Comparison of AFLPs with other markers for phylogenetic inference in wild tomatoes [*Solanum* L. section *Lycopersicon* (Mill.) Wettst.]

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Wild tomatoes (*Solanum* section *Lycopersicon*) are native to western South America. The delimitation and relationships of tomato species have differed widely depending upon whether morphological or biological species concepts are considered more important. Molecular data from mitochondrial, nuclear, and chloroplast DNA restriction fragment length polymorphisms (RFLPs), nuclear microsatellites, isozymes, and gene sequences of internal transcribed spacers of nuclear ribosomal DNA (ITS; multiple-copy), the single-copy nuclear encoded Granule-bound Starch Synthase gene (GBSSI or *waxy*), and morphology, have been used to examine hypotheses of species relationships. This study is a companion to the previous GBSSI gene sequence study and to the morphological study of relationships of all ten wild tomato species (including the recently described *S. galapagense*), with a concentration on the most widespread and variable species *S. peruvianum* s.l. These new AFLP data are largely concordant with the GBSSI and morphological data and in general support the species outlined in the latest treatment by C.M. Rick, but demonstrate the distinct nature of northern and southern Peruvian populations of *S. peruvianum*, and suggest that their taxonomy needs revision. *Solanum ochranthum* is supported as sister to wild tomatoes, and *S. habrochaites* and *S. pennellii* reside in a basal polytomy in the tomato clade.

KEYWORDS: Amplified Fragment Length Polymorphism, AFLP, congruence tests, *Lycopersicon*, phylogeny, Solanaceae, *Solanum* section *Lycopersicon*, tomato.

INTRODUCTION

All wild tomato species (*Solanum* section *Lycopersicon*) (see Table 1 for species list and authors of names) are native to western South America (Fig. 1). They are distributed along the coast and in the Andes, from Ecuador to northern Chile, and with two endemic species in the Galápagos Islands. We here informally treat wild tomatoes (Table 1) in subsection *Lycopersicon* to provide a coordinate name for their formally described outgroups in section *Juglandifolium* (Rydb.) Child and subsection *Lycopersicoides* Child. With the recently described *S. galapagense* from these islands, ten species are currently recognized (Darwin & al., 2003). Wild *S. lycopersicum* is supported as the ancestor of cultivated tomatoes, and the species occurs as a weedy escape from cultivation worldwide. All tomatoes are diploid ($2n = 24$; Rick, 1979; although rare tetraploid forms occur) and vary in breeding system from allogamous self-incompatible to facultative allogamous self-compatible to autogamous self-compatible (Rick, 1963, 1979, 1984, 1986a; Tables 1, 2). All wild tomatoes can be crossed (sometimes with difficulty) to the cultivated tomato. They are of paramount importance in breeding programs as sources of disease resistance and agronomic traits (Esquinas Alcazar, 1981; Rick, 1982a; Stevens & Rick, 1986). The tomato also serves as a model organism for genetic and developmental studies (Tanksley & McCouch, 1997; Hay & al., 2004).

There has been great controversy about the number of species in the group, their interrelationships, and their treatment in the genus *Solanum* or *Lycopersicon*. Spooner & al. (1993; Fig. 2D) provided a chloroplast DNA (cpDNA) restriction site phylogeny and morphological phylogeny that supported inclusion of *Lycopersicon* in *Solanum*. This treatment is also strongly supported by other chloroplast DNA restriction site and sequence data (Bohs & Olmstead, 1997, 1999; Olmstead & Palmer, 1997; Olmstead & al., 1999; Bohs, in press). These multiple datasets from a variety of genes unambiguously show tomatoes to be deeply nested in *Solanum*, and the majority of taxonomists are adopting

Table 1. Comparison of wild tomato species (*Solanum* L. section *Lycopersicon* subsection *Lycopersicon*) (data compiled from Müller, 1940; Luckwill, 1943; Esquinas Alcazar, 1981; Rick, 1982b, 1986b; Taylor, 1986). *Lycopersicon* synonyms in common use follow *Solanum* names.

Species	Fruit color	Breeding system[a]	Distribution and habitat[b]	Importance for breeding purposes
S. cheesmaniae (L. Riley) Fosberg [*L. cheesmaniae* L. Riley]	Yellow, orange	SC, exclusively At	En. to the Galápagos. From low elevations in the saline seashore up to 1300 m in volcanic areas	Salt tolerance, Lepidoptera and virus resistances, and genes involved in the retention of fruits and thick pericarp
S. chilense (Dunal) Reiche [*L. chilense* Dunal]	Green, purple stripes	SI, Al	Na. from S Peru to N Chile.; 0–3000 m; sympatric with *S. peruvianum*; grows in dry river beds, survives by deep roots	Drought resistance
S. chmielewskii (C. M. Rick, Kesicki, Fobes & Holle) D. M. Spooner, G. J. Anderson & R. K. Jansen [*L. chmielewskii* C. M. Rick, Kesicki, Fobes & Holle]	Green	SC, facultatively Al	Na. to S-C Peru to N Bolivia; 1500–3000 m; usually in slightly better-drained sites than *S. neorickii*	Contributed higher sugar content in the crop
S. galapagense S. Darwin & Peralta [*L. cheesmaniae* f. *minor* (Hook. f.) C. H. Müll.]	Yellow, orange	SC, exclusively At	En. to the Galápagos; from low elevations in the saline seashore	As for *S. cheesmaniae*
S. habrochaites S. Knapp & D. M. Spooner [*L. hirsutum* Dunal]	Green	Typically SI, 1-2 collections SC, but with later inbreeding depression	Na. from SW Ecuador to S-Central Peru; 500–3300 m; typically from forested regions in moist well drained soils	Cold and frost tolerance. Insect resistance (glandular hairs), and other resistances
S. lycopersicum L. [*L. esculentum* Mill.]	Red	SC, facultatively Al	Probably Na. from Ecuador and Peru, now widespread; wide range of habitats, weed in newly open areas	Moisture-tolerance, resistance to wilt, root-rotting, and leaf-spotting fungi
S. neorickii D. M. Spooner, G. J. Anderson & R. K. Jansen [*L. parviflorum* C. M. Rick, Kesicki, Fobes & Holle]	Pale green	SC, highly At	Na. from S Ecuador to S-C Peru; 1500–3000 m; moist and well-drained rocky environments, Pacific side; more widespread than *S. chmielewskii*	
S. pennellii Correll [*L. pennellii* (Correll) D'Arcy]	Green	Usually SI, some SC in southern part of species range	Na. in coastal Peru (8–16 °S); from 50 m, but typically 500–1500 m; occurs in hot dry habitats subject to dew and fog; many stomata adaxially, poor root system	Contributed drought resistance; dense pubescence of glandular hairs imparts insect resistance
S. peruvianum L. s.l. [*L. peruvianum* (L.) Mill.]	Green	Typically SI, Al, rare pop. SC, At (trend to reduced variability in Northern races)	Na. from N Peru to N Chile, 0–3000 m; Wide range of environments	Virus, bacteria, fungi, aphid, and nematode resistances
S. pimpinellifolium L. [*L. pimpinellifolium* (L.) Mill.]	Red	SC, At, facultative Al	Na. in S Ecuador and N Peru; W end of river valleys on Pacific side coastal to usually below 1000 m; often a weed in cultivated fields	Contributed to improved color and fruit quality. Insect, nematode, and disease resistances

[a]SC = self-compatible, SI = self-incompatible, At = autogamous, Al = allogamous. [b]Na. = native, En. = endemic.

Solanum as the genus name for tomatoes.

Some continue to use the *Lycopersicon* names (e.g., Nuez & al., 2004), adopting arguments of Brummitt (2002) that Linnaean nomenclature without paraphyletic taxa is a logical impossibility. Brummitt's (2002) arguments, however, only support maintenance of traditional Linnaean classifications without indicating how new discoveries showing paraphyly should be treated. It essentially is an argument for convenience and stasis, unlike arguments of De Queiroz & Gauthier (1994) who propose rankless, non-Linnaean nomenclature. We use a phylogenetic classification philosophy and a Linnaean nomenclatural system, and place tomatoes in *Solanum* where they were originally placed by Linnaeus (1753), but provide their names in the segregate genus *Lycopersicon* for ease of comparison to the literature (Table 1).

Peralta & Spooner (2001; Fig. 2F) provided a GBSSI gene sequence phylogeny of tomatoes, concentrating on the most geographically widespread and polymorphic species *S. peruvianum*. That study supported section *Juglandifolium* (*S. juglandifolium* + *S. ochranthum*) as sister to tomatoes and subsection *Lycopersicoides* (*S. lycopersicoides* + *S. sitiens*) as sister to the above, and potatoes (section *Petota*) sister to the entire "tomato" clade to include section *Juglandifolium* and subsection *Lycopersicoides*. Within subsection *Lycopersicon*, there was a basal polytomy composed of the self-incompatible and green-fruited species *S. chilense*, and the central-southern Peruvian to northern Chilean populations of *S. peruvianum*, *S. habrochaites*, and *S. pennellii*. A sister clade contained the northern Peruvian populations of *S. peruvianum* (also self-incompatible and green-fruited), *S. chmielewskii* and *S. neorickii* (self-compatible, green-fruited), and a monophyletic group composed of the self-compatible and brightly-colored (red- to orange- to yel-

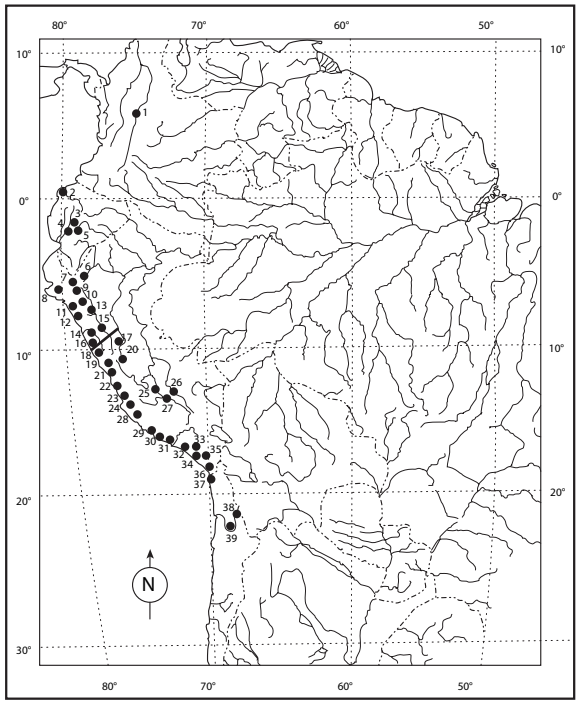

Fig. 1. Distribution map showing the tomato accessions examined here (except for *Solanum cheesmaniae* and *S. galapagense*, located at approximately 0°S and 90°W in the Galápagos Islands). A line drawn at ~10°S indicates the northern (N) and southern (S) edges of the "northern" and "southern" *S. peruvianum* populations. Map numbers correspond to those in the Appendix and Figs. 7 and 8, and to the companion GBSSI sequence study (Peralta & Spooner, 2001) and morphological study (Peralta & Spooner, in press).

low-) fruited species *S. cheesmaniae* (including accessions now recognized as *S. galapagense*), *S. lycopersicum*, and *S. pimpinellifolium*. Peralta & Spooner (in press; Fig. 2I) provided phenetic and cladistic analyses of largely the same accessions using morphological data. That study supported not only the traditionally recognized species of wild tomatoes, but also demonstrated the distinct nature of the northern and southern Peruvian populations of *S. peruvianum*, and suggested that they may represent distinct species.

