KURTZIANA

Classification of wild tomatoes: a review

Iris Edith Peralta[*, **] & David M. Spooner[*]

*United States Department of Agriculture, Agricultural Research Service, Department of Horticulture, University of Wisconsin, 1575 Linden Drive, Madison, Wisconsin 53706-1590, USA.

** Facultad de Ciencias Agrarias, Universidad Nacional de Cuyo, Casilla de Correo 7, Chacras de Coria, 5517 Mendoza, Argentina. IADIZA, Casilla de Correo 507, 5500 Mendoza, Argentina. Miembro de la Carrera del Investigador. CONICET.

Resumen

Peralta, I. E. & D. M. Spooner. 2000. Clasificación de los tomates silvestres: una revisión. *Kurtziana* 28 (1): 45-54.

Las especies de tomates silvestres son nativas del oeste de América de Sur. Su posición genérica dentro de las Solanáceas ha sido controvertida desde el Siglo XVIII. Linneo en 1753 ubicó a los tomates en *Solanum* mientras que Miller, un contemporáneo de Linneo, los incluyó dentro del nuevo género *Lycopersicon*. Posteriormente, la mayoría de los botánicos siguieron la clasificación de Miller. Las clasificaciones basadas en morfología o en estudios de cruzamientos han propuesto diferente número de especies o categorías supraespecíficas. Sobre la base de la cruzamientos entre especies se han identificado dos grupos; uno de ellos incluye especies autocompatibles que pueden cruzarse fácilmente con el tomate cultivado, el otro comprende especies autoincompatibles que no pueden cruzase fácilmente con esta especie. Recientes investigaciones moleculares, utilizando grupos externos adecuados, han mostrado que los tomates y las papas están muy relacionados filogenéticamente y apoyan la inclusión de los tomates dentro de *Solanum*, clasificación que hemos adoptado aquí. Se discute acerca del conflicto de los objetivos de las clasificiones basados en la predicción o la estabilidad, una continua controversia en sistemática.

Palabras clave: *Lycopersicon*, *Solanum*, tomates, clasificación.

Abstract

Peralta, I. E. & D. M. Spooner. 2000. Classification of wild tomatoes: a review. *Kurtziana* 28 (1): 45-54.

Wild tomatoes are native to western South America. The generic status of wild tomatoes within the Solanaceae has been controversial since the eighteen century. Linnaeus in 1753 placed tomatoes in *Solanum* while Miller, a contemporary of Linnaeus, classified tomatoes in a new genus *Lycopersicon*. The majority of later botanists have followed Miller. Differing numbers of species and conflicting supraspecific classifications have been proposed, based on morphology or crossing studies. Two major crossability groups have been identified, one that includes mainly self-compatible species that easily cross with the cultivated tomato, and another that comprises self-incompatible species not easily cross with the cultivated tomato. Recent molecular investigations using appropriate outgroups have shown that tomatoes and potatoes are close related phylogenetically, and support the inclusion of tomatoes within *Solanum*, the classification advocated here. We discuss the conflicting goals of classifications based on predictivity versus stability, a continuing controversy in systematics.

Key words: *Lycopersicon*, *Solanum*, tomatoes, classification.

Wild Tomato distribution and species characters

Wild tomatoes (*Solanum* L. subsect. *Lycopersicum*, an autonym of *Solanum* section *Lycopersicum* (Mill.) Wettst.) are entirely American in distribution, growing in the western South American Andes from central Ecuador, through Peru, to northern Chile, and in the Galapagos Islands, where the endemic species *S. cheesmaniae* grows (Table 1, Fig. 1). In addition, *S. lycopersicum*, the wild ancestor of cultivated tomatoes, is more widespread, and perhaps more recently distributed into Mexico, Colombia, Bolivia, and other South American regions (Rick & Holle, 1990). Wild tomatoes grow in a variety of habitats, from near sea level to over 3,300 m.s.m. in elevation (Rick, 1973; Taylor, 1986). These habitats include the arid Pacific coast to the mesic uplands in the high Andes. Numerous valleys, formed by rivers draining into the Pacific, characterize the western side of the Andes. Wild tomato populations grow at different altitudes in these narrow valleys, are geographically isolated, and are adapted to particular microclimatic and soil conditions. Certainly, the diverse geography and habitats as well as different climates contributed to wild tomato diversity (Warnock, 1988).

Wild tomatoes are herbaceous plants, although can also undergo secondary growth. In their natural habitats, wild tomatoes probably behave as annuals because frost or drought kill the plants after the first growing season (Müller, 1940). In all species the shoots are initially erect, but later, due to the weight of the branches, the plants become prostrate and can root at the nodes. *Solanum lycopersicum*, *S. habrochaites*, *S. chilense*, and some races of *S. peruvianum* are robust and can maintain the erect habit longer until they reach 80-100 cm in height. All species can produce long branches; *S. peruvianum*, *S. pimpinellifolium* and *S. lycopersicum* branches can grow to more than 4 m long. Pubescence has been considered an important taxonomic character (Luckwill, 1943), distinguishing especially *S. habrochaites* and *S. pennellii*.

