Untangling the origin of *Cucumis sativus* and *Cucumis melo* and their dissemination into Europe and beyond

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Writer's Comment: In Professor Gepts' course on the evolution of crop plants I learned about the origins and patterns of domestication of many crops we consume and use today. As this was the only plant biology course I took during my time at UC Davis, I wasn't sure what to expect. We were assigned to write a term paper on the origin of domestication of a crop of our choosing. Upon reading the list of possible topics I noticed a strange pairing, cucumber/melon. I thought that it was just a typing error, but to my surprise cucumbers and melons are closely related and from the same genus. I wanted to untangle the domestication history of the two crops, and I quickly learned that uncovering the origins requires evidence across many different disciplines. Finding the origin of a crop is challenging; as new evidence from different fields comes forward, the origins of domestication often shift.

Instructor's Comment: In a predominantly urbanized and developed society like California, agriculture—let alone the origins of agriculture—is an afterthought. Yet, the introduction of agriculture some 10,000 years ago represents one of the most significant milestones in the evolution of humanity. Since then, humans and crops have developed a symbiotic relationship of mutual dependency for continued survival. In her term paper, Aimee Levinson describes in a lucid and succinct way the domestication and subsequent dissemination of two related crops, cucumber and melon. The challenge in this endeavor is that the topic is not amenable to direct observation given the occurrence of key events in the, sometimes distant, past. Instead, science

reconstructs the past using different types of evidence, such as genetic, archaeobotanical, historical, and linguistic to develop a, hopefully, consistent scenario. Aimee used this approach to compare and contrast the origins and subsequent dispersal of melon and cucumber, two crops that add culinary pleasures to our daily meals.

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Abstract

The Cucurbitaceae family contains some of the earliest domesticated crops in the world. Evidence that *Cucumis sativus* was domesticated in India near the Himalayas has been consistent in the literature. However, finding the origin of domestication of *Cucumis melo* has been more challenging. Scientists and historians were certain that *C. melo* originated in Africa alongside *Citrullus lanatus* (watermelon) and other wild *Cucumis* plants of the same ploidy; however, recent DNA data has shown that it is more probable that *C. melo* was a part of an Asian or Australian clade and originated in India near the Himalayas as well. *C. sativus* and *C. melo* were once considered to be closely related based on morphological data, but newer genetic research has proven that they are phylogenetically more distant. The dissemination of cucumbers and melons into Europe and beyond has also been debated. Cucumbers seemed to be common and widespread throughout Europe and the Mediterranean Basin during the times of the ancient Greeks and Romans, but historical and linguistic evidence has shown that cucumbers were wrongly identified and that various ancient painting and writings actually depict variations of oblong vegetable melons. Using a combination of historical, linguistic, genetic, and botanical evidence has allowed researchers in the field to untangle and better understand the origin of domestication, routes of dissemination, and relatedness of *C. melo* and *C. sativus*.

Introduction

Cucumber (*Cucumis sativus*) and melon (*Cucumis melo*) are both widely cultivated crops within the large Cucurbitaceae family. The

Cucurbitaceae family, also referred to as cucurbits and the gourd family, consists of 118 genera and 800 species, making it one of the most genetically diverse groups of plants (Weng and Sun 2012; Robinson and Decker-Walters 1997). Cucurbits are distributed throughout the equatorial tropical and subtropical regions in both the new and old world; while some species grow in mild temperate regions, none of them are frost-tolerant (Pitrat et al 1999; Robinson and Decker-Walters 1997). There are five primary genera: *Cucurbita* (squash, pumpkin, zucchini, and gourds), *Lagenaria* (mostly inedible gourds), *Luffa* (fruit used as scrubbing sponges), *Citrullus* (watermelon), and *Cucumis* (cucumbers, melons, gherkins) (Courteau 2011). The fruits produced from cucurbits, extremely diverse in size, shape, color, and ornamentation, are technically called pepos because they have hard rinds, fleshy pulp, and many flattened seeds (Robinson and Decker-Walters 1997). The cucurbitaceae family also holds the world record for heaviest and largest fruit, with a cultivated pumpkin weighing in at 2624.6 lbs in 2016 (Giantpumpkin.com). Following tomatoes and onions, cucumbers and melons are some of most widely cultivated vegetable crops in the world (Pitrat et al 1999).

