

COLLAPSE OF MORPHOLOGICAL SPECIES IN THE WILD POTATO *SOLANUM BREVICAULE* COMPLEX (*SOLANACEAE*: SECT. *PETOTA*)¹

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The major cultivated potato, *Solanum tuberosum*, and six other related cultivated species, are hypothesized to have arisen from a group of weedy relatives indigenous to the central Andes of central Peru, Bolivia, and northern Argentina. A major problem hindering investigations of the origins of the cultivated species has been a continuing debate over the species boundaries of their putative progenitors. This study investigated the morphological phenetic species boundaries of these putative progenitors and five cultivated taxa, here collectively referred to as the *Solanum brevicaule* complex. Two hundred fifteen accessions of 30 taxa in the *S. brevicaule* complex and 42 accessions of six taxa outside of the complex were assessed for 53 morphological traits in replicate plots in a common garden, resulting in a total of over 81 000 data points. Phenetic analyses of these data are unable to support 30 taxa, suggesting instead a single variable complex at best only weakly divided into three widely intergrading sets of populations: (1) Peruvian and geographically adjacent Bolivian accessions (including wild species and all the cultigens), (2) Bolivian and Argentinian accessions and *S. verrucosum* from Mexico (including only wild species), and (3) the Bolivian and Argentinian wild species *S. oplocense*. These and other data suggest that Hawkes's 1990 treatment (*The Potato: Evolution, Biodiversity, and Genetic Resources*, Smithsonian Institution Press, Washington, DC.) of 232 morphological species is an overestimate for sect. *Petota*.

Key words: potato; section *Petota*; Solanaceae; *Solanum brevicaule* complex; South America.

The genus *Solanum* L. is one of the five largest genera of flowering plants, with 1400 species, according to Maberley (1993). If D'Arcy's (1991) most recent estimate of 1000 species for *Solanum* is used, it is among the 13 largest. *Solanum* sect. *Petota* Dumort., the potato and its wild relatives, contains 232 of these species, according to the latest classification of the group (Hawkes, 1990). An alternative classification (Child, 1990), supported by morphological and chloroplast DNA (cpDNA) data (Spooner, Anderson, and Jansen, 1993), places all of the tuber-bearing species in sect. *Petota*, and the nine non-tuber-bearing species of sect. *Petota* in sect. *Etuberosum*

(Bukasov and Kameraz) A. Child, sect. *Juglandifolium* (Rydb.) A. Child, and sect. *Lycopersicum* (Mill.) Wettst. Even with the recent transfers of nine species of *Lycopersicon* Mill. to *Solanum* (Spooner, Anderson, and Jansen, 1993) and 32 species of *Cyphomandra* Sendtner to *Solanum* (Bohs, 1995), wild potatoes comprise over one-fifth of this large genus.

Section *Petota* has been the subject of extensive historical and recent taxonomic work. Section *Petota* has been partitioned variously into 36 series (Bukasov, 1978) or 21 series (Hawkes, 1990). Treatments differ widely regarding the affiliation of species into series, hypotheses of species boundaries, ranks of infraspecific taxa, and the interpretation of "intermediate" or taxonomically difficult populations as hybrids (Spooner and van den Berg, 1992a). Harlan and de Wet (1971) highlighted the lack of agreement of the taxonomic treatments of potatoes (comparing Bukasov, 1933; Bukasov and Kameraz, 1959; Hawkes, 1963), and of maize, sorghum, and wheat to argue that traditional taxonomy had little practical use for plant breeders. They constructed an alternative hierarchical "gene pool classification" based solely on varying possibilities of artificial gene transfer among species.

Our research reevaluates the morphological support for discrete species in the "*S. brevicaule* complex." This complex was first recognized by Ugent (1966; first published in Ugent, 1970) as a taxonomically confusing group of putative ancestors of the cultivated potato species, endemic to central Peru, Bolivia, and northern Argentina. All members of the *S. brevicaule* complex (1) have pinnately dissected leaves, (2) round fruits, (3) rotate to rotate-pentagonal corollas, (4) are largely sexually compatible (Hawkes, 1958; Pandey, 1962; Hawkes and Hjerting, 1969, 1989; Ochoa, 1990), (5) are hypothesized to form occasional natural hybrid swarms (Hawkes and

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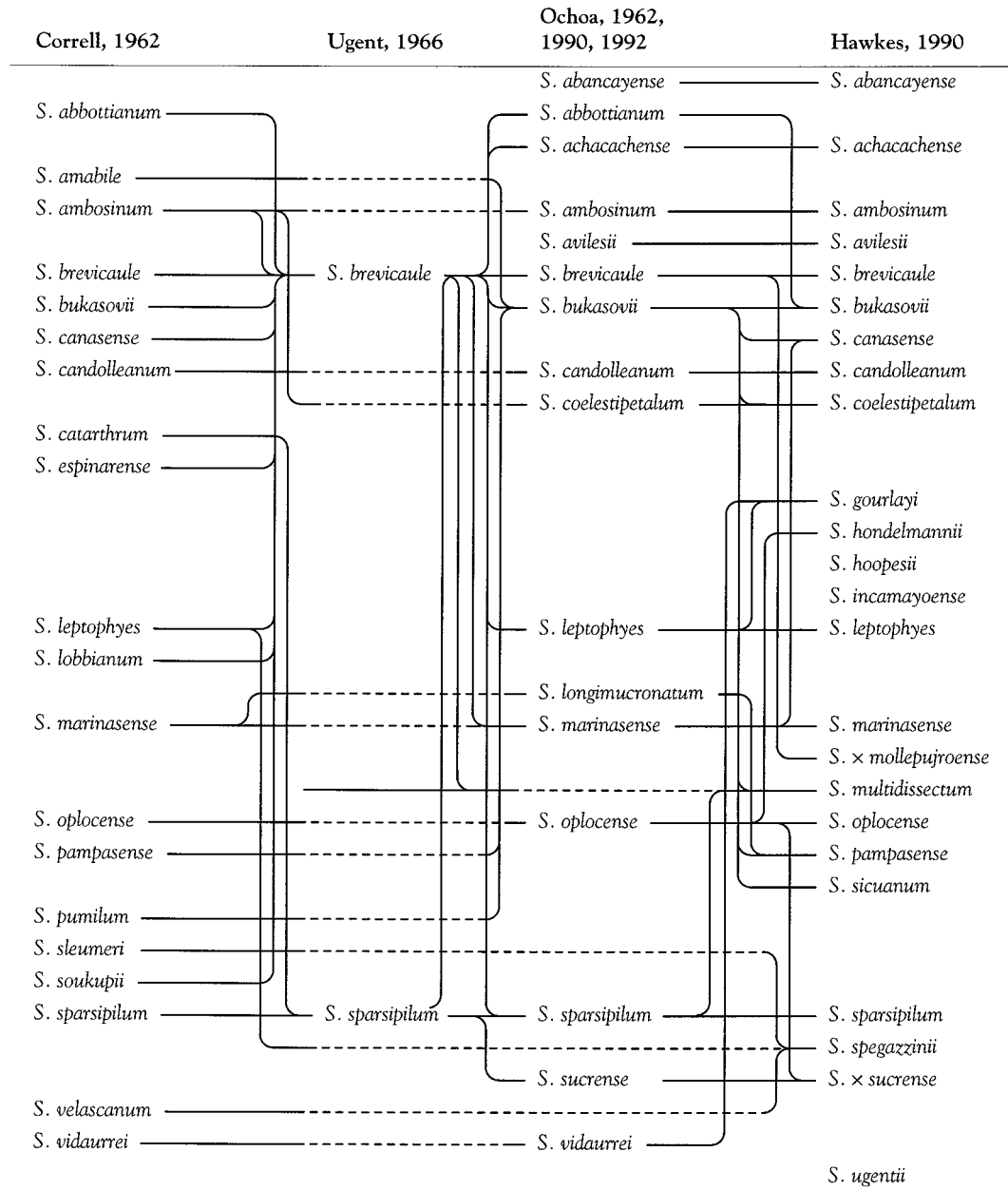


Fig. 1. Chronological flow chart of hypotheses of species boundaries of members of the *S. brevicaule* complex according to Correll (1962), Ugent (1966), Ochoa (1962, 1990, 1992), and Hawkes (1990) (Table 1). Dotted lines indicate that an author did not treat the species.

Hjerting 1969, 1989; Hawkes 1978), (6) have Endosperm Balance Numbers (a phenomenon of sexual compatibility based on ratios of maternal/paternal genomes in the endosperm [Johnston and Hanneman, 1980, 1982; Hanneman, 1994]) matching their ploidy levels, and (7) are frequently confused in the literature, herbarium, and germplasm collections regarding identifications (Ugent, 1966; Grun, 1990; Spooner and van den Berg 1992a; Spooner et al., 1994).

Members of the *S. brevicaule* complex are classified in most taxonomic treatments in series *Tuberosa* (Rydb.) Hawkes. Ploidy levels include diploids, tetraploids, pentaploids, and hexaploids. *Solanum gourlayi* has two ploidy levels (diploid and tetraploid), and *S. oplocense* has

three (diploid, tetraploid, and hexaploid). Wild members of the *S. brevicaule* complex (25 taxa) are difficult to distinguish from the cultivated members (seven taxa) and from each other. Two wild species members of the complex, *S. leptophyes* Bitter and *S. sparsipilum* (Bitter) Juz. and Bukasov, are believed to be immediate progenitors of the cultigens, and other members have been implicated as contributing germplasm to the cultigens through hybridization as weeds (Ugent, 1970). No qualitative characters distinguish these species, and they differ only by widely overlapping character states (Spooner and van den Berg, 1992b; Spooner, van den Berg, and Bamberg, 1995; Van den Berg, Groendijk-Wilders, and Kardolus, 1996). Most new taxa in sect. *Petota* have been described with-

TABLE 1. Alternative classifications of wild taxa of the *Solanum brevicaulis* complex, as illustrated in Fig. 1. Accepted taxa are listed as boldface and left justified; synonyms are indented. The taxonomic decisions by Ugent (1966) only appear in a thesis and were not effectively published. The most recent decision of Ochoa is used when his treatments conflict.

