

Taxonomy of Mexican and Central American Members of *Solanum* Series *Conicibaccata* (sect. *Petota*)

DAVID M. SPOONER,^{1,2} RONALD G. VAN DEN BERG,³ ANTONIO RIVERA-PEÑA,⁴
PETER VELGUTH,⁵ ALFONSO DEL RIO,⁵ and ALBERTO SALAS-LÓPEZ⁶

¹Vegetable Crops Research Unit, USDA, Agricultural Research Service, Department of Horticulture,
University of Wisconsin, 1575 Linden Drive, Madison, Wisconsin 53706-1590;

²Author for correspondence (dspooner@facstaff.wisc.edu);

³Plant Taxonomy Group, Wageningen University, P. O. Box 8010, 6700 ED Wageningen, The Netherlands;

⁴Programa Nacional de Papa, Instituto Nacional Investigaciones Forestales Agrícolas y Pecuarias (INIFAP),
Apdo. Postal 31, Suc. "A", C. P. 52 140, Metepec, Estado de México, Mexico;

⁵Department of Horticulture, University of Wisconsin, 1575 Linden Drive, Madison, Wisconsin 53706-1590;

⁶International Potato Center (CIP), Apartado 1558, La Molina, Lima 12, Peru

Communicating Editor: Jeff H. Rettig

ABSTRACT. Members of *Solanum* series *Conicibaccata* in Mexico and Central America are very similar. All are tetraploids ($2n = 4x = 48$). Recent authors have recognized three or four species: *S. agrimonifolium*, *S. woodsonii*, *S. longiconicum* (sometimes included in the next), and *S. oxycarpum*. We had difficulty distinguishing these species in the herbarium, and needed to resolve species boundaries for ongoing floristic studies. We studied this group in the field throughout Mexico, Guatemala, Costa Rica, and Panama, grew collections in the greenhouse, studied herbarium specimens, determined ploidy levels through flow cytometry, and generated molecular data using Random Amplified Polymorphic DNA. Molecular data distinguish *S. agrimonifolium*, *S. longiconicum*, and *S. oxycarpum*. *Solanum woodsonii* was not available for molecular analysis. All four species can be distinguished morphologically, but only by leaf character states that overlap in range, by pubescence differences that are best observed in living specimens, and by a seed spot character that is only evident on living or recently gathered specimens.

Species of *Solanum* L. sect. *Petota* Dumort. include the potato and its relatives and occur from the southwestern United States to southern Chile. The section consists of seven cultivated and 225 wild species, according to the latest comprehensive taxonomic treatment of Hawkes (1990). Hawkes (1990) partitioned the section into 19 tuber-bearing series and two non-tuber-bearing series.

Series *Conicibaccata* Bitter is the second largest of these 19 tuber-bearing series, containing about 40 diploid ($2n = 2x = 24$), tetraploid ($2n = 4x = 48$) and hexaploid ($2n = 6x = 72$) species, distributed from southern Mexico to northern Bolivia. Most occur in South America, but three or four species, all tetraploids, grow in Mexico and Central America. Existing treatments (Correll 1962; Hawkes 1990) differ in their recognition of species. These authors distinguished the Mexican and Central American species by leaflet shape and pubescence, numbers of lateral and interjected leaflets, size of corolla acumens, and anther morphology (Table 1). Most of these character states overlap in range. Correll (1962) and Hawkes (1990) agreed regarding the recognition of *S. agrimonifolium* Rydb. and *S. woodsonii* Correll, but disagreed regarding *S. longiconicum* Bitter and *S. oxycarpum* Schiede (Fig. 1). Correll (1962) placed *S. longiconicum* in synonymy with *S. oxycarpum*.

Castillo and Spooner (1997) investigated the species boundaries and interrelationships of 23 of the 40 species of ser. *Conicibaccata* using germplasm collections,

with phenetic analyses of morphological data of plants grown in a common screen house environment, and cladistic analysis of chloroplast DNA (cpDNA) restriction site data. They found 1) the diploids and polyploids formed two separate clades based on cpDNA, 2) some members of the series likely belonged to a separate series *Piurana*, 3) most species were extremely similar, and apparently could be distinguished only by character states that overlap in range, and 4) among the polyploids, *S. agrimonifolium* and *S. oxycarpum* formed a close phenetic group. No formal taxonomic decisions were made in that study, awaiting additional germplasm and molecular data. Recent additional collections of ser. *Conicibaccata* allowed a better resolution of these species, needed for our floristic studies of sect. *Petota* in North America, Mexico, and Central America.

MATERIALS AND METHODS

Field Studies, Greenhouse Observations, and Herbarium Data.

We saw living plants of all species in the field during germplasm collecting expeditions in Mexico (Spooner et al. 1991, 2000), Guatemala (Spooner et al. 1998), Costa Rica (Spooner et al. 2001), and Panama (collections in September, 2000). We examined living plants of all species in greenhouses in Wisconsin, and obtained ploidy determinations, and RAPD data, of all but *S. woodsonii*. We also searched Venezuela (Spooner et al. 1995) for possible sites of *S. woodsonii* as cited by Correll (1962). We assembled herbarium data from AGUAT, B, BIGUA, BM, BR, C, CAS, CIP, CR, EAP, ENCB, F, G, GH, HAL, IEB, INB, INIFAP, K, LL, M, MEXU, MICH, MO, MPU, MSC, NA, NY, OXF, P, PMA, PTIS, S, TAES, TEX, US, USCG, USJ, UVAL, W, WAG, WIS, and Z. The herbaria INB and PTIS will appear in the 9th edition of Index Herbariorum, cur-

TABLE 1. Morphological characters used by Correll (1962) and Hawkes (1990) in their keys and descriptions to differentiate the Mexican and Central American members of *Solanum* ser. *Conicibaccata*.

Taxon	Leaf pubescence	Pairs of lateral leaflets	Number of interjected leaflets	Leaflets	Corolla acumens	Lobe at base of anther
<i>Solanum agrimonifolium</i>	subglabrous to sparsely pubescent	7–9	many, up to 20	sessile to subsessile, elliptic lanceolate to narrowly lanceolate	short	absent
<i>S. longiconicum</i> (synonym of <i>S. oxycarpum</i> by Correll)	completely glabrous to almost glabrous	3–4	0	short petiolulate, narrowly lanceolate	short	absent
<i>S. oxycarpum</i>	scattered pustulate hairs above, finer shorter hairs below (Correll); glabrous or with sparse short hairs (Hawkes)	(3) 4–5 (6)	0 (typically) to 2	subsessile, narrowly lanceolate to ovate lanceolate or elliptic lanceolate (Correll); narrowly lanceolate (Hawkes)	prominent (Correll)	absent
<i>S. woodsonii</i>	dense short hairs	2–3	0 (typically) to few	elliptic to oval	short	present

rently Holmgren et al. (1990), but currently can be accessed at <http://www.nybg.org/bsci/ih/ih.html>. The herbarium CIP is at the International Potato Center in La Molina, Peru, and INIFAP is at the Mexican National Potato Program in Toluca, Mexico. Specimens from Guatemala and Honduras are listed by Spooner et al. (1998), from Costa Rica by Spooner et al. (2001), and from Mexico and Panama here. Germplasm accessions (available at the US potato genebank in Sturgeon Bay, Wisconsin) are denoted by an asterisk under "Additional specimens examined."

Leaf Dissection. Numbers of lateral and interjected leaflets have been important in past treatments of Mexican and Central American members of ser. *Conicibaccata* (Table 1), and are practical and readily accessible characters for many herbarium specimens of this group that lack or have poorly pressed flowers or fruits. We therefore assessed each of these two characters, and their sum, from 53 herbarium specimens of *S. agrimonifolium*, 45 of *S. longiconicum*, 55 of *S. oxycarpum*, and 22 of *S. woodsonii* (Table 2).

We initially identified specimens by prior determinations of Correll (1962) and Hawkes (1997), using his database of localities described there) and by identifications of germplasm provided by these workers at on-site visits to the United States Potato Genebank (National Research Support Program-6, NRSP-6; Bamberg et al. 1996), and by distributional data as shown in Fig. 2. All leaf dissection characters were analyzed for their means, ranges, and

standard deviations. Leaf dissection differences among taxa were examined for significant differences by the Tukey-Kramer HSD test in JMP statistical software (SAS 1995).

RAPDs. A total of 18 10-mer RAPD primers were selected based on clearly discernable polymorphic bands based on prior (Spooner et al. 1996, 1997; Miller and Spooner 1999) and unpublished studies in sect. *Petota*. The RAPD primers are (Operon Technologies, Alameda, CA) OPA2, OPA110, OPAA-1, OPAA-6, OPAA-16, OPAB-8, OPAC-9, OPAC-15, OPAE-3, OPAG-2, OPAG-4, OPAG-9, OPD-1, OPE-18, OPG-6, OPM-12, OPU-3, and OPV-8. Polymerase Chain Reaction (PCR) amplifications were performed in 15 μ L reaction volumes containing 50 mM Tris-HCl pH 8.0, 100mM NaCl, 0.1 mM EDTA, 5mM DTT, 50% glycerol, 1.0% Triton X-100 as reaction buffer, 25 mM MgCl₂, 200 μ M each of dATP, dCTP, dGTP and dTTP; 1 unit of Taq DNA Polymerase (Promega, Madison, WI), 15 ng genomic DNA template, and 0.2 μ M of a random primer. PCR amplification was performed in a Perkin-Elmer Cetus DNA Thermal Cycler 9600 (Norwalk, CT) programmed for 1 cycle@94°C/4 min; 3 cycles@94°C/15 sec, 35°C/15 sec, 72°C/75 sec; 40 cycles@94°C/15 sec, 40°C/15 sec, 72°C/75 sec; 1 cycle@72°C/7 min; and then 4°C hold. All RAPD products were fractionated by electrophoresis in 1.5% agarose gels and visualized by ethidium bromide staining 0.5 μ g/ml in 1 \times TAE buffer.