C. sativus are annuals primarily grown as a vine winding up trellises, but can be grown as a bush for home gardens (UC Davis 2012). Cucumbers are a common botanical fruit eaten as a vegetable worldwide; 80% of cucumbers are produced in Asia, followed by 10.6% in Europe, and 4.3% in the Americas (fao.org/faostat). Picked while still immature, cucumbers are often sliced and eaten fresh, or pickled (Weng and Sun 2012). There are almost 100 varieties of cucumbers; the most common varieties include English, Persian, and kirby (UC Davis 2012). C. sativus was originally a monoecious plant, producing both male and female yellow-hued flowers on the same plant, but selection has led cultivars to become gynoecious, where the plants are predominantly female and produce only a small proportion of male flowers, allowing for greater yield (Nonnecke 1992; Couteau 2011). Most *C. sativus* plants are self-incompatible and are pollinated by bees (Nonnecke 1992). Cucumbers are 95% water and have little nutritional value, but are valued for their fresh taste and crisp texture (Robinson and Decker-Walters 1997). They have also been used as an anti-inflammatory in traditional medicine (Robinson and Decker-Walters 1997). Cucumbers have not changed very much in many centuries, but have been selected to increase yield, decrease bitterness, and increase resistance to pathogens such as cucumber

mosaic virus (Nonnecke 1992).

C. melo are known as melons, musk melons, sweet melons, and a variety of other names (Nonnecke 1992). This is the most diverse group within the genus *Cucumis*, showing great morphological and physiological variation among varieties (Esteras et al 2012). Some melons have netted rinds while others are smooth. The rind colors range from green, white, yellow, and tan, and the flesh color can be green, pink, orange or white (Robinson and Decker-Walters 1997). Typically, melons are harvested as mature fruit when sugars are present, but some varieties are grown for their young and immature fruit (Paris et al 2011). *C. melo* is also a tendril-bearing annual vine that twines around any nearby support (Paris et al 2011). Like most cucurbits, melons grow best in the heat and are extremely sensitive to frost (Robinson and Decker-Walters 1997). In addition, they are highly susceptible to the same diseases as cucumber. For the most part *C. melo* is andromonoecious, predominantly staminate with hermaphroditic yellow flowers, unlike *C. sativus* (Nonnecke 1992). *C. melo* cannot cross with *C. sativus*, but all members of *C. melo* can cross with each other, producing numerous varieties of melons and making it more difficult to untangle the center of origin and routes of dissemination (Lovegren 2016).

Results and Discussion

The centers of origin and routes of dissemination of *Cucumis sativus* and *Cucumis melo* have been difficult to correctly identify due to confusion of archaeobotanical remains (fossilized seeds of melon and cucumber cannot be well distinguished), African-biased genetic phylogenies, and misinterpretations of ancient paintings and writings (Lovegren 2016; Sebastian et al 2010). It was thought for many years that *Cucumis melo* originated in Africa due to the numerous wild African *Cucumis* species, but recent research has shown that it is included in a clade from Asia/Australia and thus originated in India (Sebastian et al 2010). By contrast, it is quite certain in the literature that *Cucumis sativus* originated in India because wild cucumbers grow on the Indian subcontinent and a closely related species grows in the Eastern Himalayas (Sebastian et al 2010).

