



**A Reexamination of Species Boundaries Between *Solanum megistacrolobum*
and *S. toralapanum* (*Solanum* sect. *Petota*, series *Megistacroloba*):
Morphological Data**

Robert B. Giannattasio; David M. Spooner

Systematic Botany, Vol. 19, No. 1 (Jan. - Mar., 1994), 89-105.

Stable URL:

<http://links.jstor.org/sici?sici=0363-6445%28199401%2F03%2919%3A1%3C89%3AAROSBB%3E2.0.CO%3B2-A>

Systematic Botany is currently published by American Society of Plant Taxonomists.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/aspt.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

A Reexamination of Species Boundaries between *Solanum megistacrolobum* and *S. toralapanum* (*Solanum* sect. *Petota*, series *Megistacroloba*): Morphological Data

ROBERT B. GIANNATTASIO and DAVID M. SPOONER¹

Vegetable Crops Research Unit, Agricultural Research Service, U.S.D.A.,
Department of Horticulture, University of Wisconsin, 1575 Linden Drive,
Madison, Wisconsin 53706-1590

¹Author for reprint requests

ABSTRACT. *Solanum megistacrolobum* and *S. toralapanum* are two phenetically similar wild potato (*Solanum* sect. *Petota*) species, classified in series *Megistacroloba*, that together are distributed from southern Peru to northwestern Argentina. They have variously been synonymized, recognized as varieties of *S. megistacrolobum*, or recognized as distinct species. This study examines 26 morphological characters of 115 living accessions of these two species, plus six accessions of two related species in series *Megistacroloba*, *S. boliviense* and *S. sogarandinum*. All measurements were taken from living accessions planted in a common garden plot. *Solanum megistacrolobum* and *S. toralapanum* could be distinguished phenetically only by a combination of the 21 characters that showed statistically significant differences between the two taxa. No individual characters provided consistent discrimination, and there was frequent overlap of "species-specific" characters between taxa. Our results most closely fit the contemporary treatment of *S. megistacrolobum* and *S. toralapanum* at the varietal level.

The genus *Solanum* L. is estimated to contain 1000–1100 species (D'Arcy 1991), including the potato and its wild relatives (*Solanum* sect. *Petota* Dumort.). The latest taxonomic interpretation of sect. *Petota* (Hawkes 1990) includes 232 species divided into 21 taxonomic series, but there are widely conflicting treatments of sect. *Petota*. They differ regarding species boundaries, the rank of infraspecific taxa, the placement of species into series, and hypotheses of interspecific hybridization (Spooner and Sytsma 1992; Spooner and van den Berg 1992a).

One series containing species illustrating many of these alternative hypotheses is series *Megistacroloba* Cárđ. and Hawkes, distributed from southern Peru through Bolivia to northwestern Argentina. The series is generally characterized by plants with a rosette habit, or with short stems, terminal leaf lobes larger than the laterals and with lateral leaf lobes typically broadly decurrent on the basiscopic side, long pedicels with articulation near the apex, and sub-stellate to rotate, usually purple corollas. All species are diploid ($2n = 24$), self-incompatible, and largely interfertile (Buck 1966; Hawkes 1990; Ochoa 1990; Pandey 1960). Correll (1962) includes 11 species in series *Megistacroloba*, Gorbatenko (1989) 16 species, Hawkes (1990) 11 species, and Ochoa (1990) seven species and one nomenclaturally designated hy-

brid species. One taxonomic controversy within series *Megistacroloba* concerns the taxonomic status and hypotheses of hybridization of *S. megistacrolobum* Bitter and *S. toralapanum* Cárđ. and Hawkes. Ochoa (1984) recognizes them as conspecific, but later (Ochoa 1990) regards them as varieties of a single species [as *S. megistacrolobum* var. *megistacrolobum* and var. *toralapanum* (Cárđ. and Hawkes) Ochoa]. They have been recognized as distinct species by Correll (1962), Gorbatenko (1989) and Hawkes (1990).

Solanum megistacrolobum is characterized by a rosette habit or with stems slightly elongate; leaves simple to pinnately lobed with 0–10 decurrent lateral leaflets, paired or unpaired; peduncles 0–5.5 cm long; pedicels 2–9 cm long; inflorescence with 1–8 flowers; calyces with upright posture and corollas lilac to purple, pentagonal to sub-stellate (Correll 1962; Hawkes 1990; Hawkes and Hjerting 1989; Ochoa 1990). Also, the leaves of *S. megistacrolobum* have a weak to strong "parsley-like" odor (Hawkes 1990; Hawkes and Hjerting 1989; Ochoa 1990). There is much variation, however, for all of these features. *Solanum megistacrolobum* has been recognized as a potential source of valuable traits such as frost resistance and drought tolerance (Brücher 1959; Hawkes and Hjerting 1989; Ochoa 1990).

Solanum toralapanum is morphologically sim-

TABLE 1. Morphological characters used by prior taxonomists to distinguish *S. megistacrolobum* and *S. toralapanum*.

Character	<i>S. megistacrolobum</i>	<i>S. toralapanum</i>
1. Primary lateral leaflet	Narrowly decurrent	Broadly decurrent
2. Length of peduncle	0–5.5 cm	6–8 cm
3. Posture of calyx acumen	Straight to appressed	Spreading to recurved
4. "Parsley-like" odor of leaf	Strong	None

ilar to *S. megistacrolobum*. It is characterized by a rosette habit or with stems slightly elongate; leaves simple to pinnately lobed with 0–8 decurrent lateral leaflets, paired or unpaired; peduncles 6–8 cm long; pedicels 1–5 cm long; inflorescence with 1–several (exact number not stated) flowers; calyces with spreading to recurved posture and corollas lilac to purple, rotate-pentagonal to sub-stellate (Correll 1962; Hawkes 1990; Hawkes and Hjerting 1989; Ochoa 1990). The leaves of *S. toralapanum* lack the parsley-like odor characteristic of *S. megistacrolobum*. There is much variation for all of these features within *S. toralapanum* except for the parsley-like leaf odor, which is not known to occur in this taxon.

The main characters that have been used in the past to distinguish *S. megistacrolobum* from *S. toralapanum* (Hawkes 1990; Hawkes and Hjerting 1989; Ochoa 1990) are outlined in Table 1. Our preliminary observations of living germplasm accessions at the National Research Support Program-6 (NRSP-6; formerly known as the Inter-Regional Potato Introduction Project, IR-1) however, noted much inter- and intraspecific morphological variability. There also is some distributional and possible ecological differentiation between the two species. *Solanum toralapanum* grows from 3000–4500 m, often more to the east of *S. megistacrolobum* on the east-facing Andean mountain slopes and valleys (Fig. 1; Table 2). Our accessions of *S. toralapanum* are from areas 3–10, 16, 17, 19, 21, 26, and 33 (Fig. 1). Both species are mapped from regions 4, 7, 16, 19, 21, 26, and 33. *Solanum megistacrolobum* grows from 2700–4450 m, on upland valleys and intermontane basins in the eastern Andean cordillera (Hawkes and Hjerting 1989; Fig. 1). Hawkes and Hjerting (1989) state that *S. toralapanum* grows in wetter sites than *S. megistacrolobum*, but Ochoa (1990) lists the habitat of *S. megistacrolobum* as moist.

Brücher (1959) notes extensive morphologi-

cal variability within *S. megistacrolobum* that he ascribes to different growth responses in different environments. Correll (1962) recognizes an apparent morphological connection between *S. megistacrolobum* and *S. toralapanum* but felt the extremes should be maintained as separate species. These morphological and distributional patterns led Ochoa (1984) to synonymize *S. toralapanum* under *S. megistacrolobum*. Johns et al. (1987) invalidly treat *S. toralapanum* as a variety of *S. megistacrolobum*. Hawkes and Hjerting (1989) state that plants phenotypically intermediate between *S. megistacrolobum* and *S. toralapanum* breed true and are probably the result of introgression between them. Ochoa (1990) cites unpublished studies at the International Potato Center, Peru (CIP), documenting extensive intraspecific variability within *S. megistacrolobum* and *S. toralapanum* that he attributes to a combination of genotypic variability and environmental plasticity. Ochoa (1990) formally transferred *S. toralapanum* to a variety of *S. megistacrolobum*.

