

## A reexamination of infraspecific taxa of a wild potato, *Solanum microdontum* (*Solanum* sect. *Petota*: *Solanaceae*)

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**Key words:** *Solanaceae*, *Solanum* sect. *Petota*, *Solanum microdontum*. — Potatoes, subspecies, systematics, varieties.

**Abstract:** Current taxonomic interpretations of *Solanum microdontum* BITTER partition the species into two or three infraspecific taxa, variously recognized as subspecies or varieties. The present study reexamines these taxa using morphological data from four individuals each of 69 accessions from most of the range of the species, planted in a common field plot. Our results show that the character states used to recognize infraspecific taxa in *S. microdontum* often vary within accessions and have no correlation with geography. We conclude that past hypotheses have used typological concepts and that infraspecific taxa are not warranted. This study questions other hypotheses of infraspecific taxa in sect. *Petota*.

*Solanum microdontum* BITTER is a highly variable species distributed from northern Bolivia (La Paz Prov.) to northwestern Argentina (La Rioja Prov.). It is a member of sect. *Petota*, a group of 232 species (as interpreted by HAWKES 1990) related to the cultivated potato. The species is self-incompatible and diploid ( $2n = 2x = 24$ ), except for some scattered triploid cytotypes in the southern part of the range in Argentina (OKADA 1981). Many populations of *S. microdontum* are distinguished by entire leaves, but intra- and interpopulational variability encompasses morphotypes with pinnately-dissected leaves more similar to those of other wild species. This variability has been partitioned into six species, three subspecies, and six varieties, but current classifications reduce this variability to one species with two subspecies: subsp. *microdontum* and subsp. *gigantophyllum* (BITTER) HAWKES & HJERT. (HAWKES 1990; Table 1) or three varieties, var. *microdontum*, var. *metriophyllum* BITTER, and var. *montepuncoense* OCHOA (OCHOA 1990). Var. *microdontum* and var. *metriophyllum* are equivalent nomenclaturally to subsp. *microdontum* and subsp. *gigantophyllum*, respectively; var. *montepuncoense* is distinct, and is a possible interspecific hybrid (see below). This study investigates the morphological and geographical patterns of variability in *S. microdontum* to find if infraspecific taxa are warranted.

Table 1. Morphological characters used by HAWKES & HJERTING (1969, 1989), HAWKES (1990), and OCHOA (1990) to separate infraspecific taxa of *Solanum microdontum*, and elevational and distributional data<sup>1</sup>

<i>Character</i>	subsp. <i>microdontum</i> <sup>2</sup>	subsp. <i>gigantophyllum</i> <sup>3</sup>
Habit	spreading	upright or decumbent
Plant height	up to 0.5 m	up to 2 m
Stem diameter	1.5–3 (–5) mm	3–10 (–20) mm
Stem wing width	0–1 (–2.5) mm	2–5 mm
Stem wing morphology	straight, entire	undulate, denticulate
Terminal leaflet length	up to 8 cm	up to 18 cm
Terminal leaflet width	up to 5 cm	up to 9 cm
Number of flowers/inflorescence	1–8 (–15) flowers	5–20 (–35) flowers
Distribution	18°S–24°S	17°S–29°S
Elevation (m)	(1600–) 1800–2700 (–3200)	(1000–) 1200–2500 (–3200)

<sup>1</sup> OCHOA (1990) recognizes a third infraspecific taxon, var. *montepuncoense*, differing from these two by conical fruits (round to oval in the other infraspecific taxa; see text).

<sup>2</sup> OCHOA (1990) treats this taxon as *S. microdontum* var. *microdontum*.

<sup>3</sup> OCHOA (1990) treats this taxon as *S. microdontum* var. *metriophyllum*.

## Material and methods

**Material.** We chose 69 accessions of *S. microdontum* available in the germplasm collection of the Inter-Regional Potato Introduction Project (IR-1; HANNEMAN & BAMBERG 1986; Table 2, Fig. 1). We obtained identities of the accessions from HAWKES & HJERTING (1969, 1989), supplemented by identities from HANNEMAN & BAMBERG (1986). J. G. HAWKES, C. M. OCHOA, and other visiting taxonomists identified these accessions from living germplasm accessions planted at the IR-1 Station at Surgeon Bay, Wisconsin, for identification (SPOONER & BAMBERG 1991). For convenience, we use the subspecies designations of HAWKES (1990) here. We chose the accessions to maximize the taxonomic and geographic diversity in the group available at IR-1, and they cover most of the geographical range of *S. microdontum*. We mapped all accessions to one of 29 generalized regions (Fig. 1). 33 of these 69 accessions were identified as subsp. *gigantophyllum*, 19 as subsp. *microdontum*, 13 variously designated as “hybrids” or “intermediates”, and four were undesignated as to subspecies. We planted the seeds in a greenhouse in early May, transferred the seedlings to peat pots in late May, and transplanted nine individuals per accession together in rows in a field plot at Sturgeon Bay in early June.

**Data measurement.** We scored 20 quantitative and one qualitative character (Table 3) in late August after flowering had commenced. We used the first four surviving and flowering plants per row for all measurements, and used the means of four plants as representative of each accession. Leaf measurements were made of the largest leaf per plant.

