Tracing Tomato Timelines: The Domestication of *Solanum lycopersicum*

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Writer's Comment: As a kid, I loved gardening with my dad. While we rotated through various squash and herbs every year, the one plant that could always be found in our backyard garden bed was the tomato. Fast forward to this past year when I had the honor of working in Distinguished Professor Dr. Venkatesan Sundaresan's lab, studying methods of clonal asexual reproduction in tomatoes. Then, the perfect opportunity for me to build on my tomato knowledge presented itself in the form of the PLB 143 term paper, where Distinguished Professor Dr. Paul Gepts challenged students to dive into the history of the evolution of a crop of choice— and mine was quite obvious. As is with many subjects, looking back in history can guide future research and discoveries while building a better understanding of processes all around us. I hope that this paper not only captures my passion for agriculture but also highlights my fascination with tracing various forms of evidence to recreate an evolutionary timeline.

Instructor's Comment: Why is a course dealing primarily with evolutionary and historic events that affected our crops still relevant in our contemporary societies? Because these events generally have long-term consequences related to environmental adaptation (think global climate change) and geographic distribution of our crops and their wild ancestors (think ownership of biocultural diversity). Samantha's excellent paper on the origin of tomato provides an first-class example of the types of evidence used to trace back the dissemination and center of domestication of tomato in the Americas and its human-mediated dispersal to other continents, especially Europe. In the case of tomato, an ingenious combination of botanical, historical, and linguistic information sheds light on the evolutionary and anthropic selection and dissemination steps that have made tomato, the all-important, world-wide vegetable crop it is today. For example, did you know that tomato – a

mainstay of Italian cuisine - appeared in Europe only in the 16th century after Columbus' voyages? Well, you definitely have to read Samantha's paper!

—Paul Gepts, Department of Plant Sciences

Abstract

Solanum lycopersicum, the tomato plant, is the second most important vegetable crop in the world. Cultivated for its fruit, the globally grown crop is believed to have originated in Mesoamerica or South America. While early researchers theorized a linear domestication path based on botanical evidence, new research has revealed potential de-domestication events before reaching the modern fruit we know today. Historical evidence such as references to tomatoes in European herbals and Spanish journals allow us to trace the spread of tomatoes across the globe. Moreover, linguistic studies show a Nahuatl origin before the Spaniards brought the tomato to Europe, which led to its expansion. Despite the lack of archaeological evidence, genetic studies have greatly elucidated the tomato's center of origin and have painted a picture of the movement of the tomato's wild ancestor to the plump fruit harvested all across the world. An analysis of the existing research on *S. lycopersicum* allows us to trace its evolution from the New World to the Old World, and back.

Introduction

With over 100 million tons of fresh fruit production annually, the tomato plays a significant role not only in worldwide diets but also in budding agricultural research (Food and Agriculture Organization). Scientifically named *Solanum lycopersicum*, the tomato offers high levels of nutrients through a plethora of cuisines and preparations. Despite the vegetable-like uses of tomatoes, it is classified as a fruit and, more specifically, a berry (Bjarnadottir 2019). It belongs to the nightshade or *Solanaceae* family, along with other vegetable crops such as potatoes, eggplants, and bell

peppers (Costa and Heuvelink 2018). Tomatoes make up nearly 20% of all vegetable crop consumption, and with a growing list of over 10,000 cultivars, the tomato is grown in large quantities all across the globe (Reimers and Keast 2016, Moore 2021). While they are often eaten fresh, the majority of tomatoes are processed into canned tomatoes or tomato paste, which opens up a larger variety of uses for the fruit.

Water makes up 95% of a tomato, with carbohydrates and fibers making up the remaining 5%. Even still, the tomato remains an excellent source of vitamins and minerals that contribute to blood pressure control, bone health, tissue growth, and cell function, among other things. Tomatoes are also the main source of the antioxidant lycopene, which has been found to protect important biomolecules from damage and degradation and promotes cell communication (Bjarnadottir 2019). Recent studies have found that lycopene plays a big role against Alzheimer's and cardiovascular diseases, and also shows some anticancer activity (Kumar *et al.* 2017).