There are many hypotheses about the interrelationships and hybridization of *S. megistacrolobum* and *S. toralapanum*. None of these distinguish phenetic from cladistic concepts. Brücher (1959) hypothesizes hybridization between *S. megistacrolobum* and *S. acaule* Bitter ($2n = 48$; series *Acaulia*). Correll (1962) states that *S. megistacrolobum* and *S. toralapanum* are closely allied. He also hypothesizes occasional hybridization between the two, as well as hybridization of *S. megistacrolobum* with *S. acaule* and *S. sanctae-rosae* Hawkes ($2n = 24$; series *Megistacroloba*). Hawkes and Hjerting (1969) hypothesize hybridization or introgression between *S. megistacrolobum* and *S. boliviense* Dunal ($2n = 24$; series *Megistacroloba*), *S. acaule*, *S. infundibuliforme* Philippi ($2n = 24$; series *Cunealata*), *S. microdontum* Bitter ($2n = 24$; series *Tuberosa*) and *S. gourlayi* Hawkes ($2n = 24$; series *Tuberosa*) or *S. oplocense* Hawkes [with diploid ($2n = 24$), tet-

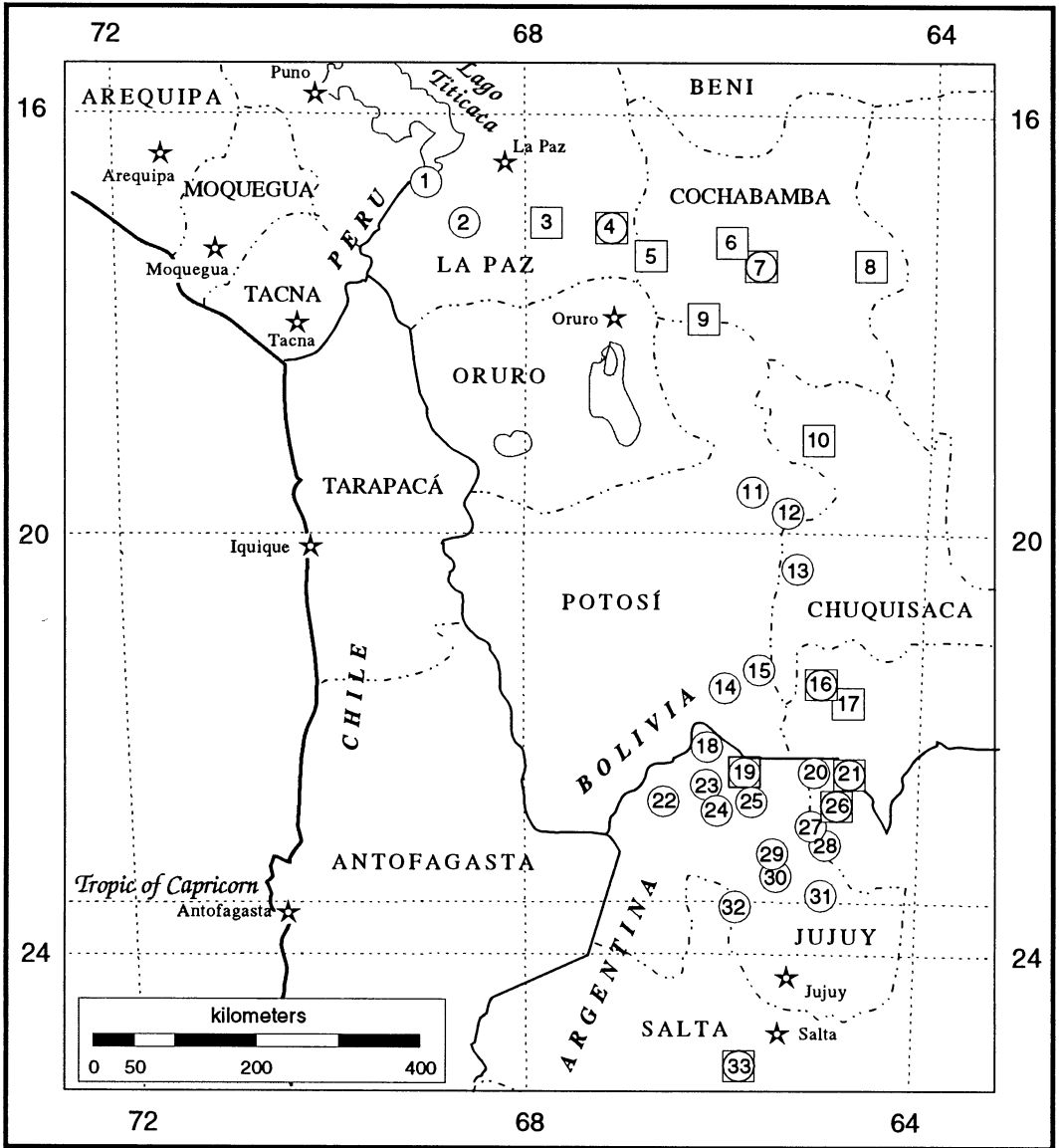


FIG. 1. Map showing the 33 generalized areas of the accessions of *Solanum acaule* subsp. *aemulans*, *S. boliviense*, *S. megistacrolobum* and *S. toralapanum* examined in this study or in a companion study (Giannattasio and Spooner 1994) using nuclear RFLPs (see Table 2). Some species other than *S. megistacrolobum* and *S. toralapanum* were collected outside of this map area. Examined accessions of *S. megistacrolobum* are from circled areas; *S. toralapanum* are from squared areas; accessions of both species were examined from areas with an overlaid circle and square.

raploid ($2n = 48$), and hexaploid ($2n = 72$) cytotypes; series *Tuberosa*]. They designate *S. ×brucherii* Correll ($2n = 24$; series *Acaulia*) as a natural hybrid between *S. megistacrolobum* and *S. acaule*. Ugent (1970) hypothesizes that *S. raphanifolium* Cárđ. and Hawkes ($2n = 24$; series

Megistacroloba) is of hybrid origin between *S. canasense* Hawkes ($2n = 24$; series *Tuberosa*) and *S. megistacrolobum*. *Solanum megistacrolobum* is hypothesized to be a diploid parent (with *S. stenotomum* Juz. and Buk.; $2n = 24$; series *Tuberosa*) of the cultivated diploid species, *S. ajanhuiri* Juz.

TABLE 2. Accessions examined. Those examined in this morphological study are marked with an M in the second column. Those marked with a D were used in a separate DNA study (Giannattasio and Spooner 1994). Vouchers are deposited at the herbarium of the National Research Support Program, Sturgeon, Bay, Wisconsin. ¹ acl = *S. acaule*, blb = *S. bulbocastanum*, blv = *S. boliviense*, brd = *S. brevidens*, can = *S. canasense*, meg = *S. megistacrobium*, rap = *S. raphanifolium*, sgr = *S. sogarandinum*, tor = *S. toralapanum*. ² M = Accession used in the morphological study. D = Accession used in the DNA study. ³ United States Department of Agriculture Plant Introduction Numbers. ⁴ Generalized map areas. See Fig. 1. ⁵ Collector unknown; accession from the Erin Baur Sortiment Genebank, Germany. ⁶ Collector unknown; accession from the Commonwealth Potato Collection, Scotland.

Taxon ¹	Study ²	PI ³	Area ⁴	Collector	Locality
1. meg	M, D	473361	1	Hawkes et al. 5058	Bolivia. La Paz: 31 km from Desaguadero, on road to Puno; 3950 m; 16°34'S, 69°02'W.
2. meg	M, D	473360	2	Hawkes et al. 4853	Bolivia. La Paz: 4 km past Caquiaviri on road to Río Desaguadero; 4000 m; 17°03'S, 68°38'W.
3. meg	M, D	498258	4	Ochoa 11916	Bolivia. La Paz: between Tres Cruces and Río Seco; 3500 m; 17°06'S, 67°21'W.
4. meg	M, D	498263	7	Ochoa 12098	Bolivia. Cochabamba: Toralapa; 3600 m; 17°26'S, 65°43'W.
5. meg	M	265873	11	EBS ⁵ 1793	Bolivia. Potosí: Potosí; 19°35'S, 65°45'W.
6. meg	M	265874	11	EBS 1808	Bolivia. Potosí: 8 km from Potosí on road to Don Diego; 19°35'S, 65°45'W.
7. meg	M, D	473356	11	Hawkes et al. 4317	Bolivia. Potosí: below Potosí on road to Lecherías; 3950 m; 19°35'S, 65°45'W.
8. meg	M	473358	11	Hawkes et al. 4589	Bolivia. Potosí: 0.5 km below Potosí on road to Lecherías; 3950 m; 19°35'S, 65°45'W.
9. meg	M	473359	11	Hawkes et al. 4590	Bolivia. Potosí: 0.7 km below Potosí on road to Lecherías; 3950 m; 19°35'S, 65°45'W.
10. meg	M, D	210034	12	Hjerting 1028	Bolivia. Potosí: Alkatayo; 19°50'S, 65°30'W.
11. meg	M	283082	13	EBS 1787	Bolivia. Chuquisaca: Sivingamayo; 3800 m; 20°20'S, 65°04'W.
12. meg	M	473357	13	Hawkes et al. 4323	Bolivia. Chuquisaca: 126 km on road from Potosí to Carmargo, near Payacota; 3500 m; 20°24'S, 65°18'W.
13. meg	M	473497	13	Astley 49	Bolivia. Chuquisaca: 130 km from Potosí on road to Camargo; 19°35'S, 65°45'W.
14. meg	M, D	498259	14	Ochoa 11960	Bolivia. Potosí: Sud Chichas; 4250 m, 20°40'S, 67°00'W.
15. meg	M	498260	15	Ochoa 11962	Bolivia. Potosí: Sud Chichas; pass of Machu Cruz in route to Tupiza; 4100 m; 21°27'S, 65°43'W.
16. meg	M	498261	15	Ochoa 11963	Bolivia. Potosí: Sud Chichas; pass of Machu Cruz in route to Tupiza; 4100 m; 21°27'S, 65°43'W.
17. meg	M	498262	15	Ochoa 11964	Bolivia. Potosí: Sud Chichas; pass of Machu Cruz in route to Tupiza; 4100 m; 21°27'S, 65°43'W.
18. meg	M	265578	16	Correll 654	Bolivia. Tarija: Iscayachi; 21°31'S, 65°03'W.
19. meg	M, D	545897	16	Hoopes et al. 99	Bolivia. Tarija: Méndez; 4 km from Iscayachi on road to Tarija; 3500 m; 21°27'S, 64°58'W.
20. meg	M, D	545898	16	Hoopes et al. 101	Bolivia. Tarija: Aviles; 11 km from Iscayachi on road to Villazón; 3540 m; 21°34'S, 65°02'W.
21. meg	M	458347	18	Hoffman 1682	Argentina. Jujuy: 19 km E of Santa Catalina on the way to El Angosto; 4200 m; 21°55'S; 66°08'W.

