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RESEARCH IN CONTEXT

Origin and emergence of the sweet dessert watermelon, *Citrullus lanatus*

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• **Background and Aims** Watermelons, *Citrullus* species (Cucurbitaceae), are native to Africa and have been cultivated since ancient times. The fruit flesh of wild watermelons is watery, but typically hard-textured, pale-coloured and bland or bitter. The familiar sweet dessert watermelons, *C. lanatus*, featuring non-bitter, tender, well-coloured flesh, have a narrow genetic base, suggesting that they originated from a series of selection events in a single ancestral population. The objective of the present investigation was to determine where dessert watermelons originated and the time frame during which sweet dessert watermelons emerged.
• **Key Findings** Archaeological remains of watermelons, mostly seeds, that date from 5000 years ago have been found in northeastern Africa. An image of a large, striped, oblong fruit on a tray has been found in an Egyptian tomb that dates to at least 4000 years ago. The Greek word *pepon*, Latin *pepo* and Hebrew *avattiah* of the first centuries CE were used for the same large, thick-rinded, wet fruit which, evidently, was the watermelon. Hebrew literature from the end of the second century CE and Latin literature from the beginning of the sixth century CE present watermelons together with three sweet fruits: figs, table grapes and pomegranates. Wild and primitive watermelons have been observed repeatedly in Sudan and neighbouring countries of northeastern Africa.
• **Conclusions** The diverse evidence, combined, indicates that northeastern Africa is the centre of origin of the dessert watermelon, that watermelons were domesticated for water and food there over 4000 years ago, and that sweet dessert watermelons emerged in Mediterranean lands by approximately 2000 years ago. Next-generation ancient-DNA sequencing and state-of-the-art genomic analysis offer opportunities to rigorously assess the relationships among ancient and living wild and primitive watermelons from northeastern Africa, modern sweet dessert watermelons and other *Citrullus* taxa.

Key words: Archaeobotany, citron watermelon, *Citrullus lanatus*, Cucurbitaceae, colocynth, crop history, dessert watermelon, egusi watermelon, evolution under domestication, fruit sweetness, talmudic cucurbits.

INTRODUCTION

Watermelons, *Citrullus* Schrad., are among the most widely grown vegetable crops in the warmer parts of the world (Maynard, 2001; Wehner *et al*., 2001; Wehner, 2008). Over 3 400 000 hectares are planted annually, with production exceeding 102 000 000 t (http://faostat.fao.org/site/339/default.aspx). Few food items are as refreshing and appreciated on hot summer days as chilled slices of watermelon.

Citrullus ($2n = 2x = 22$) is a xerophytic genus native to Africa (Whitaker and Davis, 1962; Robinson and Decker-Walters, 1997). Other cultivated members of the genus, besides the familiar sweet dessert watermelon, are the citron and egusi watermelons and the colocynth (Jeffrey, 2001). The sweet dessert watermelon, though, has considerably less DNA sequence polymorphism than the others (Maggs-Kölling *et al*., 2000; Levi *et al*., 2000, 2001; Dane *et al*., 2004, 2007; Hwang *et al*., 2011; Nimmakayala *et al*., 2014*a*, *b*), indicating that it originated from a single founder population. The progenitor of the sweet dessert watermelon has been widely believed to be the colocynth or the citron watermelon and, recently, genomic sequencing has fostered the suggestion that the progenitor is the egusi watermelon (Guo *et al*., 2013). Another widely held belief is that sweet watermelons first diffused to Europe via Moorish Spain somewhat prior to 961 CE, from the Indian subcontinent, facilitated by Islamic conquests (Watson, 1983). However, there is much evidence showing that the history of the sweet dessert watermelon matches none of the above beliefs concerning progenitor or geographic origin. My objective is to gather and assess this evidence, and trace the origin and emergence of the sweet dessert watermelon.

SOURCES OF EVIDENCE

Crop plant history is best assessed using a multidisciplinary approach that encompasses botany, horticulture, cookery, philology and archaeology (Harlan and de Wet, 1973; Dalby, 2003; Zohary *et al*., 2012). Sources of evidence concerning the history of cucurbits have taken the form of archaeological artefacts, iconography and literature (Janick *et al*., 2007; Paris, 2000, 2012; Paris *et al*., 2012*a*, *b*, *c*).

Archaeological artefacts

The time and area where a crop was domesticated can be signalled by archaeological finds but the degree of confidence that can be afforded to artefacts is a function of their abundance, distribution and state of preservation (Harlan and de Wet, 1973;

Ladizinsky, 1998). Most plant remains decay quickly, within several years (Day, 2013). Soft, watery plant parts, such as foliage and fruits, are much less likely to be preserved than hard, dry parts, such as seeds. However, in dry situations, such as arid climates or caves, remains can be preserved for thousands of years. The Egyptian custom of placing everyday items in tombs has increased the chances of preserving remains of plants (Manniche, 1989). Much archaeological attention has been devoted to remains of staple food crops, but less effort has been focused on vegetables such as cucurbits (Maynard and Maynard, 2000).

Iconography

Iconography has been especially useful for understanding the evolution under domestication and diffusion of cucurbits, but the degree of confidence that can be afforded to iconography is a function of its detail and accuracy (Eisendrath, 1961; Zeven and Brandenburg, 1986; Paris, 2000; Paris *et al*., 2011). Stunningly detailed and realistic illustrations of a colocynth plant are in two early medieval manuscripts on medicine descended from the same lost archetype (Hummer and Janick, 2007). Over most of the medieval period, though, images of plants are successively poor copies from long-lost archetypes dating to the Roman period and so inaccurate as to be useless for taxonomic identification (Pächt, 1950; Opsomer *et al*., 1984; Collins, 2000; Givens, 2006). Late in the medieval period, new, original depictions of plants were produced with sufficient detail and accuracy to allow identification of species (Paris *et al*., 2009, 2011). Images from late 14th-century northern Italy show both red-fleshed dessert watermelons and white-fleshed citron watermelons (Paris *et al*., 2013). However, based on these depictions alone, it cannot be ascertained how long prior to 1400 CE dessert and citron watermelons had been in Europe or where they originated.

Literature

Literature would appear to be the most likely source of evidence for fruit sweetness. As a rule, though, food items, including fruits and vegetables, were considered by ancient writers to be familiar to everyone and in no need of description, being discussed only concerning their supposed dietary or medicinal qualities (Dalby, 2003). Fortunately, some off-hand descriptions of the commodity can often be gleaned in the context of medicine, religion, travel and cookery (Paris *et al*., 2012*b*). Such is the case, too, regarding the watermelon. No direct description is made of its characteristically smooth, glossy, green-striped rind, or the taste, texture or colour of its flesh or seeds.

Adjectives tend to be used differently across languages, contexts, geographic areas and periods of time (Paris *et al*., 2012*b*). For example, ‘sweet’ can be synonymous with sugary or simply not bitter, not sour, not spicy or not salty. What might have been considered sweet in ancient times might not be considered sweet today, due to later development or introduction of cultigens with greater sweetness. The adjective ‘red’ has been variously used to include orange, purple and brown, and ‘yellow’ to include orange. Although red fruit flesh is non-existent in melons, *Cucumis melo* L., in some literature from the Renaissance to the present day, melon fruit-flesh has been described as ‘red’ or ‘pink’.

Nouns are often used inconsistently, denoting different taxa across places or times (Kroll, 2000). The word ‘melon’ in American English can refer to either or both *Citrullus* and *Cucumis melo* (Mohr, 1986; Goldman, 2002) and the medieval Latin *melones* was used for both (Paris *et al*., 2009, 2013). Also, the medieval Latin *pepo* referred to watermelon in southern Europe and to melon in northern Europe (Paris *et al*., 2012*b*). In Arabic, *battikh* usually are watermelons but can be melons or inclusive of both (Watson, 1983; Nasrallah, 2007; Amar and Lev, 2011). Generally, though, the word *battikh* was applied to melons by writers hailing from the far reaches of the Islamic Empire, Khorasan and Persia in the north-east and Andalusia in the west, but was applied to watermelons everywhere else (Paris *et al*., 2012*b*). The focus here will be restricted to informative literature in which taxonomic identity as *Citrullus* can be inferred, based on one or more of its diagnostic features.

DIAGNOSTIC FEATURES OF *CITRULLUS*

The Cucurbitaceae exhibit much parallel variation among genera and species in the size, shape and coloration of the fruits (Vavilov, 1951). As a result, throughout human history, the identities of various cucurbits, cultivated and wild, have been confused.

Citrullus is readily distinguished from other cucurbit genera by the pinnatifid shape of its leaf laminae (Paris *et al*., 2013). The flowers are solitary, 2–3 cm in diameter, with five light yellow petals. Most of the flowers are staminate, a pistillate or hermaphroditic flower appearing at every seventh or eighth leaf axil (Rosa, 1928; Porter, 1933). Most cultivars are monoecious, but many old or indigenous cultivars are andromonoecious (Pangalo, 1930; Fursa, 1981; Mohr, 1986; Gouda, 2007). The plants usually begin to flower 40–60 d after sowing and are naturally self- and cross-pollinated by bees (Mohr, 1986; Maynard, 2001; Wehner, 2008). Ovaries and primordial fruits are lanate, becoming glabrous, smooth and glossy as they grow. Usually 25–40 d ensue from anthesis to fruit maturity, but the external indications of fruit ripening are subtle (Woodward, 1937; Thompson and Kelly, 1957). The earliest cultivars, which require 65 d from sowing to first harvest, bear small fruits ($\leq$5 kg). As much as 100 d are required to reach maturity in the very large-fruited cultivars. If stored in a cool, shady place, dessert watermelons can keep for weeks or even months without serious deterioration of their quality (Keith-Roach, 1924; Rushing, 2001).