Wild tomato species also present taxonomically significant differences in leaf, inflorescence, flower and fruit characters (Table

1). Leaves are imparipinnate, with 2-6 opposite or sub-opposite, sessile or petiolate pairs of leaflets. There is great interspecific variation in leaf dissection, and much intraspecific variation in *S. peruvianum* (Rick, 1963), from pinnate to bipinnate with primary, secondary and tertiary leaflets, and interjected leaflets. The number of leaves per sympodium is another valuable taxonomic character, either 2 or 3 (Rick et al., 1990).

The basic inflorescence is a cyme with different kinds of branching including monochasial, dichotomous, and polychotomous (Luckwill, 1943). The development of inflorescence bracts also is considered an important taxonomic character (Rick et al., 1990).

Flowers are typically yellow, and as in other Solanaceae, gamosepalous at the base and gamopetalous. The self-compatible species (Table 1) typically have smaller stellate flowers and the stigma is often included or flush with the anther. The self-incompatible species (Table 1) have larger stellate-rotate or rotate flowers and exerted stigmas. Tomatoes have a characteristic stamen morphology, with anthers connivent laterally to form a flask-shaped cone, with an elongated sterile tip at the apex (except in *S. pennellii*). Flowers are buzz pollinated.

Fruit size, color and pubescence also are highly variable and taxonomically useful (Rick et al., 1990; Table 1), and too are seed size, color and radial walls of the seed coat cells (Luckwill, 1943; Lester 1991).

Taxonomic History

Ever since the cultivated tomato was introduced to Europe in the sixteenth century, botanists have recognized the close relationship of tomatoes with the genus *Solanum*, and commonly referred to them as *S. pomiferum* during the seventeenth century (Luckwill, 1943). Tournefort (1694) was the first to consider cultivated tomatoes as a distinct genus, *Lycopersicon* ("wolf peach", Greek). Tournefort placed species with large multilocular fruits in the genus *Lycopersicon,* but kept the bilocular species in *Solanum*. However, we now know that some species have two to many locules. In Species Plantarum, Linnaeus (1753) classified

tomatoes in the genus *Solanum*, and described *S. lycopersicum* and *S. peruvianum*. Jussieu (1789) also included tomatoes in *Solanum*. Miller (1754), though, followed Tournefort and formally described the genus *Lycopersicon*. Later, Miller (1768) published diagnoses for *L. esculentum* (the type species), *L. peruvianum* and *L. pimpinellifolium*. Miller's circumscription of the genus also included the potato, *S. tuberosum*, and two other species of *Solanum* under *Lycopersicon* (Miller, 1768), but he ultimately merged *Lycopersicon* and *Solanum* (Miller, 1807). Following Tournefort and Miller's early work, a number of classical and modern authors recognized *Lycopersicon* (e.g., Dunal, 1813; 1852; Bentham & Hooker, 1873; Müller, 1940; Luckwill, 1943; Correll, 1958; D'Arcy, 1972, 1987, 1991; Hunziker, 1979; Rick, 1979, 1988; Rick et al., 1990; Symon, 1981, 1985; Taylor, 1986; Warnock, 1988; Hawkes, 1990).

However, Wettstein (1895), in his classical revision of the *Solanaceae*, included *Lycopersicon* under *Solanum*, a treatment followed by a minority of later authors (MacBride, 1962; Seithe, 1962; Heine, 1976; Fosberg, 1987). Börner (1912) also recognized the close affinity between tomatoes and potatoes, and proposed a new genus *Solanopsis* to segregate them. D'Arcy (1972, 1987) in his revision of *Solanum* treated *Lycopersicon* as distinct. D'Arcy (1987), later recognized polymorphism in the anther characters that largely separated the two genera, and questioned if perhaps *Lycopersicon* should be merged into *Solanum*.

Lester (1991) studied the relationships among domesticated pepinos, potatoes and tomatoes using seed coat characters and other data. He recognized that these three groups could be included in a single genus segregated from *Solanum*, but decided for practical reasons to treat them in *Solanum* section *Basarthrum*, *Solanum* section *Petota*, and *Lycopersicon*, respectively.

In another taxonomic treatment, Child (1990; Fig. 1) placed the tomatoes in *Solanum* subgenus *Potatoe* (G. Don) D'Arcy, section *Lycopersicum*, subsection *Lycopersicum*, and distributed them in three series *Eriopersicon* (C. H. Müll.) Child, *Lycopersicon*, and *Neolycopersicon* (Correll)

Child. He also hypothesized that *Solanum* subsection *Lycopersicoides* Child and section *Juglandifolium* (Rydb.) Child are the closest relatives of subsection *Lycopersicum*.

Two most recent and complete taxonomic treatments of tomatoes are those of Müller (1940) and Luckwill (1943; Fig. 1). Müller (1940) considered *Lycopersicon* as a distinct genus and divided it into two subgenera, *Eulycopersicon* C. H. Müll. with two species possessing glabrous and red- to orange-colored fruits, and *Eriopersicon* C. H. Müll. with four species bearing pubescent green fruits. Three years later, Luckwill (1943) adopted the same supraspecific categories but recognized different infraspecific taxa and five species in the subgenus *Eriopersicon* (Fig. 1). These treatments have become outdated as the number of species and races collected from South America has increased considerably (Rick, 1971, 1991; Holle et al., 1978, 1979; Taylor, 1986).