Based on cpDNA restriction site data (Castillo and Spooner

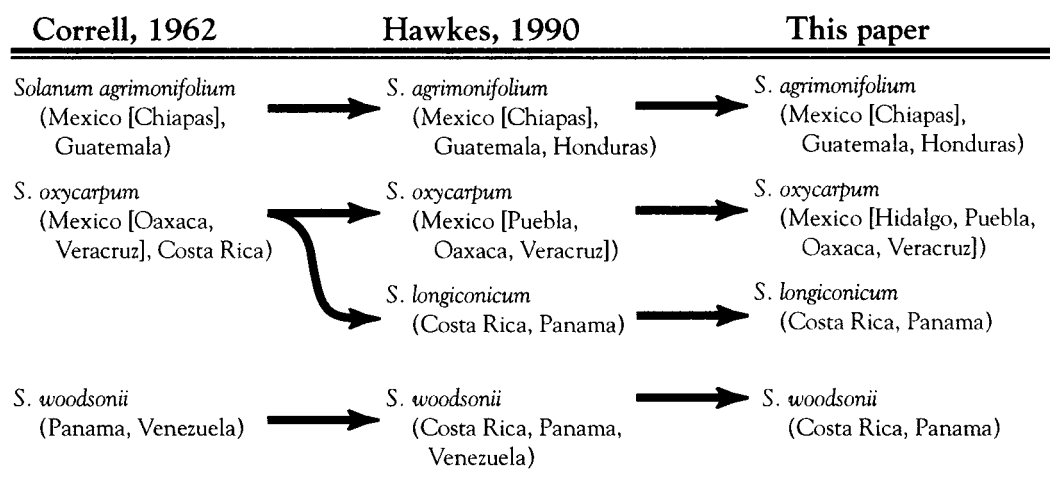


FIG. 1. Alternative classifications of the Mexican and Central American species of *Solanum* series *Conicibaccata*.

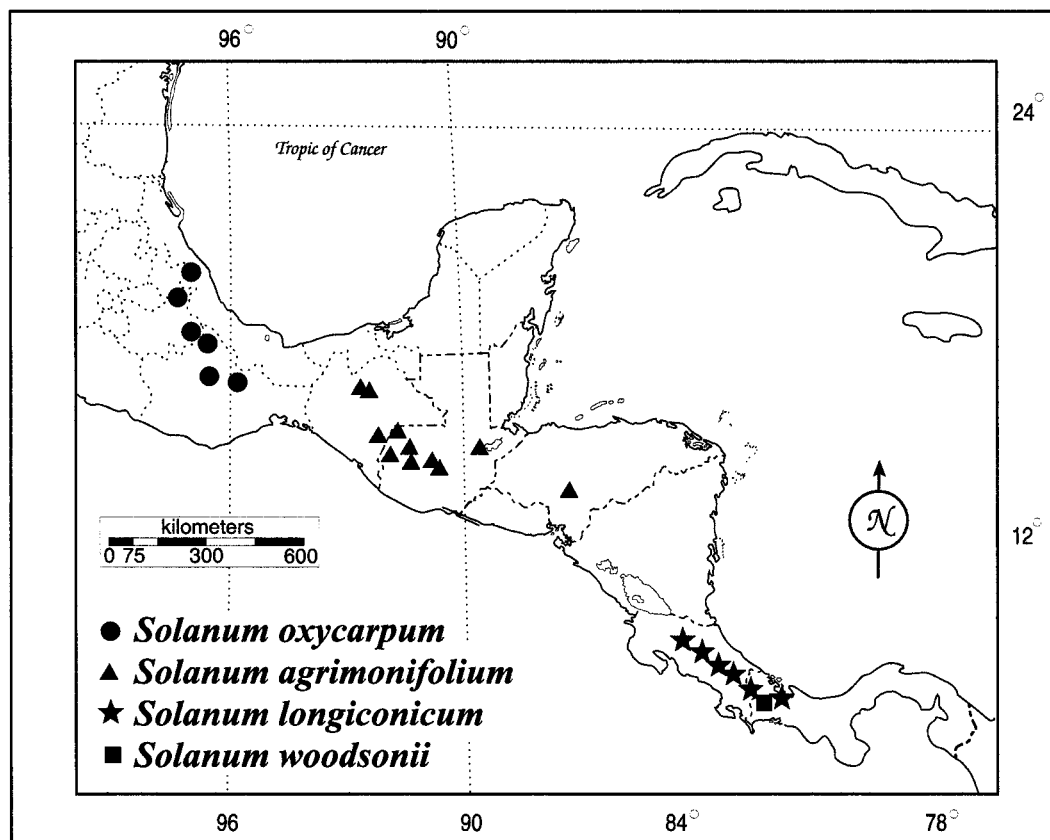


FIG. 2. Distributions of the Mexican and Central American species of *Solanum* series *Conicibaccata*.

1997; Spooner and Castillo, 1997), *S. buesii* Vargas, *S. laxissimum* Bitter, *S. santolallae* Vargas, and *S. violaceimarmoratum* Bitter (all diploid representatives of ser. *Conicibaccata*) were chosen as immediate outgroups to the polyploid species, while *S. piurae* Bitter and *S. bulbocastanum* Dunal were chosen as more distant outgroups.

RAPD data were analyzed using NTSYS-pc[®] version 2.02k (Rohlf 1992). Similarity matrices (in SIMQUAL) were generated using Jaccard's similarity matrix, which ignores shared absent bands (Jaccard 1908), and a simple matching coefficient that treats all data combinations as equivalent. Clustering was performed using the unweighted pair-group method (UPGMA) in SAHN, and neighbor-joining analysis (NJ). Cophenetic correlation coefficients (COPH, in MXCOMP) were used to measure distortion between the similarity matrices and the resulting four phenograms (Rohlf and Sokal 1981; Sokal 1986).

Ploidy Levels. All prior chromosome counts of *S. agrimonifolium*, *S. longiconicum*, and *S. oxycarpum* have been determined to be tetraploid, $2n = 4x = 48$ (Hanneman and Bamberg 1986; Bamberg et al. 1996; Castillo and Spooner 1997). Castillo and Spooner (1997) showed that diploid members of ser. *Conicibaccata* differed from polyploids by narrower terminal and lateral leaflets and longer petioles. Because of variation in leaflet shape and petiole length among these species (Table 1) we wished to investigate new collections to see if some of them might have been diploids. We also wished to see if there were species-specific differences in DNA content among the polyploids.

Flow cytometry determines nuclear DNA content by measuring the fluorescence emission of isolated nuclei, then relating this observed fluorescence to DNA amount by comparison to a known standard. We used flow cytometry to assess ploidy levels of 12 accessions of *S. agrimonifolium*, nine of *S. longiconicum*, and three of *S. oxycarpum*; five of these accessions previously had been count-

ed as $2n = 4x = 48$ (Table 2). Leaf samples were prepared for flow cytometric analysis of DNA content according to the methods of Dickson et al. (1992), except for the use of *Vigna radiata* (L.) R. Wilczek 'Berken' as an internal standard. Fifty mg of plant leaves (25 mg of *Solanum* and 25 mg of *Vigna radiata*) were placed in 1 ml of chopping buffer and chopped for 1 min with a single edged razor blade. The solution was filtered through a 10 μ nylon mesh, centrifuged to pellet nuclei, and the pellet resuspended in 200 μ l stain (propidium iodide at 100 μ g per ml and containing DNase-free RNase [Boehringer Mannheim] in chopping buffer). The internal standard *Vigna radiata* has 1.06 pg DNA per 2C nucleus, a value established independently by both reassociation kinetics and Feulgen methods (M. D. Bennett, pers. comm.). Eighteen of the accessions were run based on two independent samples run on different days, and five were from one leaf sample.

A computer program, WinMDI, allowed the selection of peaks and calculated mean channel number representing sample and *Vigna* DNA from histograms generated for each sample. DNA content of samples was calculated by (sample mean channel number \times *Vigna* DNA content) / (*Vigna* mean channel number) = unknown sample DNA content. DNA contents among taxa were examined for significant differences by the Tukey-Kramer HSD test in JMP statistical software (SAS 1995).

RESULTS

Leaf Dissection. The Tukey-Kramer HSD test determined that numbers of lateral leaflets were significantly different ($P = 0.05$) among *S. agrimonifolium*, *S. oxycarpum*, and *S. longiconicum* plus *S. woodsonii*, but not

TABLE 2. Accessions of *Solanum* sect. *Petota* examined for leaf dissection (Fig. 3), RAPDs (Fig. 5), and ploidy as determined by flow cytometry. ¹Multiple herbarium entries represent separate leaf counts. Vouchers from Mexico and Panama are listed in this paper, from Guatemala and Honduras in Spooner et al. (1998), and from Costa Rica in Spooner et al. (2001). ²R designates accessions used in the RAPD study; the number following R corresponds to the number following the species on Fig. 4. ³The ploidy level as inferred from flow cytometry is listed as 4x, while preexisting mitotic chromosome counts are listed as 2n = 48.

