# Reexamination of Series Relationships of Mexican and Central American Wild Potatoes (Solanum sect. Petota): Evidence from Chloroplast DNA Restriction Site Variation

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ABSTRACT. Chloroplast DNA restriction analysis has been used to test the series classifications of the Mexican and Central American representatives of *Solanum* sect. *Petota* of Rydberg, Bukasov, Hawkes, and Correll. Three clades are supported: 1. all species in series *Morelliformia*, *Pinnatisecta*, and *Polyadenia* exclusive of *S. bulbocastanum* and *S. cardiophyllum*. Subclades within clade 1 include *S. trifidum* and *S. tarnii*; *S.* × *michoacanum* and *S. pinnatisectum*; *S. brachistotrichum* and *S. stenophyllidium*; *S. clarum* and *S. morelliforme*; and series *Polyadenia*; 2. *S. bulbocastanum* and *S. cardiophyllum*; 3. *S. verrucosum* (a Mexican diploid), the Mexican polyploid species, and the South American species. Within clade 3, series *Conicibaccata* forms a well-defined subclade, whereas *S. verrucosum*, series *Longipedicellata*, series *Demissa*, and the South American species form another. In reference to the latest classification of Hawkes, series *Conicibaccata* and *Polyadenia* are supported as monophyletic; the Mexican diploids are paraphyletic; and series *Demissa*, *Longipedicellata*, and *S. verrucosum* (series *Tuberosa*) form one monophyletic assemblage. Species within series *Longipedicellata* and *Demissa* are polyploid, possibly of hybrid origin, and may need less conservative markers or biparentally-inherited probes to distinguish them. These molecular results are compared to the diverse data sets that have led to this classification.

*Solanum* sect. *Petota* Dumort., the potato and its wild relatives, traditionally has been considered to be taxonomically difficult, and conflicting taxonomic interpretations of species boundaries and series relationships are common. The group contains much morphological and physiological variability. An earlier taxonomic interpretation of the group (Correll 1962) recognized 157 species, while the latest (Hawkes 1990) recognizes 232 species.

Bitter (1912) was the first to describe series in *Solanum* sect. *Petota* (series *Conicibaccata* and *Maglia*), although he failed to designate series affiliations for many species. Rydberg (1924) divided the Mexican and Central American potatoes into five informal groups (Bulbocastana, Juglandifolia, Oxycarpa, Pinnatisecta, Tuberosa) but failed to designate rank. Hawkes (1944) validated these names as series (except Oxycarpa = series *Conicibaccata*) and described series *Cuneoalata*. Since that time, 25 additional series have been validly published: series *Megistacroloba* (Cárdenas and Hawkes 1945); *Trifida* (Correll 1950); *Cardiophylla*, *Polyadenia* (Correll 1952); *Circaeifolia*, *Piurana* (Hawkes 1954); *Morelliformia*

(Hawkes 1956a); *Acaulia*, *Andigena*, *Commersoniana*, *Demissa*, *Etuberosa*, *Longipedicellata*, *Vaviloviana* (Bukasov and Kameraz 1959); *Ingifolia* (Ochoa 1962); *Clara*, *Minutifoliola*, *Tarijensa*, *Yungasensa* (Correll 1962); *Olmosiana* (Ochoa 1965); *Lignicaulia* (Hawkes 1989); *Bukasoviana*, *Chomatophylla*, *Pyriformia*, *Simpliciora* (Gorbatenko 1989). Gorbatenko (1989) published series *Lignicaulia* as a later homonym. The date of publication on Gorbatenko (1989) is ambiguous, because the latest date listed on the volume is August 9, after the words (transliterated) "Podpisano v petsat" = signed off for printing. This was not the publication date, however, which was 21 Sep 1989 (letter from Gorbatenko to Hawkes). Hawkes (1989) was released on 29 Aug 1989. The following names have been treated as series but invalidly published: Looseriana (Bukasov 1939); Andreana (Hawkes 1944); Glabrescentia, Transaequatorialia (Bukasov and Kameraz 1959); Borealia (Correll 1962); Alticola, Berthaultiana, Chilotana, Cisaequatorialia, Collina, Subacaulia, and Verrucosa (Bukasov 1978).

Figure 1 provides a chronological flow chart detailing the hypotheses of species boundaries

and series affiliations of the Mexican and Central American species by Rydberg (1924), Bukasov (1939, 1978), Hawkes (1944, 1963, 1966, 1978, 1990), Correll (1952, 1962), and Flores Crespo (1966). This study reinvestigates these alternative hypotheses using chloroplast DNA (cpDNA). The resulting cpDNA cladograms are compared to characters that have been used in the past to address questions of series affiliations. This study is an extension of a cpDNA study (using 22 accessions of 20 species) of these species that examined genome relationships within the group (Spooner et al. 1991a). The prior study provided partial support for a hypothesis by Hawkes (1990) concerning the origin of Solanum sect. Petota in Mexico and Central America (as a B genome) with later migrations and evolution to an A genome in South America. These events were later followed by a return migration of A genome species to Mexico and Central America with A × B hybridizations and polyploidy to produce species in series Longipedicellata (4x) and Demissa (6x).

## MATERIALS AND METHODS

*Plants.* Seeds of 48 accessions of 35 species of Solanum sect. Petota (table 1), representing all eight Mexican and Central American series, and four of the 13 South American series, were obtained from the Inter-Regional Potato Introduction Project (IR-1) in Sturgeon Bay, Wisconsin (Hanneman and Bamberg 1986). Six of these series are confined to Mexico and Central America: series Bulbocastana, Morelliformia, Pinnatisecta, Polyadenia, Longipedicellata, and Demissa, whereas two, Conicibaccata and Tuberosa, are represented both in this region and in South America (table 1). The first four series are diploid ($2n = 24$), series Longipedicellata is tetraploid ($2n = 48$), series Demissa is hexaploid ($2n = 72$), series Conicibaccata is diploid, tetraploid, and hexaploid, and series Tuberosa is diploid, tetraploid, and hexaploid (including the tetraploid cultigen, S. tuberosum L.). In addition, some series contain triploid and pentaploid cytotypes (Hawkes 1990). Solanum brevidens Philippi, a species of series Etuberosa native to the Andes of Argentina and Chile, was used as the outgroup. Although the outgroup relationships of Solanum sect. Petota are not fully resolved, Hawkes (1990) includes S. brevidens in sect. Petota but in a distinct subsection (subsect. Estolonifera Hawkes) separated from all of the other species here examined (subsect. Potatoe G. Don). Additionally, Hosaka et al. (1984) and Spooner et al. (1990) provided a cpDNA cladistic analysis that indicated the outgroup status of series Etuberosa. Identifications used are those provided in Hanneman and Bamberg (1986), which are based on many years of on-site determinations of living accessions at the Inter-Regional Potato Introduction Station by Donovan Correll, Jack Hawkes, J. Peter Hjerting, Carlos Ochoa, Katsuo Okada, and Donald Ugent (Spooner and Bamberg 1991); vouchers are deposited at the Inter-Regional Potato Introduction Station.

*DNA Isolation and Restriction-Site Comparison.* Pooled leaf samples of one to eight plants per accession were collected from two-month old plants for DNA extraction. Preparations of total DNA were made from five gm of fresh leaf tissue using the procedure of Doyle and Doyle (1987) and purified over CsCl/ethidium bromide gradients. Restriction endonuclease digestions, agarose-gel electrophoresis, bidirectional transfer of DNA fragments from agarose gels to nylon filters, labelling of recombinant probes by nick translation, filter hybridization, and autoradiography were conducted following the methods of Palmer (1986). Twenty-two endonucleases were used to examine cpDNA variation in Solanum (table 2). Membranes were probed with 12 Pst I and two Sal I clones that represent nearly the entire chloroplast genome of Petunia A. L. Juss. (Sytsma and Gottlieb 1986). Five clones of Nicotiana L. were used to represent the small single-copy region between the inverted repeats (courtesy of J. Palmer and R. Olmstead).

