

**SPECIES AND SERIES BOUNDARIES OF *SOLANUM* SERIES
LONGIPEDICELLATA (SOLANACEAE) AND PHENETICALLY
SIMILAR SPECIES IN SER. *DEMISSA* AND SER. *TUBEROSA*:
IMPLICATIONS FOR A PRACTICAL TAXONOMY OF
SECTION *PETOTA*¹**

DAVID M. SPOONER,^{2,5} RONALD G. VAN DEN BERG,³ AND
JOSEPH T. MILLER⁴

²Vegetable Crops Research Unit, USDA, Agricultural Research Service, Department of Horticulture, University of Wisconsin,
1575 Linden Drive, Madison, Wisconsin 53706-1590 USA;

³Department of Plant Taxonomy, Agricultural University Wageningen, P.O. Box 8010, 6700 ED Wageningen, The Netherlands; and

⁴CSIRO Plant Industry, GPO Box 1600, Canberra ACT, 2601 Australia

Species boundaries were assessed by phenetic analyses of morphological data for all species of wild potatoes (*Solanum* section *Petota*) assigned to ser. *Longipedicellata*: *S. fendleri*, *S. hjertingii*, *S. matehualae*, *S. papita*, *S. polytrichon*, and *S. stoloniferum*. These six tetraploid species grow in the southeastern United States (*S. fendleri*) and Mexico (all six species). We also analyzed morphologically similar species in ser. *Demissa* (*S. demissum*) and ser. *Tuberosa* (*S. avilesii*, *S. gourlayi*, *S. verrucosum*). We chose *S. verrucosum* and *S. demissum* as Mexican representatives, and *S. avilesii* and *S. gourlayi* as South American representatives of other series that are difficult to distinguish from ser. *Longipedicellata*. We also analyzed morphologically more dissimilar species in ser. *Tuberosa* (*S. berthaultii*) and ser. *Yungasensia* (*S. chacoense*). The results support only three species in ser. *Longipedicellata*: (1) *S. polytrichon*, (2) *S. hjertingii* + *S. matehualae*, (3) *S. fendleri* + *S. papita* + *S. stoloniferum*. *Solanum avilesii*, *S. gourlayi*, and to a lesser extent *S. demissum* and *S. verrucosum* are very similar to members of ser. *Longipedicellata* and are difficult to distinguish practically from them, despite differences in chromosome numbers and crossability relationships. These data help document and explain the extensive taxonomic difficulty in sect. *Petota*, highlight conflicts between biological and morphological species concepts, and add to a growing body of evidence that too many wild potato species are recognized.

Key words: phenetics; potato; sect. *Petota*; Solanaceae; *Solanum* series *Longipedicellata*; species concepts; taxonomy.

Solanum L. sect. *Petota* Dumort., the potato and its wild relatives, is distributed from the southwestern United States to southern Chile, with a concentration of diversity in the Andes. The latest comprehensive taxonomic treatment of the group (Hawkes, 1990) recognized 232 species, partitioned into 21 series. However, nine of these species are members of separate non-potato clades and are alternatively treated in sect. *Etuberosum* (Buk. and Kameraz) A. Child, sect. *Lycopersicum* (Mill.) Wettst., or sect. *Juglandifolium* (Rydb.) A. Child (Child, 1990; Spooner, Anderson, and Jansen, 1993; Contreras and Spooner, 1999). There are several disagreements regarding the number of species and their assignment to series throughout sect. *Petota* (Spooner and Sytsma, 1992; Spooner and van den Berg, 1992a).

Our study examines species boundaries of all six tetraploid ($2n = 4x = 48$) wild potato species in *Solanum* ser. *Longipedicellata* Juz., all of which have Endosperm Balance Numbers (EBN, see below) of 2. The standard citation of this ploidy

and EBN combination is $4x(2EBN)$. These six species are *S. fendleri* A. Gray, *S. hjertingii* Hawkes, *S. matehualae* Hjert. & T.R. Tarn, *S. papita* Rydb., *S. polytrichon* Rydb., and *S. stoloniferum* Schlttdl. & Bouchet. They grow in the southeastern United States (*S. fendleri*) and Mexico (all six species) and constitute all the members of ser. *Longipedicellata* except for *S. × vallis-mexici* Juz., a localized triploid of putative hybrid origin between *S. verrucosum* Schlttdl. (ser. *Tuberosa* Rydb. [Hawkes]) and *S. stoloniferum* (Hawkes, 1990).

The treatment of section *Petota* by Hawkes (1990) is the latest of many often-conflicting attempts at formal infrasectional classifications (Spooner and Sytsma, 1992; Spooner and van den Berg, 1992a). Hawkes's (1990) series classification has been discordant with phylogenies from chloroplast DNA restriction site data (cpDNA; Spooner and Sytsma, 1992; Spooner and Castillo, 1997), and Amplified Fragment Length Polymorphisms (AFLPs; Kardolus, 1998). The cpDNA data group all members of ser. *Longipedicellata* into a large clade that also includes all other Mexican and Central American polyploid species, the diploid Mexican species *S. verrucosum*, and most of the South American species. The AFLP data place all members of ser. *Longipedicellata* into a single clade, sister to *S. verrucosum*; sister to this clade is *S. brachycarpum* Correll (ser. *Demissa*); sister to this clade are South American species. Morphological data show *S. fendleri* (ser. *Longipedicellata*) to be distinguished from other South American species in the *Solanum brevicaule* complex only by character states that overlap in range (van den Berg et al., 1998). In summary, members of ser. *Longipedicellata* are difficult to distinguish

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⁵ Author for reprint requests (dsponer@facstaff.wisc.edu).

from members of other series in Mexico and in South America. It may be a natural group based partly on crossability data (below), shared tetraploid genomes, and restriction to North America and Mexico, but this is unresolved. We designed our study to explore the status of the six species in ser. *Longipedicellata* and the morphological distinction of this series from similar series.

We analyzed morphologically similar species in ser. *Demissa* Juz. [*S. demissum* Lindl. 6x(4EBN)] and ser. *Tuberosa* [*S. avilesii* Hawkes & Hjert., *S. gourlayi* Hawkes, and *S. verrucosum*, all 2x(2EBN)], and morphologically more dissimilar species in ser. *Tuberosa* [*S. berthaultii*, 2x(2EBN)] and ser. *Yungasensia* Correll [*S. chacoense* Bitter, 2x(2EBN)]. We chose *S. demissum* and *S. verrucosum* as Mexican representatives and *S. avilesii* and *S. gourlayi* as South American representatives of other series that are morphologically similar to members of ser. *Longipedicellata*. *Solanum demissum* was examined by Spooner, van den Berg, and Bamberg (1995) with morphological data, and forms a close phenetic group with the South American ser. *Acaulia*, rather than with ser. *Demissa*. We re-examine it here because of morphological similarity to *S. stoloniferum*, *S. fendleri*, and *S. verrucosum* (see below).

Our study is designed to be compared to a similar morphological study of the *Solanum brevicaule* complex, a group of ~30 South American wild potato taxa, including diploids, tetraploids, and hexaploids, that are very similar to the cultivated potato. The species boundaries of this complex were investigated by van den Berg, Groendijk-Wilders, and Kardolus (1996), and van den Berg et al. (1998) with morphological data, and Miller and Spooner (1999) with molecular data. The two latter studies were concordant in suggesting that these 30 taxa could at best be partitioned into three species. These studies showed that although *S. fendleri* could be distinguished from members of this complex, this could only be done with multivariate techniques using quantitative character states that overlap in range. The present study includes four species as “placeholders” that were investigated in common between these studies: *S. fendleri* (ser. *Longipedicellata*), *S. avilesii*, *S. gourlayi*, and *S. verrucosum* (ser. *Tuberosa*).

Morphological criteria and species boundaries—Correll (1962) and Hawkes (1990) provided the latest comprehensive treatments of sect. *Petota* and therefore will form the basis for comparison to our study. They had slightly different concepts regarding affiliations of species to ser. *Longipedicellata*, ser. *Demissa*, and ser. *Tuberosa*. Correll (1962) distinguished ser. *Longipedicellata* with “more or less petiolulate leaflets” and with “rotate-stellate corollas,” and ser. *Demissa* (including *S. verrucosum*) with “corolla[s] mostly rotate-pentagonal, sometimes rotate-substellate or rotate-stellate, occasionally somewhat 10–15-lobulate.” He keyed out members of ser. *Tuberosa* (Correll placed most species assigned here by Hawkes [1990] in ser. *Transaequatorialia* Buk. ex Kameraz) largely by geographical data and provided no species-specific characters. Hawkes (1990) distinguished ser. *Longipedicellata* by having a corolla with a “completely circular appearance with acumens standing out sharply from it,” or with corollas “occasionally substellate to pentagonal.” He stated that “the corolla lobes [of ser. *Tuberosa*] are not formed so as to give a circular appearance to the flower.” Hawkes (1990) distinguished ser. *Demissa* (excluding *S. verrucosum* placed in ser. *Tuberosa* by Correll [1962]) by “corolla lobes very short and flat, with

small acumens (1.5–2 mm long), giving the flowers a ten-lobed appearance.”

Members of these series are morphologically similar to each other in floral and vegetative traits, and the species distinctions can be vague. Gray (1886) noted the similarity of *S. fendleri* to the cultivated potato *S. tuberosum* L. (ser. *Tuberosa*) and synonymized it under *S. tuberosum* var. *boreale* A. Gray. Problems in distinguishing members of different series also were noted by Correll (1962, p. 364): “In my opinion, the confusing of some plants of *S. verrucosum* with some plants of *S. demissum* is excusable. In fact, many plants collected in nature cannot be placed with certainty into either category, while specimens of cultivated plants of both *S. verrucosum* and *S. demissum* are exceedingly variable.” Correll (1962, pp. 380–382) continued: “Vegetatively, many plants of *S. fendleri*, *S. demissum*, *S. verrucosum*, and *S. stoloniferum* found in nature approach one another very closely, and because of this I have leaned heavily on the shape of the corolla for separation of these plants. . . It must be noted, however, that variations are frequent and must be taken into consideration. . . All of these species, however, are exceedingly variable, especially in the size of the corolla, and the amount of pubescence present on the plant.”

Both authors also had slightly different concepts regarding species boundaries within ser. *Longipedicellata*. We summarize the characters they use in the keys and descriptions in Table 1 and provide a comparison of their species boundaries and affiliations to species and series in Fig. 1.

Biological criteria used to define ser. *Longipedicellata*—Members of *Solanum* ser. *Longipedicellata* are characterized by three key biological criteria (1) AABB genomes, (2) 4x(2EBN) crossability relationships, and (3) free interspecific crossability.

Genome hypotheses of ser. *Longipedicellata*—Within sect. *Petota* and the closest non-tuber-bearing relatives in section *Etuberosum*, chromosome pairing relationships have been interpreted by genome formulae (Marks, 1955; Matsubayashi, 1955, 1991; Hawkes, 1958, 1990; Irikura, 1976). Most authors agree on a five-genome hypothesis, although they do not use standard letter designations. The latest review of genome hypotheses by Matsubayashi (1991) designates genomes as A, B, C, D, and E. The A genome and its superscripted minor variants are part of the genomes of all diploid and polyploid species except for the non-tuber-bearing species of *Solanum* section *Etuberosum* that are designated as E genome species. The B genome is associated with the Mexican tetraploid wild species of ser. *Longipedicellata*; the C genome is associated with the Mexican, Central, and South American wild species of the ser. *Conicibaccata*; and the D genome with the Mexican hexaploid wild species of ser. *Demissa*.

Meiotic studies show the tetraploid species of ser. *Longipedicellata* to form 24 bivalents at metaphase I and generally to form 12 bivalents and 12 univalents in artificial hybrids with a typical A genome diploid, *S. chacoense*. Matsubayashi (1955, 1991), Irikura (1976), Ramanna and Hermsen (1979), and Hawkes (1990) postulated that members of ser. *Longipedicellata* are strict allotetraploids, with distinct A and B genomes. Hawkes (1990) suggested that the B genome was a primitive indigenous genome from Mexico, that the A genome was a recent migrant from South America, and that the members of ser. *Longipedicellata* are allopolyploid derivatives of

TABLE 1. Morphological characters used by Correll (1962) and Hawkes (1990) in their keys and descriptions to differentiate the six species of *Solanum* ser. *Longipedicellata*. Dashed lines indicate characters not mentioned by authors.