Species	Country	State	Collector	Leaf dissection ¹	RAPDs ²	Ploidy ³
Mexican and Central American members of <i>Solanum</i> ser. <i>Conicibaccata</i>						
<i>S. oxycarpum</i>	Mexico	Hidalgo	Hernández 3427	MEXU		
<i>S. oxycarpum</i>	Mexico	Hidalgo	Hernández and Hernández 4772	ENCB, MEXU		
<i>S. oxycarpum</i>	Mexico	Hidalgo	Rivera-Peña et al. 944	INIFAP, MEXU, WAG	R1	
<i>S. oxycarpum</i>	Mexico	Oaxaca	Anderson and Anderson 4850	ENCB		
<i>S. oxycarpum</i>	Mexico	Oaxaca	Flores S-797	K		
<i>S. oxycarpum</i>	Mexico	Oaxaca	Rivera 1245	MEXU		
<i>S. oxycarpum</i>	Mexico	Oaxaca	Rivera-Peña et al. 952	PTIS (2), WAG	R2	
<i>S. oxycarpum</i>	Mexico	Oaxaca	Rivera-Peña et al. 953	INIFAP, MEXU	R3	2n = 48
<i>S. oxycarpum</i>	Mexico	Oaxaca	Tarn et al. 272			4x
						2n = 48
<i>S. oxycarpum</i>	Mexico	Puebla	Rivera-Peña et al. 951	MEXU (2), PTIS, WAG	R4	
<i>S. oxycarpum</i>	Mexico	Puebla	Tarn et al. 182		R5	4x
<i>S. oxycarpum</i>	Mexico	Veracruz	Balls and Gourlay 5513	K (3)		
<i>S. oxycarpum</i>	Mexico	Veracruz	Flores-C. S-792	MEXU, K		
<i>S. oxycarpum</i>	Mexico	Veracruz	Dorantes et al. 1618	ENCB, MEXU		
<i>S. oxycarpum</i>	Mexico	Veracruz	Hawkes and Hernandez 1064	K (6)		
<i>S. oxycarpum</i>	Mexico	Veracruz	Hawkes et al. 1643	K (2)		
<i>S. oxycarpum</i>	Mexico	Veracruz	Hawkes et al. 1645	K (2)		
<i>S. oxycarpum</i>	Mexico	Veracruz	Hawkes et al. 1649	K		
<i>S. oxycarpum</i>	Mexico	Veracruz	Norris and Taranto 16840	MEXU		
<i>S. oxycarpum</i>	Mexico	Veracruz	Ochoa 14213		R6	
<i>S. oxycarpum</i>	Mexico	Veracruz	Rivera-Peña et al. 949	INIFAP, MEXU, PTIS, WAG		
<i>S. oxycarpum</i>	Mexico	Veracruz	Schiede s. n. (type of <i>S. oxycarpum</i>)	HAL (photo at K)		
<i>S. oxycarpum</i>	Mexico	Veracruz	Tarn et al. 286			4x
						2n = 48
<i>S. oxycarpum</i>	Mexico	Veracruz	Ventura 3868	ENCB (2), IEB, MEXU		
<i>S. oxycarpum</i>	Mexico	Veracruz	Ventura 17479	ENCB, IEB, MEXU		
<i>S. oxycarpum</i>	Mexico	Veracruz	Ventura 19639	ENCB, IEB, MEXU		
<i>S. oxycarpum</i>	Mexico	Veracruz	Zamora 1009	IEB, MEXU (2)		
<i>S. agrimonifolium</i>	Mexico	Chiapas	Breedlove 6696	MEXU		
<i>S. agrimonifolium</i>	Mexico	Chiapas	Breedlove 12343	MEXU		
<i>S. agrimonifolium</i>	Mexico	Chiapas	Flores C. S-948	MEXU		
<i>S. agrimonifolium</i>	Mexico	Chiapas	Flores C. S-952	MEXU		
<i>S. agrimonifolium</i>	Mexico	Chiapas	Flores C. S-948	K (3)		
<i>S. agrimonifolium</i>	Mexico	Chiapas	Hawkes 1019	K (4)		
<i>S. agrimonifolium</i>	Mexico	Chiapas	Rivera-Peña et al. 959	INIFAP, MEXU, PTIS, WAG		
<i>S. agrimonifolium</i>	Mexico	Chiapas	Rivera-Peña et al. 960	WAG		
<i>S. agrimonifolium</i>	Mexico	Chiapas	Rivera-Peña et al. 961	INIFAP, MEXU, PTIS, WAG (2)		
<i>S. agrimonifolium</i>	Mexico	Chiapas	Rivera-Peña et al. 963	INIFAP		
<i>S. agrimonifolium</i>	Mexico	Chiapas	Spooner et al. 4227			4x
						2n = 48
<i>S. agrimonifolium</i>	Mexico	Chiapas	Tarn et al. 277			4x
<i>S. agrimonifolium</i>	Guatemala	Chimaltenango	Schwabe s.n.	MEXU		
<i>S. agrimonifolium</i>	Guatemala	Chimaltenango	Spooner et al. 7050		R7	4x
<i>S. agrimonifolium</i>	Guatemala	Chimaltenango	Spooner et al. 7051	WAG	R8	4x
<i>S. agrimonifolium</i>	Guatemala	Huehuetenango	Graham 145A	K (photo LL)	R9	
<i>S. agrimonifolium</i>	Guatemala	Huehuetenango	Purpus 6977 (type of <i>S. agrimonifolium</i>)	F		
<i>S. agrimonifolium</i>	Guatemala	Huehuetenango	Spooner et al. 7061	WAG	R10	4x
<i>S. agrimonifolium</i>	Guatemala	Huehuetenango	Spooner et al. 7062	PTIS		4x
<i>S. agrimonifolium</i>	Guatemala	Huehuetenango	Spooner et al. 7063	WAG		
<i>S. agrimonifolium</i>	Guatemala	Huehuetenango	Spooner et al. 7073	WAG		4x
<i>S. agrimonifolium</i>	Guatemala	Huehuetenango	Spooner et al. 7074	WAG		4x
<i>S. agrimonifolium</i>	Guatemala	Huehuetenango	Steyrmark 49938	K (photo F)		
<i>S. agrimonifolium</i>	Guatemala	Quezaltenango	Graham 136		R11	
<i>S. agrimonifolium</i>	Guatemala	Quezaltenango	Hawkes et al. 1868	K (2)		
<i>S. agrimonifolium</i>	Guatemala	Quezaltenango	Spooner et al. 7019	WAG	R12	
<i>S. agrimonifolium</i>	Guatemala	San Marcos	Beaman 3252	ENCB		

TABLE 2. Continued.

Species	Country	State	Collector	Leaf dissection ¹	RAPDs ²	Ploidy ³
<i>S. agrimonifolium</i>	Guatemala	San Marcos	Hawkes et al. 1851	K (4)		
<i>S. agrimonifolium</i>	Guatemala	San Marcos	Hawkes et al. 1853	K (2)		
<i>S. agrimonifolium</i>	Guatemala	San Marcos	Hawkes et al. 1854	K (2)		
<i>S. agrimonifolium</i>	Guatemala	San Marcos	Spooner et al. 7021	WAG	R13	4x
<i>S. agrimonifolium</i>	Guatemala	San Marcos	Spooner et al. 7026	WAG		4x
<i>S. agrimonifolium</i>	Guatemala	Solalá	Spooner et al. 7036	WAG		4x
<i>S. agrimonifolium</i>	Guatemala	Totonicipán	Hawkes et al. 1889	K		
<i>S. agrimonifolium</i>	Guatemala	Totonicipán	Hawkes et al. 1891	K (2)		
<i>S. agrimonifolium</i>	Guatemala	Totonicipán	Hawkes et al. 1892	K		
<i>S. agrimonifolium</i>	Guatemala	Totonicipán	Spooner et al. 7006	PTIS		4x
<i>S. agrimonifolium</i>	Honduras	Morazán	Hawkes et al. 2035	K		
<i>S. agrimonifolium</i>	Honduras	Morazán	Hawkes et al. 2137	K		
<i>S. longiconicum</i>	Costa Rica	Alajuela	Hope s.n.			4x
						2n = 48
<i>S. longiconicum</i>	Costa Rica	Alajuela	Spooner et al. 7109	PTIS, WAG	R14	4x
<i>S. longiconicum</i>	Costa Rica	Alajuela	Spooner et al. 7122	PTIS, WAG	R15	4x
<i>S. longiconicum</i>	Costa Rica	Cartago	Burger 7969	MO		
<i>S. longiconicum</i>	Costa Rica	Cartago	Burger and Liesner 6466	CR		
<i>S. longiconicum</i>	Costa Rica	Cartago	Hawkes 1128	K		4x
						2n = 48
<i>S. longiconicum</i>	Costa Rica	Cartago	Hawkes 1130	K	R16	
<i>S. longiconicum</i>	Costa Rica	Cartago	Mesén 496	K		
<i>S. longiconicum</i>	Costa Rica	Cartago	Mesén 505	K		
<i>S. longiconicum</i>	Costa Rica	Cartago	Mesén 506	K		
<i>S. longiconicum</i>	Costa Rica	Cartago	Mesén 515	K		
<i>S. longiconicum</i>	Costa Rica	Cartago	Mesén 517	K		
<i>S. longiconicum</i>	Costa Rica	Cartago	Orozco 525	K		
<i>S. longiconicum</i>	Costa Rica	Cartago	Oviedo 522	K		
<i>S. longiconicum</i>	Costa Rica	Cartago	Oviedo 523	K		
<i>S. longiconicum</i>	Costa Rica	Cartago	Oviedo 524	K		
<i>S. longiconicum</i>	Costa Rica	Cartago	Spooner et al. 7101	PTIS, WAG	R17	4x
<i>S. longiconicum</i>	Costa Rica	Cartago	Spooner et al. 7103	PTIS, WAG		4x
<i>S. longiconicum</i>	Costa Rica	Cartago	Spooner et al. 7133	PTIS, WAG	R18	4x
<i>S. longiconicum</i>	Costa Rica	Cartago	Spooner et al. 7136	PTIS, WAG		
<i>S. longiconicum</i>	Costa Rica	Cartago	Werklé 18	F (photo at B)		
<i>S. longiconicum</i>	Costa Rica	Cartago	Werklé 65 (type of <i>S. longiconicum</i>)	F (photo at B)		
<i>S. longiconicum</i>	Costa Rica	Heredia	Pittier 18	K (photo at G)		
<i>S. longiconicum</i>	Costa Rica	Heredia	Skutch 3580	K		
<i>S. longiconicum</i>	Costa Rica	Heredia	Spooner et al. 7105	PTIS, WAG	R19	4x
<i>S. longiconicum</i>	Costa Rica	Heredia	Spooner et al. 7107	PTIS (2)	R20	4x
<i>S. longiconicum</i>	Costa Rica	Limon	Spooner et al. 7116	PTIS, WAG		
<i>S. longiconicum</i>	Costa Rica	San José	Mesén 501	K		
<i>S. longiconicum</i>	Costa Rica	San José	Mesén 513	K		
<i>S. longiconicum</i>	Costa Rica	San José	Roesl 630 (type of <i>S. manoteranthum</i>)	F (photo at M)		
<i>S. longiconicum</i>	Panama	Chiriquí	Davidson et al. 314	F		
<i>S. longiconicum</i>	Panama	Chiriquí	Grayum 6439	MO		
<i>S. longiconicum</i>	Panama	Chiriquí	Knapp 1609	MO		
<i>S. longiconicum</i>	Panama	Chiriquí	Hammel et al. 6717	MO		
<i>S. longiconicum</i>	Panama	Chiriquí	Spooner et al. 7411	CIP, PMA, PTIS		
<i>S. woodsonii</i>	Panama	Chiriquí	Spooner et al. 7405	CIP, EAP, PMA, (2) PTIS		
<i>S. woodsonii</i>	Panama	Chiriquí	Spooner et al. 7413	CIP (4), EAP (3), PMA (4), PTIS (4)		
<i>S. woodsonii</i>	Panama	Chiriquí	Woodson and Scherry 399 (type GH, MO of <i>S. woodsonii</i>)			
South American members of <i>Solanum</i> ser. <i>Conicibaccata</i> (all 2n = 24)						
<i>S. buesii</i>	Peru	Cusco	Ochoa 13637		R21	
<i>S. laxissimum</i>	Peru	unknown	Erwin Baur Sortiment 1888		R22	
<i>S. santolallae</i>	Peru	Cuzco	Commonwealth Potato Collection 2078		R23	
<i>S. santolallae</i>	Peru	Cuzco	Hawkes et al. 5113		R24	
<i>S. violaceimar-moratum</i>	Bolivia	La Paz	Ochoa and Salas 11901		R25	
<i>Solanum</i> sect. <i>Petota</i> ser. <i>Bulbocastana</i> and ser. <i>Piurana</i> (all 2n = 24)						
<i>S. bulbosastanum</i>	Guatemala	Huehuetenango	Spooner et al. 7057		R26	
<i>S. piurae</i>	Peru	Piura	Hawkes 2443		R27	

between the latter two species. This test also determined that both numbers of interjected leaflets and the sum of lateral and interjected leaflets were significantly different only between *S. agrimonifolium* and all other species. Histograms, means, ranges, and standard deviations of these data are shown in Fig. 3. Figure 4 illustrates variation in leaf shapes of these species.