*Data Analysis.* Solanum brevidens was used as the outgroup. Restriction site data were analyzed using Wagner parsimony, which weights equally site gains and site losses, using PAUP (version 3.0r, D. Swofford, Illinois Natural History Survey, Urbana). The equally most parsimonious trees were sought by heuristic searching using the options COLLAPSE, TBR (tree bisection-reconnection) branch swapping, and MULPARS. A consensus tree was constructed of equally-parsimonious Wagner trees. Character-state changes were placed on trees using the accelerated transformation method (ACCTRAN). Additionally, the character-state weighting method of Albert et al. (1992) was used with weights of 1.1 and 1.3. The COLLAPSE and

| Rydberg 1924 | Bukasov 1939 | Hawkes 1944 | Correll 1952 | Correll 1962 Crespo 1966 | Hawkes 1963, 66, 78 | Bukasov 1978 | Hawkes 1990 |

Row labels (left): BUL, MOR, CLA, TRI, CAR, PIN, POL, CON, TUB, LON, DEM, VRR, BRL, UNK
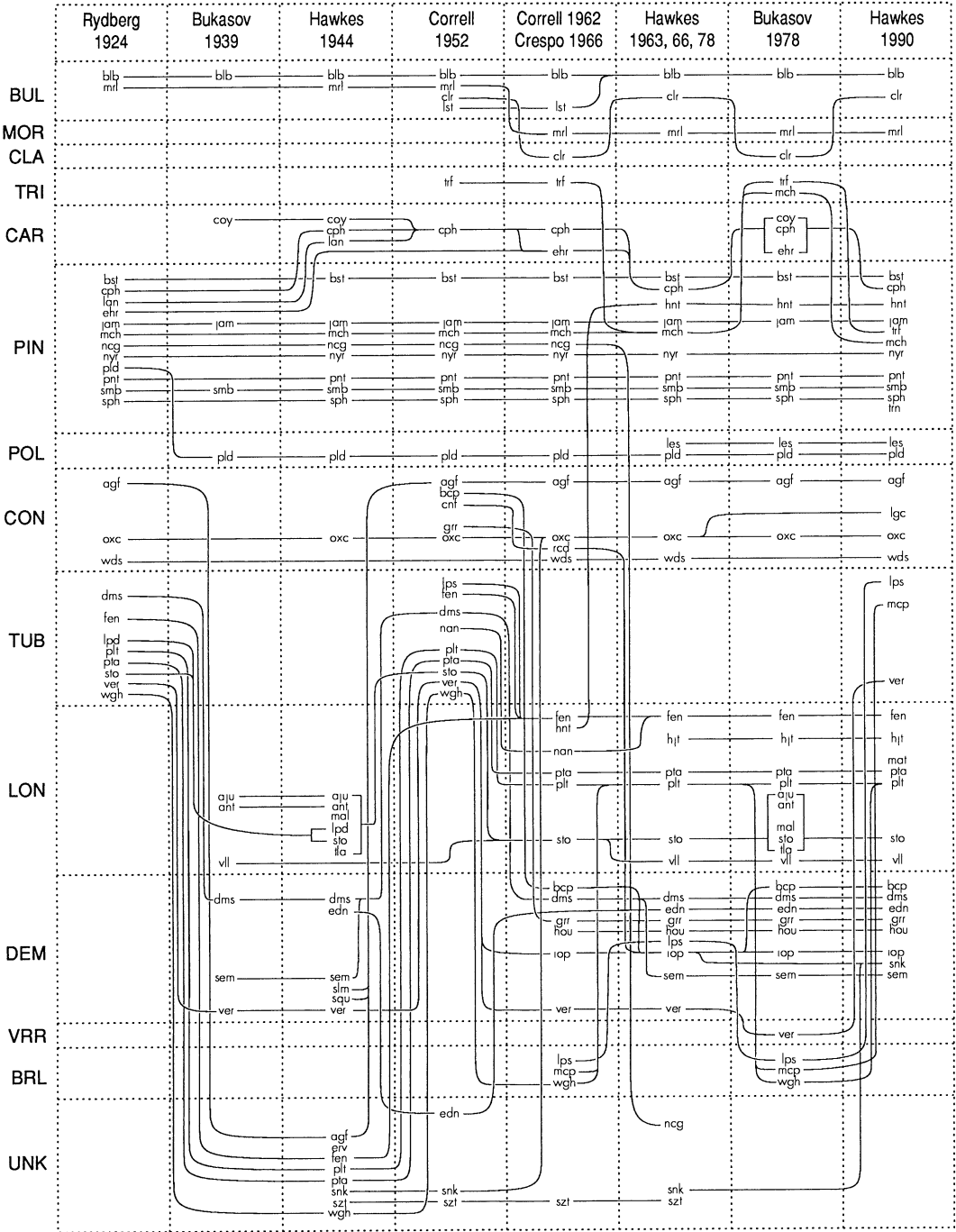
FIG. 1. Chronological flow chart of hypotheses of series relationships of the Mexican and Central American species of *Solanum* sect. *Petota* according to Rydberg (1924), Bukasov (1939, 1978), Hawkes (1944, 1963, 1966, 1978, 1990), Correll (1952, 1962), and Flores Crespo (1966). Subspecies, varieties, and uncontested synonyms are not listed. The following standardized abbreviations follow Hawkes (1990), Huamán and Ross (1985), and Simmonds (1963), except for the abbreviations preceeded by an asterisk, which are first designated here: agf *S. agrimonifolium*, aju *S. ajuscoense* Buk., ant *S. antipoviczii* Buk., bcp *S. brachycarpum*, blb *S. bulbocastanum*, *BRL

MULPARS options were used with either TBR or nearest neighbor interchanges (NNI) branch swapping routines. Additional trees and character placements were examined using Mac-Clade (version 2.97c, W. & D. Maddison). Because of the large size of this data set, the generation of bootstrap confidence values (Felsenstein 1985) was not feasible, but the confidence values of some of these clades in a reduced data set are available in Spooner et al. (1991a).

## RESULTS

This study involved 26 accessions of 15 additional species (table 1), and 22 additional mutations (table 2) than examined in an earlier study (Spooner et al. 1991a). Of a total of 131 site mutations (table 3), 88 occurred in more than one accession and, thus, were phylogenetically informative. Wagner parsimony produced 2017 collapsed, equally-parsimonious, 152-step trees with a consistency index of 0.862/0.807, with/without autapomorphies. One randomly-chosen tree is depicted in figure 2 (as a phylogram), with unique mutations, homoplastic losses, and homoplastic gains indicated along each branch. Of the 21 convergent character-state changes required in the depicted tree (fig. 2), 14 (67%) involve more likely homoplastic losses (including gain/losses) and seven (33%) involve less likely homoplastic gains (including loss/gains). Of the latter, three of the seven involve convergences with the outgroup. A strict consensus tree of these 2017 trees is depicted in figure 3.

The character-state weighting method (1.3 weight), using the COLLAPSE and MULPARS options along with the more "global" TBR branch swapping routine, generated 32 equally-parsimonious trees after nearly 100 hours of computation time on a MacIIsi. Branch swapping, however, was not completed on most trees when the run was intentionally terminated. To facilitate more rapid analysis, these 32 trees were used as starting trees with the nearest-neighbor interchanges (NNI) branch swapping option. This character-state weighted analysis ran to completion and resulted in 48 equally-parsimonious trees. These 48 trees were then used as starting trees in a second analysis with a character state of 1.1. The NNI branch swapping option generated the same 48 trees as found with the 1.3 character-state weighting analysis. These 48 trees represent a subset of the 2017 most-parsimonious Wagner trees. A strict consensus tree of these 48 trees, however, differs only slightly from the Wagner strict consensus tree (See fig. 3) and only in or near the terminal clades.

