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CHLOROPLAST DNA EVIDENCE FOR THE INTERRELATIONSHIPS OF TOMATOES, POTATOES, AND PEPINOS (SOLANACEAE)[1]

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We used chloroplast DNA restriction site analysis to test hypotheses of relationships of *Solanum* subgenus *Potatoe* (including potatoes and pepinos), two other *Solanum, Cyphomandra* (the tree tomatoes), and *Lycopersicon* (the tomatoes). *Capsicum* and *Datura* were used as outgroups. The results support two main clades among the taxa we studied: 1) *Solanum* subgenus *Potatoe* and *Lycopersicon*; and 2) other *Solanum* and *Cyphomandra*. Within the first clade, the following groups were supported: a) sect. *Basarthrum* and sect. *Anarrhichomenum*; b) sect. *Etuberosum*; c) sect. *Petota*; d) sect. *Juglandifolium*, including subsect. *Lycopersicoides*; and e) the genus *Lycopersicon*. These results, in combination with an analysis of morphological data, advocate the controversial, but previously suggested, treatment of *Lycopersicon* as congeneric with *Solanum* in subgenus *Potatoe*. Thus, the cultivated tomato will be recognized as *Solanum lycopersicum* L. *Solanum chmielewskii* and *Solanum lycopersicum* var. *cerasiforme* are proposed as new combinations; *Solanum neorickii* is proposed as a new name for *Lycopersicon parviflorum*. Our data also suggest that *Cyphomandra* should be included within *Solanum*.

The Solanaceae is one of the economically most important and larger families of angiosperms. There has been much change in recent years regarding generic circumscription in the family. In 1979, D'Arcy estimated it to contain 83 genera and 2,671 species, but the most recent estimate is 96 genera and about 2,300 species (D'Arcy, 1991). The genus *Solanum* is by far the largest of the genera, and like the Solanaceae, its number of species has been revised recently. It is presently interpreted to contain 1,000–1,100 species (D'Arcy, 1991), in contrast to larger earlier estiamtes of 1,400 (D'Arcy, 1979) to 2,000 species (Correll, 1962; Hawkes, 1963). D'Arcy (1972) divided *Solanum* into seven subgenera, including subgenus *Potatoe,* which contains the domesticated potato (*S. tuberocum* L.) and pepino (*S. muricatum*).

The focus of this study is on the interspecific relationships of *Solanum* subgenus *Potatoe* and *Lycopersicon* (the tomatoes). *Lycopersicon* has been recognized as a distinct genus by most students of the Solanaceae (Miller, 1754; Dunal, 1852; Muller, 1940; Luckwill, 1943; Correll, 1962; D'Arcy, 1972, 1987, 1991; Hunziker, 1979; Rick, 1979, 1988; Symon, 1981, 1985; Taylor, 1986; Warnock, 1988; Hawkes, 1990; Rick, Laterrot, and Philouze, 1990). Others, however, merge *Lycopersicon* with *Solanum* (MacBride, 1962; Seithe, 1962; Heine, 1976; Fosberg, 1987; Child, 1990).

The relationships of these genera have been the subject of great debate since Linnaeus (1753) treated the tomatoes and potatoes as members of the genus *Solanum. Lycopersicon* was recognized as a distinct genus in the following year by Miller (1754). There have been numerous studies examining phylogenetic relationships among groups within subgenus *Potatoe.* These investigations have employed data from morphology (Dunal, 1852; Bitter, 1912a; Börner, 1912; Correll, 1958, 1962; D'Arcy, 1972, 1979, 1982, 1987, 1991; Anderson, 1979b; Hunziker, 1979; Seithe and Anderson, 1982; Taylor, 1986; Rick, 1988; Child, 1990; Hawkes, 1990; Child and Lester, 1991; Lester, 1991), breeding systems or crossability, including somatic hybridizations (Wann and Johnson, 1963; Anderson, 1977; Melchers, Sacristan, and Holder, 1978; Hermsen and Taylor, 1979; Rick, 1979; Whalen and Anderson, 1981; Handley et al., 1986; Austin et al., 1988; Fish, Karp, and Jones, 1988; Deverna et al., 1990; Anderson and Bernardello, 1991; Matsubayashi, 1991; Mione and Anderson, 1992), amino acid sequences of plastocyanin or the small subunit of ribulose-1,5-biphosphate carboxylase (Boulter et al., 1979; Martin et al., 1986), flavonoids (Steinharter, Cooper-Driver, and Anderson, 1986), genetic linkage studies (Bonierbale, Plaisted, and Tanksley, 1988), mitochondrial DNA (McClean and Hanson, 1986), chromosome morphology and evolution (Bernardello and Anderson, 1990), chloroplast DNA (Palmer and Zamir, 1982; Hosaka et al., 1984; Hosaka and Hanneman, 1988; Spooner, Sytsma, and Smith, 1991; Olmstead and Palmer, 1992; Spooner and Sytsma, 1992), and nuclear DNA (Debener, Salamini, and Gebhardt, 1990; Miller and Tanksley, 1990). With the exception of the morphological data sets, no studies have surveyed all major groups of *Ly-*

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TABLE 1. *Morphological comparisons among the immediate relatives of tomatoes, potatoes, and pepinos. In this table,* Lycopersicon *is recognized as a genus following D'Arcy (1972), but the classification of subgenus* Potatoe *follows Child (1990) to differentiate groups not recognized by D'Arcy (1972)*

	Tubers[a]	Pubescence[b]	Anthoclades[c]	Articulation[d]	Anther dehiscence[e]	Anther connation[f]	Anther appendages[g]	Corolla pigments[h]	Flower symmetry[i]
Lycopersicon									
subgenus *Lycopersicon*	A	A	3.7	H	L	C	A	C	S
subgenus *Eriopersicon*	A	A	3.7	H	L	C	A	C	S
Solanum subgenus *Potatoe*									
subsect. *Lycopersicum*									
ser. *Neolycopersicon*[j]	A	A	3.7	B[k]	P	C	U	C	A
subsect. *Lycopersicoides*	A	A	3.7	H	P	F	U	C	S
sect. *Basarthrum*	A	B	3.5	B	P	F	U	A	S
sect. *Anarrhichomenum*	A	A	3.3	B	P	F	U	A	S
sect. *Juglandifolium*	A	A	3.6	H	P	F	U	C	S
sect. *Etuberosum*	A	A	3.5	B	P	F	U	A	S
sect. *Petota*	P	A	3.5	H	P	F	U	A	S
Solanum nigrum (outgroup for the morphological analysis)	A	A	1.5	B	P	F	U	A	S

