SOLANACEAE SYSTEMATICS

Species limits of *Solanum berthaultii* Hawkes and *S. tarijense* Hawkes and the implications for species boundaries in *Solanum* sect. *Petota*

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Solanum berthaultii and *S. tarijense* are two wild potato (sect. *Petota*) species distributed from Bolivia to northern Argentina. All authors have accepted them as good species since their publication in 1944, but they have been hypothesized to hybridize extensively with each other and with other species, despite their classification into different series and superseries by some authors. This study is a molecular counterpart (AFLPs, plastid DNA restriction site data, survey of a plastid DNA deletion) to a prior morphological study of these two species. AFLP data show weak support for separate species status for some accessions, but with many exceptions. In agreement with the morphological results we place *S. tarijense* into synonymy of *S. berthaultii*, and use herbarium specimen data for a taxonomic treatment to include a description, synonymy, and mapping of all accessions. We show similar taxonomic problems in sect. *Petota* and suggest that there will be a continuing trend of reduction of names in wild potatoes.

KEYWORDS: AFLP, plastid DNA, *Solanum berthaultii*, *Solanum* sect. *Petota*, *Solanum tarijense*

INTRODUCTION

Solanum L. sect. *Petota* Dumort., the potato and its wild relatives, are distributed in the Americas from the southwestern United States to Chile, Argentina, and Uruguay (Hijmans & Spooner, 2001). The section is taxonomically difficult, and conflicting interpretations of species boundaries and interrelationships are common. Hawkes (1990) recognized 232 species, divided into 21 series. Spooner & Salas (2006) question many of these series and list only 189 species, despite the description of 10 new species since Hawkes (1990), and predict yet further reductions in names with continuing research. Many of the species are morphologically very similar, often distinguished by apparently minor differences of pubescence or leaf shape (Spooner & van den Berg 1992a). Boundaries of many species series are minor and apparently artificial, and alternative taxonomic treatments are common (Spooner & van den Berg, 1992a).

Natural interspecific hybridization is believed to be common among many species of sect. *Petota* (Ugent, 1970a, b; Hawkes, 1962a, b, 1990; Okada & Clausen, 1982, 1985; Spooner & al., 1991; Miller & Spooner, 1996; Clausen & Spooner, 1998). Hybrid speciation has been implicated in the formation of many species at both diploid and polyploid levels, and introgression and interspecific hybridization not leading to speciation is believed to be a common cause for much of the taxonomic difficulty in sect. *Petota*. For example, Hawkes & Hjerting (1969) interpret 9.5% of the specimens they examined for the treatment of sect. *Petota* in Argentina, Brazil, Paraguay and Uruguay as natural hybrids, and Hawkes & Hjerting (1989) provide extensive lists of hybrids for 25 of the 35 wild species of sect. *Petota* treated in Bolivia (Spooner & van den Berg, 1992a). Hawkes (1990) designates eighteen species as hybrids, exclusive of all hybrids in ser. *Longipedicellata* (where he recognized seven species) and ser. *Demissa* (eight species), and five of the seven cultivated species.

The present paper is a molecular counterpart to a morphological study (Spooner & van den Berg, 1992b) of two diploid species of section *Petota* which have been hypothesized to show extensive introgression and hybridization, *S. berthaultii* and *S. tarijense*. Hawkes (1944) described *S. berthaultii* as a glandular species with blue to violet, pentagonal to substellate corollas, and placed it in ser. *Tuberosa* (Rydb.) Hawkes, and *S. tarijense* with white, stellate corollas and placed it in ser. *Commersoniana* Buk. Gibson (1971) interpreted a third character when he showed *S. berthaultii* to possess long, glandular trichomes with a single ovoid gland at the tip (Gregory & al., 1986; Type B trichomes), and indicated that *S. tarijense* lacks such trichomes. Both species also possess a dense indument of short glandular trichomes with tetralobulate heads (Type B trichomes). *Solanum berthaultii* was believed to be confined to central Bolivia and *S. tarijense* largely overlapping this distribution further south in Bolivia, and continuing south to northern Argentina (Hawkes & Hjerting, 1989). Both species have similar phenology, hab-

itat preferences, and are entirely interfertile (Gibson, 1979; Hawkes, 1990; Ochoa, 1990). Hawkes (1956) suggested that *S. berthaultii* and *S. tarijense* "linked" ser. *Tuberosa* and ser. *Commersoniana*.

Hawkes (1963) and Hawkes & Hjerting (1969) treated *S. berthaultii* as a hybrid species between *S. tarijense* and "a blue-flowered mountain species, possibly *S. sparsipilum*." Hawkes & Hjerting (1989) subsequently reversed their opinion regarding the hybrid origin of *S. berthaultii*, but continued to hypothesize extensive hybridization between *S. berthaultii* and *S. tarijense*. Fifteen percent of the *S. berthaultii* and *S. tarijense* accessions listed in Hanneman & Bamberg (1986) and 24% of the specimens cited in Hawkes & Hjerting (1989) are listed as natural interspecific *S. berthaultii* × *S. tarijense* hybrids. Further mention of these in this paper will be "hybrids" for simplicity.

The purpose of this study is to use molecular data from Amplified Fragment Length Polymorphisms (AFLPs), plastid DNA restriction site data, and a 241-bp plastid deletion to explore support for *S. berthaultii*, *S. tarijense*, and their hybrids. We chose AFLPs because of their ability to produce the polymorphisms needed to distinguish closely related taxa. AFLPs combine restriction enzyme reactions with the Polymerase Chain Reaction (PCR), revealing high levels of polymorphism (Vos & al., 1995). They have been shown to have high congruence with many other marker types (Powell & al., 1996; Milbourne & al., 1997; Russell & al., 1997), particularly within closely related species (Spooner & al., 2005b). Within section *Petota*, AFLPs have been used to study species boundaries or diversity of closely related members of series *Longipedicellata* Buk. (van den Berg & al., 2002), Mexican diploid wild potatoes (Lara-Cabrera & Spooner, 2004), the *Solanum brevicaule* complex (Spooner & al., 2005a), *Solanum tuberosum* L. (Kim & al., 1998), and *S. acaule* (McGregor & al., 2002). Outside of sect. *Petota*, Mace & al. (1999) and Furini & Wunder (2004) used AFLPs to examine relationships of *Solanum melongena* L. (eggplant) and its close relatives.

Spooner & Sytsma (1992), Castillo & Spooner (1997), Spooner & Castillo (1997), and Rodríguez & Spooner (1997) discovered four main clades in sect. *Petota*. *Solanum berthaultii* was a member of a largely unresolved clade 4. In this study, we added additional accessions of *S. berthaultii*, *S. tarijense*, their hybrids, and three other accessions in clade 4 (Appendix).

Hosaka (2002, 2003) showed that many populations of *S. berthaultii*, *S. tarijense*, their hybrids, *S. neorossii*, and most landrace populations of *S. tuberosum* from Chile, but not any other wild species, possess a 241 bp plastid DNA deletion in an intergenic region flanking the 3′ end of the *trnV-UAC* gene (Kawagoe & Kikuta, 1991). We screened this deletion to search for taxonomic and geographic patterns in *S. berthaultii*, *S. tarijense*, and their hybrids.

MATERIALS AND METHODS

Plants. — Seeds from 77 accessions of *S. berthaultii*, *S. tarijense*, their hybrids, and related ingroup and outgroup species of *S. alandiae* (1 accession), *S. arnezii* (4), *S. bulbocastanum* (2), *S. chacoense* (14), *S. chomatophilum* (2), *S. gourlayi* (3), *S. neorossii* (5), *S. pinnatisectum* (2), *S. spegazzinii* (1), *S. sparsipilum* (3), *S. vernei* (2), and *S. verrucosum* (2) (118 accessions in total) were obtained from the United States Potato Genebank (NRSP-6; http://www.ars-grin.gov/nr6/) at Sturgeon Bay, Wisconsin (Appendix). All of these collections are from the US Germplasm System, are preceded by "PI" (Plant Introduction) and have a six-digit number identifying the collection. One accession of PI 473336 had two separate DNA extractions from different individuals grown from separate seeds of the accession. The additional species were chosen to represent the cladistic diversity in sect. *Petota* based on plastid DNA analyses as described above. We chose *S. arnezii* and *S. chacoense* because Hawkes (1990) placed these in series *Commersoniana* (with *S. tarijense*); *S. neorossii* because some accessions of this species shared the 241-bp deletion with *S. berthaultii*, *S. tarijense* and their hybrids (Hosaka, 2003); and the other species in clade 4 as diverse representatives of this clade. Identifications of these accessions have been provided in past years by visiting taxonomists during on-site visits to NRSP-6 to inspect living representatives of the accessions in field plots. Herbarium vouchers are deposited at the U.S. Potato Introduction Station Herbarium (PTIS).