Both consensus trees provide support for three main clades for the Mexican and Central American species (series designations fide Hawkes 1990):

CLADE 1. All of the Mexican diploid species in series *Morelliformia, Pinnatisecta,* and *Polyadenia,* exclusive of *S. bulbocastanum* Dun. in Poir. and *S. cardiophyllum* Lindl.

CLADE 2. *Solanum bulbocastanum* (series *Bulbocastana*) and *S. cardiophyllum* (series *Pinnatisecta*).

CLADE 3. *Solanum verrucosum* Schldl. (a dip-

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series Borealia (an invalidly published name treated as a series by Correll 1962) Correll, bst *S. brachistotrichum* (Bitter) Rydb., BUL series *Bulbocastana,* CAR series *Cardiophylla* Correll, *CLA series *Clara* Correll, clr *S. clarum,* cnf *S. confusum* Correll, CON series *Conicibaccata,* coy *S. coyoacanum* Buk., cph *S. cardiophyllum* Lindley, DEM series *Demissa,* dms *S. demissum* Lindley, edn *S.* × *edinense* Berth., ehr *S. ehrenbergii* (Bitter) Rydb., *erv *S. ervendbergii* Rydb., fen *S. fendleri,* grr *S. guerreroense,* hjt *S. hjertingii,* hnt *S. hintonii* Correll, hou *S. hougasii,* iop *S. iopetalum,* jam *S. jamesii,* lan *S. lanciforme* Rydb., les *S. lesteri* Hawkes and Hjert., lgc *S. longiconicum* Bitter, LON series *Longipedicellata,* lpd *S. longipedicellatum* Bitter, lps *S. leptosepalum* Correll, lst *S. longistylum* Correll, mal *S. malinchense* Hawkes, mat *S. matehuale* Hjert. and Tarn, mch *S.* × *michoacanum,* mcp *S. macropilosum* Correll, *mon *S. montoperanthum* Bitter, MOR series *Morelliformia* Hawkes, mrl *S. morelliforme* Hawkes, nan *S. nannodes* Correll, ncg *S. nicaraguense* Rydb., nyr *S. nayaritense* Bitter, oxc *S. oxycarpum* Schiede, PIN series *Pinnatisecta,* pld *S. polyadenium,* plt *S. polytrichon,* POL series *Polyadenia,* pnt *S. pinnatisectum,* pta *S. papita* Rydb., rcd *S. reconditum* Correll, sem *S. semidemissum* Juz., slm *S. salamanii* Hawkes, smb *S.* × *sambucinum* Rydb., snk *S. schenckii* Bitter, sph *S. stenophyllidium,* squ *S. squamulosum* M. Martens and Galeotti, sto *S. stoloniferum,* szt *S. schizostigma* Bitter, tla *S. tlaxcalense* Hawkes, *TRI series *Trifida* Correll, trf *S. trifidum,* trn *S. tarnii* Hawkes and Hjert., TUB series *Tuberosa* (Rydb.) Hawkes, UNK Series unknown, vav *S. vavilovii* Juz. and Buk., ver *S. verrucosum* Schldl., vll *S.* × *vallis-mexici* Juz., *VRR series *Verrucosa* Buk., wds *S. woodsonii* Correll, wgh *S. wightianum* Rydb.

TABLE 1.   Additional *Solanum* sect. *Petota* accessions assessed for cpDNA variation. See Spooner et al. (1991a) for the 22 previously-examined populations. Duplicate accessions within species examined in Spooner et al. (1991c) (not listed here), are designated as accessions 1, 2 or 3. [1]USDA Plant Introduction Numbers (see Hanneman and Bamberg 1986). [2,3]*Spooner et al. 4217; Spooner et al. 4078* (see Spooner et al. 1991c, for these collections; PI numbers not yet assigned).

| Series/species | PI[1] | 2n |
|---|---|---|
| series *Conicibaccata* Bitter | | |
| 1. *S. agrimonifolium* Rydb. 2 | 243350 | 48 |
| 2. *S. agrimonifolium* 3 | 243349 | 48 |
| 3. *S. oxycarpum* Schiede | 230479 | 48 |
| series *Demissa* Buk. | | |
| 4. *S. brachycarpum* Correll | 230459 | 72 |
| 5. *S. guerreroense* Correll 1 | 161727 | 72 |
| 6. *S. guerreroense* Correll 2 | 161730 | 72 |
| 7. *S. hougasii* Correll 1 | 161174 | 72 |
| 8. *S. hougasii* Correll 2 | 161726 | 72 |
| 9. *S. iopetalum* (Bitter) Hawkes | 275181 | 72 |
| series *Longipedicellata* Buk. | | |
| 10. *S. fendleri* A. Gray 2 | 275163 | 48 |
| 11. *S. hjertingii* Hawkes | 186559 | 48 |
| 12. *S. polytrichon* Rydb. | 255522 | 48 |
| 13. *S. stoloniferum* Schldl. and Bouché | 186544 | 48 |
| series *Bulbocastana* (Rydb.) Hawkes | | |
| 14. *S. clarum* Correll 1 | SHGF 4217[2] | 24 |
| 15. *S. clarum* 2 | 283099 | 24 |
| series *Pinnatisecta* (Rydb.) Hawkes | | |
| 16. *S. cardiophyllum* Lindley 1 | 347759 | 24 |
| 17. *S. cardiophyllum* 2 | 545734 | 24 |
| 18. *S. jamesii* Torrey 1 | 275168 | 24 |
| 19. *S. jamesii* 2 | 458424 | 24 |
| 20. *S.* × *michoacanum* (Bitter) Rydb. | SHG 4078[3] | X |
| 21. *S. pinnatisectum* Dunal 2 | 347766 | 24 |
| 22. *S. stenophyllidium* Bitter | 518629 | 24 |
| 23. *S. trifidum* Correll | 255536 | 24 |
| series *Polyadenia* | | |
| 24. *S. lesteri* Hawkes and Hjert. | 442694 | 24 |
| 25. *S. polyadenium* Greenman 2 | 347769 | 24 |
| 26. *S. polyadenium* 3 | 161728 | 24 |

loid species of series *Tuberosa*), the Mexican polyploid species (series *Longipedicellata*, series *Demissa*), series *Conicibaccata* (Mexican, Central

and South American diploids, tetraploids, and hexaploids) and the South American species.

## DISCUSSION

An earlier study using some of these accessions (Spooner et al. 1991a) focused on the implications of cpDNA restriction site data for hypotheses of genome divergence. The present study added 26 additional accessions of important Mexican and Central American species (table 1) to address questions of series affiliations in the group. All Mexican and Central American species, covering all eight series from this region that were available from the Inter-Regional Potato Introduction Project (Hanneman and Bamberg 1986) were used, supplemented by *S.* × *michoacanum* (Bitter) Rydb., collected on a recent germplasm collecting expedition to Mexico (Spooner et al. 1991c). Twenty-seven of the 32 Mexican and Central American species (excluding putative hybrids) recognized by Hawkes (1990) were analyzed in the present study. Not analyzed were *S. hintonii* Correll, *S. leptosepalum* Correll, *S. longiconicum* Bitter, *S. macropilosum* Correll, and *S. matehuale* Hjert. & T. R. Tarn, which were unavailable from the Inter-Regional Potato Introduction Project. The following systematic insights are provided:

*CLADE 1,* Solanum trifidum, S. tarnii. *Solanum trifidum* Correll is a distinctive species. Correll (1950, 1952) segregated it into monotypic series *Trifida* on the basis of its three-parted leaves and winged petioles and related it to *S. bulbocastanum* (series *Bulbocastana*) because of the dull appearance and texture of leaves of the latter. Hawkes (1956a) transferred *S. trifidum* to series *Pinnatisecta* without comment. When the species was described, its fruits were unknown, but later collections showed them to be long-conical, unlike all of the other then known members of series *Pinnatisecta* (with round fruits). Correll (1962) interpreted this elongated fruit shape "definitely" to exclude *S. trifidum* from series *Pinnatisecta* and suggested a relationship with series *Conicibaccata*, characterized by conical fruits. *Solanum hintonii* (series *Pinnatisecta* fide Hawkes 1963, 1966, 1978, 1990) recently also was found to possess conical fruits (Spooner et al. 1991c), and conical fruits also are known in other series (see discussion under series *Conicibaccata* below). The present analysis clearly indicates that conical fruits are convergent in *Solanum* sect. *Petota*.