	Correll (1962)	Ugent (1966)	Ochoa (1962, 1990, 1992)	Hawkes (1990)
<i>Solanum abbotianum</i> Juz.		<i>S. brevicaulis</i> subsp.	<i>S. abbotianum</i> Ochoa	<i>S. abbotianum</i>
<i>S. amabile</i> Vargas		<i>brevicaule</i>	<i>S. abbotianum</i>	<i>S. abbotianum</i>
<i>S. ambosinum</i> Ochoa		<i>S. leptophyes</i>	<i>S. achacachense</i>	<i>S. achacachense</i>
<i>S. coelestipetalum</i> Vargas		<i>S. pachytrichum</i>	<i>S. ambosinum</i>	<i>S. ambosinum</i>
<i>S. ochoae</i> Vargas		<i>S. gourlayi</i>	<i>S. avilesii</i>	<i>S. avilesii</i>
<i>S. brevicaulis</i> Bitter		<i>S. soukupii</i>	<i>S. avilesii</i> Hawkes and Hjert.^a	<i>S. brevicaulis</i>
<i>S. liriunianum</i> M. Cárdenas and Hawkes		<i>S. punoense</i>	<i>S. candellarianum</i> M. Cárdenas	<i>S. liriunianum</i>
<i>S. colominense</i> M. Cárdenas		<i>S. liriunianum</i>	<i>S. brevicaulis</i>	<i>S. colominense</i>
<i>S. achacachense</i> M. Cárdenas		<i>S. colominense</i>	<i>S. mollepujroense</i>	<i>S. colominense</i>
<i>S. bukasovii</i> Rybin		<i>S. spinarense</i>	<i>S. bukasovii</i>	<i>S. bukasovii</i>
<i>S. canasense</i> Hawkes var. <i>canasense</i>		<i>S. achacachense</i>	<i>S. amabile</i>	<i>S. canasense</i>
<i>S. lechnovichi</i> Hawkes		<i>S. leptophyes</i> f. <i>gourlayi</i>	<i>S. canasense</i>	<i>S. lechnovichi</i>
<i>S. fragariaefractum</i> Hawkes		(Rybin) Ugent	<i>S. canasense</i> var. <i>alba</i>	<i>S. punoense</i>
<i>S. canasense</i> var. <i>alba</i> Vargas		<i>S. bukasovii</i>	<i>S. canasense</i> var. <i>calcense</i>	<i>S. soukupii</i>
<i>S. canasense</i> var. <i>calcense</i> Vargas		<i>S. abbotianum</i>	<i>S. canasense</i> var. <i>intihuatanense</i>	<i>S. spinarense</i>
<i>S. punoense</i> Hawkes		<i>S. multi-dissectum</i>	<i>S. canasense</i> var. <i>lechnovichi</i>	<i>S. canasense</i> var. <i>alba</i>
<i>S. canasense</i> var.		<i>S. neohawkesii</i>	<i>S. canasense</i> var. <i>lechnovichi</i>	<i>S. canasense</i> var. <i>calcense</i>
<i>intihuatanense</i> Vargas		<i>S. lobbianum</i> f. <i>multidissectum</i>	<i>S. canasense</i> var. <i>lechnovichi</i>	<i>S. canasense</i> var. <i>intihuatanense</i>
<i>S. lechnovichi</i> var. <i>latifolium</i> Vargas		<i>S. canasense</i> var. <i>neohawkesii</i>	<i>S. canasense</i> var. <i>lechnovichi</i>	<i>S. lechnovichi</i> var. <i>latifolium</i>
<i>S. canasense</i> var. <i>neohawkesii</i> (Ochoa)		<i>S. multi-dissectum</i> subsp.	<i>S. lechnovichi</i> var. <i>latifolia</i>	<i>S. amabile</i>
Correll		<i>neohawkesii</i> (Ochoa) Hawkes	<i>S. lechnovichi</i> var. <i>latifolia</i>	<i>S. canasense</i> var. <i>latifolium</i>
<i>S. neohawkesii</i> Ochoa		<i>S. brevicaulis</i> subsp. <i>canasense</i>	<i>S. neohawkesii</i>	<i>S. canasense</i> var. <i>lechnovichi</i>
<i>S. canasense</i> var. <i>xerophyllum</i> (Vargas)		(Hawkes) Ugent	<i>S. ochoae</i>	<i>S. canasense</i> var. <i>xerophyllum</i>
Correll		<i>S. canasense</i>	<i>S. pampasense</i>	(Vargas) Hawkes
<i>S. lechnovichi</i> var. <i>xerophyllum</i> Vargas		<i>S. lechnovichi</i>	<i>S. pumilum</i>	<i>S. candolleianum</i>
<i>S. candolleianum</i> P. Berthault		<i>S. fragariaefractum</i>	<i>S. punoense</i>	<i>S. mandonii</i>
<i>S. mandonii</i> A.D.C.		<i>S. canasense</i> var. <i>alba</i>	<i>S. sicuanum</i>	<i>S. coelestipetalum</i>
<i>S. spinarense</i> Vargas		<i>S. lechnovichi</i> var. <i>latifolia</i>	<i>S. soukupii</i>	<i>S. ochoae</i>
<i>S. spagazzinii</i> Bitter		<i>S. canasense</i> var. <i>calcense</i>	<i>S. soukupii</i> var. <i>spinarense</i>	<i>S. gourlayi</i> subsp. <i>gourlayi</i>
<i>S. pachytrichum</i> Hawkes		<i>S. canasense</i> var.	<i>S. bukasovii</i> var. <i>multidissectum</i>	<i>S. gourlayi</i> subsp. <i>salense</i> A.M. Clausen and K.A. Okada
<i>S. leptophyes</i> f. <i>gourlayi</i> (Hawkes)		<i>intihuatanense</i>	(Hawkes) Ochoa	<i>S. gourlayi</i> subsp. <i>vidaurrei</i> (M. Cárdenas) Hawkes and Hjert.
Correll		<i>S. ochoae</i>	<i>S. multi-dissectum</i>	<i>S. vidaurrei</i>
<i>S. lobbianum</i> Bitter		<i>S. lechnovichi</i> var. <i>xerophylla</i>	<i>S. candolleianum</i>	<i>S. vidaurrei</i>
<i>S. lobbianum</i> f. <i>multidissectum</i>		<i>S. canasense</i> var. <i>xerophyllum</i>	<i>S. mandonii</i>	<i>S. gourlayi</i> subsp. <i>pachytrichum</i> (Hawkes)
(Hawkes) Correll		<i>S. canasense</i> var. <i>lechnovichi</i>	<i>S. coelestipetalum</i>	Hawkes and Hjert.
<i>S. multi-dissectum</i>		<i>S. x</i> <i>sparsipitum</i>	<i>S. leptophyes</i>	<i>S. pachytrichum</i>
<i>S. marinasense</i> Vargas		<i>S. tuberosum</i> subsp.	<i>S. gourlayi</i>	<i>S. pachytrichum</i>
<i>S. cuzcoense</i> Ochoa		<i>sparsipitum</i> Bitter	<i>S. pachytrichum</i>	<i>S. hondelmannii</i> Hawkes and Hjert.^b
<i>S. marinasense</i> var. <i>dentifolium</i> Vargas		<i>S. catarthrum</i>	<i>S. leptophyes</i> f. <i>gourlayi</i>	<i>S. hoopesii</i> Hawkes and K.A. Okada
<i>S. marinasense</i> f.		<i>S. anomalocalyx</i>	<i>S. longimucronatum</i>	<i>S. incayoiense</i> K.A. Okada and A.M. Clausen
<i>longimucronatum</i>		<i>S. calcense</i>	<i>S. marinasense</i>	<i>S. leptophyes</i>
<i>S. longimucronatum</i> Vargas		<i>S. mollepujroense</i>	<i>S. marinasense</i> var. <i>dentifolium</i>	<i>S. marinasense</i>
<i>S. oplocense</i> Hawkes		<i>S. membranaceum</i>	<i>S. cuzcoense</i>	<i>S. marinasense</i> var. <i>dentifolium</i>
<i>S. pampasense</i> Hawkes		<i>S. sparsipitum</i> var.	<i>S. oplocense</i>	<i>S. pampasense</i> f. <i>glabrescens</i>
<i>S. pampasense</i> f.		<i>llallaguanianum</i>	<i>S. subandigenum</i> Hawkes var.	<i>S. x mollepujroense</i>^c
<i>glabrescens</i> Correll		<i>S. sparsipitum</i>	<i>canaguense</i> M. Cárdenas	<i>S. multi-dissectum</i>
<i>S. pumilum</i> Hawkes		<i>S. tuberosum</i> subsp. <i>sparsipitum</i>	<i>S. sparsipitum</i>	<i>S. fragariaefractum</i>
<i>S. sleumeri</i> Correll		<i>S. aracc-papa</i> Juz.	<i>S. tuberosum</i> subsp. <i>sparsipitum</i>	<i>S. lobbianum</i> f. <i>multidissectum</i>
<i>S. soukupii</i> Hawkes		<i>S. catarthrum</i>	<i>S. catarthrum</i>	<i>S. oplocense</i>
		<i>S. anomalocalyx</i>	<i>S. anomalocalyx</i>	<i>S. pampasense</i>

TABLE 1. Continued.

Correll (1962)	Ochoa (1962, 1990, 1992)	Hawkes (1990)
<i>S. sparsipilum</i> (Bitter) Buk.	<i>S. brevimucronatum</i>	<i>S. longimucronatum</i>
<i>S. tuberosum</i> subsp. <i>sparsipilum</i> Bitter	<i>S. lapazense</i>	<i>S. marinacense</i> f. <i>longimucronatum</i>
<i>S. calcense</i> Hawkes	<i>S. calcense</i>	<i>S. sicuanum</i>^d
<i>S. anomalocalyx</i> var. <i>brachystylum</i> M. Cárdenas and Hawkes	<i>S. fragariaefructum</i>	<i>S. sparsipilum</i> subsp. <i>sparsipilum</i>
<i>S. anomalocalyx</i> var. <i>anomalocalyx</i> var. <i>murale</i> M. Cárdenas and Hawkes	<i>S. anomalocalyx</i> var. <i>llallaguanianum</i>	<i>S. tuberosum</i> subsp. <i>sparsipilum</i>
<i>S. anomalocalyx</i> var. <i>murale</i> M. Cárdenas and Hawkes	<i>S. anomalocalyx</i> var. <i>brachystylum</i>	<i>S. catarthrum</i>
<i>S. anomalocalyx</i> var. <i>murale</i> M. Cárdenas and Hawkes	<i>S. anomalocalyx</i> var. <i>brachystylum</i>	<i>S. anomalocalyx</i>
<i>S. membranaceum</i> Vargas	<i>S. calcense</i> var. <i>urubambae</i>	<i>S. brevimucronatum</i>
<i>S. atlandiae</i> M. Cárdenas	<i>S. membranaceum</i>	<i>S. lapazense</i>
<i>S. sparsipilum</i> var. <i>llallaguanianum</i> (M. Cárdenas and Hawkes) Correll	<i>S. sparsipilum</i> var. <i>llallaguanianum</i>	<i>S. anomalocalyx</i> var. <i>llallaguanianum</i>
<i>S. sucrense</i> Hawkes	<i>S. ruitz-zeballosii</i> M. Cárdenas	<i>S. anomalocalyx</i> var. <i>brachystylum</i>
<i>S. anomalocalyx</i> Hawkes	<i>S. sucrense</i>	<i>S. anomalocalyx</i> var. <i>murale</i>
<i>S. brevimucronatum</i> Hawkes	<i>S. vidaurrei</i>	<i>S. calcense</i> var. <i>urubambae</i>
<i>S. lapazense</i> Hawkes		<i>S. membranaceum</i>
<i>S. anomalocalyx</i> var. <i>llallaguanianum</i> M. Cárdenas and Hawkes		<i>S. sparsipilum</i> var. <i>llallaguanianum</i>
<i>S. calcense</i> var. <i>urubambae</i> Vargas		<i>S. ruitz-zeballosii</i>
<i>S. velascanum</i> Bitter and Wittm.		<i>S. sparsipilum</i> subsp. <i>calcense</i> (Hawkes)
<i>S. famatinae</i> Bitter and Wittm.		Hawkes
<i>S. vidaurrei</i> M. Cárdenas		<i>S. calcense</i>
		<i>S. spegazzinii</i>
		<i>S. famatinae</i>
		<i>S. steueneri</i>
		<i>S. × sucrense</i>^e
		<i>S. subandigenum</i> var. <i>canariquense</i>
		<i>S. ugentii</i>

^a Ochoa (1990) incorrectly referred to this taxon as *S. candellarianum* (see Spooner and van den Berg, 1992a).
^b Hawkes (1990) recognized *S. hondelmannii* as a distinct species, while Ochoa (1990) considered it a "hybrid variant" of *S. oplocense*, possibly involving *S. chacoense* or *S. lituinum*.
^c Hawkes (1990) considered *S. × mollepujroense* a hybrid between *S. gourlayi* subsp. *pachytrichum* and *S. sparsipilum*.
^d Hawkes (1990) used the new name *S. sicuanum* because *S. pumilum* Hawkes is a homonym.
^e Astley and Hawkes (1979) and Hawkes (1990) considered *S. × sucrense* to be of hybrid origin between *S. oplocense* and *S. tuberosum* subsp. *andigena*.

TABLE 2. Accessions of *Solanum* sect. *Petota* examined. Vouchers are deposited at the herbarium of the National Research Support Program, Sturgeon Bay, Wisconsin.

