

Compendium of Plant Genomes

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The Tomato Genome

Compendium of Plant Genomes

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The Tomato Genome

 Springer

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We dedicate this volume to Prof. Steven Tanksley without whom the tomato system and genome would never have been developed to the exceptional utility and quality they serve today.



Preface

The Tomato Genome Sequence: How Did It Happen and Why Does It Matter?

The tomato genome sequencing project was initiated as part of the International Solanaceae Project (SOL) by a large international consortium of 10 countries (Korea, China, UK, India, The Netherlands, France, Japan, Spain, Italy and the United States). The tomato was chosen as reference species for the Solanaceae due to the high level of macro and micro-syteny within this plant family which comprises more than 3000 species among which some are important crops such as the fruit-bearing vegetables tomato, eggplant, and pepper, and the tuber-bearing potato, in addition to a number of medicinal and ornamental plants. The goal of the tomato genome sequencing project was to generate new information and resources allowing to shed light on how a common set of genes can give rise to a wide range of morphologically and ecologically distinct organisms, and how a better understanding of the genetic basis of plant diversity can be harnessed to meet the needs of the fast growing world population for a sustainable food crop production. It is important to mention that the launching of the tomato genome sequencing project would have not been possible without the use of the rich resources previously generated using this plant species. Undoubtedly, the project took advantage of the large collection of EST sequences, the high number of genetic markers, the dense and saturated genetic maps, and the well-characterized genomic libraries already available (<http://sgn.cornell.edu>).

In many ways, the project represented a unique scientific and human adventure where the participants shared the scientific effort and the financial outlay and worked in close collaboration. Starting with conventional sequencing technologies the project shifted to the new high-throughput sequencing technologies, just emerging at the time. In this regard, the tomato genome sequencing project accompanied the transition from the old to the new sequencing era. Indeed, the Sanger sequencing method was initially used, but the advent of next-generation (NextGen) sequencing technologies has prompted the consortium to adopt these promising techniques. In retrospect, we can now say that the choice of these pioneering technologies was a wise decision, although it posed a risk at the time because there was no prior experience where the NextGen sequencing technologies have been applied *de novo* to sequence a large and complex eukaryotic genome. The consortium

had to overcome the difficulties of high-throughput data processing and assembly of “reads” without any possibility to rely on past experience in this area. An important challenge was the buildup of a pipeline for the genome sequence assembly, and in this respect, one of the most striking aspects of the project’s success had been to produce finally a high-quality assembled tomato genome sequence using for the first time the new sequencing technologies.

Due to the estimated elevated cost of producing a high-quality sequence of the complete tomato genome, the initial strategy was the preferred sequencing of the euchromatin region where the majority of genes reside. This approach presents the advantage to target only 25 % of the total tomato genome thus allowing to significantly reduce the sequencing effort. The BAC-by-BAC sequencing strategy built on the existing saturated tomato genetic map, and made use of the genetic markers to select seed BACs within the gene-rich part of the tomato genome. The starting point for sequencing the genome was BACs anchored to the genetic map, and this minimal tiling path then extends from seed BACs to cover the whole genome. Once completed, the BAC-by-BAC tomato genome sequence was anticipated to provide a framework for shotgun sequencing of other Solanaceae species. While this approach enabled a rapid progress at the early phases of the project, it struck quickly with the difficulty of selecting BACs to power the sequencing pipeline. Finally, the slowness of this process became a serious obstacle pushing the consortium to seek other alternatives to reinvigorate the project. The advent of next-generation sequencing technologies offered an attractive option despite the lack of experience in applying these techniques to complex genomes. Switching to high-throughput sequencing launched the project into a new and original adventure where you have to discover simultaneously both the problems and their solutions. In particular, the consortium realized that these approaches require massive use of bioinformatics tools that had to be acquired and implemented in a short period of time.

