REEXAMINATION OF SERIES RELATIONSHIPS OF SOUTH AMERICAN WILD POTATOES (SOLANACEAE: *SOLANUM* **SECT.** *PETOTA*): EVIDENCE FROM CHLOROPLAST **DNA RESTRICTION SITE VARIATION**¹

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Chloroplast DNA (cpDNA) restriction enzyme site analysis was used to test hypotheses of series and superseries affiliations of 76 taxa, representing 11 of the 13 South American series (material unavailable for two series) of wild potatoes (Solanum sect. Petota) recognized in the latest classification by Hawkes. The cladistic results, combined with those from earlier cpDNA studies of 30 taxa of the Mexican and Central American species (representing eight series; ser. Conicibaccata and ser. Tuberosa have representatives in Mexico and in South America), support four main clades for 17 of the 19 series examined in sect. Petota: (1) the Mexican and Central American diploid species, exclusive of *S. bulbocastanum, S. cardiophyllum*, and *S. verrucosum*, (2) *S. bulbocastanum* and *S. cardiophyllum* (ser. Bulbocastana, ser. Pinnatisecta), (3) South American diploid species constituting all of ser. Piurana, but also members of ser. Conicibaccata, ser. Megistacroloba, ser. Tuberosa, and ser. Yungasensia, (4) all Mexican and Central American polyploid species (ser. Longipedicellata, ser. Demissa), *S. verrucosum* (diploid Mexican species in ser. Tuberosa), and South American diploid and polyploid members of ser. Acaulia, ser. Circaeifolia, ser. Commersoniana, ser. Conicibaccata, ser. Lignicaulia, ser. Maglia, ser. Megistacroloba, ser. Tuberosa, and ser. Yungasensia. Each of these clades contains morphologically and reproductively very diverse species, and there are no evident morphological features that unite members within a clade to therefore distinguish them. These results strongly suggest a need for a reevaluation of the series and superseries classifications of sect. Petota.

Key words: chloroplast DNA; phylogeny; potato; Solanaceae; Solanum sect. Petota; systematics; taxonomy.

Species of Solanum L. sect. Petota Dumort., the potatoes and their wild relatives, grow from the southwestern United States to south-central Chile. According to the classifications of Correll (1962) and Hawkes (1990), sect. Petota contains both tuber- and nontuber-bearing species. An alternative classification (Child, 1990), later supported by morphological and chloroplast DNA (cpDNA) data (Spooner, Anderson, and Jansen, 1993), places all of the tuber-bearing species in sect. Petota, and the nontuberbearing species in sect. Etuberosum (Bukasov and Kameraz) A. Child, sect. Juglandifolium (Rydb.) A. Child, and sect. Lycopersicum (Mill.) Wettst. Ploidy in sect. Petota (sensu stricto) includes diploid (2n = 2x = 24), tetraploid (2n = 4x = 48), and hexaploid (2n = 6x = 72)levels, with occasional triploid and pentaploid populations.

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Section *Petota* is taxonomically difficult, with much disagreement regarding species boundaries, number of series and affiliation of species to series, rank of infraspecific taxa, and hypotheses of hybridization (Spooner and Sytsma, 1992; Spooner and van den Berg, 1992a). Correll (1962) recognized 148 tuber-bearing species, partitioned into 24 series. Hawkes (1990) recognized 224 tuber-bearing species, partitioned into 19 series. Ochoa has provided floristic treatments for Peru (Ochoa, 1962) and Bolivia (Ochoa, 1990), and has published many new South American species in sect. *Petota*, where he usually designated affiliations of species to series. For the purposes of discussion, we use the series classification of Hawkes (1990) in this paper.

Endosperm Balance Numbers (EBN) are interspecific isolating mechanisms, based on endosperm breakdown in EBN cross-incompatible hybrids, that have been used with distributional and morphological data to speculate about relationships in sect. Petota (Hawkes, 1990; Hawkes and Jackson, 1992; Ortiz and Ehlenfeldt, 1992). The Endosperm Balance Number hypothesis (Johnston et al., 1980) suggests that normal seed development depends on a 2:1 maternal to paternal balance of genetic factors in the endosperm, independent of ploidy. Species are assigned EBN's based on their ability to cross within EBN levels, irrespective of ploidy level. Endosperm Balance Numbers of species belonging to sect. Petota have been published by Hanneman and Bamberg (1986), Hawkes and Jackson (1992), and Ochoa (1992a). Within sect. Petota, species can be 2x(1EBN), 2x(2EBN), 4x(2EBN),

Table 1.	Distribution, pl	loidy, Endosperm	Balance Numbers	s (EBN), and s	superseries d	esignations of th	e 19 tuber-bearing	series of Solanum sect.
Petota	, according to t	he putative evolut	tionary progressio	n of series and	d superseries	of Hawkes (199	0) and Hawkes and	d Jackson (1992).

Series	Distribution	Ploidy (EBN)	Superseries ^a
Morelliformia Hawkes	Mexico, Guatemala	2 <i>x</i> (1EBN)	SP
Bulbocastana (Rydb.) Hawkes	Mexico, Guatemala	2x(1EBN)	SP
Pinnatisecta (Rydb.) Hawkes	SW USA, Mexico	2x(1EBN)	SP
Polyadenia Correll	Mexico	2x(1EBN)	SP
Commersoniana Bukasov	Brazil, Uruguay, Argentina	2x(1EBN)	SP
Circaeifolia Hawkes	Bolivia	2x(1EBN)	SP
Lignicaulia Hawkes	Peru	2x(1EBN)	SP
Olmosiana Ochoa	Peru	2x(1EBN)	SP
Yungasensia Correll ^b	Peru, Bolivia, Brazil, Paraguay, Ar- gentina	2x(2EBN)	SA
Megistacroloba Cárdenas and Hawkes	Peru, Bolivia, Argentina	2x(2EBN)	RP
Cuneoalata Hawkes	Argentina, Bolivia, Peru	2x(2EBN)	RP
Conicibaccata Bitter-southern South Americac	Peru, Bolivia	2x(2EBN)	RP
Maglia Bitter	Chile	2x, $3x$ (?EBN)	RP
Tuberosa (Rydb.) Hawkes-southern South America ^e	Peru, Bolivia, Argentina, Chile	2 <i>x</i> (2EBN), 4 <i>x</i> (4EBN), 6 <i>x</i> (4EBN)	RP
Piurana Hawkes	Colombia, Ecuador, Peru	2x(2EBN), 4x(2EBN)	RA
Ingifolia Correll	Peru	$2x(1\text{EBN})^{d}$	RA
<i>Conicibaccata</i> —northern South America ^c , southern Mexico and Central America	Venezuela, Colombia, Ecuador, southern Mexico and Central America	2 <i>x</i> (1EBN), 4 <i>x</i> (2EBN), 6 <i>x</i> (4EBN)	RA
Tuberosa—northern South America ^c , Mexico	Colombia, Ecuador, Mexico	2 <i>x</i> (1EBN), 4 <i>x</i> (2EBN), 6 <i>x</i> (4EBN)	RA
Acaulia	Ecuador, Peru, Bolivia, Argentina	4x(2EBN), 6x(4EBN)	RA
Longipedicellata Juz.	SW USA, Mexico	4 <i>x</i> (2EBN)	RA
Demissa Juz.	Mexico and Central America	6x(4EBN)	RA

^a Superseries designations according to Hawkes (1990) and Hawkes and Jackson (1992). SP = primitive Stellata; SA = advanced Stellata; RP = primitive Rotata; RA = advanced Rotata (see text).