Map location ^a	Taxon ^b	PI number ^c	Country, department, or province
1	<i>Solanum stenotomum</i> subsp. <i>goniocalyx</i>	230512	Peru, Amazonas
1	<i>S. stenotomum</i> subsp. <i>stenotomum</i>	230513	Peru, Amazonas
2	<i>S. ambosinum</i>	365362	Peru, Ancash
3	<i>S. ambosinum</i>	498209	Peru, Ancash
3	<i>S. ambosinum</i>	498210	Peru, Ancash
3	<i>S. ambosinum</i>	498211	Peru, Ancash
3	<i>S. ambosinum</i>	498212	Peru, Ancash
3	<i>S. ambosinum</i>	498213	Peru, Ancash
4	<i>S. stenotomum</i> subsp. <i>goniocalyx</i>	195214	Peru, Huanuco
4	<i>S. stenotomum</i> subsp. <i>stenotomum</i>	205527	Peru, Huanuco
5	<i>S. medians</i>	458402	Peru, Lima
6	<i>S. medians</i>	265872	Peru, Lima
6	<i>S. medians</i>	283081	Peru, Lima
6	<i>S. medians</i>	320260	Peru, Lima
6	<i>S. medians</i>	473496	Peru, Lima
7	<i>S. bukasovii</i>	365304	Peru, Lima
8	<i>S. multidissectum</i>	210043	Peru, Junin
9	<i>S. multidissectum</i>	210044	Peru, Junin
10	<i>S. ambosinum</i>	365315	Peru, Huancavelica
10	<i>S. bukasovii</i>	473492	Peru, Huancavelica
10	<i>S. bukasovii</i>	473493	Peru, Huancavelica
10	<i>S. bukasovii</i>	473494	Peru, Huancavelica
11	<i>S. pampasense</i>	442697	Peru, Apurimac
12	<i>S. canasense</i>	473355	Peru, Ayacucho
12	<i>S. multidissectum</i>	210052	Peru, Ayacucho
12	<i>S. pampasense</i>	275274	Peru, Ayacucho
12	<i>S. pampasense</i>	458381	Peru, Ayacucho
12	<i>S. stenotomum</i> subsp. <i>goniocalyx</i>	195186	Peru, Ayacucho
13	<i>S. stenotomum</i> subsp. <i>goniocalyx</i>	195188	Peru, Ayacucho
14	<i>S. leptophyes</i>	473451	Peru, Ayacucho
15	<i>S. bukasovii</i>	414155	Peru, Apurimac
15	<i>S. multidissectum</i>	473354	Peru, Apurimac
16	<i>S. abancayense</i>	442700	Peru, Apurimac
16	<i>S. abancayense</i>	458403	Peru, Apurimac
16	<i>S. abancayense</i>	458404	Peru, Apurimac
17	<i>S. stenotomum</i> subsp. <i>stenotomum</i>	195204	Peru, Cuzco
18	<i>S. canasense</i>	210035	Peru, Cuzco
18	<i>S. canasense</i>	246533	Peru, Cuzco
18	<i>S. canasense</i>	473348	Peru, Cuzco
18	<i>S. leptophyes</i>	473445	Peru, Cuzco
18	<i>S. multidissectum</i>	473349	Peru, Cuzco
18	<i>S. sparsipilum</i>	230502	Peru, Cuzco
18	<i>S. sparsipilum</i>	246536	Peru, Cuzco
18	<i>S. sparsipilum</i>	473385	Peru, Cuzco
18	<i>S. stenotomum</i> subsp. <i>stenotomum</i>	205526	Peru, Cuzco
19	<i>S. marinasense</i>	498255	Peru, Cuzco
20	<i>S. multidissectum</i>	473353	Peru, Cuzco
20	<i>S. multidissectum</i>	498304	Peru, Cuzco
21	<i>S. acroscopicum</i>	365314	Peru, Arequipa
21	<i>S. acroscopicum</i>	365315	Peru, Arequipa
22	<i>S. marinasense</i>	498254	Peru, Arequipa
23	<i>S. multidissectum</i>	210055	Peru, Cuzco
23	<i>S. multidissectum</i>	473352	Peru, Puno
24	<i>S. bukasovii</i>	568933	Peru, Puno
24	<i>S. bukasovii</i>	568954	Peru, Puno
25	<i>S. canasense</i>	265863	Peru, Puno
25	<i>S. canasense</i>	442696	Peru, Puno
25	<i>S. canasense</i>	458376	Peru, Puno
26	<i>S. leptophyes</i>	458378	Peru, Puno
27	<i>S. acroscopicum</i>	230495	Peru, Tacna
28	<i>S. candolleanum</i>	498227	Bolivia, La Paz
29	<i>S. achacachense</i>	558032	Bolivia, La Paz
29	<i>S. brevicale</i>	545970	Bolivia, La Paz
29	<i>S. candolleanum</i>	498226	Bolivia, La Paz
29	<i>S. candolleanum</i>	498313	Bolivia, La Paz
29	<i>S. candolleanum</i>	545972	Bolivia, La Paz
30	<i>S. sparsipilum</i>	498284	Bolivia, La Paz
31	<i>S. leptophyes</i>	473342	Bolivia, La Paz
31	<i>S. leptophyes</i>	473343	Bolivia, La Paz

TABLE 2. Continued.

Map location ^a	Taxon ^b	PI number ^c	Country, department, or province
31	<i>S. sparsipilum</i>	473384	Bolivia, La Paz
31	<i>S. tuberosum</i> subsp. <i>andigena</i>	280995	Bolivia, La Paz
32	<i>S. canasense</i>	265865	Bolivia, La Paz
32	<i>S. multidissectum</i>	458393	Bolivia, La Paz
32	<i>S. stenotomum</i> subsp. <i>goniocalyx</i>	458393	Bolivia, La Paz
32	<i>S. tuberosum</i> subsp. <i>andigena</i>	280991	Bolivia, La Paz
33	<i>S. tuberosum</i> subsp. <i>andigena</i>	258917	Bolivia, Cochabamba
34	<i>S. brevicaule</i>	473378	Bolivia, Cochabamba
34	<i>S. brevicaule</i>	498111	Bolivia, Cochabamba
34	<i>S. brevicaule</i>	498112	Bolivia, Cochabamba
34	<i>S. brevicaule</i>	498114	Bolivia, Cochabamba
34	<i>S. brevicaule</i>	498115	Bolivia, Cochabamba
34	<i>S. brevicaule</i>	498218	Bolivia, Cochabamba
34	<i>S. brevicaule</i>	545967	Bolivia, Cochabamba
34	<i>S. brevicaule</i>	545969	Bolivia, Cochabamba
34	<i>S. brevicaule</i>	545971	Bolivia, Cochabamba
34	<i>S. microdontum</i>	545884	Bolivia, Cochabamba
34	<i>S. sparsipilum</i>	473375	Bolivia, Cochabamba
34	<i>S. sparsipilum</i>	498140	Bolivia, Cochabamba
34	<i>S. stenotomum</i> subsp. <i>stenotomum</i>	545980	Bolivia, Cochabamba
35	<i>S. hondelmannii</i>	545879	Bolivia, Cochabamba
35	<i>S. sparsipilum</i>	498134	Bolivia, Cochabamba
36	<i>S. avilesii</i>	498091	Bolivia, Santa Cruz
36	<i>S. avilesii</i>	498092	Bolivia, Santa Cruz
36	<i>S. avilesii</i>	498093	Bolivia, Santa Cruz
37	<i>S. leptophyes</i>	545985	Bolivia, Oruro
38	<i>S. tuberosum</i> subsp. <i>andigena</i>	258879	Bolivia, Oruro
39	<i>S. leptophyes</i>	545985	Bolivia, Potosi
39	<i>S. leptophyes</i>	545987	Bolivia, Potosi
39	<i>S. leptophyes</i>	545992	Bolivia, Potosi
39	<i>S. leptophyes</i>	545997	Bolivia, Potosi
40	<i>S. gourlayi</i> subsp. <i>gourlayi</i> 2×	537026	Bolivia, Potosi
40	<i>S. gourlayi</i> subsp. <i>pachytrichum</i>	545865	Bolivia, Potosi
40	<i>S. gourlayi</i> subsp. <i>pachytrichum</i>	545866	Bolivia, Potosi
40	<i>S. gourlayi</i> subsp. <i>pachytrichum</i>	545867	Bolivia, Potosi
40	<i>S. hondelmannii</i>	498071	Bolivia, Potosi
40	<i>S. hondelmannii</i>	545876	Bolivia, Potosi
40	<i>S. hondelmannii</i>	545877	Bolivia, Potosi
40	<i>S. hondelmannii</i>	545878	Bolivia, Potosi
40	<i>S. oplocense</i> 6×	442693	Bolivia, Potosi
40	<i>S. sparsipilum</i>	498285	Bolivia, Potosi
40	<i>S. sucrense</i>	442691	Bolivia, Potosi
40	<i>S. sucrense</i>	473382	Bolivia, Potosi
40	<i>S. sucrense</i>	473388	Bolivia, Potosi
41	<i>S. oplocense</i> 6×	458392	Bolivia, Potosi
41	<i>S. sucrense</i>	473506	Bolivia, Potosi
42	<i>S. oplocense</i> 4×	498070	Bolivia, Potosi
42	<i>S. oplocense</i> 6×	473368	Bolivia, Potosi
42	<i>S. oplocense</i> 6×	545909	Bolivia, Potosi
42	<i>S. sucrense</i>	545888	Bolivia, Potosi
43	<i>S. oplocense</i> 6×	498068	Bolivia, Potosi
43	<i>S. oplocense</i> 6×	545906	Bolivia, Potosi
44	<i>S. gourlayi</i> subsp. <i>pachytrichum</i>	545975	Bolivia, Chuquisaca
44	<i>S. gourlayi</i> subsp. <i>pachytrichum</i>	545976	Bolivia, Chuquisaca
44	<i>S. gourlayi</i> subsp. <i>pachytrichum</i>	545977	Bolivia, Chuquisaca
44	<i>S. gourlayi</i> subsp. <i>pachytrichum</i>	545978	Bolivia, Chuquisaca
44	<i>S. hondelmannii</i>	473365	Bolivia, Chuquisaca
44	<i>S. hondelmannii</i>	498067	Bolivia, Chuquisaca
44	<i>S. hondelmannii</i>	545869	Bolivia, Chuquisaca
44	<i>S. hondelmannii</i>	545870	Bolivia, Chuquisaca
44	<i>S. hondelmannii</i>	545871	Bolivia, Chuquisaca
44	<i>S. hondelmannii</i>	545872	Bolivia, Chuquisaca
44	<i>S. tuberosum</i> subsp. <i>andigena</i>	265882	Bolivia, Chuquisaca
45	<i>S. hoopesii</i>	545881	Bolivia, Chuquisaca
45	<i>S. hoopesii</i>	545883	Bolivia, Chuquisaca
45	<i>S. sucrense</i>	545915	Bolivia, Chuquisaca
45	<i>S. sucrense</i>	549008	Bolivia, Chuquisaca
45	<i>S. ugentii</i>	546030	Bolivia, Chuquisaca
45	<i>S. ugentii</i>	546032	Bolivia, Chuquisaca

TABLE 2. Continued.