TABLE 2. Continued.

Taxon ¹	Study ²	PI ³	Area ⁴	Collector	Locality
22. meg	M	458349	18	<i>Okada</i> 3933	Argentina. Jujuy: 24 km E of Santa Catalina; 4200 m; 21°57'S, 66°04'W.
23. meg	M	473116	18	<i>Okada</i> 3914	Argentina. Jujuy: 10 km W of Santa Catalina; 4000 m; 21°57'S, 66°04'W.
24. meg	M	473117	18	<i>Okada</i> 3917	Argentina. Jujuy: 10 km W of Santa Catalina; 4000 m; 21°57'S, 66°04'W.
25. meg	M, D	473118	18	<i>Okada</i> 3926	Argentina. Jujuy: 10 km W of Santa Catalina; 4000 m; 21°57'S, 66°04'W.
26. meg	M	473119	18	<i>Okada</i> 3931	Argentina. Jujuy: 24 km W of Santa Catalina; 4200 m; 21°57'S, 66°04'W.
27. meg	M	473120	18	<i>Okada</i> 3934	Argentina. Jujuy: 24 km W of Santa Catalina; 4200 m; 21°57'S, 66°04'W.
28. meg	M	473122	18	<i>Okada</i> 3983	Argentina. Jujuy: Oratorio; 4000 m; 22°05'S, 66°07'W.
29. meg	M, D	473121	18	<i>Okada</i> 3977	Argentina. Jujuy: Cabrerillas W to Oratorio; 3900 m; 22°05'S, 66°07'W.
30. meg	M, D	458348	19	<i>Okada</i> 3906	Argentina. Jujuy: Tafna; 3600 m; 22°06'S, 65°44'W.
31. meg	M	473115	19	<i>Okada</i> 3886	Argentina. Jujuy: Río Chico; 3620 m; 22°08'S, 65°44'W.
32. meg	M	473135	19	<i>Okada</i> 4442	Argentina. Jujuy: Quebrada del Chorro; 3900 m, 22°08'S, 65°38'W.
33. meg	M	473136	19	<i>Okada</i> 4442	Argentina. Jujuy: on slope from ravine of Chorro; 3900 m; 22°08'S, 65°38'W.
34. meg	M, D	473137	19	<i>Okada</i> 4444	Argentina. Jujuy: top of Quebrada del Chorro, along path from Casa Colorada to Molulo; 3700 m, 22°08'S, 65°38'W.
35. meg	M, D	275148	20	<i>Hjerting</i> 255	Argentina. Jujuy: between Lizoite and Abra de Lizoite; 3600 m; 22°15'S, 65°13'W.
36. meg	M	473112	20	<i>Hoffman</i> 1663	Argentina. Jujuy: Cajas; 4000 m; 22°15'S, 65°18'W.
37. meg	M, D	435072	20	<i>Okada</i> 5823	Argentina. Salta: Santa Victoria; 3800 m; 22°15'S, 64°58'W.
38. meg	M, D	473158	21	<i>Okada</i> 5839	Argentina. Salta: on the way from Lizoite; 3400 m; 22°16'S, 65°11'W.
39. meg	M	473139	22	<i>Okada</i> 4452	Argentina. Jujuy: Pucará; 3700 m; 22°24'S, 66°34'W.
40. meg	M	473153	23	<i>Okada</i> 5772	Argentina. Jujuy: 3 km SW of Timon Cruz; 4140 m; 22°13'S, 66°09'W.
41. meg	M	473154	23	<i>Okada</i> 5774	Argentina. Jujuy: 1 km W of Oros; 4000 m; 22°16'S, 66°21'W.
42. meg	M	473155	23	<i>Okada</i> 5775	Argentina. Jujuy: 3 km W of Oros; 3980 m; 22°16'S, 66°21'W.
43. meg	M	473156	23	<i>Okada</i> 5776	Argentina. Jujuy: 4 km W of Oros; 3940 m; 22°16'S, 66°21'W.
44. meg	M	473157	23	<i>Okada</i> 5782	Argentina. Jujuy: 4 km W of Oros; 3840 m; 22°16'S, 66°21'W.
45. meg	M	458350	24	<i>Okada</i> 3989	Argentina. Jujuy: Rinconada; 3800 m; 22°26'S, 66°10'W.
46. meg	M	458351	24	<i>Okada</i> 4018	Argentina. Jujuy: Rinconada, near Abra de Fundiciones; 4200 m; 22°33'S, 66°17'W
47. meg	M	473123	24	<i>Okada</i> 3992	Argentina. Jujuy: Sierra de Rinconada; 3900 m; 22°26'S, 66°07'W.

TABLE 2. Continued.

Taxon ¹	Study ²	Pf ³	Area ⁴	Collector	Locality
48. meg	M	473124	24	<i>Okada 4006</i>	Argentina. Jujuy: Rinconada; 4000 m; 22°26'S, 66°10'W.
49. meg	M	473125	24	<i>Okada 4008</i>	Argentina. Jujuy: Rinconada; 4000 m; 22°26'S, 66°10'W.
50. meg	M	473126	24	<i>Okada 4024</i>	Argentina. Jujuy: 8 km SW of Rinconada; 4020 m; 22°26'S, 66°10'W.
51. meg	M	473152	24	<i>Okada 5526</i>	Argentina. Jujuy: Salveayoc, 5 km SW of Rinconada; 4000 m; 22°26'S, 66°10'W.
52. meg	M	473162	24	<i>Okada 5996</i>	Argentina. Jujuy: on the way from Orosmayo; 4100 m; 22°35'S, 66°21'W.
53. meg	M, D	458346	25	<i>Hoffman 1629</i>	Argentina. Jujuy: Cochinoca; 3650 m; 22°44'S, 65°54'W.
54. meg	M	458352	25	<i>Okada 4421</i>	Argentina. Jujuy: El Angosto; 4000 m; 24°02'S, 65°35'W.
55. meg	M	473131	25	<i>Okada 4422</i>	Argentina. Jujuy: Laguna River, on the way from Casa Colorado to El Durazno; 4000 m; 22°28'S, 65°41'W.
56. meg	M	473160	25	<i>Okada 5956</i>	Argentina. Jujuy: Sierra de Cochinoca; 3700 m; 22°34'S, 65°53'W.
57. meg	M	473161	25	<i>Okada 5957</i>	Argentina. Jujuy: Sierra de Cochinoca; 3700 m; 22°34'S, 65°53'W.
58. meg	M	473114	26	<i>Hoffman 1729</i>	Argentina. Salta: Poscaya; 3420 m; 22°28'S, 65°06'W.
59. meg	M	265879	27	<i>EBS 1783</i>	Argentina. Jujuy: Tres Cruces; 3800 m; 22°55'S, 65°35'W.
60. meg	M	275147	27	<i>Hjerting 366</i>	Argentina. Jujuy: between Condor and Abra del Condor; 3800 m; 22°53'S, 65°16'W.
61. meg	D	233125	27	<i>CPC⁶ 2482</i>	Argentina. Jujuy: between Condor and Abra del Condor; 3800 m; 22°53'S, 65°16'W.
62. meg	M, D	473109	27	<i>Hoffman 1598</i>	Argentina. Jujuy: Cuesta Azul Pampa; 3400 m; 23°04'S, 65°24'W.
63. meg	M	473111	27	<i>Hoffman 1618</i>	Argentina. Jujuy: Condor; 4000 m; 22°54'S, 65°17'W.
64. meg	M	473113	27	<i>Hoffman 1701</i>	Argentina. Jujuy: Condor; 4000 m; 22°54'S, 65°17'W.
65. meg	M	473127	27	<i>Okada 4358</i>	Argentina. Jujuy: near La Cueva; 3900 m; 22°55'S, 65°22'W.
66. meg	M	473132	27	<i>Okada 4428</i>	Argentina. Jujuy: La Cueva; 3900 m; 22°55'S, 65°22'W.
67. meg	M	473133	27	<i>Okada 4430</i>	Argentina. Jujuy: La Cueva; 3900 m; 22°55'S, 65°22'W.
68. meg	M	473134	27	<i>Okada 4431</i>	Argentina. Jujuy: La Cueva; 3900 m; 22°55'S, 65°22'W.
69. meg	M	473148	27	<i>Okada 4567</i>	Argentina. Jujuy: between Esquina Blanca and Tres Cruces; 3700 m; 22°57'S, 65°32'W.
70. meg	M	473150	27	<i>Okada 4573</i>	Argentina. Jujuy: 14 km NE of Iturbe; 3700 m; 22°59'S, 65°21'W.
71. meg	M	473524	27	<i>EBS 2945</i>	Argentina. Jujuy: valley of Humahuaca, Azul Pampa; 23°04'S, 65°24'W.
72. meg	M	473149	27	<i>Okada 4569</i>	Argentina. Jujuy: 3 km past Abra de Azul Pampa towards Iturbe; 3700 m; 22°58'S, 65°26'W.
73. meg	M	473140	28	<i>Okada 4460</i>	Argentina. Jujuy: Palca de Aparso; 3800 m; 23°06'S, 65°06'W

TABLE 2. Continued.