Rick (1960, 1979) proposed an infrageneric classification based on crossing relationships. He recognized nine wild tomato species, classified into two complexes. The *L. esculentum* complex included seven species, mainly self-compatible, and easily crossed with the cultivated tomato. Within this group, three species have mostly glabrous, pigmented fruits, while the others have pubescent, green fruits. The *L. peruvianum* complex included the self-incompatible species *S. peruvianum* and *S. chilense*, having pubescent green fruits that seldom crossed with *L. esculentum* (Table 1, Fig. 1).

Different criteria used in classification, morphology and crossability, therefore has led to different numbers of species, subspecies, and varieties, and in conflicting hypotheses of interspecific relationships (Fig. 1). In their morphology-based taxonomic treatments, Müller (1940) and Luckwill (1943) divided the highly polymorphic *S. peruvianum* into two varieties and four subspecies, respectively. In addition, Müller (1940) described a new species, *L. glandulosum* C. H. Müll., and Luckwill (1943) recognized *L. pissisi* Phil. as a separate species (Fig. 1).

Based on intercrossability and morphological data, Rick and Lamm (1955) recognized *L. chilense* as a separate species, and included *L.*

Table 1

COMPARISON OF WILD TOMATO SPECIES (*SOLANUM* L. SUBSECTION *LYCOPERSICUM*) (DATA COMPILED FROM MULLER, 1940; LUCKWILL, 1943; RICK, 1986; TAYLOR, 1986). THE SYNONYMS IN *LYCOPERSICON* ARE LISTED ONLY WHEN THE SPECIFIC EPITHET DIFFERS BETWEEN GENERA

Species	Fruit color	Breeding system	Distribution and Habitat	Comments
S. lycopersicum L. (*L. esculentum*)	Red	SC[a], facultative allogamous	Native from Ecuador and Peru, widespread in America. Wide range of habitats, weed in open areas	Putative origin of cultivated forms
S. cheesmaniae Riley	Yellow, yellow green, orange, purple	SC, exclusively autogamous	Endemic of the Galapagos Archipelago. Low elevations of the saline seashore	Closely related to *S. lycopersicum* and *S. pimpinellifolium*
S. pimpinellifolium B. Juss.	Red	SC, autogamous, facultative allogamous	Low elevations in Southern Ecuador and Peru (coastal to usually below 1000 m), western end of river valleys on Pacific side. Weed in cultivated fields	Closely related to *S. lycopersicum* (some natural introgression with it)
S. chmielewskii (Rick, Kesickii, Fobes & Holle) D. M. Spooner, G. J. Anderson & R. K. Jansen	Green	SC, facultatively allogamous	1500-3000 m, Pacific side, South-Central Peru; moist habitats; slightly better-drained sites that *S. neorickii*	Sympatric with *S. neorickii*
S. neorickii D. M. Spooner, G. J. Anderson, & R. K. Jansen (*L. parviflorum*)	Pale green	SC, highly autogamous	1500-3000 m, Pacific side, South Ecuador to South-Central Peru; moist and well-drained rocky environments; more common than *S.chmielewskii*	Sympatric with *S. chmielewskii*; evolved from *S. chmielewskii*; yet no natural introgression reported with *S. neorickii*
S. habrochaites S. Knapp & D. M. Spooner (*L. hirsutum*)	Green	Typically SI[a], 1-2 collections SC, but with later inbreeding depression	Typically high elevations (500-3300 m) in moist, well drained soils; South-Western Ecuador to South-Central Peru	Insect resistant (glandular hairs), and other resistances
S. chilense (Dunal) Reiche	Small green with purple stripe	SI, allogamous	Sea level-3000 m; Southern Peru to Northern Chile, sympatric with *S. peruvianum*; grows in dry river beds, survives by deep roots	Typically prostate habit; post-syngamic barriers with *S. peruvianum*, but Northern most pops. of *S. peruvianum* almost fully sexually compatible with *S. chilense*
S. peruvianum L.	Green	Typically SI, allogamous, rare pop SC, autogamous (trend to reduced variability in Northern races)	Sea level-3000 m; Northern Peru to Northern Chile. Wide range of environments	Erect habit; characterized by tremendous variability, even within single accessions (many informal races recognized)
S. pennellii Correll	Green	Usually SI, some SC in Southern range	50 m, but typically 500-1500 m; North-Central to South-Central Peru (8-16 °S); hot dry habitats, but subject to heavy dew; (many stomata adaxially, poor root system)	Covered with glandular hairs imparts insect resistance; hybridizes unilaterally (as male) with many other species except *S. chilense* or *S. peruvianum*

[a] SC=self-compatible; SI= self-incompatible

glandulosum within *S. peruvianum.* They also examined a photograph of the original type collection of *L. pissisi,* and concluded that this specimen was not related to *S. peruvianum* (Fig. 1). *Solanum peruvianum* grows throughout much of the range of the wild tomatoes.

