Species Limits and Hypotheses of Hybridization of Solanum berthaultii Hawkes and S. tarijense Hawkes: Morphological Data

David M. Spooner; Ronald G. van den Berg

Taxon, Vol. 41, No. 4. (Nov., 1992), pp. 685-700.

Species limits and hypotheses of hybridization of *Solanum berthaultii* Hawkes and *S. tarijense* Hawkes: morphological data

David M. Spooner[1] & Ronald G. van den Berg[2]

Summary

Spooner, D. M. & Berg, R. G. van den: Species limits and hypotheses of hybridization of *Solanum berthaultii* Hawkes and *S. tarijense* Hawkes: morphological data. – *Taxon* 41: 685-700. 1992. – ISSN 0040-0262.

Solanum berthaultii Hawkes and *S. tarijense* Hawkes have been recognized as distinct species by all authors since their description in 1944. Some authors have considered them as sister species, but more recently they have been treated as unrelated species belonging to separate superseries. Hypotheses of species boundaries and hybridization have been examined using principal components analysis, stepwise discriminant analysis, canonical discriminant analysis, and one-way analysis of variance. 25 morphological characters measured on four individuals from each of 84 living accessions from throughout their natural range were analysed. Extensive intra-accession, intraspecific, and interspecific variability have been found in many characters, including those previously given great taxonomic weight. 9 characters show no statistically significant differences between species or putative interspecific hybrids. The remaining 16 characters show statistically significant differences between species and putative hybrids, but show so much variability that repeatable identifications of some accessions would require the use of population samples. The data suggest the possibility that the two species should be treated as one. Other currently-recognized species within *S.* sect. *Petota* may need to be reevaluated for synonymy. The results also question the hypotheses of extensive hybridization, interpretation of series designations, and the phylogenetic interpretation of corolla shape at the superseries level in *S.* sect. *Petota*.

Introduction

Solanum L. sect. *Petota* Dumort., the potato and its wild relatives, are distributed in the Americas from the southwestern United States to southern Chile. The group is taxonomically difficult, and conflicting interpretations of species boundaries and interrelationships are common. An earlier interpretation (Correll, 1962) recognized 157 species, while the latest (Hawkes, 1990) recognizes 232 species, divided into 21 series. Various regional treatments have been published (Montaldo & Sanz, 1962; Ochoa, 1962, 1990; Flores Crespo, 1966; Hawkes & Hjerting, 1969, 1989), and, since 1962, 176 new taxa have been described, 140 of these by Ochoa, including 77 new varietal and form names of cultivated Bolivian species (Ochoa, 1988).

Many species are morphologically very similar, often distinguished by apparently minor differences of pubescence or leaf shape (Correll, 1962; Hawkes, 1990). In addition, series boundaries are sometimes unclear and apparently overlapping, and alternative placement of species into different series is common (Spooner & Sytsma, 1992; Spooner & Berg, 1992). Despite strong reproductive isolation between some major

---

[1] Vegetable Crops Research Unit, Agricultural Research Service, USDA, Department of Horticulture, University of Wisconsin, 1575 Linden Drive, Madison, Wisconsin 53706, U.S.A.

[2] Department of Plant Taxonomy, Wageningen Agricultural University, Generaal Foulkesweg 37, P.O. Box 8010/6700 ED, Wageningen, The Netherlands.

Table 1. Features used to distinguish *Solanum berthaultii* and *S. tarijense*

Character	*S. berthaultii*	*S. tarijense*
glandular trichomes[1]	A + B	A
corolla color[2]	pale blue-violet to mauve	white
corolla shape	pentagonal to substellate	stellate
distribution	central Bolivia	central Bolivia south to northern Argentina

[1] Ochoa (1980) is the first taxonomist to concur with Gibson (1971, 1976) in separating *S. berthaultii* and *S. tarijense* by the presence/absence of Type B trichomes.

[2] Correll (1962) includes white and blue for both species; Ochoa (1990) lists *S. berthaultii* as purple to lilac, occasionally whitish, and *S. tarijense* as white; Hawkes (1990) and Hawkes & Hjerting (1969, 1989), consider deviations of species-specific colors to be caused mainly by hybridization.

groups (e.g., the Mexican diploids isolated from the South American species and the Mexican polyploids), natural and artificial interspecific and even interseries and intersuperseries hybrids are common (Hawkes, 1958, 1990).

Natural interspecific hybridization has been hypothesized to be a major evolutionary mechanism in *Solanum* sect. *Petota* (Ugent, 1970a; Hawkes, 1990), and hybrid speciation has been implied in the formation of many species: *S. ajanhuiri* Juz. & Buk. (Huamán & al., 1980, 1982, 1983; Johns & al., 1987), *S. bruecheri* Correll (Hawkes & Hjerting, 1969; Hawkes, 1990), *S. chaucha* Juz. & Buk. (Jackson & al., 1977), *S. curtilobum* Juz. & Buk. (Hawkes, 1962a), *S. demissum* Lindley (Hawkes, 1966), *S. doddsii* Correll (Hawkes & Hjerting, 1989), *S. edinense* Berthault (Hawkes, 1944, 1966; Ugent, 1967), *S. guerreroense* Correll and *S. hougasii* Correll (Hawkes, 1966), *S. indunii* Okada & A. Clausen (Okada & Clausen, 1982), *S. iopetalum* (Bitter) Hawkes (Hawkes, 1966), *S. juzepczukii* Buk. (Hawkes, 1962a; Schmiediche & al., 1980), *S. litusinum* Ochoa (Hawkes, 1990), *S. michoacanum* (Bitter) Rydb. (Correll, 1962), *S. raphanifolium* Cárdenas & Hawkes (Ugent, 1970b), *S. rechei* Hawkes & Hjerting (Hawkes & Hjerting, 1969; Okada & Hawkes, 1978), *S. ruiz-lealii* Brücher (Hawkes & Hjerting, 1969), *S. sambucinum* Rydb. (Hawkes, 1963, 1966; Hawkes & Lester, 1968), *S. sucrense* Hawkes (Astley & Hawkes, 1979), *S. semidemissum* Juz. (Hawkes, 1963; Ugent, 1967), *S. setulosistylum* Bitter (Hawkes, 1963), *S. subandigena* Hawkes (Hawkes & Hjerting, 1989), *S. trigalense* Cárdenas (Hawkes, 1990), *S. tuberosum* subsp. *andigena* Hawkes (Brücher, 1964; Hawkes, 1956a; Cribb & Hawkes, 1986; Matsubayashi, 1991), *S. vallis-mexici* Juz. (Hawkes, 1963, 1966), *S. viirsooi* Okada & A. Clausen (Okada & Clausen, 1985), *S. zudaniense* Cárdenas (Hawkes, 1990).

Additionally, introgression and interspecific hybridization not leading to speciation is believed to be common (Hawkes, 1962b). Hawkes & Hjerting (1969) interpret 9.5 % of the specimens they examined for the treatment of *S.* sect. *Petota* in Argentina, Brazil, Paraguay and Uruguay as natural hybrids. Similarly, Hawkes & Hjerting (1989) provide extensive lists of putative hybrids for 25 of the 35 wild species of *S.* sect. *Petota* in Bolivia.

The present paper focuses on two species that have been hypothesized to show extensive introgression and hybridization, *Solanum berthaultii* Hawkes and *S. tarijense* Hawkes.