TABLE 2. Newly reported chloroplast DNA restriction site mutations within *Solanum* sect. *Petota*. See Spooner et al. (1991a) for previously-examined mutations (1–109) and enzymes used. Mutations 110–130 are unique to the new accessions examined here. See table 3 for the complete data matrix. Mutation 131 is shared with *S. polyadenium* (PI 347770) of our previous study. The mutations are listed with the apomorphic state first, followed by the pleisiomorphic state (relative to *S. brevidens*). Parentheses indicate where small fragments were not seen but were hypothesized to exist because length mutations were not seen with other enzymes. [1] Species numbers from table 1.

| No. | Enzyme | Region | Size (Kb) | Species[1] |
|-----|--------|--------|-----------|------------|
| 110 | *Bgl* II | P6 | 2.4 + 1.6 = 4.0 | 18 |
| 111 | *Cla* I | P8 | 3.7 = 2.6 + 1.1 | 12 |
| 112 | *Cla* I | P18/P19 | 1.2 + (0.5) = 1.7 | 7 |
| 113 | *Cla* I | P6 | 7.3 + 1.6 = 8.9 | 24 |
| 114 | *Dra* I | P3 | 3.3 + 2.5 = 5.8 | 15 |
| 115 | *Dra* I | P10 | 4.6 + 3.0 = 7.6 | 23 |
| 116 | *Dra* I | P10 | 1.5 + 1.5 = 3.0 | 17 |
| 117 | *Eco* RI | P18/P19 | 2.0 = 1.4 + 0.6 | 14 |
| 118 | *Eco* RI | P3 | 1.8 + (0.4) = 2.2 | 21 |
| 119 | *Eco* RI | P6 | 3.4 + 0.8 = 4.2 | 2 |
| 120 | *Eco* RV | P8/P10 | 4.9 + 2.8 = 7.7 | 25 |
| 121 | *Eco* RV | T39/T40 | 2.4 + 0.1 = 2.5 | 24 |
| 122 | *Eco* O 109 | P10 | 6.3 + 4.9 = 11.2 | 16, 17 |
| 123 | *Hinc* II | P10 | 1.8 + 1.0 = 2.8 | 16, 17 |
| 124 | *Hinc* II | P10 | 2.4 = 1.9 + 0.6 | 2 |
| 125 | *Hinc* II | T38/T39/T40 | 2.2 = 1.6 + 0.6 | 16, 17 |
| 126 | *Hind* III | P10 | 3.0 = 1.9 + 1.1 | 14 |
| 127 | *Hind* III | P10 | 3.6 = 2.5 + 1.1 | 23 |
| 128 | *Hpa* II | T38/T39 | 1.7 + 1.5 = 3.2 | 17 |
| 129 | *Hph* I | P16/S6 | 1.0 + 0.7 = 1.7 | 16, 17 |
| 130 | *Hph* I | P10 | 3.0 + 3.0 = 6.0 | 16 |
| 131 | — | P16/S6 | 300 bp deletion | 24–26 |

*Solanum tarnii* Hawkes and Hjert. (with round fruits) was placed by Hawkes et al. (1988) in series *Pinnatisecta*. They recognized the morphological similarity of *S. tarnii* to *S. trifidum*, but made no definite statement of series affiliations. Both species are found on or near the trans-volcanic belt of Mexico, with *S. trifidum* restricted to the west in the states of Michoacán and Jalisco and *S. tarnii* to the east in the states of Hidalgo, Queretaro and Veracruz. The single cpDNA mutation that unites them (fig. 2) suggests they are sister taxa.

**Solanum jamesii, S. × michoacanum, S. nayaritense, S. pinnatisectum.** *Solanum × michoacanum* (as *S. michoacanum*) was initially considered related to *S. jamesii* Torr. or *S. nayaritense* Bitter (Bitter 1913; Correll 1952; Rydberg 1924). *Solanum pinnatisectum* Dunal and *S. jamesii* are the only two species in sect. *Petota* that possess pinnatifid pseudostipular leaflets, suggesting their close relationship. This is further indicated by the shared presence of three coumarins

in *S. pinnatisectum*, *S. jamesii*, and *S. sambucinum* Rydb., a putative hybrid between *S. pinnatisectum* and *S. cardiophyllum* (Harborne 1960; Hawkes 1990). The relationship of *S. jamesii*, *S. × michoacanum*, *S. nayaritense*, and *S. pinnatisectum* is supported in this analysis by a single cpDNA mutation in some of the Wagner trees (fig. 2).

Correll (1962) noted artificial hybrids between *S. bulbocastanum* and *S. pinnatisectum* (Graham et al. 1959; Magoon et al. 1958; Swaminathan 1955) that matched the morphology of *S. × michoacanum* and suggested that this latter species was of natural hybrid origin between the two. Hawkes (1963) made no mention of this hypothesis and synonymized *S. trifidum* under *S. michoacanum*, but later (Hawkes 1978) recognized *S. trifidum* as a distinct species. Bukasov (1978) grouped *S. michoacanum* and *S. trifidum* under series *Trifida*. Hawkes (1990) accepted Correll's hybridization hypothesis. Recently, Spooner et al. (1991c) have used molecular markers that failed to support the diploid hy-

TABLE 3.   Data matrix of 131 restriction site mutations for all 48 accessions. The states 0, 1, and 9 represent site absence, site presence, and missing data, respectively.

*S. bulbocastanum* 1

00010111101001100100110110110000001000100001000000111000101101011000000000111
0100010100011101000111101011010101000001000000011110000

*S. bulbocastanum* 2

00010111101001100100110110110000001000100001000000111000101101011000100000111
0100010100011101000111101011010101000001000000011110000

*S. clarum* 1

00110110110011100001010000010001001100190011100000010010101000011000010111011
00000101100110001001110010011000010010010000000111110000

*S. clarum* 2

00110110110011100001010000010001001100190011100000010010101000011000010111011
00000101100110001101110010011000010000000000000011010000

*S. morelliforme* 1

00110111110011100001010000010011000100110101000010000010101000010000010111011
00000111100110001101110010011000010000010000000011910000

*S. morelliforme* 2

00110110110011100000010000010001001100190011100000010010101000011000110111011
00000101100110001001110010011000010000010000000111110000

*S. brachistotrichum*

00110111110011100001010000010000001000110001000000001011010100001100000101110011
00000101100110001101110010011001010000010000000111110000

*S. jamesii* 1

00110111110011100001010000010000001000110001000000010010101000011000010111011
00000101100110001101010010011001010000100000000111110000

*S. jamesii* 2

00110111110011100001010000010000001000100010000000100101010000011000010111011
00000101100110001101010010011001110000010000000111110000

*S.* × *michoacanum*

00110111110011100001010000010000101000110001000000010010101000011000010111011
00000101100110001101010010011001010000100000000111110000

*S. nayaritense*

00110111110011100001010000010000001000110001000000100101010000110000101110111
00000101100110001101010010011001010000010000000111110000

*S. pinnatisectum* 1

0011011111100110000010100000100001010001100010000000010019101000011000010111011
00000101100110001101010010011001010000010000000111110000

*S. pinnatisectum* 2

00110111110011100001010000010000101000110001000000010010101000011000010111011
00000101100110001101010010011001010000011000000111110000

*S. stenophyllidium*

00110111110011100001010000010000001000110001000000010110101000011000010111011
00000101100110001101110010011001010000010000000111110000

*S. cardiophyllum* 1

00110111101011100100010010110000001000100001000000100010100101011000000010111
0100010100011101010111101011010101000001000011110110110

TABLE 3.   Continued.