There is considerable intra-accession variation for numbers of lateral and interjected leaflets, as determined by duplicates of the same collections (Table 2). Only four of the 34 collections accessed with more than one plant per collection had invariant numbers of lateral and interjected leaflets. For *S. agrimonifolium*, the largest intra-accession variation was in *Graham S-748* with numbers of lateral and interjected leaflets in three separate plants as (7,10; 7,15; 7,29); in *S. oxycarpum*, *Rivera-Peña et al. 949* with (5,2; 5,3; 6,7); in *S. longiconicum*, *Spooner et al. 7109* with (4,6; 5,3), and in *S. woodsonii*, *Spooner et al. 7413* with (3,0; 4,0; 5,2).

Seed Spot. A new character distinguishing *S. longiconicum* from *S. agrimonifolium* and *S. oxycarpum* was discovered by Spooner et al. (2001). *Solanum longiconicum* has a seed spot that is evident on recently extracted fresh and dried seeds, formed by the purple embryo showing through the light green seed coat. This character is difficult to use on most herbarium specimens, however, because few specimens have mature fruits, they must be dissected to see the character, and we have found it difficult to see seed spots on old specimens. Our recent field work in Panama discovered the first fruiting specimens of *S. woodsonii* (*Spooner et al. 7413*), and shows that this species lacks this seed spot, making *S. longiconicum* the only one of these four species possessing this character.

RAPDs. Eighteen RAPD primers were used to generate 64 RAPD bands polymorphic among the 27 accessions examined in this study, with 4.9% missing data (available at http://www.hort.wisc.edu/faculty/spooner/data_files.htm). All analyses (UPGMA and NJ trees constructed with J or SM coefficients) gave nearly identical topologies, with only minor differences in placement of the phylogenetically most-distant taxa *S. bulbocastanum* and *S. piurae*. All trees had cophenetic correlations (r) from 0.92–0.97, indicating excellent fits to the similarity matrices (Rohlf 1997). The neighbor joining tree constructed with Jaccard's coefficient (Fig. 5, $r = 0.92$) is presented as representative.

The RAPD data distinguish two main groups of the Mexican and Central American polyploid members of ser. *Conicibaccata*, one consisting of *S. agrimonifolium* and *S. oxycarpum* and a second containing *S. longiconicum*. *Solanum agrimonifolium* and *S. oxycarpum* are separated on an internal branch, but show less difference between them than either does to *S. longiconicum*. The diploid members of ser. *Conicibaccata* (*S. buesii*, *S. laxissimum*, *S. santolallae*, *S. violaceimarmoratum*) cluster most closely to the polyploid members, followed by *S. piurae* (ser. *Piurana*) and *S. bulbocastanum* (ser. *Bulbocastana*).

Ploidy Levels. The coefficient of variation of the data peaks in these analyses ranged from 2.8 to 6.0%. The 24 accessions of *S. agrimonifolium*, *S. longiconicum*, and *S. oxycarpum* analyzed by flow cytometry proved to have a DNA content within a very narrow range, and each averaged 2.99 pg/2C nucleus (overall variance = 0.004). There were no significant differences in DNA content among taxa as determined by the Tukey-Kramer HSD test. The very narrow range of DNA contents in all 24 wild potato accessions, and relationship of five of these to prior counts of $2n = 4x = 48$ make our data easy to interpret as all species to be $2n = 4x = 48$.

DISCUSSION

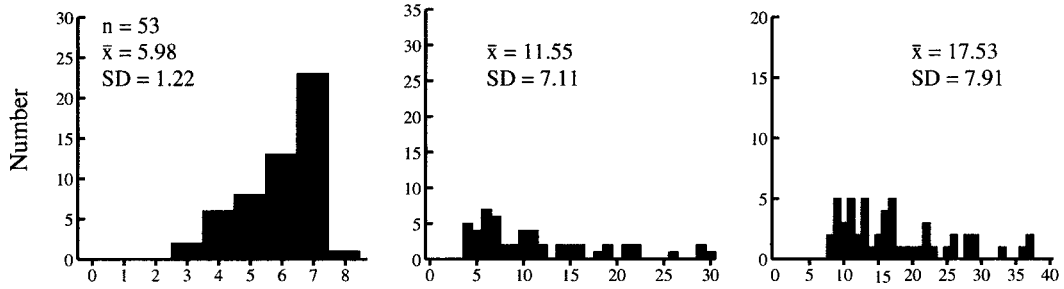
The RAPD data are entirely concordant with topologies produced from cpDNA restriction site data in sect. *Petota*, with separation of the diploid and polyploid members of ser. *Conicibaccata*, and with *S. piurae* and *S. bulbocastanum* as progressively more distantly related (Castillo and Spooner 1997; Spooner and Castillo 1997). The data are also concordant with the morphological data of Castillo and Spooner (1997) in indicating a close morphological similarity of *S. agrimonifolium* and *S. oxycarpum*.

The cpDNA and morphological results of Castillo and Spooner (1997) used only a few accessions of *S. agrimonifolium* and *S. oxycarpum* and suggested that they may be conspecific. Our morphological (Figs. 3, 4) and RAPD (Fig. 5) results support their recognition at some rank. They are morphologically very similar and indeed can be difficult to distinguish on herbarium sheets. Their morphological and RAPD similarity could be used to support their recognition at the subspecies, rather than at the species rank, as was done with *S. toralapanum* Cárdenas and Hawkes (Giannatasio and Spooner 1994) and *S. astleyi* Hawkes and Hjert. and *S. boliviense* Dunal (Spooner et al. 1997). Unlike the taxa in that study, however, *S. agrimonifolium* and *S. oxycarpum* have allopatric distributions (Fig. 2). The combined morphological, distributional, and molecular data lead us to maintain them at the species rank.

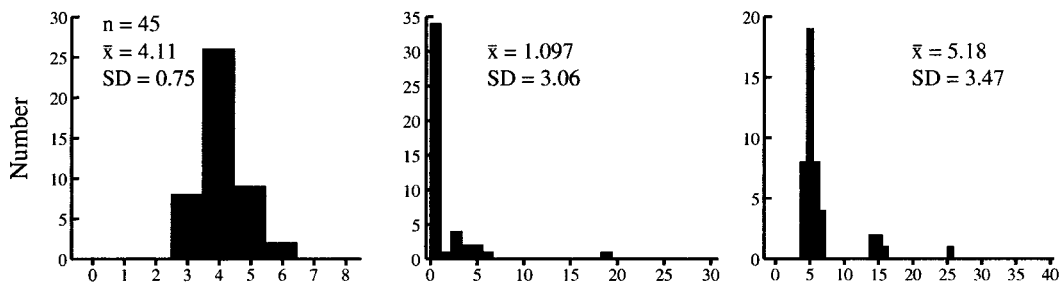
Correll (1962) made *S. longiconicum* a synonym of *S. oxycarpum*. His decision was understandable, considering his access to limited herbarium collections and their morphological similarity, especially on herbarium sheets. Our new collections and field observations, including the discovery of a diagnostic seed spot character (Spooner et al. in press, and above), and our RAPD results (Fig. 5) provide sufficient new data to recognize *S. longiconicum* and *S. oxycarpum* as distinct species.

Combined numbers of lateral leaflets and interjected leaflets usually distinguish *S. agrimonifolium*, despite some overlap with the other species (Figs. 3, 4). The glabrous to nearly glabrous and shiny leaves of *S. longiconicum* make it very easy to distinguish from the other species in the greenhouse and in the field, but it

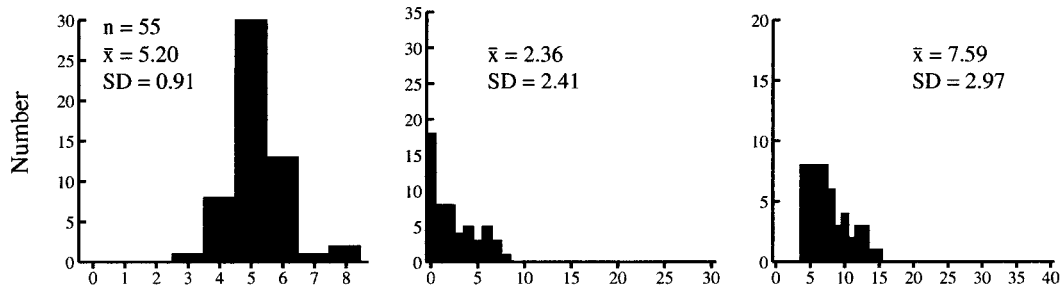
Solanum agrimonifolium



Solanum longiconicum



Solanum oxycarpum



Solanum woodsonii

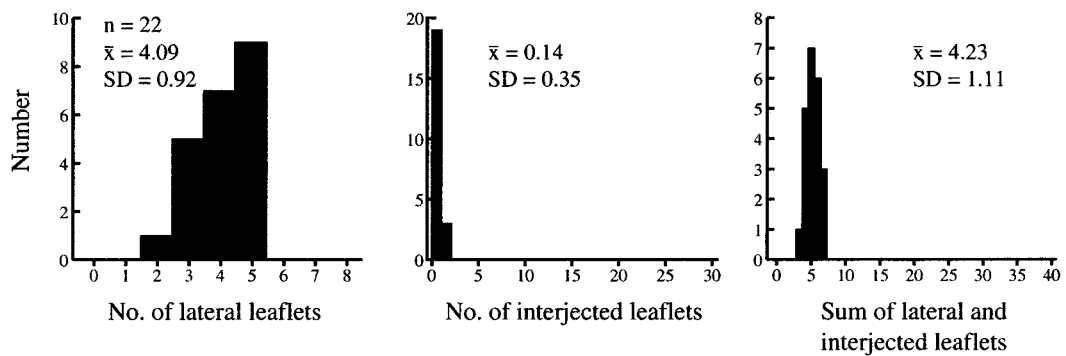


FIG. 3. Distribution of numbers of lateral and interjected leaflets in Mexican and Central American members of *Solanum* series *Conicibaccata*.