Plant growth conditions and DNA extraction. — Plants were grown in a greenhouse in Madison, Wisconsin, and DNA was extracted from lyophilized leaf tissue from single individuals grown from different seeds of one plant per accession (except PI 473336 with two separate DNA extractions from two seeds of the accession) of two-month-old plants, using the medium-scale DNA extraction procedure from the International Potato Center (1999). For plastid DNA restriction site analysis, DNA was further purified over CsCl ethidium bromide gradients.

AFLP data generation and analyses. — The restriction and ligation reaction of 1X T4 Ligase buffer (with ATP), 0.05 M NaCl, 0.045 mg/mL BSA, 1 µM *Eco*RI or *Pst*I adapter, 5 µM *Mse*I adapter, 5 U *Eco*RI or *Pst*I and *Mse*I, 1 U T4 DNA Ligase, and 500 ng of DNA in a total of 11 µL was incubated overnight at room-temperature. The preselective amplification in a total of 13 µL containing 1X PCR Buffer with 20 mM $MgCl_2$, 0.2 mM dNTPs, 0.3 µM each *Eco*RI+1 or *Pst*I+1 and *Mse*I+1, 0.5 U *Taq* DNA polymerase (Takara *Ex Taq*, Madison, WI, U.S.A.), and 3 µL of a 1 : 10 diluted reaction amplified for 2 min at 72°C, 20 cycles of 94°C for 20 sec, 56°C for 30 sec, and 72°C for 2 min, followed by 72°C for 2 min, and a final extension of 60°C for 30 min. Next followed

the selective amplification (SA) in 8 µL with 2 µL of a 1 : 20 diluted PSA in 1X PCR buffer, 2 mM $MgCl_2$, 0.2 mM dNTPs, 0.625 µM each D4-PA labeled *Eco*RI + 3 or *Pst*I + 3 and unlabeled *Mse*I + 3, and 0.2 U *Taq* DNA polymerase (SIGMA® JumpStart *Taq* polymerase, Saint Louis, MO, U.S.A.); amplified at 94°C for 2 min, 10 cycles of 94°C for 20 sec, 66°C for 30 sec, decreasing 1°C per cycle, and 72°C for 2 min, 25 cycles of 94°C for 30 sec, 56°C for 30 sec, and 72°C for 3 min, and a final extension of 60°C for 30 min. AFLP assays were performed using the following six primer combinations, following advice of collaborators from the Scottish Crop Research Institute: (EAAC + MCCA, EACA + MCAC, PAC + MACT, PAG + MACC, PAT + MAAC, PCA + MAGG. Samples were prepared as follows for the CEQ™ 8000; 1 µL of SA, 35 µL SLS (Beckman Coulter, Inc.), and 0.66 µL of DNA size standard 400 (Beckman Coulter, Inc.). On the CEQ™ 8000, samples were denatured at 90°C for 2 min, injected at 1 kV for 30 sec, and separated at 5 kV for 55 min. To analyze the results, the Analysis Parameter Set was modified as cubic for the model and PA ver. 1 for the Dye Mobility Calibration. The fragment list was then filtered to exclude all dyes but D4 and rfu values less than 3,600. Data were converted to 0 (absent) and 1 (present).

AFLP data were analyzed cladistically and phenetically. Cladistic analyses were performed using PAUP vers. 4.0b8 (Swofford, 2001), using Fitch parsimony (Farris, 1970). *Solanum chomatophilum* was designated as outgroup, following results of Castillo & Spooner (1997) and Spooner & Castillo (1997). To find multiple tree islands, we used a four-step search strategy (modified from Olmstead & Palmer, 1994): (1) one hundred thousand replicates initially were run using random order entry starting trees with nearest-neighbor interchange (NNI); (2) the shortest trees from this analysis were used individually as starting trees with the tree-bisection reconnection (TBR) method; (3) the resulting trees were searched with NNI, retaining all most parsimonious trees (MULPARS); (4) the resulting trees were searched with TBR and MULPARS. A bootstrap analysis was conducted on 1,000 replicates with TBR and MULPARS. Phenetic analyses used NTSYS-pc® vers. 2.02k (Rohlf, 1997). Distance matrices were generated using Jaccard's matrix and clustering was performed using the unweighted pair group method (UPGMA) and Neighbor-Joining.

Plastid DNA restriction site data generation and analysis. — We added 23 additional accessions of *S. berthaultii*, *S. tarijense*, their hybrids, and four other species to the phylogenetic tree of Spooner & Castillo (1997) (Appendix). Procedures follow that study, including screening cpDNA variation with 22 restriction endonucleases: *Ava*I, *Bam*HI, *Ban*I, *Bcl*I, *Bgl*II, *Bst*NI, *Cla*I, *Dra*I, *Eco*O109, *Eco*RI, *Eco*RV, *Hin*cII, *Hin*dIII, *Hpa*I, *Hpa*II, *Hph*I, *Nci*I, *Nsi*I, *Sst*I, *Xba*I, *Xho*I, and *Xmn*I. Membranes were probed with twelve *Pst*I and two *Sal*I clones of *Petunia* (Sytsma & Gottlieb, 1986), and five clones of *Nicotiana* in the small single-copy region (Olmstead & Palmer, 1992) covering the entire plastid genome. *Solanum palustre* was designated as outgroup, following results of Spooner & al. (1993). The data were analyzed cladistically as for AFLPs.

Plastid DNA 241-bp deletion assay. — The PCR marker assay of Hosaka (2002) was used to determine the presence or absence of the 241 bp plastid DNA deletion in the intergenic region flanking the 3′ end of the *trnV-UAC* gene, in 65 accessions of *S. berthaultii*, *S. tarijense*, and their hybrids. Our PCR assay was from DNA of a single individual per accession except for two accessions of *S. tarijense* or *S. tarijense*/*S. berthaultii* hybrids (PIs 473242, 545885) that Hosaka (2003) discovered to have polymorphism within populations, where we screened 16 and 20 individuals respectively per accession.

Herbarium studies. — We gathered herbarium specimens, including types, of these study species from worldwide herbaria. We used the results from this study, and the prior morphological study (Spooner & van den Berg, 1992b) to decide taxonomic limits of *S. berthaultii* and *S. tarijense*.

RESULTS

AFLPs. — The six AFLP primer combinations produced 958 polymorphic bands and there were no missing data; raw data are available from the corresponding author. For AFLP analysis, we examined two subsets of species: (1) all accessions, (2) all species minus the hybrids of *S. berthaultii* and *S. tarijense*.

No bands are species-specific to the accessions of *S. berthaultii* or *S. tarijense* (the hybrids excluded from the analysis). Only five of the 958 polymorphic bands are present in all accessions of *S. berthaultii*, but these are present in 46% to 75% or more of the accessions of *S. tarijense* (average 65%). One polymorphic band was present in all accessions of *S. tarijense*, but this was present in 70% of the accessions of *S. berthaultii*. Hence, there is no support for species-specific or near species-specific bands to distinguish these two species.