Taxon	Pubescence of stem, leaves, and calyx	Pairs of lateral leaflets	Pairs of interjected leaflets	Size difference between terminal and lateral leaflets	Petiole length	Corolla diameter (mm)	Corolla color	Style length and style exertion	Calyx length	Anther length	No. of flowers
<i>Solanum fendleri</i> subsp. <i>fendleri</i>	coarsely pubescent	(2-)3(-4)	0-several	—	petiolulate, sometimes subsessile	20-30	white to purple	7-10 (1.5) mm	4-7 mm	3.5-6 mm	several
<i>S. fendleri</i> subsp. <i>arizonicum</i>	coarsely pubescent	—	—	terminal leaflet larger than laterals	(sub)sessile	20-30	—	—	—	3 mm	—
<i>S. hjertingii</i>	glabrous	—	—	—	usually petiolulate	20-30	white to pale blue	—	—	—	—
<i>S. matehualae</i>	glabrous	2-3(-4)	0-1	terminal leaflet occasionally larger than laterals	petiolulate	20-25	dark purple	12-13 (8) mm	3-4 mm	4-5 mm	few
<i>S. polytrichon</i>	white spreading hairs	2-4	>5	terminal leaflet usually larger than laterals	shortly petiolulate sometimes sessile	20-30	white to mauve	6-10 mm	5 mm	4-5 mm	up to 15
<i>S. papita</i>	coarsely pubescent	(2-)3-4 (-5)	4	—	sessile to shortly petiolulate	10-15	pale lilac to dark purple	5-7.5(2) mm	4-6 mm	3-4 mm	up to 4
<i>S. stoloniferum</i> subsp. <i>stoloniferum</i>	coarsely pubescent	(3-)4-5	0-many	no size difference, sometimes terminal slightly larger	petiolulate	20-30	white to medium purple	8-10 mm	5-9 mm	5-6 mm	numerous
<i>S. stoloniferum</i> subsp. <i>moreletiae</i>	coarsely pubescent	3-4(-5)	0-2	—	—	20-30	very dark purple	—	<5 mm	—	—

Correll (1962)

Series *Longipedicellata*

S. fendleri
S. hintonii
S. nanmodes
S. papita
S. polytrichon
S. stoloniferum

Series *Borealia*

S. wightianum

Hawkes (1990)

Series *Longipedicellata*

S. fendleri
S. hjertingii
S. matehualae
S. papita
S. polytrichon
S. stoloniferum

Series *Pinnatisecta*

S. hintonii

Fig. 1. Comparison of species boundaries and affiliations of species to series of *Solanum* series *Longipedicellata* according to Correll (1962) and Hawkes (1990). Lines connect only points of disagreement between treatments.

hybridization between these A and B genome diploids. See Spooner, van den Berg, and Bamberg (1995) for a summary of these genome formulae by different authors for ser. *Longipedicellata*, ser. *Demissa*, and ser. *Tuberosa*.

Endosperm Balance Numbers—A major isolating mechanism in section *Petota* is governed by a strong crossing barrier evidenced by endosperm breakdown in hybrids differing by EBN compatibilities, referred to as the Endosperm Balance Number (EBN) hypothesis (Johnston et al., 1980; Hanneman, 1994). Species are assigned an EBN based on their ability to cross within EBN levels, using standard tester species. Within sect. *Petota*, species are 2x(1EBN), 2x(2EBN), 4x(2EBN), 4x(4EBN), and 6x(4EBN). Doubling ploidy doubles EBN (Hanneman, 1994). The 4x(2EBN) condition is rare in sect. *Petota*, possessed by all members of ser. *Longipedicellata*, but only two other Mexican and Central American species, *S. agrimonifolium* Rydb. and *S. oxycarpum* Scheide in Schldl. (members of ser. *Conicibaccata*), and a few other South American species.

Crossing relationships among species of ser. *Longipedicellata*—Hawkes (1966, 1990) and Matsubayashi (1991) documented that artificial interspecific hybrids within ser. *Longipedicellata* are fully interfertile. This contrasts sharply with general lack of intercrosability among species in the Mexican and Central American 6x(4EBN) species of ser. *Demissa*. In summary, species of ser. *Longipedicellata* are freely intercrossable with each other but have a strong EBN-based biological isolating mechanism from members of ser. *Demissa* and ser. *Tuberosa* and possess unique (putative) AABB genomes.

Purpose of the present study—This study contributes to our goal to produce a monograph of *Solanum* sect. *Petota* for North and Central America. It follows a morphological study of the six Mexican and Central American species in ser. *Demissa* (Spooner, van den Berg, and Bamberg, 1995), chloroplast DNA (cpDNA) restriction site studies of the ~30 wild potato species of North and Central America (Spooner and Sytsma, 1992), cpDNA studies of the Mexican and Central American species *S. bulbocastanum* and *S. cardiophyllum* (Rodríguez and Spooner, 1997), and field trips to Mexico and

Central America (Spooner et al., 1991, 1998, 2000, in press; Rodríguez et al., 1995). It also is part of a goal to better define species boundaries and relationships of wild potatoes to better classify the holdings of the world's genebanks. We pose the following two questions in this study: (1) What is the pattern of character state variation in the six tetraploid species of ser. *Longipedicellata*, and does this provide morphological support for these species? (2) Is there a practical taxonomic separation of members of ser. *Longipedicellata* from phenetically similar members of ser. *Tuberosa* using *S. avilesii*, *S. gourlayi*, and *S. verrucosum* as placeholders in reference to an earlier study of the *S. brevicaulis* complex (van den Berg et al., 1998; Miller and Spooner, 1999), and to *S. demissum* (ser. *Demissa*)?

MATERIALS AND METHODS

Species—We analyzed a total of 113 accessions (Table 2) and mapped the North and Central American ones to 48 generalized geographic regions (Fig. 2). This included all six species of ser. *Longipedicellata*: *S. fendleri* (32 accessions), *S. hjertingii* (10), *S. matehualae* (1; the only accession available of this rare species), *S. papita* (14), *S. polytrichon* (13), and *S. stoloniferum* (29). We did not classify *S. fendleri* and *S. stoloniferum* to the subspecies of Hawkes (1990; Fig. 1) because not all accessions are identified to subspecies (Bamberg et al., 1996) and because of the uncertainty of many of these identifications. We also analyzed morphologically similar species in ser. *Demissa* (*S. demissum*, 4), ser. *Tuberosa* (*S. avilesii*, 2; *S. gourlayi*, 3; and *S. verrucosum*, 3); and yet morphologically more dissimilar species in ser. *Tuberosa* (*S. berthaultii*, 1) and ser. *Yungasensia* (*S. chacoense*, 1).

All accessions were from the National Research Support Program-6 (NRSP-6; formerly the Inter-Regional Potato Introduction Project, IR-1; Bamberg et al., 1996). They represent the maximum geographic distribution available from the NRSP-6 collection (Fig. 2), and nearly the entire geographic ranges for these species as mapped by Hawkes (1966). Vouchers are deposited at the NRSP-6 herbarium in Sturgeon Bay, Wisconsin (PTIS, see <http://www.nybg.org/bsci/ih/ih.html>). Identifications of these accessions have been provided in past years by visiting taxonomists during on-site visits to NRSP-6 to identify living representatives in field plots.

To aid in communicating intra-accession variation and interspecific similarity of all six species within ser. *Longipedicellata* and morphologically similar species in ser. *Tuberosa* (*S. avilesii*, *S. gourlayi*, and *S. verrucosum*), and ser. *Demissa* (*S. demissum*) we show leaf variation (Fig. 3). We selected these accessions to illustrate variation within and between accessions, species, and series.

Seeds were planted in a greenhouse in early May, seedlings were transferred to peat pots in late May, and six individuals per accession were transplanted together in rows in a field plot at the University of Wisconsin Hancock Agricultural Experiment Station in early June. The study was replicated in the same field, for a total of 12 plants planted per accession.

Data measurement—The middle three of the six plants per row were measured for each accession. We measured 47 quantitative and seven qualitative characters (Table 3) when the plants were in full bloom in August, or in September for fruits, that set naturally in the field. Trichome density (characters 3–4) was assessed from young, fully expanded leaves in the interveinal areas, using a hand-held clear acetate strip with different numbers of points per square centimetre. Leaf measurements were made on the largest leaf per plant. Floral characters were measured on the uppermost inflorescence. Corolla colors were measured with the aid of the Royal Horticultural Society Colour Charts (Royal Horticultural Society, 1986), based on recommendations of Tucker, Maciarelo, and Tucker (1991). Because of varying colors and color intensities from blue to violet and white, and difficulty of ordering the colors by eye, we determined color intensity from charts with a Minolta chroma meter CR-221®. The 48 scored RHS colors, ordered by their corresponding intensity values, are: 155A (white, 102.3), 91D (94.1), 92D (93.1), 85D (93.0), 84D (92.3), 91C (86.2), 84C (83.6), 92C (82.7), 85C (82.2), 91B (77.7), 81A

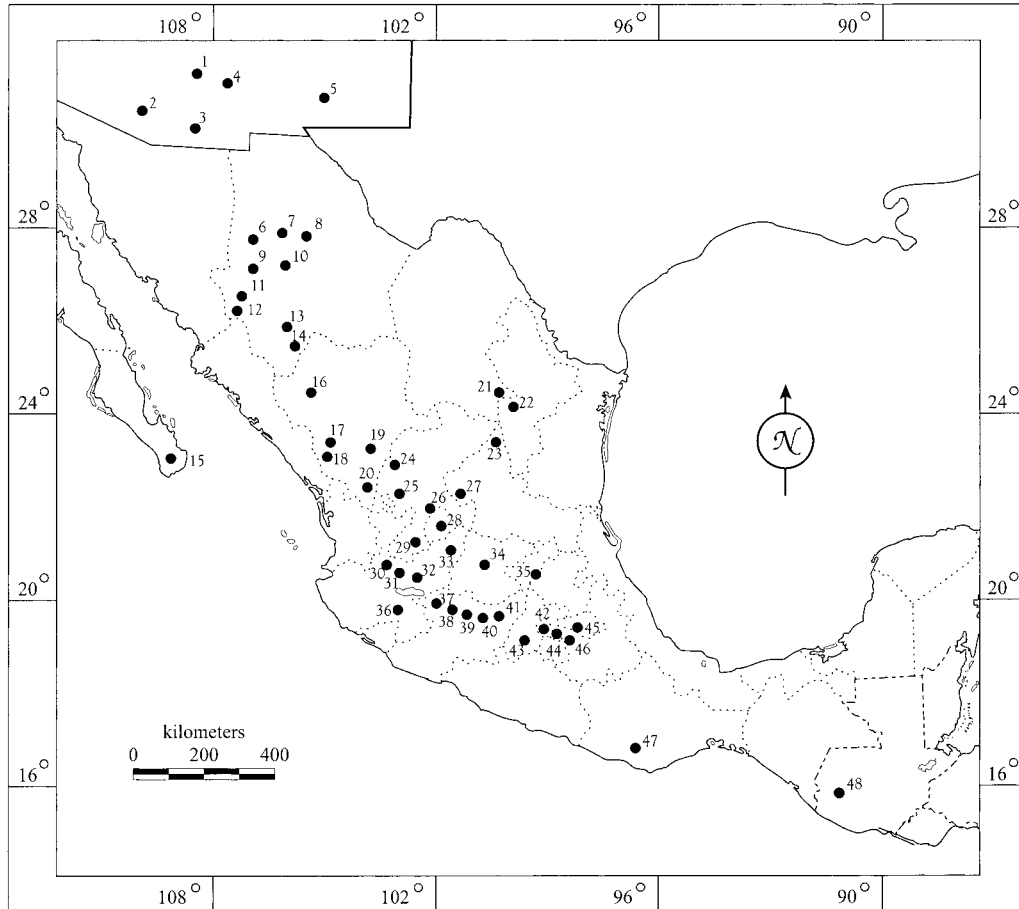


Fig. 2. Map showing the 48 generalized areas of the accessions of *S. demissum*, *S. fendleri*, *S. hjertingii*, *S. matehualae*, *S. papita*, *S. polytrichon*, *S. stoloniferum*, and *S. verrucosum* examined in this study. *Solanum avilesii*, *S. berthaultii*, *S. chacoense*, and *S. gourlayi* from South America are not mapped. Numbers are cited as generalized map areas in Table 2 and in Fig. 6.

(76.0), 85B (75.2), 84B (74.3), 95D (72.1), 92B (71.9), 85A (69.6), 93D (66.8), 91A (63.4), 94C (63.1), 86D (59.9), 90D (59.0), 84A (57.3), 88C (56.6), 92A (55.7), 90C (53.3), 82A (52.1), 94B (50.8), 83D (50.4), 86C (50.2), 93C (49.1), 88B (47.5), 90B (45.2), 86B (44.8), 88A (43.2), 83C (42.4), 98C (41.0), 77A (39.0), 90A (38.3), 93B (37.3), 94A (37.2), 83B (33.9), 86A (31.4), 79B (31.0), 83A (27.9), 79A (25.1), 93A (24.6), 89C (23.2), 89B (dark purple, 17.9). Raw data are available from the authors upon request.

