

Bolivia potato germplasm collecting expeditions 1993, 1994: Taxonomy and new germplasm resources

David M. Spooner¹, Ronald G. van den Berg², Willman García³ & María Luisa Ugarte³

¹ Vegetable Crops Research Unit, USDA, Agricultural Research Service, Department of Horticulture, University of Wisconsin, 1575 Linden Drive, Madison, WI 53706-1590, USA; ² Department of Plant Taxonomy, Agricultural University Wageningen, P.O. Box 8010, 6700 ED Wageningen, The Netherlands; ³ Instituto Boliviano de Tecnología Agropecuaria, Proyecto de Investigación de la Papa (PROINPA), Calle Man Cesped 923, Casilla 4285, Cochabamba, Bolivia

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Summary

We conducted joint Bolivia/The Netherlands/United States wild potato (*Solanum* sect. *Petota* Dumort.) germplasm collecting expeditions in Bolivia from February 1–April 15, 1993, and January 1–February 26, 1994. The goals of the expeditions were to collect germplasm and gather data for continuing taxonomic studies of the approximately 43 taxa of Bolivian wild potatoes accepted by current taxonomists. We made 223 collections, 135 as true seed collections, 54 as tubers, 19 only as herbarium collections. Two recent taxonomic treatments of Bolivian wild and cultivated potatoes have clarified the taxonomy and distribution of these plants, but there are continuing disagreements between treatments regarding species boundaries and interrelationships. These disagreements, and the variability we observed in natural populations, present problems for identifications. We summarize the state of germplasm collections for Bolivia, provide our field data regarding the taxonomy of Bolivian wild potatoes, provide recommendations for future collecting, and provide new chromosome counts for *S. hoopesii*, *S. ugentii*, and *S. yungasense*.

Introduction

This paper summarizes results of our germplasm collections and taxonomic field data of a three-month (February 1–April 15, 1993) and a two-month (January 1–February 26, 1994) potato (*Solanum* sect. *Petota*) germplasm collecting expedition to Bolivia. *Solanum* sect. *Petota* is widely distributed from the southwestern United States to south-central Chile, and consists of seven cultivated and 225 wild species, according to the latest taxonomic interpretation (Hawkes, 1990). Bolivia is the second most species-rich country (after Peru) for wild and cultivated potatoes, and harbors all seven of these cultivated species and approximately 43 wild taxa (species, subspecies, varieties; Table 1).

Correll (1962), Hawkes & Hjerting (1989), and Ochoa (1990) provide thorough summaries of collections made in Bolivia for taxonomic studies and

germplasm collections. Prior to our expedition there were good germplasm collections for some species from most their Bolivian range, such as *S. acaule*, *S. berthaultii*, *S. megistacrolobum*, *S. sparsipilum*, *S. sucrense*. Others, however, had no or few collections, such as *S. achacachense*, *S. astlewi*, *S. bombycinum*, *S. chacoense*, *S. flavoviridens*, *S. gourlayi* subsp. *vidaurrei*, *S. litusinum*, *S. neocardenasii*, *S. neovavilovii*, *S. soestii*, *S. virgultorum*, *S. yungasense* (Table 1). The Instituto Boliviano de Tecnología Agropecuaria, Proyecto de Investigación de la Papa (PROINPA), the Dutch/German genebank (BGRC), and the Technical Advisory Committee of the United States National Research Program-6 (NRSP-6; formerly known as the Inter-Regional Potato Introduction Project, IR-1) targeted Bolivia as a high priority area for field work. The goals of the expedition were to collect wild species germplasm (the cultivated species are well-represented

Table 1. Wild potato taxa accepted for Bolivia by Hawkes & Hjerting (1989) and Ochoa (1990), with number of NRSP-6 Bolivian accessions available before the 1993 and 1994 expeditions to Bolivia (those in parentheses with sufficient data to map at least to level of province). The planning maps are deposited at NRSP-6

Species	Total Bolivian NRSP-6 accessions before expeditions (No. mapped)
1. <i>S. acaule</i> Bitter	77 (70)
2. <i>S. achacachense</i> Cárdenas	1 (1)
3. <i>S. alandiae</i> Cárdenas	12 (12)
4. <i>S. arnezii</i> Cárdenas	4 (4)
5. <i>S. astleyi</i> Hawkes & Hjert.	2 (2)
6. <i>S. avilesii</i> Hawkes & Hjert.	3 (3)
7. <i>S. berthaultii</i> Hawkes	12 (12)
8. <i>S. boliviense</i> Dunal	12 (12)
9. <i>S. bombycinum</i> Ochoa	0
10. <i>S. brevicaule</i> Bitter	11 (11)
11. <i>S. canasense</i> Hawkes	1
12. <i>S. candolleanum</i> Berthault	5 (5)
13. <i>S. capsicibaccatum</i> Cárdenas	4 (3)
14. <i>S. chacoense</i> Bitter	0
15. <i>S. circaefolium</i> Bitter subsp. <i>circaefolium</i>	3 (3)
16. <i>S. circaefolium</i> subsp. <i>quimense</i> Hawkes & Hjert.	4 (4)
17. <i>S. doddsii</i> Correll	12 (11)
18. <i>S. flavoviridens</i> Ochoa	0 (0)
19. <i>S. gardarillasii</i> Cárdenas	5 (4)
20. <i>S. gourlayi</i> subsp. <i>gourlayi</i>	7 (5)
21. <i>S. gourlayi</i> subsp. <i>vidaurrei</i> (Cárdenas) Hawkes & Hjert.	0
22. <i>S. hondelmannii</i> Hawkes & Hjert.	16 (15)
23. <i>S. hoopesii</i> Hawkes & K.A. Okada	3 (3)
24. <i>S. infundibuliforme</i> Philippi	7 (6)
25. <i>S. leptophyes</i> Bitter	19 (19)
26. <i>S. litusinum</i> Ochoa	0
27. <i>S. megistacrolobum</i> Bitter	28 (21)
28. <i>S. microdontum</i> Bitter	15 (13)
29. <i>S. neocardenasii</i> Hawkes & Hjert.	2 (2)
30. <i>S. neorosii</i> Hawkes & Hjert.	0
31. <i>S. neovavilovii</i> Ochoa	0
32. <i>S. okadae</i> Hawkes & Hjert.	4 (4)
33. <i>S. oplocense</i> Hawkes	22 (19)
34. <i>S. soestii</i> Hawkes & Hjert.	0
35. <i>S. sparsipilum</i> (Bitter) Juz. & Buk.	46 (39)
36. <i>S. sucrensis</i> Hawkes	30 (24)
37. <i>S. tarijense</i> Hawkes	14 (13)
38. <i>S. toralapanum</i> Cárdenas and Hawkes	25 (25)
39. <i>S. ugentii</i> Hawkes & K.A. Okada	3 (3)
40. <i>S. vernei</i> Bitter & Wittm. subsp. <i>vernei</i>	0
41. <i>S. virgultorum</i> (Bitter) Cárdenas & Hawkes	0
42. <i>S. yungasense</i> Hawkes	0
43. <i>S. violaceimarmoratum</i> Bitter	7 (7)

at PROINPA and the International Potato Center (CIP) of under-represented species, to increase them quickly to make them freely available internationally, and to study their species boundaries and interrelationships.