Fruits of dessert watermelons can weigh from 1 to 100 kg or more, but most commercially available watermelons range from 3 to 13 kg (Mohr, 1986; Maynard, 2001; Wehner, 2008). Fruit shape is often spherical but can be globular, oval or oblong. The watermelon rind consists of two layers. The thin, glossy outer layer, or exocarp, is typically boldly striped or otherwise patterned in two shades of green. The green colours can range from light to dark, and the stripes are jaggedly edged and range in breadth from very narrow to very broad. The thick inner layer of the rind, or mesocarp, is wet, white and hard. Underneath the rind is the watery fruit flesh or endocarp, the

portion of the fruit that is usually eaten. Early in development, the fruit flesh is hard, white or otherwise pale-coloured, and insipid. In citron watermelons, the fruit flesh remains hard, nearly colourless and tasteless to fruit maturity (Xu *et al*., 2012). In sweet dessert watermelons, the flesh of the maturing fruit becomes tender and accumulates carotenoid pigments and sucrose (Elmstrom and Davis, 1981; Brown and Summers, 1985; Soteriou *et al*., 2014). Colour begins to accumulate between 2 and 3 weeks after anthesis, first around the developing seeds and thereafter gradually spreading throughout the endocarp (Perkins-Veazie *et al*., 2012). Depending on the genotype, the flesh of ripe watermelon fruits can range in colour from red to pink, orange, yellow, a mixture of these colours, green and white (Gusmini and Wehner, 2006). The range in texture of the ripe fruit flesh has been variously described as crisp, soft or liquefied, and coarsely or finely grained. Each fruit can contain 200 or more seeds that, to the casual observer, are seemingly scattered throughout the flesh and, to the consumer, are of great annoyance. The seeds of sweet watermelons are hard, flat and oval and, depending on cultivar, generally range in length from 8 to 16 mm and can be black, brown, tan, white, yellow or red, and can be patterned with a second colour.

Sweetness of watermelon fruit flesh can be easily and objectively assessed by squeezing out drops from a cut piece on the surface of a refractometer, a device that measures soluble solids content (Tucker, 1934; Thompson and Kelly, 1957). By modern standards, a minimum of 8 % soluble solids is required in dessert watermelons, and the best cultivars can regularly achieve 11 % or more soluble solids (Mohr, 1986; Maynard, 2001; Wehner, 2008).

Watermelons are sometimes confused with melons, *Cucumis melo*, as both are often large and sweet. The most salient features distinguishing them are the shape of the leaf laminae, distribution of staminate and pistillate (or hermaphroditic) flowers on the plant, range of fruit shape, fruit surface features, wetness of the fruit, thickness of the fruit rind, fruit flesh colour, and shape, colour and distribution of seeds within the fruit (Paris *et al*., 2012*b*). In the field, watermelons ripen evenly over the course of the harvest season but melons ripen in two distinct waves (Rosa, 1924; McGlasson and Pratt, 1963; Pratt *et al*., 1977). Watermelons have no well-marked indicators of fruit ripening but melons typically become aromatic and yellow, and abscise from the plant upon ripening (Isenberg *et al*., 1987; Nonnecke, 1989). Watermelons have a much longer shelf-life than most melons but are subject to breakage if not handled carefully (Whitaker and Davis, 1962; Robinson and Decker-Walters, 1997). In watermelons, the seeds are distributed within the fruit flesh but in melons the fruit flesh is free of seeds.

NOMENCLATURE AND TAXONOMY OF *CITRULLUS*

The nomenclature and taxonomy of the genus *Citrullus* has, unfortunately, been confused from the outset. Watermelons were designated *Cucurbita citrullus* by Linné in his *Species Plantarum* of 1753, in the same genus with pumpkin, squash and bottle gourd. The word *citrullus* was the northern European medieval Latin word for watermelon. It is a misnomer, though, being the diminutive of the classical Latin *citrium*, the citron watermelon (discussed later). Originally and more appropriately, *citrullus* was the southern European medieval Latin word for a small-fruited cucurbit, the cucumber, *Cucumis sativus* L. (Italian *cetriolo*) (Paris *et al*., 2011). Subsequent permutations of names for the genus and for the species of watermelons were recently discussed by Renner *et al*. (2014) in a much-needed proposal to conserve the name *Citrullus lanatus*.

Three species of *Citrullus* – *C. ecirrhosus* Cogn., *C. rehmii* De Winter and *C. naudinianus* (Sond.) Hooker f. (Chomicki and Renner, 2015) – are not cultivated. A fourth, *C. colocynthis* (L.) Schrad., the colocynth, is sparingly cultivated. The widely cultivated citron, egusi and dessert watermelons have been variously treated as subspecies, botanical varieties or cultivar groups within one species, *C. lanatus* (Thunb.) Matsum. & Nakai (Table 1). The nomenclature is confusing, though, the epithet *lanatus*, as a subspecies, being applied to the citron and, as a botanical variety, being applied to the dessert watermelon. The taxonomy is questionable, too. Crossings of dessert with citron watermelons have resulted in hybrid progenies with reduced pollen fertility and massive preferential segregation (Levi *et al*., 2003; Wehner, 2008; McGregor and Waters, 2013). Although few attempts at crossing dessert and egusi watermelons have been described, there are two reports indicating that degree of success was dependent on the direction of the cross (Fursa, 1983; Gusmini *et al*., 2004). Genomic sequencing has revealed that the citron, egusi and dessert watermelons differ significantly in genome organization (Guo *et al*., 2013; Reddy *et al*., 2013; Chomicki and Renner, 2015), leading Chomicki and Renner (2015) to propose that each be

TABLE 1. *English names and equivalent specific, sub-specific, botanical-variety, and cultivar-group names (non-inclusive) of cultivated* Citrullus

English name	Species[1]	Subspecies[2]	Botanical variety[3]	Cultivar-group(s)[4]
Dessert watermelon	*C. lanatus* (Thunb.) Matsum. & Nakai	*vulgaris* (Schrad.) Fursa; *cordophanus* Ter-Avan.	*lanatus*; *colocynthoides* Schweinf.	Dessert; Cordophanus
Citron watermelon	*C. amarus* Schrad.	*lanatus*	*citroides* Bailey	Citroides
Egusi watermelon	*C. mucosospermus* (Fursa) Fursa	*mucosospermus* Fursa	*mucosospermus* Fursa	Mucosospermus
Colocynth	*C. colocynthis* (L.) Schrad.	–	–	–

[1]After Renner *et al*. (2014); Chomicki and Renner (2015).
[2]After Fursa (1972).
[3]There are very many designated botanical varieties; only four equivalent to the four listed subspecies are listed here.
[4]After Jeffrey (2001).

considered a separate species, for a total of seven in the genus *Citrullus* (Table 1). Accordingly, the citron watermelon is *C. amarus* Schrad., the egusi watermelon is *C. mucosospermus* (Fursa) Fursa and the dessert watermelon retains the name *C. lanatus* (Renner *et al*., 2014).

Caution must be exercised in identifying species of *Citrullus* based solely on individual phenotypic characteristics (Wehner, 2008). Features that are deemed characteristic of one species can occur, albeit rarely, in others. Bitterness of the fruit flesh is not exclusive to colocynths and hardness of the fruit flesh is not exclusive to citron watermelons. Wild *Citrullus* have small, spherical fruits with broad dark stripes, and hard, usually bitter, pale-coloured and seedy fruit flesh (Fig. 1). The dessert, citron and egusi watermelons have often been confused with one another and with colocynths, even though colocynth leaves are smaller, more elongate and greyer, with coarse, adpressed rather than soft spreading hairs, and the flowers are smaller and greenish-yellow. Colocynth fruits do not exceed 10 cm in diameter; usually they are $\leq$8 cm and are extremely bitter, and as they mature their exterior fades from brightly striped green to light yellow and their flesh desiccates. Colocynth seeds are small, $\leq$8 mm long and, significantly, are distinguished from dessert watermelon seeds by their having a smooth surface and no bulging of the edges next to the hilum (Schweinfurth, 1883; Montasir and Hassib, 1956; Chakravarty, 1966, 1982).

DISTRIBUTION AND USAGE

The current distribution of wild relatives of a crop can provide valuable evidence for a more accurate assessment of crop-plant history. *Citrullus ecirrhosus*, *C. rehmii* and *C. naudinianus* are native to deserts of southern Africa. Though congeneric with the dessert watermelon, they are relatively distant to it geographically and genetically (Chomicki and Renner, 2015).

Citrullus colocynthis, the colocynth, grows wild in the deserts spanning northern Africa to southwestern Asia. Colocynths have small, spherical and extremely bitter fruits valued for medicinal use of extracts from their dry, spongy pulp or extraction of the oil from their seeds (Clément-Mullet, 1866; Darby *et al*., 1977; Amar and Hazot, 2003).