The phenetic and cladistic results are similar and only the cladistic results are discussed here. Parsimony analysis of all accessions produced six equally parsimonious trees with a tree length of 6,467, consistency index of 0.1361, rescaled consistency index of 0.3753, and retention index of 0.0501. A strict consensus tree of these six trees (Fig. 1) showed low (< 50%) bootstrap support in the external nodes for all but the outgroups (members of plastid DNA clades 1, 2, and 3 of Castillo & Spooner, 1997, and Spooner & Castillo, 1997), and the topology of these

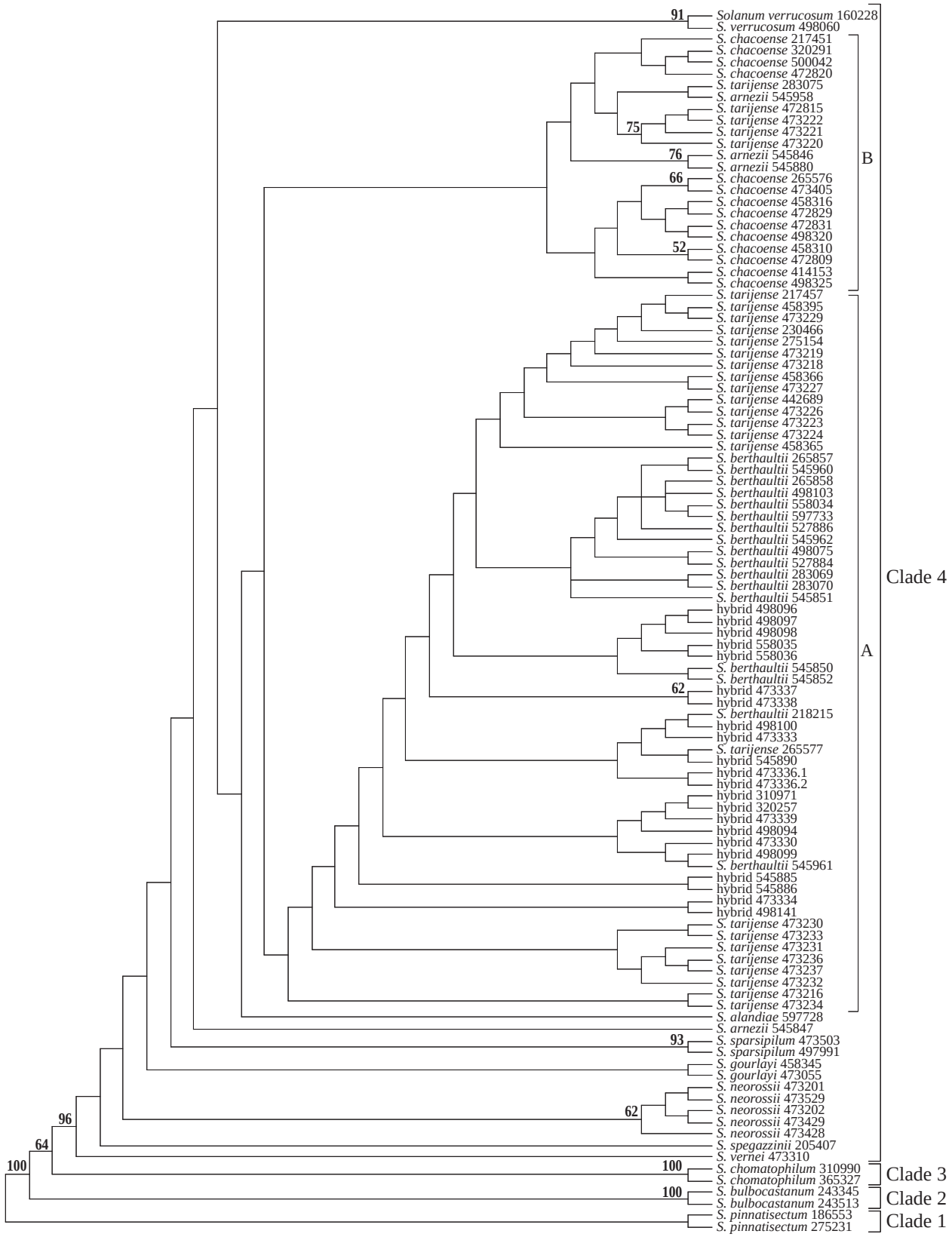

Fig. 1. The strict consensus cladogram of the six most parsimonious 6,472-step Fitch trees using AFLP data of all accessions examined. Clades 1–4 refer to prior plastid DNA restriction site clades (see text) that are also present in the present AFLP data and clades 4A and 4B are discussed in the text. The numbers above branches represent bootstrap values over 50%.

outgroups follows these studies. All other species are members of clade 4 arranged as *S. vernei*, *S. spegazzinii*, *S. neorossii*, *S. gourlayi*, *S. sparsipilum*, *S. arnezii* (one of four accessions), *S. alandiae*, *S. verrucosum*. Then, all accessions of *S. berthaultii*, *S. tarijense*, their hybrids, *S. chacoense* and three accessions of *S. arnezii*, that form clade A + B (Fig. 1).

Clade A is composed entirely of accessions of *S. berthaultii*, *S. tarijense* and their hybrids, and there are no species-specific clades. Clade B is composed of all accessions of *S. chacoense* and *S. arnezii* (the latter synonymized by Ochoa [1990] in *S. chacoense*) and five accessions of *S. tarijense*. Four of these five accessions of *S. tarijense* are the southern-most accessions of *S. tarijense* (southern Salta Province, Argentina, from Fig. 2 of Spooner & van den Berg, 1992b); the remaining accession, PI 283075 has no known locality data and may be from this area. As shown by Spooner & van den Berg (1992b) and Gibson (1979), the populations of *S. tarijense* from southern Salta Province have an unusually high concentration of Type-B trichomes typically characterizing *S. berthaultii*.

Cladistic analysis of all accessions except the *S. berthaultii* and *S. tarijense* hybrids results in 77 equally parsimonious trees with a tree length of 5,281, consistency index of 0.1630, rescaled consistency index of 0.3806, and retention index of 0.0630. A strict consensus tree of these 77 trees (Fig. 2), collapses clades A + B into a single clade, but with a subclade containing 21 of the 28 accessions of *S. tarijense*.

Plastid DNA restriction site data. — Twenty-four restriction site variants were identified with the 27 accessions examined (Table 1). Cladistic analysis of these accessions, added to the dataset of Spooner & Castillo (1997) produced over 5,000 (our upper limit of saving trees) equally parsimonious trees with a tree length of 338, consistency index of 0.65, rescaled consistency index of 0.54, and retention index of 0.83. A strict consensus tree of these 5,000 trees (Fig. 3) placed 22 of the 24 accessions of *S. berthaultii*, *S. tarijense*, and their hybrids in clade 4a of Spooner & Castillo (1997) and two accessions in grade 4b–d. Five accessions of *S. tarijense* (PIs 414152, 442689, 473217, 473231, 473244) are in a well supported clade (98% bootstrap support) supported by three restriction site variants and the 241 bp deletion. All five of these accessions are from northern Salta Province in Argentina and adjacent southern Bolivia in Tarija Department. However, two other accessions (PIs 458364, 473216) are also from this area in northern Salta Province.

Plastid DNA restriction site data, therefore, identifies a clade of five accessions of *S. tarijense* clustered in northern Argentina and adjacent southern Bolivia, but is unable to support *S. berthaultii*, *S. tarijense*, or their hybrids as a species group because it places them in the largely unresolved clade 4a + grades 4b–d composed of South American diploid and polyploid species, Mexican polyploid species, and *S. verrucosum* (diploid, Mexico).

Plastid DNA deletion. — Hosaka (2003) assessed the presence (1) or absence (2) of the 241 bp deletion in 30 accessions of *S. berthaultii* and 82 accessions of *S. tarijense* (112 accessions) by a PCR-based reaction, from a pooled sample of "many" young leaves from separate individuals per accession. We reassessed 61 accessions of the 112 accessions assessed by Hosaka (2003) and our data matched his (Appendix). Hosaka reported polymorphism within two accessions but his pooling protocol was not able to determine if the polymorphism was caused by heteroplasmy or intrapopulational variation. *Solanum berthaultii*/*S. tarijense* PI 545885 had 4 individuals possessing the deletion and 16 individuals lacking it; *S. tarijense* PI 473242 had 6 individuals possessing the deletion and 12 individuals lacking it. We made the following three new plastid DNA deletion determinations: *S berthaultii* 558034 and 597733, and *S. tarijense* 230466 (2).