Materials and methods

Prior to the expedition, we mapped available NRSP-6 Bolivian germplasm accessions (Bamberg & Martin, 1993) onto 1:3,000,000-scale base maps, and compared these to species distributions as mapped in Hawkes & Hjerting (1989) and Ochoa (1990). We also obtained distributions from the herbarium specimens at the Herbario Nacional Forestal Dr. Martín Cárdenas in Cochabamba (BOLV), the Herbario Nacional de Bolivia, La Paz (LPB), the NRSP-6 herbarium (PTIS; Bamberg and Spooner, 1994), and the University of Wisconsin-Madison Department of Botany (WIS). Herbarium codes follow Holmgren et al. (1990, the new PTIS acronym will be published in the forthcoming edition 9).

We found localities with the following geographic references: 1) Paynter (1992); 2) Gonzales Moscoso (1984); 3) United States Department of Interior (1955); 4) the 1:250,000-scale topographic maps from the Bolivia Instituto Geográfico Militar (the maps of Andean Bolivia currently available commercially from the Instituto Geográfico Militar are SD 19-14, SE 19-2, SE 19-3, SE 19-6, SE 19-7, SE 19-8, SE 19-10, SE 19-11, SE 19-12, SE 19-15, SE 19-16, SE 20-5, SE 20-9, SE 20-13, SE 20-14, SF 19-3, SF 19-4, SF 19-7, SF 19-8, SF 19-11, SF 19-12, SF 20-1, SF 20-2, SF 20-5, SF 20-6, SF 20-9, SF 20-10; see Parry & Perkins (1987) for coverage); 5) 1:500,000-scale aerial photos covering part of La Paz Province (from the Instituto Geográfico Militar); 6) a nine-sheet set of 1:100,000-scale 'Mapa Hidrográfico de Bolivia' (Instituto Geográfico Militar); and 7) a 1:3,000,000-scale 'Mapa Político de Bolivia' (Instituto Geográfico Militar). We purchased and bound these maps in a book, and they are available for study, along with our base maps with germplasm localities, at NRSP-6.

We collected on many passable roads by jeep, or in other areas on foot, with the aid of pack animals. We were aided by local residents who led us to sites of wild potatoes. Bolivian type localities were visited to the precision of the locality data. We obtained precise latitude and longitude data (to a precision of 300 m)

by a Global Positioning System, and altitudes with an altimeter.

Herbarium vouchers were dried in the field, and a complete set of duplicates was deposited at BOLV, with duplicates distributed to the International Potato Center, Lima, Peru (not in Holmgren et al., but cited in Ochoa's publications as CIP), the Department of Plant Taxonomy, Wageningen Agricultural University (WAG), and PTIS. We extracted seed and cleaned tubers at PROINPA. By written agreement with PROINPA, true seeds and tubers of all collections with fewer than 200 seeds or 5 tubers from the 1993 expedition were imported into the United States for increase at NRSP-6, and those from the 1994 expedition to the Dutch/German genebank. Germplasm from the first increase will be shared between PROINPA (address on title page), CIP (International Potato Center, Apartado Postal 5969, Lima, Peru), NRSP-6 (Potato Introduction Station, 4312 Hwy. 42, Sturgeon Bay, Wisconsin 54235-9620, U.S.A.), and BGRC (Institute of Crop Science and Plant Breeding, Federal Research Center of Agriculture, D-3300 Braunschweig, Germany).

A full report is deposited at PROINPA, CIP, NRSP-6, the United States Germplasm Services Laboratory in Beltsville, Maryland, and the International Plant Genetic Resources Institute Offices in Cali, Colombia and Rome, Italy. All locality data are available online from the United States, USDA GRIN (Germplasm Resources Information Network) system. Collections from the 1993 expedition are *D.M. Spooner, Ronald G. van den Berg, Willman García* and *Maria Luisa Ugarte 6500-6773*; those of the 1994 expedition are *Ronald G. van den Berg, D.M. Spooner, Willman García, and Maria Luisa Ugarte 600-656*.

Results and discussion

Chromosome counts. All are somatic counts from root tips. See immediately above for collectors. *Solanum chacoense* Bitter, 608, 633: $2n = 24$; *Solanum doddsii* Correll, 609: $2n = 24$; *Solanum hoopesii* Hawkes and K.A. Okada, 6683, 6685: $2n = 48$; *Solanum tuberosum* subsp. *andigena* Hawkes, 605: $2n = 48$; *Solanum ugentii* Hawkes and K.A. Okada, 6687: $2n = 48$; *Solanum yungasense* Hawkes, 601, 602, 604, 606, 6738: $2n = 24$; *Solanum yungasense* Hawkes 603: $2n = 36$.

Taxonomy. This expedition was greatly aided by the recent floristic treatments of the Bolivian wild potatoes (Hawkes & Hjerting, 1989; Ochoa, 1990). These works provide an invaluable summary of locality data, distribution maps, hypotheses of species boundaries and interrelationships, crossability and evaluation data, and taxonomic keys. However, they differ regarding species boundaries, rank of infraspecific taxa, hypotheses of hybridization, and affiliation of species to series (Spooner & van den Berg, 1992a). These disagreements are caused by the following four problems:

1) Inconsistencies between treatments. Hawkes & Hjerting (1989) base their study on 1610 Bolivian collections, Ochoa (1990) on 853. Of these 2463 collections, 350 are in common between these treatments, resulting in a total data base of 2113 collection numbers, of which Hawkes & Hjerting (1989) used 76% and Ochoa (1990) 40%. Thus, only 16% was examined in common between treatments. An analysis of the identifications of these 350 numbers examined in common illustrates a critical point about potato taxonomy. Not counting type specimens, identifications differ in 20% of the cases. Some distinct taxa, such as *S. acaule*, *S. boliviense*, *S. gandarillasii*, *S. infundibuliforme*, *S. neocardenasii*, and *S. okadae* usually were identified the same, but others frequently differed. For example, identifications differed 38% of the time among the similar species *S. brevicaulis*, *S. gourlayi*, *S. hondelmannii*, *S. leptophyes*, *S. oplocense*, *S. pachytrichum*, *S. sucrense*, *S. sparsipilum*, and *S. vidaurrei*.