**Data analysis.** We analyzed the data by principal components analysis (PCA), stepwise discriminant analysis (SDA), and canonical discriminant analysis (CDA), by the PRINCOMP, STEPDISC, and CANDISC procedures in SAS (SAS Institute, Inc. 1988) using the standardized means of four plants per accession as character scores. The SDA and CDA analyses were performed after excluding the four accessions unidentified as to subspecies or intermediates. The SDA analysis used a 0.15 significance level to enter groups. To search for geographic patterns on the PCA, accession labels had the geographic area designations (Table 2, Fig. 1) added to the taxon labels. Means and standard deviations of

Table 2. Specimens examined in this study<sup>1</sup>

Region	Taxon	PI Number <sup>2</sup>	Collector and number <sup>3</sup>
1	int	473363	HHCH 4737
2	mcd	498128	HHA 6531
3	mcd	498124	HHA 6502
3	mcd	498125	HHA 6504
4	int	473362	HHCH 4359
5	mcd	498126	HHA 6513
5	mcd	498127	HHA 6517
6	gig	498123	HHA 6653
7	mcd	498121	HHA 6650
8	gig	473173	OKA 5902
8	gig	473174	OKA 5912
8	gig	473175	OKA 5913
9	int	320306	HHR 3830
9	mcd	320307	HHR 3863
9	mcd	320309	HHR 3868
9	int	320310	HHR 3871
9	int	473166	HOF 2075
9	gig	473169	OKA 5452
9	gig	473172	OKA 5893
9	int	473177	OKA 5928
10	gig	473176	OKA 5918
11	gig	473180	OKA 6327
11	gig	473179	OKA 6326
12	mcd	473312	OKA 6881
13	und	558100	OKA 7634
13	mcd	458356	OKA 4478
13	mcd	458357	OKA 4479
13	mcd	473167	OKA 4480
14	mcd	458355	OKA 4398
14	und	558099	OKA 7612
14	mcd	500039	OKA 7620
15	mcd	500040	OKA 7621
16	int	320304	HHR 3777
16	int	320305	HHR 3781
17	gig	320319	HHR 3753
18	gig	265881	EBS 1802
19	int	500033	OKA 7524
19	gig	500034	OKA 7526
19	und	558097	OKA 7530
19	und	558098	OKA 7538
19	gig	500035	OKA 7543
19	gig	500036	OKA 7541
19	gig	500037	OKA 7544
19	int	500064	OKA 7528
19	gig	558101	OKA 7587
20	gig	473170	OKA 5614
21	gig	473168	OKA 4897
21	int	473171	OKA 5623

Table 2 (continued)

Region	Taxon	PI Number <sup>2</sup>	Collector and number <sup>3</sup>
21	int	458358	OKA 482022
22	mcd	320318	HHR 3710
22	mcd	500032	OKA 7493
22	int	500038	OKA 7656
22	mcd	500041	OKA 7658
23	gig	320314	HHR 3681
24	gig	320313	HHR 3663
25	gig	218222	EBS 187B
25	gig	218223	EBS 190
25	gig	218224	EBS 447
26	gig	320311	HHR 3464
26	gig	498386	HAW 3473
27	gig	265575	COR A705
27	gig	458354	OKA 2910
28	gig	458353	OKA 2896
29	gig	473178	OKA 6092
— <sup>4</sup>	gig	208866	BRU 45
—	gig	218225	EBS 523
—	gig	218226	EBS 626
—	mcd	310979	ALAN 6411
—	gig	473525	EBS 2636

<sup>1</sup>mcd *Solanum microdontum* subsp. *microdontum*, gig subsp. *gigantophyllum*, int putative “intermediates” or “hybrids”, und undetermined as to subspecies.

<sup>2</sup>USDA plant introduction number.

<sup>3</sup>Collectors: ALAN S. ALANDIA, BRU H. BRÜCHER, COR D. CORRELL, EBS Collections from the EDWIN BAUER Sortiment Genebank, Germany, HAW J. G. HAWKES, HHA J. G. HAWKES, J. P. HJERTING, and I. AVILÉS, HHCH J. G. HAWKES, J. P. HJERTING, P. CRIBB, and Z. HUAMÁN, HHR J. G. HAWKES, J. P. HJERTING, and K. RAHN, HOF W. HOFFMANN, OKA A. OKADA.

<sup>4</sup>Locality data vague or unknown.

the presumed taxonomically important characters (Table 1) were graphically portrayed by geographic area (Fig. 2) and by taxon (Fig. 3).

## Results

**Analysis of the taxonomically important characters by taxon.** We measured seven of the eight morphological characters used by taxonomists to distinguish the subspecies of *S. microdontum* (Table 1; no habit differences were observed in our field plots and this character was not measured). Figure 3 presents a taxon-specific analysis of the means, ranges, and standard deviations of six of these seven quantitative characters. F tests indicate that three of these seven characters, terminal leaflet length, terminal leaflet width, and stem wing width differ significantly between the subspecies and putative intermediates, but with extensive overlap of absolute measurements. The remaining four characters, plant height, stem diameter,