Characters distinguishing Solanum berthaultii *and* S. tarijense. – *S. berthaultii* and *S. tarijense* were validly named in 1944 (Hawkes, 1944), and have been accepted by all subsequent authors (Table 1). *S. berthaultii* was described as a glandular species with blue to violet, pentagonal to substellate corollas, and placed in *S.* ser. *Tuberosa* (Rydb.) Hawkes, characterized by pentagonal to rotate corollas. *S. tarijense* was described with white, stellate corollas and placed in *S.* ser. *Commersoniana* Buk., characterized by stellate corollas. Subsequently, Gibson (1971) pointed out a third qualitative difference between the two species. *S. berthaultii* possesses 650-950 μm long glandular trichomes, with an ovoid gland at the tip, 20-60 μm in diameter, which continuously discharges a clear viscous exudate not bound by a membrane (Gregory & al., 1986). *S. tarijense* lacks such trichomes. Both species also possess a dense indument of short glandular trichomes, 120-210 μm in length, with 4-lobulate heads 50-70 μm in diameter, in which the glandular material is membrane-bound and only released upon mechanical rupture. Gibson (1976) named the short glandular trichome "Type A" and the longer one "Type B" (Fig. 1), a terminology used by all subsequent authors. The species may occur sympatrically in dry Andean habitats, generally at elevations of 2000-3000 m (Hawkes, 1990). *S. berthaultii* is confined to central Bolivia in the provinces of Cochabamba, Santa Cruz, Sucre, and Potosí; *S. tarijense* largely overlaps this distribution in central Bolivia, and continues south to northern Argentina (Hawkes & Hjerting, 1989). Both species have similar phenology, habitat preferences, and are interfertile (Gibson, 1979; Hawkes, 1990).

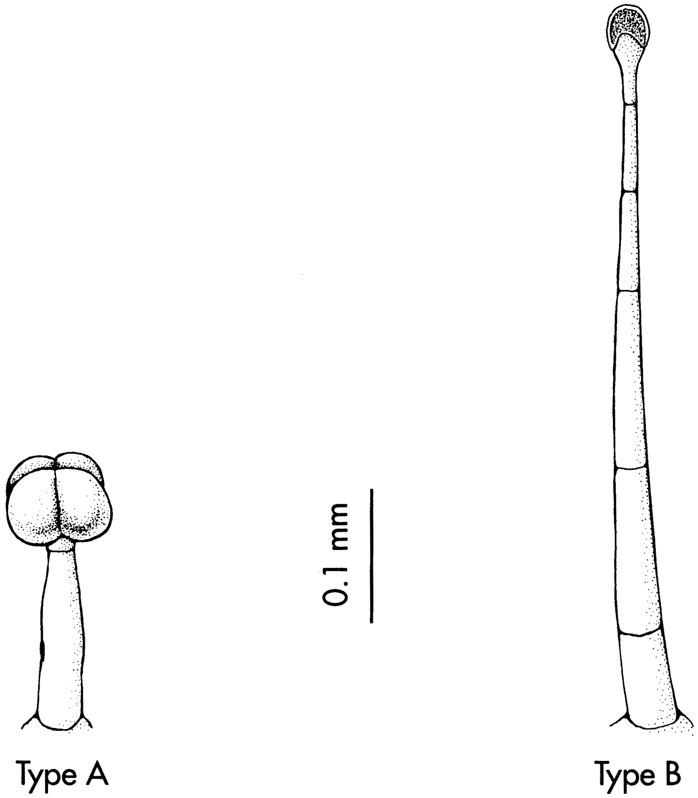

Fig. 1. Type A and Type B glandular trichomes in *Solanum* sect. *Petota.*

Table 2. Previous taxonomic classifications of *Solanum berthaultii* and *S. tarijense* with comments on their origins

Reference	Taxonomic classification *S. berthaultii*	 *S. tarijense*
Hawkes (1944)	*S.* ser. *Tuberosa*	*S.* ser. *Commersoniana*
Brücher & Ross (1953)[1]	*S.* ser. *Tuberosa*	*S.* ser. *Commersoniana*
Bukasov (1955)	*S.* ser. *Andigena*	*S.* ser. *Glabrescentia*
Hawkes (1956b)[2]	*S.* ser. *Tuberosa*	*S.* ser. *Commersoniana*
Bukasov & Kameraz (1959)[3]	*S.* ser. *Transaequatorialia*	*S.* ser. *Glabrescentia*
Correll (1962)	*S.* ser. *Tarijensia*	*S.* ser. *Tarijensia*
Hawkes (1963)[4]	*S.* ser. *Tuberosa*	*S.* ser. *Commersoniana*
Hawkes & Hjerting (1969)[5]	*S.* ser. *Tuberosa*	*S.* ser. *Commersoniana*
Bukasov (1978)	*S.* ser. *Berthaultiana*	*S.* ser. *Tarijensia*
Gorbatenko (1989)[6]	*S.* ser. *Tarijensia*	*S.* ser. *Tarijensia*
Hawkes & Hjerting (1989)[7]	*S.* ser. *Tuberosa*	*S.* ser. *Commersoniana*
Hawkes (1990)[8]	*S.* ser. *Tuberosa*	*S.* ser. *Yungasensia*
Ochoa (1990)[9]	*S.* ser. *Commersoniana*	*S.* ser. *Commersoniana*

[1] *S. berthaultii* is of autopolyploid origin from *S. vernei.*

[2] *S. berthaultii* may form a link between *S.* ser. *Tuberosa* and *S.* ser. *Commersoniana* (Cárdenas, 1956, who does not mention *S. berthaultii,* makes an identical assumption for *S. tarijense*).

[3] *S.* ser. *Transaequatorialia* was not validly published; Gorbatenko (1989) provided a validly published substitute, *S.* ser. *Bukasoviana.*

[4] *S. berthaultii* is a natural hybrid between *S. tarijense* and some blue-flowered mountain species, possibly *S. sparsipilum.*

[5] Some populations of *S. berthaultii* and *S. tarijense* suggest introgression with *S. gourlayi, S. vernei,* or *S. vidaurrei.*

[6] Gorbatenko (1989) divided *S.* ser. *Tarijensia* into *S.* subser. *Tarijensia* (containing *S. tarijense*) and *S.* subser. *Berthaultiana* (containing *S. berthaultii*).

[7] *S. berthaultii* not formed by hybridization between *S. tarijense* and some other blue-flowered species, but widespread natural hybrids between *S. berthaultii* and *S. tarijense* occur.

[8] *S.* ser. *Tuberosa* in *S.* superser. *Rotata, S.* ser. *Yungasensia* in *S.* superser. *Stellata.* Hybridization and introgression is hypothesized to occur between *S. berthaultii* and *S. tarijense* in Bolivia and between *S. tarijense* and some purple-flowered species in Argentina.