Data analysis—For phenetic analyses, accessions were averaged over the two replicates (six plants in total). Thus the accession is the Operational Taxonomic Unit, OTU. Each character was analyzed for its mean, range, and standard deviation. Differences among taxa were determined by one-way ANOVA ($P = 0.05$), using species as the grouping criterion by one-way ANOVA in JMP statistical software (SAS, 1995). Dendrograms including all accessions were produced by NTSYS-pc^r version 1.70 (Rohlf, 1992). Averages for each character were standardized (STAND) and similarity matrices (in SIMINT), using average taxonomic distance (DIST), Manhattan distance (MANHAT), and product-moment correlation (CORR) were generated. Clustering was performed using the unweighted pair-group method (UPGMA) in SAHN. Co-phenetic correlation coefficients (COPH and MXCOMP) were used to measure distortion between the similarity matrices and the resultant three phenograms (Rohlf and Sokal, 1981; Sokal, 1986). Principal components analysis (PCA), canonical discriminant analysis (CDA), and stepwise discriminant analysis (SDA) were performed by SAS Version 7 (SAS, 1998) using PRINCOMP, CANDISC, and STEPDISC, with the means of six individuals per accession. The PCA, CDA, and SDA were run twice, once with all taxa and

all characters. They were run again with only the six species of ser. *Longipedicellata* and with a reduced character set that showed significant differences among any two pairs of species in ser. *Longipedicellata*, using the Tukey-Kramer HSD test in JMP software (SAS, 1995). The dendrograms were produced only with all taxa and all characters.

PCA and CDA are both ordination techniques, but PCA makes no assumptions about group membership of OTUs. 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, 1998). Cluster analysis, like PCA, makes no assumptions about group membership; it produces trees based on average similarity of all data. It is convenient graphically for studies such as this one with many OTUs, because of ease of labeling the terminal branches. PCA and dendrograms therefore are more appropriate to explore phenetic structure without any assumptions of species boundaries, while CDA is an appropriate technique to test preexisting classifications. Because these phenetic approaches use very different algorithms and operate under very different assumptions about the data set, we used all three analyses in our exploration of phenetic structure in *Solanum* ser. *Longipedicellata* and the other species outside of this series.

RESULTS

Character state variation—The Tukey-Kramer HSD test determined that 38 of the 54 characters were significantly different ($P = 0.05$) between at least two species. We illustrate

TABLE 2. Accessions of *Solanum* sect. *Petota* examined. Vouchers are deposited at the herbarium of the U.S. Potato Introduction Station (PTIS) in Sturgeon Bay, Wisconsin, USA.

Accession number	Species ^a	Map locality ^b	PI ^c	Collector	Locality
1	avl	S	498091	<i>Hawkes et al. 6519</i>	Bolivia. Santa Cruz: Valle Grande. 26 km from Valle Grande on the road to Pucará, Aqua de Oro; 2850 m, 18°38'S, 64°09'W.
2	avl	S	498093	<i>Hawkes et al. 6522</i>	Bolivia. Santa Cruz: Valle Grande. 28 km from Valle Grande on the road to Pucará; 2850 m, 18°38'S, 64°09'W.
3	ber	S	498102	<i>Hawkes et al. 6547</i>	Bolivia. Cochabamba: E. Arce. 16 km along the road from Anzaldo to Mollepujro, near Alfamayo; 2570 m, 17°55'S, 65°55'W.
4	chc	S	566746	<i>Okada et al. 4825</i>	Argentina. Salta: Rosaría de Lerma, between Alisal and Chorrillos, 1900 m, 24°19'S, 65°42'W.
5	dms	14	275207	<i>Hawkes et al. 1296</i>	Mexico. Chihuahua: Municipio Balleza, near Vergel, by the side of a small lake, not far from the fire tower; 2600 m, 25°26'N, 105°32'W.
6	dms	48	275211	<i>Hawkes et al. 1782</i>	Guatemala. Huehuetenango: Sierra de los Cuchumatanes, 28 miles from Huehuetenango; 3500 m, 15°40'N, 91°28'W.
7	dms	43	558386	<i>Spooner et al. 4010</i>	Mexico. México: Near roadside, near junction of road S of Route 130 and spur road that goes directly to the top of Nevado de Toluca; 3465 m, 19°09'N, 99°48'W.
8	dms	41	558392	<i>Spooner et al. 4064</i>	Mexico. Michoacán: 21 km N of Route 15; at junction of road N of Route 15 just W of Cd. Hidalgo, past San Pedro Jacuaro and road to steam wells at Los Azufres; 2750 m, 19°49'N, 100°39'W.
9	fen	1	458418	<i>Ugent & Ruhde 12-78</i>	United States. Arizona: Apache. Hwy 666, 1.9 km NE of the Greenlee County line; 2400 m, 33°47'N, 109°09'W.
10	fen	1	564042	<i>Salas et al. 23</i>	United States. Arizona: Apache County. Alpine vicinity. Hwy 666, 1.2 miles NE of Greenlee County line, at the pulloff. On W side of road under very large pines, especially in rotting fallen logs; 2400 m, 33°47'N, 109°09'W.
11	fen	2	564024	<i>Salas et al. 1</i>	United States. Arizona: Pima County. Coronado National Forest. About 0.6 miles past the 24 mile marker. Just past the emergency station turnoff. Just off the road on both sides; 2400 m, 32°25'N, 110°44'W.
12	fen	3	275162	<i>Hawkes 1177</i>	United States. Arizona: Cochise County. Chiricahua Mountains, Barfoot Park; 2450 m, 31°54'N, 109°16'W.
13	fen	3	275163	<i>Hawkes 1180</i>	United States. Arizona: Cochise County. Chiricahua Mountains, Rustler Park; 2550 m, 31°53'N, 109°16'W.
14	fen	3	458420	<i>Ugent & Ruhde 1-78</i>	United States. Arizona: Cochise County. Barfoot Park, Coronado National Forest, 24.1 km from the NW park entrance; 2480 m, 31°54'N, 109°16'W.
15	fen	3	564025	<i>Salas et al. 3</i>	United States. Arizona: Cochise County. About 1 mile SW of Sierra Vista Estates in Ramsey Canyon (private property). About 0.2 miles from the visitor center in the stream bottoms; 1900 m, 31°26'N, 110°19'W.
16	fen	4	275161	<i>Hawkes 1174</i>	United States. New Mexico: Catron County. Mogollon Mountains, 15 miles from Willow Creek on the road to Glenwood; 2200 m, 33°23'N, 108°46'W.
17	fen	4	564041	<i>Salas et al. 20</i>	United States. New Mexico: Catron County. Reserve vicinity. At 12 miles NE of Reserve on Hwy 12 to town of Apache Creek. Take Cox Canyon road ca. 15 miles to John Kerr lookout tower peak (tower has been removed). Along roadside about 0.5 mile up primitive trail; 2500 m, 33°48'N, 108°28'W.
18	fen	5	275156	<i>Hawkes 1156</i>	United States. New Mexico: Otero County. Lincoln National Forest. Lane located about a quarter of a mile S of Cloudcroft; 2600 m, 32°56'N, 105°43'W.
19	fen	5	458409	<i>Ugent & Ruhde 14-78</i>	United States. New Mexico: Otero County. E edge of Cloudcroft, across from the school; 2595 m, 32°57'N, 105°43'W.
20	fen	5	564034	<i>Salas et al. 12</i>	United States. New Mexico: Otero County. Cloudcroft vicinity. At 8 miles N of Cloudcroft on Hwy 82, take the gravel road to Sixteen Springs Canyon to the cemetery (about 6.2 miles). Only found at base of trees; 2350 m, 32°59'N, 105°34'W.
21	fen	6	498001	<i>Tarn et al. 16</i>	Mexico. Chihuahua: About 5 km W of Madera on the road to Sirupa; 2050 m, 29°08'N, 108°08'W.
22	fen	6	498004	<i>Tarn et al. 15</i>	Mexico. Chihuahua: About 15 km along the road from Madera to Sirupa; 2100 m, 29°07'N, 108°09'W.
23	fen	6	498238	<i>Ochoa 14196</i>	Mexico. Chihuahua: Madera; 2075 m, 29°12'N, 108°07'W.
24	fen	7	497994	<i>Tarn et al. 5</i>	Mexico. Chihuahua: 23 km along brecha to Sta. Clara from km 92 on Hwy 45 from Chihuahua to Delicias; 1800 m, 28°58'N, 106°27'W.
25	fen	8	251062	<i>Hawkes 1230</i>	Mexico. Chihuahua: Majalca, 40 miles NW of Chihuahua, near the village; 2100 m, 29°08'N, 106°05'W.
26	fen	9	497996	<i>Tarn et al. 7</i>	Mexico. Chihuahua: Along the road from La Junta to Tomochic. On the E side of the Papigochic River; 2090 m, 28°19'N, 107°21'W.
27	fen	9	497997	<i>Tarn et al. 8</i>	Mexico. Chihuahua: 15 km towards San Juanito from the La Junta to Yepachic Hwy; 2070 m, 28°14'N, 107°27'W.
28	fen	9	497998	<i>Tarn et al. 9</i>	Mexico. Chihuahua: 27 km along the road to San Juanito from the La Junta to Yepachic Hwy; 2060 m, 28°14'N, 107°27'W.
29	fen	9	497999	<i>Tarn et al. 10</i>	Mexico. Chihuahua: 30 km along the road to San Juanito from the La Junta to Yepachic Hwy; 2040 m, 28°14'N, 107°27'W.
30	fen	9	498000	<i>Tarn et al. 11</i>	Mexico. Chihuahua: Near Cebolla, 36 km along the road from the La Junta to Yepachic Hwy; 2060 m, 28°14'N, 107°27'W.

TABLE 2. Continued.

Accession number	Species ^a	Map locality ^b	PI ^c	Collector	Locality
31	fen	9	498241	<i>Ochoa 14205</i>	Mexico. Chihuahua: Route Tomochic-Basasiachic; 1975 m, 28°12'N, 107°47'W.
32	fen	10	497995	<i>Tarn et al. 6</i>	Mexico. Chihuahua: 17 km from Cuauhtemoc towards La Junta; 2090 m, 28°26'N, 107°00'W.
33	fen	11	558398	<i>Spooner et al. 4245</i>	Mexico. Chihuahua: In arroyos on SE side of rail road line at San Rafael, on N side of town; 2150 m, 27°30'N, 107°53'W.
34	fen	12	558397	<i>Spooner et al. 4241</i>	Mexico. Chihuahua: At rail road km 171.5, about 3 km SW of Bauchivo Rail road station, Los Mochis-Chihuahua rail road, about 250 m SE of rail road line across stream; 1550 m, 27°18'N, 108°05'W.
35	fen	13	262895	<i>Gentry 18006</i>	Mexico. Chihuahua: Between Guadalupe and Calvo and Tecolate; 26°49'N, 106°25'W.
36	fen	14	283102	<i>Hawkes 1314</i>	Mexico. Chihuahua: 11 miles from Vergel on road from Parral; 2500 m, 26°16'N, 105°27'W.
37	fen	15	558395	<i>Spooner et al. 4237</i>	Mexico. Baja California Sur: In the Sierra La Laguna, on a footpath to La Laguna, marsh on top of Sierra, ENE of Todos Santos; 1600 m, 23°32'N, 110°01'W.
38	fen	15	558396	<i>Spooner et al. 4239</i>	Mexico. Baja California Sur: In the Sierra La Laguna, on a footpath to La Laguna marsh on top of Sierra, ENE of Todos Santos; 1750 m, 23°32'N, 109°59'W.
39	fen	16	498038	<i>Tarn et al. 140</i>	Mexico. Durango: Just before km 103 on Hwy 39 between Santa Teresa and Santiago Papasquiari; 2150 m, 24°48'N, 105°08'W.
40	fen	36	558449	<i>Spooner et al. 4118</i>	Mexico. Jalisco: New microwave tower road to top of Nevado de Colima, at edge of cornfield, 6 km from beginning of this road which begins about 0.5 km SE of La Mesa and el Fresno; 1775 m, 19°35'N, 103°32'W.
41	grl	S	210038	<i>Hjerting 962</i>	Argentina. Jujuy: Between Iturbe and Tres Cruces, km 1313; 3500 m, 22°56'S, 65°24'W.
42	grl	S	473019	<i>Okada 4333</i>	Argentina. Jujuy: Quebrada de Sepulturas, Puerta de Potrereros; 3000 m, 23°39'S, 65°36'W.
43	grl	S	473063	<i>Okada 4832</i>	Argentina. Salta: 8 km NW of Las Cuevas, Quebrada Munal; 3340 m, 24°19'S, 66°06'W.
44	hjt	21	186559	<i>Hawkes 1113</i>	Mexico. Coahuila: Near Saltillo, Municipio Arriaga, Cañon de Los Lirios, Chupadero; situated in the Sierra Madre Oriental; 2000 m, 25°25'N, 101°00'W.
45	hjt	21	186560	<i>Hawkes 1114</i>	Mexico. Coahuila: Near Saltillo, Municipio Arriaga, Cañon de los Lirios, situated in the Sierra Madre Oriental; 2250 m, 25°25'N, 101°00'W.
46	hjt	21	251063	<i>Hawkes 1355</i>	Mexico. Coahuila: Saltillo. E of Saltillo, Cañon de Los Lirios, 4 miles W of the Lirios village; 2200 m, 25°25'N, 101°00'W.
47	hjt	21	251065	<i>Hawkes 1357</i>	Mexico. Coahuila: Saltillo. 19 miles from Saltillo, Route 57, entering at Puerto de Flores on the track to Rancho Las Vacas; 2100 m, 25°25'N, 101°00'W.
48	hjt	21	283103	<i>Hawkes 1353</i>	Mexico. Coahuila: Saltillo. School of Agriculture, about 5 miles S of Saltillo; 1760 m, 25°25'N, 101°00'W.
49	hjt	21	498019	<i>Tarn et al. 159</i>	Mexico. Coahuila: Near Saltillo, Los Lirios, 50 km from Saltillo on the road to Allende, in the village itself; 2340 m, 25°22'N, 100°38'W.
50	hjt	21	545713	<i>Tarn et al. 158</i>	Mexico. Coahuila: Road to Sierra Hermosa, 6.3 km along road turning off from Hwy 57 at km 29 from Saltillo; 2200 m, 25°30'N, 100°45'W.
51	hjt	21	545714	<i>Tarn et al. 160</i>	Mexico. Coahuila: Los Lirios, 50 km from Saltillo on the road to Allende. 700 m S of the village go up the slope towards the woods; 2340 m, 25°22'N, 100°38'W.
52	hjt	21	545715	<i>Tarn et al. 163</i>	Mexico. Coahuila: 5 km E of San Antonio de las Alazanas, village of Efigenia; 2350 m, 25°16'N, 100°36'W.
53	hjt	22	251067	<i>Hawkes 1378</i>	Mexico. Nuevo León: Cerro Potosí. Below Las Canoas on the edge of La Joya de Abajo; 2500 m, 24°52'N, 100°13'W.
54	mat	23	498050	<i>Tarn et al. 155</i>	Mexico. San Luis Potosí: Sierra de Catorce, road turning off 10 km west of Cedral (north of Matehuala), track to Real de Catorce, 2 km above tunnel; 2740 m, 23°42'N, 100°54'W.
55	plt	17	255547	<i>Graham 358</i>	Mexico. Durango: Km 972, Hwy 40, Durango-El Salto; 23°54'N, 105°01'W.
56	plt	26	184770	<i>Hawkes 1101</i>	Mexico. Zacatecas: 726.5 km from Mexico towards Zacatecas; 2100 m, 22°47'N, 102°35'W.
57	plt	27	545780	<i>Tarn et al. 212</i>	Mexico. San Luis Potosí: Hwy 49 at 67 km W of Zacatecas, then 1 km N along the track to Villa de Ramos; 2160 m, 22°39'N, 101°57'W.
58	plt	29	545786	<i>Tarn et al. 233</i>	Mexico. Zacatecas: Hwy 54, 10 km SW of Jalpa, 26.3 km along the track towards Tlaltenango; 2400 m, 21°39'N, 103°08'W.
59	plt	29	545788	<i>Tarn et al. 236</i>	Mexico. Zacatecas: Hwy 54, 10 km SW of Jalpa, 28.2 km along the track towards Tlaltenango; 2520 m, 21°40'N, 103°09'W.
60	plt	30	558447	<i>Spooner et al. 4093</i>	Mexico. Jalisco: Along Volcán Tequila microwave tower road S of city of Tequila, 8.6 km from rail road tracks at base of Volcán Tequila; 2000 m, 20°49'N, 103°51'W.
61	plt	31	558446	<i>Spooner et al. 4086A</i>	Mexico. Jalisco: On N side of Route 15 W of Guadalajara, about 3 km W of La Venta; 1670 m, 20°43'N, 103°34'W.

