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History, Origin and Early Cultivation of Tomato (Solanaceae)

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INTRODUCTION

Tomatoes rank fourth among the leading world vegetables. In 2001, over 100 million metric tons were produced, with the 15 leading countries being (in descending order) China, US, India, Turkey, Egypt, Italy, Spain, Brazil, Islamic Republic of Iran, Mexico, Greece, Russian Federation, Ukraine, Chile, and Uzbekistan (FAO 2002; Fig. 1.1). There has been a general upward trend in tomato production during the period 1992-2002 (Fig. 1.2). Interestingly, the countries that produce higher yields (Fig. 1.3) do not possess the ideal climate for the tomato crop and have less land area devoted to tomato production (Fig. 1.4). Northern European countries, as well as Canada and New Zealand, produce most of their tomatoes under controlled greenhouse conditions. Tomato consumption has also shown a general increased trend of consumption over a period of time (FAO 2002). Tomatoes supply a mean of 12.1 kg/cap/yr, and tomato consumption is higher in Mediterranean and Arab countries (usually between 40 and 60 kg/cap/yr). Tomatoes are highly popular in Egypt, Italy, Israel, Lebanon, Turkey and United Arab Emirates (60-70 kg/cap/yr), whereas people from Greece and Libya have the highest preference consuming more than 100 kg of tomatoes per capita and year. Tomatoes are also a popular food in Latin and North America.

Tomatoes rank second among the leading vegetables of the US (Ensminger et al. 1995), with a production of 10.25 million metric tons in

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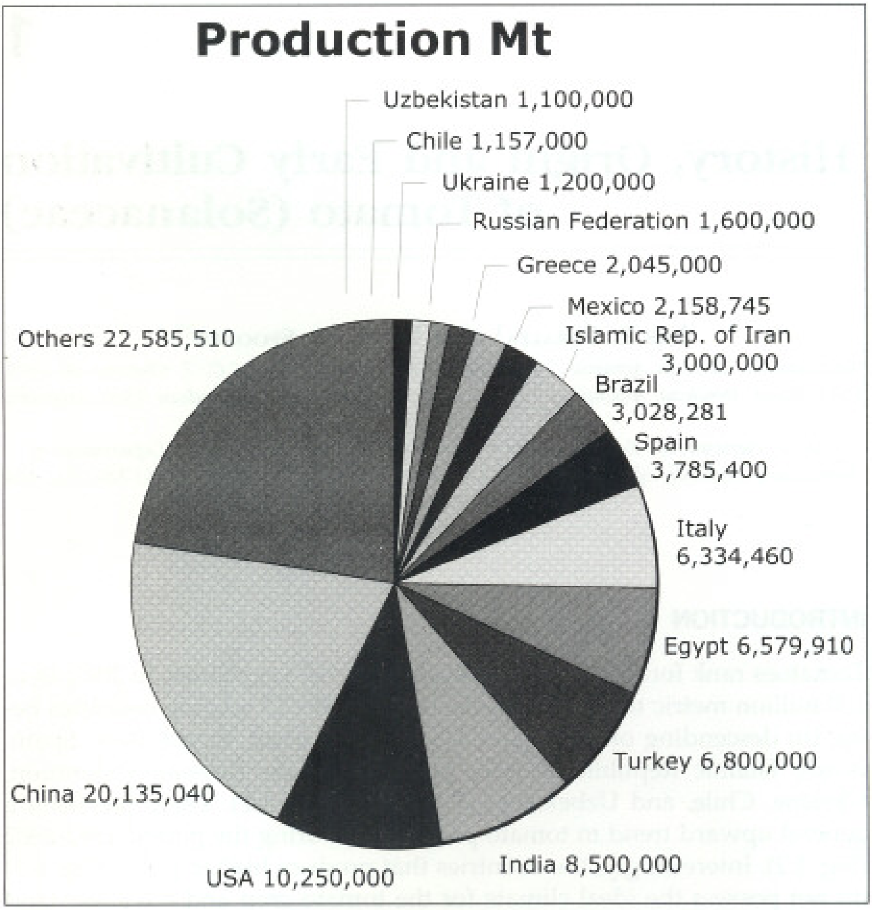

Fig. 1.1 Tomato production worldwide, 2001.

2001. Much of the US production is processed, with major products being canned tomatoes, ketchup, chilli sauce, juice, paste, powder, puree, salad dressings, sauces, soups, and vegetable and juice cocktails.

The US farmgate (point of first sale) value of tomatoes in 2001 was 1.12 billion dollars for fresh tomatoes and 0.54 billion dollars for processed tomatoes ($1.66 billion dollars total) (USDA, National Statistics Service 2002a). California and Florida clearly dominate the US market, with Florida accounting for 40.3% of the fresh US market, and California accounting for 24.1% of the fresh market and 90.7% of the processed market (USDA, National Statistics Service 2002b). Tomato consumption has substantially increased in the US since the beginning of the last century. In 1920, the per capita consumption was only 8.2 kg/yr, which in 1978 increased to