Taxon ¹	Study ²	PI ³	Area ⁴	Collector	Locality
74. meg	M	473163	28	<i>Okada 6734</i>	Argentina. Jujuy: Aparso; 3800 m; 23°06'S, 65°10'W.
75. meg	M	473164	28	<i>Okada 6737</i>	Argentina. Jujuy: 2 km S of Aparso; 3650 m; 23°06'S, 65°10'W.
76. meg	M	473110	29	<i>Hoffman 1615</i>	Argentina. Jujuy: Chalcamayo; 3880 m; 23°14'S, 65°33'W.
77. meg	M	473141	30	<i>Okada 4506</i>	Argentina. Jujuy: Sierra Alta; 3660 m; 23°23'S, 65°32'W.
78. meg	M	473142	30	<i>Okada 4509</i>	Argentina. Jujuy: Sierra Alta; 3200 m; 23°23'S, 65°32'W.
79. meg	M	473143	30	<i>Okada 4512</i>	Argentina. Jujuy: Sierra Alta; 3300 m; 23°23'S, 65°32'W.
80. meg	M	473144	30	<i>Okada 4514</i>	Argentina. Jujuy: Sierra Alta; 3300 m; 23°23'S, 65°32'W.
81. meg	M	473145	30	<i>Okada 4515</i>	Argentina. Jujuy: Sierra Alta; 3300 m; 23°23'S, 65°32'W.
82. meg	M	473147	30	<i>Okada 4524</i>	Argentina. Jujuy: Sierra Alta; 3300 m; 23°23'S, 65°32'W.
83. meg	M, D	473146	30	<i>Okada 4520</i>	Argentina. Jujuy: Sierra Alta; 3300 m; 23°23'S, 65°32'W.
84. meg	M, D	473128	31	<i>Okada 4362</i>	Argentina. Jujuy: along path from Casa Colorada de Molulo, Ventura River; 4000 m; 23°33'S, 65°12'W.
85. meg	M	473129	31	<i>Okada 4411</i>	Argentina. Jujuy: Piedra Parada; 3700 m; 23°35'S, 65°10'W.
86. meg	M, D	500031	31	<i>Okada 7606</i>	Argentina. Jujuy: 7 hr E of Tilcara by mule, between Peña Parada and Portrero de Ventura; 3500 m; 23°35'S, 65°13'W.
87. meg	M	473130	32	<i>Okada 4415</i>	Argentina. Jujuy: on the path from El Durazno to Casa Colorada; 3800 m; 23°10'S, 65°39'W.
88. meg	M, D	473159	32	<i>Okada 5954</i>	Argentina. Jujuy: 21 km from Abra Pampa along Route 7; 3700 m; 23°35'S, 65°51'W.
89. meg	M, D	275149	33	<i>Hjerting 316</i>	Argentina. Jujuy: Piedra Molino; 3700 m; 25°10'S, 65°52'W.
90. meg	M	500029	33	<i>Okada 7504</i>	Argentina. Salta: Cuesta del Obispo, Encantado valley; 3450 m; 25°10'S, 65°52'W.
91. meg	M	500030	33	<i>Okada 7516</i>	Argentina. Salta: 2 h by foot from Isonza following ravine; 3500 m; 25°20'S, 65°53'W.
92. meg	M	233124	Z	<i>CPC 2535</i>	Bolivia. Unknown.
93. meg	M	310977	Z	<i>Alandia 64-9</i>	Bolivia. Unknown.
94. meg	M, D	310978	Z	<i>Alandia 64-10</i>	Bolivia. Unknown.
95. tor	M	310936	3	<i>Ugent 4853</i>	Bolivia. La Paz: Ayopaya; 10 km from Hacienda Sailapata; 16°30'S, 66°35'W.
96. tor	M, D	546014	3	<i>Hawkes et al. 200</i>	Bolivia. La Paz: Loayza; 11.2 km from Ayo Ayo on the road to Caracato; 3960 m; 17°03'S, 67°53'W.
97. tor	M, D	498257	4	<i>Ochoa 11914</i>	Bolivia. La Paz: Inquisive; Huanecta, between Tres Cruces and Quime; 4450 m; 17°04'S, 67°18'W.
98. tor	M, D	498142	5	<i>Hawkes et al. 6572</i>	Bolivia. Cochabamba: Ayopaya; road from Cruce de Challa to Independencia, Abra de Ornoni; 3730 m; 17°15'S, 66°54'W.

TABLE 2. Continued.

Taxon ¹	Study ²	PI ³	Area ⁴	Collector	Locality
99. tor	M, D	498143	5	<i>Hawkes et al. 6589</i>	Bolivia. Cochabamba: Ayopaya; 24 km from Independencia on road to Challa; 3730 m; 17°14'S, 66°54'W.
100. tor	M, D	498144	6	<i>Hawkes et al. 6613</i>	Bolivia. Cochabamba: Chapare; 35 km from Tranca de Sacaba on road to Palca; 3760 m; 17°14'S, 66°03'W.
101. tor	M, D	498145	6	<i>Hawkes et al. 6616</i>	Bolivia. Cochabamba: Chapare; 35 km from Tranca de Sacaba; 3760 m; 17°14'S, 66°03'W.
102. tor	M	498146	6	<i>Hawkes et al. 6622</i>	Bolivia. Cochabamba: Chapare; 0.5 km from Palca, 40 km from Tranca de Sacaba on road to Palca; 3730 m; 17°13'S, 66°03'W.
103. tor	M, D	473389	7	<i>Hawkes et al. 4758</i>	Bolivia. Cochabamba: Toralapa; 71.5 km from Cochabamba on Santa Cruz road; 3500 m; 17°26'S, 65°43'W.
104. tor	M, D	545928	8	<i>Hoopes et al. 174</i>	Bolivia. Cochabamba: Chapare; 9 km from turn-off at Aguirre from the Cochabamba-Chapare road; 3500 m; 17°18'S, 64°44'W.
105. tor	M, D	545892	8	<i>Hoopes et al. 175</i>	Bolivia. Cochabamba: Chapare; 9 km from turn-off at Aguirre from the Cochabamba-Chapare road; 3500 m; 17°18'S, 64°44'W.
106. tor	M, D	545998	9	<i>Hawkes et al. 251</i>	Bolivia. Cochabamba: Ibañes; 18.2 km from Sacaca on road to Oruro; 3900 m; 18°00'S, 66°26'W.
107. tor	M, D	458396	10	<i>Hawkes et al. 4556</i>	Bolivia. Chuquisaca: Oropeza; 29 km from Sucre toward Ravelo; 3300 m; 19°02'S, 65°17'W.
108. tor	M, D	458397	16	<i>Hawkes et al. 4695</i>	Bolivia. Tarija: Méndez; 32 km from Tarija toward Iscayachi; 3000 m; 21°31'S, 64°45'W.
109. tor	M, D	545926	17	<i>Hoopes et al. 94</i>	Bolivia. Tarija: Méndez; Cuesta de Sama; 2950 m; 21°29'S, 64°53'W.
110. tor	M, D	472805	19	<i>Hoffman 1851</i>	Argentina. Salta: 56 km E of Cajas; 3150 m; 22°15'S, 65°18'W.
111. tor	D	320303	21	<i>Hawkes et al. 3829</i>	Argentina. Salta: 16 to 16.7 km from Santa Victoria on road from Yavi to Santa Victoria; 3450 m; 22°15'S, 64°58'W.
112. tor	M	472804	21	<i>Hoffman 1738</i>	Argentina. Salta: 9 km SW of Santa Victoria, Cuesta Parada; 3350 m; 22°15'S, 64°58'W.
113. tor	M, D	472806	21	<i>Hoffman 1926</i>	Argentina. Salta: 10 km SE of Santa Victoria; 3300 m; 22°15'S, 64°58'W.
114. tor	M, D	472808	21	<i>Okada 5436</i>	Argentina. Salta: 50 km E of Abra Lizoite; 3500 m; 22°13'S, 65°14'W.
115. tor	M, D	472807	26	<i>Hoffman s.n.</i>	Argentina. Salta: Santa Victoria department; 22°25'S, 64°55'W.
116. tor	M, D	320302	33	<i>Hawkes et al. 3727</i>	Argentina. Salta: 21.4 km from Escoipe on road to Cachi, Cuesta del Obispo; 3200 m; 25°10'S, 65°51'W.
117. tor	M, D	195210	Z	<i>CPC 1773</i>	Bolivia. Unknown.
118. blv	M, D	265861	10	<i>EBS 1847</i>	Bolivia. Chuquisaca: 8 km from Tarabuco on road to Zudañez; 19°10'S, 64°57'W.
119. blv	M	310974	Z	<i>Alandia 64-6</i>	Bolivia. Unknown.
120. blv	M	310975	Z	<i>Alandia 64-7</i>	Bolivia. Unknown.
121. blv	M	498215	Z	<i>Ochoa 11929</i>	Bolivia. Chuquisaca: Kkucha Tambo, on road from Sucre to Guerraloma; 2940 m.
122. blv	D	265860	Bol	<i>EBS 1795</i>	Bolivia. Unknown: E of Siclla; 3600 m.

TABLE 2. Continued.