TABLE 2. Continued.

Accession number	Species ^a	Map locality ^b	PF ^c	Collector	Locality
62	plt	32	558451	<i>Spooner et al. 4140</i>	Mexico. Jalisco: On microwave tower road to Cerro Grande, SE of Santa Fe, 0.7 km downhill of top of tower; 2230 m, 20°30'N, 103°02'W.
63	plt	35	186545	<i>Hawkes 1090</i>	Mexico. Querétaro: San Juan del Río, ESE of town, near the Mexico highway; 2000 m, 20°20'N, 100°00'W.
64	plt	35	498276	<i>Ochoa 14184</i>	Mexico. Querétaro: Route San Juan del Río-Palmillas; 2040 m, 20°17'N, 99°54'W.
65	plt	35	545789	<i>Tarn et al. 297</i>	Mexico. Querétaro: Hwy 57, km 154 from Mexico City, between Palmillas and San Juan del Río, near Palma de Romero; 2200 m, 20°20'N, 99°57'W.
66	plt	35	558454	<i>Spooner et al. 4146</i>	Mexico. Querétaro: On E side of Route 57, SE of San Juan del Río, about 2 km N of Palmillas; 2150 m, 20°20'N, 99°56'W.
67	plt	37	255546	<i>Graham 315</i>	Mexico. Michoacán: Hwy 110, Guadalupe-Jiquilpan; 19°59'N, 102°46'W.
68	pta	8	283101	<i>Hawkes 1259</i>	Mexico. Chihuahua: Majalca, 40 miles NW of Chihuahua, near the village; 2150 m, 29°08'N, 106°05'W.
69	pta	17	249929	<i>Correll 20075</i>	Mexico. Durango: 18 miles W of Durango, Río Chico; 23°05'N, 103°10'W.
70	pta	17	275227	<i>Hawkes 1482</i>	Mexico. Durango: Near Hacienda Otinapa, Rancho Alamito, high valley of Río Chico; 2300 m, 24°57'N, 103°54'W.
71	pta	18	498035	<i>Tarn et al. 139</i>	Mexico. Durango: 17 km S of El Salto on the track to La Peña; 2790 m, 23°47'N, 104°40'W.
72	pta	18	545732	<i>Tarn et al. 138</i>	Mexico. Durango: 18 km S of El Salto on the track to La Peña; 2810 m, 23°47'N, 104°40'W.
73	pta	19	545726	<i>Tarn et al. 125</i>	Mexico. Durango: 3 km beyond La Flor on the track to Las Bayas; 2700 m, 24°33'N, 104°06'W.
74	pta	19	545728	<i>Tarn et al. 128</i>	Mexico. Durango: S of Durango, 68 km along the track from La Ferreria to La Flor; 2680 m, 24°24'N, 104°28'W.
75	pta	20	545723	<i>Tarn et al. 113</i>	Mexico. Durango: Along the track from Huejuquilla to Santa Lucia de la Sierra, 2 km E of Las Canoas; 2750 m, 22°40'N, 104°21'W.
76	pta	24	498028	<i>Tarn et al. 117</i>	Mexico. Zacatecas: Sierra de Sombrerete. From San Martín, near Hwy 45, 5 km along the track to the microwave tower; 2760 m, 23°38'N, 103°39'W.
77	pta	24	498030	<i>Tarn et al. 120</i>	Mexico. Zacatecas: Hwy 45, 18 km NW of Sombrerete towards Vicente Guerrero, at junction with side track to El Alamo; 2380 m, 23°38'N, 103°39'W.
78	pta	24	545724	<i>Tarn et al. 119</i>	Mexico. Zacatecas: Sierra de Sombrerete, just below the microwave tower, 8 km from San Martín; 3000 m, 23°38'N, 103°39'W.
79	pta	25	498027	<i>Tarn et al. 114</i>	Mexico. Zacatecas: 26 km W of Valparaiso on road to Huejuquilla; 2310 m, 22°46'N, 103°34'W.
80	pta	26	251740	<i>Hawkes 1473</i>	Mexico. Zacatecas: 82 miles from Fresnillo on the road from Zacatecas, El Alamo, 7 miles from the Durango border; 2350 m, 23°30'N, 103°10'W.
81	pta	26	275229	<i>Hawkes 1488</i>	Mexico. Zacatecas: 4.2 miles from the Durango border, along the road from Durango to Zacatecas; 2250 m, 23°30'N, 103°35'W.
82	sto	14	283108	<i>Hawkes 1301</i>	Mexico. Chihuahua: Municipio Balleza, Vergel, on the edge of the village when entering from Parral; 2750 m, 25°26'N, 105°32'W.
83	sto	20	545740	<i>Tarn et al. 110</i>	Mexico. Durango: Along track from Huejuquilla to Santa Lucia de la Sierra, 30 km W of turn to San Juan Capistrano; 2610 m, 22°40'N, 104°21'W.
84	sto	28	545781	<i>Tarn et al. 217</i>	Mexico. Aguascalientes: Hwy 70, about 33 km from Aguascalientes, 10.2 km along the track past Milpillillas de Arriba towards Potrero los López; 2460 m, 21°57'N, 102°36'W.
85	sto	28	545793	<i>Tarn et al. 222</i>	Mexico. Aguascalientes: Hwy 70, at km 49 just before Calvillo, then N thru San Isidro and 12 km N of La Labor, beyond Temascal towards La Dongoja; 2300 m, 22°03'N, 102°44'W.
86	sto	29	545792	<i>Tarn et al. 224</i>	Mexico. Zacatecas: Hwy 70, 12 km NW of Jalpa, 14 km along the track SE towards Tlachichila; 2220 m, 21°36'N, 102°51'W.
87	sto	33	255534	<i>Graham 366</i>	Mexico. Jalisco: N of Lagos de Moreno; 21°21'N, 101°55'W.
88	sto	34	283109	<i>Hawkes 1452</i>	Mexico. Guanajuato: 18 miles from Dolores Hidalgo on the road to Guanajuato; 2250 m, 20°51'N, 101°24'W.
89	sto	35	558455	<i>Spooner et al. 4149</i>	Mexico. Querétaro: On E side of Route 57, SE of San Juan del Río, about 2 km N of Palmillas; 2150 m, 20°20'N, 99°56'W.
90	sto	38	275248	<i>Hawkes 1520</i>	Mexico. Michoacán: Sierra de los Tarascos, 42 km from Carapan on the Uruapan road, near Paracho; 2300 m, 19°35'N, 102°03'W.
91	sto	38	275249	<i>Hawkes 1521</i>	Mexico. Michoacán: Sierra de los Tarascos, 43 km from Carapan on the Uruapan road, Grahamnja Villa Imelda; 2300 m, 19°35'N, 102°03'W.
92	sto	39	239410	<i>Graham 385</i>	Mexico. Michoacán: Quiroga Patzcuaro; 19°31'N, 101°36'W.
93	sto	39	558477	<i>Spooner et al. 4278</i>	Mexico. Michoacán: 4.1 km NW of Route 120 by Santa Maria Huiramangaro on road to San Francisco Pichataro; 2330 m, 19°31'N, 101°47'W.
94	sto	40	558468	<i>Spooner et al. 4074</i>	Mexico. Michoacán: On W side of Route 120 S of Morelia, just S of El Reparo; 2080 m, 19°34'N, 101°19'W.
95	sto	40	558469	<i>Spooner et al. 4080</i>	Mexico. Michoacán: Along Route 120 S of Morelia, 27.5 km (by roadside markers), S of Morelia; 2080 m, 19°34'N, 101°21'W.
96	sto	41	255525	<i>Graham 222</i>	Mexico. Michoacán: 22 km S of Morelia; 19°42'N, 101°07'W.
97	sto	41	338620	<i>Rowe 6</i>	Mexico. Michoacán: E of Morelia; 19°42'N, 101°07'W.

TABLE 2. Continued.

Accession number	Species ^a	Map locality ^b	PI ^c	Collector	Locality
98	sto	41	338621	Rowe 7	Mexico. Michoacán: Mount Punguato, near Morelia; 2000 m, 19°42'N, 101°07'W.
99	sto	41	365401	Tarn 187	Mexico. Michoacán: Morelia-Guadalajara road, Hwy 15, at 387 km, on left of road; 2080 m, 19°42'N, 101°07'W.
100	sto	41	558465	Spooner et al. 4058	Mexico. Michoacán: On road from Route 15 to San Pedro Jacuaro, 6 km NW of Route 15; 2270 m, 19°43'N, 100°39'W.
101	sto	41	558466	Spooner et al. 4066	Mexico. Michoacán: S slope of Cerro Punhuato, 2 km E of E end of Morelia, NE Route 15; 2080 m, 19°41'N, 101°07'W.
102	sto	41	558467	Spooner et al. 4069	Mexico. Michoacán: About 3 km W of W edge of Morelia, on N side of Route 15, about 0.5 km E of road diverting S to Cointzio; 2000 m, 19°41'N, 101°17'W.
103	sto	42	186555	Hawkes 1107	Mexico. Federal District: Above Contreras, Cuatro Dinamos, between the first and second hydro-electric plants; 2600 m, 19°18'N, 99°17'W.
104	sto	43	161178	Correll 14263	Mexico. Michoacán: Near San Juan de las Huertas, the lower slopes of Nevada de Toluca; 19°43'N, 101°07'W.
105	sto	43	545794	Tarn et al. 240	Mexico. México: Toluca-Sultepec Road #3, at about 32 km take turn to Coatepec. At 2.7 km turn E following tracks 7.7 km towards El Picacho. South of Agua Bendita; 2670 m, 18°57'N, 99°51'W.
106	sto	43	558462	Spooner et al. 4005	Mexico. México: Along roadside by cornfield just NE of Calimaya, about 2 km W of Route 55, S of Toluca; 2600 m, 19°10'N, 99°37'W.
107	sto	44	558472	Spooner et al. 4151	Mexico. México: San Luis Huexotla, 4 km SE of Texcoco; 2250 m, 19°29'N, 98°52'W.
108	sto	45	545834	Tarn et al. 262	Mexico. Tlaxcala: Road from Teacalco to Torre Forestal, 350 m before Estación Microondas (N slope of Volcán Malinche); 2830 m, 19°18'N, 98°02'W.
109	sto	46	310964	Ugent 1288	Mexico. Puebla: Popocatepetl; 2835 m, 18°60'N, 98°43'W.
110	sto	47	558475	Spooner et al. 4187	Mexico. Oaxaca: 3.0 km S of Miahuatlan de Porfirio Diaz-San Pedro Coatlán road, on road to San Miguel Coatlán; 2110 m, 16°13'N, 96°43'W.
111	ver	21	498061	Tarn et al. 161	Mexico. Coahuila: Road from Saltillo towards E, between Jame and Cienega de la Purisima, at the highest part of the road; 2720 m, 25°25'N, 100°44'W.
112	ver	36	558488	Spooner et al. 4127	Mexico. Jalisco: New microwave tower road to top of Nevado de Colima which begins about 0.5 km SE of La Mesa y el Fresnito; 1.5 km W of Estación de Vigilancia de Sedue; 3410 m, 19°34'N, 103°35'W.
113	ver	44	545811	Tarn et al. 251	Mexico. México: Along Hwy 142 from Oaxtepec to Xochimilco, 6.1 km N of Morelos-México state boundary, 3 km W towards CICITEC and 1 km along track; 2930 m, 19°06'N, 98°57'W.