These conflicting identifications could result from various causes: 1) Species may be characterized by minor characters that are not easily discerned, and one taxonomist misidentified a collection. 2) Species may be characterized by a combination of character states, some of which may be variable between individual herbarium sheets of a collection. 3) There are some poorly defined species in sect. *Petota*. 4) Interspecific hybridization blurs species boundaries.

Taxonomic studies are needed to examine these alternatives in sect. *Petota*. A recent study of the Bolivian species *S. berthaultii* Hawkes and *S. tarijense* Hawkes (Spooner & van den Berg, 1992b) showed extensive overlap of morphological characters used to distinguish them, and this may result from causes 1–4. Combined morphological and molecular data for *S. megistacrolobum* and *S. toralapanum* (Giannattasio & Spooner, 1994a, b) supported the interpretation of Ochoa (1990), in recognizing these taxa as varieties or subspecies (cause 2), not as species (Hawkes & Hjerting, 1989). Data supporting cause 3 has been

advanced for the Colombian and Ecuadorian species *S. andreanum* Baker and its synonyms (Spooner et al., 1993), and varieties within the Bolivian and Argentinian species *S. microdontum* (van den Berg & Spooner, 1992).

2) Inconsistencies within treatments. Hawkes & Hjerting (1989) and Ochoa (1990) take very different approaches in keying out the Bolivian species, especially in the taxonomically difficult ser. *Tuberosa*. Hawkes & Hjerting (1989) mainly use pubescence, whereas Ochoa (1990) mainly uses height, dividing ser. *Tuberosa* into two groups (less than 40 cm tall, greater than 50 cm tall). However, heights used in Ochoa's keys do not match natural variability of these plants as outlined in Ochoa's same publication in the descriptions or list of species for *S. avilesii*, *S. brevicaulis*, *S. okadae*, *S. microdontum*, *S. oplocense*, and *S. vidaurrei*.

3) Imprecise terminology to distinguish taxa. Hawkes & Hjerting (1989) frequently use subjective terms for habit and pubescence within the ser. *Tuberosa* key that hinders its use. Height terms include 'plant of medium vigor' compared to 'plant delicate'. Pubescence terms include 'pubescence medium-lengthed', vs. 'pubescence variable'. Precise measurements or use of standard terms (such as those provided in Harrington & Durrell, 1957) are needed.

4) Variability that exceeds species boundaries. We consider the under-documentation of natural variability within and between populations to be the greatest problem hindering the objective evaluation of species boundaries in sect. *Petota* (Spooner & van den Berg, 1992a). For example, Hawkes & Hjerting (1989) distinguish *S. hondelmannii* from *S. sparsipilum* and *S. sucrense* in part by 'leaflets apically acuminate', vs. 'leaflets acute to acuminate'. Our topotype collections of *S. hondelmannii* (6663), and of collections from localities cited as representative material by Hawkes & Hjerting (1989) (6660) show that both character states are present within populations and even on individual plants. Both Hawkes & Hjerting (1989) and Ochoa (1990) distinguish *S. avilesii* from *S. brevicaulis* by the erect habit and 1–3 pairs of lateral leaflets of the former and rosette habit and 3–5 pairs of lateral leaflets of the latter. Our collections (6632, 6634) document plants growing in the sun of more upright habit and smaller numbers of lateral leaflets, while plants growing in the shade to be smaller, and with larger numbers of lateral leaflets.

Wild potatoes are weedy species and may have formed hybrid populations that complicate the inter-

pretation of species boundaries (Hawkes & Hjerting, 1989). This variability has presented potato taxonomists with inherent difficulties. Although the keys of Hawkes & Hjerting (1989) and Ochoa (1990) do not work in all instances, they may have intuitively interpreted species boundaries well. However, we need to give identifications now to best organize our genebank collections and provide information to breeders and other users. Outlined below are our field and literature observations that explain our identifications of our collections (Table 2), some of which are likely to change with future study. We group these collections into the following related groups (without implying formal synonymy) to outline taxonomic problems and assist users to choose collections based on their needs.

Solanum chacoense, *S. arnezii*, *S. doddsii*, *S. flavoviridens*, *S. yungasense*. We informally group here the following phenetically similar species: *S. arnezii*, *S. chacoense*, *S. doddsii*, *S. flavoviridens*, and *S. yungasense*. We informally call this the 'S. chacoense' group because this is the earliest name, but identified all our collections to individual species based on morphology and expectations from distributions in Hawkes & Hjerting (1989) and Ochoa (1990). In Bolivia, these species occur from 600–2300 m, on the eastern slopes of the Andes mountains, and, except *S. gandarillasii* and *S. neocardenasii*, occupy the lowest elevations of wild potato species in Bolivia (see Fig. 5 of Hawkes & Hjerting, 1989).

Much taxonomic disagreement within the Bolivian potato flora occurs among the *S. chacoense* group (Spooner & van den Berg, 1992a). For example, Hawkes & Hjerting (1989) distinguish *S. chacoense* from *S. yungasense* by the narrower stem wings of the former, but Ochoa (1990) describes *S. chacoense* and *S. yungasense* as having wings of equal width (but generally more sinuous in *S. yungasense*). Hawkes & Hjerting (1989) distinguish *S. chacoense* from *S. yungasense* by the white corollas of the former and the yellow corollas of the latter, but Ochoa (1990) states *S. yungasense* can have white or yellow-white corollas. Hawkes & Hjerting (1989) accept both *S. arnezii* and *S. chacoense* as distinct species and distinguish *S. arnezii* with yellow corollas, *S. chacoense* with white. Ochoa (1990) synonymizes *S. arnezii* under *S. chacoense*, without mentioning the yellow corollas. Hawkes & Hjerting (1989) use corolla color to help identify populations as natural interspecific hybrids with *S. chacoense*. For example, they use corolla color variation to help designate *S. doddsii* as a natural hybrid between

S. alandiae and *S. chacoense*, and a population at the Valle Grande airport in Santa Cruz Province as a hybrid between *S. chacoense* and *S. berthaultii*. Ochoa (1990) accepts *S. doddsii* as a species, and makes no mention of corolla color variability.

