Sixteenth-century tomatoes in Europe: who saw them, what did they look like, and where did they come from?

Tinde van Andel[1,2,3], Rutger Vos[1], Ewout Michels[1,2], Anastasia Stefanaki[1,3]

[1] Naturalis Biodiversity Center, Leiden, the Netherlands.
[2] Institute for Biology, Leiden University, Leiden, the Netherlands.
[3] Biosystematics group, Wageningen University, Wageningen, the Netherlands

Corresponding Author:
Tinde van Andel
Darwinweg 2, 2333 CR Leiden, the Netherlands
Email address: tinde.vanandel@naturalis.nl

Abstract

Background. Soon after the Spanish conquest of the Americas, the first tomatoes were presented as curiosities to the European royals and drew the attention of sixteenth-century Italian naturalists. Despite of their scientific interest in this New World crop, most Renaissance botanists did not specify where these 'golden apples' or 'pomi d'oro' came from. The debate on the first European tomatoes and their origin is often hindered by erroneous dating, botanical misidentifications and inaccessible historical sources. The discovery of a tomato specimen in the sixteenth-century 'En Tibi herbarium' kept at Leiden, the Netherlands led to claims that its DNA would reveal the 'original' taste and pest resistance of early tomatoes.
Methods. Recent digitization efforts greatly facilitate research on historic botanical sources. Here we provide an overview of the ten remaining sixteenth-century tomato specimens, early descriptions and 13 illustrations. Several were never published before, revealing what these tomatoes looked like, who saw them, and where they came from.
Results. Our survey shows that the earliest tomatoes in Europe came in a much wider variety of colors, shapes and sizes than previously thought, with both simple and fasciated flowers, round and segmented fruits. Pietro Andrea Matthioli gave the first description of a tomato in 1544, and the oldest specimens were collected by Ulisse Aldrovandi and Francesco Petrollini in c. 1551 from plants grown in the Pisa botanical garden by their teacher Luca Ghini. The oldest illustrations were made in Germany in the early 1550s, but the Flemish Rembert Dodoens published the first image in 1553. The names of early tomatoes in contemporary manuscripts suggest both a Mexican and a Peruvian origin. The 'En Tibi' specimen was collected by Petrollini around Bologna in 1558 and thus is not the oldest extant tomato. Although only 1.2%

of its DNA was readable, recent molecular research shows that the En Tibi tomato was a fully domesticated, but quite heterozygous individual and genetically close to three Mexican and two Peruvian tomato landraces. Molecular research on the other sixteenth-century tomato specimens may reveal other patterns of genetic similarity and geographic origin. Clues on the 'historic' taste and pest resistance of the sixteenth-century tomatoes should not be searched in their degraded DNA, but rather in those landraces in Central and South America that are genetically close to them. The indigenous farmers growing these traditional varieties should be supported to conserve these heirloom varieties *in-situ*.

Introduction

Soon after Christopher Columbus' first voyage to the Americas, the first New World crops were taken to Europe as curiosities and presented to the royal courts (Pardo Tomás & López Terrada, 1993; Katz, 2009). Seeds of maize, marigold and chili peppers were planted in noblemen's gardens as exquisite novelties, where they attracted the interest of early sixteenth-century scholars (Daunay, Laterrot & Janick, 2007; Egmond, 2016). One of the American crops that travelled from indigenous gardens through the hands of Spanish colonizers to Iberian Kings was the tomato (*Solanum lycopersicum* L.). The Spanish conquistador Hernán Cortés is often said to be the first person to have transferred the tomato to Europe after seizing the Aztec city of Tenochtitlan (now Mexico City) in 1521 (Jenkins, 1948; Gentilcore, 2010). Decades later, the Franciscan friar Bernardino de Sahagún (c. 1577: 49) reported that the Aztecs cultivated a great variety of tomatoes of different sizes, shapes and colors. The Spanish later adopted their Nahuatl term *tomatl* as *tomate* (Long, 1995).

The port of Seville was the principal point of entry for products from the New World. Still, there is no record of the introduction of the tomato in this Spanish port, as plant transfers were rarely considered important enough to document (Long, 1995). Due to the many Italian merchants sailing under Portuguese and Spanish flags, these new exotic plants quickly reached Italy (Rotelli, 2018). Soon after the first tomato seeds sprouted in the gardens of Italian aristocrats in the 1540s, they became the object of study by Renaissance naturalists, who described and depicted these 'golden apples' with great interest (Daunay, Laterrot & Janick, 2007; Egmond, 2018). From an unknown aphrodisiac to an essential ingredient in national dishes, the subsequent European history of the tomato has been extensively studied (e.g., Sturtevant, 1919; McCue, 1952; Gentilcore, 2010; Metro-Roland, 2013).

Despite their scientific interest in this recently introduced crop, most sixteenth-century botanists did not specify where their tomatoes came from. An exception was the Venetian naturalist Pietro Antonio Michiel, who mentioned that the fruits were known as 'love apples' by some and as 'Peruvian apples' by others (De Toni, 1940). Although Jenkins (1948) classified the latter name as dubious, it gave rise to the alternative hypothesis that the first European tomatoes were brought from Peru, shortly after Francisco Pizarro's conquest of the Inca emperors in 1531 (Bailey, 1886; Peralta, Spooner & Knapp, 2008).

The geographic origin of tomato domestication has been debated for at least two centuries (Klee and Resende, 2020). Evidence for the 'South American theory' was provided early on by the discovery of wild relatives of tomato along the coastline between Ecuador and northern Chile (Jenkins, 1948; Peralta, Spooner & Knapp, 2008). Molecular studies have demonstrated a high genetic and morphological diversity of traditional tomato varieties on the eastern slopes of the Andes in Ecuador and Peru (Blanca et al., 2015; Knapp & Peralta, 2016). The current model for tomato domestication is that the small-fruited *Solanum lycopersicum* L. var. *cerasiforme* (Alef.)

Fosberg was developed from the red-fruited wild species *S. pimpinellifolium* L in South America. This 'pre-cultivar' spread northwards to Mesoamerica, where indigenous people further domesticated this pea-sized tomato into the very variable *S. lycopersicum* L. var. *lycopersicum* (Lin et al., 2014, Blanca et al. 2015; Klee & Resende, 2020). The exact time and place of domestication of the tomato are still not known with certainty for either Mexico, Ecuador or Peru (Bai & Lindhout, 2007), but there is a diminishing genetic diversity from Ecuador to Mexico (Lin et al. 2014; Blanca et al. 2015).

In 1989, Sergio Toresella, an expert on medieval herbals, examined a well-preserved tomato specimen in a sixteenth-century book herbarium kept at Naturalis Biodiversity Center in Leiden, the Netherlands. He claimed that this plant collection was made in Ferrara (Italy) between 1542 and 1544 and therefore was the oldest existing herbarium (Toresella, 1992). This meant that the anonymous Italian who contributed with 'En Tibi herbarium' had collected the earliest European tomato specimen (Houchin, 2010; Thijsse, 2012; Egmond, 2016). As such, the collector predated compatriots Pietro Andrea Matthioli, who described this 'new species of eggplant' in 1544, and naturalist Ulisse Aldrovandi, previously suggested to have collected the first specimen in 1551 (McCue, 1952; Peralta, Spooner &Knapp, 2008).

The Leiden specimen was also thought to be older than a tomato collection in Rome herbarium , dated pre-1553 (De Toni, 1910), which was attributed first to the painter Gherardo Cibo (Penzig, 1905) and later to the physician Francesco Petrollini (Chiovenda, 1909). The 'En Tibi tomato', however, with its simple flowers and round fruit, did not resemble the well-known sixteenth-century woodcut illustration of a tomato plant with double flowers and elongated, segmented fruits, claimed as typical for the early European tomatoes (Sturtevant, 1919; Daunay, Laterrot & Janick, 2007). This woodcut is often inaccurately attributed to Matthioli (e.g., Houchin, 2010), but was published eight years after his death by Camerarius in his commentaries on Matthioli, first in black and white (1586) and four years later in color (Camerarius, 1586: 821; 1590: 378). In the Aldrovandi manuscripts, kept at the University of Bologna, there is an undated list of seeds sent by Aldrovandi to Camerarius that mentions 'Pomum amoris flore rubro non compressum' (Aldrovandi manuscripts 136 VII, c. 26).

