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Phylogenetic Relationships of Wild Potatoes, *Solanum* Series *Conicibaccata* (Sect. *Petota*)

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ABSTRACT. *Solanum* sect. *Petota* series *Conicibaccata* is a group of 40 wild potato species, composed of diploids, tetraploids, and hexaploids, distributed from central Mexico to central Bolivia. This study examined their species boundaries and interrelationships by phenetic analyses of morphological data and cladistic analyses of chloroplast DNA restriction site data. Mitotic chromosome counts were obtained for 114 accessions; species whose first counts are reported here are *S. garcia-barrigae*, *S. orocense*, and *S. sucubunense*. Most results were concordant in showing three main groups of species: 1) tetraploids and hexaploids from central Mexico to southern Ecuador; 2) diploids from northern Peru to Bolivia, included in a cpDNA clade of diploids and hexaploids assigned to ser. *Demissa* and ser. *Tuberosa*, and 3) diploids and tetraploids from southern Colombia to Peru, cladistically related to members of ser. *Piurana*. Some species boundaries, and even series boundaries of ser. *Conicibaccata* and ser. *Piurana*, are supported morphologically only by a combination of widely overlapping character states, none of which is constant for a species. Other species have no support, and it is likely that too many species are recognized in the group. The cladistic analysis of chloroplast DNA data suggested that some species represent a combination of apospecies and plesiospecies, and some populations are of possible hybrid origin.

The genus *Solanum* L. contains about 1,000 to 1,100 species (D'Arcy 1991) and is one of the largest genera of angiosperms. *Solanum* sect. *Petota* Dumort., the potato and its wild relatives, includes 232 species as recognized by Hawkes (1990), or 223 species with the exclusion of nine nontuber-bearing species alternatively placed in sect. *Etuberosum* (Bukasov and Kameraz) A. Child, sect. *Juglandifolium* (Rydb.) A. Child, and sect. *Lycopersicon* (Mill.) Wettst. (Child 1990; Spooner et al. 1993). The tuber-bearing species are distributed from the southwestern United States to southern Chile, from sea level to over 4,500 m, with a concentration of diversity in the Andes. Section *Petota* contains diploids ($2n = 2x = 24$), tetraploids ($2n = 4x = 48$) and hexaploids ($2n = 6x = 72$), with occasional triploids and pentaploids. Section *Petota* is taxonomically difficult with much disagreement regarding species boundaries, affiliation of species to series, rank of infraspecific taxa, and hypotheses of hybridization (Spooner and van den Berg 1992a).

Solanum ser. *Conicibaccata* Bitter presents many problems regarding species and series boundaries and is in need of revision. Bitter (1912) was the first to recognize series in sect. *Petota*. When Bitter (1912) first described the two series *Conicibaccata* and *Maglia* Bitter, the morphological distinction between the conical fruits of the former and rounded to ovoid fruits of the latter presented few taxonomic problems. As new species and series were described, these distinctions became imprecise and assignment of species to series varied widely among taxonomists, as summarized in Spooner and Sytsma (1992) and Spooner and van den Berg (1992a). The latest taxonomic treatment of sect. *Petota* (Hawkes 1990) recognized 19 tuber-bearing series.

Correll (1962), Hawkes (1990), and Ochoa (1990) defined series *Conicibaccata* on the basis of long conical fruits, in contrast to short conical or spherical fruits of other series. However, the distinction between long conical and short conical fruits is not always clear, especially with some species in ser. *Demissa* Juz. (*S. brachycarpum* Correll, *S. iopetalum* [Bitter] Hawkes), ser. *Pinnatisecta* (Rydb.) Hawkes (*S. hintonii* Correll, *S. trifidum* Correll and some populations of *S. pinnatisectum* Dunal), ser. *Polyadenia* Correll (*S. lesteri* Hawkes and Hjert.) and ser. *Piurana* Hawkes (*S. tuquerrense* Hawkes). In addition, some species placed in ser. *Conicibaccata* have short conical to ovoid fruits (e.g., *S. chomatophilum* Bitter). Nothing is known about

the genetic control or homology of fruit shapes in sect. *Petota*.

Conicibaccata is the second largest series in sect. *Petota*, after ser. *Tuberosa* (Rydb.) Hawkes. Hawkes (1990) circumscribed ser. *Conicibaccata* to contain 40 species, including diploids (17 species), tetraploids (12), and hexaploids (2), distributed from central Mexico to central Bolivia (Table 1; nine species do not yet have chromosome numbers reported). All members of ser. *Conicibaccata* distributed from Mexico to Ecuador are tetraploids and hexaploids, while all species in Peru and Bolivia are diploids, with the exception of *S. nemorosum* (6*x*) from northern Peru, *S. nubicola* (4*x*) from central Peru, and *S. bombycinum* (4*x*) from Bolivia near the Peruvian border.

Some species, such as *S. agrimonifolium*, *S. colombianum*, and *S. moscopanum*, are widespread, but most apparently are narrowly restricted endemics. Twenty seven of the 40 species in ser. *Conicibaccata* are known from only type collections, or occur in very restricted areas; these are *S. ayacuchense*, *S. bombycinum*, *S. buesii*, *S. burkartii*, *S. calacalinum*, *S. contumazaense*, *S. donachui*, *S. garcia-barrigae*, *S. irosinum*, *S. jaenense*, *S. limbaniense*, *S. lobbianum*, *S. multiflorum*, *S. nemorosum*, *S. neovalenzuelae*, *S. neovargasii*, *S. neovavilovii*, *S. nubicola*, *S. orocense*, *S. pamplonense*, *S. pillahuatense*, *S. salasianum*, *S. solisii*, *S. subpanduratum*, *S. sucubunense*, *S. urubambae*, and *S. villuspetalum* (Correll 1962; Hawkes 1990; Spooner et al. 1992, 1994a, 1995; or from original descriptions).

Recent publications of wild potato germplasm collecting expeditions reported problems in the field identification of members of ser. *Conicibaccata* (Spooner et al. 1992, 1995), and identifications of accessions of the United States National Germplasm System held at the National Research Support Program-6 (NRSP-6) in Sturgeon Bay, Wisconsin (Spooner and van den Berg 1992a). The biggest problem in identification is lack of a comprehensive treatment of ser. *Conicibaccata*. Hawkes (1990) provided keys to only 23 of the 40 species he included in the series, because he was unable to examine types for the remaining 17. Earlier treatments (e.g., Correll 1962; Ochoa 1962, 1981, 1990; Hawkes 1963; Hawkes and Hjerting 1989) treated species from only portions of the range of the series or did not include recently described taxa.

Members of ser. *Conicibaccata* often are very similar morphologically, and new species descriptions frequently lacked diagnoses to similar taxa. Species are distinguished in the literature mainly by differences in leaf shape and pubescence, corolla color and size, and fruit shape. Most species apparently differ only by overlapping ranges of quantitative character states, but this variation frequently was either not described, or was described in qualitative ways. Additional support for some species was sometimes provided by ploidy level, crossing data, and serology (Hawkes 1990; López and Hawkes 1991a,b).

Restriction site analyses of cpDNA have been useful for elucidating phylogenetic relationships within the genera and families (Sytsma and Hahn 1994, 1996). Within the Solanaceae, chloroplast DNA restriction site analyses addressed both family (Olmstead and Palmer 1992; Spooner et al. 1993) and generic level relationships. Generic level studies have examined *Jaltomata* Schltdl. (Mione et al. 1994), *Lycopersicon* Miller (Palmer and Zamir 1982), *Nicotiana* L. (Olmstead and Palmer 1991), *Physalis* L. (Martinez, in press), and *Solanum* (Hosaka et al. 1984; Hosaka and Hanneman 1988; Spooner and Sytsma 1992; Bruneau et al. 1995; Olmstead and Palmer 1997; Spooner and Castillo 1997). The studies in *Solanum* sect. *Petota* have defined some clear maternal lineages, but many groups of species remain unresolved. For example, a study of the 30 Mexican and Central American species of *Solanum* sect. *Petota* (Spooner and Sytsma 1992), and a later analysis of 76 South American species (Spooner and Castillo 1997) define four major clades within sect. *Petota*, but relationships among these clades are largely unresolved.

A problem with interpreting species relationships based on cpDNA phylogenies arises if hybridization has occurred (Doyle 1992). Chloroplast DNA is predominately maternally inherited in the Solanaceae (Corriveau and Coleman 1988; Harris and Ingram 1991), and hybridization is believed to be a common evolutionary event in sect. *Petota* (Hawkes 1990). Twenty-seven diploid, tetraploid, and hexaploid species are of putative hybrid origin in sect. *Petota* (Spooner and van den Berg 1992b). However, the only species of ser. *Conicibaccata* of putative hybrid origin is hexaploid *S. moscopanum*. Hawkes (1954) suggested it arose by hybridization between the sympatric tetraploid species *S. colombianum* and an unknown diploid species. The only other hypothesis of hybridization involving ser. *Conicibaccata* was advanced by Hawkes (1966), who suggested that members of the Mexican and Central American hexaploid ser. *Demissa* arose from hybridization between Mexican and Central American representatives of ser. *Conicibaccata* or ser. *Longipedicellata* Juz. and the diploid

TABLE 1. *Solanum* ser. *Conicibaccata* and other species used for comparison in this study.

Taxon, publication date of basionym	Distribution	Accessions examined[a]	Affiliation to series[b] (by author)				
			Original description	Correll 1962	Ochoa 1962	Hawkes 1963	Hawkes 1990
S. agrimonifolium Rydb. 1924	Mexico, Guatemala	C(4), M(12)	TUB	CON		CON	CON
S. albicans (Ochoa) Ochoa 1960	Ecuador, Peru	C(1)	ACA	ACA	ACA	ACA	ACA
S. andreanum Baker 1884	Colombia, Ecuador	C(1)		TRN[c]		TUB	TUB
S. ayacuchense Ochoa 1959	Peru				CON	CON	CON
S. bombycinum Ochoa 1983	Bolivia		CON				CON
S. brachycarpum (Correll) Correll 1950	Mexico	C(4), M(4)	CON	DEM		DEM	DEM
S. buesii Vargas 1943	Peru	C(1), M(1)	CON	CON	CON	CON	CON
S. burkartii Ochoa 1977	Peru		CON				CON
S. cajamarquense Ochoa 1959	Peru	C(1)	TUB	MIN	TUB	TUB	TUB
S. calacalinum Ochoa 1981	Ecuador		CON				CON
S. cardiophyllum Lindl. 1848 (two accessions as out-groups)	Mexico	C(2)		CAR		PIN	PIN
S. chilliasense Ochoa 1981	Ecuador	C(1)	PIU				PIU
S. chomatophilum Bitter 1924	Ecuador, Peru	C(4), M(7)		PIU	CON	PIU	CON
S. colombianum Dunal 1852[d]	Venezuela, Colombia, Ecuador	C(58), M(36)		CON	CON	CON	CON
S. contumazaense Ochoa 1964	Peru	C(1), M(1)	TUB				CON
S. donachui (Ochoa) Ochoa 1982	Colombia		CON				CON
S. flahaultii Bitter 1913	Colombia	C(13), M(5)	CON	CON		CON	CON
S. garcia-barrigae Ochoa 1978	Colombia	C(2), M(2)	CON				CON
S. irosinum Ochoa 1981	Peru	C(1), M(2)	CON				CON & TUB[e]
S. jaenense Ochoa 1960	Peru		TUB		TUB	CON	CON
S. laxissimum Bitter 1916	Peru	C(2), M(2)			CON	CON	CON
S. limbaniense Ochoa 1974	Peru	C(1), M(1)	CON				CON
S. lobbianum Bitter 1913	Colombia	C(3), M(1)		TRN		TUB	TUB
S. longiconicum Bitter 1912	Costa Rica, Panama	C(2), M(1)		CON		CON	CON
S. minutifoliolum Correll 1961	Ecuador	C(1)		MIN			TUB
S. moscopanum Hawkes 1954	Colombia, Ecuador	C(18), M(17)	CON	CON		CON	CON
S. multiflorum Vargas 1956	Peru		CON	TRN	CON	CON	CON
S. nemorosum Ochoa 1983	Peru		CON				CON
S. neovalenzuelae L. E. López 1986	Colombia	C(1), M(1)	CON				CON
S. neovargasii Ochoa 1962	Peru		CON		CON	CON	CON
S. neovavilovii Ochoa 1983	Bolivia		CON				CON
S. nubicola Ochoa 1970	Peru		TUB				CON
S. orocense Ochoa 1980	Colombia	C(3), M(2)	CON				CON
S. otites Dunal 1852	Colombia, Venezuela	C(2), M(1)		CON		CON	CON
S. oxycarpum Schiede 1841	Mexico, Central America	C(4), M(8)		CON		CON	CON
S. pamplonense L. E. López 1983	Colombia	C(1), M(1)	CON				CON
S. paramoense Pittier 1926	Venezuela	C(2)		TRN		TUB	TUB or CON[f]
S. paucijugum Bitter 1912	Ecuador	C(10), M(8)		CON		CON	CON
S. pillahuatense Vargas 1956	Peru		CON	CON	CON	CON	CON
S. salasianum Ochoa 1989	Peru		CON				CON
S. santolallae Vargas 1943	Peru	C(3), M(2)	CON	CON	CON	CON	CON
S. solisii Hawkes 1944	Ecuador	C(1), M(1)		PIU		PIU	PIU
S. subpanduratum Ochoa 1979	Venezuela	C(1), M(1)	CON				CON
S. sucubunense Ochoa 1980	Colombia	C(2), M(1)	CON				CON
S. suffrutescens Correll 1961	Ecuador	C(1)		ING		TUB	TUB
S. trinitense Ochoa 1964	Peru		TUB				CON
S. tundalomense Ochoa 1963[g]	Ecuador	C(3), M(3)	CON				CON
S. tuquerrense Hawkes 1954	Colombia, Ecuador	C(13), M(9)	PIU	ING		PIU	PIU

TABLE 1. Continued.

Taxon, publication date of basionym	Distribution	Accessions examined[a]	Affiliation to series[b] (by author)				
			Original description	Correll 1962	Ochoa 1962	Hawkes 1963	Hawkes 1990
S. urubambae Juz. 1937	Peru	C(1)		CON	CON	CON	CON
S. verrucosum Schltdl. 1841	Mexico	C(2)		DEM		DEM	TUB
S. villuspetalum Vargas 1956	Peru		CON	TRN	CON	CON	CON
S. violaceimarmoratum Bitter 1912	Bolivia	C(4), M(7)		CON		CON	CON
S. woodsonii Correll 1961	Panama			CON		CON	CON
Unknown species "a"	Colombia	C(1), M(1)					
Unknown species "b"	Colombia	C(1), M(1)					
Unknown species "c"	Colombia	C(1)					
Unknown species "d"	Ecuador	C(1)					
Unknown species "e"	Colombia	C(1)					

[a]C = Number of specimens used in the chloroplast DNA study, M = morphological study; those species without codes were not available for this study. [b]Series abbreviations after Hawkes (1990), and Simmonds (1963): ACA = ser. *Acaulia* Juz.; CAR = ser. *Cardiophylla* Correll, 1952; CON = ser. *Conicibaccata* Bitter; DEM = ser. *Demissa* Juz.; ING = ser. *Ingifolia* Ochoa; MIN = *Minutifoliola* Correll; PIN = ser. *Pinnatisecta* (Rydb.) Hawkes; PIU = ser. *Piurana* Hawkes; TRN = ser. *Transaequatorialia* (never validly described); TUB = ser. *Tuberosa* (Rydb.) Hawkes. [c]Hawkes (1990) synonymized under ser. *Tuberosa* (Rydb.) Hawkes. [d]Hawkes (1990) listed *S. cacetanum* Ochoa (Ochoa 1980) in his treatment, but Ochoa (1992b) synonymized it under *S. colombianum*. [e]Hawkes (1990) was unsure of the series affiliations of *S. irosinum* and placed it under both ser. *Conicibaccata* and ser. *Tuberosa*. [f]Ochoa (1992b) synonymized under *S. tuberosum* L.; Hawkes (1990) placed *S. paramoense* under ser. *Tuberosa*, but stated "Without berries it is difficult to be certain whether [*S. paramoense*] fits into ser. *Conicibaccata* or *Tuberosa*." [g]Hawkes (1990) synonymized under *S. colombianum*.

species *S. verrucosum* (ser. *Tuberosa*). Hawkes (1990) also hypothesized widespread introgression among species in sect. *Petota* subsequent to habitat disturbance that disrupted supposedly formerly distinct habitats.

Biparentally inherited characters can highlight discrepancies between maternal phylogenies and species phylogenies that may be caused by hybridization (Doyle 1992). Like cpDNA, all biparentally inherited markers have potential strengths and weaknesses. Morphological characters are useful because they are readily observed and measured and form the basis of most species circumscriptions and hypotheses of hybridization. However, morphology can be influenced by the environment, and little is known about the genetic basis of morphological characters, especially those commonly used taxonomically in potatoes (Ortiz and Huáman 1994). Also, hybrid taxa often display unilateral expression or transgressive segregation of individual character states (Rieseberg and Wendel 1993).

We conducted an integrated morphological and molecular (cpDNA) study of *Solanum* ser. *Conicibaccata*. The objectives were to investigate: 1) the species boundaries and phenetic structure within ser. *Conicibaccata* with morphological data, and 2) their phylogenetic relationships with cladistic analyses of cpDNA restriction site data.

MATERIALS AND METHODS

Species. We used 181 accessions for cpDNA analyses, and 139 for morphological analyses (Table 1, Appendix 1). All accessions were from NRSP-6 (Bamberg et al. 1996). Many were collected on recent field trips to Mexico (Spooner et al. 1991), Venezuela and Colombia (Spooner et al. 1995), and Ecuador (Spooner et al. 1992), and represent the maximum geographic distribution available (Appendix 1; Figs. 1–3). Identities of recent collections often were not clear in the field and were identified as expected based on type localities or our best interpretation from the literature. We could not examine all recently collected accessions in the living state at Sturgeon Bay because some were still held in United States quarantine.

The low numbers of accessions examined of some species represent their presumed rarity and not their under-representation in the genebank. Vouchers are deposited at the NRSP-6 herbarium (Bamberg and Spooner 1994) in Sturgeon Bay, Wisconsin [PTIS, to appear in Edition 9 *Index Herbariorum* (Holmgren et al. 1990)], the International Potato Center Herbarium (not in Holmgren et al., 1990, but cited in publications by Carlos Ochoa as OCH and CIP), and in various national herbaria in the country of origin.

Chloroplast DNA. Pooled leaf samples of six plants per accession were collected from 2-month-old plants for DNA extraction. Preparations of total DNA were made from about 5 g of fresh leaf tissue by the procedure of Doyle and Doyle (1987), substituting 6× CTAB for 2× CTAB (Smith et al. 1991). DNA was purified over CsCl/ethidium bromide gradients. Restriction endonuclease digestions, agarose-gel electrophoresis, unidirectional

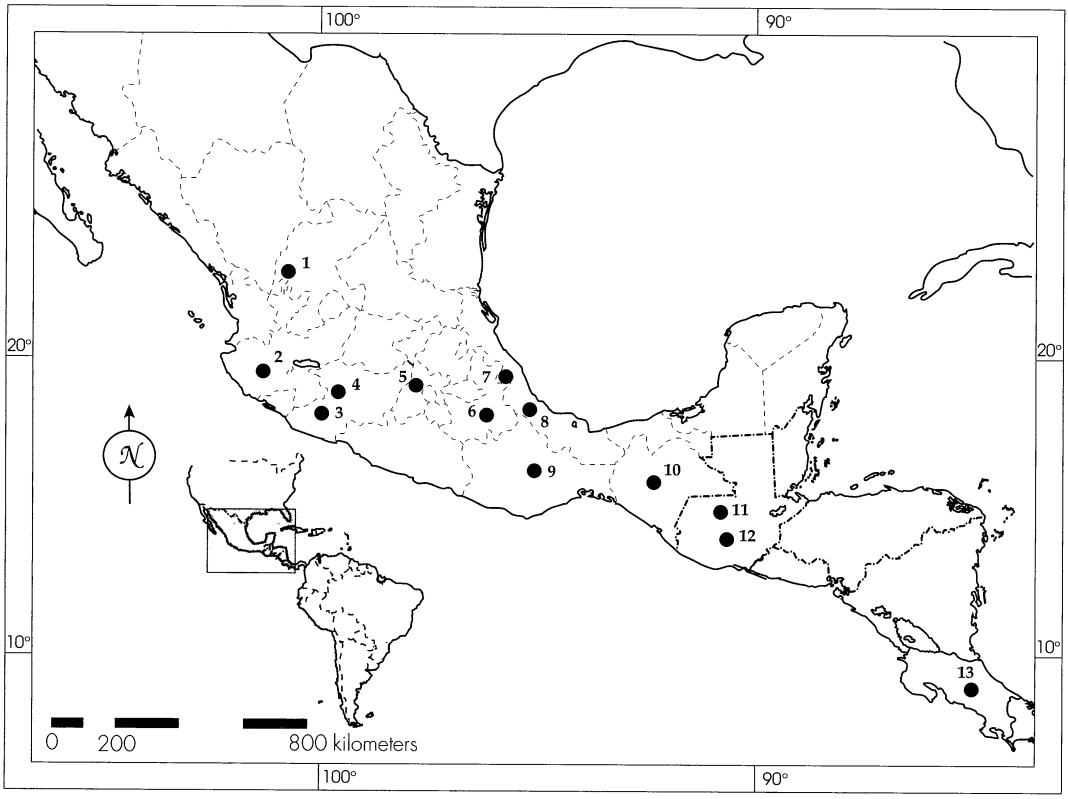


FIG. 1. Map of Mexico and Central America showing generalized collection localities 1–13 of the accessions examined in this study. Numbers are cited as generalized map areas in Appendix 1.

