Sixteenth-century tomatoes in Europe: who saw them, how they looked like, and where they came from

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Abstract

Background. Soon after the Spanish conquest of the Americas, the first tomatoes were presented as curiosities to the European elite 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, triggered research on its geographical provenance and morphological comparison to other tomato specimens and illustrations from the same time period.

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. We compare our historical findings with recent molecular research on the chloroplast and nuclear DNA of the 'En Tibi' specimen.

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, possibly from plants grown in the Pisa botanical garden by their teacher Luca Ghini. The oldest tomato illustrations were made in Germany and Switzerland in the early 1550s, but the Flemish Rembert Dodoens published the first image in 1553. The names of early tomatoes in

40   contemporary manuscripts suggest both a Mexican and a Peruvian origin. The 'En Tibi'
41   specimen was collected by Petrollini around 1558 and thus is not the oldest extant tomato.
42   Recent molecular research on the ancient nuclear and chloroplast DNA of the En Tibi specimen
43   clearly shows that it was a fully domesticated tomato, and genetically close to three Mexican
44   landraces and two Peruvian specimens that probably also had a Mesoamerican origin. Molecular
45   research on the other sixteenth-century tomato specimens may reveal other patterns of genetic
46   similarity, past selection processes, and geographic origin. Clues on the 'historic' taste and pest
47   resistance of the sixteenth-century tomatoes will be difficult to predict from their degraded DNA,
48   but should be rather sought in those landraces in Central and South America that are genetically
49   close to them. The indigenous farmers growing these traditional varieties should be supported to
50   conserve these heirloom varieties *in-situ*.
51

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 farms through the hands of Spanish colonizers to European aristocrats' gardens was the tomato (*Solanum lycopersicum* L.). After the conquest of the Aztec city of Tenochtitlan (now Mexico City) in 1521 by Hernán Cortez, the Franciscan friar and chronicler 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 (Jenkins, 1948; Rotelli, 2018). Still, there is no record of the introduction of the tomato in this Spanish port, or its cultivation in the royal Iberian gardens (Jenkins, 1948), as plant transfers were rarely considered important enough to document (Long, 1995). Due to the many Italian merchants sailing under Portuguese and Spanish flags, and the fact that the Kingdom of Naples was under Spanish rule, 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 (*Poma amoris da alcuni et del Peru*, 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), but the Mexican origin

92   of the cultivated tomato was still considered (Peralta & Spooner 2007). The current model for the
93   tomato domestication process is that the small-fruited *Solanum lycopersicum* var. *cerasiforme*
94   (Dunal) D.M.Spooner, G.J.Anderson & R.K.Jansen originated from the red-fruited wild species
95   *S. pimpinellifolium* L, which spread slowly northwards from the Peruvian desert to Mesoamerica,
96   adapting itself gradually to wetter environments, unrelated to human activity (Blanca et al.,
97   2021). Later, indigenous people took the wild Mexican cherry-sized tomato to South America,
98   where it was domesticated, and brought it back to Mesoamerica, where they further domesticated
99   it into the very variable big-fruited *S. lycopersicum* L. var. *lycopersicum* (Blanca et al., 2021;
100   Blanca 2021). Details on the exact time and place of domestication of the tomato are still not
101   known with certainty for either Mexico, Ecuador or Peru (Bai & Lindhout, 2007), but there is a
102   diminishing genetic diversity from Ecuador to Mexico (Lin et al., 2014; Blanca et al., 2015).
103
104   In 1989, Sergio Toresella, an expert on medieval herbals, examined a well-preserved tomato
105   specimen in a sixteenth-century book herbarium kept at Naturalis Biodiversity Center in Leiden,
106   the Netherlands. He claimed that this plant collection was made in Ferrara (Italy) between 1542
107   and 1544 and therefore was the oldest existing herbarium (Toresella, 1992). This meant that the
108   anonymous Italian maker of this 'En Tibi herbarium' had collected the earliest European tomato
109   specimen (Houchin, 2010; Thijsse, 2012; Egmond, 2016). As such, the collector would have
110   predated compatriots Pietro Andrea Matthioli, who described a 'new species' in his section on
111   mandrake in 1544 (McCue, 1952), and naturalist Ulisse Aldrovandi, who collected in 1551 a
112   specimen of a cultivated tomato, preserved at the Bologna Herbarium, that was considered as the
113   earliest extant specimen (Peralta, Spooner &Knapp, 2008).
114
115   The Leiden specimen was also thought to be older than a tomato in a herbarium in Rome, dated
116   pre-1553 (De Toni, 1910), which was attributed first to the painter Gherardo Cibo (Penzig, 1905)
117   and later to the physician Francesco Petrollini (Chiovenda, 1909). However, the 'En Tibi
118   tomato', with its simple flowers and round fruit (see
119   https://data.biodiversitydata.nl/naturalis/specimen/L.2111092), did not resemble the well-known
120   sixteenth-century woodcut illustration of a tomato plant with double flowers and elongated,
121   segmented fruits, claimed as typical for the early European tomatoes (Sturtevant, 1919; Daunay,
122   Laterrot & Janick, 2007). This woodcut is often inaccurately attributed to Matthioli (e.g.,
123   Houchin, 2010), but was published eight years after his death by Camerarius in his commentaries
124   on Matthioli, first in black and white (1586) and four years later in color (Camerarius, 1586: 821;
125   1590: 378). In the Aldrovandi manuscripts, kept at the University of Bologna, there is an undated
126   list of seeds sent by Aldrovandi to Camerarius that mentions '*Pomum amoris flore rubro non
127   compressum*' (Aldrovandi manuscripts 136 VII, c. 26).
128
129   The finding of the 'oldest extant tomato' in the Netherlands led to claims in the popular media
130   that the DNA of this 'primitive tomato' could disclose potential ancient resistances to pests and
131   diseases lacking in modern crops. It was suggested that the En Tibi tomato could help plant

132   breeders develop new cultivars with the 'original taste' of the sixteenth-century tomatoes (Van
133   Santen, 2012; De Boer, 2013). The genomic diversity stored in herbarium specimens creates
134   ample opportunities for genome-scale population and domestication studies (Staats et al., 2013).
135   Comparing the DNA of traditional crop specimens to the increasingly available online genetic
136   information on crop accessions worldwide can also provide detailed information on geographic
137   origins, past selection processes and historic migration routes of plants and people (van Andel et
138   al., 2016; Larranaga, van Zonneveld & Hormaza, 2021). Unfortunately, the sampling of
139   historical collections has had limited success due to their highly degraded DNA, although
140   significant progress is being made with new 'ancient genomics' methods (Bakker et al., 2020).
141
142   At the same time, ongoing digitization efforts greatly facilitate the research on sixteenth-century
143   herbaria, illustrations, publications and manuscripts (Koning et al., 2008; Van Andel, 2017).
144   However, the literature on early tomato descriptions and depictions often lacks detailed links to
145   the original sources. The latter can now be directly inspected online and sometimes reveal other
146   authors, editions, dates and species than previously thought. Our recent revision of the En Tibi
147   herbarium uncovered that it was not made in Ferrara in 1542-3 as had been suggested, but in
148   Bologna around 1558 by the Italian botanist Francesco Petrollini, who also made the so-called
149   'Erbario Cibo' kept in Rome (Stefanaki et al., 2018; 2019).
150
151   This paper aims to provide a more accurate overview of early sixteenth-century descriptions,
152   illustrations and particularly herbarium specimens of the tomato. Some of the published sources
153   have been digitally available for some years, but several images and most of the herbarium
154   specimens have never been published so far. We show that the earliest tomatoes in Europe came
155   in a variety of colors, shapes and sizes, and reveal that some 'early tomatoes' were, in fact,
156   misidentified and represent other, related species. We compare these findings with recent
157   molecular research on 'En Tibi' specimen's nuclear DNA (Michels, 2020) and choloroplast
158   DNA (Kakakiou, 2021), which shed new light on its probable geographic origin.
159

Materials & Methods

161   We performed a literature review, starting with studies on the introduction of the tomato in
162   Europe (e.g., Jenkins, 1948. McCue, 1952, Daunay, Laterrot & Janick, 2007; Gentilcore, 2010)
163   and on early modern naturalists in Italy, France, Central Europe and the Low Countries (e.g., De
164   Toni, 1907, 1910, 1940; Findlen, 1994, 2017; Egmond, 2016, 2018, Rotelli, 2018.). We also
165   reviewed modern taxonomic and molecular studies on the origin of the tomato (e.g., Peralta,
166   Spooner & Knapp, 2008; Lin et al., 2014; Blanca et al., 2021). We consequently traced the
167   original sixteenth-century manuscripts cited in these works via online repositories (e.g., google
168   books, the Biodiversity Heritage Library, https://www.europeana.eu).
169
170   We searched for tomato specimens in sixteenth-century herbaria (for an overview of the c. 32
171   herbaria that were probably produced in that century, see Thijsse, 2016) by reviewing scientific

