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What did 16th-century tomatoes look like?

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Soon after the Spanish conquest of the Americas, the first tomatoes were presented as curiosities to the European elite and drew the attention of 16th-century Italian naturalists. Despite their scientific interest in this New World crop, most Renaissance botanists did not specify where these "golden apples" or "pomi d'oro" came from. It is likely that tomatoes were brought to Europe after the Spanish sieged the Aztec city of Tenochtitlan (now Mexico City) in 1521 and after they conquered the Peruvian Inca emperors in 1531. Tomatoes and other New World domesticates must have been brought to the Spanish court, and were probably planted in the royal gardens in Madrid, after which they were likely shipped from Sevilla to Italy, but no written evidence have been found so far for these events. The debate on the first European tomatoes and their origin is often hindered by erroneous dating, botanical misidentifications and inaccessible historical sources. So, who saw the first 16th-century tomatoes that entered Europe? What did they look like? Who made the first botanical description, collection and/or illustration? And where did these tomatoes come from?

Recent digitization efforts greatly facilitate research on historic botanical sources. Van Andel et al. (2022) provide an overview of the ten remaining 16th-century tomato specimens, early descriptions and 13 illustrations. Several of these specimens, descriptions, garden inventories and illustrations had never been digitized and/or published before. The historical findings are compared to recent molecular research on the ancient chloroplast and nuclear DNA of the tomato specimen in the "En Tibi book herbarium" (Vos et al. 2022), dated around 1558 and produced in Bologna by the Italian botanist Francesco Petrollini, and by some claimed to be the oldest tomato specimen.

Our survey showed that the earliest tomatoes in Europe came in a much wider variety of colors, shapes and sizes than previously thought, with both white and yellow, simple and fasciated flowers, round and segmented fruits in various colors. Pietro Andrea Matthioli gave the first description of a tomato in 1544, and the oldest specimens were collected by Ulisse Aldrovandi (Fig. 1) in c. 1551 and Francesco Petrollini (Fig. 2), possibly from plants grown in the Pisa botanical garden by their teacher Luca Ghini. The "En Tibi" specimen thus is not the oldest extant tomato. Due to the close network of Renaissance

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Fig. 1. Tomato specimen by Aldrovandi, Bologna, c. 1551.



Fig. 2. Specimen by Petrollini in the "En Tibi" herbarium, c. 1558.



Fig. 3. Specimen by Caspar Bauhin (1577–1624), Basel.

botanists, tomato seeds rapidly spread to northwest Europe, and also were planted in Caspar Bauhin's garden in Basel. The oldest tomato illustrations were made in the early 1550s in Germany (by Leonhard Fuchs and Georg Oellinger) and Switzerland (by Conrad Gessner), but the Flemish Rembert Dodoens published the first image in 1553. The names of early tomatoes in contemporary manuscripts varied a lot but some suggest a Mexican and others a Peruvian origin.

DNA analysis of the 464-year-old "En Tibi" specimen recovered only 1.2 % of its genome, but still showed that it was a fully domesticated tomato. It clustered neatly with the domesticated tomatoes in a comparison with genome assemblies of 114 accessions of wild species and traditional cultivars from Latin America that were retrieved from an earlier published 360-tomato resequencing project. The "En Tibi tomato" was genetically close to three Mexican landraces and two Peruvian specimens that probably also had a Mesoamerican origin.

Molecular research on the other 16th-century tomato specimens may reveal other patterns of genetic similarity, past selection processes, and geographic origin. Clues on the "historic" taste and pest resistance of the 16th-century tomatoes should be sought in those landraces in Central and South America that are genetically close to them. With decreasing crop diversity and the social, economic and ecological challenges faced by small farmers of indigenous descent to preserve their traditional agricultural practices, 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. The indigenous farmers growing traditional tomato varieties should be supported to conserve these heirloom varieties in-situ.

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