Our collections within the *S. chacoense* group document broad dentate stem wings on collections from the Yungas Region of La Paz Province, which we provisionally identify as *S. yungasense* (600, 601, 602, 603, 604, 606, 607, 6732, 6735, 6738, 6739), and on plants from the border of or to the southeast of this region which we provisionally identify as *S. arnezii* (624, 634, 636, 637, 6692). We provisionally identify plants with narrow wings and pure white corollas as *S. chacoense* (608, 621, 633, 645), plants similar to *S. chacoense* but with corollas white tinged with blue or light blue as *S. doddsii* (609, 614, 615, 617, 630, 631, 641, 644, 6649, 6651, 6701), and plants in the area of the type locality of *S. litusinum* as *S. litusinum* (642, 643).

Solanum yungasense occurs on the eastern slopes of the Andes from southern Peru (Puno Province) to adjacent east-central Bolivia (La Paz Province), at elevations of 1100–1900 m (Hawkes & Hjerting, 1989; Ochoa, 1990). An earlier report of *S. yungasense* from Argentina (Correll, 1962) was reidentified as *S. chacoense* by Hawkes & Hjerting (1969), showing the difficulty of distinguishing these species. Our 11 germplasm collections of *S. yungasense* cover the entire Bolivian range of the species, except the northernmost Bolivian population in Larecaja Province; we searched for this latter population unsuccessfully.

Ochoa (1984, 1990) reports both diploid and triploid populations of *S. yungasense* but cites no vouchers and therefore we cannot tell how these cytotypes are distributed within populations or geographically. Hawkes & Hjerting (1989) report two diploid counts from collections near the type locality in La Paz Province, Department of Sud Yungas. Despite Ochoa's (1984) report of triploids, Hawkes & Hjerting (1989) state 'we very much doubt that any triploid forms of this species have been found'. Our collections show diploid and triploid plants from a single population (603, 604), confirming Ochoa's (1990) report of triploids. We made separate collections from this one population because the tubers of 603 had tan skin, and those of 604 had purple skin.

Hawkes introduced two germplasm samples of *S. yungasense* to England in the 1940's, but they soon died (Hawkes & Hjerting, 1989). Our collections of this species are all from tubers and currently are being

Table 2. Summary of new collections of *Solanum* sect. *Petota* from the 1993 and 1994 expeditions to Bolivia

	Map areas ¹	Total	Seeds	Tubers	Herb.
<i>Solanum acaule</i>	5, 9, 21, 28, 30(2), 32 33, 58, 65, 74, 79	12	12		8
<i>S. alandiae</i>	35(3), 36	4	3		4
<i>S. arnezii</i>	40, 41, 53(2), 59	5	1	4	5
<i>S. berthaultii</i>	25, 26, 37, 41, 62	5	4	1	5
<i>S. boliviense</i> ²	34, 63, 64(2), 65, 73	6	6		6
<i>S. bombycinum</i>	1	1			1
<i>S. brevicaule</i> ³	5, 8, 9(2), 10, 11(2) 29(2), 31(2), 32, 37 54, 64(2), 68, 71, 73(3), 78	22	16	1	19
<i>S. candolleanum</i>	1, 5, 6, 7(2)	5	2	3	5
<i>S. chacoense</i>	18, 38, 57, 61	4	1	4	4
<i>S. circaeifolium</i> ⁴	8(2), 20(2), 22, 24 35, 54	8	4	2	8
<i>S. doddsii</i>	36(2), 38, 39(4), 41 53, 55, 56	11	5	7	11
<i>S. gandarillasii</i>	39(2), 42(2)	4	2		4
<i>S. hoopessii</i>	58(2), 60(2), 61(3)	7	6		6
<i>S. infundibuliforme</i>	67, 68, 70, 74, 75, 76(2), 77, 79	9	5		8
<i>S. juzepczukii</i>	30	1		1	1
<i>S. litusinum</i>	38(2)	2		1	2
<i>S. megistacrolobum</i> subsp. <i>megistacrolobum</i>	24, 25, 26, 31, 32, 33, 54, 66, 67, 71, 74(2), 76(3), 80	16	13		15
<i>S. megistacrolobum</i> subsp. <i>toralapanum</i>	29(2), 54, 58(2)	5	5		4
<i>S. microdontum</i>	37(2), 40(3), 41, 56, 81, 82(2)	10	2	4	10
<i>S. neovavilovii</i>	1	1		1	1
<i>S. okadae</i>	20(5)	5	5		5
<i>S. oplocense</i> ⁵	46(2), 52, 54(2), 77(2), 79	8	5		8
<i>S. soestii</i>	20(4)	4	1	2	4
<i>S. sparsipilum</i> ⁶	2, 20, 22, 23, 24(4), 25, 28, 29(2), 30, 32 44, 62, 68, 69, 70, 72(2)	21	18	1	17
<i>S. tarijense</i>	37, 39(2), 41(2), 42, 43, 44, 45, 46, 53, 62(2), 81(3)	16	14		14
<i>S. tuberosum</i> subsp. <i>andigena</i>	3(2), 4, 5(4), 7, 12 19	10	2	9	7

Table 2. Continued.

<i>S. ugentii</i>	58(4)	4	2	2	4
<i>S. vidaurrei</i> ⁷	65, 73(2)	3	1		3
<i>S. violaceimarmoratum</i>	15, 27	2			2
<i>S. yungasense</i>	13(4), 14, 15, 16(2), 17(3), 18	12		10	11
Grand totals		223	135	54	202

¹ Refer to Fig. 1.

² Included here (see Taxonomy section for explanations of footnotes 2–6) is *S. astleyi*.

³ Included here are *S. achacachense*, *S. avilesii*, *S. gourlayi*, *S. leptophyes*.

⁴ Included here is *S. capsicibaccatum*, and all varieties from both species.

⁵ Included here is *S. hondelmannii*.

⁶ Included here are *S. sucrense* and *S. virgultorum*.

⁷ As *S. gourlayi* ssp. *vidaurrei* in Hawkes and Hjerting (1989).

grown at BGRC and United States quarantine, with the attempt to produce seeds and/or tuber increases. If the collections survive, they will be the first germplasm collections available for distribution.