172 studies on these historical collections (e.g., Kessler, 1870; Caruel, 1858; Camus & Penzig, 1885;
173 Penzig, 1905; Speta & Grims, 1980; Soldano, 2000). Where available, we checked the published
174 species lists, and otherwise the indices and specimens of these herbaria, for references to '*pomo*',
175 '*mala*', '*lycopersicon*', '*Lycopersicum*', '*Solanum*', etc. We approached several libraries and
176 museums in Italy, France, Germany, Poland and Switzerland to request digital images of
177 specimens and illustrations in manuscripts that had not yet been published. We provided links to
178 digital sources of the historical specimens, literature, manuscripts and images that we reviewed
179 for this study. We listed the local and pre-Linnaean scientific names for tomatoes mentioned in
180 the original published sources, manuscripts, and handwritten texts on botanical vouchers,
181 illustrations or herbarium labels. We checked each historical specimen, description and depiction
182 for visible or written evidence of different shapes, sizes and colors of flowers and fruits. We
183 scrutinized all historical material for possible clues of the geographical origins of the tomatoes.
184 Finally, we report on two recent molecular studies on the genetic affinities of the sixteenth-
185 century tomato specimen in the En Tibi herbarium (Michels, 2020; Kakakiou, 2021).
186

Results

The first mention of a tomato (1544)

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

212

213   But where did Matthioli see his first tomato? According to Ubriszy Savoia (1993), his (former)

214   teacher Luca Ghini (c. 1490-1556) had obtained the seeds from the Venetian patrician and

215   naturalist Pietro Antonio Michiel (1510-1576). Next to his house in Venice, Michiel cultivated

216   numerous exotic plants from faraway places, including the Americas, the Near East and northern

217   Africa. His objective was to spread these botanical novelties among his network, so he sent seeds

218   and sprouts of plants to his friends (De Toni, 1940). Michiel was given the charge to curate the

219   Padua garden from 1551 to 1555 when Luigi Squalermo (1512-1570), better known as

220   Anguillara, was prefect. Anguillara had followed Ghini's classes and worked in his teacher's

221   private garden in Bologna, and in 1546 became the first prefect of the Padua garden (Minelli,

222   2010). In 1543, Anguillara assisted Ghini in amassing materials for the Pisa garden (Findlen,

223   2017), so it is more likely that Anguillara (and not Michiel) provided Ghini with tomato seeds,

224   also because the Padua garden was founded in 1545 (Palmer, 1985), a year after Matthioli

225   described the first European tomato. Michiel apparently started to expand his Venice garden

226   upon his return from Padua in 1555 (De Toni, 1940).

227

228   Ghini taught medical botany in Pisa from 1544 to 1555, where he founded the first university

229   botanical garden supported by the Grand Duke of Tuscany, Cosimo I de' Medici (De Toni,

230   1907). Cosimo attempted to import and acclimatize various American plants (Gentilcore, 2010),

231   and Ghini enriched the garden with exotic species and taught his many pupils to press and dry

232   botanical specimens between paper (Findlen, 2017). According to McCue (1952: 292), the Pisa

233   garden catalogue manuscript from 1548 'does not include any plant identifiable as the tomato'.

234   However, the inventory of this catalogue brought to light by De Toni (1907: 439) lists a plant

235   named '*Thumatulum pomum vulgo dictum rubrum et luteum*' (Table 1) and suggests that the

236   catalogue with 620 species could have been started already in 1545.

237

238   Matthioli did not travel much after he reached his forties (from 1541 onwards he stayed in the

239   small town of Gorizia, near the current border with Slovenia) and simply sent lists of

240   Dioscoridean plants that he had not yet seen or identified to his colleagues (Palmer, 1985). He

241   often included the knowledge of his fellow scientists or local people in the many editions of his

242   books without citing them (Arber, 1986). Ghini had sent many dried specimens to Matthioli,

243   accompanied by written opinions on their identification (De Toni, 1907; Palmer, 1985). If Ghini

244   had already planted his first tomato seeds in the Pisa garden in 1544 (Ubriszy Savoia, 1993), it

245   was likely his description of the tomato that ended up in Matthioli's first edition of his

246   Commentaries on Dioscorides in 1544.

247

248   **The first tomato specimen (1551)**

249   One of Ghini's best-known disciples was Ulisse Aldrovandi (1522-1605), who became famous

250   for his 16-volume herbarium with over 4000 specimens kept at the botanical garden in Bologna.

251   The tomato specimen is preserved in the first volume (Fig. 1A), which Aldrovandi started in

252   1551, and is therefore considered the oldest extant botanical voucher of this New World crop
253   (Table 1). Thorough work has been carried out to trace the origin of Aldrovandi's specimens, but
254   unfortunately for the tomato specimen this information has not survived (Soldano, 2000).
255   Aldrovandi kept an extensive correspondence with other naturalists. From his letters, we know
256   that around 1551, plants were sent to him by Michiel, then employed in the Padua botanical
257   garden (Minelli, 2010), by Ghini from the Pisa garden (Ubriszy Savoia, 1993) and by his
258   companion and guide in the field Francesco Petrollini (Soldano, 2000; Stefanaki et al., 2019).
259
260   Petrollini, whose birth and death dates remain unknown, also attended classes by Ghini and
261   graduated in Bologna in 1551. Two of his tomato specimens have survived: one in his extensive
262   work herbarium, which is known to have consisted of several book volumes by 1553 (De Toni,
263   1910) and is kept in the Bibliotheca Angelica in Rome, and one in the En Tibi herbarium (c.
264   1558) that was made on commission, possibly for the Habsburg emperor Ferdinand I (Stefanaki
265   et al., 2019). The tomato specimen in the Rome herbarium has immature fruits. A separate fruit
266   glued on top of the page, partly destroyed by insects, is an immature eggplant and belongs to
267   another specimen (Fig. 1B). We know that Petrollini graduated two years before Aldrovandi and
268   guided him in his early steps in the field. It is, therefore, likely that he started his work herbarium
269   earlier than Aldrovandi (De Toni, 2010), but the tomato appears only in the third volume. The
270   tomato in the En Tibi herbarium is thus not the oldest preserved tomato specimen in the world,
271   although it is the earliest surviving specimen with (the remains of) a mature fruit (Fig. 1C).
272
273   We traced 17 surviving sixteenth-century herbaria in Italy, Germany, France, Switzerland and
274   the Netherlands (Supplementary Table 1), eight of which contain tomato specimens (Fig. 1A-J).
275   We have no indication of tomato specimens in other surviving herbaria produced in this time
276   period. The oldest extant herbarium was compiled by Michele Merini, also a pupil of Ghini, in
277   the Pisa botanical garden between 1540-1545. His herbarium is not available online, but its
278   contents were published by Chiovenda (1927), and it does not contain a tomato specimen.
279   Another disciple of Ghini, Andrea Cesalpino, also made a herbarium in the Pisa garden between
280   1555-1563. Although he mentions the tomato in his *De plantis Libri XVI* (Cesalpino, 1583),
281   there is no tomato among his vouchers (Caruel, 1858). The first herbaria made in France (by
282   Jehan Girault in 1558) and the Low Countries (by Petrus Cadé in 1566, see Christenhusz, 2004)
283   do not have a tomato specimen either. The second herbarium produced in France, that of the
284   German botanist Leonhard Rauwolf, contains a tomato (Fig. 1D), but this specimen was
285   collected during Rauwolf's field trip in northern Italy in 1563 (Stefanaki et al., 2021). Tomato
286   specimens are also included in the herbaria Estense (Ferrara, Italy), Bauhin (three specimens;
287   Basel, Switzerland), Ratzenberger (Kassel, Germany) and the *Herbarium Vivum* of Hieronymus
288   Harder (Ulm, Germany); all these collections have been compiled towards the end of the
289   sixteenth century (Supplementary Table 1, Fig. 1A-J).
290
291   **The first image of a tomato (1553)**