[9] *S. berthaultii* and *S. tarijense* are closely related; *S. berthaultii* not of hybrid origin between *S. tarijense* and *S. sparsipilum.*

Series relationships and hybridization of Solanum berthaultii *and* S. tarijense *(Table 2).* – Hawkes (1956b) was the first to note a similarity between the two species and suggested that they formed a phyletic "link," connecting *S.* ser. *Tuberosa* and *S.* ser. *Commersoniana.* Hawkes (1963) and Hawkes & Hjerting (1969) treated *S. berthaultii* as a hybrid derivative of *S. tarijense* and "a blue-flowered mountain species, possibly *S. sparsipilum* (Bitter) Juz. et Buk." Hawkes & Hjerting (1989) subsequently reversed their opinion regarding the hybrid origin of *S. berthaultii* but continued to assume extensive hybridization between *S. berthaultii* and *S. tarijense.* 15 % of the *S. berthaultii* and *S. tarijense* accessions listed in Hanneman & Bamberg (1986) and 24 %

Table 3. Examined accessions of *Solanum berthaultii* (ber), *S. tarijense* (tar) and their putative hybrids (hyb), as indicated by specialists, with geographical origin as mapped in Fig. 2.

Origin	Identity	Collection	Accession[1]
1	ber	Ross 382	265857
1	ber	Ross s.n.	265858
1	hyb	Ochoa s.n.	310927
1	ber	Hawkes & al. 4531C	473331
2	ber	Hawkes & al. 6668	498109
2	ber	Hoopes & al. 190	545960
3	ber	Hawkes & al. 6541	498100
3	ber	Hawkes & al. 6544	498101
3	ber	Hawkes & al. 6547	498102
3	ber	Hawkes & al. 6548	498103
3	ber	Hawkes & al. 6549	498104
3	ber	Hawkes & al. 6552	498105
3	ber	Hawkes & al. 6554	498106
3	ber	Hawkes & al. 6556B	498107
3	ber	Hawkes & al. 6557	498108
3	ber	Hawkes & al. 6542	----------
4	hyb	Hawkes & al. 6451	498096
4	hyb	Hawkes & al. 6453	498097
5	hyb	Hawkes & al. 6438	498094
6	hyb	Correll B619	265577
6	hyb	Hawkes & al. 6442	498095
7	ber	Ross 326	218215
7	ber	Ross 351	283069
8	hyb	Hawkes & al. 4543	473333
9	hyb	Hawkes & al. 4538	473332
10	tar	Hawkes & al. 4569	458394
10	hyb	Hawkes & al. 4570	473335
11	hyb	Hawkes & al. 4574	473336
11	hyb	Hawkes & al. 4728	473338
11	ber	Astley 044	498075
12	tar	Hawkes & al. 4667	414152
12	tar	Hawkes & al. 4673	458395
13	tar	Sleumer 4002	217457
13	tar	Hjerting 151	275154
13	tar	Hoffman 1890	414148
13	tar	Hoffman 2017	414149
13	tar	Hoffman 1885	414159
13	tar	Hoffman 1892	442689
13	tar	Hoffman 1876	458364
13	tar	Hoffman 1902	458365
13	tar	Hoffman 1886	458366
13	tar	Hoffman 1876A	473218
13	tar	Hoffman 1870	473219
13	tar	Okada 5873	473223
13	tar	Okada 5874	473224
13	tar	Okada 5876	473225
13	tar	Okada 5877	473226
13	tar	Okada 5878	473227
13	tar	Okada 5879	473228
13	tar	Okada 5880	473229
13	tar	Okada 5881	473230
13	tar	Okada 5882	473231
13	tar	Okada 5883	473232
13	tar	Okada 5884	473233
13	tar	Okada 5886	473234
13	tar	Okada 5887	473235
13	tar	Okada 5888	473236
13	tar	Okada 5889	473237
13	tar	Okada 5890	473238
13	tar	Okada 5891	473239
13	tar	Okada 6232	473240
13	tar	Okada 6233	473241
13	tar	Okada 6234	473242
13	tar	Okada 6238	473243
13	tar	Okada 6239	473244
13	tar	Okada 6320	473245
13	tar	Hoffman 1867 x 1886	498399
14	tar	Sleumer 4024	217458
15	tar	Hoffman 1713	473216
15	tar	Hoffman 1717	473217
15	tar	Hoffman 1713 x 1717	----------
16	tar	Okada 4818	472815
16	tar	Okada 5632	473220
16	tar	Okada 5633	473221
16	tar	Okada 5634	473222
16	tar	Okada 7491	500043
16	tar	Okada 7303	500054
16	tar	Okada 7492	500055
16	tar	Okada 7494	----------
16	tar	Okada 7495	----------
	tar	CPC 2667	230466
	hyb	Alandia 64-2	310971
	tar	Ochoa 12001	498290
	ber	LaPointe 31284-1	----------

---

[1] Plant introduction (PI) number (see Hanneman & Bamberg, 1986) when assigned.

of the specimens cited in Hawkes & Hjerting (1989) are listed as natural interspecific *S. berthaultii* × *S. tarijense* hybrids. Additionally, Hawkes & Hjerting (1969, 1989) list natural interspecific hybrids between *S. berthaultii* and *S. chacoense* Bitter, *S. sparsipilum*, and *S. sucrense* Hawkes, and between *S. tarijense* and *S. chacoense*, *S. gourlayi* subsp. *pachytrichum* (Hawkes) Hawkes & Hjerting, *S. hondelmannii* Hawkes & Hjerting, *S. microdontum* Bitter, and *S. spegazzinii* Bitter. Considerable disagreement occurs between various authors regarding the placement of *S. berthaultii* and *S. tarijense* into series (the names in quotation marks have not been validly published), with *S. berthaultii* variously placed in *S.* ser. *Andigena* Buk. & Kameraz, *"Berthaultiana"*, *Commersoniana*, *Tarijensia* Correll, *"Transaequatorialia"*, or *Tuberosa;* and *S. tarijense* placed in *S.* ser. *Commersoniana*, "*Commersoniana/Tuberosa* intermediate", *"Glabrescentia"*, *Tarijensia*, or *Yungasensia* Correll (Table 2). Hawkes (1989, 1990) placed major phylogenetic importance on stellate corollas to define *S.* superser. *Stellata* Hawkes (containing *S. tarijense*) vs. pentagonal to rotate corollas to characterize *S.* superser. *Rotata* Hawkes (containing *S. berthaultii*). He thus considered these species as quite unrelated.

The purpose of this study is to reexamine the distinctness of *Solanum berthaultii* and *S. tarijense*, using many of the same accessions and all of the taxonomic characters used by prior taxonomists, and to discuss the implications of the results for species circumscriptions and assumptions of putative hybridization within *S.* sect. *Petota*.

Materials and methods

Materials. – Seeds from 84 accessions of *Solanum berthaultii*, *S. tarijense*, or putative interspecific hybrids of the two were obtained from the Inter-Regional Potato Introduction Project (IR-1) at Sturgeon Bay, Wisconsin (Hanneman & Bamberg, 1986; Table 3, Fig. 2). Identifications of living representatives of the accessions in field plots have been provided over the years by Jack G. Hawkes, J. Peter Hjerting, Carlos Ochoa or Armando Okada during on-site visits to IR-1 (Spooner & Bamberg, 1991). Identifications of Bolivian collections were compared to those in Hawkes & Hjerting (1989); where identifications differed, determinations follow this latter source. Seeds were planted in a greenhouse in early May, 1990, seedlings were transferred to peat pots in late May, and nine individuals per accession were transplanted together in rows in a field plot at Sturgeon Bay in early June.