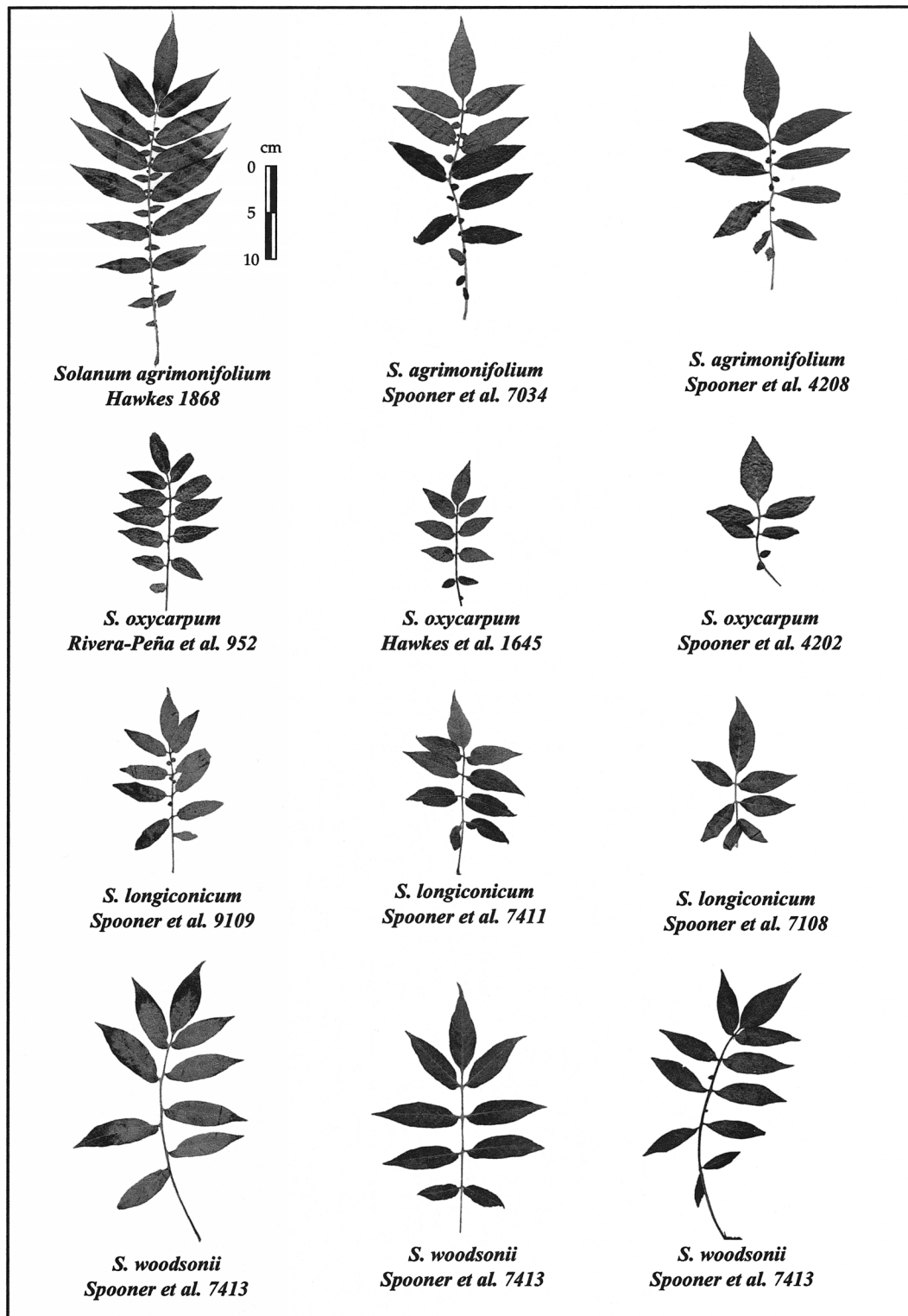


FIG. 4. Variation in leaves of all four species of Mexican and Central American representatives of *Solanum* series *Conicibaccata*.

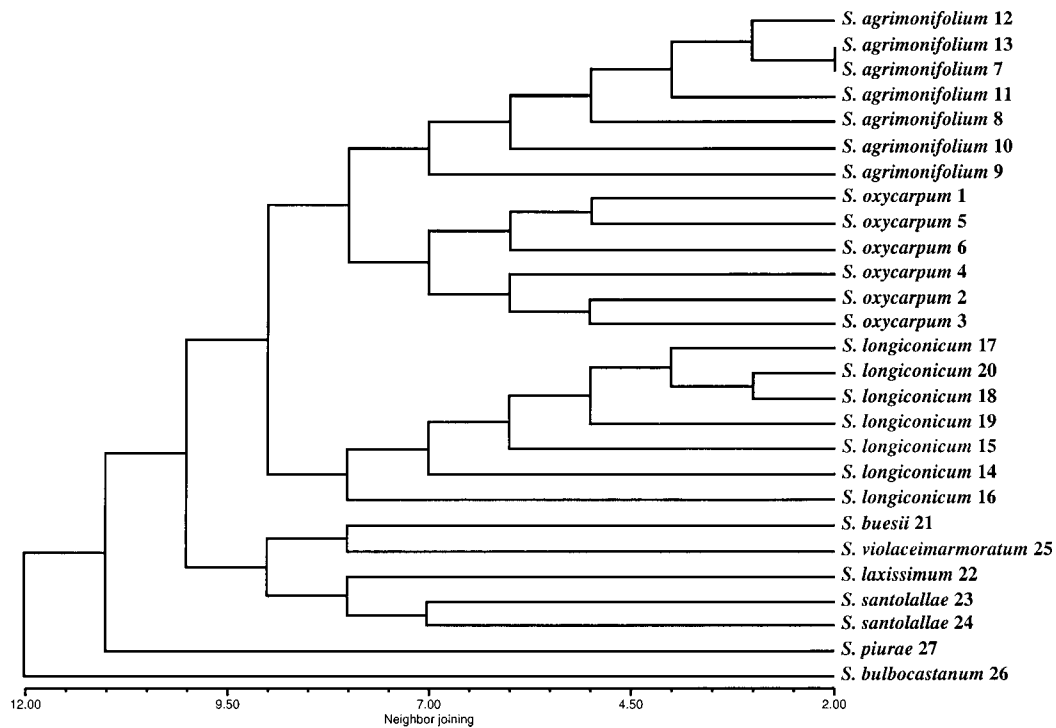


FIG. 5. Neighbor-joining tree (Jaccard's coefficient) based on 64 polymorphic RAPD fragments of the Mexican and Central American species of *Solanum* series *Conicibaccata* and comparison species. The numbers after the species correspond to those in Table 2.

is more difficult to observe these leaf surface differences on herbarium specimens. An additional character distinguishing *S. longiconicum* is its purple seed spot that is evident on recently extracted fresh and dried seeds, as mentioned above. Also, *S. longiconicum* frequently has corollas pure white to purple or lavender, while most specimens of *S. agrimonifolium*, *S. oxycarpum*, and *S. woodsonii* have purple corollas that are only very rarely white in *S. agrimonifolium* and *S. oxycarpum*. *Solanum woodsonii* is most similar to *S. oxycarpum* in leaf shape and dissection and lack of a seed spot, and these species are most difficult to distinguish. They differ by leaf sizes (*S. woodsonii* typically larger) and have significantly different numbers of lateral leaflets, but with overlap of ranges (*S. oxycarpum* more leaflets).

In summary, we do not consider that there is an easy or even "correct" decision on taxonomic limits for these four species. Our decision to maintain *S. agrimonifolium*, *S. longiconicum*, and *S. oxycarpum* as distinct species was influenced by the RAPD data that may merely be showing geographical differentiation among populations of a widespread polymorphic taxon. Our decision to recognize *S. oxycarpum* and *S. woodsonii* as distinct species is based on very limited material of the latter, and additional collections, or future molecular tests, may show greater intergradation of them. The larger leaves distinguishing *S. woodsonii* is not present

on our collection 7405 that was collected in very deep shade, or even on the type that also appears to be a shade-grown plant, as wild potatoes usually grow much smaller in shade. The wide geographical separation of *S. oxycarpum* and *S. woodsonii* also influences our decision, with full realization of disjunct species distributions. Our key frankly will be difficult to use for plants with incomplete specimens or immature material.

TAXONOMIC TREATMENT

SOLANUM SERIES *CONICIBACCATA* Bitter, Feddes Repert. Spec. Nov. Regni Veg. 11: 381. 1912.—Lectotype, chosen by D'Arcy (1972), *S. oxycarpum* Scheide in Schltldl.

Solanum [rankless] *Oxycarpa* Rydb., Bull. Torrey Bot. Club 51: 146, 172. 1924.

[Note: This description applies only to the Mexican and Central American members of ser. *Conicibaccata*]. Plants to 0.2–2.5 m tall; stems 2–13 mm wide at base, green to purple, simple to branched; leaves odd pinnate, lateral leaflets with apex acuminate, base oblique, rounded to cuneate; terminal leaflet ovate to elliptical, apex acute to acuminate, base attenuate; interstitial leaflets absent or present; pseudostipular leaves auriculate; inflorescence terminal, sometimes later displaced lat-

erally; pedicel 15–30 mm long; calyx tube 1.5–5 mm long, lobes 1–8 mm long, short and acute to long attenuate; corolla 2–3 cm in diam, rotate to rotate-pentagonal with short acumens, white to blue to purple, sometimes lined or mottled; filaments 1.5–2 mm long,

anthers 4–5.5 mm long, cordate at base; style exceeding stamens by 2–3.6 mm; fruits conical, rounded to pointed at tip, medium to deep green or sometimes tinged with purple, 1.1–5 cm long. Chromosome number: $2n = 4x = 48$.