292   Although the tomato was common in Mexico at the time of the Spanish conquest, no images of
293   tomatoes made in the New World exist (Daunay, Laterrot & Janick, 2007). An uncolored
294   woodcut illustration, published in 1553 in a Latin herbal by the Flemish doctor and botanist
295   Rembert Dodoens, can be considered the first image of a tomato (Fig. 2A). A year later
296   (Dodoens, 1554), he published a colored version of the same woodcut (Fig. 2B). Also known
297   under his Latinized name Dodonaeus, Dodoens studied at several universities and travelled to
298   France, Germany and Italy from 1535 to 1546, where he may have seen the tomato for the first
299   time. In 1548, he settled in Mechelen (currently Belgium), then a hotspot of sixteenth-century
300   naturalists, who studied exotic plants in the gardens of local noblemen. In a later edition of his
301   herbal, Dodoens (1583) acknowledged the people who supplied him with plants. One of them,
302   Jean de Brancion, had a beautiful garden with many exotic species, obtained via his extensive
303   international network (Egmond, 2010). In Aldrovandi's manuscripts, kept at the University of
304   Bologna, there are several lists of seeds sent to De Brancion (Frati, Ghigi & Sorbelli, 1907), of
305   which one, dated 10 January 1571, contains a '*Pomum pomiferum*' listed just before the
306   eggplant, indicated as '*Mala insane purpurea*' (Aldrovandi manuscripts 136 V, c. 137v).
307   Another possibility is that Dodoens obtained a tomato plant from the garden of the Antwerp
308   apothecary Pieter van Coudenberghe, created in 1548 and containing more than 600 exotic plants
309   (Vandewiele, 1993).
310
311   On 22 September 1553, in the same year that Dodoens published the first woodcut, two tomato
312   plants were depicted by the Swiss naturalist Conrad Gesner (Table 1, Fig. 2C-D). Unfortunately,
313   his *Historia Plantarum*, a beautiful collection with hundreds of colored plant illustrations, was
314   never published. Gesner had travelled to Italy in 1544, where he met Ghini to study his
315   collections (Findlen, 2017), which provides us with a clue to where he may have obtained his
316   tomato seeds. Later, Gesner (1561) wrote that the tomato was grown by Pieter van
317   Coudenberghe in Antwerp (a possible source of Dodoens' tomato), by Vuoysselus in Breslau
318   (now Poland) and in German gardens by Joachimus Kreichius in Torgau and in Nuremberg by
319   George Oellinger. Apothecary Oellinger (Ollingerus) also had three drawings made by Samuel
320   Quichelberg (1529-1567) of the different tomato varieties that he had planted (Fig. 2G-I). His
321   vast collection of naturalist drawings, *Magnarum medicinae partium herbariae et zoographiae*,
322   was finished in 1553 but never published until Lutze and Retzlaff (1949) published a selection of
323   his work.
324
325   In the meantime, from c. 1550 to his death in 1576, the Venetian nobleman Michiel worked on
326   his garden inventory, finalized in a five-volume illustrated manuscript now held by the Marciana
327   library in Venice (De Toni, 1940). Michiel attempted to describe all plants he knew, so the
328   species that figure in his work may have grown in the Padua garden, in his own Venice estate, or
329   they were sent to him as dried specimens (De Toni, 1940). The third volume (Libro Rosso I)
330   features a description of the tomato (Table 1). When he started his manuscript, Michiel was still
331   in Padua and may have seen the tomato there. The watercolor image in this manuscript is

332   possibly made by Domenico Dalle Greche (Fig. 2F). Another drawing in Michiel's manuscript
333   (Supplementary Fig. 1) was mentioned as one of the earliest depicted tomatoes in Europe
334   (Egmond, 2018), but the depicted plant has simple, lobed leaves and symmetrical, depressed and
335   deeply furrowed fruits. We agree with De Toni's identification of this illustration as an Ethiopian
336   eggplant (*Solanum aethiopicum* L.), probably a member of the kumba cultivar group (PROTA,
337   2015).
338

339   Another candidate for the earliest extant European drawing of the tomato is a watercolor image
340   (Fig. 2E) in a manuscript by the German botanist Leonhart Fuchs, dated between 1549 and 1561
341   and known as the 'Vienna Codex' (Meyer, Trueblood & Heller, 1999; Baumann, Baumann &
342   Baumann-Schleihauf, 2001). This manuscript was meant to become an extended version of his
343   famous herbal *De historia stirpium commentarii insignes* (Fuchs, 1542), widely considered a
344   masterpiece with 500 very accurate woodcut illustrations and the first known European
345   publication of New World plants such as maize, tobacco, marigold and chili pepper (Meyer,
346   Trueblood & Heller, 1999). The tomato, however, was not yet described in this famous herbal,
347   nor its later editions. It does appear in the Vienna Codex as a drawing (Fig. 2E) and in the text,
348   which reported that this unfamiliar 'apple' was only known from gardens and that it was not
349   mentioned by the ancient Greeks, Romans or even the Moors. The manuscript was never
350   published, but Meyer, Trueblood & Heller (1999) suggested that the drawing may be earlier than
351   the woodcut of Dodoens (1553).
352

353   In 1586, decades after the first tomato illustrations in the 1550s and eight years after Matthioli's
354   death in 1578, an uncolored woodcut of a tomato plant (Fig. 2M) appeared in *De Plantis Epitome*
355   *Utilissima*, an enlargement of Matthioli's work published in Latin by Joachim Camerarius (1586:
356   821). A colored version of the same woodcut (Fig. 2N) is published four years later, again by
357   Camerarius, but this time in German (1590: 378), although this image is often attributed to
358   Matthioli (e.g., Houchin, 2010).
359

360   **The first names of tomatoes**
361   In 1548, Grand Duke Cosimo I was presented some tomatoes from his Florentine Estate. A letter
362   from 1548 mentions that the Florentine *pomidoro* arrived safely at the ducal household (Table 1).
363   This letter is the earliest written evidence of the term 'golden apples' in Italian (Gentilcore,
364   2010). The Latin translation of this local name ('*mala aurea*') quickly follows in 1554, while
365   Aldrovandi's name '*mali insani*' refers to its resemblance to the botanically related eggplant or
366   *melanzana* (Table 1). Other early sixteenth-century names of the tomato reveal that it came in
367   different colors (red, golden, brown, yellow) or that it was related to the mandrake
368   ('*Mandragorae species*').
369

370   The terms '*pomum amoris*' or '*pomme d'amour*' are often said to refer to the alleged aphrodisiac
371   properties of the tomato (Smith, 1994). The French term was likely added by a French translator

372 of Matthioli's work (Peralta, Spooner & Knapp, 2008) and could also be a corruption of '*pome*
373 *dei Moro*' (apples of the Moors, Houchin 2010) or '*pomi d'oro*'. Two years before Matthioli's
374 first description of the tomato in 1544, the term '*amoris poma*' was already coined by Fuchs
375 (1542: 532) in his description of the eggplant. Michiel also described the eggplant as '*Pomes da*
376 *mouri da Galli*, *Melongena da Arabi*', a fruit brought by the Moors or Arabs (De Toni, 1940).
377 *Solanum melongena* L. was indeed introduced to Europe during the Middle Ages by Arab traders
378 from India (Daunay, Laterrot & Janick, 2007).
379
380 The Spanish gave the name 'love apple' first to the Mexican tomatillo (*Physalis ixocarpa* Lam.),
381 of which the calyx splits open to reveal the fruit, apparently reminding them of female genitals.
382 Later the Spanish transferred this name to the tomato (Gentilcore, 2010). Although the Italians
383 never adopted the Spanish name '*tomate*', derived from the Nahuatl '*tomatl*' (Long, 1995), the
384 appearances of '*thumatulum*' in the inventory of the Pisa garden, '*tumatl*' in the inventory of the
385 Bologna garden and '*Tumatle Americanorum*' in Guilandinus (1572), successor of Anguillara in
386 the Padua garden, suggest that some early modern botanists knew this name. However, the local
387 term '*poma/pomo*' was more common (Table 1).
388
389 The name '*Saliunca*' in the En Tibi herbarium was erroneously given to the tomato specimen, a
390 mistake made by the scribe who wrote the plant names next to the specimens: the name was
391 meant for the preceding specimen (nr. 293) of *Valeriana celtica* L. (Stefanaki et al., 2018).
392 According to Ubriszy Savoia (1993: 581), Aldrovandi's term '*Tembul quibusd.*' (another type of
393 Tembul) refers to *Solanum betaceum* Cav., the South American tree tomato, but this species was
394 only introduced in European botanical gardens in 1836.
395
396 The remark that 'some people knew the tomatoes as Peruvian apples' was made both by Michiel
397 (De Toni, 1940) and Anguillara (1561), which is not surprising as they were friends and worked
398 together in the Padua garden from 1551 to 1555 (Minelli, 2010). Several other Andean plants
399 figure in Michiel's garden inventory (De Toni, 1940), such as coca (*Erythroxylum coca* Lam.)
400 and 'quina de India' (probably *Cinchona* sp.). As Michiel never published his garden inventory,
401 Anguillara (1561) was quoted for this South American provenance by C. Bauhin in his annotated
402 edition of Matthioli's commentaries (C. Bauhin 1598: 761, Table 1). According to Jenkins
403 (1948), however, there is nothing in the historical record that suggests a Peruvian origin of the
404 tomato. Nevertheless, De Candolle (1885) argued that sixteenth century botanists had received
405 the plant from Peru. De Candolle based this on J. Bauhin & Cherler (1651, published
406 posthumously) who mentioned the name '*Pomi del Peru*' as a vernacular Italian name. They also
407 mentioned the name '*Mala Peruviana*', citing *Hortus Eystetensis* (Besler, 1613) as the source,
408 but this name is not mentioned in the tomato illustration in this book. Gray & Trumbull (1883)
409 assume that Anguillara mistook the tomato for *Datura stramonium* L., an American Solanaceae
410 described as '*mala peruviana*' by Guilandinus (1572). Despite his closeness to Ghini, there is no
411 evidence that Anguillara made a herbarium, so no specimen of the 'Poma del Peru' exists. In the