[a] A, absent; P, present.
[b] A, bayonet hairs absent, various types of unicellular to multicellular hairs present; B, bayonet hairs present, as well as various types of unicellular to multicellular hairs.
[c] Anthoclades are patterns of lateral branching and associated inflorescences. The numbers follow the classification of Child and Lester (1991).
[d] A, pedicel articulation above the base; B, pedicel articulation at the base. Section *Etuberosum* has pedicel articulation basal to very slightly above the base, and is scored as basal for the morphological analysis.
[e] L, longitudinal introrse slits; P, poricidal. The distinction between poricidal and longitudinal introrse dehiscence is not always clear. Members of ser. *Neolycopersicon,* subsect. *Lycopersicoides,* and sect. *Juglandifolium* have anthers that are initially poricidal and later develop introrse slits. Anthers of some species of sect. *Petota* occasionally develop introrse slits (Correll, 1962; Child, 1990).
[f] C, connate; F, free. There are two types of anther connation in subgenus *Potatoe.* The genus *Lycopersicon* and *Solanum pennellii* (ser. *Neolycopersicon*) have anthers connate by means of interlocking marginal hairs, while *Solanum dulcamara* (sect. *Dulcamara*) has anthers connate by means of union of tissue (Rick, 1947). We here score anther connation of the former type. *Solanum pennellii,* like *Lycopersicon,* has anthers connate by means of interlocking marginal hairs, but they are not as tightly held together as in *Lycopersicon,* and are sometimes separated in mature herbarium specimens. *Solanum pennellii* has both self-compatible and self-incompatible populations. Anthers from self-compatible populations are more tightly held together than those from self-incompatible populations (C. Rick, personal communication).
[g] A, anthers with sterile apical appendages; U, anthers unappendaged.
[h] C, carotenoids, corollas yellow; A, anthocyanins, corollas pink to blue, or white.
[i] S, symmetrical; A, asymmetrical.
[j] D'Arcy (1982) treated *S. pennellii* (placed by Child [1990] in ser. *Neolycopersicon*) as a member of the genus *Lycopersicon.*
[k] Rick and Tanksley (1981) note an anomalous specimen of *S. pennellii* from the northernmost part of its range with medial articulation.

copersicon or *Solanum* subgenus *Potatoe.* Furthermore, there has yet to emerge a consensus on the relationships of these species.

Members of *Solanum* subgenus *Potatoe* and *Lycopersicon* are very similar morphologically. The majority are herbs (some vines) with dissected leaves (some simple), with symmetrical, five-merous flowers (asymmetrical in *S. pennellii*), baccate fruits, and "hairy" seeds, the hairs formed by lignified extensions of the sporoderm (D'Arcy, 1972; Anderson, 1979b; Child, 1990; Lester, 1991).

There are few, but sometimes conspicuous morphological differences among the taxa of *Solanum* subgenus *Potatoe* and *Lycopersicon* (Table 1). Unique features defining sections or series include tubers in sect. *Petota* (Hawkes, 1990), bayonet hairs in sect. *Basarthrum,* here informally referred to as "pepinos" (Seithe and Anderson, 1982), distinct anthoclade types (= patterns of lateral branching and associated inflorescences) within each of sects. *Anarrhichomenum* and *Juglandifolium* (Child and Lester, 1991), and zygomorphic flowers in ser. *Neolycopersicon* (Correll, 1958; Child, 1990). Shared features between groups include articulation of the pedicel, connate stamens, corolla pigments (Child, 1990), and anther appendages (Luckwill, 1943; Child, 1990).

The base chromosome number of members of *Solanum* subgenus *Potatoe* and *Lycopersicon* is $x = 12$. Most species are diploid, except in *Solanum* sect. *Petota,* which has 27% polyploids (ranging from triploids to hexaploids; Hawkes, 1990). The majority of these species (including *Lycopersicon*) are characterized by the widespread occurrence of gametophytic self-incompatibility, which is rare in the rest of *Solanum* (Whalen and Anderson, 1981). Despite genomic differentiation (Matsubayashi, 1991) and/or embryo-endosperm incompatibilities (Ehlenfeldt and Hanneman, 1984, 1992), many taxa within *Solanum* sect. *Petota* (Hawkes, 1958, 1979; Johnston et al., 1980; Matsubayashi, 1991) and within *Lycopersicon* (Rick, 1979) can be crossed artificially to produce advanced-generation hybrids. In contrast, crossing is generally difficult within members of *Solanum* sects. *Basarthrum* (Anderson, 1979b; Anderson and Bernardello, 1991) and *Etuberosum* (Ramanna and Hermsen, 1981).

Chloroplast DNA (cpDNA) is an excellent marker to address phylogenetic relationships within and between genera (Palmer et al., 1988). Although the use of cpDNA has some potential problems (Doyle, 1992), it has much power to resolve relationships, especially when integrated with other data. The purpose of our study is to investigate

TABLE 2. *Taxa examined in this study*

Taxon	USDA plant introduction or collection number	Source[a]	Locality
Capsicum pubescens Ruíz Lopez and Pavón	*Anderson 1554*	1	Unknown
Cyphomandra diploconos (Martius) Sendtner	Unknown	2	Brazil
Datura inoxia Miller	*Spooner 2989*	3	US–Wisconsin
Lycopersicon esculentum Miller	124034	4	Peru
L. chmielewskii Rick, Kesickii, Fobes & Holle	379030	4	Peru
L. peruvianum (L.) Miller	127832	4	Peru
Solanum agrimonifolium Rydb.	243351	5	Guatemala
S. albornozii Correll	498206	5	Ecuador
S. appendiculatum Dunal	*Anderson 656*	1	Mexico
S. brevidens Philippi	245763	5	Chile
S. bulbocastanum Dunal	255516	5	Mexico
S. dulcamara L.	*Spooner 2988*	3	US–Wisconsin
S. etuberosum Lindley	498311	5	Chile
S. fernandezianum Philippi	320270	5	Chile
S. jasminoides Pax	*Olmstead S-86*	6	Colombia
S. lycopersicoides Dunal	LA1964	7	Peru
S. macrocarpon L. f.	441914	8	Brazil
S. muricatum Aiton	*Anderson 844*	1	Ecuador
S. nigrum L.	304600	8	Unknown
S. ochranthum Dunal	230519	5	Peru
S. phureja Juz. & Buk.	283123	5	Ecuador
S. pseudocapsicum L.	368425	8	Yugoslovia
S. quitoense Lam.	Unknown	8	Unknown
S. sitiens I. M. Johnston	498279	5	Chile
S. suaveolens Kunth and Bouché	390819	8	Peru
S. taeniotrichum Correll	*Anderson 1423*	1	Costa Rica
S. verrucosum Schldl.	310966	5	Mexico

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ingroup and outgroup relationships of *Solanum* subgenus *Potatoe* and *Lycopersicon* with cpDNA, coupled with a reanalysis of morphological data. We compare these results to prior phylogenetic hypothesis to produce a synthetic hypothesis of relationships of these species.

MATERIALS AND METHODS

Species—We analyzed 17 accessions of *Solanum* subgenus *Potatoe,* four other *Solanum,* three *Lycopersicon,* and one accession each of *Cyphomandra, Capsicum,* and *Datura* (Table 2). All examined members are diploids ($2n = 24$; Pickersgill, 1977; Anderson, 1979b; Rick, 1979; Whalen, Costich, and Heiser, 1981; Palomino, Viveros, and Bye, 1988; Hawkes, 1990; Pringle and Murray, 1991), except *Solanum nigrum,* a hexaploid (Edmonds, 1979). These taxa represent much of the ingroup variability in *Solanum* subgenus *Potatoe* and *Lycopersicon.* Although we used only one accession for each species in this analysis, our ongoing studies within selected lineages of *Solanum* subgenus *Potatoe* (Spooner, Sytsma, and Smith, 1991; Spooner and Sytsma, 1992; Anderson and Jansen, unpublished data) show that intraspecific variation does not adversely affect phylogenetic relationships between sections of *Solanum.* Voucher specimens are deposited at the herbarium of Inter-Regional Potato Introduction Station, Sturgeon Bay, Wisconsin; the herbarium of the University of Colorado, Boulder, Colorado (COLO); or the George Safford Torrey Herbarium, University of Connecticut, Storrs, Connecticut (CONN).