The switch to a whole genome sequencing approach that combines both next-generation sequencing and Sanger sequencing boosted the project leading to a high-quality assembled tomato genome sequence within a relatively short period of time. The present book tells the tale of the tomato genome sequencing adventure with the various chapters describing in great detail every step of the sequencing project. Chapters 1 and 2 provides a brief review of the birth of the tomatoes in the Andean regions of South America, the history of their botanical classification along with other wild and cultivated Solanaceae as well as information about the main production areas. The following chapters deal with gene and QTL mapping in tomato with a particular emphasis on the new opportunities that the tomato genome sequences are providing for the genetic and molecular dissection of complex traits and how it helps breeders to shape new and better tomato varieties. The chapter on tomato resources for functional genomics describes the main resources, strategies, and tools currently available for linking genes to phenotypes in tomato. The chapters devoted to the generation of the tomato genome sequence per se emphasize the sequencing and assembling strategies

used in the project and the genome quality evaluation and the finishing methods. A separate chapter is dedicated to the annotation of the tomato genome with the aim to provide the best gene structures, a high-quality functional description for the protein-coding genes. The sequencing of the chloroplast and mitochondrial genomes, described in a specific chapter, adds to the understanding of the plant evolutionary history of tomato based on the phylogenetic position inferred from the organelles sequences information. The following two chapters review recent research on the timing and formation of ancient genome duplications and their evolutionary effects on the shaping of modern Solanaceae genomes. They also address the synteny among Solanaceae genomes providing insight into the modes and tempo of plant genome evolution and illustrating how a better knowledge of genome synteny and colinearity can facilitate the mobilization of resources from one species to other in this agronomically important family. The last chapter describes the tomato-centric databases and other generic resources freely accessible to Solanaceae community.

While the effort to produce an improved assembly with a larger coverage of the tomato genome is ongoing, the present version of the tomato genome (The Tomato Genome Consortium, Nature 2012) is among, if not the best quality of, all dicot genomes published to date, excluding Arabidopsis. Producing a reference tomato genome sequence represented a major breakthrough and has provided invaluable resource that has opened new avenues for research. Building on this resource enabled the development of a variety of genome-wide approaches like whole genome transcriptomic profiling that is nowadays becoming a routine method for expression studies. Likewise, genotyping-by-sequencing is currently spreading as a method of choice and mapping by sequencing is being increasingly used. The access to a complete genome sequence also fostered epigenetics studies allowing to establish a genome-wide mapping of various epigenetic marks. More recently, genome editing is experiencing a rapid growth to address the functional significance of candidate genes in the tomato model. These are some of the main areas that have been impacted by the acquisition of a high-quality reference genome for tomatoes, but most likely, we are only at the dawn of these dramatic developments and more unexpected ones will break out in the future.

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Sophie Colvine and François Xavier Branthôme

Abstract

Originating from South America, tomato is now produced all over the world. After a slow propagation in European Mediterranean countries since the sixteenth century, it has started to be largely cultivated in the twentieth century. It has experienced spectacular growth over the last 50 years both for processing tomato and fresh market. The growth of global trade reflects the rise in consumption, with a recent increase in Asia, notably in China, which has become the first producer in the last years.

Keywords

Tomato · Production · Trade · Processing · Fresh market

Although still a matter of debate, the birth of the tomato is generally located in the Andean regions of South America. In this century of rampant and frenetic globalisation, the slower-paced journeys that took it from Peru, then Mexico, to the shores of the Caribbean and South East Asia and from Southern Italy to Northern Europe before reaching North America are pretty mind boggling.

But, the tomato's travels have not just been geographic. It has been consumed and indeed grown since well before the Christian era (500 years BC in Mexico) but first had to convince the cultures and people it encountered that it was safe. Its heart-shaped form and red colours conquered the Moors who discovered it in Spain, but it was subsequently considered to be an aphrodisiac by the Italian Herbalist, Pietro Andrea Mattioli, who gave it the name of 'love apple' in 1544, or as 'highly toxic' by the English Physician and Herbalist, John Gerard in the late sixteenth century. The suspicions it raised relegated it to the status of an ornamental plant hidden away at the bottom of the garden throughout the seventeenth and early eighteenth centuries. The most that can be said is that its colour and taste brightened and spiced up a few soups around 1730 in England

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while at the same time on the other side of the Atlantic, scientists strongly discouraged its consumption due to its links with Mandrake and Deadly Nightshade, both members of the Solanaceae family. For the tomato to be definitively considered as a food in its own right, it needed President Thomas Jefferson's political influence and strength of conviction in 1809, a cultural and industrial revolution and, almost 30 years later, again in the US, a media offensive by the New York Times. It would be a further 30 years until, in 1869, Henry John Heinz founded the company in Pittsburgh whose name and flagship product remain inextricably linked to the tomato.