*S. cardiophyllum* 2
00110111101011100100010010110000001000100001000000100010100101011000000010111
0100010100011101010111101011010101000011000011110111100

*S. trifidum*
00110111110011100001010000010000001000110001000000010011101000011000010111011
00000101100110001101110010011001010001010000001100000

*S. tarnii*
00110111110011100011010000010000001000110001000000010011101000011000010111011
00000101100110001101110010011001010000010000011110000

*S. lesteri*
00110111110011100001011000010100001000010001010000001001011100001100001011010
0001010111011010110110001001100101010001000100011110001

*S. polyadenium* 1
00110111110011100001011000010100001000010001010000010010111000011000010111010
0001010111011010110110001001100101000001000000111110001

*S. polyadenium* 2
00110111110011100001011000010100001000010001010000010010111000011000010111010
0001010111011010110110001001100101000001000000111110001

*S. polyadenium* 3
00110111110011100001011000010100001000010001010000010010111000011000010111010
0001010111011010110110001001100101000001001000111110001

*S. agrimonifolium* 1
01111101000001100100010010110000001011110000000100110011101111111100000010101
0110100000110101011011110101001001000001000000111110000

*S. agrimonifolium* 2
01111101000001100100010010110000001010110000000100110011101111111100000010101
0110100000110101011011110101001001000001010000111110000

*S. agrimonifolium* 3
01111101900001100100010010110000001010110000000100110011101111011100000010101
0110100000110101011011110101001001000001000000001110000

*S. colombianum*
01101101900001100100010010110000001011110000000100110011101111011100000010101
0110100000110101011011110101001001000001000000111110000

*S. oxycarpum*
01111101900001100100010010110000001010100000000100100011101111011100000010101
0110100000110101011011110101001001000001000000111110000

*S. chomatophilum*
00111111900011100100010011110000001010110010000001100110001110111010000010101
011001010000191010100111110000011010000010000000111110000

*S. stoloniferum*
00111101100011100100010010110000001010110000000000110011101111011100000010101
011000000000101010100111110010010010000010000000111110000

*S. fendleri* 1
00111111110001110010001001010000001010100000001000100011101111011100000010101
011000000000010101001111100100100100000010000000111110000

TABLE 3.   Continued.

*S. fendleri* 2

  0011111110001110010001001010000000101010000000100010001110111101110000010101
  0110000000000101010011111001001001000001000000111110000

*S. papita*

ı 0011111110001110010001001010000000101010000000100010001110111101110000010101
  0110000000000101010011111001001001000001000000111110000

*S. polytrichon*

  0011111110001110010001001010000000101010000000100010001110111101110000010101
  0110000000001010101001111100100100000000100000011110000

*S.hjertingii*

  0011111110001110010001001010000000101010000000100010001110111101110000010101
  0110000000000101010011111001001001000001000000111110000

*S. iopetalum*

  0011111110001110010001001010000000101010000000100010001110111101110000010101
  0110000000000101010011111001001001000001000000111110000

*S. guerreroense* 1

  0011111110001110010001001010000000101010000000100010001110111101110000010101
  0110000000000101010011111001001001000001000000111110000

*S. guerreroense* 2

  0011111110001110010001001010000000101010000000100010001110111101110000010101
  0110000000000101010011111001001001000001000000111110000

*S. hougasii* 1

  0011111110001110010001001010000000101010000000100010001110111101110000010101
  0110000000000101010011111001001001000001000000111110000

*S. hougasii* 2

  0011111110001110010001001010000000101010000000100010001110111101110000010101
  0110000000000101010011111001001001100001000000111110000

*S. schenckii*

  0011111110001110010001001010000000101010000000100010001110111101110000010101
  0110000000000101010011111001001001000001000000111110000

*S. demissum*

  0011111110001110010001001010000000101010000000100010001110111101110000010101
  0110000000000101010011111001001001000001000000111110000

*S. brachycarpum*

  0011111110001110010001001010000000101010000000100010001110111101110000010101
  0110000000000101010011111001001001000001000000111110000

*S. verrucosum*

  0011111110001110010001001010000000101010000000100010001110111101110000010101
  0110000000000101010011111001001001000001000000111110000

*S. alandiae*

  0011111110001110010001001010000000101010000000100010001110111101110000010101
  0110000000010101010011111001001001000001000000111110000

*S. tuberosum andigena*

  0011110110001110010001001011000000101019000900100011001110111101110000010101
  0110000000010101010011111001001001000001000000111110000

TABLE 3. Continued.

*S. chancayense*

    001110111000111001000100111100000010101900090009000110011101111011100000010101
    011001010001110101001111100100110100000100000011110000

*S. circaeifolium*

    001111111000111001000100101000000010101000000010001000111011111011100000010101
    011000000000101010100111110010010010000010000011110000

*S. brevidens*

    111101111001000011000000101110100110001100090000011100101011011010100010101111
    100001010001110001011110100100010100000100000011110000

bridization hypothesis of *S. raphanifolium* (Ugent 1970), another member of *Solanum* sect. *Petota*. In light of these results, similar molecular tests should be conducted on the *S.* × *michoacanum* hybridization hypothesis, now possible because of the recent acquisition of germplasm of this rare species (Spooner et al. 1991c). The single cpDNA mutation uniting *S.* × *michoacanum* and *S. pinnatisectum* (fig. 2) indicates that if the hybridization hypothesis is correct, *S. pinnatisectum* or a related species would be likely maternal parents.

**Solanum brachistotrichum, S. stenophyllidium.** *Solanum brachistotrichum* (Bitter) Rydb. and *S. stenophyllidium* Bitter share similar sparse, downward-pointing pubescence, and have been suggested to be closely related by Correll (1952, 1962) and Hawkes (1963, 1990). Both species are restricted to Mexico (Correll 1962; Hawkes 1966, 1990) and are allopatric. They are distinguished only by minor differences in shape and size of leaves. The cpDNA evidence is concordant with pubescence in linking these as sister species.