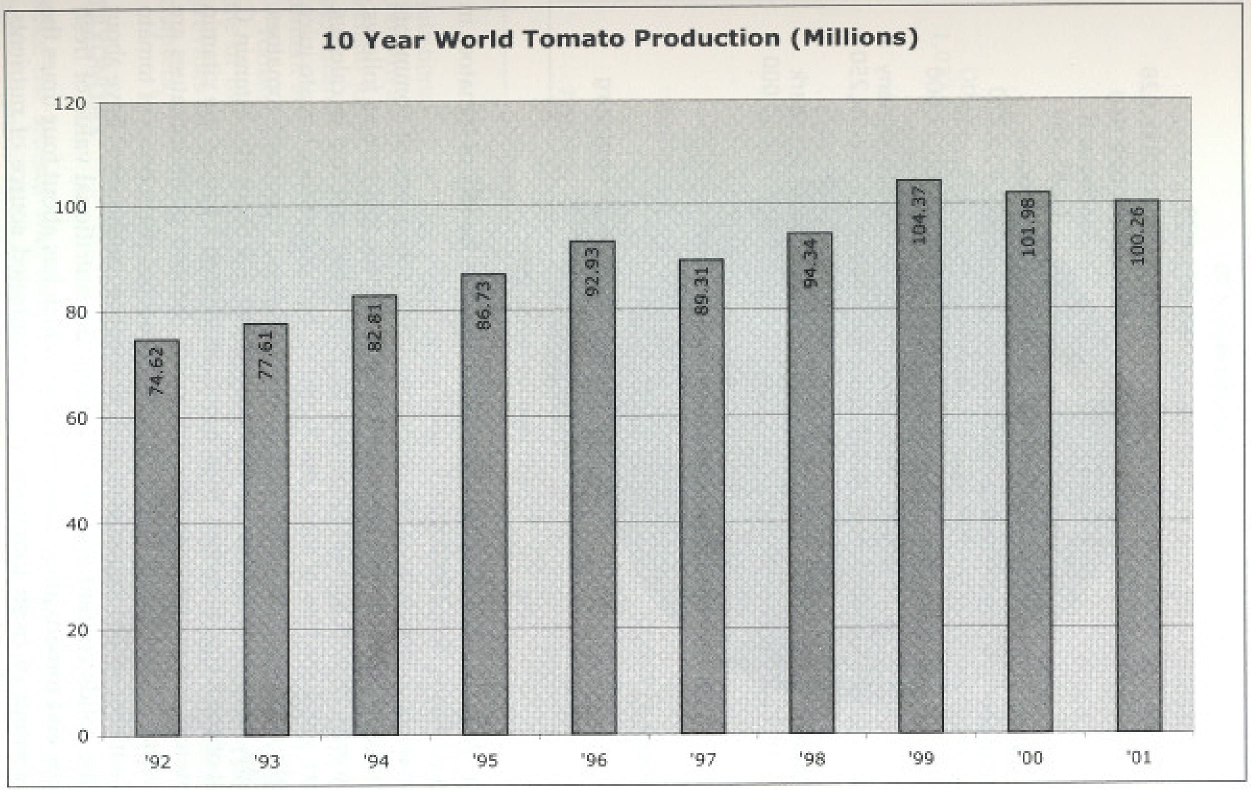

Fig. 1.2 Tomato production worldwide, 1992-2001.

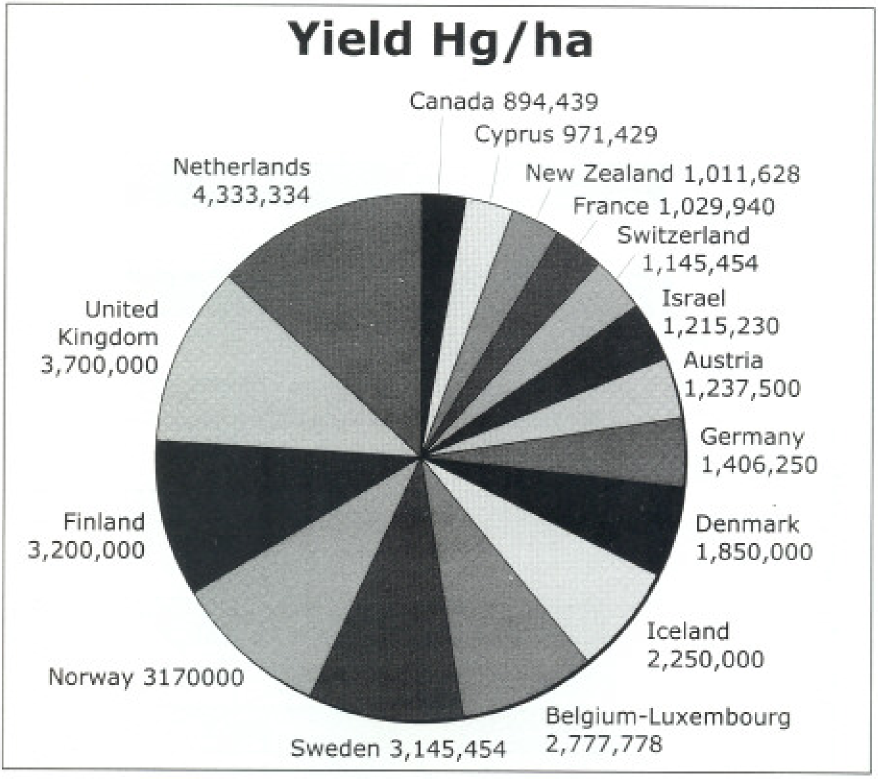

Fig. 1.3 Tomato yield worldwide, 2001.

25.5 kg/yr (Rick 1978), and now is 40.5 kg /yr, but mostly of tomatoes in preserved forms (FAO 2002).

Tomato is a rich source of nutrients (Table 1.1). General comments (Ensminger et al. 1995) made in particular from this table are as follows: Fresh tomatoes and tomato juices are high in water and low in calories. Both are good sources of vitamins A and C, but unfortified tomato juice has only about 2-3 the vitamin C content of raw, ripe (red) tomatoes. Similarly, canned tomatoes contain only about 3-4 times the vitamin C content of fresh ripe tomatoes. Ripe tomatoes contain 3-4 times the vitamin A as mature green tomatoes, but otherwise red and green tomatoes are about equal in nutritional value. Tomato puree and plain types of tomato sauce (without added ingredients such as meat or mushrooms) have about twice the solids content and about double the nutritional value of fresh tomatoes and tomato juice. Tomato paste, which has about four times the solids content of fresh tomatoes, is a concentrated source of nutrients, making it a valuable contribution when used in preparation of pastas, pizzas, and other foods. Ketchup and chilli sauce are about equal in