DNA isolation and restriction-site comparison—Pooled leaf samples of one to eight plants per accession were collected from 2-month-old plants for DNA extraction. We made preparations of total DNA from 5 g of fresh leaf tissue by the procedure of Doyle and Doyle (1987) and purified the DNA over CsCl/ethidium bromide gradients. Restriction endonuclease digestions, agarose-gel electrophoresis, bidirectional transfer of DNA fragments from agarose gels to nylon filters, labeling of recombinant probes by nick-translation, filter hybridization, and autoradiography followed methods in Palmer (1986). Eighteen restriction endonucleases were used to examine cpDNA variation in *Solanum*: *Ava* I, *Bam* HI, *Ban* I, *Bcl* I, *Bgl* II, *Bst* NI, *Bst* XI, *Cla* I, *Eco* O 109, *Eco* RI, *Eco* RV, *Hae* II, *Hinc* II, *Hind* III, *Hph* I, *Nci* I, *Nsi* I, and *Xmn* I. We probed membranes with 12 *Pst* I and two *Sal* I clones of *Petunia* (Sytsma and Gottlieb, 1986) or 43 clones of *Nicotiana* (Olmstead and Palmer, 1992) covering nearly the entire chloroplast genome.

Data analysis—*Molecular data analysis*—*Capsicum* and *Datura* were used as outgroups. Some mutations, especially those observed with the larger *Petunia* probes and for the taxa outside of subgenus *Potatoe,* were difficult to score and were eliminated from the analysis. Phylogenetic

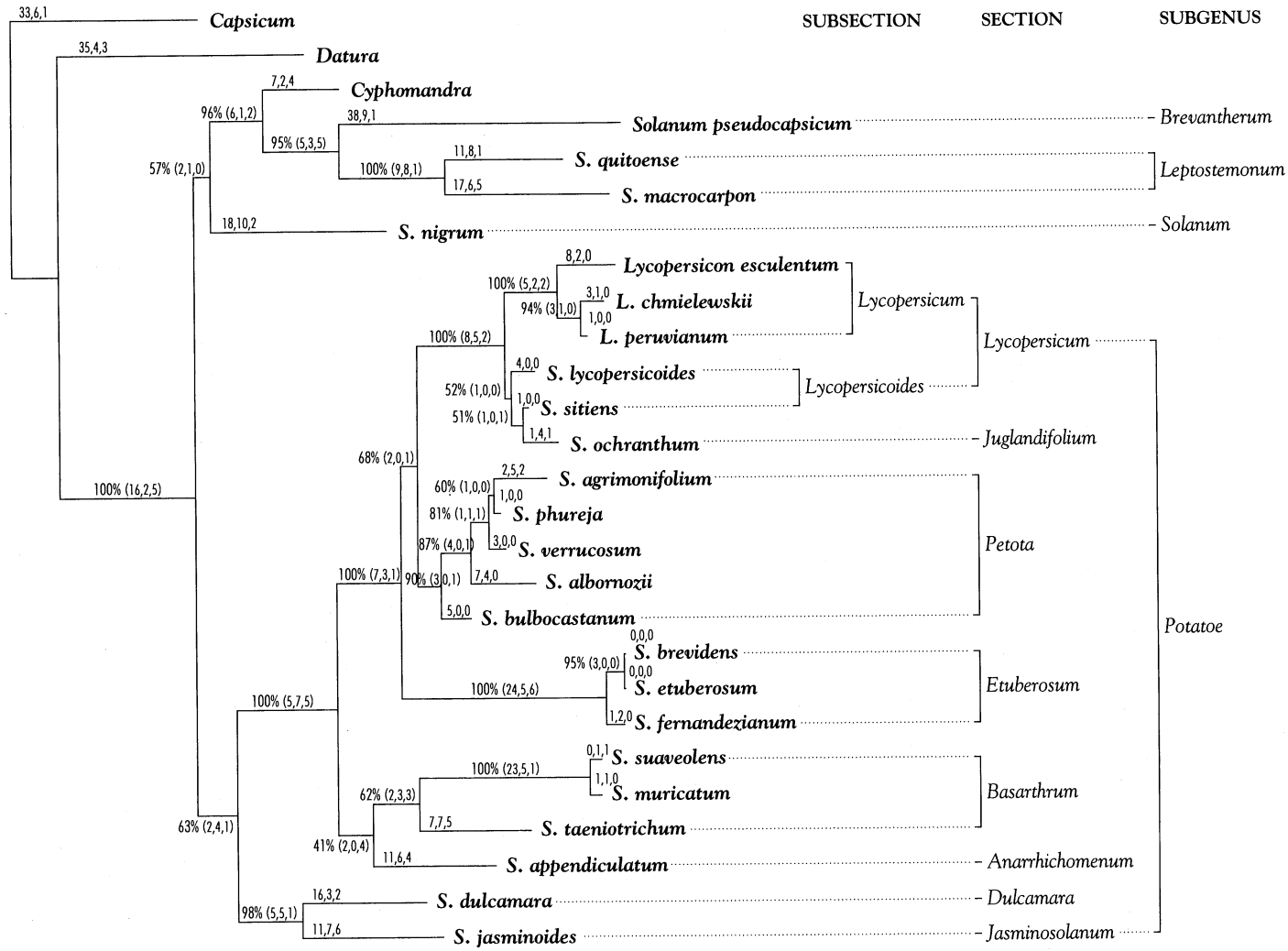


Fig. 1. One of two most-parsimonious 608-step Wagner trees (as a phylogram) of the cpDNA data, and the single most-parsimonious weighted tree (1.1 and 1.3 weights of site gains over site losses), with overlayed bootstrap values and number of mutations supporting each branch (ordered as unique mutations, parallel losses, and parallel gains). The taxonomy follows Child (1990), except that the names in *Lycopersicon* are used here.

reconstructions were performed with PAUP, version 3.0r (Swofford, 1991). The data were analyzed using Wagner parsimony (Farris, 1970), which gives equal weight to site gains and site losses. The most-parsimonious trees were sought using BRANCH AND BOUND, COLLAPSE, and ACCTRAN (accelerated transformation) optimization, which favors reversals over parallelisms. Alternate topologies were tested with the CONSTRAINTS option. Additionally, the character-state weighting method of Albert, Mishler, and Chase (1992) was used with weights of 1.1 and 1.3 given to site gains. Ancestral states were designated as question marks. For weighted analyses, length mutations were given equal weight. Bootstrap values (Felsenstein, 1985) on resulting branches were obtained from 100 replicates.

Morphological data analysis—We assembled the major morphological features distinguishing the immediate relatives of tomatoes, potatoes, and pepinos from the literature (Table 1). Our morphological analysis is intended only to show cladistic relationships using these taxonomically important characters and does not constitute an in-depth morphological study of *Solanum* subgenus *Potatoe* and *Lycopersicon.* Character states were polarized using *S. nigrum* as an outgroup. We scored anthoclade types as a five-state ordered character, based on the hypotheses of Child and Lester (1991). Pedicel articulation in sect. *Etuberosum* is basal to very slightly above the base and we scored it as basal. We scored the genus *Lycopersicon* and *Solanum pennellii* as having connate anthers, although connate anthers are not always evident in mature specimens of the latter (see Table 1). Red-fruited members of *Lycopersicon* (subgenus *Lycopersicon*) differ from the green-fruited ones (subgenus *Eriopersicon*) primarily by carotenoid pigments in the fruits. Because of lack of information about fruit pigments in the outgroup, this character was not scored and these two series were treated as one group. As with the cpDNA data, phylogenetic reconstructions were performed with PAUP, version 3.0r (Swofford, 1991), using Wagner parsimony. The most-parsimonious trees were sought using EXHAUSTIVE, COLLAPSE.