De Candolle (1886) wrote that the *Cucumis sativus* center of domestication can most likely be located in India, in turn spreading towards China in the east. Wild cucumbers have been found over

much of the Indian subcontinent and cultivated cucumbers have been dispersed throughout China from 2,000 years ago (Paris 2016; Paris et al 2011). The genetic Indian germplasm of *C. sativus* is heterogeneous; there is great genetic diversity in Indian varieties compared to cucumbers in the rest of the world (Lv et al 2012). It is likely that cucumbers were domesticated on the Indian subcontinent by 3,000 BC and that China was a secondary center of genetic diversification of *C. sativus* (Esteras et al 2012). Documented Chinese history explains that cucumbers were introduced from India via the Silk Road by Zhang Qian, a Chinese diplomat, and was selected on by Chinese farmers for over a thousand years (Lv et al 2012). This helps explain the huge genetic differentiation of *C. sativus* in China (Lv et al 2012).

For a long time, historians assumed that *C. sativus* was common in the ancient Mediterranean societies of the Greeks, Romans, Egyptians and Jews; however, it is now known that they were eating a vegetable variation of *C. melo,* not *C. sativus* (Paris et al 2011). *C. sativus* only arrived to the Mediterranean Basin and Europe sometime in the medieval period between 500 and 1150 CE, about the time of Islamic conquests (Esteras et al 2012; Paris et al 2011). Cucumber was introduced into Europe by at least two independent diffusions. One diffusion was via the Silk Road through Persia and into eastern and northern Europe and the other was via sea from Persia or the Indian subcontinent into western and southern Europe (Paris et al 2011). In a study using 23 highly polymorphic SSR microsatellite markers on a large cucumber collection, results showed that independent migrations of *C. sativus* out of India to other parts of the world have occurred and that three distinct populations correlate with geographic regions (Lv et al 2012). One population is from China; another includes Europe, America, Central and West Asia; the last, and most diverse, is in India and the Xishuangbanna, an area within southernmost China (Lv et al 2012). The first realistic iconography of *C. sativus* in the Mediterranean region dates to around 1335 in the Manfred de Monte Imperiali from Pisa, Italy (Paris and Janick 2008; Paris et al 2011). Images from French and Italian manuscripts of late medieval time period are very detailed, allowing researchers to accurately assess the fruit and to determine the presence of *C. sativus* (Paris et al 2011).

The phylogenetic placement of cucumber has been disputed. Taxonomical studies showed that *C. sativus* is an offshoot in the evolution of *C. melo* (Mallick and Masui 1985), but this was later discredited.

Research at the University of Munich asserted that previous phylogenetic work had been biased towards African origin by excluding some Australian relatives (Sebastian et al 2010). Since *C. sativus* and *Cucumis sativus* var. *hardwickii* are the only cucurbits that have 7 (2n=14) chromosomes, researchers believed that *C. sativus* var. *hardwickii*, a Chinese species first found in the Himalayan foothills of Nepal, may be the wild progenitor (Pitrat et al 1999; Robinson and Decker-Walters 1997). Others believe that *C. sativus* var. *hardwickii* is a feral derivative and that *Cucumis sativus* var. *hystrix*, a Southeastern Asian species, may be the wild progenitor to cucumber as they are morphologically similar (Hancock 2012). DNA sequencing of plastid and nuclear markers for about 100 *Cucumis* species show that *C. sativus* var. *hystrix* is in fact the closest relative to *C. sativus*—their divergence is 8 million years old according to molecular clock data—which further suggests that cucumber is of Indian/Asian origin (Weng and Sun 2012, Sebastian et al 2010, Renner et al 2007).

Melons have been cultivated for several thousand years (Robinson and Decker-Walters 1997). The center of origin and region of domestication for *Cucumis melo* has been more difficult to identify than that of *C. sativus*. Nineteenth-century taxonomists thought *C. melo* was likely to have been domesticated in Asia/India because melons had been cultivated there for centuries and many inedible forms grow wild in India (Robinson and Decker 1997). More modern authorities on the matter asserted for many years that melons originated in Africa alongside *Citrullus lanatus* and many wild melons. They backed up this claim with historical records, archeological remains, and chromosomal number comparisons until new research was found in the last few years (Robinson and Decker 1997; Lovegren 2016). *C. melo* has 12 basic chromosomes (2n=24), just like many other African melon types, so it was assumed to have African origin and that it was traded early on to Asia (Weng and Sun 2012; Kerje and Grum 2000). The comparative plasmid and nuclear DNA work of Sebastian et al (2010) at the University of Munich showed that the wild progenitor of *C. melo* occurs in India, not Africa.