Taxon ¹	Study ²	PI ³	Area ⁴	Collector	Locality
123. sgr	M, D	230510	Peru	Ochoa 1440	Peru. La Libertad: near Santiago de Chuco; 3550 m; 08°09'S, 78°11'W.
124. sgr	M, D	365360	Peru	Ochoa S-54	Peru. Ancash: Acrana; 3500 m; 09°30'S, 77°45'W.
125. alb	D	266381	Peru	Correll P863	Peru. Cajamarca: 6 km from the entrance to Hacienda Porcón; 3500 m.
126. pne	D	473431	Peru	Ochoa 7990	Peru. Unknown.
127. aem	D	472793	30	Okada 4361	Argentina. Jujuy: Piedra Rosada, by the Ventura River; 4000 m; 23°35'S, 65°12'W.
128. acl	D	472801	Arg	Okada 6083A	Argentina. La Rioja: Sierra de Famatina, La Encrucijada; 3050 m; 28°58'S, 67°42'W.
129. brd	D	245763	Chil	Correll C14	Chile. Region IX: road from Cherquenco to Refugio Llaima; 800 m; 38°40'S, 71°53'W.
130. blb	D	275200	Guat	Hawkes 1796	Guatemala. Huehuetenango: 5 km S of Malacatancito, road from Huehuetenango to Quezaltenango; 1800 m.
131. can	D	265864	Peru	EBS 1831	Peru. Cuzco: 4 km on the road from Cuzco to Pisac; 3800 m.
132. rap	D	473369	Peru	Hawkes et al. 5138	Peru. Cuzco: 25 km on road from Cuzco to Puno; 3200 m.

et Buk. ($2n = 24$; series *Tuberosa*; Huamán et al. 1980, 1982, 1983; Johns et al. 1987). Okada and Clausen (1982) document the occurrence of natural triploid ($2n = 36$) hybrids between *S. megistacrolobum* and *S. acaule* subsp. *acaule* in northwestern Argentina and formally name them *S. ×indunii* Okada and Clausen. They further suggest that some populations of *S. acaule* subsp. *aemulans* Bitter and Wittm. ($2n = 48$) are hybrids between *S. acaule* subsp. *acaule* and *S. megistacrolobum* or *S. ×indunii*. They also question Hawkes and Hjerting's (1969) hypothesis of the hybrid origin of *S. ×brucherii* (see above) and suggest that it is related to *S. gourlayi*. Hawkes and Hjerting (1989) mention "intermediate forms" between *S. megistacrolobum* and *S. toralapanum* that they believe are the result of introgression between the two. They also designate natural hybrids of *S. megistacrolobum* with *S. acaule*, *S. infundibuliforme*, *S. sparsipilum* (Bitter) Juz. and Buk. ($2n = 24$; series *Tuberosa*) and *S. stenotomum*; and of *S. toralapanum* with *S. acaule*. Ochoa (1990) hypothesizes natural hybridization between some populations of *S. megistacrolobum* and *S. toralapanum* and *S. megistacrolobum* and *S. infundibuliforme*. He suggests a "connecting link" of *S. megistacrolobum* to series *Acaulia* and believes that *S. megistacrolobum* hybridizes naturally with *S. acaule*. Hawkes (1990)

reverses his earlier hypothesis relative to the origin of *S. ×brucherii* (see above), and designates it as a hybrid between *S. gourlayi* and *S. infundibuliforme* (Hawkes and Hjerting 1969).

The objective of this study is to assess the nature, extent, and geographical partitioning of morphological differences between *S. megistacrolobum*, *S. toralapanum*, and two other species in series *Megistacroloba*; *S. boliviense* and *S. sogarandinum* Ochoa. We chose these latter two species from the many others mentioned above because of their close phenetic resemblance to *S. megistacrolobum* and *S. toralapanum*. A separate study (Giannattasio and Spooner 1994) examines a subset of these taxa and other species for differences in single- to low-copy nuclear DNA. These combined data will be used to assess taxonomic boundaries and possible patterns of hybridization involving *S. megistacrolobum* and *S. toralapanum*.

MATERIALS AND METHODS

Plants. This study uses 93 accessions of *S. megistacrolobum*, 22 of *S. toralapanum*, four of *S. boliviense*, and two of *S. sogarandinum* (Table 2), chosen from the germplasm bank of NRSP-6 (Hanneman and Bamberg 1986), and grown in an experimental field plot at Sturgeon Bay, Wis-

TABLE 3. Characters used in phenetic analysis of *Solanum megistacrolobum* and *S. toralapanum*. Characters with an asterisk (*) were significantly different (0.05 level or greater) and used for a separate phenetic analysis.

Leaf characters

*1. Leaf length (cm). *2. Ratio: leaf width/leaf length. *3. Length of terminal leaflet lamina (cm). *4. Ratio: terminal leaflet width/terminal leaflet length. *5. Ratio: distance from base of petiole to widest part of terminal leaflet/leaf length. *6. Length of primary lateral leaflet (cm). *7. Degree of decurrency of the primary lateral leaflet; measured by the length of the primary leaflet five mm basiscopic to the midrib (cm). 8. Density of adaxial pubescence: glabrous (0), puberulent (1), intermediate (2), dense (3). *9. Density of abaxial pubescence: glabrous (0), puberulent (1), intermediate (2), dense (3). *10. Parsley-like leaf odor: absent (0), slight (1), moderate (2), extreme (3). *11. Ratio: distance from base to widest part of terminal leaflet/terminal leaflet length. *12. Number of leaflets.

Floral characters (see Spooner and van den Berg 1992b, for illustrations of characters 22, 23, 24, and 25)

*13. Number of flowers per inflorescence. *14. Length of peduncle (cm). *15. Distance from base of peduncle to articulation (cm). *16. Position of the pedicel articulation; measured by the ratio of character 15/total pedicel length. 17. Width of calyx lobe (cm). *18. Length of calyx lobe (cm). *19. Ratio: length of acumen/length of calyx lobe. *20. Posture of calyx acumen: tightly appressed (1), moderately appressed (2), spreading to recurved (3). *21. Color of corolla: whitish blue (1), blue (2), deep blue to purple (3). *22. Radius of corolla: longest distance between center of corolla and tip of petal (cm). 23. Petal lobe length (cm). *24. Corolla shape; ratio between the petal lobe length and petal lobe width. 25. Ratio: radius from center of corolla to base of corolla lobe/radius of corolla. 26. Length of anther (cm).

consin. The accessions of *S. megistacrolobum* and *S. toralapanum* were chosen to represent the widest possible geographic range of these species. They are mapped into 33 generalized geographic regions (Fig. 1). The accessions were planted from seed in early June 1990; eight seedlings per accession were planted in rows in a common field plot in early July, and all measurements were taken in late August when the plants were in flower.

Character Measurement. The middle four surviving plants per row were measured for each accession. A total of 26 characters (Table 3) were measured on each plant. Of these, 21 characters were quantitative and five were qualitative. Leaf characters were measured using the fourth true leaf of each plant. Floral characters were taken from the uppermost inflorescence. The means of these four plants were used as representative of the accession. In rare cases, a character was lacking entirely (i.e., primary lateral leaflet length), and the average of that character per species was substituted for the missing character. Many herbarium specimens of members of sect. *Petota* collected in the wild are incomplete, have been collected at different growth stages, or have been collected under different environments. Also, many wild potato species, including *S. megistacrolobum* and *S. toralapanum*, are thought to exhibit morphological

plasticity under different environments (Brücher 1959; Correll 1962; Hawkes 1990; Hawkes and Hjerting 1989; Ochoa 1990). Our study with living plantings grown in one location, with measurements taken from serial organs at the same growth stage, standardizes environments and measurements of organs at the same serial stage.

Data Analysis. Each character was analyzed for its mean, range, standard deviation, and significance by one-way ANOVA in Minitab (Ryan et al. 1985). These analyses were performed twice, once for all taxa, and again for a subset of the taxa that occurred in the 33 geographic areas that had only one species per area (i.e., omitting all accessions from areas 4, 7, 16, 19, 21, 26, and 33). This second analysis was done to test whether morphological intermediacy between species was caused by hybridization or primary divergence. Phenetic analyses of all accessions were produced by NTSYS-pc®, version 1.70 (Rohlf 1992). Averaged data 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). These analyses were performed twice, once for all characters, and again for a subset of the characters that were significantly different (0.05 level) between *S. megistacrolobum* and *S. toralapanum*. Principal Components Analyses (PCA) also were performed from similarity matrices (CORR) and EIGEN. As in the UPGMA analysis, PCA were performed twice, once for all characters, and again for a subset of the characters that were significantly different (0.05 level) between *S. megistacrolobum* and *S. toralapanum*.

RESULTS

One-way ANOVA of the entire data set demonstrated that 21 of the 26 characters (81%), including the four major characters used previously to distinguish *S. megistacrolobum* and *S. toralapanum* (Table 1), were significantly different (0.05 level or greater) between them. The five characters not showing this significance were characters 8, 17, 23, 25 and 26 (Table 3). Our data show extensive intra-accession, intra-specific and interspecific variability for most characters (Fig. 2). For example, while none of the *S. toralapanum* examined were found to possess the parsley-like leaf odor characteristic of *S. megistacrolobum*, 74 out of the 93 accessions of *S. megistacrolobum* had at least one of the four individuals per accession lacking this odor. Many of these accessions also had individuals with strong odor, however, demonstrating high intra-accession variability for this character.

One-way ANOVA of the reduced data set that eliminated taxa from areas of general geographic co-occurrence of *S. megistacrolobum* and *S. toralapanum* (see above) demonstrated that 19 of the 26 characters (73%), including the four major characters used previously to distinguish them, were significantly different (0.05 level or greater). In general, however, there was little difference in levels of significance of characters relative to the entire data set. All further analyses used all accessions.

The phenograms using all 26 characters generated by DIST and EUCLID had the greatest cophenetic correlation coefficients (0.87), were equal in topology, and differed only in the scaling of the phenograms. These phenograms,

however (not shown here, but see Giannattasio 1992), intermixed 17 accessions of *S. megistacrolobum* and 21 accessions of *S. toralapanum* on one cluster of the phenogram, and therefore, provided poor separation of the two species.