Solanum astleyi/*S. boliviense*. Hawkes & Hjerting (1989) distinguish *S. astleyi* from *S. boliviense* by the former having simple leaves, or if lateral leaf lobes are present, these with broad wings decurrent on the leaf rachis, and the latter having simple leaves, or if lateral leaf lobes are present, these having distinct leaflets. Our topotype collections of *S. astleyi* (6531) and our other collections of *S. boliviense* (6524, 6532, 6535, 6612, 6619) are variable for these characters. Because of the similarity of these sympatric species, and variability within populations, we question Hawkes & Hjerting's (1989) designation of natural interspecific hybrid populations between these two, and suspect that they fail to document natural variability in *S. boliviense*. Our field data suggest to us that Ochoa (1990) may be correct in designating the two taxa as conspecific. Until we can complete further studies of this problem, we will identify all of our collections (including the topotype collection of *S. astleyi*) as *S. boliviense*.

Solanum berthaultii/*S. tarijense*. Recent studies (Spooner & van den Berg, 1992b) demonstrated extensive morphological variability within and between 84 germplasm accessions of these two species. One of the characters used to distinguish the species (corolla shape) showed no statistically significant difference between them, and other characters, while statistically significant between species, showed much overlap between species. As in our prior study, we noted on this expedition variability of 'species-specific' charac-

ters (e.g., *S. berthaultii* 6503 has corollas on different plants in the same population pure white to deep blue). Also, we observed plants at the type locality of *S. berthaultii* (at the base of Cerro San Pedro in Cochabamba) that had white corollas, intermixed within the more common plants there with blue corollas like the description of *S. berthaultii*. We also found an area of possible co-occurrence of species (*S. tarijense* 6529, and *S. berthaultii* 6530), in an area hypothesized by Hawkes & Hjerting (1989) to be an area of hybridization (Dept. Potosi, Prov. Saavedra, 70 km south of Sucre). Despite this apparent variability within populations, we generally were able to identify our collections to species on a complex of species-specific characters, providing support from our intuitive field observations for the interpretation of these as species. Molecular studies complementing the morphological study are in progress.

Solanum capsicibaccatum/*S. circaeifolium*. These species, and *S. soestii*, are the sole members of ser. *Circaeifolia*. All are distributed in Bolivia. Hawkes & Hjerting (1989) and Ochoa (1990) both treat *S. soestii* as a good species, and we have no problem identifying it. Hawkes & Hjerting (1989) recognize *S. capsicibaccatum* and *S. circaeifolium*, with the latter divided into subsp. *circaeifolium* and subsp. *quimense*. Ochoa (1990), however, distinguishes a single species, *S. circaeifolium* with two varieties, var. *circaeifolium* and var. *capsicibaccatum*.

The key in Hawkes & Hjerting (1989) uses pubescence to distinguish *S. capsicibaccatum* and *S. circaeifolium*, and leaf dissection and pubescence to distinguish the subspecies of *S. circaeifolium*. Ochoa (1990) uses leaf dissection to key out varieties of *S.*

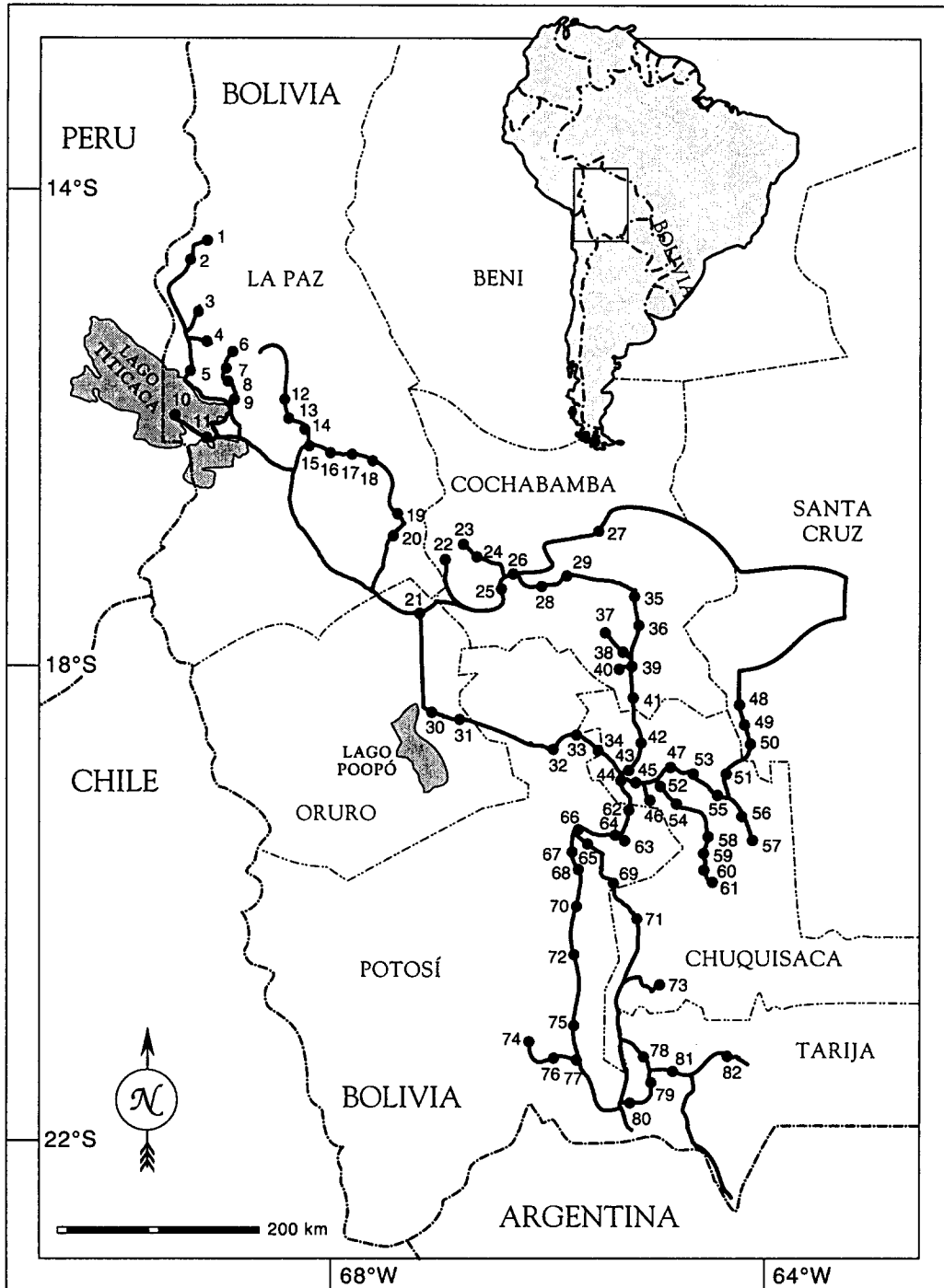


Fig. 1. Routes of the 1993 and 1994 expeditions to Bolivia. The numbers refer to generalized collection sites (see Table 2).

circaeifolium. Two of our collections (6767, 650) from the area of the type collection of *S. circaeifolium* subsp. *circaeifolium* show the typical simple leaves of this subspecies, suggesting this is a good taxon, but we observed much variation for pubescence and leaf dis-

section in *S. circaeifolium* making identification of its subspecies unclear. We here conservatively identify all our collections of these two species as *S. circaeifolium*.