Citron watermelons or 'tsamma', which grow wild and are widely cultivated in southern Africa, are usually spherical and weigh several kilograms, but can be oblong and quite large, and vary widely in fruit rind striping and colour pattern. Citrons have hard, bland, sometimes bitter, watery flesh that is white, light green or yellow (Rubatsky, 2001; Jensen, 2012; McGregor, 2012). They are an important source of water, an article of cooked food and provide animal fodder in resource-poor, remote parts of southern Africa (Welman, 2011; Jensen, 2012; Mujaju *et al*., 2011), and are elsewhere a minor crop (Pangalo, 1930; Cizik, 1952; Bush, 1978; Laghetti and Hammer, 2007). Their seeds vary widely in size and colour, and are difficult to distinguish from those of dessert watermelons.

Egusi watermelons, indigenous to western Africa, are usually spherical with bitter flesh, and are distinguished by their peculiar soft mucilaginous seed coats (Badra *et al*., 1982; Achigan-Dako *et al*., 2008, 2015; Jensen *et al*., 2011). Egusis are cultivated for the consumption of their seeds, which vary widely in size and shape (Oyolu, 1977; Fursa, 1983; Djè *et al*., 2010; Minsart *et al*., 2011).

Dessert watermelons have been reported as growing wild in northeastern Africa (Schweinfurth, 1883; Muschler, 1912; Andrews, 1950; Abdel-Magid, 1989; Robinson, 2005; Gouda, 2007; Mariod *et al*., 2009). The fruits of wild or 'spontaneous' plants are small, spherical and striped with hard, pale-coloured, bitter, bland or sweetish flesh, and are used as a source of clean water during the long dry season as well as for food and animal fodder. Cultigens indigenous to Kordofan (Sudan) (Fig. 1) vary widely in fruit size, colour, striping pattern, flesh colour and taste, and seed size and colour (Hassan *et al*., 1984). Modern dessert watermelon cultivars also vary widely in fruit size, colour, striping pattern and seed size and colour, but their fruit flesh has much improved quality, being tender, highly coloured and sweet.

CITRULLUS FROM ANCIENT EGYPT, LIBYA, SUDAN, EUROPE AND ISRAEL

Artefacts

De Vartavan and Asensi Amoros (1997) listed ten sites in Egypt, dating from the pre-dynastic and dynastic eras, that contain remains of watermelon, *Citrullus lanatus*. Schweinfurth (1883), an accomplished botanist, identified foliage placed in the coffin of the Egyptian priest Nibsoni at Dayr al-Bahari (near Luxor) dating to ~1000 BCE, as of a desert ecotype of the dessert watermelon, which he named as botanical variety *colocynthoides*. Germer (1988) listed Egyptian remains, including seeds over 4500 years old and fruits over 4000 years old considered to belong to *C. lanatus* var. *colocynthoides*. Wasylikowa and van der Veen (2004) recovered watermelon seeds, 5000 years old, in an assemblage of wild seeds and fruits in southwest Libya. De Vartavan (1999) presented photographs of five individual seeds taken from the tomb of Tutankhamen (1323 BCE); significantly, the seeds have distinctly bulging margins flanking the hilum end and therefore these seeds are of watermelon, not colocynth. A watermelon fruit with seeds from ~1500 BCE has been reported from foundation deposits of a temple in Sudan (van Zeist, 1983). Watermelon seeds along with remains of other food plants have been reported from two sites across the Mediterranean, at Krania in central Greece (Margaritis, 2006–2007) and on the eastern island of Samos (Kučan, 2000), dating to ~800 and 650 BCE, respectively.

Citrullus seeds have also been recovered from post-dynastic Egypt through the Coptic period, and the findings are listed by de Vartavan and Asensi Amoros (1997). More recently, seeds dating to the Roman period were uncovered in an archaeological site at Qusayr al-Qadim on the shore of the Red Sea in Egypt (Cox and van der Veen, 2008; van der Veen, 2011). These seeds were described as having a rough surface and a photograph of them clearly shows bulges and creases adjacent to the hilum, and thus these could not be of colocynth. The seeds are relatively small, 10–11 mm in length, too long to be colocynths but small enough that it is likely that the fruits were consumed for their flesh rather than their seeds. In contrast, seeds dating to the Islamic period at the same site are larger, ~15 mm long, and cracked open in the same way that watermelon seeds are consumed by people today. Seeds of similar

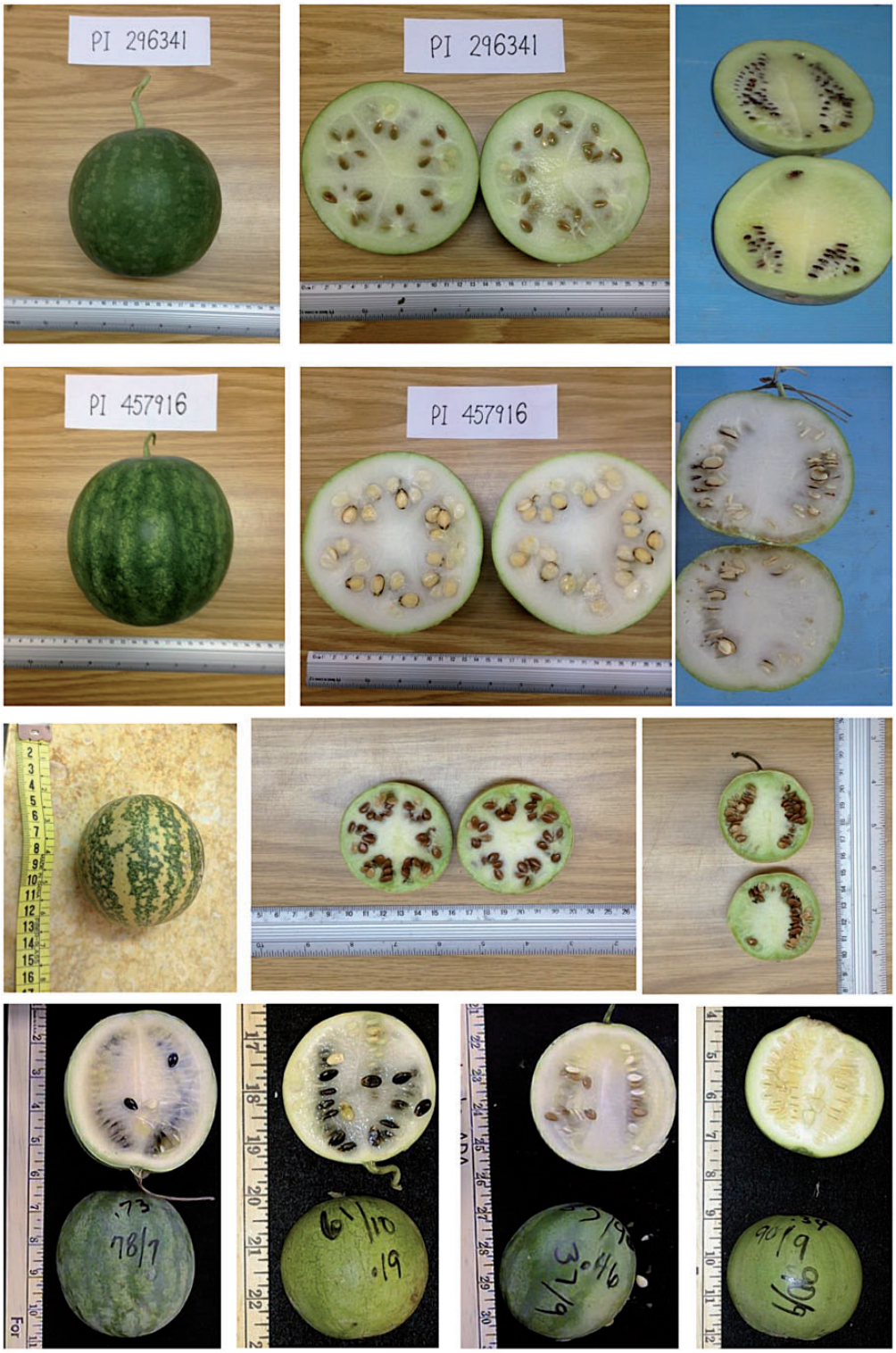

Fig. 1. Fruits of wild and primitive *Citrullus*. (Top three rows) Small, spherical, broadly dark-striped mature fruits with bitter, hard, greenish white or white flesh. (First row, left to right) Whole, equatorially cut and longitudinally cut fruits of *C. amarus*, citron watermelon, PI 296341 (South Africa), 14 cm diameter. (Second row) Whole, equatorially cut and longitudinally cut fruits of *C. mucosospermus*, egusi watermelon, PI 457916 (Liberia), 14 cm diameter. (Third row) Whole, equatorially cut and longitudinally cut fruits of *C. colocynthis*, colocynth, Paqqu'a 16 (Israel), 6–8 cm diameter. Photographs by the author. (Bottom row) Small, spherical mature fruits, 8–13 cm in diameter with white flesh, of accessions from northeastern Africa, probably *C. lanatus*, dessert watermelon. (Left to right) PI 193963, Agaruen Hills, Ogaden, Ethiopia, collected 26 October 1950, http://www.ars-grin.gov/cgi-bin/npgs/html/acchtml.pl?1164951; PI 481871, Wadi Noori, 26 km S of Jebel Marra, Darfur, Sudan, from non-irrigated sorghum field, collected 15 November 1981, http://www.ars-grin.gov/cgi-bin/npgs/acc/display.pl?1376807; PI 254622, Bol El Homar, Kordofan, Sudan, collected 18 December 1958, http://www.ars-grin.gov/cgi-bin/npgs/html/acchtml.pl?1195486; PI 525084, Hemidat, Qena, Egypt collected 1985, http://www.ars-grin.gov/cgi-bin/npgs/html/acchtml.pl?1420020. Photographs by A. Davis, USDA/ARS.

appearance to those from the Roman period at Qusayr al-Qadim have also been reported from the Roman outpost of Mons Claudians in Egypt, an inland site ~300 km to the south, in the eastern desert (van der Veen, 1999). Seeds of *Citrullus* dating to the second century CE have been found in a cave above the Dead Sea near 'En Gedi in eastern Israel (Kislev and Simhoni, 2009). These seeds, too, are similar in size and have bulges and creases near the hilum end. Clearly then, watermelons were used in Egypt and neighbouring Israel during Roman times.