412 extensive collection of Aldrovandi's manuscripts, however, there are many lists of objects
413 (plants, animals, minerals) that he received from all over the world, including South American
414 locations such as the Tumbes province in Peru, the Ecuadorian capital Quito, Cumana
415 (Venezuela) and Uraba in Colombia (Frati, Ghigi & Sorbelli, 1907). It is unfortunately unknown
416 whether Aldrovandi received his tomato specimen directly from his contacts overseas and, if so,
417 from which location. Guilandinus (1572) referred to the tomato as '*tumatle*', using its Nahuatl
418 name, and wrote that it came from '*Themistithan*', according to Jenkins (1948) a corruption of
419 Tenochtitlan, the Aztec name for what is now Mexico City. Aldrovandi also made a
420 '*Themistitani catalogus*' of natural objects received from this area, next to lists of specimens
421 from other Mexican locations such as 'Iztapalapa', 'Jucatan insula' and 'Tlaxcala' (Frati, Ghigi
422 & Sorbelli, 1907: 181). Still, we do not know whether tomatoes are listed in these manuscripts.
423
424 The name 'Ethiopian apple' written next to the tomato specimen in the anonymous Ducale
425 Estense herbarium (Fig. 1I, Table 1) refers to an African origin. This demonstrates the existing
426 confusion between *Solanum lycopersicum* and the related Old-World species *S. aethiopicum*,
427 also depicted in Michiels manuscript (Supplementary Fig. 1). Besides the tomato specimens,
428 there are also three specimens of *S. aethiopicum* in C. Bauhins' herbarium, one of which was
429 named '*poma amoris racemosa*' and possibly came from his own garden (Supplementary Fig. 2).
430 The word '*Ettiopia*' or '*aethiopicum*' in those days did not refer to the current country of
431 Ethiopia but was used as a general term to indicate the African continent (De Toni, 1940).
432
433 The name *Lycopersicon* means 'wolf peach', after the Greek words for wolf (*lykos*) and peach
434 (*persikon*), and was first used by the Greek physician Galen (AD 131–200) for designating a
435 plant from Egypt with malodorous sap, just like tomato leaves. Which species Galen had in mind
436 while describing the wolf peach has been lost in centuries of translations and misinterpretations
437 of the classical texts during the Middle Ages (Palmer, 1985). Galen had never seen any New
438 World plant, but a major aim of the Renaissance naturalists was to search for plant specimens
439 that matched descriptions by the classical authors (Palmer, 1985; Stefanaki et al., 2019).
440 However, the German botanist Fuchs argued in his manuscript that as the Greek and Latin
441 authors did not mention the tomato, the plant should not carry any of the classical names (Meyer,
442 Trueblood & Heller, 1999). The Greek name was used in Latin as specific epithet of *Solanum*
443 *lycopersicum* L. by Linnaeus (1753), after which Miller (1754) applied it as the genus name for
444 the cultivated tomato (*Lycopersicum esculentum* Mill). Modern taxonomy has brought the
445 tomato back to the genus *Solanum* (Peralta, Spooner & Knapp, 2008). Another attempt of
446 sixteenth-century naturalists to trace the tomato in ancient literature led them to the '*Glaucium*'
447 of Dioscorides: De Lobel (1571, 1576), for example, described, not without doubts, the tomato
448 under poppies.
449
450 **The morphology of early tomatoes**

451 The woodcut illustration of the elongated, segmented tomatoes by Camerarius (1586; 1590)
452 became widely known, as Matthioli's *Commentaries on Dioscorides* continued to be a bestseller
453 after his death. However, the sixteenth-century herbarium specimens and the images of small
454 spherical tomatoes in unpublished manuscripts remained locked up in royal treasure rooms,
455 libraries, and universities. This has led to the idea that the earliest tomatoes introduced to Europe
456 were 'large and lumpy', a 'mutation' from a smoother, more diminutive Mesoamerican form,
457 and probably 'the direct ancestor of some modern cultivated tomatoes' (Smith, 1994:15).
458 According to Sturtevant (1919), there were no indications that the round tomato was known
459 among the early botanists before 1700.
460
461 From our review of the sixteenth-century descriptions, images and herbarium specimens, it
462 becomes clear that different landraces of tomatoes were introduced early on in Europe. These
463 represented a great variety in flower and fruit shape, size and color, as was already suggested by
464 Daunay, Laterrot & Janick (2007) and Peralta, Spooner & Knapp (2008). Several tomato
465 illustrations (e.g., Camerarius, 1586) and specimens like those of C. Bauhin (Fig. 1E-G) show
466 duplications of sepals and petals, exserted styles and deeply furrowed (segmented) fruits, while
467 the specimens in the En Tibi and Rauwolf herbaria (Fig. 1C-D) and Oellinger's third drawing
468 (Fig. 2I) have simple flowers (5 petals) and small, spherical fruits (Table 2).
469
470 Although the drawing in Fuchs' manuscript (Vienna Codex, 1549-1556/1561) is often
471 considered 'unnatural' and 'false' (Meyer, Trueblood & Heller, 1999; Koning et al., 2008), the
472 task assigned to artist Albrecht Meyer was to represent the variation in flowers and fruits, instead
473 of depicting an individual plant. Fuchs wrote that he had seen at least three different varieties and
474 decided to include all in one illustration (Meyer, Trueblood & Heller, 1999: 629; Peralta,
475 Spooner & Knapp, 2008). Dominico dalle Greche also included several fruit types in his drawing
476 for Michiel (Fig. 2F). According to McCue (1952), the reference by Cesalpino (1583) to the
477 white color of the flowers was incorrect, but Camerarius (1590) described and depicted white-
478 colored flowers as well. The different tomato names, '*aurea*' (golden), '*rubrum*' (red), '*luteum*'
479 (yellow) and '*croceum*' (orange-yellow, golden-yellow), also indicate that the fruits came in
480 different colors.
481
482 Tomatoes underwent a dramatic increase in fruit size during domestication: some modern
483 cultivars produce fruit a thousand times larger than their wild counterparts (Lin et al., 2014).
484 Wild tomato species generally have flowers with five to six sepals, petals and stamens, and
485 bilocular fruits. Through a mutation known as fasciation, flowers will produce up to eight petals
486 and an increased number of locules, which leads to multisegmented, elongated fruits. Humans
487 probably selected fasciated tomatoes for their large fruits, but only a small portion of all modern
488 tomato cultivars is multilocular (Barrero & Tanksley, 2004). The fact that the first tomato
489 described in Europe was segmented (Matthioli, 1544, Table 2) proves that the early sixteenth-

490   century tomatoes did not come from wild plants but represented a crop that had reached a fairly
491   advanced stage of domestication (Bai & Lindhout, 2007).