Rick (1963) analyzed the morphological, ecological, and reproductive variation of *S. peruvianum,* and recognized 40 informally designated races. A few of these are widespread coastal races, but the majority are locally distributed mountain races. Rick (1986a) identified four groups of these 40 races that were isolated by reproductive barriers. Three groups of races occur in northern Peru: a Chamaya-Cuvita group, a Marañón group, and a Chotano-*humifusum* group. The races from central and southern Peru comprise the fourth group of *S. peruvianum* races, reproductively isolated from the northern races. Rick (1986a) also confirmed the crossing barriers between the northern and southern races. The northern races crossed to a limited degree among themselves and with *S. chilense, S. habrochaites* and *S. lycopersicum.* He also hypothesized that the Río Marañón races of *S. peruvianum* were ancestral to the wild tomatoes.

Molecular Systematics

Isozymes were extensively used to examine intra- and interspecific genetic variation in wild tomatoes (Rick, 1983, 1986a; Rick & Fobes, 1975a,b; Rick & Tanksley, 1981; Rick & Holle, 1990; Rick et al., 1974, 1976, 1977). These studies showed that within- and between-population variability was low in the self-compatible species *S. cheesmaniae, S. lycopersicum,* and *S. neorickii.* Variability was greater in the facultatively allogamous *S. pimpinellifolium,* and there was a geographic component to the variability, with the northern Peruvian populations, the most polymorphic. The self-incompatible populations of *S. habrochaites* from northwestern Peru showed more variability than the self-compatible northern and southern populations. Isozyme polymorphism increased in the almost exclusively self-incompatible *S. pennellii,* and was greatest in the self-incompatible *S. chilense* and *S. peruvianum.*

Not surprising, more genetic variation, examined with other molecular markers (RAPDs and RFLPs), has been found for the cultivated tomato and its putative ancestor in the primary center of diversity (western South America)

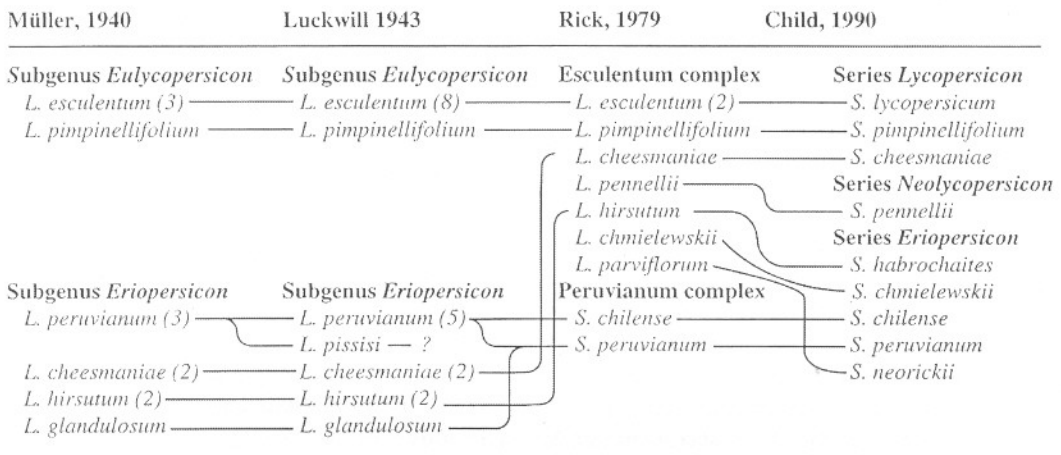| Müller, 1940	Luckwill 1943	Rick, 1979	Child, 1990
Subgenus *Eulycopersicon*	**Subgenus *Eulycopersicon***	**Esculentum complex**	**Series *Lycopersicon***
L. esculentum (3)	*L. esculentum (8)*	*L. esculentum (2)*	*S. lycopersicum*
L. pimpinellifolium	*L. pimpinellifolium*	*L. pimpinellifolium*	*S. pimpinellifolium*
		L. cheesmaniae	*S. cheesmaniae*
		L. pennellii	**Series *Neolycopersicon***
		L. hirsutum	*S. pennellii*
		L. chmielewskii	**Series *Eriopersicon***
		L. parviflorum	*S. habrochaites*
Subgenus *Eriopersicon*	**Subgenus *Eriopersicon***	**Peruvianum complex**	*S. chmielewskii*
L. peruvianum (3)	*L. peruvianum (5)*	*S. chilense*	*S. chilense*
	L. pissisi — ?	*S. peruvianum*	*S. peruvianum*
L. cheesmaniae (2)	*L. cheesmaniae (2)*		*S. neorickii*
L. hirsutum (2)	*L. hirsutum (2)*		
L. glandulosum	*L. glandulosum*		

Fig. 1.- Comparison of four major taxonomic treatments of tomatoes, showing differences in number of species, subspecies and varieties (numbers in parentheses), infrageneric classifications (under bold headings), and treatment of synonyms (connecting lines). Some new names or new combinations in *Solanum* were made by Spooner et al. (1993), and Knapp & Spooner (1999) but these authors make no determination regarding infrasectional relationships. Child (1990) did not list *S. chmielewskii* and *S. neorikii,* but we include them within series *Eriopersicon* because they match his concept of this series.

than in the Old World (Williams & St. Clair, 1993; Villand et al., 1998). The authors concluded that more genetic diversity could be discovered at a faster rate by collecting in the primary center of diversity and by sampling over a wide range of environments. Molecular markers are promising tools to predict genetic variation as well as to identify beneficial genes, especially in wild relatives of the cultivated tomato (Tanksley & McCouch, 1997).