Images

Depictions of numerous plants have been preserved in ancient Egyptian tombs. An illustration of a round, striped fruit, attached by a thin stem to a short section of vine, including two highly dissected leaves, was reproduced by Keimer (1924, p. 170) (Fig. 2). Given the shape of the leaves and striping of the fruit, this depiction undoubtedly represents a specimen of *Citrullus*. Another image shows nine round, striped fruits resembling small watermelons neatly placed in a basket adjacent to two large snake melons and two other baskets containing smaller fruits (Feliks, 2005, p. 303). An image, more than 4000 years old, of a fairly large, oblong, boldly striped fruit laid on a tray, has been identified as representing watermelon, *C. lanatus* (Manniche, 1989, p. 92).

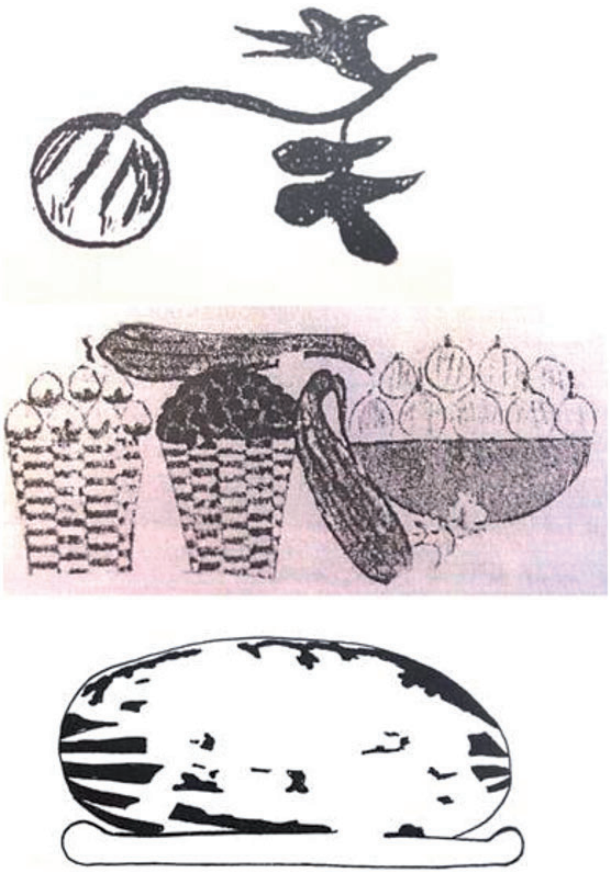

FIG. 2. Ancient images of *Citrullus* from Egyptian tombs. (Top) A spherical, striped fruit with an adjacent section of foliage (Keimer, 1924). (Centre) Fruits and vegetables, including a basket of small, round, striped *Citrullus* fruits, the two large, long fruits being snake melons, *Cucumis melo* Flexuosus Group (Feliks, 2005). (Bottom) An oblong, striped fruit on a tray (Manniche, 1989).

Literature

Biblical Hebrew. The Children of Israel, during their sojourn in the Sinai Desert, longed for five vegetables they knew from the Land of Egypt, in the following order: *qishu'im*, *avattihim*, *hazir*, *bezalim* and *shumim* (*Numbers* 11:5). These have been identified by Feliks (1968) and Janick *et al*. (2007) as snake melons (*Cucumis melo*), watermelons (*Citrullus lanatus*), leeks (*Allium porrum* L., Amaryllidaceae), onions (*A. cepa* L.) and garlics (*A. sativum* L.), respectively. The Hebrew word *avattihim* is probably derived from an ancient Egyptian language root (Loret, 1892; Darby *et al*., 1977; Manniche, 1989).

Centuries later, during a time of famine in the Land of Israel, an incident is recorded of the desperate use of *paqqu'ot* in a kitchen preparation (*2 Kings* 4:39–40). These *paqqu'ot*, which resulted in a pottage that was bitter, have been identified as colocynths (*Citrullus colocynthis*) (Feliks, 1968; Janick *et al*., 2007). At a later time, ~600 BCE, the word for a cucurbit field was *miqsha* (*Isaiah* 1:8). This word is derived from *qishu'im*, indicating that snake melons had been a more common or widely produced commodity than the *avattihim*.

Greek literature (400 BCE–355 CE). The *pepon* of classical Greek literally indicates a sun-ripened fruit and is thought to refer specifically to watermelon, *Citrullus lanatus* (Liddell and Scott, 1948; Andrews, 1958; Stol, 1987; Grant, 2000). Hippocrates, in his *Regimen* (400 BCE), wrote that the *pepones* are easily digested (Jones, 1967). Theophrastus, the botanist, did not use the word *pepon* in his *Enquiry into Plants* (~300 BCE) (Hort, 1976). He did use three other words for cucurbits – *sikyos* for snake melons, *sikya* probably for a form of bottle gourd, *Lagenaria siceraria* (Mol.) Standl., and *kolokynta* for perhaps bottle gourd or watermelon – only stating that there were no specific cultivars, although some were better and others were worse.

Dioscorides, in the second volume of *On Medical Matters* (~70 CE), wrote that the flesh of the *pepon* is easily digestible and diuretic, and that the rind of the *pepon* is to be applied on top of the head of a child suffering from heat stroke (Osbaldeston and Wood, 2000; Beck, 2005). Clearly, the *pepon* was a large, wet, thick-rinded fruit. Dioscorides described various medicinal uses of other cucurbits, including the *sikyos* (snake melons, *Cucumis melo*), *sikyos agrios* (wild *sikyos*, squirting cucumbers, *Ecballium elaterium* (L.) A. Rich.), *kolokyntha edodimos* (edible *kolokyntha*, bottle gourds, *Lagenaria siceraria*) and *kolokyntha agria* (wild *kolokyntha*, colocynths, *Citrullus colocynthis*) (Janick *et al*., 2007). The colocynth was described as most effective when the green colour of the rind had faded.

Galen, in *On the Properties of Foods* (~180 CE), wrote that the *pepon* was cold and wet and that the *melopepon* (apple-*pepon*) was less so, having a milder effect on the body (Grant, 2000; Powell and Wilkins, 2003). The *pepon* was more diuretic than the *melopepon*, the *sikyos* (snake melons) and the *kolokynte* (bottle gourds). The *kolokynte* were bad for digestion eaten raw, but were a food eaten after boiling, frying or roasting.

Athenaeus, in *The Learned Banqueters* (∼200 CE), quoted thousands of lines of verse written by ∼1000 authors from various times and localities across the Greek-speaking world (Olson, 2006). Phaenias is quoted as writing that the *kolokynte* are inedible raw, but edible after being stewed or baked. Euthydemus of Athens wrote that the *kolokyntin* is the Indian (= eastern) *sikya*. Menodorus wrote that the Indian *kolokynton*, which is called the *sikya*, is generally stewed but the regular *kolokynton* is usually baked. However, the inhabitants of Hellespont are quoted as using the word *sikyai* for long cucurbits and *kolokuntai* for round cucurbits. Diphilus wrote that the *kolokynte* are not very nutritious but add moisture to the body, and are more easily digested when eaten with water and vinegar or when seasoned. Diocles stated that the best *kolokyntas* are round, very large, sweet (*glukeian*) and easy to digest. Hermippus was quoted 'What a big head he has! As big as a *kolokunte*!' and Phrynichus used the diminutive *kolokuntion*. Thus, among the Greeks, there was an inconsistency in the usage of *kolokynte*. For Phaenias and Menodorus, they were not eaten raw but only after being cooked or baked, suggestive of bottle gourds. For Diocles and Hermippus, and perhaps Theophrastus before them, they were something large, round, moist and easy to digest, and the best ones were sweet, a description suggestive of watermelons.

Oribasius, in his *Medical Compilations* (∼355 CE), wrote that the fruit flesh of the *peponon* was abundantly moist and diuretic and that of the *melopeponon* was less moist and less diuretic (Grant, 1997). The *sikyon*, snake melon (Janick *et al.*, 2007), was not quite as diuretic as the *kolokyntus*. The *kolokyntus* was not distinctly flavoured but moist and could be prepared in many ways. Some, after allowing the fruits to become large, at which time they desiccate and become like shoe leather, use them for storage. Clearly, then, to Oribasius the *kolokyntus* was the bottle gourd.

