American Journal of Botany 84(5): 671–685. 1997.

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

DAVID M. SPOONER[2] AND RAUL CASTILLO T.[3]

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

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. *Cuneoalata,* 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 nontuber-bearing 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.

[1] Manuscript received 22 March 1996; revision accepted 10 October 1996.

The authors thank Harvey Ballard, Jr., Lynn A. Bohs-Sperry, Robert E. Hanneman, Jr., Richard G. Olmstead, and R. G. van den Berg for reviews; Kenneth J. Sytsma for *Petunia* chloroplast DNA probes; Richard G. Olmstead for the *Nicotiana* chloroplast DNA probes; Brian Karas for technical assistance; and Andrew Wynn Rouse for artwork. Names are necessary to report factually and available data; however, the USDA neither guarantees nor warrants the standard of the product, and the use of the name by USDA implies no approval of the product to the exclusion of others that may also be suitable.

[2] Author for correspondence (email: dspooner@facstaff.wisc.edu).

[3] Present address: Departamento Nacional Recursos Fitogenéticos y Biotecnología, Instituto Nacional de Investigaciones Agropecuarias, Casilla 17-01-340, Quito, Ecuador (email: castillo@fitogen.sc.iniap.gov.ec).

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, ploidy, Endosperm Balance Numbers (EBN), and superseries designations of the 19 tuber-bearing series of *Solanum* sect. *Petota*, according to the putative evolutionary progression of series and superseries of Hawkes (1990) and Hawkes and Jackson (1992).

Series	Distribution	Ploidy (EBN)	Superseries[a]
Morelliformia Hawkes	Mexico, Guatemala	2*x*(1EBN)	SP
Bulbocastana (Rydb.) Hawkes	Mexico, Guatemala	2*x*(1EBN)	SP
Pinnatisecta (Rydb.) Hawkes	SW USA, Mexico	2*x*(1EBN)	SP
Polyadenia Correll	Mexico	2*x*(1EBN)	SP
Commersoniana Bukasov	Brazil, Uruguay, Argentina	2*x*(1EBN)	SP
Circaeifolia Hawkes	Bolivia	2*x*(1EBN)	SP
Lignicaulia Hawkes	Peru	2*x*(1EBN)	SP
Olmosiana Ochoa	Peru	2*x*(1EBN)	SP
Yungasensia Correll[b]	Peru, Bolivia, Brazil, Paraguay, Argentina	2*x*(2EBN)	SA
Megistacroloba Cárdenas and Hawkes	Peru, Bolivia, Argentina	2*x*(2EBN)	RP
Cuneoalata Hawkes	Argentina, Bolivia, Peru	2*x*(2EBN)	RP
Conicibaccata Bitter—southern South America[c]	Peru, Bolivia	2*x*(2EBN)	RP
Maglia Bitter	Chile	2*x*, 3*x*(?EBN)	RP
Tuberosa (Rydb.) Hawkes—southern South America[c]	Peru, Bolivia, Argentina, Chile	2*x*(2EBN), 4*x*(4EBN), 6*x*(4EBN)	RP
Piurana Hawkes	Colombia, Ecuador, Peru	2*x*(2EBN), 4*x*(2EBN)	RA
Ingifolia Correll	Peru	2*x*(1EBN)[d]	RA
Conicibaccata—northern South America[c], southern Mexico and Central America	Venezuela, Colombia, Ecuador, southern Mexico and Central America	2*x*(1EBN), 4*x*(2EBN), 6*x*(4EBN)	RA
Tuberosa—northern South America[c], Mexico	Colombia, Ecuador, Mexico	2*x*(1EBN), 4*x*(2EBN), 6*x*(4EBN)	RA
Acaulia	Ecuador, Peru, Bolivia, Argentina	4*x*(2EBN), 6*x*(4EBN)	RA
Longipedicellata Juz.	SW USA, Mexico	4*x*(2EBN)	RA
Demissa Juz.	Mexico and Central America	6*x*(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 2*x*, to be 2*x*(1EBN).

4*x*(4EBN), and 6*x*(4EBN) (Hanneman, 1994). Many of the 2*x*(1EBN) species occur in Mexico and Central America, but eight tuber-bearing 2*x*(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 2*x*(1EBN) species possessing white stellate corollas, and remnant or derivative 2*x*(1EBN) species remain there (primitive *Stellata*), (2) 2*x*(1EBN) species retaining white stellate corollas (also primitive *Stellata*) migrated into South America in the early Pliocene, (3) 2*x*(1EBN) species evolved to 2*x*(2EBN) species with white but less stellate corollas (advanced *Stellata*), (4) the ''advanced *Stellata*'' evolved to 2*x*(2EBN), 4*x*(4EBN), and 6*x*(4EBN) species with more rotate corollas (primitive *Rotata*), (5) finally, the ''primitive *Rotata*'' at various ploidy levels and EBN's evolved to 2*x*(2EBN), 4*x*(2EBN), and 6*x*(4EBN), and a few 2*x*(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* 4*x*(2EBN) (six species) and ser. *Demissa* 6*x*(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. verrucosum* 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* (4*x*) and ser. *Demissa* (6*x*) 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 electrophoresis, 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 ^{32}P-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: *Ava*I, *Bam*HI, *Ban*I, *Bcl*I, *Bgl*II, *Bst*NI, *Cla*I, *Dra*I, *Eco*O109, *Eco*RI, *Eco*RV, *Hin*cII, *Hin*dIII, *Hpa*I, *Hpa*II, *Hph*I, *Nci*I, *Nsi*I, *Sst*I, *Xba*I, *Xho*I, and *Xmn*I. Membranes were probed with 12 *Pst*I and two *Sal*I 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 single- to 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 5 000 equally parsimonious trees were possible for the data set, and we had to constrain the program to save no more than 5 000 trees when the MULPARS 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 5 000 trees as a constraint tree and performed an inverse constraint analysis using procedures for searching shortest trees. Wagner parsimony produced 5 000 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 cpDNA variation. Species are assigned to series according to the classifications of Correll (1962), Ochoa (1962, 1963, 1972, 1979, 1981, 1990, 1992b), and Hawkes (1990), and ordered according to the putative evolutionary progression of series and superseries of Hawkes (1990) and Hawkes and Jackson (1992).

