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## NOMENCLATURE FOR WILD AND CULTIVATED TOMATOES

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An efficient way to communicate ideas about our world is to build a common language, including scientific names of biological organisms that are named according a Latin binomial nomenclature first used for all plants by Linnaeus (1753). In binomial nomenclature a name is composed of two parts, the first refers to the genus and the second, often called the epithet, refers to the species, followed by the author(s) of the name. Species epithets can refer to striking characteristics of the plant (e.g. *Solanum tuberosum*), where the plant was found (e.g. *Solanum peruvianum*) or are sometimes used to honor particular people (e.g. *Solanum neorickii*).

How are plants named? *Species plantarum*, written by the Swedish botanist and Doctor Carl Linnaeus and published in 1753, is considered the starting point for scientific nomenclature of plants. The International Code of Botanical Nomenclature (ICBN, McNeill et al., 2006; revised and updated every 6 years at International Botanical Congresses, the most recent held in Vienna in 2005) provides a framework to properly name species and other taxonomic ranks, as well as a set of rules to determine the priority of plant names when competing names refer to the same organism. In cultivated plants, new forms or cultivars have been generated by domestication and artificial selection. The application of the ICBN to cultivated taxa could produce complex scientific names of limited utility to either taxonomists or plant breeders. For that reason a different set of nomenclatural rules can be used for cultivated plants, laid out in the International Code of Nomenclature for Cultivated Plants (ICNCP, Brickell et al., 2004).

### The names of wild tomatoes

In a taxonomic treatment of tomatoes and their wild relatives it is important to study the diversity and distribution of the species as well as their natural history. Species delimitation is a synthetic interpretation of our knowledge of a group (Spooner et al., 2003), and what constitutes a species is a hypothesis that changes over time as more information becomes available.

Wild tomatoes are native of western South America, distributed from Ecuador to northern Chile, and with two endemic species in the Galápagos Islands (Darwin et al., 2003; Peralta and Spooner, 2005). They grow in variety of habitats, from near sea level to over 3,300 m in elevation, in arid coastal lowlands and adjacent lomas where the Pacific winds drop scarce rainfall and humidity; in isolated valleys in the high Andes, and in deserts like the severe Atacama Desert in northern Chile. Andean topography, diverse ecological habitats, and different climates have all contributed to wild tomato diversity.

We have recently completed an in-depth study of tomatoes and their wild relatives, with the aim to provide new species definitions, revised and updated the nomenclature and to synthesize

knowledge about these plants. We have treated tomatoes in the large genus *Solanum*, rather than as the segregate genus *Lycopersicon*, based on a weight of evidence coming largely, but not exclusively, from studies of DNA sequences. In the past decade, several molecular phylogenetic studies of the Solanaceae have unambiguously showed tomatoes to be deeply nested within *Solanum* (Spooner et al., 1993; Bohs and Olmstead, 1997, 1999; Olmstead and Palmer, 1997; Olmstead and al., 1999; Peralta and Spooner, 2001; Bohs, 2005; Spooner et al., 2005). We propose a phylogenetic classification philosophy that simply states the hypothesis that tomatoes may have more "predictivity" under *Solanum*, and also apply a Linnaean nomenclatural system (hierarchical) to provide the valid names of wild species under *Solanum* and their equivalents in *Lycopersicon* for ease of comparison to the literature (Table 1).