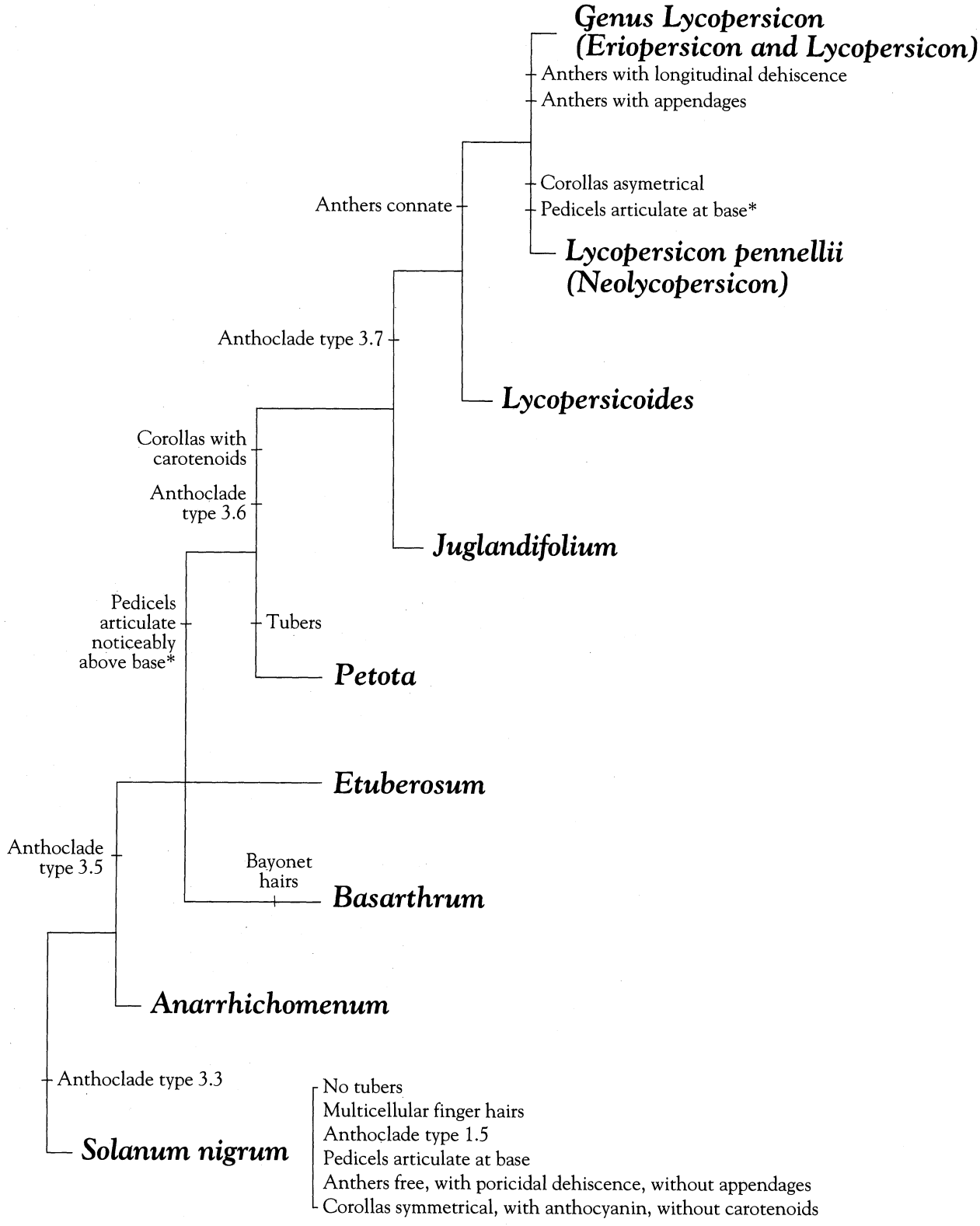


Fig. 2. The single most-parsimonious Wagner tree of the morphological data separating members of *Solanum* subgenus *Potatoe*. The taxonomy follows Child (1990), except that the names in *Lycopersicon* are used here.

RESULTS

Chloroplast DNA — A total of 473 site mutations were identified, 231 of which were phylogenetically informative. Data are available on request from DMS. All characters were site mutations except three insertions or deletions (one shared by *S. pseudocapsicum* and *S. macrocarpon,* and two shared by members of sect. *Etuberosum*). PAUP 3.0r with Wagner parsimony produced two most-parsimonious 608-step trees with a consistency index of 0.631 (without autapomorphies). These two trees differed only in the placement of *S. appendiculatum* within a monophyletic assemblage including other members of sect. *Basarthrum,* or separate from and basal to this clade. Weighted parsimony, with weights of 1.1 and 1.3 in favor of gains over losses, generated a single most-parsimonious tree identical with one of the Wagner trees. This tree (Fig. 1) supports two main clades among the species we studied:

1. *Solanum* subgenus *Potatoe* and *Lycopersicon.* Within this clade, the following clades were supported: a. sect. *Basarthrum* and sect. *Anarrhichomenum*; b. sect. *Etuberosum*; c. sect. *Petota*; d. sect. *Juglandifolium,* including subsect. *Lycopersicoides*; and e. the genus *Lycopersicon.*
2. Other members of *Solanum* and *Cyphomandra.*

We used the CONSTRAINTS option with Wagner parsimony to examine how many steps were required to obtain the following two alternative topologies: 1) *Lycopersicon* as a sister taxon to the rest of the ingroup; and 2) *Lycopersicon* as a sister taxon to *Solanum* subgenus *Potatoe.* The first alternative topology produced six most-parsimonious 649-step trees; the second topology produced four most-parsimonious 648-step trees. These alternative trees (not shown) are 41 and 40 steps longer than the most-parsimonious tree (Fig. 1). Consensus trees of these alternative analyses retained the major groups our analysis found at the sectional level, but exhibited an unresolved polychotomy within the remaining members of subgenus *Potatoe.*

Morphology — Wagner parsimony produced a single most-parsimonious tree, 13 steps long, with a consistency index of 0.923 (without autapomorphies). The only homoplastic character was pedicel articulation (Fig. 2, see asterisk). This tree, like the cpDNA tree, included *Lycopersicon* in *Solanum* subgenus *Potatoe* and was topologically identical with the weighted molecular tree, except for one unresolved trichotomy.

DISCUSSION

Phylogenetic position of Lycopersicon — *Taxonomic implications* — The most noteworthy finding of our study is the support for the sister group relationship of tomatoes and potatoes. A strict reliance on cpDNA for making phylogenetic or taxonomic conclusions is problematical if introgression or lineage sorting has occurred (Doyle, 1992). Although we have no evidence for either of these processes, they cannot be ruled out in the evolutionary history of *Solanum* subgenus *Potatoe* and *Lycopersicon.* Nonetheless, the large number of molecular characters, and general concordance of the molecular and morphological data, provide strong support for merging *Solanum* and *Lycopersicon.* The characters that separate the two genera (Table 1) are minor when viewed in reference to the range of morphological diversity in *Solanum.* According to D'Arcy (1991), "Many of the 62 sections [of *Solanum*] now recognized are of such distinctive appearance that in other plant groups they would be recognized as separate genera." Thus, *Lycopersicon* could be treated as a separate genus, but given its position in the phylogram generated from our data, either *Solanum* would be paraphyletic (see Fig. 1) or several other genera would have to be recognized.