Wild tomato species are valuable genetic sources to improve important agronomic traits and to introgress resistance to diseases and stress tolerances in the cultivated tomato (Es-quinas Alcazar, 1981; Laterrot, 1989; Rick, 1982, 1986b, 1987; Rick et al. 1987; Stevens & Rick, 1986). For these reasons, tomatoes have been identified among the eight major species/gene-ra for priority conservation status by the International Board for Plant Genetic Resources, and presently more than 62,000 accessions are conserved in genebanks (Cross, 1998).

Phylogenetic relationships in tomatoes have been studied using molecular markers. Two studies have been based on organellar DNA. A cladistic analysis of eight species of *Lycopersicon* and two species of *Solanum* as outgroups was conducted with chloroplast DNA (cpDNA) restriction site data (Palmer & Zamir, 1982). The DNA was cut with 25 restriction enzymes and 39 variable sites were observed, of which 14 bands were phylogenetically informative. This analysis supported *S. pennelli* placed with tomatoes, a species that by prior treatments had been placed in *Lycopersicon* or *Solanum*. It also supported the red fruited species as a monophyletic group. Pigmented fruit was considered a derived feature within *Lycopersicon* (Palmer & Zamir, 1982). The data were insufficient to completely resolve relationships within tomatoes as evidenced by two internal trichotomies and identical cpDNA for *S. chilense* and the three accessions of *S. peruvianum*. Of great interest was that cpDNA polymorphism was observed within the widely distributed and morphologically variable species *S. peruvianum* for which six accessions were examined, and that these two groups of accessions were placed in different clades.

Restriction fragment polymorphisms of mitochondrial DNA (mtDNA; McClean & Hanson, 1986) were used to compare nine species of *Lycopersicon* and two closely related *Solanum* species, utilizing a phenetic approach. The mtDNA divergence is higher than that in cpDNA, indicating that the DNA of the two genomes is evolving at different rates. The studies of McClean and Hanson (1986) were incongruent with the cpDNA results of Palmer and Zamir (1982) and with the morphological and crossing data. Differential organellar introgression, lineage sorting, or possible incorrect assessment of homology of the mtDNA bands may be possible explanations for the incongruence.

Miller and Tanksley (1990) used single- to low-copy nuclear restriction fragment length polymorphisms (RFLPs) to analyze the phenetic relationships within tomatoes. They found two major groups, one corresponding to inbreeding species with red fruits, and the other to outbreeding species with green fruits. However, one accession of *S. peruvianum* (outbreeding, green fruits) was an exception in that it grouped with the inbreeding red-fruited species. They confirmed many isozyme results in showing a gradation of RFLP variation from the self-com-patible species to the self-incompatible ones, with most found in *S. peruvianum*. The RFLP diversity of the self-compatible species was greater between populations than within populations. As a matter of fact, there was more genetic variation in a single accession of the self-incompatible species *S. peruvianum* than among all 34 accessions of the self-compatible species.

More recently, the treatment of tomatoes in *Solanum*, and indeed as a monophyletic sister group to potatoes, has been supported by cpDNA restriction site data, using 18 restriction endonucleases and cloned heterologous probes (Spooner et al., 1993). This study also conducted a cladistic analysis of tomatoes, potatoes, and outgroups with morphological data, as gleaned from the literature, that similarly supported this sister group relationship. The only characters shown here that separated potatoes and tomatoes were presence/absence

of tubers, corolla pigmentation, anthoclade types (patterns of lateral branching and associated inflorescences), and anther morphology (free vs. connate; anthers without or with sterile apical appendages, anthers opening by terminal pores vs. longitudinal dehiscence). The close relationship of tomatoes and potatoes is also suggested by genetic linkage data (Bonierbale & al., 1988; Gerhardt et al., 1991; Tanksley et al., 1992). Treatments of tomatoes in *Solanum* are beginning to gain acceptance in the taxonomic literature (Bohs & Olmstead, 1997; Olmstead & Palmer, 1997).

Intron DNA sequences of the single-copy nuclear structural gene for granule-bound starch synthase (*waxy*) are considered useful to analyze phylogenetic relationships (Ballard and Spooner, pers. com.) as shown for *Ipomoea* (Miller et al., 1999). We currently are using *waxy* intron DNA sequences to examine relationships of all nine species of wild tomatoes. Our preliminary cladistic analysis of *waxy* data supports the paraphyly of the most common and widespread species *S. peruvianum*. The allogamous species are basal while all autogamous and facultative allogamous species are derived (Peralta et al., 1997).

Conclusions

Many of the discrepancies in taxonomic treatments of the wild tomatoes have arisen from the application of different classification concepts. The classifications of Müller (1940), Luckwill (1943), and Child (1990) were based on morphology, while Rick (1979) used the biological species concept. These treatments are partly discordant with relationships as shown by phenetic (Miller & Tanksley, 1990) or cladistic (Palmer & Zamir, 1982; Spooner et al., 1993) analyses of molecular data.