Solanum megistacrolobum/*S. toralapanum*. These species are morphologically very similar, and have been the subject of continuing taxonomic debate. They were recognized as distinct species by Brücher (1959), Correll (1962) and Hawkes & Hjerting (1989). Ochoa (1984) originally synonymized the two, but later (1990) recognized them at the varietal level (as *S. megistacrolobum* Bitter var. *megistacrolobum* and *S. megistacrolobum* var. *toralapanum* (Cárdenas and Hawkes) Ochoa). The difficulty in distinguishing these taxa is evident from a comparison of the identifications of identical herbarium material by Hawkes & Hjerting (1989) and Ochoa (1990) where, excluding types, identifications differ in 26% of the cases.

Morphological and molecular studies (Giannattasio & Spooner, 1994a, 1994b) showed extensive overlap of characters from both data sets, but the taxa were weakly supported by multivariate techniques. These results, combined with the distributional data (with *S. toralapanum* growing more to the east of *S. megistacrolobum*) support Ochoa's (1990) treatment of the taxa as varieties.

However, because the taxonomic treatments of Hawkes & Hjerting (1989) use subspecies, and Ochoa (1990) varieties, identical taxa in sect. *Petota* are provided separate names. This situation is common in flowering plants, and recent recommendations (Hamilton & Reichard, 1992) have suggested the use of subspecies over varieties when only one infraspecific taxon is used. Therefore, Giannattasio & Spooner (1994b) made the new combination *S. megistacrolobum* subsp. *toralapanum* to begin to solve this problem of unequal use of infraspecific categories in potatoes.

Series Tuberosa. The greatest disagreement in contemporary treatments of Bolivian wild potatoes is in the series *Tuberosa* (Spooner & van den Berg, 1992). This group includes the 38% disagreement relating to independent identifications mentioned above for *S. brevicaulle*, *S. gourlayi*, *S. hondelmannii*, *S. leptophyes*, *S. oplocense*, *S. pachytrichum*, *S. sucrense*, *S. sparsipilum*, and *S. vidaurrei*. Because of inconsistencies between treatments reported above, and other problems we report below, we are unsure of the identity of many of our collections. We tentatively divide these species into three widely overlapping groups, but are unsure of species limits within or between any of them. We subjectively divide them based on size, with Group 1 generally including lower-growing plants under about 20 cm, Group 2 of taller plants over about 20 cm,

and Group 3 similar to Group 2 but with smaller stigmas.

Tuberosa Group 1, *Solanum achacachense*/*S. avilesii*/*S. brevicaulle*/*S. gourlayi*/*S. leptophyes*. Hawkes & Hjerting (1989) say that after studying herbarium specimens and living material they 'firmly believe that we have reached the right conclusions' concerning the species boundaries of *S. gourlayi* and *S. leptophyes*. Yet Correll (1962) reduced *S. gourlayi* to a form of *S. leptophyes*, and Ochoa (1990) synonymized *S. gourlayi* to *S. leptophyes*. Correll (1962) treated *S. achacachense* as a synonym of *S. brevicaulle*. Ugent (1966) united the species mentioned above (with the exception of *S. avilesii*), and other taxa from Argentina to Peru, under *S. brevicaulle*. Hawkes & Hjerting (1989) did not accept this reduction.

Our collections show similar problems. For example, 6632 and 6634 include variability within populations of broad-leaved plants, conforming to the description of *S. avilesii*, and narrower-leaved plants, conforming to the description of *S. brevicaulle*. We refer all these collections to the oldest species name, *S. brevicaulle*.

Tuberosa Group 2, *Solanum candolleianum*/*S. hoopesii*/*S. sparsipilum*/*S. sucrense*/*S. ugentii*/*S. virgultorum*/*S. tuberosum* 'weedy' populations. *Solanum sucrense* illustrates the morphological similarity of part of this group and the tenuous data maintaining them as separate. Ochoa (1979) designated *S. sucrense* as synonymous with *S. sparsipilum*, but later (Ochoa, 1990) recognized both as species, but without any reference to his earlier synonymy. Ochoa (1990) keys out *S. sparsipilum* from *S. sucrense* from numbers of interjected and lateral leaflets that do not match his illustration of representative material of *S. sparsipilum*. Our examination of these characters in the field in Bolivia and plantings at Sturgeon Bay showed these characters, and the additional characters provided in Hawkes & Hjerting (1989) of stigma morphology and shininess of leaves to vary extensively within accessions and even on individual plants. Astley & Hawkes (1979) state that *S. sucrense* is of natural origin from *S. tuberosum* subsp. *andigena* and *S. oplocense*. They support this hypothesis by artificial reconstruction of the hybrid, and comparison of seed and fruit set of these to putative parents. Their study, however, assumes the species are distinct and provides no data to distinguish them.

We also found it hard to distinguish other weedy wild potato species from certain forms of the cultivated potato classified as *S. tuberosum* subsp. *andigena*. The morphological similarity of most wild species to

the cultivars is striking, leaving only characters like smaller tubers and longer stolons to identify the 'wildness' of the species. Wild species like *S. sparsipilum* are considered as potential parental species to cultivars, but could as well be interpreted as escapes from cultivation. We have used the species name *S. sparsipilum* (the earliest name in the group) for the group of weedy species of robust stature, resembling the cultivars of subsp. *andigena*. However, collections *S. hoopesii* (6679, 6680) and *S. ugentii* (6687) collected at or near the type locality have been denoted with their species names, although we are not able to distinguish these species from *S. sparsipilum* and the similar forms of *S. tuberosum* subsp. *andigena*.