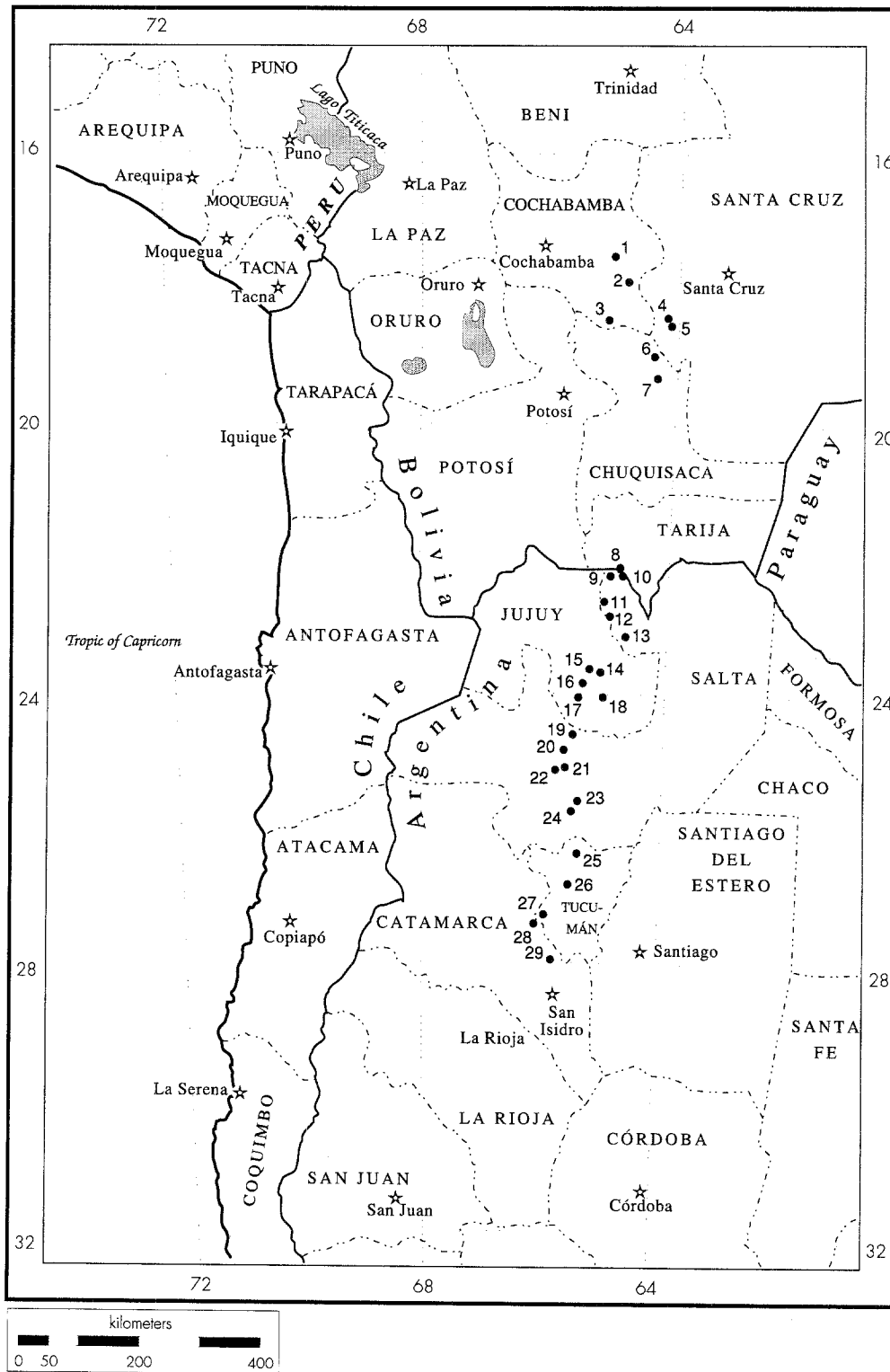


Fig. 1. The 29 geographic areas to which we mapped the 69 accessions examined in this study (see Table 2). This covers nearly the entire geographic range of the species, which extends from Bolivia (La Paz Province) to Argentina (La Rioja Province)

Table 3. Characters and states used in numerical phenetics of *Solanum microdontum*. Terminology after HAWKES (1990)

Habit	1. Plant height (cm)
Stem	2. Diameter (mm). 3. Wing width (mm). 4. Wing morphology: undulate (1), straight (2)
Leaves	5. Leaf length (cm). 6. Leaf width (cm). 7. Ratio of leaf length/length from axis of widest point of leaf to apex. 8. Terminal leaflet length (cm). 9. Terminal leaflet width (cm). 10. Number of primary lateral leaflet pairs. 11. Number of interjected lateral leaflets
Peduncle	12. Length (cm)
Pedicel	13. Length (mm). 14. Ratio of pedicel length/length from base of pedicel to articulation
Inflorescence	15. Flower number
Calyx	16. Total length (mm). 17. Ratio of total length/lobe length. 18. Acumen length (mm)
Corolla	19. Diameter to apex of corolla lobe (mm). 20. Ratio of diameter to apex of corolla lobe/diameter to base of corolla lobe. 21. Ratio of width of corolla lobe at base/length from a line drawn across widest point of corolla lobes

stem wing morphology, and number of flowers per inflorescence showed no significant differences (0.05 level). In addition, total leaf width and number of lateral leaflets differed significantly (0.001, 0.005, respectively) between subspecies and putative intermediates, but also with much overlap between taxa.

**Principal components analysis.** Figures 4 and 5 present the results of the PCA. Factors 1, 2, and 3 accounted for 20.2, 13.2, and 9.1% of the variation, respectively, for a total variation of 42.5%. Factor 1 had high positive loadings on leaf length, terminal leaflet length, terminal leaflet width, stem diameter, and stem wing width; factor two had high positive loadings on leaf width and number of primary lateral leaflets. Factors 1 and 2 roughly separate the subspecies, with the intermediates located in a zone of contact between them; factors 1 and 3 provide much less separation. This same PCA analysis, coding the OTU's by the 29 geographic areas (PCA not shown) indicates no geographic pattern.