Southern transfers to nylon membranes (Biotrans™), filter hybridization, and autoradiography followed methods in Palmer (1986).

Chloroplast clones were radiolabeled by ^{32}P-dCTP by the oligo-labelling method of Feinberg and Vogelstein (1984). Two µg of each DNA sample were digested with 22 restriction endonucleases to examine cpDNA variation in *Solanum*: *Ava*I, *Bam*HI, *Ban*I, *Bcl*I, *Bgl*II, *Bst*NI, *Cla*I, *Dra*I, *Eco*O109, *Eco*RI, *Eco*RV, *Hinc*II, *Hind*III, *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* Juss. (Sytsma and Gottlieb 1986), and five clones of *Nicotiana* in the small single-copy region (Olmstead and Palmer 1992) covering the entire chloroplast genome.

Based on results of Spooner and Sytsma (1992), two accessions of *S. cardiophyllum* were used as outgroups. Rodríguez and Spooner (1997) showed that these two accessions of *S. cardiophyllum* fell in two clades basal to our ingroup, one in the *S. cardiophyllum* and *S. bulbocastanum* Dunal clade, and the other in the typical Mexican diploid species clade including *S. pinnatisectum* (Spooner and Sytsma 1992). The outgroups were rooted, therefore, as paraphyletic. Phylogenetic reconstructions were performed with PAUP, version 3.1.1 (Swofford 1993). The data were analyzed using Wagner parsimony (Farris 1970), which gives equal weight to site gains and site losses. To find multiple islands, a four-step search strategy was employed (modified from Olmstead and Palmer 1994): 1) 10,000 random-addition sequence replicates initially were run with nearest neighbor joining (NNI) to generate starting trees; 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, and saving all most parsimonious trees (MULPARS on), and 4) the resulting trees were searched with TBR and MULPARS on. A bootstrap analysis (Felsenstein 1985) was conducted on 1,000 replicates using Wagner parsimony, TBR, and MULPARS off.

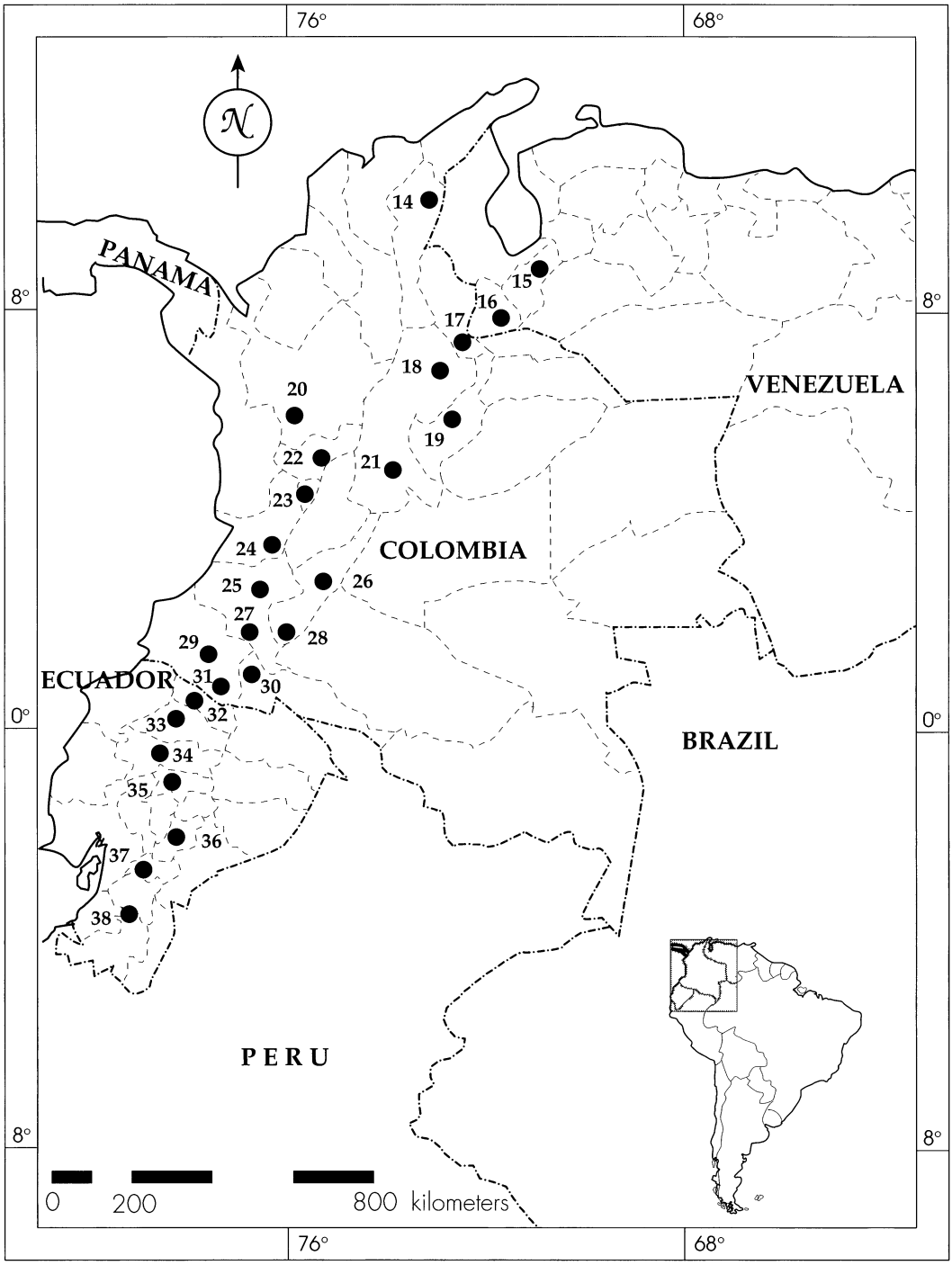


FIG. 2. Map of northwestern South America showing generalized collection localities 14–38 of the accessions examined in this study. Numbers are cited as generalized map areas in Appendix 1.

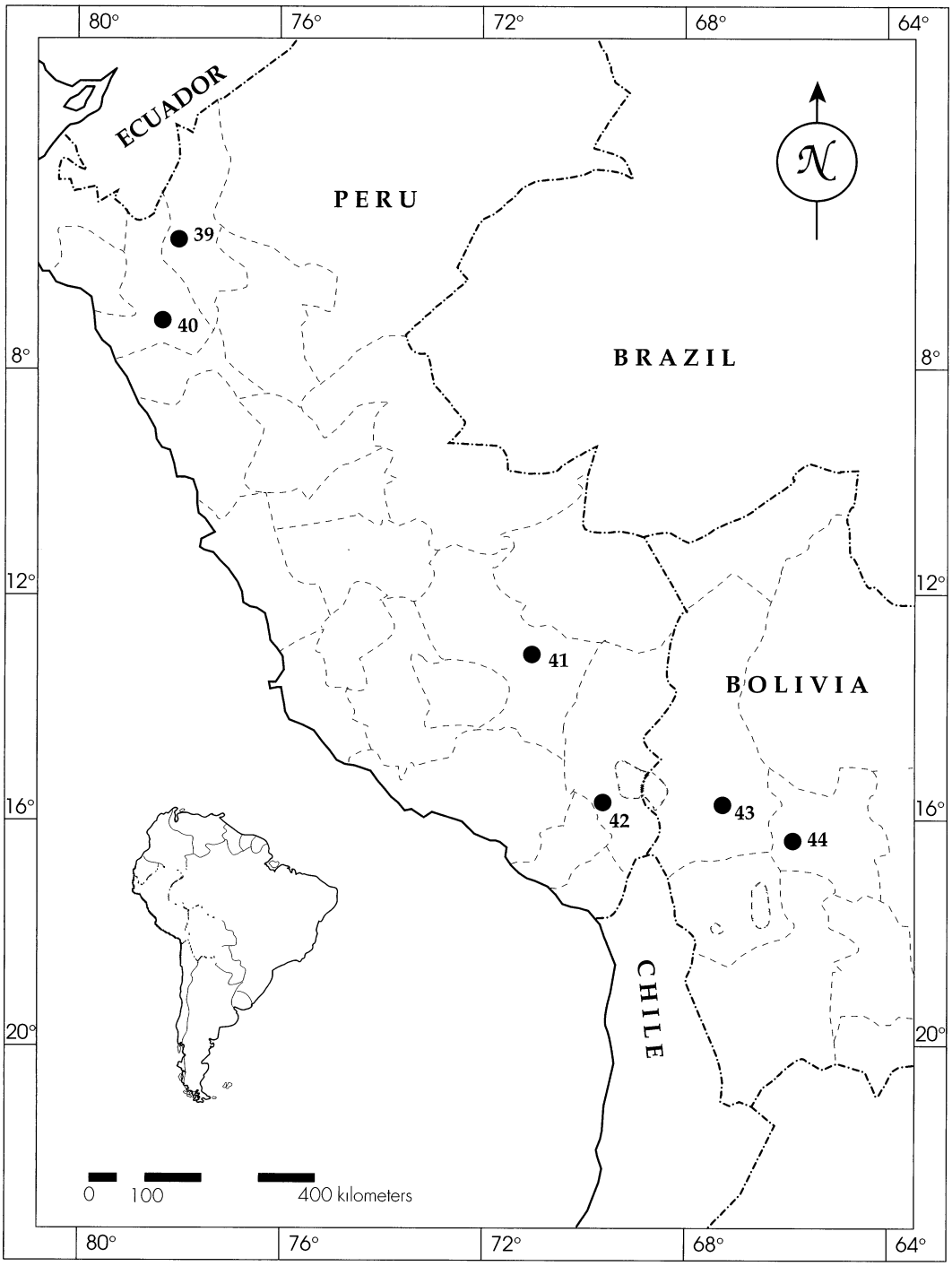


FIG. 3. Map of Peru and northern Bolivia showing generalized collection localities 39–44 of the accessions examined in this study. Numbers are cited as generalized map areas in Appendix 1.

Morphology. Most accessions of ser. *Conicibaccata* grow poorly in the field at Sturgeon Bay, but plants thrive in pots in a shaded screenhouse that apparently provides conditions more like their natural habitats. Seeds were planted in a greenhouse in early May, seedlings were transferred to pots in late May, and six individuals per accession were transplanted together in rows in the shaded screenhouse in early June. Hand pollinations ensured fruit set for all species. Character states (Table 2) were measured at anthesis in August, and in September for mature fruit characters. The middle four plants per row were measured for all characters, and means of the four plants were used as representative of each accession (thus the accession is the Operational Taxonomic Unit, OTU). Leaves were chosen from the middle of the plant. Corolla colors in sect. *Petota* vary from uniform throughout, to speckled throughout, or with two separate colors (a predominant color on the outside and a secondary color in a smaller area in the center). To assess this variation, we scored the predominant corolla color as that occupying the greatest area of the corolla, and the secondary color as the color in the center or secondary color in speckled areas. Uniform colored corollas received two identical scores. Fruits were measured when mature. Each character was analyzed for its mean, range, and standard deviation.

Dendrograms including all accessions were produced by NTSYS-pc®, version 1.70 (Rohlf 1992). Averages for each character were standardized (STAND) and similarity matrices (in SIMINT) were generated using average taxonomic distance (DIST), Manhattan distance (MANHAT), and product-moment correlation (CORR). Clustering was performed using the unweighted pair-group method (UPGMA) in SAHN. Cophenetic correlation coefficients (COPH, in MXCOMP) were used to measure distortion between the similarity matrices and the resultant three phenograms (Rohlf and Sokal 1981; Sokal 1986). Principal components analysis (PCA, using correlation matrices), canonical discriminant analyses (CDA), and stepwise discriminant analyses (SDA) were conducted using the means of four individuals per accession (SAS Institute Inc. 1989). PCA and CDA are both ordination techniques, but PCA makes no assumptions of group membership of OTU's. It attempts to portray multidimensional variation in the data set in the fewest possible dimensions, while maximizing the variation. CDA uses assigned groups to derive a linear combination of the variables (morphological characters) that

TABLE 2. Characters used in the morphological analysis. See Materials and Methods for descriptions of characters 28 and 29. Character numbers correspond to those in Figs. 9–11.

Stem characters

1. Diameter of stem 10 cm above ground (mm). 2. Pubescence of stem: glabrous (0), pilose (1), densely pilose (3). 3. Color of stem: green (1), green mottled with purple (2), purple (3). 4. Morphology of stem wing: no wings (0), straight (1), wavy (2). 5. Width of stem wing (mm).

Leaf characters

6. Ratio: length of pseudostipular leaf/width. 7. Length of leaf (mm). 8. Ratio: length of leaf/width. 9. Ratio: length from axis of widest point of leaf to apex/length of leaf. 10. Widest leaflet pair from apex. 11. Length of terminal leaflet lamina (mm). 12. Ratio: length of terminal leaflet lamina/width. 13. Ratio: length from axis of widest point of terminal leaflet to apex/length of terminal leaflet lamina. 14. Length of petiolule of terminal leaflet (mm). 15. Length of petiolule of distal most lateral leaflet. 16. Ratio: length of most distal lateral leaflet lamina/width. 17. Ratio: length from axis of widest point of distal most lateral leaflet to apex/length of lateral leaflet. 18. Ratio: length of terminal leaflet/length first lateral leaflet. 19. Adaxial pubescence: glabrous (0), puberulent (1), pubescent (2). 20. Abaxial pubescence: glabrous (0), puberulent (1), pubescent. 21. Number of pairs of lateral leaflets. 22. Number of interstitial leaflets. 23. Margin of leaflets; straight (1), undulate (2), sinuate (3). 24. Interstitial leaflet(s) at base of terminal leaflet: absent (0), present (1). 25. Length of largest interstitial leaflet (mm). 26. Width of terminal leaflet 5 mm from apex (mm).

Floral characters (see Spooner and van den Berg 1992b, for illustrations of character 30)

27. Number of flowers per inflorescence. 28. Primary color of corolla: white (1), pink (2), deep blue or purple (3). 29. Secondary color of corolla (see text): white (1), pink (2), deep blue or purple (3). 30. Radius of corolla, largest distance from center of corolla and tip of petal (mm). 31. Ratio: radius of corolla/distance from center of corolla to junction of corolla lobes. 32. Ratio: width of corolla lobe measured at base of corolla junction/petal lobe length. 33. Length of anther (mm). 34. Ratio: length of calyx lobe from the base of lobe to the bottom of acumen/width of calyx lobe at base of junction of calyx lobes. 35. Length of calyx (mm). 36. Length of calyx acumen (mm). 37. Calyx pubescence; glabrous (0), puberulent (1), pubescent (2). 38. Length of pedicel (mm). 39. Ratio: length from base of pedicel to articulation/pedicel length. 40. Peduncle length (mm).

Fruit characters

41. Length of fruit (mm). 42. Ratio: length of fruit/width at widest dimension. 43. Ratio: length of fruit from axis of widest point to apex/length of fruit. 44. Ratio: width of fruit at widest dimension/width of fruit at narrowest dimension.

produces the greatest separation of the groups (SAS Institute, Inc., 1989). CDA and SDA were performed on the entire data set using species as classification variables. Reiterations of these analyses using species and larger groups of species (see below) as classification variables also were performed for subsets of the entire data set based on the cpDNA results.

Chromosome Counts. Mitotic chromosome counts were obtained from root tips of 4–6 week old plants by an alcoholic hydrochloric acid-carmine procedure (Smith 1974). Counts were made from 10–15 cells per accession. Only approximate counts were possible with the tetraploids ($2n = 48$) and hexaploids ($2n = 72$); therefore possible aneuploidy was not detected.

Results

Chloroplast DNA. Sixty of the 181 accessions shared identical cpDNA restriction site variants with other accessions and were not used in the PAUP analyses but were later added to the tree. A total of 227 restriction site variants were identified (listed in Castillo 1995), 156 of which were phylogenetically informative. All characters were restriction site variants except for one length variant, a 200 base pair deletion autapomorphic to *S. andreanum* (Castillo 1995). Over 3,000 equally-parsimonious trees were possible for the data set, and we had to constrain the program to saving no more than 3,000 trees when the MULPARS option was in effect because of computer memory restrictions. Wagner parsimony analysis produced 3,000 most-parsimonious 417-step trees with a consistency index of 0.414 (without autapomorphies). We further tested the shortest length of these trees by loading a strict consensus tree of these 3,000 trees as a constraint tree and performed an inverse constraint analysis using procedures for searching shortest trees as described in Materials and Methods. No shorter trees were found.

A randomly chosen Wagner tree is presented as a phylogram to show branch lengths and distributions of characters (Fig. 4). A strict consensus tree of the 3,000 Wagner trees (Fig. 5) identifies eight clades, exclusive of the outgroups:

Clade A. All but 15 of the 111 polyploid accessions of ser. *Conicibaccata*, unknown *Solanum* species "a" (C1296; tetraploid), both accessions of *S. paramoense* (tetraploid, ser. *Tuberosa*).

Clade B. One of the four accessions of *S. brachycarpum*, (hexaploid, ser. *Demissa*).

Clade C. Ten of the 18 diploid accessions of ser. *Conicibaccata*, *S. verrucosum*, (diploid, ser. *Tuberosa*), three of the four accessions of *S. brachycarpum* (hexaploid, ser. *Demissa*), two accessions of *S. colombianum* (one counted as tetraploid, ser. *Conicibaccata*), one of the two accessions of *S. longiconicum* (tetraploid, ser. *Conicibaccata*).

Clade D. *Solanum buesii* (diploid, ser. *Conicibaccata*).

Clade E. *Solanum albicans* (hexaploid, ser. *Acaulia*).

Clade F. *Solanum limbaniense* (diploid, ser. *Conicibaccata*).

Clade G. *Solanum andreanum* (diploid, ser. *Tuberosa*), *S cajamarquense* (diploid, ser. *Tuberosa*), *S. chilliasense*, (diploid, ser. *Piurana*), *S. chomatophilum* (diploid, ser. *Conicibaccata*), one of the 58 accessions of *S. colombianum* (tetraploid, ser. *Conicibaccata*), *S. contumazaense* (diploid, ser. *Conicibaccata*), *S. irosinum* (diploid, ser. *Conicibaccata*), *S. paucijugum* (tetraploid, ser. *Conicibaccata*), one of the three accessions of *S. tundalomense* (hexaploid, ser. *Conicibaccata*), *S. tuquerrense* (tetraploid, ser. *Piurana*), *S. solisii* (diploid, ser. *Piurana*). An analysis of 76 South American species (Spooner and Castillo 1997) shows that clade G includes species best placed in a redefined ser. *Piurana*. For discussion purposes, we will refer to clade G as "ser. *Piurana*."

Clade H. *Solanum minutifoliolum* (diploid, ser. *Tuberosa*), *S. suffrutescens* (diploid, ser. *Tuberosa*), unknown *Solanum* species "b" (570640; diploid), unknown *Solanum* species "c" (583324, diploid), unknown *Solanum* species "d" (567823, diploid), unknown *Solanum* species "e" (C1294, diploid). We reexamined these six accessions of clade H in the global analysis of sect. *Petota* by Spooner and Castillo (in press). This study did not use the restriction endonucleases *Ban*II, *Bst*XI, *Hae*II, *Kpn*I, *Pvu*II, and *Ssp*I of that study, necessitating 25 missing character states for these six accessions in a total data matrix of 210 characters. The results of this study and the global analysis maintain clade H as a distinctive clade, coordinate with clades 3 and 4 of Spooner and Castillo (1997). The results do not change the cladistic structure of the other clades, except for removing *S. albornozii* from clade 3 to its own clade (Fig. 6).