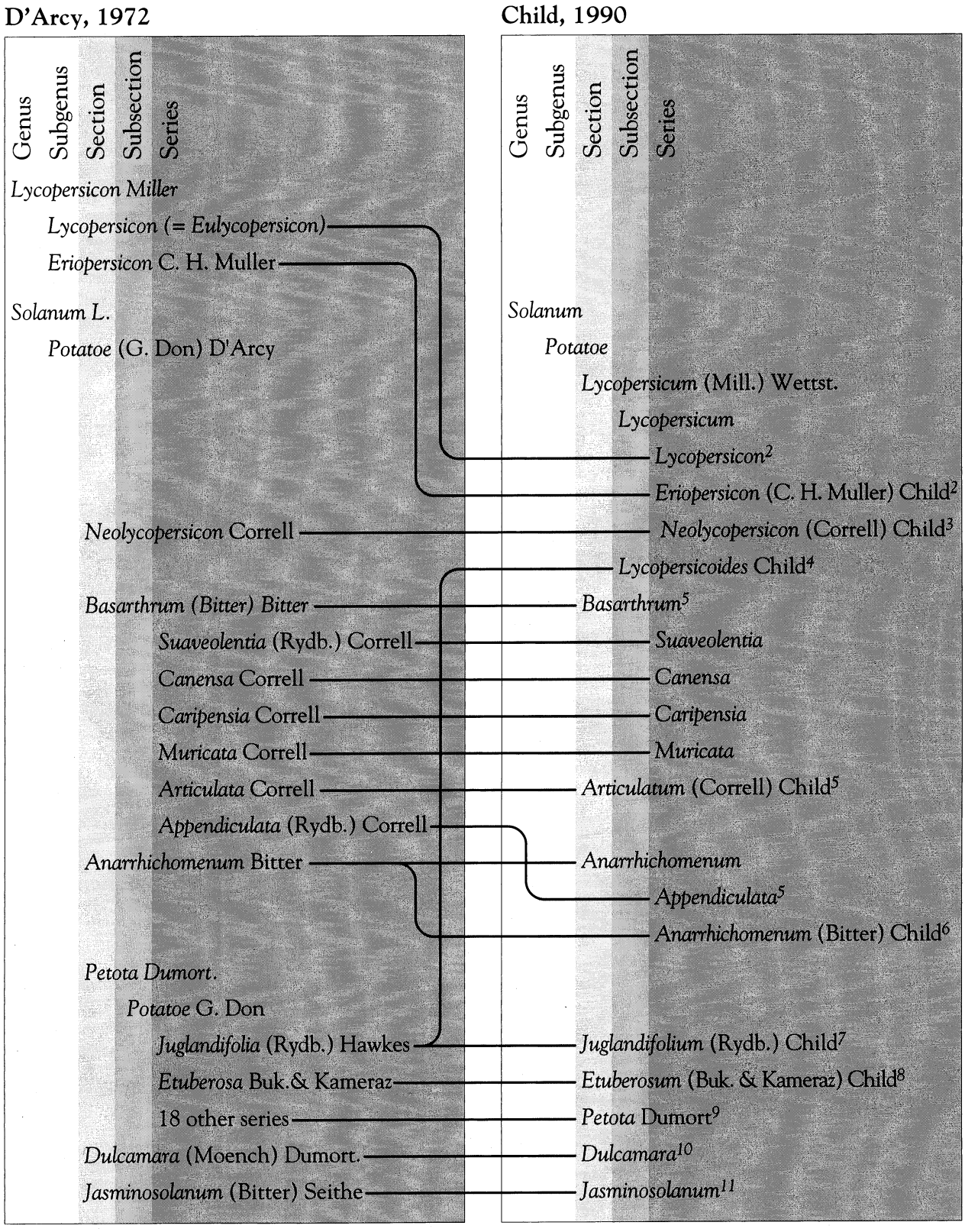
The close relationship between *Solanum* sect. *Petota* and *Lycopersicon* was supported previously by morphological, chemical, and molecular data. We interpret our data, combined with prior data, to provide overwhelming evidence for the cladistic relationship of *Solanum* subgenus *Potatoe* and *Lycopersicon.* Thus, we will treat *Lycopersicon* hereafter as a member of the genus *Solanum,* subgenus *Potatoe.* The classification of Child (1990, Fig. 3) most recently reflects this treatment, and consequently we will follow it relative to his treatment of *Lycopersicon* in *Solanum* subgenus *Potatoe,* but point out discordancies between our data and his classification below.

Nomenclatural changes — There has been much discussion about the unnatural status of the genus *Solanum* and its possible split into separate monophyletic genera (Börner, 1912; D'Arcy, 1991; Olmstead and Palmer, 1992). Based on pedicel articulation above the base and pinnately dissected leaves, Börner (1912) erected the genus *Solanopsis* to include members of *Solanum* subgenus *Potatoe,* including *Lycopersicon.* Bitter (1912a) immediately rejected Börner's generic concept and maintained *Lycopersicon* and *Solanum* as separate genera. Lester (1991) suggested that subgenus *Potatoe* (including *Lycopersicon*) may form a separate genus, and raised the possibility that *Solanopsis* may have to be reconsidered. Splitting *Solanum* into smaller monophyletic genera, such as *Solanopsis,* awaits further data on cladistic relationships throughout the Solanaceae. While our study does not provide data to answer this larger question, it does suggest that the genus *Solanopsis* may have to be reconsidered if *Solanum* eventually is subdivided.

The relationship of *Cyphomandra* to *Solanum* also has been controversial (Child, 1984, 1990; Bohs, 1989; Child and Lester, 1991). Our cpDNA data and that of Olmstead and Palmer (1992) provide support for the inclusion of *Cyphomandra* in *Solanum* (Fig. 1).

Child (1990) divided *Lycopersicon* into three series (including *L. pennellii*), grouped under *Solanum* subsect. *Lycopersicum* of subgenus *Potatoe* (Fig. 3). He suggested that subsect. *Lycopersicum* evolved recently and shared a common ancestry with sects. *Articulatum* (cladistically related to sect. *Basarthrum,* see Fig. 1), *Juglandifolium,* or *Etuberosum.* Child (1990) implied with his quote "The treatment here is to be deemed a taxonomic ploy for the benefit of a schema" that he was unsure of the relationship of *Lycopersicon* to *Solanum.* He provided series and section names to be used in *Lycopersicon* if additional evidence showed separated generic status. However, he did not provide existing names of *Lycopersicon* as *Solanum* at the species level, or make new combinations. We supply the following new name and new combinations in *Solanum,* with previously used *Lycopersicon* synonyms, for

Comparison of recent classifications of *Lycopersicon* and *Solanum* subgenus *Potatoe*[1]



the ten taxa of *Lycopersicon* accepted by Rick, Laterrot, and Philouze (1990):

Solanum agrimoniifolium (Dunal in DC.) J. F. Macbr., *Field Museum of Natural History, Botanical Series* 13: 159. 1962.

Lycopersicum hirsutum Dunal, Solanorum generumque affinium synopsis 4. 1816, not *L. hirsutum* Dunal in DC., Prodromus systematis naturalis regni vegetabilis 13: 25. 1852. *Lycopersicon agrimoniifolium* Dunal in DC., Prodromus systematis naturalis regni vegetabilis 13: 24. 1852, '*agrimoniæfolium*'.

A new combination in *Solanum* based on *L. hirsutum* cannot be made because the name is occupied by *S. hirsutum* Dunal, Solanorum generumque affinium synopsis 158. 1816. *Solanum agrimoniifolium* is the first name used for this taxon in the genus *Solanum.*

Solanum cheesmaniae (Riley) Fosb., *Phytologia* 62. 181. 1987.

Lycopersicon cheesmaniae Riley, *Bulletin of Miscellaneous Information* 1925: 227. 1925, '*cheesmanii*'.