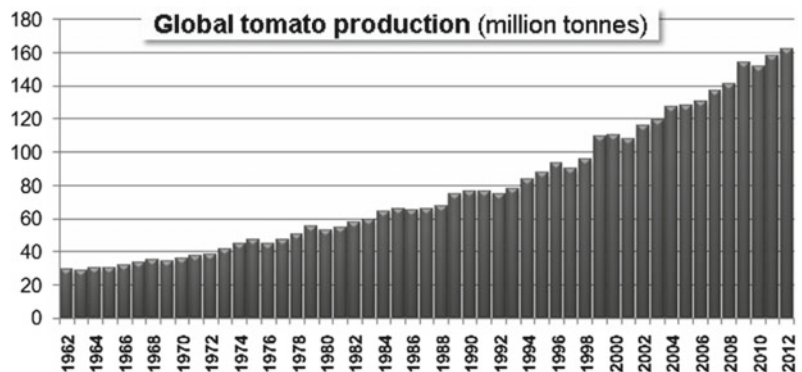
Now grown in all latitudes, or almost, the tomato has experienced spectacular growth over the last 50 years (Fig. 1.1). As a member of the Solanaceae family, it is often compared to the potato which holds the record for annual worldwide consumption with more than 376 million tonnes of potatoes produced in 2013 according to the FAO. The tomato is more modest by comparison and currently settles for an annual production level of 164 million tonnes.

Nonetheless, the tomato outclasses its cousin in terms of production growth (Table 1.1). Admittedly, potato cultivation already stood at nearly 271 million tonnes in 1961, precisely ten times that of the tomato, but during the last 50 years, the amounts of tomatoes produced worldwide have multiplied by 5.8, jumping from less than 28 million tonnes in 1961 to nearly 164

million tonnes in 2013. This growth is all the more pronounced in Asia and especially China, the world's biggest producer with just over a quarter of total production, where there has been a sevenfold increase in production while in India production has been multiplied by 18. Over the same period, potato production *only* increased by 20 %, weighing-in at just 376 million tonnes in 2013, or barely twice that for tomatoes! These figures however only account for commercial production and exclude family farming and subsistence production which can be fairly significant in certain regions.

The reasons for this growth lie in a dramatic improvement in agricultural productivity which reflects the wide interest in both vegetables making it possible to expand production way beyond what would have been expected based on existing surface area increases alone. Average figures given by the FAO (currently 34 t/ha compared to 16 t/ha in 1961) give only a rough idea of the astonishing progress made by agronomy. Average yields for processing tomato fields in California which are frequently used as an example, have quite simply jumped from 25 t/ha in 1961 to 105 t/ha in 2014 and some farmers even manage to reach spectacular yields of 150 t/ha. In other words, the quality of fruit harvested from the same field has increased fourfold in the space of just two generations. Under glass, average yields are now around 400 t/ha and can even reach 1000 t/ha!

Fig. 1.1 Global tomato production (million tonnes)



(Source : FAO)

Table 1.1 Main tomato-producing countries (2012)

	Production (tonnes)	Area harvested
China	50,000,000	1,000,000
India	17,500,000	870,000
USA	13,206,950	150,140
Turkey	11,350,000	300,000
Egypt	8,625,219	216,395
Iran	6,000,000	160,000
Italy	5,131,977	91,850
Spain	4,007,000	48,800
Brazil	3,873,985	63,859
Mexico	3,433,567	96,651
Uzbekistan	2,650,000	60,000
Russia	2,456,100	117,700
Ukraine	2,274,100	85,700
Nigeria	1,560,000	270,000
Portugal	1,392,700	15,400
Morocco	1,219,071	15,639
Tunisia	1,100,000	28,900
Iraq	1,100,000	62,500
Greece	979,600	16,000
Indonesia	887,556	56,042
Cameroon	880,000	150,000

Source: FAO

And examples abound in the main tomato-producing countries of China, India, Turkey, Egypt, Italy, Iran, Spain, Brazil and Mexico and so on. The tomato has continued to travel which has subsequently led to its being selected, improved, made more resistant, more productive, fleshier, redder and eventually taken from the fields and tables to the processing factories. As a standard-bearer for the Mediterranean diet, the tomato has quickly adapted to modern lifestyles. It has even become emblematic for a few leaders in the global food industry, including some that have themselves engaged in the lengthy process of selecting varieties and, just a few decades ago, ‘invented’ the illustrious ancestors of those jointly used by the processing industry today.