While there are biennial and perennial tomatoes, *S. lycopersicum* is typically grown as an annual crop (OECD 2017). Its growth and ripening following flower fertilization are typically accompanied by a color change from green to red fruit, but color variations of tomatoes exist within different cultivars. Ripening of tomato fruit is regulated through ethylene production, which has recently been manipulated to de-green tomatoes that are harvested too early (Quinet *et al* 2019). Other relatively new tomato-related technologies include the use of artificial intelligence to manage greenhouse conditions, the breeding of tomatoes to increase pest resistance, and the use of plant growth-promoting rhizobacteria to promote stress tolerance and crop yield (Nyaku and Danquah 2019).

China is the leading producer of fresh tomatoes, followed by India, Turkey, and then the United States; these four countries accounted for around 60% of worldwide tomato production in 2017, totaling over 170 million tons worth tens of billions of

dollars (Nag 2020). In 2020, world tomato production exceeded 180 million tons, with China producing about 35% of the fresh fruit (Branthome 2022). Within the United States, California is the leader in processing tomato production, while Florida is the leader in fresh tomato production; the U.S. produces over $2 billion worth of commercial tomatoes annually (Reimers and Keast 2019).

Tomatoes have an unmistakable influence on cuisines all around the world. With its acidic, sweet, and umami flavors, we can observe the use of tomatoes in the grilled kebabs of the Middle East and simple egg and tomato stir-frys in Southeast Asia. Despite their early misclassification as poisonous in Europe, we also see tomatoes in Italian pasta and pizza sauces, French dishes like ratatouille, and refreshing Greek salads (Smith 2013). Spaniards, who are credited with introducing tomatoes to Europe, use tomatoes in dishes like paella. Following British colonization, Indian recipes began including tomatoes, leading to dishes like butter chicken and other curries (Authentica World Cuisine, Kanjilal 2021). And long before the cultivation of the modern tomatoes we are familiar with, the Aztecs prepared a salsa-like mixture of tomatoes, chilies, and squash seeds (Cutler 1998).

Tomatoes have recently been employed as a focus for genetic, fruit development, pest and disease resistance, and evolution research. It is regarded as the cornerstone for genetic research on all crops within the *Solanaceae* family, and acts as a model for fleshy fruit development and biology (Lin *et al* 2014). However, human breeding of tomatoes has affected the ability of researchers to trace the genetic history of tomatoes. Crosses with distantly related relatives during tomato domestication have led to introgressions that can mask the true genetic identity of the crop (Razifard *et al* 2020). This unintended side effect of tomato domestication means researchers cannot dismiss other forms of evidence in order to better understand the tomato's origins.

Results and Discussion

This composition will analyze three types of evidence—historical, linguistic, and botanical—to trace the history of tomato domestication and evolution. A literature review of current knowledge regarding the tomato will allow us to better understand its origins.

Historical Evidence

European herbalists began to take note of the tomato in their writings in the 1500s when the tomato was introduced to Europe. Despite the common agreement that tomatoes were introduced to Europe by the Spaniards, the timing of Spanish conquests makes it difficult to pinpoint where the Spaniards obtained the fruits. Between the capture of Mexico City in 1521 and the Peruvian conquest in 1531, either location could have been the Spaniards' source of tomatoes (Labate *et al* 2007). While previous names such as "Mala peruviana" and "Pomi del Peru" suggested a Peruvian origin, other scientists such as Alexander von Humboldt believed cultivation began in Mexico (Jenkins 1948). Pietro Andrea Matthioli, the first Italian to write about the tomato in 1544, described it as another species within the mandrake family, comparing the fruit to an apple and its preparation to an eggplant (Jenkins 1948). He explained that, in Italy, the tomato was prepared with salt and pepper, and fried in oil (OECD 2017, Jenkins 1948).

John Gerard was the first botanist to write about the tomato in England (OECD 2017). He explained that this plant grows in hot environments like Italy and Spain, where he was able to retrieve some seeds for his own garden. In his herbal, Gerard describes both yellow and red fruit. Curiously, one particular excerpt from his writing stands out: "… I have in the hottest time of Summer cut away the superfluous branches from the mother root, and cast them carelesly in the allies of my Garden, the which (notwithstanding the extreme heate of the Sun, the hardnesse of the trodden allies, and at that time when no rain at all did fal) have growne as fresh

where I cast them, as before I did cut them off…" (Gerard 1636, pp. 346). This line seems to speak about the adaptability of the tomato and bears a striking resemblance to the Dump Heap theory posited much later on by Edgar Anderson in 1952. Anderson posits that the disposal of food waste could have supported the survival of plants that grow to be adapted to highly disturbed areas; these dump heaps could have been the origin of domestication for some plants (Anderson 1952). Perhaps the "weedy" abilities of Gerard's tomatoes offer a connection to wild ancestors, like early *S. lycopersicum* varieties in Mexico that regressed wild traits and weed-like capabilities in order to better adapt to new environments (which will be detailed in *Botanical Evidence*).