Other studies using fewer accessions also have investigated phylogenetic relationships in subsection *Lycopersicon* with data from cpDNA restriction site data, (Palmer & Zamir, 1982; Fig. 2A), mitochondrial DNA (mtDNA) restriction sites (McClean & Hanson, 1986; Fig. 2B), nuclear RFLPs (Miller & Tanksley, 1990; Fig. 2C), isozymes (Breto & al., 1993; Fig. 2E), ITS gene sequence data (Marshall & al., 2001; Fig. 2G), and nuclear DNA microsatellites (Alvarez & al., 2001; Fig. 2H).

The Amplified Fragment Length Polymorphism (AFLP) technique used in this study combines restriction enzyme reactions with the Polymerase Chain Reaction (PCR), revealing high levels of polymorphism (Vos & al., 1995). AFLP data have been shown to be useful in phylogenetic studies and to have generally high congruence with many other marker types (Powell & al., 1996; Milbourne & al., 1997; Russell & al., 1997). These data have been successfully used to study relationships of species within genera (Spooner & Lara-Cabrera, 2001). Within section *Petota* AFLPs have been used to study the phylogeny of 19 wild potato taxa and three taxa of *Solanum* section *Lycopersicon* (Kardolus & al., 1998); species within *Solanum* series *Longipedicellata* (van den Berg & al., 2002); and species within Mexican diploid wild potatoes (Lara-Cabrera & Spooner, 2004), with results concordant to some current taxonomic hypotheses. Elsewhere in Solanaceae, Mace & al. (1999a) studied members of the solanaceous tribe *Datureae* (*Datura* L. and *Brugmansia* Pers.), and Mace & al. (1999b) studied the genetic relationships among cultivated and wild eggplants [members of *Solanum* subgenus *Leptostemonum* (Dunal) Bitter]; both datasets found consistent results with ITS sequences, isozymes and morphology.

The purpose of this study is to explore the utility of AFLPs to elucidate phylogenetic relationships of wild tomatoes, and to explore its congruence with other molecular and morphological results.

MATERIALS AND METHODS

Plants. — We analyzed a total of 65 accessions, including all ten recognized species of tomatoes (Figs. 3–5). Most of these accessions correspond to the GBSSI (Peralta & Spooner, 2001) and morphological studies (Peralta & Spooner, in press), except for the addition of eight new accessions of *S. peruvianum* and the deletion of 11 accessions of *S. peruvianum* relative to the GBSSI study. For efficiency of comparison with prior studies, we used the same 39 generalized geographic regions published in those papers (Appendix, Fig. 1); accessions were not used here for map localities 1, 2, 20, 25. All tomato accessions, representing much of the ingroup variation, were obtained from the C.M. Rick Tomato Genetics Resource Center, Department of Vegetable Crops, University of California, Davis (TGRC). The late Dr. Charles Rick, former curator of this genebank, kindly provided advice on the choice of accessions, based on geographic distribution, morphology, genetic diversity, and breeding behavior (Table 1, Fig. 1). The wild potato accessions were obtained from the U.S. Potato Genebank in Sturgeon Bay, Wisconsin (Bamberg & al., 1996). Outgroups were chosen based on Spooner & al. (1993) and Peralta & Spooner (2001) to represent immediate outgroups of tomatoes in *Solanum* section *Juglandifoli-*

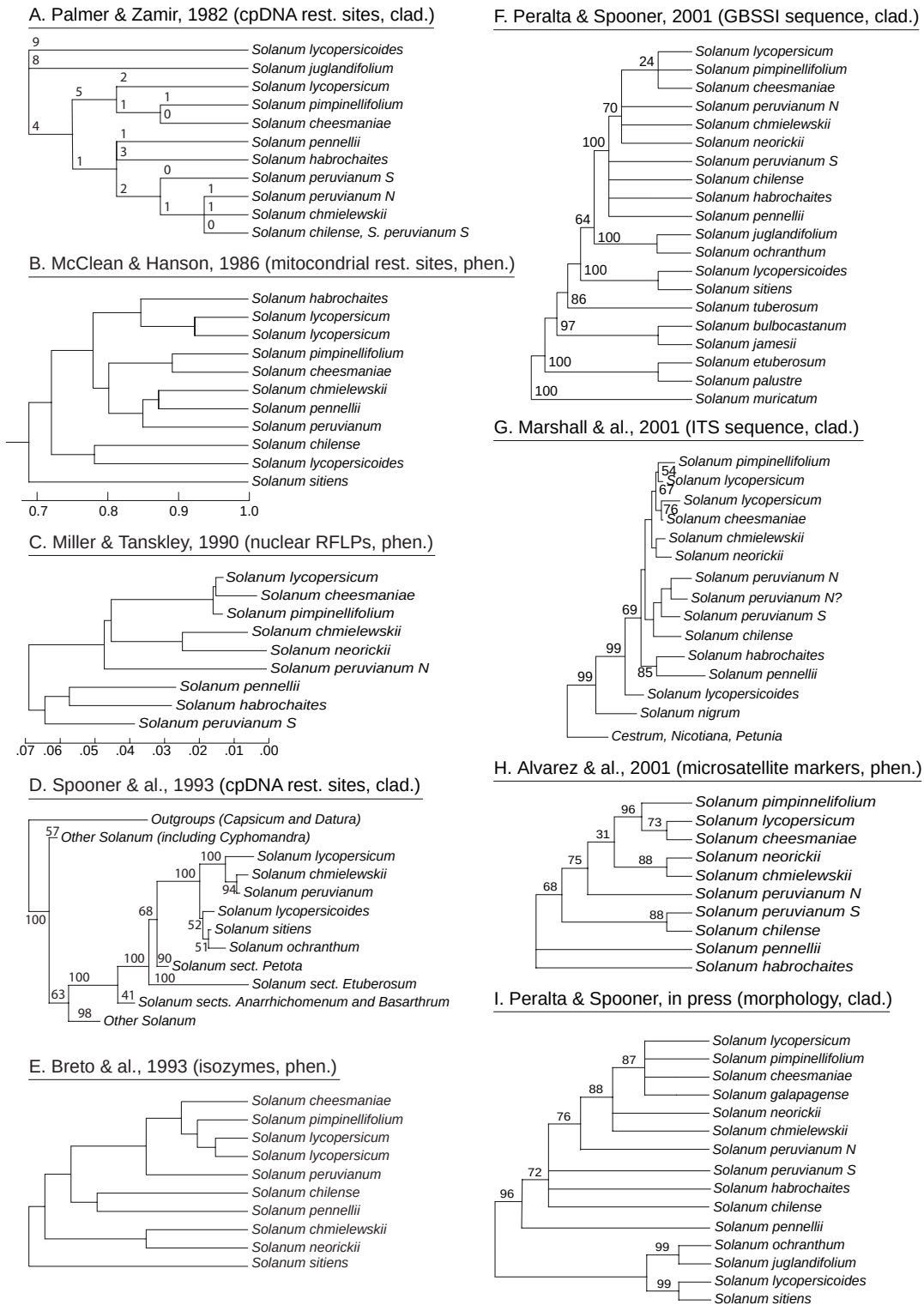

Fig. 2. An abstracted summary of cladistic (clad.) and phenetic (phen.) studies of tomatoes and outgroups using morphological, isozyme, and molecular data, including similarity coefficients (lines below trees, B, C) restriction sites supporting each branch (A), or bootstrap values over 50% (D, F, G, H, I); the study in E showed no statistics to support the tree. The trees are shortened when necessary to show summary results and use the *Solanum* equivalents of *Lycopersicon* names (Table 1). The letters N and S following *S. peruvianum* indicate northern (N) and southern (S) accessions of that species corresponding to the companion GBSSI sequence study (Peralta & Spooner, 2001) and morphological study (Peralta & Spooner, in press), as delineated in Fig. 1 and as used in Figs. 2, 6-9.

Fig. 3. Leaves of tomato and outgroup species; Figs. 3–5 have the species arranged in the same order but the accessions are sometimes different. See Table 2 for explanation of LA codes. A, *S. lycopersicum* (*LA1673*); B, *S. pimpinellifolium* (*LA2646*); C, *S. cheesmaniae* (*LA1450*); D, *S. galapagense* (*LA317*); E, *S. neorickii* (*LA247*); F, *S. chmielewskii* (*LA1306*); G, *S. peruvianum* northern population (*LA2152*); H, *S. peruvianum* northern population (LA2561); I, *S. peruvianum* southern population (*LA1947*); J, *S. peruvianum* southern population (*LA1647*); K, *S. chilense* (*LA2884*); L, *S. habrochaites* (*LA1353*); M, *S. pennellii* (*LA1376*); N, *S. ochranthum* (*LA3650*); O, *S. juglandifolium* (*LA2134*); P, *S. lycopersicoides* (*LA2772*); Q, *S. sitiens* (*LA2876*). Scale bars = 1 cm in C and D, 2 cm in A, B, E, F, G, H, I, J, K, M, P and Q, and 3 cm in L, N and O.