The finding of the 'oldest extant tomato' in the Netherlands led to claims in the popular media that the DNA of this 'primitive tomato' could reveal ancient resistance to pests and diseases lacking in modern crops. Moreover, the En Tibi tomato could help plant breeders develop new cultivars with the 'original taste' of the sixteenth-century tomatoes (Van Santen, 2012; De Boer, 2013). The genomic diversity stored in herbarium specimens creates ample opportunities for genome-scale population and domestication studies (Staats et al., 2013). Comparing the DNA of traditional crop specimens to the increasingly available online genetic information on crop accessions worldwide can also provide detailed information on geographic origins and historic migration routes of plants and people (van Andel et al., 2016; Larranaga, van Zonneveld &

Hormaza, 2021). Unfortunately, the sampling of historical collections has had limited success due to their highly degraded DNA, although significant progress is being made with new 'ancient genomics' methods (Bakker et al., 2020).

At the same time, ongoing digitization efforts greatly facilitate the research on sixteenth-century herbaria, illustrations, publications and manuscripts (Koning et al., 2008; Van Andel, 2017). However, the literature on early tomato descriptions and depictions often lacks detailed links to the original sources. The latter can now be directly inspected online and sometimes reveal other authors, editions, dates and species than previously thought. Our recent revision of the En Tibi herbarium uncovered that it was not made in Ferrara in 1542-3 as had been suggested, but in Bologna around 1558 by the Italian botanist Francesco Petrollini, who also made the so-called 'Erbario Cibo' kept in Rome (Stefanaki et al., 2018; 2019).

This paper aims to provide a more accurate overview of early sixteenth-century descriptions, illustrations and particularly herbarium specimens of the tomato. Some of the published sources have been digitally available for some years, but several images and most of the herbarium specimens have never been published so far. We show that the earliest tomatoes in Europe came in a variety of colors, shapes and sizes, and reveal that some 'early tomatoes' were, in fact, misidentified and represent other, related species. We compare these findings with recent molecular research on ancient DNA of the 'En Tibi' specimen (Michels, 2020), which sheds new light on this crop's historic migration routes from the Americas to Europe.

Materials & Methods

We performed a literature review, starting with studies on the introduction of the tomato in Europe (e.g., Jenkins, 1948. McCue, 1952, Daunay, Laterrot & Janick, 2007; Gentilcore, 2010) and on early modern naturalists in Italy, France, Central Europe and the Low Countries (e.g., De Toni, 1907, 1910, 1940; Findlen, 1994, 2017; Egmond, 2016, 2018, Rotelli, 2018.). We also reviewed modern taxonomic and molecular studies on the origin of the tomato (e.g., Peralta, Spooner & Knapp, 2008; Lin et al., 2014). We consequently traced the original sixteenth-century manuscripts cited in these works via online repositories (e.g., google books, the Biodiversity Heritage Library, https://www.europeana.eu).

We searched for tomato specimens in all known sixteenth-century herbaria by reviewing scientific studies on these historical collections (e.g., Kessler, 1870; Caruel, 1858; Camus & Penzig, 1885; Penzig, 1905; Speta & Grims, 1980; Soldano, 2000). Where available, we checked the published species lists, and otherwise the indices and specimens of these herbaria, for references to 'pomo', 'mala', 'lycopersicon', '*Lycopersicum*', '*Solanum*', etc. We approached several libraries and museums in Italy, France, Germany, Poland and Switzerland to request digital images of specimens and illustrations in manuscripts that had not yet been published. We provided links to digital sources of the historical specimens, literature, manuscripts and images

that we reviewed for this study. We listed the local and pre-Linnaean scientific names for tomatoes mentioned in the original published sources, manuscripts, and handwritten texts on botanical vouchers, illustrations or herbarium labels. We checked each historical specimen, description and depiction for visible or written evidence of different shapes, sizes and colors of flowers and fruits. We scrutinized all historical material for possible clues of the geographical origins of the tomatoes. Finally, we report recent molecular results on the genetic affinities of the sixteenth-century tomato specimen in the En Tibi herbarium.

Results

The first mention of a tomato (1544)

In 1544, the Italian physician and botanist Pietro Andrea Matthioli (1501-1578) was the first person to mention the tomato in Europe, in the first edition of his commentary in Italian on the famous classical herbal *De Materia Medica* by Pedanius Dioscorides (c. 60 AD), entitled: '*Di Pedacio Dioscoride Anazarbeo libri cinque della historia, et materia medicinale trodotti in lingua volgare Italiana*'. In his chapter on mandrake (*Mandragora*), he adds: "Another species [of eggplant, *Solanum melongena* L.] has been brought to Italy in our time, flattened like the mele rose [a type of apple] and segmented, green at first and when ripe of a golden color, which is eaten in the same manner [as the eggplant: fried in oil with salt and pepper, like mushrooms]" (Matthioli, 1544: 326). Matthioli's first publication is not available online, so we relied on the translation by McCue (1952). Unfortunately, there is no illustration. The second edition (Matthioli, 1548) had the same text and still did not mention any local name for the tomato. Matthioli's work became a bestseller, selling over 30,000 copies, and he constantly enlarged the book with augmented editions (Palmer, 1985). In 1554, Matthioli translated his commentary in Latin, expanding his text about the tomato, which he described after the eggplant: "Another species has already begun to be imported, flattened, round like apples, ribbed like melons, at first green, in some plants turning gold and in others red. They are colloquially called *pomi d'oro*, that is, *mala aurea*. Eaten in the same way [as eggplant with oil, salt and pepper, like mushrooms. That said by Hermolao (Matthioli, 1554: 479). The same text appears after the description of the *melanzane* (eggplant) in many of the later versions of his book, named *pomi d'oro* in the Italian and *mala aurea* in the Latin editions. Unfortunately, Matthioli has never produced or commissioned an image of a tomato during his life (Table 1).

But where did Matthioli see his first tomato? According to Ubriszy Savoia (1993), his (former) teacher Luca Ghini (c. 1490-1556) had obtained the seeds from the Venetian patrician and naturalist Pietro Antonio Michiel (1510-1576). Next to his house in Venice, Michiel cultivated numerous exotic plants from faraway places, including the Americas, the Near East and northern Africa. His objective was to spread these botanical novelties among his network, so he sent seeds and sprouts of plants to his friends (De Toni, 1940). Michiel was given the charge to curate the

Padua garden from 1551 to 1555 when Luigi Squalermo (1512-1570), better known as Anguillara, was prefect. Anguillara had followed Ghini's classes and worked in his teacher's private garden in Bologna, and in 1546 became the first prefect of the Padua garden (Minelli, 2010). In 1543, Anguillara assisted Ghini in amassing materials for the Pisa garden (Findlen, 2017), so it is more likely that Anguillara (and not Michiel) provided Ghini with tomato seeds, also because the Padua garden was founded in 1545 (Palmer, 1985), a year after Matthioli described the first European tomato. Michiel apparently started to expand his Venice garden upon his return from Padua in 1555 (De Toni, 1940).

Ghini taught medical botany in Pisa from 1544 to 1555, where he founded the first university botanical garden supported by the Grand Duke of Tuscany, Cosimo I de' Medici (De Toni, 1907). Cosimo attempted to import and acclimatize various American plants (Gentilcore, 2010), and Ghini enriched the garden with exotic species and taught his many pupils to press and dry botanical specimens between paper (Findlen, 2017). According to McCue (1952: 292), the Pisa garden catalogue manuscript from 1548 'does not include any plant identifiable as the tomato'. However, the inventory of this catalogue brought to light by De Toni (1907: 439) lists a plant named 'Thumatulum pomum vulgo dictum rubrum et luteum' (Table 1) and suggests that the catalogue with 620 species could have been started already in 1545.