We are attempting to resolve these discrepancies by analyzing more accessions, especially from the most widely distributed and genetically variable species *S. peruvianum*. We are analyzing these accessions with explicit morphological techniques, coordinated with molecular data from *waxy*, and using appropriate outgroups in *Solanum*. A modern revision that incorporates insights from different areas is in progress (Peralta, 2000).

The systematic placement of tomatoes in *Solanum* is still controversial in that it has yet to gain universal acceptance, especially in the breeding literature. This example dramatically illustrates two main and often competing goals in taxonomy of predictive natural classifications (treatment in *Solanum*, our taxonomic decision) and the maintenance of nomenclatural stability (treatment in *Lycopersicon*, the taxonomic decision of Lester [1991] and others). In reality, the overall predictive value of classifications, based on any classification philosophy, has rarely, if ever been tested empirically, and we are aware of no such tests in crops. It is not possible to resolve or even summarize these many issues here, and we simply state our hypothesis that tomatoes may be more "predictivity" classified in *Solanum*, despite these tests. Classification philosophies remain under discussion in the systematic community and involve many additional questions such as reliance on nomenclatural types and classification ranks (Moore, 1998). The economic importance of tomatoes highlights these competing goals and hypotheses of classification. It will surely stimulate discussion within the scientific community of taxonomists and breeders to highlight the relative value of these classifications that emphasize predictivity versus stability.

Literature Cited

Bentham, G. & J. D. Hooker. 1873. Solanaceae. *Genera Plantarum*, 2: 882-913. Lovel Reeve & Co. Londini.

Bohs, L. & R. G. Olmstead. 1997. Phylogenetic relationships in *Solanum* (Solanaceae) base on *ndhF* sequences. *Syst. Bot.* 22: 5-17.

Bonierbale, M. W., Steinharter, T. P. & S. D. Tanksley. 1988. RFLP maps based on a common set of clones reveal modes of chromosomal evolution in potato and tomato. *Genetics* 120: 1095-1103.

Börner, C. 1912. *Solanum* L. und *Solanopsis* gen. nov. *Abh. Naturwiss. Vereine Bremen*, 21: 282.

Child, A. 1990. A synopsis of *Solanum* subgenus *Potatoe* (G. Don) D'Arcy [*Tuberarium* (Dun.) Bitter (s.l.)]. *Feddes Repert.* 101: 209-235.

Correll, D. S. 1958. A new species and some nomenclatural changes in *Solanum*, section *Tuberarium. Madroño* 14: 232-236.

Cross, R. J. 1998. Review paper: global genetic resources of vegetables. *Pl. Var. Seeds* 11: 1, 39-60.

D'Arcy, W. G. 1972. *Solanaceae* studies II: typification of subdivisions of *Solanum. Ann. Missouri Bot. Gard.* 59: 262-278.

————— 1987. The circumscription of *Lycopersicon. Solanaceae Newslett.* 2: 60-61.

————— 1991. The *Solanaceae* since 1976, with a review of its biogeography, in J. G. Hawkes, R. N. Lester, M. Nee & N. Estrada (eds.). *Solanaceae* III: *taxonomy, chemistry, evolution*, pp. 75-137. Royal Botanic Gardens, Kew.

Dunal, M. F. 1813. *Histoire Naturelle, Medicinale et Economique des Solanum.* Paris, Strasbourg, Montpellier.

Dunal, M. F. 1852. *Solanaceae*, in A.L.P.P. de Candolle (ed.). *Prodromus systematis naturalis regni vegetabilis*, 13: 1-690.

Esquinas Alcazar, J. T. 1981. Genetic resources of tomatoes and wild relatives. *Rep. Int. Board Pl. Breed. Resources.* No.AGP: IBPGR-80-103, pp.1-65. Rome.

Fosberg, F. R. 1987. New nomenclatural combination for Galapagos plant species. *Phytologia* 62: 181-183.

Gerhardt C., E. Ritter, A. Barone, T. Debener, B. Walkemeier, U. Schachtchabel, H. Kaufmann, R. D. Thompson, M. W. Bonierbale, M. W. Ganal, S. D. Tanksley, and F. Salamini. 1991. RFLP maps of potato and their aligment with the homoeologous tomato genome. *Theor. Appl. Genet.* 83:49-57.

Hawkes, J. G. 1990. *The potato: evolution, biodiversity and genetic resources.* Belhaven Press, London.

Heine, H. 1976. *Flore de la Nouvelle Caledonie*, vol.7. Musée National d'Histoire Naturelle, Paris.

Holle, M., Rick, C. M. & D. G. Hunt. 1978. Catalog of collections of green-fruited *Lycopersicon* species and *Solanum pennellii* found in watersheds of Peru. *TGC report* 28:49-78.

Holle, M., Rick, C. M. & D. G. Hunt. 1979. Catalog of collections of green-fruited *Lycopersicon* species and *Solanum pennellii* found in watersheds of Peru. *TGC report* 29:73-91.