**Solanum clarum, S. morelliforme.** *Solanum clarum* Correll and *S. morelliforme* Hawkes are united in our analysis by three cpDNA mutations. The closest approach any taxonomist has made to suggest their relationship has been Correll (1952), who grouped them (with *S. bulbocastanum*) in series *Bulbocastana*. All three of these species possess entire leaves, rare in sect. *Petota*. Correll (1952) speculated that series *Bulbocastana* was an unnatural group and later (Correll 1962) segregated all of these species into monotypic series (series *Bulbocastana, Clara, Morelliformia*), a classification later followed by Bukasov (1978). Hawkes (1963, 1966, 1978, 1990) united *S. bulbocastanum* and *S. clarum* in series *Bulbocastana* but maintained monotypic series

*Morelliformia*. Hawkes (1990) characterized series *Bulbocastana* by its larger flowers, broader anthers not adhering laterally, and terrestrial habit, in contrast to series *Morelliforme* with smaller flowers, narrower anthers adhering laterally, and an epiphytic habit. Other characters supporting Hawkes's classification are: 1. *Solanum bulbocastanum* and *S. clarum* are self-incompatible; *S. morelliforme* is self-compatible (Hawkes 1958; Marks 1968). 2. *S. bulbocastanum* and *S. clarum* share similar serological reactions (Gell et al. 1960; Hawkes and Lester 1966), different from *S. morelliforme*. Data suggesting alternative relationships to the classification of Hawkes are: 1. Despite all previous statements about the terrestrial habit of *S. clarum* (e.g., Correll 1962; Hawkes 1990) the species in nature grows in moss, in epiphytic-like conditions (Spooner, pers. obs.), and has been collected before as an epiphyte (*Hawkes et al. 1849*, collected as an epiphyte on *Abies*—data from Hawkes's original collection notes). 2. Crossability data have suggested an isolated relationship for both *S. clarum* and *S. morelliforme*, distinct from all other tested species in sect. *Petota*, with *S. bulbocastanum* showing relationships with other Mexican diploid species (Graham and Dionne 1961a). 3. Despite hypotheses of reproductive isolation of *S. clarum*, fertile $F_1$ hybrids have been made between *S. clarum* and *S. morelliforme*, although the hybrids exhibited chromosomal structural differences and sterility in the $F_2$ generation (Marks 1968). 4. Marks (1969) demonstrated by pachytene analysis that *S. clarum* and *S. morelliforme* share characteristically large telochromomeres (although on different chromosomes) unknown in the rest of sect. *Petota*. 5. Both species are morphologically similar vegetatively (Hawkes and Lester
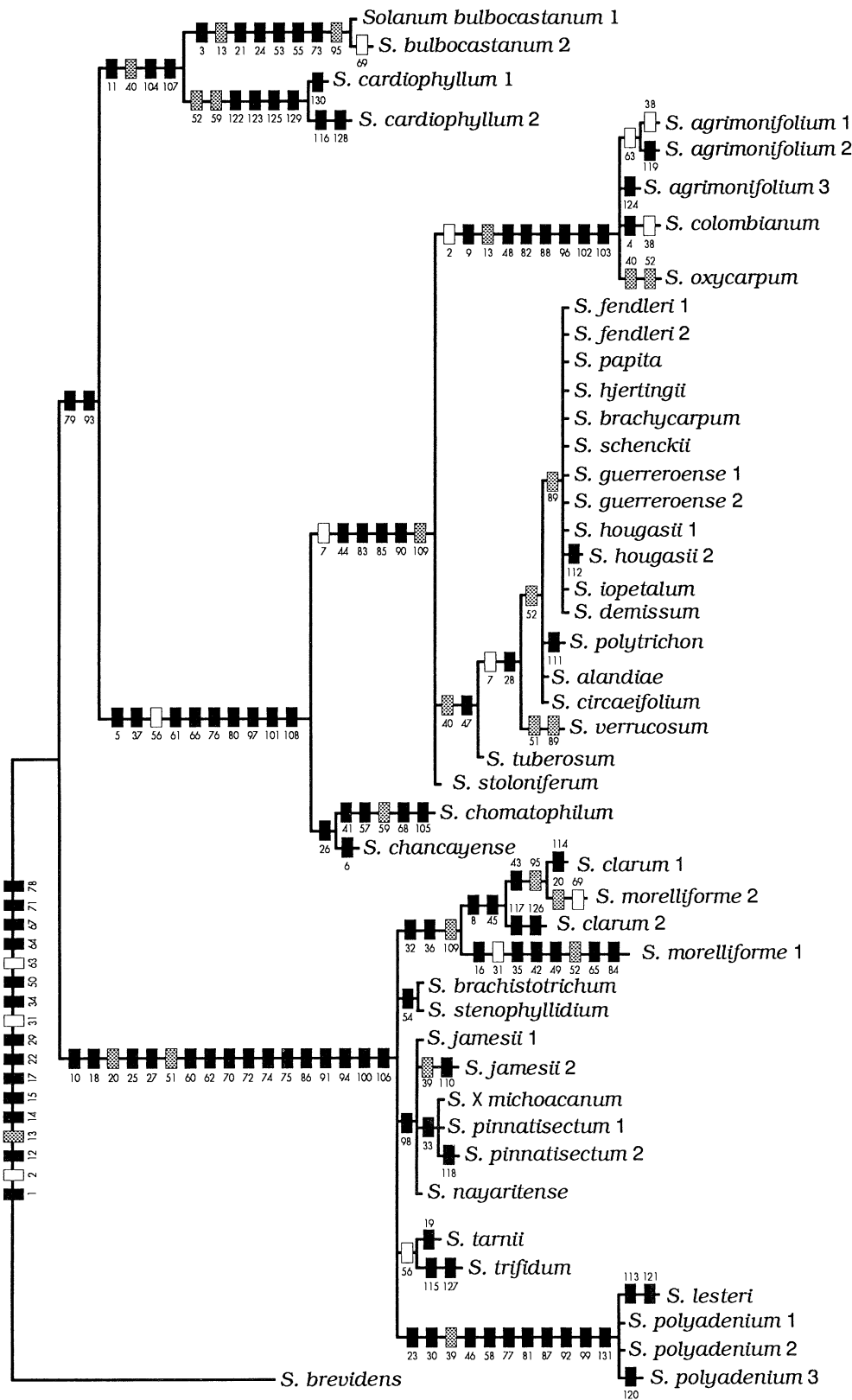
1966) as they both are entire-leaved, low-growing species (less than 0.7 dm) vs. 1 m or more for *S. bulbocastanum*.

Our data indicate that *S. clarum* and *S. morelliforme* are sister taxa, with no relationship with *S. bulbocastanum*. In this regard, the molecular evidence and vegetative morphology, habit, and chromosomal features are concordant, whereas the molecular evidence is discordant with the evidence from serology, flower morphology, and self-compatibility/self-incompatibility. The cpDNA data of the four accessions of these two species fail to resolve them into species-specific clades (fig. 2). This pattern was unexpected, but similar patterns have been demonstrated in other cpDNA studies (Doebley 1989; Doyle et al. 1990; Spooner et al. 1991b). It could be the result of introgression, matriarchal lineage sorting (Neigel and Avise 1986), poorly-understood species relationships, or lack of resolution of the cpDNA tree caused by homoplasy and a small number of synapomorphic characters. This analysis does not address these alternatives.

**Solanum lesteri, S. polyadenium.** *Solanum lesteri* Hawkes and Hjert. and *S. polyadenium* Greenm. are very similar species. Both have a dense indument of short glandular trichomes with a two-cell stalk and a tetralobulate head [Type A glandular trichomes, Gibson (1976)], and both have a characteristic "mousy" odor unique to series *Polyadenia*. This combination of characters is so distinctive that there has been no disagreement of their placement in series *Polyadenia* since Bukasov (1939), although series *Polyadenia* was not validly described until Correll (1952). The 10 restriction site mutations and one deletion mutation make this an extremely well-supported group, concordant with trichome and odor characters.