A feminine ending to the epithet is necessary because the species was named after Miss L. Evelyn Cheesman. This species name unfortunately is very similar to *S. cheesemannii* Gerasimanko, named after another person. These names are neither orthographic variants or homonyms (Fosberg, 1987).

Solanum chilense (Dunal in DC.) Reiche, *Anales de la Universidad de Chile, Santiago* 124: 742. 1909.

Lycopersicon chilense Dunal in DC., Prodromus systematis naturalis regni vegetabilis 13: 24. 1852.

Solanum chmielewskii (Rick, Kesickii, Fobes, and Holle) Spooner, Anderson, and Jansen, comb. nov.

Lycopersicon chmielewskii Rick, Kesickii, Fobes, and Holle, *Theoretical and Applied Genetics* 47: 58. 1976.

Solanum lycopersicum L., Species plantarum 185. 1753.

Lycopersicon esculentum Miller, The gardeners dictionary, ed. 8: *Lycopersicon* No. 2. 1768. ≡ *Lycopersicon lycopersicum* (L.) Karsten, Deutsche flora, ed. 1: 966. 1882.

The conservation of the name, *L. esculentum* Miller against *L. lycopersicum* (L.) Karsten does not preclude the use of *Solanum lycopersicum* L. (see Terrell, Broome, and Reveal [1983], and Appendix IIIB of Greuter et al. [1988]).

Solanum lycopersicum var. *cerasiforme* (Dunal) Spooner, Anderson, and Jansen, comb. nov.

Lycopersicon esculentum var. *cerasiforme* (Dunal) A. Gray, Synoptical flora of North America, vol. 2, 2d ed.: 226. 1886. *Lycopersicon cerasiforme* Dunal, Historie naturelle, médicale et économique des *Solanum* 113. 1813.

See Terrell, Broome, and Reveal (1983) who point out that changes in the Sydney Code regarding autonyms created the autonym *Lycopersicon cerasiforme* var. *cerasiforme,* with the publication of *Lycopersicon cerasiforme* Dunal var. γ *leptophyllum* Dunal in DC., Prodromus systematis naturalis regni vegetabilis 13: 26. 1852. Variety *cerasiforme* took precedence over D'Arcy's (1978) new combination made before the Sydney Code, *Lycopersicon esculentum* var. *leptophyllum,* (Dunal) D'Arcy, *Annals of the Missouri Botanical Garden* 65: 771. 1978.

Solanum neorickii Spooner, Anderson, and Jansen, nom. nov.

Lycopersicon parviflorum Rick, Kesickii, Fobes, and Holle, *Theoretical and Applied Genetics* 47: 57. 1976.

This new name honors Dr. Charles Rick, an authority on the breeding, genetics, and taxonomy of *Lycopersicon.* A new name in *Solanum* is required because the name, *Solanum parviflorum,* has been used before, the earliest being *Solanum parviflorum* Usteri, *Annalen der Botanik* 6: 61. 1793. An earlier name honoring Dr. Rick (*Solanum rickii* Correll, *Wrightia* 2. 1961) is a synonym of *S. sitiens* Johnston, *Revista Chilena de Historia Natural* 33: 25. 1929 (Marticorena and Quezada, 1977).

Solanum pennellii Correll, *Madroño* 14: 233. 1958.

Lycopersicon pennellii (Correll) D'Arcy, *Phytologia* 5: 240. 1982.

Solanum peruvianum L., Sp. pl. 186. 1753.

Lycopersicon peruvianum (L.) Miller, The gardeners dictionary, ed. 8: *Lycopersicon* No. 5. 1768.

Solanum pimpinellifolium B. Juss. in Linnaeus, Centuria I. plantarum 8. 1755.

Lycopersicon pimpinellifolium (B. Juss.) Miller, The gardeners dictionary, ed. 8: *Lycopersicon* No. 4. 1768.

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Fig. 3. A comparison of the classifications of *Solanum* subgenus *Potatoe* of D'Arcy (1972) and Child (1990). 1. Not included on this figure are six sections placed in subgenus *Potatoe* by Child (1990) and not discussed in this study. 2. Series *Lycopersicon* (with three red-fruited species) and ser. *Eriopersicon* (with six green-fruited species) traditionally have been considered as the immediate wild relatives of tomatoes. The group is distributed naturally along western South America from Ecuador to northern Chile, and the Galapagos Islands (*S. cheesmaniae* [Riley] Fosberg); *S. lycopersicum* L. (= *L. esculentum* Miller nomen. cons.) is naturalized in Mexico and Central America. 3. Series *Neolycopersicon* is monotypic, including *S. pennellii* Correll, distributed along the coastal Peruvian deserts. D'Arcy (1982) treats this as *Lycopersicon pennellii* (Correll) D'Arcy. 4. Subsection *Lycopersicoides* includes two species: *S. lycopersicoides* Dunal (distributed in southern Peru and adjacent northern Chile), and *S. sitiens* I. M. Johnston (= *S. rickii* Correll), distributed in northern Chile (Rick, 1988). 5. Section *Basarthrum* (sensu D'Arcy, 1972; Anderson, 1979b) includes 22 species distributed from central Mexico to Peru. The treatment of Child (1990) is similar, except *S. sanctae-marthae* Bitter (distributed in northern Colombia and not available as living material) is placed in the monotypic section *Articulatum,* and *S. appendiculatum* Dunal (distributed from central Mexico to Guatemala) is placed in series *Appendiculata.* 6. Section *Anarrhichomenum* includes seven species of vines distributed from Guatemala, south to Peru. 7. Section *Juglandifolium* includes two species: *S. juglandifolium* Dunal, distributed in Colombia and Ecuador, and *S. ochranthum* Dunal, distributed in Colombia, Ecuador, and Peru (Rick, 1988). 8. Section *Etuberosum* includes three species, distributed in south-central Chile and adjacent southwestern Argentina (Spooner, Douches, and Contreras-M., 1992). 9. The latest taxonomic interpretation of sect. *Petota* (Hawkes, 1990) includes 232 species, partitioned among 19 series, distributed from the southwestern United States to south-central Chile. This may be an overestimate of the species diversity in the group (Spooner and van den Berg, 1992). 10. The size of sect. *Dulcamara* is unclear and in need of revision. Child (1990) describes the group as containing Eurasian climbing shrubs. *Solanum dulcamara* L. is naturalized and weedy in many places outside of its natural range. 11. The size of sect. *Jasminosolanum* is unclear and in need of revision. Child (1990) lists 15 species from Mexico, south to Argentina, and Brazil. *Solanum jasminoides* Pax is native to South America and naturalized elsewhere.