Hunziker, A. T. 1979. South American *Solanaceae*: a synoptic survey, in J. G. Hawkes, R. N. Lester & A. D. Skelding (eds.). *The biology and taxonomy of Solanaceae.* Linnean Soc. Symp., Ser.7, pp. 49-85. Academic Press, London.

Jussieu, A. L. de. 1789. *Genera Plantarum.* Paris.

Laterrot, H. 1989. The tomato. Advantages and use of wild varieties for varietal creation. *Rev. Hort.* 295: 13-17.

Lester, R. N. 1991. Evolutionary relationships of tomato, potato and pepino, and wild species of *Lycopersicon* and *Solanum*, in J. G. Hawkes, R. N. Lester, M. Nee & N. Estrada (eds.). *Solanaceae* III: taxonomy, chemistry, evolution, pp. 283-301. Royal Botanic Gardens, Kew.

Linnaeus, C. 1753. *Species Plantarum*, 1st ed. Holmiae, Stockholm.

Luckwill, L. C. 1943. The genus *Lycopersicon*: an historical, biological, and taxonomical survey of the wild and cultivated tomatoes. *Aberdeen Univ. Stud.* 120: 1-44.

MacBride, J. F. 1962. Flora of Peru: *Solanaceae. Field Mus. Nat. Hist., Bot. Ser.* 13: 3-267.

McClean, P. E. & M. R. Hanson. 1986. Mitochondrial DNA sequence divergence among *Lycopersicon* and related *Solanum* species. *Genetics* 112: 649-667.

Miller, P. 1754. *The gardeners dictionary*, Abridged 4th ed. London.

Miller, P. 1768. *The gardeners dictionary*, Abridged 8th ed. London.

Miller, P. 1807. *The gardener's and botanist's dictionary.* Posth. ed. London.

Miller, J. C. & S. D. Tanksley. 1990. RFLP analysis of phylogenetic relationships and genetic variation in the genus *Lycopersicon. Theor. Appl. Genet.* 80: 437-448.

Miller, R. E., Rausher, M. D. & P. S. Manos. 1999. Phylogenetic Systematics of *Ipomoea* (*Convolvulaceae*) based on ITS and Waxy. *Syst. Bot.* 24: 209-227

Moore, G. 1998. A comparison of traditional and phylogenetic nomenclature. *Taxon* 47: 561-579.

Müller, C. H. 1940. A revision of the genus *Lycopersicon. U.S.D.A. Misc. Publ.* 382: 1-28 + 10pl.

Olmstead, R. G. & J. D. Palmer. 1997. Implications for phylogeny, classification, and biogeography of *Solanum* from cpDNA restriction site variation. *Syst. Bot.* 22: 19-29.

Palmer, J. D. & D. Zamir. 1982. Chloroplast DNA evolution and phylogenetic relationships in *Lycopersicon. Proc. Natl. Acad. Sci. U.S.A.* 79: 5006-5010.

Peralta, I. E., H. Ballard & D. M. Spooner. 1997. *Waxy* gene intron phylogeny of tomatoes, *Solanum* subsect. *Lycopersicum* (*Solanaceae*). *Amer. J. Bot.* 84: 222.

Peralta, I. E. 2000. Phylogeny of wild tomatoes (*Solanum* L. section *Lycopersicum* [Mill.] Wettst. subsection *Lycopersicum*) based on morphology and *waxy* gene sequences. Ph.D. Thesis, University of Wisconsin-Madison

Rick, C. M. 1960. Hybridization between *Lycopersicon esculentum* and *Solanum pennellii*. Phylogenetic and cytogenetic significance. *Proc. Natl. Acad. Sci. U.S.A.* 46: 78-82.

——— 1963. Barriers to interbreeding in *Lycopersicon peruvianum*. *Evolution* 17: 216-232.

——— 1971. *Lycopersicon*, in: I. L. Wiggins & D. M. Porter (eds.). *Flora of the Galapagos Islands*, pp. 468-471. Stanford Univ. Press, Palo Alto, California.

——— 1973. Potential genetic resources in tomato species: clues from observations in native habitats, in A. M. Srb (ed.), *Genes, Enzymes, and Populations*, pp. 255-269. Plenum, New York.

——— 1979. Biosystematic studies in *Lycopersicon* and closely related species of *Solanum*, in J. G. Hawkes, R. N. Lester & A. D. Skelding (eds.). *The biology and taxonomy of Solanaceae*. Linnean Soc. Symp., Ser.7, pp. 667-677. Academic Press, London.

——— 1982. The potential of exotic germplasm for tomato improvement, in I. K. Vasil, W. R. Scowcroft & K. J. Frey (eds.). *Plant Improvement and Somatic Cell Genetics*, pp. 1-28. New York, Academic Press.

——— 1983. Tomato (*Lycopersicon*), in: S. D. Tanksley & T. J. Orton (eds.). *Isozymes, in Plant Genetics and Breeding*, pp. 147-165. Elsevier Sci. Publ. Amsterdam.

——— 1986a. Reproductive isolation in the *Lycopersicon peruvianum* complex, in: W. G. D'Arcy (ed.). *Solanaceae: biology and systematics*, pp. 477-495. Colombia Univ. Press, New York.

