The Tomato (*Solanum lycopersicum* L., Solanaceae) and Its Botanical Relatives

2

Sandra Knapp and Iris Edith Peralta

Abstract

The cultivated tomato, *Solanum lycopersicum* L., is a member of the small section *Lycopersicon* along with its 12 wild relatives. An additional four species from sections *Juglandifolia* and *Lycopersicoides* are traditionally considered as tomato wild relatives. These species are all endemic to South America, but the cultivated tomato itself has achieved worldwide distribution with the help of human populations. Tomato and its wild relatives are part of a larger monophyletic group (the Potato clade) that also contains the potatoes and their wild relatives. Here we review the taxonomic and phylogenetic history, relationships and species-level taxonomy of the cultivated tomato and its wild relatives, and highlight important studies of diversity that remain to be undertaken in the group, especially in light of global environmental and climatic change.

S. Knapp (✉)
Department of Life Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, UK
e-mail: s.knapp@nhm.ac.uk

I.E. Peralta
Facultad de Agronomía, Universidad Nacional del Cuyo, Almirante Brown 500, 5505 Chacras de Coria, Argentina

I.E. Peralta
Instituto Argentino de Investigaciones de las Zonas Áridas, (IADIZA-CCT CONICET Mendoza), Calle Adrián Ruiz Leal s/n, 5500 Mendoza, Argentina

Introduction

The cultivated tomato, *Solanum lycopersicum* L., belongs to the diverse family Solanaceae, which includes more than 3000 species, occupying a wide variety of habitats (Knapp 2002). The Solanaceae contain many species of economic use, such as food (tomatoes, potatoes, peppers and eggplants), medicines (deadly nightshade, henbane, datura) and ornamental purposes (petunias). *Solanum lycopersicum* was previously recognized as *Lycopersicon esculentum* Mill., but data from both morphology and molecular sequences support its

inclusion in the large genus *Solanum* L., and a revised new nomenclature has resulted (Peralta and Spooner 2001, 2005; Spooner et al. 2005; Peralta et al. 2006, 2008a). Morphological characters, phylogenetic relationships and geographical distribution have demonstrated that tomatoes (*Solanum* sect. *Lycopersicon* (Mill.) Wettst.) and their immediate outgroups in *Solanum* sect. *Lycopersicoides* (A. Child) Peralta and sect. *Juglandifolia* (Rydb.) A. Child form a sister clade to potatoes (sect. *Petota* Dumort.), with *Solanum* sect. *Etuberosum* (Buk. and Kameraz) Child being sister to potatoes + tomatoes (Spooner et al. 1993; Peralta and Spooner 2001; Spooner et al. 2005; Peralta et al. 2008a; Rodriguez et al. 2010; Särkinen et al. 2013). Analyses of multiple data sets from a variety of genes unambiguously establish tomatoes to be deeply nested in *Solanum* (Bohs and Olmstead 1997, 1999; Olmstead and Palmer 1997; Olmstead et al. 1999; Peralta and Spooner 2001; Bohs 2005; Särkinen et al. 2013). The monophyletic *Solanum* with the inclusion of all traditional segregate genera (*Cyphomandra* Mart. ex Sendtn., Bohs 1995; *Lycopersicon* Mill., Spooner et al. 1993; *Normania* Lowe and *Triguera* Cav., Bohs and Olmstead 2001) is one of the ten most species-rich genera of angiosperms (Frodin 2004, see also Solanaceae Source, http://www.solanaceaesource.org). It contains several crops of economic importance in addition to the tomato, such as the potato (*S. tuberosum* L.) and the aubergine or eggplant (*S. melongena* L.), as well as other minor crops (naranjilla, *S. quitoense* Lam.; tamarillo or tree tomato, *S. betaceum* Cav. and pepino, *S. muricatum* Aiton). The majority of taxonomists as well as most plant breeders and other users have accepted the re-integration of tomatoes to *Solanum* (e.g. Caicedo and Schaal 2004; Fridman et al. 2004; Schauer et al. 2006; Mueller et al. 2005; Tomato Genome Consortium 2012; see also http://tgrc.ucdavis.edu/key.html). The tomato and all of its wild relatives were treated in a taxonomic monograph by Peralta et al. (2008a).

The tomatoes and their close relatives are easily distinguished from any other group of *Solanum* species by their bright yellow flowers and pinnate or pinnatifid, non-spiny leaves; the only other species in the genus with bright yellow flowers is *S. rostratum* Dunal, a spiny member of sect. *Androceras* (Nutt.) Whalen of the Leptostemonum clade (Whalen 1979) and *S. huayavillense* Del Vitto, a member of the Morelloid clade (Barboza et al. 2013). Here we provide a brief review of the history of generic classification of the tomatoes and their wild relatives, species diversity and relationships amongst wild tomatoes, the position of the tomato in the Solanaceae and timing of relevant diversification events in the family and review the history of tomato introduction from its native range to a worldwide distribution as a cultivated plant.

Generic Position of the Tomato and Its Relatives

The system of giving plants a genus and species name began with Linnaeus in the first edition of *Species Plantarum* (1753); before that plant names were long sentences (polynomials) in Latin that described the plant and distinguished it from others. In his first edition of *The Gardener's Dictionary* (Miller 1731) Philip Miller, the English botanist and curator of the Chelsea Physic Garden, used the generic name *Lycopersicon* meaning "wolf peach", a term previously coined by de Tournefort (1694), and included a number of taxa with multi-locular fruits ("roundish, soft, fleshy Fruit, which is divided into several Cells, wherein are contain'd many flat Seeds"), all colour variants of the cultivated tomato (*S. lycopersicum*). In the same work, Miller also recognized *Solanum*, and included within it the eggplant as "*Solanum Americanum, spinosum, foliis Melongenae, fructu mammoro*" and the potato as "*Solanum tuberosum, esculentum*" (Miller 1731). His definition of *Lycopersicon* was confined to plants that we would today recognize as cultivars of *S. lycopersicum*, the cultivated tomato.

In *Species Plantarum*, Linnaeus (1753) classified tomatoes in the genus *Solanum*, and described *S. lycopersicum* and *S. peruvianum*. The French botanist Adrian de Jussieu (1789), in his classification, also included tomatoes in *Solanum*. Miller (1754), however, continued to

use both the generic name *Lycopersicon* and polynomial nomenclature in the abridged 4th edition of *The Gardener's Dictionary*. He expanded his definition of *Lycopersicon* by including "*Lycopersicon radice tuberose, esculentum*" (the potato) within it, using the following reasoning (Miller 1754): "This Plant was always ranged in the Genus of *Solanum*, or Nightshade, and is now brought under that Title by *Dr. Linnaeus*; but as *Lycopersicon* has now been establish'd as a distinct Genus, on account of the Fruit being divided into several Cells, by intermediate Partitions, and as the Fruit of this Plant [the potato] exactly agrees with the Characters of the other species of this Genus, I have inserted it here." The editor of the posthumously published edition of *The Gardener's and Botanist's Dictionary* (Miller 1807), Thomas Martyn, merged *Lycopersicon* and *Solanum*, and recognized all Miller's species as members of *Solanum*. Miller (1754) did not recognize the tomatoes by their elongate anther cones, used by later authors (e.g. D'Arcy 1972; Nee 1999; Hunziker 2001) to justify the segregation of the genus *Lycopersicon*, but instead, based his genus on fruit characters.