Latin literature (77–516 CE). Pliny, in his *Historia Naturalis* (∼77 CE), described the *pepo* as *refrigerant maxime*, a very refreshing or cooling food (Book 20, 6:11). In contrast, the *melopepo* (apple-*pepo*) was a new introduction resembling a quince that, upon ripening, turned yellow, became aromatic and, significantly, spontaneously detached from the plant (Book 19, 23:67). Pliny, like Dioscorides, described the *colocynthis* as better used for medical preparations when faded rather than green (Book 20, 6:14–17) (Rackham, 1950; Jones, 1951).

Quintus Gargilius Martialis, in his *Medicinae ex Oleribus et Pomis* (∼260 CE), wrote that the *pepone* are good to eat after removal of the rind and pits (Maire, 2007). Some eat them with vinegar and a mixture of mint and onion. He repeated Dioscorides' prescription to use the rind of the *pepon* as an alleviant of sunstroke. Other cucurbits discussed are the *cucurbita* and the *cucumere*, which are identified as the bottle gourd (*Lagenaria siceraria*) and the snake melon (*Cucumis melo*), respectively (Janick *et al.*, 2007).

An edict on maximum prices, *De Pretiis Rerum Venalium*, was issued by the Roman Emperor Diocletian, in both Latin and Greek (301 CE) (Lauffer, 1971). In it, four cucurbits are listed sequentially – *cucurbitae*, *cucumeres*, *melopepones* and *pepones* – with the corresponding Greek *kolokynthai*, *sikyon*, *melopeponon* and *peponon*, respectively. Evidently, each of these four was a food item that was distinct and economically important enough to be named specifically.

A Latin cookbook, designated *De Re Coquinaria*, is attributed to an individual who is thought to have been named Apicius and lived in the first century. The original work has been lost, but a supplemented version (∼400 CE) has been preserved. This book has several recipes for cucurbits (Flower and Rosenbaum, 1958). One recipe calls for dressed *pepones et melones*. Others call for cooked *cucurbita* (bottle gourds) and cooked or dressed *cucumeres* (snake melons). Another, for a fricassee, calls for *citrium*, which first has to be 'cleaned inside and outside, diced and boiled'. The citron, *Citrus medica* (Rutaceae), is found elsewhere in this work but Flower and Rosenbaum (1958) indicated that this recipe would make no sense in the case of *Citrus medica*. Instead, *citrium* is defined by Latinists as a cucurbit (Andrews, 1863; Lewis and Short, 1951). *Citrium* is the forerunner of the English word 'citron', *citre* in French, for the hard-fleshed watermelon used in cooking or otherwise processed. Indeed, the citron watermelon, to be included in a fricassee, would require cleaning inside (removal of the seeds) and outside (removal of the rind).

De Observantia Ciborum (∼510 CE), attributed to a Pseudo-Hippocrates, lists 101 foods, including three cucurbits (Mazzini, 1984). *Cucumere* (snake melons) are high on the list, at no. 18 and first among the vegetables. *Cucurbitae* (bottle gourds) are much further down, at no. 67. *Pepone*, at no. 80, are listed among sweet, juicy fruits that are usually eaten raw when ripe, pomegranates, grapes and figs.

Anthimus, in *De Observatione Ciborum Epistula* (∼516 CE), a book intended for the ruler of northeastern France, mentioned three cucurbits (Grant, 2007). The *cucurbitas* (bottle gourds) were cooked when young and tender and the *cucumeres* (snake melons), which were not always available, were eaten whole, with the seeds. The *melones* were to be eaten well-ripened, the flesh with the seeds still mixed in being preferable.

Hebrew literature (200–400 CE). Three large codices of Jewish Law were compiled in Israel during the first centuries CE. They are easily searched on-line (Mekhon Mamre, 2015). The *Mishna*, compiled by Rabbi Yehuda the President in northern Israel around 200 CE, consists of six *sedarim* (orders) that are divided into a total of 63 *massakhtot* (tractates), each of which contains a highly variable number of *mishnayot* (statements). The *Tosefta*, probably compiled a century later, is structured similarly to the *Mishna* but is not as well edited, containing most of the same tractates, but these often differ in content. The *Jerusalem Talmud*, written in northern Israel around 400 CE, closely follows the *Mishna* and has much additional rabbinical commentary but, unfortunately, it too was never fully edited.

The *Mishna*, *Tosefta* and *Jerusalem Talmud* contain some tractates that focus on issues concerning agriculture, crops and foods, including cucurbits. There are statements that allude to the three cucurbits mentioned in the Hebrew Bible, the *qishu'im* (snake melons, *Cucumis melo*), *paqqu'ot* (colocynths, *Citrullus colocynthis*) and *avattihim* (singular *avattiah*). Several other cucurbits are also discussed, the *delu'im* (bottle gourds, *Lagenaria siceraria*), of which there were three cultivars, the *qarmulin* (sponge gourds, *Luffa aegyptiaca* Mill.), the *yeroqat hamor* (squirting cucumber, *Ecballium elaterium*) and the *melafefonot* (sing. *melafefon*) (Feliks, 1967; Janick *et al.*, 2007).

Four cucurbits, the *qishu'im* (snake melons), *delu'im* (bottle gourds), *avattihim* and *melafefonot*, are considered together in the first chapter of the tractate *Kil'ayim*, which focuses on prohibitions regarding intermingling of plantings or 'crossing' in gardens or fields (Feliks, 1967; Janick *et al*., 2007). The cucurbits, as vine-crop vegetables having large, prominent fruits, were prohibited, in some combinations, from being planted close to one another, in order to prevent the intermingling of their vines (*Mishna*, *Kil'ayim* 1:5; *Tosefta*, *Kil'ayim* 1:4). There are elements of practicality in this prohibition, such as not having to search for snake melons within the rampant foliage of bottle gourds. In other instances, the prohibitions are consistent with modern scientific knowledge. For example, if the edible-fruited bottle gourd was grown in the same vicinity as the utilitarian, bitter-fruited bottle gourd, both of which are *Lagenaria siceraria*, some of the resulting plants would likely have been hybrids bearing worthless, inedible fruits. The texts, though, also contain recantations of Mediterranean agricultural folklore, such as: 'A person takes a seed from the flesh of an *avattiah* and a seed from the flesh of an apple and puts them together in the same hole and they can unite and become an intermingling. This is called in the Greek language *molefefon*' (*Jerusalem Talmud*, *Kil'ayim* 1:2, p. 2a). Thus the myth of the apple-*pepo* was carried across three languages, Greek, Latin and Hebrew. There is in a subsequent passage this comment: 'Prohibited is the insertion of cuttings from grapevines into an *avattiah* lest it throw its waters into them' (*Jerusalem Talmud*, *Kil'ayim* 1:8, p. 4a). Thus, the *avattiah*, like the Greek *pepon*, was a watery fruit.

The same four cucurbits, the *qishu'im*, *delu'im*, *avattihim* and *melafefonot*, being foodstuffs, were also discussed in the first chapter of *Ma'asrot*, the tractate on tithing (*Mishna*, *Ma'asrot* 1:4,5; *Tosefta*, *Ma'asrot* 1:5,6; *Jerusalem Talmud*, *Ma'asrot* 1:4,5). Prior to eating, the *qishu'im* (snake melons) and the *delu'im* (bottle gourds) were to undergo *piqqus*, rubbing off of the hairs on their surfaces (Paris, 2012). As young cucurbit fruits are softly hairy but the hairs naturally slough off as the fruits grow and mature, the snake melons and bottle gourds must have been consumed when they were young and tender. The harvested fruits were gathered in a pile for tithing and, in the *Jerusalem Talmud* (*Ma'asrot* 1: 4, p. 4a), this pile had a special name, *paqqesusiyya*, a derivative of *piqqus* and forerunner of the Arabic word for snake melons, *faqqous*.

The *avattihim*, in contrast, were to be tithed after they underwent *shilluq* (*Ma'asrot* 1:4–6), a word which usually means scalding or blanching (Lieberman, 1955, p. 671; Feliks, 2005, p. 65). However, *shilluq* has a rarely used, second meaning of slicking or polishing (Even-Shoshan, 2003, p. 1908). The great 12th-century scholar Maimonides, in his *Commentary on the Mishna* (∼1168), explained that *shilluq* of *avattihim* meant *yahliq beyado*, smoothing by hand of the fruit surface to remove the *zihuv* (yellowing) on it (Qafah, 1963). Yellow-coloured dust accumulates on fruits over the course of growth and ripening in the field, in the rainless Middle Eastern summer. 'Smoothing' would result in a cleaner, more attractive product for marketing. Also, the *avattihim* were not to be offered for sale in a pile. Instead, they were laid out separately, side by side (*Mishna, Ma'asrot* 1:5). This arrangement had a special name, *shallequqiyya* (*Jerusalem Talmud*, *Ma'asrot* 1:4, p. 4a). The laying out one by one of the *avattihim* suggests that they were too fragile to be piled on top of one another and, indeed, as Maimonides explained in his *Commentary*, the laying out of the fruits was a precaution to prevent breakage.