**Stepwise discriminate analysis.** Stepwise discriminate analysis supports three groups, *S. microdontum* subsp. *microdontum*, subsp. *gigantophyllum*, and their putative intermediates, using the following seven characters arranged in a decreasing order of discriminant utility: terminal leaflet length, leaf width, stem wing width, plant height, corolla diameter to apex of corolla lobe, stem diameter, and number of flowers per inflorescence. The last four of these characters, plant height, corolla diameter to apex of corolla lobe, stem diameter, and number of flowers per inflorescence were not significantly different between groups (0.05 level).

**Canonical discriminate analysis.** Figure 6 presents the results of the CDA. All three groups are well-supported with only slight overlap between subsp. *microdontum* and the putative intermediates. Three reiterations of the CDA were run with random substitutions of the taxon identifications. Two of these reiterations involved 12 changes in the identifications, and one involved six changes. All changes

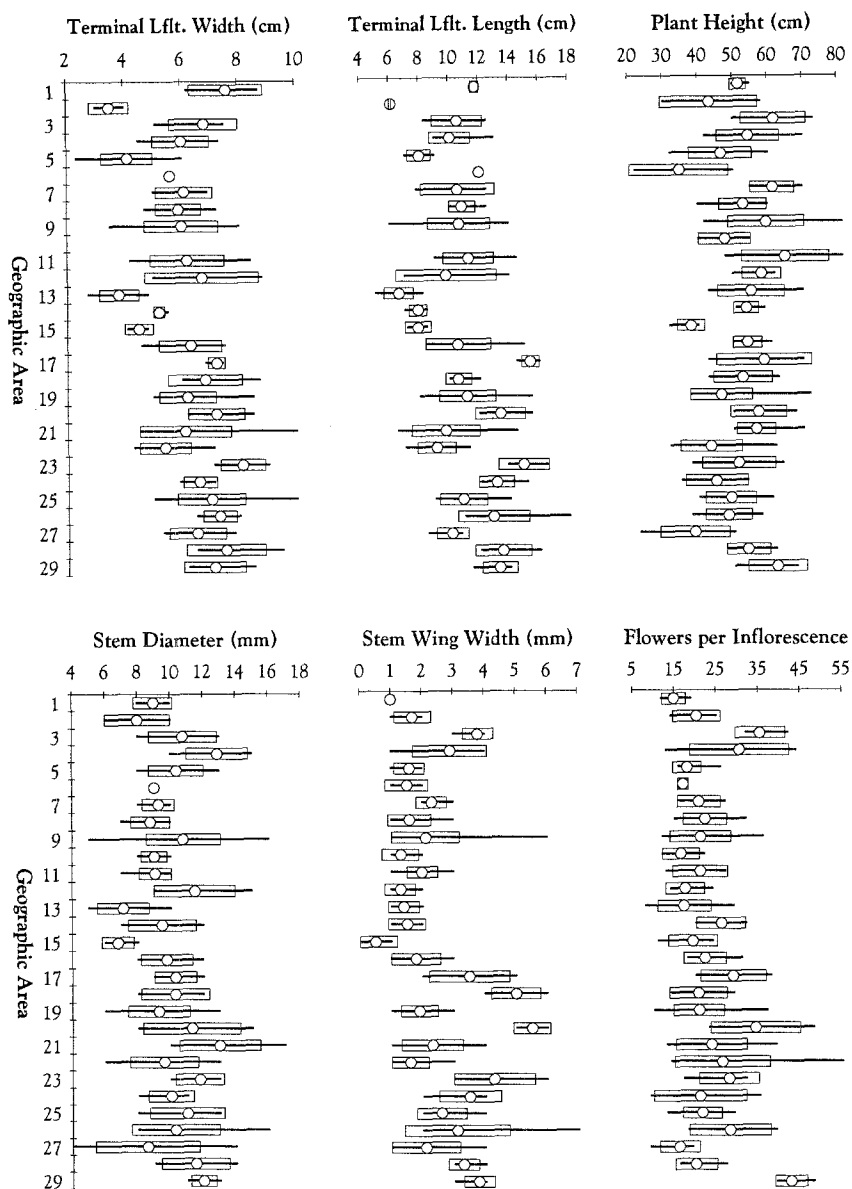


Fig. 2. Means, ranges, and one standard deviation of the six presumed taxonomically important quantitative characters distinguishing *Solanum microdontum* subsp. *microdontum* and subsp. *gigantophyllum*, analyzed by geographic area (see Fig. 1). All 69 examined accessions are grouped here

involved all taxa. Although plots of these CDA showed greater overlap of taxa, all three groups were still supported as significant at the 0.01 level using the four multivariate test statistics in SAS (SAS Institute, Inc. 1988; Hotelling-Lawley Trace, Pillai's Trace, Roy's Greatest Root, Wilks' Lambda).