——— 1986b. Germplasm resources in the wild tomato species. *Acta Hort.* 190: 39-47.

——— 1987. Genetic resources in *Lycopersicon*. *Pl. Biol.* 4: 17-26.

——— 1988. Tomato-like nightshades: affinities, autoecology, and breeders opportunities. *Econ. Bot.* 42: 145-154.

——— 1991. Tomato resources of South America reveal many genetic treasures. *Diversity* 7: 54-56.

——— & R. Lamm. 1955. Biosystematic studies on the status of *Lycopersicon chilense*. *Amer. J. Bot.* 42: 663-675.

——— R. W. Zobel, & J. F. Fobes. 1974. Four peroxidase loci in red-fruited tomato species: genetics and geographic distribution. *Proc. Natl. Acad. Sci. USA* 71: 835-839.

——— & J. F. Fobes, 1975 a. Allozymes of Galapagos tomatoes: polymorphism, geographic distribution and affinities. *Evolution* 29: 443-457.

——— & J. F. Fobes, 1975 b. Allozymes variation in the cultivated tomatoes and closely related species. *Bull. Torrey Bot. Club.* 102: 376-384.

——— E. Kesicki, J. F. Fobes & M. Holle. 1976. Genetic and biosystematic studies on two new sibling species of *Lycopersicon* from Interandean Perú. *Theor. Appl. Genet.* 47: 55-68.

——— J. F. Fobes & M. Holle. 1977. Genetic variation in *Lycopersicon pimpinellifolium*: evidence of evolutionary change in mating systems. *Pl. Syst. Evol.* 127: 139-170.

——— & S. D. Tanksley. 1981. Genetic variation in *Solanum pennelli*: comparison with two other sympatric tomato species. *Pl. Syst. Evol.* 139: 11-45.

——— J. W. DeVerna, R. T. Chetelat & M. A. Stevens. 1987. Potential contributions of wide crosses to improvement of processing tomatoes. *Acta Hort.* 200: 45-55.

——— & M. Holle. 1990. Andean *Lycopersicon esculentum* var. *cerasiforme*: genetic variation and its evolutionary significance. *Econ. Bot.* 44 (3 Suppl.): 69-78.

——— H. Laterrot & J. Philouze. 1990. A revised key for the *Lycopersicon* species. *TGC report* 40: 31.

Seithe, A. 1962. Die Haararten der Gatung *Solanum* L. und ihre taxonomische Verwertung. *Bot. Jahrb. Syst.* 81: 261-336.

Spooner, D. M., Anderson, G.J. & R.K. Jansen. 1993. Chloroplast DNA evidence for the interrelationships of tomatoes, potatoes, and pepinos (*Solanaceae*). *Amer. J. Bot.* 80: 676-688.

Stevens, M. A. & C. M. Rick. 1986. Genetics and breeding, in J. G. Atherton & J. Rudich (eds.). *The tomato crop: a scientific basis for improvement*, pp. 35-109. Chapman and Hall, London.

Symon, D. E. 1981. The solanaceous genera *Browallia, Capsicum, Cestrum, Cyphomandra, Hyoscyamus, Lycopersicon, Nierembergia, Physalis, Petunia, Salpichroa, Withania,* naturalized in Australia. *J. Adelaide Bot. Gard.* 3: 133-166.

———— 1985. The *Solanaceae* of New Guinea. *J. Adelaide Bot. Gard.* 8: 1-177.

Tanksley, S. D., M. W. Ganal, J. P. Prince, M. C. de Vicente, M. W. Bonierbale, P. Broun, T. M. Fulton, J. J. Giovannoni, S. Grandillo, G. B. Martin, R. Messeguer, J. C. Miller, L. Miller, A. H. Paterson, O. Pineda, M. S. Röder, R. A. Wing, W. Wu, & N. D. Young. 1992. High density molecular linkage maps on the tomato and potato genomes. *Genetics* 132: 1141-1160.

Tanksley, S. D. & S. R. McCouch. 1997. Seed banks and molecular maps: unlocking genetic potential from the wild. *Science* 277: 1063-1066.

Taylor, I. B. 1986. Biosystematic of the tomato, in J. G. Atherton & J. Rudich (eds.). *The tomato crop: a scientific basis for improvement*, pp. 1-34. Chapman and Hall, London.

Tournefort, J. P. de. 1694. *Élémens de Botanique.*

Villand, J., P. W. Skorch, T. Lai, P. Hanson, C. G. Kuo, & J. Nienhuis. 1998. Genetic variation among tomato accessions from primary and secondary centers of diversity. *Crop Sci. (Madison)* 38:1339-1347.

Warnock, S. J. 1988. A review of taxonomy and phylogeny of the genus *Lycopersicon.* *HortScience* 23: 669-673.

Wettstein, R. von. 1895. *Solanaceae*, in A. Engler & K. Prantl (eds.). *Die Natürlichen Pflanzenfamilien*, 4: 4-38: Nachtrage 292-293.

Williams, C. E. & D. A. St Clair. 1993. Phenetic relationships and levels of variability detected by restriction fragment length polymorphism and random amplified polymorphic DNA analysis of cultivated and wild accessions of *Lycopersicon esculentum. Genome* 36: 619-30.