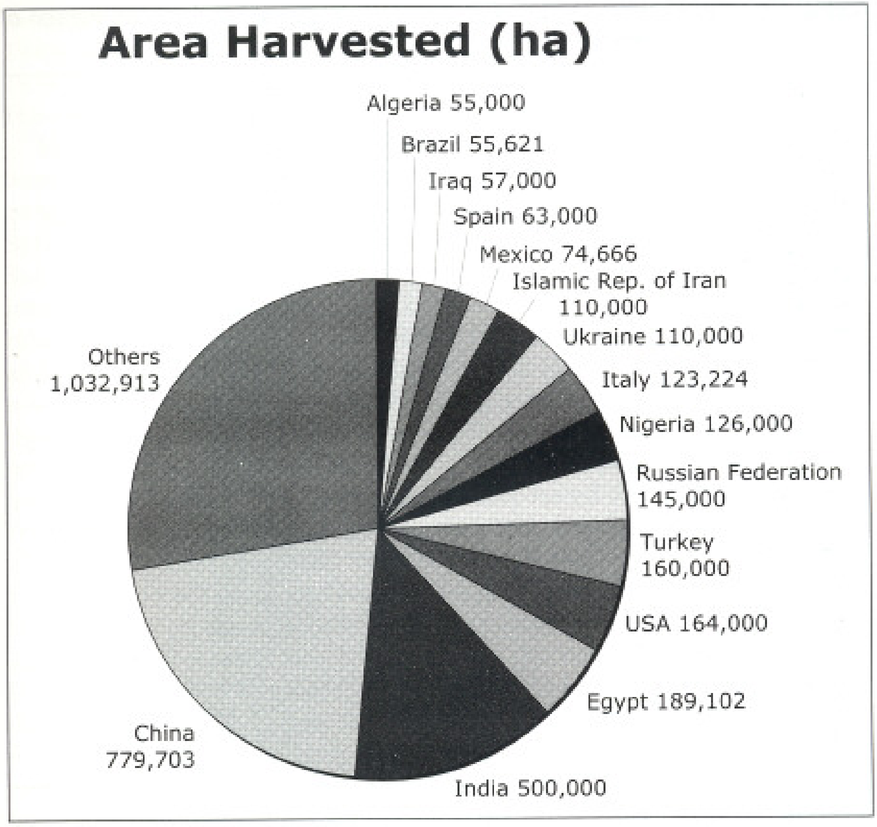

Fig. 1.4 Area of tomato harvest worldwide, 2001.

nutritional value, since each item is made with similar ingredients and contains about 32% solids (about 5 times the content of fresh tomatoes and tomato juice). However, the nutrients per calorie of these products are significantly less than those furnished by tomato paste, because the solids content and caloric values are boosted by added salt and sugar.

Tomato popularity and its high level of consumption make this vegetable one of the major sources of vitamins and minerals in human diet, and provides healthy benefits that will be discussed further in the following chapters.

TAXONOMY

Since the tomato was introduced to Europe in the sixteenth century, early botanists recognized the close relationships of tomatoes with the genus *Solanum*, and commonly identified them as *S. pomiferum* (Sabine 1820, Luckwill 1943a). Anguillara (1561) identified the newly introduced

Table 1.1 *Chemical composition of tomato fruit (figures for a small tomato of 100 g; after Ensminger et al. 1995).*

Moisture	95%
Food energy	22 kcal
Protein	1 g
Fats	0.2 g
Carbohydrates	4.7 g
Fiber	0.5 g
Calcium	13.0 mg
Phosphorus	27.0 mg
Sodium	3.0 mg
Magnesium	17.7 mg
Potassium	244.0 mg
Iron	0.50 mg
Zinc	0.20 mg
Copper	0.01 mg
Vitamin A	900.0 IU
Vitamin D	0
Vitamin E (α-Tocopherol)	0.40 mg
Vitamin C	23 mg
Thiamin	0.06 mg
Riboflavin	0.04 mg
Niacin	0.70 mg
Panthothenic Acid	0.33 mg
Vit. B-6 (pyridoxine)	0.10 mg
Folacin (folic acid)	39.00 mcg
Biotin	4.00 mcg
Vitamin B-12	0

tomato as a plant named *Lycopersicon*, which means "wolf peach", by the Greek naturalist Galen fourteen centuries earlier. However, the actual plant described by Galen is unknown, and it certainly did not refer to any form of tomato because all tomato species are not native of the Old World. Tournefort (1694) was the first to consider cultivated tomatoes within a distinct genus under the early name *Lycopersicon*. He used the multilocular character of the fruit as a criterion to differentiate *Lycopersicon* from *Solanum*. Tournefort listed nine taxa but only seven of them correspond to fasciated-fruited varieties that differed in the color and size of their fruits, and the other two described taxa belong to different Solanaceae (Luckwill 1943a).

Linnaeus (1753) classified tomatoes in the genus *Solanum*, and under the specific name of *Solanum lycopersicum* grouped all the cultivated multilocular forms that Tournefort described as separate species. He also described a second wild species from Peru, *S. peruvianum*. Jussieu (1789), in his natural classification, also included tomatoes in *Solanum*. On the other hand, Miller (1754) reconsidered Tournefort's classification and formally described the genus *Lycopersicon*. This classification of tomatoes under *Lycopersicon* continued as the prevailing treatment by several classical and modern authors (e.g., Dunal 1813, 1852, Bentham and Hooker 1873, Müller 1940a, Luckwill 1943a, Correll 1958, D'Arcy 1972, 1987, 1991, Hunziker 1979, Rick 1979, 1988, Symon 1981, 1985, Taylor 1986, Warnock 1988, Hawkes 1990, Rick et al. 1990b).