In summary, our data and that of Hosaka (2003) found the deletion taxonomically distributed as *S. berthaultii*

Table 1. Plastid DNA restriction enzyme site variants found in the accessions of *Solanum* sect. *Petota* examined (Appendix). The variants are listed with the apomorphic state first, followed by the plesiomorphic state (relative to *S. palustre*). Parentheses indicate where small fragments were hypothesized to exist because length mutations were not seen with other enzymes. Character states of these accessions, added to the prior study of Spooner & Castillo (1997) are available from the corresponding author.

Mutation number[a]	Enzyme	Region	Size (kb)
New	All	P3	241 bp deletion
New	*Ava*I	P16/S6	3.3 = 2.1 + 1.2
New	*Eco*RV	P3/P16	10.8 = 7.4 + 3.4
New	*Nci*I	T40	4.4 = 2.6 + 1.8
New	*Cla*I	P3	1.6 + 1.5 = 3.1
4	*Bam*HI	P3	9.9 = 6.0 + 3.9
5	*Bam*HI	P3	12.2 = 9.9 + 2.3
48	*Cla*I	P6/P8	1.2 = 1.1 + 0.1
52	*Cla*I	P3	1.8 = 1.5 + (0.3)
55	*Cla*I	T36/T37	7.1 = 6.6 + 0.5
65	*Dra*I	P8	2.1 = 2.0 + (0.1)
66	*Dra*I	P8/P10	8.0 + 1.4 = 9.4
68	*Dra*I	P6	12.6 = 9.1 + 3.5
73	*Dra*I	P3	1.2 = 1.1 + (0.1)
75	*Dra*I	P3	4.0 = 2.2 + 1.8
78	*Dra*I	P16	3.0 = 1.6 + 1.4
83	*Dra*I	S6	2.5 = 1.5 + 1.0
85	*Dra*I	P12/P18/P19	12.2 = 9.1 + 3.1
86	*Dra*I	T36/T37	1.5 = 1.3 + (0.2)
89	*Dra*I	T38/T39	5.0 = 3.0 + 2.0
111	*Eco*RI	T36/T37	2.5 = 1.7 + 0.8
113	*Eco*RI	T39/T40	2.3 = 1.3 + 1.0
139	*Hinc*II	P3	3.5 = 3.1 + 0.4
200	*Xba*I	T40	1.5 = 1.0 + 0.5

[a]The mutations are numbered relative to Table 3 of Spooner & Sytsma (1992).

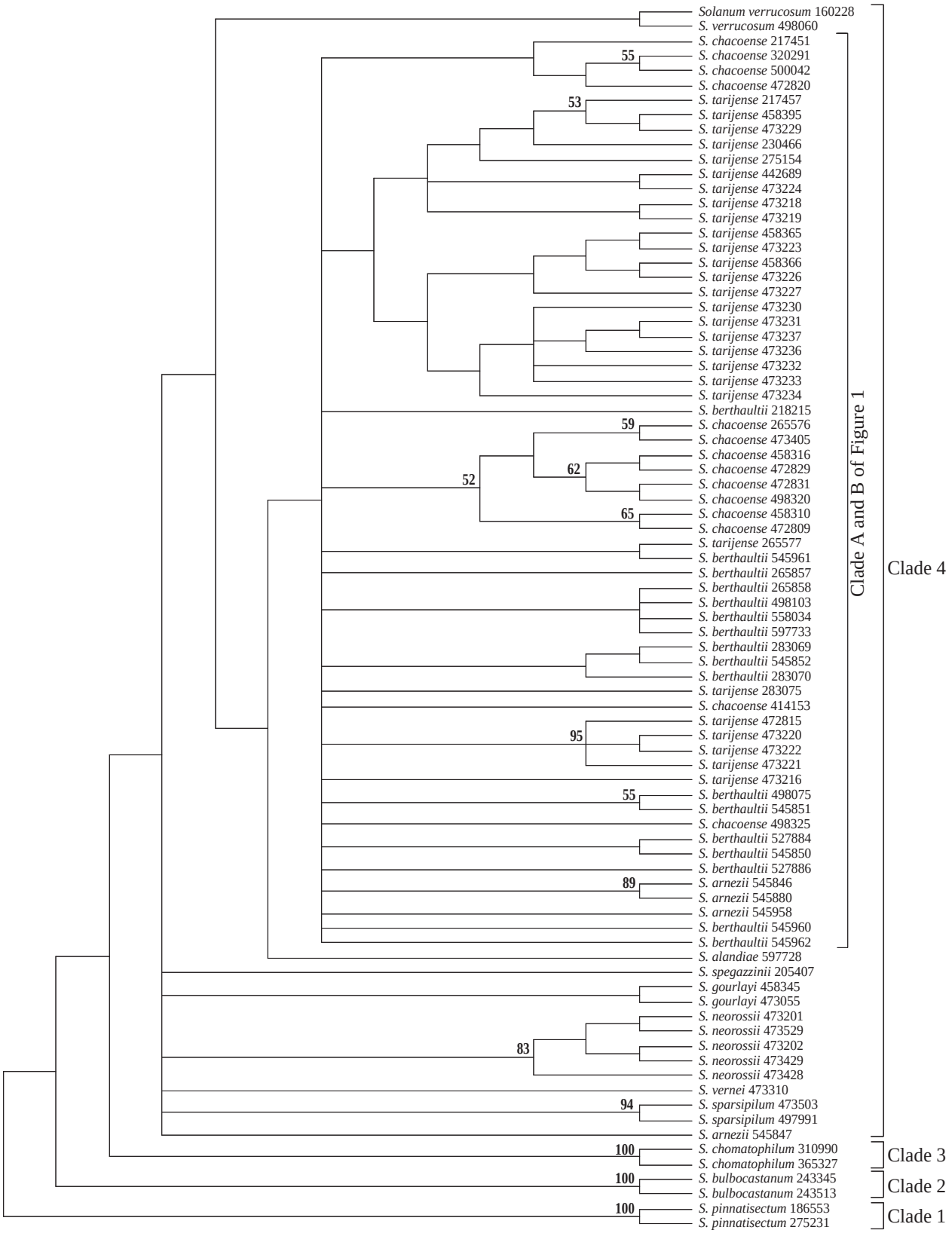

Fig. 2. The strict consensus cladogram of the 77 most parsimonious 5,281-step Fitch trees using AFLP data of all accessions except the *S. berthaultii* × *S. tarijense* hybrids. The numbers above branches represent bootstrap values over 50%.

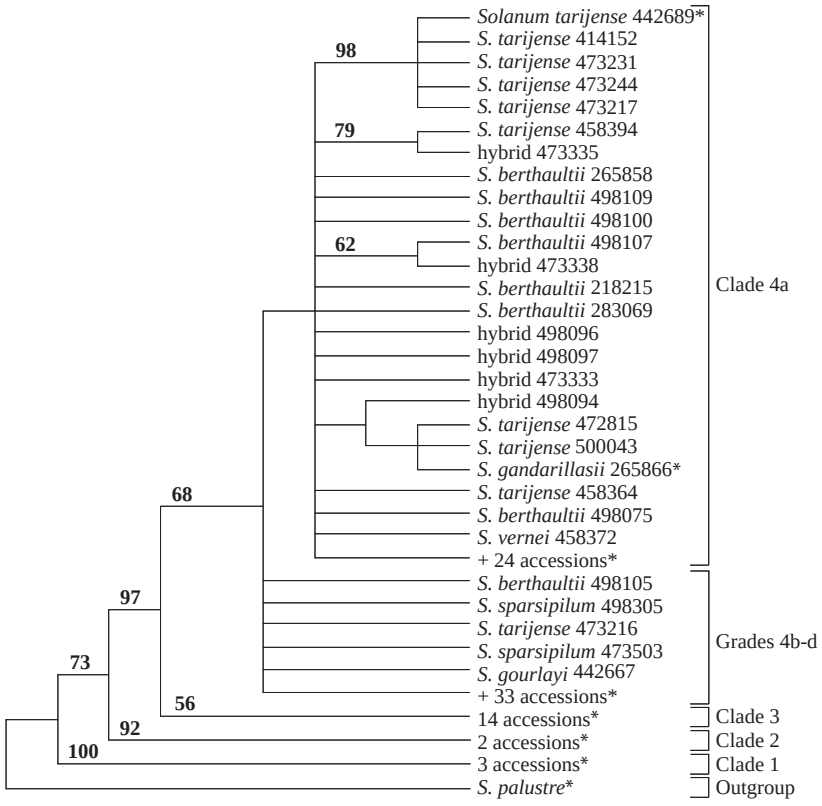

Fig. 3. The strict consensus cladogram based on plastid DNA of the 5,000 most parsimonious 338-step Wagner trees of all accessions examined placed in the larger dataset of Spooner & Castillo (1997), with designations of clades 1–4 following that paper. The accessions designated by asterisks are from prior analyses; all accessions of *S. berthaultii* and *S. tarijense* from this and prior analyses are listed here. The numbers above branches represent bootstrap values over 50%.