Species	PI[a]	Ploidy[b], EBN[c]	Series[d]			Superseries[f]
			Correll	Ochoa	Hawkes[e]	
Solanum palustre Poepp.	245763	2*x*(1EBN)	*Etuberosum*		*Etuberosa*	
S. morelliforme Bitter and G. Muench	243357	2*x*(?EBN)	*Morelliformia*		*Morelliformia*	SP
S. bulbocastanum Dunal	275187	2*x*(1EBN)	*Bulbocastana*		*Bulbocastana*	SP
S. cardiophyllum Lindl.	347759	2*x*(1EBN)	*Cardiophylla*		*Pinnatisecta*	SP
S. hintonii Correll	558400	?*x*(?EBN)	*Longipedicellata*		*Pinnatisecta*	SP
S. pinnatisectum Dunal	275234	2*x*(1EBN)	*Pinnatisecta*		*Pinnatisecta*	SP
S. commersonii Dunal	243503	2*x*(1EBN)	*Commersoniana*		*Commersoniana*	SP
S. capsicibaccatum Cárdenas	205560	2*x*(1EBN)	*Circaeifolia*	*Circaeifolia*	*Circaeifolia*	SP
S. lignicaule Vargas	473351	2*x*(1EBN)	*Transaequatorialia*	*Tuberosa*	*Lignicaulia*	SP
S. arnezii Cárdenas	545847	2*x*(?EBN)	*Yungasensia*	*Commersoniana*	*Yungasensia*	SA
S. chacoense Bitter	217451	2*x*(2EBN)	*Commersoniana*	*Commersoniana*	*Yungasensia*	SA
S. chacoense	414153					
S. huancabambense Ochoa	458400	2*x*(2EBN)	*Conicibaccata*	*Tuberosa*	*Yungasensia*	SA
S. tarijense Hawkes	442689	2*x*(2EBN)	*Tarijensa*	*Commersoniana*	*Yungasensia*	SA
S. hastiforme Correll	498242	2*x*(?EBN)	*Megistacroloba*		*Megistacroloba*	RP
S. megistacrolobum Bitter	210034	2*x*(2EBN)	*Megistacroloba*	*Megistacroloba*	*Megistacroloba*	RP
S. raphanifolium Cárdenas and Hawkes	265862	2*x*(2EBN)	*Megistacroloba*	*Megistacroloba*	*Megistacroloba*	RP
S. sanctae-rosae Hawkes	473200	2*x*(2EBN)	*Megistacroloba*		*Megistacroloba*	RP
S. sogarandinum Ochoa	365360	2*x*(2EBN)	*Megistacroloba*	*Megistacroloba*	*Megistacroloba*	RP
S. infundibuliforme Phil.	472887	2*x*(2EBN)	*Cuneoalata*	*Cuneoalata*	*Cuneoalata*	RP
S. laxissimum Bitter	283088	2*x*(2EBN)	*Conicibaccata*	*Conicibaccata*	*Conicibaccata*	RP
S. limbaniense Ochoa	473468	2*x*(?EBN)			*Conicibaccata*	RP
S. santolallae Vargas	195168	2*x*(?EBN)	*Conicibaccata*	*Conicibaccata*	*Conicibaccata*	RP
S. violaceimarmoratum Bitter	473395	2*x*(2EBN)	*Conicibaccata*	*Conicibaccata*	*Conicibaccata*	RP
S. maglia Schltdl.	245087	2*x*(?EBN)	*Tuberosa*		*Maglia*	RP
S. alandiae Cárdenas	498086	2*x*(?EBN)	*Transaequatorialia*	*Tuberosa*	*Tuberosa* 3	RP
S. avilesii Hawkes and Hjert.	498093	2*x*(?EBN)		*Tuberosa*	*Tuberosa* 3	RP
S. berthaultii Hawkes	265857	2*x*(2EBN)	*Berthaultiana*	*Commersoniana*	*Tuberosa* 3	RP
S. brevicaule Bitter	498115	2*x*(2EBN)	*Transaequatorialia*	*Tuberosa*	*Tuberosa* 3	RP
S. candolleanum P. Berthault	498227	2*x*(2EBN)[g]	*Transaequatorialia*	*Tuberosa*	*Tuberosa* 3	RP
S. doddsii Correll	442690	2*x*(2EBN)	*Transaequatorialia*		*Tuberosa* 3	RP
S. gandarillasii Cárdenas	265866	2*x*(2EBN)	*Transaequatorialia*	*Tuberosa*	*Tuberosa 3*	RP
S. gourlayi Hawkes ssp. *gourlayi*	442667	2*x*(2EBN)		*Tuberosa*	*Tuberosa* 3	RP
S. hondelmannii Hawkes and Hjert.	498067	2*x*(?EBN)		*Tuberosa*	*Tuberosa* 3	RP
S. incamayoense K.A. Okada and A.M. Clausen	473068	2*x*(?EBN)			*Tuberosa* 3	RP
S. kurtzianum Bitter and Wittm.	320271	2*x*(2EBN)	*Transaequatorialia*		*Tuberosa* 3	RP
S. microdontum Bitter	310979	2*x*(2EBN)	*Transaequatorialia*	*Tuberosa*	*Tuberosa* 3	RP
S. neocardenasii Hawkes and Hjert.	498129	2*x*(?EBN)		*Tuberosa*	*Tuberosa* 3	RP
S. neorossii Hawkes and Hjert.	473201	2*x*(?EBN)			*Tuberosa* 3	RP
S. okadae Hawkes and Hjert.	498065	2*x*(?EBN)		*Tuberosa*	*Tuberosa* 3	RP
S. oplocense Hawkes	435079	6*x*(4EBN)	*Transaequatorialia*	*Tuberosa*	*Tuberosa* 3	RP
S. pampasense Hawkes	210046	2*x*(2EBN)	*Piurana*	*Tuberosa*	*Tuberosa* 3	RP
S. spegazzinii Bitter	205407	2*x*(2EBN)	*Transaequatorialia*		*Tuberosa* 3	RP
S. sucrense Hawkes	442691	4*x*(4EBN)	*Transaequatorialia*	*Tuberosa*	*Tuberosa* 3	RP
S. sucrense	498302					
S. vernei Bitter and Wittm.	320333	2*x*(2EBN)	*Transaequatorialia*		*Tuberosa* 3	RP
S. vidaurrei Cárdenas	472995	2*x*(?EBN)	*Transaequatorialia*	*Tuberosa*	*Tuberosa* 3	RP
S. leptophyes Bitter	473448	2*x*(2EBN)	*Transaequatorialia*	*Tuberosa*	*Tuberosa* 2, 3	RP
S. sparsipilum (Bitter) Juz. and Bukasov	310993	2*x*(2EBN)	*Transaequatorialia*	*Tuberosa*	*Tuberosa* 2, 3	RP
S. abancayense Ochoa	442700	2*x*(2EBN)		*Tuberosa*	*Tuberosa* 2	RP
S. ambosinum Ochoa	498208	2*x*(2EBN)	*Transaequatorialia*	*Tuberosa*	*Tuberosa* 2	RP
S. bukasovii Juz.	266385	2*x*(2EBN)	*Transaequatorialia*	*Tuberosa*	*Tuberosa* 2	RP
S. canasense Hawkes	210035	2*x*(2EBN)	*Transaequatorialia*	*Tuberosa*	*Tuberosa* 2	RP
S. chancayense Ochoa	442699	2*x*(1EBN)	*Transaequatorialia*	*Tuberosa*	*Tuberosa* 2	RP
S. immite Dunal	458401	2*x*(1EBN)[g]	*Piurana*	*Tuberosa*	*Tuberosa* 2	RP
S. marinasense Vargas	310946	2*x*(2EBN)	*Piurana*	*Tuberosa*	*Tuberosa* 2	RP
S. medians Bitter	283081	2*x*(2EBN)	*Tuberosa*	*Tuberosa*	*Tuberosa* 2	RP
S. mochiquense Ochoa	283114	2*x*(1EBN)	*Piurana*	*Tuberosa*	*Tuberosa* 2	RP
S. multidissectum Hawkes	210043	2*x*(2EBN)	*Transaequatorialia*	*Tuberosa*	*Tuberosa* 2	RP

TABLE 2. Continued.