More recently, the phylogenetic relationships within the Solanaceae have been examined with molecular data. Spooner et al. (1993) examined outgroup relationships of tomato to potato and other members of the Solanaceae based on chloroplast DNA restriction site data (Fig. 1.5). Subsequent molecular studies unequivocally supported tomato to be firmly internested in the genus *Solanum* L., then this tomato-potato sister group relationship is now clearly established (Olmstead and Palmer 1997, Bohs and Olmstead 1997, 1999, Peralta and Spooner 2001). Based on these results, a new phylogenetic classification has assigned tomato to the genus *Solanum* (Spooner 2005). This classification of tomatoes in *Solanum* matches the original treatment of Linnaeus (1753), as well as prior taxonomists who insightfully foresaw this generic relationship based on morphological data (Wettstein 1895, MacBride 1962, Seithe 1962, Heine 1976, Fosberg 1987, Child 1990). Börner (1912) also recognized the close affinities among tomatoes and potatoes, and proposed a new genus *Solanopsis* to segregate them. Although most taxonomists today place tomato in *Solanum*, most agronomists and horticulturists do not use this name (see Doco et al. 1997, Shichijo et al. 2001, Van der Heuvel 2001, Weller et al. 2001). Most users of the classification in *Lycopersicon* clearly base their reluctance to use the *Solanum* names on tradition or the practical goal of maintaining familiar names rather than adherence to any particular classification philosophy. In this chapter tomato species are classified in the genus *Solanum* and their comparative *Lycopersicon* synonyms are given in Table 1.2.

Hypotheses of ingroup relationships within tomato also have varied greatly. Müller (1940a), Luckwill (1943a), and Child (1990) classified tomato based on morphological criteria, while Rick (1963, 1979) and Rick et al. (1990b) classified tomato quite differently based on biological (interbreeding) criteria. Peralta and Spooner (2001) produced a phylogeny of tomato based on DNA sequences of the single-copy GBSSI (*waxy*) gene, and Spooner et al. (2005) based on Amplified Fragment Length Polymorphisms. The results support allogamy, self-incompatibility, and green fruits as primitive in tomatoes, and most closely match the classification of Child (1990). One of the self-incompatible species, the highly polymorphic *Solanum peruvianum* L., was supported to consist of one group of populations from northern Peru and another group of populations from central to southern Peru. A phenetic morphological study by Peralta and Spooner (2003) supported all species, including the "northern" and "southern" group of populations of *S. peruvianum* as distinct taxa. Peralta et al. (2005) used these results, and morphological data, to divide the former *S.*

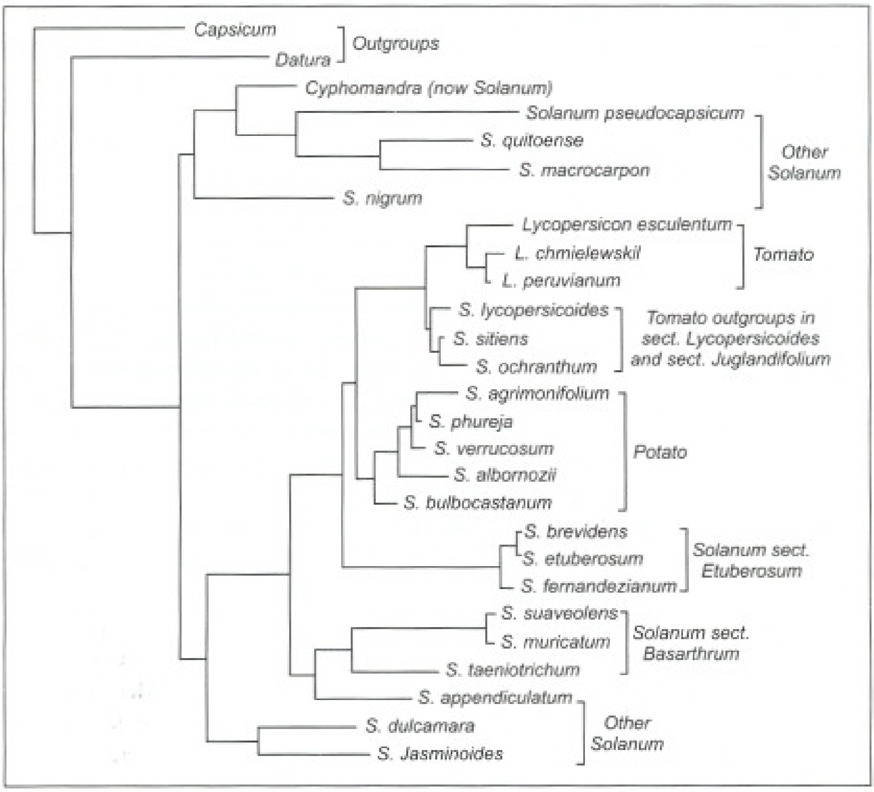

Fig. 1.5 One of two-most parsimonious cladograms (as a phylogram) of chloroplast DNA restriction site data examining wild tomatoes (here labeled *Lycopersicon*), their sister groups (*Solanum* sect. *Lycopersicoides*, sect. *Juglandifolium), wild* potatoes (*Solanum* sect. *Petota*), and further outgroups in *Solanum* sect. *Etuberosum*, sect. *Basarthrum*, and other *Solanum* (modified from Spooner et al., 1993).

peruvianum into four species. A taxonomic monograph of tomato, based partly on these new molecular and morphological data, is in preparation by the present authors and Sandra Knapp (Natural History Museum, London).

DISTRIBUTION, HABITATS, MORPHOLOGY, MATING SYSTEMS AND GENETIC RESOURCES OF WILD TOMATOES

The wild relatives of the cultivated tomato are native of western South America along the coast and high Andes from central Ecuador, through Peru, to northern Chile, and in the Galápagos Islands (Table 1.2). The most likely ancestor of cultivated tomatoes is the wild cherry tomato (usually identified as *S. lycopersicum* var. *cerasiforme*), which is more widespread,

Table 1.2 *Comparison of wild tomato species (*Solanum *L. section* Lycopersicon *(data comapiled from* Müller, *1940a;* Luckwill *1943a;* Esquinas Alcazar *1981;* Rick *1982b, 1986b;* Taylor *1986;* Peralta *et al., 2005). The Lycopersicon synonyms follow the Solanum names.*