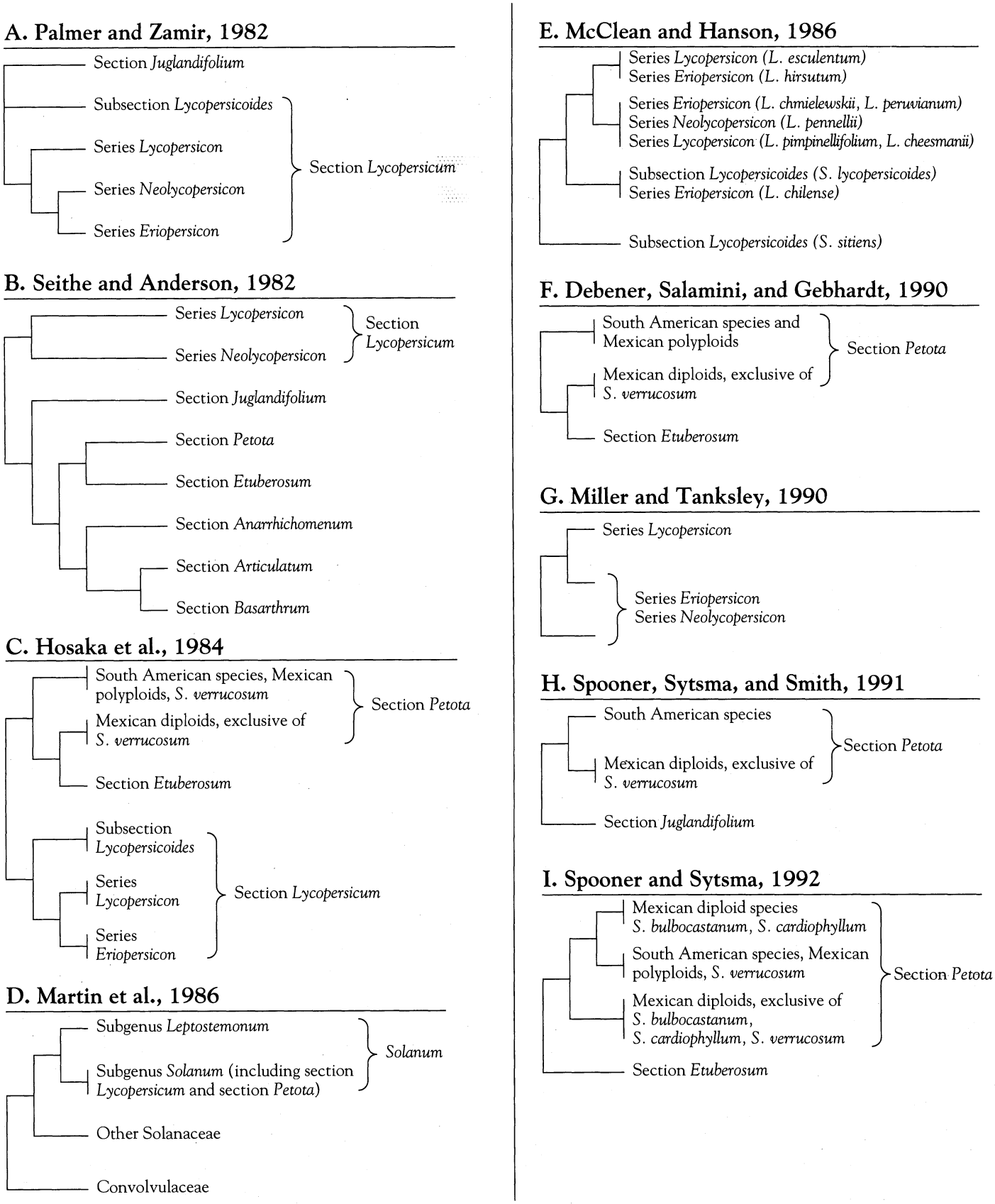

Fig. 4. Hypotheses of relationships of selected members of *Solanum* sect. *Petota,* advanced by Palmer and Zamir (1982), using cpDNA data; Seithe and Anderson (1982), using trichome types; Hosaka et al. (1984), using cpDNA data; Martin et al. (1986), using partial amino acid sequences of the small subunit of Rubisco; McClean and Hanson (1986), using mitochondrial DNA data; Debener, Salamini, and Gebhardt (1990), using single- to low-copy nuclear DNA; Miller and Tanksley (1990), using single- to low-copy nuclear DNA; Spooner, Sytsma, and Smith (1991), using

Despite firm evidence for the monophyly and genetic and morphological similarity of *Lycopersicon* and other members of *Solanum* subgenus *Potatoe,* there are likely to be practical and philosophical arguments against the subsumption of *Lycopersicon* into *Solanum.* The name *Lycopersicon esculentum* P. Miller was conserved over the earlier valid name, *L. lycopersicum* (L.) Karsten (Terrell, Broome, and Reveal, 1983) at the Fourteenth International Botanical Congress in Berlin in 1897. D'Arcy (1991) states "The conservation action at Berlin . . . may be taken as supporting the case for the use of the separate genus [*Lycopersicon*] for the tomato." Similarly, although Lester (1991) concludes that subgenus *Potatoe,* including *Lycopersicon,* is monophyletic, he argues for a "practical . . . classification which is simple and easy to use, even though this may be . . . artificial." Symon (1981) states "If there is a utilitarian component in nomenclature, it is convenient to have this crop and its related species in a distinct genus rather than being lost in a welter of *Solanum* names." Continued use of names in *Lycopersicon* for practical reasons may persist.

Subsectional and series relationships of subgenus Potatoe—As Fig. 1 shows, all the members of subgenus *Potatoe,* including *Lycopersicon,* form a monophyletic group (Fig. 1). The cpDNA data support sister group relationships between 1) sects. *Basarthrum* and *Anarrhichomenum,* and 2) sect. *Etuberosum* to sects. *Petota* and *Lycopersicum,* including sect. *Juglandifolium.* Series *Eriopersicon* (*Lycopersicon chmielewskii, L. peruvianum*) and ser. *Lycopersicon* (*L. esculentum*) are supported as distinct clades. However, because only one species was used in ser. *Lycopersicon,* more taxa need to be examined to provide better support for the latter.

Child's (1990) new classification is compared to the widely used classification of D'Arcy (1972) in Fig. 3 to highlight differences in classifications of *Solanum* subgenus *Potatoe.* For convenience, all further discussion will follow Child's (1990) classification, except as noted. Our data match D'Arcy's (1972) classification by uniting members of subsect. *Lycopersicoides* and sect. *Juglandifolium* under ser. *Juglandifolia* (of D'Arcy). However, he advocates treatment of *Lycopersicon* and *Solanum* as separate genera, and placement (along with Correll, 1962 and Hawkes, 1990) of sects. *Juglandifolium* and *Etuberosum* in subsect. *Potatoe* (of D'Arcy), that our data do not support. Our cpDNA data suggest that Hawkes' (1989, 1990) subsect. *Estolonifera* Hawkes, including ser. *Etuberosa* and ser. *Juglandifolia* (of D'Arcy) is polyphyletic. Our data support much of Child's classification except that sect. *Juglandifolium* as he recognizes it makes sect. *Lycopersicum* paraphyletic (see Fig. 1). In addition to these differences, Child's and D'Arcy's classifications differ in the sectional placement of ser. *Appendiculata,* and in the rank of sects. *Articulatum, Etuberosum,* and *Juglandifolium* (Fig. 3).

Our cpDNA tree shows many areas of agreement and conflict with other hypotheses of cladistic or phenetic relationships in subgenus *Potatoe* (Fig. 4A–I). Our support for ser. *Eriopersicon* (including *L. chmielewskii* and *L. peruvianum*) and ser. *Lycopersicon* (including *L. esculentum*) is congruent with the cpDNA results of Palmer and Zamir (1982, Fig. 4A). Our results mostly agree with cpDNA studies of Hosaka et al. (1984, Fig. 4C). The only discordance concerns sect. *Etuberosum,* placed by us as the sister group to sects. *Petota, Lycopersicum,* and *Juglandifolium,* and by Hosaka et al. (1984) as the sister group to the Mexican diploid members of sect. *Petota* (*S. bulbocastanum, S. cardiophyllum* Lindley, *S. pinnatisectum* Dunal, *S. polyadenium* Greenman; exclusive of *S. verrucosum* Schldl.). Our placement of sect. *Etuberosum,* however, is supported by only three cpDNA mutations. Crossing data indicate a close relationship between sects. *Etuberosum* and *Petota.* Members of sect. *Etuberosum* ($2n$) can be crossed with some $2n$ members of sect. *Petota* (Hermsen and Taylor, 1979). The hybrids have reduced pairing and complete sterility, but fertility can be restored by allopolyploidy (Hermsen, Ramanna, and Sawor, 1981). Also, crosses producing fertile hybrids can be made between sect. *Etuberosum* and sect. *Petota* by the use of bridging species (Ehlenfeldt and Hanneman, 1984). We consider the relationship of sect. *Etuberosum* to be equivocal, therefore, and in need of further study.