Map location ^a	Taxon ^b	PI number ^c	Country, department, or province
46	<i>S. sucrensis</i>	498306	Bolivia, Chuquisaca
47	<i>S. oplocense</i> 4×	442682	Argentina, Jujuy
47	<i>S. oplocense</i> 4×	473184	Argentina, Jujuy
47	<i>S. oplocense</i> 4×	473198	Argentina, Jujuy
47	<i>S. oplocense</i> 6×	458360	Argentina, Jujuy
47	<i>S. oplocense</i> 6×	458361	Argentina, Jujuy
47	<i>S. oplocense</i> 6×	473182	Argentina, Jujuy
47	<i>S. oplocense</i> 6×	473185	Argentina, Jujuy
47	<i>S. oplocense</i> 6×	473190	Argentina, Jujuy
47	<i>S. tuberosum</i> subsp. <i>andigena</i>	473251	Argentina, Jujuy
48	<i>S. gourlayi</i> subsp. <i>gourlayi</i> 4×	210038	Argentina, Jujuy
48	<i>S. gourlayi</i> subsp. <i>gourlayi</i> 4×	442673	Argentina, Jujuy
48	<i>S. gourlayi</i> subsp. <i>gourlayi</i> 4×	473049	Argentina, Jujuy
48	<i>S. oplocense</i> 4×	435079	Argentina, Jujuy
48	<i>S. oplocense</i> 6×	473187	Argentina, Jujuy
48	<i>S. oplocense</i> 6×	558107	Argentina, Jujuy
48	<i>S. oplocense</i> 6×	558108	Argentina, Jujuy
49	<i>S. gourlayi</i> subsp. <i>gourlayi</i> 2×	414145	Argentina, Jujuy
49	<i>S. gourlayi</i> subsp. <i>gourlayi</i> 2×	473011	Argentina, Jujuy
49	<i>S. gourlayi</i> subsp. <i>gourlayi</i> 2×	500022	Argentina, Jujuy
49	<i>S. gourlayi</i> subsp. <i>gourlayi</i> 4×	472918	Argentina, Jujuy
49	<i>S. gourlayi</i> subsp. <i>gourlayi</i> 4×	473014	Argentina, Jujuy
49	<i>S. gourlayi</i> subsp. <i>gourlayi</i> 4×	473015	Argentina, Jujuy
49	<i>S. gourlayi</i> subsp. <i>gourlayi</i> 4×	473016	Argentina, Jujuy
49	<i>S. gourlayi</i> subsp. <i>gourlayi</i> 4×	473017	Argentina, Jujuy
49	<i>S. gourlayi</i> subsp. <i>gourlayi</i> 4×	473026	Argentina, Jujuy
49	<i>S. gourlayi</i> subsp. <i>gourlayi</i> 4×	473039	Argentina, Jujuy
49	<i>S. gourlayi</i> subsp. <i>gourlayi</i> 4×	558068	Argentina, Jujuy
49	<i>S. gourlayi</i> subsp. <i>vidaurrei</i>	472991	Argentina, Jujuy
49	<i>S. gourlayi</i> subsp. <i>vidaurrei</i>	473004	Argentina, Jujuy
49	<i>S. gourlayi</i> subsp. <i>vidaurrei</i>	473007	Argentina, Jujuy
49	<i>S. vernei</i> subsp. <i>ballsii</i>	320333	Argentina, Jujuy
49	<i>S. vernei</i> subsp. <i>ballsii</i>	473303	Argentina, Jujuy
49	<i>S. vernei</i> subsp. <i>ballsii</i>	473304	Argentina, Jujuy
49	<i>S. vernei</i> subsp. <i>ballsii</i>	473305	Argentina, Jujuy
49	<i>S. vernei</i> subsp. <i>vernei</i>	500068	Argentina, Jujuy
49	<i>S. vernei</i> subsp. <i>vernei</i>	558150	Argentina, Jujuy
50	<i>S. gourlayi</i> subsp. <i>gourlayi</i> 2×	558067	Argentina, Jujuy
51	<i>S. gourlayi</i> subsp. <i>vidaurrei</i>	472911	Argentina, Salta
51	<i>S. gourlayi</i> subsp. <i>vidaurrei</i>	473000	Argentina, Salta
52	<i>S. gourlayi</i> subsp. <i>vidaurrei</i>	472995	Argentina, Salta
52	<i>S. gourlayi</i> subsp. <i>vidaurrei</i>	472998	Argentina, Salta
52	<i>S. gourlayi</i> subsp. <i>vidaurrei</i>	498332	Argentina, Salta
52	<i>S. vernei</i> subsp. <i>vernei</i>	458374	Argentina, Salta
53	<i>S. vernei</i> subsp. <i>ballsii</i>	458369	Argentina, Salta
53	<i>S. vernei</i> subsp. <i>ballsii</i>	458370	Argentina, Salta
53	<i>S. vernei</i> subsp. <i>ballsii</i>	458371	Argentina, Salta
53	<i>S. vernei</i> subsp. <i>ballsii</i>	458372	Argentina, Salta
53	<i>S. vernei</i> subsp. <i>ballsii</i>	500070	Argentina, Salta
53	<i>S. vernei</i> subsp. <i>vernei</i>	473309	Argentina, Salta
54	<i>S. gourlayi</i> subsp. <i>gourlayi</i> 2×	473095	Argentina, Salta
54	<i>S. gourlayi</i> subsp. <i>gourlayi</i> 2×	473098	Argentina, Salta
55	<i>S. gourlayi</i> subsp. <i>gourlayi</i> 2×	473065	Argentina, Salta
55	<i>S. gourlayi</i> subsp. <i>gourlayi</i> 2×	473075	Argentina, Salta
55	<i>S. gourlayi</i> subsp. <i>gourlayi</i> 2×	473077	Argentina, Salta
55	<i>S. incamayoense</i>	473060	Argentina, Salta
55	<i>S. incamayoense</i>	473066	Argentina, Salta
55	<i>S. incamayoense</i>	473067	Argentina, Salta
55	<i>S. incamayoense</i>	473068	Argentina, Salta
55	<i>S. incamayoense</i>	473069	Argentina, Salta
55	<i>S. incamayoense</i>	473089	Argentina, Salta
55	<i>S. incamayoense</i>	500048	Argentina, Salta
55	<i>S. spgazzinii</i>	442686	Argentina, Salta
55	<i>S. tuberosum</i> subsp. <i>andigena</i>	473269	Argentina, Salta
56	<i>S. gourlayi</i> subsp. <i>gourlayi</i> 4×	558062	Argentina, Salta
56	<i>S. spgazzinii</i>	472971	Argentina, Salta
56	<i>S. vernei</i> subsp. <i>vernei</i>	558148	Argentina, Salta
57	<i>S. spgazzinii</i>	472988	Argentina, Tucuman
57	<i>S. vernei</i> subsp. <i>vernei</i>	458373	Argentina, Tucuman
57	<i>S. vernei</i> subsp. <i>vernei</i>	473308	Argentina, Tucuman

TABLE 2. Continued.

Map location ^a	Taxon ^b	PI number ^c	Country, department, or province
58	<i>S. spagazzinii</i>	320299	Argentina, Catamarca
58	<i>S. spagazzinii</i>	472984	Argentina, Catamarca
58	<i>S. vernei</i> subsp. <i>vernei</i>	320332	Argentina, Catamarca
59	<i>S. spagazzinii</i>	275143	Argentina, La Rioja
59	<i>S. spagazzinii</i>	458337	Argentina, La Rioja
59	<i>S. spagazzinii</i>	472966	Argentina, La Rioja
59	<i>S. spagazzinii</i>	472990	Argentina, La Rioja
	UNMAPPED:		
	<i>S. brachistotrichum</i>	320265	Mexico, Chihuahua
	<i>S. brachistotrichum</i>	498216	Mexico, Chihuahua
	<i>S. brachistotrichum</i>	498217	Mexico, Chihuahua
	<i>S. brachistotrichum</i>	545812	Mexico, Aguascalientes
	<i>S. brachistotrichum</i>	545815	Mexico, Aguascalientes
	<i>S. brachistotrichum</i>	545816	Mexico, Aguascalientes
	<i>S. brachistotrichum</i>	558460	Mexico, Jalisco
	<i>S. curtilobum</i>	186181	Peru
	<i>S. curtilobum</i>	225649	Colombia
	<i>S. curtilobum</i>	258900	Bolivia
	<i>S. fendleri</i>	251062	Mexico, Chihuahua
	<i>S. fendleri</i>	275156	United States, New Mexico
	<i>S. fendleri</i>	458412	United States, New Mexico
	<i>S. fendleri</i>	458413	Mexico, Chihuahua
	<i>S. fendleri</i>	458420	United States, Arizona
	<i>S. fendleri</i>	458422	United States, Arizona
	<i>S. fendleri</i>	497995	Mexico, Chihuahua
	<i>S. fendleri</i>	497998	Mexico, Chihuahua
	<i>S. fendleri</i>	498238	Mexico, Chihuahua
	<i>S. fendleri</i>	558395	Mexico, Baja California
	<i>S. fendleri</i>	558396	Mexico, Baja California
	<i>S. medians</i>	230507	Peru
	<i>S. medians</i>	310994	Peru
	<i>S. stenotomum</i> subsp. <i>stenotomum</i>	234011	Bolivia
	<i>S. stenotomum</i> subsp. <i>stenotomum</i>	234012	Bolivia
	<i>S. stenotomum</i> subsp. <i>stenotomum</i>	234015	Bolivia
	<i>S. tuberosum</i> subsp. <i>andigena</i>	225628	Colombia, Santander
	<i>S. tuberosum</i> subsp. <i>andigena</i>	281038	Peru
	<i>S. tuberosum</i> subsp. <i>andigena</i>	281208	Peru
	<i>S. tuberosum</i> subsp. <i>tuberosum</i>	161401	Mexico, Federal Distrito
	<i>S. tuberosum</i> subsp. <i>tuberosum</i>	245796	Chile, Los Lagos
	<i>S. tuberosum</i> subsp. <i>tuberosum</i>	245815	Chile, Chiloé
	<i>S. tuberosum</i> subsp. <i>tuberosum</i>	245835	Chile, Chiloé
	<i>S. verrucosum</i>	275256	Mexico, Michoacán
	<i>S. verrucosum</i>	275257	Mexico, Michoacán
	<i>S. verrucosum</i>	310996	Mexico, Puebla
	<i>S. verrucosum</i>	365404	Mexico, México
	<i>S. verrucosum</i>	498010	Mexico, Hidalgo
	<i>S. verrucosum</i>	498061	Mexico, Coahuila
	<i>S. verrucosum</i>	545745	Mexico, Nuevo León
	<i>S. verrucosum</i>	545747	Mexico, México
	<i>S. verrucosum</i>	558482	Mexico, México

^a Generalized map areas of members of the *Solanum brevicaule* complex, see Fig. 1; taxa outside of the complex and some cultivated taxa outside the map area of the wild species are not mapped.

^b Ploidy level is indicated when there is polymorphism within the taxon.

^c United States Department of Agriculture Plant Introduction Numbers.

out reference to similar taxa. Taxonomists in the group have evidently relied, therefore, largely or entirely on intuitive judgments (“Gestalt approach”). Correll (1962) discussed the problems of distinguishing some members of the complex (*S. abbotianum*, *S. brevicaule*, *S. canasense*, *S. leptophyes*, *S. multidissectum*), and remarked “If all of these were placed together as one highly variable species it would probably be in the best interest of science.” Hawkes and Hjerting (1989) discussed their taxonomic concepts and stated “The whole group of species [*S. brevicaule* complex, in part] is undoubtedly a

difficult one which can only be fully understood by studying living material as well as herbarium specimens. This we have now been able to do, and consequently we fully believe that we have reached the right conclusions.” Determining the purported species differences is aggravated by Correll’s (1962) and Hawkes’s (1990) sole reliance on geography in some key couplets. Brücher (1985) also synonymized members of the complex, but the accepted species and synonymy differed. For example, under *S. leptophyes* Brücher included *S. famatinae*, *S. pachytrichum*, *S. punoense*, *S. puberulo-fructum*, *S.*