^b Correll (1962) described ser. *Yungasensa*, a spelling used by later authors. The spelling *Yungasensia* conforms to the rules of botanical nomenclature (Spooner and van den Berg, 1992a).

^c Hawkes (1990) and Hawkes and Jackson (1992) partitioned ser. *Conicibaccata* and ser. *Tuberosa* into primitive *Rotata* and advanced *Rotata*, and placed the geographical boundary that divided each group in northern South America. They were not specific regarding the actual boundary, and for the purposes of this paper we place it at the Ecuador-Peru boundary.

^d Ochoa (1992a) first reported the EBN of the two species Hawkes (1990) places in this series (*S. ingaefolium* Ochoa, *S. raquialatum* Ochoa), previously reported as 2x, to be 2x(1EBN).

4x(4EBN), and 6x(4EBN) (Hanneman, 1994). Many of the 2x(1EBN) species occur in Mexico and Central America, but eight tuber-bearing 2x(1EBN) species occur in South America (Table 1).

Hawkes (1989) further grouped the 19 tuber-bearing series into superseries Stellata Hawkes and superseries Rotata Hawkes. Hawkes (1990) and Hawkes and Jackson (1992) informally divided each superseries into primitive and advanced groups (Table 1), based on Endosperm Balance Numbers (EBN), corolla colors and shapes, and geographical distribution. They hypothesized the following evolutionary scenario: (1) sect. Petota arose in Mexico and Central America as 2x(1EBN) species possessing white stellate corollas, and remnant or derivative 2x(1EBN) species remain there (primitive *Stellata*), (2) 2x(1EBN) species retaining white stellate corollas (also primitive Stellata) migrated into South America in the early Pliocene, (3) 2x(1EBN) species evolved to 2x(2EBN) species with white but less stellate corollas (advanced Stellata), (4) the "advanced Stellata" evolved to 2x(2EBN), 4x(4EBN), and 6x(4EBN) species with more rotate corollas (primitive *Rotata*), (5) finally, the "primitive Rotata" at various ploidy levels and EBN's evolved to 2x(2EBN), 4x(2EBN), and 6x(4EBN), and a few 2x(1EBN) species (apparently as an EBN reversal), with very rotate corollas (advanced Rotata). They designated members of the widespread ser. Conicibaccata and ser. *Tuberosa* in southern South America as primitive *Rotata*, and those in northern South America and Mexico and Central America as advanced *Rotata*. The "south" and "north" geographical boundaries in South America delimiting these groups were not explicitly stated by these authors; for the purposes of this paper we place it at the Ecuador-Peru boundary (Table 1). No quantitative analyses of corolla shapes were conducted to support the superser. *Stellata/Rotata* hypothesis.

Genomic data have contributed to hypotheses of relationships of the Mexican and Central American ser. Longipedicellata and ser. Demissa. Hawkes (1990), following Marks (1955), Irikura (1976), Ramanna and Hermsen (1979), and Matsubayashi (1981), hypothesized all members of the polyploid Mexican and Central American ser. Longipedicellata 4x(2EBN) (six species) and ser. Demissa 6x(4EBN) (six species) to be of allopolyploid origin, containing a common A genome. He designated both series as advanced Rotata. The other genomes are designated as B in ser. Longipedicellata, and B, C, or D in ser. Demissa. The sole resident Mexican diploid A genome species, S. verrucosum, is a putative A genome contributor to species in ser. Demissa (Hawkes, 1990). Prior cpDNA analyses of the Mexican and Central American species (Spooner, Sytsma, and Conti, 1991; Spooner and Sytsma, 1992) provided partial support for this hypothesis by demonstrating the paraphyletic nature of the

Mexican and Central American diploid species (or their derivatives), and the close cladistic relationship of *S. ver-rucosum* with members of ser. *Longipedicellata* and ser. *Demissa*.

In previous broad-scale phylogenetic studies using cpDNA, Hosaka et al. (1984) examined cladistic relationships of 26 species representing 14 of the series of Hawkes (1963), and outgroups in sect. Etuberosum, sect. Juglandifolium, and sect. Lycopersicum, from total cpDNA digests with eight restriction endonucleases. Spooner, Sytsma, and Conti (1991) and Spooner and Sytsma (1992) examined cladistic relationships of 30 species of all eight of the Mexican and Central American series, five species of two of the South American series, and sect. Etuberosum (outgroup) with sequential probing of the entire chloroplast genome, using 22 restriction endonucleases. The purpose of the present study is to provide a global analysis of series relationships in sect. Petota by expanding these prior studies to include representatives of all available remaining series in sect. Petota, and to compare these data to the evolutionary/biogeographic hypotheses of other workers.

MATERIALS AND METHODS

Species—We examined 78 accessions of 76 ingroup taxa, representing 11 of the 13 South American series (Tables 1, 2), and one accession of sect. *Etuberosum* (outgroup). One diploid ingroup taxon from Argentina is undescribed. Two species, *S. chacoense* and *S. sucrense*, are represented by two separate accessions per species. Five species, *S. curtilobum, S. doddsii, S. raphanifolium, S. sucrense*, and *S. tuberosum*, are of putative hybrid origin (of 27 total putative hybrid species in sect. *Petota* listed in Spooner and van den Berg, 1992b). Many of the other putative hybrid species are in ser. *Longipedicellata* (4x) and ser. *Demissa* (6x) and were investigated in Spooner and Sytsma (1992). Most of the remaining 232 species of sect. *Petota* listed by Hawkes (1990) are rare and not available. This cpDNA study, combined with that of Spooner, Sytsma, and Conti (1991) and Spooner and Sytsma (1992) examined 17 of the 19 tuber-bearing species (only ser. *Ingifolia* and ser. *Olmosiana* were not studied).

For comparison of results to Spooner and Sytsma (1992), we included previously examined accessions of S. cardiophyllum, S. chancayense, S. colombianum, and S. pinnatisectum, and different accessions of species previously examined (S. bulbocastanum, S. morelliforme, and S. verrucosum). Solanum palustre was used as an outgroup based on results of Spooner, Anderson, and Jansen (1993). This species is referred to in earlier studies as S. brevidens, but was combined with this species in a recent revision (Contreras and Spooner, in press). All accessions were from the United States Potato Introduction Project in Sturgeon Bay, Wisconsin, referred to as the National Research Support System-6 (NRSP-6; Bamberg et al., 1996). Identifications of most of these accessions have been provided by visiting taxonomists to the genebank (Hanneman, 1989). Most identifications were provided by Jack Hawkes (University of Birmingham, England), Carlos Ochoa (International Potato Center, Lima, Peru), and K. Armando Okada (Instituto Nacional de Tecnología Agropecuaria, Balcarce, Argentina). Herbarium vouchers are at PTIS [the new herbarium code to appear in the forthcoming edition of Index Herbariorum (Holmgren, Holmgren, and Barnett, 1990; Bamberg and Spooner, 1994)].