Archaeobotanical remains of the *Cucumis genus* are few and far between as the seed coats are thin and the fruits do not have lignified rinds (Paris 2016). Seeds of the *Cucumis* genus have been found, but distinguishing *C. melo* and *C. sativus* fossilized seeds from one another has proven to be difficult (Robinson and Decker-Walters 1997). Some of the earliest melon remains were found in the Indus Valley of India from

2300 BC and 1600 BC and in western central India around the year 1600 BC (Lovegren 2016). Melon seeds from 3000 BC have been found in the "Burnt City" of southeastern Iran, one of the first cities in human history and a major center of diversification of crops, suggesting that *C. melo* spread rather quickly from India to Iran (Lovegren 2016). However as previously stated, melons do not preserve well and it is unclear if the seeds were truly *C. melo*. Melon seeds have also been discovered in the Chinese provinces of Zhejiang and Shaanxi dating back to 3000 BC and 2000 BC, respectively (Lovegren 2016). This demonstrates the early dissemination of melons from India into China, where they became a very important fruit. However, these seeds may be from the conomon melon, an oriental pickling melon that was domesticated in China (Lovegren 2016; Robinson and Decker-Walters 1997). Evidence from an autopsy of a mummified woman from the Han dynasty show that her stomach was full of *C. melo* melon seeds, proving that at the latest, melons were present in China by 206 BC to 220 AD (Lovegren 2016).

De Candolle (1986) explained the importance of using linguistic data to better understand the origin and domestication of crops; however, in the study of cucurbits, linguistic data has been misleading at times (Paris and Janick 2008). The Munda—aboriginal inhabitants of India—had many words for *C. melo* melons. Sanskrit-speaking Indo-Aryans began to move into India during the 1st and 2nd millennium BC and adopted the Munda words for melons including *carbhatah* and *cirbhita* (Lovegren 2016). These words are the root of the Latin word *cucurbit* (Paris and Janick 2010-2011). Although archaeobotanical evidence of melon in Persia is lacking, much linguistic data shows that Persians were familiar with the fruit (Lovegren 2016). When the Persians invaded India in 5th century BC, they adapted the Munda/Sanskrit word *carbhatah* into the Persian word for melon *kharbuz(a)* and supposedly brought *C. melo* back with them into Persia (Lovegren 2016).

Linguistic and historical data becomes even more confusing when trying to decipher if it was *C. melo* or *C. sativus* present in ancient Mediterranean civilizations. Until recently, it was assumed that cucumbers were widespread throughout these civilizations. A lot of the confusion comes from assuming that the Latin word *cucumis* is the same as cucumber, and while cucumis is indeed the root of the word, it is not always describing cucumbers but, rather, melons (Paris and Janick 2010-2011). In addition, depictions Cucurbits in these ancient

civilizations have been misinterpreted as cucumbers because of their oblong cucumber-like shape (Paris and Janick 2010-2011).