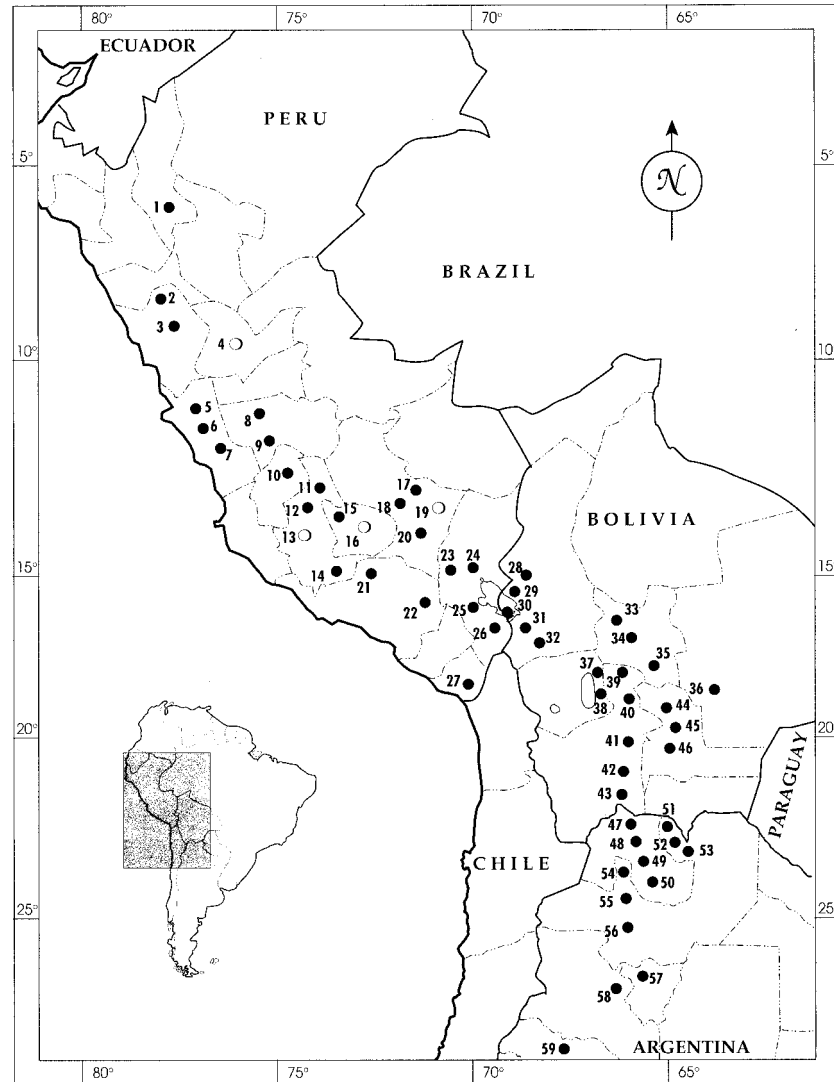


Fig. 2. Map showing the 59 generalized areas of the accessions of the *S. brevicaule* complex examined in this study. Solid circles are areas with good locality data; open circles are localities that can be mapped only to department (or province). Generalized map areas correspond to those in Table 2.

sleumeri, *S. spegazzinii*, *S. vidaurrei*, a treatment at variance with other major treatments (Table 1, Fig. 1).

We studied the *S. brevicaule* complex using comparative morphological data from germplasm collections grown in a common garden. The goal was to investigate phenetic species boundaries from a large statistical sample of populations and characters, including all characters used by prior workers in the group. We addressed the following questions: (1) What taxa are supported by morphological phenetic analyses of the *S. brevicaule* complex (how many clusters are apparent as recognizable and discrete taxa)? (2) Is there a geographical component to morphological variation? (3) Do the morphological groups correspond to past taxonomic interpretations?

MATERIALS AND METHODS

Species—The circumscription and composition of the *S. brevicaule* complex differ dramatically among all prior taxonomic treatments. For

our study, we broadly defined the group to include all putative members proposed previously (Table 1, Fig. 1). These taxa follow, with the ploidy levels listed for all that are not diploid: *S. achacachense*, *S. ambosinum*, *S. avilesii*, *S. brevicaule*, *S. bukasovii*, *S. canasense*, *S. gourlayi* subsp. *gourlayi* (both diploid and tetraploid populations examined), *S. gourlayi* subsp. *pachytrichum*, *S. gourlayi* subsp. *vidaurrei*, *S. hondelmannii*, *S. leptophyes*, *S. marinasense*, *S. medians*, *S. multidissectum*, *S. oplocense* (both tetraploid and hexaploid populations examined, the diploid populations not available), *S. pampasense*, *S. sparsipilum*, *S. spegazzinii*, *S. sucrense* (tetraploid). We also added six wild taxa that our field and genebank experience suggested might be additional members of the group: *S. abancayense*, *S. acroscopicum*, *S. candolleianum*, *S. hoopesii* (tetraploid), *S. incamayoense*, *S. ugentii* (tetraploid), and five cultivated taxa: *Solanum curtilibum* (pentaploid), *S. stenotomum* subsp. *stenotomum*, *S. stenotomum* subsp. *goniocalyx*, *S. tuberosum* subsp. *andigena* (tetraploid), and *S. tuberosum* subsp. *tuberosum* (tetraploid). We also analyzed the putative outgroup taxa *S. brachistotrichum* (Bitt.) Rydb. (ser. *Pinnatisecta* [Rydb.] Hawkes), *S. fendleri* A. Gray (tetraploid, ser. *Longipedicellata* Bukasov), *S. microdontum* Bitt. (ser. *Tuberosa*), *S. ver-*

TABLE 3. Characters used in the phenetic analysis of the *Solanum brevicaule* complex. All measurements for the quantitative characters are in millimetres, except as noted below.

Stem characters

1. Color of stem: (1) entirely green, (2) mostly green, (3) equally green and purple, (4) mostly purple, (5) entirely purple. 2. Diameter of stem at base. 3. Plant height (cm).

Leaf characters

4. Length of adaxial leaf pubescence (μm). 5. Density of adaxial leaf pubescence (number of hairs/cm²). 6. Length of abaxial leaf pubescence (μm). 7. Density of abaxial leaf pubescence (number of hairs/cm²). 8. Length of leaf. 9. Ratio: length of leaf/width of leaf. 10. Ratio: length from widest part of leaf to apex/length of leaf. 11. Number of lateral leaflet pairs. 12. Number of interjected leaflets. 13. Number of secondary lateral leaflets (= leaflets positioned on the lateral leaflet petiolules). 14. Leaflet margins: undulate (0), straight (1). 15. Length of terminal leaflet. 16. Ratio: length of terminal leaflet/width of terminal leaflet. 17. Ratio: length from widest part of terminal leaflet to apex/length of terminal leaflet. 18. Width of terminal leaflet from a point 5 mm below apex. 19. Terminal leaflet base: (0) evidently cuneate, (1) truncate to slightly cuneate, (2) truncate to slightly cordate, (3) evidently cordate. 20. Length of most distal lateral leaflet petiolule. 21. Angle of most distal lateral leaflet from rachis, as measured by ratio: one half of width between apices of most distal lateral leaflet pair/length of most distal lateral leaflet. 22. Ratio: terminal leaflet length/length of most distal lateral leaflet. 23. Width of most distal lateral leaflet. 24. Ratio: length from widest part of most distal lateral leaflet to apex/length of most distal lateral leaflet. 25. Width of wing of rachis of most distal lateral leaflet. 26. Width of most distal lateral leaflet from a point 5 mm below apex. 27. Ratio: length of most distal lateral leaflet/width of most distal lateral leaflet. 28. Decurrency of most distal lateral leaflet as measured by width of basicopic decurrent tissue from a point on the petiole 5 mm basicopic to the junction of the petiolule and petiole. 29. Length of leaf from apex to widest point. 30. Length of most distal lateral leaflet from apex to widest point. 31. Ratio: length of third most distal lateral leaflet/length of second most distal lateral leaflet.

Floral characters

32. Length of peduncle. 33. Number of peduncle forks. 34. Number of flowers per inflorescence. 35. Ratio: number of flowers inflorescence/number of forks per inflorescence. 36. Length of pedicel. 37. Ratio: length of pedicel from base to articulation/length of pedicel. 38. Length of calyx acumen. 39. Length of calyx lobe. 40. Ratio: length of calyx lobe/width of calyx lobe. 41. Radius of corolla. 42. Ratio: length from center of corolla to base of corolla lobe/radius of corolla. 43. Ratio: width of corolla lobe at base of junction of corolla lobes/length from lobe at base to tip of corolla lobe. 44. Length of anther. 45. Length of style exertion from apex of anthers apex of stigma. 46. Diameter of style. 47. Ratio: diameter of style/diameter of stigma. 48. Length of stigma. 49. Diameter of stigma/length of stigma. 50. Color of adaxial corolla interpetolar tissue (see Materials and Methods). 51. Color of abaxial corolla interpetolar tissue. 52. Color of adaxial corolla ray. 53. Color of abaxial corolla ray.

nei Bitt. and Wittm. subsp. *ballsii* (Hawkes) Hawkes and Hjert. (ser. *Tuberosa*), *S. vernei* subsp. *vernei*, and *S. verrucosum* Schltld. (ser. *Tuberosa*) (Table 2). We chose *S. brachistotrichum* as a representative of a primitive member of sect. *Petota* (Hawkes, 1990; Spooner and Sytsma, 1992). We chose *Solanum fendleri* and *S. verrucosum* because these Mexican species appeared to us to be possible morphological candidates for inclusion into the complex, and because *S. verrucosum* is the most northern representative of ser. *Tuberosa*. We chose *S. microdontum* and *S. vernei* as South American members of ser. *Tuberosa* that are phenetically distinct from the members of the complex. In total, we analyzed three individuals of 215 accessions, encompassing 30 taxa of the *S. brevicaule* complex, and three individuals of 42 accessions, encompassing six taxa outside of the complex (Table 2).

We mapped these accessions to 59 generalized areas, ranging from northern Peru to northern Argentina (Fig. 2). All accessions came from the National Research Support Program-6 (NRSP-6; Bamberg et al., 1996). Identifications of the species 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). Vouchers are deposited at the NRSP-6 herbarium in Sturgeon Bay, Wisconsin (PTIS [Bamberg and Spooner, 1994], to appear in Edition 9 of *Index Herbariorum* [Edition 8 is Holmgren, Holmgren, and Barnett, 1990]).

Seeds were planted in a greenhouse in early May and transferred to peat pots in late May. Two replicates each of six plants per accession were transplanted into a completely randomized design in early June at the Hancock, Wisconsin State Agricultural Experimental Station.

Data measurement—The middle three of the six plants per row were measured for each accession. A total of 53 characters (Table 3) were measured on each plant, except for the pubescence characters 4–7 that were measured from a single individual per accession, using a binocular microscope. Trichomes (characters 4, 6) were measured with the aid of an ocular micrometer from young, fully expanded leaves in the interveinal areas, not from the veins where they typically are longer. When

lengths varied, an average length was scored. Leaf measurements were made on the largest leaf per plant. Floral characters were measured on the uppermost inflorescence. Corolla colors were measured with the R.H.S. Colour Charts (Royal Horticultural Society, 1986), based on recommendations of Tucker, Maciarello, and Tucker (1991). Because of varying colors and color intensities from blue to violet and white, and the difficulty of ordering colors by eye, we determined color intensity from charts with a Minolta chroma meter CR-221[®]. The 22 scored RHS colors, ordered by their corresponding intensity values are: 155 A-D (white, 93), 91D (85.3), 76C (82.8), 91C (78.2), 75B (74.4), 91B (70.4), 84B (66.8), 85A (62.7), 91A (57.6), 86D (53.5), 77B (52.6), 84A (51.7), 87B (48.8), 90C (47.2), 86C (45.1), 86B (39.8), 87A (39.6), 88A (39.2), 77A (34.8), 94A (33.1), 86A (27.4), 89A (dark purple, 11.5). Data are deposited in Miller (1997).

Data analysis—For phenetic analyses, accessions were averaged over two replicates (six plants in total). Principal Components Analysis (PCA) was produced by NTSYS-pc version 1.70 (Rohlf, 1992); Canonical Discriminant Analysis (CDA) and Stepwise Discriminant Analysis (SDA) were produced using SAS (SAS, 1989). PCA were performed from the correlation matrix on standardized data using procedures STAND, EIGEN, and PROJ. CDA and SDA used CANDISC and STEPDISC. CDA was conducted first with the entire data set, and then with a subset of the data based on the initial CDA results.

The mean, range, and standard deviation of each character were calculated in Microsoft Excel[®]. Character correlations were explored by a PCA analysis of the characters that showed statistically significant differences in the SDA analysis.