**Analysis of the taxonomically important characters by geographic area.** Figure 2 presents a geographic analysis of the means, ranges, and standard deviations of the six taxonomically important quantitative characters of all accessions by geo-

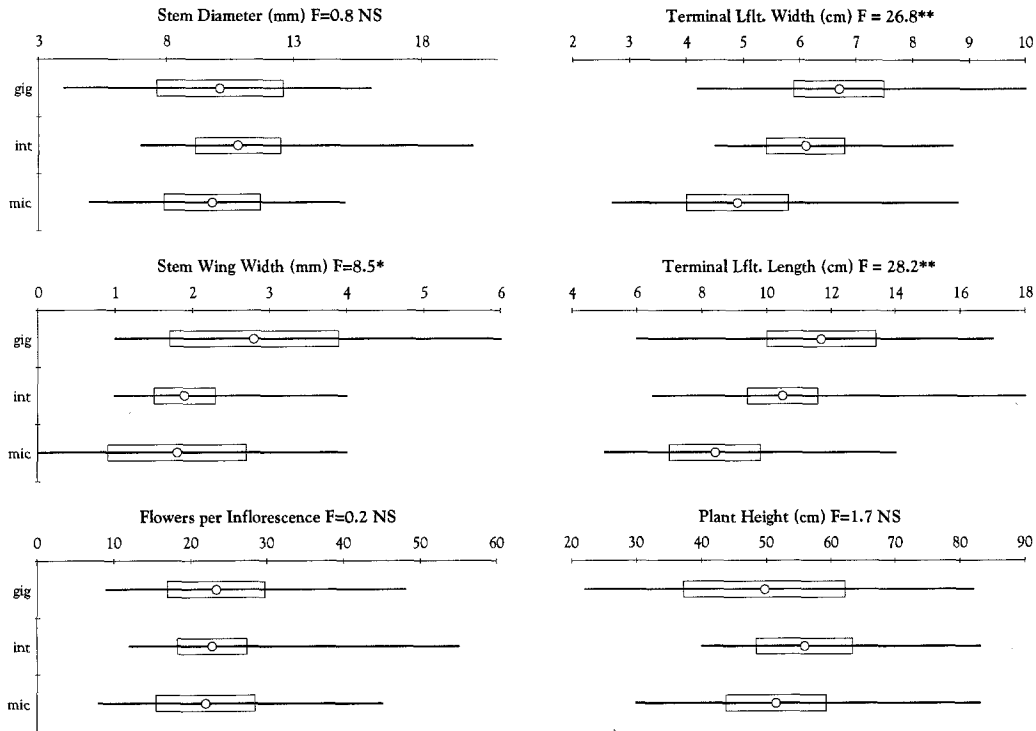


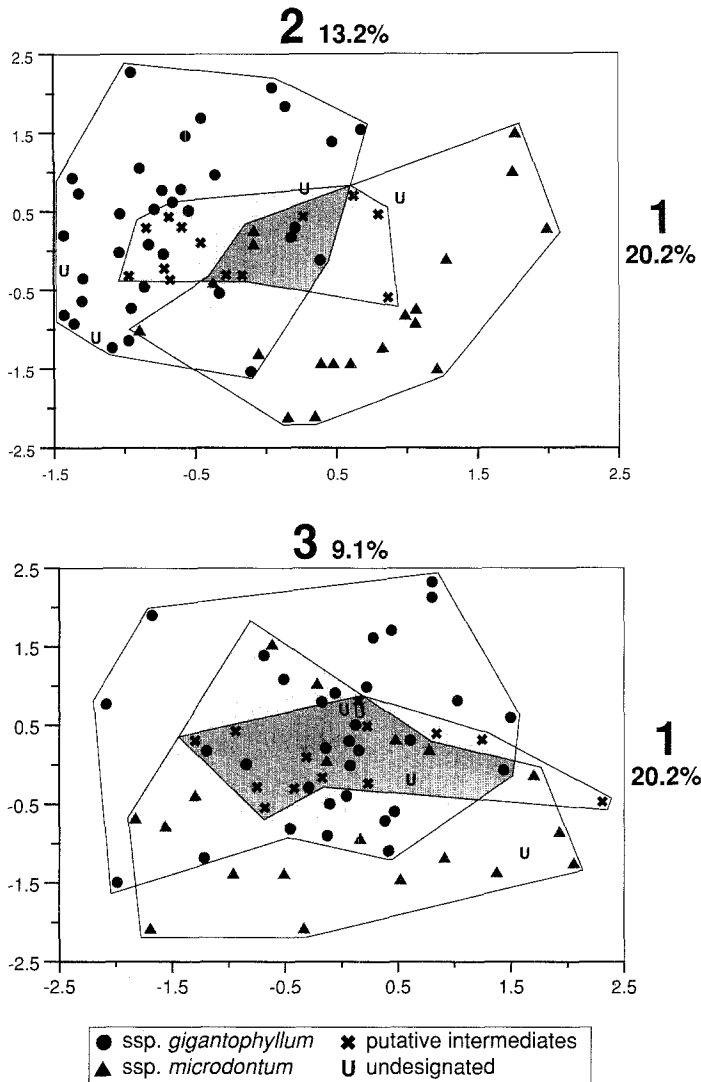
Fig. 3. Means, ranges, and one standard deviation of the mean of the six presumed taxonomically important characters distinguishing *Solanum microdontum* subsp. *microdontum* (mcd), subsp. *gigantophyllum* (gig), and putative intermediates (int) analyzed by taxon. The four unidentified accessions are not included here. NS Not significant, \* significant at 0.01, \*\* significant at 0.001

graphic regions (Table 2). No north-south geographic pattern is present. The seventh taxonomically important character, wing morphology, was qualitative, and likewise showed no north-south geographic pattern. Wings were undulate (a putative subsp. *gigantophyllum* character) in 262 of the 276 individuals examined. Only one accession (PI 500064 of region 19; Table 2, Fig. 1) had all four individuals examined with straight stem wings. The remaining 10 individuals with straight stem wings occurred in areas 5, 7, 8, 9, 11, and 22 (Fig. 1).