Species	Lycopersicon *synonyms*	*Fruit color*	*Breeding system*	*Distribution and Habitat*	*Comments and interesting features for breeding purposes*
S. lycopersicum L.	*L. esculentum* Miller	Red	SC, facultative allogamous	Native from Ecuador and Peru, widespread in America. Wide range of habitats, weed in newly open areas	Moisture-tolerance, resistance to wilt, root-rotting, and leaf-spotting fungi
S. cheesmaniae (Riley) Fosberg	*L. cheesmaniae* Riley	Yellow, yellow green, orange, purple	SC, exclusively autogamous	Endemic of the Galápagos Archipelago. From low elevations in the saline seashore up to 500 m in volcanic areas	Closely related to *S. galapagense*. Salt tolerance, lepidoptera and virus resistances, and genes involved in the retention of fruits and thick pericarp
S. galapagense S. *Darwin* and *Peralta*	*Part of L. cheesmaniae L. Riley (previously known as forma or var. minor)*	Pale to deep orange	SC, exclusively autogamous	Endemic of the Galápagos Archipelago. Mostly occurring on coastal lava to within 1 m of high tide mark within range of salt spray, but occasionally inland up to 50 m	Closely related to *S. cheesmaniae*. Salt tolerance.
S. pimpinellifolium B. Juss.	*L. pimpinellifolium* (B. Juss.) Miller	Red	SC, autogamous, facultative allogamous	Central Peru to central chile, dry coastal habitats, 0 – 500 m, but exceptionally upto 1400 m.	Closely related to *S. lycopersicum* (some natural introgression with it). Contributed to improve color and fruit quality. Insect, nematode, and disease resistances.

(Contd.)

(*Contd.*)

S. arcanum Peralta	Part of *L. peruvianum* (L.) Miller	Green	SI	100-2800 m; N Peru, lomas, dry valleys, and dry rocky slopes	
S. chilense (Dunal) Reiche	*L. chilense* Dunal	Small green with purple stripe	SI, allogamous	Sea level-3250 m; S Peru to N Chile, grows in dry river beds, survives by deep roots	Typically erect becoming decumbent; post-syngamic barriers with *S. peruvianum*. Drought resistance
S. chmielewskii (C. M. Rick, Kesicki, Fobes & M. Holle), D. M. Spooner, G. J. Anderson & R. K. Jansen	*L. chmielewskii* C. M. Rick, Kesicki, Fobes & M. Holle	Green	SC, facultatively allogamous	1600-3200 m, Pacific side, South-Central Peru to N Bolivia; moist habitats; slightly better-drained sites that *S. neorickii*	Sympatric with *S. neorickii*. Contributed to improve high sugar content in the crop
S. corneliomuelleri *J. F. Macbr.*	Part of *L. peruvianum (L.) Miller*; also known as *Lycopersicon glandulosum* C. F. Mull.	Green	SI	Landslides and rocky slopes, (40)200-3300 m, Central to S Peru	
S. habrochaites S. Knapp & D. M. Spooner	*L. hirsutum* Dunal	Green	Typically SI, 1-2 collections SC, but with later inbreeding depression	Typically high elevations, (40) 200-3300 m, in moist well drained soils; Central Ecuador to Central Peru	Cold and frost tolerance. Insect resistance (glandular hairs), and other resistances
S. huaylasense Peralta	Part of *L. peruvianum* (L.) Miller	Green	SI	Rocky slopes, (940) 1700-3000 m, N Peru, Ancash along Río Santa.	

(*Contd.*)

(*Contd.*)

S. neorickii C.M. Rick, Kesicki, Fobes & M. Holle, D.M. Spooner, G.J. Anderson, & R.K. Jansen	*L. parviflorum* C. M. Rick, Kesicki, Fobes & M. Holle	Pale green	SC, highly autogamous	(920)1950-2600 m, Pacific side, South Ecuador to South-central Peru; moist and well-drained rocky environments; more common than *S. chmielewskii*.	Sympatric with *S. chmielewskii*; probably evolved from *S. chmielewskii*; yet no natural introgression reported with *S. neorickii*.
S. pennellii Correll	*L. pennellii* (Correll) D'Arcy	Green	Usually SI, some SC in Southern range	sea level to 2300 m; N cent to S cent Peru (8-16 °S); hot dry habitats but subject to dew and fog; (many stomata adaxially, poor root system).	Drought resistence; covered with glandular hairs imparts insect resistance; hybridizes unilaterally (as male) with many other species except *S. chilense* or *S. peruvianum*.
S. peruvianum L.	*L. peruvianum* (L.) Miller	Green	Typically SI, allogamous,	Sea level-600 m; Central Peru to N Chile. Coastal lomas formations and occasionally as a weed at fields edges.	Virus, bacteria, fungi, aphid, and nematode resistances.

and perhaps more recently distributed into Mexico, Colombia, Bolivia, and other South American countries (Rick and Holle 1990). The prior taxonomies recognized the cherry tomato as *L. esculentum* var. *cerasiforme* or *S. lycopersicon* var. *cerasiforme* but we do not recognize this variety and combine all variants of this species (cultivated and wild) into *S. lycopersicon*. The wild cherry tomato grows spontaneously in tropical and subtropical areas worldwide, where it might have been accidentally introduced or escaped from cultivation.

Wild tomatoes grow in a variety of western South American habitats, from near sea level to over 3,300 m in elevation (Rick 1973, Taylor 1986). These habitats include the arid Pacific coastal lowlands and adjacent lower valleys to 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 and geographically isolated valleys, and are adapted to particular microclimatic and soil conditions. Certainly, the Andean geography, diverse ecological habitats, and different climates contributed to wild tomato diversity (Warnock 1988).

Wild tomatoes are perennial herbaceous plants, although in their natural habitat tomatoes most probably behave as annuals and might die after the first growing season due to frost or drought. They have an erect or prostrate growth habit, and possess taxonomically useful differences in leaf, inflorescence, flower, fruit, and seed characters. Leaves are pinnately dissected with 2-6 opposite or sub-opposite, sessile, subsessile or petiolate pairs of leaflets. There is great interspecific variation in leaf dissection with primary, secondary, tertiary, and interjected leaflets. The basic inflorescence is a cyme with different branching patterns (monochasial, dichotomous, and polychotomous), and with or without axial bracts. Flowers are typically yellow; the anthers are united 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 are variable (Table 1.2), as are seed size, color and development of radial walls of the seed coat cells (Müller 1940a, Luckwill 1943a). Fruits are usually bilocular in the wild species, and bilocular or multilocular in the cultivated varieties.