PCA and CDA are both ordination techniques, but PCA makes no assumptions of group membership of OTUs (Operational Taxonomic Units). It attempts to portray multidimensional variation in the data set in the fewest possible dimensions, while maximizing the variation. CDA uses assigned groups to derive a linear combination of the variables (morphological characters) that produces the greatest separation of the groups (SAS, 1989). Because these phenetic approaches use very dif-

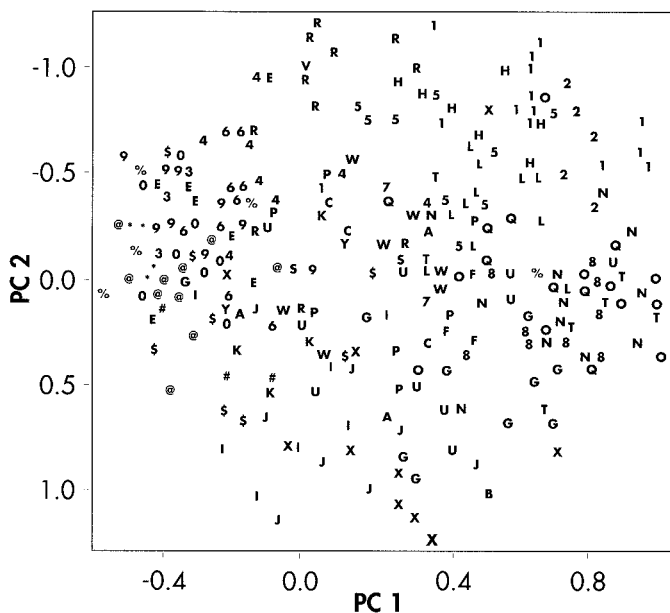


Fig. 3. Principal Components Analysis of members of the *S. brevicaulle* complex and other species in sect. *Petota*, based on 53 morphological characters (Table 3). Taxon codes are: *Solanum abancayense*, A; *S. achacachense*, B; *S. acroscopicum*, C; *S. ambosinum*, E; *S. avilesii*, F; *S. brevicaulle*, G; *S. brachistotrichum* (outgroup, OG), H; *S. bukasovii*, I; *S. canasense*, J; *S. candolleanum*, K; *S. fendleri* (OG), L; *S. gourlayi* (2x) O; *S. gourlayi* (4x) N; *S. gourlayi* subsp. *pachytrichum*, P; *S. gourlayi* subsp. *vidaurrei*, Q; *S. hondelmannii*, R; *S. hoopesii*, S; *S. incamayoense*, T; *S. leptophyes*, U; *S. microdontum* (OG), V; *S. medians*, W; *S. multidissectum*, X; *S. marinasense*, Y; *S. oplocense*, (4x) 2; *S. oplocense* (6x) 1; *S. pampasense*, 3; *S. sucrense*, 4; *S. spagazzinii*, 5; *S. sparsipilum*, 6; *S. ugentii*, 7; *S. verrucosum* (OG), 8; *S. vernei* subsp. *ballsii* (OG), 9; *S. vernei* subsp. *vernei* (OG), zero; *S. curtilibum*, # sign; *S. stenotomum* subsp. *stenotomum*, dollar sign; *S. stenotomum* subsp. *goniocalyx*, percent sign; *S. tuberosum* subsp. *tuberosum*, asterisk; *S. tuberosum* subsp. *andigena*, @ sign.

ferent algorithms and operate under different assumptions about the data set, we used both analyses in our exploration of phenetic structure in the *S. brevicaulle* complex and outgroups.

RESULTS

Phenetic results—The entire data set resulted in over 81 000 data points. The PCA of the entire data set is presented in Fig. 3. Principal components 1 and 2 account for 17 and 10% of the variation, respectively, for a total of 27%. The third principal component raises the total to 36% but does not change the overall pattern and is not presented. PCA axis 1 is most highly influenced by (presented in decreasing order of loadings) (1) length of leaf, (2) diameter of stem at base, (3) width of most distal lateral leaflet, (4) shape of terminal leaflet base, and (5) length of most distal lateral leaflet from apex to widest point; PCA axis 2 by (1) ratio: length of leaf from widest point of leaf to apex/length of leaf, (2) ratio: length of leaf/width of leaf, (3) ratio: length from center of corolla to base of corolla lobe/radius of corolla, (4) ratio: width of corolla lobe at base of junction of corolla lobes/length from lobe at base to tip of corolla lobe, (5) ratio: length of most distal lateral leaflet/width of most distal lateral leaflet. PCA (Fig. 3) fails to resolve sharply discrete phenetic groups, and no further subdivision is possible.

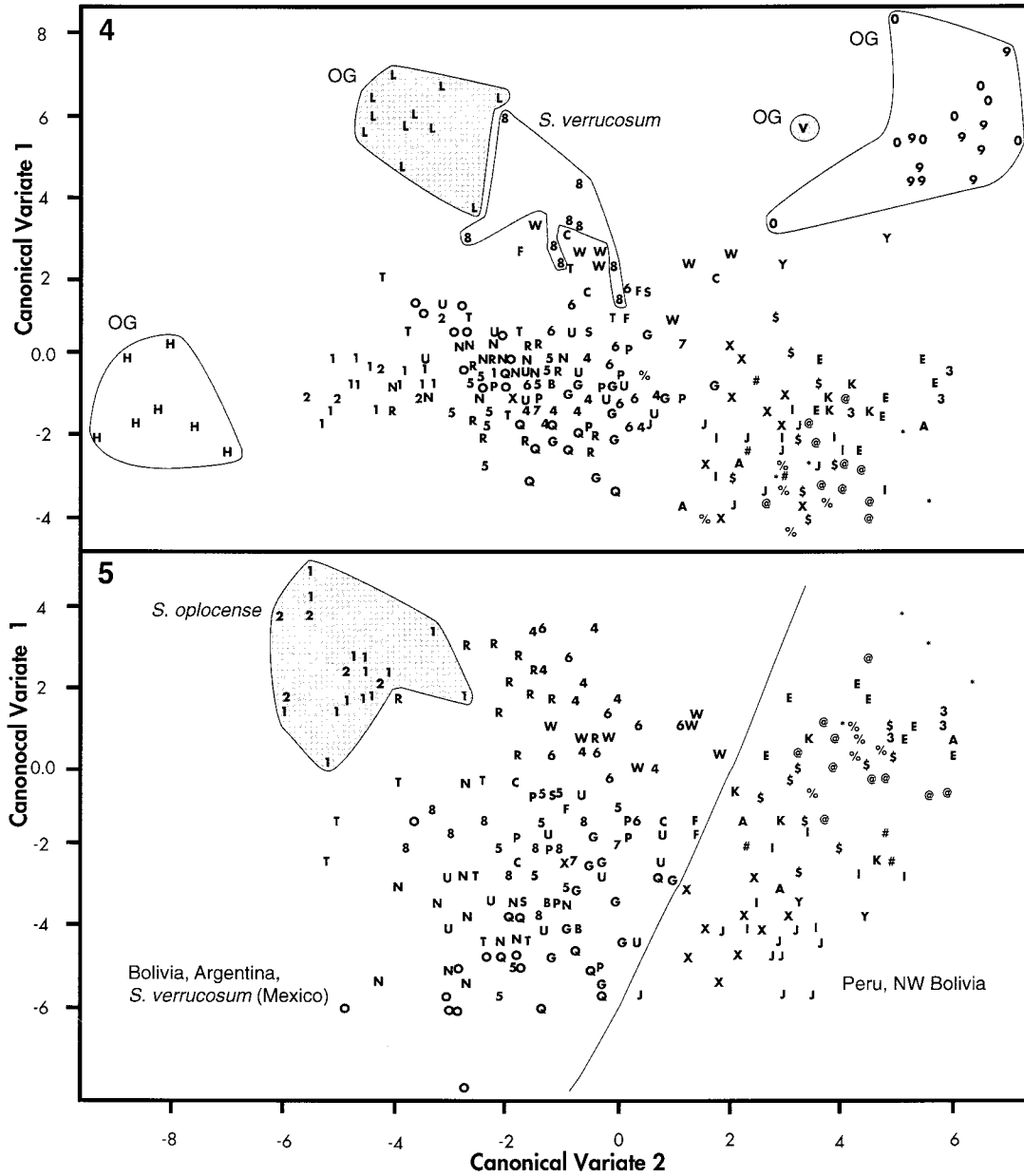
The CDA of the entire data set is presented in Fig. 4. CDA axis 1 is most highly influenced by (presented in order of decreasing levels of canonical structure) (1) number of interjected leaflets, (2) shape of terminal leaflet base, (3) density of adaxial leaf pubescence, (4) diameter of style, (5) number of lateral leaflet pairs; CDA axis 2 by (1) length of terminal leaflet, (2) color of stem, (3) length of most distal lateral leaflet from apex to widest point, (4), length of abaxial leaf pubescence, and (5) ratio: length of leaf/width of leaf.

The CDA of the entire data set shows more phenetic structure, but the only groups well differentiated are five non-*S. brevicaulle* complex taxa (*S. brachistotrichum*, *S. fendleri*, *S. microdontum*, *S. vernei* subsp. *ballsii*, and *S. vernei* subsp. *vernei*). One non-*S. brevicaulle* complex taxon, *S. verrucosum* (ser. *Tuberosa*, Mexico), is not well separated from the complex.

Based on the results of the CDA of the entire data set, the CDA was performed again after eliminating *S. brachistotrichum*, *S. fendleri*, *S. microdontum*, *S. vernei* subsp. *ballsii*, and *S. vernei* subsp. *vernei* (Fig. 5). CDA axis 1 is most highly influenced by (1) diameter of style, (2) shape of terminal leaflet base, (3) density of abaxial leaf pubescence, (4) number of interjected leaflets, (5) length of stigma; CDA axis 2 by (1) length of terminal leaflet, (2) width of most distal lateral leaflet, (3) length of most distal lateral leaflet from apex to widest point, (4) length of leaf from apex to widest point, (5) length of leaf. The five most important characters in distinguishing species in the SDA, ranked by decreasing importance, are (1) width of most distal lateral leaflet, (2) density of abaxial leaf pubescence, (3) shape of terminal leaflet base, (4) plant height, and (5) diameter of style.

This CDA analysis of the reduced data set shows more phenetic structure than the PCA and CDA of the entire data set, but there are no clear gaps to differentiate most species. OTUs fall along a geographical axis, with accessions from Peru and adjacent northwestern Bolivia (*S. candolleanum*) grading into accessions from Bolivia and Argentina (and *S. verrucosum* from Mexico), except for a single accession of *S. multidissectum* (Peru) that clusters with other accessions from Bolivia and Argentina. *Solanum oplocense* is distinct in the Bolivian and Argentinian cluster. However, there is no appreciable phenetic structure separating these groups. Our most liberal taxonomic interpretation based on our data is to recognize only three taxa: (1) Peruvian and immediately adjacent Bolivian accessions (including wild species and all the cultigens) (2) Bolivian and Argentinean accessions and *S. verrucosum* from Mexico (including only wild species), and (3) the Bolivian and Argentinian wild species *S. oplocense*.

Our results corroborate a morphological phenetic analysis (PCA) of the *S. brevicaulle* complex by van den Berg, Groendijk-Wilders, and Kardolus (1996) who studied 43 accessions of 15 taxa of the complex. They similarly showed poor phenetic structure in the complex, with much overlap of the best characters defining taxa. As in the present study, they discovered length of terminal leaflet to be an important character to discriminate species (Fig. 6), as well as stem width and plant height. Their analyses of a smaller data set of characters and accessions distinguished *S. achacachense*, *S. brevicaulle*, *S. gourlayi*



Figs. 4–5. 4. Canonical discriminant analysis of the entire data set of members of the *S. brevicaule* complex and other species in sect. *Petota*, based on 53 morphological characters (Table 3). Taxon codes are as in Fig. 3. Outgroup taxa are highlighted in shade. 5. Canonical discriminant analysis of the reduced data set of members of the *S. brevicaule* complex (eliminating *S. brachistotrichum*, *S. fendleri*, *S. microdontum*, and *S. vernei*), based on 53 morphological characters (Table 3). Species codes are as in Fig. 3. *Solanum oplocense* is highlighted in shade. The line divides accessions of Peru and immediately adjacent Bolivia (*S. candolleianum*) from those of Bolivia and Argentina (and *S. verrucosum* from Mexico).

subsp. *vidaurrei*, and some, but not all accessions of *S. spegazzinii*.