492

493   Table 2 shows that most sixteenth-century specimens lack preserved fruits: juicy tomatoes
494   cannot be easily pressed into botanical vouchers. They are bulky and will not keep their shape
495   when pressed, and due to their moisture, the specimens will quickly start to mold. Petrollini's
496   first tomato specimen had only an immature fruit, but when preparing the tomato specimen in the
497   En Tibi herbarium, he skillfully removed the juicy insides of the tomato and pressed the skin of
498   the fruit to represent its round shape (Fig. 1C). Ratzenberger's fruits seem to have spoiled and
499   have been removed from the specimen (Fig. 1J). Harder found a solution: he pressed a flowering
500   specimen and drew the roots, ripe and golden fruits later on the paper (Fig. 1H).

501

502   **Genetic origin of the En Tibi tomato**
503   What was the geographical origin of the early tomatoes that sparked the interest of the
504   Renaissance botanists? The sixteenth-century literature, specimens and illustrations do not
505   answer this question. The Peruvian origin mentioned by Michiel and Anguillara is not specific,
506   and apart from Guilandinus (1572), the other early sources do not discuss any geographical
507   origin. The knowledge on tomatoes circulating in Europe during the sixteenth-century came from
508   plants that were already cultivated in gardens, as is evident from the detailed morphological
509   descriptions on fruit shape and color, characters that were only observable in living plants. The
510   provenance from the obscure New World was not of interest to most sixteenth-century scholars,
511   who tried hard to trace the tomato in the writings of ancient Greek authors. Regarding herbarium
512   specimens, we only know that the Rauwolf tomato was collected somewhere in N. Italy
513   (Stefanaki et al., 2021), while C. Bauhin's tomatoes were possibly cultivated in his garden in
514   Basel.

515

516   The question of geographical origin may also be approached by genomic research on the crop's
517   earliest herbarium specimens. Recently, DNA was extracted from a leaf of the tomato specimen
518   in the En Tibi herbarium (c. 1558, Bologna, kept at Naturalis), and its whole genome was
519   sequenced using Illumina TruSeq technology (Michels, 2020) and published online
520   (https://www.ncbi.nlm.nih.gov/bioproject/PRJNA566320; sequencing read archive number
521   SRS5407108). The En Tibi genome was then mapped to the Heinz 1706 reference genome (The
522   Tomato Genome Consortium, 2012), with an average sequencing depth of 2.28 (Michels, 2020).
523   Only 9.9 Mbp were recovered with ≥10x depth, which equated to 1.2% of the reference genome.
524   This indicated that the specimen's DNA had severely fragmented over the past 475 years. Data
525   on genome assemblies of 114 accessions of wild species and traditional cultivars from Latin
526   America were retrieved from the 360-tomato resequencing project (Lin et al., 2014;
527   https://solgenomics.net/organism/Solanum_lycopersicum/tomato_360) and cropped to span only
528   the 1.2% of the sequenced En Tibi genome with sufficient coverage.

529

530   To identify the En Tibi tomato's nearest neighbors, Michels (2020) performed a network
531   clustering analysis (NeighborNet, Bryant 2003). Dimensionality reduction analyses were carried
532   out on the remaining SNPs to investigate coarse genetic similarity among the accessions. In Fig.
533   3, the lengths of the terminal branches are proportional to the number of autapomorphies,
534   distinctive genetic features that are unique to each taxon. Wild populations are generally more
535   genetically diverse (and thus have higher numbers of autapomorphies) than domesticated ones,
536   because of the founder events of domestication and deliberate inbreeding. The highly diverse,
537   wild *Solanum pimpinellifolium* accessions (dark green circles) spread out on the left (Fig. 3A).
538   On the right, the En Tibi tomato clustered in the group of domesticated tomatoes (*S.*
539   *lycopersicum*) from both Central and South America, with very short branches (Fig. 3B). The
540   graph also shows that some accessions of the cherry tomato (*S. lycopersicum* var. *cerasiforme*)
541   are genetically close to the large-fruited domesticated tomato varieties on both parts of the
542   continent. In contrast, other accessions of cherry tomatoes appear to be truly wild, given their
543   long branches.
544
545   Table 3 shows the genetically close varieties to the En Tibi tomato, and some of the associated
546   data stored for these accessions in the C.M. Rick Tomato Genetics Resource Center (TGRC,
547   https://tgrc.ucdavis.edu) at the University of California at Davis, USA. While the three Mexican
548   accessions are characterized as 'Latin American cultivars' (probably landraces are meant here),
549   the other three accessions are classified in the TGRC database as 'wild'. However, C-61 was
550   collected from a family garden and C-281 in open vegetation along a road in the (once) heavily
551   forested eastern Andean foothills. Very little information from the farmers themselves is stored
552   for the accessions close to the En Tibi tomato. B-249 is the only one with a vernacular name
553   (Zocato, no language indicated), and B-153 was collected on a market but said to grow wild. For
554   C-281, the sentence "Indian women: no word in Quechua" in the database suggests that the
555   collector tried to obtain information from a local person, but communication was not possible.
556   The presumably 'wild state' of some of the accessions close to the En Tibi tomato does not
557   coincide with the molecular data, which show that the sixteenth-century tomato was a fully
558   domesticated crop. Combined with the absence of farmers' knowledge in the database, the
559   information in the TGRC database on the domestication status of these accessions is
560   questionable. Some of the nearest neighbors of the En Tibi tomato that were listed as 'wild' in
561   the germplasm data may have escaped from cultivation. Compared to genuinely wild accessions,
562   the branches of these presumably feralized ones are so short that they are very likely to have
563   passed through domestication processes and/or possible hybridization with cultivated tomatoes.
564
565   Michels (2020) also found that the En Tibi tomato specimen was more heterozygous than all
566   recently collected accessions from Mesoamerica sequenced by Lin et al. (2014), which had a
567   narrower genetic background. This means that the sixteenth-century specimen was less inbred or
568   domesticated than its current counterparts in Mexico. However, some South American

569 domesticated tomatoes had even higher heterozygosity, perhaps due to gene flow between
570 landraces and crop wild relatives (Michels, 2020).

571

Discussion

573 Recently, the chloroplast DNA of the En Tibi specimen was completely retrieved at high
574 coverage by Kakakiou (2021). Consequently, the En Tibi plastome was mapped to the
575 chloroplast genome of *S. lycopersicum* (NC_007898) and haplotype networks were constructed
576 using the Median-Joining (MJ) method and the accessions of the 360-tomato resequencing
577 project (Lin et al., 2014) to reveal the nearest relatives and give clues regarding its origin. The En
578 Tibi specimen was placed in the same node as all Mesoamerican individuals, together with some
579 Ecuadorian and Peruvian accessions of *S. lycopersicum* var. *cerasiforme* (Kakakiou, 2021).

580

581 The molecular research on the En Tibi tomato does not provide a definite answer to the exact
582 locality of its domestication, and it was impossible to appoint the En Tibi as a direct ancestor of
583 some modern tomato varieties. However, its predecessor likely came from Mesoamerica. The
584 latest study on the origin of domesticated tomatoes (Blanca 2021; Blanca et al. 2021) proposed a
585 domestication model considering that the wild forms of *S. lycopersicum* var. *cerasiforme* from
586 Mexico have travelled with indigenous people to South America, probably as a weed among
587 maize grains, where it hybridized with wild individuals of *S. pimpinellifolium*. This hypothesis
588 also considered that as part of the domestication process, people then started to select these
589 hybrids and took them back to Mexico, where they generated *S. lycopersicum* var. *lycopersicum*
590 with larger fruits. The Peruvian cherry tomato accessions that were close to the En Tibi tomato
591 were probably also cultivated, and carried some Mesoamerican ancestry that could reflect the
592 domestication model outlined by Blanca et al. (2021).

593

594 As more than 98% of its genome could not be read, it is impossible to reconstruct complete gene
595 sequences coding for taste or natural resistance to pest and diseases (Michels, 2020), despite
596 anticipation of this earlier (Van Santen 2012, De Boer, 2013). To reconstruct the 'original'
597 flavor, nutritional qualities and adaptations to the (a)biotic environment of sixteenth-century
598 tomatoes, assuming that these tomatoes possessed those traits and that they were lost through
599 intensive breeding for yield in modern cultivars (Klee & Resende, 2020), research should focus
600 on traditional landraces currently grown by small farmers in Central and South America that
601 most resemble historic varieties.

