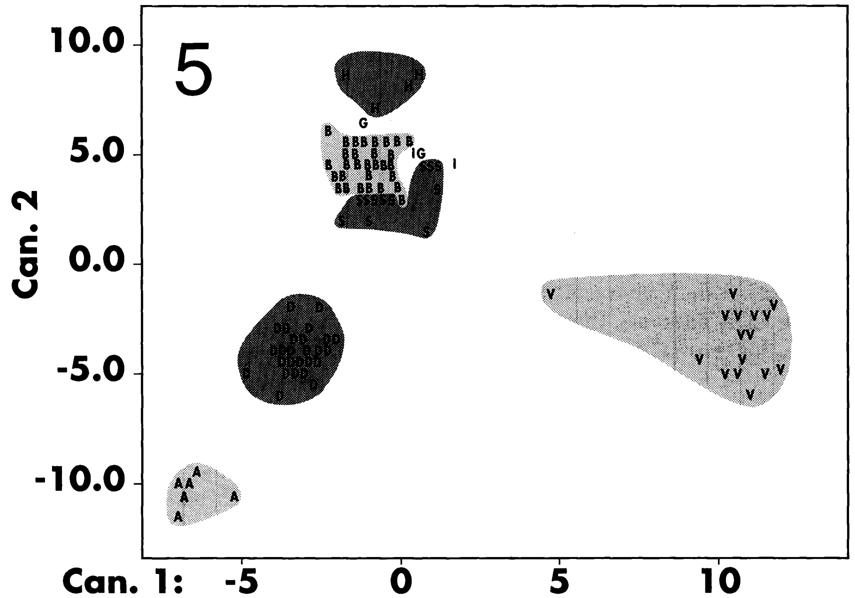


FIG. 4. Principal components analysis based on 37 morphological characters (Table 4). A = *S. albicans*, B = *S. brachycarpum*, D = *S. demissum*, G = *S. guerreroense*, H = *S. hougasii*, I = *S. iopetalum*, S = *S. schenckii*, and V = *S. verrucosum*.

ysis, their taxonomic status is unclear. Hawkes distinguished *S. guerreroense* from other species of series *Demissa* by its combination of conical fruits and well dissected leaves with many interjected leaflets. *Solanum guerreroense* generally has more interjected leaflets and more flowers per inflorescence, but is not distinguished by number of lateral leaflets and conical fruits. Hawkes (1990) distinguished *S. iopetalum* from the very similar *S. brachycarpum* by lateral leaflets decreasing in length proximally and by deep purple corollas. The leaflet difference (character 17, Fig. 2) fails to distinguish *S. iopetalum* from *S. brachycarpum* (and from *S. demissum*). Although both accessions of *S. iopetalum* have deep purple corollas, so do a very few accessions of *S. brachycarpum* (character 31). *Solanum hougasii* is somewhat more distinct in all analyses (Figs. 3–5). More field work in Mexico is needed to seek more specimens of the apparently rare species *S. guerreroense, S. hougasii,* and *S. iopetalum,* to help resolve their taxonomic status.

The extensive variation of putative species-specific character states in members of series *Demissa* and in *S. albicans* and *S. verrucosum* shows the difficulty of obtaining discrete character states useful for the practical taxonomic needs of keys and diagnoses of taxa. A similar pattern of extensive variation and overlapping character states occurs in the recognition of subspecies in the wild potato species *S. megistacrolobum* Bitter (Giannattasio and Spooner 1994a, b). Such a polythetic classification [grouping taxa that have the greatest number of shared features, no single feature of which is essential to group membership or is sufficient to make an organism a member the group (Sokal and Sneath 1963; Stuessy 1990)] may be the rule in sect. *Petota*. A similar pattern of character state variation occurs in many wild potato species from Bolivia. A comparison by Spooner et al. (1994) of recent taxonomic treatments of Bolivian wild potatoes by experienced taxonomists (Hawkes and Hjerting 1989; Ochoa 1990) showed that independent identifications of identical herbarium specimens differed in 20% of the cases. Such problems are common in sect. *Petota*. This lack of repeatability in identifications may occur with some of the taxa examined in this study because of broadly overlapping character states defining species. It suggests that some species boundaries have to be more broadly circumscribed.

Our results show the difficulty of performing cladistic analyses in these species based on morphological data. The only workable method to perform cladistic analyses in cases similar to the example shown in this study would be to divide quantitative data into ranges of variation as suggested by Chappill (1989), but such approaches are invalid (Farris 1990).