The phenograms using only the 21 statistically significant characters did a much better job of distinguishing *S. megistacrolobum* from *S. toralapanum*. As above, the phenograms generated by DIST and EUCLID had the greatest cophenetic correlation coefficients (0.83), were equal in topology, and differed only in the scaling of the phenograms. The phenogram generated by DIST is shown in Figure 3. The cophenetic correlation coefficients for the phenograms generated by CORR and MANHAT were 0.65 and 0.77, respectively.

This second analysis, using only those characters showing statistically significant differences between *S. megistacrolobum* and *S. toralapanum*, largely separated them into two separate clusters of the phenogram, with the exception of five of the 93 accessions of *S. megistacrolobum* that clustered with *S. toralapanum*, and two that clustered between *S. boliviense* and *S. sogarandinum*. Also, one accession of *S. toralapanum* clustered with three of the four accessions of *S. boliviense*. Both accessions of *S. sogarandinum* and three of the four accessions of *S. boliviense* clustered among themselves, separated by the two "misplaced" accessions of *S. megistacrolobum*. The remaining accession of *S. boliviense* clustered with two of the five "misplaced" accessions of *S. megistacrolobum* in the *S. toralapanum* cluster (Fig. 3).

PCA using all 26 characters (not shown here, but see Giannattasio 1992), like the UPGMA, provided somewhat poor separation of *S. megistacrolobum* and *S. toralapanum* by showing contiguous distribution of taxa along the first three PCA axes, with much interdigitation between species. The first three principal components axes accounted for 24.1%, 12.5%, and 7.8%, for a total of 44.4% of the total variation.

PCA of the reduced data set using the 21 statistically significant characters also showed contiguous distribution but with less interdigitation of taxa (Fig. 4). This analysis, like the UPGMA analysis, grouped both accessions of *S. sogarandinum*, but provided a better grouping of all four accessions of *S. boliviense*. The first three principal components axes accounted for 27.7%, 13.9%, and 9.8%, for a total of 51.4% of the total variation. The six highest loadings on PCA axis

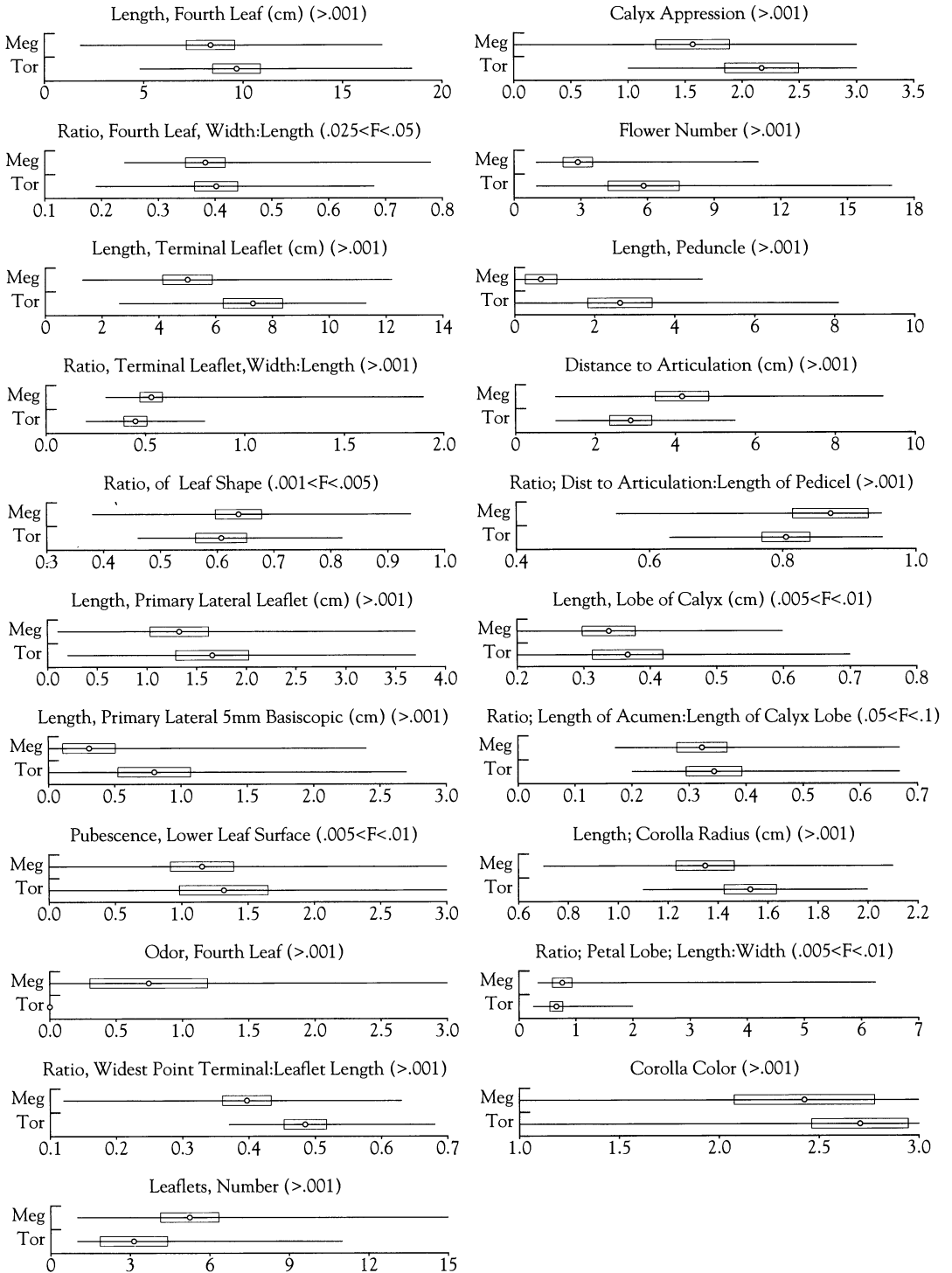


FIG. 2. Means, ranges and one standard deviation of the mean for the 21 characters showing significant differences (0.05 level or greater) between *Solanum megistacrolobum* (meg) and *S. toralapanum* (tor). See Table 3 for an explanation of character states.

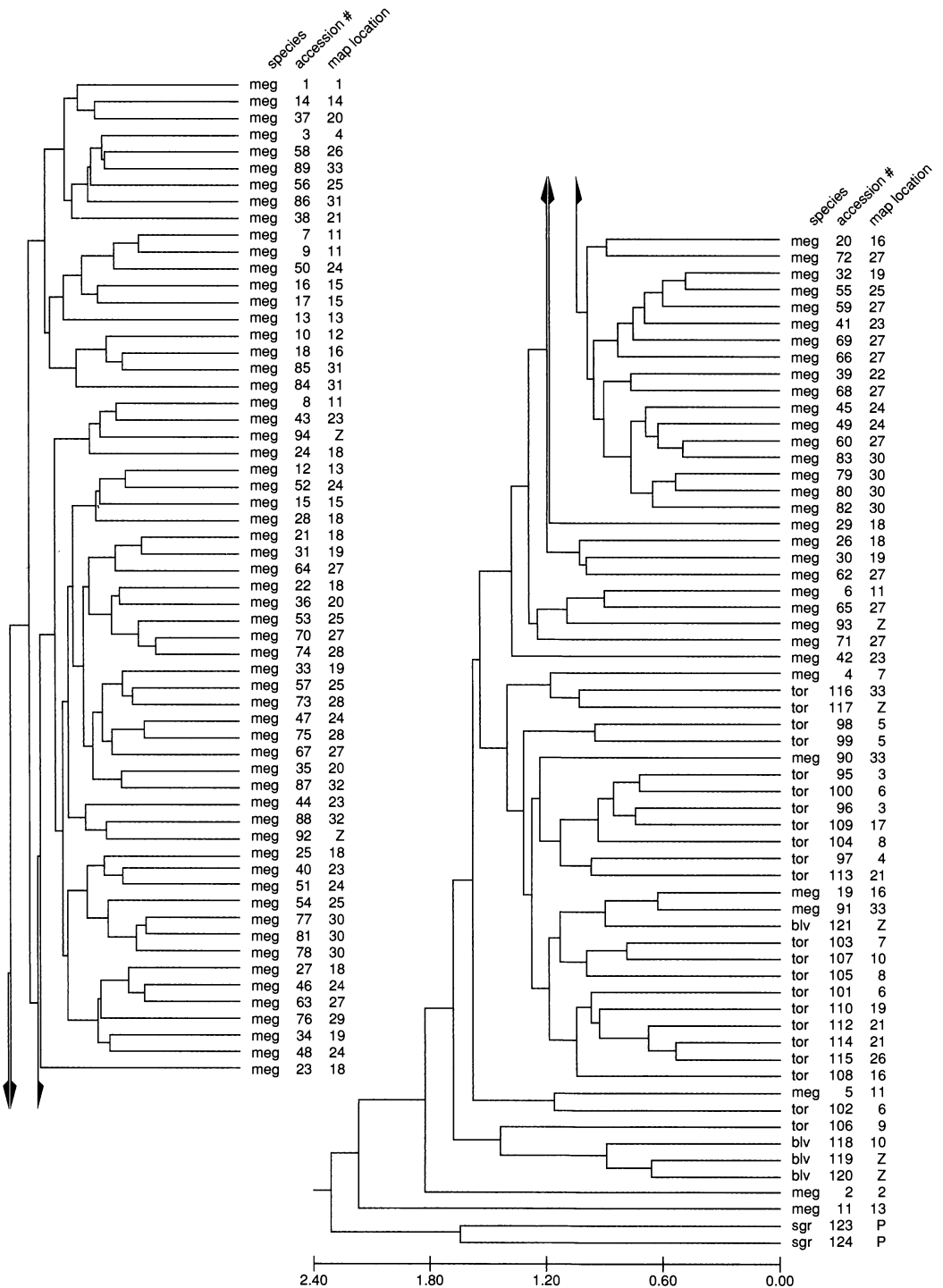


FIG. 3. UPGMA phenogram (DIST similarity option) based on the 21 of the 26 morphological characters that showed statistically significant differences between *Solanum megistacrolobum* (meg) and *S. toralapanum* (tor). *Solanum boliviense* = blv; *S. sogarandinum* = sgr. See Table 2 for a listing of accession numbers and map locations. The letters refer to locations outside of Figure 1. P = Peru; Z = unknown location.