Fig. 4. Flowers of tomato and outgroup species. A, *S. lycopersicum* (*LA1226*); B, *S. pimpinellifolium* (*LA1581*); C, *S. cheesmaniae* (*LA166*); D, *S. galapagense* (LA317); E, *S. neorickii* (*LA2200*); F, *S. chmielewskii* (*LA1306*); G, *S. peruvianum* northern population (*LA2328*); H, *S. peruvianum* northern population (*LA2562*); I, *S. peruvianum* southern population (*LA1954*); J, *S. peruvianum* southern population (*LA1647*); K, *S. chilense* (*LA1930*); L, *S. habrochaites* (*LA1223*); M, *S. pennellii* (*LA1926*); N, *S. ochranthum* (*LA3650*); O, *S. juglandifolium* (*Spooner & al. 5088*); P, *S. lycopersicoides* (*LA2772*); Q, *S. sitiens* (*LA2876*). Scale bars = 0.5 cm in E–G; 1 cm in A–D, H–Q.

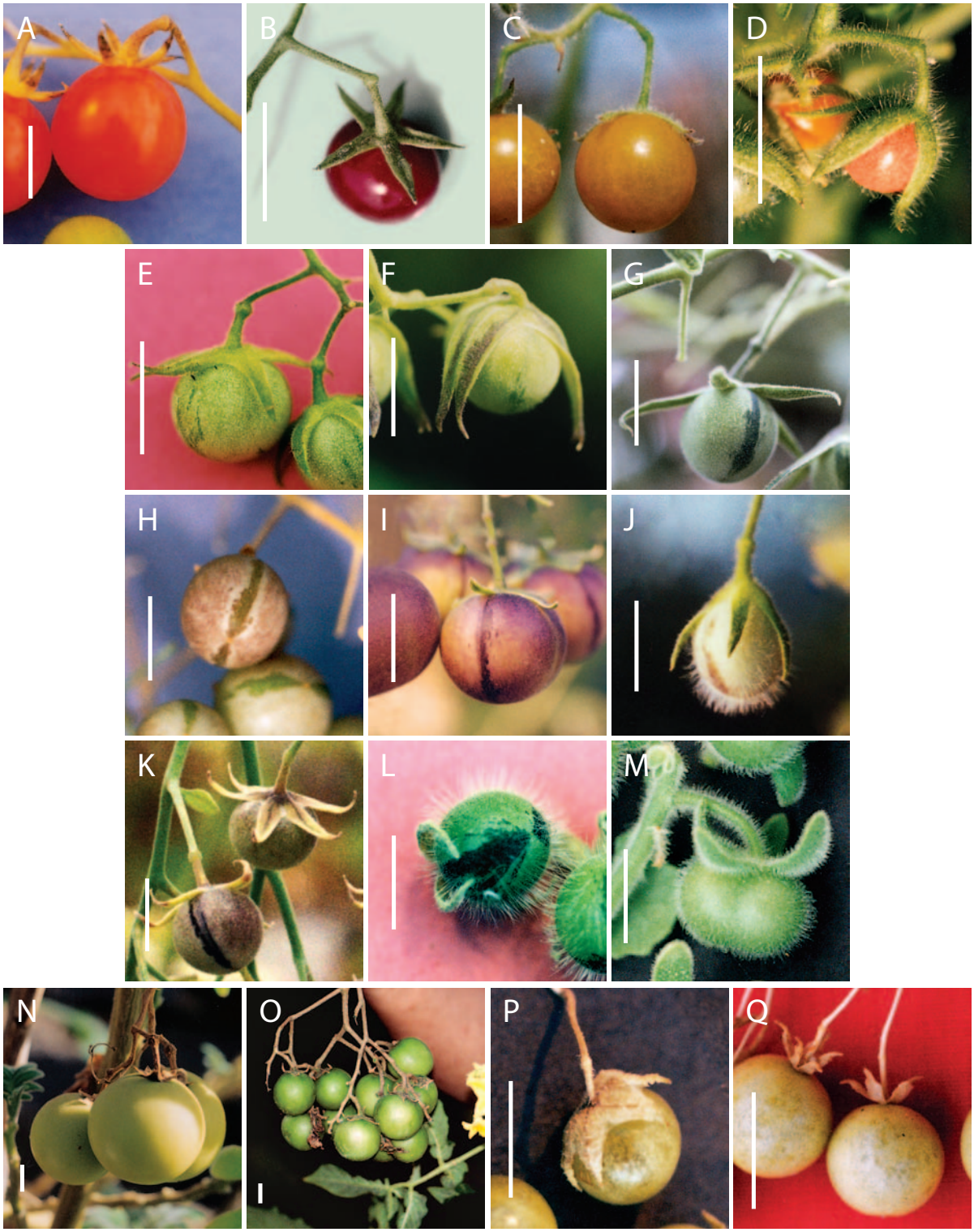

Fig. 5. Fruits of tomato and outgroup species. A, *S. lycopersicum* (*LA1673*); B, *S. pimpinellifolium* (*LA1237*); C, *S. cheesmaniae* (*LA1450*); D, *S. galapagense* (*LA317*); E, *S. neorickii* (*LA2200*); F, *S. chmielewskii* (*LA2663*); G, *S. peruvianum* northern population (*LA2548*); H, *S. peruvianum* northern population (*LA1365*); I, *S. peruvianum* southern population (*LA153*); J, *S. peruvianum* southern population (*LA1609*); K, *S. chilense* (*LA1930*); L, *S. habrochaites* (*LA1353*); M, *S. pennellii* (*LA716*); N, *S. ochranthum* (*Spooner & al. 5000*); O, *S. juglandifolium* (*Castillo & al. 1206*); P, *S. lycopersicoides* (*LA2772*); Q, *S. sitiens* (*LA2876*). Scale bars = 1 cm throughout.

um (*S. ochranthum*) and subsection *Lycopersicoides* (*S. lycopersicoides*, *S. sitiens*), then further outgroups in section *Petota* (*S. cardiophyllum*, *S. ehrenbergii*, *S. pinnatisectum*), and section *Etuberosum* (*S. etuberosum*). These latter accessions (those with six-digit Plant Introduction or "PI" numbers) were from the National Research Support Program-6 (NRSP-6; Bamberg & al., 1996; Appendix).

Vouchers for all these accessions were field-grown in Wisconsin, U.S.A. and Mendoza, Argentina in 2000 and duplicates are deposited in BM, DAV, MERL and WIS. Some of the LA (TGRC) accessions are represented by herbarium specimens collected by C. M. Rick and colleagues and deposited in a variety of herbaria, mostly in South America; where appropriate, the location of these original herbarium vouchers is cited, rather than our field-grown vouchers. Where original vouchers do not exist, we have cited the voucher numbers as given by the TGRC as Rick & al. followed by our field grown voucher number if different. A database of tomato specimens is available from the authors and complete exsiccatae will be published in our monograph of the group (Peralta, Knapp, and Spooner, in prep.).

AFLP primer selection and amplification. — Total genomic DNA was extracted from a single individual per accession from fresh leaves of 2-month-old plants, following the procedure of Doyle & Doyle (1987), and purified over CsCl/ethidium bromide gradients. AFLPs (Vos & al., 1995) were generated for all accessions using four primer combinations, chosen on advice of Glenn Bryan of the Scottish Crop Research Institute, Dundee, based on clarity of band pattern, number of markers, and well-distributed markers in a potato (*Solanum* section *Petota*) mapping population (unpublished data). These were: *Pst*I+AC, *Mse*I+AGC; *Pst*I+AG, *Mse*I+ACC; *Pst*I+AG, *Mse*I+AGT; *Pst*I+CT, *Mse*I+AGG. DNA was double-digested with the restriction enzyme combination *Pst*I-*Mse*I. Appropriate linkers were ligated to digested DNA and two rounds of PCR were initiated. Fragments were separated by polyacrylamide gels and markers scored with proprietary technology developed by KeyGene N. V. (Wageningen, The Netherlands). Bands were scored as presence or absence and no attempt was made to differentiate homozygotes from heterozygotes based on differential band intensity.

Cladistic analysis. — Phylogenetic reconstruction was performed using PAUP version 4.0b8 (Swofford, 2001), using Fitch parsimony (Farris, 1970). *Solanum etuberosum* was designated as the farthest outgroup, following results of Spooner & al. (1993). To find multiple tree islands, we used a four-step search strategy (modified from Olmstead & Palmer, 1994). (1) Five hundred thousand replicates initially were run using random order entry starting trees with nearest-neighbor interchange (NNI). (2) The shortest trees from this analysis were used individually as starting trees with the tree-bisection-reconnection (TBR) method. (3) The resulting trees were searched with NNI, retaining all most parsimonious trees (MULPARS). (4) The resulting trees were searched with TBR and MULPARS. The resulting trees were used to compute a strict consensus tree. A bootstrap analysis was conducted on 100 replicates with TBR and MULPARS. We also performed a cladistic analysis of 48 taxa common to AFLP and GBSSI data, and ten taxa common to AFLP, GBSSI, cpDNA, and ITS data.

Phenetic analysis. — AFLP data were analyzed using NTSYS-pc® version 2.02k (Rohlf, 1997). Similarity matrices (in SIMQUAL) were generated using DICE similarity matrix, which places less weight on shared absent bands, as an appropriate algorithm for AFLPs that are predominately dominant markers. Clustering was performed using the unweighted pair-group method (UPGMA) and the Neighbor-Joining method in SAHN. We chose the tree that had the highest cophenetic correlation coefficient of the tree to the similarity matrix as determined by COPH and MXCOMP in NTSYS-pc.