The *melafefonot* were to be tithed after they were lifted out of the *yora* (*Tosefta*, *Ma'asrot* 1:6), a cauldron or large kettle of boiling water (Lieberman, 1955, p. 672; Feliks, 2005, p. 65). If the *melafefonot* are dessert melons, as indicated by Feliks (1968) and Janick *et al.* (2007), then the reason for dipping them in boiling water is perplexing. Feliks (2005, p. 55), though, in his analysis of the tithing of figs (*Jerusalem Talmud*, *Ma'asrot* 1:3), interpreted the instruction *mesheyuru* as meaning ripening of the second yield in the fig orchard. He explained that fig trees ripen their fruits in two waves over the course of the summer and, accordingly, the weak consonant *alef* (') must have dropped out of the word *meshey*[*e'*]*uru*. If the *melafefonot* also ripened in two waves over the course of the growing season, then the *alef* (') must have dropped out of *y*[*e'*]*ora* and the passage becomes logical. Specifically, the grower was not obliged to tithe the second wave of ripening *melafefonot* fruits until it was lifted out of the field (*eno hayav 'ad sheya'alan min haye'ora*)! This statement is parallel to the previous ones concerning the snake melons, bottle gourds and *avattihim*: fruit vegetables were to be tithed after harvesting, when they were gathered.

Significantly, in the second and third chapters of the tractate on tithing, the *avattihim*, but not the other cucurbits, are discussed together with three other fruits, the *te'enim* (figs), *eshkol* (cluster of table grapes) and *rimmonim* (pomegranates). They were exempt from tithing if they were picked in the garden or field and eaten there (*Mishna*, *Ma'asrot* 2:6; *Jerusalem Talmud*, *Ma'asrot* 2:4, p. 11a). Evidently, the *avattihim*, like the other three, were common fruits that were eaten raw without any culinary preparation, and were juicy and sweet. The text specifies that figs were simply chosen and eaten, grapes were picked from a cluster one by one and eaten, pomegranates were plucked and eaten, and *avattihim* were sliced and eaten (Feliks, 2005; Perez, 2005).

The tractate on fruit stems, *'Oqazin*, instructs that a pomegranate or an *avattiah* that withers at one of its ends, or in the middle, is not normally eaten and thus not among the items that can result in ritual impurity (*Mishna*, *'Oqazin* 2:3). Cucurbit plants, as well as fruit-bearing trees, often set more fruits than can be supported through fruit maturity and ripening, the excess withering before reaching maturity. The *avattiah*, like the pomegranate, was eaten when ripe.

The tractate on tithing, *Ma'asrot*, also instructs that the seeds of the *melafefon* were to be tithed and those of the *avattiah* were not (*Jerusalem Talmud*, *Ma'asrot* 1:2, 2b). The reason, explained by one of the rabbis, is that the seeds of the *melafefon* are eaten and those of the *avattiah* are not, being used only for sowing (Feliks, 2005, pp. 39–40).

One of the topics discussed in the tractate on contributions, *Terumot*, is the amount of time, post-harvest, that various fruits and vegetables are acceptable as contributions. As the young, succulent snake melons and bottle gourds were highly perishable, they were deemed suitable as contributions for only 1 d (*Tosefta*, *Terumot* 4:5). The *melafefonot* were deemed suitable for contribution for 3 d. For the *avattihim*, though, no time restriction is specified as, apparently, they kept for a longer, indefinite period of time.

The *paqqu'ot* fruits, colocynths, were not used as food and not subject to tithing (Feliks, 1968, p. 202). The oil extracted from the seeds was used for illumination (*Mishna*, *Shabbat* 2: 2; *Tosefta*, *Shabbat* 2: 3; *Jerusalem Talmud*, *Shabbat* 2: 2). The dry shells of *paqqu'ot* fruits are mentioned in the tractate on tools (*Mishna*, *Kelim* 17: 17).

DISCUSSION

Domesticated plants are derived from small samples of wild source populations, and thus are themselves founder populations that contain only a small fraction of the genetic diversity in their wild ancestors (Ladizinsky, 1985). Cultigens have various traits that were selected early and continually in the domestication process, such as lack of bitterness, increased size of the harvested parts, increased yield and novel coloration (Heslop-Harrison and Schwarzacher, 2012). The sweet dessert watermelon, *Citrullus lanatus*, which has relatively little genetic diversity (Levi *et al*., 2000, 2001; Dane *et al*., 2004; Nimmakayala *et al*., 2014*a*, *b*; Reddy *et al*., 2015), follows this general pattern of crop-plant domestication. The fruit flesh of wild and primitive *Citrullus* is bitter or insipid, hard and pale-coloured (Wehner, 2008). Non-bitterness of the fruits was probably the first and most important trait to be selected in the process of watermelon domestication and, in effect, success in its selection acted as a preadaptive evolutionary event (Cohen *et al*., 2014) for subsequent selection for tender and sweet fruit flesh. As non-bitterness is conferred by a single recessive gene (Chambliss *et al*., 1968; Navot *et al*., 1990; Wehner, 2007), this trait should have been relatively easy to maintain if isolation from neighbouring wild populations was feasible. The modes of inheritance of hard versus tender and of insipid versus sweet flesh in *Citrullus* have not been illuminated.

The present investigation, which has focused mainly on ancient literature, has attempted to define a narrower time frame and geographic range within which the dessert watermelons having non-bitter, tender, highly coloured, sweet flesh were developed. The latest possible date for this time frame is provided by illustrations of both red-flesh sweet dessert watermelons and white-flesh citron watermelons in illustrated manuscripts prepared in northern Italy dating to the end of the 14th century (Paris *et al*., 2009, 2013). Botanists of the European Renaissance, such as Fuchs (1542), Gerard (1597), Dalechamps (1613) and Chabrey (1666), observed various cultivars of watermelons that had red and sweet or white and insipid flesh, and noted that the finest watermelons were found in warm regions. The adaptation of watermelons to warm, sunny climates indicates that much of their history lies to the south of Europe (Paris *et al*., 2013).

Although it is agreed that the genus *Citrullus* is of African origin (Whitaker and Davis, 1962; Maynard and Maynard, 2000; Zohary *et al*., 2012), there has been major disagreement concerning where in Africa the dessert watermelon originated. Much of the controversy stems from phenotypic variations that overlap among citron, egusi and dessert watermelons and colocynths. Wild and primitive *Citrullus* fruits, regardless of taxon, typically have hard, bitter or bland, weakly coloured flesh and, as indicated by Wehner (2008), this situation has repeatedly been a source of incorrect taxonomic identifications. For example, both the citron watermelon PI 296341 and the egusi watermelon PI 457916 have small, spherical, striped fruits with hard, bitter flesh (Fig. 1). As discussed by Chomicki and Renner (2015), in but few cases have voucher specimens been preserved and thus taxonomic identifications often cannot be verified. Accounts of seed sample origins and germplasm descriptions that could help assign taxonomic identity are sometimes lacking, for example a case involving a cross between a dessert watermelon and a purported colocynth (Shimotsuma, 1958). Further confusion has been generated by the inconsistent use of nomenclature; for example, Pangalo (1930) applied the name *colocynthoides* to the citron watermelon even though he knew that name had been given a half-century earlier by Schweinfurth (1883) to the wild watermelons of the Nile Valley. Thus, some conclusions drawn from crossing experiments within *Citrullus* have been based on questionable or incorrect taxonomic identities of the parents. Confused taxonomy, together with the weakness of crossability barriers among species of *Citrullus*, has resulted in several hypotheses for the origin of the sweet dessert watermelon.

One hypothesis for the origin of the dessert watermelon is that it is descended from the colocynth of northern Africa (Singh, 1978; Sain *et al*., 2002; McCreight *et al*., 2013). *Citrullus lanatus* and *C. colocynthis* have been observed to cross spontaneously in the field (Fulks *et al*., 1979). However, the hybrid plants exhibit chromosome irregularities and lower fertility (Whitaker and Davis, 1962; Shimotsuma, 1963; Sain *et al*., 2002; Wehner, 2008). Results of investigations using techniques of molecular genetics and genomics indicate that colocynths are more distant from dessert watermelons than are citron watermelons (Jarret and Newman, 2000; Levi *et al*., 2000, 2001, 2013; Dane *et al*., 2004; Dane and Lang, 2004; Dane and Liu, 2007; Chomicki and Renner, 2015).

A second, widely accepted hypothesis for the origin of the dessert watermelon is that it is descended from the citron watermelon of southern Africa (Robinson and Decker-Walters, 1997; Maynard and Maynard, 2000; Rubatsky, 2001). However, the findings of 4000-year-old artefacts of watermelon in Egypt are contradictory, as farming was not yet under way in southern Africa at that time (Zohary *et al*., 2012; Mead and Martens, 2013). Massive preferential segregation (Levi *et al*., 2003) and reduced pollen fertility (McGregor and Waters, 2013) occur in progenies of crosses between citron and dessert watermelons. Moreover, there are major differences in genome organization between the two (Guo *et al*., 2013; Reddy *et al*., 2013; Chomicki and Renner, 2015).

A third, newer hypothesis is that 'the recent progenitor of modern cultivated watermelon' is the egusi watermelon of western Africa (Guo *et al*., 2013). Egusi and dessert watermelons are sister species that diverged only 3.1 million years ago (Chomicki and Renner, 2015). However, the egusi watermelons have peculiar soft, thick, moist, mucilaginous seed coats not reported in any other *Citrullus*. The wild-type PI 457916 has this trait (Fig. 1) and egusis were domesticated for the consumption of their seeds, not their flesh. Besides the unidirectional crossing ability between dessert and egusi watermelons (Fursa, 1983; Gusmini *et al*., 2004), egusi watermelons have high nucleotide divergence of reproductive barrier genes from the dessert watermelons, for which has been offered the tenuous explanation that 'the domestication of watermelon could be a

possible force responsible for the rapid evolution of reproductive barriers' (Guo *et al*., 2013).