Based on morphological characters, phylogenetic relationships, and geographic distribution, we proposed the segregation of four species within the highly polymorphic green-fruited species *S. peruvianum* sensu lato (sensu lato refers to a broad concept of a species): *S. arcanum*, *S. huaylasense*, *S. peruvianum*, and *S. corneliomulleri*. The first two have been described as new species (Peralta et al., 2005) from Perú, while the latter two had already been named by Linnaeus (1753) and MacBride (1962) respectively. We recognize yet another new yellow- to orange-fruited species, *S. galapagense*, segregated from *S. cheesmaniae*; both are endemic to the Galápagos Islands (Darwin et al., 2003; Knapp and Darwin, in press). In total, we recognize 13 species of wild tomatoes, including the cultivated tomato (*Solanum lycopersicum*) and its weedy escaped forms that are distributed worldwide (Table 1). This is an increase from the nine species of tomatoes traditionally recognized (Rick et al., 1990). We are treating these 13 species, in addition to four closely related species (*S. juglandifolium*, *S. lycopersicoides*, *S. ochranthum*, *S. sitiens*), in the taxonomic series *Systematic Botany Monographs* (Peralta et al., in press).

### **Cultivated tomatoes and the history of their scientific naming**

Tomatoes were introduced into Europe from the Americas and became known to botanists about the middle of the sixteenth century, thus the scientific naming of tomatoes, including wild species, is linked to concepts of diversity in *Solanum lycopersicum*, the cultivated species. Pietro Andrea Matthioli (1544) described tomatoes for the first time with the common name "Pomi d'oro" (Golden Apples) in the first edition (written in Italian) of his 'Commentary' upon the work of the 1st century Greek botanist Dioscorides of Anazarbos. In the Latin edition, Matthioli (1554) referred to tomatoes as "Mala aurea" (the Latin equivalent of Golden Apple). Matthioli greatly enriched the tomato description with Italian traditional knowledge and uses of plants previously not known in Europe, and many editions of Matthioli's work were translated in different languages throughout Europe (Watson, 1989). Other early herbalists referred to the tomato as "mala peruviana" or "pommi del Peru" (Peruvian Apples), "pomi d'oro", "mala aurea", "poma aurea", pomme d'Amour, "pomum amoris" or often used polynomial names like *Poma amoris fructu luteo* or *Poma amoris fructu rubro*. Some of these common names like "pomum amoris" were also used for eggplants (*S. melongena*) and "mala peruviana" was used for a species of another solanaceous genus, *Datura* (Jimson weed or thorn apple). Different names in different languages were used to name tomatoes in the time before standardized scientific naming. Pre-Linnaean botanists usually used polynomial, or phrase, names, consisting of several words describing the plant itself and distinguishing it from all others. They did not employ today's genus and species concepts, but did seek to name plants in a way that reflected their affinities. Interestingly, early botanists recognized the close relationship of tomatoes with the genus *Solanum*, and commonly referred to them as *S. pomiferum* (Luckwill, 1943). Tournefort (1694) was the first to name cultivated tomatoes as *Lycopersicon* ("wolf peach" in Greek). Tournefort placed

forms with large multilocular fruits in the set of plants he called *Lycopersicon*, but kept the plants with bilocular fruits as *Solanum*. Linnaeus (1753) began to consistently use Latin binomials in *Species Plantarum*, as polynomials were becoming too complicated and difficult to memorize. He classified tomatoes in the genus *Solanum* and described *S. lycopersicum* (the cultivated tomato) and *S. peruvianum*. The very next year Miller (1754) followed Tournefort (1694) and formally described the genus *Lycopersicon*. Miller did not approve of Linnaeus's binomial system, and he continued to use polynomial phrase names for all plants until 1768 (Miller, 1768). Miller's circumscription of the genus *Lycopersicon* also included potatoes as "*Lycopersicon radice tuberosa, esculentum*" supported by the argument that "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 established 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."

Later, Miller (1768) began to use Linnaeus' binomial system and published descriptions under *Lycopersicon* for several species, among them were *L. esculentum*, *L. peruvianum*, *L. pimpinellifolium* and *L. tuberosum* (potatoes). In the posthumously published edition of *The gardener's and botanist's dictionary* (Miller, 1807) the editor, Thomas Martyn, followed Linnaeus and merged *Lycopersicon* back into *Solanum*. Following Miller's early work, a number of classical and modern authors recognized tomatoes under *Lycopersicon*, but other taxonomists included tomatoes in *Solanum*.