As such, the tomato has long been the leading processed ‘vegetable’ in the world. The diversity of processed tomato products makes it

impossible to list the countless forms in which the tomato is consumed everywhere on a daily basis throughout the world. Indeed, the quantities of tomatoes used for sauces, diced tomatoes, pastes, on pizzas, for passata, in ketchup, peeled, chopped, frozen, or powdered tomatoes, to name just a few of the most common forms, increase regularly each year. Here, also, growth has been astonishing with the global industry increasing its production from 22 million tonnes in the 1990s to nearly 40 million tonnes by the end of 2010. No other vegetable can boast consumption figures in processed form that represent nearly a third of its fresh volumes. This is indeed the case for the tomato which to be consumed the world over is only processed (and cultivated solely for this purpose) in what boils down to a quite a small number of countries. The leader among them is California which accounted for nearly a third of worldwide production over the last

10 years with an average annual volume of over 10 million tonnes (Fig. 1.2). One of the strengths of the American industry is the size of its companies, including 9 which rank among the top 12 biggest tomato businesses in the world.

As a relative newcomer in 2000, the Chinese industry has quickly become one of the global leaders. It owes its heavy-weight status to the strength of its exports of pastes which account for virtually all of its products. The other advantage China has is to have spotted and developed markets that were practically ignored until the late 1990s thanks to a particularly competitive commercial policy.

The historical processor and uncontested leader in the European industry is Italy. It only recently relinquished its place as world leader to China, a position it occupied for a long time in quantitative terms due to robust sales of pastes but also the diversity of exported products and the domination it holds in the canned sector, especially peeled tomatoes.

Italy however remains the world leader in terms of revenue. In 2013, business generated nearly 2.1 billion US Dollars for the Italian industry whereas Chinese and American sales only amounted to 984 and 715 million US Dollars, respectively.

Nevertheless, the processing tomato is also taken in Spanish, Portuguese, Chilean, Iranian, Turkish and Greek industries, to name just those key players in international trade. They all operate on a global level each with their specific characteristics in terms of processing techniques, products, packaging, customers or geographic zones. These nine countries account for 80 % of global processing power for the export market for paste alone which is the main processed tomato product marketed today. The price of this growing concentration of processing hubs is that a significant number of regions are increasingly dependent on supplies of processed tomato products.

The growth of global trade reflects the rise in consumption (Fig. 1.3). 40 million tonnes of the 159 million tonnes of fresh tomatoes identified by the FAO are consumed each year throughout the world in processed form. In good years or bad, this amount rises by the equivalent of one million tonnes of fresh tomatoes each year, but the components of global consumption of processed tomato products (the different product categories) evolve at the whims of cultural choices, social and economic constraints, political events and dietary patterns, etc.

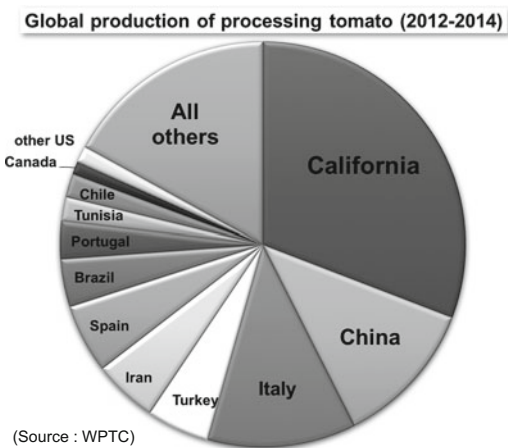


Fig. 1.2 Global production of processing tomato (2012–2014)