A fourth hypothesis is that the dessert watermelon originated and was first domesticated in northeastern Africa (Fig. 3). Accordingly, the wild, often hard, bitter or insipid watermelons given the botanical variety name *colocynthoides* by Schweinfurth (1883) and subspecies *cordophanus* by Ter-Avanesyn (1966) (Table 1) are living representatives of the ancestor of the sweet dessert watermelon (Fursa and Gavrilyuk, 1990). Wild watermelons are widespread in Sudan (Andrews, 1950) and occur in areas of savannah and desert (Bebawi and Neugebohrn, 1991; Hassan *et al*., 2009), centred in the Nile Valley (Schweinfurth, 1873, 1883; Gouda, 2007; Mariod *et al*., 2009), to the west in Kordofan (Ter-Avanesyn, 1966) and Darfur (Robinson, 2005) and to the east in Shaqadud (Abdel-Magid, 1989). Their distribution extends north into Egypt (Muschler, 1912; Shimotsuma, 1963), and perhaps south to Kenya (Jeffrey, 1967, 2001) and east to Ethiopia (Fig. 1). The largest extant population of wild dessert watermelons may be one that has been reported adjacent to the Nile River in Sudan (Mariod *et al*., 2009). The wild population at Shaqadud, in the eastern desert some 140 km northeast of Khartoum, is exploited by local residents for water and sustenance (Abdel-Magid, 1989). Landraces in Darfur are used as a source of water (Keith-Roach, 1924). Wild watermelons are known in Sudan as *gurum* (Ziyada and Elhussien, 2008; Mariod *et al*., 2009) and in central and southern Egypt as *gurma* (Schweinfurth, 1883; Issa Bey, 1930; Manniche, 1989). Unfortunately, *Citrullus* samples derived from Sudan and Egypt have not been subjected to extensive molecular-genetic scrutiny. Results from DNA-sequence-based, systematic investigations of *Citrullus* have been presented for only a few accessions from Egypt and none from Sudan (Levi *et al*., 2013; Nimmakayala *et al*., 2014*b*). Two of the Egyptian accessions, listed as US plant introductions PI 525081 and PI 525083, which had been previously thought, based on phenotype, to be a colocynth and a citron, respectively, were observed by Levi *et al*. (2013) to cluster with dessert watermelons. Next-generation sequencing of ancient DNA (Brown *et al*., 2014), if applied to comparing watermelon artefacts with modern *Citrullus*, can be expected to identify the artefacts taxonomically. The latest sequencing and genomics technologies (Guo *et al*., 2013; Levi *et al*., 2013; Nimmakayala *et al*., 2014*a*, *b*; Chomicki and Renner, 2015) also should be directed to comparing the wild and primitive watermelons from northeastern Africa with modern, sweet dessert watermelons as well as other *Citrullus* taxa. If applied to such germplasm, the results can be expected to determine whether the dessert watermelon, *Citrullus lanatus*, indeed exhibits a clear wild/domesticated dimorphism or merely a continuum from wild to domesticated gene pools reflective of continual selection for improved horticultural traits (Abbo *et al*., 2014).

Archaeological artefacts, mostly seeds, and images found in tombs of ancient Egyptian nobility provide important evidence for the presence of *Citrullus* in northeastern Africa >4000 years ago (Schweinfurth, 1883; Keimer, 1924; Darby *et al*., 1977; Germer, 1985; de Vartavan and Asensi Amoros, 1997; Zohary *et al*., 2012). However, the Arabist Watson (1983) has questioned whether the various findings are of watermelon, *C. lanatus*, or colocynth, *C. colocynthis*. Both *C. lanatus* var. *colocynthoides* and *C. colocynthis* have been recorded as wild plants in Egypt (Muschler, 1912) and these two taxa are easily confused. Besides taking no account of the Hebrew-language evidence, Watson dismissed all of the archaeological, iconographic and other literary evidence from pre-Islamic times as indicating colocynth or melon rather than watermelon, and promulgated that sweet watermelons originated in the Indian subcontinent and diffused westward as a result of Islamic conquests. There can be no mistaking, though, that seeds >10 mm long, with bulges adjacent to the hilum and having a rough surface, are not of colocynths. The photographs and drawings of seeds presented by de Vartavan (1999) and Wasylikowa and van der Veen (2004) prove that watermelons were present in Egypt and Libya thousands of years ago. Seeds of *Citrullus* that date from the Roman period at Qusayr al-Qadim in Egypt (Cox and van der Veen, 2008; van der Veen, 2011) and, several hundred kilometres to the north, near the Dead Sea in Israel (Kislev and Simhoni, 2009), shown in clear photographs, likewise cannot be of colocynths. Hence, there can be no remaining doubt that watermelons were present in Egypt and its immediate neighbours for centuries, even millennia, prior to the rise of Islam.

Although the watermelon must have been a familiar item valued by the Egyptians of pharaonic times, from the remains alone it is not clear whether the fruits were gathered from wild or cultivated plants. However, the image of a large, oblong, striped fruit in an Egyptian tomb, >4000 years old (Manniche, 1989, p. 92), is suggestive of a cultivated watermelon. The wild and primitive watermelons of northeastern Africa are typically spherical (Schweinfurth, 1883; Ter-Avanesyn, 1966) (Fig. 1), and therefore this oblong-shaped specimen obviously deviates from the wild type. This fruit appears on a tray served, undoubtedly, to a royal receiver, surely indicating the esteem given to this item and that it was to be eaten fresh (Chomicki and Renner, 2015). Indeed, this fruit could not have been a citron watermelon because citron fruit flesh is too hard to be enjoyed fresh in large quantity. Although melons, *Cucumis melo*, are large fruits and can be striped, the striping of mature, ripe melons is rarely as stark as that shown in the image. As this large, striped fruit was enjoyed fresh, it must have been non-bitter and tender-fleshed, and its oblong shape indicates that it was taken from a cultivated plant. However, this fruit was not necessarily sweet, at least not according to modern standards (Mohr, 1986; Maynard, 2001). The longing for *avattihim* by the Children of Israel (*Numbers* 11:5) places them, at the time of the Exodus, in the same category as the *qishu'im* (snake melons) and various Alliaceae. Like the snake melons, leeks, onions and garlics, the *avattihim* of that early time were probably eaten fresh, pickled or cooked, not better tasting than snake melons and certainly not sweet like modern dessert watermelons.

Greek, Latin and Hebrew writers of the first centuries CE clearly distinguished watermelons, melons and colocynths. Physicians writing in Greek, from Hippocrates (~400 BCE) (Jones, 1967) to Dioscorides (first century) (Osbaldeston and Wood, 2000; Beck, 2005), Galen (second century) (Grant, 2000; Powell and Wilkins, 2003) and Oribasius (fourth century) (Grant, 1997), indicated that the *pepon* was wet, abundantly cooling, easily digested and diuretic. The *pepon* must have been large enough to be placed on the head of a child and quite wet and cooling so as to reduce fever, as instructed by Dioscorides. To Pliny, the *pepo* was a food that was most cooling (Rackham, 1950; Jones, 1951). The *Jerusalem Talmud*