Data measurement. – 23 quantitative and 2 qualitative characters were measured (Table 4) in late August, 1990 after flowering had commenced. The first four surviving plants per row were measured for all characters, and means of four plants were used to represent each accession, except for a few examples when only three plants per accession were available (the accession represents the Operational Taxonomic Unit, OTU). Measurements of leaves were made on the largest leaf per plant. Scoring presence/absence of glandular tips of Type B trichomes (character 14, Table 4) was conducted on young leaves because in rare cases the glandular tips of these trichomes were not evident on older leaves. Mehlenbacher & al. (1983, 1984) demonstrate intra- and interaccession variability in the density of Type B trichomes, but scoring for their presence/absence here was done without regard to their density.

Data analysis. – The data were analysed by one-way analysis of variance available in Minitab (Ryan & al., 1985), principal components analysis available in NTSTS-pc,

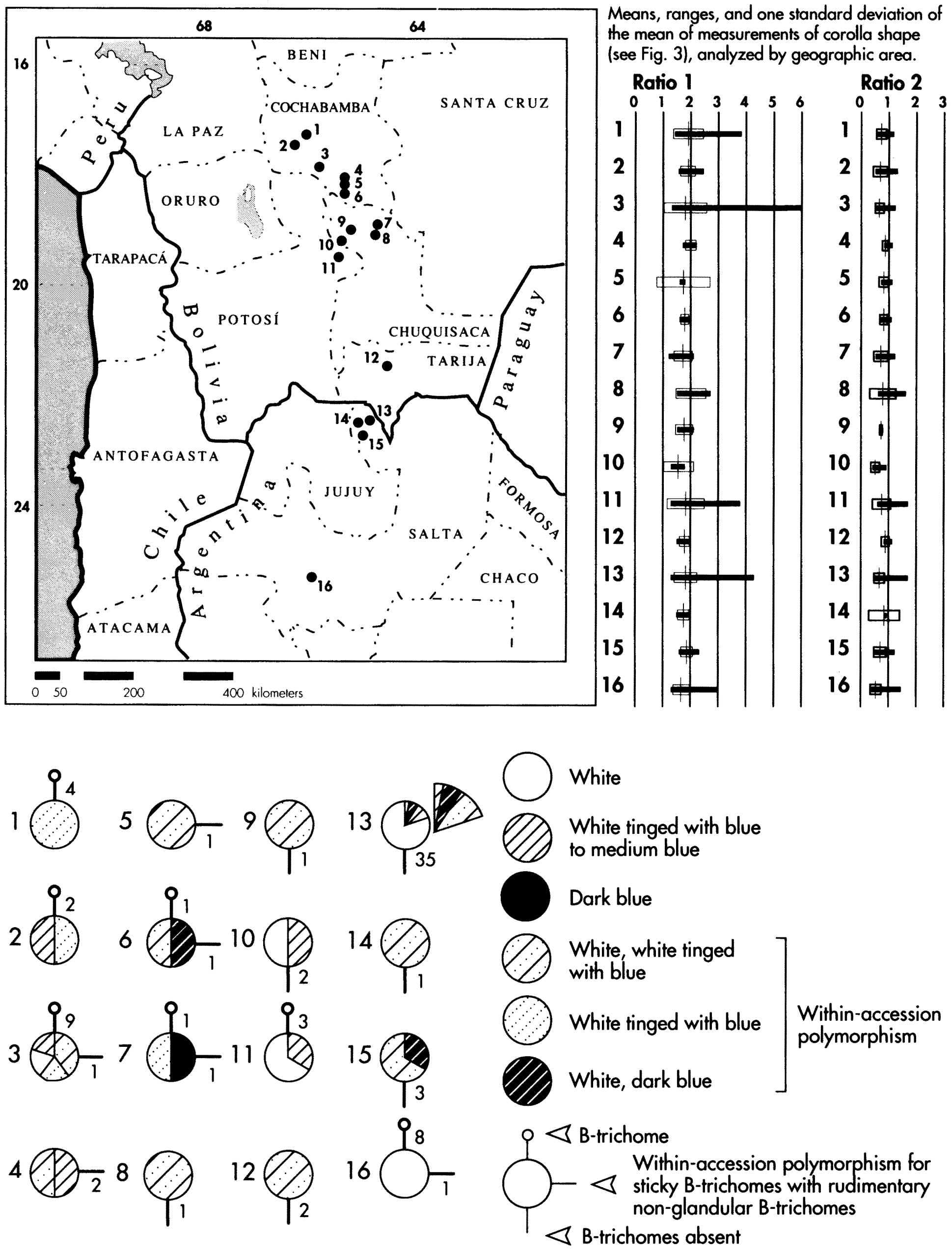

Fig. 2. Geographical origin of 80 of the 84 accessions of *Solanum berthaultii*, *S. tarijense*, and putative hybrids, grouped into clusters of localities, illustrating the geographic distribution of their corolla color and corolla shape and variability of indumentum characters.

Table 4. Characters and states used in numerical phenetics of *Solanum berthaultii* and *S. tarijense* (see Fig. 1, 3). Terminology after Hawkes (1990).

1. Leaf length (cm).
2. Leaf width (cm).
3. Leaf length : length from axis of widest point of leaf to apex.
4. Terminal leaflet length (cm).
5. Terminal leaflet width (cm).
6. Terminal leaflet length : length from axis of widest point of leaflet to apex.
7. Terminal leaflet petiolule length (mm).
8. Primary dorsal lateral leaflet length (cm).
9. Primary dorsal lateral leaflet width (cm).
10. Primary dorsal lateral leaflet length : length from axis of widest point of leaflet to apex.
11. Primary dorsal lateral leaflet petiolule length (mm).
12. Number of primary lateral leaflet pairs.
13. Number of secondary and tertiary interjected lateral leaflets.
14. B trichomes: with well-formed glandular tip (0), rudimentary glandular tip (0.5), glandular tip absent (1).
15. Pedicel length (mm).
16. Pedicel length : length from base of pedicel to articulation.
17. Total calyx length.
18. Total calyx length : calyx lobe length.
19. Calyx lobe width at base (mm).
20. Sepal acumen length (mm).
21. Corolla color: white (0), white tinged with blue to medium blue (1), dark blue (2).
22. Radius to apex of corolla lobe (mm).
23. Radius to apex of corolla lobe : radius to base of corolla lobe (R1).
24. Width of corolla lobe at base : length from a line drawn across widest point of corolla lobes (R2).
25. Anther length (mm).

version 1.50 (Exeter Software, Setauket, New York), stepwise discriminant analysis, and canonical discriminant analysis (Anonymous, 1988), using the standardized means of four plants per accession as character scores. Stepwise discriminant analysis requires continuous characters. Because presence/absence of type B trichomes (character 14) and corolla color (character 21) were scored as discrete characters with only three qualitative character states each, they were not used in this analysis. Character distributions of the three groups (*Solanum berthaultii*, *S. tarijense*, and putative hybrids) and one-way analysis of variance were implimented by means of the ONEWAY option in Minitab (Ryan & al., 1985), using observations on individual plants. Corolla shape, a character given much taxonomic weight by Hawkes (1990), required two separate measurements (see Fig. 3). Hawkes (1990, App. 3, Fig. III.2) defined a stellate corolla as one in which measurement 4 (length of corolla lobe) was greater than measurement 3 (width of corolla lobe), and a rotate corolla as one in which measurement 4 was one-half the length of measurement 3 (Ratio 2 in Fig. 3).