Mating systems have played an important role in the evolution of wild tomato species, varying from allogamous self-incompatible, to facultative allogamous, and self-compatible, to autogamous and self-compatible (Rick 1963, 1979, 1986a; Table 1.2). The self-incompatibility system in tomatoes is gametophytic and controlled by a single, multiallelic S locus (Rick 1982a). Large flowers and greater stigma exsertion from the anther tube have been associated with self-incompatibility resulting in greater outcrossing and genetic variation in wild tomatoes (Rick 1982a). Similarly, in the self-compatible species *S. pimpinellifolium*, greater outcrossing and genetic variation is related to large flowers and greater stigma exsertion; marginal populations of this species are highly autogamous with little or no genetic variation, bearing small flowers, with little or no stigma exsertion (Rick et al. 1977). Self-incompatibility is most probably regulated by different unlinked genes or gene complexes (Rick 1982a), and changes in mating systems in wild tomatoes occurred from self-incompatibility, as the ancestral condition, to self-compatibility, which probably never reversed to self-incompatibility. Change from self-incompatibility to self-compatibility is expected to have arisen infrequently and independently (Rick 1982a). Hybridization is another possible source of genetic variation. Evidence of natural interspecific hybridization and gene flow among wild self-compatible tomato species have been documented in native sympatric populations of *S. pimpinellifolium* and *S. lycopersicum*, and cultivated tomatoes in Ecuador and Peru (Rick 1958). The reciprocal introgression of traits into both taxa generates complex morphological gradation between them that makes their taxonomic identification difficult (Rick 1958).

The traditional breeding for pure lines in the cultivated tomato has narrowed its genetic base (Stevens and Rick 1986). Fortunately, genetic resources from the primary center of diversity provide a wealth of useful genetic traits to improve the crop (Rick 1982b, 1995). All wild tomato species are diploid ($2n = 2x = 24$) and can be crossed (but sometimes with difficulty) to the cultivated tomato (Rick 1979). They are of great use in breeding programs as sources of disease resistances and agronomic traits (Esquinas Alcazar 1981, Rick 1982b, 1986b, Rick et al. 1987, Stevens and Rick 1986, Laterrot 1989). The International Plant Genetic Resources Institute (IPGRI) recognized the need for maintaining valuable vegetable genetic resources and nominated tomatoes for priority conservation status. Ross (1998) considered that the diversity of tomato is likely to be well conserved, and cited 62,832 accessions maintained in gene banks around the world, although most of these accessions are *S. lycopersicum*. The genetic variation among *S. lycopersicum* accessions at the Asian Research and Development Center (ARDC–one of the largest collections of cultivated tomato germplasm) was evaluated with Random Amplified Polymorphic DNA (RAPDs) by Villand et al. (1998). RAPD diversity was greater in accessions from the primary center (Ecuador, Peru, Chile), and for breeding purposes variation can be obtained at a faster rate by sampling accessions from this area than from other geographic regions. The largest and most important collection of wild species genetic resources exists at the Tomato Genetics Resources Center (TGRC, University of California, Davis).

Tomato also serves as a model organism to understand the basic genetics of diploid plants. Features that enhance the usefulness of tomatoes for genetic studies are: the naturally occurring variability in the species, selfpollination that lead to the expression of recessive mutations, the possibility of controlled hybridization within and among species, the lack of gene duplication, and the possibility to easily identify the 12 chromosomes (Rick 1978). In recent years there have been great advances in tomato genetics. New methodological approaches like molecular mapping of important agronomical characters have provided powerful tools for the improvement of the tomato crop (Tanksley and McCouch 1997).

DOMESTICATION OF CULTIVATED TOMATOES—PERU OR MEXICO?

Methods for Inferring Location of Crop Origins

Two competing hypotheses have been advanced to ascertain the place of domestication of the cultivated tomato, one from Peru, and another from Mexico. How does one search for origins of crops? The first systematic attempt was outlined by DeCandolle (1886). He used an eclectic approach based on the following four criteria: 1) "Botany", or observing natural spontaneous geographic distributions of the crop or its putative wild relatives. These data could be gathered from floras or herbaria, but this could be complicated by recent adventive introductions; 2) "Archaeology and paleontology", gathered from fossil evidence of plant remains in caves, burial sites, or other preserved deposits; 3) "History", searching for evidence in early accounts of peoples; 4) "Philology", or linguistic evidence, or comparison of native names of plants to prior languages. DeCandolle, however, placed the least credence on the linguistic evidence. Since DeCandolle's time, additional techniques have been used in determining the origin of crops which include radiocarbon dating, scanning electron microscopy, palynology, refined archaeological methods as flotation techniques, and genetic and molecular evidence (Smith 1995).

Peruvian Hypothesis

DeCandolle (1886) advanced the Peruvian hypothesis for the site of domestication of tomato. He reviewed botanical (Bauhin 1623, Ruiz and Pavón 1797), linguistic (Roxburgh 1832), and historical (Hernández 1651) evidence and concluded: 1) there were no unambiguous natural records of tomato outside of the Americas before its European discovery there; 2) Bauhin (1623) referred to tomato as "mala peruviana" and "pomi del Peru," which suggested initial domestication and transport of tomato from Peru to Europe; 3) its origin was from the wild cherry tomato (*S. lycopersicum)* that by DeCandolle's time was known to occur from coastal Peru, Mexico, to southwestern US (California); 4) the distribution of cultivated tomato and its progenitor outside of Peru originated by garden escapes; and 5) the plant was domesticated before the discovery of America but not very long before that. This Peruvian origin was later supported by other authors (Moore 1935, Müller 1940a,b, Luckwill 1943a,b).