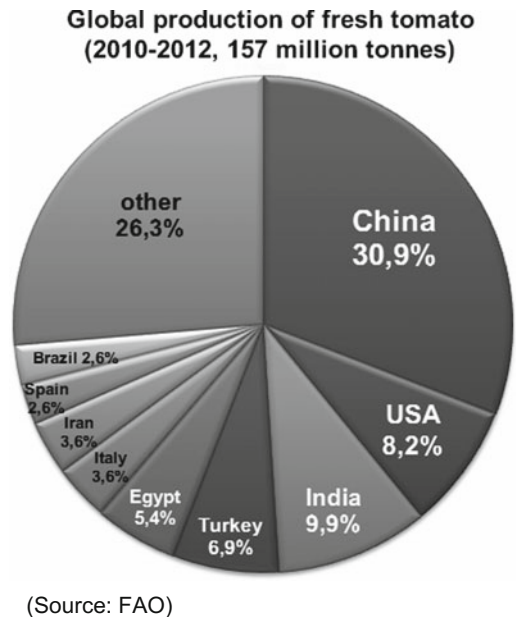


Fig. 1.3 Global production of fresh tomato

According to FAO figures, average global consumption per capita was 20.5 kg in 2009, with variations from 0 to more than 100 kg in North Africa and the Middle East. This compares to around 31 kg in the European Union and 44 kg in the US. In terms of processed tomatoes, it was 6 kg in 2011 according to WPTC figures, which shows a 50 % increase over the last 15 years (4 kg in 1995). This is both a little and a lot since this level of individual consumption is just over one kilogramme of paste, whereas in 2013 just one third of the world's population consumed more than this threshold. Although eating habits and consumption levels can be incredibly varied from one continent to the other, the most surprising example is without doubt China. It is both the world's leading supplier of pastes and the biggest consumer of tomatoes and now accounts for more than 42 million tonnes per year. Out of this impressive total, only one million tonnes (2.5 %) are consumed in processed form, i.e. the equivalent of about 800 grams of fresh tomatoes per year and per person. On the other hand, the impression tomatoes has made on culinary cultures and dietary traditions, however different they may be, in Italy and the USA can be clearly seen in the individual consumption ratios. Although far from holding any records in the discipline, American or Italian consumers each consume more than 30 kilos of tomatoes every year in the form of pastes, sauces, pizzas, etc. For someone living in Parma, Rome or Naples, fresh tomatoes remain a must which accompanied with mozzarella, basil or olive oil, still represent more than 56 % of annual consumption. In Sacramento, Houston or Springfield, fresh tomatoes are rarer and ketchup, sauces and other processed forms of tomato now account for more than three-quarters of annual tomato consumption!

The tomato's forms, tastes and circumstances may differ, but whether fresh or processed, it constitutes a universally recognised foodstuff that is independent of age, religion and culture. With each minute that passes, 300 tonnes of tomatoes

disappear. 228 tonnes are taken up by fresh consumption and 72 tonnes are consumed in processed form. Whatever the latitude or longitude, these two markets complement each other, grow together and feed off each other. Nevertheless, everything, or nearly everything, sets these two faces of the same crop apart. First, the varieties are all derived from common ancestors destined for the fresh market. Some varieties occasionally got confused as 'dual-purpose' varieties but now they are totally differentiated between the fresh and processed sectors. Second, there is the period and type of cultivation; annual and under glass in once case and highly seasonal and open-field in the other. Cultivating and harvesting fresh tomatoes is highly dependent on the availability of manpower while it is increasingly mechanised for the processed sector and then there are the regions of production, logistical restrictions, techniques and costs, etc. But in the end, the amounts consumed, whether fresh or processed, are rising in line with each other at just over a 25 and 75 %, respectively of global consumption.

The tomato's journeys via winds and currents, through different cultures, skills, culinary arts, across changing land and seasons as well as for different economic reasons and industrial logistics have sometimes been unexpected and eventful but have built up a long and rich history. They brought the wild cherry tomato all the way from Peru to the individual ketchup portion consumed in the fast food restaurants of Shanghai. Every day it becomes a little more universal, it unveils yet more new qualities while research demonstrates its contribution to health, advances its farming attributes and positions it in a more environmentally friendly global approach. The journey and the story do not stop there. Its colours and forms, its contents, its strengths and its virtues are yet more complex and secret, but that is for genetics to discover.