A number of classical and twentieth century authors have recognized the genus *Lycopersicon* mainly based on the anther morphology (e.g. Dunal 1813, 1852; Bentham and Hooker 1873; Müller 1940; Luckwill 1943; Correll 1958; D'Arcy 1972, 1987, 1991; Hunziker 1979, 2001; Rick 1979, 1988; Child 1990; Rick et al. 1990;

Symon 1981, 1985; Hawkes 1990), but others continued to recognize the tomatoes as members of the genus *Solanum* (MacBride 1962; Seithe 1962; Heine 1976; Fosberg 1987). Today, tomatoes are widely accepted as members of the large and diverse genus *Solanum*, based on the results of both morphological and molecular analyses (see Peralta et al. 2008a for details).

Species Diversity and Relationships of Wild Tomato Relatives

Solanum sect. *Lycopersicon* consists of 13 closely related taxa; the cultivated tomato, *Solanum lycopersicum*, exists only as a domesticated or feral plant (Peralta et al. 2008a), and 12 wild species (Table 2.1): *Solanum arcanum*, *S. cheesmaniae*, *S. chilense*, *S. chmielewskii*, *S. corneliomulleri*, *S. galapagense*, *S. habrochaites*, *S. huaylasense*, *S. neorickii*, *S. pennellii*, *S. peruvianum* and *S. pimpinellifolium* (Peralta et al. 2005; Spooner et al. 2005; Peralta et al. 2008a). All of the wild species of section *Lycopersicon* occur on the western slopes of the Andes in dry desert or pre-desert environments (Fig. 2.1; for distributions and environments of all species see Table 2.1). Four species have been segregated from the green-fruited species *S. peruvianum* sensu lato (s.l.); two of them, *S. arcanum* and *S. huaylasense*, were described as new (Peralta et al. 2005) from Peru, while the other two, *S. peruvianum* and *S. corneliomulleri*
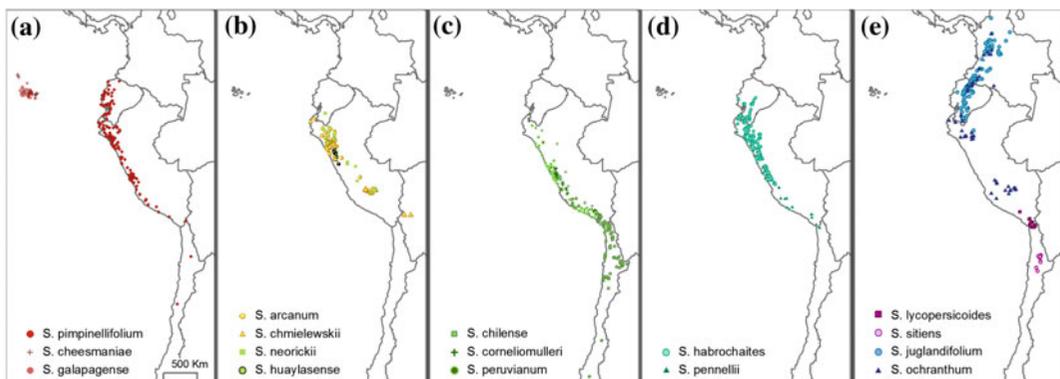

Fig. 2.1 Distribution maps of tomato wild relatives

Table 2.1 Tomatoes and their wild relatives (Peralta et al. 2008a 'Lycopersicon group' corresponds to the red- and orange-fruited species)

Species	Distribution	Habitat (elevational range)	Section according to Peralta et al. (2008a, b)
Solanum arcanum Peralta	Northern Peru	Dry inter-Andean valleys and in coastal lomas (seasonal fog-drenched habitats); 100–4000 m	*Lycopersicon* 'Arcanum group'
Solanum cheesmaniae (L. Riley) Fosberg	Galápagos Islands	Dry, open, rocky slopes; sea level—1300 m	*Lycopersicon* 'Lycopersicon group'
Solanum chilense (Dunal)Reiche	Coastal Chile and southern Peru	Dry, open, rocky slopes; sea level—4000 m (B. Igic, pers. comm. has suggested the higher elevation plants represent a new species)	*Lycopersicon* 'Eriopersicon group'
Solanum chmielewskii (C.M. Rick, Kesicki, Fobles & M. Holle) D.M. Spooner, G. J. Anderson & R.K. Jansen	Southern Peru and northern Bolivia	Dry inter-Andean valleys, usually on open, rocky slopes; often on roadcuts; 1200–3000 m	*Lycopersicon* 'Arcanum group'
Solanum corneliomulleri J.F. Macbr.	Southern Peru (Lima southwards)	Dry, rocky slopes; 20–4500 m (low elevation populations associated with landslides in southern Peru)	*Lycopersicon* 'Eriopersicon group'
Solanum galapagense S.C. Darwin & Peralta	Galápagos Islands	Dry, open, rocky slopes; seashores; sea level—1600 m	*Lycopersicon* 'Lycopersicon group'
Solanum habrochaites S. Knapp & D.M. Spooner	Andean Ecuador and Peru	Montane forests, dry slopes and occasionally coastal lomas; 10–4100 m	*Lycopersicon* 'Eriopersicon group'
Solanum huaylasense Peralta	Rio Santa river drainage, north-central Peru	Dry, open, rocky slopes; 950–3300 m	*Lycopersicon* 'Eriopersicon group'
Solanum juglandifolium Dunal	Andean Colombia, Ecuador and Peru	Montane cloud forests; 1000–3200 m	*Juglandifolia*
Solanum lycopersicoides Dunal	Southern Peru and northern Chile	Rocky slopes and ravines; 1250–3600	*Lycopersicoides*
Solanum lycopersicum L.	Globally cultivated domesticate	Cultivated; sea level—4000 m	*Lycopersicon* 'Lycopersicon group'
Solanum neorickii D.M. Spooner, G.J. Anderson & R.K. Jansen	Southern Ecuador to southern Peru	Dry inter-Andean valleys; 500–3500 m	*Lycopersicon* 'Arcanum group'
Solanum ochranthum Dunal	Andean Colombia, Ecuador and Peru	Montane cloud forests; 1850–4100 m	*Juglandifolia*
Solanum pennellii Correll	Northern Peru to northern Chile	Dry slopes and washes, usually in flat areas; sea level—4100 m	*Lycopersicon* 'Neolycopersicon group'
Solanum peruvianum L.	Central Peru to northern Chile	Dry coastal deserts and lomas; sea level—3000 m	*Lycopersicon* 'Eriopersicon group'
Solanum pimpinellifolium L.	Southwestern Ecuador to northern Chile (many northern populations in Ecuador are admixture with *S. lycopersicum*; Peralta et al. 2008a, b; Blanca et al. 2013)	Dry slopes, plains and around cultivated fields; sea level—3000 m	*Lycopersicon* 'Lycopersicon group'
Solanum sitiens I.M. Johnst	Northern Chile	Dry ravines and slopes (hyperarid areas); 2000–3500 m	*Lycopersicoides*

For further details of crossability and other biological parameters of wild tomatoes see Grandillo et al. (2011)

had already been named by Linnaeus (1753) and MacBride (1962), respectively. In addition, *S. galapagense*, a yellow to orange-fruited plant, was segregated from *S. cheesmaniae*; both species are endemic to the Galápagos Islands (Darwin et al. 2003). Lucatti et al. (2013) have suggested that *S. galapagense* and *S. cheesmaniae* should be considered conspecific but we think the morphological and combined molecular evidence argues against the lumping of these taxa; this will only obscure the useful differences already seen and used by plant breeders from these two taxa at whatever rank they are recognized (Grandillo et al. 2011). Peralta et al. (2008a) put these 12 species into three informal species groups ('Arcanum', 'Eriopersicon' and 'Neolycopersicon', see Table 2.1) based on a combination of morphological and molecular analyses. All members of sect. *Lycopersicon* are diploid (2*n* = 24) (Peralta and Spooner 2001; Nesbitt and Tanksley 2002), characterized by a high degree of genomic synteny (Chetelat and Ji 2007; Stack et al. 2009; Tomato Genome Consortium 2012), and are to some degree intercrossable (Taylor 1986). Non-phylogenetic schemes (Müller 1940; Luckwill 1943; Rick 1979) for the relationships of tomatoes and their wild relatives have been treated in detail by Peralta et al. (2008a), so we will not treat them here.