KEY TO THE MEXICAN AND CENTRAL AMERICAN MEMBERS OF *SOLANUM* SERIES *CONCIBACCATA*

1. Leaves with (3)6–7(8) pairs of lateral leaflets and 4–31 interjected leaflets; corollas bluish purple *S. agrimonifolium*.
1. Leaves with (2)3–6(8) pairs of lateral leaflets and 0–6(8) interjected leaflets, corollas white to blue to purple.
 2. Leaves shiny, glabrous or with scattered 1–2 celled short hairs; fresh seeds greenish with a conspicuous purple spot caused by the purple embryo showing through the seed coat; corollas pure white to blue or purple *S. longiconicum*.
 2. Leaves not shiny, but finely to coarsely pubescent; fresh seeds greenish throughout and without a spot; corollas typically bluish purple to purple, only rarely white) 3
 3. Larger leaves typically 15–25 cm long, with (3)4–6(8) pairs of lateral leaflets; southeastern Mexico *S. oxycarpum*.
 3. Leaves typically 25–40 cm long, with (2)3–5 pairs of lateral leaflets; western Panama *S. woodsonii*.

SOLANUM AGRIMONIFOLIUM Rydb., Bull. Torrey Bot. Club 51: 154. 1924.—TYPE: MEXICO. Chiapas: Cerro del Boquerón, Sep 1913, *Purpus* 6977 (holotype: US!, [photo: K!, PTIS!]; isotypes: BM!, F! [photo: PTIS!], GH! [photos: K!, F!, PTIS!], MO! [photo: PTIS!], NY [2!] [photos: LL!, PTIS!]).

Plants 0.5–2 m tall; finely pubescent above and below, blades 13–30 cm long, 10–19 cm wide, petioles 1–5 cm long; lateral leaflets (3)5–7(8) pairs, sessile to subsessile with petiolules to 2 mm long; interjected leaflets 4–31; inflorescence with 8–38 flowers; calyx lobes 3–8 mm long, long attenuate; corolla 2–3 cm diam, bluish purple to purple; fruits 2–5 cm long.

Distribution and Habitat (Fig. 2). Southern Mexico (Chiapas), southeast through Guatemala and central Honduras, 1600–3800 m; in wet habitats, in organic soils, in full sun to partial shade, often in cloud forests. Common habitats include recently logged or otherwise recently disturbed areas in valleys, streamsides, upland marshes, or roadside ditches.

Additional Specimens Examined (germplasm collections at NRSP-6 from Mexico are denoted by an asterisk; see Spooner et al. [1998] for specimens from Guatemala and Honduras). MEXICO. **Chiapas:** steep slopes on SE side of Zontehuitz near summit, Municipality of Chamula, 9400 ft, 31 Jul 1964, *Breedlove* 6696 (CAS, LL, MEXU); steep heavily wooded northeast slope of Zontehuitz near summit, Municipality of San Cristóbal las Casas, 9300 ft, 20 Jul 1965 *Breedlove* 11137 (CAS, F, LL); steep northeast slope of Zontehuitz near summit, Municipality of San Cristóbal las Casas, 21 Sep 1965, *Breedlove* 12343 (CAS, MEXU, F, LL); steep canyon, SW side of Cerro Mozotal, 11 km NW of the junction of the road to Motozintla along the road to El Porvenir and Siltepec, Municipality of Motozintla de Mendoza, 2100 m, *Breedlove* 25761 (CAS); high ridge near Niquivil at the junction with a small side ridge to Cerro Boquerón, Municipality of Motozintla de Mendoza, 2600 m, 16 Dec 1976, *Breedlove* 42787 (CAS); Barrio Emiliano Zapata, high mountains between

Huixtla and Motozintla, 2180 m, 9 Jul 1966, *Flores* C. S-948 (MEXU); Cerro Zontehuitz, almost at the top by the microwave station, 2800 m, 9 Jul 1966, *Flores* C. S-952 (MEXU); San Cristóbal las Casas, Cerro Zontehuitz, on path to Los Ángeles, at the highest point, 2900 m, 13 Jul 1949, *Hawkes et al.* 1019 (B, K, LL, P); Fraylesca, near Siltepec, 2000 m, 12 Mar 1945, *Matuda* 5246 (F, LL, MEXU, NA); Amatenango del Valle, 1835 m, 13 Jun 1945, *Matuda* 30161 (MEXU); Cerro Huitepec, W of San Cristóbal, Municipality of Zinacantan, 17 Jul 1985, *Méndez* G. 8353 (MO); Montana Alcolliades, route from Motozintla to Porvenir, Las Silvas, 2830 m, 14 Sep 1980, *Ochoa* 14147 (US); Cerro Zontehuitz, 9.7 km up microwave tower road, turning off the San Cristóbal de las Casas to Tenejapa road, 16°48.87'N, 92°34.96'W, 2800 m, 10 Oct 1997, *Rivera-Peña et al.* 959 (INIFAP, MEXU, PTIS, WAG)*; 50 m walk downhill from the uppermost antenna cluster on Cerro Zontehuitz, by the lower of the two shrines, 16°49.10'N, 92°34.82'W, 2950 m, 10 Oct 1997, *Rivera-Peña et al.* 960 (INIFAP, MEXU, PTIS, WAG)*; 17.4 km N of Rt 190 just S of Motozintla on road to El Porvenir, ca 50 m W of road, 15°24.22'N, 92°10.72'W, 2410 m, 11 Oct 1997, *Rivera-Peña et al.* 961 (INIFAP, MEXU, PTIS, WAG)*; 1.2 km N of town square of El Porvenir, on road to Siltepec, ca 100 m W of road, 15°27.96'N, 92°16.84'W, 2850 m, 11 Oct 1997, *Rivera-Peña et al.* 963 (INIFAP); Cerro Boquerón, Sep 1913, *Rydberg* s. n. (NY, F, GH, MO, US); 6.9 km N of Route 190 beginning S of Motozintla de Mendoza on road to Siltepec, in woods on W side of road, in Ejido Benito Juárez, 15°22'N, 92°17'W, 2005 m, 25 Sep 1988, *Spooner et al.* 4208 (IBUG, INIFAP, PTIS)*; Cerro del Boquerón at Barrio Pizarrin, in woods, on W side of road, 17.4 km N of Route 190 of Motozintla de Mendoza on road to Siltepec, 15°25'N, 92°18'W, 2330 m, 25 Sep 1988, *Spooner et al.* 4211 (INIFAP, PTIS, WIS)*; 12.1 km along road to microwave tower of Zontehuitz, from San Cristóbal de las Casas-Tenejapa road, 0.1 km downhill from microwave tower, along roadside, 16°20'N, 92°17'W, 2790 m, 30 Sep 1988, *Spooner et al.* 4227 (IBUG, INIFAP, PTIS, WIS)*; road from

San Cristóbal de las Casas to Cerro Zontehuitz, 9.7 km along road to microwave tower, turning off the road to Tenejapa, 16°49'N, 92°35'W, 2750 m, 21 Oct 1984, *Tarn et al.* 277 (PTIS)*; road from San Cristóbal de las Casas to Cerro Zontehuitz, 9.8 km along road to microwave tower, turning off road to Tenejapa, 16°49'N, 92°35'W, 2760 m, 21 Oct 1984, *Tarn et al.* 278 (K [cult.], PTIS)*; road from San Cristóbal de las Casas to Cerro Zontehuitz, about 10 km along road to microwave tower, turning off the road to Tenejapa, 16°48'N, 92°35'W, 2760 m, 23 Oct 1984, *Tarn et al.* 280 (PTIS)*.

Solanum longiconicum Bitter, *Repert Spec. Nov. Regni Veg.* 10: 534. 1912.—TYPE: COSTA RICA. Cartago: Irazú, massif of the Irazú, defrichements du Roble, 2000 m, 10 Jul 1891, *A. Tonduz* 4235 (lectotype, chosen here: K! [photos BM! G! Z!]; isolecotypes: BR, CR!, G [3]!, US! Z! [photo LL!, WAG!]).

Solanum manoteranthum Bitter, *Repert Spec. Nov. Regni Veg.* 11: 383. 1912.—TYPE: COSTA RICA. San José: Volcán Barba, *A. Roesl* s. n. (holotype: M! [photos: BM! F!, LL!, PTIS!]).

Plants 0.2–2 m tall; glabrous or with only scattered 2–3 celled short hairs above and below, leaves shiny, blades 8–28 cm long, 5–20 cm wide, petioles 1–5 cm long; lateral leaflets (2)3–5(6) pairs, sessile or with petiolules to 1 cm long; interjected leaflets 0 (most commonly) to rarely 6; inflorescence with 8–16 flowers; calyx lobes 1–3 mm long, short and acute to short attenuate; corolla 2–3 cm in diam, white or light to dark blue to purple, or white with blue to purple stripes or mottling; fruits 1.1–3.9 cm long.

Distribution and Habitat (Fig. 2). Central Costa Rica to western Panama, 1400–3600 m (one Costa Rican record at 1050 m); in wet habitats, in organic soils, in full sun or partial shade, in areas of cloud forests, including disturbed habitats such as landslides, roadcuts, moist garbage heaps, recently plowed soil in forest clearings, recently burned forests, roadside ditches, forest edges, or on rotting tree stumps. When growing in primary forests, it occurs near sunny openings such as paths or streams or treefalls.

Additional Specimens Examined (see Spooner et al. [2001] for specimens and germplasm from Costa Rica). PANAMA. **Chiriquí:** Boquete District, Bajo Chorro, 6000 ft, 18 Feb 1939, *Davidson* 314 (F); at boundary with Prov. Bocas del Toro, along continental divide to ca. 1 km E of Cerro Pate Macho, 8°23'N, 82°23'W, 2100–2200 m, 7 Feb 1986, *Grayum* 6439 (MO); S of Paso Respingo trail to high ridge N of Volcán summit, 10,000–10,800 ft, 4 Apr 1979, *Hammel et al.* 6717 (MO); summit and ridge N of Cerro Pando, 8°55'N, 82°44'W, 2400–2500 m, 15 Oct 1981, *Knapp* 1609 (MO); Distrito y Corregimiento Boquete, E base of Cerro Pata de Macho, ca 100 m S of continental divide at border with Province of Bocas del Toro, located on 1:50,000-

scale map 3742 III, 8°49'N, 82°23'W, 2000 m, Sep 8 2000, *Spooner et al.* 7411 (CIP, PMA, PTIS)*; Distrito Renacimiento; Corregimiento Río Sereno; growing along a path at summit of continental divide separating Panama and Costa Rica, about path leading to the stone division marker at the summit of Cerro Pando, 8°55'14'N, 82°42'46' W, 2445 m, Sep 12 2000, *Spooner et al.* 7414 (CIP, PMA, PTIS)*. **Chiriquí and Bocas del Toro border:** Cerro Horqueta, along foot path from the northern base of Volcán Barú (Volcán de Chiriquí), NW out of Bajo Boquete, walking north to Laguna Escondida, at a local place name (no houses) called Culebras, on both sides of continental divide, 8°51'26'N, 82°28'33'W, 1970 m, Sep 8 2000, *Spooner et al.* 7412 (CIP, PMA, PTIS)*.