Matthioli did not travel much after he reached his forties (from 1541 onwards) and simply sent lists of Dioscoridean plants that he had not yet seen or identified to his colleagues (Palmer, 1985). He often included the knowledge of his fellow scientists or local people in the many editions of his books without citing them (Arber, 1986). Ghini had sent many dried specimens to Matthioli, accompanied by written opinions on their identification (De Toni, 1907; Palmer, 1985). If Ghini had already planted his first tomato seeds in the Pisa garden in 1544 (Ubriszy Savoia, 1993), it was likely his description of the tomato that ended up in Matthioli's first edition of his Commentaries on Dioscorides in 1544.

The first tomato specimen (1551)

One of Ghini's best-known disciples was Ulisse Aldrovandi (1522-1605), who became famous for his 16-volume herbarium with over 4000 specimens kept at the botanical garden in Bologna. The tomato specimen is preserved in the first volume (Fig. 1A), which Aldrovandi started in 1551, and is therefore considered the oldest extant botanical voucher of this New World crop (Table 1). Aldrovandi left detailed records on where his specimens came from, but unfortunately for the tomato specimen, this information has not survived (Soldano 2000). Aldrovandi kept an extensive correspondence with other naturalists. From his letters, we know that around 1551, plants were sent to him by Michiel, then employed in the Padua botanical garden (Minelli, 2010), by Ghini from the Pisa garden (Ubriszy Savoia, 1993) and by his companion and guide in the field Francesco Petrollini (Soldano, 2000; Stefanaki et al., 2019).

Petrollini, whose birth and death dates remain unknown, also attended classes by Ghini and graduated in Bologna in 1551. Two of his tomato specimens have survived: one in his extensive work herbarium, which is known to have consisted of several book volumes by 1553 (De Toni, 1910) and is kept in the Bibliotheca Angelica in Rome, and one in the En Tibi herbarium (c. 1558) that was made on commission, possibly for the Habsburg emperor Ferdinand I (Stefanaki et al., 2019). The tomato specimen in the Rome herbarium has immature fruits. A separate fruit glued on top of the page, partly destroyed by insects, is an immature eggplant and belongs to another specimen (Fig. 1B). We know that Petrollini graduated two years before Aldrovandi and guided +him in his early steps in the field. It is, therefore, likely that he started his work herbarium earlier than Aldrovandi (De Toni, 2010), but the tomato appears only in the third volume. The tomato in the En Tibi herbarium is thus not the oldest preserved tomato specimen in the world, although it is the earliest surviving specimen with (the remains of) a mature fruit (Fig. 1C).

We traced 17 surviving sixteenth-century herbaria in Italy, Germany, France, Switzerland and the Netherlands (Supplementary Table 1), eight of which contain tomato specimens (Fig. 1A-J). The oldest herbarium was compiled by Michele Merini, also a pupil of Ghini, in the Pisa botanical garden between 1540-1545. His herbarium is not available online, but its contents were published by Chiovenda (1927), and it does not contain a tomato specimen. Another disciple of Ghini, Andrea Cesalpino, also made an herbarium in the Pisa garden between 1555-1563. Although he mentions the tomato in his *De plantis Libri XVI* (Cesalpino, 1583), there is no tomato among his vouchers (Caruel, 1858). The first herbaria made in France (by Jehan Girault in 1558) and the Low Countries (by Petrus Cadé in 1566, see Christenhusz, 2004) do not have a tomato specimen either. The second herbarium produced in France, that of the German botanist Leonhard Rauwolf, contains a tomato (Fig. 1D), but this specimen was collected during Rauwolf's field trip in northern Italy 1563 (Stefanaki et al., 2021). Tomato specimens are also included in the herbaria Estense (Ferrara, Italy), Bauhin (three specimens; Basel, Switzerland), Ratzenberger (Kassel, Germany) and the Herbarium Vivum of Hieronymus Harder (Ulm, Germany); all these collections have been compiled towards the end of the sixteenth century (Supplementary Table 1, Fig. 1A-J).

The first image of a tomato (1553)

Although the tomato was common in Mexico at the time of the Spanish conquest, no images of tomatoes made in the New World exist (Daunay, Laterrot & Janick, 2007). An uncolored woodcut illustration, published in 1553 in a Latin herbal by the Flemish doctor and botanist Rembert Dodoens, can be considered the first image of a tomato (Fig. 2A). A year later (Dodoens, 1554), he published a colored version of the same woodcut (Fig. 2B). Also known under his Latinized name Dodonaeus, Dodoens studied at several universities and travelled to France, Germany and Italy from 1535 to 1546, where he may have seen the tomato for the first

time. In 1548, he settled in Mechelen (currently Belgium), then a hotspot of sixteenth-century naturalists, who studied exotic plants in the gardens of local noblemen. In a later edition of his herbal, Dodoens (1583) acknowledged the people who supplied him with plants. One of them, Jean de Brancion, had a beautiful garden with many exotic species, obtained via his extensive international network (Egmond, 2010). In Aldrovandi's manuscripts, kept at the University of Bologna, there are several lists of seeds sent to De Brancion (Frati, Ghigi & Sorbelli, 1907), of which one, dated 10 January 1571, contains a 'Pomum pomiferum' listed just before the eggplant, indicated as 'Mala insane purpurea' (Aldrovandi manuscripts 136 V, c. 137v). Another possibility is that Dodoens obtained a tomato plant from the garden of the Antwerp apothecary Pieter van Coudenberghe, created in 1548 and containing more than 600 exotic plants (Vandewiele, 1993).

On 22 September 1553, in the same year that Dodoens published the first woodcut, two tomato plants were depicted by the Swiss naturalist Conrad Gesner (Table 1, Fig. 2C-D). Unfortunately, his *Historia Plantarum*, a beautiful collection with hundreds of colored plant illustrations, was never published. Gesner had travelled to Italy in 1544, where he met Ghini to admire his collections (Findlen, 2017), which provides us with a clue to where he may have obtained his tomato seeds. Later, Gesner (1561) wrote that the tomato was grown by Pieter van Coudenberghe in Antwerp (a possible source of Dodoens' tomato), by Vuoysselus in Breslau (now Poland) and in German gardens by Joachimus Kreichius in Torgau and in Nuremberg by George Oellinger. Apothecary Oellinger (Ollingerus) also had three drawings made by Samuel Quichelberg (1529-1567) of the different tomato varieties that he had planted (Fig. 2G-I). His vast collection of naturalist drawings, *Magnarum medicinae partium herbariae et zoographiae*, was finished in 1553 but never published until Lutze and Retzlaff (1949) printed a selection of his work.

In the meantime, from c. 1550 to his death in 1576, the Venetian nobleman Michiel worked on his garden inventory, finalized in a five-volume illustrated manuscript now held by the Marciana library in Venice (De Toni, 1940). Michiel attempted to describe all plants he knew, so the species that figure in his work may have grown in the Padua garden, in his own Venice estate, or they were sent to him as dried specimens (De Toni, 1940). The third volume (Libro Rosso I) features a description of the tomato (Table 1). When he started his manuscript, Michiel was still in Padua and may have seen the tomato there. The watercolor image in this manuscript is possibly made by Domenico Dalle Greche (Fig. 2F). Another drawing in Michiel's manuscript (Supplementary Fig. 1) was mentioned as one of the earliest portrayed tomatoes in Europe (Egmond, 2018), but the depicted plant has simple, lobed leaves and symmetrical, depressed and deeply furrowed fruits. We agree with De Toni's identification of this illustration as an Ethiopian eggplant (*Solanum aethiopicum* L.), probably a member of the kumba cultivar group (PROTA, 2015).

Another candidate for the earliest extant European drawing of the tomato is a watercolor image (Fig. 2E) in a manuscript by the German botanist Leonhart Fuchs, dated between 1549 and 1561 and known as the 'Vienna Codex' (Meyer, Trueblood & Heller, 1999; Baumann, Baumann & Baumann-Schleihauf, 2001). This manuscript was meant to become an extended version of his famous herbal *De historia stirpium commentarii insignes* (Fuchs, 1542), widely considered a masterpiece with 500 very accurate woodcut illustrations and the first known European publication of New World plants such as maize, tobacco, marigold and chili pepper (Meyer, Trueblood & Heller, 1999). The tomato, however, was not described in this famous herbal, nor in its later editions. It does appear in the Vienna Codex as a drawing (Fig. 2E) and in the text, which reported that this unfamiliar 'apple' was only known from gardens and that it was not mentioned by the ancient Greeks, Romans or even the Moors. The manuscript was never published, but Meyer, Trueblood & Heller (1999) suggested that the drawing may be earlier than the woodcut of Dodoens (1553).