Chloroplast DNA—Pooled leaf samples of six plants per accession were collected from 2-mo-old plants for DNA extraction. Preparations of total DNA were made from 5 g of fresh leaf tissue by the procedure of Doyle and Doyle (1987). DNA was purified over CsCl/ethidium bromide gradients. Restriction endonuclease digestions, agarose-gel elec-

trophoresis, unidirectional Southern transfers to nylon membranes (Biotrans[®]ICN Biochemicals, Costa Mesa, CA), filter hybridization, and autoradiography followed methods in Palmer (1986).

Chloroplast clones were radiolabeled by ³²P-dCTP by the oligo-labeling method of Feinberg and Vogelstein (1984). Two micrograms of each DNA sample were digested with 22 restriction endonucleases to examine cpDNA variation: *AvaI, Bam*HI, *BanI, BcII, BgIII, BstNI, ClaI, DraI, Eco*O109, *Eco*RI, *Eco*RV, *HincII, HindIII, HpaI, HpaII, HphI, NciI, NsiI, SstI, XbaI, XhoI,* and *XmnI.* Membranes were probed with 12 *PstI* and two *SaII* clones of *Petunia* (Sytsma and Gottlieb, 1986), and five clones of *Nicotiana* in the small single-copy region (Olmstead and Palmer, 1992) covering the entire chloroplast genome.

Phylogenetic reconstructions were performed with PAUP, version 3.1.1 (Swofford, 1993). The data were analyzed using Wagner parsimony (Farris, 1970). To find multiple islands, we used a four-step search strategy (modified from Olmstead and Palmer, 1994). (1) Ten thousand replicates initially were run using random order entry starting trees with nearest neighbor joining (NNI). (2) The shortest trees from this analysis were used individually as starting trees with the tree bisection-reconnection method (TBR). (3) The resulting trees were searched with NNI, retaining all most parsimonious trees (MULPARS). (4) The resulting trees were searched with TBR and MULPARS. Additionally, the character-state weighting method of Albert, Mishler, and Chase (1992) was used with weights of 1.1 and 1.3 given to site gains. A bootstrap analysis was conducted on 100 replicates with NNI and MULPARS (Felsenstein, 1985). Decay analyses were conducted with inverse constraint searches in PAUP. A separate PAUP analysis was conducted with the elimination of all five species of putative hybrids investigated (Materials and Methods) except S. raphanifolium. This species was not supported as a hybrid by data from cpDNA, nuclear ribosomal DNA, and singleto low-copy nuclear DNA restriction site data (Spooner, Sytsma, and Smith, 1991; Giannattasio and Spooner, 1994).

RESULTS

A total of 200 restriction enzyme site variants were identified (Tables 3, 4), 89 of which were phylogenetically informative. All characters were restriction enzyme site variants. Over 5000 equally parsimonious trees were possible for the data set, and we had to constrain the program to save no more than 5000 trees when the MUL-PARS option was in effect because of computer memory restrictions. We further tested the shortest length of this tree by loading a strict consensus tree of these 5000 trees as a constraint tree and performed an inverse constraint analysis using procedures for searching shortest trees. Wagner parsimony produced 5000 most parsimonious 319-step trees (e.g., Fig. 1) with a consistency index of 0.49 (without autapomorphies), and a retention index of 0.79. Weighted parsimony, with weights of 1.1 and 1.3 in favor of gains over losses, generated trees identical to two of the Wagner trees.

A strict consensus tree supported four clades (Figs. 1,2). The following discussion of these clades uses the series and superseries classification of Hawkes (1990; Tables 1,2): (1) the Mexican and Central American diploid species, exclusive of *S. bulbocastanum*, *S. cardiophyllum*, and *S. verrucosum*; (2) *S. bulbocastanum* and *S. cardiophyllum* (ser. *Bulbocastana* and ser. *Pinnatisecta*, respectively), (3) South American diploid species constituting all seven members of ser. *Piurana*, but also members of ser. *Conicibaccata*, ser. *Megistacroloba*, ser. *Tuberosa*, and ser. *Yungasensia*, (4) *S. verrucosum* (diploid Mexican species in ser. *Tuberosa*), and South American diploid and polyploid members of ser. *Acaulia*, ser. *Cir*-

Table 2.	Solanum sect.	Petota accessions	examined for cp	DNA variation	. Species a	ure assigned t	o series a	ccording to the	classification:	s of Correll
(1962), Ochoa (1962,	, 1963, 1972, 1979	9, 1981, 1990, 199	92b), and Hawk	es (1990),	and ordered a	according	to the putative	evolutionary j	progression
of ser	ies and superse	ries of Hawkes (1	990) and Hawke	s and Jackson	(1992).					

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	S. medians Bitter	283081	2x(2EBN)	Tuberosa	Tuberosa	Tuberosa 2	RP
S. mochiquense Ochoa 283114 2x(1EBN) Piurana Tuberosa Tuberosa 2 RP	S. mochiquense Ochoa	283114	2x(1EBN)	Piurana	Tuberosa	Tuberosa 2	RP
S. multidissectum Hawkes 210043 2x(2EBN) Transaequatorialia Tuberosa Tuberosa 2 RP	S. multidissectum Hawkes	210043	2x(2EBN)	Transaequatorialia	Tuberosa	Tuberosa 2	RP

TABLE 2. Continued.

		Plaidub		Series ^d		
Species	\mathbf{PI}^{a}	EBN ^c	Correll	Ochoa	Hawkes ^e	Superseries ^f
S. scabrifolium Ochoa	365363	2 <i>x</i> (?EBN)		Tuberosa	Tuberosa 2	RP
S. acroglossum Juz.	365313	$2x(2EBN)^{g}$	Piurana	Tuberosa	Piurana	RA
S. albornozii Correll	498206	$2x(2EBN)^{g}$	Piurana		Piurana	RA
S. hypacrarthrum Bitter	473477	$2x(1\text{EBN})^{g}$	Piurana	Tuberosa	Piurana	RA
S. pascoense Ochoa	365339	2x(2EBN)	Transaequatorialia	Tuberosa	Piurana	RA
S. paucissectum Ochoa	473489	2x(2EBN)	Piurana	Piurana	Piurana	RA
S. piurae Bitter	310997	$2x(2EBN)^{g}$	Piurana	Piurana	Piurana	RA
S. tuquerrense Hawkes	498177	4x(2EBN)	Ingaeifolia	Piurana	Piurana	RA
S. agrimonifolium Rydb.	243349	4x(2EBN)	Conicibaccata		Conicibaccata	RA
S. colombianum Dunal	218217	4x(2EBN)	Conicibaccata	Conicibaccata	Conicibaccata	RA
S. longiconicum Bitter	186568	4x(?EBN)	Conicibaccata		Conicibaccata	RA
S. moscopanum Hawkes	498159	6x(4EBN)	Conicibaccata	Conicibaccata	Conicibaccata	RA
S. subpanduratum Ochoa	498289	4x(?EBN)		Conicibaccata	Conicibaccata	RA
S. tundalomense Ochoa	473474	4x(?EBN)		Conicibaccata	Conicibaccata	RA
S. andreanum Baker	498148	2x(?EBN)	Transaequatorialia	Tuberosa	Tuberosa 1	RA
S. verrucosum Schltdl.	275260	2x(2EBN)	Demissa		Tuberosa 1	RA
S. curtilobum Juz. and Bukasov	225649	$4x(4\text{EBN})^{h}$		Tuberosa	Tuberosa cult.	R
S. tuberosum L. ssp. tuberosum	161401	4x(4EBN)	Tuberosa	Tuberosa	Tuberosa cult.	R
S. acaule Bitter	225620	4x(2EBN)	Acaulia	Acaulia	Acaulia	RA
Undescribed species	473204	2 <i>x</i> (?EBN)				

^a USDA plant introduction numbers (Bamberg et al., 1996).