Two other sets of species complete the tomato wild relatives in the broad sense (Table 2.1). *Solanum* sect. *Juglandifolia* contains the two woody tomato-like nightshades *S. ochranthum* and *S. juglandifolium*. These two species are partially sympatric and they are morphologically similar, both being woody perennials with rampant, liana-like stems up to 30 m in length (Correll 1962; Rick 1988; Peralta and Spooner 2005; Peralta et al. 2008a). Based on evidence from molecular sequence data (Peralta et al. 2008a) sect. *Juglandifolia* is the sister group of the wild tomatoes in the strict sense. Sister to both groups is *Solanum* sect. *Lycopersicoides*, comprising the allopatric sister species *S. lycopersicoides* and *S. sitiens*. These four tomato-like nightshade species have in common several morphological features that make them intermediate between tomato and potato (Rick 1988; Stommel 2001; Smith and

Peralta 2002). Tomato-like morphological characters that together differentiate them from most of other *Solanum* species include yellow corollas, pedicels articulated above the base, pinnately segmented non-prickly leaves, and lack of tubers (Correll 1962; Rick 1988). These four allied outgroup species are diploids (2*n* = 24), but strong reproductive barriers isolate them from the core tomato group (Rick 1988; Correll 1962; Child 1990; Stommel 2001; Smith and Peralta 2002; Grandillo et al. 2011). Overall, crosses between the cultivated tomato and all but two (*S. ochranthum* and *S. juglandifolium*) of these wild species are possible, although with varying degrees of difficulty (Rick 1979; Rick and Chetelat 1995; Pertuzé et al. 2002; Grandillo et al. 2011). Although, using special techniques, introgression lines have been developed between *S. lycopersicoides* and *S. lycopersicum* (Chetelat et al. 1998; Canady et al. 2006). These have been useful in the elaboration of genetic maps (Chetelat and Meglic 2000), and for the understanding of cold, pest and pathogen resistances (Davis et al. 2009).

Cladistic and phenetic studies of species boundaries and relationships within the tomatoes and all their wild relatives have used a combination of molecular and morphological data (Palmer and Zamir 1982; Spooner et al. 1993; McClean and Hanson 1986; Miller and Tanksley 1990; Bretó et al. 1993; Marshall et al. 2001; Alvarez et al. 2001; Peralta and Spooner 2001, 2005; Spooner et al. 2005; Rodríguez et al. 2010). These studies used a variety of techniques, data sets and analysis types; the reader is referred to the primary literature and to the summary of the results of these studies in Peralta et al. (2008a) for further details of specific algorithms used and parameters set. The four species with brightly coloured fruits (*S. cheesmaniae*, *S. galapagense*, *S. lycopersicum*, *S. pimpinellifolium*) unambiguously form a closely related monophyletic group in all molecular analyses and this relationship has been suggested by all who have studied tomatoes previously (Müller 1940; Luckwill 1943; Rick 1979).

Rodriguez et al. (2010) used a set of nuclear COSII (conserved orthologous set II, Wu et al.

2006) markers to investigate the test their utility for phylogeny reconstruction in both potato and tomato. They did not intend to provide a definitive phylogenetic reconstruction for these groups, but instead focused on identifying markers that would be useful for future studies. Their analysis of the tomato clade, however, provided robust and well-supported hypotheses of species relationships in which the "red-orange-clade" comprising *S. lycopersicum*, *S. pimpinellifolium*, *S. galapagense* and *S. cheesmaniae* was consistently recovered with bootstrap values of 100 % and posterior probabilities of 1 (Rodriguez et al. 2010). Relationships amongst the green-fruited species revealed several different topologies, suggesting different gene genealogies, and whether section *Juglandifolia* or *Lycopersicoides* is sister to the tomatoes sensu stricto was unresolved, in contrast to previous studies (see above). Their Bayesian analysis (Rodríguez et al. 2010) using 18 COSII markers showed two sister group relationships in the "red-orange clade"—*S. galapagense* + *S. cheesmaniae* and *S. lycopersicum* + *S. pimpinellifolium*. This is in accordance with geography (Darwin et al. 2003; Peralta et al. 2008a) with the two Galápagos endemics most closely related to each other, and *S. lycopersicum* most closely related to its wild progenitor (Tomato Genome Consortium 2012). Koenig et al. (2013) recovered *S. galapagense* as sister to *S. lycopersicum* and *S. pimpinellifolium* sister to them (they did not include *S. cheesmaniae*), but they suggest this result stems from potential incomplete lineage sorting resulting from the extremely close relationship amongst the red- and orange-fruited species. Causse et al. (2013) also showed that repeated introgressions from wild species over the course of modern tomato breeding have resulted in extensive variation at the molecular level, perhaps obscuring the relationships of the cultivated species to one or other of its close wild relatives.

All those studying the cultivated tomato have unambiguously placed its evolutionary origins with the other tomato species with brightly coloured berries. These are all species of dry, desert habitats, suggesting there is much genetic variation yet to mine in the very close relatives of

S. lycopersicum to help tomatoes deal with environmental change to come.

Tomatoes in the Solanaceae

Tomato is a flagship species in the Solanaceae, and has been extensively used in studies on the evolution and development of fruit characters in particular (Lippman and Tanksley 2001; van der Knaap et al. 2002; Seymour et al. 2013). The Solanaceae themselves are members of the derived Asterid Clade of flowering plants (Angiosperm Phylogeny Group 2009) and molecular dating analyses coupled with fossil evidence suggests they arose just after the Cretaceous/Tertiary boundary, approximately 59 Million years ago (Bell et al. 2010) to ca. 49 Million years ago (Mya; 46.2–53.7 Mya) (Särkinen et al. 2013; see Fig. 2.2). Fossils available for stratigraphic calibration of the phylogenetic tree of the family are few (Särkinen et al. 2013) and all dates presented here must be considered minimum ages; it may be that older fossils are found that change the absolute, but not relative, ages of the clades mentioned here.

Solanum lycopersicum belongs to the large clade Solanoideae (sometimes defined as a subfamily) whose members possess berries as a fruit type (with some modifications, see Knapp 2002). The stem age of the Solanoideae is estimated at ca. 21 Mya (19.0–23.3 Mya), around the same time that many of the major clades within the family began to diversify rapidly (Särkinen et al. 2013). *Solanum* itself has a stem age of ca. 17 Mya (14.5–17.7 Mya) and a crown age of ca. 15.5 Mya (13.3–17.5 Mya, see Fig. 2.2). Stem and crown ages differ due to differential inclusion of putative common ancestors (extinct taxa) in the group to be analyzed (see Baum and Smith 2012). This hyper-diverse genus with its more than 1200 species (see Knapp et al. 2004) is relatively young and the start of its diversification occurred in the mid-Miocene.