In 1586, decades after the first tomato illustrations in the 1550s and eight years after Matthioli's death in 1578, an uncolored woodcut of a tomato plant (Fig. 2M) appeared in *De Plantis Epitome Utilissima*, an enlargement of Matthioli's work published in Latin by Joachim Camerarius (1586: 821). A colored version of the same woodcut (Fig. 2N) was published four years later, again by Camerarius, but this time in German (1590: 378), although this image is often attributed to Matthioli (e.g., Houchin, 2010).

The first names of tomatoes

In 1548, while Matthioli still has no name for the tomato, Grand Duke Cosimo I was presented some tomatoes from his Florentine Estate. A letter from 1548 mentions that the Florentine pomidoro arrived safely at the ducal household (Table 1). This letter is the earliest written evidence of the term 'golden apples' in Italian (Gentilcore, 2010). The Latin translation of this local name ('mala aurea') quickly follows in 1554, while Aldrovandi's name 'mali insani' refers to its resemblance to the botanically related eggplant or melanzana (Table 1). Other early sixteenth-century names of the tomato reveal that it came in different colors (red, golden, brown, yellow) or that it was related to the mandrake ('Mandragorae species').

The term 'pomum amoris' is often said to refer to the alleged aphrodisiac properties of the tomato (Smith, 1994). Still, the name could also be a corruption of 'pomi d'oro' (Peralta, Spooner & Knapp, 2008) or 'pome dei Moro' (apples of the Moors, Houchin 2010). Two years before Matthioli's first description of the unnamed tomato in 1544, the term 'Amoris poma' was already coined by Fuchs (1542: 532) in his description of the eggplant. Michiel also described the eggplant as 'Pomes da mouri da Galli, Melongena da Arabi', a fruit brought by the Moors or Arabs (De Toni, 1940). *Solanum melongena* L. was indeed introduced to Europe during the Middle Ages by Arab traders from India (Daunay, Laterrot & Janick, 2007).

The Spanish gave the name ‘love apple’ first to the Mexican tomatillo (*Physalis ixocarpa* Lam.), of which the calyx splits open to reveal the fruit, apparently reminding them of female genitals. Later the Spanish transferred this name to the tomato (Long, 1995). Although the Italians never adopted the Spanish name ‘tomate’, derived from the Nahuatl ‘tomatl’, the appearances of ‘*Thumatulum*’ in the inventory of the Pisa garden and ‘*Tumatle Americanorum*’ in Guilandinus (1572), successor of Anguillara in the Padua garden, suggest that some early modern botanists knew this name. However, the local term ‘poma’/‘pomo’ was more common (Table 1).

The name ‘Saliunca’ in the En Tibi herbarium was erroneously given to the tomato specimen, a mistake made by the scribe who wrote the plant names next to the specimens: the name was meant for the preceding specimen (nr. 293) of *Valeriana celtica* L. (Stefanaki et al., 2018). According to Ubriszy Savoia (1993: 581), Aldrovandi’s term ‘Tembul quibusd.’ (another type of Tembul) refers to *Solanum betaceum* Cav., the South American tree tomato, but this species was only introduced in European botanical gardens in 1836.

The remark that ‘some people knew the tomatoes as Peruvian apples’ was made both by Michiel (De Toni, 1940) and Anguillara (1561), which is not surprising as they were friends and worked as colleagues in the Padua garden from 1551 to 1555 (Minelli, 2010). Several other Andean plants figure in Michiel’s garden inventory (De Toni, 1940), such as coca (*Erythroxylum coca* Lam.) and ‘quina de India’ (probably *Cinchona* sp.). As Michiel never published his garden inventory, Anguillara (1561) was quoted for this South American provenance by Bauhin in his annotated edition of Matthioli’s commentaries (Bauhin 1598: 761, Table 1). According to Jenkins (1948), however, there is nothing in the historical record that suggests a Peruvian origin of the tomato. Gray & Trumbull (1883) assume that Anguillara mistook the tomato for *Datura stramonium* L., an American Solanaceae described as ‘mala peruviana’ by Guilandinus (1572). Despite his closeness to Ghini, there is no evidence that Anguillara made a herbarium, so no specimen of the ‘Poma del Peru’ exists. In the extensive collection of Aldrovandi’s manuscripts, however, there are many lists of objects (plants, animals, minerals) that he received from all over the world, including South American locations such as the Tumbes province in Peru, the Ecuadorian capital Quito, Cumana (Venezuela) and Uraba in Colombia (Frati, Ghigi & Sorbelli, 1907). Unfortunately, the catalogues have not yet been digitized, so we could not verify whether Aldrovandi received his tomato specimen directly from his contacts overseas and, if so, from which location. Guilandinus (1572) referred to the tomato as ‘tumatle’, using its Nahuatl name, and wrote that it came from ‘Themistithan’, according to Jenkins (1948) a corruption of Tenochtitlan, the Aztec name for what is now Mexico City. Aldrovandi also made a ‘Themistitani catalogus’ of natural objects received from this area, next to lists of specimens from other Mexican locations such as Iztapalapa, ‘Jucatan insula’ and Tlaxcala (Frati, Ghigi & Sorbelli, 1907: 181). Still, we do not know whether tomatoes are listed in these manuscripts.

The name ‘Ethiopian apple’ written next to the tomato specimen in the anonymous Ducale Estense herbarium (Fig. 1I, Table 1) refers to an African origin. This demonstrates the existing confusion between *Solanum lycopersicum* and the related Old-World species *S. aethiopicum*, also depicted in Michiels manuscript (Supplementary Fig. 1). Besides the tomato specimens, there are also three specimens of *S. aethiopicum* in Bauhins’ herbarium, one of which was named ‘poma amoris racemosa’ and possibly came from his own garden (Supplementary Fig. 2). The word ‘Ettiopia’ or ‘aethiopicum’ in those days did not refer to the current country of Ethiopia but was used as a general term to indicate the African continent (De Toni, 1940).

The name *Lycopersicon* means ‘wolf peach’, after the Greek words for wolf (lykos) and peach (persikon), and was first used by the Greek physician Galen (AD 131–200) for designating a plant from Egypt with malodorous sap, just like tomato leaves. Which species Galen had in mind while describing the wolf peach has been lost in centuries of translations and misinterpretations of the classical texts during the Middle Ages (Palmer, 1985). Galen had never seen any New World plant, but a major aim of the Renaissance naturalists was to search for plant specimens that matched descriptions by the classical authors (Palmer, 1985; Stefanaki et al., 2019). However, the German botanist Fuchs argued in his manuscript that as the Greek and Latin authors did not mention the tomato, the plant should not carry any of the classical names (Meyer, Trueblood & Heller, 1999). The Greek name was later Latinized to *Lycopersicum*, and the species epithet *esculentum* (edible) was added. Modern taxonomy has brought the tomato back to the genus *Solanum* (Peralta, Spooner & Knapp, 2008). Another attempt of sixteenth-century naturalists to trace the tomato in ancient literature led them to the ‘Glaucium’ of Dioscorides: De Lobel (1571, 1576), for example, described, not without doubts, the tomato under poppies.

The morphology of early tomatoes

The woodcut illustration of the elongated, segmented tomatoes by Camerarius (1586; 1590) became widely known, as Matthioli’s *Commentaries on Dioscorides* continued to be a bestseller after his death. However, the sixteenth-century herbarium specimens and the images of small spherical tomatoes in unpublished manuscripts remained locked up in royal treasure rooms, libraries, and universities. This has led to the idea that the earliest tomatoes introduced to Europe were ‘large and lumpy’, a ‘mutation’ from a smoother, more diminutive Mesoamerican form, and probably ‘the direct ancestor of some modern cultivated tomatoes’ (Smith, 1994:15). According to Sturtevant (1919), there were no indications that the round tomato was known among the early botanists before 1700.