However, another measure is necessary to assess corolla shape, because some corollas have narrow to deep incisions at the junction of the two corolla lobes, providing a different type of stellate corolla that would not be detected by Ratio 2. Although this incision could result from a tear down the junction of the connate corolla lobes in a normally rotate corolla, giving the false impression of a stellate corolla, many plants had this incision at all stages of corolla development, and care was taken to measure intact corollas. Ratio 1 (Fig. 3), the ratio between the radius of the corolla measured from the center of the corolla to the tip of the corolla lobes (measurement 1) and the distance between the center of the flower and the junction of the two corolla lobes (measurement 2) measures this shape.

Results

Simple statistics. – Despite much overlap in the range, the sample means of 16 of the 25 characters measured were statistically significant at the 0.05 level or more (Fig. 4). Extensive variability and overlap in all characters, however, precluded any consistent species-specific character, or combination of characters, to distinguish *Solanum berthaultii* from *S. tarijense.*

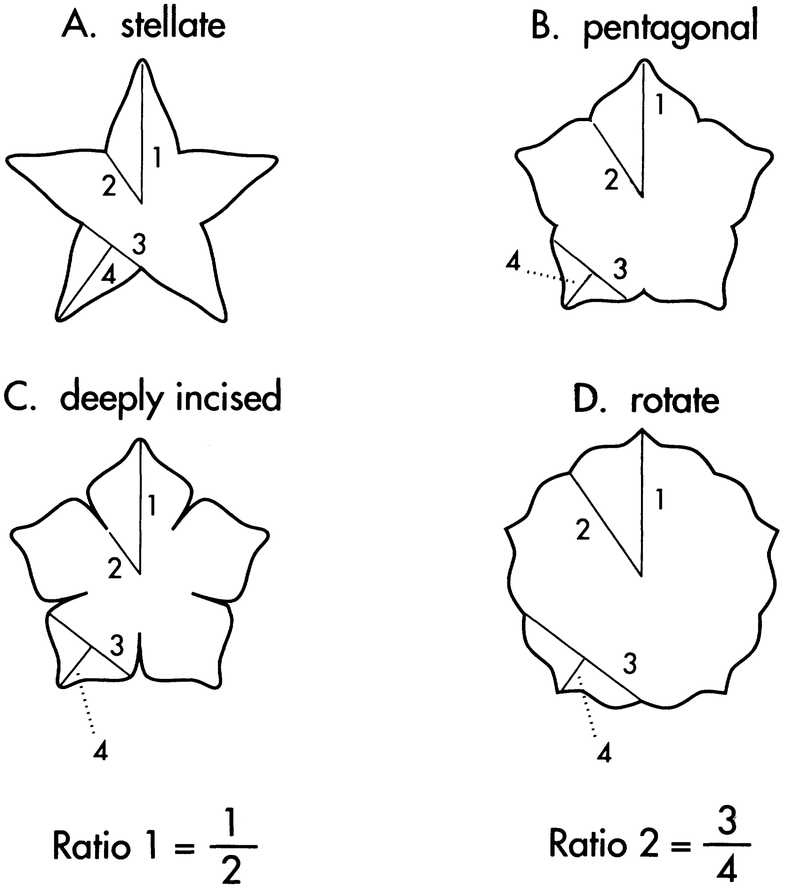

Fig. 3. Stylized corolla shapes (modified from Hawkes, 1990), and indication of the measurements taken for the numerical taxonomic study.

Principal components analysis. – In the PCA of the accessions, Factors 1, 2, and 3 accounted for 26.7, 12.8 and 11.6 % of the variation, respectively. Although there is some partitioning of accessions of *Solanum berthaultii* along the first principal component, there is extensive overlap of *S. berthaultii, S. tarijense,* and putative interspecific hybrids. Coding the accessions by geographic area, rather than by taxon, shows them geographically intermixed.

Stepwise discriminant and canonical discriminant analyses. – A stepwise discriminant analysis used eight characters (25, 16, 19, 6, 5, 22, 11, 7, given in decreasing order of importance) to try and discriminate the taxa (Table 4). The canonical discriminant analysis was able to provide some discrimination, but with considerable overlap, between *Solanum berthaultii, S. tarijense,* and putative hybrids (Fig. 5).

Observations on taxonomically important characters. – Great intra-accession, intraspecific and interspecific variability is encountered for all three characters used by prior taxonomists to differentiate *Solanum berthaultii* and *S. tarijense* (presence/absence of Type B trichomes, corolla color, corolla shape). A geographic analysis of these characters is presented in Fig. 2. Intra-accession variability in presence/absence of Type B trichomes was encountered in 8 of the 64 accessions. Although Type B trichomes are present in all individuals in the extreme northernmost portion of the range (Fig. 2, areas 1 and 2 in Prov. Cochabamba, Bolivia), plants lacking them occur immediately southward. Type B trichomes are entirely absent in the central part of the range (areas 12-15 in southern Bolivia and adjacent northern Argentina), but reappear in its southernmost portion (area 16 in Prov. Salta, Argentina), corroborating similar findings by Gibson (1979). Corolla color likewise shows extensive intra-accession, intraspecific, and interspecific variability. Although corolla color varied continuously from pure white to dark-blue, and our measure (Table 4, character 21) was a step-wise approximation of this continuous variation, intra-accession variability was encountered in 30 of the 84 accessions. The only geographic area with constant corolla color is area 16 where all accessions examined had pure white corollas, a *S. tarijense* character, but most of these accessions possessed Type B trichomes, a *S. berthaultii* character. Within the 19 accessions of *S. berthaultii*, deviations from the combination of Type B glandular trichomes and corollas blue or tinged with blue were found in eight cases. Similarly, within *S. tarijense*, deviations from the combination of no Type B trichomes and white corollas was found within 22 of the 53 accessions. Corolla shape, the third classic taxonomic character, as measured by both Ratio 1 and Ratio 2 (Fig. 3), exhibited no statistically significant differences between any of the taxa and no geographic pattern (Fig. 2). In some accessions, corolla shape varied tremendously from very stellate to rotate.

Discussion

Of the three taxonomic characters that have traditionally been used to separate *Solanum berthaultii* and *S. tarijense*, the presence or absence of Type B trichomes has been most cited (e.g., Ochoa, 1980, 1990; Hawkes & Hjerting, 1989; Hawkes 1990). Intraspecific variation for trichome density or morphology is recognized in many species of flowering plants and may be correlated with differential predator pressure in different geographic regions (Levin, 1973). The lack of a strong geographic pattern for this character (Fig. 2), combined with the results of the PCA and canonical