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

[a] USDA plant introduction numbers (Bamberg et al., 1996).
[b] 2*x* = 24, 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 (5*x* = 60), but is listed in Bamberg et al. (1996) and Hanneman (1994) as a tetraploid (4*x* = 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 2*n* pollen (Watanabe and Peloquin, 1989, 1991) and 2*n* 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 2*x*(2EBN) germplasm from the wild species into the 4*x*(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. 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 number	Enzyme	Region	Size (kb)
1	*Bam*HI	P10	3.4 ↔ 2.8 + 0.6
2	*Bam*HI	P10	2.4 + (0.1) = 2.5
3	*Bam*HI	P10	2.7 = 2.5 + (0.2)
4	*Bam*HI	P6	5.7 = 3.6 + 2.1
5	*Bam*HI	P3	12.2 = 9.9 + 2.3
6	*Bam*HI	P3	9.9 = 6.0 + 3.9
7	*Bam*HI	P3	6.8 + 3.1 = 9.9
8	*Bam*HI	P16/S6	18.2 = 14.4 + 3.8
9	*Bam*HI	P16/S6	2.3 + 1.6 = 3.9
10	*Bam*HI	S8	7.6 = 3.8 + 3.8
11	*Bam*HI	P12/P14	5.9 = 3.5 + 2.4
12	*Bam*HI	IR2	2.9 + 0.4 = 3.3
13	*Ban*I	P8	1.9 + 1.4 = 3.3
14	*Ban*I	P3	4.4 = 2.9 + 1.5
15	*Ban*II	P10	1.8 + 1.0 = 2.8
16	*Ban*II	P10	2.3 + (0.1) = 2.4
17	*Ban*II	P10	3.1 = 2.4 + 0.7
18	*Ban*II	P10/P8	7.6 = 3.8 + 3.8
19	*Ban*II	P3	2.0 + 1.5 = 3.5
20	*Ban*II	P6	2.3 + 0.9 = 3.2
21	*Ban*II	S8	3.8 = 2.1 + 1.7
22	*Ban*II	P18/P19	0.75 + (0.05) = 0.8
23	*Bgl*II	P10	3.1 + 2.5 = 5.6
24	*Bgl*II	P10/P8	2.5 + 3 = 5.5
25	*Bgl*II	P3	3.7 = 2.4 + 1.3
26	*Bgl*II	S8	3.3 ↔ 2.3 + 1.0
27	*Bgl*II	P12/P14	0.7 = 0.4 + 0.3
28	*Bst*NI	P10	5.1 + 1.4 = 6.5
29	*Bst*NI	P10	2.6 = 2.0 + 0.6
30	*Bst*NI	P6/P8	0.8 + 0.6 = 1.4
31	*Bst*NI	P8	0.6 = 0.4 + 0.2
32	*Bst*NI	P6	2.0 + 0.3 = 2.3
33	*Bst*NI	P3	0.3 + 0.3 = 0.6
34	*Bst*NI	P3	1.1 + 0.7 = 1.8
35	*Bst*NI	P3	1.0 = 0.8 + 0.2
36	*Bst*NI	P3	1.2 + 0.1 = 1.3
37	*Bst*NI	P16/S6	2.7 + 1.2 = 3.9
38	*Bst*NI	P16/S6	2.5 + 1.4 = 3.9
39	*Bst*NI	S8	4.6 = 3.3 + 1.3
40	*Bst*NI	S8	1.5 = 1.3 + 0.2
41	*Bst*NI	P14	0.8 = 0.7 + 0.1
42	*Bst*XI	P6	16.6 = 12.4 + 4.2
43	*Bst*XI	P16/S6	23 = 13 + 10
44	*Bst*XI	S8	4.0 = 2.9 + 1.1
45	*Bst*XI	T39/T40	4.8 = 4.0 + 0.8
46	*Bst*XI	T39/T40	7.0 = 4.7 + 2.3
47	*Cla*I	P10	9.0 = 6.4 + 2.6
48	*Cla*I	P6/P8	1.2 = 1.1 + 0.1
49	*Cla*I	P6	8.9 = 5.3 + 3.6
50	*Cla*I	P6	8.9 = 7.4 + 1.5
51	*Cla*I	P6/P3	6.3 = 5.3 + 1.0
52	*Cla*I	P3	1.8 = 1.5 + (0.3)
53	*Cla*I	P16/S6	3.5 = 3.2 + 0.3
54	*Cla*I	P18/P19	7.5 + 7.5 = 15
55	*Cla*I	T36/T37	7.1 = 6.6 + 0.5
56	*Cla*I	T36/T37	7.1 = 5.8 + 1.3
57	*Cla*I	T39/T40	1.5 = 1.4 + (0.1)
58	*Cla*I	T40	2.4 = 1.5 + 0.9
59	*Dra*I	P8/P10	6.6 + 1.4 = 8.0
60	*Dra*I	P10	1.0 = 0.8 + (0.2)
61	*Dra*I	P8/P10	3.4 = 3.1 + (0.3)
62	*Dra*I	P8/P10	8.0 = 6.4 + 1.6
63	*Dra*I	P10	1.0 = 0.9 + (0.1)
64	*Dra*I	P8/P10	4.6 + 2.4 = 7.0
65	*Dra*I	P8	2.1 = 2.0 + (0.1)
66	*Dra*I	P8/P10	8.0 + 1.4 = 9.4
67	*Dra*I	P10	0.65 + 0.65 = 1.3
68	*Dra*I	P6	12.6 = 9.1 + 3.5
69	*Dra*I	P6/P3	3.5 = 2.5 + (1.0)
70	*Dra*I	P6	9.1 = 6.8 + 2.3
71	*Dra*I	P6	12.6 = 6.3 + 6.3
72	*Dra*I	P6	6.3 = 5.0 + 1.3
73	*Dra*I	P3	1.2 = 1.1 + (0.1)
74	*Dra*I	P3	3.4 = 2.3 + 1.1
75	*Dra*I	P3	4.0 = 2.2 + 1.8
76	*Dra*I	P3	5.8 = 4.8 + 1.0
77	*Dra*I	P3	4.4 + 2.4 = 6.8
78	*Dra*I	P16	3.0 = 1.6 + 1.4
79	*Dra*I	P16/S6	3.8 ↔ 2.3 + 1.5
80	*Dra*I	S6	3.2 = 2.5 + (0.7)
81	*Dra*I	S6	3.5 = 2.2 + 1.3
82	*Dra*I	S6	2.0 = 1.5 + 0.5
83	*Dra*I	S6	2.5 = 1.5 + 1
84	*Dra*I	S6	3.0 = 1.6 + 1.4
85	*Dra*I	P12/P18/P19	12.2 = 9.1 + 3.1
86	*Dra*I	T36/T37	1.5 = 1.3 + (0.2)
87	*Dra*I	T37	2.1 = 1.8 + (0.3)
88	*Dra*I	T37	2.1 = 1.6 + (0.5)
89	*Dra*I	T38/T39	5.0 = 3.0 + 2.0
90	*Dra*I	T38/T39	5.0 = 4.5 + (0.5)
91	*Dra*I	T38	3 = 1.6 + 1.4
92	*Dra*I	T39/T40	2 = 1.2 + 0.8
93	*Dra*I	T39/T40	1.2 = 0.7 + 0.5
94	*Dra*I	T40	1.2 = 1.1 + 0.1
95	*Eco*RI	P10	2.1 ↔ 1.8 + 0.3
96	*Eco*RI	P10	7.6 = 5.4 + 2.2
97	*Eco*RI	P10	2.5 = 1.9 + 0.6
98	*Eco*RI	P10	0.6 = 0.4 + (0.2)
99	*Eco*RI	P10	0.6 = 0.5 + (0.1)
100	*Eco*RI	P6	0.7 = 0.5 + (0.2)
101	*Eco*RI	P3	1.5 = 1.2 + 0.3
102	*Eco*RI	P3	2.0 = 1.1 + 0.9
103	*Eco*RI	P16/S6	1.6 + (0.1) = 1.7
104	*Eco*RI	P16/S6	2.0 = 1.6 + 0.4
105	*Eco*RI	P16/S6	5.8 = 4.1 + 1.7
106	*Eco*RI	S8	2.2 = 1.6 + 0.6
107	*Eco*RI	S8	1.5 = 1.4 + (0.1)
108	*Eco*RI	S8	3.4 = 2.8 + 0.6
109	*Eco*RI	S8	3.3 = 2.9 + (0.4)
110	*Eco*RI	IR2	4.6 = 2.6 + 2.0
111	*Eco*RI	T36/T37	2.5 = 1.7 + 0.8
112	*Eco*RI	T40	2.8 = 2.3 + 0.5
113	*Eco*RI	T39/T40	2.3 = 1.3 + 1.0
114	*Eco*RV	P10	2.7 = 2.0 + 0.7
115	*Eco*RV	P8/P10	11.6 = 6.6 + 5.0
116	*Eco*RV	P6/P3	17.3 ↔ 12.0 + 5.3
117	*Eco*RV	P3	22 = 18 + 4
118	*Eco*RV	P3	10.8 = 7.4 + 3.4
119	*Eco*RV	P3	7.4 = 6.7 + 0.7
120	*Eco*RV	P16/S6	13.2 = 6.6 + 6.6
121	*Eco*RV	S8	1 = 0.8 + (0.2)
122	*Eco*RV	P18/P19	1.5 = 1.1 + 0.4
123	*Eco*RV	T37/T38	11 = 8 + 3
124	*Eco*O109	P10/P19	11.2 = 6.3 + 4.9
125	*Eco*O109	P6	2.9 = 2.1 + 0.8
126	*Eco*O109	P6	2.1 = 1.5 + 0.6
127	*Eco*O109	P3	6.1 = 5.3 + 0.8
128	*Eco*O109	P14/IR-2	7.3 = 6.4 + 0.9
129	*Eco*O109	T39/T40	6.4 = 4.4 + 2.0
130	*Hae*II	P8/P10	9.5 = 7.0 + 2.5
131	*Hae*II	P10	17 = 8.6 + 8.4

TABLE 3. Continued.