The tomato (*S. lycopersicum*) and its relatives belong to Särkinen et al.'s (2013) *Solanum* Clade I, and within that to the Potato clade (see Fig. 2.2), whose stem age was calculated at ca. 14.3 Mya (12.5–16.3 Mya), with the tomato and its relatives diverging from the potatoes (section *Petota*) at ca.
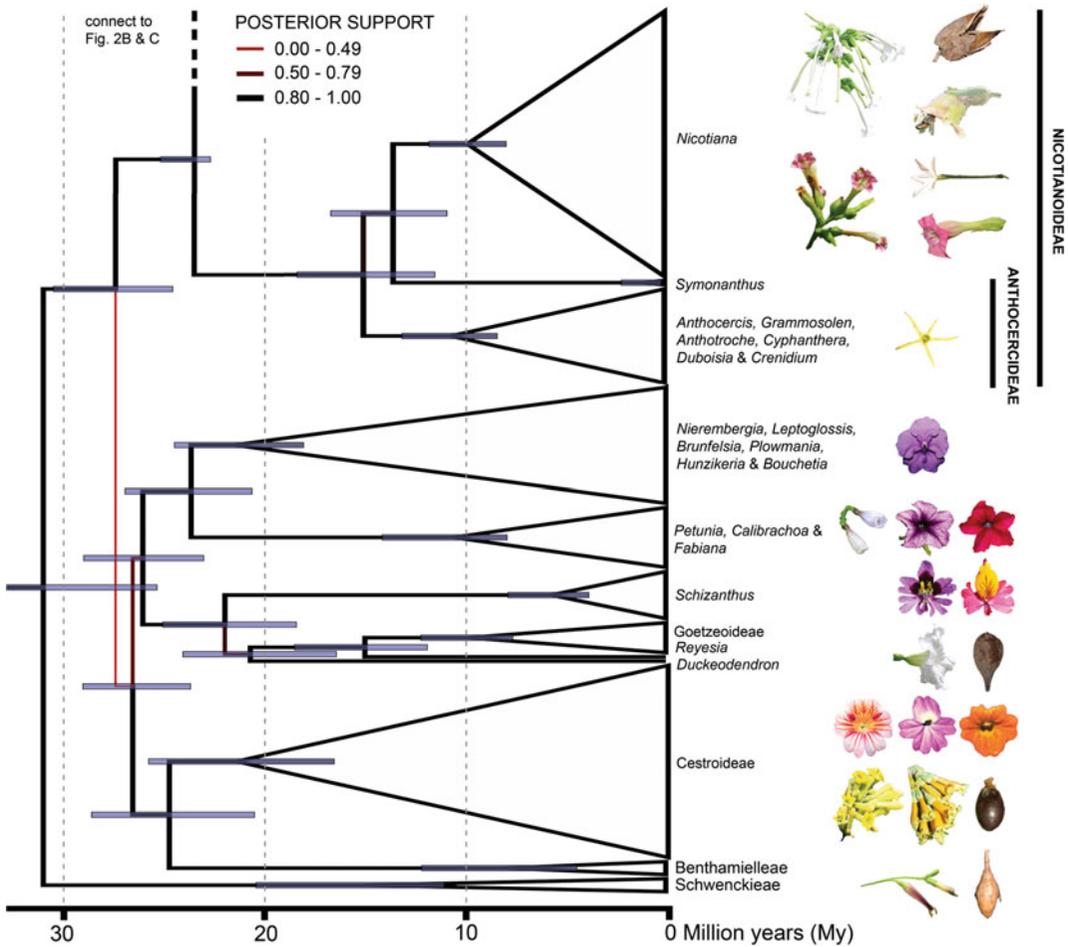
Fig. 2.2 Dated Solanaceae phylogeny; only major clades shown with representative flowers/fruits alongside. *Grey bars* correspond to date ranges as seen in text (from Särkinen et al. 2013, reproduced with permission from *BMC Evolutionary Biology* 13:214 (2013). doi:10.1186/1471-2148-13-214)

8 Mya (6.6–9/9 Mya). Within the tomato clade in the strict sense (excluding sections *Juglandifolia* and *Lycopersicoides*) species diversification was calculated to have a minimum age of ca. 2 Mya (1.2–2.6 Mya). The cultivated tomato itself belongs to a very recently derived group within the clade and is not a wild species, but instead is a domesticated plant derived from its wild progenitor, *S. pimpinellifolium*, by humans.

Tomatoes Travelling

The origins of crop plants can be difficult to decipher, due at least in part to human transport and use around the world with the globalization that began in the sixteenth century when Europeans first colonized the New World (Mann 2011). Even modern molecular tools can fail to unambiguously resolve origins, especially in groups like tomatoes, where spread has been global and wild species have been extensively used in breeding (Grandillo et al. 2011). How and when *Solanum lycopersicum* was first brought from the Americas to Europe has been debated since the late nineteenth century (de Candolle 1886; Jenkins 1948). The earliest description in the European botanical literature of a tomato dates from the sixteenth century in Pietro Andrea Matthioli's (Latinized as Petrus
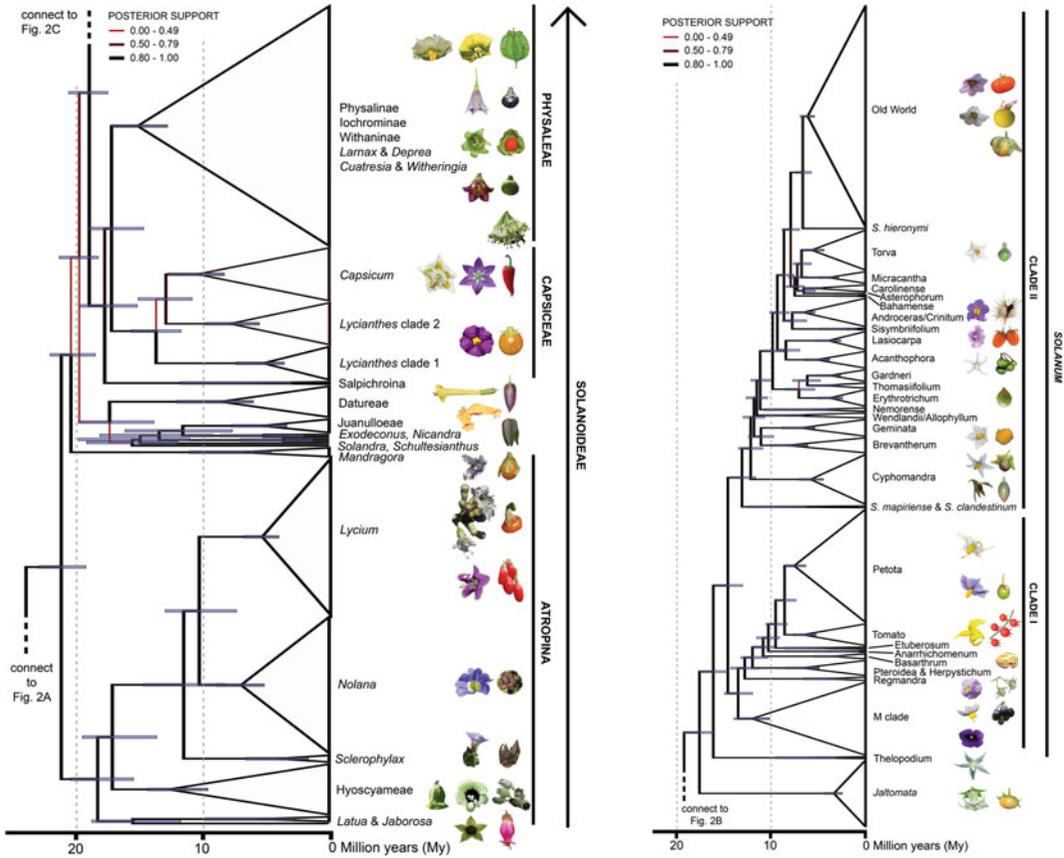
Fig. 2.2 (continued)