Tuberosa Group 3 *S. hondelmannii*/*S. oplocense*. Hawkes & Hjerting (1989) recognize both *S. hondelmannii* and *S. oplocense*, but Ochoa (1990) considers *S. hondelmannii* 'a hybrid variant' of *S. oplocense*. The characters used by Hawkes & Hjerting (1989) to distinguish *S. hondelmannii* from *S. oplocense* are: large number of lateral leaflets (4–5 vs. (2) 3–4 (5)) larger number of interjected leaflets (2–3 (11) pairs vs. 0–1 (5) pairs); longer petiolules (5–10 (20) mm vs. 1–2 (13) mm); shorter style exsertion (2 (5) mm vs. 5–6 (8) mm); larger stigma (broader than the style against minute, not exceeding the thickness of the style); and 'constant diploid chromosome number' (*S. oplocense* comprises diploid, tetraploid, and hexaploid cytotypes). In our collections, the leaf characters vary greatly, precluding our reliable identifications now. The collection made at the type locality of *S. hondelmannii* (6663) lacked flowers, but we observed the minute stigma often (6557, 6559, 6575). We have used the species name *S. oplocense* for these and similar accessions with minute stigmas.

Solanum bombycinum, *S. neovavilovii*, *S. violaceimarmoratum*. Hawkes & Hjerting (1989) and Ochoa (1990) place these species as the sole Bolivian representatives of ser. *Conicibaccata*, a series of 40 species, distributed from southern Mexico to central Bolivia, partly characterized by conical fruits. Hawkes & Hjerting (1989) discussed, but did not formally treat *S. bombycinum* and *S. neovavilovii*, while Ochoa (1990) treated all three.

The species boundaries and interrelationships of these taxa are unresolved. When Ochoa (1983a) described *S. bombycinum*, he reported its tetraploid chromosome number ($2n = 48$) and placed it in ser. *Conicibaccata*. He stated (Ochoa 1983a, 1990) it had affinities with *S. villuspetalum* Vargas, a southern Peru-

vian diploid member of the series. Hawkes & Hjerting (1989, in text) initially suggested *S. bombycinum* was conspecific with *S. villuspetalum*, but stated later (Hawkes & Hjerting, 1989, in postscript) 'it is likely that *S. bombycinum* could be a distinct species'.

When Ochoa (1983b) described *S. neovavilovii* he reported its diploid chromosome number ($2n = 24$) and placed it in ser. *Conicibaccata*. However, he stated it could have affinity with *S. bukasovii* and *S. leptophyes*, two species he placed in ser. *Tuberosa* (Ochoa 1962, 1990), and *S. limbaniense* Ochoa, a species he placed in ser. *Conicibaccata* (Ochoa, 1974). Later (Ochoa, 1990) he rejected his hypothesis of relationships to *S. bukasovii* and *S. leptophyes* and related *S. neovavilovii* solely to *S. limbaniense*. Hawkes & Hjerting (1989), however, rejected Ochoa's (1990) hypothesis of relationship to *S. limbaniense*, and state the species is conspecific with *S. violaceimarmoratum* (also diploid). These changing hypotheses of species boundaries and interrelationships show the extreme similarity of these wild potato species and the need for their reevaluation.

Our expedition collected *S. bombycinum* and *S. neovavilovii* at their type localities, in La Paz Province, near the Peruvian border. Both localities are separated by about 5 km, and the plants grow alongside the horse trail from Pelechuco to Mojos. From Bolivia, the only access to these sites is from the town of Pelechuco, then hiking 12–15 hours north, through the town of Queara, on the horse trail to Mojos. This route crosses a 4700 m snow-covered mountain crest, and pack animals, a guide, and camping gear are required.

The type locality of *S. neovavilovii*, 'Moyapampa' (not 'Mayupampa' as in publications), is about 3 km north of Queara. Moyapampa is a flat clearing, bordered by wooded hills on either side, descending from Queara in the valley of Rio Queara. We found *S. neovavilovii* there, in organic soil along the trail and on moss-covered rocks next to the trail at Moyapampa. We were unable to find the species there on our visit on March 28, 1993, and found immature conical fruits on our visit on February 19, 1994. We were able to collect tubers, however.

The type of *S. bombycinum* is 'Dept. La Paz: Prov. Franz Tamayo, between Cheke-Chekeni and Chullumayo, 2000 m, on the horse trail to Mojos, February, 1983'. Our guides told us that 'Cheke-Chekeni' was an area name (uninhabited) approximately a one hour hike south of Moyapampa on the trail to Mojos, and that 'Chullumayo' referred to the general area of Río Chullumayo, a tributary flowing from the east into Río

Queara. We found *S. bombycinum* next to the horse trail 5 m south of the bridge crossing of Río Chullumayo, at 2850 m. Because the horse trail ascends for many kilometers on either side of the bridge crossing, the 2000 m elevation provided in the type description is in error. The population consisted of about 25 plants, some with flowers and immature conical fruits. We could find no tubers, and therefore have no germplasm of this rare species.

Phenology. Timing is one of the most important aspects of planning a collecting expedition. In Bolivia, wild potatoes occur in seasonal wet-dry climates, with flowering generally occurring during or after the rainy season that generally falls during December–February. We planned our expeditions based on dates of collections of herbarium material in Ochoa (1990; Hawkes & Hjerting (1989) do not provide collecting dates) or in unpublished collecting reports and verbal recommendations by Robert Hoopes (who led collaborative Bolivian/NRSP-6 expeditions to Bolivia in 1986, 1987). Most collecting dates mentioned in Ochoa (1990) are in the months of February and March, with many fewer reports in December, January, and April.

Most of our fruit collections were from early February–late March. We planned the 1994 expedition in January to search for members of the *S. chacoense* group that we thought flowered and fruited earlier than other potato species. This is because in 1993, we collected *S. arnezii* and *S. chacoense* in early March. Two of these collections had mature flowering and fruiting plants, and two had withering plants with very mature fruits. In 1994, we revisited these and other populations of *S. arnezii* and *S. chacoense* in mid-January, where we collected mature fruits from some, but not all of them. Because late 1993/1994 was much drier than late 1992/1993, it is hard to compare phenology between years. Also, we collected *S. yungasense* in mid-March, 1993, and early January and mid-February, 1994. We never found fruits of *S. yungasense*, although some populations of this species had flowering and even aging plants at both times. Local people who were familiar with the various populations provided various reports of when fruits were produced, covering months throughout the year, and we do not know when these populations produce fruits in nature. Hawkes & Hjerting (1989), and Ochoa (1990) both describe round fruits for *S. yungasense*, but these may have been from greenhouse grown plants originally collected as tubers.