Mutation number	Enzyme	Region	Size (kb)
132	*Hinc*II	P10	2.3 = 1.9 + 0.4
133	*Hinc*II	P10/P8	1.4 = 0.7 + 0.7
134	*Hinc*II	P8/P6	4.9 + 3.1 = 8.0
135	*Hinc*II	P6	3.1 = 2.5 + 0.6
136	*Hinc*II	P6	6.1 = 5.5 + 0.6
137	*Hinc*II	P3	3.5 ↔ 2.7 + 0.8
138	*Hinc*II	P3	4.9 = 3.5 + 1.4
139	*Hinc*II	P3	3.5 = 3.1 + 0.4
140	*Hinc*II	T38	1.6 + (0.6) = 2.2
141	*Hinc*II	T39/T40	5.8 = 3.8 + 2.0
142	*Hind*III	P8	2.2 + 0.7 = 2.9
143	*Hind*III	P3	4.0 = 2.9 + 1.1
144	*Hind*III	P3	12.4 + 1.0 = 13.4
145	*Hind*III	P3/P16	13.2 = 9.5 + 3.7
146	*Hind*III	T36/T37	6.6 = 4.4 + 2.2
147	*Hind*III	T36/T37	6.6 = 5.6 + 1.0
148	*Hpa*II	P10	0.8 = 0.6 + (0.2)
149	*Hpa*II	P10	2.1 + 1.0 = 3.1
150	*Hpa*II	P10	1.7 = 1.5 + 0.2
151	*Hpa*II	P8	1.6 = 1.3 + 0.3
152	*Hpa*II	P8	1.4 = 1.3 + (0.1)
153	*Hpa*II	P6	1.9 = 1.5 + (0.4)
154	*Hpa*II	P16/S6	2.2 = 2.0 + 0.2
155	*Hpa*II	P16/S6	1.5 = 1.0 + 0.5
156	*Hpa*II	S8	0.9 = 0.8 + (0.1)
157	*Hpa*II	P18	2.5 = 1.4 + 1.1
158	*Hpa*II	T39/T40	3.3 + 2.5 = 5.8
159	*Hpa*II	T39/T40	3.2 = 1.7 + 1.5
160	*Hpa*II	T39/T40	2.6 = 1.4 + 1.2
161	*Hph*I	P10	11.4 = 9.9 + 1.5
162	*Hph*I	P10	7.2 = 3.6 + 3.6
163	*Hph*I	P10	11.4 = 7.2 + 4.2
164	*Hph*I	P3/P6	2.2 = 1.5 + 0.7
165	*Hph*I	P3	3.0 = 2.2 + 0.8
166	*Hph*I	P3	2.5 + (0.2) = 2.7
167	*Hph*I	P3	2 = 1.4 + 0.6
168	*Hph*I	P16/S6	1.7 = 1.0 + 0.7
169	*Hph*I	P16/S6	1.1 = 0.6 + 0.5
170	*Hph*I	T36/T37	3.4 = 2.4 + 1.0
171	*Hph*I	T39/T40	3.2 = 1.7 + 1.5
172	*Kpn*I	P3	12.5 = 9.4 + 3.1
173	*Nci*I	P10	5.5 = 4.9 + 0.6
174	*Nci*I	P6	2.7 + (0.4) = 3.1
175	*Nci*I	S8	1.7 + (0.4) = 2.1
176	*Nci*I	P18/P19	4.2 = 3.1 + 1.1
177	*Nsi*I	P10	8.4 = 6.6 + 1.8
178	*Nsi*I	P10	18.6 = 12.0 + 6.6
179	*Nsi*I	P8/P6	14.7 = 10.6 + 4.1
180	*Nsi*I	P6	4.5 = 3.5 + 1
181	*Nsi*I	P3	2.9 = 2.0 + 0.9
182	*Nsi*I	T38	5.0 = 2.5 + 2.5
183	*Pvu*II	IR2/T36/T37	15.3 = 11.5 + 3.8
184	*Ssp*I	P10	2.1 = 1.7 + (0.4)
185	*Ssp*I	P8	1.9 = 1.0 + 0.9
186	*Ssp*I	P8	1.4 = 1.3 + (0.1)
187	*Ssp*I	P6	1.9 = 1.1 + 0.8
188	*Ssp*I	P6/P3	3.4 + 2.1 = 5.5
189	*Ssp*I	P6/P3	3.7 + 2.1 = 5.8
190	*Ssp*I	P3	2.7 = 1.5 + 1.2
191	*Ssp*I	T36/T37	1.2 = 1.0 + (0.2)
192	*Sst*I	P8/P10	6.0 = 5.1 + 0.9
193	*Sst*I	P8/P10	8.9 = 6.0 + 2.9
194	*Sst*I	P6/P3	18 = 9 + 9
195	*Sst*I	P3	3.8 = 3.4 + (0.4)
196	*Sst*I	S6/S8	10.5 = 6.8 + 3.6
197	*Sst*I	P3	1.1 = 0.9 + (0.2)
198	*Xba*I	P16/S6	4.7 = 3.1 + 1.6
199	*Xba*I	P18/P19	2.6 = 1.4 + 1.2
200	*Xba*I	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 2*x*(1EBN) species, such as *S. chancayense, S. circaeifolium, S. lignicaule,* and *S. mochiquense,* have white and/or stellate corollas. In addition, *S. gandarillasii,* 2*x*(2EBN) and *S. colombianum,* 4*x*(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

TABLE 4. Data matrix of 200 restriction enzyme site variants for 78 accessions of *Solanum* sect. *Petota*, and one accession of sect. *Etuberosum* (outgroup). The states 0, 1, and 9 represent site absence, site presence, and missing data, respectively.

Outgroup (sect. Etuberosum)	
Solanum palustre (outgroup)	
10111101011001001100100011101010001000111011010110100000000000011100	
00100000110000001010000001100110001011001110110101111010110000010111111	
10100001011001000100001001101100100111910101010110101000011	
Ingroup (sect. Petota)	
Solanum abancavense	
00111001011101001100100010101010001000111001010100100000010000000111100	
00100000090000000100000011100110001011001110101101111010000010111101111	
10000001000010010100000000100110011011101109011110101000000	
S. acaule	
00111000011101001100100010101010001000111001010100100000010000000101000	
00100000010000000000000011100110001011001110101101111010000010111101111	
10000001000010010100000000100110011011101110001111010100000000	
S. acroglossum	
01111001011101001000100010111000001001111001010100100000010000000111000	
00000000010000000000100111001100010110011101101110010001011111101111	
10000001000010000100001001101100111011101110101111010100001010	
S. agrimonifolium	
00111100011101001100100010101010001000111001010100100000010000000111000	
00100000010010000010000011100110001011001110101101111010000010011101111	
10000001000110010110000011001000111011101110000111010101000000	
S. alandiae	
00111001011101001100100010101010001000111001010000100000010000000111000	
00100000010000000000000011100110001011000110101101111010000010111101111	
10000001000010010100000000100110011011101110101111010100000000	
S. albornozii	
00111001011101001100100101010001000100111001010100100000010000000111110	
00010000910099000010010011100110000011000011010110111101000001011110111	
00000001100010000100001001101100110011011000011111101000001 0	
S. ambosinum	
00111001011101001100100110101010001000111001010100100000010000000111100	
00100000090000000100000011100110001011001110101101111010000010111101111	
10000001000010010100000000100110011011101110901111010100000099	
S. andreanum	
01111001011101011100100010101010001001111001010100100000010000000111101	
00000000001001000100001011000011100101100111010111011110100000101111011	
10000011000010000100001001101100110111011101110101111010100000010	
S. arnezii	
00111001011101001100100010101010001000111001010000100000010000009110000	
00100000010000010000000011100110001011000110101101111010000010111101111	
10000001000010010100000001001100110111011101110101111010100000000	
S. avilesii	
00111001011101001100100010101010001000111001010000110000010000000111000	
00100000010000010000000011100110001011000110101101111010000010111101111	
10000001000010010100000001001100110111011101110101111010100000000	
S. berthaultii	
00111001011101001100100010101010001000111001010000110000010000000111000	
00100000010000010000000011100110001011000110101101111010000010111101111	
10000001000010010100000001001100110111011101110101111010100000000	
S. brevicaule	
00111001011101001100100010101010001000111001010100100010010000000111100	
00100000010000000000000011100110001011001110101101111010000010111101111	
10000001000010010100000001001100110111011101110101111010100000001	
S. bukasovii	
00111009011101001100100010101010001000111001010100100000010000000111000	
00100000010010000100000011100110001011001110101101111010000010111101111	
10000001000010010100000001001100110111011101110001111010100000009	
S. bulbocastanum	
01111001010001101100100010101010011010111001110100100000010000000111000	
00100000000000000000010011101110001111000101001011111010001001010110111	
10000001001010000000001001101100110111011101110101111000011	
S. canasense	
00111000011101001100100010101010001000111001010100100000010000000111100	
00100000010010000100000011100110001011001110101101111010000010111101111	
10000001000010010100000000100110011011101110001111010100000000	
S. candolleanum	
00111001011101001100100010101010001000111001010100100000010000000111100	
00100000010010000100100011100110001010001110101101111010000010111101111	
10000001000010010100000000100110011011101110901111010100000000	
S. capsicibaccatum	
00111001011101001100110010101010001000111001010100100000010000000111000	
00100000010000000000000011100110001011001110101101111010000010111101111	
10000001000010010010001000100111001101110011010111101010000000	
S. cardiophyllum	
00011001011001101100100010101010101000101001010100100001010000000111000	
00100000000000000000001001110011010101100011010010111011001001010110110	
10000001001010010100011001111110011011111110101011011100000011	
S. chacoense PI 217451	
00111001011101001100100010101010001000111001010000100000010000000001100	
00000000010000010000000011100110001011000110101101111010000010111101111	
10000001000010010100000001001100110111011101110101111010100000000	
S. chacoense PI 414153	
00111001011101001100100010101010001000111001010000100000010000000111000	
00100000000000010000000011100110001011000110101101111010000010111101111	
10000001000010010100000001001100110111011101110001111010100000000	
S. chancavense	
00111001011101001100000010101010001001111001010100100000010000000111100	
00000000000000001010010011100110001011001110101101111010000010111101111	
10000001000010000100001101101100110111011101110101111010100000010	
S. colombianum	
00101100011101001100100010101010001000111001010100100000010000000111100	
00100000010010000010000011100110001011001110101101111011000010111101111	
00000001000010010110000011001100110111011109011110101010000	
S. commersonii	
00111001111101001100100010101010001000111001010000100000010000000111000	
00100000010000010000000011100110001011000110101101111010000010111101111	
10000001000010010100000001001100110111011101110101111010100000000	
S. curtilobum	
00111000011101001100100010101010001000111001010100100000010000000111000	
00100000010010000100000011100110001011000110101101111010000010111101111	
10000001000010010100000001001100110111011101110001111010100000000	
S. doddsii	
00111001011101001100100010101010001000111001010000100000010000000111000	
00100000010000010000000011100110001011000110101101111010000010111101111	
10000001000010010100000001001100110111011101110101111010100000000	