Andrea Matthiolus and sometimes also written as Mattioli) Italian language commentary upon the work of the first century Greek botanist Dioscorides of Anazarbos (Mattioli 1544). Tomatoes were classified and identified by comparison with plants already known in Europe and from classical Greek references, and, following this tradition, Mattioli (1544) described tomatoes in his section "Della Mandragorae," (On Mandrakes) as: "Portansi à i tempi nostri d'un'altra spetie in Italia stiacciante come le mele rose, and fatte a spicci, de colour prima verdi and come son mature, di color d'oro, lequali pur si mangiano nel medesmo modo" (Another species has been brought to Italy in our time, flattened like the "mele rose" [variety of apple] and segmented, green at first and when ripe of a golden colour, which is eaten in the same manner). Most probably the oldest illustration of tomatoes is a

watercolour part of the unpublished manuscript of Leonard Fuchs (see frontispiece of Peralta et al. 2008a, b), and it is considered a "chimera" since represent in one plant fruits of different shapes and colours (round, flat, segmented, red and yellow) and even green fruits with stripes that might correspond to a wild species. This painting demonstrates that various different types of tomatoes (perhaps even wild species) were known in Europe by mid-sixteenth century. The earliest published illustration of a tomato is a rather crude woodcut of a plant with eight-parted flowers and fascinated fruits in Dodoens' herbal (1554) published in the Netherlands. Contemporaneous published illustrations of tomatoes in the sixteenth and seventeenth century literature (see Fig. 2.3) all depict plants with large, fascinated flowers and multi-locular fruit, clearly showing that tomatoes came to Europe not as

Fig. 2.3 An early wood cut illustration of *Solanum lycopersicum* (Mattioli 1590), showing the fasciated flowers and large multi-locular fruits present in early European tomatoes. *Source* Reproduced with permission of the Library of the Natural History Museum, London

small-fruited wild species, but as domesticated, large-fruited plants. These early introductions were said to have yellow (Mattioli 1544; Besler 1613) or red (Besler 1613) fruits.

de Candolle (1886) suggested the tomato was introduced from Peru for both historical and botanical reasons, and subsequent workers on the group (Müller 1940; Luckwill 1943). Jenkins (1948) suggested that Mexico was the area from which the plants were introduced to Europe, based mostly on linguistic (the Nahuatl name for *S. lycopersicum* is 'jitomatl', very like tomato) evidence and the lack of archaeological or linguistic evidence for any domestication in South America. Peralta and Spooner (2007) considered the origins for the cultivated tomato to be uncertain, and concluded that evidence is inconclusive

regarding either a Mexican or a Peruvian initial site of domestication. Recent work with high density molecular markers has helped to shed light on some aspects of the story (see below).

Small-fruited cherry tomatoes were considered to be the wild progenitors of *S. lycopersicum* (de Candolle 1886; Müller 1940; Luckwill 1943; Rick and Holle 1990); these small-fruited plants are otherwise morphologically nested within the variation of the cultivated tomato and they are often seen growing in what appear to be wild conditions. Nesbitt and Tanksley (2001), however, suggested that many of these plants with small fruits were the results of admixtures with the wild species, *S. pimpinellifolium*. Molecular analyses of SNPs in a large collection of small-fruited tomatoes (Ranc et al. 2008) showed that cherry-type tomatoes were a complex mixture of *S. pimpinellifolium* and *S. lycopersicum* and did not form a distinct, recognizable group either based on morphology or molecules. Blanca et al. (2013) used the SOLCap platform to analyze a different set of small and large-fruited tomatoes from both germplasm collections and wild origin. They found that a set of Andean accessions could be distinguished from both *S. pimpinellifolium* and *S. lycopersicum*, but that these plants did not all have small fruits. Accessions from the eastern slopes of the Andes in Ecuador and Peru were suggested to be early cultivars, with Mesoamerican accessions also distinct from those found elsewhere in the world. Blanca et al. (2013) hypothesize that the plants from Ecuador and Peru represent early domesticates, pre-breeding populations, and that the tomato was truly developed as a cultivated plant in Mexico and Mesoamerica after being taken there in pre-Columbian times. European heritage varieties show more molecular similarity to Mesoamerican accessions than to South American ones. The similarity of climate in Mexico and the European Mediterranean may have contributed to the ease of introduction of the tomato post-1520.

Blanca et al. (2013) distinguish these pre-breeding Andean populations at the varietal level as var. *cerasiforme*. This has been traditional in the tomato literature for plants of *S. lycopersicum* with small fruits, but we consider these

plants to be the product of domestication, not of evolution by natural selection, and thus should not be named using the *International Code of Nomenclature for algae, fungi, and plants* (McNeill et al. 2012). In addition, Blanca et al. (2013) found that the South American accessions they identified as distinct had a wide range of fruit sizes; the accessions were better distinguished using a panel of morphological characteristics (similar to those used to distinguish *S. pimpinellifolium* and *S. lycopersicum* by Peralta et al. 2008a), thus use of 'cerasiforme' could cause confusion. We suggest this distinct set of accessions be named according to the *International Code of Nomenclature for Cultivated Plants* (Brickell et al. 2009), as has been done for potatoes (Huamán and Spooner 2002). These conventions for naming pertain to "plants whose origin or selection is primarily due to the intentional actions of mankind" (Brickell et al. 2009). As Blanca et al. (2013) point out, further sampling of South American traditional cultivars is necessary to better understand these patterns. New collecting in the Andes where tomato pre-breeding and early domestication occurred is a priority before this diversity disappears.

Diversity within the cultivated species is likely to be well conserved ex situ; Ross (1998) cited 62,832 accessions of mainly of *S. lycopersium* maintained in gene banks around the world. A wealth of studies using isozymes (Rick and Holle 1990) and molecular markers (Williams and St. Clair 1993; Villand et al. 1998; Blanca et al. 2013) have demonstrated the high genetic diversity of landrace cultivars in South America.

Nevertheless, areas close to the origin of tomatoes have not been sufficiently explored to recover these valuable genetic resources. The richness of cultural values in Andean communities is also reflected by their crop diversity, traditional cultivation and culinary practices. Small farmers developed a sustainable agriculture using ancestral land practices that are less aggressive to the environment, select crops adapted to the local conditions and maintain their own seed. Social, economic and ecological factors are affecting the in situ conservation of these genetic resources. Recently, germplasm recuperation efforts have been focused in tomato local landraces or "criollos" in Bolivia (Gonzáles et el. 2011) and Argentina (Peralta et al. 2008b, Fig. 2.4). These landraces were incorporated in the Argentinean Vegetable Crop Germplasm Bank System (Clausen et al. 2008, http://inta.gob.ar/documentos/red-de-bancos-y-colecciones-de-germoplasma/), evaluated in the field for agronomic and fruit quality traits and their potential use in breeding programmes (Peralta et al. 2008b). Traditional tomato varieties are characterized by their fruit qualities, mainly metabolites (Asprelli et al. 2016), antioxidants (Di Paola Naranjo et al. 2016a, b) and organic volatiles (Cortina et al. 2016), and typical flavour that consumers appreciate and now demand, although their seeds are not longer available. Recovery and return of these locally adapted varieties to their original communities will contribute to their sustainable maintenance. In basic research, the value of these Andean accessions has been demonstrated in their contribution to understanding the role of epigenetics in the

Fig. 2.4 Fruits from three tomato landraces from Argentina. "Platense": plurilocular, round, flattened and segmented; "Corazón de Buey": plurilocular, heart shape, slighly segmented; and "Largo": 2 or 3 locules, elongated. These landraces are cultivated for their quality traits (flavor, color, aroma) by local farmers in rural Argentina

determination of relevant agronomic traits (Quadrana et al. 2014). Additional collections and characterization of South American traditional cultivars are necessary not only for understanding diversity patters and evolutionary relationships, but also to reveal the domestication history and elucidate the genetics of agronomic and quality traits. Recuperation, conservation and uses of local landraces, particularly those from South and Central America, in tomato breeding is essential to incorporate valuable traits, such as fruit flavour and nutritional and health beneficial components, that humans have selected for over the course of improvement of tomatoes in local situations.