Congruence tests among AFLP, cpDNA, GBSSI, ITS, and morphological studies. — Different tests have been developed that assess the general null hypothesis of homogeneity between datasets. We tested congruence among our new AFLP results to the cpDNA (Palmer & Zamir, 1982), GBSSI (Peralta & Spooner, 2001), ITS (Marshall & al., 2001) and morphology (Peralta & Spooner, in press) datasets through three methods: (1) distance matrix-based comparisons, (2) character-based comparisons, and (3) visual qualitative comparison of trees. Two comparative datasets were constructed. The larger comparative dataset contained 47 identical tomato accessions from our AFLP and GBSSI studies and contained one additional accession of *S. etuberosum* as outgroup. The smaller comparative dataset contained only 10 accessions that were common to all studies cited above (all tomato species except *S. neorickii* were included, the northern and southern accessions of *S. peruvianum* were included as separate taxa, and *S. lycopersicoides* was the common outgroup). We reconstructed a cpDNA matrix from Palmer & Zamir (1982) and obtained the ITS matrix from Marshall & al. (2001). We realigned the indels of the latter after deletion of nine taxa to construct a common 10-taxon data matrix of tomatoes (with *S. lycopersicoides* as outgroup).

Our morphological data (Peralta & Spooner, in press) included a predominately quantitative dataset of 66 characters for 41 taxa common to AFLP and GBSSI studies, and a subset of 10 taxa common to AFLP, cpDNA, GBSSI, and ITS studies for phenetic analyses (Table 2). Our morphological data also included a quali-

tative dataset of 26 characters for 10 taxa common to AFLP, cpDNA, GBSSI, and ITS for cladistic analysis (Table 3).

Distance-based comparisons of six datasets (AFLP, cpDNA, GBSSI, ITS, morphology cladistics, morphology phenetics; Table 2) were conducted by first constructing pair-wise distance matrices. For the GBSSI and ITS data we used the Jukes & Cantor (1969) distance method and for the cpDNA restriction site data we used Nei & Li (1979); both available in PAUP. For the AFLP data we used the DICE matrix, and for the morphological data we used the distance algorithm for phenetic comparisons, and simple matching algorithm for cladistic comparisons, both present in NTSYS-pc. The comparison of matrices test assumes that the two matrices have been obtained independently. The program takes two symmetric similarity or dissimilarity matrices and plots one matrix against the other, element by element. The product-moment correlation coefficient, r, between their associated path-length matrices, and the Mantel test statistic, Z, to measure the degree of relationship between the two matrices were computed with the Mantel test (Mantel, 1967) as performed in NTSYS-pc. The correlation coefficient varies from 0 (no correspondence of matrices) to 1 (perfect correspondence). We interpret the significant association of the matrices by using the critical values of matrix correlations coefficient found in Appendix of Lapointe & Legendre (1992). We also analyzed distance values between three pairs of species representing close, intermediate, and far species comparisons (Table 4).

Character-based comparisons of five datasets (AFLP, cpDNA, GBSSI, ITS, morphology; Table 3) used the incongruence length difference (ILD) test, also called the partition homogeneity test of data partition congruence, of Farris & al. (1995), available in PAUP version 4.0b8 (Swofford, 2001). The ILD test is based on an expectation that data partitions which reflect different topologies will have higher overall homoplasy in combination, than will data partitions that reflect a single topology. Consequently, combined analysis of incongruent datasets should yield trees that are significantly longer than the sum of the tree lengths inferred from each data partition separately (Hipp & al., 2004). The ILD statistic, D, shows the difference between tree lengths of combined partitions and the sum of tree lengths of data partitions analyzed separately: $D = L_{(1+2+\ldots+N)}-(L_1+L_2+\ldots+L_N)$, where L_N is the length of the most parsimonious tree(s) found for each data partition N, and $L^{(1+2+\ldots+N)}$ is the length of the most parsimonious tree(s) for the combined data. By comparing D to a distribution generated by randomly partitioning the combined data according to the number and size of the original data partitions, the ILD test provides a p-value that estimates the type I error rate, i.e., the probability of rejecting the null hypothesis that the data partitions are congruent with another. If two datasets are highly incongruent then the sum of their minimal trees should be significantly shorter than that of the sum of tree lengths from random partitions of the combined data and the null hypothesis will be rejected (Hoot & al., 1997). To reject the null hypothesis usually the type I error rate is set at 5%. When P values ≥ 0.05 the null hypothesis is accepted, concluding that the data sets are significantly homogeneous. All combinations were run on 100 replicates, heuristic search option with simple addition sequence, TBR, and MULPARS in effect. The ILD test has been criticized by Yoder & al. (2001), but their criticisms have been refuted by Hipp & al. (2004).

RESULTS

In this paper we use the ranks of Child (1990) as a convenient temporary reference to tomato groups, although these ranks will change in our monograph of tomatoes and their relatives (Peralta & al., in prep.). Spooner & al. (1993) present a graphical display of Child's nomenclaturally nested tomato and potato nomenclature.

Cladistic analysis. — The four AFLP primer combinations produced 328 characters with 0.6% missing data. Thirty-five characters were uninformative in the cladistic analysis. Fitch parsimony analysis produced 296 most parsimonious 1174-step trees with a consistency index of 0.25 and a retention index of 0.50 (Fig. 6). A strict consensus tree of these 296 trees (Fig. 7) shows tomatoes (*Solanum* section *Lycopersicon* subsection *Lycopersicon*) and their immediate outgroup relatives (*S. ochranthum* representing section *Juglandifolium*, and *S. lycopersicoides* + *S. sitiens* representing section *Lycopersicon* subsection *Lycopersicoides*) to form a sister clade to potatoes (section *Petota*; *S. cardiophyllum*, *S. ehrenbergii*, *S. pinnatisectum*) and further outgroups (*S. etuberosum*; section *Etuberosum*). *Solanum pennellii* and *S. habrochaites* are part of a basal polytomy in the tomato clade. All brightly-colored-fruited, self compatible species (*S. cheesmaniae*, *S. galapagense*, *S. lycopersicum*, *S. pimpinellifolium*) form a well supported clade (100% bootstrap). *Solanum chmielewskii*, *S. neorickii*, and four accessions of the self-incompatible northern *S. peruvianum* from the Río Marañón drainage form a clade (52% bootstrap support). Only one accession from northern Peru (LA 1984) grouped with the southern *S. peruvianum*. Interestingly Rick (1986a) considered this accession as a crossing bridge between northern and southern populations of *S. peruvianum*.

Phenetic results. — Because AFLPs are dominant markers, a case could be made that they should be

Table 2. Distance matrix-based comparisons as determined by Mantel tests of association among 17 pairs of similarity matrices derived from AFLPs (this study), ITS (Marshall & al., 2001), cpDNA (Palmer & Zamir, 1982), GBSSI (Peralta & Spooner, 2001), and morphology data (Peralta & Spooner, in press). In the first 15 pairs, the distance matrix comparisons were statistically associated (α = 0.05) according to the critical values of the cross-product matrix correlation coefficient Appendix of Lapointe & Legendre (1992). See text for explanation of different sample sizes.

Comparisons	Number of accessions per comparison of dissimilarity matrices	Matrix correlation r (= normalized Mantel statistic Z)	Approximate Mantel *t* test	P (random Z ≥ obs. Z)
AFLP/GBSSI	10	0.858	3.149	0.0002
cpDNA/GBSSI	10	0.831	2.880	0.0137
AFLP/GBSSI	48	0.822	7.119	0.0002
AFLP/cpDNA	10	0.765	3.056	0.0014
cpDNA/morphology cladistics	10	0.675	3.056	0.0009
AFLP/morphology cladistics	10	0.669	3.089	0.0003
cpDNA/morphology phenetics	10	0.594	2.241	0.0062
AFLP/morphology phenetics	10	0.579	2.232	0.0130
GBSSI/morphology phenetics	10	0.562	1.865	0.0327
GBSSI/morphology cladistics	10	0.557	2.200	0.0070
ITS/morphology phenetics	10	0.532	1.777	0.0524
AFLP/ITS	10	0.471	1.732	0.0091
ITS/morphology cladistics	10	0.410	1.690	0.0629
AFLP/morphology phenetics	41	0.324	2.368	0.0374
GBSSI/ITS	10	0.261	0.832	0.1402
GBSSI/morphology phenetics	41	0.255	2.164	0.0331
ITS/cpDNA	10	0.092	0.322	0.3394

analyzed with phenetic methods (Koopman & al., 2001). The cophenetic correlation coefficient (r, varies from 0 = poor correlation to 1 = perfect correlation) of DICE/Neighbor Joining was 0.735, vs. 0.961 for DICE/UPGMA (Fig. 8). A phenetic analysis is designed to distinguish similar groups of individuals that could be interpreted to support species status of grouped accessions.

Table 3. Character-based comparisons as determined by the incongruence length difference (ILD) test, also called the partition homogeneity test, among pairs of similarity matrices derived from AFLP (this study), ITS (Marshall & al., 2001), cpDNA (Palmer & Zamir, 1982), GBSSI (Peralta & Spooner, 2001), and morphological data (Peralta & Spooner, in press). P values ≥ 0.05 (the first nine comparisons designated by an asterisk) indicate congruent trees between pairs of data. See text for explanation of different sample sizes.

Comparisons	Number of accessions per tree	P value
*ITS/cpDNA	10	0.58
*AFLP/GBSSI	10	0.22
*AFLP/GBSSI	48	0.15
*GBSSI/morphology	10	0.10
*AFLP/ITS	10	0.08
*GBSSI/ITS	10	0.06
*AFLP/cpDNA	10	0.06
*ITS/morphology	10	0.05
*AFLP/morphology	10	0.05
cpDNA/morphology	10	0.02
cpDNA/GBSSI	10	0.01

The cladogram and phenogram outline almost the same set of species groups, and place outgroup taxa similarly. The phenogram could represent the phylogeny when similarities are mainly due to shared derived characteristics (Futuyma, 1998). Like the cladogram, the phenogram groups all the brightly-colored-fruited species, groups *S. pennellii* and *S. habrochaites* (adjacent on the cladogram), groups all accessions of *S. chilense*, largely separates the northern and southern accessions of *S. peruvianum*, separates the four northern accessions of *S. peruvianum* from other northern accessions, and groups them with *S. chmielewskii* and *S. neorickii*.