***Alternative Hypotheses of Relationships among Members of Series* Demissa, S. albicans, *and* S. verrucosum.** Our analysis examined all six hexaploid species of series *Demissa,* one species from series *Acaulia* (*S. albicans*), and one species from series *Tuberosa* (*S. verrucosum*). Because series *Tuberosa* comprises approximately 100 species, and series *Acaulia* two species, we cannot make definitive statements about the boundaries of these three series. Within the context of our study, however, *S. albicans* and *S. demissum* are more similar to each other than to the other species, and the rationale for assigning them to different series is unclear.

All species of series *Demissa* are hypothesized to have *S. verrucosum* as a parent, and *S. albicans* is believed to be of hybrid origin between *S. acaule* and another species (Marks 1955, 1965; Hawkes 1956, 1990; Matsubayashi 1991). Hybridization complicates the use of morphology to construct possible hybrid origins because hybrids often express individual character states from only one parent or show transgressive segregation (Rieseberg and Wendel 1993). Our study only reexamines species boundaries with the morphological criteria used by previous taxonomists (Table 1) and does not address possible hybrid origins. Our phenetic results suggest three alternative hypotheses for the relationships of these taxa.

HYPOTHESIS 1, CONVERGENCE. The morphological similarities of *S. demissum* (series *Demissa*) and *S. albicans* (series *Acaulia*) may be due to convergent evolution. In addition to the morphological characters grouping *S. albicans* and

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FIG. 5. Canonical discriminate analysis based on 37 morphological characters (Table 4). Species codes as in Fig. 4.

S. demissum, these species (and the morphologically similar *S. acaule*) grow in upland habitats periodically subjected to frosts. These morpho-ecological similarities were noted by many workers, and explained as convergences related to upland habitats (Correll 1962; Ugent 1981; Hawkes 1990; Ochoa 1990).

HYPOTHESIS 2, COMMON ANCESTOR. *Solanum acaule* is morphologically very similar to *S. albicans* and has been hypothesized to be a parent in its hybrid origin. *Solanum albicans* and *S. demissum* may both have *S. acaule* as a common ancestor. Our phenetic results cannot prove this cladistic alternative, and the difficulties of cladistic analyses of morphological data in this group are shown above. Our phenetic results can show only that *S. albicans* and *S. demissum* are more similar to each other morphologically than either is to all other species in series *Demissa* and *S. verrucosum,* to suggest that *S. acaule* may be the common ancestor. Long-distance dispersal of *S. acaule* may have occurred from South America to Mexico, with subsequent hybridization with *S. verrucosum* in Mexico and with another diploid species in South America (each contributing $2n$ gametes) to produce independently *S. demissum* and *S. albicans,* respectively.

HYPOTHESIS 3, PROGENITOR-DERIVATIVE RELATIONSHIP. The phenetic resemblance of *S. albicans* and *S. demissum* suggests that *S. albicans* may have evolved directly from *S. demissum,* or *S. demissum* from *S. albicans,* by long-distance dispersal and subsequent divergence of either species. Long-distance dispersal of *S. acaule* or *S. albicans* to Mexico, or *S. demissum* to South America (hypotheses 2 and 3) never has been considered (Correll 1962; Ugent 1981; Hawkes 1990; Ochoa 1990). However, two extant examples in sect. *Petota* show its potential. *Solanum fendleri* A. Gray is distributed from the southwestern United States to northwestern Mexico, with disjunct populations across the Gulf of California in the Laguna Mountains at the southern tip of Baja California Sur, Mexico (Spooner et al. 1991), ca. 220 km west of the mainland populations as mapped by Hawkes (1966). Similarly, *S. fernandezianum* Phil. is restricted to Masatierra Island in the Juan Fernández Archipelago, over 650 km west of its close relatives in sect. *Etuberosum* in Chile (Hawkes 1990). Although the distance between the southern distribution of *S. demissum* in Guatemala and the northern distribution of *S. acaule* in Ecuador is longer (ca. 1,300 km), the potential for long-distance dispersal is evident. *Solanum acaule, S. albicans, S. demissum,* and *S. fendleri,* like *S. fernandezianum,* not only are self-compatible, but set abundant seed without the apparent aid of pollinators (pers. obs.), suggesting that long-distance dispersal of single seeds could result in successful colonization. Also, the wide distribution of *S. acaule,* from Ecuador to northern Argentina, attests to its dispersal ability.

In summary, our results show extensive overlap of species specific character states in the constituent members of series *Demissa, S. albicans,* and *S. verrucosum.* They will be useful with other data to help determine species boundaries and the evolutionary history of series *Demissa* and its potential relatives. The results show the difficulty of cladistic analyses using morphology in this group, and question the assignment of species into series. Objective morphological and molecular studies are needed throughout the section to demonstrate patterns of character state variation, refine taxonomic interpretations, and test alternative hypotheses.

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