^a Species abbreviations follow Hawkes (1990). avl = *S. avilesii*, ber = *S. berthaultii*, chc = *S. chacoense*, dms = *S. demissum*, fen = *S. fendleri*, grl = *S. gourlayi*, hjt = *S. hjertingii*, mat = *S. matehualae*, plt = *S. polytrichon*, pta = *S. papita*, sto = *S. stoloniferum*, ver = *S. verrucosum*.

^b Map numbers correspond to Fig. 2; S refers to unmapped accessions from South America.

^c United States Department of Agriculture Plant Introduction Numbers.

the means, ranges, and standard deviations of 24 of these 38 characters, and chose them based on using all 19 characters of the SDA of the reduced data set, and then five important characters based on the PCA and CDA analyses of the reduced data set. All characters are highly polymorphic, and there are few absolute species-specific character states within ser. *Longipedicellata* (Fig. 4).

Phenetic results—The entire data set resulted in over 36 600 data points. A PCA of the entire data set is presented in Fig. 5. Principal components 1, 2 and 3 account for 17.9, 10.9, and 7.9% of the variation, respectively, for a total of 36.7%. PCA axis 1 is most highly influenced by (presented in decreasing order of loadings) (1) length of most distal lateral leaflet lamina, (2) ratio: length of most distal lateral leaflet lamina from its widest point to apex/length of lamina, (3) leaf length, (4) leaf width across the most distal lateral leaflet pair, (5) length of anther; PCA axis 2 by (1) width of most distal lateral leaflet 5 mm below apex, (2) width of terminal leaflet 5 mm below apex, (3) length of terminal leaflet lamina, (4) ratio: length of terminal leaflet lamina from its widest point to apex/length of lamina, (5) ratio: length of most distal lateral leaflet lamina/

width of lamina; PCA axis 3 by (1) ratio: length of terminal leaflet lamina/width of lamina, (2) shape of most distal lateral leaflet base, (3) shape of terminal leaflet base, (4) corolla ratio 1, (5) ratio: length of calyx lobe/width. The PCA (interpreting axes 1, 2 and 1, 3 as a unit) separates *S. berthaultii*, *S. chacoense*, *S. demissum*, and only very weakly separates *S. gourlayi* and *S. verrucosum*, and intermixes other species.

The dendrogram of the entire data set produced by DIST (Fig. 6) had the highest cophenetic correlation coefficient (0.76), only slightly higher than those produced by MANHAT, 0.75; CORR was 0.58. Rohlf (1992) stated that cophenetic correlations between 0.8 and 0.9 could be interpreted subjectively as good fits to the cluster analysis, and those between 0.7 and 0.8 as poor fits. It clearly separates the morphologically most dissimilar species, *S. chacoense* and *S. berthaultii*, at the very base of the tree. All four accessions of *S. demissum* cluster near the base of the tree. The other non-ser. *Longipedicellata* species cluster among ser. *Longipedicellata* species. All three accessions of *S. verrucosum* cluster. The two accessions of *S. avilesii* and three accessions of *S. gourlayi* (ser. *Tuberosa*) are intercalated in the members of ser. *Longipedicellata*. Regarding ser. *Longipedicellata*, *S. matehualae* and *S.*

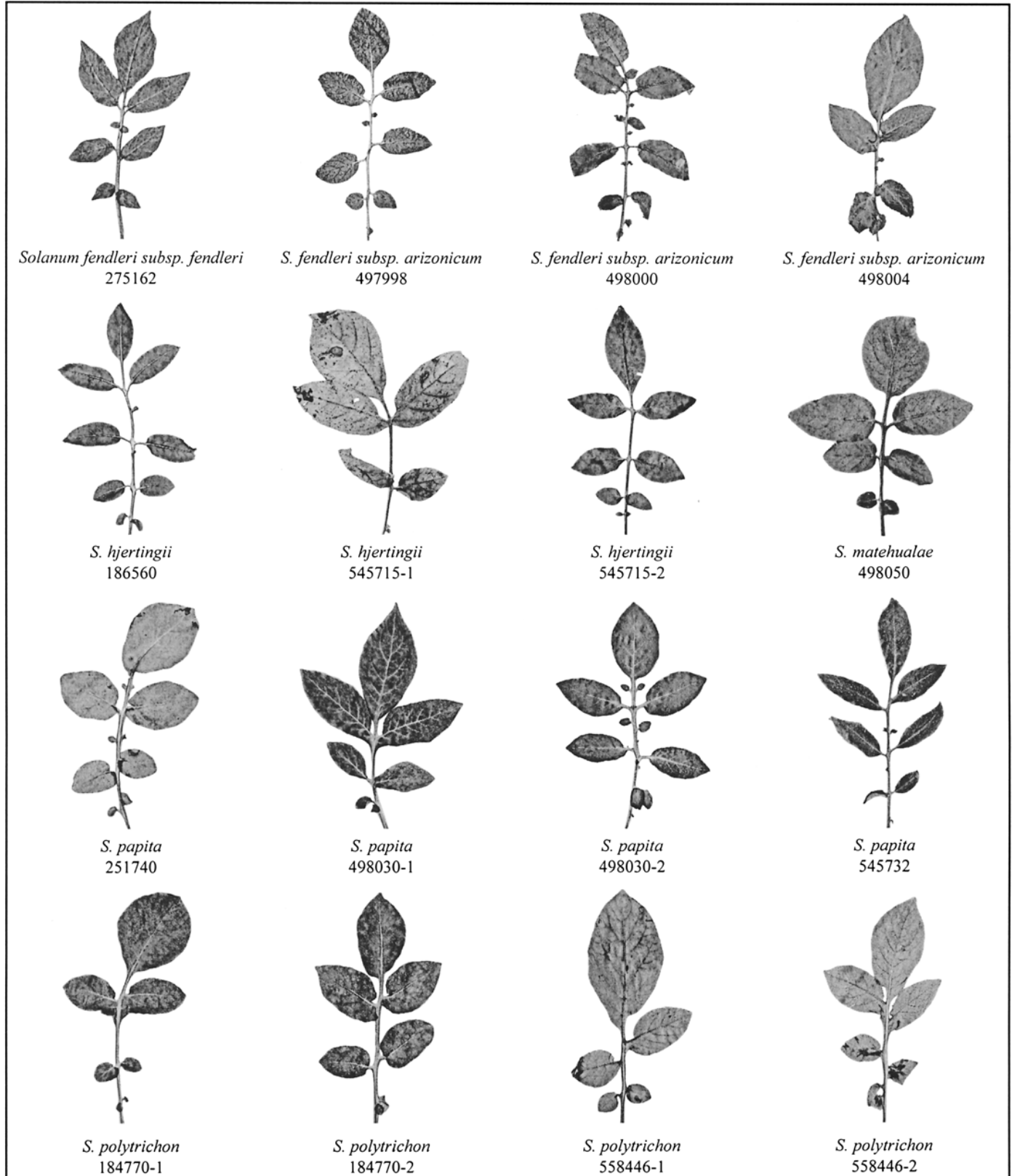


Fig. 3. Representative leaves of all six species of series *Longipedicellata*, followed by leaves of the phenetically similar species *S. avilesii*, *S. gourlayi* and *S. verrucosum* (ser. *Tuberosa*) and of *S. demissum* (ser. *Demissa*).

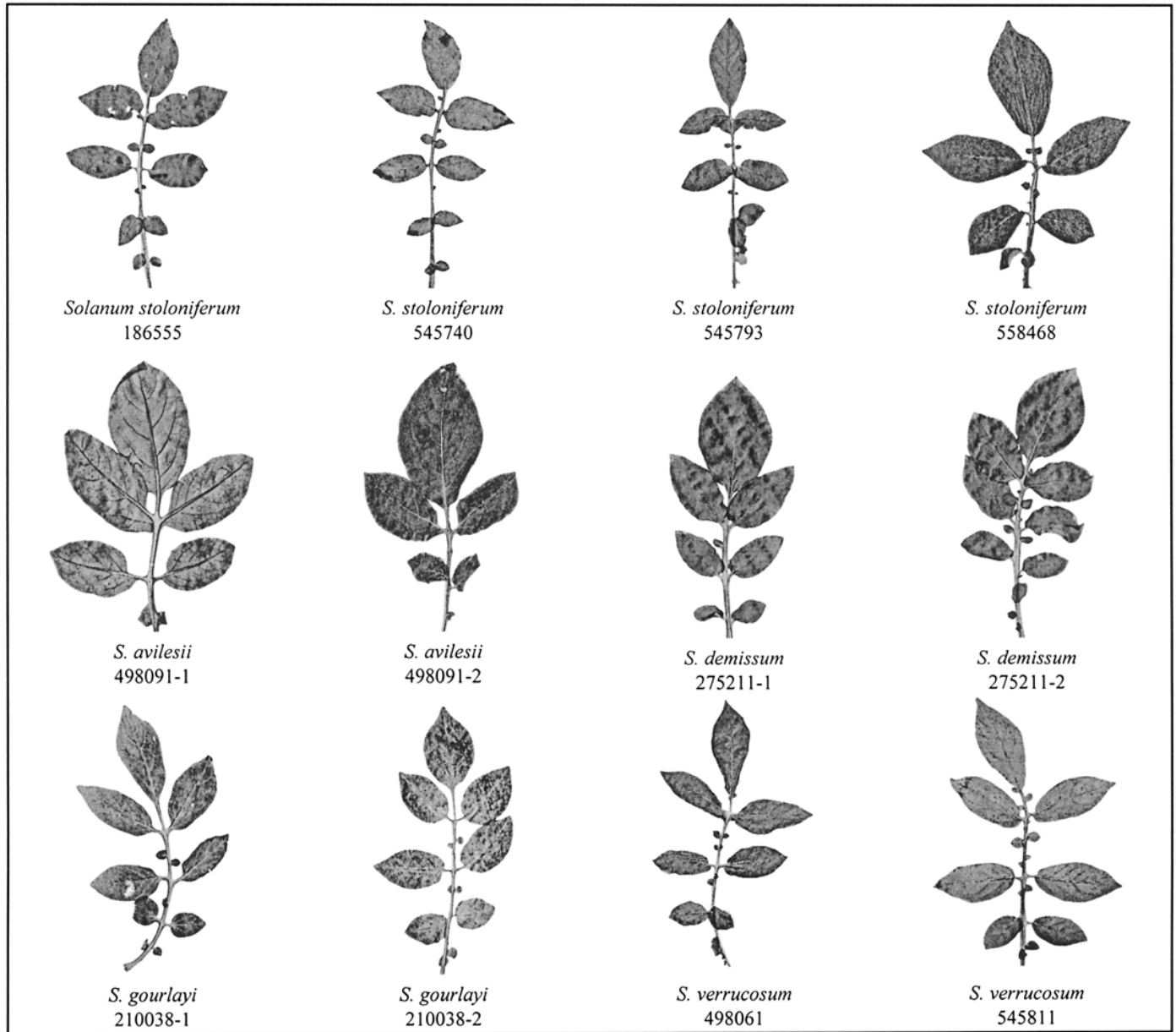


Fig. 3. Continued.

hjertingii form a cluster. All other species, *S. fendleri*, *S. papita*, *S. polytrichon*, and *S. stoloniferum* are intermixed on the tree.