(1 population with, 30 without, 1 polymorphic), *S. tarijense* (19 populations with, 43 without, 1 polymorphic), hybrids (4 populations with, 20 without, 1 polymorphic). Geographically, the deletion is widely distributed throughout the range of both species from near the northern part of the range in Bolivia, Cochabamba Department, south to northern Argentina in Salta Province. The only other wild species to possess this deletion, *S. neorossii*, is sympatric with *S. tarijense* in northern Argentina in the Provinces of Jujuy and Salta.

DISCUSSION

Species boundaries and relationships of *S. berthaultii* and *S. tarijense*. — AFLPs (but not plastid DNA restriction site data or the deletion data) place some accessions of *S. berthaultii* and *S. tarijense* into species-specific clades, but with many exceptions. Our data are unable to determine if the weak pattern of differentiation in some accessions is caused by primary divergence or disruption of possible former differentiation by hybridization. Okada & Clausen (1982, 1985) and Clausen & Spooner (1998) documented local hybridization of morphologically distinct species elsewhere in sect. *Petota*, and Hawkes & Hjerting (1969, 1989) speculate that such hybridization is rampant in many of the species. Hawkes & Hjerting (1989) speculate that *S. berthaultii* and *S. tarijense* formerly had separate (north/south) distributions and came together through habitat disturbance caused by humans (Anderson's [1948] "hybridization of the habitat" hypothesis). Whatever the cause of the taxonomic problems in *S. berthaultii* and *S. tarijense*, all datasets show the inability to reliably distinguish *S. berthaultii* and *S. tarijense*, and we conclude that it is better to classify both as a single highly polymorphic taxon. Their maintenance as distinct species is neither natural phylogenetically nor practical taxonomically. AFLP data show five accessions to be in a clade with *S. chacoense* (Fig. 1). While this may signal their relationship to *S. chacoense*, morphological data show them to have the trichome and other traits falling within our expanded concept of *S. berthaultii*. Perhaps these southern-most accessions are combining AFLP markers by gene flow from *S. chacoense*, similar to the pattern shown by Schmidt-Lebuhn & al. (2006), who discovered that samples from different species in the genus *Polylepis* (Rosaceae) sometimes clustered according to geographic proximity rather than systematic affiliation.

The morphological study of Spooner & van den Berg (1992b) also questioned the validity of separate species of *S. berthaultii* and *S. tarijense*. Multivariate analyses failed to support separate species, there is great overlap of three "species-specific" characters (presence/absence Type B trichomes, corolla color, corolla shape) within "non-hy-

brid" species, and a geographic analysis of these characters showed them to be distributed throughout the range of both species. For example, intra-accession variability for presence/absence of Type B trichomes was encountered in 8 of the 64 accessions. Corolla colors varied continuously from pure white to dark-blue, and their measure showed only one geographic area in the extreme south of Salta Province to have all corollas pure white (a *S. tarijense* character, but most of these accessions possessed Type B trichomes, a *S. berthaultii* character). Corolla shapes exhibited no statistically significant differences between any of the taxa and varied from white to blue within many accessions. Despite these morphological problems, all authors (Correll, 1962; Hawkes & Hjerting, 1969, 1989; Hawkes, 1990; Ochoa, 1990; Gorbatenko, 2006) have accepted these species as distinct, and Hawkes even separated them into different superseries.

The taxonomic problems we show here with *S. berthaultii* and *S. tarijense* signal taxonomic problems to be faced in the future when a comprehensive taxonomic treatment of *Solanum* sect. *Petota* is attempted. We are currently conducting morphological and molecular studies in the context of an NSF-funded worldwide taxonomic treatment of *Solanum* (http://www.nhm.ac.uk/research-curation/projects/solanaceaesource//). We will be forced to make similar decisions of morphologically similar species, and we delay the construction of comprehensive keys until we have an opportunity to examine species from throughout the range of the group. Our data suggest, however, that *S. berthaultii* is closely related to *S. arnezii*, *S. chacoense*, and *S. yungasense* from which it differs by the possession of a dense indumentum of short Type-A trichomes, and frequent possession of longer Type-B trichomes.

Species concepts in *Solanum* sect. *Petota*. — Previous taxonomists of sect. *Petota* were splitters (Spooner & van den Berg, 1992a). For example, Spooner & al. (2004) reduced the 33 species, 12 subspecies, and 5 nothospecies of sect. *Petota* from North and Central America recognized by Hawkes (1990) to 25 species and 4 nothospecies. Van den Berg & al. (1998), Miller & Spooner (1999), and Spooner & al. (2005a) showed the inability to distinguish many species in the *Solanum brevicaule* complex. Spooner & Salas (2006) summarize taxonomic uncertainties in sect. *Petota* and suggest that continuing research will show the need for further reductions of names in sect. *Petota*.

TAXONOMIC TREATMENT

Because two competing names, *S. berthaultii* and *S. tarijense*, were published simultaneously and have never been synonymized, one must be chosen here for the species. *Solanum berthaultii* is chosen in honor of Pierre Berthault, a French *Solanum* taxonomist who published a treatise on *S. tuberosum* and its wild relatives in 1911.

Many of the herbarium specimens cited below, especially from C and K, were cultivated in field plots and greenhouses in Birmingham, England, and Copenhagen, Denmark, where the collaborators Jack Hawkes and Peter Hjerting, respectively, worked; from the herbarium of the International Potato Center (CIP) and other herbaria cultivated in fields in Peru (likely in Huancayo in the central Andes) where Carlos Ochoa worked, and from PTIS, cultivated at Sturgeon Bay, Wisconsin, U.S.A., where germplasm from many specimens were cultivated. These cultivated specimens sometimes are labeled as such but many times not so; our descriptions are from non-cultivated specimens to the best of our knowledge.

Types and other herbarium collections in the literature for these specimens as others in sect. *Petota* frequently are cited from herbaria not in *Index Herbariorum*: CIP, CPC (the Commonwealth Potato Collection), JGH (the personal herbarium of Jack Hawkes), and OCH (the personal herbarium of Carlos Ochoa). Hawkes gave most of his specimens to K in 1997, but some duplicates are distributed elsewhere, Ochoa has distributed most specimens from his personal herbarium and those at CIP widely, but most at CUZ and many types at US. CPC still has a herbarium, but most types have been distributed to K. We have not seen all of the types originally from these four herbaria but cite them below where they now reside. We did not see these types when they were at the original locations, but only later when they were deposited in their current institutional herbaria.

Donovan Correll took many photos of wild potato specimens (mainly types) from worldwide herbaria and used these in his treatment of *Solanum* sect. *Petota* and outgroup relatives (Correll, 1962). The photos are all serially numbered and duplicates are deposited in many herbaria; we cite his photos by his negative numbers. As a note for future workers, Spooner searched for these negatives for years in places where Correll worked and by contacting his widow. The only place where he located some of the negatives were at the Donovan Correll archives at the Harry Ransom Research Center at the University of Texas, Austin, Texas.