^b $2x = 2\hat{4}$, taken from summary in Hawkes (1990) unless otherwise noted.

^c Endosperm Balance Numbers (see text).

^d All recognized as series under sect. *Petota* except sect. *Etuberosum*. Missing series affiliations are caused by species descriptions later than these publications, or the author did not designate a series.

^e Hawkes (1990) divided ser. *Tuberosa* into three putative natural groups based on geography: *Tuberosa* group 1, Mexico south to Ecuador; group 2, Peru; group 3, Bolivia south to Chile.

^f SP = primitive *Stellata*; SA = advanced *Stellata*; RP = primitive *Rotata*; RA = advanced *Rotata* (see text).

^g EBN first reported by Ochoa (1992a).

^h Solanum curtilobum is listed in Hawkes (1990), and Ochoa (1990) as a pentaploid (5x = 60), but is listed in Bamberg et al. (1996) and Hanneman (1994) as a tetraploid (4x = 48). The accession was introduced to NRSP-6 as a tuber, later propagated sexually.

caeifolia, ser. *Commersoniana*, ser. *Conicibaccata*, ser. *Cuneoalata*, ser. *Lignicaulia*, ser. *Maglia*, ser. *Megistacroloba*, ser. *Tuberosa*, and ser. *Yungasensia*. Clade 4 has five groups of species in the strict consensus tree (Fig. 2; three of them labeled as groups 4a-c for discussion). Groups within these clades similarly intermix series. PAUP analyses done without the four putative hybrids investigated in this study resulted in the same four clades as in Fig. 2.

DISCUSSION

Hybridization in sect. Petota-Chloroplast DNA is predominately maternally inherited in the Solanaceae (Hosaka et al., 1984; Corriveau and Coleman, 1988; Harris and Ingram, 1991). All discussions of the translation of this maternal phylogeny to a species phylogeny must take into account the widespread hybridization and introgression that may be common in sect. Petota. Hybrid speciation has been hypothesized to have formed 27 named wild and cultivated species, and introgressive hybridization is believed to be common among many other species (Hawkes, 1962, 1990; Hawkes and Hjerting, 1969, 1989; Ugent, 1970). Many of the wild species having the same EBN levels can hybridize freely, although some hybrids may show reduction in fertility or vigor in later generations (Hawkes, 1958, 1990). Both 2n pollen (Watanabe and Peloquin, 1989, 1991) and 2n eggs (Werner and Peloquin, 1991) are common among the wild species. Sexual polyploidization may be common in nature (Hawkes and Jackson, 1992; Ortiz and Ehlenfeldt, 1992), allowing for hybridization of 2x(2EBN) germplasm from the wild species into the 4x(4EBN) species. If hybridization has occurred across clades, these chloroplast DNA gene trees may not reflect the true species phylogeny (e.g., Doyle, 1992).

Previous cpDNA results—Data from this study were not combined in a PAUP analysis with those of Spooner and Sytsma (1992) because not all restriction endonucleases were identical in both studies. However, comparison with the four accessions examined in common and with the restriction enzyme site variants defining clades (of 18 endonucleases in common between studies) make the comparison of these studies clear. Clades 1 and 2 of Spooner and Sytsma (1992) are the same as clades 1 and 2 in this study. Clade 3 of Spooner and Sytsma (1992) is subdivided as clades 3 and 4 here. Assignments of species from the analysis of Spooner and Sytsma (1992) to clades of this study are: S. chancayense (ser. Tuberosa) and S. chomatophilum Bitter (ser. Conicibaccata) to clade 3; all members of ser. Demissa and ser. Longipedicellata (except S. stoloniferum Schltdl. and Bouchet), S. alandiae (ser. Tuberosa) and S. circaeifolium Bitter (ser. Circaeifolia) to clade 4 group 4a; all polyploid members of ser. Conicibaccata to Clade 4 group 4b; S. tuberosum (ser. Tuberosa) and S. stoloniferum to clade 4 but not in any of the five groups in this clade.

This comparison also indicates that the sole Mexican

TABLE 3. Continued.

Enzyme

DraI

DraI

DraI

DraI

DraI

Region

P8/P10

P8/P10

P10

P8

P10

Mutation

number

63

64

65

66

67

Size (kb)

1.0 = 0.9 + (0.1)

2.1 = 2.0 + (0.1)

0.65 + 0.65 = 1.312.6 = 9.1 + 3.53.5 = 2.5 + (1.0)9.1 = 6.8 + 2.312.6 = 6.3 + 6.36.3 = 5.0 + 1.31.2 = 1.1 + (0.1)3.4 = 2.3 + 1.14.0 = 2.2 + 1.85.8 = 4.8 + 1.04.4 + 2.4 = 6.83.0 = 1.6 + 1.4 $3.8 \leftrightarrow 2.3 + 1.5$ 3.2 = 2.5 + (0.7)3.5 = 2.2 + 1.32.0 = 1.5 + 0.52.5 = 1.5 + 13.0 = 1.6 + 1.412.2 = 9.1 + 3.11.5 = 1.3 + (0.2)2.1 = 1.8 + (0.3)2.1 = 1.6 + (0.5)5.0 = 3.0 + 2.05.0 = 4.5 + (0.5)3 = 1.6 + 1.42 = 1.2 + 0.81.2 = 0.7 + 0.51.2 = 1.1 + 0.1 $2.1 \leftrightarrow 1.8 + 0.3$ 7.6 = 5.4 + 2.22.5 = 1.9 + 0.60.6 = 0.4 + (0.2)0.6 = 0.5 + (0.1)0.7 = 0.5 + (0.2)1.5 = 1.2 + 0.32.0 = 1.1 + 0.91.6 + (0.1) = 1.72.0 = 1.6 + 0.45.8 = 4.1 + 1.72.2 = 1.6 + 0.61.5 = 1.4 + (0.1)3.4 = 2.8 + 0.63.3 = 2.9 + (0.4)4.6 = 2.6 + 2.02.5 = 1.7 + 0.82.8 = 2.3 + 0.52.3 = 1.3 + 1.02.7 = 2.0 + 0.711.6 = 6.6 + 5.0 $17.3 \leftrightarrow 12.0 + 5.3$ 22 = 18 + 410.8 = 7.4 + 3.47.4 = 6.7 + 0.713.2 = 6.6 + 6.61 = 0.8 + (0.2)1.5 = 1.1 + 0.411 = 8 + 311.2 = 6.3 + 4.92.9 = 2.1 + 0.82.1 = 1.5 + 0.66.1 = 5.3 + 0.87.3 = 6.4 + 0.96.4 = 4.4 + 2.09.5 = 7.0 + 2.517 = 8.6 + 8.4

4.6 + 2.4 = 7.0

8.0 + 1.4 = 9.4

TABLE 3. Chloroplast DNA restriction enzyme site variants in *Solanum* sect. *Petota*. The variants are listed with the apomorphic state first, followed by the plesiomorphic state (relative to *S. palustre*). A double arrow indicates that the mutation could not be polarized because the outgroup differed from all other species. Parentheses indicate where small fragments were hypothesized to exist because length mutations were not seen with other enzymes. See Table 4 for character states.