Structure Within Clade A. Clade A contains all but 15 of the 111 tetraploid and hexaploid accessions of ser. *Conicibaccata*, with ten of these 15 exceptions all *S. paucijugum* of clade G (Fig. 5). Clade A contains a polytomy of 54 clades (but drawn for simplicity as only 32 clades on Fig. 5 with

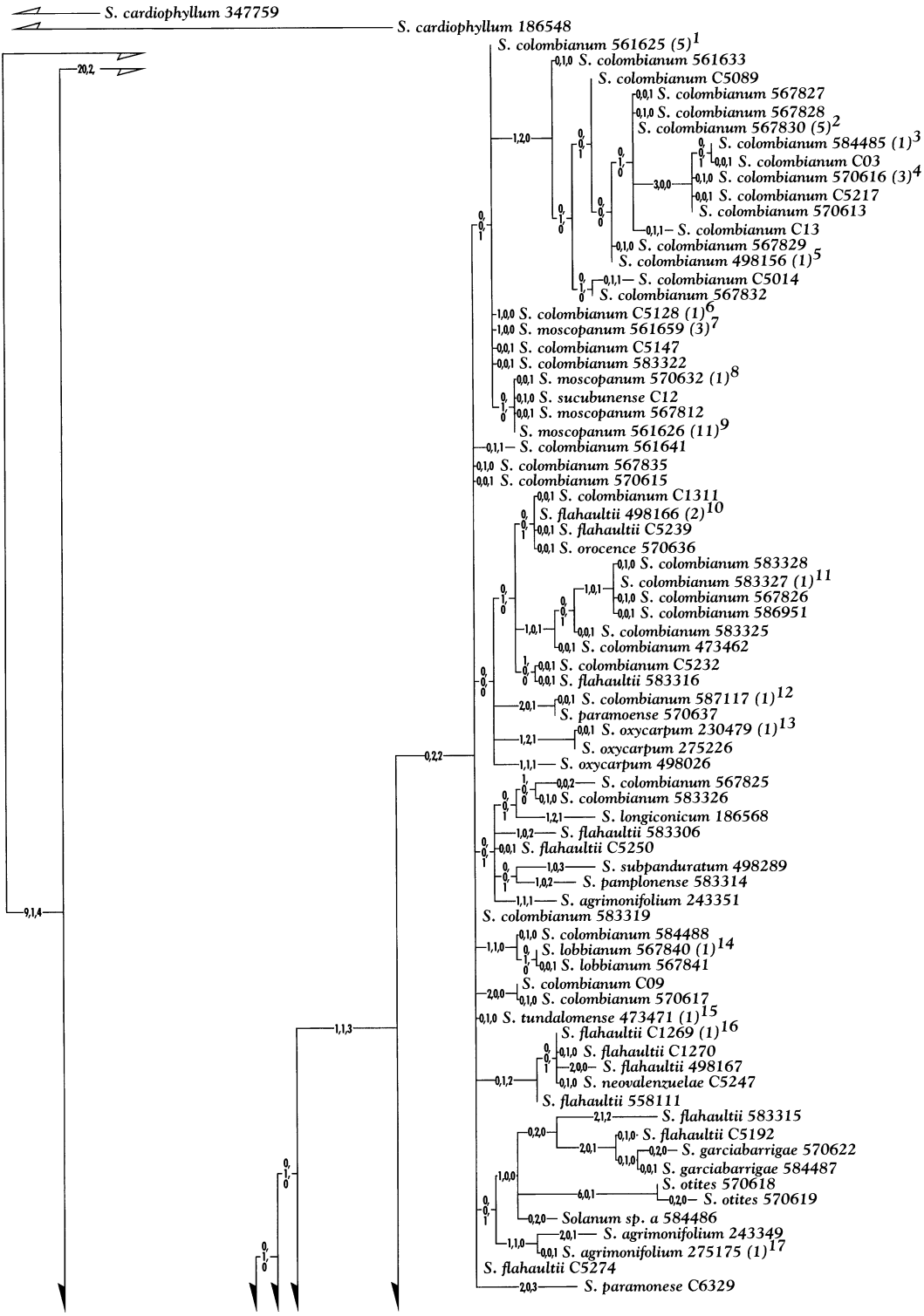
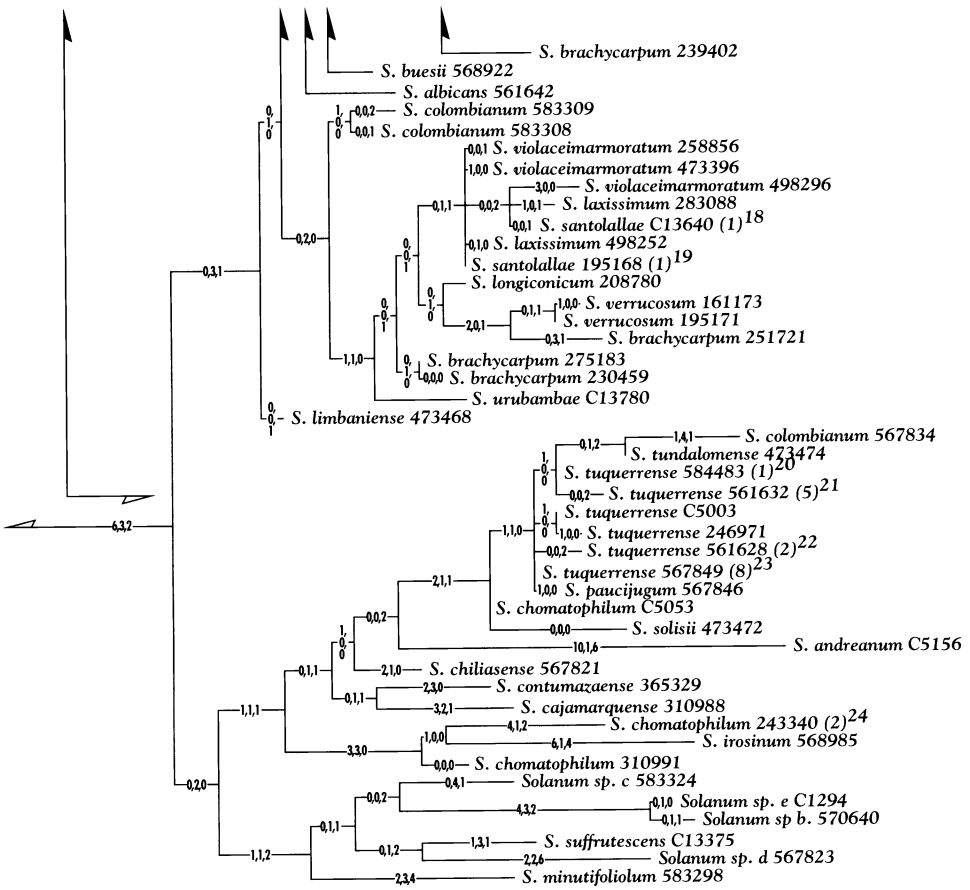

S. cardiophyllum 347759
S. cardiophyllum 186548
S. colombianum 561625 (5)1
S. colombianum 561633
S. colombianum C5089
S. colombianum 567827
S. colombianum 567828
S. colombianum 567830 (5)2
S. colombianum 584485 (1)3
S. colombianum C03
S. colombianum 570616 (3)4
S. colombianum C5217
S. colombianum 570613
S. colombianum C13
S. colombianum 567829
S. colombianum 498156 (1)5
S. colombianum C5014
S. colombianum 567832
S. colombianum C5128 (1)6
S. moscopanum 561659 (3)7
S. colombianum C5147
S. colombianum 583322
S. moscopanum 570632 (1)8
S. sucubunense C12
S. moscopanum 567812
S. moscopanum 561626 (11)9
S. colombianum 561641
S. colombianum 567835
S. colombianum 570615
S. colombianum C1311
S. flahaultii 498166 (2)10
S. flahaultii C5239
S. orocence 570636
S. colombianum 583328
S. colombianum 583327 (1)11
S. colombianum 567826
S. colombianum 586951
S. colombianum 583325
S. colombianum 473462
S. colombianum C5232
S. flahaultii 583316
S. colombianum 587117 (1)12
S. paramoense 570637
S. oxycarpum 230479 (1)13
S. oxycarpum 275226
S. oxycarpum 498026
S. colombianum 567825
S. colombianum 583326
S. longiconicum 186568
S. flahaultii 583306
S. flahaultii C5250
S. subpanduratum 498289
S. pamplonense 583314
S. agrimonifolium 243351
S. colombianum 583319
S. colombianum 584488
S. lobbianum 567840 (1)14
S. lobbianum 567841
S. colombianum C09
S. colombianum 570617
S. tundalomense 473471 (1)15
S. flahaultii C1269 (1)16
S. flahaultii C1270
S. flahaultii 498167
S. neovalenzuelae C5247
S. flahaultii 558111
S. flahaultii 583315
S. flahaultii C5192
S. garciabarrigae 570622
S. garciabarrigae 584487
S. otites 570618
S. otites 570619
Solanum sp. a 584486
S. agrimonifolium 243349
S. agrimonifolium 275175 (1)17
S. flahaultii C5274
S. paramonese C6329

FIG. 4



the elimination of 22 multiple identical accessions in unresolved clades). Nine clades are resolved (labeled a-i). Some of these clades support the monophyly of currently recognized species, while others do not.

For example, clade Aa contains 25 accessions of *S. colombianum*, distributed from central Colombia (Quindío Department) to northern Ecuador (Pichincha Province). These species have relatively small (usually 10–18 mm diameter), entirely white corollas, but a similar morphotype of *S. colombianum* (561625) with small white corollas occurs on an unresolved branch of clade A. Members of clade Aa do not cluster in the morphological results.

Clade Ab, on the other hand, contains 15 accessions of *S. colombianum*, *S. flahaultii* (three of

FIG. 4. One of 3,000 equally-parsimonious 417-step Wagner trees (drawn as a phylogram) of cpDNA restriction enzyme site variants (ordered as unique variants, parallel losses, and parallel gains supporting each branch, respectively) in *Solanum* ser. *Conicibaccata* and related series. Sixty accessions were invariant for cpDNA restriction site variants, and were later added to the tree. The number of additional identical accessions are indicated in parentheses on the tree: [1]*Solanum colombianum* C5081, 561627, 561657, 567837, 590923; [2]*S. colombianum* C14, 310983, 498151, 567831, 567833; [3]*S. colombianum* 570614; [4]*S. colombianum* C5280, 583312, 583318; [5]*S. colombianum* 320346; [6]*S. colombianum* 561652; [7]*S. moscopanum* 561653, 567824, 567838; [8]*S. moscopanum* 570631; [9]*S. colombianum* 5212b, *S. moscopanum* 230517, 498155, 567843, 567844, 570626, 570628, 570629, 570630, 570633, *S. sucubunense* 583320; [10]*S. orocense* C1306, 583307; [11]*S. colombianum* 586950; [12]*S. colombianum* 587118; [13]*S. oxycarpum* 275225; [14]*S. lobbianum* 567842; [15]*S. tundalomense* 473476; [16]*S. flahaultii* 583317; [17]*S. agrimonifolium* 275177; [18]*S. violaceimarmoratum* 473395; [19]S. *santolallae* 473372; [20]*S. tuquerrense* 561647; [21]*S. tuquerrense* 338614, 561646, 583300, 583310, 590926; [22]*S. paucijugum*, 561650, *S. tuquerrense* 561645; [23]*S. paucijugum* C5149, C5150, 561643, 561644, 561651, 561654, 583299, 583303; [24]*S. chomatophilum* 266387, 310943.

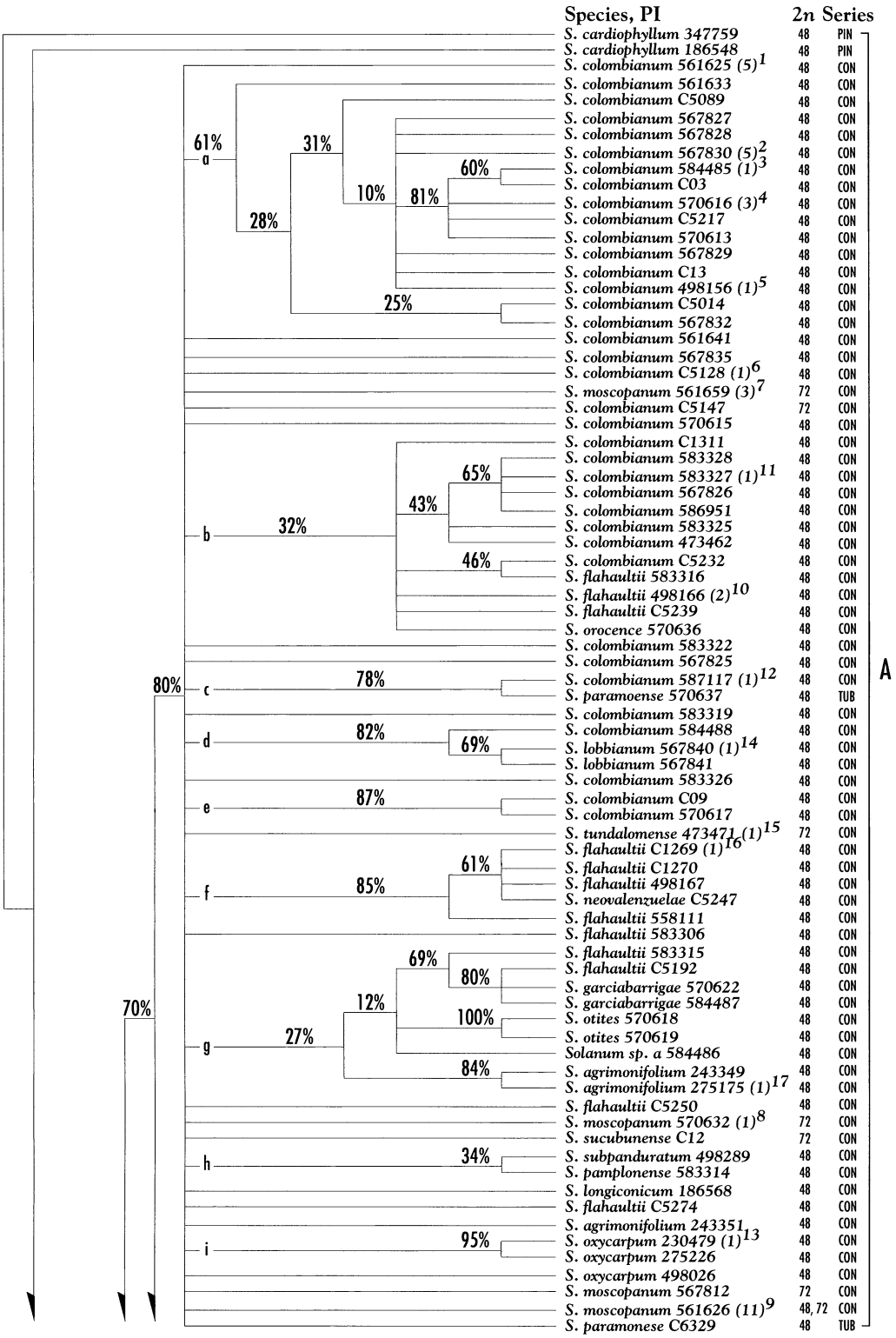
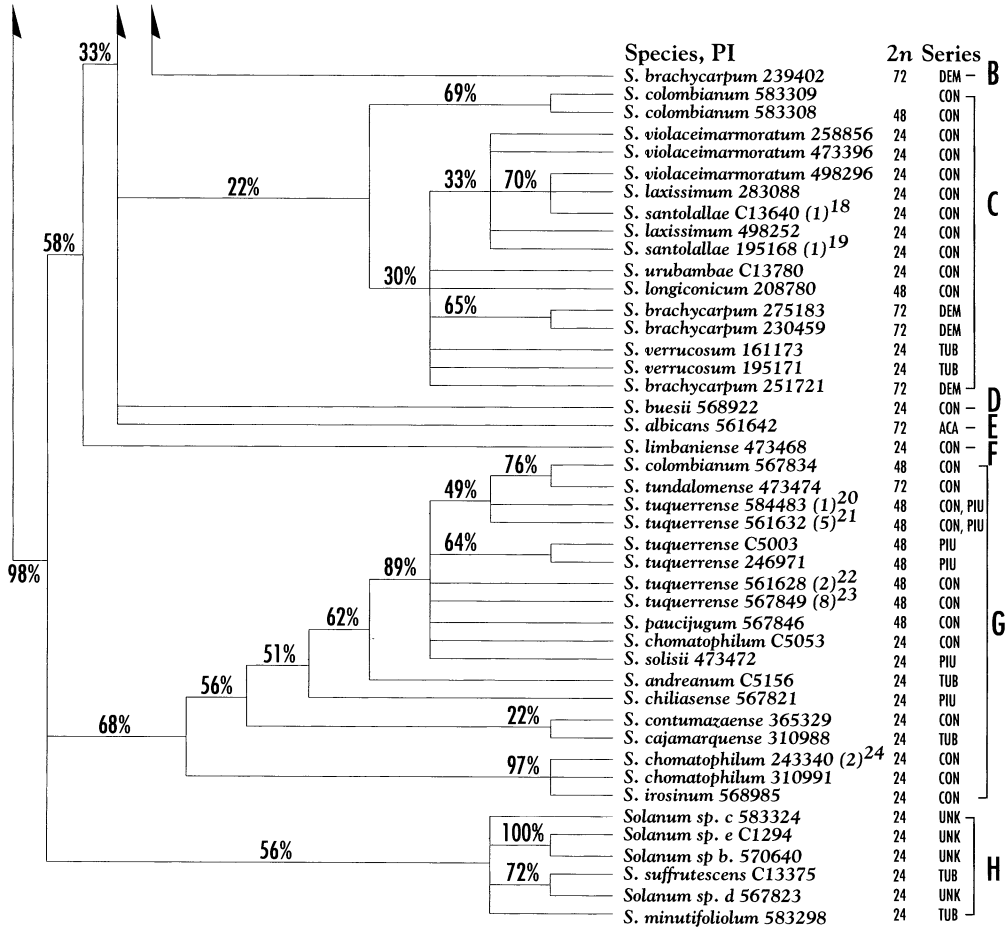

Species, PI
2n
Series
S. cardiophyllum 347759 48 PIN
S. cardiophyllum 186548 48 PIN
S. colombianum 561625 (5)1 48 CON
S. colombianum 561633 48 CON
S. colombianum C5089 48 CON
S. colombianum 567827 48 CON
S. colombianum 567828 48 CON
S. colombianum 567830 (5)2 48 CON
S. colombianum 584485 (1)3 48 CON
S. colombianum C03 48 CON
S. colombianum 570616 (3)4 48 CON
S. colombianum C5217 48 CON
S. colombianum 570613 48 CON
S. colombianum 567829 48 CON
S. colombianum C13 48 CON
S. colombianum 498156 (1)5 48 CON
S. colombianum C5014 48 CON
S. colombianum 567832 48 CON
S. colombianum 561641 48 CON
S. colombianum 567835 48 CON
S. colombianum C5128 (1)6 48 CON
S. moscopanum 561659 (3)7 72 CON
S. colombianum C5147 72 CON
S. colombianum 570615 48 CON
S. colombianum C1311 48 CON
S. colombianum 583328 48 CON
S. colombianum 583327 (1)11 48 CON
S. colombianum 567826 48 CON
S. colombianum 586951 48 CON
S. colombianum 583325 48 CON
S. colombianum 473462 48 CON
S. colombianum C5232 48 CON
S. flahaultii 583316 48 CON
S. flahaultii 498166 (2)10 48 CON
S. flahaultii C5239 48 CON
S. orocence 570636 48 CON
S. colombianum 583322 48 CON
S. colombianum 567825 48 CON
S. colombianum 587117 (1)12 48 CON
S. paramoense 570637 48 TUB
S. colombianum 583319 48 CON
S. colombianum 584488 48 CON
S. lobbianum 567840 (1)14 48 CON
S. lobbianum 567841 48 CON
S. colombianum 583326 48 CON
S. colombianum C09 48 CON
S. colombianum 570617 48 CON
S. tundalomense 473471 (1)15 72 CON
S. flahaultii C1269 (1)16 48 CON
S. flahaultii C1270 48 CON
S. flahaultii 498167 48 CON
S. neovalenzuelae C5247 48 CON
S. flahaultii 558111 48 CON
S. flahaultii 583306 48 CON
S. flahaultii 583315 48 CON
S. flahaultii C5192 48 CON
S. garciabarrigae 570622 48 CON
S. garciabarrigae 584487 48 CON
S. otites 570618 48 CON
S. otites 570619 48 CON
Solanum sp. a 584486 48 CON
S. agrimonifolium 243349 48 CON
S. agrimonifolium 275175 (1)17 48 CON
S. flahaultii C5250 48 CON
S. moscopanum 570632 (1)8 72 CON
S. sucubunense C12 72 CON
S. subpanduratum 498289 48 CON
S. pamplonense 583314 48 CON
S. longiconicum 186568 48 CON
S. flahaultii C5274 48 CON
S. agrimonifolium 243351 48 CON
S. oxycarpum 230479 (1)13 48 CON
S. oxycarpum 275226 48 CON
S. oxycarpum 498026 48 CON
S. moscopanum 567812 72 CON
S. moscopanum 561626 (11)9 48, 72 CON
S. paramonese C6329 48 TUB
A
61%
a
31%
28%
10%
81%
60%
25%
b
32%
43%
65%
46%
80%
c
78%
d
82%
69%
e
87%
f
85%
61%
70%
g
27%
12%
69%
80%
100%
84%
h
34%
i
95%

FIG. 5



the 13 accessions examined), and *S. orocense*. These accessions are distributed at the northeastern limit of sect. *Petota* in the Andes, from western Venezuela (Mérida State) to adjacent northeastern Colombia (Boyacá, Norte de Santander Departments). These accessions vary greatly in vegetative and floral morphology and corolla color (white to violet).

Clade Ac contains three Venezuelan accessions assigned to different series (*S. colombianum* of ser. *Conicibaccata*, *S. paramoense* of ser. *Tuberosa*). A separate accession of *S. paramoense* is included elsewhere in the polyploid ser. *Conicibaccata* clade. Spooner et al. (1995) first reported the fruit shape of *S. paramoense* as globose to globose-ovoid, typical of ser. *Tuberosa*, not ser. *Conicibaccata*, and this is the only species within clade A that lacks conical fruits.