From our review of the sixteenth-century descriptions, images and herbarium specimens, it becomes clear that different landraces of tomatoes were introduced early on in Europe. These represented a great variety in flower and fruit shape, size and color, as was already suggested by Daunay, Laterrot & Janick (2007) and Peralta, Spooner & Knapp (2008). Several tomato

449 illustrations (e.g., Camerarius, 1586) and specimens like those of Bauhin (Fig. 1E-G) show
450 duplications of sepals and petals, exserted styles and deeply furrowed (segmented) fruits, while
451 the specimens in the En Tibi and Rauwolf herbaria (Fig. 1C-D) and Oellinger's third drawing
452 (Fig. 2I) have simple flowers (5 petals) and small, spherical fruits (Table 2).
453
454 Although the drawing in Fuchs' manuscript (Vienna Codex, 1549-1556/1561) is often
455 considered 'unnatural' and 'false' (Koning et al. 2008; Meyer, Trueblood & Heller, 1999), the
456 task assigned to artist Albrecht Meyer was to represent the variation in flowers and fruits, instead
457 of depicting an individual plant. Fuchs wrote that he had seen at least three different varieties and
458 decided to include all in one illustration (Meyer, Trueblood & Heller, 1999: 629). Dominico
459 dalle Greche also included several fruit types in his drawing for Michiel (Fig. 2F). According to
460 McCue (1952), the reference by Cesalpino (1583) to the white color of the flowers was incorrect,
461 but Camerarius (1590) described and depicted white-colored flowers as well. The different
462 tomato names, 'aurea' (golden), 'rubrum' (red), 'luteum' (yellow) and 'croceum' (orange-
463 yellow, golden-yellow), also indicate that the fruits came in different colors.
464
465 Tomatoes underwent a dramatic increase in fruit size during domestication: some modern
466 cultivars produce fruit a thousand times larger than their wild counterparts (Lin et al., 2014).
467 Wild tomato species generally have flowers with five to six sepals, petals and stamens, and
468 bilocular fruits. Through a mutation known as fasciation, flowers will produce up to eight petals
469 and an increased number of locules, which leads to multisegmented, elongated fruits. Humans
470 probably selected fasciated tomatoes for their large fruits, but only a small portion of all modern
471 tomato cultivars is multilocular (Barrero & Tanksley, 2004). The fact that the first tomato
472 described in Europe was segmented (Matthioli, 1544, Table 2) proves that the early sixteenth-
473 century tomatoes did not come from wild plants but represented a crop that had reached a fairly
474 advanced stage of domestication (Bai & Lindhout, 2007).
475
476 Table 2 shows that most sixteenth-century specimens lack preserved fruits: juicy tomatoes
477 cannot be easily pressed into botanical vouchers. They are bulky and will not keep their shape
478 when pressed, and due to their moisture, the specimens will quickly start to mold. Petrollini's
479 first tomato specimen had only an immature fruit, but when preparing the tomato specimen in the
480 En Tibi herbarium, he skillfully removed the juicy insides of the tomato and pressed the skin of
481 the fruit to represent its round shape (Fig. 1C). Ratzenberger's fruits seem to have spoiled and
482 have been removed from the specimen (Fig. 1J). Harder found a solution: he pressed a flowering
483 specimen and drew the roots, ripe and golden fruits later on the paper (Fig. 1H).
484
485 **Genetic origin of the En Tibi tomato**
486
487 What was the geographical origin of the early tomatoes that sparked the interest of the
488 Renaissance botanists? The sixteenth-century literature, specimens and illustrations do not

answer this question. The Peruvian origin mentioned by Michiel and Anguillara is not specific, and apart from Guilandinus (1572), the other early sources do not discuss any geographical origin. The knowledge on tomatoes circulating in Europe during the sixteenth-century came from plants that were already cultivated in gardens, as is evident from the detailed morphological descriptions on fruit shape and color, characters that were only observable in live plants. The provenance from the obscure New World was not of interest to most sixteenth-century scholars, who tried hard to trace the tomato in the writings of ancient Greek authors. Regarding herbarium specimens, we only know that the Rauwolf tomato was collected somewhere in Northern Italy (Stefanaki et al., 2021), while Bauhin tomatoes were possibly cultivated in his garden in Basel.

The question of geographical origin may also be approached by genomic research on the crop's earliest herbarium specimens. Recently, DNA was extracted from a leaf of the tomato specimen in the En Tibi herbarium (c. 1558, Bologna, kept at Naturalis), and the genome was sequenced using the Illumina TruSeq platform (Michels, 2020). The En Tibi genome was mapped to the Heinz 1706 reference genome (The Tomato Genome Consortium, 2012), with an average sequencing depth of 2.28 (Michels, 2020). Only 9.9 Mbp were recovered with ≥10x depth, which equated to 1.2% of the reference genome. This indicated that the specimen's DNA had severely fragmented over the past 475 years. Data on genome assemblies of 114 accessions of wild species and traditional cultivars from Latin America were retrieved from the 360-tomato resequencing project (Lin et al. 2014) and cropped to span only the 1.2% of the sequenced En Tibi genome with sufficient coverage.

To identify the En Tibi tomato's nearest neighbors, Michels (2020) performed a network clustering analysis (NeighborNet, Bryant 2003). Dimensionality reduction analyses were carried out on the remaining SNPs to investigate coarse genetic similarity among the accessions. In Fig. 3, the lengths of the terminal branches are proportional to the number of autapomorphies, distinctive genetic features that are unique to each taxon. Wild populations are generally more genetically diverse (and thus have higher numbers of autapomorphies) than domesticated ones, because of the founder events of domestication and deliberate inbreeding. The highly diverse, wild *Solanum pimpinellifolium* accessions (dark green circles) spread out on the left (Fig. 3A). On the right, the En Tibi tomato clustered in the group of domesticated tomatoes (*S. lycopersicum*) from both Central and South America, with very short branches (Fig. 3B). The graph also shows that some accessions of the cherry tomato (*S. lycopersicum* var. *cerasiforme*) that once travelled from South to Mesoamerica are genetically close to the large-fruited domesticated tomato varieties on both parts of the continent. In contrats, other accessions of cherry tomatoes appear to be truly wild, given their long branches.

Table 3 shows the genetically close varieties to the En Tibi tomato, and some of the associated data stored for these accessions in the C.M. Rick Tomato Genetics Resource Center (TGRC, https://tgrc.ucdavis.edu) at the University of California at Davis, USA. While the three Mexican

accessions are characterized as ‘Latin American cultivars’ (probably landraces are meant here), the other three accessions are classified in the TGRC database as ‘wild’. However, C-61 was collected from a family garden and C-281 in open vegetation along a road in the (once) heavily forested eastern Andean foothills. Very little information from the farmers themselves is stored for the accessions close to the En Tibi tomato. B-249 is the only one with a vernacular name (Zocato, no language indicated), and B-153 was collected on a market but said to grow wild. For C-281, the sentence “Indian women: no word in Quechua” in the database suggests that the collector tried to obtain information from a local person, but communication was not possible. The presumably ‘wild state’ of some of the accessions close to the En Tibi tomato does not coincide with the molecular data, which show that the sixteenth-century tomato was a fully domesticated crop. Combined with the absence of farmers’ knowledge in the database, the information in the TGRC database on the domestication status of these accessions is questionable. Some of the nearest neighbors of the En Tibi tomato that were listed as ‘wild’ in the germplasm data may have escaped from cultivation. Compared to genuinely wild accessions, the branches of these presumably feralized ones are so short that they are very likely to have passed through domestication processes.