Congruence tests. — The distance-matrix Mantel tests of associations (Table 2) showed that all pairs of matrices compared were statistically correlated at (α = 0.05) as determined by the criterion of Lapointe & Legendre (1992), except in the last three cases: GBSSI/ITS, GBSSI/morphology phenetics, and ITS/cpDNA. It is interesting to note that increasing the number of taxa, from 10 to 41, in the GBSSI/morphology phenetics comparison, lowered the correlation coefficient from 0.562 to 0.255. A similar trend was found in the AFLP/morphology phenetics matrices comparison with 10 and 41 taxa. In both cases the matrices were significantly correlated. The matrix correlation coefficients

Table 4. Genetic and morphological distances of selected pairs of species, chosen to represent close, intermediate, and far species comparisons.

	Marker, distance algorithm, and distance values				
Pairs of taxa	AFLP (DICE)	GBSSI (Jukes-Cantor)	cpDNA (Nei-Li)	ITS (Jukes-Cantor)	Morphology cladistic (simple matching)
S. lycopersicum/S. pimpinellifolium (close comparison)	0.851	0.999	0.917	0.980	0.885
S. lycopersicum/S. pennellii (intermediate)	0.542	0.991	0.791	0.877	0.307
S. lycopersicum/S. lycopersicoides (far)	0.233	0.964	0.500	0.932	0.269

The AFLP (this study), GBSSI (Peralta & Spooner, 2001) and cpDNA (Palmer & Zamir, 1982) comparisons used the same accessions when possible among studies; the morphology cladistic data (Peralta & Spooner, in press) were general species values. *Solanum lycopersicum* (LA1673 for AFLP and GBSSI; cultivar T6 at UC Davis for cpDNA); *S. pennellii* (LA716 for AFLP, GBSSI, cpDNA); *S. lycopersicoides* (LA2386 for AFLP; LA1990 for GBSSI; LA1964 for cpDNA).

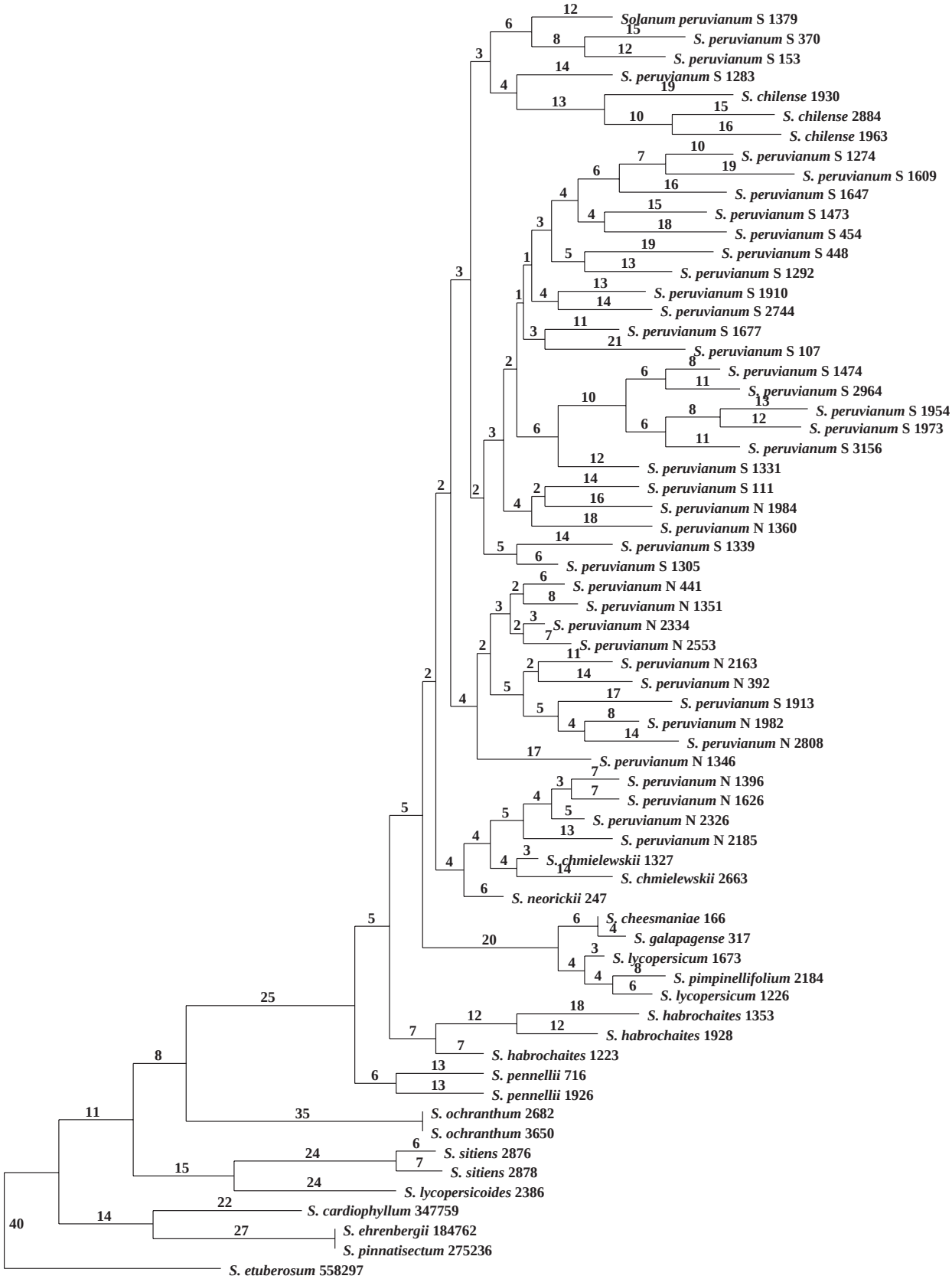

Fig. 6. One representative phylogram of the 296 most parsimonious 1174-step Fitch trees, consistency index 0.25, retention index 0.50. Numbers indicate branch lengths; accession codes correspond to Table 2.

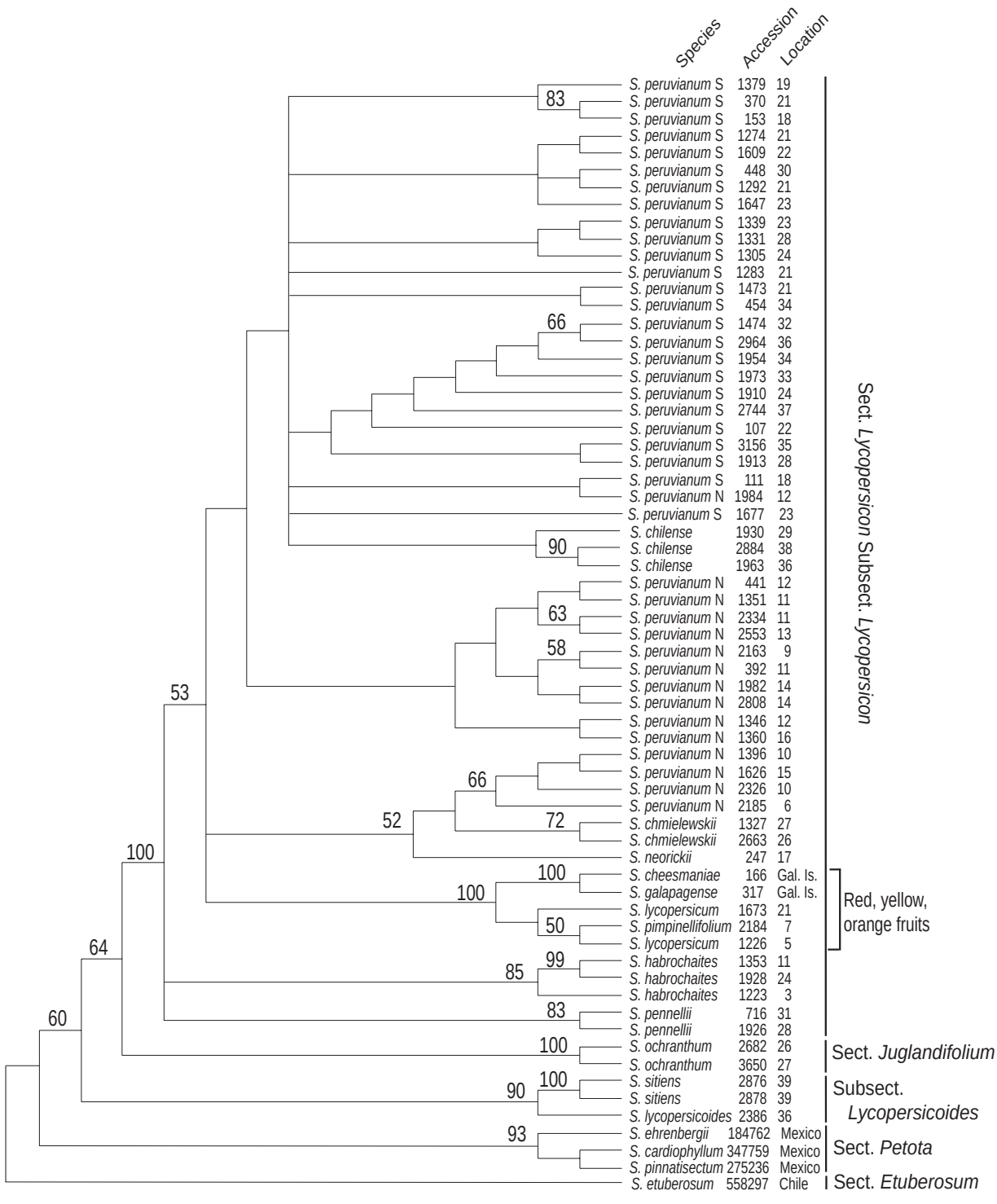

Fig. 7. The strict consensus cladogram of the 296 most parsimonious 1174-step Fitch trees. Location codes correspond to Fig. 1, with the locations in Chile, Galápagos Islands (Gal. Is.), and Mexico outside the map area; accession codes correspond to Table 2. The numbers above each branch represent bootstrap values over 50%.