602

603 The accessions sequenced by Lin et al. (2014) in the 360-tomato project reflect centuries of
604 human migration and trade, which has caused extensive gene flow between tomato varieties. The
605 information was obtained from online genomic data, and germplasm institutes store very little
606 information on exact localities or morphological, nutritional and agronomical qualities of these
607 accessions or on the farmers that grow them. Moreover, this resequencing project did not capture
608 the entire tomato diversity in the Americas. Increased sampling of landraces in the Andes and

609 Mesoamerica is essential to fully characterize tomato diversity (Knapp & Peralta, 2016). With
610 decreasing crop diversity and the social, economic and ecological challenges faced by small
611 farmers of indigenous descent to preserve their traditional agricultural practices (Knapp &
612 Peralta, 2016; Petropoulos, Barros & Ferreira, 2019), tracing the 'sisters' of the En Tibi tomato
613 back to Mexican or Peruvian smallholders' gardens will be difficult. The landraces that were
614 genetically close to the En Tibi tomato were collected between 36 and 52 years ago: they may
615 have already disappeared from indigenous gardens and survive only as seeds in germplasm
616 institutes.
617

Conclusions

619 The earliest tomatoes that reached Europe came in a wide variety of colors, shapes and sizes:
620 with both simple and fasciated flowers, round and segmented fruits. The first description of a
621 tomato was published by Matthioli in 1544, while the oldest specimens were collected by
622 Aldrovandi and Petrollini in c. 1551 in the Pisa botanical garden. The earliest illustrations were
623 made in Germany and Flanders in the early 1550s. The names of early tomatoes in contemporary
624 manuscripts suggest both a Mexican and a Peruvian origin. The 'En Tibi' specimen was
625 collected by Petrollini around 1558 and thus is not the oldest extant tomato, although it is the
626 first specimen that shows a mature fruit. Although only 1.2% of its nuclear DNA was recovered,
627 molecular research on its genome and plastome shows that the En Tibi specimen was a fully
628 domesticated tomato, and genetically close to three Mexican landraces and two Peruvian tomato
629 accessions that most probably also had a Mesoamerican origin.
630

631 Molecular research on the other sixteenth-century tomato specimens may reveal additional
632 patterns of genetic similarity and geographic origin. Clues on the 'historic' taste and pest
633 resistance of the sixteenth-century tomatoes are difficult to find in their degraded DNA, but
634 should rather be sought in those landraces in Central and South America that are genetically
635 close to them. The indigenous farmers growing these traditional varieties should be supported to
636 conserve these heirloom varieties *in-situ*.
637

638 Sequencing the ancient DNA of the other nine sixteenth-century tomato specimens highlighted in
639 our paper may provide different but equally exciting snapshots of historic genetic variation. This
640 may lead to different, similar-looking landraces in either South- or Mesoamerica. Further
641 digitization, translation and online publication of Aldrovandi's manuscripts, archives of botanical
642 gardens and correspondence between Renaissance naturalists will probably reveal more details
643 on the first New World crops in Europe, their geographic origin and arrival date.
644

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661

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905   **Figure 1: All extant specimens of tomatoes in sixteenth-century herbaria, in chronological**
906   **order.** (A) Ulisse Aldrovandi (c. 1551), Vol 1, p. 368. The pair of leaves at the bottom of the
907   page belong to a *Citrullus*. Photo credit: University of Bologna. (B) Francesco Petrollini (pre-
908   1553) Photo credit: Biblioteca Angelica, Rome, c.49r, Erbario Cibo B, vol. 3. (C) Francesco
909   Petrollini (c. 1558), L.2111092, 'En Tibi tomato'. Photo credit: Naturalis, Leiden. (D) Leonhard
910   Rauwolf (1563), Photo credit: Naturalis, Leiden. (E) Caspar Bauhin (1577-1624) B15-075.2A.
911   Photo credit: Herbaria Basel, University of Basel. (F) Bauhin B15-075.2B_1. Photo credit:
912   Herbaria Basel, University of Basel. (G) Bauhin B15-075.2B_2. Photo credit: Herbaria Basel,
913   University of Basel. (H) Hieronymous Harder (1576-1594), Photo credit: Bayerische
914   Staatsbibliothek München, Cod.icon. 3, fol. 140v. (I) Ducale Estense herbarium (1570-1580),
915   Photo credit: Archivio di Stato di Modena. (J) Caspar Ratzenberger (1592), Photo credit:
916   Naturkundemuseum Kassel. Written permission to publish these images is provided in
917   Supplementary Figure 3.
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920   **Figure 2: Published and unpublished 16th century tomato illustrations, in chronological**
921   **order.** (A) Dodoens (1553), (B) Dodoens (1554), (C) Gesner (1553), image credit:
922   Universitätsbibliothek der FAU Erlangen-Nürnberg, MS 2386, 37v, (D) Gesner manuscript
923   (1553), image credit: Universitätsbibliothek der FAU Erlangen-Nürnberg, MS 2386, 42r, (E)
924   Fuchs (1549-1556-1561), image credit: Österreichische Nationalbibliothek, (F) Domenico Dalle
925   Greche / Michiel (1550-1576), image credit: Biblioteca Marciana, (G) Oellinger manuscript
926   (1553: 541), image credit: Universitätsbibliothek der FAU Erlangen-Nürnberg, MS 2362, 541,
927   (H) Oellinger (1553: 543), image credit: Universitätsbibliothek der FAU Erlangen-Nürnberg, MS
928   2362, 543, (I) Oellinger (1553: 545), image credit: Universitätsbibliothek der FAU Erlangen-
929   Nürnberg, MS 2362, 545, (J) Libri Picturati (1565-1569) A f(olio) 81r, image credit: Jagiellonian
930   library, (K) Libri Picturati A 28 f(olio) 81v, image credit: Jagiellonian library, (L) De Lobel
931   (1572), (M) Camerarius (1586: 821), (N) Camerarius (1590: 378), (O) Bauhin (1598). Written
932   permission to publish these images is provided in Supplementary Figure 3.
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935   **Figure 3: Results of the Neighbor Net clustering analysis, showing the genetic similarity of**
936   **the wild relatives and the domesticated tomato specimens analyzed by Michel (2020).** (A)
937   Wild individuals of *S. pimpinellifolium* and *S. lycopersicum* L. var. *cerasiforme* from Peru (green
938   circles) and Ecuador (bright green circles) show a high genetic diversity (left of the figure), while
939   a dense cluster of domesticated, genetically less diverse tomatoes is visible on the right, which
940   includes the En Tibi specimen. (B) Enlargement of the cluster with domesticated tomatoes from
941   Figure 3A, showing the nearest neighbors of the En Tibi tomato (dark gray circle), indicated with
942   a red arrow. All distances expressed in Kimura 2-parameter substitutional distance; parsimony-
943   uninformative SNPs excluded. Image credit: Ewout Michels and Rutger Vos.
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953 **Supplementary Figure 1: Drawing of *Solanum aethiopicum* in the manuscript of Pietro**
954 **Antonio Michiel (1510-1576).** Artist unknown, manuscript: *I cinque libri di piante. Codice*
955 *Marciano, 1551-1575*. Image credit: Biblioteca Marciana, Venice.
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958 **Supplementary Figure 2: Specimen of *Solanum aethiopicum*, collected by Caspar Bauhin**
959 **between 1577 and 1624.** Image credit: Herbaria Basel, University of Basel.
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962 **Supplementary Figure 3: Written permission of the various herbaria and libraries to**
963 **publish the images of the specimens and illustrations.**
964

Table 1

Sixteenth-century descriptions, specimens and illustrations of the tomato, ordered by author and chronologically.

1 **Table 1: Sixteenth-century descriptions, specimens and illustrations of the tomato, ordered by author and chronologically.**

Author (birth-death year) *Title of source*	Year of publication(s) with online links	Representation	Names
Pietro Andrea Matthioli (1501-1578) *Commentaries on Dioscorides*	1544, 1548, 1549, 1554, 1557-1560, 1562, 1565, 1568	Text	'another species' [of eggplant] (1544, 1548); pomi d'oro, mala aurea (1554 onwards)
Anonymous *Pisa garden catalogue*	1545-1548? De Toni (1907: 439)	Text	Thumatulum pomum vulgo dictum rubrum et luteum
Vincenzo Ferrini (Pisa) to Pier Francesco Riccio (Florence) *Letter about showing tomatoes to Cosimo I*	31 October 1548 López-Terrada (n.d.)	Text	pomidoro
Ulisse Aldrovandi (1522–1605) *Herbarium*	1551, herbarium vol. 1, fol. 368	Herbarium specimen	Pomum amoris. Mali insani species. Tembal quibusd.
Bologna public garden plant catalogue	1568-1582		Tumatl. seu Pomum amoris quibusdam
Rembert Dodoens (c. 1517-1585) *De stirpium historia… Cruydeboeck*	1553: 428 1554: Part III, chapter 82: 471	Uncolored woodcut, text Colored woodcut, text	pomum amoris, pomum aureum, Goldt apffel, guldt appel, pome d'amours poma amoris, gulden appelen
Leonhard Fuchs (1501-1566). Manuscript, Vienna Codex 11, 122, p. 159 (text), 161 (drawing)	1549-1556 (-1561) Partly published (Meyer, Trueblood & Heller, 1999; Baumann, Baumann & Baumann-Schleihauf, 2001).	Text, watercolor drawing	malus aurea, pomum luteum/rubrum/ croceum, goldt Apffelkraut, pomme d'amour
Georg Oellinger (1487–1557) *Magnarum Medicinae partium herbariae* .... (manuscript).	c. 1553, f. 541, 543, 545 Partly published by Lutze & Retzlaff (1949)	Watercolor drawings	Mala aurea seu Poma amoris; Poma amoris maiora Lutea ;
Conrad Gesner (1516-1565) *Historia plantarum* (manuscript)	1553 (22 September) p. 37 verso, p. 42 recto	Watercolor drawings	Pomo amoris vel aurea, Goldöpfel, pomi d'oro