Mexican Hypothesis

Jenkins (1948) developed the Mexican hypothesis. He pointed out that the first reference to tomato in Europe was made by Matthiolus (1544) who provided a short description of tomato. Matthiolus (1554) amplified the description where he first provided the Italian name "pomi d'oro", and Latin name "mala aurea." A later edition of his work (Matthiolus 1586) provided an illustration showing an unambiguously identified tomato plant that made his concept of tomato clear, but there was no reference to its geographical origin. Only later, Anguillara (1561) first used the name "pomi del Peru," along with the name "pomi d'oro," but his reference is ambiguous as to whether he was referring to the same plant. Jenkins argued that "pomi del Peru" was used by early botanists to refer to other solanaceous plants such as *Datura stramonium* L. and had nothing to do with tomato, weakening DeCandolle's linguistic evidence.

Jenkins's second argument was that there was no evidence for pre-Colombian domestication of tomatoes in South America, yet good evidence for early domestication in Mexico. This comes from a reference from Guilandini (1572) who referred to tomato as "tumatle ex Themistitan," using an indigenous Mexican name for tomato. Jenkins interpreted the name "Themistitan" as a variant spelling of "Temixtitan" which in turn is a corruption of "Tenochtitlan", the native name for Mexico City. He therefore concluded that tomatoes came from Mexico. During the seventeenth century the Nahua name "tomatl" was often mentioned by botanists, and variants of this name are used in different languages at present (tomate in Spanish, tomato in English, etc.). Interestingly, the early name "Pomi d'oro" is still used in Italy. According to Jenkins (1948), evidence for early Mexican domestication also came from Hernández (1651) who documented early cultivation of tomato in Mexico at least before 1578 (the year of his death) and possibly from Acosta (1590); although Acosta could be referring to Mexico or Peru. Nevertheless, Yakovleff and Herrera (1935) considered that Acosta documented the uses of tomatoes in ancient Peru.

Jenkins's third argument was that there was considerably more variation of the landrace cultivars in Mexico than in Peru. Following ideas of Vavilov (1926), Jenkins argued that var. *cerasiform*, the small bilocular fruit form of *S. lycopersicum*, was introduced into Mexico in pre-Columbian times and it was domesticated in the central area that he considered as a secondary center of diversity. Jenkins agreed with DeCandolle (1886) that *S. lycopersicum* was the progenitor of the domesticated cultivars, but disagreed with the place of domestication in Peru.

Our Conclusion

We consider the question of the original site of domestication of cultivated tomato to be unsolved, and likely to forever be so. Like DeCandolle (1886), we consider linguistic evidence to be a weak source of data, and the existing linguistic sources for tomato are scant, ambiguous, and subject to various interpretations. Contrary to Jenkins's (1948) statements that there are no indigenous Peruvian names for tomato, Horkheimer (1973) documented a Quechua name for tomato (pirca), and Yakovleff and Herrera (1935) cited another Quechua name (pescco-tomate) possibly referring to the small bilocular fruit form of *S. lycopersicum*. The historical evidence also is sparse and ambiguous in their references to tomatoes. From the analysis of the original description by Hernández (1651), it is not clear that the plant cited as "tomatl" referred to the true tomatoes or a native *Physalis* species. Unless some new document is uncovered that clearly identifies introductions of tomato to Europe from a certain area (see McCue 1952, for a comprehensive summary of historical references), the first European site of introduction will forever remain unknown. However, even such a clear reference would not determine a first site of domestication, viz. Mexico vs. Peru.

Jenkins's (1948) Vavilovian argument of more diversity of cultivars in Mexico is not supported by comparative data (Villand et al. 1998) from South America (Ecuador, Peru and Chile). Tomatoes from Europe and North America share similar isozymes with those from Mexico and Central America, suggesting the tomato was introduced to Europe and North America from Mexico or Central America (Rick and Fobes 1975). Nevertheless, comparisons among genetic variability of primitive tomato cultivars found in Mexico, Central America and Peru, and modern varieties have neither substantiated nor disproved the hypothesis that Mexico was the centre of domestication (Rick et al. 1974, Rick and Fobes 1975, Rick and Holle 1990). Rick and Holle (1990) provided an isozyme study of different accessions of var. *cerasiforme* of the wild cherry tomato (*S. lycopersicum*) from South America, but they did not include cultivars or landraces from Mexico. The only comparative molecular studies (RAPDs and/or nuclear RFLPs) of diversity of landrace cultivars (Williams and St. Clair 1993, Villand et al. 1998) of tomato do not address the Peruvian/Mexican hypothesis.

A molecular study may be useful to elucidate the origin of tomato domestication by comparing a large number of accessions. However, it would be complicated by relative lack of variation within *S. lycopersicum* (including its landraces), and by the difficulty to identify existing landraces from Mexico and Peru as truly native today. The only putative archaeological evidence of tomato is decorated functional ceramics "spindle whorls" produced by the native Quimbaya culture (500-1000 AD) of Colombia (McMeekin 1992). However, our examination of the figures in this publication do not convince us that these are unequivocally tomato flowers, and could be other *Solanum* flowers (possibly potato). Like Rick and Holle (1990), we conclude that none of the evidence is conclusive regarding either a Mexican or a Peruvian initial site of domestication, and that tomatoes may have been domesticated independently in both areas.

EARLY HISTORY OF THE CULTIVATED TOMATO IN EUROPE

What were the first morphotypes of cultivated tomatoes exported from the Americas and where did they come from? McCue (1952) examined these questions through an extensive search from the literature, herbarium specimens, and early drawings. Despite this extensive search, we still know very little. The first European contact with Mexico was in 1519 (taking of Mexico City), and with Peru in 1531 (completion of the Peruvian conquest). Botanists at that time were mainly interested in the medicinal and culinary properties of plants and had little interest or knowledge of distribution or origin of cultivars. The first tomato references mentioned above were from sixteenth century herbalists, who were mainly interested with the medicinal values or "virtues" of plants, but they knew them only from exchange among botanical gardens.