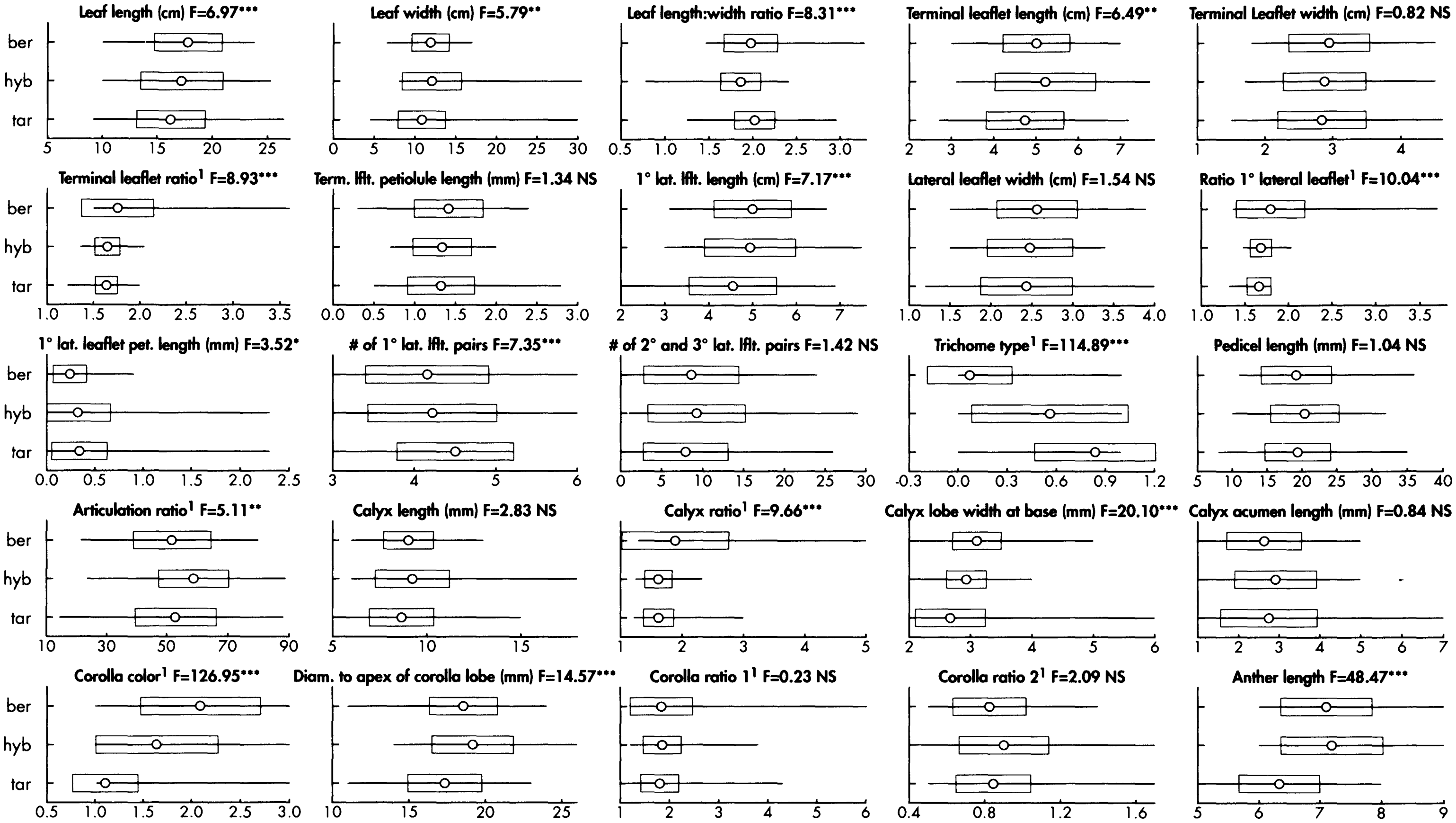

Fig. 4. Means, ranges, and one standard deviation of the mean of the 25 characters examined for *Solanum berthaultii* (ber), *S. tarijense* (tar), and putative interspecific hybrids (hyb). ¹ See Table 4 for complete character states. NS = not significant. * = significant at 0.005, ** = 0.01, *** = 0.001.

discriminant analysis (Fig. 5), the lack of known ecological and biological isolating mechanisms between the taxa, and the treatment of trichome variation in other plant groups, make the use of this character to separate *S. berthaultii* and *S. tarijense* as distinct species questionable. Despite extensive overlap of characters, however, some of the OTU's of *S. tarijense* cluster together in the PCA, and the discriminant analyses indicates some discrimination of groups.

Prior reports of variability in *Solanum berthaultii* and *S. tarijense*, however, underestimated its extent (Correll, 1962; Ochoa, 1990; Hawkes & Hjerting, 1989; Hawkes, 1990). The extensive overlap of morphological characters (Fig. 4) and of accessions in the PCA and canonical discriminant analyses (Fig. 5) was unexpected in light of the prior universal acceptance of the two species and especially of their placement in separate superseries (Table 2). Whether this pattern represents the initial stages of species formation or results from extensive hybridization aided by the recent disruption of formerly well defined specific habitats is unknown. The extensive variability of characters at all levels (intra-accession, intraspecific, interspecific) in this group, however, suggests that *S. berthaultii* and *S. tarijense* should at least be considered as closely related if not conspecific.

Species concepts in Solanum *sect.* Petota. – Recent treatments of *S.* sect. *Petota* (Correll, 1962; Ochoa, 1962, 1990; Hawkes & Hjerting, 1969, 1989; Bukasov, 1978, 1985; Hawkes, 1990) have stressed a morphological species concept. All have emphasized the need to use genetically constant characters and to recognize species as

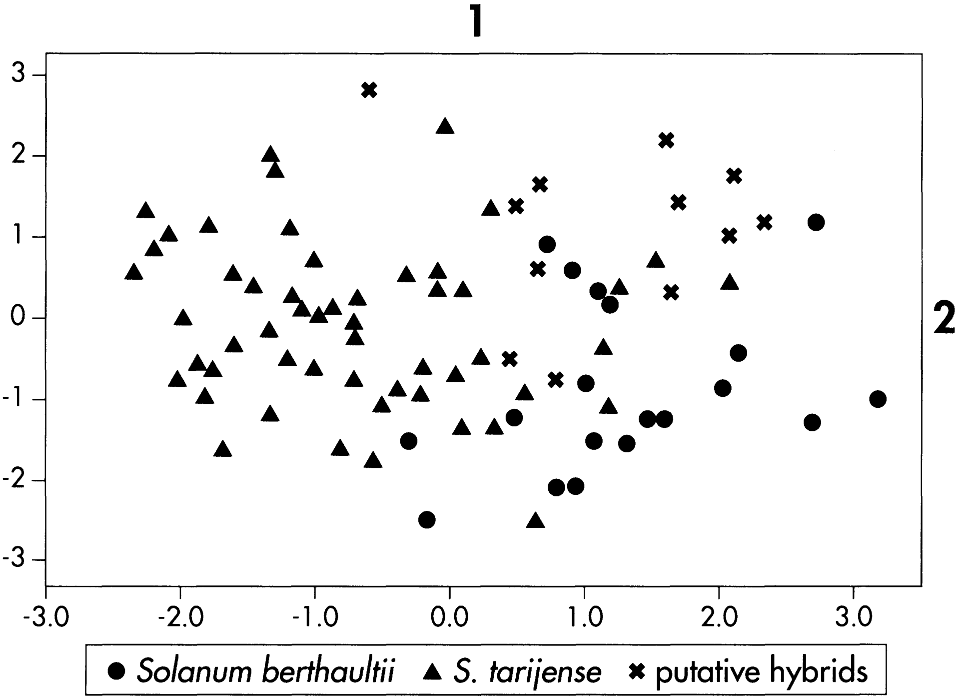

Fig. 5. Scatter-diagram generated by plotting the two canonical variables of OTU's of *Solanum berthaultii, S. tarijense*, and their putative hybrids.

distinct only when clear gaps in variability are encountered, and all have attempted to reduce the extensive synonymy of prior workers. Bukasov (1978, 1985) stressed character correlations. Correll (1962) demonstrated environmental variability caused by growth of identical accessions in different habitats and decried the practice of describing new species from plants under cultivation. He also hypothesized that much variability was caused by sexually sterile interspecific hybrids being maintained vegetatively by tubers. Ochoa (1962) argued that introgression confounded species boundaries. Hawkes (1990) and Hawkes & Hjerting (1969, 1989) emphasized hybridization and introgression more than any other taxonomists working in *S.* sect. *Petota.* They suggested that the taxonomic confusion in the group may have resulted from its recent evolution, with sympatric species initially maintained by ecogeographical factors, but now with their boundaries blurred by recent hybridization and introgression, aided by man-made disruption of previously well-defined habitats. Hawkes (1990) and Hawkes & Hjerting (1969, 1989) have tested many of these hypotheses by artificial crosses, but the general lack of statistical analyses and intra- and interspecific crossing controls makes their results only tentative.