The CDA of the entire data set is not shown. CDA axis 1 is most highly influenced by (presented in order of decreasing levels of total canonical structure): (1) ratio: length of fruit/width of fruit at its wider dimension, (2) fruit length, (3) style curvature, (4) ratio: length of pedicel/length from base of pedicel to articulation, (5) ratio: length of calyx lobe/width; CDA axis 2 by (1) corolla ratio 1, (2) radius of corolla, (3) ratio: length of calyx lobe/width, (4) adaxial leaf pubescence type, (5) length of style. This analysis separates (1) *S. berthaultii*, (2) *S. chacoense*, (3) *S. demissum*, (4) a group of *S. gourlayi* + *S. hjertingii* + *S. matehualae*, and (5) a group of *S. avilesii* + *S. fendleri* + *S. papita*, + *S. stoloniferum* + *S. polytrichon* + *S. verrucosum*.

A PCA of the reduced data set (only ser. *Longipedicellata*, only 38 of 54 characters) is presented in Fig. 7. Principal components 1, 2, and 3 account for 20, 13.4, and 10.4% of the variation, respectively, for a total of 43.8%. PCA axis 1 is most highly influenced by (presented in decreasing order of loadings) (1) radius of corolla, (2) length of stamen, (3) pedicel length, (4) length of style, (5) number of interjected leaflets; PCA axis 2 by (1) ratio: length of terminal leaflet lamina from its widest point to apex/length of lamina, (2) length of terminal leaflet lamina, (3) pedicel pubescence posture, (4) length of calyx acumen, (5) width of most distal lateral leaflet 5 mm below apex; PCA axis 3 by (1) length of style, (2) length of style exertion from apex of anther column, (3) ratio: length of terminal leaflet lamina/width of lamina, (4) density of adaxial pubescence, (5) width of terminal leaflet 5 mm below apex. It somewhat separates (1) *S. polytrichon*, (2) *S. hjertingii*

TABLE 3. Characters used in the phenetic analysis of *Solanum* series *Longipedicellata* and comparison species in series *Demissa* and ser. *Tuberosa*. All measurements are in millimeters, except as noted below.

Stem characters
1. Stem diameter at base.
2. Plant height (cm).
Leaf characters
3. Density of adaxial leaf pubescence (Materials and Methods): (10) 0–10 hairs cm ² (30) 11–30 hairs cm ² (50) 31–50 hairs cm ² (70) 51–70 hairs cm ² .
4. Ratio: density of adaxial/abaxial leaf pubescence.
5. Adaxial leaf pubescence type: (1) glabrous to glabrescent, (2) strigose, (3) pubescent to pilose.
6. Abaxial leaf pubescence type: (1) glabrous to glabrescent, (2) strigose, (3) pubescent to pilose.
7. Leaf length.
8. Leaf width across the most distal lateral leaflet pair.
9. Ratio: leaf length/length from apex of leaf to junction of second most distal lateral leaflet pair.
10. Number of lateral leaflet pairs.
11. Number of interjected leaflets.
12. Length of terminal leaflet petiolule.
13. Length of terminal leaflet lamina.
14. Ratio: length of terminal leaflet lamina from its widest point to apex/length of lamina.
15. Ratio: length of terminal leaflet lamina/width of lamina.
16. Width of terminal leaflet from a point 5 mm below apex.
17. Shape of terminal leaflet base: (1) cuneate, (2) truncate, (3) cordate.
18. Length of most distal lateral leaflet petiolule.
19. Length of most distal lateral leaflet lamina.
20. Ratio: length of most distal lateral leaflet lamina from its widest point to apex/length of lamina.
21. Ratio: length of most distal lateral leaflet lamina/width of lamina.
22. Width of most distal lateral leaflet from a point 5 mm below apex.
23. Width of decurrent tissue of most distal lateral leaflet as measured 3 mm basiscopic to junction of petiolule with rachis.
24. Shape of most distal lateral leaflet base: (1) cuneate, (2) truncate, (3) cordate.
25. Length between junctions of most distal lateral leaflet and second-most distal lateral leaflet.
26. Ratio: length of most distal lateral leaflet/length of second-most distal lateral leaflet.
27. Length of stipules.
28. Ratio: length of stipules/width.
Floral characters (see Spooner and van den Berg 1992b) for illustrations of characters 38, 39 (corolla ratio 1), and 40 (corolla ratio 2).
29. Peduncle length.
30. Pedicel length.
31. Ratio: length of pedicel/length from base of pedicel to articulation.
32. Pedicel pubescence posture: (1) tightly appressed, (2) slightly spreading up to about 10°, (3) widely spreading.
33. Number of flowers per inflorescence.
34. Length of calyx.
35. Length of calyx lobe.
36. Length of calyx acumen.
37. Ratio: length of calyx lobe/width.
38. Radius of corolla.
39. Corolla ratio 1: radius of corolla/radius to junction of petal lobes.
40. Corolla ratio 2: width of corolla lobe at base/length from a line drawn across widest point of corolla lobes.
41. Adaxial corolla color (see Materials and Methods) of interpetalar tissue.
42. Ratio: adaxial corolla color of interpetalar tissue/abaxial corolla color of interpetalar tissue.
43. Ratio: adaxial corolla color of interpetalar tissue/adaxial corolla color of ray of petal.
44. Ratio: abaxial corolla color of interpetalar tissue/abaxial corolla color of ray of petal.
45. Color of adaxial corolla acumen (0) same as body of ray, (1) lighter or darker than body of ray.
46. Color of abaxial corolla acumen (1) same as body of ray, (2) lighter or darker than body of ray.
47. Length of stamen.
48. Length of anther.
49. Length of style.
50. Length of style exertion from apex of anther column.
51. Style curvature: (1) straight, (2) curved.
Fruit characters
52. Fruit length.
53. Ratio: length of fruit/width of fruit at its widest dimension.
54. Ratio: width of fruit at its widest dimension/width of fruit at its narrowest dimension.

+ *S. matehualae*, (3) *S. fendleri* + *S. papita* + *S. stoloniferum*.

The CDA of the reduced data set is shown in Fig. 8. CDA axis 1 is most highly influenced by (presented in order of decreasing levels of total canonical structure): (1) length of style, (2) length of style exertion from apex of anther column, (3) density of adaxial leaf pubescence, (4) style curvature, (5)

corolla ratio 1; CDA axis 2 by (1) pedicel pubescence posture, (2) abaxial leaf pubescence, (3) adaxial corolla color of interpetalar tissue, (4) ratio: length of terminal leaflet lamina from its widest point to apex/length of lamina, (5) ratio: length of terminal leaflet lamina/width of lamina. This final analysis, using only members of ser. *Longipedicellata*, and a reduced data set of only 38 characters, separates three groups: (1) *S.*

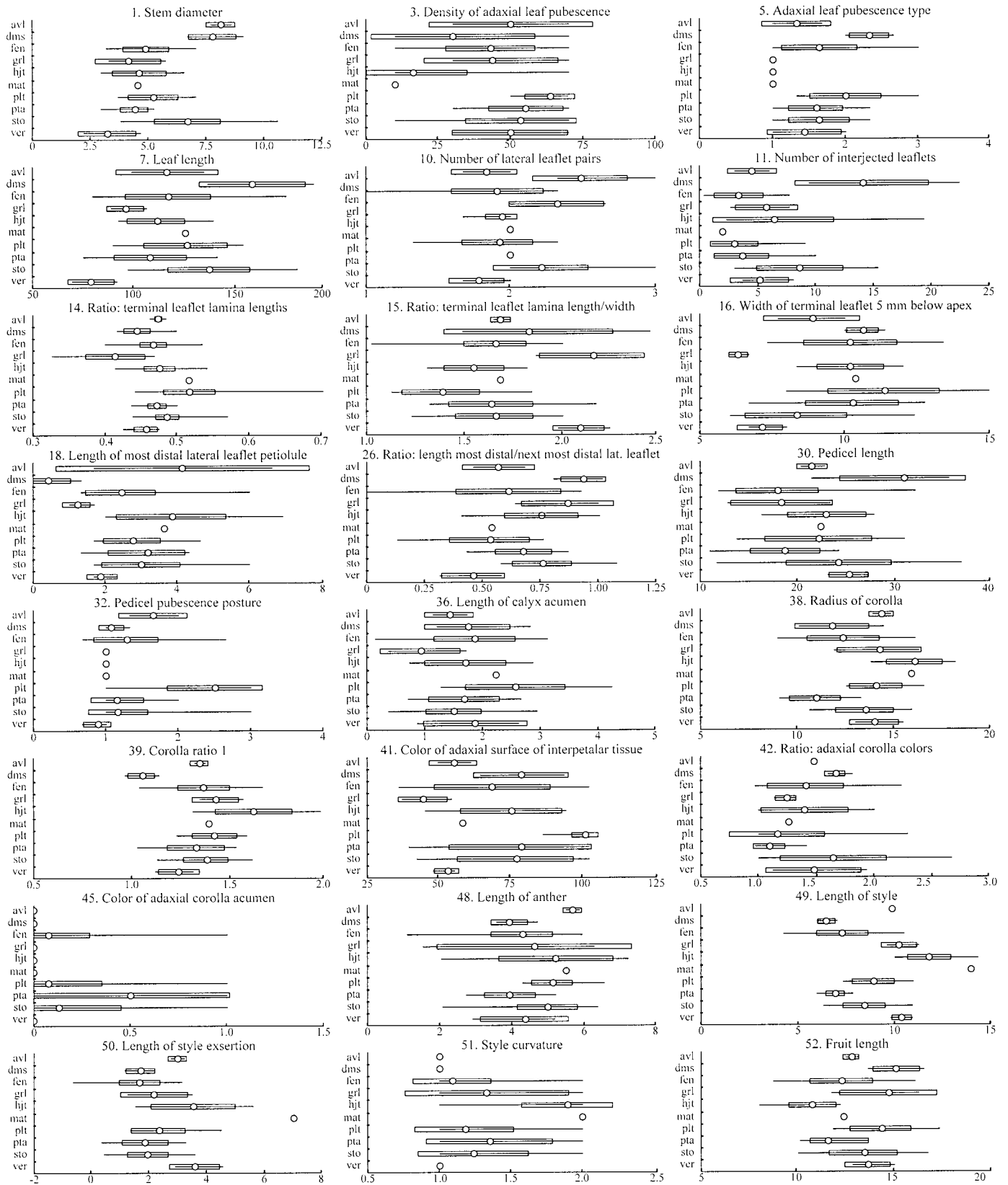


Fig. 4. Means, ranges, and one standard deviation of the mean for 24 of the 54 characters examined in this study showing the greatest differences among taxa of *Solanum avilesii* = avl; dms = *S. demissum*; fen = *S. fendleri*, grl = *S. gowlayi*, hjt = *S. hjertingii*, mat = *S. matehualae*; plt = *S. polytrichon*; pta = *S. papita*; sto = *S. stoloniferum*; ver = *S. verrucosum*.

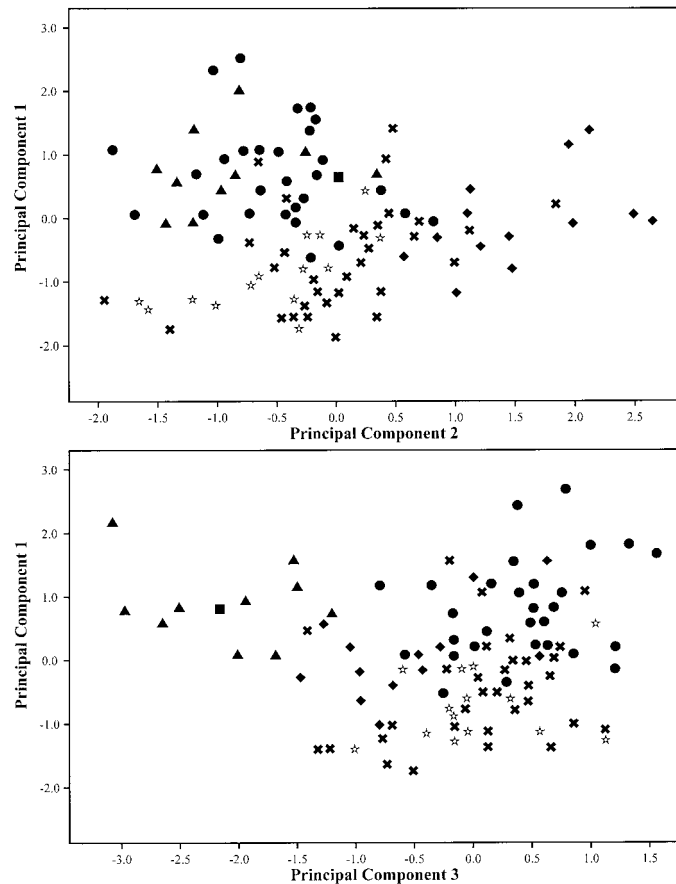


Fig. 5. Principal components analysis of the entire data set based on 54 morphological characters (Table 3). A = *Solanum avilesii*; B = *S. berthaultii*; C = *S. chacoense*; D = *S. demissum*; × = *S. fendleri*; G = *S. gourlayi*, ▲ = *S. hjertingii*, ■ = *S. matehualae*; ◆ = *S. polytrichon*; ★ = *S. papita*; ● = *S. stoloniferum*; v = *S. verrucosum*.

polytrichon, (2) *S. hjertingii* + *S. matehualae*, and (3) *S. fendleri* + *S. papita* + *S. stoloniferum*.