Clade Ad contains three accessions of *S. lobbianum* from Volcán del Ruiz, central Colombia, and one accession initially identified as *S. colombianum* 584488 from ca 170 km to the east. All four accessions have blue corollas, are densely pubescent, and may be related. The accessions of *S. lobbianum* from Volcán del Ruiz co-occur with the

FIG. 5. Strict consensus tree of 3,000 most-parsimonious Wagner trees of the cpDNA restriction site variants in *Solanum* ser. *Conicibaccata* and related species, with overlaid bootstrap values. The number of additional identical accessions are indicated in parentheses and are listed in Fig. 4. Each accession is followed by its ploidy level (diploid = 24, tetraploid = 48, hexaploid = 72), and code indicating series assignment of Hawkes (1990): CON = ser. *Conicibaccata*, DEM = ser. *Demissa*, PIU = ser. *Piurana*, TUB = ser. *Tuberosa*, PIN = ser. *Pinnatisecta*. Clades A-H are discussed in the text. Clade G is ser. *Piurana* in the discussion.

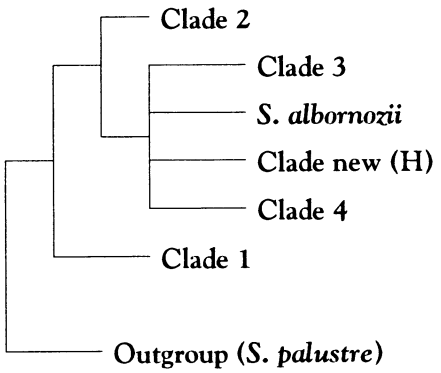


FIG. 6. Cladistic relationships of clade H in this study to a global analysis of cpDNA relationships in sect. *Petota* (Spooner and Castillo 1997; see text).

small white corolla phenotype of clade Aa (567831; Spooner et al. 1995).

Clade Ae has a geographic component in that it contains two accessions from the same general locality in southern Colombia, near the type locality of *S. cacetanum*. Ochoa (1980) described this species, but later (Ochoa 1992b) synonymized it with *S. colombianum*.

Clade Af contains five of the 13 accessions of *S. flahaultii* and *S. neovalenzuelae*. The morphological data (Figs. 7, 8) show that some accessions of both species cluster near each other.

Clade Ag contains two of the 13 accessions of *S. flahaultii* (the other accessions on clades Ab, Af, and individually elsewhere on clade A), *S. garcia-barrigae*, *S. otites*, unknown species "a," and three of the four accessions of *S. agrimonifolium*. Some accessions of *S. flahaultii* are very similar morphologically to *S. garcia-barrigae*, but there is less similarity to *S. otites*, *S. agrimonifolium*, and unknown species "a" (Figs. 7, 8).

Clade Ah contains *S. subpanduratum* from Venezuela and the morphologically dissimilar *S. pamplonense* from Colombia (Figs. 7, 8).

Clade Ai contains three of the four accessions of *S. oxycarpum*; the other is on an unresolved branch of Clade A.

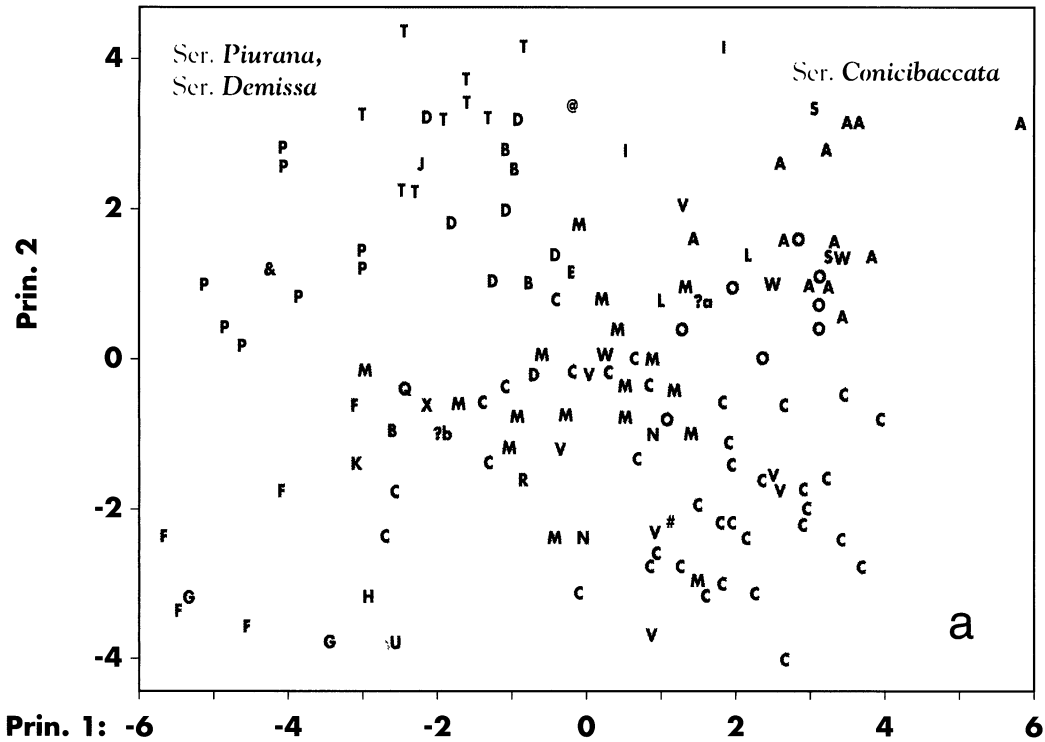
The remaining unresolved clades contain *S. agrimonifolium*, *S. colombianum*, *S. flahaultii*, *S. longiconicum*, *S. moscopanum*, *S. oxycarpum*, *S. paramoense*, *S. sucubunense*, and *S. tundalomense*. *Solanum agrimonifolium*, *S. colombianum*, *S. flahaultii*, *S. oxycarpum*, and *S. paramoense* also occur on other resolved clades within clade A. The 19 hexaploids of *S. moscopanum* and *S. sucubunense* occur in seven separate unresolved clades, widely distributed from central Colombia to southern Ecuador (map areas 24, 25, 27, 34, 36, 37, 38; map area 27, respectively; Appendix 1, Fig. 2). The other hexaploid member of ser. *Conicibaccata* (*S. nemorosum* from northern Peru) was not examined.

STRUCTURE WITHIN CLADES C AND G. Clades C and G, like clade A, have unresolved polytomies that fail to separate species, and that include taxa with multiple identical accessions for all cpDNA restriction site variants (Figs. 4, 5). Clade C contains all accessions of four diploid species in ser. *Conicibaccata*: *S. laxissimum*, *S. santolallae*, *S. urubambae*, and *S. violaceimarmoratum*. Two other diploid species of ser. *Conicibaccata*, *S. buesii* and *S. limbaniense*, form a polytomy or are basal to clade C, respectively (Fig. 5).

Four other species of ser. *Conicibaccata*, *S. chomatophilum*, *S. contumazaense*, *S. irosinum*, and *S. paucijugum*, are on the moderately well supported clade G (Figs. 4, 5). A global cladistic analysis of sect. *Petota* by Spooner and Castillo (1997) indicates that this clade contains all members of ser. *Piurana* and species from four other series.

Morphology. The PCA axes 1 and 2 of all accessions (Fig. 7) accounted for 14.9% and 9.0% of the total variation, for a total of 23.9%; axis 3 accounted for an additional 8.3%, but did not change the overall pattern and is not presented. Axis 1 is most highly influenced (highest positive or negative eigenvector values) by the following four

FIG. 7A,B. Principal components analysis based on 44 morphological characters (Table 2) examined in this study. Species codes are: *S. agrimonifolium* (A), *S. brachycarpum* (B), *S. buesii* (E), *S. chomatophilum* (D), *S. colombianum* (C), *S. contumazaense* (@), *S. flahaultii* (F), *S. garcia-barrigae* (G), *S. irosinum* (I), *S. laxissimum* (L), *S. limbaniense* (J), *S. lobbianum* (H), *S. longiconicum* (#), *S. moscopanum* (M), *S. neovalenzuelae* (K), *S. orocense* (N), *S. otites* (R), *S. oxycarpum* (O), *S. pamplonense* (Q), *S. paucijugum* (P), *S. santolallae* (S), *S. solisii* (&), *S. subpanduratum* (U), *S. sucubunense* (X), *S. tundalomense* (W), *S. tuquerrense* (T), *S. violaceimarmoratum* (V), *Solanum* unknown taxa "a" (?a), "b" (?b). Fig. 7a based on all taxa; Fig. 7b based only on ser. *Conicibaccata* taxa, and additionally excluding *S. chomatophilum*, *S. contumazaense*, *S. irosinum*, *S. limbaniense*, and *S. paucijugum* (see text). Balloons outline ser. *Conicibaccata* from ser. *Piurana* and ser. *Demissa* (*S. brachycarpum*) in a, and polyploid ser. *Conicibaccata* from South America, polyploid ser. *Conicibaccata* from Mexico and Central America, and diploid ser. *Conicibaccata* in b.


Ser. Piurana,
Ser. Demissa
Ser. Conicibaccata
a
Prin. 2
Prin. 1: -6 -4 -2 0 2 4 6
4 2 0 -2 -4

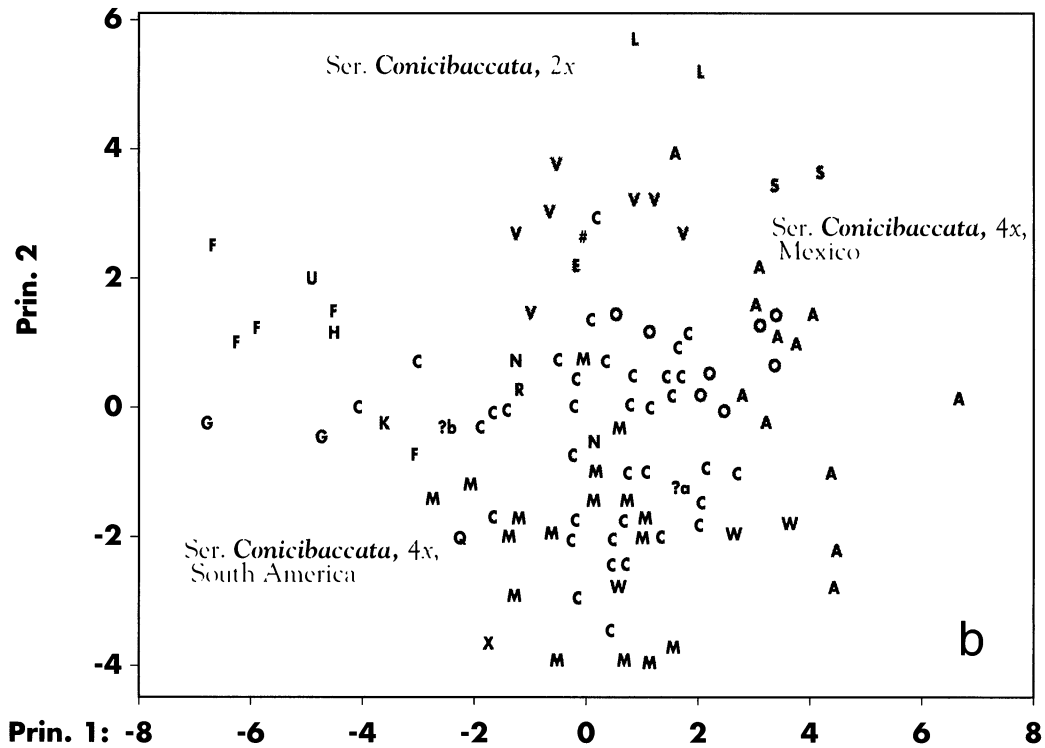
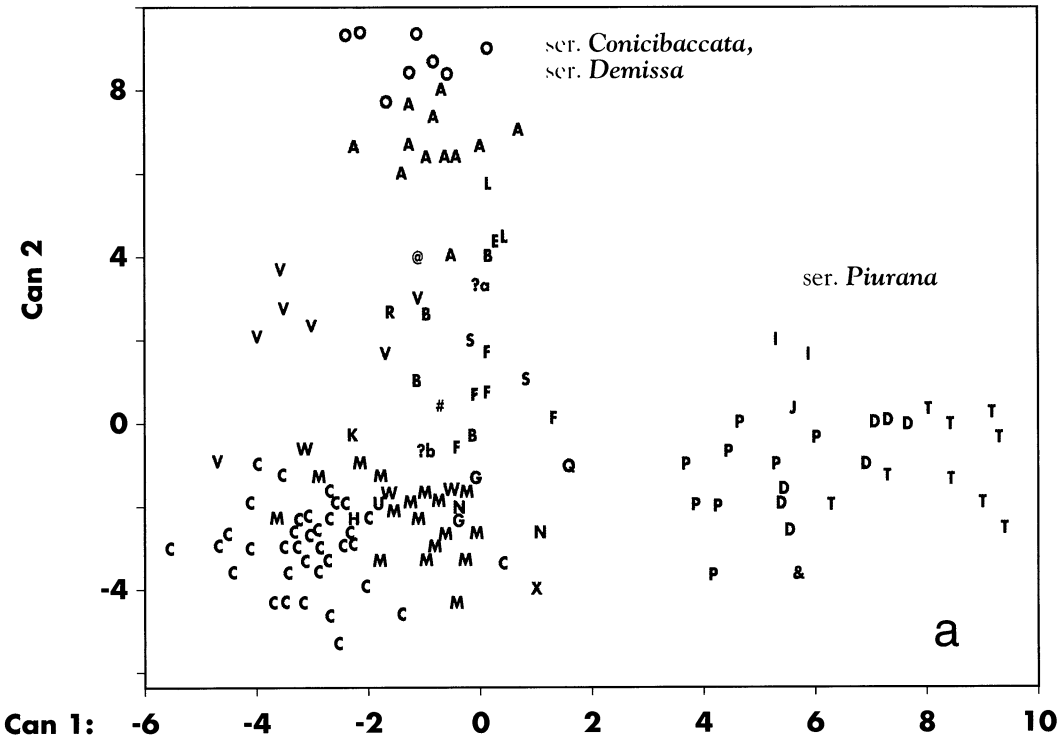

Ser. Conicibaccata, 2x
Ser. Conicibaccata, 4x,
Mexico
Ser. Conicibaccata, 4x,
South America
b
Prin. 2
Prin. 1: -8 -6 -4 -2 0 2 4 6 8
6 4 2 0 -2 -4

FIG. 7


ser. Conicibaccata,
ser. Demissa
ser. Piurana
a
Can 2
Can 1:
8
4
0
-4
-6
-4
-2
0
2
4
6
8
10

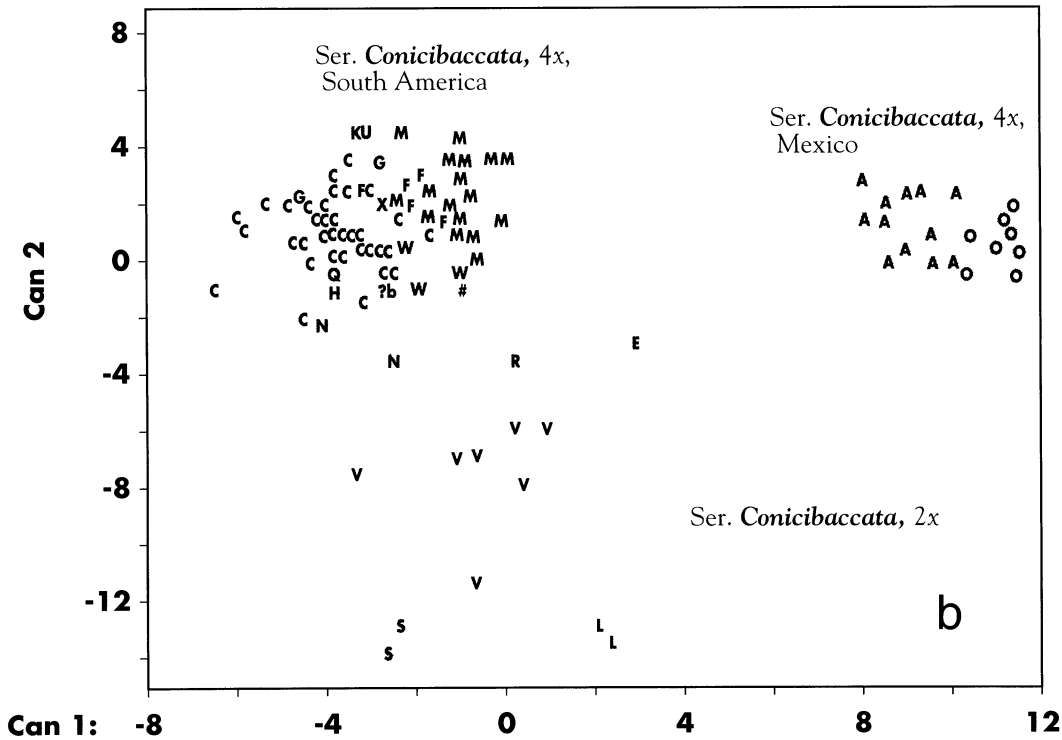

Ser. Conicibaccata, 4x,
South America
Ser. Conicibaccata, 4x,
Mexico
Ser. Conicibaccata, 2x
b
Can 2
Can 1:
8
4
0
-4
-8
-12
-8
-4
0
4
8
12

FIG. 8

characters: diameter of stem, length of leaf, position of widest leaf pair, and number of lateral leaflets; axis 2 by the following four characters: margin of leaflets, primary color of corolla, secondary color of corolla, and length of pedicel. The PCA (Fig. 7a) separated ser. *Piurana* (clade G) and the two accessions of *S. brachycarpum* (ser. *Demissa*, clade C) from ser. *Conicibaccata* quite well, and included unknown species "b" from clade H. This analysis intermixed many multiple accessions of different species; i.e., there was poor species-specific clustering for most species.

The phenogram of all accessions produced by DIST (not shown; Castillo 1995) had the greatest cophenetic correlation coefficient (0.741); the others were: MANHAT (0.689), CORR (0.636). The results of the DIST phenogram were very similar to that of the PCA and are not discussed further.

In order to examine phenetic structure better within ser. *Conicibaccata*, the PCA was run again without members of ser. *Demissa* and ser. *Piurana* (as defined in Fig. 7a). Axes 1 and 2 (Fig. 7b) accounted for 12.4% and 10.8% of the total variation, for a total of 23.2%; axis 3 added an additional 8.6%, but did not change the overall pattern and is not presented. Axis 1 is most highly influenced by the same four character states of axis 1 of the entire data set, and axis 2 by width of stem wings, length of petiolule of terminal leaflet, terminal leaflet shape (character 19, Table 2), and length of petiolule of most distal lateral leaflet. This analysis similarly intermixed multiple accessions of different species, but weakly separated three groups: 1) *S. agrimonifolium* and *S. oxycarpum* (tetraploids from Mexico and Central America); 2) the South American *Conicibaccata* diploids, and 3) and the South American tetraploids.

The CDA's of the entire data set and reduced data set (excluding ser. *Demissa* and ser. *Piurana*) are presented in Figs. 8a,b. The SDA identified the following five characters to be the most important in discriminating taxa within the entire data set, ranked from the most important first: number of lateral leaflets, primary color of corolla, margin of leaflets, diameter of stem, length of terminal leaflet/first lateral leaflet; and for the reduced data set the following five characters: number of lateral leaflets, primary color of corolla, length of petiolule of most distal lateral leaflet, length of terminal leaflet/lateral leaflet, and terminal leaflet length/width. The CDA of the entire data set clearly separated all accessions of ser. *Piurana* from all accessions of ser. *Conicibaccata*, but *S. brachycarpum* was included within the ser. *Conicibaccata* cluster, unlike the results of the phenogram and PCA.

The CDA of the reduced data set, similar to the PCA, separated *S. agrimonifolium* and *S. oxycarpum* (tetraploids from Mexico and Central America), the South American diploids, and the South American tetraploids, but the separation is better. Separation of species in the reduced data set is better than in all other analyses, but is best in *S. agrimonifolium* and *S. oxycarpum*, and in the South American diploid cluster. Separation among many South American tetraploid species is poor. Despite multivariate support of some groups, especially with the CDA, there is much overlap of even the best character states separating species (Fig. 9).

To investigate the morphological differences between diploid and polyploid members of ser. *Conicibaccata*, OTU's were classified as diploid or polyploid and analyzed with SDA. These results identified the following five characters as the most important to distinguish the diploids from the polyploids, and are ranked by the most important first: longer leaves, narrower terminal leaflets, narrower lateral leaflets, more "open" leaves having longer lateral leaflet petiolules, and shorter pedicels. There was extensive overlap between the individual morphological character states best distinguishing diploid and polyploid *Conicibaccata* (Fig. 10), and they were separated only with multivariate techniques (Figs. 7b, 8b).

To investigate the differences between ser. *Conicibaccata* and ser. *Piurana* (redefined as mentioned above to include four species in ser. *Conicibaccata* placed here by the cpDNA and morphological results, and to exclude *S. limbaniense*), OTU's were assigned to one of these two redefined series and analyzed with SDA. These results identified the following five characters (ranked by the most important first) to distinguish series *Conicibaccata*

FIG. 8A,B. Canonical discriminant analysis based on 44 morphological characters examined in this study (Table 2). Species codes as in Fig. 7. Fig. 8a based on all taxa; Fig. 8b based only on ser. *Conicibaccata* taxa, and additionally excluding *S. chomatophilum*, *S. contumazaense*, *S. irosinum*, *S. limbaniense*, and *S. paucijugum* (see text). Balloons outline ser. *Conicibaccata* from ser. *Piurana* in a, and polyploid ser. *Conicibaccata* from South America, polyploid ser. *Conicibaccata* from Mexico and Central America, and diploid ser. *Conicibaccata* in b.