TABLE 4. Continued.

S. gandarillasii

0011100101110100110110001010101000100011100101000010000001000000011100
0010100001000001000000001110011000101100011010110111101000001011110111
1000000100001001010000000100110011011101110101111010100000000

S. gourlayi

0011100101110100110010001010101000100011100101010010001001000000011100
0000000001000000000000000111001100010110011001011011110100000101110111
1000000100001001010000000100110011011101110101111010100000001

S. hastiforme

0011100001110100110010001010101000100011100101010010000000100000011100
0010000000100100001000000111001100010110011101011011110100000101110111
1000000100001001010000000100110011011101110001111010100000099

S. hintonii

0011100101101100110010001000111000100001100101010000100001000000011000
0000000000000000000010011100010001011001110100101011000010010101101111
1001010000100000010100100110111000111111101010010001001010

S. hondelmannii

0011100101110100110010001010101000100011100101000011000001000000011000
0010000000100000100000000111001100010110001001011011110100000101110111
1000000100001001010000000100110011011101110101111010100000000

S. huancabambense

0011100101110100110010001010101000100111100101010010000001000000011000
0000001000000000000000100111001100010110011101011011110100000101110111
1000000100001000010000100110110011011101110101111010100000010

S. hypacrarthrum

0011100101110100110010001010101000100111100101010010000001000000011100
0000000009000000000000000111001100010110011101011011110100000101110111
1000000100001000010000100190110011011101110101111010100000010

S. immite

0011100101110100110010001010101000100111100101010010000001000000011100
0000000000000000000000100111001100010110011101011011110100000101110111
1000000100001000010000100110110011011101110101111010100000010

S. incamayoense

0011100101110100110010001010101000100011100101010010001001000000011100
0000000001000000000000000111001100010110011001011011110100000101110111
1000000100001001010000000100110011011101110101111010100000001

S. infundibuliforme

0011100101110100110010001010101000100011100101110010010001000000011000
0010000000000000000000000111001100010110011101011011110100000101110111
1000100100001001010000000110110011011101110101111010100000001

S. kurtzianum

0011100101110100110010001010101000100011100101000010000001000000011000
0010000000100000100000000111001100010110001101011011110100000101110111
1000000100001001010000000100110011011101110101111010100000000

S. laxissimum

0011100101110100010010001010101000110011100101000010000001000000011000
1110000000100000100000000111001100010110011101011011110100000101110111
1000000100001001010000000100110011011101110101111010100000100

S. leptophyes

0011100001110100110010001010101000100011100100010010000001000000011000
0010000101001100010000001110011001101110111010110111101000001011110111
1000000100001001010000000100110011011101110001111010100000000

S. limbaniense

0011100001110100110010001010101000100011100101010010000001000001011100
0010000000100100001000000111001100110110011101011011110100000101110111
1000000100001001010000000100110011011101110001111010100000000

S. lignicaule

0011100101110100110010001010101000100011100101010010000001000000011100
0010000000100000000000000111001100010110011101011011110100000101110101
1000000100001001010000000100110011011101110001110010100000000

S. longiconicum

0011110001110100110010001010101000100011100101010010000001000010011101
0010010001001000001000000111001100010110011111011011110100000101110111
1000000100001001011000001100010111011101110011111010101000000

S. maglia

0011100101110100110010001010101000100011100101000011000001000000011000
0010000000100000100000000111001100010110001101011011110100000101110111
1000000100001001010000000100110011011101110101111010100000000

S. marinasense

0011100101110100110010001010101000100011100101010010000001000000011100
0010000000100000001000000111001100010110011101011011110100000101110111
1000000100001001010000000100110011011101110901111010100000000

S. medians

0011100001110100110010001010101000100011100101010010000001000000011100
0010000000100100001000000111001100010110011101011011110100000101110111
1000000100001001010000000100110011011101110001111010100000000

S. megistacrolobum

0011100001110100110010001010101000100011100101010010000001000000011100
0010000000100100900000000111001100010110001101011011110100000101110111
1000000100001001010000000100110011011101110001111010100000000

S. microdontum

0011100100110101110000001010101000100011100101000010000001000001011000
0010000000100000100000000111101100010110001101011011110100000101110111
1000000100001001010000000100110011011101110101111000100000000

S. mochiquense

0011100101110100110010001010101000100111100101010010000001000000011100
0000000000000000101001001110010000101100111010110111101000001011110111
1000000100001000010000110110110011011101110101111010100000010

S. morelliforme

0011100101111000010010001000101000100001100101010000000000111100011100
0010000000100000000000110111010100010110011101001010110000000199011011
1009010000100000010100100100111000111111101010010101001000

S. moscopanum

0011110001110100110010001010101000100011100101010010000001000010011100
0010000000100100001000001110011000101100111010110111101000001011110111
1000000100001001011000001100110011011101110001111010101000000

S. multidissectum

0011100001110100110010001010101000100011100101010010000001000000011100
0010000000100100001100000111001100110110011101011011110100000101110111
1000000100001001010000000100110011011101110001111010100000000

S. neocardenasii

0011100101110100110010001010101000100011100101000010000001000000011000
0010000000100000100000000111001100010110001101011011110100000101110111
1000000100001001010000000100110011011101110101111010100000000

TABLE 4. Continued.