of all comparisons varied greatly with the AFLP/GBSSI the highest (Z = 0.858), and the ITS/cpDNA the lowest (Z = 0.092). The ILD tests (Table 3) show the ITS/cpDNA, AFLP/GBSSI (both 10 and 48 taxon comparisons), the GBSSI/morphology, AFLP/ITS, GBSSI/ITS, AFLP/cpDNA, ITS/morphology, and AFLP/mor-

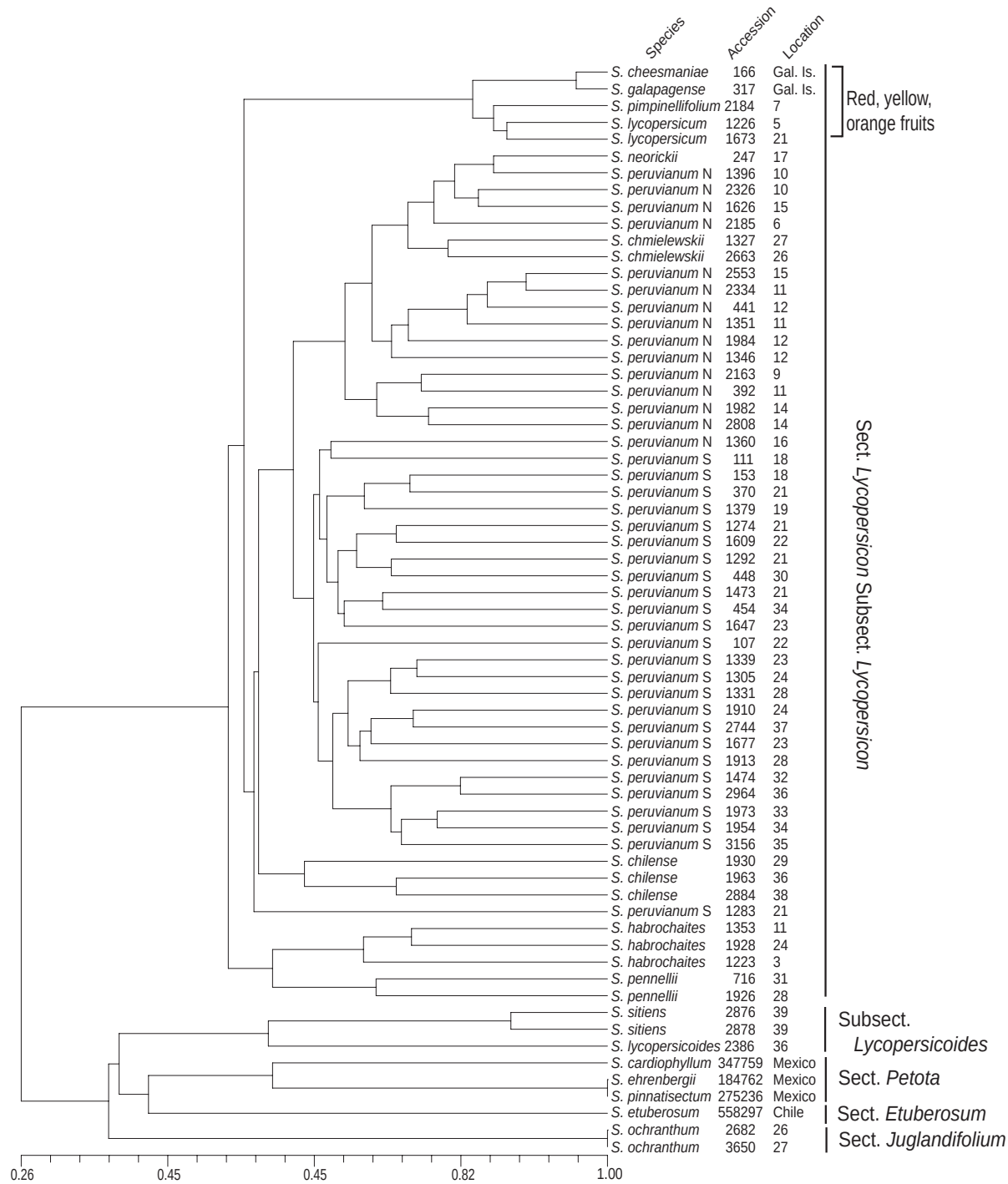

Fig. 8. The UPGMA dendrogram (DICE similarity matrix). Location codes correspond to Fig. 1, with the locations in Chile, Galápagos Islands (Gal. Is.), and Mexico outside the map area; accession codes correspond to Table 2.

phology datasets to be congruent at a P value ≥ 0.05. The other comparisons (cpDNA/morphology, cpDNA/GBSSI) proved to be incongruent.

A combined AFLP and GBSSI Fitch tree (48 taxa; 1652 characters) produced 34 most parsimonious 994-step trees with a consistency index of 0.35 and a retention index of 0.56. A strict consensus tree of these 34 trees (not shown) present a topology very similar to the AFLP strict consensus tree (Fig. 7), including showing the relationship *S. chmielewskii*, *S. neorickii*, and four accessions of the self-incompatible northern *S. peruvianum* from the Río Marañón drainage. A combined

AFLP, GBSSI, cpDNA, ITS tree, and morphology analysis (10 taxa; 2299 characters of which 148 were parsimony informative) produced two most-parsimonious 577-step trees with a consistency index of 0.816 and a retention index of 0.603. A consensus tree of these two trees (Fig. 9) shows: (1) The brightly-colored-fruited species as monophyletic supported by 100% bootstrap, with *S. pimpinellifolium* sister to *S. cheesmaniae* and *S. lycopersicum*, (2) *S. chmielewskii* and a northern population of *S. peruvianum* to be a sister clade to the above supported by 65% bootstrap, (3) *S. chilense* and a southern population of *S. peruvianum* to form a well supported clade (98% bootstrap), and (4) *S. habrochaites* and *S. pennellii* to be a well supported clade (98%), but forming a basal polytomy with clade 3. *Solanum lycopersicoides* forms an outgroup to tomatoes that have a 51% bootstrap value.

The distance comparisons between three pairs of species (Table 4) were difficult to compare among marker types because different distance algorithms were appropriate for AFLPs, GBSSI, cpDNA restriction sites, ITS sequences, and morphology. For AFLPs (analyzed by DICE) the distance values ranged from 0.233–0.851; for GBSSI (Jukes-Cantor) ranged from 0.964–0.999, cpDNA (Nei-Li) ranged from 0.500–0.917, ITS (Jukes-Cantor) 0.877–0.980, and morphology cladistic data ranged from 0.269–0.885. The distance values estimated from sequence data (GBSSI and ITS) with Jukes-Cantor were higher than those estimated for other kinds of markers using a different algorithm. The distance values were intermediate for cpDNA (Nei-Li) and lower for AFLP (DICE) and morphology cladistic (simple matching). All markers showed a similar trend, except ITS, in the genetic and morphological distances of selected pairs of species (Table 4), being higher for closely related species (*S. lycopersicum/S. pimpinellifolium*), intermediate between a self-compatible brightly-colored-fruited species (*S. lycopersicum*) and a self-incompatible green fruited species (*S. pennellii*), and lower for a species of the tomato clade (*S. lycopersicum*) and a species of the outgroup (*S. lycopersicoides*). Contrary to this trend, the ITS genetic distance estimated with Jukes-Cantor was higher for the far species comparisons (0.932) than for the intermediate (0.877).

The two congruence tests gave different results regarding the rejected comparisons. That is, the ILD test found cpDNA/morphology and cpDNA/GBSSI to be incongruent, while the matrix comparison method established that GBSSI/ITS, GBSSI/morphology phenetics, and ITS/cpDNA were not statistically correlated. Notably, the comparison of cpDNA/GBSSI gave a high matrix correlation coefficient (0.831), but did not pass the ILD test.

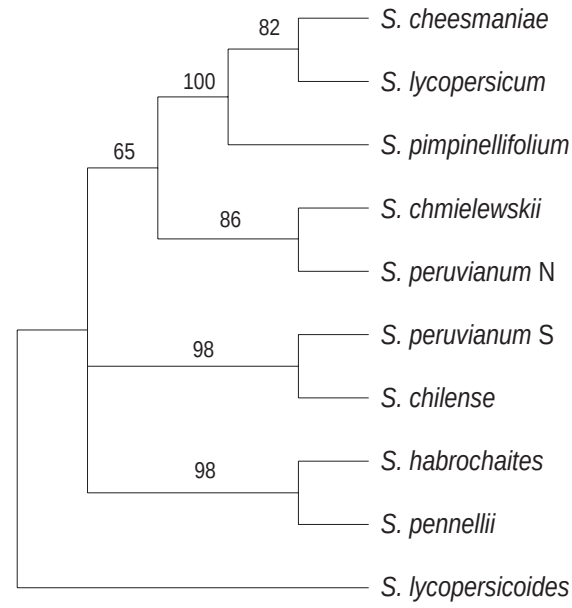

Fig. 9. The single combined AFLP, GBSSI, cpDNA, and ITS 530-step Fitch tree (10 taxa; 2275 characters). The numbers above each branch represent bootstrap values over 50%.

DISCUSSION

Our AFLP cladistic results are completely concordant with the cpDNA results of Spooner & al. (1993), Bohs & Olmstead (1997, 1999), Olmstead & Palmer (1997) and Olmstead & al. (1999) in supporting the sister group relationship of tomatoes, including section *Juglandifolium* and subsection *Lycopersicoides* (when examined), to potatoes. The present AFLP cladistic results also show various degrees of congruence with prior molecular and morphological studies of tomatoes and outgroups in section *Juglandifolium* and subsection *Lycopersicoides* (Fig. 2, Table 5). These results are sometimes difficult to compare because of different marker types (molecules vs. morphology; organellar [cpDNA and mitochondrial DNA] vs. nuclear inheritance; codominant markers such as isozymes, nuclear RFLPs and microsatellites vs. dominant markers such as AFLPs; multiple copy gene DNA sequences such as ITS vs. single copy gene sequences such as GBSSI). As well, some results are analyzed phenetically, others cladistically. Despite these many differences in marker types and analytical methods, it is illuminating to examine the congruence of these tomato datasets by visual comparison of phenograms and cladograms.