Summary

The cultivated tomato, *Solanum lycopersicum*, is a member of the large and diverse genus Solanum of the derived Asterid family Solanaceae. It belongs to a group of 13 closely related species all of which occur in arid habitats on the west coast of South America. The tomatoes are sister to the potatoes, and began to diversify only very recently, after the rise of the Andes and the development of the arid western deserts. Tomatoes were probably brought to Europe by the Spanish from Mesoamerica, and thence distributed worldwide. Traditional, early cultivars from the eastern slopes of the Andes in Ecuador and Peru are distinct from other cultivated populations but harbour a great diversity of fruit size and are not only small-fruited. Further collecting of feral populations and local varieties from South America will contribute to elucidate the diversity and origins of the cultivated tomato, as well as to reveal the genetics of agronomic and quality traits. Efforts to conserve the variation in *S. lycopersicum* itself, and not only related wild species, in its area of origin are a priority. Tomato landraces, selected and adapted to their local environments, are promising genetic sources to incorporate valuable traits in cultivated varieties.

References

Alvarez AE, van de Wiel CCM, Smulders MJM, Vosman B (2001) Use of microsatellites to evaluate genetic diversity and species relationships in the genus *Lycopersicon*. Theor Appl Genet 103:1283–1292

APG III (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Bot J Linn Soc 161:105–121

Asprelli PD, Sance M, Insani M, Asis R, Valle EM, Carrari F, Galmarini CR, Peralta IE (2016) Agronomic performance and fruit nutritional quality of an Andean tomato collection. Acta Horticulturae (in press)

Barboza GE, Knapp S, Särkinen TE (2013) Grupo VII. Moreloide. In: Anton AM, Zuloaga FO (eds), Barboza GE (coord) Flora Argentina vol 13, Solanaceae. IOBDA- IMBIV, CONICET, Buenos Aires, pp 231–264

Baum DA, Smith SD (2012) Tree thinking: an introduction to phylogenetic biology. Roberts and Co., Greenwood

Bell CD, Soltis DE, Soltis PS (2010) The age and diversification of the angiosperms re-visited. Am J Bot 97:1296–1303

Bentham G, Hooker JD (1873) Solanaceae. Genera Plant 2:882–913

Besler B (1613) Hortus eystettensis. Published by the author, Nuremberg

Blanca J, Cañizares J, Cordero L, Pascual L, Diez MJ, Nuez F (2013) Variation revealed by SNP genotyping and morphology provides insight into the origin of the tomato. PLoS ONE 7(10):e48198

Bohs L (1995) Transfer of *Cyphomandra* (Solanaceae) and its species to *Solanum*. Taxon 44:583–587

Bohs L (2005) Major clades in *Solanum* based on ndhF sequences. In: Keating RC, Hollowell VC, Croat TB (eds) A Festschrift for William G. D'Arcy: the legacy of a taxonomist. Monographs in Systematic Botany from the Missouri Botanical Garden, vol 104. Missouri Botanical Garden Press, St. Louis, pp 27–49

Bohs L, Olmstead RG (1997) Phylogenetic relationships in *Solanum* (Solanaceae) based on ndhF sequences. Syst Bot 22:5–17

Bohs L, Olmstead RG (1999) *Solanum* phylogeny inferred from chloroplast DNA sequence data. In: Nee M, Symon DE, Lester RN, Jessop JP (eds) Solanaceae IV: advances in biology and utilization. Royal Botanic Gardens, Kew, pp 97–110

Bohs L, Olmstead RG (2001) A reassessment of *Normania* and *Triguera* (Solanaceae). Plant Syst Evol 228:33–48

Bretó MP, Asins MJ, Carbonell EA (1993) Genetic variability in *Lycopersicon* species and their genetic relationships. Theor Appl Genet 86:113–120

Brickell CD, Alexander C, David JC, Hetterscheid WLA, Leslie AC, Malecot V, Jin XB, Cubey JJ (2009) International code of nomenclature for cultivated plants (ICNCP or Cultivated Plant Code) incorporating the rules and recommendations for naming plants in cultivation, 8th edn. Adopted by the International Union of Biological Sciences International Commission for the Nomenclature of Cultivated Plants. Regnum Vegetabile 151; Scripta Horticulturae 10. International Society for Horticultural Science, Leuven, Belgium

Caicedo AL, Schaal BA (2004) Population structure and phylogeography of *Solanum pimpinellifolium* inferred from a nuclear gene. Mol Ecol 13:1871–1882

Canady MA, Ji Y, Chetelat RT (2006) Homeologous recombination in *Solanum lycopersicodes* introgression lines of cultivated tomato. Genetics 174:1775–1778

Causse M, Desplat N, Pascual L, Le Paslier M-C, Sauvage C, Bauchet G, Bérard A, Bounon R, Tchoumakov M, Brunel D, Bouchet J-P (2013) Whole genome resequencing in tomato reveals variation associated with introgression and breeding events. BMC Genom 14:791

Chetelat RT, Ji Y (2007) Cytogenetics and evolution. In: Razdan MK, Mattoo AK (eds) Genetic improvement of solanaceous crops, vol 2, Tomato. Science, Enfield, pp 77–112

Chetelat RT, Meglic Y (2000) Molecular mapping of chromosome segments introgressed from *Solanum lycopersicoides* into cultivated tomato (*Lycopersicon esculentum*). Theor Appl Genet 100:232–241

Chetelat RT, Rick CM, Cisneros P, Alpert KB, DeVerna JW (1998) Identification, transmission, and cytological behavior of *Solanum lycopersicoides* Dun. monosomic alien addition lines in tomato (*Lycopersicon esculentum* Mill.). Genome 41:40–50

Child A (1990) A synopsis of *Solanum* subgenus *Potatoe* (G. Don) D'Arcy section *Tuberarium* (Dunal) Bitter (s.l.). Feddes Rep 101:209–235

Clausen AM, Ferrer ME, Formica ME (2008) Situación de los recursos Fitogenéticos en la Argentina. II Informe Nacional 1996–2006. Publicaciones Regionales. Ediciones INTA

Correll DS (1958) A new species and some nomenclatural changes in *Solanum* section *Tuberarium*. Madroño 14:232–236

Correll DS (1962) The potato and its wild relatives. Contr Texas Res Found Bot Studies 4:1–606

Cortina PR, Asis R, Peralta IE, Asprelli PD, Santiago AN (2016) Determination of volatile organic compounds in Andean tomato landraces by headspace solid phase microextraction-gas chromatography-mass spectrometry. J Braz Chem Soc 1–12. http://jbcs.sbq.org.br/imagebank/pdf/160126AR.pdf

D'Arcy WG (1972) Solanaceae studies II: typification of subdivisions of *Solanum*. Ann Mo Bot Gard 59:262–278

D'Arcy WG (1987) The circumscription of Lycopersicon. Solanaceae Newsl 2:60–61

D'Arcy WG (1991) The Solanaceae since 1976, with a review of its biogeography. In: Hawkes JG, Lester RN, Nee M, Estrada N (eds) Solanaceae III: taxonomy, chemistry, evolution. Royal Botanic Gardens, Kew, pp 75–137

Darwin SC, Knapp S, Peralta IE (2003) Taxonomy of tomatoes in the Galapagos Islands: native and introduced species of *Solanum* section *Lycopersicon* (Solanaceae). Syst Biodivers 12:29–53