The relationship of series *Polyadenia* to other series, however, always has been controversial. Gell et al. (1960) used serological data to suggest a relationship of series *Polyadenia* to series *Bulbocastana, Demissa* and *Longipedicellata*, although Hawkes (1990) indicated the data of Gell et al. (1960) for series *Bulbocastana* was in error and series *Bulbocastana* shared serological patterns

with series *Pinnatisecta* and *Cardiophylla*. Hawkes and Lester (1966), using different antisera, reported that although series *Polyadenia* had a distinct serological pattern, it suggested a "link" between series *Bulbocastana, Cardiophylla* and *Pinnatisecta*, or possibly a "link" between series *Demissa, Longipedicellata*, and *Tuberosa*. Hawkes (1958) summarized crossing data between *S. polyadenium* with members of series *Cardiophylla, Pinnatisecta* and *Tuberosa*, proposing possible relationships with these series. Bukasov (1939) related series *Polyadenia* to a large group of species with rotate corollas (informally treated as "Rotata"), while Hawkes (1989) formalized this system taxonomically, but placed series *Polyadenia* in superseries *Stellata*. Spooner et al. (1991a) discounted the monophyly of superseries *Stellata* and *Rotata*. Our cpDNA data indicate that series *Polyadenia* is firmly imbedded within clade 1 and is not a sister species (possibly the concept of "link" of the above authors) to the Mexican polyploids or the South American species, as suggested by Hawkes (1958) and Hawkes and Lester (1966). The molecular data are discordant with results of crossability relationships and serology with respect to the relationships of series *Polyadenia*.

All three accessions of *S. polyadenium* and *S. lesteri* are characterized by a 400 bp deletion in a fragment hybridizing to both our *Petunia* P16 and S6 probes. Because small insertion/deletion mutations are common in cpDNA (Palmer et al. 1985), this mutation (as well as other unique insertion/deletion mutations) was not scored by Spooner et al. (1991a) that used only one accession of *S. polyadenium*. Hosaka et al. (1988) found a 400 bp deletion unique to *S. tuberosum* ssp. *tuberosum*, which is apparently homologous to the B3 fragment of Heinhorst et al. (1988), adjacent to the *rbc*L gene on the *atp* side. The 400 bp deletion of series *Polyadenia* hybridizes to our *Petunia* probes P16 and S6, and is apparently located on the B11a fragment of Heinhorst et al. (1988), adjacent to the *rbc*L gene but on the side opposite the *atp* gene.

*CLADE 2.* **Solanum bulbocastanum, S. cardiophyllum.** The derived nature of *S. cardi-*

←

FIG. 2. One of 2017 equally-parsimonious 152-step Wagner trees (drawn as a phylogram of cpDNA restriction site mutations in *Solanum* sect. *Petota*. Gray and open boxes represent convergent gains or loss/gains and convergent losses or gain/losses, respectively, solid boxes represent unique mutations. Mutations 110–131 are listed in table 2, mutations 1–109 are listed in table 2 of Spooner et al. (1991a).

SERIES

*Solanum bulbocastanum* 1
S. *bulbocastanum* 2 — Bulbocastana

CLADE 2

S. *cardiophyllum* 1
S. *cardiophyllum* 2 — Pinnatisecta

S. *agrimonifolium* 1
S. *agrimonifolium* 2
S. *agrimonifolium* 3
S. *colombianum*
S. *oxycarpum* — Conicibaccata

S. *stoloniferum*

S. *fendleri* 1
S. *fendleri* 2
S. *papita*
S. *hjertingii*
S. *polytrichon* — Longipedicellata

S. *brachycarpum*
S. *schenckii*
S. *guerreroense* 1
S. *guerreroense* 2
S. *hougasii* 1
S. *hougasii* 2
S. *iopetalum*
S. *demissum* — Demissa

CLADE 3

S. *circaeifolium* — Circaeifolia

S. *verrucosum*
S. *alandiae*
S. *tuberosum* — Tuberosa

S. *chancayense*

S. *chomatophilum* — Conicibaccata
S. *clarum* 1 — Bulbocastana
S. *morelliforme* 2 — Morelliformia
S. *clarum* 2 — Bulbocastana
S. *morelliforme* 1 — Morelliformia

S. *brachistotrichum*
S. *stenophyllidium*
S. *jamesii* 1
S. *jamesii* 2
S. X *michoacanum*
S. *pinnatisectum* 1
S. *pinnatisectum* 2 — Pinnatisecta
S. *nayaritense*
S. *tarnii*
S. *trifidum*

CLADE 1

S. *lesteri*
S. *polyadenium* 1
S. *polyadenium* 2 — Polyadenia
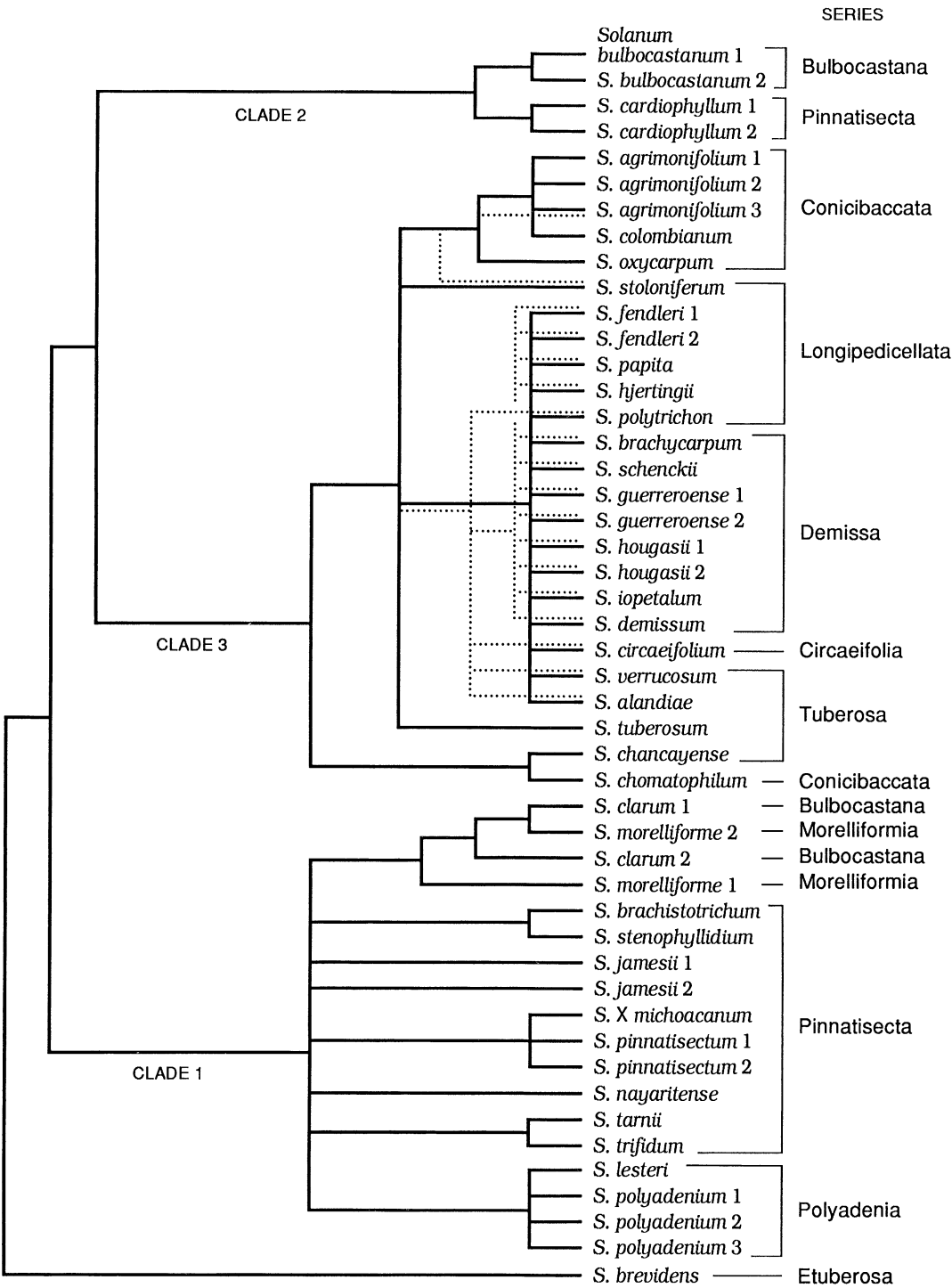S. *polyadenium* 3

S. *brevidens* — Etuberosa

FIG. 3. The strict consensus tree (solid lines) of 2017 equally-parsimonious 152-step Wagner trees. The three major clades, as discussed in the text, are indicated. The strict consensus tree of the 48 equally-parsimonious weighted trees is identical to the Wagner consensus tree, except for the dashed lines.