Pietro Antonio Michiel (1510-1576), I *Cinque Libri di Piante*, vol. 3 (Libro Rosso 1: nr. 46 (illustration possibly by Domenico Dalle Greche)	1550-1576 Partly published by DeToni (1940)	Text, watercolor drawing	Licopersicon Galeni, pomodoro da volgari, melongiana da latini, Poma amoris; Poma del Peru. 'If I should eat of this fruit, cut in slices in a pan with butter and oil, it would be injurious and harmful to me' (McCue, 1952)
Francesco Petrollini *Erbario B*: Vol. 3, nr.722	before 1553	Herbarium specimen, text (in index)	Malus insana. Mandragorae species. Poma amoris
Francesco Petrollini En Tibi herbarium	c. 1558: Nr. 294	Herbarium specimen	Puma Amoris
Anguillara (Luigi Squilerno, 1512-1570) *Semplici*….	1561: 217 written between 1549-1560	Text	Lycopersico di Galeni Pomi d'oro, Pomi del Perù
Leonhard Rauwolf (1535-1596), *herbarium*	1563	Herbarium specimen	Poma aurea
Ducale Estense (anonymous, herbarium)	1570-1598: nr. 142	Herbarium specimen	Pomi di Ettiopia ouer pomi d'oro
Mathias De Lobel (Lobelius, 1538-1616) *Stirpium Adversaria Nova Plantarum seu stirpium historia Kruydtboeck*	1571: p. 108 1576: p. 108 1581: 331-332	Text Text Text, uncolored woodcut	Poma amoris, Pomum aureum, Lycopersiumc quorumdam, an Glaucium Dioscoridis?, Golt opffel, Gulden appelen, Pommes dorées, Gold apel. Memita of the Arabs?, Pommes d'orées, Gold appel
Melchior Wieland (Guilandinus, 1520-1589), *Papyrus*…. (1572)	1572: 90-91	Text	Americanorum tumatle Tumatle ex Themistithan
Hieronymous Harder (1523-1607).	1576-1594	Herbarium specimen, drawing	Solanum marinum alii Poma amoris, Portugalischer nachtschatt
Andrea Cesalpino (1519-1603) *De plantis Libri XVI*	1583, lib. IV: 211	Text	Mala insana rotundiora, specie Mali Appii, specie Malii rosei

Libri Picturati (1565-1569?)	A28.080, A28.080v	Two drawings	Pomme d'amour, pomum amoris,
Joachim Camerarius the Younger (1534-1598) edited version of Matthioli's *Commentaries*	1586: 821 1590: 378-379	Uncolored woodcut Colored woodcut	Poma amoris Goldöpffel, Poma aurea, Amoris poma, Lycopersico, pomme d'amours, pomi d'oro
Caspar Ratzenberger (1533-1603) *Herbarium* Vol. 3: 490-PICT0240	1556-1592	Herbarium specimen	Pomidoria, poma aurea, Lieboepffel, Goldoepffel
Caspar Bauhin (1560-1624) *Phytopinax*	1596: p. 302-303	Text	Solanum pomiferum fructu rotundo, striato, molli. Poma amoris & Pomum aureum Dodon.
Caspar Bauhin, edited version of Matthioli's *Commentaries*	1598: 761	Text, uncolored woodcut	Citing many names used by others and Poma Peruuiana Anguil[lara]
Caspar Bauhin (1560-1624)	1577-1624	Herbarium specimen + label B15-075.2A	Solanum pomiferum fructu molli C.B. Aurea mala, Dodo. Poma amoris Lob. Cam. Apud Matth. Tab. Basileae ex horto.
Caspar Bauhin (1560-1624)	1577-1624	Herbarium specimen + label B15-075.2B_1_	Solanum pomiferum fructu rotundo striato molli, C. Bauh. Lycopersicon Galeni, Anguillar. Poma amoris, Dod. Gal. Lob. Tab. 403. 2. Ex hortulo nostro.
Casper Bauhin (1560-1624)	1577-1624	Herbarium specimen + label B15-075.2B_2	Solanum pomiferum fructu rotundo striato molli, C. Bauh. Lycopersicon Galeni, Anguillar. Poma amoris, Dod. Gal. Lob. Tab. 403. 2. Ex hortulo nostro.

Table 2

Morphological characters of early sixteenth-century tomatoes mentioned in descriptions or visible in herbarium specimens and illustrations, arranged chronologically.

1 **Table 2: Morphological characters of early sixteenth-century tomatoes mentioned in**
2 **descriptions or visible in herbarium specimens and illustrations, arranged chronologically.**

Author / artist (year)	Collection	Flowers	Fruit shapes	Fruit colors
Matthioli (1544)	Description	-	'Segmented'	'Blood red, gold'
Aldrovandi (1551)	Specimen	Simple	No fruit	-
Petrollini (pre-1553)	Specimen	Simple	Small immature fruit	-
Fuchs (1549-1556/1561)	Description, drawing	Simple and fasciated ('9 petals')	Either spherical or oblong, smooth or deeply grooved	Golden, saffron, red, striped, whitish-yellow
Dodoens (1553)	Description, uncolored woodcut	Fasciated	Ribbed, round, somewhat flattened	Red, yellow or whitish
Dodoens (1554)	Description, colored woodcut	Fasciated	Ribbed, round, somewhat flattened	Red
Gesner (1553)	Color drawings	Fasciated, single?	Round and smooth; elongated and ribbed	Red, white, yellow, brown
Oellinger (1553)	Color drawings	Fasciated and simple	Ribbed and segmented Round and smooth	Red, orange, yellow, whitish?
Petrollini (1558)	Specimen L.2111092	Simple	Round, smooth	Red
Michiel / Dalle Greche (1553-1565)	Color drawing	Simple	Spherical, elongated, ribbed, smooth	Red, yellow
Rauwolf (1563)	Specimen	Simple	No fruit	-
De Lobel (1581)	Text, uncolored woodcut	Fasciated	Ribbed, round, flattened, 'big like oranges'	Red, yellow
Camerarius (1586, 1590)	Description, (un)colored woodcut	Fasciated, white	Ribbed/ segmented, elongated	'Red, golden yellow, brown, some very big'
Bauhin (1598)	Description, uncolored woodcut	Fasciated, white, yellow	Ribbed, round, flattened, hairy	'varying in color'
Harder (1576–1600)	Specimen+drawing	Simple	Round, smooth	Red
Libri Picturati (1565-1569?)	Drawings	Fasciated	Round, flattened, ribbed	Red
Cesalpino (1583)	Description	White	Round, elongated and ribbed/furrowed	Golden, red

Bauhin (1577-1624)	Specimen B15-075.2A	Fasciated?	No fruit	-
Bauhin (1577-1624)	Specimen B15-075.2B_1	Fasciated	No fruit, label description: ribbed, round, soft	-
Bauhin (1577-1624)	Specimen B15-075.2B_2	Fasciated	No fruit, label description: ribbed, round, soft	-
Bauhin (1596)	Description	-	Ribbed, round, soft, some suppressed and wider	Golden yellow (most), some red, pink, white (rare)
Bauhin (1598)	Uncolored woodcut	Fasciated	Ribbed, round, soft	-
Ducale Estense (1570-1598)	Specimen	Fasciated	No fruit	-
Ratzenberger (1556-1592)	Specimen	Fasciated?	Round	Red?