The accessions used in the 360-tomato resequencing project (Lin et al., 2014) reflect centuries of human migration and trade, which has caused extensive gene flow between tomato varieties. Although it is impossible to appoint the En Tibi as a direct ancestor of some modern tomato varieties, its direct ancestors likely came from Mesoamerica. Michels (2020) also found that the En Tibi tomato specimen was more heterozygous than all recently collected accessions from Mesoamerica sequenced by Lin et al. (2014), which had a narrower genetic background. This means that the sixteenth-century specimen was less inbred or domesticated than its current counterparts in Mexico. However, some South American domesticated tomatoes had even higher heterozygosity, perhaps due to gene flow between landraces and crop wild relatives (Michels, 2020).

Discussion

The genomic research on the En Tibi tomato does not provide a definite answer to the discussion on the locality of tomato domestication (Mexico vs Peru). As more than 98% of its genome could not be read, it is impossible to reconstruct complete gene sequences coding for taste or natural resistance to pest and diseases (Michels, 2020), despite anticipation of this earlier (Van Santen 2012, De Boer, 2013). To reconstruct the ‘original’ flavor, nutritional qualities and adaptations to the (a)biotic environment of sixteenth-century tomatoes lost through intensive breeding for yield in modern cultivars (Klee & Resende, 2020), research should focus on traditional landraces currently grown by small farmers in Central and South America that most resemble historic varieties.

The accessions sequenced by Lin et al. (2014) in the 360-tomato project were obtained from online genomic data, and germplasm institutes store very little information on exact localities or morphological, nutritional and agronomical qualities of these accessions or on the farmers that grow them. Moreover, this resequencing project did not capture the entire tomato diversity in the Americas. Increased sampling of landraces in the Andes and Mesoamerica is essential to fully characterize tomato diversity (Knapp & Peralta, 2016). With decreasing crop diversity and the social, economic and ecological challenges faced by small farmers of indigenous descent to preserve their traditional agricultural practices (Knapp & Peralta, 2016; Petropoulos, Barros & Ferreira, 2019), tracing the 'sisters' of the En Tibi tomato back to Mexican or Peruvian smallholders' gardens will be difficult. The landraces that were genetically close to the En Tibi tomato were collected between 36 and 52 years ago: they may have already disappeared from indigenous gardens and survive only as seeds in germplasm institutes.

Conclusions

The earliest tomatoes that reached Europe came in a wide variety of colors, shapes and sizes: with both simple and fasciated flowers, round and segmented fruits. The first description of a tomato was given by Matthioli in 1544, the oldest specimens were collected by Aldrovandi and Petrollini in c. 1551 in the Pisa botanical garden and the earliest illustrations were made in Germany and Flanders in the early 1550s. The names of early tomatoes in contemporary manuscripts suggest both a Mexican and a Peruvian origin. The 'En Tibi' specimen was collected by Petrollini around Bologna in 1558 and thus is not the oldest extant tomato. Although only 1.2% of its DNA was recovered, molecular research shows that the En Tibi tomato was a fully domesticated, quite heterozygotic and genetically close to three Mexican and two Peruvian tomato landraces.

Molecular research on the other sixteenth-century tomato specimens may reveal additional patterns of genetic similarity and geographic origin. Clues on the 'historic' taste and pest resistance of the sixteenth-century tomatoes should not be searched in their degraded DNA, but rather in those landraces in Central and South America that are genetically close to them. The indigenous farmers growing these traditional varieties should be supported to conserve these heirloom varieties *in-situ*.

Sequencing the ancient DNA of the other nine sixteenth-century tomato specimens highlighted in our paper may provide different but equally exciting snapshots of historic genetic variation. This may lead to different, similar-looking landraces in either South- or Mesoamerica. Further digitization, translation and online publication of Aldrovandi's manuscripts, archives of botanical gardens and correspondence between Renaissance naturalists will probably reveal more details on the first New World crops in Europe, their geographic origin and arrival date.

Acknowledgements

We would like to thank the staff of libraries and universities who provided us with digital images of specimens, illustrations, rare books and manuscripts: Adriano Soldano, Annalisa Managlia, Martina Caroli and Silvia Tebaldi of the University of Bologna (Aldrovandi herbarium), Gerda van Uffelen of the Hortus Botanicus Leiden and Izabela Korczyńska of the Jagiellonian library in Krakow (Libri Picturati), Gisela Glaeser of the Universitätsbibliothek der FAU Erlangen-Nürnberg (Oellinger and Gesner illustrations), Raffaella Alterio and Mario Setter, of the Biblioteca Angelica (Erbario B), Rome, Karien Lahaise, Naturalis library (literature), Jurriaan de Vos, University of Basel (Bauhin herbarium), the staff of the Archivio di Stato di Modena (Ducale Estense herbarium), the staff of Biblioteca Marciana, Venice and Alessandro Moro (Michiel's illustrations), Peter Mansfeld, Naturkundemuseum Kassel (Ratzenberger herbarium), Sophie Schrader, Bayerische Staatsbibliothek München (Harder herbarium), and Peter Prokop of the Österreichische Nationalbibliothek, Vienna (Fuchs illustration). DNA extraction was carried out by Barbara Gravendeel (Naturalis) and sequencing was carried out by Elio Schijlen (Wageningen University).

References

Anguillara LM. 1561. *Semplici, li quali in più parerei a diversi nobili huomini scritti Appaiono*. Venice: Vincenzo Valgrisi.

Arber A. 1986. *Herbals, their origins and evolution: A chapter in the history of botany, 1470–1670*. Cambridge: Cambridge University Press.

Bai Y, Lindhout P. 2007. Domestication and breeding of tomatoes: What have we gained and what can we gain in the future? *Annals of Botany* 100(5): 1085–1094. doi: https://doi.org/10.1093/aob/mcm150

Bailey LH. 1886. *Notes on tomatoes*. East Lansing: Agricultural College of Michigan.

Bakker FT, Antonelli A, Clarke JA, Cook JA, Edwards SV, Ericson PG, Faurby S, Ferrand N, Gelang M, Gillespie RG, Irestedt M, Lundin K, Larsson E, Matos-Maraví P, Müller J, Von Proschwitz T, Roderick GK, Schliep A, Wahlberg N, Wiedenhoeft J, Källersjö, M. 2020. The Global Museum: Natural history collections and the future of evolutionary science and public education. *PeerJ* 8: e8225. Doi: 10.7717/peerj.8225.

Barrero LS, Tanksley SD. 2004. Evaluating the genetic basis of multiple- locule fruit in a broad cross section of tomato cultivars. *Theoretical and Applied Genetics* 109: 669–679. Doi: 10.1007/s00122-004-1676-y.

Bauhin C. 1596. *Phytopinax, seu, Enumeratio plantarum ab herbariis nostro …… plantarum viuis iconibus*. Basel: Sebastianum Henricpetri. Available at https://www.biodiversitylibrary.org/item/30648#page/346/mode/1up

Bauhin C. 1598. *Petri Andrea Matthioli opera quae extant omnia*. Frankfurt: Nikolaus Basse. Available at https://play.google.com/books/reader?id=W99s3SJjLaAC&hl=en_GB&pg=GBS.PA760

Baumann B, Baumann H, Baumann-Schleihauf S. 2001. *Die Kräuterbuch–Handschrift des Leonhart Fuchs*. Stuttgart: Ulmer.

Blanca J, Montero-Pau J, Sauvage C, Bauchet G, Illa E, Díez MJ, Francis D, Causse M, Van der Knaap E, Cañizares J. 2015. Genomic variation in tomato, from wild ancestors to contemporary breeding accessions. *BMC genomics* 16(1): 1-19.

Bryant D. 2003. Neighbor-Net: an agglomerative method for the construction of phylogenetic networks. *Molecular Biology and Evolution* 21(2): 255–65. Doi: 10.1093/molbev/msh018.

Camerarius J. 1586. *De Plantis Epitome Utilissima*. Frankfurt am Main: Peter Fischer, Heinrich Dack. Available at https://archive.org/details/BIUSante_07755x01

Camerarius, J. 1590. *Kreutterbuch Desz Hochgelehrten vnnd weitberühmten Herrn D. Petri Andreae Matthioli: Jetzt widerumb mit viel schönen neuwen Figuren*…. Frankfurt am Main: Peter Fischer, Heinrich Dack. Available at: http://digital.ub.uni-duesseldorf.de/vester/content/titleinfo/4025416

Camus J, Penzig OAJ. 1885. *Illustrazione del ducale Erbario Estense conservato nel R. Archivio di Stato in Modena*. Modena: GT Vincenzi e nipoti.