Of the ten studies compared here (Fig. 2A–I and this study, Table 5), only four included enough taxa to address the outgroup relationship of tomatoes. All four studies (Fig. 2D, F, G, and this study, Table 5) support the

close outgroup relationships of tomatoes to *Solanum* section *Juglandifolium* and subsection *Lycopersicoides*. Both GBSSI and AFLP results showed congruence supporting *Solanum* section *Juglandifolium* as the closest outgroup to tomatoes. Only two studies of eight that include *S. habrochaites* and *S. pennellii* (Fig. 2C and G, Table 5) support their grouping. Five of the seven studies including northern and southern accessions of *S. peruvianum* (relative to the GBSSI results, Fig. 2F) separated them into different groups (Fig. 2C, F, H, I, and this study, Table 5). These two geographical groups exhibit moderate breeding barriers (Rick, 1986a). Two of the six studies that included northern and southern populations of *S. peruvianum* and *S. chilense* supported the grouping of the latter with the southern populations of *S. peruvianum* (Fig. 2H and this study, Table 5). Four of the seven studies grouped *S. chmielewskii* and *S. neorickii* (Fig. 2C, E, G, H, Table 5). Eight of the nine studies grouped all the species with brightly colored fruits (Fig. 2A, C, E, F, G, H, I, and this study, Table 5). Four of the seven studies grouped the brightly-colored-fruited species exclusively with *S. chmielewskii* and *S. neorickii* (Fig. 2C, G, H, I, Table 5).

Wendel & Doyle (1998) discuss thirteen possibilities leading to discordant phylogenetic results, and divide them into three classes: (1) technical causes, (2) organism-level processes, and (3) gene and genome-level processes. We consider the following seven possibilities to be possible here, including: technical causes of (1a) insufficient data, (1b) taxon sampling, and (1c) gene choice; organism level processes of (2a) hybridization and introgression, (2b) rapid diversification, and (2c) lineage sorting; and gene and genome-level processes of (3c) paralogy, possibly with the ITS data.

Our GBSSI sequence, morphological, and present AFLP results included multiple accessions of all taxa, with a concentration on the most widespread and polymorphic species, *S. peruvianum*. Use of several appropriate outgroups reduced problems of taxon sampling; none of the other studies included such wide sampling. Insufficient taxon sampling in other studies precluded addressing many of the questions of congruence we pose here with AFLP, GBSSI (Peralta & Spooner, 2001) and morphological (Peralta & Spooner, in press) studies. Genealogical differences due to hybridization or introgression may be the cause of discordance with the cpDNA results. Chloroplast DNA is maternally inherited in *Solanum*, and cpDNA data frequently shows discordant results with biparentally-inherited markers, particularly in groups with high levels of natural interspecific hybridization, as in some tomato species (Rick, 1958). The ILD test is sensitive to character incongruence caused by genealogical discordance, and this may be reflected in our cpDNA/GBSSI dataset comparison. Hipp & al. (2004) discussed the possible causes that appear to affect increasing the probability of Type-I errors in ILD test results (the error of incorrectly rejecting the correct hypothesis of congruence). Differences among site substitution rates, overall evolutionary rates, levels of noise, and size of the data partition being tested may also affect the sensitivity of the ILD test (Hipp & al., 2004). In tomato, mtDNA divergence is higher than that of cpDNA, indicating that the DNA of the two organelles is evolving at different rates (McClean & Hanson, 1986). Rapid diversification and lineage sorting are always possible causes of discordance with recently evolved groups; this may be the case in tomatoes, as suggested by poor resolution (polytomies) in some terminal clades (Peralta & Spooner, 2001). As mentioned above, discordance could have been caused by methodological differences in phenetic versus cladistic analyses.

Our three methods for examining congruence among studies (distance matrix-based comparisons, character-based comparisons, and visual comparisons) gave different answers concerning the appropriateness of combining different datasets for phylogeny reconstruction of tomato. Different tests might produce different interpretations about the congruence of two datasets. Knowledge about possible biases in the data caused by biology of the species is needed for interpreting the meaning of incon-

Table 5. Comparison of hypotheses of relationships inferred from molecular and morphological characters of tomato and outgroups in *Solanum*, analyzed with cladistic or phenetic methods. Letters in the header correspond to Fig. 2. √ indicates concordant results, X discordant results, / lack of resolution due to polytomies in cladistic results, and insufficient species were included in the study or cannot be resolved because of insufficient outgroup sampling.

Hypothesis of relationships	A	B	C	D	E	F	G	H	I	This study
Sect. *Juglandifolium* (*S. juglandifolium* and *S. ochranthum*) and/or subsect. *Lycopersicoides* (*S. lycopersicoides* and *S. sitiens*) are sister to tomatoes or group with them	–	–	–	√	–	√	√	–	–	√
Solanum pennellii and *S. habrochaites* group together	/	X	√	–	–	/	√	/	X	/
Northern and southern *S. peruvianum* separate into different groups	X	–	√	–	–	√	/	√	√	√
Solanum chilense groups with all southern *S. peruvianum*, which are separate from all northern *S. peruvianum*	X	–	–	–	–	/	/	√	/	√
Solanum chmielewskii and *S. neorickii* group together	–	–	√	–	√	/	√	√	/	/
Red to orange to yellow-fruited species group together	√	X	√	–	√	√	√	√	√	√
Red to orange to yellow-fruited species group together and with *S. chmielewskii* and *S. neorickii*	–	–	√	–	X	/	√	√	√	X

gruence. We make the following conclusions, therefore, based on general congruence of AFLP, GBSSI, and morphological results: (1) *Solanum* section *Juglandifolium* is sister to the tomatoes, with subsection *Lycopersicoides* basal to the above, with potatoes (section *Petota*) sister to the entire group. (2) The four species with brightly-colored fruits form a monophyletic group. (3) The widespread and highly polymorphic species *S. peruvianum* is not monophyletic and is in need of taxonomic revision. (4) The self-compatible green-fruited species *S. chmielewskii* and *S. neorickii* are related to at least some northern *S. peruvianum* populations. (5) *Solanum chilense* is in the same clade as southern *S. peruvianum*. (6) *Solanum pennellii* and *S. habrochaites* group or form a basal polytomy relative to the other tomatoes.

AFLPs have provided better resolution to terminal clades that were poorly resolved with GBSSI sequence data, suggesting that these species have diverged only recently. AFLPs have been found to be useful in other cases where DNA sequence data fail to reveal variability (Beardsley & al., 2003; Despres & al., 2003). The relatively high marker number per gel, and ease and repeatability, appear to make AFLPs a very useful marker type within some genera containing closely related diploid species, despite some homoplasy present in the data.

Note added in proof: A manuscript (Peralta & al.) describing the new segregate taxa from *Solanum peruvianum*) L. s.l. is in press (Syst. Bot.).

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Appendix. Accessions of tomatoes (*Solanum* sect. *Lycopersicon* subsection *Lycopersicon*) and outgroups, examined for AFLP variation, with indications if they also were examined for morphological and GBSSI gene sequence variation in the studies of Peralta & Spooner (2001, in press). Some accessions are represented by herbarium specimens collected by C. M. Rick and colleagues and are deposited in a variety of herbaria, mostly in South America. Where original vouchers do not exist, we grew plants from seeds obtained from the C. M. Rick Tomato Genetics Resource Center (CMR) (http://tgrc.ucdavis.edu) and produced new vouchers. We cite both the CMR collection numbers (when available) and new I. E. Peralta vouchers. Forms of *S. habrochaites*, *S. pennellii*, and *S. peruvianum* as listed in the database of germplasm at the CMR are indicated in parentheses after the species name. Locality data for all accessions follow Peralta & Spooner (2001), with the exception of additional accessions listed below.

Taxon / Map locality[a] / Dataset[b] / Accession number[c] / Voucher[d] / Breeding system[e]