As a geographical, historical, cultural and artistic link, the tomato already has a great history. It also has a bright future.

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.

Keywords

Taxonomy · Tomato · *Solanum lycopersicum* · Wild relatives · Systematics

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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 *Leplostemonum* 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 tuberosa, 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*

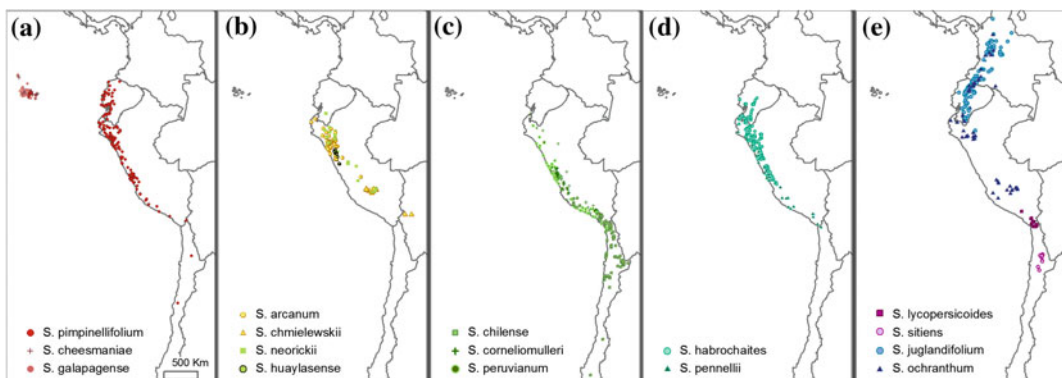


Fig. 2.1 Distribution maps of tomato wild relatives

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)
<i>Solanum arcanum</i> Peralta	Northern Peru	Dry inter-Andean valleys and in coastal lomas (seasonal fogs-drenched habitats); 100–4000 m	<i>Lycopersicon</i> 'Arcanum group'
<i>Solanum cheesmanii</i> (L. Riley) Fosberg	Galápagos Islands	Dry, open, rocky slopes; sea level—1300 m	<i>Lycopersicon</i> 'Lycopersicon group'
<i>Solanum chilense</i> (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)	<i>Lycopersicon</i> 'Eriopersicon group'
<i>Solanum chmielewskii</i> (C.M. Rick, Kasicki, 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	<i>Lycopersicon</i> 'Arcanum group'
<i>Solanum cornelium</i> Mullert J.F. Macbr.	Southern Peru (Lima southwards)	Dry, rocky slopes; 20–4500 m (low elevation populations associated with landslides in southern Peru)	<i>Lycopersicon</i> 'Eriopersicon group'
<i>Solanum galapagensis</i> S.C. Darwin & Peralta	Galápagos Islands	Dry, open, rocky slopes; seashores; sea level—1600 m	<i>Lycopersicon</i> 'Lycopersicon group'
<i>Solanum habrochaites</i> S. Knapp & D.M. Spooner	Andean Ecuador and Peru	Montane forests, dry slopes and occasionally coastal lomas; 10–4100 m	<i>Lycopersicon</i> 'Eriopersicon group'
<i>Solanum huaylasense</i> Peralta	Río Santa river drainage, north-central Peru	Dry, open, rocky slopes; 950–3300 m	<i>Lycopersicon</i> 'Eriopersicon group'
<i>Solanum juglandifolium</i> Dunal	Andean Colombia, Ecuador and Peru	Montane cloud forests; 1000–3200 m	<i>Juglandifolia</i>
<i>Solanum lycopersicoides</i> Dunal	Southern Peru and northern Chile	Rocky slopes and ravines; 1250–3600	<i>Lycopersicoides</i>
<i>Solanum lycopersicum</i> L.	Globally cultivated domestic	Cultivated; sea level—4000 m	<i>Lycopersicon</i> 'Lycopersicon group'
<i>Solanum neorickii</i> D.M. Spooner, G.J. Anderson & R.K. Jansen	Southern Ecuador to southern Peru	Dry inter-Andean valleys; 500–3500 m	<i>Lycopersicon</i> 'Arcanum group'
<i>Solanum ochranthum</i> Dunal	Andean Colombia, Ecuador and Peru	Montane cloud forests; 1850–4100 m	<i>Juglandifolia</i>
<i>Solanum pennellii</i> Correll	Northern Peru to northern Chile	Dry slopes and washes, usually in flat areas; sea level—4100 m	<i>Lycopersicon</i> 'Neolyopersicon group'
<i>Solanum peruvianum</i> L.	Central Peru to northern Chile	Dry coastal deserts and lomas; sea level—3000 m	<i>Lycopersicon</i> 'Eriopersicon group'
<i>Solanum pimpinellifolium</i> L.	Southwestern Ecuador to northern Chile (many northern populations in Ecuador are admixture with <i>S. lycopersicum</i> ; Peralta et al. 2008a, b; Blanca et al. 2013)	Dry slopes, plains and around cultivated fields; sea level—3000 m	<i>Lycopersicon</i> 'Lycopersicon group'
<i>Solanum sitens</i> I.M. Johnston	Northern Chile	Dry ravines and slopes (hyperarid areas); 2000–3500 m	<i>Lycopersicoides</i>