Caruel T. 1858. *Illustratio in hortum siccum Andreae Caesalpini*. Florence: Le Monnier.

Cesalpino A. 1583. *De plantis Libri XVI*. Florence: Georgi Marescotti. Available at https://www.biodiversitylibrary.org/bibliography/60929#/summary

Chiovenda E. 1909. Francesco Petrollini, botanico del secolo XVI. *Annali di Botanica* 7: 339–447.

Chiovenda E. 1927. Un antichissimo erbario anonimo del Museo Botanico di Firenze. *Annali di Botanica* 17: 119–139.

Christenhusz MJ. 2004. The hortus siccus (1566) of Petrus Cadé: a description of the oldest known collection of dried plants made in the Low Countries. *Archives of Natural History* 31(1): 30-43.

Daunay MC, Laterrot H, Janick J. 2006. Iconography of the Solanaceae from Antiquity to the XVIIth century: A rich source of information. *Acta Horticulturae* 745: 59-88.

De Boer M. 2013. De smaak van een eeuwenoude tomaat. Naturalis Biodiversity Center: het maatschappelijk belang van biodiversiteit. *NRC Handelsblad Supplement* 7 September 2013: 4.

De Lobel M, Pena P. 1571. *Stirpium Adversaria Nova*. London: Thomas Purfoot. Available at https://bibdigital.rjb.csic.es/viewer/13064/?offset=#page=131&viewer=picture&o=search&n=0&q=amoris

De Lobel M. 1576. *Plantarum seu stirpium historia*. Antwerp: Christopher Plantin. Avaialble at https://bibdigital.rjb.csic.es/viewer/13070/?offset=#page=1&viewer=picture&o=ocr&n=0&q=amoris

De Sahagún B. c. 1577. *Historia general de las cosas de Nueva España por el fray Bernardino de Sahagún: el Códice Florentino. Libro X: del pueblo, sus virtudes y vicios, y otras naciones*. Florence: Mss. Biblioteca Medicea Laurenziana, Florence. Available at http://www.wdl.org/es/item/10621/#collection=florentine-codex.

De Toni GB. 1907. Spigolature Aldrovandiane. VI. Le piante dell'antico Orto Botanico di Pisa ai tempi di Luca Ghini. *Annali di Botanica Volume V* (3): 421-440.

688 De Toni GB. 1910. Spigolature Aldrovandiane IX. Nuovi documenti intorno Francesco
689 Petrollini, prima guida di Ulisse Aldrovandi nello studio delle piante. *Atti del Reale Istituto*
690 *Veneto di Scienze, Lettere ed Arti* 69: 815–825.
691 De Toni GB. 1940. *Michiel, Pietro Antonio. I cinque libri di piante. Codice Marciano, 1551-*
692 *1575*. Venice: Officine Grafiche Carlo Ferrari.
693 Dioscorides P. c. 60 AD. *De Materia Medica*.
694 Dodoens R. 1553. *De stirpium historia commentariorum imagines ad vivum expressae…*
695 Antwerp: Ioannis Loei. Available at
696 https://www.biodiversitylibrary.org/page/6726576#page/2/mode/1up
697 Dodoens R. 1583. *Stirpium Historiae Pemptades Sex sive Libri XXX*. Antwerp: Christopher
698 Plantin. Available at
699 https://bibdigital.rjb.csic.es/viewer/10942/?offset=#page=1&viewer=picture&o=search&n=0
700 &q=
701 Egmond F. 2010. *The world of Carolus Clusius: Natural history in the making, 1550–1610*.
702 London: Pickering & Chatto.
703 Egmond F. 2016. The garden of nature: visualizing botanical research in northern and southern
704 Europe in the 16th century. In: Ferdinand J, ed. *From art to science: Experiencing nature in*
705 *the European garden 1500-1700*. Treviso: ZeL Edizioni, 18-33.
706 Egmond F. 2018. European exchanges and communities. In: Curry A, Jardine N, Secord JA,
707 Spary EC, eds. *Worlds of Natural History*. Cambridge: Cambridge University Press, 78-93.
708 Findlen P. 1994. *Possessing nature: Museums, collecting, and scientific culture in Early Modern*
709 *Italy*. Berkeley: University of California Press.
710 Findlen P. 2017. The death of a naturalist: Knowledge and community in late Renaissance Italy.
711 In: Manning G, Klestinec C. *Professors, Physicians and Practices in the History of Medicine*.
712 Cham: Springer, 127-168.
713 Frati L, Ghigi A, Sorbelli A. 1907. *Catalogo dei manoscritti di Ulisse Aldrovandi*. Bologna:
714 Nicola Zanichelli, 127-168
715 Fuchs L. 1542. *De Historia Stirpium Commentarii insignes*. Basel: Officina Isingriniana.
716 Available at
717 https://bibdigital.rjb.csic.es/viewer/13865/?offset=#page=77&viewer=picture&o=bookmark&
718 n=0&q=
719 Gentilcore D. 2010. *Pomodoro! A history of the tomato in Italy*. New York: Columbia University
720 Press.
721 Gesner C. 1561. *In hoc volumine continentur ....De hortus Germaniae*. Argentorati: Iosias
722 Rihelius. Available at https://www.biodiversitylibrary.org/item/33559#page/1/mode/1up
723 Gray A, Trumbull JH. 1883. Review of De Candolle's origin of cultivated plants; with
724 annotations upon certain American species. *American Journal of Science* 3(148): 128-138.
725 Guilandinus M. 1572. *Papyrus, hoc est commentarius in tria C. Plinij maioris de papyro capita*.
726 Venice: Antonium Ulmum. Available at

https://play.google.com/store/books/details?id=Lq4vsSs34OkC&rdid=book-Lq4vsSs34OkC&rdot=1
Houchin R. 2010. Praten over tomaten: Introductie van tomaat (*Solanum lycopersicum* L.) in de Lage Landen. In: Bakels CC, Fennema K, Out W, Vermeeren C., eds. *Van planten en slakken*. Leiden, Sidestone Press, 81-102.
Jenkins, JA. 1948. The origin of the cultivated tomato. *Economic Botany 2*(4): 379-392.
Katz E. 2009. Chili pepper, from Mexico to Europe: Food, imaginary and cultural identity. In: Medina FX, Ávila R, De Garine, I. *Food, Imaginaries and Cultural Frontiers: Essays in honour of Helen Macbeth.* Guadalajara: Universidad de Guadalajara, 213-232.
Kessler HF. 1870. *Das älteste und erste Herbarium Deutschlands, im Jahre 1592 von Dr. Caspar Ratzenberger angelegt: gegenwärtig noch im Königlichen Museum zu Cassel befindlich*. Kassel: Freyschmidt. Available at http://mdz-nbn-resolving.de/urn:nbn:de:bvb:12-bsb11018583-2
Klee HJ, Resende Jr. MF. 2020. Plant domestication: Reconstructing the route to modern tomatoes. *Current Biology* 30(8): R359-R361.
Knapp S, Peralta IE. 2016. *The tomato (Solanum lycopersicum L., Solanaceae) and its botanical relatives*. London: Natural History Museum.
Koning J, van Uffelen G, Zemanek A, Zemanek B. 2008. *Drawn after nature: the complete botanical watercolours of the 16th-century Libri Picturati*. Leiden: Brill.
Larranaga N, Van Zonneveld M, Hormaza JI. 2021. Holocene land and sea-trade routes explain complex patterns of pre-Columbian crop dispersion. *New Phytologist* 229(3): 1768-1781.
Lin T, Zhu G, Zhang J, Xu X, Yu Q, Zheng Z, Zhang Z, Lun Y, Li S, Wang X, Huang Z, Li J, Zhang C, Wang T, Zhang Y, Wang A, Zhang Y, Lin K, Li K, Xiong G, Xue Y, Mazzucato A, Causse M, Fei Z, Giovannoni JJ, Chetelat RT, Zamir D, Städler T, Li J, Ye Z, Du Y, Huang S. 2014. Genomic analyses provide insights into the history of tomato breeding. *Nature Genetics* 46(11): 1220-1226.
Long J. 1995. De tomates y jitomates en el siglo XVI. *Estudios de Cultura Náhuatl* 25: 239–252.
López-Terrada M. n.d. The history of the arrival of the tomato in Europe: an initial overview. Traditiom. Available at http://traditom.eu/fileadmin/traditom/downloads/TRADITOM_History_of_the_arrival_of_the_tomato_in_Europe.pdf
Luztze E, Retzlaff H. 1949. *Herbarium des Georg Oellinger anno 1553 zu Nürnberg*. Salzburg: Akademischer Gemeinschaftsverlag.
Matthioli PA. 1544. *Di Pedacio Dioscoride Anazarbeo libri cinque della historia, et materia medicinale trodotti in lingua volgare Italiana*. Venice: Nicolo de Bascarini.
Matthioli PA. 1548. *Commentarii, in libros sex Pedacii Dioscorides Anarzabei, de materia medica.*,Venice: Valgrisius. Available at https://classic.europeana.eu/portal/nl/record/92004/NKCR___NKCR__5_H_000058__45VM8U7_cs.html?utm_source=new-website&utm_medium=button