## Discussion

**Taxonomy.** HAWKES & HJERTING's (1960) original concept of subsp. *microdontum* and subsp. *gigantophyllum* incorporated a geographical concept for this rank, and made no mention of possible sympatric distribution. Their subsequent distributional data (HAWKES & HJERTING 1969, 1989; Table 1), however, indicated almost complete sympatry of these two subspecies. However, their theory (HAWKES 1980; HAWKES & HJERTING 1969, 1989) and practice of subspecies designations are contradictory, with discordant textual accounts, specimen citations, and mapped records. They overlook their own distributional data and maintain a geographical (allopatric) concept for subspecies, with subsp. *microdontum* as the "northern" taxon, subsp. *gigantophyllum* as the "southern" one, with "intermediates" "largely"





Figs. 4, 5. Plots of principal components 1,2 and 1,3 of the 21 morphological characters of *Solanum microdontum* subsp. *microdontum* (circles), subsp. *gigantophyllum* (triangles), putative intermediates (X), and taxa undesignated as to subspecies (U)

confined to a vaguely defined area of geographical overlap. For example, HAWKES & HJERTING (1969: 317) state: "Forms intermediate between [subsp. *microdontum* and subsp. *gigantophyllum*] also occur in the zone of overlap between them", and add (p. 318): "In general there is no difficulty in placing a specimen into one or the other of the two subspecies unless it comes from the zone of intergradation between them. The forms from this zone are roughly intermediate in all characters between the two subspecies." HAWKES & HJERTING (1989: 319) hypothesize introgression between these taxa, and conclude (p. 318): "The various phenotypes derived from certain habitat differences, as well as genotypic differences in some cases, have formed a continuum which can be divided only into two subspecies,

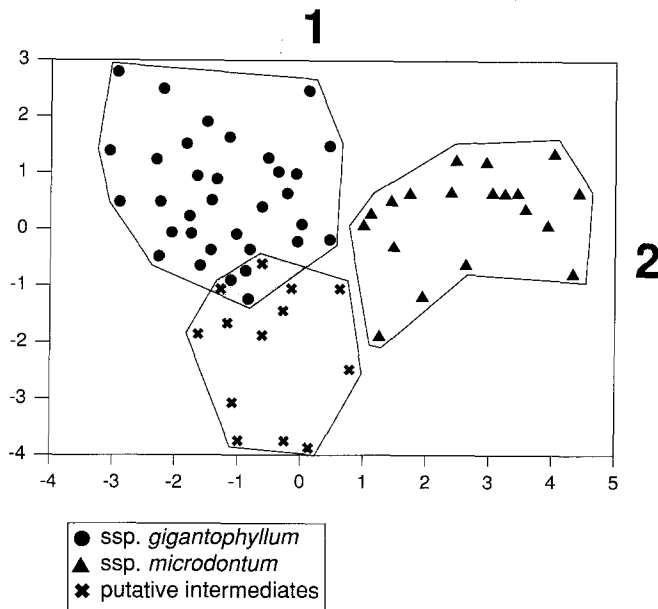


Fig. 6. Plots of the first two canonical variates distinguishing *Solanum microdontum* subsp. *microdontum* (circles), subsp. *gigantophyllum* (triangles), putative intermediates (X)

*microdontum* and *gigantophyllum*.” No evidence is presented, however, for habitat differences or sexual incompatibilities.

OCHOA (1990) provides little insight into his taxonomic concepts separating var. *microdontum* from var. *metriophyllum* (subsp. *gigantophyllum*), other than the morphological differences in his key and descriptions similar to those of HAWKES & HJERTING (1969, 1989) (Table 1). Unfortunately, his distribution maps do not account for varietal distributions. His specimen citations, however, like HAWKES & HJERTING (1969, 1989), indicate sympatric distributions (var. *microdontum* in the Bolivian Depts of Cochabamba and Santa Cruz; var. *metriophyllum* in the Bolivian Depts of Cochabamba, La Paz, and Tarija). Unlike HAWKES & HJERTING (1969, 1989), OCHOA (1990) does not hypothesize hybridization or intergradation between the two taxa.

Although factors 1 and 2 of the PCA roughly separate the putative taxa, prior identifications apparently have been based on size of leaves or leaflets, or possibly the width of the wing of the stem. There are no qualitative characters separating the taxa, and the extreme differences in size and dissection of the leaves vary both within populations and geographic areas. Viewed without reference to prior taxonomic determinations, the PCA simply indicates a continuous distribution of variability of a highly polymorphic taxon.

The SDA and CDA are designed to provide better discrimination than PCA by searching for gaps among predetermined groups, and are designed to provide the most “optimistic” separation of groups. If the results of these analyses were literally translated into a taxonomy, there would be three, not two taxa among these examined populations. Each “taxon” would be defined by arbitrary breaks in a continuum of variability, without any correlation with habitats, geography,

or other known isolating mechanisms. Because of sympatric distributions, a continuum of morphological variability, and lack of isolating mechanisms between “taxa”, however, we interpret the two subspecies and putative intermediates to constitute one polymorphic taxon. We interpret hypotheses of subspecies and hybrids to arise from a typological concept influenced by extremes of the variation, but with no documentation and/or appreciation for normal variability in a highly polymorphic taxon.