Choice of a lectotype is necessary because Bitter cited two syntypes (*A. Tonduz* 4235 and *C. Wercklé* 65). We rejected the latter because it was destroyed at B and only exists as photos (at F, G, GH, LL, NY, US).

Solanum oxycarpum Scheide in *Schldtl., Hort.* hal. 1: 5, tab 3. 1841.—TYPE: MEXICO. Veracruz: in rocky places at Malpays de La Joya, Jun 1929, *C. Schiede* s. n. (lectotype, chosen by Hawkes [1957]: HAL, [photos: K!, PTIS!]).

Plants 0.3–2 m tall; finely to coarsely pubescent above and below, blades 13–25 cm long, 7–15 cm wide, petioles 0.5–5 cm long; lateral leaflets (3)4–6(8) pairs, sessile to subsessile with petiolules to 3 mm long; interjected leaflets 0–8; inflorescence with 8–25 flowers; calyx lobes 3–7 mm long, acute to long-attenuate; corolla 2–3 cm in diam, purple; fruits 2–3.5 cm long.

Distribution and Habitat (Fig. 2). Southeastern Mexico (Hidalgo, Oaxaca, Puebla, Veracruz); from 1870–2870 m; in wet habitats, in organic soils, in full sun to partial shade, growing among shrubs and in pine-oak-alder forests, frequently in pockets of volcanic rocks, often growing among ferns and mosses.

Additional Specimens Examined. MEXICO. **Hidalgo:** mountains NE of Ixtlán de Juárez on road to Tuxtepec, 20-Jul 1968, *Anderson & Anderson* 4850 (ENCB); Municipality of Tenango de Doria, 11 km W of Tenango de Doria, 2100 m, 6 Jul 1979, *Hernandez M.* 3427 (MEXU); 20 km E of Metepec, Municipality of Metepec, 2130 m, 11 Aug 1980, *Hernandez M. and Hernandez V.* 4772 (CAS, ENCB, MEXU); on Metepec-Tenango de Doria Rd, 16 km NE of intersection of this road with road entering Metepec, on S side of road, 20°18.94'N, 98°15.50'W, 2280 m, 4 Oct 1997, *Rivera-Peña et al.* 944 (INIFAP, MEXU, PTIS, WAG)*. **Oaxaca:** Km 25 on the road to Teotitlán from Huautla, right side of a canyon, 8 Nov 1964, *Flores C.* 5-797 (K, LL); Yotao, *Galeotti* 1225P (W); in Sierra Madre Oriental, 29 km E of Teotitlán, 2300 m, 25 Sep 1957, *Graham* 323 (LL); District of Mixe, Municipality of Totontepec, Totontepec, 17°15'N, 96°02'W, 2 Nov 1989, *Rivera R.* 1245 (MEXU); Km 25 on the road from Teotitlán to Huatla, ca 20 m S of road above stream, 18°10.52'N, 97°00.36'W, 2240

m, 4 Oct 1997, *Rivera-Peña et al.* 952 (INIFAP, MEXU, PTIS, WAG)*; Km 27.2 on road from Teotitlán to Huatla, at Puerto Soledad, 18°09.95'N, 96°59.87'W, 2370 m, 4 Oct 1997, *Rivera-Peña et al.* 953 (INIFAP, MEXU)*; District Mixe, Municipality of Totontepec, Totontepec, 17°15'N, 96°00'W, 1900 m, 6 Oct 1986, *Reyes 484* (K, MEXU); 21.8 km N of Ixtlán de Juárez on Hwy 175 to Tuxtepec, 17°28'N, 96°30'W, 2870 m, 17 Oct 1984, *Tarn et al.* 272 (PTIS)*; same locality, 22 Sep 1988, *Spooner et al.* 4200 (INIFAP, IBUG, PTIS); 27 km N of N end of Ixtlán de Juárez on Rt 175 to Tuxtepec, 17°31'N, 96°31'W, 2850 m, 22 Sep 1988, *Spooner et al.* 4202 (INIFAP, PTIS); 8.5 m E. of Rt 135 on road to Huatla, 18 Oct 1981, *Warnock 2506* (TEX). **Puebla:** from Tehuacan to Puebla Rd., turn NE on road to Zoquitlán, 22 km up road, by divergence of road to Coyomeapa, 18°17.84'N, 97°03.96'W, 2640 m, 4 Oct 1997, *Rivera-Peña et al.* 951 (INIFAP, MEXU, PTIS, WAG)*; road from Tehuacan to Oaxaca, turning off at Coxcatlán, 21 km towards Zoquitlán, La Griega, where road divides to Zoquitlán and Coyomeapa, 20°40'N, 100°14'W, 2660 m, 24 Oct 1987, *Tarn et al.* 180 (PTIS)*; road from Tehuacán to Oaxaca turning off at Coxcatlán towards Zoquitlán, 22 km along this road, 1 km past La Griega towards Coyomeapa, 20°40'N, 100°14'W, 2640 m, 24 Oct 1983, *Tarn et al.* 182 (K, PTIS)*. **Veracruz:** Perote, La Joya, 1950 m, 23 Sep 1938, *Balls and Gourlay 5513* (BM, K); La Joya, Jalapa to Perote Rd, Rafael Ramírez, 2100 m, 29 Aug 1972, *Dorantes et al.* 1618 (CAS, ENCB, F, MEXU, TAES, TEX); La Joya Mexico to Veracruz to Jalapa Rd, 100 m on right side of rd, 30 Sep 1964, *Flores C. S-792* (K, LL, MEXU); pedregal de La Joya, 18°14'N, 96°07'W, 2000 m, 27 Aug 1953, *Graham 1* (PTIS)*; upper outskirts of La Joya, 2080 m, 12 Aug 1949, *Hawkes and Hernández 1064* (B, K, LL, MEXU, MPU, P, WAG); near Perote, km 306.5 from Mexico, road from Las Vigas to Jalapa, upper edge of La Joya village, Milpais de La Joya, walled enclosure on the S side of the road, 19°34'N, 97°14'W, 2100 m, 8 Oct 1958, *Hawkes et al.* 1634 (PTIS); near Perote on the road from Las Vigas to Jalapa, upper edge of La Joya village, Milpais de La Joya, 2100 m, 8 Oct 1958, *Hawkes et al.* 1643 (K)*; near Perote, road from Las Vigas to Jalapa, upper edge of the La Joya village, Malpais de La Joya, 19°34'N, 97°14'W, 2100 m, 8 Oct 1958, *Hawkes et al.* 1645 (C, K, MPU, PTIS, US)*; Km 305.5 from Mexico on the road from Las Vigas to Jalapa, Malpais de La Joya, 19°40'N, 98°35'W, 2150 m, 8 Oct 1958, *Hawkes et al.* 1649 (C, K, P, PTIS)*; Municipality of Acajete, along road, Rt 140, 1 km NW of La Joya, 19°37'N, 97°02'W, 2175 m, 7 Sep 1986, *Nee 32990* (NY); old lava field about 4 mi W of Jalapa, 5000 ft, 28 Aug 1970, *Norris & Taranto 16840* (CAS, MEXU); La Joya, route from Jalapa to Puebla, near Perote, 2050 m, 10 Oct 1980, *Ochoa 14213* (PTIS, US)*; La Joya, along Perote to Jalapa road, ca 100 m S of road by the restaurants by the road, 19°36'.74'N, 97°, 2188 m, 2 Oct 1997, *Rivera-Peña et al.* 949 (INIFAP, MEXU, PTIS, WAG)*; Malpais de La Joya between Perote and Jalapa, about 32 km from Perote, Km 176 on

Rt 140, 19°37'N, 97°02'W, 2200 m, 1 Nov 1984, *Tarn et al.* 286 (PTIS)*; Malpais de La Joya between Perote and Jalapa, about 32 km from Perote, Km 176 on Rt 140, 19°37'N, 97°02'W, 2200 m, 1 Nov 1984, *Tarn et al.* 287 (PTIS)*; turning off Rt 140 between Perote and Las Vigas, go S from Sierra de Agua (N slope of Cerro Cofre de Perote); 14 km above Pescados, Rajas, 19°33'N, 97°10'W, 2840 m, 2 Nov 1984, *Tarn et al.* 288 (PTIS)*; Llano Grande, Municipality of Las Vigas, 2115 m, 15 Jul 1971, *Ventura A. 3868* (ENCB, IEB, MEXU); La Joya, Municipality of Acajete, 2050 m, 12 Jul 1980, *Ventura A. 17479* (ENCB, IEB, MEXU); Piedra Blanca, Municipality of Las Vigas, 2250 m, 13 Jul 1982, *Ventura A. 19639* (ENCB, IEB, MEXU); Along Xalapa to Vigas Rd, 200 m E of the road, at the altitude of Toxtlaocoaya, Municipality of Las Vigas, 19°37'N, 97°03'W, 2200 m, 30 Aug 1989, *Zamora C. 1009* (IEB, MEXU). **Locality unknown:** *Liebmann 1394*, 1841–1843 (C [photo K]).

Spooner et al. (2000) noted overlap in numbers of lateral and interjected leaflets in the field in Mexico between *S. agrimonifolium* and *S. oxycarpum*, which led them to question the distinctness of these two species. A collection from Hidalgo (*Rivera-Peña et al.* 944) from within the geographic range of *S. oxycarpum* was especially problematical because of its many lateral and interjected leaflets, this resembling some populations of *S. agrimonifolium*. Our data from three herbarium specimens of this collection (Table 2) show numbers of lateral and interjected leaflets of (8,4; 7,6; 8,7), with the latter counts (specimen at WAG) having the highest numbers of leaflets for *S. oxycarpum*. However, other specimens from outside the range of *S. agrimonifolium* are nearly as dissected (e.g., *Rivera 1245* [MEXU], from Oaxaca with 6,8). Collection *Rivera-Peña et al.* 944 is on the high end of variation for dissection for *S. oxycarpum* (Fig. 3). The RAPD data show it to cluster with other accessions of this species, leading us to recognize it as *S. oxycarpum*.