Subsequent evidence of tomatoes in the 17th and 18th centuries suggests that they were domesticated as ornamentals (OECD 2017). Strangely, despite the previous understanding that tomatoes could be eaten, they were widely feared by the public and believed for a period of time to be poisonous. In the late 18th century, the tomato was nicknamed the "poison apple"; they were considered exotic fruits and mostly eaten by upper-class Europeans, who could afford pewter tableware (Smith 2013). Unfortunately, the acidity of the tomatoes leached lead from pewter plates, causing an increase in deaths due to lead poisoning (Crang *et al* 2018). As a result, the tomato was blamed for the deaths.

Also in the 18th century, the tomato made its way (back) to North America. William Salmon reported the tomato as an ornamental plant in 1710 as it arrived in commercial harbors on the East Coast, but it continued to take on a notorious reputation. Due to its classification within the *Solanaceae* family, also known as the nightshade family, tomatoes were believed to carry the same toxins as deadly nightshades. These myths were finally debunked in the 1800s when a New Jersey resident ate a tomato on the Salem courthouse steps (Rick 1978). Subsequent Italian cultivars of tomatoes began to make their way to the United States, followed by the breeding of new varieties for commercial sale and an increase in knowledge regarding the incredible nutritional value of tomatoes.

Despite its tropical origins, the tomato is now widely grown across the globe, mostly in temperate regions (OECD 2017).

Linguistic Evidence

In 1532, following Spanish colonization in the New World, Bernardo de Sahagun wrote about the tomato and its origin in Nahuatl language. The Aztecs referred to the fruit as "*tomatl*," which comes from the roots "tom," meaning plump or swollen, and "atl," meaning water (Davis 2015, Veschi 2020). When the Spanish brought the New World tomato to the Old World, they referred to the fruit as "*tomate*". It is important to mention that there has been no discovery of any South American Indian word for tomato, which points towards Central or North American origins (Jenkins 1948).

When tomatoes arrived in Europe, the Italian naturalist Pietro Matthioli referred to the tomato as "*Pomi d'oro*" which is still used as the common Italian word for tomato today, pomodoro. In Matthioli's original reference, the tomato is described to be yellow, which likely inspired the name "*Pomi d'oro*," or "apple of gold" (Jenkins 1948). The Flemish botanist Rembert Dodoens wrote in his herbal, Cruijdeboeck, in 1554 several names referring to the tomato, including "Apples of love" and its French equivalent, "*Pommes d'amours*"- inspired by Matthioli's Italian name for the plant (Davis 2015).

In 1561, Italian botanist Luigi Anguillara's *Semplici* suggested that "Lycopersico" and "Pomi d'oro" were synonymous for the tomato. One significant record refers to the tomato as "tomato from Themistitan," which refers to Tenochtitlan- the Aztec capital in ancient Mexico (Jenkins 1948). An account from 1590 by José de Acosta, a Spanish Jesuit missionary, in his *Historia natural y moral de las Indias* (Natural and Moral History of the Indies), describes *Lycopersicon esculentum* as a round and juicy berry, good for eating on its own or as a sauce (Acosta and Mignolo 2002).

During the 17th and 18th centuries, various scientists posited a variety of names for the tomato, including "Pomum de oro" and "Solanum pomiferum" (Jenkins 1948). However, in 1753, Linnaeus formally named the tomato *Solanum lycopersicum*. Around the same time, other botanists like Phillip Miller placed the tomato in its own genus, *Lycopersicon* (from Greek "wolf-peach"), calling the tomato *Lycopersicum esculentum* (Labate et al 2007). Despite these arguments, *S. lycopersicum* remains the most used scientific name today (Labate *et al* 2007).