**Synonymy of *Solanum microdontum* BITTER**, Feddes Repert. Spec. Nov. Regni Veg. **10**: 535. 1912.

*Solanum simplicifolium* subsp. *microdontum* (BITTER) HAWKES, Scott. Pl. Breed. Sta., Ann. Rep. 1956: 92. 1956. Nomen invalidum. Type: Argentina [Salta]: Toldos, near Bermejo, 1800 m, December 1903, FIEBRIG 2498 (holotype: B, destroyed; neotype, designated by HAWKES & HJERTING, 1960: W; isotypes: F! M, LL! SI, U!; photograph of LL isotype in HAWKES & HJERTING 1969: pl. 97).

*Solanum bijugum* BITTER, Feddes Repert. Spec. Nov. Regni Veg. **10**: 533. 1912. Type: Argentina [Salta]: Toldos, near Bermejo, November 26, 1903, FIEBRIG 2253 (holotype: B, destroyed; photograph: F! US, herb. of J. G. HAWKES; photograph of specimen in herbarium of J. G. HAWKES in HAWKES & HJERTING 1969: pl. 98).

*Solanum gigantophyllum* BITTER, Feddes Repert. Spec. Nov. Regni Veg. **11**: 368. 1912. *Solanum simplicifolium* subsp. *gigantophyllum* (BITTER) BITTER, Feddes Repert. Spec. Nov. Regni Veg. **12**: 445. 1913. *Solanum microdontum* subsp. *gigantophyllum* (BITTER) HAWKES & HJERTING, Phytol. **9**: 144. 1960. *Solanum microdontum* var. *gigantophyllum* (BITTER) OCHOA, Phytologia **57**: 321. 1985. Type: Argentina [Tucumán]: Cuesta del Garabatal near Siambon, Sierra de Tucumán, January 27, 1874, LORENTZ & HIERONYMUS 802 (holotype: GOET!).

*Solanum simplicifolium* BITTER, Feddes Repert. Spec. Nov. Regni Veg. **11**: 369. 1912. Type: Argentina [Salta]: Quebrada de San Lorenzo, March 9, 1873, LORENTZ & HIERONYMUS s.n. (holotype: B, destroyed; photographs: F! GH, US).

*Solanum simplicifolium* subsp. *gigantophyllum* var. *metriophyllum* BITTER, Feddes Repert. Spec. Nov. Regni Veg. **12**: 445. 1913. *Solanum microdontum* var. *metriophyllum* (BITTER) OCHOA. The potatoes of South America: Bolivia: 243. 1990. Lectotype (chosen by OCHOA, 1990; June 13, 1991): Argentina: Tucumán: Arcas-Trancas, January 1897, SPEGAZZINI s.n. (LP!, herb. no. 14217).

*Solanum simplicifolium* subsp. *gigantophyllum* var. *mollifrons* BITTER, Feddes Repert. Spec. Nov. Regni Veg. **12**: 445. 1913. Type: Argentina: Salta: Pampa Grande, January 1897, SPEGAZZINI s.n. (holotype: B, destroyed).

*Solanum simplicifolium* subsp. *gigantophyllum* var. *trimerophyllum* BITTER, Feddes Repert. Spec. Nov. Regni Veg. **12**: 446. 1913. Type: Argentina: Salta: Pampa Grande, January 1897, SPEGAZZINI s.n. (holotype: B, destroyed).

*Solanum simplicifolium* var. *variabile* (as var. *variabilis*) BRÜCHER & ROSS, Lilloa **26**: 465. 1953. Syntypes: Argentina: Catamarca: 1949, BRÜCHER 184, 185, 188, 264 (GOET).

*Solanum cevallos-tovari* CÁRDENAS, Bol. Soc. Per. Bot. **5**: 13, pl. I(C), Figs. 1–3. 1956. Type: Bolivia: Santa Cruz: Valle Grande, La Forteleza, March 1955, CÁRDENAS 5087 (holotype: BOLV).

*Solanum higuerae* CÁRDENAS, Bol. Soc. Per. Bot. **5**: 20, pl. I(F), Figs. 1–8. 1956. Type: Bolivia: Santa Cruz: Valle Grande, between Pucara and Higuera, March 1955, CÁRDENAS 5067 (holotype: BOLV; isotype: LL, photo LL!).

*Solanum tafiense* nomen nudum, mentioned in HAWKES & HJERTING (1989: 313) and OCHOA (1990: 240).

BITTER (1913) described both *S. simplicifolium* subsp. *gigantophyllum* var. *mollifrons* and var. *trimerophyllum* from type material with identical locality and collector data. It is unknown if they represent the same collection. A collection bearing these same data is deposited in LPS (fragment LL!) marked as "*Solanum simplicifolium* var. *mollifrons*" by BITTER, and may represent type material.