S. necrossii

00111001011101001100100010101010001000111001010000100000010000000010000
00100000010000010000000011100110001011000110111010111010000010111101111
10000001000010010100000001001100110111011101111010000000

S. okadae

00111001011101001100100010101010001000111001010000100000010000000011000
00100000010000010000000011100110001011000110111010111010000010111101111
10000001000010010100000000001100110111011101111010000000

S. oplocense

00111001011101001100100010101010001000111001010000100000010000000011000
00100000000000010000000011100110001011000110111010111010000010111101111
10000001000010010100000001001100110111011101111010000000

S. pampasense

00111011011101001100100010101010000000111001010000100000010000000011100
00100000000000010000000011100110001001000110111010111010000010111010111
11000001000010010100000001001100110111011101111010111010000000

S. pascoense

00111101011101001000100010111010001001111000010101100000010000000011101
00000000011000000110010011100110001010011101101111010111000100000111110111
10000010000100001000010011011001101110110011010111010000001000

S. paucissectum

01111001011101011100100010101010001001111001010100100000010000000011000
00000000010000001000010011111011000101100111010110111010000010111101111
10000010000100001000010011011001101110111110111010100000010

S. pinnatisectum

00111001011011001100100010001110001000011001010100000000010000000011100
00100000000000000000010011100010001011001110100101011000010010101101111
10010100001000000101001001101110001101111101010010001001010

S. piurae

01111001011101011100100000101010001001111001010100100010010000000011100
00000000010000001000010011111011000101100111010111111101000001011110111
10000001000010000100001001101100110111011101011101000000010

S. raphanifolium

00111000011101001100100010101010001000111001010100100000010000000111100
00100100010010000010000011100110000011001110101101111010000011011110111
10000001000010010100000000100110011011101110001111010100000000

S. sanctae-rosae

00111000011101001100100010101010001000111001010100100000010001001111000
00101000010000000010000011100110001011001110001101111010000010111101111
10000001000010010100000000100110011011101110001111010100000000

S. santolallae

00111009011101001100100010101010001000111001010000100000010000000011000
00100000010000010000000011100110001011000110111010111010000010111101111
10000001000010010100000000100110011011101110101111010100000000

S. scabrifolium

00111000011101001110100010101010001000111001010100100000010000000011100
00100000010010000100000011100110011011001110101101111010000010111001111
10000001000010010100000000100110011011101110001111010100000000

S. sogarandinum

00111001011101001100100010101010001001111001010100100000010000000011100
00000000010000001000010011100110001011001110101101111010000010111101111
10000001000010000100001101101100110111011101011110100100000010

S. sparsipilum

00111001011101001100100010101010001000111001010100100000010000000011100
00100000010010000000000011100110001011001100101101111010000010111101111
10000001000010010100000001001100110111011101011110100100000001

S. spegazzinii

00111001011101001100100010101010001000111001010000100000010000000011000
00100000010000010000000011100110001011000110101101111010000010111101111
10000001000010010100000001001100110111011101011110100100000000

S. subpanduratum

00111100011101001100100010101010001000111001010100100000010000000111100
00100100010010100010000011100110001011001110101101111010000010111101111
10000001000010010110000011001100110111011100011110101010100000

S. sucrense PI 442691

00111000011101001100100010101010001000111001010100100000010000000011000
00100000010010000100000011100110001011000110101101111010000010111101111
10000001000010010100000001101100110111011100011110101010000000

S. sucrense PI 498302

00111001011101001100100010101010001000111001010100100000010000000011100
00100000010000000000000011100110001011001100101101111010000001991110111
10000001000010010100000001001100110111011101011110101010000001

S. tariiense

00111000101110100110010001010101000100011100101010010000001000000011000
00100000010000010000000011100110001011000110111010111010000010111101111
10000001000010010100000001001100110111011101111010111010000000

S. tuberosum

00111000011101001100100010101010001000111001010100100000010000000111000
00100000010000000000009011100110001011000110101101111010000010111101111
10000001000010010100000001001100110111011100011110101010000000

S. tundalomense

00111001011101011100100010101010001001110001010100100000011000000111100
00000000010100001000010011110110000011001110101101111010000019911101111
10000001000010010100001001101100110111011101111010111010000090

S. tuquerrense

01111001011101011100100010101010001001190010101001000001100000011110000
00000000010100001001010011110110001011001110101101111010000010111101111
10000001000010101100001001101100110111011101111010111010000010

S. vernei

00111001011101001100100010101010001000111001010100100000010000000011000
00100000010000010000000011100110001011000110101101111010000010111101111
10000001000010010100000001001100110111011101111010111010000000

S. verrucosum

00111001011101001100100010101010001000111001010000100000010000000011000
00100000010000010000000011100110001011010110101101111010000010111101111
10000001000010010100000000001100110111011101111010111010000000

S. vidaurrei

00111001011101001100100010101010001000111001011100100110010000100111100
00100000000000000000000011100110001011001100101101111010000010111101111
10001001000010010100000001001100110111011101111010111010000001

S. violaceimarmoratum

00111001011101001100100010101010001000111001010000100000010000000011000
00100000010000010000000011100110001011001110101101111010000010111101111
10000001000010010100000001001100110111011101111010111010000000

S. sect. Petota undescribed species

00111001011101001100100010101010011000111001010000100000010000000011000
00100000010000010000000011100110001011000110101101111000000010111101111
10000001000010010100000001001100110111011101111010111010000000

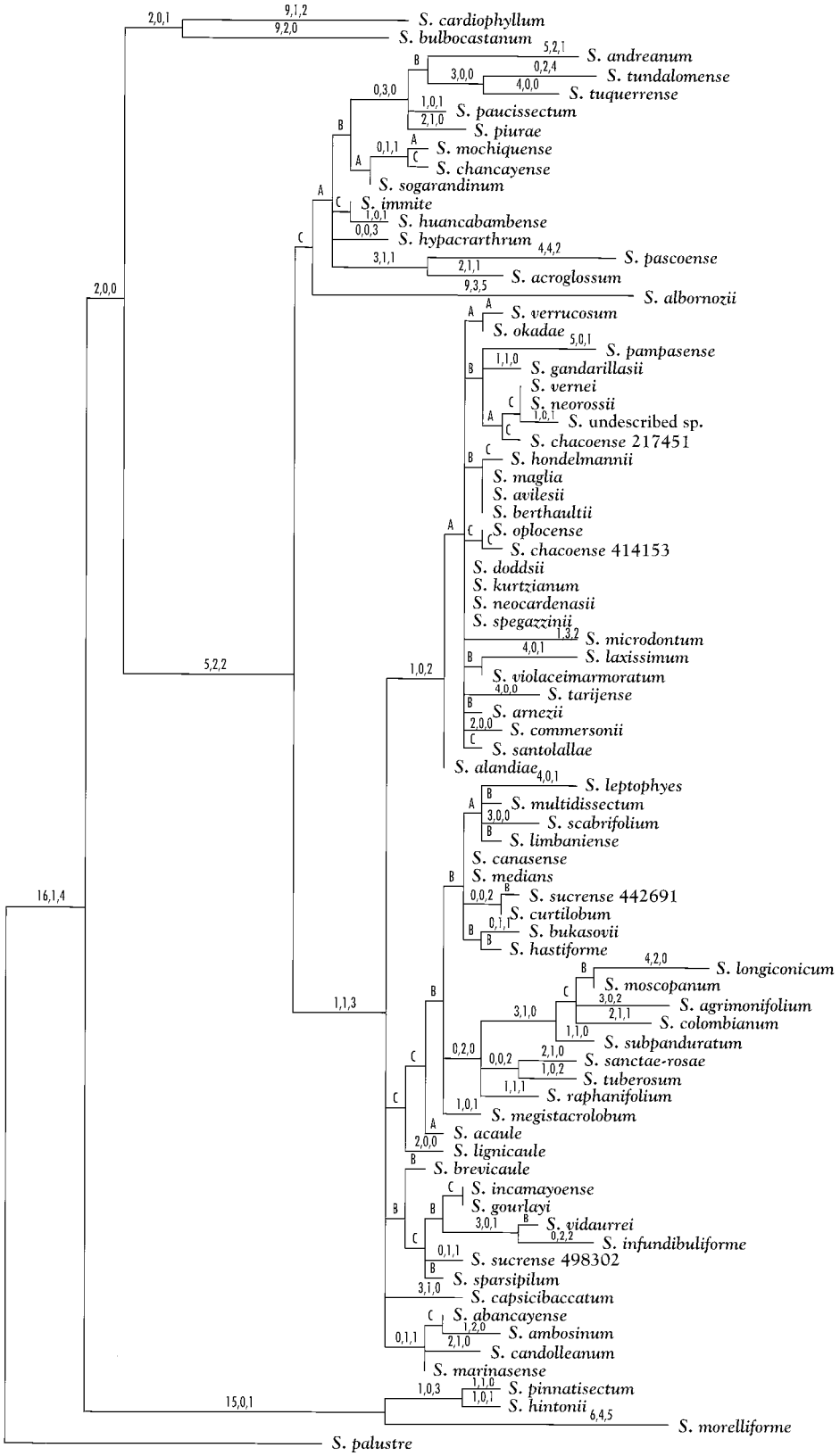

Fig. 1. One of 5000 equally parsimonious 319-step Wagner trees drawn as a phylogram (branch lengths proportional to character support) of cpDNA restriction site variants in *Solanum* sect. *Petota* and sect. *Etuberosum* (*S. palustre*, outgroup), with numbers of characters supporting each branch, ordered 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).