Solanum berthaultii J.G. Hawkes in Bull. Imp. Bur. Pl. Breed. Genet., Cambridge: 45, 122, Figure 32. 1944 – TYPE: BOLIVIA. Cochabamba: vicinity of Cochabamba, SE of city, Cerro de San Pedro, 8,500 ft, 18 Mar 1939, *E.K. Balls, W.B. Gourlay & J.G. Hawkes 6297* (lectotype, designated by Hawkes & Hjerting, 1989: K; isolectotypes: BM! C! K[8]! LL! UC[2]! US[2]!, photos of BM isolectotype [Correll neg.: 907]: F! LL! MO! NY! PTIS! UC!, photos of the 8 K isolectotypes: PTIS!, photo of US 1779337 isolectotypes

[Correll neg.: 760]: F! LL! UC! NY! PTIS!, photo of US 1779338 isolectotypes: PTIS!, photo of K sheet 1 of 8 [Correll neg.: 56]: F, LL! NY! UC!, photo of UC 683654 [Correll neg.: 757]: F! LL! NY!). Photo of specimen originally at CPC [Correll neg.: 759]: F! LL! NY!, photo of specimen at K [Correll neg.: 758]: F! LL!. Hawkes & Hjerting (1989) designated K as the deposition of the holotype, but we did not find a sheet designated as holotype. Ochoa (1990) designated a superfluous lectotype at US; there are two sheets at US (1779337, 1779338) and both are annotated by Ochoa as "type collection."

Solanum tarijense J.G. Hawkes in Bull. Imp. Bur. Pl. Breed. Genet., Cambridge: 20, 114, Figure 3. 1944, **syn. nov.** – TYPE: BOLIVIA. Tarija: above the left bank of a river a little above Tarija, 6,650 ft, 26 Feb 1939, *E.K. Balls, W.B. Gourlay, & J.G. Hawkes 6093* (lectotype, chosen by Hawkes & Hjerting [1969]: K [labeled sheet 2 of 4; the specimen was originally cited at CPC but transferred to K]!; isolectotypes: CPC[3], K sheets 1! 3! 4! of 4, UC! US!, photos of CPC isolectotypes [Correll neg.: 933]: UC! F! LL! NY! PTIS!, photos of another CPC isolectotypes [Correll neg.: 92]: F! LL! NY! UC!, photos of another CPC isolectotypes [Correll neg.: 934]: BM! LL! MO! NY! PTIS! UC!, photo of US isolectotype: PTIS!). Hawkes & Hjerting (1989) chose another superfluous lectotype from the personal herbarium of Hawkes.

Solanum trigalense M. Cárdenas in Bol. Soc. Peruana Bot. 5: 41, Pl. III (G). 1956 – TYPE: BOLIVIA. Santa Cruz: Prov. Vallegrande, near El Trigal on the way to Mataral, 2,100 m, Mar 1955, *M. Cárdenas 5069* (holotype: cited in personal herbarium M. Cárdenas, perhaps now at LIL where he gave his herbarium; isotype: MO!, photo of herbarium Cárdenas LL!).

Solanum vallegrandense M. Cárdenas in Bol. Soc. Peruana Bot. 5: 23, Pl. II (B). 1956 – TYPE: BOLIVIA. Santa Cruz: Prov. Vallegrande, along Vallegrande airport runway [this locality is a correction provided in Hawkes & Hjerting (1989: 144, 258), by pers. comm. from M. Cárdenas, of erroneous locality data originally reported on specimens and in the protologue, reported as "on way from Trigal to Mataral, 2000 m"], Mar 1955, *M. Cárdenas 5070* (holotype: COCH! [seen in 1993 when the herbarium still existed, perhaps now at LIL]; isotypes: BOLV!, K[3]! LL!, photos of LL isotype [Correll neg.: 831]: BM! LL! NY! PTIS! UC!, photos of K isotypes: PTIS!).

Solanum vallegrandense var. *pojoense* M. Cárdenas in Bol. Soc. Peruana Bot. 5: 24, Pl. II (C). 1956; *Solanum tarijense* var. *pojoense* (M. Cárdenas) D. Correll, Wrightia 2: 173. 1961 – TYPE: BOLIVIA. Cochabamba: Prov. Carrasco, above Pojo 2,300 m, *Cárdenas 5071* (holotype: BOLV [2]!; isotypes: K[2]!; LL!, photos of K isotypes: PTIS!, photos of LL isotype [Correll neg.: 830]: BM! LL! PTIS! UC!).

Solanum zudaniense M. Cárdenas in Bol. Soc. Peruana Bot. 5: 31, Pl. III (A). 1956; *Solanum berthaultii* f. *zudaniense* (M. Cárdenas) D.S. Correll, Wrightia 2: 184. 1961 – TYPE: BOLIVIA. Chuquisaca: between Zudáñez and Tolima, 2,000 m, Feb 1949, *M. Cárdenas 5077* (holotype: personal herbarium of M. Cárdenas, photo: LL!; isotype: K!, photos: PTIS! WAG! WIS!).

Solanum litusinum C. Ochoa in Phytologia 48: 229. 1981 – TYPE: BOLIVIA. Santa Cruz: Prov. Vallegrande, at edge of Prov. Florida, La Playa, along route from Seca to Ariruma, Mar 1978, *C. Ochoa 12027* (holotype: OCH [personal herbarium of C. Ochoa]; isotypes: CIP[2]!, photo of CIP isotype: PTIS!

Description. — Plants 0.3–1 m tall, herbaceous, terrestrial, erect. *Stems* 3–5 mm in diameter at base of plant, densely invested with short non-glandular trichomes and short glandular trichomes, 120–210 µm in length, with tetralobulate heads 50–70 µm in diameter, and often with longer glandular trichomes, 600–950 µm in length, with an ovoid gland at the tip, 20–60 µm in diameter. *Pseudostipules* 5–17 mm long, lunate. *Leaves* 10–28 cm long, 6–20 cm wide, odd-pinnate, pubescent as the stems, fresh leaves sticky to the touch and with a spicy odor; *petioles* 0.5–4.5 cm long; *lateral leaflet pairs* 3–6, often subequal except for the most proximal 1 or 2 pairs that are greatly reduced in size; leaves and leaflets varying greatly in shape and size, *most distal lateral leaflets* 2–7.5 cm long, 1–4.5 cm wide, narrowly to broadly ovate, the apex acuminate, the base typically oblique, cordate to rounded, subsessile or with petiolules up to 10 mm long; *terminal leaflet* 3–12 cm long, 1.5–4.0 cm wide, ovate to elliptical, the apex acute to acuminate, the base attenuate; *interjected leaflets* 0–25, sessile to short petiolate, ovate to orbicular. *Inflorescences* generally in distal half of plant; *peduncle* 3–9.5 cm long. *Flowers* 5–15; *pedicels* 12–22 mm long, articulate at or above the middle; *calyx* 5–15 mm long, the lobes long-attenuate, the acumens 1–3 mm long; *corolla* 1.1–2.5 cm in diameter, substellate to pentagonal, the acumens 1–3 mm, edges of corolla flat, not folded dorsally, pure white to rarely creamy white or faintly yellowish to medium blue to dark blue to lilac above and below; *anthers* 5–9 mm long, two of them very slightly shorter than the other three, connate; *style* 11–14 mm long, exceeding stamens by 2–5 mm, straight, stigma clavate to capitate. *Fruits* 1.5–2.5 cm long, globose to slightly ovoid, medium to deep green, often with scattered white dots. *Seeds* from living specimens green-white throughout.

Chromosome number and EBN. — $2x = 2n = 24$ (2EBN) (Spooner & Salas, 2006; Hijmans & al., in press). Voucher: Spooner & al., 6503 from Cochabamba, Bolivia (PTIS).

Phenology. — Flowering and fruiting from January to March.

Distribution. — Central-eastern Bolivia (Cochabamba Department), south to northern Argentina (Provinces of Catamarca, Jujuy and Salta) (Fig. 4), in generally dry rocky areas in the open or among spiny shrubs or cacti, or a weed at the edges of cultivated fields or roadsides, or along streamsides; (1,200) 1,600–2,100 (3,950) m.