Two taxa are very similar to *S. microdontum* and warrant further morphological and molecular study to determine their affinities: *S. microdontum* var. *montepuncoense* OCHOA and *S. guzmanguense* M. WHALEN & SAGÁST. No known germplasm of either of these taxa is yet available, however, and we refrain from making taxonomic judgements until these studies are completed. The former differs from *S. microdontum* (with round to ovoid fruits) by its longconical fruits. It is distributed in Bolivia, Cochabamba Province, near the northern end of the range of *S. microdontum* and at the southern end of the range of *S. violaceimarmoratum* BITTER. HAWKES & HJERTING (1989) hypothesize var. *montepuncoense* to be a natural interspecific hybrid between these two taxa.

WHALEN & al. (1986) described *S. guzmanguense* from a few populations of a very limited distribution in northern Peru, Cajamarca Department, c. 1100 km by air north of the northern range of *S. microdontum* in northern Bolivia, La Paz Province. They state "[*Solanum guzmanguense*] does not seem to be related to any of the other known Peruvian wild potatoes" . . . "Upon study of other wild potato species from other Andean regions, the nearest relationship of *S. guzmanguense* proved to be with *S. simplicifolium*." The type of *S. simplicifolium* has entire leaves, a feature we found to vary within populations, and we here synonymize it to *S. microdontum*, in agreement with HAWKES & HJERTING (1989) and OCHOA (1990). WHALEN & al. (1986) distinguish *S. guzmanguense* from *S. simplicifolium* by pubescence (glabrate to sparsely and inconspicuously ciliate in *S. guzmanguense*; coarsely pubescent with simple uniseriate trichomes in *S. simplicifolium*), longer pedicels (2.5–4.5 cm long; vs. 1.5–2.5 cm long), larger corollas (4–6 cm in diameter; vs. 2.5–4.0 cm in diameter), glabrous styles (papillose in *S. simplicifolium*), and simple leaves (simple to compound in *S. simplicifolium*). Our study shows that the distinguishing characters of overall pubescence, leaf dissection, and style pubescence are insufficient to discriminate *S. guzmanguense* from *S. microdontum*, but the pedicel length and corolla diameter of *S. guzmanguense* exceed that found in *S. microdontum* (pedicel length range = 1.4–3.3 cm; corolla diameter range = 2.0–4.0 cm).

**Implications of this study.** Intraspecific taxa and even species in sect. *Petota* often are distinguished by what on the surface appear to be minor characters with overlapping character states like habit, pubescence, number of lateral or interjected leaflets, or colors or shapes of the calyx or corolla (SPOONER & VAN DEN BERG 1992). Our ongoing field and herbarium work make it clear that there are many fewer than the 232 species in sect. *Petota* recognized by HAWKES (1990). The ease of crossability within morphologically very different taxa with distinct geographic ranges in sect. *Petota* (HAWKES 1958) dissuades us from using the biological species concept alone to circumscribe taxa in this group. Our concept of species and subspecies in sect. *Petota*, therefore, largely rests on morphological criteria, with

subspecies used for phenetically distinct geographical components of these species, but with intermediate taxa in narrow zones of sympatry. We agree with HAMILTON & REICHARD (1992) and STUESSY (1990) that if one infraspecific category is to be used, subspecies represent a suitable solution to the ambiguities caused by the equal use of varieties and subspecies by different authors.

The acceptance of infraspecific taxa within *S. microdontum* by HAWKES, HJERTING, or OCHOA questions the reliability of infraspecific taxa they accept elsewhere in sect. *Petota*. Using the criteria of minor morphological differences and large sympatric distributions between taxa, we are conducting similar investigations for the following infraspecific taxa recognized by these authorities: 1. *S. acaule* BITTER subsp. *acaule* and subsp. *punae* (JUZ.) HAWKES & HJERT. (accepted by HAWKES 1990); 2. *S. bulbocastanum* DUNAL subsp. *bulbocastanum*, subsp. *dolichophyllum* (BITTER) HAWKES, and subsp. *partitum* (CORRELL) HAWKES (HAWKES 1990); 3. *S. cardiophyllum* LINDLEY subsp. *cardiophyllum*, subsp. *ehrenbergii* BITTER, and subsp. *lanceolatum* (BERTH.) BITTER (HAWKES 1990); 4. *S. circaefolium* BITTER subsp. *circaeifolium* and subsp. *quimense* HAWKES & HJERT. (HAWKES & HJERTING 1989, HAWKES 1990); 5. *S. circaefolium* var. *circaeifolium* and var. *capsicibaccatum* (CÁRDENAS) OCHOA (OCHOA 1990); 6. *S. fendleri* A. GRAY subsp. *fendleri* and subsp. *arizonicum* HAWKES (HAWKES 1990); 7. *S. vernei* BITTER & WITTM. subsp. *vernei* and subsp. *balsii* HAWKES & HJERT. (HAWKES & HJERTING 1969, HAWKES 1990).

The wild species of *Solanum* have tremendous proven and potential utility as breeding material to improve our modern cultivars (ROSS 1986, HANNEMAN 1990, SPOONER & BAMBERG 1991). *Solanum microdontum* has disease and pest resistances to bacterial, fungal, and viral pathogens, insect and nematode pests, and frost (HAWKES & HJERTING 1989). *Solanum microdontum* is part of the pedigree of "Conestoga" (PLAISTED & HOOPES 1989), a cultivar approved for 171 acres of "seed" potatoes in the United States and Canada in 1989 (NATIONAL POTATO COUNCIL 1990). An understanding of the species and infraspecific diversity in *S. microdontum* and the other wild species will greatly help breeders using the wild species. They can better plan breeding programs by choosing or avoiding related materials based on wild species evaluations or prior breeding results.

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