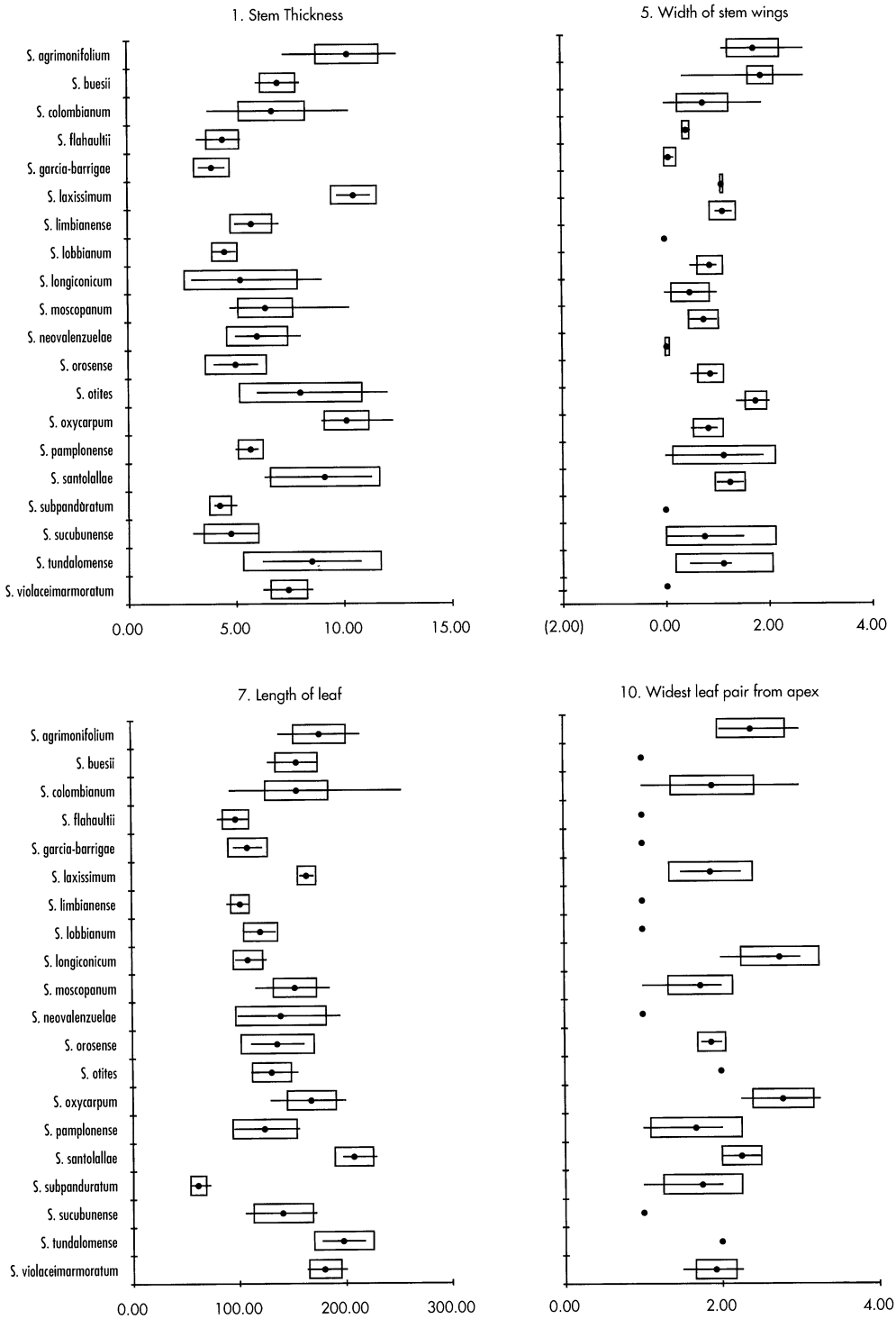


FIG. 9. Means, ranges, and one standard deviation of the mean for eight of the 44 morphological characters most important in separating species in the PCA and CDA analyses (Figs. 7, 8) in ser. *Conicibaccata*, excluding species in the ser. *Piurana* clade and ser. *Demissa*.

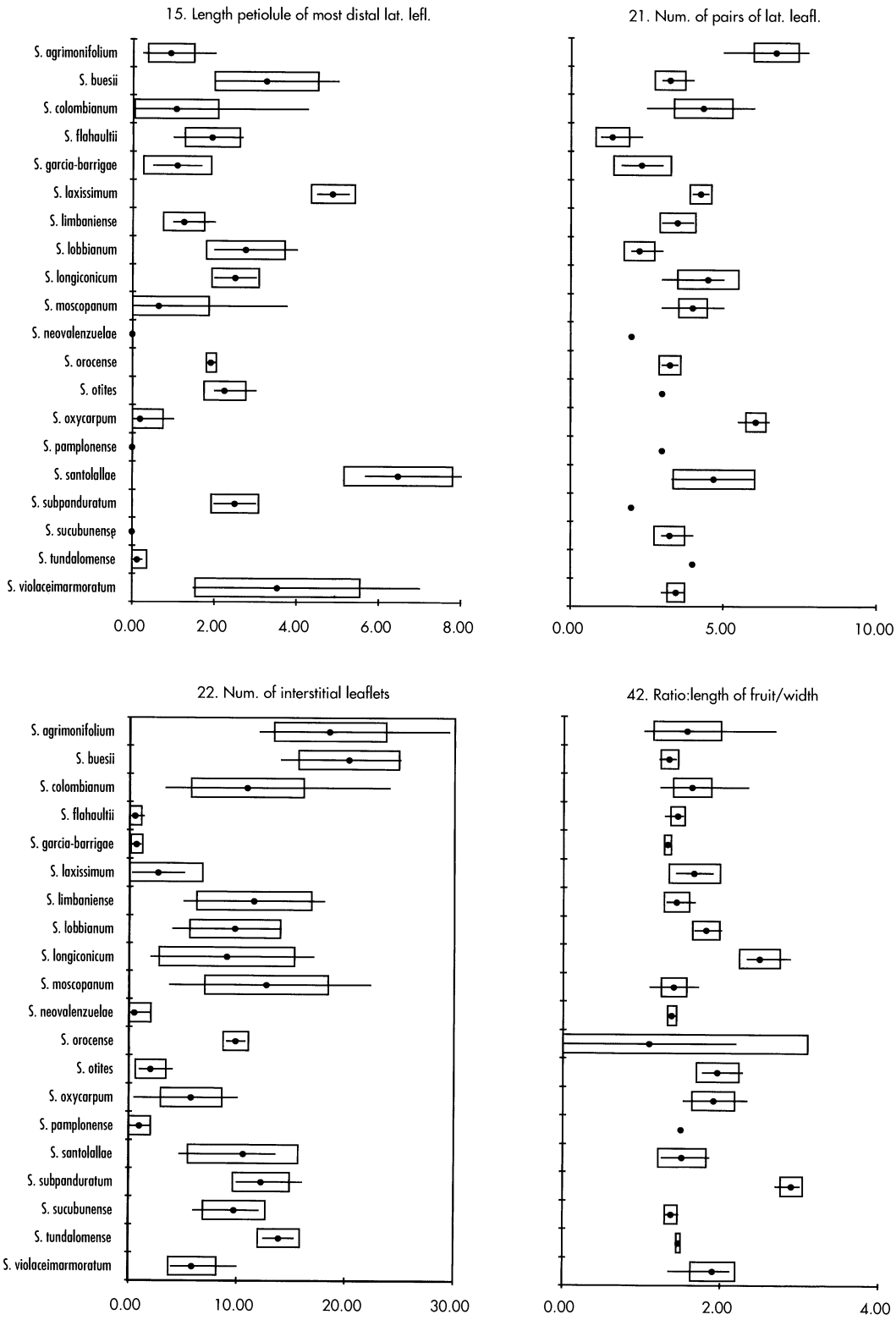

15. Length petiolule of most distal lat. lefl.
21. Num. of pairs of lat. leafl.
22. Num. of interstitial leaflets
42. Ratio:length of fruit/width
S. agrimonifolium
S. buesii
S. colombianum
S. flahaultii
S. garcia-barrigae
S. laxissimum
S. limbaniense
S. lobbianum
S. longiconicum
S. moscopanum
S. neovalenzuelae
S. orocense
S. otites
S. oxycarpum
S. pamplonense
S. santolallae
S. subpanduratum
S. sucubunense
S. tundalomense
S. violaceimarmoratum
0.00
2.00
4.00
6.00
8.00
5.00
10.00
10.00
20.00
30.00

FIG. 9.

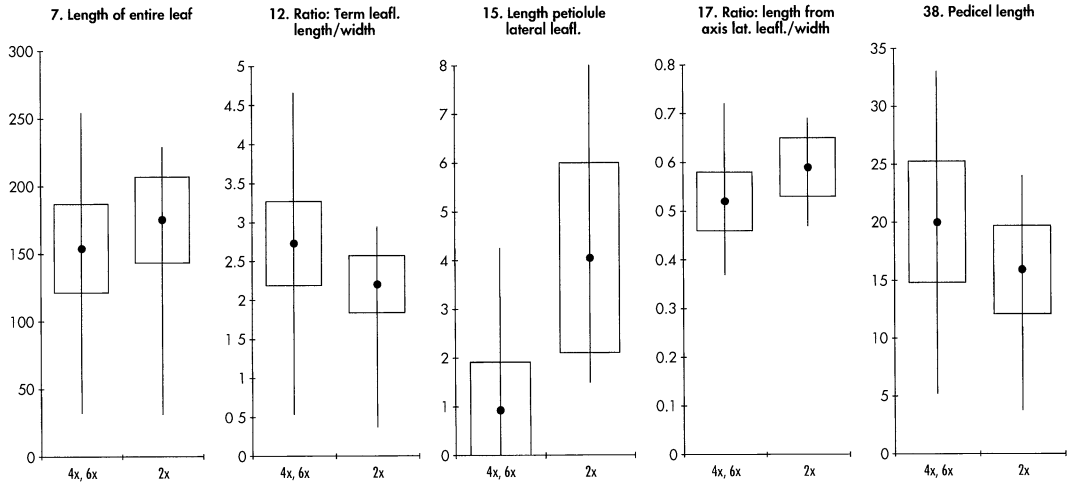


FIG. 10. Means, ranges, and one standard deviation of the mean for five of the 44 morphological characters most important in separating diploid from polyploid members of ser. *Conicibaccata* in the CDA analysis, excluding species in the ser. *Piurana* clade: (*S. chomatophilum*, *S. contumazaense*, *S. irosinum*, *S. paucijugum*) and *S. limbaniense*.

from ser. *Piurana*: wider stems, fewer interstitial leaflets, straighter leaf margins, lighter secondary corolla color, and smaller corollas. As above with the differences separating ploidy level groups in ser. *Conicibaccata*, there was extensive overlap between character states best distinguishing ser. *Conicibaccata* and ser. *Piurana* (Fig. 11).

Chromosome Counts. Mitotic chromosome counts (polyploid counts are approximations) were obtained for 112 accessions of *Solanum* sect. *Petota* (Appendix 1). New species counts are: *S. garcia-barrigae*, *S. orocense*, and *S. sucubunense*.

Concordance of Data Sets. The cpDNA analyses (Figs. 4, 5) defined eight clades (A-H), in addition to the outgroups. The cpDNA and morphological results, with few exceptions, are concordant in supporting three main groups of species: 1) polyploid members of ser. *Conicibaccata* exclusive of *S. paucijugum*; 2) diploid members of ser. *Conicibaccata*, exclusive of *S. chomatophilum*, *S. contumazaense*,

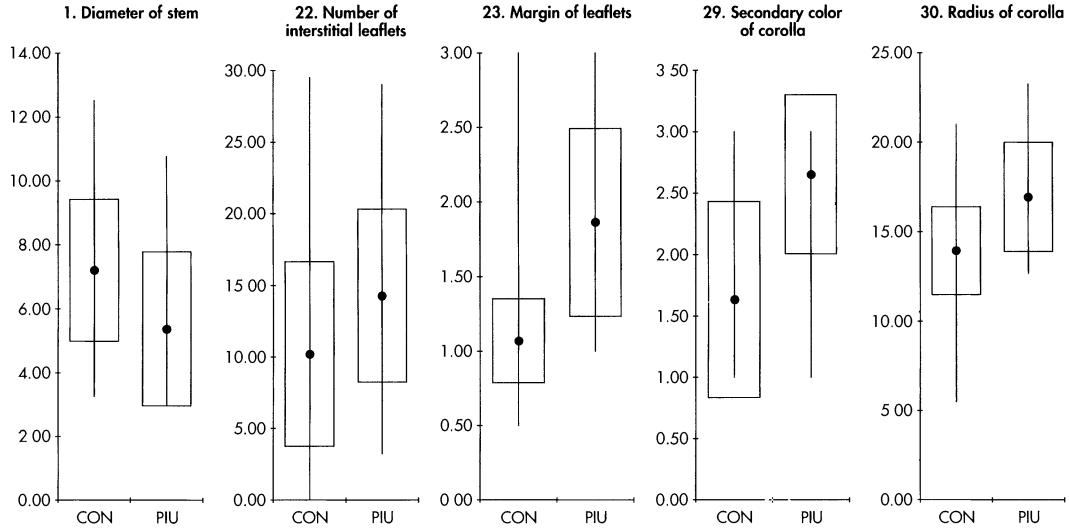


FIG. 11. Means, ranges, and one standard deviation of the mean for five of the 44 morphological characters most important in separating members of ser. *Conicibaccata* from ser. *Piurana* in the CDA analysis.

S. irosinum, and with cpDNA results, three of the four accessions of *S. brachycarpum* and *S. verrucosum*, and two accessions of *S. colombianum* (one of these, 583308) counted as a tetraploid), and 3) ser. *Piurana*, including the four species of ser. *Conicibaccata* excluded above (*S. chomatophilum*, *S. contumazaense*, *S. irosinum*, *S. paucijugum*). *Solanum limbaniense* is sister to diploid ser. *Conicibaccata* and members of ser. *Acaulia*, ser. *Demissa*, and ser. *Tuberosa* on the cpDNA analysis, and clusters with ser. *Piurana* on the morphological analyses. *Solanum buesii* is part of a polytomy with other diploid *Conicibaccata* and members of these other series on the cpDNA analyses, and clusters with other diploid ser. *Conicibaccata* in the morphological analyses.

Discordances within or between data sets consist of the following: 1) *Solanum brachycarpum* is found in both clades B and C; the one accession in clade B was not examined morphologically; 2) *Solanum tundalomense* (hexaploid, ser. *Conicibaccata*) clusters with the polyploid members of ser. *Conicibaccata* in the morphological analyses, and three of the four accessions in the cpDNA analysis also, but with one accession in clade G (ser. *Piurana*) of the cpDNA analysis; 3) *Solanum* species "b" (diploid) clusters with the polyploid ser. *Conicibaccata* in the PCA (Fig. 7b) and CDA (Fig. 8b), but is part of clade H, distinct from ser. *Conicibaccata* and ser. *Piurana*, and 4) three accessions of *S. colombianum* (567834, 583308, 583309; two counted as tetraploid, one uncounted) are separated from the other polyploid members of this species on clades C and G.

Discussion

Apospecies and Plesiospecies Within the Polyploid ser. Conicibaccata Clade. Cladistic theory can be used to group species into related taxa and to recognize species, but there is much controversy regarding the applicability of cladistic theory at the species level (Luckow 1995). Much of this controversy has arisen only recently from the interpretation of large data sets using molecular phylogenetic data. Molecular studies have detected considerable cpDNA polymorphisms within species (Harris and Ingram 1991; Soltis et al. 1992; this study). Some extend cladistic theory to the extreme of arguing that clades fixed for minor genetic traits even in the absence of traditional morphological characters should be recognized as species (Davis and Nixon 1992). Others advance phylogenetic species concepts but do not recommend recognition of species defined only by minor genetic traits (Olmstead 1995).

Another controversy relates to the recognition of paraphyletic species, i.e., those including a common ancestor and some but not all of its descendants (Rieseberg and Brouillet 1994), or the recognition of metaspecies, i.e., a group defined within a polytomous clade but with apomorphies distinguishing some derivative populations (de Queiroz and Donoghue 1988). Olmstead (1995) proposes the term "apospecies" for monophyletic groups of populations fixed for a trait(s) derived from within both metaspecies and paraphyletic species, and the term "plesiospecies" for the remaining ancestral populations. Our cpDNA data could be interpreted to recognize some apospecies [i.e., that subset of *S. colombianum* clade Aa, *S. lobbianum* on clade Ad if *S. colombianum* 554488 were reidentified as this species (below), *S. otites* on clade Ag], some plesiospecies (*S. colombianum* in a broad sense, to the exclusion of many apospecies derived from it, and some polyphyletic species (*S. flahaultii*, clades Ab, Af, Ag).

The discordance between morphological species as currently defined, and cpDNA clades could be caused by the following processes: 1) populations may have arisen from a progenitor highly polymorphic for cpDNA that has not yet sorted out between species [the matriarchal lineage sorting concept of Neigel and Avise (1986)]; 2) interspecific hybridization, thought to be common in sect. *Petota*, and 3) many of these populations represent a wide array of variability that are artificially and inappropriately divided into species and there are too many species recognized in the group.

Morphological Character States Distinguishing ser. Conicibaccata and ser. Piurana. Hawkes (1990) included 15 species in ser. *Piurana*, distributed from Colombia south to Peru. *Solanum irosinum* and *S. paucijugum* always have been treated in ser. *Conicibaccata*, but *S. chomatophilum* alternatively has been treated in ser. *Piurana* (Correll 1962; Hawkes 1963), and *S. contumazaense* in ser. *Tuberosa* (Ochoa 1964; Table 1). Our combined cpDNA and morphological data are concordant in including these four species in ser. *Piurana*, except that *S. contumazaense* clusters morphologically with ser. *Piurana* on the PCA (Fig. 7a) and ser. *Conicibaccata* on the CDA (Fig. 8a).

These results raise the question of the morphological distinction between ser. *Conicibaccata* and ser. *Piurana*, neither of which has been circumscribed clearly. Most species in ser. *Piurana* are character-

ized by globose to short ovoid fruits and coriaceous leaves with revolute margins when dry, but there are many exceptions. Series *Conicibaccata* has been defined largely by its long conical fruits but the apparent overlap of long conical fruits with ovoid conical fruits in other series is mentioned above. We determined *S. chomatophilum*, *S. paucijugum*, and *S. irosinum* to have ovoid conical fruits, and *S. contumazaense* to have round fruits. We did not measure revolute vs. simple leaf margins on dried leaves, or leaf texture. The distinction between coriaceous vs. membranous leaves is not always clear, but we observed *S. chomatophilum*, *S. paucijugum*, and *S. irosinum* to have more coriaceous leaves in contrast to more membranous leaves of other *Conicibaccata*. The five most important character states separating ser. *Conicibaccata* and ser. *Piurana* in our study are listed above; all show much overlap (Fig. 11). These data suggest that *S. chomatophilum*, *S. contumazaense*, *S. paucijugum*, and *S. irosinum* should be included in ser. *Piurana*, but that this clade is not easily defined morphologically.

Relationships Between Diploid and Polyploid Members of ser. Conicibaccata. Hawkes (1990) and Hawkes and Jackson (1992) hypothesized that polyploid ser. *Conicibaccata* arose from diploid ser. *Conicibaccata*, but this would require a mutation in Endosperm Balance Number (EBN). A major isolating mechanism in section *Petota* is governed by a strong crossing barrier evidenced by endosperm breakdown in hybrids differing by EBN compatibilities [the Endosperm Balance Number hypothesis (Johnston et al. 1980; Hanneman 1994)]. Species are assigned an EBN based on their ability to cross within EBN levels, using standard tester species. Within sect. *Petota*, species are $2x$(1EBN); $2x$(2EBN), e.g., ser. *Conicibaccata*, *S. verrucosum*; $4x$(2EBN), e.g., ser. *Conicibaccata*, Mexican ser. *Longipedicellata*; $4x$(4EBN); and $6x$(4EBN), e.g., ser. *Conicibaccata*, ser. *Demissa*. Doubling ploidy doubles EBN (Hanneman 1994). Many wild potato species commonly produce $2n$ gametes (Watanabe and Peloquin 1991), and interspecific hybrids within and between ploidy levels are easily made within EBN levels. Hybrids via $2n$ gametes among $2x$(2EBN) ser. *Conicibaccata* species would lead to $4x$(4EBN), not 4x(2EBN), the condition of the ser. *Conicibaccata* tetraploids, necessitating an EBN reduction mutation.

Hawkes (1990) and Hawkes and Jackson (1992) further hypothesized that *S. brachycarpum* and its relatives in ser. *Demissa* are of hybrid origin between the tetraploid members of ser. *Conicibaccata* or ser. *Longipedicellata* and *S. verrucosum*. This hypothesis is compatible with the EBN hypothesis [e.g., $4x$(2EBN) X $2x$(2EBN) = $6x$(4EBN)].