Mutation	Engrana	Danian	Size (lab)	68	DraI	P6
number	Enzyme	Region	Size (kb)	69	DraI	P6/P3
1	Bam HI	P10	$3.4 \leftrightarrow 2.8 + 0.6$	70	DraI	P6
2	Bam HI	P10	2.4 + (0.1) = 2.5	71	DraI	P6
3	<i>Bam</i> HI	P10	2.7 = 2.5 + (0.2)	72	DraI	P6
4	<i>Bam</i> HI	P6	5.7 = 3.6 + 2.1	73	DraI	P3
5	Bam HI	P3	12.2 = 9.9 + 2.3	74	DraI	P3
6	BamHI	P3	9.9 = 6.0 + 3.9	75	DraI	P3
7	Bam HI	P3	6.8 + 3.1 = 9.9	76	DraI	P3
8	BamHI	P16/S6	18.2 = 14.4 + 3.8	77	DraI	P3
9	BamHI	P16/S6	2.3 + 1.6 = 3.9	78	DraI	P16
10	Bam HI	S8	7.6 = 3.8 + 3.8	79	DraI	P16/S6
11	BamHI	P12/P14	5.9 = 3.5 + 2.4	80	DraI	S6
12	BamHI	IR2	2.9 + 0.4 = 3.3	81	DraI	S6
13	BanI	P8	1.9 + 1.4 = 3.3	82	DraI	S6
14	BanI	P3	4.4 = 2.9 + 1.5	83	DraI	S6
15	BanII	P10	1.8 + 1.0 = 2.8	84	DraI	S6
16	BanII	P10	2.3 + (0.1) = 2.4	85	DraI	P12/P18/P19
17	BanII	P10	3.1 = 2.4 + 0.7	86	DraI	T36/T37
18	BanII	P10/P8	7.6 = 3.8 + 3.8	87	DraI	T37
19	BanII	P3	2.0 + 1.5 = 3.5	88	DraI	T37
20	BanII	P6	2.3 + 0.9 = 3.2	89	DraI	T38/T39
21	BanII	S8	3.8 = 2.1 + 1.7	90	DraI	T38/T39
22	BanII	P18/P19	0.75 + (0.05) = 0.8	91	DraI	T38
23	BglII	P10	3.1 + 2.5 = 5.6	92	DraI	T39/T40
24	BglII	P10/P8	2.5 + 3 = 5.5	93	DraI	T39/T40
25	BglII	P3	3.7 = 2.4 + 1.3	94	DraI	T40
26	BglII	S8	$3.3 \leftrightarrow 2.3 + 1.0$	95	EcoRI	P10
27	BglII	P12/P14	0.7 = 0.4 + 0.3	96	EcoRI	P10
28	<i>Bst</i> NI	P10	5.1 + 1.4 = 6.5	97	EcoRI	P10
29	<i>Bst</i> NI	P10	2.6 = 2.0 + 0.6	98	EcoRI	P10
30	<i>Bst</i> NI	P6/P8	0.8 + 0.6 = 1.4	99	EcoRI	P10
31	<i>Bst</i> NI	P8	0.6 = 0.4 + 0.2	100	EcoRI	P6
32	<i>Bst</i> NI	P6	2.0 + 0.3 = 2.3	101	EcoRI	P3
33	<i>Bst</i> NI	P3	0.3 + 0.3 = 0.6	102	EcoRI	P3
34	<i>Bst</i> NI	P3	1.1 + 0.7 = 1.8	103	EcoRI	P16/S6
35	<i>Bst</i> NI	P3	1.0 = 0.8 + 0.2	104	EcoRI	P16/S6
36	<i>Bst</i> NI	P3	1.2 + 0.1 = 1.3	105	EcoRI	P16/S6
37	<i>Bst</i> NI	P16/S6	2.7 + 1.2 = 3.9	106	EcoRI	S8
38	<i>Bst</i> NI	P16/S6	2.5 + 1.4 = 3.9	107	EcoRI	S8
39	<i>Bst</i> NI	S 8	4.6 = 3.3 + 1.3	108	EcoRI	S8
40	<i>Bst</i> NI	S8	1.5 = 1.3 + 0.2	109	EcoRI	<u>S8</u>
41	<i>Bst</i> NI	P14	0.8 = 0.7 + 0.1	110	EcoRI	IR2
42	BstXI	P6	16.6 = 12.4 + 4.2	111	EcoRI	T36/T37
43	BstXI	P16/S6	23 = 13 + 10	112	EcoRI	T40
44	BstXI	S8	4.0 = 2.9 + 1.1	113	EcoRI	139/140
45	BstXI	T39/T40	4.8 = 4.0 + 0.8	114	EcoRV	PIO
46	BstXI	T39/T40	7.0 = 4.7 + 2.3	115	EcoRV	P8/P10
47	ClaI	P10	9.0 = 6.4 + 2.6	116	EcoRV	P6/P3
48	ClaI	P6/P8	1.2 = 1.1 + 0.1	117	EcoRV	P3
49	ClaI	P6	8.9 = 5.3 + 3.6	118	EcoRV	P3
50	ClaI	P6	8.9 = 7.4 + 1.5	119	EcoRV	P3
51	Clal	P6/P3	6.3 = 5.3 + 1.0	120	EcoRV	P16/S6
52	ClaI	P3	1.8 = 1.5 + (0.3)	121	EcoRV	S8
53	ClaI	P16/S6	3.5 = 3.2 + 0.3	122	EcoRV	P18/P19
54	ClaI	P18/P19	7.5 + 7.5 = 15	123	EcoRV	137/138
55	Clal	T36/T37	7.1 = 6.6 + 0.5	124	<i>Eco</i> 0109	P10/P19
56	Clal	136/137	1.1 = 5.8 + 1.3	125	<i>Eco</i> 0109	Po
57	Clal	T39/T40	1.5 = 1.4 + (0.1)	126	<i>Eco</i> 0109	P0 D2
58	Clal	T40	2.4 = 1.5 + 0.9	127	EcoU109	P3
59	Dral	P8/P10	6.6 + 1.4 = 8.0	128	EcoU109	P14/IR-2
60	Dral	P10	1.0 = 0.8 + (0.2)	129	ECOUIU9	139/140 D8/D10
61	Dral	P8/P10	3.4 = 3.1 + (0.3)	130	Haell	P8/P10 D10
62	Dral	P8/P10	8.0 = 6.4 + 1.6	131	Haell	P10

TABLE 3. Continued.