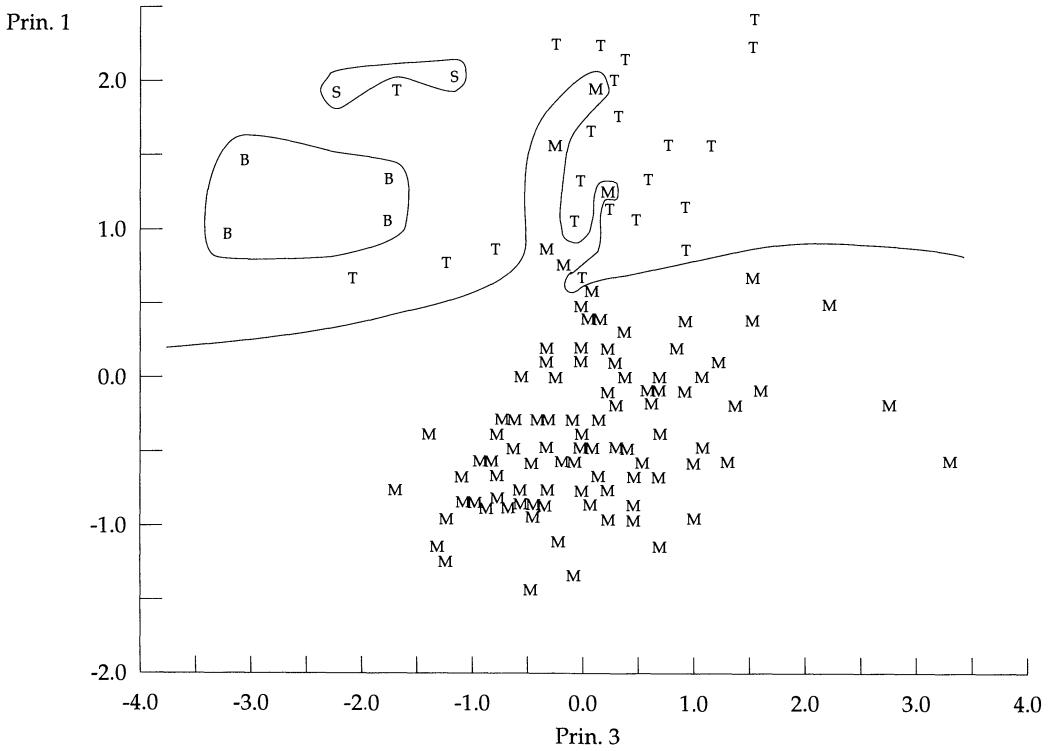
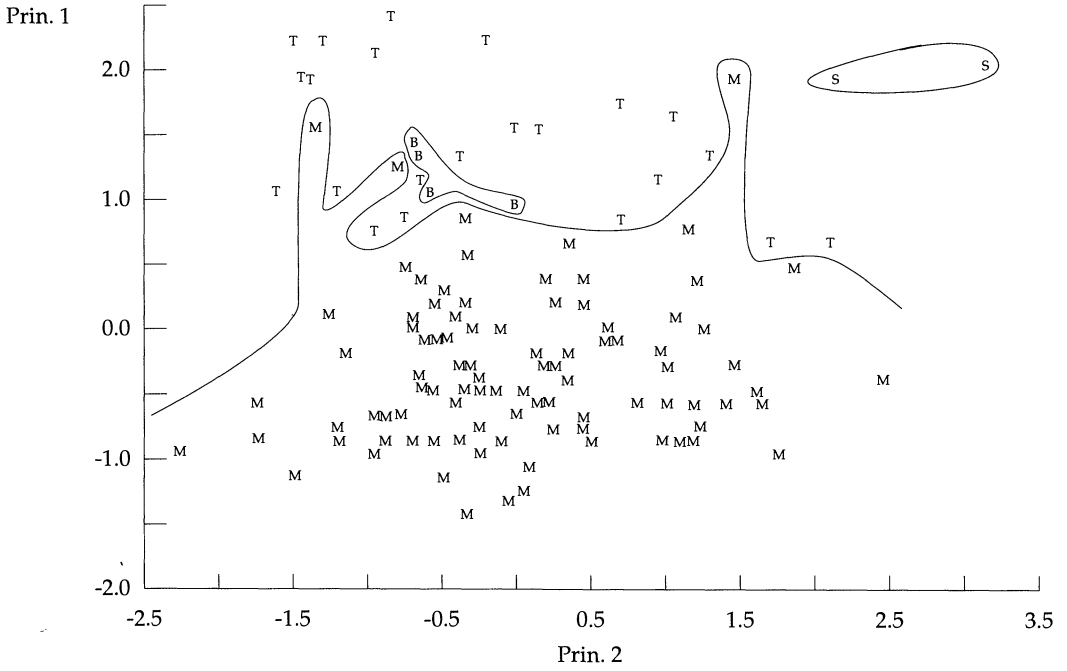


FIG. 4. Principal Components Analysis (PCA) based on the 21 morphological characters shown to be significantly different (0.05 level or greater) between *Solanum megistacrolobum* and *S. toralapanum*. B = *Solanum boliviense*, M = *S. megistacrolobum*, S = *S. sogarandinum*, and T = *S. toralapanum*.

one were for characters 14, 3, 13, 22, 11, and 10; the six highest loadings on PCA axis two were for characters 5, 6, 12, 21, 4, and 7 (Table 3). Three of these characters (7, 10, and 14) have been used by prior taxonomists to distinguish *S. megistacrolobum* and *S. toralapanum* (Table 1).

DISCUSSION

Prior descriptions of *S. megistacrolobum* and *S. toralapanum* largely distinguished the taxa by four morphological characters. These characters are so highly variable (Fig. 2), often within individual accessions, that reliance on any one of them to identify taxa could lead to frequent misidentifications. The accessions we analyzed, however, largely clustered by prior determinations, but only after eliminating the five characters that showed no statistically significant differences between *S. megistacrolobum* and *S. toralapanum*. This indicates that the morphological characters are useful, even though individual character states regularly cross species boundaries. These accessions have been identified by various taxonomists at NRSP-6 from field plantings of from 6 to 12 plants per accession, and have been accompanied by data on prior determinations and locality data (Spooner and van den Berg 1992a). It is apparent that reliably consistent determinations for some accessions require the use of many characters from more than one individual per accession. We assume that the patterns of intra- and interspecific variability documented here would be similar in replicated field plantings over different environments, but our conclusions are based on this one field planting. It also is possible that these taxa would better maintain their differences in their native environments.

The high degree of variability within these two species, and intermediacy between them, is consistent with prior observations (Brücher 1959; Correll 1962; Hawkes 1990; Hawkes and Hjerting 1989; Ochoa 1990). The high morphological variability we documented within *S. megistacrolobum* also is consistent with the high variability in their glycoalkaloid profiles shown by Johns and Osman (1986). They interpret their data to group *S. toralapanum* with *S. boliviense* (and *S. sanctae-rosae*). Our morphological data showed that most accessions of *S. megistacrolobum* and *S. toralapanum* are more similar to each other than either is to *S. boliviense*.

Some of the intermediacy between *S. megis-*

tacrolobum and *S. toralapanum* is partitioned in zones of geographical overlap between their main areas of distribution. Four of the five accessions of *S. megistacrolobum* that cluster with *S. toralapanum* (Fig. 3) co-occur with this species in areas 7, 16, and 33 (Table 2; Fig. 1). This pattern is consistent with hypotheses of inter-specific hybridization, primary divergence, or misidentification. The remaining three "misplaced" accessions of *S. megistacrolobum* are from areas 2, 11, and 13 where only one species per area occurs. The one-way ANOVA of character state differences between species for the subset of the taxa that occur in the geographic areas that had only one species per area show a similar to slightly reduced significance of characters relative to the entire data set. These results would be expected when hybridization or primary divergence were not occurring. The distributional data, therefore, are ambiguous regarding causes of morphological intermediacy between *S. megistacrolobum* and *S. toralapanum*.