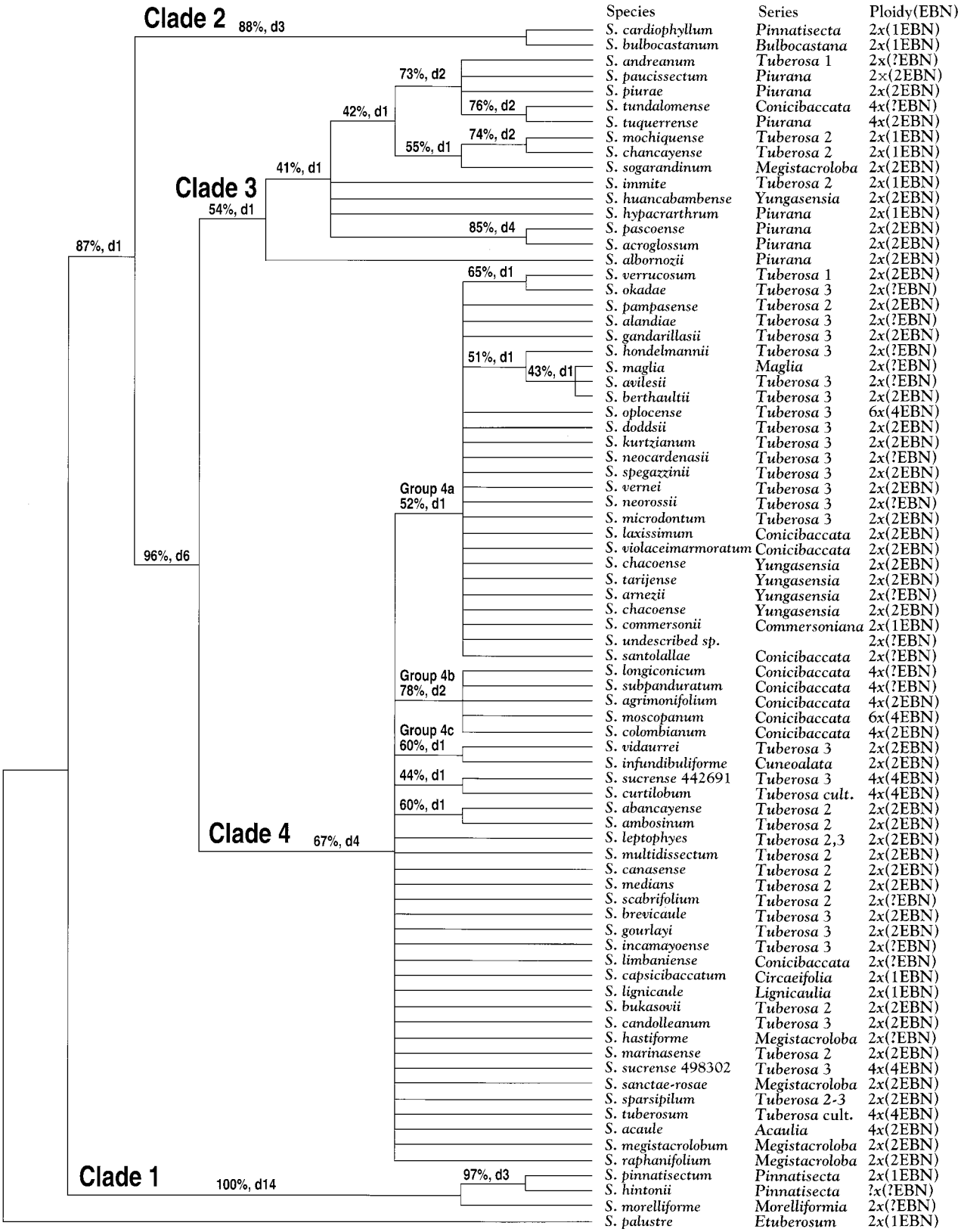

Fig. 2. The strict consensus tree of 5000 equally parsimonious 319-step Wagner trees, with bootstrap and decay values. Clades 1-4 as discussed in the text. Series affiliations (including informal ser. *Tuberosa* groups 1, 2, and 3) follow Hawkes (1990); ploidy and Endosperm Balance Numbers (EBN) from 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 2*x*(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 well-defined 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. *Conicibaccata* 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 intra- and interspecific sampling to see if this relationship is maintained, and questions the continued recognition of ser. *Cuneoalata.*

The presence of the 2*x*(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 2*x*(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 tuber-bearing 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.

LITERATURE CITED

ALBERT, V. A., B. D. MISHLER, AND M. W. CHASE. 1992. Character-state weighting for restriction site data in phylogenetic reconstruction, with an example from chloroplast DNA. *In* P. S. Soltis, D. E. Soltis, and J. J. Doyle [eds.], Molecular systematics of plants, 369–403. Chapman and Hall, New York, NY.

BAMBERG, J. B., M. W. MARTIN, J. J. SCHARTNER, AND D. M. SPOONER. 1996. Inventory of tuber-bearing *Solanum* species. Potato Introduction Station, NRSP-6, Sturgeon Bay, WI.

———, AND D. M. SPOONER. 1994. The United States Potato Introduction Station Herbarium. *Taxon* 43: 489–496.

CASTILLO, R. O., AND D. M. SPOONER. In press. Phylogenetic relationships of wild potatoes, *Solanum* series *Conicibaccata* (sect. *Petota*). *Systematic Botany*.

CHILD, A. 1990. A synopsis of *Solanum* subgenus *Potatoe* (G. Don) (D'Arcy) (*Tuberarium* (Dun.) Bitter (s.l.)). *Feddes Repertorium* 95: 238–298.

CONTRERAS-M., A., AND D. M. SPOONER. In press. Revision of *Solanum* section *Etuberosum*. *In* M. Nee, D. E. Symon, and J. P. Jessop [eds.], Solanaceae IV: taxonomy, chemistry, evolution. Royal Botanic Gardens, Kew.

CORRELL, D. S. 1962. The potato and its wild relatives. *Contributions from Texas Research Foundation, Botanical Studies* 4: 1–606.

CORRIVEAU, J. L., AND A. W. COLEMAN. 1988. Rapid screening method to detect potential biparental inheritance of plastid DNA and results for over 200 angiosperm species. *American Journal of Botany* 75: 1443–1458.

DEBENER, T., F. SALAMINI, AND C. GEBHARDT. 1990. Phylogeny of wild and cultivated *Solanum* species based on nuclear restriction fragment length polymorphisms (RFLPs). *Theoretical and Applied Genetics* 79: 360–368.

DOYLE, J. J. 1992. Gene trees and species trees: molecular systematics as one-character taxonomy. *Systematic Botany* 17: 144–163.

———, AND J. L. DOYLE. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochemical Bulletin* 19: 11–15.

FARRIS, J. S. 1970. Methods for computing Wagner trees. *Systematic Zoology* 19: 83–92.

FEINBERG, A. P., AND B. VOGELSTEIN. 1984. A technique for radiolabelling DNA restriction endonuclease fragments to high specific gravity. *Analytical Biochemistry* 137: 266–267.

FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.

GIANNATTASIO, R., AND D. M. SPOONER. 1994. A reexamination of species boundaries between *Solanum megistacrolobum* and *S. toralapanum* (*Solanum* sect. *Petota*, series *Megistacroloba*): morphological data. *Systematic Botany* 19: 89–105.

HANNEMAN, R. E., JR. 1989. The potato germplasm resource. *American Potato Journal* 66: 655–667.

———. 1994. Assignment of Endosperm Balance Numbers to the tuber-bearing solanums and their close non-tuber-bearing relatives. *Euphytica* 74: 19–25.

———, AND J. B. BAMBERG. 1986. Inventory of tuber-bearing *Solanum* species. *Wisconsin Agricultural Experiment Station Bulletin* 533: 1–216.

HARRIS, S. F., AND R. INGRAM. 1991. Chloroplast DNA and biosystematics: the effects of intraspecific diversity and plastid transmission. *Taxon* 40: 393–412.

HAWKES, J. 1958. Kartoffel. I. Taxonomy, cytology and crossability. *In* H. Kappert and W. Rudorf [eds.], Handbuch der Pflanzenzüchtung, 2nd ed., vol. 3, 1–43. Paul Parey, Hamburg.

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

———. 1963. A revision of the tuber-bearing Solanums. *In* Scottish Plant Breeding Station Record, 2nd ed., 76–181. Scottish Plant Breeding Station, Pentlandfield, Scotland.