SOLANUM WOODSONII Correll, *Wrightia* 2: 137. 1961.—

TYPE: PANAMA. Chiriquí: Volcán de Chiriquí, Potrero Muleto to summit, 3500–4000 m, 13–15 July 1940, R. E. Woodson Jr. & R. W. Schery 399 (holotype: GH! [photo: LL!]; isotypes: MO[2]! [photos: BM!, PTIS!], US! [photo: PTIS!]).

Plants 0.3–2.5 m tall; finely to coarsely pubescent above and below, blades 10–42 cm long, 6–22 cm wide, petioles 3–10 cm long; lateral leaflets (2)3–5 pairs, sessile to subsessile with petiolules to 2 mm long; interjected leaflets 0–2; inflorescence with 7–16 flowers; calyx lobes 1.5–2 mm long, acute; corolla 2.8–3.6 cm in diam, purple; fruits 1.5–2.6 cm long.

Additional Specimens Examined. PANAMA. **Chiriquí:** Potrero Muleto, 10,400 ft., Volcán de Chiriquí, *Davidson 1017* (F); Distrito y Corregimiento Boquete, E slopes of Volcán Barú (Volcán de Chiriquí), near the dirt road to the summit of the volcano from Bajo Boquete, along the way to El Salto, above Potrero Muleto,

8°49'15"N, 82°31'47"W, 3015 m, Sep 6 2000, *Spooner et al.* 7405 (CIP, EAP, PMA, PTIS)*; Distrito Bugaba; Corregimiento Cerro Punta, on N-facing slope of Volcán Barú (Volcán de Chiriquí), ascending "sendero [foot-path] de los Quetzales," a trail departing from the park guard station of Alto Respingo, reached by driving on a dirt road ca. 5 km E of the town of Cerro Punta, 8°48'46"N, 82°32'24"W, 3045 m, Sep 9 2000, *Spooner et al.* 7413 (CIP, EAP, PMA, PTIS)*.

Correll (1961) described *S. woodsonii* as possessing a small lobed dorsal base of the anther and indicated that this anther lobe "may be diagnostic." We could not find this lobe on the isotype specimen at GH nor in living material in the field in Panama.

Correll (1962) and Hawkes (1990) indicated that *S. woodsonii* is found in Venezuela. Correll (1962) cited the sole Venezuelan collection of this species as VENEZUELA. Andes of Trujillo and Mérida, 1225–4300 m, *I. Linden* 473 p. p. [FI, G, K]. He cited other specimens of this same collection (at OXF, P, US) as the type of *S. dolichocarpum* Bitter, which he synonymized under *S. colombianum* Bitter. Hawkes (1990) cited no specimen, and Hawkes (1997, database accompanying this publication) cited no specimen of *S. woodsonii* for Venezuela, but rather identified different components of *I. Linden* 473 as *S. colombianum* and *S. oites*.

We made 16 collections of ser. *Conicibaccata* throughout Venezuela (Spooner et al. 1995), and searched the Andean localities of Trujillo and Mérida and points in between. These cities are more than 100 km apart by air and therefore preclude definitive searches for the locality of *Linden* 473. We identify all of our Venezuelan collections as *S. colombianum*. Our examination of *Linden* 473 at G, OXF, P, and US show it to be *S. colombianum*. In agreement with Ochoa (1979) we do not think that *S. woodsonii* occurs in Venezuela.

ACKNOWLEDGEMENTS. We thank the following for funding collecting expeditions: United States Department of Agriculture, Agricultural Research Service; Wageningen University; the Netherlands Organization for Scientific Research (NWO); the Instituto Nacional Investigaciones Forestales Agropecuarias (INIFAP); the International Cooperative Program for Potato Late Blight (PCTI-PAPA); Fondo Terra, a funding agency of PULSAR, a private investment group headquartered in Monterrey, Mexico; the Institut für Pflanzengenetik und Kulturpflanzenforschung Gatersleben; Gemeinschaft zur Förderung der Kulturpflanzenforschung Gatersleben e. V.; the International Potato Center; and the Instituto de Investigaciones Agropecuarias, Panama (IDIAP).

We also thank Lynn Bohs and Thomas G. Lammers who provided reviews; Alan Stoner of the USDA, Agricultural Research Service, for importing herbarium and germplasm collections into the United States; Charles J. Fernandez (NRSP-6) for pointing out the seed spot character distinguishing *S. longiconicum*, and John Bamberg (NRSP-6), for increasing germplasm after passage through United States quarantine.

LITERATURE CITED

- BAMBERG, J. B., M. W. MARTIN, J. J. SCHATNER, and D. M. SPOONER. 1996. Inventory of tuber-bearing *Solanum* species: catalog of potato germplasm. Potato Introduction Station, NRSP-6, Sturgeon Bay, Wisconsin.

- CASTILLO-T., R. and D. M. SPOONER. 1997. Phylogenetic relationships of wild potatoes, *Solanum* series *Conicibaccata* (sect. *Petota*). *Systematic Botany* 22: 45–83.
- CORRELL, D. S. 1961. Four new *Solanums* in section *Tuberarium*. *Wrightia* 2: 133–141.
- . 1962. The potato and its wild relatives. Contributions from the Texas Research Foundation, Botanical Studies 4: 1–606.
- D'ARCY, W. G. 1972. Typification of subdivisions of *Solanum* L. *Annals of the Missouri Botanical Garden* 59: 262–278.
- DICKSON, E. E., K. ARUMUGANATHAN, S. KRESOVICH, and J. J. DOYLE. 1992. Nuclear DNA content variation within the Rosaceae. *American Journal of Botany* 79: 1081–1086.
- GIANNATTASIO, R. B. and D. M. SPOONER. 1994. A reexamination of species boundaries and hypotheses of hybridization concerning *Solanum megistacrolobum* and *S. toralapanum* (*Solanum* sect. *Petota*, series *Megistacroloba*): molecular data. *Systematic Botany* 19: 106–115.
- HANNEMANN, R. E. JR. and J. B. BAMBERG. 1986. Inventory of tuber-bearing *Solanum* species. Wisconsin Agricultural Experiment Station Bulletin 533: 1–216.
- HAWKES, J. G. 1957. On the lectotype of *Solanum stoloniferum* Schlechtendal et Bouché, *S. oxycarpum* Schiede and *S. verrucosum* Schlechtendal. *Wissenschaftliche Zeitschrift der Martin-Luther-Universität Halle-Wittenberg* 6(5): 849–854.
- . 1990. *The potato: evolution, biodiversity and genetic resources*. Oxford: Belhaven Press.
- . 1997. A database for wild and cultivated potatoes. *Euphytica* 93: 155–161.
- HOLMGREN, P. K., N. H. HOLMGREN, and L. C. BARNETT. 1990. *Index herbariorum, part I: the herbaria of the world*. Ed. 8. Bronx, New York: New York Botanical Garden.
- JACCARD, P. 1908. Nouvelles recherches sur la distribution florale. *Bulletin de la société vaudoise des sciences naturelles* 44: 223–270.
- MILLER, J. T. and D. M. SPOONER. 1999. Collapse of species boundaries in the wild potato *Solanum brevicaulum* complex (Solanaceae: sect. *Petota*): molecular data. *Plant Systematics and Evolution* 214: 103–130.
- OCHOA, C. M. 1979. Nueva papa silvestre Venezolana de la serie *Conicibaccata*. *Biota* 11: 331–333.
- ROHLF, F. J. 1997. *NTSYS-pc: numerical taxonomy and multivariate analysis system*. version 2.0. Setauket, New York: Exeter Software.
- and R. R. SOKAL. 1981. Comparing numerical taxonomic studies. *Systematic Zoology* 30: 459–490.
- SAS. 1995. *JMP Software*, Version 3.1. Cary, NC: SAS Institute Inc.
- SOKAL, R. R., 1986. Phenetic taxonomy: theory and methods. *Annual Review of Ecology and Systematics* 17: 423–442.
- SPOONER, D. M. and R. CASTILLO-T. 1997. Reexamination of series relationships of South American wild potatoes (Solanaceae: *Solanum* sect. *Petota*): evidence from chloroplast DNA restriction site variation. *American Journal of Botany* 84: 671–685.
- , J. B. BAMBERG, J. P. HJERTING, and J. GÓMEZ. 1991. Mexico, 1988 potato germplasm collecting expedition and utility of the Mexican potato species. *American Potato Journal* 68: 29–43.
- , R. CASTILLO-T., L. LÓPEZ J., R. PINEDA, R. LEÓN P., A. VARGAS, M. L. GARCÍA, and J. B. BAMBERG. 1995. Colombia and Venezuela 1992 wild potato (*Solanum* sect. *Petota*) collecting expedition: taxonomy and new germplasm resources. *Euphytica* 81: 45–56.
- , R. HOEKSTRA, R. G. VAN DEN BERG, and V. MARTÍNEZ. 1998. *Solanum* sect. *Petota* in Guatemala; taxonomy and genetic resources. *American Journal of Potato Research* 75: 3–17.
- , R. HOEKSTRA, and B. VILCHEZ. 2001. *Solanum* sect. *Petota*

- in Costa Rica; taxonomy and genetic resources. *American Journal of Potato Research* 78: 91–98.
- , A. RIVERA-PENA, R. G. VAN DEN BERG, and K. SCHÜLER. 2000. Potato germplasm collecting expedition to Mexico in 1997: taxonomy and new germplasm resources. *American Journal of Potato Research* 77: 261–270.
- , J. TIVANG, J. NIENHUIS, J. P. MILLER, D. S. DOUCHES, and A. CONTRERAS-M. 1996. Comparison of four molecular markers in measuring relationships among the wild potato relatives *Solanum* section *Etuberosum* (subgenus *Potatoe*). *Theoretical and Applied Genetics* 92: 532–540.
- , M. L. UGARTE, and P. W. SKROCH. 1997. Species boundaries and interrelationships of two closely related sympatric diploid wild potato species, *Solanum astleyi* and *S. boliviense*, based on RAPDs. *Theoretical and Applied Genetics* 95: 764–771.