Ingroup, *Solanum* L. section *Lycopersicon* subsection *Lycopersicon*: *S. cheesmaniae* / Gal / M, W, A / LA166 / *Peralta 1001* (BM, DAV, MERL, WIS) / Aut-SC; *S. chilense* / 29 / M, W, A / LA1930 / *Rick & al. 3172/Peralta 1181* / Allo-SI; *S. chilense* / 36 / M, W, A / LA1963 / *Rick & al. 3204/Peralta 1189* (BM, DAV, MERL, WIS) / Allo-SI; *S. chilense* / 38 / M, W, A / LA2884 / *Rick & al. 7609/Peralta 1195* (BM, DAV, MERL, WIS) / Allo-SI; *S. chmielewskii* / 27 / M, W, A / LA1327 / *Rick & al. 411/Peralta 1108* (BM, DAV, MERL, WIS) / Fac-SC; *S. chmielewskii* / 26 / M, W, A / LA2663 / *Rick & al. 6101/Peralta 1123* (BM, DAV, MERL, WIS) / Fac-SC; *S. galapagense* / Gal / M, W, A / LA317 / *Peralta 1021* (BM, DAV, MERL, WIS) / Aut-SC; *S. habrochaites* (*glabratum*) / 3 / M, W, A / *LA1223* (PI 365903) / *Rick & al. 301/Peralta 1128* (BM, DAV, MERL, WIS) / Fac-SC; *S. habrochaites* / 11 / M, W, A / LA1353 (PI 365934) / *Rick & al. 437/Peralta 1152* (BM, DAV, MERL, WIS) / Allo-SI; *S. habrochaites* / 24 / M, W, A / LA1928 / *Rick & al. 3170/Peralta 1146* (BM, DAV, MERL, WIS) / Fac-SC; *S. lycopersicum* (*cerasiforme*) / 5 / M, W, A / LA1226 (PI 379045) / *Rick & al. 309/Peralta 1038* (BM, DAV, MERL, WIS) / Aut-SC; *S. lycopersicum* (*cerasiforme*) / 21 / M, W, A / LA1673 / *Rick & al. 1985/Peralta 1046* (BM, DAV, MERL, WIS) / Aut-SC; *S. neorickii* / 17 / M, W, A / LA247 / *Ochoa 1017* (MOL) / Aut-SC; *S. pennellii* / 31 / M, W, A / LA716 (PI 246502) / *Peralta 1164* (BM, DAV, MERL, WIS) / Fac-SC; *S. pennellii* (*puberulum*) / 28 / M, W, A / LA1926 / *Rick & al. 3168/Peralta 1175* (BM, DAV, MERL, WIS) / Allo-SI; *S. peruvianum* / 6 / M, W, A / LA2185 / *Rick & al. 5030* (BM) / Allo-SI; *S. peruvianum* / 9 / M, W, A / LA2163 / *Rick & al. 5008* (BM) / Allo-SI; *S. peruvianum* / 11 / M, W, A / LA392 / *Rick & al. 141* (BM) / Allo-SI; *S. peruvianum* / 11 / W, A / LA1351 (PI 365951) / *Rick 435* (USM) / Allo-SI; *S. peruvianum* (*humifusum*) / 11 / A / LA2334 / *Rick & al. 430* (BM) / Allo-SI; *S. peruvianum* / 10 / M, W, A / LA1396 / *Rick & al. 480* (BM) / Allo-SI; *S. peruvianum* / 10 / A / LA2326 / *Rick & al. 5170* (BM) / Allo-SI; *S. peruvianum* / 13 / M, A / LA2553 / *Peralta 1554* (BM, DAV, MERL, WIS) / Allo-SI; *S. peruvianum* / 12 / M, W, A / LA441 / *Rick 128* (USM) / Allo-SI; *S. peruvianum* / 12 / A / LA1346 (PI 365950) / *Rick & al. 430* (BM) / Allo-SI; *S. peruvianum* / 12 / M, W, A / LA1984 / *Rick & al. 3665* (BM) / Allo-SI; *S. peruvianum* / 14 / M, A / LA1982 / *Rick & al. 3223/Peralta 1476* (BM, DAV, MERL, WIS) / Allo-SI; *S. peruvianum* / 14 / A / LA2808 / *Peralta 1563* (BM, DAV, MERL, WIS) / Allo-SI; *S. peruvianum* / 15 / M, W, A / LA1626 / *Peralta 1415* (BM, DAV, MERL, WIS) / Allo-SI; *S. peruvianum* / 16 / M, A / LA1360 (PI 365952) / *Rick & al. 444/Peralta 1363* (BM, DAV, MERL, WIS) / Allo-SI; *S. peruvianum* / 18 / M, W, A / LA111 / *Rick & al. 41/Peralta 1219* (BM, DAV, MERL, WIS) / Allo-SI; *S. peruvianum* / 18 / W, A / LA153 (PI 126944) / *Peralta 1226* (BM, DAV, MERL, WIS) / Allo-SI; *S. peruvianum* / 19 / M, W, A / LA1379 (PI 379018) / *Rick 463* (USM) / Allo-SI; *S. peruvianum* / 21 / M, W, A / LA1274 (PI 365940) / *Rick 356* (USM) / Allo-SI; *S. peruvianum* / 21 / M, W, A / LA370 / *Rick & al. 115* (BM) / Allo-SI; *S. peruvianum* / 21 / A / LA1292 / *Rick & al. 375/Peralta 1321* (BM, DAV, MERL, WIS) / Allo-SI; *S. peruvianum* (*glandulosum*) / 21 / A / LA1473 / *Peralta 1390* (BM, DAV, MERL, WIS) / Allo-SI; *S. peruvianum* (*glandulosum*) / 21 / M, W, A / LA1283 (PI 365942) / *Rick & Rick 365* (USM) / Allo-SI; *S. peruvianum* / 22 / W, A / LA1609 / *Rick & al. 1889* (BM) / Allo-SI; *S. peruvianum* / 22 / M, W, A / LA107 / *Rick & al. 33/Peralta 1207* (BM, DAV, MERL, WIS) / Allo-SI; *S. peruvianum* / 23 / M, A / LA1339 (PI 365949) / *Rick 423* (USM) / Allo-SI; *S. peruvianum* / 23 / A / LA1677 / *Rick & al. 1989/Peralta 1428* (BM, DAV, MERL, WIS) / Allo-SI; *S. peruvianum* / 23 / A / LA1647 / *Peralta 1426* (BM, DAV, MERL, WIS) / Allo-SI; *S. peruvianum* / 24 / M, W, A / LA1305 (PI 379015) / *Rick & al. 3889/Peralta 1328* (BM, DAV, MERL, WIS) / Allo-SI; *S. peruvianum* / 24 / M, W, A / LA1910 / *Rick 3152* (USM) / Allo-SI; *S. peruvianum* / 28 / M, W, A / LA1913 / *Rick & al. 3155* (BM) / Allo-SI; *S. peruvianum* / 28 / M, W, A / LA1331 (PI) 365946) / *Rick 415* (USM) / Allo-SI; *S. peruvianum* / 30 / M, W, A / LA448 / *Rick 202* (USM) / Allo-SI; *S. peruvianum* / 32 / M, A / LA1474 / *Peralta 1396* (BM, DAV, MERL, WIS) / Allo-SI; *S. peruvianum* / 33 / M, W, A / LA1973 / *Peralta 1470* (BM, DAV, MERL, WIS) / Allo-SI; *S. peruvianum* / 35 / M, W, A / LA3156 / *Peralta 1579* (BM, DAV, MERL, WIS) / Allo-SI; *S. peruvianum* / 34 / M, W, A / LA1954 / *Rick & al. 3195* (BM) / Allo-SI; *S. peruvianum* / 34 / M, A / LA454 / *Rick 208* (USM) / Allo-SI; *S. peruvianum* / 36 / M, W, A / LA2964 / *Peralta 1569* (BM, DAV, MERL, WIS) / Allo-SI; *S. peruvianum* / 37 / M, W, A / LA2744 / *Rick & al. 7502* (BM) / Allo-SI; *S. pimpinellifolium* / 7 / W, A / LA2184 / *Rick & al. 5029/Peralta 1075* (BM, DAV, MERL, WIS) / Aut-SC.

Outgroup, *Solanum* section *Lycopersicon* subsection *Lycopersicoides* Child: *S. lycopersicoides* / 36 / M, W, A / LA2386 / *Ochoa 14248* (MOL) / Allo-SI; *S. sitiens* / 39 / M, W, A / LA2876 / *Rick & al. 7601/Peralta 1598* (BM, DAV, MERL, WIS) / Allo-SI; *S. sitiens* / 39 / W, A / LA2878 / *Rick & al. 7603/Peralta 1599* (BM, DAV, MERL, WIS) / Allo-SI.

Outgroup, *Solanum* section *Juglandifolium* (Rydb.) Child: *S. ochranthum* / 26 / W, A / LA2682 / *Rick & al. 6120/Peralta 1586* (BM, DAV, MERL, WIS) / Allo-SI; *S. ochranthum* / 27 / W, A / LA3650 / *Rick & al. 7710/Peralta 1594* (BM, DAV, MERL, WIS) / Allo-SI.

Outgroup, *Solanum* section *Etuberosum* (Buk. & Kameraz) Child: *S. etuberosum* / S Chile / A / PI 558297 / *Spooner & Conteras 4349* (PTIS) / Aut-SC

Outgroup, *Solanum* section *Petota* Dumort.: *S. cardiophyllum* / Mexico / A / PI 347759 / *Tarn 241D* (PTIS) / Allo-SI; *S. ehrenbergii* / Mexico / A / PI 184762 / *Hawkes & García 1086* (K) / Allo-SI; *S. pinnatisectum* / Mexico / A / PI 275236 / *Hawkes & al. 1505* (K) / Allo-SI.

Locality data not found in Peralta & Spooner (2001): *S. peruvianum*, LA2334, Peru. Cajamarca: San Juan, Río Jequetepeque; LA 2326, Peru. Amazonas: Balsas, 1500–1800 m, 6°50'S, 78°01'W; LA1346, Peru. La Libertad. Casmiche, 1800–2100 m; LA2808, Peru. Ancash. Huaylas; LA1292, Peru. Lima. San Mateo. Central highway, 1 km below San Mateo; LA1473, Peru. Lima. Callahuanca, Santa Eulalia; LA1677, Peru. Lima. Between Fundo Huadquina and Topara; LA1647, Peru. Ica. Huadquina, Topara, 500 m. **Outgroups:** *S. etuberosum*, *Spooner & Contreras 4349*, Chile. Region VIII: Prov. Biobio, ca 3 km SE of Alto Biobio, on N side of Río Pangue, 300 m upstream of Puente Pangue, 440 m, 37°53'S, 71°36'W. *S. cardiophyllum*, *Tarn 241d*, Mexico. Puebla: left side of the Tehuacán to Huajuapan de León Road on the Puebla side of border, Hwy 125, almost at border of Puebla-Oaxaca states, 2060 m, 18.62ºN, 97.58ºW. *S. ehrenbergii*, *Hawkes & García 1086*, Mexico. Querétaro: San Juan del Río, SW of the town, 2050 m, 20.67ºN, 99.50ºW. *S. pinnatisectum*, *Hawkes & al. 1505*, Mexico. Jalisco: 29 mi from Guadalajara on the road to México City, Hacienda de Huejotitán, 1600 m, 20.67ºN, 103.33ºW.

[a] Map numbers correspond to Fig. 1; Chile, Mexico, and the Galápagos Islands are outside the map area.

[b] M = morphological study (Peralta & Spooner, in press); W = GBSSI gene sequence study (Peralta & Spooner, 2001). The morphological and GBSSI study accessions are listed here for ease of comparison to those papers.

[c] LA numbers are from the C. M. Rick Tomato Genetics Resource Center; PI numbers are the same United States Plant Introduction Number duplicate accessions held at the United States Department of Agriculture genebank in Geneva, New York (Geneva Plant Genetic Resources Unit, NE-9).

[d] The collector abbreviation in the database of the C. M. Rick Tomato Genetics Resource Center is SAL, an abbreviation used by Charles Rick for his collections alone or with others to indicate "South American *Lycopersicon*"; here we cite these collections as *Rick & al*. unless evidence exists to the contrary.

[e] Allo = allogamous, Aut = autogamous, Fac = facultatively allogamous, SC = self-compatible, SI = self-incompatible. Data from Rick 1963, 1979, 1984, 1986 and http://tgrc.ucdavis.edu.