766 Matthioli PA. 1554. *Commentarii in libros sex Pedacii Dioscoridis Anazarbei, de medica*
767 *materia*. Venice: Valgrisius. Available at
768 https://books.google.nl/books?id=HEhdAAAAcAAJ&printsec=frontcover&cad=0#v=onepag
769 e&q&f=true
770 McCue GA. 1952. The history of the use of the tomato: an annotated bibliography. *Annals of the*
771 *Missouri Botanical Garden* 39(4): 289-348.
772 Metro-Roland MM. 2013. Goulash nationalism: the culinary identity of a nation. *Journal of*
773 *Heritage Tourism* 8(2-3): 172-181.
774 Meyer FG, Trueblood EE, Heller JL. 1999. *The great herbal of Leonhart Fuchs: de historia*
775 *stirpium commentarii insignes, 1542.* Stanford: Stanford University Press.
776 Minelli A. 2010. Michiel, Pietro Antonio. *Dizionario Biografico degli Italiani,* Volume 74.
777 Available at https://www.treccani.it/enciclopedia/pietro-antonio-michiel_(Dizionario-
778 Biografico).
779 Palmer R. 1985. Medical botany in northern Italy in the Renaissance. *Journal of the Royal*
780 *Society of Medicine* 78(2): 149-157.
781 Pardo Tomás J, López Terrada ML. 1993. *Las primeras noticias sobre plantas Americanas en*
782 *las relaciones de viajes y crónicas de Indias (1493-1553).* Cuadernos Valencianos de Historia
783 de la Medicina y de la Ciencia XL, Serie A (Monografías). Valencia: Universitat de Valencia.
784 Penzig OAJ. 1905. Illustrazione degli erbarii di Gherardo Cibo. In: Penzig OAJ, ed.
785 *Contribuzioni alla storia della botanica*. Milan: U. Hoepli, 1–237.
786 Peralta IE, Spooner DM, Knapp S. 2008. *Taxonomy of wild tomatoes and their relatives*
787 *(Solanum sect. Lycopersicoides, sect. Juglandifolia, sect. Lycopersicon; Solanaceae).*
788 Systematic Botany Monographs 84. Laramie: American Society of Plant Taxonomists.
789 Petropoulos SA, Barros L, Ferreira ICFR. 2019. Rediscovering local landraces: Shaping
790 horticulture for the future. *Frontiers in Plant Science* 10: 126. Doi: 10.3389/fpls.2019.00126.
791 PROTA. 2015. *Bibliographic details for Solanum aethiopicum*. Wageningen: Plant Resources of
792 Tropical Africa. Available at https://uses.plantnet-
793 project.org/en/Solanum_aethiopicum_(PROTA)
794 Rotelli F. 2018. Exotic plants in Italian pharmacopoeia (16th-17th centuries). *Medicina nei*
795 *Secoli* 30(3): 827-880.
796 Smith AF. 1994. *The tomato in America: Early history, culture, and cookery*. Columbia:
797 University of South Carolina Press.
798 Soldano A. 2000. La provenienza delle raccolte dell'erbario di Ulisse Aldrovandi, Volumi I e II.
799 *Atti dell' Istituto Veneto di Scienze, Lettere ed Arti, Classe de Scienze fisiche, Matematiche e*
800 *Naturali* 158: 1-246.
801 Speta F, Grims F. 1980. Hieronymus Harder und sein „Linzer" Herbarium aus den Jahre 1599.
802 *Kataloge des Oö. Landesmuseums 105, zugleich Linzer Biologische Beiträge* 12: 307-330
803 Staats M, Erkens RH, Van de Vossenberg B, Wieringa JJ, Kraaijeveld K, Stielow B, Geml J,
804 Richardson JE, Bakker FT. 2013. Genomic treasure troves: complete genome sequencing of
805 herbarium and insect museum specimens. *PLoS ONE* 8(7): e69189.

Stefanaki A, Thijsse G, van Uffelen G, Eurlings M, van Andel TR. 2018. The En Tibi herbarium, a 16th century Italian treasure. *Botanical Journal of the Linnaean Society* 187: 397-427.

Stefanaki A, Porck H, Grimaldi IM, Thurn N, Pugliano V, Kardinaal A, Salemink J, Thijsse G, Chavannes-Mazel C, Kwakkel E, Van Andel TR. 2019. Breaking the silence of the 500-year-old smiling garden of everlasting flowers: The En Tibi book herbarium. *PLoS ONE* 14(6): e0217779.

Stefanaki A, Walter T, Porck H, Bertin A, Van Andel TR. 2021. The early book herbaria of Leonhard Rauwolf (S. France and N. Italy, 1560–1563): new light on a plant collection from the 'golden age of botany'. Researchsquare preprint server. Available at https://www.researchsquare.com/article/rs-352450/v1 Doi: 10.21203/rs.3.rs-352450/v1

Sturtevant EL. 1919. *Notes on edible plants*. Report of the New York Experiment Station of the year 1919. Albany: J.B. Lyon Company. Available at https://uses.plantnet-project.org/en/Lycopersicum_(Sturtevant,_1919)

The Tomato Genome Consortium. 2012. The tomato genome sequence provides insights into fleshy fruit evolution. *Nature* 485(7400): 635–41. Doi: 10.1038/nature11119.

Thijsse G. 2012. Gedroogde schatten. In: van Gelder E, ed. *Bloeiende kennis: Groene ontdekkingen in de Gouden Eeuw*. Hilversum: Uitgeverij Verloren, 36–54.

Toresella S. 1992. Le prime piante americane negli erbari del Cinquecento. *Le Scienze* 281: 46-57.

Ubriszy Savoia A. 1993. Le piante americane nell'Erbario di Ulisse Aldrovandi. *Webbia* 48: 579–598.

Van Santen H. 2012 De alleroudste tomaat ligt in Leiden. *NRC Handelsblad* 17 July 2012: 16.

Van Andel TR, Meyer RS, Aflitos SA, Carney JA, Veltman MA, Copetti D, Flowers JM, Havinga RM, Maat M, Purugganan MD, Wing RA, Schranz ME. 2016. Tracing ancestor rice of Suriname Maroons back to its African origin. *Nature Plants* 2(10): 1-5. Doi: 10.1038/nplants.2016.149

Van Andel TR. 2017. *Open the treasure room and decolonize the museum*. Inaugural lecture for the Clusius chair in History of Botany and Gardens. Leiden: Leiden University.

Vandewiele LJ. 1993. Wat groeide er in de tuin van Pieter van Coudenberghe? In: De Nave F, Imhof D, eds. *De Botanica in de Zuidelijke Nederlanden (einde 15de eeuw-ca. 1650)* Antwerp: Museum Plantin-Moretus and Stedelijk Prentenkabinet, 23-31.