Fig. 4. Map of *S. berthaultii* (including its synonyms as detailed in taxonomic treatment).

REPRESENTATIVE SPECIMENS EXAMINED

[Note: This list of specimens is greatly abbreviated from those deposited in the Solanaceae Source website http://www.nhm.ac.uk/research-curation/projects/solanaceaeresource/. We converted latitude and longitude from the herbarium sheets to a decimal notation and determined these when they were missing by inspection with maps or gazetteers; asterisks represent new latitude and longitude determinations. We added PI numbers in brackets to the accessions held at PTIS.]

ARGENTINA. Catamarca: Dept. Andalgalá, experimental station of the Inst. de Fitotecnia, Alto de las Juntas, 1,650 m, 5 Feb 1952, *H. Sleumer 2278* (K, LL); Jujuy: San Pedro, ridgetop woods at highest place on road from Santa Clara to Palma Sola, 24°18′11″ S, 64°30′07″ W, 1365 m, 16 Apr 2000, *M. Nee & al. 50800* (NY); Salta: Nazanero river, 22°36′ S, 65°07′12″ W, 2,550 m, 1 Jan 1970, *W. Hoffman 1717* (PTIS [PI 473217]); 2 km above de Escoipe, Route 59, 25°10′48″ S, 65°48′ W, 2,100 m, 30 Nov 1969, *K.A. Okada 5634* (PTIS [PI 473222]); Dept. Santa Victoria, Rodeo Pampa between Santa Victoria and Abra de Lizoite, 22°15′ S, 65°04′12″ W, 2,850 m, 6 Apr 1971, *W. Hoffman 1870* (PTIS [PI 473219]). BOLIVIA. Chuquisaca: between Zudáñez and Tomina, 2,200 m, Feb 1949, *M. Cárdenas 4503* (K); ca. 45 km S of Sucre on road to Potosí, 1 : 250,000-scale map SE 20–13, 19°18′36″ S, 65°10′12″ W, 2614 m, 18 Mar 1989, *D. Spooner & al. 6527* (PTIS [PI 597770]); Cochabamba: road to Sacaba, 8,200 ft, 11 Jan 1949, *W.M.A. Brooke 3005* (BM, F, NY); Prov. Arce, road from Aznaldo to Mollepujro at 15 km from Anzaldo, 17°55′01″ S, 65°55′01″ W, 2,730 m, 6 Mar 1980, *J.G. Hawkes & al. 6540* (C, K, PTIS [PI 498099]); Potosí: about 32 km from Sucre on road to Potosí, 17 Feb 1960, *D.S. Correll & al. B623* (LL); Prov. Saavedra, Retiro, 78 km from Sucre to Potosí, 19°31′59″ S, 65°16′01″ W, 2,950 m, 28 Mar 1974, *D. Astley 44B* (K, PTIS [PI 498075]); Santa Cruz: 2 km NNW of Quebrada Seca, 1,900 m, 1 Apr 1984 *Ochoa & Salas 15596*, (LPB); Prov. Florida, near Mataral, 18°6′50″ S*, 64°12′54″ W*, 1,200 m, Apr 1961, *M. Cárdenas 5069* (WIS); Tarija: 41 km from Tarija on road to Entre Ríos, 21°31′01″ S*, 64°33′ W*, 2,325 m, 13 Mar 1971, *J.P. Hjerting & al. 4673* (K, PTIS [PI 458395]); 34.1 km E of police gate at E end of Tarija, on road to Entre Ríos, 1 : 250,000-scale map SF 20–6, 21°26′24″ S*, 64°27′36″ W*, 2,369 m, 8 Oct 1988, *D. Spooner & al. 6590* (PTIS [PI 597771]).

Hawkes (1990) designated *S.* ×*trigalense* as "undoubtedly a natural hybrid between *S. chacoense* and *S. tarijense*" and Ochoa (1990) synonymizes it with *S. tarijense*. It has faintly yellowish-white corollas as some forms of *S. chacoense*, but the yellowish leaves and dense indument of Type A trichomes (no Type-B trichomes) of *S. berthaultii*. Some populations of *S. berthaultii* also have faintly yellowish corollas and appear otherwise similar to the type of *S. trigalense* (e.g., *Solomon & King 15909*).

Solanum berthaultii is very similar to *S. arnezii*, *S. chacoense*, and *S. yungasense* Hawkes. *Solanum chacoense* is highly variable and is one of the most widely distributed potato species, occurring from sea level to about 3300 m, growing from central Bolivia to central Argentina (Hawkes, 1962b; Miller & Spooner, 1996). *Solanum arnezii* grows in central Bolivia from 2,000 to 2,300 m (Hawkes & Hjerting, 1989). *Solanum yungasense* is distributed in the humid east-facing slopes of the Andes in southern Peru and adjacent Bolivia from 1,100 to 1,750 m (Hawkes & Hjerting, 1989; Ochoa, 1990). These three species are all very similar to each-other, and, like some populations of *S. berthaultii*, have white to cream colored stellate to pentagonal corollas; all three species may be conspecific. They differ from *S. berthaultii* principally by the lack of glandular pubescence.

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Appendix. Accessions examined for AFLPs, plastid DNA restriction sites, and a 241-bp plastid DNA deletion.

Species, PI accession examined, Country, Department (Bolivia, Peru) or Province (Argentina) or State (Mexico), Collector, examined for AFLP, examined for plastid restriction sites (rest.), 241-bp plastid deletion present (1), 241-bp plastid deletion absent (2).