Our CDA result provides little support to the unpublished classification of a portion of the complex by Ugent (1966; Table 1, Fig. 1). Like us, he was unable to recognize many taxa in the complex. He lumped many taxa into two species (*S. brevicaule* with three subspecies, *S. × sparsipilum*). However, Ugent’s taxa intermix populations from Peru and Bolivia, and his classification does not correlate with the geographically based separation of populations in our analysis.

Character state variation—The Principal Components Analysis of 50 of the 53 morphological characters that were statistically significant in at least one pairwise comparison of taxa based on an SDA analysis of the reduced data set is presented in Fig. 7. Three characters: (1) number of secondary lateral leaflets, (2) ratio: length of calyx lobe/width of calyx lobe, and (3) color of abaxial corolla interpetalar tissue are not significant among species. Figure 6 presents the means, ranges, and standard deviations of six of the most important characters distinguishing species on the PCA, CDA, and SDA analyses. Most char-

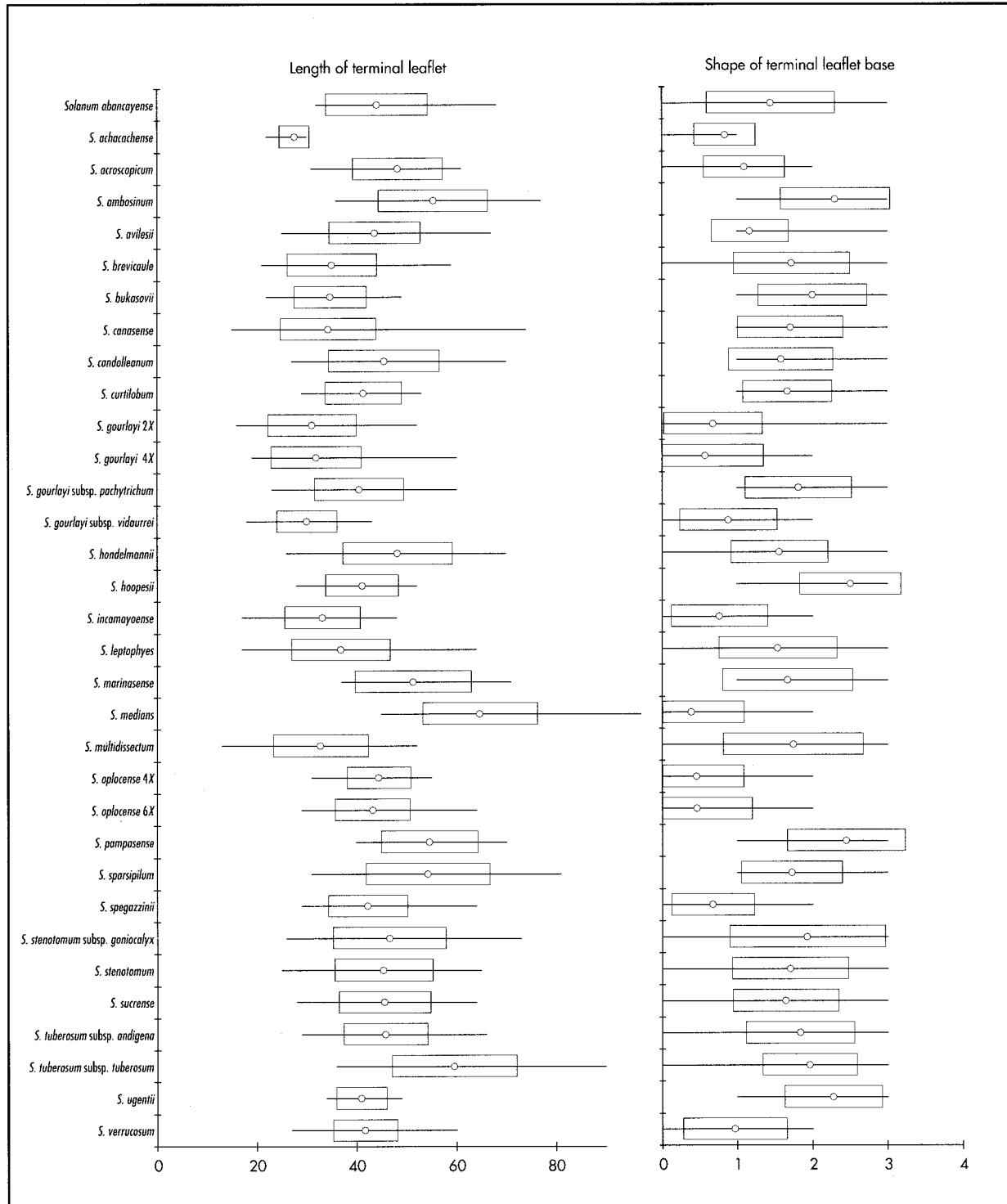


Fig. 6. Means, ranges, and one standard deviation of the mean for six of the most important characters separating taxa of the *S. brevicaule* complex.

acters, however, are highly polymorphic, and there are no species-specific character states. Phenetic structure, therefore, relies entirely on polythetic support, i.e., 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 of a group (Sokal and Sneath, 1963; Stuessy, 1990).

Principal components 1 and 2 (Fig. 7) account for 36 and 14% of the variation, respectively, for a total of 50%. This result shows high correlation of some characters of

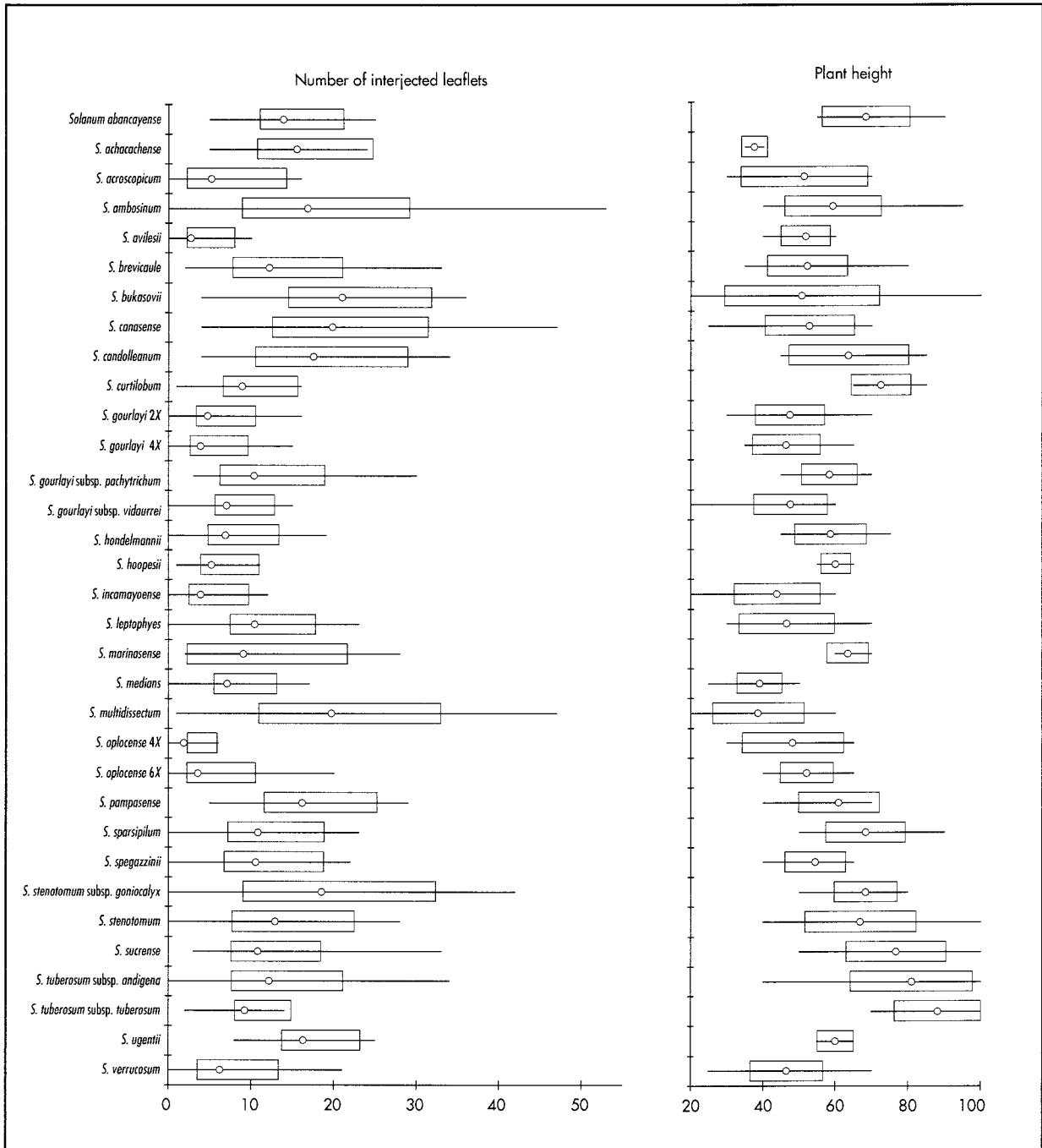


Fig. 6. Continued.

similar organs that logically might be correlated, such as stem diameter and plant height (characters 2, 3; Table 3), leaf pubescence lengths (characters 4, 6), leaf pubescence densities (characters 5, 7), length of leaf and length of terminal leaflet (characters 8,15), terminal and most distal lateral leaf shapes (characters 16,27), calyx acumen length and calyx lobe lengths (characters 38, 39), and corolla colors (characters 50, 52, 53). However, it also shows high correlations of characters of very different types, such as shape of terminal leaflet and length of calyx acumen (characters 16, 38), relative lengths of ter-

minal and most distal lateral leaflets and a corolla shape index (characters 22, 42), or angle of most distal lateral leaflet from rachis and ratio: diameter of style/diameter of stigma (characters 21, 47).

We conducted an SDA analysis by relabeling populations as (1) Peruvian and immediately adjacent Bolivian accessions (including wild species and all the cultigens), (2) Bolivian and Argentinean accessions and *S. verrucosum* from Mexico (including only wild species), and (3) the Bolivian and Argentinean wild species *S. oplacense*. The means, ranges, and standard deviations of the