Today, based on evidence from phylogenetic studies using DNA sequences and more in-depth studies of plant morphology and distribution, there is general acceptance of the treatment of tomatoes in the genus *Solanum* by both taxonomists and breeders alike. For example, the use of *Solanum* names has gained wide acceptance by the breeding and genomics community such as the Solanaceae Genomics Network (SGN) and the International SOL Project (<http://www.sgn.cornell.edu/>). These names in *Solanum* are being incorporated in germplasm bank databases as in the C.M. Rick Tomato Genetic Resources Center (<http://tgrc.ucdavis.edu/>).

In conclusion, the generic status of tomatoes has been in flux since the eighteenth century, reflecting two main and often competing goals in taxonomy, that of 1) predictive natural classifications (treatment in *Solanum*) and 2) the maintenance of nomenclatural stability (treatment in *Lycopersicon*). The economic importance of tomatoes has stimulated discussion within the scientific community of taxonomists and breeders about the relative value of classifications that emphasize predictivity versus stability (Peralta and Spooner, 2000; Spooner et al., 2003).

### Hypotheses of cultivated tomato domestication

Tomatoes were domesticated in America and two competing hypotheses have been advanced for the original place of domestication. Alfonse De Candolle (1886) used linguistic evidence like the names "mala peruviana" or "Pommi del Peru" (Peruvian apples) to suggest a Peruvian origin. He also considered the cherry tomato 'cerasiforme' types as the ancestor of the crop that spread worldwide, but recent genetic investigations have shown that the plants known as 'cerasiforme' are a mixture of wild and cultivated tomatoes rather than being "ancestral" to the cultivars (Nesbitt and Tanksley, 2002).

The Mexican hypothesis was advanced by Jenkins (1948), who also used linguistic evidence, but it is not clear that the plant cited as "tomatl" from Mexico referred to the true tomatoes or a native *Physalis* species ("tomate" or "tomatillo" is the common name in Mexico for *Physalis philadelphica*, the husk tomato, while "jitomate" refers to cultivars with large fruits of *Solanum lycopersicum*). Jenkins (1948) agreed with DeCandolle (1886) that *S. lycopersicum* from South America was the progenitor

of the European domesticated cultivars, but disagreed with the place of domestication in Peru. We consider the question of the original site of domestication of cultivated tomato to be unsolved (Peralta and Spooner, in press).

### Nomenclature of cultivated tomato

Regardless of where tomatoes were first domesticated, human beings have created a huge array of morphologically different cultivars and forms from the single species *S. lycopersicum* using traditional techniques of plant breeding. Some taxonomists (e.g. Brezhnev, 1958) have attempted to treat this diversity using the ICBN, and have created an enormously complex and almost unworkable nomenclature for wild and cultivated species that is neither predictive nor stable.

For tomato cultivars, we support a taxonomy under the Code of Nomenclature for Cultivated Plants (ICNCP; Brickell et al., 2004), which provides a framework more appropriate to name the great diversity of cultivated tomatoes, all members of the single biological species *S. lycopersicum*, generated by breeding. This taxonomy has yet to be developed on a global scale, but would be useful to standardize the naming and exchange of the wide variety of tomato cultivars in use today.

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**TABLE 1. Species list for tomatoes and their wild relatives (with equivalents in the previously recognized genus *Lycopersicon*, now part of a monophyletic *Solanum*), and with their fruit color and breeding system.**