Mutation number	Enzyme	Region	Size (kb)
132	HincII	P10	2.3 = 1.9 + 0.4
133	HincII HincII	P10/P8	1.4 = 0.7 + 0.7 4.9 + 3.1 - 8.0
134	HincII	P6	4.9 + 3.1 = 8.0 3.1 = 2.5 + 0.6
136	HincII	P6	6.1 = 5.5 + 0.6
137	HincII	P3	$3.5 \leftrightarrow 2.7 + 0.8$
138	HincII HincII	P3 P3	4.9 = 3.5 + 1.4 3.5 = 3.1 + 0.4
140	HincII	T38	1.6 + (0.6) = 2.2
141	HincII	T39/T40	5.8 = 3.8 + 2.0
142	HindIII	P8	2.2 + 0.7 = 2.9
145	HindIII	P3	4.0 - 2.9 + 1.1 12.4 + 1.0 = 13.4
145	HindIII	P3/P16	13.2 = 9.5 + 3.7
146	HindIII	T36/T37	6.6 = 4.4 + 2.2
147 148	HindIII Hpall	T36/T37 P10	6.6 = 5.6 + 1.0 0.8 = 0.6 + (0.2)
149	HpaII	P10	2.1 + 1.0 = 3.1
150	HpaII	P10	1.7 = 1.5 + 0.2
151	HpaII	P8	1.6 = 1.3 + 0.3
152	Hpall Hpall	P8 P6	1.4 = 1.3 + (0.1) 1.9 = 1.5 + (0.4)
155	HpaII	P16/S6	1.9 = 1.3 + (0.4) 2.2 = 2.0 + 0.2
155	HpaII	P16/S6	1.5 = 1.0 + 0.5
156	HpaII	S8	0.9 = 0.8 + (0.1)
157	Hpall	P18 T30/T40	2.5 = 1.4 + 1.1 3.3 + 2.5 - 5.8
158	HpaII HpaII	T39/T40	3.3 + 2.3 - 3.8 3.2 = 1.7 + 1.5
160	HpaII	T39/T40	2.6 = 1.4 + 1.2
161	HphI	P10	11.4 = 9.9 + 1.5
162	HphI HphI	P10 P10	7.2 = 3.6 + 3.6
164	Hph1 Hph1	P3/P6	11.4 = 7.2 + 4.2 2.2 = 1.5 + 0.7
165	HphI	P3	3.0 = 2.2 + 0.8
166	HphI	P3	2.5 + (0.2) = 2.7
167	HphI	P3	2 = 1.4 + 0.6
168	Hph1 Hph1	P16/S6	1.7 = 1.0 + 0.7 1.1 = 0.6 + 0.5
170	HphI	T36/T37	3.4 = 2.4 + 1.0
171	\hat{HphI}	T39/T40	3.2 = 1.7 + 1.5
172	KpnI	P3	12.5 = 9.4 + 3.1
173	NC11 NciI	P10 P6	5.5 = 4.9 + 0.6 2.7 + (0.4) = 3.1
175	NciI	S8	1.7 + (0.4) = 2.1
176	NciI	P18/P19	4.2 = 3.1 + 1.1
177	NsiI	P10	8.4 = 6.6 + 1.8
178	NsiI NsiI	P10 P8/P6	18.0 = 12.0 + 0.0 14.7 = 10.6 + 4.1
180	NsiI	P6	4.5 = 3.5 + 1
181	NsiI	P3	2.9 = 2.0 + 0.9
182	NsiI	T38	5.0 = 2.5 + 2.5
185	SspI	P10	13.3 - 11.3 + 3.8 2.1 = 1.7 + (0.4)
185	SspI	P8	1.9 = 1.0 + 0.9
186	SspI	P8	1.4 = 1.3 + (0.1)
187	SspI	P6	1.9 = 1.1 + 0.8
189	Sspi	P6/P3	3.4 + 2.1 = 5.3 3.7 + 2.1 = 5.8
190	SspI	P3	2.7 = 1.5 + 1.2
191	SspI	T36/T37	1.2 = 1.0 + (0.2)
192	SstI SatI	P8/P10	6.0 = 5.1 + 0.9
193	SSTI SstI	P8/P10 P6/P3	6.9 = 6.0 + 2.9 18 = 9 + 9
195	SstI	P3	3.8 = 3.4 + (0.4)
196	SstI	S6/S8	10.5 = 6.8 + 3.6
197	SstI Vhat	P3	1.1 = 0.9 + (0.2)
198	лраі Xhai	P10/S0 P18/P19	4.7 = 3.1 + 1.0 2.6 = 1.4 + 1.2
200	XbaI	T40	1.5 = 1.0 + 0.5

diploid A genome species, *S. verrucosum* (examined here), is maintained in the clade containing members of ser. *Longipedicellata* (except *S. stoloniferum*) and ser. *Demissa* (these species not examined here). Also, it indicates that all South American species are in clades 3 and 4, and all Mexican diploid species (exclusive of *S. verrucosum*) are in basal clades 1 and 2. These results concur with those in Spooner, Sytsma, and Conti (1991), and Spooner and Sytsma (1992), to provide partial support for Hawkes's biogeographic hypothesis suggesting that *S. verrucosum* is a parent of members of ser. *Demissa*. The cladistic relationship of *S. verrucosum* to *S. okadae* (endemic to Bolivia and Argentina) was unexpected. However, this relationship is weakly supported (Fig. 1).

Previous nuclear DNA results—Debener, Salamini, and Gebhardt (1990) examined 16 species of sect. *Petota,* and *S. palustre* (as *S. brevidens,* sect. *Etuberosum*) with 29 single- to low-copy nuclear DNA probes and seven restriction endonucleases and analyzed the data with unrooted parsimony and distance algorithms. They included members of our outgroup, and our clades 1 and 4, but not clades 2 or 3. Our results are concordant with theirs regarding the outgroup and clade 1, but not entirely so regarding clade 4. Their results placed *S. canasense* and *S. tuberosum* on one clade, and *S. chacoense, S. gourlayi, S. sparsipilum, S. spegazzinii,* and *S. vernei* on another clade. Our results placed all of these species on clade 4, but as separate groups (Fig. 2).

Series—This study provides no parallel cladistic analysis of the morphological characters defining clades within sect. *Petota.* However, other phenetic morphological studies at the species level (Spooner and van den Berg, 1992b; Giannattasio and Spooner, 1994; Spooner, van den Berg, and Bamberg, 1995; Castillo and Spooner, in press) have shown that species and subspecies can be defined only by a combination of overlapping character states. There are few, if any, discrete morphological characters useful for cladistic analyses at the species or series level in sect. *Petota.* Clades 1–4 each contains reproductively and morphologically very diverse species, and provide us with no "reciprocal illumination" to help to define these clades. All clades show a diversity of vegetative morphology and fruit shapes.