Based on these data, we would recommend most germplasm collections in Bolivia to be made from mid-February to late March. Success in finding fruits will vary greatly from year to year, depending on rainfall in the preceding months. An additional complication is presented by the very poor roads in much of Bolivia. Hawkes & Hjerting (1989) mention the compromise between a dry year where roads are passable but few fruits are present, and a wet year where roads are closed by floods and landslides but the populations produce fruits. We experienced these problems in the wet year of 1993 and the dry year of 1994.

Recommendations sites for future collecting. Based on our visits to areas where we found immature potato populations, our observations of areas passed by, and inferences of good collecting sites based on our surveys of topographic maps, we suggest the following areas for future collections of wild potatoes in Bolivia: 1. on the road from Padilla to Mataral (*S. chacoense*, *S. circaeifolium*, *S. litusinum*, and *S. neocardenasii*), 2. the road from Cochabamba to Independencia (*S. circaeifolium* and *S. okadae*), 3. the road from Soratá to Tacacoma (*S. candolleianum*, *S. circaeifolium*, and *S. virgultorum*), 4. La Paz Province from Achacachi northwest to the Peruvian border, collecting on the roads from Achacachi to Pelechuco, including side roads (*S. flavoviridens*, *S. violaceimarmoratum*), 5. hike north of Pelechuco to Queara, Río Chullumayo valley, and trail to Puina (*S. bombycinum*, *S. neovavilovii*).

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References

- Astley, D. & J.G. Hawkes, 1979. The nature of the Bolivian weed potato species *Solanum sucrensis* Hawkes. *Euphytica* 28: 685–696.
- Bamberg, J.B. & M.W. Martin, 1993. Inventory of tuber-bearing *Solanum* species. Potato Introduction Station, NRSP-6, Sturgeon Bay, Wisconsin.
- Bamberg, J. & D.M. Spooner, 1994. The United States Potato Introduction Station herbarium. *Taxon* 43: 489–496.
- Brücher, H., 1959. Kritische Betrachtungen zur Nomenklatur argentinischer Wildkartoffeln V. Die Serie *Acaulia*. *Züchter* 29: 149–156.
- Correll, D.S., 1962. The potato and its wild relatives. *Contrib. Texas Res. Found. Bot. Stud.* 4: 1–606.
- Giannattasio, R. & D.M. Spooner, 1994a. A reexamination of species boundaries between *Solanum megistacrolobum* and *S. toralapanum* (*Solanum* sect. *Petota*): morphological data. *Syst. Bot.* 19: 89–105.
- Giannattasio, R. & D.M. Spooner, 1994b. A reexamination of species boundaries and hypotheses of hybridization concerning *Solanum megistacrolobum* and *S. toralapanum* (*Solanum* sect. *Petota*): molecular data. *Syst. Bot.* 19: 106–115.
- Gonzales Moscoso, R., 1984. *Diccionario Geográfico Boliviano*. Werner Guttentag, La Paz.
- Hamilton, C.W. & S.H. Reichard, 1992. Current practice in the use of subspecies, variety, and form in the classification of wild plants. *Taxon* 41: 485–498.
- Harrington, H.D. & L.W. Durrell, 1957. *How to identify plants*. The Swallow Press, Inc., Chicago.
- Hawkes, J.G., 1990. *The potato: evolution, biodiversity and genetic resources*. Belhaven Press, Oxford.
- Hawkes, J.G. & J.P. Hjerting, 1989. *The potatoes of Bolivia: their breeding value and evolutionary relationships*. Oxford University Press, Oxford.
- Holmgren, P.K., N.H. Holmgren & L.C. Barnett, 1990. *Index herbariorum, Part 1: the herbaria of the world*. Ed. 8. *Regnum Veg.* 120: 1–693.
- Ochoa, C.M., 1962. *Los Solanum tuberíferos del Perú (Secc. Tuberarium, Sub-secc. Hyperbasarthrum)*. Priv. Publ., Lima, Peru.
- Ochoa, C.M., 1974. Nuevos *Solanum* tuberíferos silvestres del Perú. *Bol. Soc. Peruana Bot.* 7: 11–19.
- Ochoa, C.M., 1979. Exploración colectora de papas silvestres en Bolivia. *Biota* 11: 324–330.
- Ochoa, C.M., 1983a. *Solanum bombycinum*, a new tuber-bearing tetraploid species from Bolivia. *Phytologia* 60: 849–852.
- Ochoa, C.M., 1983b. *Solanum neovavilovii*: a new wild potato species from Bolivia. *Phytologia* 60: 919–923.
- Ochoa, C.M., 1984. Karyotaxonomic studies on wild Bolivian tuber-bearing *Solanum* sect. *Petota* (1). *Phytologia* 55: 17–40.
- Ochoa, C.M., 1990. *The potatoes of South America: Bolivia*. Cambridge Univ. Press, Cambridge.
- Parry, R.B. & C.R. Perkins, 1987. *World mapping today*. Butterworth and Company, London.
- Paynter, R.A. Jr. 1992. *Ornithological gazetteer of Bolivia*, Ed. 2. Bird Department, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.
- Spooner, D.M., R. Castillo T. & L.E. López J., 1993. Synonymy within wild potatoes (*Solanum* sect. *Petota*: Solanaceae): the case of *Solanum andreanum*. *Syst. Bot.* 18: 209–217.
- Spooner, D.M. & R.G. van den Berg, 1992a. An analysis of recent taxonomic concepts in wild potatoes (*Solanum* sect. *Petota*). *Genet. Res. Crop Evol.* 39: 23–37.
- Spooner, D.M. & R.G. van den Berg, 1992b. Species limits of *Solanum berthaultii* Hawkes and *S. tariiense* Hawkes: morphological data. *Taxon* 41: 685–700.
- Ugent, D., 1966. *Hybrid weed complexes in Solanum, section Tuberarium*. Ph.D. Diss., Univ. of Wisconsin, Madison, Wisconsin.
- United States Department of Interior, 1955. *Gazetteer of Bolivia: official standard names approved by the U.S. Board on geographic names*. Division of Geography, Department of Interior, U.S. Government, Washington, D.C.
- Van den Berg, R.G. & D.M. Spooner, 1992. A reexamination of infraspecific taxa of a wild potato, *Solanum microdontum* Bitter (*Solanum* sect. *Petota*: Solanaceae). *Plant Syst. Evol.* 182: 239–252.