Our results are concordant with those of Martin et al. (1986, Fig. 4D), Debener, Salamini, and Gebhardt (1990, Fig. 4F), Miller and Tanksley (1990, Fig. 4G), Spooner, Sytsma, and Smith (1991, Fig. 4H), and Spooner and Sytsma (1992, Fig. 4I). Our results conflict with those of McClean and Hanson (1986, Fig. 4E), however, because their results separate various members of ser. *Eriopersicon,* ser. *Lycopersicon,* and subsect. *Lycopersicoides.* Seithe and Anderson's (1982) hypotheses (Fig. 4B), based on trichome types, supported the recognition of major subgroups within what was formerly a single section, *Basarthrum*; these in part are similar to the groups that Child (1990) and Bitter (1912b) distinguished. The amino acid sequence data of Boulter et al. (1979) closely united *Solanum tuberosum* (sect. *Petota*) and *Solanum lycopersicum* (ser. *Lycopersicon*) relative to other Solanaceae and other angiosperm families, as in our study.

Studies using other data bases are in general agreement with the results we present. The tomato/potato genetic linkage studies of Bonierbale, Plaisted, and Tanksley (1988) were highly suggestive of the close relationship of *Solanum* sect. *Petota* and sect. *Lycopersicum,* but in the absence of comparative data from other taxa these data cannot be used cladistically. They demonstrated that the chromosomes of *S. lycopersicum* (ser. *Lycopersicon*) and a hybrid population within sect. *Petota* are homosequential except for four paracentric inversions, located on three of the 12 chromosomes. Steinharter, Cooper-Driver, and Anderson (1986) summarized flavonol data from *Sola-*

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cpDNA; and Spooner and Sytsma (1992), using cpDNA data. Some of these "trees" were produced by cladistic analyses (e.g., Palmer and Zamir, 1982), some were produced by intuitive methods from a small data set (e.g., Seithe and Anderson, 1982), and some were produced by phenetic analyses (e.g., Miller and Tanksley, 1990). Trees are simplified and redrawn by relabeling putatively related taxa under the classification of Child (1990, Fig. 1).

num sect. *Androceras,* sect. *Basarthrum,* sect. *Petota,* and sect. *Solanum.* They interpreted the data to suggest a close relationship between sect. *Basarthrum* and sect. *Petota.* Lester (1991) summarized unpublished serological studies (West, 1973; Morris, 1979; Simpson, 1979) comparing taxa within and among ser. *Lycopersicon,* ser. *Eriopersicon,* sect. *Basarthrum,* and sect. *Etuberosum.* Lester's interpretative summary of these data were that: 1) antisera to *S. tuberosum* (sect. *Petota*) and to *L. pimpinellifolium* (*Solanum* ser. *Lycopersicon*) are extremely similar; 2) members of *Solanum* sects. *Petota, Etuberosum,* and *Juglandifolium* are very similar to each other and only slightly different from tomatoes; and 3) members of *Solanum* sect. *Basarthrum* show less similarity to all of the other groups above.

Steroidal alkaloids are common in *Solanum,* and have been used by Tétényi (1987) as chemotaxonomic characters to help classify the Solanaceae at the subfamily and tribal level. Within the Solanaceae, the taxonomic distribution of the steroidal glycoalkaloid tomatine provides support to relate the former genus *Lycopersicon* to *Solanum* subgenus *Potatoe.* Tomatine occurs in subgenus *Potatoe* in: 1) Section *Dulcamara* (Moench) Dumortier (*S. dulcamara, S. kieseritzkii* C. H. Meyer); 2) Section *Etuberosum* (*S. brevidens, S. etuberosum*); 3) Section *Juglandifolium* (*S. ochranthum*); 4) Section *Lycopersicum* (known from most of the species as the only glycoalkaloid present); 5) Section *Petota* (*S. acaule* Bitter, *S. chomatophilum* Bitter, *S. clarum* Correll, *S. demissum* Lindley, *S. jamesii* Torr., *S. lesteri* Hawkes and Hjert., *S. microdontum* Bitter, *S. neocardenasii* Hawkes and Hjert., *S. okadae* Hawkes and Hjert., *S. polyadenium* Greenman, *S. stoloniferum* Schldl. and Bouché; the other species listed in the following references being synonyms of these [Bognár and Makleit, 1965; Schreiber, 1968, 1979; Roddick, 1974; Deahl, Sinden, and Young, 1993). In addition to tomatine, section *Petota* has at least 11 other glycoalkaloids. The only known occurrences of tomatine outside of subgenus *Potatoe* is in *Lycianthes rantonnetii* (Carr.) Bitter (cited by Bognár and Makleit, 1965 and Roddick, 1974 as *S. rantonnetii* Carr., but a member of the solanaceous genus *Lycianthes* [D'Arcy, 1974]) and in *S. boerhaavii* Thell., a member of *Solanum* subgenus *Solanum,* sect. *Solanum* (W. G. D'Arcy, personal communication).

Members of subsect. *Lycopersicoides* can be crossed with some members of subsect. *Lycopersicum* (Rick, 1979; Taylor, 1986; DeVerna et al., 1990). Somatic fusion hybrids with limited fertility can be made between members of ser. *Lycopersicon* and subsect. *Lycopersicoides* (Handley et al., 1986). Somatic fusion hybrids also can be made between a member of ser. *Lycopersicon* and sect. *Petota,* but the hybrids are completely sterile (Melchers, Sacristan, and Holder, 1978). Based partly on these crossing data, Rick (1979) hypothesized that ". . . [*Solanum* sect. *Juglandifolium*] is the group most closely related and probably ancestral to *Lycopersicon.*" He argued that the strong barriers to interbreeding (as a result of encountering failure in repeated artificial attempts such as embryo rescue, bridging hybrids, somatic fusion), and the morphological differences between *Lycopersicon* and *Solanum* argued against merging the two genera. Our results (Figs. 1, 2) suggest that members of *Lycopersicon* (sensu D'Arcy, 1972) evolved within *Solanum* subgenus *Potatoe,* and support merging the genera. If the failure of artificial crosses was used in part for the recognition of generic boundaries, the genus *Solanum* would have to be split into a vast number of separate genera, and there are many phenetically distinct groups within *Solanum,* many more different from each other than are tomatoes and potatoes.

Our results provide a firm basis for continuing evolutionary studies in *Solanum* subgenus *Potatoe* by providing the first synthetic phylogenetic analysis of all of its major members. Our phylogeny can form the basis for comparisons in further studies of: 1) genome evolution between clades (like the work initiated by Bonierbale, Plaisted, and Tanksley [1988] comparing sect. *Lycopersicum* and sect. *Petota,* and Bernardello and Anderson [1990] within sections *Basarthrum* and *Anarrhichomenum*); 2) the relationship between DNA evolution and breeding systems (inbreeding and outbreeding systems are diverse in most members of subgenus *Potatoe,* e.g., as shown by Anderson [1979a] in *Solanum* sect. *Basarthrum*); 3) the evolution of tuberization in potato (Ganal et al., 1991); and 4) phylogenetic relationships based on other DNA markers.

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