The SDA of the reduced data set used 19 characters to try to separate the six species of *S. ser. Longipedicellata*. The ten best characters, in decreasing order of discriminative utility, were: (1) length of style, (2) pedicel pubescence posture, (3) stem diameter at base, (4) density of adaxial leaf pubescence, (5) width of terminal leaflet 5 mm below apex (6) adaxial corolla color of interpetalar tissue, (7) style curvature, (8), ratio: abaxial corolla color of interpetalar tissue/abaxial corolla color of ray of petal, (10) fruit length.

DISCUSSION

Species distinctions within ser. *Longipedicellata*—Some, but not all of the character states used in existing keys and descriptions to distinguish taxa within ser. *Longipedicellata*, are supported by our data (compare Fig. 4 to Table 1). These characters are difficult to use for the practical needs of construction of keys and diagnoses of taxa, however, because their character states overlap among taxa. Low density of leaf trichomes (3) and short leaf trichomes (5) somewhat distinguish *S. hjertingii* and *S. matehualae*. High density of leaf trichomes (3) and long leaf trichomes (5) somewhat distinguish *S. polytrichon*, while widely spreading trichomes on the pedicel (32) do a much better job of distinguishing this species. It is hard to compare our data on numbers of lateral (10) and in-

terjected leaflets (11) to putative species-specific character states because of non-parallel descriptions and much overlap of putative character states. However, there are wide ranges and standard deviations for all species, with *S. stoloniferum* tending to have greater numbers of interjected leaflets (11). Regarding size differences between terminal and lateral leaflets, there are no statistically significant differences among species in size of the first lateral leaflets (18–22), but the terminal leaflets of *S. fendleri* and *S. polytrichon* are larger than other species, matching the descriptions, with much overlap with the other species. *Solanum papita* and *S. polytrichon* do not have longer petiolules of the terminal (12) or lateral leaflets (18). *Solanum papita* does have corollas with the smallest diameter (38) (2× our radius measure of Fig. 4, 9–13 mm, for a total of 18–26 mm), but never as small as the descriptions of 10–15 mm, with considerable overlap with other species. The ranges of corolla colors (41–46) in the descriptions matches our data but do not provide key characters for comparisons. Style length (49) and style exertion (50) distinguish *S. hjertingii* and *S. matehualae*, with overlap with other species. Length of calyx (34) and number of flowers (33) show no statistically significant difference among any species. *Solanum fendleri* and *S. papita* do not show the lowest mean anther length (48).

It is difficult to make firm generalizations about the characters most affecting structure of the ser. *Longipedicellata*

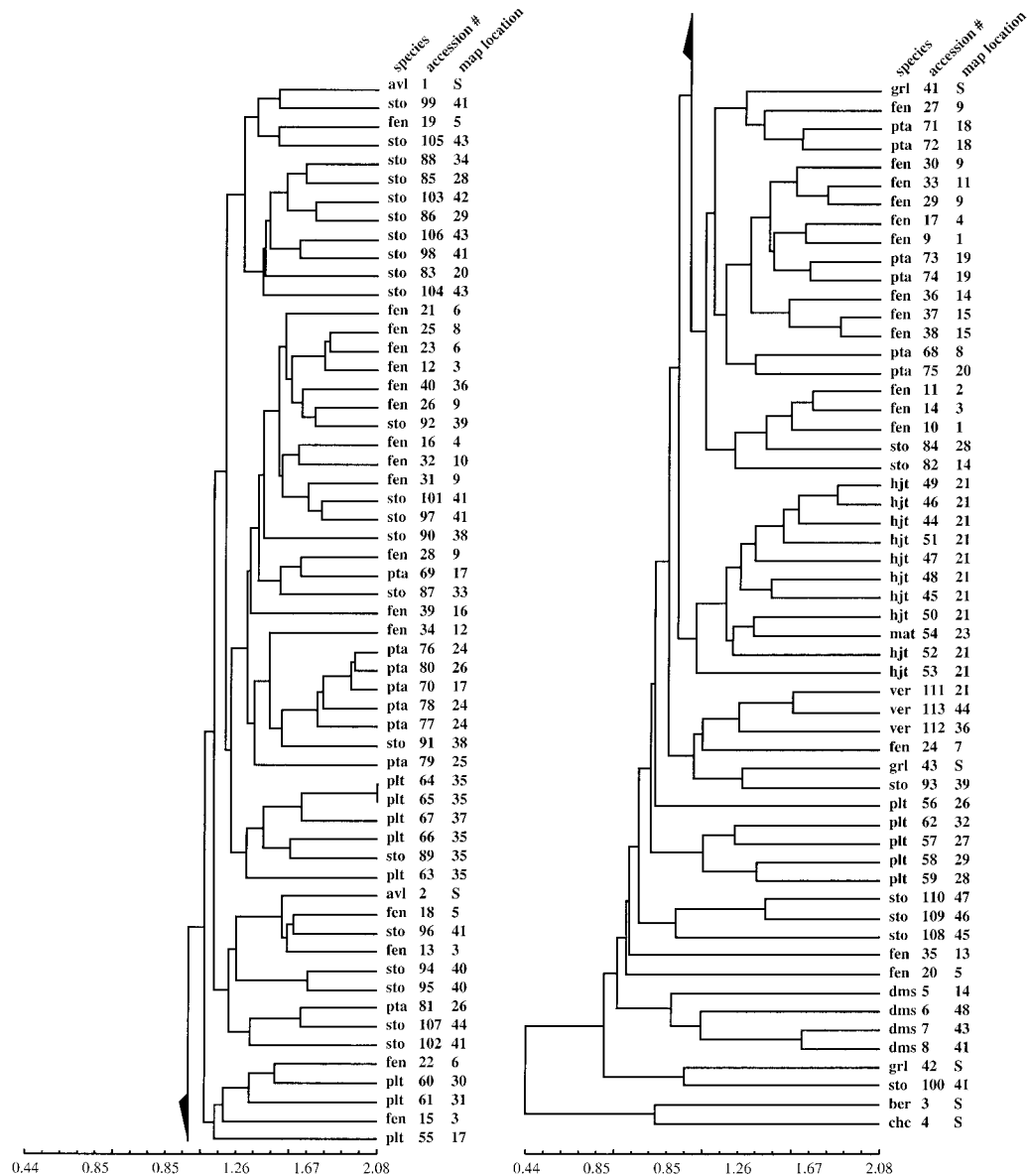


Fig. 6. UPGMA dendrogram (DIST similarity option) of the entire data set based on 54 morphological characters (Table 3). Species codes as in Fig. 4, accession numbers as in Table 2. S = South America, unmaped in Fig. 2.

PCA and CDA because of mixture of character types on different axes. However PCA axis 1 generally is most highly influenced by size of flower parts, PCA axis 2 by terminal leaflet shape and size, and PCA axis 3 by style length. The CDA axis 1 is most highly influenced by style length and curvature, and CDA axis 2 by pubescence of pedicel and leaf. The results of the two most important characters of the SDA are illuminating. The first character, length of style, characterizes *S. hjertingii* + *S. matehualae*, while the second character, pedicel pubescence, characterizes *S. polytrichon*.

Species distinctions are further complicated by intra-accession variation, illustrated in the leaves of *S. hjertingii*, *S. papita*, and *S. polytrichon* (ser. *Longipedicellata*), *S. avilesii*, *S. gourlayi*, and *S. verrucosum* (ser. *Tuberosa*), and *S. demissum* (ser. *Demissa*) (Fig. 3). Correll (1962, his plates VIII–X) dramatically illustrated such intra-accession variation in three specimens of *S. demissum* (Correll 14238), one collected in

the field in Mexico, one grown from tubers of this accession in a greenhouse in Maryland, and another grown from tubers of the same accession in a field in Wisconsin. The taxonomic difficulty of sect. *Petota* comes into focus considering such intra-accession variation and the lack of clear diagnostic characters separating species.

Phenetic structure of ser. *Longipedicellata* relies entirely on polythetic support, i.e., grouping taxa that have the greatest number of shared features, no single feature of which is essential for group membership or is sufficient to make an organism a member of a group (Sokal and Sneath, 1963; Stuessy, 1990). This pattern is proving to be the rule in species in sect. *Petota* (Spooner and van den Berg, 1992b; Giannattasio and Spooner, 1994a, b; Spooner, van den Berg, and Bamberg, 1995; Castillo and Spooner, 1997; van den Berg et al., 1998). Clearly, keys and descriptions of species that ultimately are recognized in ser. *Longipedicellata* will need to account for

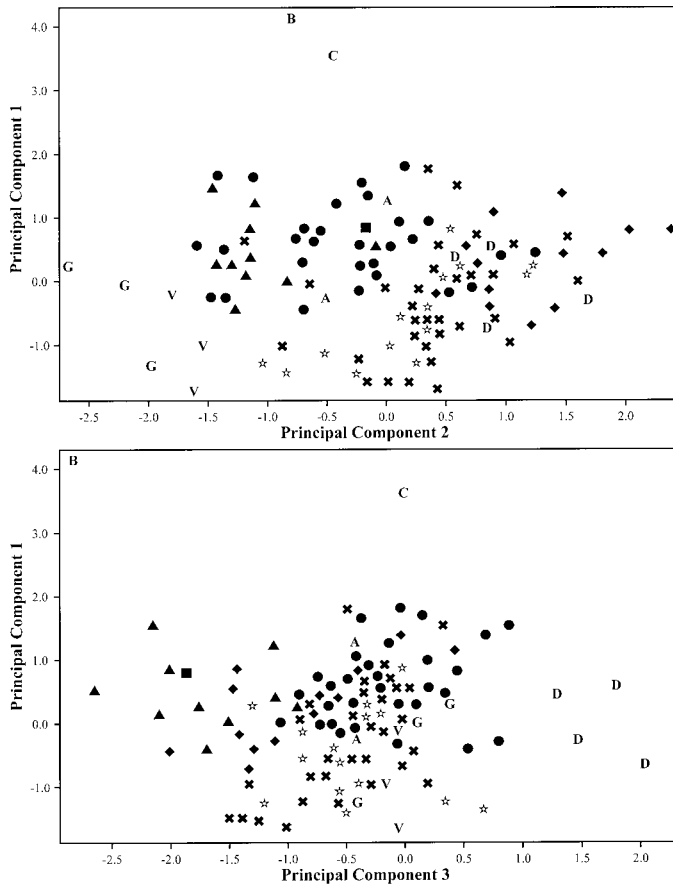


Fig. 7. Principal components analysis of the reduced data set based on 38 morphological characters. Species codes as in Fig. 5.

the intra-accession and interspecific variation inherent in the group.

Our results make a clear case for the reduction of the six species of ser. *Longipedicellata* to the three species *S. hjertingii*, *S. polytrichon*, and *S. stoloniferum* (the earliest names). We suspect that these will be the species we ultimately recognize in our potato flora of North and Central America, but we await a formal taxonomic treatment of these species for four reasons. First, our morphological data are from germplasm accessions grown in an atypical environment. However, this allowed us to measure all organs, including delicate floral organs that often are missing or poorly preserved on herbarium specimens and leaves of comparable size, and our results match our intuitive impressions of herbarium specimens collected from the wild. Second, we wish to be conservative in making taxonomic changes in this economically important group as the scientific literature reports on evaluations of wild potato species literally every month. Third, we await results of our molecular studies on this group. However, cpDNA studies of all of these species (Spooner and Sytsma, 1992; Spooner and Castillo, 1997) groups them in polytomies or includes them all in the same clade and separates them only on small branches. Fourth, we wish to study type material to insure that our collections are properly identified.

Distinction of ser. *Longipedicellata* to ser. *Demissa* and ser. *Tuberosa*—Our measurements of the corolla shape and petiolule characters used by Correll (1962) and Hawkes (1990)

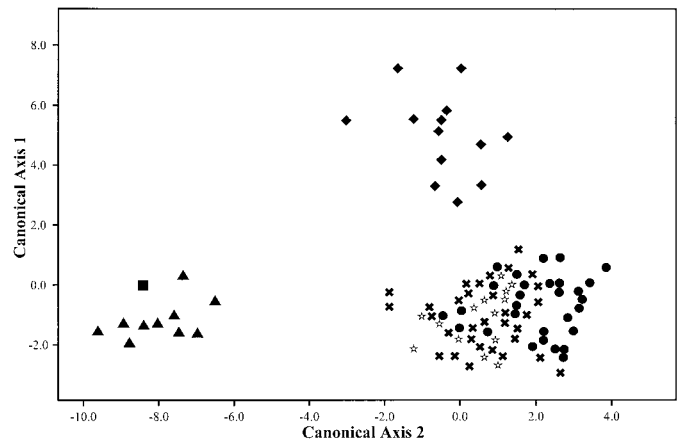


Fig. 8. Canonical discriminate analysis of the reduced data set based on 38 morphological characters. Species codes as in Fig. 5.

for ser. *Longipedicellata*, ser. *Demissa* and ser. *Tuberosa* fail to distinguish them, and our data show no series-specific character states (Fig. 4). Morphology, therefore, does not provide any absolute character states to clearly separate members of ser. *Longipedicellata* from our placeholder members of ser. *Tuberosa* (*S. avilesii*, *S. gourlayi*, and *S. verrucosum*), or ser. *Demissa* (*S. demissum*). The morphological study of the *S. brevicaula* complex (van den Berg et al., 1998) similarly showed the placeholder taxa of ser. *Longipedicellata* and ser. *Tuberosa* examined here to be distinguished from each other only by character states with overlapping ranges, not by more practical breaks between quantitative character states or by qualitative characters. This is illustrated in representative leaves of members of all of these series (Fig. 3) that show great similarity of overall form and no evident character states separating series, a pattern typical of all other character states in these series. There are simply few if any qualitative characters useful for distinguishing these species and even series. Our present results help to document and explain the reason for the continuing disagreement among taxonomists for species and series boundaries in the group (Spooner and van den Berg, 1992a).