Series and superseries concepts in Solanum *sect.* Petota. – The diagnostic criteria and the biological significance of series and superseries as currently accepted in *S.* sect. *Petota* are questionable. The recognition of series and their circumscription has been highly variable (Spooner & Sytsma, 1992; Spooner & Berg, 1992; Table 2); the most recent series circumscriptions (Hawkes, 1990) rely in part on morphological criteria that are inconstant. The placement of *S. berthaultii* and *S. tarijense* into series by previous workers is especially variable (Table 2). The variability of corolla shape shows that putting *S. berthaultii* into *S.* superser. *Rotata* (corollas pentagonal to rotate) and *S. tarijense* into *S.* superser. *Stellata* (corollas stellate) is untenable biologically. Infrasectional taxa in *S.* sect. *Petota* need thorough reexamination.

Hybridization in Solanum *sect.* Petota. – Our results showing extensive variability within *S. berthaultii* and *S. tarijense* cast doubt on other putative cases of hybridization in *S.* sect. *Petota.* Intermediate morphology may be caused by convergent evolution, retention of ancestral characters, phenotypic plasticity, as well as by hybridization (Rieseberg & al., 1988). A recent molecular analysis of *S. raphanifolium* Cárdenas & Hawkes (Spooner & al., 1991) failed to support its putative hybrid origin from *S. canasense* Hawkes and *S. megistacrolobum* Bitter (Ugent, 1970b), indicating that other such putative hybrids may be questionable. Hybrid speciation is important in the production of morphological intermediates elsewhere in flowering plants (Rieseberg & Brunsfeld, 1992), and may be common in *S.* sect. *Petota*, but each case must be considered tentative until more rigorously reexamined. Simple variability also can account for morphological intermediacy, showing the need for a reevaluation of species boundaries.

In *Solanum* sect. *Petota*, there is a continuing need to determine the constancy of characters and the gaps of morphological variability in order to circumscribe taxa more precisely. Most hypotheses of hybridization in *S.* sect. *Petota* need reinvestigation. The questionable taxonomic boundaries and hypotheses of hybridization for *S. berthaultii* shown here suggest the need for reexamination with additional characters throughout *S.* sect. *Petota.* Species boundaries and hybridization in *S. berthaultii* and *S. tarijense* are being re-evaluated by means of molecular data (isozymes, chloroplast DNA, single-copy nuclear DNA). This work will be presented later.

Acknowledgements

We thank John Bamberg and staff of the Inter-Regional Potato Project for help in acquiring, planting, and maintaining the accessions, Kandis Elliot and Andrew Wynn Rouse for artwork, Jack Hawkes and Carlos Ochoa for the loan of types and useful comments on species boundaries in *Solanum* sect. *Petota*, Peter Crump and Brian Yandell for statistical advice, and John Bamberg, Robert Hanneman, Robert Kowal, Thomas Lammers and Brigitte Zimmer for comments on an earlier draft of the manuscript.

Literature cited

Anonymous, 1988. *SAS/STAT user's guide, Release 6.03 edition.* SAS Institute, Cary, North Carolina.

Astley, D. & Hawkes, J. G. 1979. The nature of the Bolivian weed potato species *Solanum sucrense* Hawkes. *Euphytica* 28: 685-696.

Brücher, H. 1964. El origen de la papa *(Solanum tuberosum). Physis* 24: 439-452.

– & Ross, H. 1953. La importancia de las especies tuberíferas de *Solanum* del noroeste Argentino como fuente de resistencia a las enfermedades. *Lilloa* 26: 453-488.

Bukasov, S. M. 1955. Sistematika vidov kartofelja. [Systematics of potato species.] *Probl. Bot.* 2: 317-326.

– 1978. Principi sistematika kartofelja. [Principles of the systematics of potatoes.] *Trudy Prikl. Bot.* 62: 3-34.

– 1985. Principles of the systematics of potatoes [translated by A. K. Dhote]. Pp. 1-42 *in:* Kothekar, V. S. (ed.), *Systematics, breeding and seed production of potatoes.* Amerind, New Delhi.

– & Kameraz, A. J. 1959. *Osnovi selekcii kartofelja. [Bases of potato breeding.]* Sel'sko, Leningrad.

Cárdenas, M. 1956. New species of *Solanum (Tuberarium-Hyperbasarthrum)* from Bolivia. *Bol. Soc. Peruana Bot.* 5: 9-45.

Correll, D. S. 1962. The potato and its wild relatives. *Contr. Texas Res. Found., Bot. Stud.* 4: 1-606.

Cribb, P. J. & Hawkes, J. G. 1986. Experimental evidence for the origin of *Solanum tuberosum* subspecies *andigena.* Pp. 383-404 *in:* D'Arcy, W. G. (ed.), Solanaceae: *biology and systematics.* Columbia University Press, New York.

Flores Crespo, R. 1966. *Estudio preliminar del género* Solanum, *sección* Tuberarium *subsección* Hyperbasarthrum *en México.* Thesis, Universidad Nacional Autónoma, México.

Gibson, R. W. 1971. Glandular hairs providing resistance to aphids in certain wild potato species. *Ann. Appl. Biol.* 68: 113-119.

– 1976. Trapping of the spider mite *Tetranychus urticae* by glandular hairs on the wild potato *Solanum berthaultii. Potato Res.* 19: 179-182.

– 1979. The geographical distribution, inheritance and pest-resisting properties of sticky-tipped foliar hairs on potato species. *Potato Res.* 22: 223-236.

Gorbatenko, L. E., 1989. Konspekt sistemi sekcii *Petota* Dumort. roda *Solanum* L. iz južnoi Ameriki. [A conspectus of the system of the section *Petota* Dumort. of the genus *Solanum* L. in South America.] *Trudy Prikl. Bot.* 126: 92-108.

Gregory, P., Avé, D. A., Bouthyette, P. Y. & Tingey, W. M. 1986. Insect-defensive chemistry of potato glandular trichomes. Pp. 173-183 *in:* Juniper, B. & Southwood, R. (ed.), *Insects and the plant surfaces.* Arnold, London.

Hanneman, R. E. & Bamberg, J. B. 1986. Inventory of tuber-bearing *Solanum* species. *Wisconsin Agric. Exp. Sta. Bull.* 533: 1-216.

Hawkes, J. G. 1944. *Potato collecting expeditions in Mexico and South America. II. Systematic classification of the collections.* Imperial Agricultural Bureau of Plant Breeding and Genetics, Cambridge.