Davis J, Yu D, Evans W, Gokirmak T, Chetelat RT, Stotz HU (2009) Mapping of loci from *Solanum lycopersicoides* conferring resistance or susceptibility to *Botrytis cinerea* in tomato. Theor Appl Genet 119:305–314

de Candolle ALPP (1886) Origin of cultivated plants, 2nd ed. D. Appleton, New York (1959 reprint; Hafner Publishing Company, New York)

de Tournefort JP (1694) Éléments de Botanique. Imprimerie Royale, Paris

Di Paola Naranjo RD, Otaiza S, Saragusti A2, Baroni V, Carranza Adel V, Peralta IE, Valle EM, Carrari F, Asis R (2016a) Hydrophilic antioxidants from Andean tomato landraces assessed by their bioactivities in vitro and in vivo. Food Chem 206:146–155. doi:10.1016/j.foodchem.2016.03.027

Di Paola Naranjo RD, Otaiza S, Saragusti AC, Baroni V, Carranza AV, Peralta IE, Valle EM, Carrari F, Asis R (2016b) Data on polyphenols and biological activity analyses of an Andean tomato collection and their relationships with tomato traits and geographical origin. Data Brief 7:1258–1268. doi:10.1016/j.dib.2016.04.005

Dunal MF (1813) Histoire naturelle, médicale et économique des *Solanum* et des genres qui ont été confundus avec eux. France, Montpellier

Dunal MF (1852) Solanaceae. In: De Candolle AP (ed) Prodromus systematis naturalis regni vegetabilis, vol 13, pp 1–450

Fosberg FR (1987) New nomenclatural combinations for Galápagos plant species. Phytologia 62:181–183

Fridman E, Carrari F, Liu YS, Fernie AR, Zamir D (2004) Zooming in on a quantitative trait for tomato yield using interspecific introgressions. Science 305:1786–1789

Frodin D (2004) History and concepts of big plant genera. Taxon 53:753–776

Grandillo S, Chetelat R, Knapp S, Spooner D, Peralta, I, Cammareri M, Perez O, Tripodi P, Termolino P,

Chuisano ML, Ercolano MR, Frusciante L, Monti L, Pignone D (2011) 9. *Solanum* sect. *Lycopersicon*. In: Kole C (ed) Wild crop relatives: genomics and breeding resources. Volume 5—vegetables. Springer, Heidelberg, pp 129–216

Gonzáles J et al (2011) Catálogo de poblaciones de tomate nativo e introducido en Bolivia. Impresiones Poligraf, Bolivia

Hawkes JG (1990) The potato: evolution biodiversity and genetic resources. Belhaven, London

Heine H (1976) Flora de la Nouvelle Caledonie, vol 7. Museum National D'Histoire Naturelle, Paris

Huamán Z, Spooner DM (2002) Reclassification of landrace populations of cultivated potatoes (*Solanum* sect. *Petota*). Am J Bot 89:947–965

Hunziker AT (1979) South American Solanaceae: a synoptic survey. In: Hawkes JG, Lester RN, Skelding AD (eds) The biology and taxonomy of Solanaceae. Academic, London, pp 49–85

Hunziker AT (2001) Genera Solanacearum, the genera of Solanaceae illustrated arranged according to a new system. ARG Gantner, Ruggell

Jenkins JA (1948) The origin of the cultivated tomato. Econ Bot 2:379–392

Jussieu AL (1789) Genera plantarum. Herissant V & Barrios T, Paris

Knapp S (2002) *Solanum* section *Geminata*. Fl Neotrop 84:1–405

Knapp S, Bohs L, Nee M, Spooner DM (2004) Solanaceae: a model for linking genomics and biodiversity. Comp Funct Genom 5:285–291

Koenig D, Jimenez-Gómez JM, Kimura S, Fulop D, Chitwood DH, Headland LR, Kumar R, Covington MF, Kumar Devisetty U, Tat AV, Tohge T, Bolger A, Schneeberger K, Ossowski S, Lanz C, Xiong G, Taylor-Teeples, M, Brady SM, Pauly M, Weigel D, Usadel B, Fernie AR, Peng J, Sinha N, Maloof JN (2013) Comparative transcriptomics reveals patterns of selection in domesticated and wild tomato. Proc Natl Acad Sci USA 110(28):E2655–E2662. doi:10.1073/pnas.1309606110

Linnaeus C (1753) Species plantarum, 1st edn. L. Salvius, Stockholm

Lippman Z, Tanksley SD (2001) Dissecting the genetic pathway to extreme fruit size in tomato using a cross between the small-fruited wild species *Lycopersicon pimpinellifolium* and *L. esculentum* var. Giant Heirloom. Genetics 158:413–422

Lucatti AF, van Heusden AW, de Vos RCH, Visser RGF, Vosman B (2013) Differences in insect resistance between tomato species endemic to the Galapagos islands. BMC Evol Biol 13:175

Luckwill LC (1943) The genus *Lycopersicon*: an historical, biological, and taxonomical survey of the wild and cultivated tomatoes. Aberdeen Univ Stud 120:1–44

Macbride JF (1962) Solanaceae. In: Flora of Peru. Field Mus Nat Hist Bot Ser 13:3–267

Mann CC (2011) 1493: Uncovering the New World Columbus created. Alfred A. Knopf, New York

Marshall JA, Knapp S, Davey MR, Power JB, Cocking EC, Bennett MD, Cox AV (2001) Molecular systematics of *Solanum* section *Lycopersicum* (*Lycopersicon*) using the nuclear ITS rDNA region. Theor Appl Genet 103:1216–1222

Mattioli PA (1544) Di Pedacio Dioscoride Anazarbeo libri cinque della historia, et materia medicinale trodotti in lingua uolgare Italiana. N. de Bascarini, Venice

Mattioli PA (1590) Kreutterbuch deß hochgelehrten unnd weitberühmten Herrn D. Petri Andreae Matthioli. Johann Feyerabend für Peter Fischer & Heinrich Tack, Frankfurt

McClean PE, Hanson MR (1986) Mitochondrial DNA sequence divergence among *Lycopersicon* and related *Solanum* species. Genetics 112:649–667

McNeill J, Barrie FR, Buck WR, Demoulin V, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Marhold K, Prado J, Prud'homme van Reine WF, Smith GF, Wiersema JH, Turland NJ (2012) International Code of Nomenclature for algae, fungi, and plants (Melbourne Code). Regnum Vegetabile 154. Koelz Scientific Books, Königstein, Germany

Miller P (1731) The Gardener's dictionary, 1st edn. Published for the author, London

Miller P (1754) The Gardener's dictionary, Abridged 4th edn. Published for the author, London

Miller P. (1807) The gardener's and botanist's dictionary, posthumous edition, ed. Thomas Martyn. F.C. & J. Rivington, London

Miller JC, Tanksley SD (1990) RFLP analysis of phylogenetic relationships and genetic variation in the genus *Lycopersicon*. Theor Appl Genet 80:437–448

Mueller LA, Tanksley SD, Giovannoni JJ, van Eck J, Stack S, Choi D, Kim BD, Chen M, Cheng Z, Li C, Ling H, Xue Y, Seymour G, Bishop G, Bryan G, Sharma R, Khurana J, Tyagi A, Chattopadhyay D, Singh NK, Stiekema W, Lindhout P, Jesse T, Lankhorst RK, Bouzayen M, Shibata D, Tabata S, Granell A, Botella MA, Giuliano G, Frusciante L, Causse M, Zamir D (2005) The tomato sequencing project, the first cornerstone of the international Solanaceae project (SOL). Comp Funct Genom 6(3):153–158

Müller CH (1940) A revision of the genus *Lycopersicon*. USDA Misc Publ 382:1–28

Nee M (1999) A synopsis of *Solanum* in the New World. In: Nee M, Symon DE, Lester RN, Jessop JP (eds) Solanaceae IV: advances in biology and utilization. Royal Botanic Gardens, Kew, pp 285–333

Nesbitt TC, Tanksley SD (2002) Comparative sequencing in the genus *Lycopersicon*: implications for the evolution of fruit size in the domestication of cultivated tomatoes. Genetics 162:365–379