The only trend we discern among morphological characters of species in clades 1 and 2 is the presence of white (sometimes blue tinged) stellate corollas, while in clades 3 and 4 species tend to have violet to blue, rotate-pentagonal to rotate corollas. However, exceptions exist. For example, S. polyadenium (clade 1 from Spooner and Sytsma, 1992) has white but rotate-pentagonal corollas (Correll, 1962). Solanum berthaultii and S. tarijense (clade 4, group 4a) both have populations with white to violet and stellate to pentagonal corollas (Spooner and van den Berg, 1992b). Also, some of the South American 2x(1EBN) species, such as S. chancayense, S. circaeifolium, S. lignicaule, and S. mochiquense, have white and/or stellate corollas. In addition, S. gandarillasii, 2x(2EBN) and S. colombianum, 4x(2EBN) of clade 4 have white corollas, and there are intermediate corolla shapes connecting the extremes of stellate and rotate shapes (Heijdem and van den Berg, in press). Many other species

ListLi	Outgroup (sect. Etuberosum)	S. andreanum	S. capsicibaccatum
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NumberConstruction <th< td=""><td>Indroup (sect. Petota)</td><td></td><td></td></th<>	Indroup (sect. Petota)		
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3. Absence (1) $0111001100100100100100100000000000000$	1000000100000000000000001001100110010000	2. bulbocastanum	2. commersonii
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IABLE 4. Continued.			iay
S. <u>mandarillasii</u> 00111001011101001101001010101010001000	S. incanarcentse 0011100100110100100100101010100010010000	G. marinasense 00111001011010010010010101001000100011100110000	1)))]
S. <u>souriavi</u> 00110001011101001100100001010101001000101	3. intundibuliterme 00111001011101001101000101010100010001	5. mediana 0011100001100100100000101001000100001100010000	•
3. hastiforms 301110000110010010001000100010001000100	S. <u>Aurtzianum</u> 001116010111001100100001010101000000011000110000	S. madiatacrolobum 00111000001101001001000000101000000001110010000	J CONER ANL
 hintenii doll100100100100100010001000100001000010	<u>S. laxissimum</u> 0011100101101000010000101010100001000	S. microdontum 0011100100110000001001000100010001100101	CASTILLO-
8. hendelmennii 001130010110100100100010101010001000110000110000	<u>5</u> . <u>loctophos</u> 00111000011101001001000101010100010001	S. machiquense 0011100101101001100100010101000000010000	SOLANUM SI
 huancabambense outla60100100100101010100001000111100101010000	<u>S</u> . <u>limbaniense</u> 0011100001110100110010001000100011100101	G. morelliforme 0011100101111000010010010001000100001100101	LCI. I LIUIA
S. Nypactarhtum 00111001011101001100101010101000100111100101	<u>5</u> . <u>liquicaule</u> 0011100101101001001000000000000000000	S. moscopanum 00111000110100100100100101010100100010	THEODENT
3. Amoles 00111001011001100100000101001001001010000	S. londiconisum 00111000110010010010010010100001000110010000	S. multidissectum 0011100001101001001000101010100100011100101	
	3. marija 00110010111010011001001010101000100010	S. neccardensaii 001110010111010010000000010001000110010000	

TABLE 4. Continued.

TABLE 4. Continued.		
S. mecrosati 001100101101001000100010100100010001100101	S. sanctae-rosae 0011100001110100110010001000100011001010	E. tarifaise 00110001001110100100010100100010001000
S. oxadas	S. santolallas	S. tuberosum
00111001011010011001000101010101000100	001110050111010010010010101010001000110010100000	00111000011001100100000101010100010001
S. splocense	S. scabrifolium	S. tundalomense
001100101101001100100010101010100001100010000	001110000111010011101001010101010100010000	001110010111010110010001010100010011000101
S. paupacense 00111011011010011001001010101010000001100101	S. scartandinum 0011100101110100100100101010100010011100101	 Eugmerrense 0111100101111001001001010101000001100000
S. passessance	3. sparsipilum	S. vermai
0011101011010000000000001110000101110000	001110010011001001000000000100010001100101	00111001011101001001000010100010001000
S. paucissectum	S. specazzinii	S. <u>vertucosum</u>
011110010111001001001001010101010010010	001110010111010010010001000100010001100101	00111001011101001001009010100100010001100101000000
S. pinnatisactum 061119010110011001000100011100010000100	S. subpanduratum 0011110001101001100100010101010100000010000	S. <u>vidaurrei</u> 00111001011101001001000101010100100111001001001001001001100 001000000
K. pintae	S. sucrement PT 442691	S. violaceimarmoratum
0011100101110010100000001010000101000010000	00111000011101001100100010001001000110010010000	001110010111010011001000101010101000010000
S. <u>maphanifolium</u>	S. <u>sucreme</u> P1 498302	G. sect. <u>Parcia</u> undescribed species
0011100000001001001000100010001000110010010000	0011100101110120010001001010101000100	00111001001100110010001010101000011001000110000



Fig. 1. One of 5000 equally parsimonious 319-step Wagner trees drawn as a phylogram (branch lengths proportional to character support) of cpDNA restriction site variants in *Solanum* sect. *Petota* and sect. *Etuberosum* (*S. palustre*, outgroup), with numbers of characters supporting each branch, ordered as unique mutations, homoplastic gains, and homoplastic losses (the codes A, B, and C are used to represent these variants, respectively, when only one is present per branch).



Fig. 2. The strict consensus tree of 5000 equally parsimonious 319-step Wagner trees, with bootstrap and decay values. Clades 1-4 as discussed in the text. Series affiliations (including informal ser. *Tuberosa* groups 1, 2, and 3) follow Hawkes (1990); ploidy and Endosperm Balance Numbers (EBN) from Table 2.

have colored corollas with white mottling or stripes. Thus, it is difficult to use corolla colors and shapes as discrete synapomorphies uniting members of these clades.

Trends in characters affecting crossability are evident also. All species in clades 1 and 2 are 2x(1EBN). However, four of the 14 species in clade 3 and three of the 57 species in clade 4 also are 1EBN.

Clade 3 contains all of the seven representatives of ser. *Piurana* (of the 15 species recognized by Hawkes [1990]), but also seven other species from four other series (in addition, *S. chomatophilum* of ser. *Conicibaccata* is placed here from data of Spooner and Sytsma [1992]). Circumscription of ser. *Piurana* has been a continual problem. Hawkes (1990) defined it by shiny leaves with inrolled margins, but these characters vary among species assigned to this series. Correll (1962) stated "[Series *Piurana*], probably more than any [other series] may be considered a catchall. Paradoxically, its component species are held together not so much by their similarities as by their differences."