Our study demonstrates the following between *S. megistacrolobum* and *S. toralapanum*: 1) there is much intraspecific variation in all character states, 2) there are intermediate populations that appear to bridge the gap between the species, 3) no morphological characters can be used alone to distinguish the taxa consistently, 4) the taxa have contiguous and somewhat overlapping distributions, 5) the taxa are difficult to differentiate consistently, especially on the basis of key characters using single specimens, and 6) the taxa can generally be distinguished, but only by multivariate techniques, and then only with a subset of the characters. Patterns of overlapping character states used to define similar taxa have been shown to be common throughout much of *Solanum* sect. *Petota* (Spooner and van den Berg 1992a). In some cases, these taxa have not been supported by morphological reinvestigations (Spooner et al. 1993; van den Berg and Spooner 1992). Other studies, however (Spooner and van den Berg 1992b), and this one, provide weak support for the recognition of taxa at some level. The similarity of these taxa, and resulting confusion as to taxonomic status, among similar taxa is reflected in widely different treatments of sect. *Petota* by different contemporary authors (Spooner and van den Berg 1992a). The differing contemporary taxonomic treatments of *S. megistacrolobum* and *S. toralapanum* as species (Gorbatenko 1989; Hawkes and Hjerting 1989;

Hawkes 1990) or as varieties (Ochoa 1990) is one example of such disagreement.

Our experience, based on the results of the one-way ANOVA of character states, loadings on the PCA, and our personal field observations suggest that the following combination of characters best differentiate *S. megistacrolobum* and *S. toralapanum*: leaf odor, flower number, decurrency of the primary lateral leaflets, and peduncle length. The wide variability of these characters makes the construction of a dichotomous key difficult, and we refer the reader to Figure 2 for useful means and ranges of these character states.

The morphological and distributional patterns of *S. megistacrolobum* and *S. toralapanum*, that of weakly differentiated taxa, with contiguous to slightly overlapping geographic distributions, more closely fits a model of subspecies or varietal rank than one of separate species (Stuessy 1990). One biological factor also often associated with varieties or subspecies is reduced crossability between them, but this reduced crossability is not known to occur between these two taxa (Buck 1966; Hawkes 1990; Ochoa 1990; Pandey 1960), including hybrids to the F₂ generation (Hawkes and Hjerting 1989). *Solanum* sect. *Petota* includes many phenetically very distinct taxa, some with different geographic ranges, that have the ability to produce advanced generation hybrids artificially, with little or no reduction in fertility (Spooner and van den Berg 1992b). Hawkes (1990) hypothesizes that many wild potato taxa are reproductively isolated by cryptic structural differences of the chromosomes and that artificial and natural hybrids exhibit advanced generation breakdown. His data, however, are largely observational and lack detailed measurements, intraspecific crossing controls, and statistical presentation of results, and are therefore questionable (Spooner and van den Berg 1992a). A strict application of the biological species concept in much of sect. *Petota*, therefore, would lump many taxa that have distinct morphological (and perhaps agronomically important) characters. Therefore, we rely on a morphological species concept regarding *S. megistacrolobum* and *S. toralapanum*. For these reasons, our data agree most closely with Ochoa's (1990) treatment of *S. toralapanum* as a variety of *S. megistacrolobum* [as *S. megistacrolobum* var. *toralapanum* (Cárd. and Hawkes) Ochoa]. Further discussion

of taxonomic rank is provided in Giannattasio and Spooner (1994).

ACKNOWLEDGMENTS. This paper represents a portion of a M.S. thesis submitted to the Department of Horticulture at the University of Wisconsin. We thank Brian S. Yandell for statistical advice; John Doebley, Michael J. Havey, Kenneth J. Sytsma, Jonathan Wendel, Ronald G. van den Berg, and Richard Whitkus for advice on an earlier draft of the manuscript; and John Bamberg and staff of NRSP-6 for help in acquiring and growing the accessions here examined. This research was supported by the USDA and by grants from the Wisconsin Alumni Research Foundation (grants 1350601 and 1350602) to David Spooner.

LITERATURE CITED

- BUCK, R. W., Jr. 1966. Cytogenetic studies of species and interspecific hybrids of *Solanum*, section *Tuberarium*, series *Megistacroloba*. *American Potato Journal* 43: 199-206.
- BRÜCHER, V. H. 1959. Kritische Betrachtungen zur Nomenklatur argentinischer wildkartoffeln. VI. Die Serie *Alticola* (= *Megistacroloba*). *Der Züchter* 29: 257-264.
- CORRELL, D. S. 1962. *The potato and its wild relatives*. Renner, Texas: Texas Research Foundation.
- D'ARCY, WILLIAM G. 1991. The Solanaceae since 1976, with a review of its biogeography. Pp. 75-137 in *Solanaceae III: Taxonomy, chemistry, evolution*, eds. J. G. Hawkes, R. N. Lester, M. Nee and N. Estrada. R. Kew: Royal Botanic Gardens Kew and Linnean Society of London.
- GIANNATTASIO, R. B. 1992. A morphological and molecular reexamination of species boundaries and hybridization concerning *Solanum megistacrolobum* Bitter and *S. toralapanum* Cárd. and Hawkes. M.S. thesis, University of Wisconsin, Madison.
- and D. M. SPOONER. 1994. A reexamination of species boundaries and hypotheses of hybridization concerning *Solanum megistacrolobum* and *S. toralapanum* (*Solanum* sect. *Petota*, ser. *Megistacroloba*): Molecular data. *Systematic Botany* 19: 106-115.
- GORBATENKO, L. E. 1989. A conspect of the system of the section *Petota* Dumort. of the genus *Solanum* L. from South America. *Trudy po prikladnoj botanike, genetike i selekcii* 126: 92-108 (in Russian).
- HANNEMAN, R. E., Jr. and J. B. BAMBERG. 1986. Inventory of tuber-bearing *Solanum* species. *Wisconsin Agricultural Experiment Station Bulletin* 533: 1-216.
- HAWKES, J. G. 1990. *The potato: Evolution, biodiversity and genetic resources*. Washington, D.C.: Smithsonian Institution Press.
- and J. P. HJERTING. 1969. *The potatoes of Ar-*

- gentina, Brazil, Paraguay, and Uruguay. A biosystematic study. Oxford: Oxford Univ. Press.
- and ———. 1989. *The potatoes of Bolivia: Their breeding value and evolutionary relationships*. Oxford: Oxford Univ. Press.
- HUAMÁN, Z., J. G. HAWKES, and P. R. ROWE. 1980. *Solanum ajanhuiri*: An important diploid potato cultivated in the Andean altiplano. *Economic Botany* 34: 335-343.
- , ———, and ———. 1982. A biosystematic study of the origin of the cultivated diploid potato, *Solanum* × *ajanhuiri* Juz. et Buk. *Euphytica* 31: 665-676.
- , ———, and ———. 1983. Chromatographic studies on the origin of the cultivated diploid potato *Solanum* × *ajanhuiri* Juz. et Buk. *American Potato Journal* 60: 361-367.
- JOHNS, T. and S. F. OSMAN. 1986. Glycoalkaloids of *Solanum* series *Megistacrolobum* and related potato cultivars. *Biochemical Systematics and Ecology* 14: 651-655.
- , Z. HUAMÁN, C. OCHOA, and P. E. SCHMIEDICHE. 1987. Relationships among wild, weed, and cultivated potatoes in the *Solanum* × *ajanhuiri* complex. *Systematic Botany* 12: 541-552.
- OCHOA, C. M. 1984. Karyotaxonomic studies on wild Bolivian tuber-bearing *Solanum* sect. *Petota* (1). *Phytologia* 55: 17-40.
- . 1990. *The potatoes of South America: Bolivia*. Cambridge: Cambridge Univ. Press.
- OKADA, K. A. and A. M. CLAUSEN. 1982. Natural hybridization between *Solanum acaule* Bitt. and *S. megistacrolobum* Bitt. in the province of Jujuy, Argentina. *Euphytica* 31: 817-835.
- PANDEY, K. K. 1960. Self-incompatibility in *Solanum megistacrolobum* Bitt. *Phyton* 14: 13-19.
- ROHLF, F. J. 1992. *NTSYS-pc, numerical taxonomy and multivariate analysis system*. New York: Exeter Publishing, Ltd.
- and R. R. SOKAL. 1981. Comparing numerical taxonomic studies. *Systematic Zoology* 30: 459-490.
- RYAN, B. F., B. L. JOINER, and T. A. RYAN. 1985. *Minitab handbook*, 2nd ed. Boston: PWS-Kent.
- SOKAL, R. R. 1986. Phenetic taxonomy: Theory and methods. *Annual Review of Ecology and Systematics* 17: 423-442.
- SPOONER, D. S. and K. J. SYTSMAN. 1992. Reexamination of series relationships of Mexican and Central American wild potatoes (*Solanum* sect. *Petota*): Evidence from chloroplast DNA restriction site variation. *Systematic Botany* 17: 432-448.
- and R. G. VAN DEN BERG. 1992a. An analysis of recent taxonomic concepts in wild potatoes (*Solanum* sect. *Petota*). *Genetic Resources and Crop Evolution* 39: 23-37.
- and ———. 1992b. Species limits and hypotheses of hybridization of *Solanum berthaultii* Hawkes and *S. tarijense* Hawkes: Morphological data. *Taxon* 41: 685-700.
- , R. O. CASTILLO, and L. E. LÓPEZ. 1993. Synonymy within wild potatoes (*Solanum* sect. *Petota*: Solanaceae): The case of *Solanum andreanum*. *Systematic Botany* 18: 209-217.
- STUESSY, T. F. 1990. *Plant taxonomy: The systematic evaluation of comparative data*. New York: Columbia Univ. Press.
- UGENT, D. 1970. *Solanum raphanifolium*, a Peruvian wild potato species of hybrid origin. *Botanical Gazette* 131: 225-233.
- VAN DEN BERG, R. G. and D. M. SPOONER. 1992. A reexamination of infraspecific taxa of a wild potato, *Solanum microdontum* Bitter (*Solanum* sect. *Petota*: Solanaceae). *Plant Systematics and Evolution* 182: 239-252.