Name in Peralta et al. in press	<i>Lycopersicon</i> equivalent	Fruit color	Breeding system <sup>1</sup>
<i>Solanum lycopersicoides</i> Dunal	<i>Lycopersicon lycopersicoides</i> (Dunal in DC.) A. Child ex J.M.H. Shaw	Green-yellow when maturing, black when ripe	SI, allogamous
<i>Solanum sitiens</i> I.M. Johnst.	<i>Lycopersicon sitiens</i> (I.M. Johnst.) J.M.H. Shaw	Green-yellow when maturing, black when ripe	SI, allogamous
<i>Solanum juglandifolium</i> Dunal	<i>Lycopersicon ochranthum</i> (Dunal) J.M.H. Shaw	Green to yellow-green	SI, allogamous
<i>Solanum ochranthum</i> Dunal	<i>Lycopersicon juglandifolium</i> (Dunal) J.M.H. Shaw	Green to yellow-green	SI, allogamous
<i>Solanum pennellii</i> Correll	<i>Lycopersicon pennellii</i> (Correll) D'Arcy	Green	Usually SI, some SC in S of species range
<i>Solanum habrochaites</i> S. Knapp and D.M. Spooner	<i>Lycopersicon hirsutum</i> Dunal	Green with darker green stripes	Typically SI, 1-2 collections SC, but with later inbreeding depression
<i>Solanum chilense</i> (Dunal) Reiche	<i>Lycopersicon chilense</i> Dunal	Green to whitish green with purple stripes	SI, allogamous
<i>Solanum huaylasense</i> Peralta and S. Knapp	Part of <i>Lycopersicon peruvianum</i> (L.) Miller	Typically green with dark green stripes	Typically SI, allogamous,
<i>Solanum peruvianum</i> L.	<i>Lycopersicon peruvianum</i> (L.) Miller	Typically green to greenish-white, sometimes flushed with purple	Typically SI, allogamous,
<i>Solanum corneliomuelleri</i> J.F. Macbr. (1 geographic race: Misti nr. Arequipa)	Part of <i>Lycopersicon peruvianum</i> (L.) Miller; also known as <i>L. glandulosum</i> C.F. Müll.	Typically green with dark green or purple stripes, sometimes flushed with purple	Typically SI, allogamous,
<i>Solanum arcanum</i> Peralta (4 geographic races: 'humifusum', lomas, Marañon, Chotano-Yamaluc)	Part of <i>Lycopersicon peruvianum</i> (L.) Miller	Typically green with dark green stripes	Typically SI, allogamous, rare pop SC, autogamous, facultative allogamous

<i>Solanum chmeilewskii</i> (C.M. Rick, Kesicki, Fobes and M. Holle) D.M. Spooner, G.J. Anderson and R.K. Jansen	<i>Lycopersicon chmeilewskii</i> C.M. Rick, Kesicki, Fobes and M. Holle	Typically green with dark green stripes	SC, facultative allogamous
<i>Solanum neorickii</i> D.M. Spooner, G.J. Anderson and R.K. Jansen	<i>Lycopersicon parviflorum</i> C.M. Rick, Kesicki, Fobes and M. Holle	Typically green with dark green stripes	SC, highly autogamous
<i>Solanum</i> <i>pimpinellifolium</i> L.	<i>Lycopersicon</i> <i>pimpinellifolium</i> (L.) Miller	Red	SC, autogamous, facultative allogamous
<i>Solanum lycopersicum</i> L.	<i>Lycopersicon esculentum</i> Miller	Red	SC, autogamous, facultative allogamous
<i>Solanum cheesmaniae</i> (L. Riley) Fosberg	<i>Lycopersicon cheesmaniae</i> L. Riley	Yellow, orange	SC, exclusively autogamous
<i>Solanum galapagense</i> S.C. Darwin and Peralta	Part of <i>Lycopersicon</i> <i>cheesmaniae</i> L. Riley	Yellow, orange	SC, exclusively autogamous

<sup>1</sup>SI = Self-incompatible; SC = Self-compatible.

**Figure 1 (cover illustration).** The woodcut of "*Poma aurea*" or "Goldapffel" (*Solanum lycopersicum*) from Matthioli (1586), a German edition edited not by Matthioli, but by the German herbalist Joachim Camerarius. This copy has been hand-colored, but the flowers were left unpainted, presumably because their color was not known. Reproduced with permission of the Natural History Museum Botany Library.