Our results provide no answer to the question of the evolution of members of ser. *Longipedicellata*. The AABB genome hypothesis suggests an allopolyploid origin of the series, but the parental species are unknown. Even if they were known, McDade (1990) and Rieseberg and Ellstrand (1993) point out that hybridity is not always associated with additive morphology. Our results show extensive similarity of species across three currently recognized series, suggesting that it would be difficult to find clear species-specific morphological markers for putative progenitors of the series. We can only speculate about origins based on other data. Ortiz and Ehlenfeldt (1992) use EBN to speculate on the origin of the series by bilateral sexual polyploidization of two $2x(1EBN)$ species, or alternatively by bilateral sexual polyploidization of two $2x(2EBN)$ species followed by a reduction in EBN. None of these hypotheses, however, has ever been tested. The allopolyploid origin of the series can also be tested at the molecular level by searching for additivity of species-specific molecular markers (e.g., Dvorak and Zhang, 1992), or at the cytological level by genomic in-situ hybridization, GISH (e.g., Bennett, Kenton, and Bennett, 1992; Jiang and Gill, 1994).

Despite the great morphological similarity of members of ser. *Longipedicellata* to some members of ser. *Tuberosa*, they are reproductively isolated based on their 4x(2EBN) crossability, and possibly by their AABB genome constitution. This supports *S. hjertingii*, *S. polytrichon*, and *S. stoloniferum* as worthy of taxonomic recognition separate from the morphologically similar species in Mexico and South America. This example clearly demonstrates a conflict of a morphological and a biological species concept, and the continuing difficulty in the use of morphology for the preparation of keys and descriptions, and identification of specimens. Earlier we (Spooner and van den Berg, 1992a) criticized the use of geographical characters in keys of Correll (1962) and Hawkes (1990) to distinguish species. However, considering the difficulty of morphology to distinguish good biological species, this may be the only practical solution in key construction. A practical taxonomic treatment of the group using morphology likely will always be an elusive goal.

LITERATURE CITED

- BAMBERG, J. J., M. W. MARTIN, J. J. SCHARTNER, AND D. M. SPOONER. 1996. Inventory of tuber-bearing *Solanum* species: catalog of potato germplasm—1996. Potato Introduction Station, NRSP-6, Sturgeon Bay, Wisconsin, USA.
- BENNETT, S. T., A. Y. KENTON, AND M. D. BENNETT. 1992. Genomic in situ hybridization reveals the allopolyploid nature of *Milium montianum* (Gramineae). *Chromosoma* 101: 420–424.
- CASTILLO, R. O., AND D. M. SPOONER. 1997. Phylogenetic relationships of wild potatoes, *Solanum* Series *Conicibaccata* (Sect. *Petota*). *Systematic Botany* 22: 45–83.
- CHILD, A. 1990. A synopsis of *Solanum* subgenus *Potatoe* (G. Don) (D'Arcy) (*Tuberarium* (Dun.) Bitter (s.l.)). *Feddes Repertorium* 101: 209–235.
- CONTRERAS M., AND D. M. SPOONER. 1999. Revision of *Solanum* section *Euberosum* (subgenus *Potatoe*). In M. Nee, D. E. Symon, R. N. Lester, and J. P. Jessop [eds.], *Solanaceae IV, Advances in Biology and Utilization*, 227–245. Royal Botanic Gardens, Kew, UK.
- CORRELL, D. S. 1962. The potato and its wild relatives. *Contributions from the Texas Research Foundation, Botanical Studies* 4: 1–606.
- DVORAK, J., AND H. B. ZHANG. 1992. Application of molecular tools for study of the phylogeny of diploid and polyploid taxa in Triticeae. *Hereditas* 116: 37–42.
- GIANNATTASIO, R. B., AND D. M. SPOONER. 1994a. A reexamination of species boundaries between *Solanum megistacrolobum* and *S. toralapanum* (*Solanum* sect. *Petota*, series *Megistacroloba*): morphological data. *Systematic Botany* 19: 89–105.
- , AND ———. 1994b. A reexamination of species boundaries and hypotheses of hybridization concerning *Solanum megistacrolobum* and *S. toralapanum* (*Solanum* sect. *Petota*, series *Megistacroloba*): molecular data. *Systematic Botany* 19: 106–115.
- GRAY, A. 1886. Synoptical flora of North America, vol. 2, part 1. Ivison, Blakeman, Taylor and Company, London, UK.
- HANNEMAN, R. E., JR. 1994. Assignment of Endosperm Balance Numbers to the tuber-bearing *Solanums* and their close non-tuber-bearing relatives. *Euphytica* 74: 19–25.
- HAWKES, J. G. 1958. Kartoffel. I. Taxonomy, cytology and crossability. In H. Kappert and W. Rudolf [eds.], *Handbuch Pflanzenzüchtung*, 2nd ed., 1–43. Paul Parey, Berlin, Germany.
- . 1966. Modern taxonomic work on the *Solanum* species of Mexico and adjacent countries. *American Potato Journal* 43: 81–103.
- . 1990. The potato: evolution, biodiversity and genetic resources. Belhaven Press, London, UK.
- IRIKURA, Y. 1976. Cytogenetic studies on the haploid plants of the tuber-bearing *Solanum* species. II. Cytogenetical investigations on haploid plants and interspecific hybrids by utilizing haploidy (in Japanese, with English summary). *Research Bulletin of the Hokkaido National Agricultural Research Station* 115: 1–80.
- JIANG, J., AND B. S. GILL. 1994. Different species-specific chromosome translocations in *Triticum timopheevii* and *T. turgidum* support diphyletic origin of polyploid wheats. *Chromosome Research* 2: 59–64.
- JOHNSTON, S. A., T. P. M. DEN NIJS, S. J. PELOQUIN, AND R. E. HANNEMAN, JR. 1980. The significance of genetic balance to endosperm development in interspecific crosses. *Theoretical and Applied Genetics* 53: 262–269.
- KARDOLUS, J. P. 1998. A biosystematic analysis of the polyploid series *Acaulia* and related potato species. Chapter 5 of A biosystematic analysis of *Solanum acaule*, 63–84. Ph.D. dissertation, Wageningen Agricultural University, Wageningen, The Netherlands.
- MARKS, G. E. 1955. Cytogenetic studies in tuberous *Solanum* species. I. Genomic differentiation in the group *Demissa*. *Journal of Genetics* 53: 262–269.
- MATSUBAYASHI, M. 1955. Studies on the species differentiation of the section *Tuberarium* of *Solanum* III. Behavior of meiotic chromosomes in F₁ hybrid between *S. longipedicellatum* and *S. schickii* in relation to its parent species. *Science Reports of the Hyogo University of Agriculture* 2: 25–31.
- . 1991. Phylogenetic relationships in the potato and its related species. In T. Tsuchiya and P. K. Gupta [eds.], *Chromosome engineering in plants: genetics, breeding, evolution*, part B: 93–118. Elsevier, Amsterdam, The Netherlands.
- MCDADE, L. 1990. Hybrids and phylogenetic systematics I. Patterns of character expression in hybrids and their implications for cladistic analysis. *Evolution* 44: 1685–1700.
- MILLER, J. T., AND D. M. SPOONER. 1999. Collapse of species boundaries in the wild potato *Solanum brevicaulum* complex (Solanaceae, S. sect. *Petota*): molecular data. *Plant Systematics and Evolution* 214: 103–130.
- ORTIZ, R., AND M. K. EHLENFELDT. 1992. The importance of Endosperm Balance Number in potato breeding and the evolution of tuber-bearing *Solanum* species. *Euphytica* 60: 105–113.
- RAMANNA, M. S., AND J. G. T. HERMSEN. 1979. Genome relationships in tuber-bearing *Solanums*. In J. G. Hawkes, R. N. Lester, and A. D. Skelding [eds.], *The biology and taxonomy of the Solanaceae*, 647–654. Linnean Society of London Symposium Series 7. Academic Press, London, UK.
- RIESEBERG, L. H., AND N. C. ELLSTRAND. 1993. What can molecular and morphological markers tell us about plant hybridization? *Critical Reviews in Plant Sciences* 12: 213–241.
- RODRIGUEZ, A., AND D. M. SPOONER. 1997. Chloroplast DNA analysis of *Solanum bulbocastanum* and *S. cardiophyllum*, and evidence for the distinctiveness of *S. cardiophyllum* subsp. *ehrenbergii* (sect. *Petota*). *Systematic Botany* 22: 31–43.
- , O. VARGAS, E. VILLEGAS, AND D. M. SPOONER. 1995. Wild potato (*Solanum* sect. *Petota*) germplasm collection expedition to Mexico in 1993, with special reference to *Solanum bulbocastanum* Dunal and *S. cardiophyllum* Lindley. *Potato Research* 38: 47–52.
- ROHLF, F. J. 1992. NTSYS-pc, numerical taxonomy and multivariate system. Exeter Publishing, Ltd., New York, New York, USA.
- , AND R. R. SOKAL. 1981. Comparing numerical taxonomic studies. *Systematic Zoology* 30: 459–490.
- ROYAL HORTICULTURAL SOCIETY. 1986. R.H.S. colour chart. [ed. 1, 2]. Royal Horticultural Society, London, UK.
- SAS. 1995. JMP Software, Version 3.1. SAS Institute Inc., Cary, North Carolina, USA.
- . 1998. SAS Proprietary Software, Version 7. SAS Institute Inc., Cary, North Carolina, USA.
- SOKAL, R. R. 1986. Phenetic taxonomy: theory and methods. *Annual Review of Ecology and Systematics* 17: 423–442.
- , AND R. R. SNEATH. 1963. Principles of numerical taxonomy. Freeman, San Francisco, California, USA.
- SPOONER, D. M., G. J. ANDERSON, AND R. K. JANSEN. 1993. Chloroplast DNA evidence for the interrelationships of tomatoes, potatoes, and pepinos (*Solanaceae*). *American Journal of Botany* 80: 676–688.
- , J. BAMBERG, J. P. HJERTING, AND J. GOMEZ. 1991. Mexico, 1988 potato germplasm collecting expedition and utility of the Mexican potato species. *American Potato Journal* 68: 29–43.
- , AND R. CASTILLO T. 1997. Reexamination of series relationships of South American wild potatoes (*Solanaceae*: *Solanum* sect. *Petota*): evidence from chloroplast DNA restriction site variation. *American Journal of Botany* 84: 671–685.
- , R. HOEKSTRA, R. G. VAN DEN BERG, AND V. MARTINEZ. 1998. *Solanum* sect. *Petota* in Guatemala; taxonomy and genetic resources. *American Journal of Potato Research* 75: 3–17.

- , ———, AND B. VILCHEZ. In press. *Solanum* sect. *Petota* in Costa Rica: taxonomy and genetic resources. *American Journal of Potato Research*.
- , A. RIVERA-PENA, R. G. VAN DEN BERG, AND K. SCHULER. 2000. Potato Germplasm Collecting Expedition To Mexico In 1997: taxonomy and new germplasm resources. *American Journal of Potato Research* 77: 261–270.
- , 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.
- , ———, AND J. BAMBERG. 1995. Examination of species boundaries of *Solanum* series *Demissa* and potentially related species in series *Acaulia* and series *Tuberosa* (sect. *Petota*). *Systematic Botany* 20: 295–314.
- STUESSY, T. F. 1990. Plant taxonomy: the systematic evaluation of comparative data. Columbia University Press, New York, New York, USA.
- TUCKER, A. O., M. J. MACIARELLO, AND S. S. TUCKER. 1991. A survey of color charts for biological descriptions. *Taxon* 40: 201–214.
- VAN DEN BERG, R. G., N. GROENDIJK-WILDERS, AND J. P. KARDOLUS. 1996. The wild ancestors of cultivated potato: the brevicaule-complex. *Acta Botanica Neerlandica* 45: 157–171.
- , J. T. MILLER, M. L. UGARTE, J. P. KARDOLUS, J. VILLAND, J. NIENHUIS, AND D. M. SPOONER. 1998. Collapse of morphological species in the wild potato *Solanum brevicaule* complex (Solanaceae: sect. *Petota*). *American Journal of Botany* 85: 92–109.