Tomato landraces close to the En Tibi tomato (c. 1558), in order of genetic similarity

1 **Table 3: Tomato landraces close to the En Tibi tomato (c. 1558), in order of genetic**
2 **similarity**

Identifier Michel (2020)	TGRC nr. (link)	Morphological traits (TGCR database)	Geographical origin (TGCR database)	Collection year
B-153 big fruits	LA-1544	Ribbed tomatoes	Mexico: market Xol Laguna, Laguna Encantada, Campeche, Mexico.	1973
B-249 big fruits	LA-1462	Large fruit, kidney shaped, purple	Merida, Yucatan, Mexico	1971
C-233 cherry tomato	LA-1218	Small yellow fruit (1-1.5 cm).	Veracruz, Mexico	1969
C-61 cherry tomato	LA-2670	Large hairy plant, simple flowers, fruits multi-loculed, 2 cm.	Family garden, 19.5 km from San Juan del Oro, Huayvaruni-2, Rio Tambopata, Puno, Peru	1984
C-281 cherry tomato	LA-1286	Medium-sized, hairy plant, flowers very tiny, fruits various sizes.	0,5 km N of San Martin de Pangoa, Junin, Peru	1970

Figure 1

All extant specimens of tomatoes in sixteenth-century herbaria, in chronological order.

(A) Ulisse Aldrovandi (c. 1551), Vol 1, p. 368. The pair of leaves at the bottom of the page belong to a *Citrullus*. Photo credit: University of Bologna. (B) Francesco Petrollini (pre-1553) Photo credit: Biblioteca Angelica, Rome, c.49r, Erbario Cibo B, vol. 3. (C) Francesco Petrollini (c. 1558), L.2111092, 'En Tibi tomato'. Photo credit: Naturalis, Leiden. (D) Leonhard Rauwolf (1563), Photo credit: Naturalis, Leiden. (E) Caspar Bauhin (1577-1624) B15-075.2A. Photo credit: Herbaria Basel, University of Basel. (F) Bauhin B15-075.2B_1. Photo credit: Herbaria Basel, University of Basel. (G) Bauhin B15-075.2B_2. Photo credit: Herbaria Basel, University of Basel. (H) Hieronymous Harder (1576-1594), Photo credit: Bayerische Staatsbibliothek München, Cod.icon. 3, fol. 140v. (I) Ducale Estense herbarium (1570-1580), Photo credit: Archivio di Stato di Modena. (J) Caspar Ratzenberger (1592), Photo credit: Naturkundemuseum Kassel. Written permission to publish these images is provided in Supplementary Figure 3.
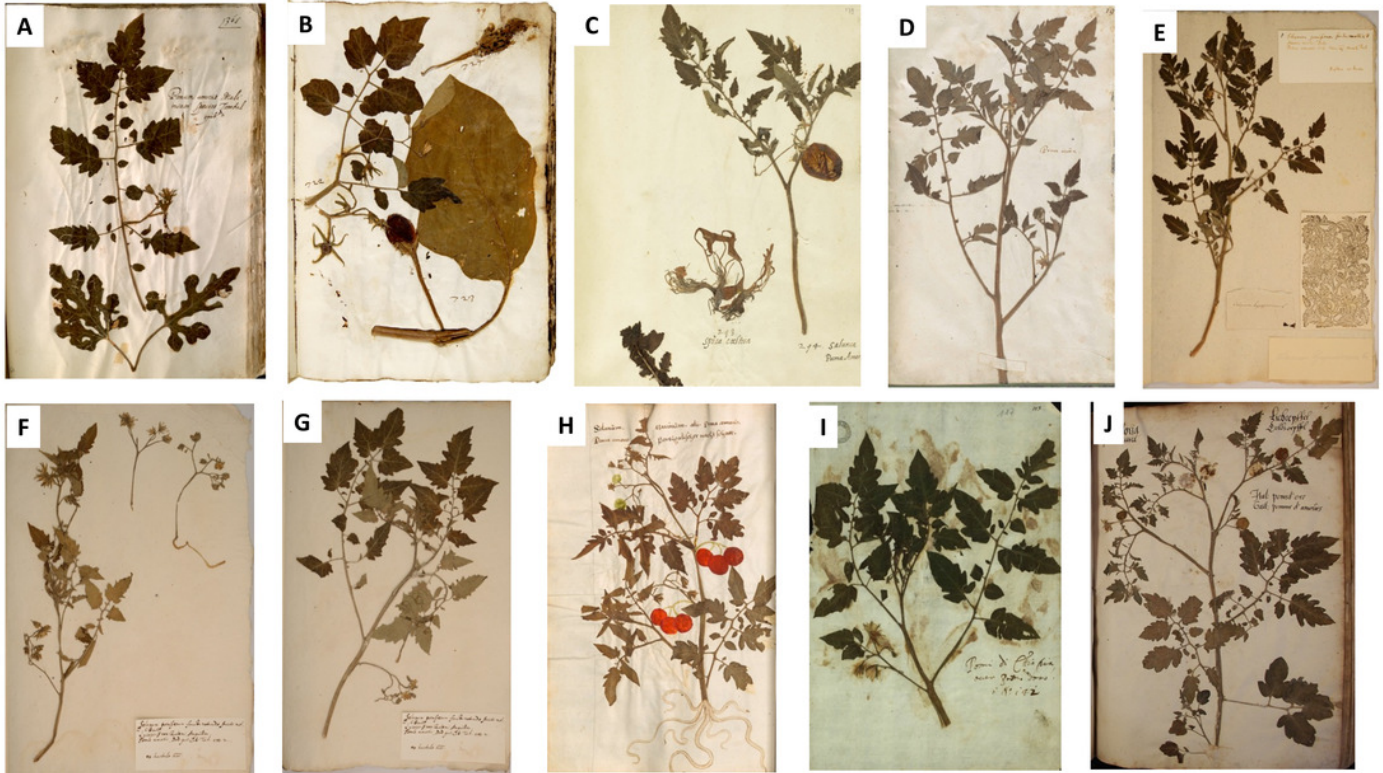
Figure 2

Published and unpublished 16th century tomato illustrations, in chronological order.

(A) Dodoens (1553), (B) Dodoens (1554), (C) Gesner (1553), image credit:
Universitätsbibliothek der FAU Erlangen-Nürnberg, MS 2386, 37v, (D) Gesner manuscript
(1553), image credit: Universitätsbibliothek der FAU Erlangen-Nürnberg, MS 2386, 42r, (E)
Fuchs (1549-1556-1561), image credit: Österreichische Nationalbibliothek, (F) Domenico
Dalle Greche / Michiel (1550-1576), image credit: Biblioteca Marciana, (G) Oellinger
manuscript (1553: 541), image credit: Universitätsbibliothek der FAU Erlangen-Nürnberg, MS
2362, 541, (H) Oellinger (1553: 543), image credit: Universitätsbibliothek der FAU Erlangen-
Nürnberg, MS 2362, 543, (I) Oellinger (1553: 545), image credit: Universitätsbibliothek der
FAU Erlangen-Nürnberg, MS 2362, 545, (J) Libri Picturati (1565-1569) A f(olio) 81r, image
credit: Jagiellonian library, (K) Libri Picturati A 28 f(olio) 81v, image credit: Jagiellonian library,
(L) De Lobel (1572), (M) Camerarius (1586: 821), (N) Camerarius (1590: 378), (O) Bauhin
(1598). Written permission to publish these images is provided in Supplementary Figure 3.
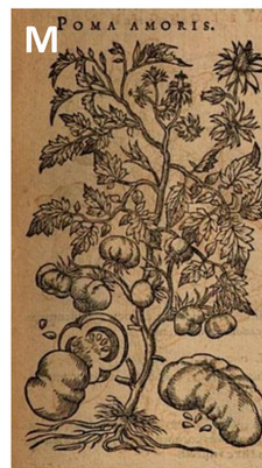
Figure 3

Results of the Neighbor Net clustering analysis, showing the genetic similarity of the wild relatives and the domesticated tomato specimens analyzed by Michel (2020).

(A) Wild individuals of *S. pimpinellifolium* and *S. lycopersicum* L. var. *cerasiforme* from Peru (green circles) and Ecuador (bright green circles) show a high genetic diversity (left of the figure), while a dense cluster of domesticated, genetically less diverse tomatoes is visible on the right, which includes the En Tibi specimen. (B) Enlargement of the cluster with domesticated tomatoes from Figure 3A, showing the nearest neighbors of the En Tibi tomato (gray circle). All distances expressed in Kimura 2-parameter substitutional distance; parsimony-uninformative SNPs excluded.