These early botanists classified new plants by comparison with plants already known in Europe and from classical Greek references. *Lycopersicon*, the ancient Greek name for the tomato attributed to Galen is a clear example. By this method, Matthiolus (1544) described tomato by comparison to mandrake, a solanaceous plant known to the classical Greek botanist Dioscorides as: "Another species (of mandrake) has been brought to Italy in our time, flattened like the melerose (variety of apple) and segmented, green at first and when ripe of a golden color, which is eaten in the same manner as the egg plant, fried in oil with salt and pepper, like mushrooms." From this we glean that early introduced tomatoes had yellow fruits. In a later edition of his work, Matthiolus (1554) cited both yellow and red fruits, and mentioned the Italian name for the tomato "pomi d'oro" and its Latin equivalent "mala aurea" or golden apple. Another early common name for tomato is "poma amoris", or "love apples," because at that time it was believed that fruits had aphrodisiacal properties. All these ancient names persisted well into the nineteenth century (Moore 1935).

The earliest tomato herbarium specimens also came from this period (McCue 1952). Jerna (1947) reported specimens labeled as "Malus insana, Mandragorae species Poma amoris" attributed to Francesso Petrolini dated between 1550 and 1560. Mattirolo (1899) mentioned another tomato specimen found in the sixteen-volume herbarium of Ulisse Aldrovandi, which was most probably cultivated in Bologna, and is the oldest extant herbarium specimen of tomato, and is now preserved at the Botanical Garden of Bologna.

Georg Oelinger was a Nürnberg aphotecarian, an avid plant collector. He cultivated tomatoes in his garden probably as curiosity or as medicinal plants. The complete edition of Oelinger's (1553) work had a picture of red- and yellow-fruited tomatoes, and all the fruits are deeply furrowed (fasciated fruits). It is clear from both illustrations that the flowers had duplications of sepals and petals (6-7-parted).

Dodoens (1553) listed the Latin, German, and French names for the tomatoes along with an illustration of the plant, but he did not mention uses. His later publications (Dodoens 1574, 1583) illustrated round fruits with furrows, flowers with 7-8 petals, and two of the flowers with exserted styles.

The illustrations in L'Obel (1576) and Tabernaemontanus (1591) were similar to Dodens's (1553). Gesner (1561) mentioned that the tomato fruit was easily grown in Germany, matured early, and had fruits varying in color from gold, red, and white; one illustration showed a plant with round fruits without furrows, and flowers with six sepals.

Teppner (1993) discussed the descriptions and illustrations of early tomatoes cultivated in Europe. He included a copy of Dodens's (1583) drawing that clearly showed a plant with large, horizontally compressed, furrowed fruits, characteristic of early tomato cultivars. According to Sabine (1820) the cherry tomato must have been introduced at the same time as a large-fruited cultivar. Nevertheless, Aymonin (in Besler 1613) considered that the cherry tomato appeared in Europe around 1625. In Europe, tomatoes initially were cultivated mainly as ornamental plants in gardens, and they were considered inedible or poisonous because they were similar to the poisonous mandrake or belladonna.

Tomatoes were first accepted for culinary purposes in southern Europe (Ray 1673, Miller 1752) during the seventeenth and eighteenth century. Filippo (1811) reported three varieties in Italy and gave instructions for their cultivation. Sabine (1820) reported four varieties of red tomatoes and two of yellow tomatoes that were cultivated in Europe; he also discussed the condition for cultivation in England based on the experience of native gardeners. Alefeld (1866) mentioned seven varieties in Germany. According to McCue (1952), Salmon (1710) mentioned tomatoes for the first time in North America. Although tomato cultivation was not difficult, the crop gained economic importance only by the end of the nineteenth century or beginning of the twentieth century when tomato breeding programs were established (Lehmann 1955, Rick 1978, 1995).

According to Rick (1995), domestication and improvement of tomato fruit production have been accompanied by changes in the position of stigma from the anther tube. The closely related wild species, and older Latin American cultivars (and their wild species progenitor), tend to have well exserted stigmas. Rick (1995) emphasized that in the absence of appropriate pollinators, flowers with exserted stigmas diminished the percentage of fruit set. Strong artificial selection for less exserted stigmas must have occurred after the tomato was first introduced to Europe, and even more selection under greenhouse culture. As a result, the stigma of most cultivars is shortened and now positioned at the mouth of the anther tube or even completely included in the anther tube. This shortening eliminated outcrossing and increased fruit yield in the modern varieties, but reduced the genetic variation of the crop.

The successful improvement of tomato agronomical traits is based on the understanding of basic genetics, continuous advancement of molecular genetic studies and breeding methods, which will be developed in the following chapters.

SUMMARY

Tomato is a major crop of world economy and supplies essential nutrients in human diets. There have long existed controversies regarding the place of domestication, early history, and taxonomy of tomato. The wild tomato species are native to western South America, from Ecuador south to northern Chile, and the Galapagos Islands. The putative progenitor of the cultivated species (*Solanum lycopersicum* = *Lycopersicon esculentum* var. *cerasiforme*) currently is widespread throughout warm regions of the world, but many of these are recent introductions. There are two competing hypotheses of the place of domestication of tomato, one supporting Peru, another in Mexico. While the Mexican origin is reasonable, we cannot discount a Peruvian origin, or even parallel domestication in both areas. Tomatoes were first recorded outside the Americas in Italy in 1544. They were cultivated first as ornamental or curiosity plants and thought by many to be poisonous. It was first accepted as a vegetable crop in southern Europe during the late sixteenth century. The first European cultivars had yellow to red flattened fruits, with deep furrows, and flowers with stigmas exserted from the anther tube. Derived cultivars had a wider range of fruit colors and shapes, smoother fruits, and stigmas included in the anther tube that led to increased fruit set but reduced the genetic variation of the crop. The taxonomy of tomato always has been controversial. This controversy involves not only generic placement in *Lycopersicum* or *Solanum*, but also hypotheses on interspecific relationships. Recent molecular data support treatment of tomato in *Solanum* (as we treat it here), and support allogamy, self-incompatibility, and green fruits as primitive of tomatoes. These studies support at least two distinct taxa in the formerly recognized *S. peruvianum*.

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*Not seen in original.