Our cladistic results (Figs. 4, 5) are ambiguous regarding the relationships of the diploid and polyploid members of ser. *Conicibaccata*, and suggest that this series may not represent a monophyletic group. The clade immediately basal to clade A is composed of one of the four accessions of *S. brachycarpum* (ser. *Demissa*), and the next basal clades are a polytomy of some other diploid members of ser. *Conicibaccata*: clade C, *S. laxissimum*, *S. santolallae*, and *S. violaceimarmoratum*, but also including diploid and hexaploid species from ser. *Demissa* and *Tuberosa*; clade D, *S. buesii* (ser. *Conicibaccata*); and clade E, a hexaploid member of ser. *Acaulia*.

The three accessions of *S. brachycarpum* in clade C may have *S. verrucosum* as a maternal parent. This concurs with the results of Spooner and Sytsma (1992) who showed eight accessions of ser. *Demissa* (including *S. brachycarpum*) and *S. verrucosum* to occur on the same clade. Additional cpDNA analyses of members of ser. *Demissa* (containing six hexaploid species from Mexico and Central America) would provide data to investigate the cladistic structure of ser. *Demissa*. Similarly, the two "misplaced" accessions of *S. colombianum*, and *S. longiconicum*, on clade C, and *S. colombianum* and *S. tundalomense* on clade G could have arisen from hybridizations with maternal parents of these respective clades. Additional data from biparentally inherited characters are needed to make conclusions regarding the monophyly of the diploid and polyploid ser. *Conicibaccata*.

Solanum lobbianum. There is controversy surrounding the identity of *S. lobbianum* (Fig. 5, Clade Ad) owing to difficulties of an incomplete type specimen (it lacks fruits), and vague locality data. The most distinctive feature of *S. lobbianum* is its densely pubescent leaves, but other members of sect. *Petota* such as *S. paucijugum* also share this character state. Clade Ad contains three accessions of *S. lobbianum* from Volcán del Ruiz, central Colombia, and one accession initially identified as *S. colombianum* 584488 from ca 170 km to the east that may be a disjunct population of *S. lobbianum*.

Hawkes (1992) identified as *S. lobbianum* two collections from central Ecuador (*Spooner, Castillo, López, 5071, 5138*) that were identified by Spooner et al. (1992) as *S. paucijugum*. Ochoa (1992a), however, identified collections from Volcán del Ruiz (Colom-

bia) as *S. lobbianum*. Our data place collection *5071* (PI 567846) with all other accessions of *S. paucijugum* in clade G (ser. *Piurana*). These results show that these separate Colombian and Ecuadorian collections, identified by Hawkes (1992) and Ochoa (1992a) as *S. lobbianum*, have distinct cpDNA restriction site patterns, but do not settle the question of the association of the type of *S. lobbianum* with a species. We identify the Colombian collections as *S. lobbianum* because of greater overall resemblance to the type specimen.

Solanum paramoense. Hawkes (1990) included *S. paramoense* (Fig. 5, Clade Ac) in ser. *Tuberosa* but had no knowledge of fruit shape and speculated that it may belong to ser. *Conicibaccata* if it were found to have conical fruits. Ochoa (1992c) reported a tetraploid chromosome number (concurring with our count) for *S. paramoense* and synonymized this species with *S. tuberosum* subsp. *andigena* (ser. *Tuberosa*). However, he did not cite a voucher, so a final comparison of our results to Ochoa's is not yet possible. Spooner et al. (1995) first reported the fruit shape of *S. paramoense* as globose to globose-ovoid, typical of ser. *Tuberosa*, not of ser. *Conicibaccata*, and this is the only species within clade A that lacks conical fruits. Our results separate the two accessions to different parts of clade 4. The conflicting data of fruit shape and cpDNA data make it difficult to speculate about the validity of *S. paramoense* as a species, or its relationships to other members of ser. *Conicibaccata*.

Unknown Wild Potato Species. Results of recent field work in Ecuador (Spooner et al. 1992) and Colombia (Spooner et al. 1995) found wild potato species not readily assigned to any taxon known to us (unknown species "a"-"e"; Appendix 1). Unknown species "a" (584486, tetraploid), "b" (570640, diploid), and "e" (C1294) occur very near each other in Colombia, César Department. Species "a" appears similar to *S. flahaultii*, but has conical fruits smaller (7–11 mm long) than any other in ser. *Conicibaccata*. Species "b" (570640) and "e" (C1294) are similar to *S. colombianum*, but have ovoid, not conical fruits, and both may be conspecific. Species "c" (583324; Colombia, Cauca Department, diploid) appears similar to *S. colombianum*, but has so many different cpDNA restriction site variants from the latter that we highlight it here as an unknown species. Species "d" (Ecuador, Chimborazo Department, diploid) is similar to *S. andreanum*, but has conical, rather than ovoid fruits.

Conclusions. Our cpDNA and morphological data discovered that most species assigned to ser. *Conicibaccata* form three major groups: 1) tetraploids and hexaploids from central Mexico to southern Ecuador; 2) diploids from northern Peru to Bolivia, together with part of a cpDNA clade of diploids and hexaploids assigned to ser. *Demissa* and ser. *Tuberosa*, and 3) diploids and tetraploids from southern Colombia to Peru, but cladistically related to other species in ser. *Piurana*. Four diploid species of unknown identity form a clade separate from other ser. *Conicibaccata* in the cpDNA results (Figs. 4–5). *Solanum limbaniense* is sister (with cpDNA) to other diploid members of ser. *Conicibaccata* (and members of ser. *Acaulia*, ser. *Demissa*, ser. *Tuberosa*), and morphologically intermediate between members of ser. *Piurana* and the ser. *Conicibaccata* diploids.

The morphological data presented here (Figs. 9–11) show the extensive overlap of character states and resulting taxonomic difficulty that has vexed all taxonomists studying this group. Some taxa form monophyletic terminal clades (apospecies) in the cpDNA analysis that cluster only by multivariate techniques of the morphological data. The cpDNA cladistic analysis suggests that: 1) some species may have a history of hybridization; 2) the cpDNA of some species may not have sorted out from a highly polymorphic ancestor; 3) this group may include a combination of apospecies and plesiospecies (including both paraphyletic species and metaspecies), and 4) there are too many species recognized in the group. An inherent problem in attempting to reconstruct phylogeny in this group may be its recent origin and the only partial sorting out of species using any technique. Maddison (1995) illustrates dichotomizing and reticulating patterns of traits within populations to argue that there is no sharp boundary between population biology and the species level, and that any marker will provide only a probability statement of phylogeny. Other markers may show different relationships, even in the absence of interspecific hybridization.

A formal taxonomic treatment of ser. *Conicibaccata* is beyond the scope of this study. We lack collections from Peru, from where many of the species are not yet available as germplasm collections, and herbarium specimens of ser. *Conicibaccata* from Peru and other countries are being used by Carlos Ochoa of the International Potato Center for his floristic studies of sect. *Petota*. We intend to eventually monograph ser. *Conicibaccata*. Considering our field experience and the present cpDNA and morphological results, however, we currently

outline two alternatives for interpreting species boundaries for the 23 species of ser. *Conicibaccata* [of 40 total species listed by Hawkes (1990)].

Our most liberal interpretation is to recognize the following 16 morphologically most distinctive taxa formerly placed in ser. *Conicibaccata*. These are: 1) *Solanum oxycarpum* (including *S. agrimonifolium*); 2) the subset of *S. colombianum* accessions in Clade Aa best distinguished by small white corollas; 3) *S. flahaultii*; 4) *S. lobbianum*; 5) *S. otites*; 6) *S. moscopanum* (including *S. tundalomense*); 7) *S. subpanduratum*; 8) the remaining polyploid accessions in series *Conicibaccata* referred to by a possible plesiospecies name (although this is not totally in concordance with the cpDNA data); 9) *S. buesii*; 10) *S. violaceimarmoratum*, and 11) *S. laxissimum* (including *S. santolallae*); within the "ser. *Piurana*"; 12) *S. chomatophilum*; 13) *S. contumazaense*; 14) *S. irosinum*; 15) *S. paucijugum*, and 16) *S. limbaniense*.

Our second, more conservative interpretation would be to recognize only eight taxa: 1) *S. colombianum* (including all other polyploid members of ser. *Conicibaccata*); 2) *S. violaceimarmoratum* (including *S. laxissimum*, *S. santolallae*, *S. urubambae*); 3) *S. buesii*, and 4) *S. limbaniense*; within ser. *Piurana*; 5) *S. chomatophilum*; 6) *S. contumazaense*; 7) *S. irosinum*, and 8) *S. paucijugum*. This second interpretation most closely matches the concordance of the morphological and cpDNA data but it possibly will be the only species concept that will maximize stable identifications. It erects highly polymorphic and broadly delimited species. It also combines pairs of taxa that can be distinguished where they sometimes co-occur in limited geographical areas and may be reproductively isolated (e.g., *S. colombianum* and *S. lobbianum* on Volcán del Ruiz, central Colombia; *S. colombianum* and *S. moscopanum* in Valle de las Papas, southern Colombia). Unfortunately, the distinction between these pairs of species is not always clear in all geographical areas. Even this more "conservative" treatment would partition the polyploid and diploid members of ser. *Conicibaccata* into two widely overlapping species (*S. colombianum* s.l., *S. violaceimarmoratum* s.l.; Fig. 10). We make no tentative decisions here regarding new species "a-e."

We think that a trend in recognizing fewer species in section *Petota* should prevail in other series as well (e.g., Spooner et al. 1994b). A comparison by Spooner et al. (1995) of alternative contemporary treatments of the Bolivian wild potatoes by Hawkes and Hjerting (1989) and Ochoa (1990), showed that identifications of identical collection numbers, excluding types, differed 20% of the time for all Bolivian taxa. They differed 38% of the time for a group of wild species related to the cultivated species (the "*S. brevicaule* complex"). Regarding ser. *Conicibaccata*, they differ in interpretations of two of the three Bolivian species (*S. bombycinum*, *S. neovavilovii*; Spooner and van den Berg 1992a, pgs. 26, 27). This lack of stable identifications suggests that the over-description and weak boundaries of species demonstrated in ser. *Conicibaccata* is typical of infrasectional taxonomy elsewhere in sect. *Petota*. Many of the 232 species recognized by Hawkes (1990) will likely lack explicit morphological and molecular support. One objective of a taxonomic system is recognition of phylogenetically meaningful units that can be reliably distinguished and named (Luckow 1995). The collapse of many species presently recognized in sect. *Petota* is inevitable.

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APPENDIX 1. Accessions of *Solanum* sect. *Petota* examined using morphology and chloroplast DNA. Vouchers are deposited at PTIS (Bamberg and Spooner, 1994).

Map[1]	Taxa	2n[2]	Study[3]	PI[4]	Collector	Locality
1	*S. cardiophyllum*	24	C	186548	*Hawkes 1,100*	Mexico. Zacatecas: 726.5 km from Mexico to Zacatecas; 2,110 m; 22°47′N, 102°35′W.
2	*S. brachycarpum*	72	C	251721	*Hawkes 1,547*	Mexico. Jalisco: Tranquitas, at W side of Nevado del Colima; 3,200 m; 19°33′N, 103°38′W.
3	*S. brachycarpum*	72	C, M	230459	*Hawkes 1,043*	Mexico. Michoacán: Zitacuaro, km 147 from Mexico to Morelia, near Zitacuaro; 2,930 m; 19°34′N, 100°22′W.
4	*S. verrucosum*	24	C	161173	*Correll 14,252*	Mexico. Michoacán: Opopeo; ca. 10 km above Opopeo; 19°24′N, 101°36′W.
5	*S. brachycarpum*	72	C	239402	*Graham 454*	Mexico. Mexico: Tenancinango; 19°34′N, 98°11′W.
5	*S. brachycarpum*	72	M	498020	*Tarn et al. 53*	Mexico. Hidalgo: Pachuca, 5.5 km along the track towards Huayacocotla; 1,950 m; 20°23′N, 98°40′W.
6	*S. brachycarpum*	72	M	498025	*Tarn et al. 181*	Mexico. Puebla: La Griega, 22 km from Tehuacán to Oaxaca, turning off at Coxatlán; 2,640 m; 20°40′N, 100°14′W.
6	*S. cardiophyllum*	24	C	347759	*Tarn et al. 241D*	Mexico. Puebla: left side of Tehuacán-Huajuapán de León road on the Puebla side of border, Highway 125; 2,060 m; 18°37′N, 97°35′W.
6	*S. oxycarpum*	48	C, M	498026	*Tarn et al. 182*	Mexico. Puebla: Tehuacán, on road from Tehuacán to Oaxaca turning off at Coxtlan towards Zoquitlán, at km 22, passing La Griega; 2,640 m; 20°40′N; 100°14′W.
7	*S. oxycarpum*	48	M	275224	*Hawkes 1,643*	Mexico. Veracruz: Perote, on road from Las Vigas to Jalapa at km 306.5 from Mexico, at La Joya village; 2,100 m; 19°34′N, 97°14′W.
7	*S. oxycarpum*	48	C, M	275225	*Hawkes 1,645*	Mexico. Veracruz: Perote, on road from Las Vigas to Jalapa, upper edge of La Joya village, at S side of road; 2,100 m; 19°34′N, 97°14′W.
7	*S. oxycarpum*	48	C, M	275226	*Hawkes 1,649*	Mexico. Veracruz: Las Vigas, on road from Las Vigas to Jalapa, at Malpais de La Joya; 2,150 m; 19°40′N, 98°35′W.
7	*S. oxycarpum*	48	M	498272	*Ochoa 14,213*	Mexico. Veracruz: La Joya; 2,050 m; 19°05′N, 97°49′W.
7	*S. oxycarpum*	48	M	545777	*Tarn et al. 286*	Mexico. Veracruz: Perote, at Malpais de la Joya between Perote and Jalapa, about 32 km from Perote on Hwy 140; 2,200 m; 19°37′N, 97°02′W.
8	*S. oxycarpum*	48	C, M	230479	*Graham 1*	Mexico. Veracruz: Pedregal de la Joya; 2,000 m; 18°14′N, 96°07′W.
9	*S. brachycarpum*	72	C, M	275183	*Hawkes 1,710*	Mexico. Oaxaca: Miahuatlán, on road from Oaxaca to Puerto Angel, 30 km S of Miahuatlán; 2,400 m; 16°17′N, 96°33′W.
9	*S. oxycarpum*	48	M	545776	*Tarn et al. 272*	Mexico. Oaxaca: Ixtlán de Juarez, 21.8 km N of Ixtlan de Juarez on Hwy 175 to Tuxtepec; 2,870 m; 17°28′N, 96°30′W.
10	*S. agrimonifolium*	48	M	545748	*Tarn et al. 277*	Mexico. Chiapas: San Cristobal de las Casas, 9.7 km from San Cristobal to Cerro Zontehuitz by road to microwave tower, turning off to Tenejapa; 2,750 m; 16°49′N, 92°35′W.
10	*S. agrimonifolium*	48	M	545749	*Tarn et al. 278*	Mexico. Chiapas: San Cristobal de las Casas, 9.8 km from San Cristobal to Cerro Zontehuitz along road to microwave tower, turning off to Tenejapa; 2,760 m; 16°49′N, 92°35′W.

APPENDIX 1. Continued

Map[1]	Taxa	$2n$[2]	Study[3]	PI[4]	Collector	Locality
10	*S. agrimonifolium*	48	M	545750	*Tarn et al. 280*	Mexico. Chiapas: San Cristobal de las Casas, 10 km from San Cristobal to Cerro Zontehuitz along road to microwave tower, turning off the road to Tenejapa; 2,760 m; 16°48′N, 92°35′W.
10	*S. agrimonifolium*	ca. 48*	M	558370	*Spooner et al. 4,208*	Mexico. Chiapas: Motozintla de Mendoza, 6.9 km N of Rt. 190 beginning S of Motozintla de Mendoza, on road to Siltepec; 2,005 m; 15°22′N, 92°17′W.
10	*S. agrimonifolium*	ca. 48*	M	558371	*Spooner et al. 4,211*	Mexico. Chiapas: Motozintla de Mendoza, at Cerro Boquerón, 17.4 km N of Rt. 190 beginning S of Motozintla de Mendoza, on road to Siltepec; 2,330 m; 15°25′N, 92°18′W.
10	*S. agrimonifolium*	ca. 48*	M	558372	*Spooner et al. 4,227*	Mexico. Chiapas: San Cristobal de las Casas, 12.1 km along road to microwave tower of Tzontehuitz, 0.1 km downhill from microwave tower; 2,790 m; 16°20′N, 92°17′W.
Mex	*S. verrucosum*	24	C	195171	*Commonwealth Potato Collection Genebank 1340.2*	Mexico.
11	*S. agrimonifolium*	48	C, M	243349	*Graham 145*	Guatemala. Quezaltenango: Mujulia; 1737 m; 14°45′N, 91°41′W.
11	*S. agrimonifolium*	48	C, M	243351	*Graham 145A*	Guatemala. Huehuetenango; 2,651 m; 15°30′N, 90°57′W.
11	*S. agrimonifolium*	48	M	243352	*Graham 145B*	Guatemala: Huehuetenango; 2,651 m; 15°30′N, 90°57′W.
12	*S. agrimonifolium*	48	M	243350	*Graham 146*	Guatemala. Huehuetenango; 2,651 m; 15°30′N, 90°57′W.
12	*S. agrimonifolium*	48	C, M	275175	*Hawkes 1,851*	Guatemala. San Marcos: San Marcos, at San Andrés Chapel, 8 km from Rt. 12 from San Marcos; 2,750 m; 15°00′N, 91°47′W.
12	*S. agrimonifolium*	48	C, M	275177	*Hawkes 1,891*	Guatemala. Totonicapán: Totonicapán, at Cerro El Quiche, 1.5 km E from Totonicapán to Los Encuentros; 3,300 m; 14°55′N, 91°22′W.
13	*S. longiconicum*	48	C, M	186568	*Hawkes 1,130*	Costa Rica. Cartago: on Panamerican Hwy, 60 km S of Cartago; 2,850 m; 09°12′N, 83°55′W.
13	*S. longiconicum*	48	C	208780	*Hope* s.n.	Costa Rica. Alajuela: Isla Bonita; 09°28′N, 84°13′W.
15	*S. colombianum*		C	587117	*Spooner et al. 6,332*	Venezuela. Mérida: San Rafael, ca. 50 m E of E side of Laguna Saisay, ca. 5.5 km by air SE of San Rafael; 3,750 m; 08°43′N, 70°50′W.
15	*S. colombianum*		C	587118	*Spooner et al. 6,339*	Venezuela. Mérida: Gavidia, 1.6 km W of school in Gavidia, on E side of Quebrada Gavidia; 3,180 m; 08°42′N, 70°57′W.
15	*S. paramoense*		C		*Spooner et al. 6,329*	Venezuela. Mérida: San Rafael, growing on SW side of Quebrada Saisay, ca. 200 m from middle of valley floor; 3,500 m; 08°45′N, 70°52′W.
15	*S. paramoense*	ca. 48*	C	570637	*Spooner et al. 6,337*	Venezuela. Mérida: Piñango, growing about 400 m W of road from El Aguila to Piñango, ca. 3 km N of El Hático, in narrow valley; 3360 m; 08°58′N, 70°48′W.
15	*S. subpanduratum*	48	C, M	498289	*Ochoa 11,208*	Venezuela. Mérida: Mérida.
16	*S. colombianum*	ca. 48*	C, M	583328	*Spooner et al. 6,309*	Venezuela. Táchira: Zumbador, along roadside, 13.4 km NW of Plaza Bolívar of Quiniquea; 2,340 m; 07°56′N, 72°03′W.
16	*S. colombianum*	ca. 48*	C	583327	*Spooner et al. 6,312*	Venezuela. Táchira: Quiniquea, on Páramo El Zumbador, along roadside, 16.1 km NW of Plaza Bolívar of Quiniquea; 2,530 m; 07°56′N, 72°03′W.