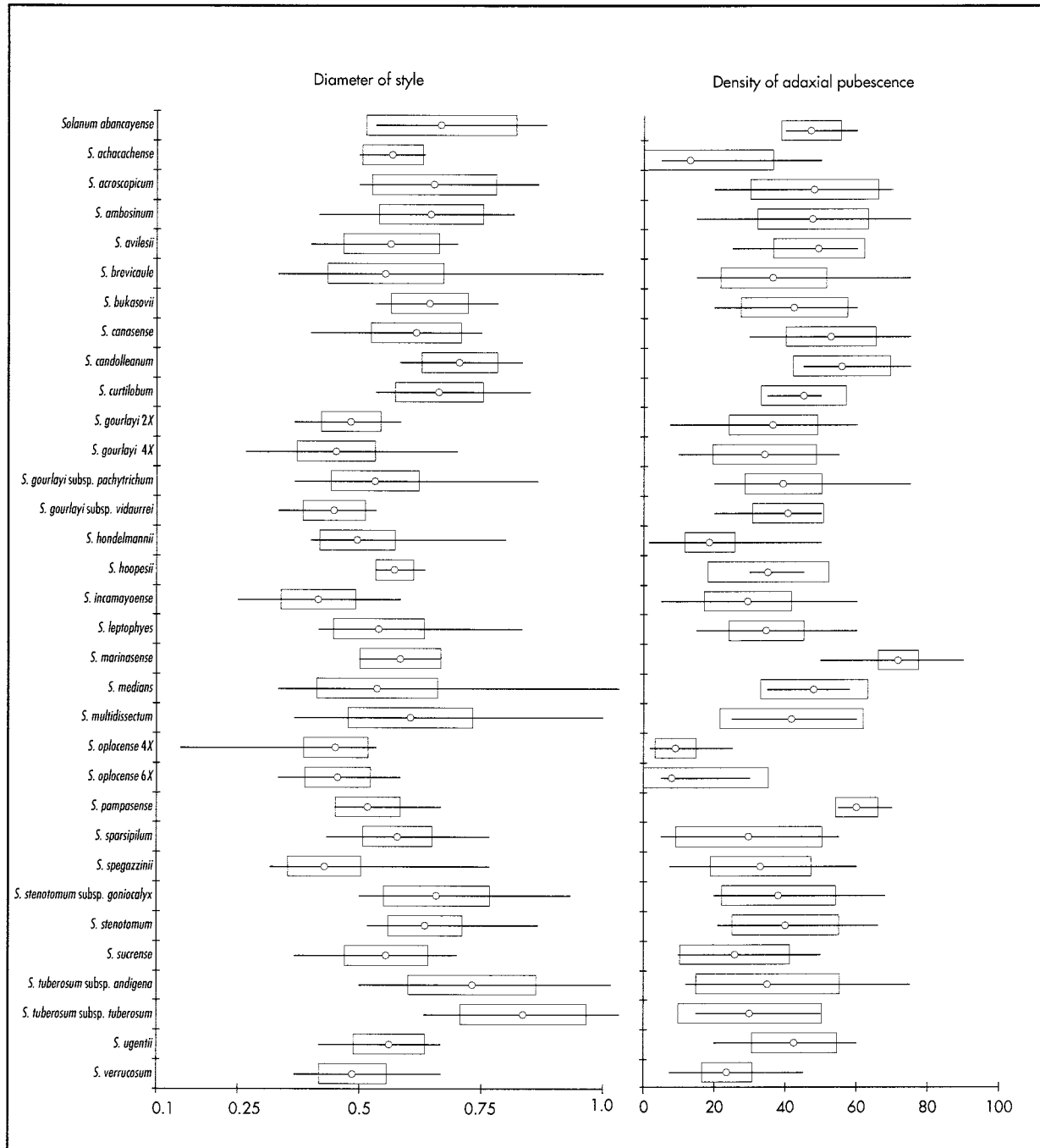


Fig. 6. Continued.

nine best characters separating these three groups are diagrammed in Fig. 8. As with the currently accepted taxa of the *S. brevicaule* complex, there is much overlap of individual character states of these three groups.

DISCUSSION

Species boundaries—The phenetic results do not support 30 morphologically distinct taxa in the *S. brevicaule* complex. Instead, one to three broadly defined taxa at most can be recognized. The phenetically most cohesive

taxon in the complex, *S. oplocense* (Fig. 5), differs from other members of the complex only by a series of widely overlapping character states (Fig. 6). The other taxa have much less support, with more overlapping of character states and with less resolution in the PCA and CDA. The morphological and geographical separation of the Peruvian from the Bolivian and Argentinian members of the complex (and *S. verrucosum*) is weak, as the segregation of OTUs into either group is not based on a clear break in phenetic structure (Fig. 5), or group-specific character states (Fig. 6).

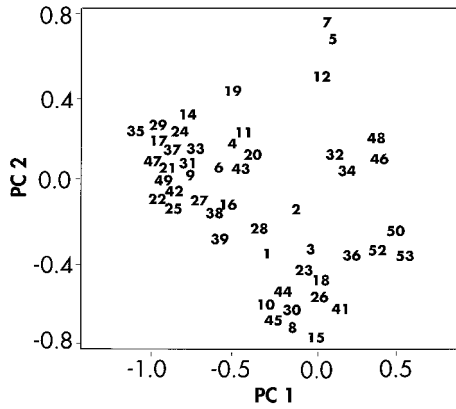


Fig. 7. Principal Components Analysis of 50 of the 53 morphological characters that were statistically significant in at least one pairwise comparison of taxa based on an SDA analysis of the reduced data set (see text). The numbers refer to character numbers in Table 3.

We have found it impossible to use morphological data to construct reliable taxonomic keys to distinguish previously recognized taxa in the complex. At best, individual characters could be used to construct keys, but they would require subjective interpretation and would not allow for consistent identifications. This polythetic circum-

scription of morphological species has been demonstrated in every study of species in sect. *Petota* to date. This includes subspecies boundaries within *S. megistacrobium* Bitter (Giannattasio and Spooner, 1994), species boundaries within *Solanum* ser. *Demissa* Bukasov (Spooner, van den Berg, and Bamberg, 1995), species differences between *S. berthaultii* and *S. tarijense* (Spooner and van den Berg, 1992b), and species boundaries within *Solanum* ser. *Circaeifolia* Hawkes (van den Berg and Groendijk-Wilders, in press).

Our results have discovered much morphological variation in the *S. brevicaule* complex, but the cause of this variation is unknown. Hawkes (1962, 1990) and Hawkes and Hjerting (1969, 1989) ascribed much of the intermediacy among species to hybridization and introgression that have occurred in recently disturbed habitats. Twenty-seven of the 232 species recognized by Hawkes are of putative hybrid origin (Spooner and van den Berg, 1992b). Hawkes and Hjerting (1969, 1989) hypothesized extensive natural hybridization. For example, 12% of the specimens listed in Hawkes and Hjerting's (1969) taxonomic treatment of Argentina, Brazil, Paraguay, and Uruguay are putative hybrid populations. Many members of the *S. brevicaule* complex are agricultural weeds that might have been spread by man. It may be possible that formerly distinct taxa in the *S. brevicaule* complex have

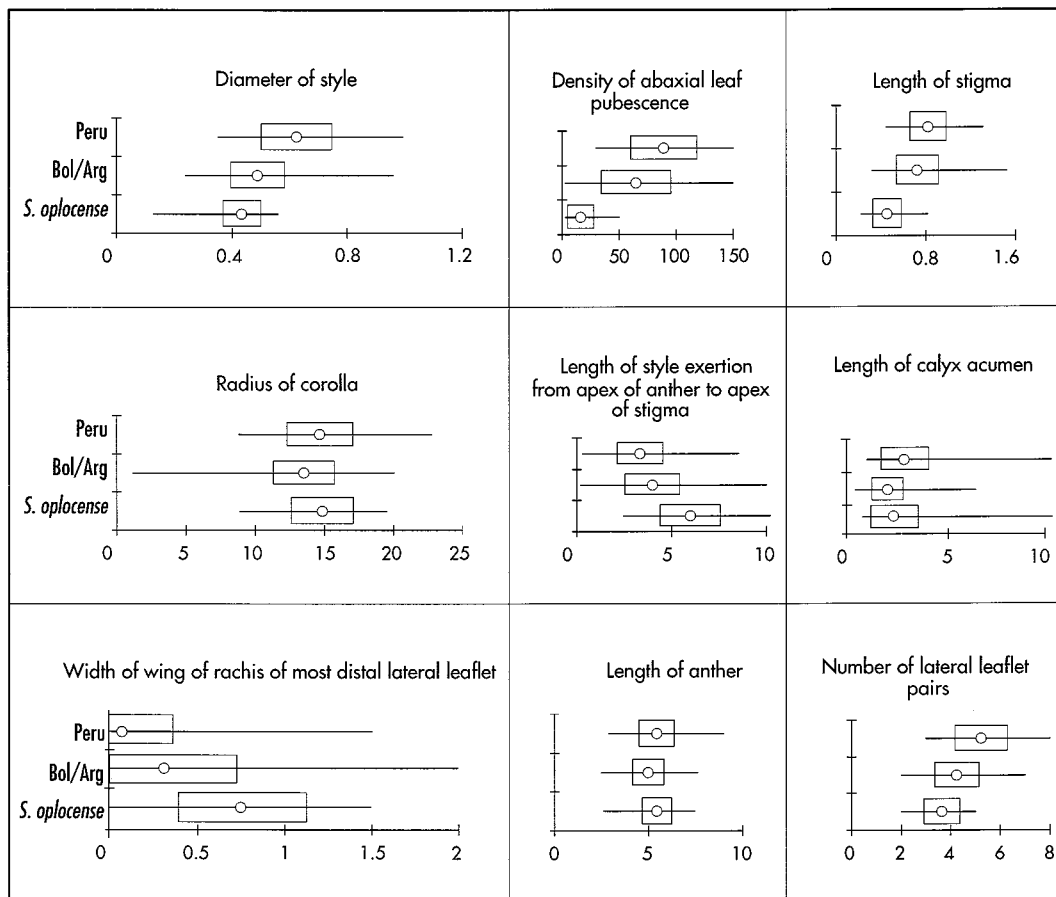


Fig. 8. Means, ranges, and one standard deviation of the mean for the nine most important characters separating taxa of the *S. brevicaule* complex, reclassified as (1) the Peruvian populations, including *S. candolleianum* from immediately adjacent Bolivia, (2) the Bolivian and Argentinian species, and (3) *S. oplocense*.

undergone recent hybridization and introgression, or that formerly distinct ranges have been disrupted by recent dispersal of weedy taxa (Hawkes, 1990). However, this is conjectural, and it is equally possible that the taxa were never well differentiated into species. Our morphological analysis of large population samples is unable to document gaps separating currently recognized taxa.

Our study is unable to differentiate many cultivated species from their putative Peruvian progenitors. We did not measure tuber traits that help to define a cultivated species because members of this complex fail to tuberize in the long-day environments of Wisconsin. However, our results question separation of cultivated and wild species that is based solely on large tubers and status as a cultivated plant. Some "wild" species, such as *S. candolleianum*, have large tubers like the cultivated species. Members of the *S. brevicaule* complex are the putative progenitors of the cultivated species, but it is equally possible that many wild species are derived from formerly cultivated populations (Ugent, 1970). The great variation of the cultivated species and sympatry with their putative wild relatives makes it possible that they are of polyphyletic origin (Ugent, 1970). A polyphyletic origin for the cultivated species has been supported by Hosaka (1995), who documented extensive cpDNA polymorphism in some members of the *S. brevicaule* complex, including the cultivated forms.

Insight into the consequences of the current taxonomy of the *S. brevicaule* complex comes from a comparison of alternative treatments of the Bolivian potato floras of Hawkes and Hjerting (1989) and Ochoa (1990). Excluding type specimens, identifications of identical collection numbers of members of the *S. brevicaule* complex differed in 38% of the cases (Spooner et al., 1994). Insights for the continued acceptance of these many difficult taxa come from taxonomic practice of genebank identifications. The NRSP-6 genebank collection of sect. *Petota* is the largest in the world for the wild species holdings (~5000 accessions of ~157 taxa [Bamberg and Spooner, 1994]). The collections historically have been identified by visiting taxonomic authorities working with living accessions planted in the field and greenhouse (Hanneman, 1989; Spooner and Bamberg, 1991). These authorities worked from field books that had full locality data, chromosome counts, and all of their prior identifications or those of others, potentially biasing identifications.

We are unsure of the basis underlying clustering of *S. verrucosum* (putative outgroup, ser. *Tuberosa* from Mexico) with members of the *S. brevicaule* complex. This species was included to represent the most northern representative of ser. *Tuberosa* (the series that includes members of the *S. brevicaule* complex) but was not expected to show affinities with the complex under study here. *Solanum verrucosum* clusters peripherally (Fig. 5) on the complex. Chloroplast DNA data poorly separated members of the *S. brevicaule* complex from *S. verrucosum* (Spooner and Castillo, 1997).

A formal taxonomic treatment of the *S. brevicaule* complex is beyond the scope of this study. Our most liberal taxonomic interpretation based on our data would be to recognize only three taxa: (1) the Peruvian populations (including *S. candolleianum* from immediately adjacent Bolivia), (2) the Bolivian and Argentinian popu-

lations, and (3) *S. oplocense* (see Fig. 8 for the major character differences separating these groups). Despite the weak morphological support for these "taxa," however, we have been unable to distinguish groups 1 and 2 even after the end of our study (we could usually distinguish *S. oplocense*), and they probably should be lumped on morphological criteria. We are continuing molecular studies of the group. We wish to have access to these data, to morphological data from replicated studies in Bolivia or Peru, and to type specimens, before we finalize taxonomic decisions. However, based on our experience in the genebank and field, the results presented here, and preliminary molecular data, collapse of species now recognized in the *S. brevicaule* complex appears inevitable.

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