*ophyllum* was used in an earlier study (Spooner et al. 1991a) to provide partial support for the A, B genome hypothesis and resulting hypotheses of genomic relationships of the origin of series *Longipedicellata* and *Demissa* (Hawkes 1990). No previous classification has united these two species (fig. 1). *Solanum cardiophyllum*, like *S. bulbocastanum* (see *S. clarum, S. morelliforme*, above), is morphologically distinct. It frequently possesses cordate leaves and typically buff-colored flowers. It was segregated in series *Cardiophylla* by Bukasov (1939, 1978), Hawkes (1944, 1956a), and Correll (1952, 1962). Correll (1962) suggested that the series should be combined with series *Pinnatisecta*, a treatment initiated by Rydberg (1924) and later followed by Hawkes (1963, 1978, 1990).

Crossing studies have provided ambiguous insights into the monophyly of the clade comprising *S. bulbocastanum* and *S. cardiophyllum* and their divergence from the other Mexican diploid species in series *Pinnatisecta*. Both species are crossable with members of series *Pinnatisecta* and with each other (Graham and Dionne 1961a, 1961b; Graham et al. 1959; Hawkes 1958; Magoon et al. 1958; Matsubayashi and Misoo 1977; Ramanna and Hermsen 1979; Swaminathan 1955). *Solanum bulbocastanum* has been suggested to be slightly divergent from members of series *Pinnatisecta* on the basis of cytological data from artificial interspecific hybrids with this group (Matsubayashi and Misoo 1977; Ramanna and Hermsen 1979).

The serological and molecular data are in conflict regarding the monophyly of the *Solanum bulbocastanum/S. cardiophyllum* clade. Both Gell et al. [1960, corrected in Hawkes (1990)] and Hawkes and Lester (1966) have interpreted serological data to suggest that series *Bulbocastana, Cardiophylla* and *Pinnatisecta* are equally related.

The monophyly of the *S. bulbocastanum/S. cardiophyllum* clade, and wide divergence of both of them from other Mexican and Central American diploid species, is entirely unexpected on the basis of all prior evidence. The species are vegetatively quite different, *S. bulbocastanum* with entire leaves and *S. cardiophyllum* with pinnately-dissected leaves, and no evident morphological characters unite them. These cpDNA results are discordant with other lines of evidence, and therefore, the relationships indicated here should be tested by other molecular, morphological, and other characters to resolve this conflict.

**CLADE 3. Series Conicibaccata.** Series *Conicibaccata* is defined largely on the basis of its long-conical fruits (Correll 1962; Hawkes 1990), although conical fruits also are found in the Mexican and Central American series *Demissa* [*Solanum guerreroense* Correll, *S. iopetalum* (Bitter) Hawkes, *S. schenckii* Bitter], series *Pinnatisecta* (*S. hintonii, S. trifidum*, and some populations of *S. pinnatisectum*), series *Polyadenia* (*S. lesteri*), as well as South American series *Circaeifolia*, and apparent overlap occurs between the "long-conical" and "conical" fruit types. Both Correll (1962) and Hawkes (1990) relied on geography to help distinguish series *Conicibaccata*. Series *Conicibaccata* and *Tuberosa* (fide Hawkes 1990) are the only two tuber-bearing series that are distributed both north and south of the isthmus of Panama. Hawkes (1990) included 40 species in series *Conicibaccata*, grouping diploids, tetraploids and hexaploids. Three of the species occur in Mexico and Central America; the other 37 occur from Colombia and Venezuela to Bolivia.

Hawkes and Hjerting (1989) relate series *Conicibaccata* to the South American series *Commersoniana* and *Tuberosa*. Hawkes (1990) hypothesized that series *Conicibaccata* evolved from species in South America and that the Mexican and Central American species of this series are northward migrants from the South American representatives of the series. This cpDNA data analysis, including both Mexican and South American representatives of series *Conicibaccata* (all examined species were tetraploids), provides strong support for the monophyly of series *Conicibaccata*, exclusive of *Solanum chomatophilum* Bitter (fig. 3), which Hawkes (1990) repositioned in series *Conicibaccata*, reversing his earlier placement in series *Piurana* (Hawkes 1963). Hawkes (1990) suggested that some of the species he included in series *Conicibaccata* may be misplaced, a possibility that will be tested in further molecular analyses. Conical fruits help characterize series *Conicibaccata*, but are known in other unrelated groups as well (see above). Perhaps there are subtle differences in fruit shapes or other unrecognized morphological characters that have led taxonomists to ally the three examined species of series *Conicibaccata* (exclusive of *S. chomatophilum*). It is possible that conical fruit shape follows different allometric growth patterns in different series and is not a homologous character state, as Donoghue (1988) and Friedman and Donoghue (1988)

have found in *Viburnum* L. Developmental studies of elongate-fruited species representative of different clades in *Solanum* sect. *Petota* may provide a similar example and provide more reliable data useful for cladistic analyses using morphology.

**Series Demissa, series Longipedicellata, Solanum verrucosum.** The greatest disagreement regarding the placement of species has involved these taxa (fig. 1). They generally differ by fruit shape (conical in some species of series *Demissa*, round in all members of series *Longipedicellata* and *S. verrucosum*), corolla acumen length (relatively smaller in series *Demissa* and *S. verrucosum* than in series *Longipedicellata*) and ploidy level ($2n = 6x = 72$ in series *Demissa*, $2n = 4x = 48$ in series *Longipedicellata*, $2n = 2x = 24$ in *S. verrucosum*). Serologically, the taxa are nearly indistinguishable (Gell et al. 1960; Hawkes and Lester 1966). Interspecific crossing relationships may differ between the series. Interspecific hybrids within series *Longipedicellata* exhibit high fertility (Magoon and Cooper 1959), but interspecific hybrids within series *Demissa* exhibit greatly reduced fertility (Hawkes 1956b; Marks 1955). These latter two studies of series *Demissa* lacked intraspecific crossing controls, however, and Marks (1965) demonstrated good fertility in an interspecific cross within series *Demissa*, suggesting that comparative interspecific crossing differences between series *Demissa* and series *Longipedicellata* may need to be reevaluated.

*Solanum verrucosum* is the only Mexican diploid species with crossing relationships with the Mexican polyploid species and the South American species, and it has been suggested to be a parent in the putative hybrid formation of series *Demissa* (Hawkes 1990). Morphologically, *S. verrucosum* is very similar to other members of series *Demissa* and has been related to them by past authors (Bukasov 1939; Correll 1952, 1962; Hawkes 1944, 1956a, 1963; Rydberg 1924; Swaminathan and Hougas 1954). Artificial hybrids are known (Hawkes 1958) and natural hybrids are hypothesized to occur (Marks 1958; Marks and Montelongo-Escobedo 1970) between *S. verrucosum* and members of series *Longipedicellata*. The close morphological similarity and/or ease of crossing relationships of *S. verrucosum*, series *Longipedicellata*, and series *Demissa* are correlated with the almost total lack of cpDNA divergence of these species (fig. 2) and suggests close relationships among them,

perhaps reflective of recent origins. It is also possible that the paternal parents of a possible hybrid origin of series *Longipedicellata* and series *Demissa* are more divergent, but that this cpDNA similarity is a reflection of recency of origin from a common maternal parent(s).

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