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 ($2n = 24$) (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 ($2n = 24$), 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).

Rodríguez 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 (Rodríguez 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.

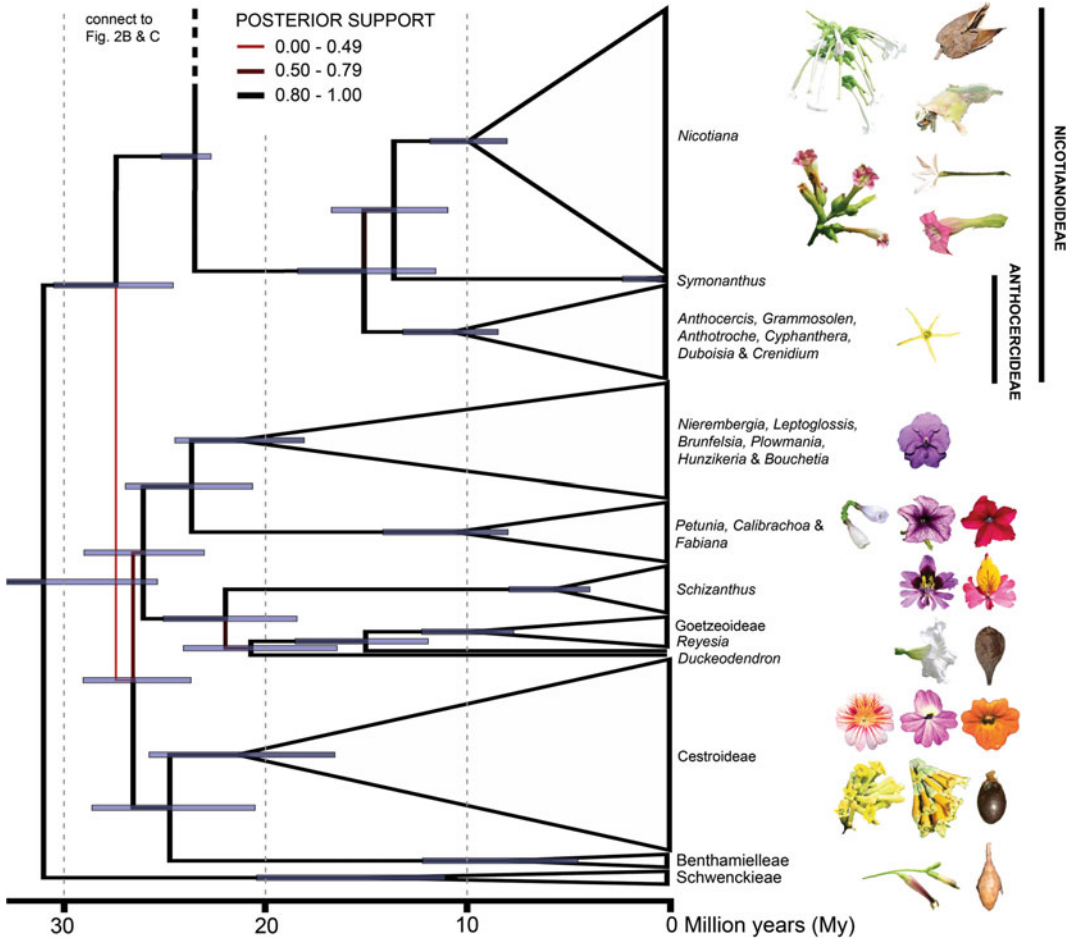


Fig. 2.2 Dated Solanaceae phylogeny; only major clades shown with representative flowers/fruits alongside. Grey bars correspond to date ranges as seen in text (from Särkinen et al. 2013, reproduced with permission from *BMC Evolutionary Biology* 13:214 (2013). doi:10.1186/1471-2148-13-214)