APPENDIX 1. Continued

Map[1]	Taxa	2n[2]	Study[3]	PI[4]	Collector	Locality
16	*S. colombianum*	ca. 48*	C	586950	*Spooner et al. 6,314*	Venezuela. Táchira: Quiniquea, on Páramo el Zumador, along roadside, 21.7 km from Plaza Bolívar of Quiniquea; 2,750 m; 07°57′N, 72°04′W.
16	*S. colombianum*	ca. 48*	C	586951	*Spooner et al. 6,316*	Venezuela. Táchira: San José de Bolívar, ca. 10 km N of San José de Bolívar on road to La Grita, 1.6 km N of Quebrada Blanca; 2,250 m; 08°01′N, 71°54′W.
16	*S. colombianum*	ca. 48*	M		*Spooner et al. 6,317*	Venezuela. Táchira: La Grita; 25 km E of Plaza Bolívar of La Grita to Pregonero; 2,900 m; 08°09′N, 71°54′W.
16	*S. colombianum*		C	583326	*Spooner et al. 6,318*	Venezuela. Táchira: La Grita, 29.9 km E of Plaza Bolívar of La Grita, on road to Pregonero; 2,840 m; 08°08′N, 71°54′W.
16	*S. colombianum*	ca. 48*	C, M	583325	*Spooner et al. 6,319*	Venezuela. Táchira: La Grita, 32 km E of Plaza Bolívar of La Grita on road on Pregonero; 2,800 m; 08°07′N, 71°54′W.
16	*S. colombianum*	ca. 48*	C	567825	*Spooner et al. 6,313*	Venezuela. Táchira: Quiniquea, on Páramo El Zumbador, along roadside 17.9 km NW of Plaza Bolívar of Quiniquea; 2,630 m; 07°56′N, 72°03′W.
16	*S. colombianum*		C	567826	*Spooner et al. 6,315*	Venezuela. Táchira: San José de Bolívar, ca. 10 km N of San José de Bolívar on road to La Grita, 1.6 km N of Quebrada Blanca; 2,250 m; 08°01′N, 71°54′W.
Ven	*S. colombianum*	48	C, M	473462	*Ochoa 11,225*	Venezuela.
14	*Solanum* unknown taxa e		C		*Castillo et al. 1,294*	Colombia. César: Manaure, above El Cinco, 27.5 km from Manaure, in Sierra del Perijá; 2,770 m; 10°22′N, 72°48′W.
14	*S. otites*	ca. 48*	C, M	570618	*Castillo et al. 1,291*	Colombia. César: Manaure, above El Cinco, 24.7 km from Manaure, in Sierra del Perijá; 2,450 m; 10°22′N, 72°48′W.
14	*S. otites*	ca. 48*	C	570619	*Castillo et al. 1,292*	Colombia. César: Manaure, above El Cinco, 26.9 km from Manaure on dirt road in Sierra del Perijá; 2,600 m; 10°22′N, 72°48′W.
14	*Solanum* unknown taxa a	ca. 48*	C, M	570640	*Castillo et al. 1,297*	Colombia. César: Manaure, above El Cinco, 34.6 km from Manaure, at Sabana Rusia in Sierra del Perijá; 3,040 m; 10°25′N, 72°48′W.
14	*Solanum* unknown taxa b	24*	C, M	584486	*Castillo et al. 1,296*	Colombia. César: Manaure, above El Cinco, 32 km from Manaure, at Sabana Rusia in Sierra del Perijá; 3,030 m; 10°24′N, 72°48′W.
17	*S. colombianum*		C		*Castillo et al. 1,311*	Colombia. Norte de Santander: Pamplona, at Cerro Loma Larga, at La Canoa, 9 km from Pamplona to Malaga, ascending 3 hours walk at E side of Páramo de Fontibón; 3,210 m; 07°21′N, 72°36′W.
17	*S. garcia-barrigae*	ca. 48*	C, M	584487	*Castillo et al. 1,302*	Colombia. Norte de Santander: Abrego, on Cerro Oroque (Jurisdicciones), 45.6 km from Abrego, W side of mountain, 50 m below antennas; 3,350 m; 07°52′N, 73°14′W.
17	*S. garcia-barrigae*	ca. 48*	C, M	570622	*Castillo et al. 1,301*	Colombia. Norte de Santander: Abrego, on Cerro Oroque (Jurisdicciones), W side of road, 40.6 km from Abrego; 3,150 M; 07°52′N, 73°14′W.
17	*S. orocense*	ca. 48*	C, M	583307	*Castillo et al. 1,304*	Colombia. Norte de Santander: Abrego, on Cerro Oroque (Jurisdicciones), 40.2 km from Abrego, then 300 m to the N from main road, before antennas; 3,100 m; 07°50′N, 73°14′W.
17	*S. orocense*	ca. 48*	C		*Castillo et al. 1,306*	Colombia. Norte de Santander: Abrego, in La Vereda, El Páramo, in Monte Oroque, 1 km E of school; 2,860 m; 08°03′N, 73°12′W.

APPENDIX 1. Continued

Map[1]	Taxa	2n[2]	Study[3]	PI[4]	Collector	Locality
17	*S. orocense*	ca. 48*	C, M	570636	*Castillo et al. 1,303*	Colombia. Norte de Santander: Abrego, on Cerro Oroque (Jurisdicciones), 45.6 km from Abrego, W side of mountain, 150 m below antennas; 3,340 m; 07°52′N, 73°14′W.
17	*S. pamplonense*	ca. 48*	C, M	583314	*López et al. 5,245*	Colombia. Norte de Santander: Pamplona, at Cerro de Oriente; 3,330 m; 07°30′N, 72°40′W.
18	*S. neovalenzuelae*	ca. 48*	C, M		*López et al. CCC 5,247*	Colombia. Santander: Bucaramanga, at Berlín, 10 km from Berlín to Las Vetas, 200 m below road; 3,650 m; 07°10′N, 72°50′W.
19	*S. flahaultii*	ca. 48*	C, M	583306	*Castillo et al. 1,287*	Colombia. Boyacá: Belén, at Páramo de Pisba, 88 km from Belén to Chita; 3,360 m; 06°02′N, 72°29′W.
19	*S. flahaultii*	ca. 48*	C		*López and Orozco CCC 5,250*	Colombia. Boyacá: Guicán, at Finca el Junco of Eduardo Carreño; 3,450 m; 06°30′N, 72°20′W.
19	*S. flahaultii*	ca. 48*	C, M	583316	*López et al. CCC 5,255*	Colombia. Boyacá: Guicán, at La Cueva, farm of Eduardo Carreño; 3,200 m; 06°30′N, 72°20′W.
19	*S. flahaultii*	48	C, M	558111	*López et al. CCC 5,174*	Colombia. Boyacá: Chita, at Páramo de La Caña; 3,300 m; 06°10′N, 72°40′W.
19	*S. flahaultii*	48	C, M	583317	*López et al. CCC 5,259*	Colombia. Boyacá: Chita, at Páramo de La Caña; 3,300 m; 06°10′N, 72°40′W.
19	*S. flahaultii*	ca. 48*	C		*López et al. CCC 5,274*	Colombia. Boyacá: Chita.
20	*S. colombianum*	ca. 48*	C		*López 03*	Colombia. Antoquia: El Jardín, 37 km from Río Sucio to El Jardín, at vereda Ventanas; 2,720 m; 05°30′N, 75°50′W.
21	*S. colombianum*		C, M	584488	*López and Orozco CCC 5,166*	Colombia. Cundinamarca: Zipaquirá, at Santa Barbara, Don Benito farm; 3,400 m; 05°02′N, 74°20′W.
21	*S. colombianum*	ca. 48*	C		*López et al. CCC 5,232*	Colombia. Cundinamarca: Usme, 33 km from Usme to Páramo de Sumapaz; 3719 m; 04°20′N, 74°11′W.
21	*S. flahaultii*	ca. 48*	C	498167	*López et al. CCC 5,168*	Colombia. Cundinamarca; Usme, 33 km from Usme to Páramo de Chusaca, 500 m on left side of road; 3,750 m; 04°20′N, 74°11′W.
21	*S. flahaultii*	ca. 48*	C		*Castillo et al. 1,269*	Colombia. Cundinamarca: Usme, at Páramo de Masamorra Cruda, 35 km from Usme to Sumapaz, 300 m E of roadside; 3,719 m; 04°20′N, 74°11′W.
21	*S. flahaultii*	ca. 48*	C		*Castillo et al. 1,270*	Colombia. Cundinamarca: Usme, 40 km from Usme to Sumapaz, 100 m E of roadside, passing a small river; 4,310 m; 04°20′N, 74°12′W.
21	*S. flahaultii*	ca. 48*	C, M	583315	*López et al. CCC 5,248*	Colombia. Cundinamarca: Usme, at Páramo de Chusacá, 33 km from Usme, 500 m W of road; 3,750 m; 04°50′N, 74°40′W.
21	*S. flahaultii*	ca. 48*	C	498166	*López et al. CCC 5,164*	Colombia. Cundinamarca: Zipaquirá, at Vereda Santa Bárbara, Don Benito farm; 3,350 m; 05°02′N, 74°20′W.
21	*S. flahaultii*	ca. 48*	C		*López et al. CCC 5,239*	Colombia. Cundinamarca: Soacha, at Las Lagunas in Granja San Jorge of Instituto Colombiano Agropecuario; 3,050 m; 01°25′N, 77°20′W.
22	*S. colombianum*	ca. 48*	C, M	567831	*Castillo et al. 1,212*	Colombia. Caldas: Manizales, 1.5 km E of road going to Nevado del Ruiz, on road from Manizales to Frezno; 3,310 m; 05°04′N, 75°19′W.

APPENDIX 1. Continued

Map[1]	Taxa	2n[2]	Study[3]	PI[4]	Collector	Locality
22	*S. colombianum*		C	567832	*Castillo et al. 1,215*	Colombia. Caldas: Manizales, on dirt road from E of Manizales passing La Enea to Termales, 15.3 km from La Esperanza; 3,370 m; 04°47′N, 75°22′W.
22	*S. lobbianum*	ca. 48*	C, M	567840	*Castillo et al. 1,211*	Colombia. Caldas: Manizales, 1.5 km E of road going to Nevado del Ruiz, on road from Manizales to Frezno, 4.5 km W of Las Letras; 3,310 m; 05°04′N, 75°19′W.
22	*S. lobbianum*	ca. 48*	C	567841	*Castillo et al. 1,213*	Colombia. Caldas: Manizales, on dirt road from E of Manizales passing La Enea to Termales, 14.5 km from La Esperanza; 3,570 m; 04°49′N, 75°22′W.
22	*S. lobbianum*	ca. 48*	C	567842	*Castillo et al. 1,214*	Colombia. Caldas: Manizales, on dirt road from E of Manizales passing La Enea to Termales, 15.3 km from La Esperanza; 3,570 m; 04°49′N, 75°22′W.
23	*S. colombianum*	48	C, M	498156	*López et al. CCC 5,158*	Colombia. Quindío: Salento, at km 20 on road from Salento to Toche (Tolima); 3,250 m; 04°55′N, 75°50′W.
23	*S. colombianum*		M	566750	*López et al. CCC 5,157*	Colombia. Quindío: Calacará, at La Línea on road to Río El Campana; 3,250 m; 04°04′N, 75°10′W.
23	*S. colombianum*	ca. 48*	C, M	567827	*Castillo et al. 1,202*	Colombia. Quindío: Armenia, above town of Calacará at La Línea, road to TV antennas at 3.5 km from deviation from road to Armenia; 3,150 m; 04°28′N, 75°35′W.
23	*S. colombianum*	ca. 48*	C	567828	*Castillo et al. 1,203*	Colombia. Quindío: Armenia, on dirt road to antennas (El Campanario), just S of La Línea, 4.4 km S on road to Armenia; 3,390 m; 04°28′N, 75°35′W.
23	*S. colombianum*	ca. 48*	C, M	567829	*Castillo et al. 1,204*	Colombia. Quindío: Armenia, on dirt road to antennas (El Campanario), just S of La Línea, 5.1 km S of road to Armenia; 3,460 m; 04°27′N, 75°35′W.
23	*S. colombianum*	ca. 48*	C, M	567830	*Castillo et al. 1,210*	Colombia. Quindío: Salento, on road from Salento to Toche, ascending E side of Cordillera Central, 200 m up hill from road, at Finca La Nevada; 3,200 m; 04°34′N, 75°31′W.
24	*S. colombianum*		C		*López et al. CCC 5,217*	Colombia. El Valle: La Florida, at km 42 on road La Florida to Herrera (Tolima); 3,200 m; 03°21′N, 76°10′W.
24	*S. colombianum*	ca. 48*	C, M	583312	*López et al. CCC 5,218*	Colombia. El Valle: Palmira, at km 47.5 on road from Palmira to Ataco (Tolima); 3,000 m; 03°20′N, 76°15′W.
24	*S. colombianum*	48	M	473407	*Hjerting 5,962*	Colombia. Tolima: El Campanario, on road towards El Campanario, between Tolima and Quindío Departments; 3,500 m; 04°04′N, 76°10′W.
24	*S. colombianum*		M	566749	*López et al. CCC 5,216*	Colombia. El Valle: Florida, at La Diana, 33 km from Florida to Herrera; 2,600 m; 03°21′N, 76°10′W.
24	*S. colombianum*	ca. 48*	C, M	570614	*Castillo et al. 1,260*	Colombia. El Valle: La Florida, 27 km from La Florida to Herrera Tolima, passing through Diana, at Monserrate in La Ermita; 2,610 m; 03°21′N, 76°10′W.
24	*S. colombianum*	ca. 48*	C	570615	*Castillo et al. 1,263*	Colombia. El Valle: La Florida, at Páramo de Cerro Pelado, 46.6 km from Florida to Laguna Los Micos, on new road to Herrera (Tolima); 3,505 m; 03°20′N, 76°05′W.
24	*S. colombianum*	ca. 48*	C, M	570616	*Castillo et al. 1,264*	Colombia. El Valle: La Florida, 48 km from La Florida to Herrera (Tolima), in Páramo Cerro Pelado, near Laguna Los Micos; 3,610 m; 03°21′N, 76°04′W.

APPENDIX 1. Continued

Map[1]	Taxa	2n[2]	Study[3]	PI[4]	Collector	Locality
24	*S. moscopanum*	ca. 72*	C, M	570633	*Castillo et al. 1,262*	Colombia. El Valle: La Florida, at Páramo of Cerro Pelado near Laguna Los Micos, 46.6 km from La Florida to Laguna Las Tinajas on new road to Herrera (Tolima); 3,505 m; 03°20′N, 76°05′W.
24	*S. moscopanum*	ca. 72*	M	570634	*Castillo et al. 1,265*	Colombia. El Valle: La Florida, at Páramo Cerro Pelado, 49 km from La Florida along a new road to Errera (Tolima); 3,600 m; 03°21′N, 76°05′W.
25	*S. colombianum*		C, M	584485	*Castillo et al. 1,259*	Colombia. Cauca: Gabriel López, 11.2 km from Gabriel López to Inzá deviation on road from Totoró to La Plata; 3,270 m, 02°30 N, 76°12 W.
25	*S. colombianum*	ca. 48*	C		*López and Cano CCC 5,014*	Colombia. Cauca: San Sebastián, at Corregimiento de Santiago, on road to Santa Rosa, at km 123 from El Bordo (Patía); 2,880 m; 01°45′N, 76°50′W.
25	*S. colombianum*	ca. 48*	C		*López et al. CCC 5,212b*	Colombia. Cauca: Totoró, at La Sabana, near San Pedro, at Elieser Vera's farm; 3,000 m; 02°40′N, 76°34′W.
25	*S. colombianum*		C, M	583319	*López et al. CCC 5,284*	Colombia. Cauca: Silva, at Las Cruses in farm of Samuel Tambá; 3,005 m; 02°54′N, 76°50′W.
25	*S. colombianum*	48	M	498154	*López et al CCC 5,211*	Colombia. Cauca: Inzá, at Los Alpes, 59 km from Inzá to Popayán; 2,900 m; 02°03′N, 75°34′W.
25	*S. colombianum*	ca. 48*	C	570613	*Castillo et al. 1,248*	Colombia. Cauca: Puracé, 25 km from Puracé on road to La Plata, 200 m to San Rafael waterfall; 3,290 m; 02°22′N, 76°23′W.
25	*S. moscopanum*	72	C, M	498155	*López et al. CCC 5,212*	Colombia. Cauca: Totoró, 15 km from Totoró to Gabriel López, at San Pedro; 3,200 m; 02°35′N, 76°25′W.
25	*S. moscopanum*	72	M	498159	*López et al. CCC 5,203*	Colombia. Cauca: Coconuco, at Paletará Valley, ca. 1 km upwards of Río Negro; 2,950 m; 02°24′N, 76°27′W.
25	*S. moscopanum*	72	M	498160	*López et al. CCC 5,204*	Colombia. Cauca: Puracé, at Pilimbalá Recreational Area, 80 m from swimming pools; 3,400 m; 02°24′N, 76°27′W.
25	*S. moscopanum*	72	M	498162	*López et al. CCC 5,207*	Colombia. Cauca: Puracé, 300 m after Bedón waterfall; 3,200 m; 02°24′N, 76°27′W.
25	*S. moscopanum*	ca. 72*	C, M	567843	*Castillo et al. 1,243*	Colombia. Cauca: Popayán, at km 45.6 from Popayán to Paletará; 2,990 m; 02°14′N, 76°29′W.
25	*S. moscopanum*	ca. 72*	C	567844	*Castillo et al. 1,256*	Colombia. Cauca: San Pedro, at La Sabana, 1 km S of San Pedro, 38.9 km north of deviation of Panamerican Highway to Totoró, on road to Gabriel López; 3,200 m; 02°31′N, 76°17′W.
25	*S. moscopanum*	ca. 72*	C	570626	*Castillo et al. 1,244*	Colombia. Cauca: Popayán, at cabaña San Rafael of Instituto Nacional de Recursos Naturales (INDERENA), 20 km from Puracé on road to La Plata; 3,390 m; 02°23′N, 76°23′W.
25	*S. moscopanum*	ca. 72*	C, M	570628	*Castillo et al. 1,247*	Colombia. Cauca: Popayán, at 25.6 km from Puracé to La Plata, 200 m from St. Rafael waterfall; 3,290 m; 02°22′N, 76°23′W.
25	*S. moscopanum*	ca. 72*	C, M	570629	*Castillo et al. 1,249*	Colombia. Cauca: Popayán, 27 km from Puracé on road to La Plata, collected by museum of Instituto Nacional de Recursos Naturales (INDERENA); 3,210 m; 02°21′N, 76°23′W.

APPENDIX 1. Continued

Map[1]	Taxa	2n[2]	Study[3]	PI[4]	Collector	Locality
25	*S. moscopanum*	ca. 72*	C, M	570631	*Castillo et al. 1,257*	Colombia. Cauca: 8 km NE of Gabriel López, on road to Inzá and La Plata from Totoró; 3,290 m; 02°30′N, 76°13′W.
25	*S. moscopanum*	ca. 72*	C, M	570632	*Castillo et al. 1,258*	Colombia. Cauca: 10.8 km NE of Gabriel López to Inzá on road to Totoró to La Plata; 3,280 m; 02°30′N, 76°12′W.
26	*S. colombianum*	ca. 48*	C		*López 09*	Colombia. Huila: El Totoró, 20.5 km from Arcadia to Vereda Agua Negra, at Ventanas farm; 2,340 m; 02°21′N, 75°20′W.
26	*S. colombianum*	ca. 48*	C	570617	*Castillo et al. 1,266*	Colombia. Huila: Algeciras, 28 km from Algeciras to Caquetá, along road side; 2,480 m; 02°29′N, 75°10′W.
27	*S. colombianum*	ca. 48*	C	567833	*Castillo et al. 1,254*	Colombia. Cauca: Valencia, at Impala, near Río Sucubún at Aurelio Cruz's farm, ca. 9 km by air from Valencia (in Valle de las Papas); 3,000 m; 01°50′N, 76°30′W.
27	*S. colombianum*	ca. 48*	C, M	583322	*López 10*	Colombia. Cauca: Valencia, at San Sebastián, 107 km from Rosas to Valencia, at Vereda Valencia-Cusiyacu; 3,080 m; 01°55′N, 76°38′W.
27	*S. colombianum*	ca. 48*	C, M		*López 13*	Colombia. Cauca: Valencia, near Río Sucubún, 6 km from Valencia to La Guada; 2,965 m; 01°54′N, 76°38′W.
27	*S. moscopanum*	ca. 72*	C, M	570630	*Castillo et al. 1,250*	Colombia. Cauca: Rosas, km 94.5 from Rosas to Valencia, 50 m E from roadside; 3,355 m; 01°58′N, 76°42 W.
27	*S. sucubunense*	ca. 72*	C		*López 12*	Colombia. Cauca: Valencia, near Río Sucubún, 6 km from Valencia to La Nevada in La Guada; 2,960 m; 01°54′N, 76°38′W.
27	*S. sucubunense*	ca. 72*	C, M	583320	*Castillo et al. 1,255*	Colombia. Cauca: Valencia, at Impala, 300 m from Río Sucubún, about 9 km SE from Valencia in Valle de la Papas; 2,959 m; 01°50′N, 76°31′W.
27	*Solanum* unknown taxa c	24*	C	583324	*Papamija* and *López 16*	Colombia. Huila: San Agustín, 4 hours by horse from Valencia to San Agustín, towards Laguna La Magdalena, at Santa Martha; 2,400 m; 01°55′N, 76°50′W.
28	*S. colombianum*	ca. 48*	C	583318	*López et al. CCC 5,279*	Colombia. Huila: Isnos, El Marmol, at Finca Chupallal de Pericoz; 2,900 m; 01°50′N, 76°45′W.
28	*S. colombianum*	ca. 48*	C		*López et al. CCC 5,280*	Colombia. Huila: Isnos, El Marmol, at Finca Chupallal de Pericoz; 3,000 m; 01°50′N, 76°45′W.
29	*S. colombianum*	48	C, M	320346	*Hawkes 2,544*	Colombia. Nariño: El Encano, 28 km from Pasto on road to Santiago at Santa María; 3,050 m; 01°25′N, 77°07′W.
29	*S. colombianum*	48	C, M	498151	*López et al. CCC 5,143*	Colombia. Nariño: El Encano, at km 32 on road from Pasto to Sibundoy; 3,050 m; 01°10′N, 77°08′W.
29	*S. colombianum*	48	M	498149	*López et al. CCC 5,139*	Colombia. Nariño: Tongua, at La Marqueza, near to Cocha Negra, then dirt road at km 15 from road Pasto to Ipiales; 3,400 m; 01°06′N, 77°24′W.
29	*S. colombianum*	48	M	498152	*López et al. CCC 5,145*	Colombia. Nariño: Pasto, at km 14 on road from Pasto to Buesaco; 2,800 m; 01°13′N, 77°17′W.
29	*S. flahaultii*		C		*López et al. CCC 5,192*	Colombia. Nariño: Pasto, at km 12 on road from Pasto to Buesaco; 3,000 m; 01°35′N, 77°20′W.