First-century Roman authors such as Columella and Pliny wrote in Latin of *cucumis*, which had been translated into English as "cucumbers," but they described *cucumis* as snake-like and hairy (Paris and Janick 2010-2011). It is common knowledge among botanists that immature melons are pubescent, covered in short soft hair, while cucumbers are glabrous, free of hair and smooth (Robinson and Decker-Walters 1997; Paris and Janick 2010-2011). It seems that Columella and Pliny were describing a vegetable melon, either a snake melon, *C. melo* var. *flexuosus*, or a chate melon, *C. melo* var. *chate*, rather than *C. sativus* (Lovegren 2016). In a city near Pompeii destroyed by the eruption of Mount Vesuvius in 79 CE, a partially preserved fresco depicts striped snake melons in a glass jar, showing that the melons of this time were pickled in addition to being eaten fresh (Paris and Janick 2010-2011). Ancient Greek writings by the philosopher and botanist Theophrastus describes *sikyos* as a crop having some sterile flowers that grow on the end of the shoot. *Sikyos* was originally translated as cucumber, but it is *C. melo* that produces staminate flowers on apical nodes (Paris and Janick 2010-2011; Robinson and Decker-Walters 1997). This again suggests that *C. sativus* was not present in ancient Mediterranean civilizations; rather, it was vegetable-like melons that were popular in the region at this this time.

Another example is found in Hebrew writings from the second and third centuries. These authors mention the crop *qishu'im* throughout the writings, which according to Jewish texts have been in Israel since biblical times; *qishu'im* has been translated to "cucumber" in English (Paris and Janick 2008; Paris and Janick 2010-2011; Paris et al 2012). But again, *qishu'im* was described as hairy—the authors even described how the hairs were removed in order for it to be eaten—which suggests that qishu'im was a vegetable variation of *C. melo* not *C. sativus* (Paris and Janick 2008; Paris et al 2012). Furthermore, in ancient Egypt, from which the Jewish people had escaped, wall paintings depicting elongated fruit have been discovered. The fruits were initially mistaken as cucumbers, but the striped and furrowed detailing of the fruits in the paintings indicates that the Egyptians were eating *C. melo* var. *flexuosus* rather than *C. sativus* (Paris and Janick 2010-2011). These snake melons, called *faqqous*, were popular in northern Africa and the Middle East, where they remain popular today (Paris 2016). *C. melo* arrived in the Caribbean Islands of

the New World on Christopher Columbus's second trip and the fruit spread rapidly to North and South America (Lovegren 2016).

Over time, as melons and cucumber spread, they developed traits of "domestication syndrome." Macro-remains of *C. melo* have been recently found, primarily preserved by being waterlogged, at eight archaeological sites throughout China, the oldest dating back to 4,600 BC (Fuller 2012). Comparing these ancient seeds to the seeds of modern domesticated melons shows that the shift to a larger seed and fruit size happened quite quickly (Fuller 2012). Data shows that *C. sativus* became less bitter and more fresh tasting, lost spines, became larger and more green, and increased yield through becoming more gynoecious (Lv et al 2012). *C. melo* developed an increase in the percent of soluble solids, a loss of bitterness, and a rapid increase in fruit and seed size (Fuller 2012; Paris et al 2012). The similar traits that evolved in both *C. melo* and *C. sativus* demonstrate how human cultivation and harvesting leads to parallel and convergent evolution in different species (Fuller 2012).

Recommended Future Lines of Research

Although sometimes contradictory, it is important to take into account genetic, archeological, linguistic, historical and botanical evidence in order to gain a more complete picture on the origin of domestication and routes of dissemination of cucumbers and melons. A majority of researchers has made it clear that archaeobotanical evidence is not the best way to study *Cucumis*, as the remains do not preserve well and the seeds of *C. melo* and *C. sativus* are practically indistinguishable from each other. Genetic labs such as Lv et al (2012), however, had little trouble pulling remains from a core via flotation to analyze with SSR markers and map regions of domestication. The use of recent genetic methods has produced data that completely uprooted what influential researchers in the field had thought for many decades was the origin of domestication of *C. melo*, moving it from Africa into India. Genetic analysis was also able to clear up the relatedness of the two species in a way phenotypic traits could not. Linguistic and historical data combined with botanical knowledge has allowed researchers to question the authenticity of ancient writings and depictions of cucumber/melon in the ancient Mediterranean societies and better understand how and when *C. melo* and *C. sativus* arrived in the region. There is still some uncertainty about the origin of

melons and the routes of dispersal for both species. A continuation of all evidence, primarily genetic, will help clear up details of domestication.

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