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

———. 1990. The potato: evolution, biodiversity, and genetic resources. Belhaven Press, London.

———, AND J. P. HJERTING. 1969. The potatoes of Argentina, Brazil, Paraguay, and Uruguay: a biosystematic study. *Annals of Botany Memoirs*: 1–525 + 150 pl.

———, AND ———. 1989. The potatoes of Bolivia: their breeding value and evolutionary relationships. Oxford University Press, Oxford.

———, AND M. T. JACKSON. 1992. Taxonomic and evolutionary implications of the Endosperm Balance Number hypothesis in potatoes. *Theoretical and Applied Genetics* 84: 180–185.

HEIJDEM, G. W. A. M., AND R. G. VAN DEN BERG. In press. Quantitative

assessment of corolla shape variation in *Solanum* sect. *Petota* by computer image analysis. *Taxon*.

HOLMGREN, P. K., N. H. HOLMGREN, AND L. C. BARNETT. 1990. Index herbariorum part I: the herbaria of the world. *Regnum Vegetabile* 120: 1–693.

HOSAKA, K. 1995. Successive domestication and evolution of the Andean potatoes as revealed by chloroplast DNA restriction endonuclease analysis. *Theoretical and Applied Genetics* 90: 356–363.

———, AND R. E. HANNEMAN, JR. 1988. Origin of chloroplast DNA diversity in the Andean potatoes. *Theoretical and Applied Genetics* 76: 333–340.

———, Y. OGIHARA, M. MATSUBAYASHI, AND K. TSUNEWAKI. 1984. Phylogenetic relationship between the tuberous *Solanum* species as revealed by restriction endonuclease analysis of chloroplast DNA. *Japanese Journal of Genetics* 59: 349–369.

IRIKURA, Y. 1976. Cytogenetic studies on the haploid plants of the tuber-bearing *Solanum* species. II. Cytogenetical investigations on haploid plants and interspecific hybrids by utilizing haploidy (in Japanese, with English summary). *Research Bulletin of the Hokkaido National Agricultural Research Station* 115: 1–80.

JOHNSTON, S. A., T. P. M. DEN NIJS, S. J. PELOQUIN, AND R. E. HANNEMAN, JR. 1980. The significance of genic balance to endosperm development in interspecific crosses. *Theoretical and Applied Genetics* 57: 5–9.

MARKS, G. E. 1955. Cytogenetic studies in tuberous *Solanum* species. I. Genomic differentiation in the group *Demissa*. *Journal of Genetics* 53: 262–269.

MATSUBAYASHI, M. 1981. Species differentiation in tuberous *Solanum* and the origin of cultivated potatoes (in Japanese). *In* Japanese Society of Breeding [ed.], Recent advances in breeding, vol. 22, 86–106. Keihatso Shuppan, Tokyo.

NEIGEL, J. E., AND J. C. AVISE. 1986. Phylogenetic relationships of mitochondrial DNA under various demographic modes of speciation. *In* S. Karlin and E. Nevo [eds.], Evolutionary processes and theory, 515–534. Academic Press, Inc., Orlando, Florida.

OCHOA, C. M. 1962. Los *Solanum* tuberiferos silvestres del Peru (Secc. *Tuberarium*, Sub-secc. *Hyperbasarthrum*), Privately published, Lima, Peru.

———. 1963. Un nuevo *Solanum* tuberifero silvestre del Ecuador. *Anales científicos de la Universidad Agraria, Lima, Peru.*

———. 1972. Un nuevo taxon y sinonimia de algunas especies tuberiferas peruanas de *Solanum. Darwiniana* 17: 416–432.

———. 1979. Nueva papa silvestre venezolana de la serie *Conicibaccata. Biota* 11: 331–333.

———. 1981. Colombian tuber bearing Solanums in the *Conicibaccata* series. *Phytologia* 49: 484–487.

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

———. 1992a. Determinations of chromosome number (2*n*) and Endosperm Balance Number (EBN) in some little-known tuber bearing *Solanum. Phytologia* 73: 180–182.

———. 1992b. New synonyms in the tuber bearing *Solanum. Phytologia* 73: 166–168.

OLMSTEAD, R. G., AND J. D. PALMER. 1992. A chloroplast DNA phylogeny of the Solanaceae: subfamily relationships and character evolution. *Annals of the Missouri Botanical Garden* 79: 346–360.

———, AND ———. 1994. Chloroplast DNA and systematics: a review of methods and data analysis. *American Journal of Botany* 81: 1205–1224.

ORTIZ, R., AND M. K. EHLENFELDT. 1992. The importance of Endosperm Balance Number in potato breeding and the evolution of tuber-bearing *Solanum* species. *Euphytica* 60: 105–113.

PALMER, J. D. 1986. Isolation and structural analysis of chloroplast DNA. *Methods in Enzymology* 118: 167–186.

RAMANNA, M. S., AND J. G. T. HERMSEN. 1979. Genome relationships in the tuber-bearing Solanums. *In* J. G. Hawkes, R. N. Lester, and A. D. Skelding [eds.], The biology and taxonomy of the Solanaceae, 647–654. Linnean Society of London Symposium Series 7, Academic Press, London.

SOLTIS, D. E., P. S. SOLTIS, AND B. G. MILLIGAN. 1992. Intraspecific chloroplast DNA variation: systematic and phylogenetic implications. *In* P. S. Soltis, D. E. Soltis, and J. J. Doyle [eds.], Molecular systematics of plants, 117–150. Chapman and Hall, New York, NY.

SPOONER, D. M., G. J. ANDERSON, AND R. K. JANSEN. 1993. Chloroplast DNA evidence for the interrelationships of tomatoes, potatoes, and pepinos (Solanaceae). *American Journal of Botany* 80: 676–688.

———, R. CASTILLO T., AND L. E. LÓPEZ J. 1993. Synonymy within wild potatoes (*Solanum* sect. *Petota*: Solanaceae): the case of *Solanum andreanum. Systematic Botany* 18: 209–217.

———, AND K. J. SYTSMA. 1992. Reexamination of series relationships of Mexican and Central American wild potatoes (*Solanum* sect. *Petota*): evidence from chloroplast DNA restriction site variation. *Systematic Botany* 17: 432–448.

———, ———, AND E. CONTI. 1991. Chloroplast DNA evidence for genome differentiation in wild potatoes (*Solanum* sect. *Petota*: Solanaceae). *American Journal of Botany* 78: 1354–1366.

———, ———, AND J. F. SMITH. 1991. A molecular reexamination of diploid hybrid speciation of *Solanum raphanifolium. Evolution* 45: 757–764.

———, AND R. G. VAN DEN BERG. 1992a. An analysis of recent taxonomic concepts in wild potatoes (*Solanum* sect. *Petota*). *Genetic Resources and Crop Evolution* 39: 23–37.

———, AND ———. 1992b. Species limits and hypotheses of hybridization of *Solanum berthaultii* Hawkes and *S. tarijense* Hawkes: morphological data. *Taxon* 41: 685–700.

———, ———, AND J. B. BAMBERG. 1995. Examination of species boundaries of *Solanum* series *Demissa* and potentially related species in series *Acaulia* and series *Tuberosa* (sect. *Petota*). *Systematic Botany* 20: 295–314.

SWOFFORD, D. L. 1993. PAUP: phylogenetic analysis using parsimony, version 3.1.1. Computer program distributed by the Illinois Natural History Survey, Champaign, IL.

SYTSMA, K. A., AND L. D. GOTTLIEB. 1986. Chloroplast DNA evolution and phylogenetic relationships in *Clarkia* sect. *Peripetasma* (Onagraceae). *Evolution* 40: 1248–1261.

UGENT, D. 1970. The potato. *Science* 170: 1161–1166.

WATANABE, K., AND S. J. PELOQUIN. 1989. Occurrence of 2n pollen and *ps* gene frequencies in cultivated groups and their related wild species in tuber-bearing Solanums. *Theoretical and Applied Genetics* 78: 329–336.

———, AND ———. 1991. The occurrence and frequency of 2n pollen in 2x, 4x, and 6x wild, tuber-bearing *Solanum* species from Mexico, and Central and South America. *Theoretical and Applied Genetics* 82: 621–626.

WERNER, J. A. AND S. J. PELOQUIN. 1991. Occurrence and mechanisms of 2*n* egg formation in 2*x* potato. *Genome* 34: 975–982.