APPENDIX 1. Continued

Map[1]	Taxa	2n[2]	Study[3]	PI[4]	Collector	Locality
29	*S. tuquerrense*	48	C, M	338614	*Hawkes 2,547*	Colombia. Nariño: Tuquerres, 30 km from Tuquerres, on road from Pasto to Ipiales, at Finca Chautalán; 01°05′N, 77°37′W.
29	*S. tuquerrense*	48	M	498177	*López et al. CCC 5,126*	Colombia. Nariño: Cumbal, at El Tambillo at Llano Grande Farm; 3,350 m; 00°54′N, 77°47′W.
29	*S. tuquerrense*	ca. 48*	C	583310	*López et al. CCC 5,179*	Colombia. Nariño: Cumbal, at Vereda Tambillo in Llano Grande, farm of Billy Bert; 3,380 m; 00°58′N, 77°45′W.
29	*S. tuquerrense*	ca. 48*	C	590926	*López et al. CCC 5,180*	Colombia. Nariño: Cumbal, at Vereda Tambillo in Llano Grande, farm of Billy Bert; 3,280 m; 00°58′N, 77°45′W.
30	*S. colombianum*	48	M	498150	*López et al. CCC 5,141*	Colombia. Putumayo: Sibundoy, at Motilón Cristal place; 2,550 m; 01°12′N, 76°55′W.
30	*S. colombianum*	ca. 48*	C		*López 14*	Colombia. Putumayo: Santiago, 0.8 km from the border of Nariño and Putumayo, to Santiago; 3,100 m; 01°08′N, 77°24′W.
31	*S. colombianum*		C	583309	*López and Cano CCC 4,939*	Colombia. Nariño: La Victoria, on road to La Estrella, 6 km from La Victoria; 2,540 m; 00°52′N, 77°51′W.
31	*S. colombianum*	ca. 48*	C	583308	*López et al. CCC 4,524*	Colombia. Nariño: Ipiales, at km 23 on road to La Victoria; 2,800 m; 00°58′N, 77°50′W.
Col	*S. colombianum*	48	C, M	310983	*Erwin Baur Sortiment 2,179*	Colombia.
32	*S. tuquerrense*	ca. 48*	C	583300	*Spooner et al. 5,098*	Ecuador. Carchi: Tulcán, SW side of dirt road, 7.1 km S of junction of roads to Tulcán and Rumichaca; 3,260 m; 00°44′N, 77°43′W.
32	*S. tuquerrense*	ca. 48*	C	567849	*Spooner et al. 5,100*	Ecuador. Carchi: Tulcán, at Hacienda Troya, 5.8 km E of road from Tulcán to Ibarra; 3,230 m; 00°44′N, 77°41′W.
33	*S. tuquerrense*	ca. 48*	C		*Spooner et al. 5,003*	Ecuador. Imbabura: Cotacachi, at Cotacachi-Cayapas National Park, 7.5 km N from main entrance, on W side of dirt road at base of cliff; 3,870 m; 00°20′N, 78°20′W.
33	*S. tuquerrense*	ca. 48*	C, M	561646	*Spooner et al. 5,111*	Ecuador. Imbabura: Ibarra, at Curiquingue, 17 km from main road from Ibarra-Tulcán to El Olivo, following road to Yuracruz; 3,450 m; 00°20′N, 78°04′W.
34	*S. colombianum*		C		*Spooner et al. 5,128*	Ecuador. Napo: Papallacta, a transplanted plant originally from farm of Cumbal family, 4 hr horse ride W of Baeza, 15.6 km from Papallacta on road to Baeza; 2,500 m; 00°06′N, 78°40′W.
34	*S. colombianum*	ca. 48*	C, M	561625	*Spooner et al. 5,004*	Ecuador. Pichincha: Cayambe, by trail on W end of Laguna San Marcos, near S end of lake; 3,450 m; 00°06′N, 77°58′W.
34	*S. colombianum*	ca. 48*	C, M	561627	*Spooner et al. 5,006*	Ecuador. Pichincha: Cayambe, by road at S end of Laguna San Marcos; 3,450 m; 00°08′N, 77°58 W.
34	*S. colombianum*	ca. 48*	C, M	561633	*Spooner et al. 5,025*	Ecuador. Pichincha: Quito, 15.5 km W of Lloa, in Quebrada La Palma, on N side road; 2,720 m; 00°12′S, 78°38′W.
34	*S. colombianum*	ca. 48*	C, M	561657	*Spooner et al. 5,119*	Ecuador. Napo: Papallacta, along old Quito-Baeza road, 4.9 km E of statue of Virgin; 3,720 m; 00°06′S, 78°40′W.
34	*S. colombianum*	ca. 48*	C, M	567837	*Spooner et al. 5,120*	Ecuador. Napo: Papallacta, along old Quito-Baeza road, 7.4 km E of statue of Virgin at crest of sierra; 3,520 m; 00°06′S, 78°40′W.

APPENDIX 1. Continued

Map[1]	Taxa	2n[2]	Study[3]	PI[4]	Collector	Locality
34	*S. moscopanum*	ca. 72*	C, M	561626	*Spooner et al. 5,005*	Ecuador. Pichincha: Cayambe, 4.1 km W of guardhouse at S end of Laguna San Marcos; 3,680 m; 00°07′N, 77°58′W.
34	*S. paucijugum*	ca. 48*	C, M	583303	*Spooner et al. 5,096a*	Ecuador. Cotopaxi: Cotopaxi National Park, 1.3 km E of center of fenced deer enclosure at Estación Boliche; 3,630 m; 00°36′S, 78°38′W.
34	*S. paucijugum*	ca. 48*	C, M	583299	*Spooner et al. 5,096b*	Ecuador. Cotopaxi: Cotopaxi National Park, 1.3 km E of center of fenced in deer enclosure at Estación Boliche; 3,630 m; 00°36′S, 78°38′W.
34	*S. paucijugum*	ca. 48*	C, M	561644	*Spooner et al. 5,094*	Ecuador. Cotopaxi: Cotopaxi National Park, on N side of park road, 0.8 km E of northern most park control station; 3,460 m; 00°36′S, 78°40′W.
34	*S. tuquerrense*	ca. 48*	C, M	561645	*Spooner et al. 5,097*	Ecuador. Cotopaxi: Cotopaxi National Park, at km 6, ca. 200 m N of Río Daule on park road to Mariscal Sucre; 3,350 m; 00°40′S, 78°39′W.
34	*S. paucijugum*	ca. 48*	C, M	561650	*Spooner et al. 5,129*	Ecuador. Cotopaxi: Cotopaxi National Park, 10.5 km E of Proyecto Llamas Station on road to Refugio Cotopaxi, 0.4 km W of Centro Administrativo Mariscal Sucre; 3,610 m; 00°39′S, 78°30′W.
34	*S. tuquerrense*	ca. 48*	C	584483	*Spooner et al. 5,019*	Ecuador. Pichincha: Quito, at Mount Pichincha, on road to antennas, on W side of Quito; 3,870 m; 00°10′S, 78°32′W.
34	*S. tuquerrense*	ca. 48*	M	561631	*Spooner et al. 5,022*	Ecuador. Pichincha: Quito, at Mount Pichincha, on road to antennas, on W side of Quito; 3,670 m; 00°10′S, 78°32′W.
34	*S. tuquerrense*	ca. 48*	C, M	561632	*Spooner et al. 5,023*	Ecuador. Pichincha: Quito, at Mount Pichincha, on road to antennas, on W side of Quito, about antenna cluster; 3,870 m; 00°10′S, 78°32′W.
34	*S. tuquerrense*	ca. 48*	C, M	561647	*Spooner et al. 5,118*	Ecuador. Pichincha: Baeza, along Quito-Baeza road, 7.2 km W of statue of Virgin; 3,660 m; 00°17′S, 78°14′W.
35	*S. colombianum*	ca. 48*	C		*Spooner et al. 5,089*	Ecuador. Cotopaxi: Pilaló, 8.5 km from gasoline station at N end of Pilaló on road to La Maná; 3,000 m; 00°57′S, 79°00 W.
35	*S. colombianum*	ca. 48*	C, M	561652	*Spooner et al. 5,135*	Ecuador. Tungurahua: Baños, 1 km S on new road to Runtún; 3,200 m; 01°26′S, 78°25′W.
35	*S. tuquerrense*	ca. 48*	C, M	561628	*Spooner et al. 5,007*	Ecuador. Cotopaxi: Cotopaxi National Park, 5.3 km from its entrance, ca. 60 m E of road; 3,450 m; 00°39′S, 78°49′W.
36	*S. albicans*	72	C	561642	*Spooner et al. 5,070*	Ecuador. Chimborazo: Palmira, at Estación Moyocancha of Chimborazo University, 11.4 km E of Tixán-Palmira road; 3,750 m; 02°09′S, 78°43′W.
36	*S. andreanum*	24*	C		*Spooner et al. 5,156*	Ecuador. Morona Santiago: San Vicente, ca. 5 km W of San Vicente, on old footpath on S side of Río Upano; 2,450 m; 02°12′S, 78°23′W.
36	*S. colombianum*	ca. 48*	C, M	567835	*Spooner et al. 5,083*	Ecuador. Tungurahua: Baños, just E of Quebrada Mandur, in farm of Silva family, on NW slopes of Volcán Tungurahua, at escuela Constancio Vigil; 2,900 m; 01°26′S, 78°28′W.
36	*S. minutifoliolum*	24[2a]	C	583298	*Spooner et al. 5,080*	Ecuador. Tungurahua: Baños; 0.5–1.5 km S of end of new road from Baños to Runtún; 2,850 m; 01°26′S, 78°25′W.

APPENDIX 1. Continued

Map[1]	Taxa	2n[2]	Study[3]	PI[4]	Collector	Locality
36	*S. colombianum*	ca. 72*	C		*Spooner et al. 5,147*	Ecuador. Chimborazo: Laguna Negra, on N end of Laguna Negra, by dirt road; 3,410 m; 02°10′S, 78°30′W.
36	*S. moscopanum*	ca. 72*	C	567824	*Spooner et al. 5,144*	Ecuador. Chimborazo: Saguán, in Quebrada Chullubamba, on E side of Saguán in area of Alfapamba, 14 km S of Chunchi; 3,000 m; 02°21′S, 78°52′W.
36	*S. paucijugum*	ca. 48*	C		*Spooner et al. 5,149*	Ecuador. Chimborazo: Guamote, 42 km from Guamote to Atillo; 3,510 m; 02°06′S, 78°30′W.
36	*S. paucijugum*	ca. 48*	C		*Spooner et al. 5,150*	Ecuador. Chimborazo: Guamote, 42 km from Guamote to Atillo; 3,510 m; 02°06′S, 78°30′W.
36	*S. paucijugum*	ca. 48*	C, M	561643	*Spooner et al. 5,084*	Ecuador. Chimborazo: Sicalpa, in Quebrada Camal, on N side of road from Sicalpa-Pallatanga, 13.2 km SW of Sicalpa road junction with road to Ocpote; 3,770 m; 01°44′S, 78°48′W.
36	*S. paucijugum*	ca. 48*	C, M	561651	*Spooner et al. 5,130*	Ecuador. Tungurahua: Ambato, 30.5 km SE of Ambato on road to Guaranda, at Tamboloma; 3,580 m; 01°18′S, 78°46′W.
36	*S. paucijugum*	ca. 48*	C, M	561654	*Spooner et al. 5,151*	Ecuador. Chimborazo: Guamote, 36 km from Guamote to Atillo; 3,600 m; 02°05′S, 78°37′W.
36	*S. paucijugum*	ca. 48*	C, M	567846	*Spooner et al. 5,071*	Ecuador. Chimborazo: San Juan, 10.5 km of San Juan, on road to Guaranda by Loma Tililog, on S side of road; 3,725 m; 01°38′S, 78°50′W.
36	*S. solisii*	48	C, M	473472	*Ochoa 10,990*	Ecuador. Tungurahua: at Río Yanyahua.
36	*S. tundalomense*	48	C, M	473471	*Ochoa 10,986*	Ecuador. Tungurahua.
36	*S. tuquerrense*	48	C, M	246971	*Correll E. 437*	Ecuador. Chimborazo: 13 km from San Juan towards Guaranda; 01°37′S, 79°00′W.
36	*Solanum* unknown taxa d	24*	C	567823	*Spooner et al. 5,078*	Ecuador. Chimborazo: San Isidro de Yungilla, 4.4 km N of San Isidro, on dirt road E of Río Chimbo; 2,740 m; 01°49′S, 78°50′W.
37	*S. chilliasense*	24[2a]	C	567821	*Spooner et al. 5,057*	Ecuador. El Oro: Chilla, on Cordillera de Chilla, 1 km S of transmission tower on top of Cerro Sharayunta; 3,275 m; 03°29′S, 79°35 W.
37	*S. moscopanum*	ca. 72*	C, M	561653	*Spooner et al. 5,140*	Ecuador. Cañar: Juncal, in Quebrada Talanquera just S of Cerro Torre, N of San Antonio; 3,500 m; 02°28′S, 78°56′W.
37	*S. moscopanum*	ca. 72*	C, M	561659	*Spooner et al. 5,139*	Ecuador. Cañar: Carshau, on Cerro Carshau, 500 m NE on road to antennas in Quebrada Guallicanga, 8 km N of main Cañar-Guayaquil road; 3,480 m; 02°28 S, 78°57 W.
37	*S. moscopanum*	ca. 72*	C	567838	*Spooner et al. 5,143*	Ecuador. Cañar: Aguarongo, S of Quebrada Aguarongo, ca. 300 m E of railroad tracks, at km 44, N of Hacienda El Carmen, by old road from Chunchi to Tambo; 3,200 m; 02°25′S, 78°58′W.
38	*S. colombianum*	ca. 48*	C	590923	*Spooner et al. 5,050*	Ecuador. Azuay: Cumbe, At Chorro Blanco on E side of road Cuenca to Loja, 18 km S of road junction to Loja and Girón; 3,235 m; 03°09′S, 79°01′W.
38	*S. colombianum*	ca. 48*	C		*Spooner et al. 5,081*	Ecuador. Tungurahua: Baños, on path to Chontal, ca. 5 km by air SW of Baños; 2,959 m; 01°26′S, 78°26′W.

APPENDIX 1. Continued

Map[1]	Taxa	2n[2]	Study[3]	PI[4]	Collector	Locality
38	*S. colombianum*		M	561640	*Spooner et al. 5,062*	Ecuador. Cañar: Cañar, at hacienda Cocha Huma, 200–400 m W of dirt road, on hill E side of flat bog called Cocha Huma; 3,410 m; 02°32′S, 78°47′W.
38	*S. colombianum*	ca. 48*	C, M	561641	*Spooner et al. 5,063*	Ecuador. Cañar: Cañar, at Hacienda Cocha Huma, 200–400 m W of dirt road, on hill E side of flat bog called Cocha Huma; 3,410 m; 02°32′S, 78°47′W.
38	*S. colombianum*	ca. 48*	C	567834	*Spooner et al. 5,047*	Ecuador. Azuay: Cumbe, 31.2 km S of junction of roads to Girón and Cuenca at Estación Cumbe, on road Cuenca to Loja; 3,270 m; 03°15′S, 79°03′W.
38	*S. moscopanum*	ca. 72*	C, M	567812	*Spooner et al. 5,040*	Ecuador. Loja: Loja, on Loja-Zamora road, ca. 500 m SE from crest of hill at Loja-Zamora Provinces boundary, 2,750 m; 03°59′S, 79°09′W.
38	*S. tundalomense*	72	C, M	473474	*Ochoa 11,004*	Ecuador. Azuay: at Portete de Tarqui.
38	*S. tundalomense*	72	C	473476	*Ochoa 11,009*	Ecuador. Azuay: at Portete de Tarqui.
38	*S. chomatophilum*		C		*Spooner et al. 5,053*	Ecuador. Azuay: Cumbe, on E side of old road from Cuenca-Loja, 1 km S of La Jarata, 64 km S of road junction to Loja-Girón Estación Cumbe, km 56 marker; 3,335 m; 03°19′S, 79°06′W.
Ecu	*S. moscopanum*	72	C, M	230517	*Ochoa 2,104*	Ecuador.
Ecu	*S. suffrutescens*	24[2a]	C		*Ochoa 13,375*	Ecuador.
Ecu	*S. tundalomense*	72	M	473475	*Ochoa 11,080*	Ecuador.
39	*S. chomatophilum*	24	C, M	310991	*Hawkes 2,492*	Peru. Amazonas: Chachapoyas, at Cerro de Leimebamba.
39	*S. chomatophilum*	24	M	473460	*Ochoa 11,061*	Peru. Amazonas: Cuatra Cuello.
40	*S. chomatophilum*	24	C, M	243340	*Ochoa 1,512*	Peru. Cajamarca: Cajamarca.
40	*S. chomatophilum*	24	C, M	266387	*Correll P. 862*	Peru. Cajamarca: Cajamarca, near entrance to Hacienda Porcon; 3,535 m; 06°10′S, 78°20′W.
40	*S. chomatophilum*	24	C, M	310943	*Ugent 5,416*	Peru. Cajamarca: Cajamarca, at Hacienda Porcon; 3,535 m; 06°10′S, 78°20′W.
40	*S. chomatophilum*	24	M	310990	*Hawkes 2,433*	Peru. Cajamarca: Cajamarca, at Hacienda Porcon; 3,000 m.
40	*S. irosinum*	24[2a]	M	583305	*Ochoa 15,210*	Peru. Cajamarca.
40	*S. irosinum*	24[2a]	C, M	568985	*Ochoa 11,646*	Peru. Cajamarca.
41	*S. buesii*	24[2a]	C, M	568922	*Ochoa 13,629*	Peru. Cuzco.
41	*S. santolallae*	24	C, M	195168	*Commonwealth Potato Collection Genebank 2,078.2*	Peru. Cuzco: Paucartambo, at Pillahuata; 13°20′S, 71°30′W.
41	*S. santolallae*	24	C, M	473372	*Hawkes 5103*	Peru. Cuzco: Paucartambo, at Pillahuata; 2,200 m; 13°08′S, 71°25′W.
41	*S. urubambae*	24[2a]	C		*Ochoa 13,780*	Peru. Cuzco: Urubamba.
42	*S. limbaniense*	24	C, M	473468	*Ochoa 5,123*	Peru. Puno: 3,520 m.
Per	*S. chomatophilum*	24	M	243341	*Ochoa 1,664*	Peru.
Per	*S. cotumazaense*	24	C, M	365329	*Ochoa S-90*	Peru.
Per	*S. cajamarquense*[5]		C	310988	*Hawkes 2,436*	Peru. Cajamarca: Chiquiden, on highway from Cajamarca to Chiclayo.
Per	*S. laxissimum*	24	C, M	283088	*Erwin Baur. Sortiment 1,888*	Peru.

APPENDIX 1. Continued

Map[1]	Taxa	2n[2]	Study[3]	PI[4]	Collector	Locality
Per	*S. santolallae*	24	C		*Ochoa 13,640*	Peru.
43	*S. violaceimarmoratum*	24	C, M	258856	*Gandarillas s.n.*	Bolivia. La Paz: Unduavi.
43	*S. violaceimarmoratum*	24	M	498314	*Zavaleta 1,579*	Bolivia. La Paz: Unduavi, 10 km from Unduavi to Coroico; 2,730 m; 16°10′S, 67°44′W.
43	*S. violaceimarmoratum*	24	M	473397	*Hawkes et al. 5,040*	Bolivia. La Paz: Yungas, 6 km from Unduavi to Coroico; 3,275 m; 16°19′S, 67°50′W.
43	*S. violaceimarmoratum*	24	M	473398	*Hawkes et al. 5,042*	Bolivia. La Paz: Yungas, 10 km from Unduavi to Coroico; 3,225 m; 16°19′S, 67°54′W.
43	*S. violaceimarmoratum*	24	C, M	498296	*Ochoa 11,901*	Bolivia. La Paz: Saavedra, at Caspichaca, 5 km before Chullina, between Mataro and Chullina; 3,500 m.
44	*S. violaceimarmoratum*	24	C, M	473395	*Hawkes et al. 4,436*	Bolivia. Cochabamba: Chapare, at km 104 on road from Cochabamba to Chapare and Villa Tunari, just 20 m before a hotel; 3,025 m; 19°14′S, 64°27′W.
44	*S. violaceimarmoratum*	24	C, M	473396	*Hawkes et al. 4,474*	Bolivia. Cochabamba: Chapare, at km 100 on road from Cochabamba to Tunari, by roadside; 3,150 m; 19°14′S, 64°27′W.
Bol	*S. laxissimum*	24	C, M	498252	*Ochoa 11,855*	Bolivia.

[1]Generalized map areas, see Figs. 1–3; those collections with vague locality data are listed after known localities from that country. [2]Sporophytic chromosome numbers; those with asterisk are counts first reported here; with [2a]are reported in Ochoa 1992c; others are reported in Bamberg et al. (1996). [3]C = accession used in the cpDNA study, M = accession used in the morphological study. [4]United States Department of Agriculture Plant Introduction (PI) Numbers, those with missing numbers are recent collections with PI numbers not yet assigned. [5]The accession of *S. cajamarquense* used here is an artificial interspecific hybrid made at NRSP-6 between *S. cajamarquense* as the maternal parent, and *S. contumazaense* PI 365329 as the paternal parent.