– 1956a. Taxonomic studies on the tuber-bearing solanums. 1: *Solanum tuberosum* and the tetraploid species complex. *Proc. Linn. Soc. London* 166: 97-144.

– 1956b. A revision of the tuber-bearing solanums. *Annual Rep. Scott. Pl. Breed. Sta.* 1956: 37-109.

– 1958. Kartoffel. I. Taxonomy, cytology and crossability. Pp. 1-43 *in:* Kappert, H. & Rudorf, W. (ed.), *Handbuch der Pflanzenzüchtung*, ed. 2, 3. Parey, Berlin.

– 1962a. The origin of *Solanum juzepczukii* Buk. and *S. curtilobum* Juz. et Buk. *Z. Pflanzenzücht.* 47: 1-14.

– 1962b. Introgression in certain wild potato species. *Euphytica* 11: 26-35.

– 1963. A revision of the tuber-bearing solanums (second edition). *Rec. Scott. Pl. Breed. Sta.* 1963: 76-181.

– 1966. Modern taxonomic work on the *Solanum* species of Mexico and adjacent countries. *Amer. Potato J.* 43: 81-103.

– 1989. Nomenclatural and taxonomic notes on the infrageneric taxa of the tuber-bearing solanums *(Solanaceae). Taxon* 38: 489-492.

– 1990. *The potato: evolution, biodiversity and genetic resources*, ed. 3. Belhaven Press, London.

– & Hjerting, J. P. 1969. The potatoes of Argentina, Brazil, Paraguay, and Uruguay: a biosystematic study. *Ann. Bot. Mem.* 3.

– & – 1989. *The potatoes of Bolivia: their breeding value and evolutionary relationships.* Oxford University Press, Oxford.

– & Lester, R. N. 1968. Immunological studies on the tuber-bearing solanums. III. Variability within *S. bulbocastanum* and its hybrids with species in series Pinnatisecta. *Ann. Bot. (London)* 32: 165-186.

Huamán, Z., Hawkes, J. G. & Rowe, P. R. 1980. *Solanum ajanhuiri:* an important diploid potato cultivated in the Andean altiplano. *Econ. Bot.* 34: 335-343.

– , – & – 1982. A biosystematic study of the origin of the cultivated diploid potato, *Solanum* ×*ajanhuiri* Juz. et Buk. *Euphytica* 31: 665-676.

– , – & – 1983. Chromatographic studies on the origin of the cultivated diploid potato *Solanum* ×*ajanhuiri* Juz. et Buk. *Amer. Potato J.* 60: 361-367.

Jackson, M. T., Hawkes, J. G. & Rowe, P. R. 1977. The nature of *Solanum* ×*chauca* Juz. et Buk., a triploid cultivated potato of the South American Andes. *Euphytica* 26: 775-783.

Johns, T., Huamán, Z., Ochoa, C. & Schmiediche, P. E. 1987. Relationships among wild, weed, and cultivated potatoes in the *Solanum* ×*ajanhuiri* complex. *Syst. Bot.* 12: 541-552.

Levin, D. A. 1973. The role of trichomes in plant defense. *Quart. Rev. Biol.* 48: 3-15.

Matsubayashi, M., 1991. Phylogenetic relationships in the potato and its related species. Pp. 93-118 *in:* Tsuchiya, T. & Gupta, P. K. (ed.), *Chromosome engineering in plants: genetics, breeding, evolution, Part B.* Elsevier, Amsterdam.

Mehlenbacher, S. A., Plaisted, R. L. & Tingey, W. M. 1983. Inheritance of glandular trichomes in crosses with *Solanum berthaultii. Amer. Potato J.* 60: 699-708.

– , – & – 1984. Heritability of trichome density and droplet size in interspecific potato hybrids and relationship to aphid resistance. *Crop Sci. (Madison)* 24: 320-322.

Montaldo, A. & Sanz, C. 1962. Las especies de papas silvestres y cultivadas de Chile. *Agric. Técn.* 22: 66-152.

Ochoa, C. M. 1962. *Los* Solanum *tuberíferos del Peru. (Secc.* Tuberarium, *sub-secc.* Hyperbasarthrum). Privately published, Lima.

– 1980. A new tuber-bearing *Solanum* potentially useful for breeding for aphid resistance. *Amer. Potato J.* 57: 387-390.

– 1988. New Bolivian taxa of *Solanum* (sect. *Petota*). *Phytologia* 65: 103-113.

– 1990. *The potatoes of South America: Bolivia.* Cambridge University Press, Cambridge.

Okada, K. A. & Clausen, A. M. 1982. Natural hybridization between *Solanum acaule* Bitt. and *S. megistacrolobum* Bitt. in the province of Jujuy, Argentina. *Euphytica* 31: 817-835.

– & – 1985. Natural triploid hybrids between *Solanum acaule* Bitter and *S. infundibuliforme* Philippi in the Province of Jujuy, Argentina. *Euphytica* 34: 219-231.

– & Hawkes, J. G. 1978. *Solanum* ×*rechei*, especie silvestre de papas de origen hibrido de la Sierra de Famatina (Provincia de La Rioja, Argentina). *Kurtziana* 11: 55-74.

Rieseberg, L. H. & Brunsfeld, S. J. 1992. Molecular evidence and plant introgression. Pp. 151-176 *in:* Soltis, P. S., Soltis, D. E., & Doyle, J. J. (ed.), *Molecular systematics of plants.* Chapman & Hall, London.

– , Soltis, D. E. & Palmer, J. D. 1988. A molecular reexamination of introgression between *Helianthus annuus* and *H. bolanderi (Compositae). Evolution* 42: 227-238.

Ryan, B. F., Joiner, B. L. & Ryan, T. A. 1985. *Minitab handbook,* 2. ed. PWS-Kent, Boston, Massachusetts.

Schmiediche, P. E., Hawkes, J. G. & Ochoa, C. M. 1980. Breeding of the cultivated potato species *Solanum* ×*juzepczukii* Buk. and *Solanum* ×*curtilobum* Juz. et Buk. I. A study of the natural variation of *S.* ×*juzepczukii, S.* ×*curtilobum* and their wild progenitor, *S. acaule* Bitt. *Euphytica* 29: 685-704.

Spooner, D. M. & Bamberg, J. B. 1991. The Inter-Regional Potato Introduction Project (IR-1), U.S. center for potato germplasm. *Diversity* 7(4): 32-35.

– & Berg, R. G. van, 1992. An analysis of recent taxonomic concepts in wild potatoes (*Solanum* sect. *Petota*). *Gen. Res. Crop Evol.* (in press).

– & Sytsma, K. J. 1992. Reexamination of series relationships of Mexican and Central American wild potatoes (*Solanum* sect. *Petota*): evidence from chloroplast DNA restriction site variation. *Syst. Bot.* 17: 432-448.

– , – & Smith, J. F. 1991. A molecular reexamination of diploid hybrid speciation of *Solanum raphanifolium. Evolution* 45: 757-764.

Ugent, D. 1967. Morphological variation in *Solanum* ×*edinense,* a hybrid of the common potato. *Evolution* 21: 696-712.

– 1970a. The potato: what is the origin of this important crop plant, and how did it first become domesticated? *Science* 170: 1161-1166.

– 1970b. *Solanum raphanifolium*, a Peruvian wild potato species of hybrid origin. *Bot. Gaz. (Crawfordsville)* 131: 225-233.