***Solanum berthaultii* Hawkes**, 218215, Bolivia, Potosí, EBS 191, AFLP, rest., (2). 265857, Bolivia, Cochabamba, EBS 1799, AFLP, (2). 265858, Bolivia, Cochabamba, EBS 1846, AFLP, rest., (2). 283069, Bolivia, Chuquisaca, EBS 1842, AFLP, rest., (2). 283070, Bolivia, Chuquisaca, EBS 1843, AFLP, (2). 498075, Bolivia, Potosí, *Astley 044*, AFLP, rest., (2). 498103, Bolivia, Cochabamba, *Hawkes & al. 6548*, AFLP, (2). 498105, Bolivia, Cochabamba, *Hawkes & al. 6552*, AFLP, rest., (1). 498107, Bolivia, Cochabamba, *Hawkes & al. 6556B*, AFLP, rest., (2). 498109, Bolivia, Cochabamba, *Hawkes & al. 6668*, AFLP, rest., (2). 527884, Bolivia, Chuquisaca, *Hoopes & al. 038*, AFLP, (2). 527886, Bolivia, Potosí, *Hoopes & al. 042*, AFLP, (2). 545850, Bolivia, Chuquisaca, *Hoopes & al. 52*, AFLP, (2). 545851, Bolivia, Chuquisaca, *Hoopes & al. 76*, AFLP, (2). 545852, Bolivia, Chuquisaca, *Hoopes & al. 81*, AFLP, (2). 545960, Bolivia, Cochabamba, *Hoopes & al. 190*, AFLP, (2). 545961, Bolivia, Cochabamba, *Hoopes & al. 195*, AFLP, (2). 545962, Bolivia, Chuquisaca, *Hoopes & al. 300*, AFLP, (2). 558034, Bolivia, *LaPointe 31284-1*, AFLP, (2). 597733, Bolivia, Cochabamba, *Spooner & al. 6503*, AFLP, (2). ***S. tarijense* Hawkes**, 217457, Argentina, Salta, *Sleumer 4002*, AFLP, (2). 230466, Bolivia, CPC 2667, AFLP, (2). 265577, Bolivia, Cochabamba, *Correll B619*, AFLP, (2). 275154, Argentina, Salta, *Hjerting 151*, AFLP, (2). 283075, EBS 1833, AFLP, (2). 414152, Bolivia, Tarija, *Hawkes & al. 4667*, AFLP, rest., (1). 442689, Argentina, Salta, *Hoffman 1892*, AFLP, (1). 458364, Argentina, Salta, *Hoffman 1876*, AFLP, rest., (2). 458365, Argentina, Salta, *Hoffman 1902*, AFLP, (2). 458366, Argentina, Salta, *Hoffman 1886*, AFLP, (2). 458394, Bolivia, Chuquisaca, *Hawkes & al. 4569*, AFLP, rest., (2). 458395, Bolivia, Tarija, *Hawkes & al. 4673*, AFLP, (2). 472815, Argentina, Salta, *Okada 4818*, AFLP, rest., (2). 473216, Argentina, Salta, *Hoffman 1713*, AFLP, rest. 473217, Argentina, Salta, *Hoffman 1717*, AFLP, rest., (1). 473218, Argentina, Salta, *Hoffman 1876A*, AFLP, (1). 473219, Argentina, Salta, *Hoffman 1870*, AFLP, (2). 473220, Argentina, Salta, *Okada 5632*, AFLP, (2). 473221, Argentina, Salta, *Okada 5633*, AFLP, (2). 473222, Argentina, Salta, *Okada 5634*, AFLP, (2). 473223, Argentina, Salta, *Okada 5873*, AFLP, (2). 473224, Argentina, Salta, *Okada 5784*, AFLP, (2). 473226, Argentina, Salta, *Okada 5877*, AFLP, (2). 473227, Argentina, Salta, *Okada 5878*, AFLP, (1). 473229, Argentina, Salta, *Okada 5880*, AFLP, (1). 473230, Argentina, Salta, *Okada 5881*, AFLP, (1). 473231, Argentina, Salta, *Okada 5882*, AFLP, rest., (1). 473232, Argentina, Salta, *Okada 5883*, AFLP. 473233, Argentina, Salta *Okada 5884*, AFLP, (1). 473234, Argentina, Salta, *Okada 5886*, AFLP, (2). 473236, Argentina, Salta, *Okada 5888*, AFLP. 473237, Argentina, Salta, *Okada 5889*, AFLP, (2). 473242, Argentina, Salta, *Okada 6234* (1/2); 473244, Argentina, Salta, *Okada 6239*, AFLP, rest., (1). 500043, Argentina, Salta, *Okada 7491*, AFLP, rest., (2). ***S. berthaultii* × *S. tarijense* hybrids**, 310971, Bolivia, Cochabamba, *Ochoa s.n.*, AFLP. 320257, Bolivia, *Alandia 64-5*, AFLP, (2). 473330, Bolivia, Cochabamba, *Hawkes & al. 4422*, AFLP. 473333, Bolivia, Chuquisaca, *Hawkes & al. 4543*, AFLP, rest., (2). 473334, Bolivia, Chuquisaca, *Hawkes & al. 4562*, AFLP. 473335, Bolivia, Chuquisaca, *Hawkes & al. 4570*, AFLP, rest., (2). 473336.1 and .2, Bolivia, Potosí, *Hawkes & al. 4574*, AFLP, (2). 473337, Bolivia, Potosí, *Hawkes & al. 4727*, AFLP. 473338, Bolivia, Potosí, *Hawkes & al. 4728*, AFLP, rest., (2). 473339, Bolivia, Chuquisaca, *Hawkes & al. 4729*, AFLP, (2). 498094, Bolivia, Cochabamba, *Hawkes & al. 6438*, AFLP, rest. 498096, Bolivia, Cochabamba, *Hawkes & al. 6451*, AFLP, rest., (2). 498097, Bolivia, Cochabamba, *Hawkes & al. 6453*, AFLP, rest., (2). 498098, Bolivia, Cochabamba, *Hawkes & al. 6454*, AFLP, 498099, Bolivia, Cochabamba, *Hawkes & al. 6540*, AFLP, 498100, Bolivia, Cochabamba, *Hawkes & al. 6541*, AFLP, rest., (2). 498141, Bolivia, Chuquisaca, *Hawkes & al. 6656*, AFLP. 545885, Bolivia, Cochabamba, *Hoopes & al. 30*, AFLP, (1/2) 545886, Bolivia, Chuquisaca, *Hoopes & al. 78*, AFLP, (2). 545890, Bolivia, Potosí, *Hoopes & al. 133*, AFLP, (2). 558035, Bolivia, *LaPointe 31284-2*, AFLP, (2). 558036, Bolivia, *LaPointe 31284-3*, AFLP. ***S. alandiae* Cárdenas**, 597728, Bolivia, Cochabamba, *Spooner & al. 6644*, AFLP. ***S. arnezii* Cárdenas**, 545958, Bolivia, Chuquisaca, *Hoopes & al. 297*, AFLP. 545846, Bolivia, Chuquisaca, *Hoopes & al. 154*, AFLP. 545880, Bolivia, Chuquisaca, *Hoopes & al. 157*, AFLP, 545847. Bolivia, Chuquisaca, *Hoopes & al. 159*, AFLP. ***S. bulbocastanum* Dunal**, 243345, Mexico, Federal District, *Graham 26X27*, AFLP. 243513, Mexico, Morelos, ROC S-398 × S-379, AFLP. ***S. chacoense* Bitter**, 217451, Argentina, Jujuy, *Sleumer 3566*, AFLP. 320291, Argentina, Salta, *Hawkes & al. 3633*, AFLP. 500042, Argentina, Salta, *Okada 7490*, AFLP. 472820, Argentina, Salta, *Okada 5608*, AFLP. 265576, Argentina, Catamarca, *Correll 707a*, AFLP. 473405, Argentina, Catamarca, *Hjerting 6378*, AFLP. 458316, Argentina, La Rioja, *Okada 6045*, AFLP. 472829, Argentina, La Rioja, *Okada 6116*, AFLP. 472831, Argentina, La Rioja, *Okada 6118*, AFLP. 498320, Argentina, La Rioja, *Okada* 2838 × 2839, AFLP. 458310, Argentina, Córdoba, *Okada 4812*, AFLP. 472809, Argentina, San Luis, *Hawkes & al. 3187*, AFLP. 414153, Paraguay, Presidente Hayes, *Bordas s.n.*, AFLP. 498325, Argentina, Corrientes, *Okada 7309*, AFLP. ***S. chomatophilum* Bitter**, 310990, Peru, Cajamarca, *Hawkes 2433*, AFLP. 365327, Peru, Amazonas, *Ochoa S-71*, AFLP. ***S. gourlayi* Hawkes**, 442667, Argentina, Salta, *Baldwin 708*, AFLP, rest. 458345. Argentina, Salta, *Baldwin 7327*, AFLP. 473055, Argentina, Jujuy, *Baldwin 72343*, AFLP. ***S. neorossii* Hawkes & Hjert.**, 473201, Argentina, Salta, *Baldwin 71279*, AFLP. 473529, Argentina, EBS 3011, AFLP. 473202, Argentina, Salta, *Baldwin 71280*, AFLP. 473429, Argentina, Salta, *Hawkes & al. 3878*, AFLP. 473428, Argentina, Salta, *Hawkes & al. 3873*, AFLP. ***S. pinnatisectum* Dunal**, 186553, Mexico, Guanajuato, *Hawkes 1092*, AFLP. 275231, Mexico, Queretaro, *Hawkes 1426*, AFLP. ***S. spegazzinii* Bitter**, 205407, Argentina, *Brücher 19*, AFLP. ***S. sparsipilum* (Bitter) Juz. & Bukasov**, 473503, Bolivia, Cochabamba, *Astley 012*, AFLP, rest. 497991, Bolivia, Potosí, EBS 2290, AFLP. 498305, Peru, Cuzco, *Hawkes & al. 5418*, AFLP, rest. ***S. vernei* Bitter & Wittm.**, 458372, Argentina, Salta, *Okada 4477*, AFLP, rest., 473310. Argentina, Salta, *Baldwin 74498*, AFLP. ***S. verrucosum* Schltdl.**, 160228, Mexico, Federal District, *Correll 14217B*, AFLP. 498060, Mexico, Nuevo León, *Tarn &. al. 094*, AFLP.

Abbreviations: CPC, Commonwealth Potato Collection, Scotland; EBS, Erwin Baur Sortiment Genebank, Germany; ROC, Rockefeller Foundation