Botanical Evidence

Based on the variety of wild tomato fruit sizes found, it was once believed that the original tomatoes featured a small, blueberry-sized fruit. These ancestral tomatoes were bred roughly 7,000 years ago to produce a medium, cherry-sized fruit, then bred to the larger tomatoes we consume today (Pankau 2020). Typically—and certainly in the case of the tomato—an increase in fruit size is a desired trait, and therefore the evolutionary growth from a small blueberry-sized tomato to a medium cherry-sized tomato to a modern tomato is reasonable. Even in more recent journal articles from 2008, 2012, and 2014, it was posited that the ancestor of our modern tomato is *Solanum pimpinellifolium* (SP), which bred into intermediate-sized *S. lycopersicum* var. *cerasiforme* (SLC), before reaching cultivated *S. lycopersicum* var. *lycopersicum* (SLL) (Ranc *et al* 2008, Blanca *et al* 2012, Lin *et al* 2014).

However, in a 2020 journal article, a research team utilized genomic evidence to trace the domestication history of the tomato. Razifard *et al* discovered that the pathway of domestication to our modern tomato was not as linear as previously perceived, and instead likely featured a regression of domesticated traits before the re-domestication to the tomato cultivars we see today. In particular, the journal article pinpoints the origins of SP to be in South America. They hypothesized a divergence of SLC from the South American SP around 78,000 years ago in nearby locations

such as Peru, Ecuador, and San Martin, as well as locations further north such as Mexico, Central America, and Northern South America. Interestingly, we see that the South American SLC has many of the favorable traits observed in the tomato domestication syndrome: thicker pericarps, lower dry weight, and lower levels of soluble solids and citric acid, among other characteristics. On the other hand, these traits were diminished in northern SLC groups, with smaller fruits, thinner pericarps, and higher levels of citric acid (Razifard *et al* 2020).

There appears to be an increasing consensus that SP originated in western South America and an expanding acceptance of theories similar to those of Razifard *et al* (OECD 2017, Pankau 2020). These blueberry-sized tomatoes were possibly never domesticated by humans, and modern tomatoes come from naturally diverged SLC groups (Razifard *et al* 2020). In having to adapt to different stresses as they spread northwards, these SLC groups lost some traits of the tomato domestication syndrome (Razifard and Caicedo 2020). The weedy nature of the crop comes into mind when we consider the different environments SLC had to grow into as it migrated, possibly along human migration routes or natural routes like birds or other animals (Pankau 2020). SLL groups, which are most closely related to northern SLC groups, were domesticated by residents of Central America and Southern Mexico—like the Aztecs—and subsequently carried over to Europe following the conquest of Mexico City (Estabrook 2015, Razifard and Caicedo 2020).

Recommended Lines of Future Research

Notably, there is a distinct lack of archaeological evidence regarding the tomato and its origins. Alphonse de Candolle discussed the tomato in his *Origin of Cultivated Plants* and its missing puzzle piece in his four types of evidence towards crop origins (Jenkins 1948). This is not to say archaeological evidence does not exist. Claims of tomato-like carvings on ceramic spindle

whorls have been made, although the florets depicted could also be in reference to other species such as the potato (Denham 2014). Future research may include finding ways to fill in this gap in knowledge, potentially through further excavations of Aztec sites to find remains that point to the possible domestication of the tomato.

Future research may also include a better understanding of how *S. lycopersicum* var. *cerasiforme* made its way north from the west coast of South America to Mexico and Central America. Similarly, it may be beneficial to understand the circumstances that lead to the regression of traits that differentiates SLC groups in South America and those in Mexico, Central America, and Northern South America (Razifard and Caicedo 2020). Another question that remains unanswered is why SLC diverged from *S. pimpinellifolium* in the first place. The emergence of traits similar to the modern domestication syndrome seems too coincidental to not be driven by human selection, but we must recall that SLC divergence seemingly occurred before human presence in the area. One possible explanation could be animal-driven selection, but overall the overlap of SLC traits with human preference remains a mysterious phenomenon (Razifard *et al* 2020)

An improved understanding of the domestication and evolutionary history of the tomato provides insight into the development of new varieties that can adapt to a changing world. As the viability and amount of agricultural land decreases, knowledge of origins and diversity becomes increasingly more valuable in order to cultivate sustainable crops. By piecing together the puzzle that is tomato evolution, we make connections between species and varieties that allow us to breed a more resilient and high-yield plant.

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