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

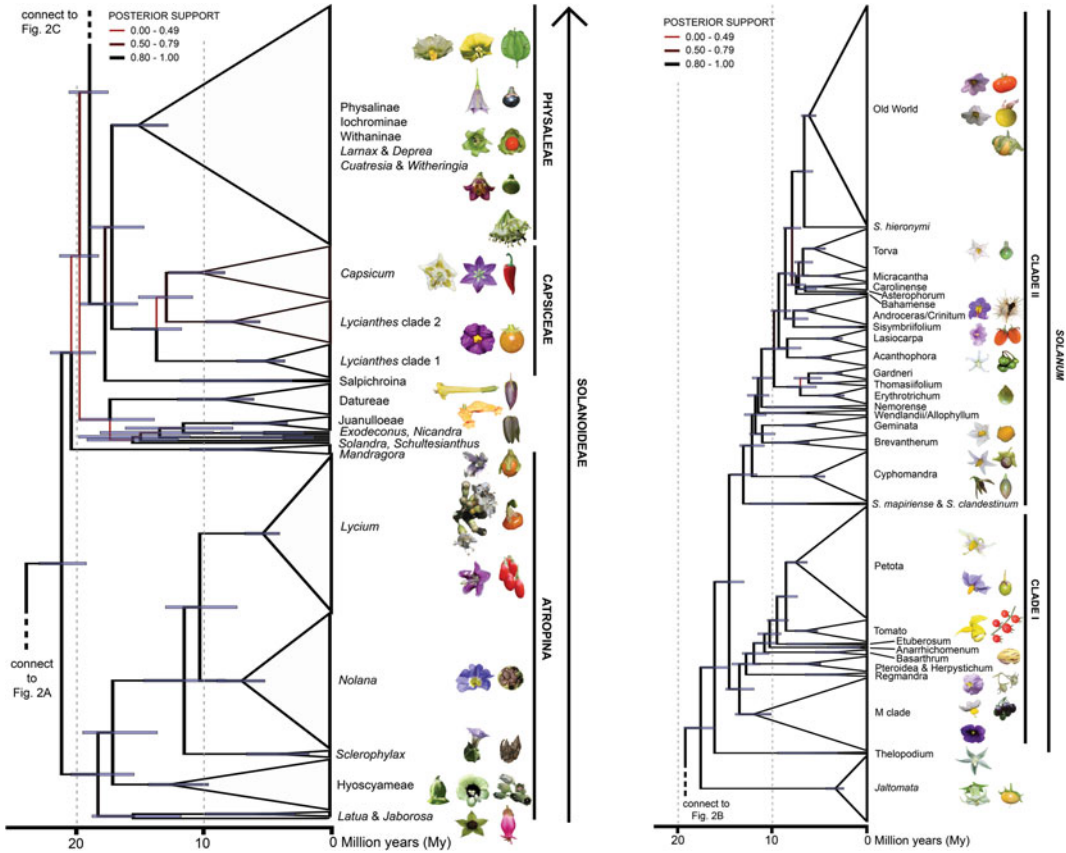


Fig. 2.2 (continued)

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 stiaciante 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 medesimo 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 fasciated 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, fasciated 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 (González et al. 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, slightly 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