Olmstead RG, Palmer JD (1997) Implications for phylogeny, classification, and biogeography of *Solanum* from cpDNA restriction site variation. Syst Bot 22:19–29

Olmstead RG, Sweere JA, Spangler RE, Bohs L, Palmer JD (1999) Phylogeny and provisional

classification of the Solanaceae based on chloroplast DNA. In: Nee M, Symon DE, Lester RN, Jessop JP (eds) Solanaceae IV: advances in biology and utilization. Royal Botanic Gardens, Kew, pp 111–137

Palmer JD, Zamir D (1982) Chloroplast DNA evolution and phylogenetic relationships in Lycopersicon. Proc Natl Acad Sci USA 79:5006–5010

Peralta IE, Spooner DM (2001) Granule-Bound Starch Synthase (GBSSI) gene phylogeny of wild tomatoes (*Solanum* L. section *Lycopersicon* [Mill.] Wettst. subsection *Lycopersicon*). Am J Bot 88:1888–1902

Peralta IE, Spooner DM (2005) Morphological characterization and Relationships of wild tomatoes (Solanum L. Section Lycopersicon [Mill.] Wettst. Subsection Lycopersicon). Monogr Syst Bot Mo Bot Gard 104:227–257

Peralta IE, Spooner DM (2007) History, origin and early cultivation of tomato (Solanaceae). In: Razdan MK, Mattoo AK (eds) Genetic improvement of Solanaceous crops, vol 2, tomato. Science, Enfield, pp 1–27

Peralta IE, Knapp S, Spooner DM (2005) New species of wild tomatoes (*Solanum* section *Lycopersicon*: Solanaceae) from Northern Peru. Syst Bot 30(2):424–434

Peralta IE, Knapp S, Spooner DM (2006) Nomenclature for wild and cultivated tomatoes. Feature article. Rep Tomato Genet Coop 56:6–12

Peralta IE, Spooner DM, Knapp S (2008a) Taxonomy of wild tomatoes and their relatives (*Solanum* sections *Lycopersicoides*, *Juglandifolia*, *Lycopersicon*; Solanaceae). Syst Bot Monogr 84:1–186

Peralta IE, Makuch M, García Lampasona S, Occhiuto PN, Asprelli PD, Lorello IM, Togno L (2008b) Catálogo de poblaciones criollas de pimiento, tomate y zapallo colectadas en valles andinos de la Argentina. Editorial INTA, Mendoza

Pertuzé RA, Ji Y, Chetelat RT (2002) Comparative linkage map of the *Solanum lycopersicoides* and *S. sitiens* genomes and their differentiation from tomato. Genome 45:1003–1012

Quadrana L, Almeida J, Asís R, Duffy T, Dominguez PG, Bermúdez L, ContiG, Corrêa da Silva JV, Colot V, Asurmendi S, Fernie AR, Rossi M, Peralta I, Carrari F (2014) Natural occurring epialleles determine vitamin E accumulation in tomato fruits. Nat Comm 5:4027. doi:10.1038/ncomms5027

Ranc N, Muños S, Santoni S, Causse M (2008) A clarified position for *Solanum lycopersicum* var. *cerasiforme* in the evolutionary history of tomatoes (Solanaceae). BMC Plant Biol 8:130

Rick CM (1979) Biosystematic studies in *Lycopersicon* and closely related species of *Solanum*. In: Hawkes JG, Lester RN, Skelding AD (eds) The biology and taxonomy of Solanaceae, Linn Soc Symp Ser 7. Academic, New York, pp 667–677

Rick CM (1988) Tomato-like nightshades: affinities, autoecology, and breeders opportunities. Econ Bot 42:145–154

Rick CM, Chetelat RT (1995) Utilization of related wild species for tomato improvement. Acta Hortic 412: 21–38

Rick CM, Holle M (1990) Andean *Lycopersicon esculentum* var *cerasiforme* genetic variation and its evolutionary significance. Econ Bot 43(Suppl. 3):69–78

Rick CM, Laterrot H, Philouze J (1990) A revised key for the *Lycopersicon* species. Tomato Genet Coop Rep 40:31

Rodriguez F, Wu F, Ané C, Tanksley S, Spooner DM (2010) Do potatoes and tomatoes have a single evolutionary history, and what proportion of the genome supports this history? BMC Evol Biol 9:191

Ross RJ (1998) Review paper: global genetic resources of vegetables. Plant Var Seeds 11:39–60

Särkinen T, Bohs L, Olmstead RG, Knapp S (2013) A phylogenetic framework for the evolutionary study of the nightshades (Solanaceae): a dated 1000-tip tree. BMC Evol Biol 13:214

Schauer N, Semel Y, Roessner U, Gur A, Balbo I, Carrari F, Pleban T, Perez-Melis A, Bruedigam C, Kopka J, Willmitzer L, Zamir D, Fernie AR (2006) Comprehensive metabolic profiling and phenotyping of interspecific introgression lines for tomato improvement. Nat Biotechnol 24:447–454

Seithe A (1962) Die Haararten der Gattung *Solanum* L. und ihre taxonomische Verwertung. Bot Jahrb Syst 81:261–336

Seymour G, Ostergaard L, Chapman NH, Knapp S, Martin C (2013) Fruit ripening and development. Ann Rev Plant Biol 64:219–241

Smith SD, Peralta IE (2002) Ecogeographic surveys as tools for analyzing potential reproductive isolating mechanisms: an example using *Solanum juglandifolium* Dunal, *S. ochranthum* Dunal, *S. lycopersicoides* Dunal, and *S. sitiens* I.M. Johnston. Taxon 51:341–349

Spooner DM, Anderson GJ, Jansen RK (1993) Chloroplast DNA evidence for the interrelationships of tomatoes, potatoes, and pepinos (Solanaceae). Am J Bot 80:676–688

Spooner DM, Peralta IE, Knapp S (2005) Comparison of AFLPs to other markers for phylogenetic inference in wild tomatoes [*Solanum* L. section *Lycopersicon* (Mill.) Wettst. subsection *Lycopersicon*]. Taxon 54:43–61

Stack SM, Covey PA, Anderson LK, Bedinger PA (2009) Cytogenetic characterization of species hybrids in the tomato clade. Tomato Genet Coop Rep 59:57–61

Stommel JR (2001) USDA 97L63, 97L66 and 97L97: tomato breeding lines with high fruit beta-carotene content. HortScience 36:387–388

Symon DE (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

Symon DE (1985) The Solanaceae of New Guinea. J Adelaide Bot Gard 8:1–177

Taylor IB (1986) Biosystematics of the tomato. In: Atherton JG, Rudich J (eds) The tomato crop: a scientific basis for improvement. Chapman and Hall, London, pp 1–34

Tomato Genome Consortium (2012) The tomato genome sequence provides insights into fleshy fruit evolution. Nature 485:635–641

Van der Knaap E, Lippman ZB, Tanksley SD (2002) Extremely elongated tomato fruit controlled by four quantitative trait loci with epistatic interactions. Theor Appl Genet 104:241–247

Villand J, Skroch PW, Lai T, Hanson P, Kuo CG, Nienhuis J (1998) Genetic variation among tomato accessions from primary and secondary centers of diversity. Crop Sci 38:1339–1347

Whalen MD (1979) Taxonomy of *Solanum* section *Androceras*. Gentes Herb 11:359–426

Williams CE, St. Clair DA (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 *Lycopersicum esculentum*. Genome 36:619–630

Wu F, Mueller LA, Crouzillat D, Petiard V, Tanksley SD (2006) Combining bioinformatics and phylogenetics to identify large sets of single copy, orthologous genes (COSII) for comparative, evolutionary and systematics studies: a test case in the Euasterid plant clade. Genetics 174:1407–1420

Springer