All prior classifications have recognized ser. Conicibaccata as a distinctive series, except for some confusion with ser. Demissa (Spooner and van den Berg, 1992a). All polyploid members of ser. Conicibaccata form a welldefined group 4b of clade 4. These are separated from all other diploid species of the series [two in clade 3 (including S. chomatophilum from Spooner and Sytsma, 1992), three in clade 4 group 4a, and one in clade 4 outside group 4a]. Conical fruits have defined ser. Coni*cibaccata* when used in combination with corolla shape. Conical fruits also occur in ser. Circaeifolia, ser. Demissa, ser. Pinnatisecta, and ser. Polyadenia (Hawkes, 1990; Spooner and Sytsma, 1992; Spooner and van den Berg, 1992a). Members of these series are found on clades 1, 3, and 4 (Fig. 2). There have been no taxonomic schemes suggesting that the polyploid and diploid members of ser. Conicibaccata form separate clades. Series Conicibaccata contains 40 species (Hawkes, 1990), but only ten have been examined here. A wider morphological and cpDNA study examining diploid and polyploid species of ser. Conicibaccata (Castillo and Spooner, in press) examines this series.

Clade 4 group 4c contains S. infundibuliforme and S. vidaurrei. Classifications have separated them into the series Cuneoalata and Tuberosa or Transaequatorialia, respectively (Table 2). Solanum vidaurrei is recognized as a subspecies of S. gourlayi by Hawkes (1990), but as a species by Ochoa (1990). Both taxa are morphologically similar and have leaves with narrow to linear leaflets. Correll (1962, p. 413) noted this similarity and believed the species were allied, even though he maintained them in different series. All of the diagnostic characters of ser. Cuneoalata, however (Correll, 1962; Hawkes, 1990; Ochoa, 1990), such as decurrent wings on the leaves, are present in other series. The sister group relationship shown here suggests the need for greater intraand interspecific sampling to see if this relationship is maintained, and questions the continued recognition of ser. Cuneoalata.

The presence of the 2x(1EBN) condition in *S. palustre* (sect. *Etuberosum*, outgroup) and in the two most basal clades 1 and 2 supports this as a primitive trait in sect.

Petota as suggested by Hawkes (1990) and Hawkes and Jackson (1992). The presence of the 2x(1EBN) condition in separate parts of clades 3 and 4 suggests that it has evolved independently in South America. Because of possible hybridization of all species in sect. *Petota*, however, the value of EBN as a phylogenetic marker awaits corroboration of this maternal phylogeny with those constructed with other biparentally inherited markers.

Members of Hawkes's ser. *Tuberosa* groups 1–3, defined on a purely geographical basis (Tables 1,2) are not supported. The two members of *Tuberosa* group 1 are separated in clades 3 and 4, members of ser. *Tuberosa* group 2 are separated in clades 3 and 4, and ser. *Tuberosa* group 3 occurs entirely in clade 4.

Two species, S. chacoense and S. sucrense, had two accessions per species examined here; the accessions differed from each other by five and seven cpDNA restriction site variants, respectively. Intraspecific cpDNA polymorphisms have been shown to be common in sect. Petota (Hosaka and Hanneman, 1988; Spooner, Sytsma, and Smith, 1991; Hosaka, 1995), as in many other plants (Soltis, Soltis, and Milligan, 1992). Both accessions of these two species remained in clade 4 group 4a and in the polytomy exclusive of group 4a, respectively, despite their high polymorphism. Additional studies are needed to determine whether infraspecific cpDNA variation exists in other species in sect. Petota, and how it affects cladistic structure. The cause of this variation is unknown. Equally likely hypotheses are hybridization and introgression, which are believed to be widespread in sect. *Petota* (above) or lineage sorting (Neigel and Avise, 1986).

Hosaka and Hanneman (1988) and Hosaka (1995) used cpDNA to investigate the wild progenitors of the cultivated species S. curtilobum, S. tuberosum, and other cultivated species. They analyzed total cpDNA banding patterns using three restriction endonucleases, with trees constructed manually. Putative progenitors of cultivated species that they and we included were S. brevicaule, S. bukasovii, S. canasense, S. candolleanum, S. leptophyes, S. multidissectum, and S. sparsipilum. They designated eight cpDNA types and arranged them from primitive to advanced based on outgroup analysis of Hosaka et al. (1984). Our analysis examined fewer accessions of these seven species, but with more endonucleases, sequential probing of cpDNA, and parsimony analysis. Our results place these seven species with S. curtilobum and S. tuberosum, on a largely unresolved polytomy of clade 4, consistent with the hypothesis that these are potential ancestors to the cultivated potato species. Our consensus results show that despite the high cpDNA intraspecific polymorphism, there are few informative synapomorphic characters at this level. This suggests that cpDNA restriction site analysis will be of limited value in elucidating the wild progenitors of S. tuberosum or the six other cultivated species.

Spooner and van den Berg (1992b) used morphological data to investigate species boundaries of *S. berthaultii* and *S. tarijense* and their putative interspecific hybrids. They showed extensive overlap of diagnostic morphological characters used to distinguish the two taxa. *Solanum berthaultii, S. avilesii,* and *S. maglia* have identical cpDNA RFLP profiles and form a clade; *S. tarijense* is

removed from it by five restriction site variants (four of these autapomorphies for *S. tarijense*). The relevance of these four cpDNA restriction site variants to recognizing species limits between *S. berthaultii* and *S. tarijense* awaits further intraspecific cpDNA sampling.

Hawkes (1990) placed *S. andreanum* in ser. *Tuberosa.* Our results place *S. andreanum* in clade 3, with the members of ser. *Piurana*, and members of four other series (Fig. 2). On the basis of field data and morphological examinations of accessions throughout the range of the species, including type specimens, Spooner, Castillo, and López (1993) synonymized five species under *S. andreanum*. These previously had been placed by Correll (1962), Ochoa (1981), and Hawkes (1990) into five separate series, including ser. *Piurana*. These alternative treatments suggest the tenuous nature of the morphological characters used to separate series in sect. *Petota*. Our cpDNA results (Fig. 2) likewise question series in sect. *Petota*.

The incongruence between the clades as defined by these cpDNA data and the series as circumscribed by prior authors or the superseries of Hawkes (1990) suggests a need for a reevaluation of series boundaries in sect. Petota. Previous criticisms of the validity of series (Spooner and van den Berg, 1992a) have highlighted the lack of clear criteria defining them, lack of phylogenetic analyses, and the widely divergent series classifications among authors. Our results, and those of Spooner, Sytsma, and Conti (1991) and Spooner and Sytsma (1992), provide the most complete chloroplast DNA phylogeny of sect. Petota, with an examination of 17 of the 19 tuberbearing series recognized by Hawkes (1990). Additional cpDNA studies are needed to examine the two series not yet available, ser. Ingifolia, with two species from Peru, and ser. Olmosiana, with one species from Peru (Hawkes, 1990). Obviously, based on the results of S. chacoense and S. sucrense, more intraspecific sampling is needed to determine the extent of infraspecific variation and to see whether the four clades are maintained.

The relatively low resolving power of cpDNA in terminal clades of sect. *Petota* also suggests the need for additional studies with less conservative maternally inherited and biparentally inherited molecular markers. Such studies are needed to (1) test the concordance of phylogenies from different sources, (2) test the maintenance of the four clades discovered here, and (3) discover whether species and series relationships can be better resolved. Perhaps no molecular markers will completely partition many of the morphologically very similar species into clades. Rather, the cpDNA data may indicate that Hawkes's estimate of 232 species is an overestimate of the species diversity in the group.

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