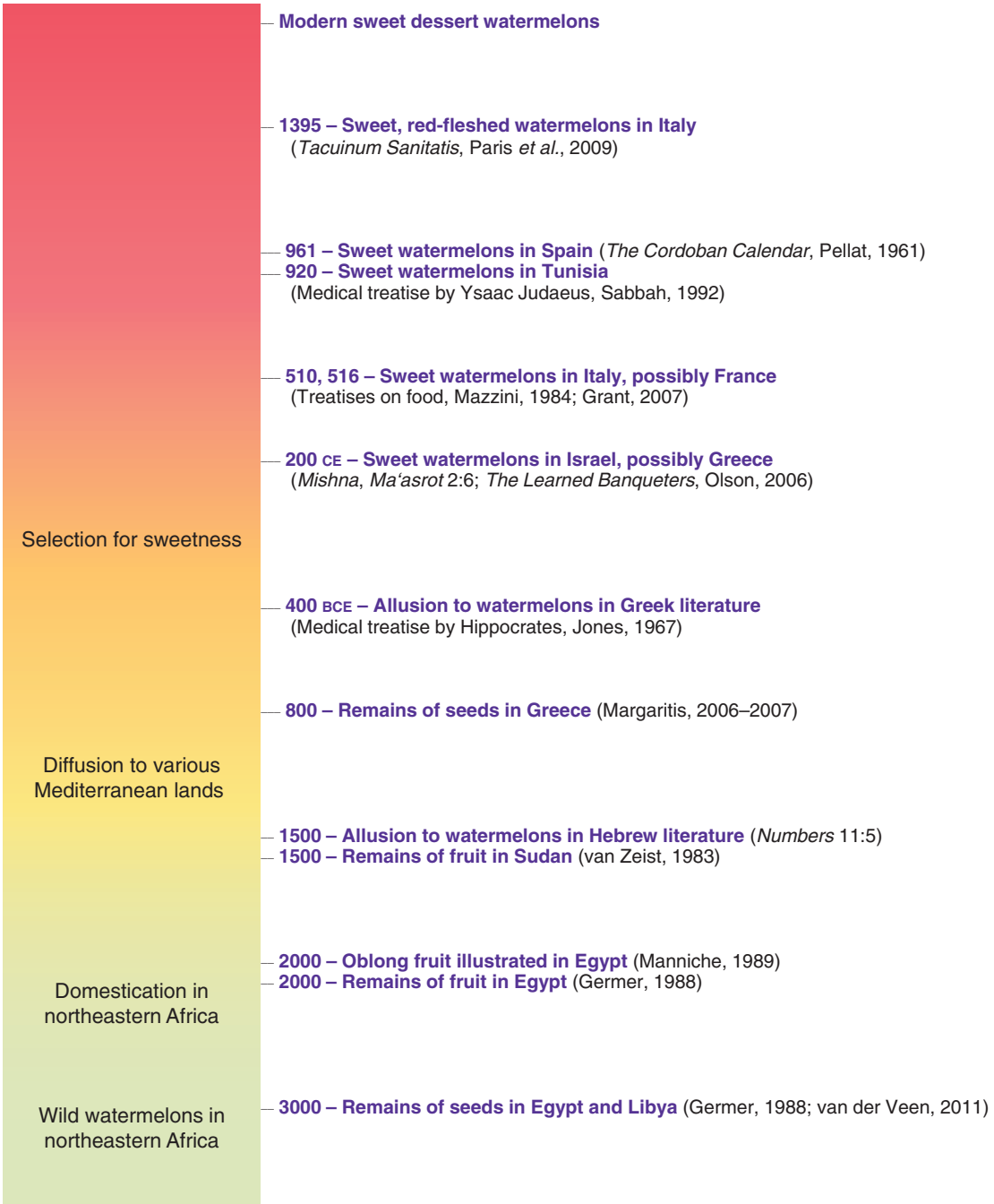

FIG. 3. Schematic timeline with highlights of the evidence, in chronological order from bottom to top, for the origin and emergence of the sweet dessert watermelon. Column at left shows a gradient of watermelon fruit-flesh colour from greenish white or white of wild and primitive watermelons to intense red of modern watermelons. On this gradient are indicated the existence of wild dessert watermelons, *Citrullus lanatus*, in northeastern Africa prior to 3000 BCE, and the timing of domestication, diffusion to lands outside of northeastern Africa, and selection for fruit flesh sweetness. The timing of the intermediate colours in the gradient is speculative, the only basis being the orange fruit flesh illustrated in a floor mosaic from southern Israel dating to ~425 CE (Avital and Paris, 2014) and the red fruit flesh illustrated in a *Tacuinum Sanitatis* manuscript from northern Italy dating to ~1395 (Paris *et al.*, 2009). Column at right indicates the timing of the highlights of archaeological, iconographic and literary evidence in accordance with the corresponding speculated intermediate fruit flesh colours.

(*Kil'ayim* 1:8, p. 4a) indicates that the *avattiah* was a watery fruit. The *pepon* of the Greek physicians, the *pepo* of the Latin encyclopaedist Pliny and the *avattiah* of the Hebrew scholars were one and the same large, watery fruit – the watermelon. The *melopepon*, the supposed hybrid of an apple with a *pepon*, had a less moisturizing and cooling effect, according to Galen and Oribasius. The *melopepo* may indeed have been a new introduction, as stated by Pliny (first century), because it is not mentioned by his contemporary, Dioscorides. According to Pliny, the *melopepo* became yellow and aromatic and spontaneously detached from the plant when it ripened. Thus the *melopepo* is without question the melon, *Cucumis melo*, an edible

cucurbit that typically yellows and becomes aromatic, and is the only one that abscises from the plant upon ripening (Whitaker and Davis, 1962; Robinson and Decker-Walters, 1997). The same taxonomic identity of the Hebrew rendition, *melafefon*, is established by the identical mythical perception of its being an apple-*pepon* admixture (*Jerusalem Talmud*, *Kil'ayim* 1:2, p. 2a). The *kolokyntha agria* or *colocynthis*, colocynth, described by the Greek physicians and by Pliny, was a familiar, highly regarded commodity for medicinal preparations and as such could not possibly be undistinguished from the watermelon (Amar and Lev, 2011). To some of the Greek writers quoted by Athenaeus (Olson, 2006), the edible, cultivated *kolokunte* were large and could be sweet, and thus distinguished from the inedible, wild *kolokyntha agria*, the colocynth. Indeed, the extremely bitter *paqqu'ot* (*2 Kings* 4:39–40), colocynths, were already clearly distinguished in biblical times from the cultivated, non-sweet but pleasant-tasting *avattihim* (Feliks, 1968; Janick *et al*., 2007). The *paqqu'ot*, like the *yeroqat hamor* (squirting cucumber, *Ecballium elaterium*), are absent from the tractate on tithing, *Ma'asrot*, and thus they were not food items, although they were used for other purposes (Feliks, 1968; Janick *et al*., 2007). Moreover, the Latin recipe book of Apicius distinguished between two kinds of watermelons, using the word *pepones* for fruits that were dressed and eaten fresh and the word *citrium* for a fruit that was cooked (Flower and Rosenbaum, 1958).

The Hebrew-language literature provides considerably more information concerning the cucurbit food crops than does the contemporary and near-contemporary Greek and Latin literature. Four cucurbits, the *qishu'im*, *delu'im*, *avattihim* and *melafefonot*, are discussed together in some passages. Each of these four must have been widely cultivated, often in the same field, because there are prohibitions on planting them too close to one another (*Mishna*, *Kil'ayim* 1:5; *Tosefta*, *Kil'ayim* 1:4). Likewise, each must have been grown for the consumption of its fruits because the tractate on tithing contains a number of pertinent instructions concerning each of them. Prior to eating, the *qishu'im* (snake melons) and the *delu'im* (bottle gourds) were to undergo *piqqus*, rubbing off of the hairs, and thus these fruits were consumed when young (Feliks, 1968; Janick *et al*., 2007). In contrast, the *avattihim* and the *melafefonot* were to undergo *shilluq*, smoothing of the fruit surface to remove accumulated dust (Qafah, 1963), and thus these fruits were to be eaten mature, upon ripening (*Mishna*, *Tosefta* and *Jerusalem Talmud, Ma'asrot* 1:4–6). The use of the *avattihim* when they were ripe, like pomegranates, is confirmed in the tractate on fruit stems (*Mishna*, *'Oqazin* 2:3).

The descriptions of the *pepon*/*pepo*/*avattiah* as being watery with a thick rind and the *melopepon*/*melopepo*/*melafefon* as becoming yellow and aromatic and spontaneously detaching from the plant when ripe, are sufficient to identify them as watermelons and melons, respectively. Other traits mentioned in the Hebrew literature reinforce these identifications. The *melafefonot*, but not the *avattihim*, ripened in two main waves over the course of the growing season (*Tosefta*, *Ma'asrot* 1:6). Ripening in waves is a well-known characteristic of melon crops (Rosa, 1924; McGlasson and Pratt, 1963; Pratt *et al*., 1977). For tithing, the *avattihim* were to be laid out individually rather than stacked (*Mishna*, *Ma'asrot* 1:5). Indeed, the watermelons of yesteryear had fragile rinds and thus were highly subject to splitting. They were replaced during the mid-20th century by newly bred cultivars having tough-rinded fruits (Parris, 1949; Ivanoff, 1954). After harvest, the *avattihim* were fit for contribution for an indefinite period, but the *melafefonot* could be contributed only during the first 3 d after harvest (*Tosefta*, *Terumot* 4:5). Whilst dessert watermelons have a shelf-life of several weeks or months (Keith-Roach, 1924; Rushing *et al*., 2001), muskmelons and cantaloupes, if not refrigerated, have a shelf-life of only 3–4 d (Burger *et al*., 2010).

In the tractate on tithing, watermelons are discussed with figs, table grapes and pomegranates (*Mishna*, *Ma'asrot* 2:6, 3:9; *Jerusalem Talmud*, *Ma'asrot* 2:4, 3:4), fruits which are juicy and sweet, and therefore the watermelons of the time must have been likewise. Although the watermelons and melons are usually mentioned together in the Jewish literature, only the watermelons are mentioned with the other three sweet fruits. Sweet melons are thought to have originated in Khorasan, Central Asia, reaching the Mediterranean Basin much later, in the 11th century, and these are the *battikh* that diffused westward after the rise of Islam (Paris *et al*., 2012*b*).

Diocles was quoted by Athenaeus (second century) as saying that the best *kolokyntas* are *glukeian*, sweet (Olson, 2006). The early sixth-century *De Observantia Ciborum* lists the *pepone* among pomegranates, grapes and figs, confirming the presence of sweet watermelons in what is now Italy (Mazzini, 1984). The early sixth-century writing of Anthimus (Grant, 2007) indicates that the *melones* were eaten when they were ripe and freshly cut, the seeds still mixed in the flesh. Anthimus, evidently, used the word *melones* for watermelons, the same word used for them in the 14th- and 15th-century *Tacuinum Sanitatis* (Paris *et al*., 2009). Hence, by the second decade of the sixth century, at the very latest, the eating of sweet, ripe watermelons had spread beyond Israel and Greece to Italy and possibly France (Fig. 3). Sweet watermelons had diffused to Europe centuries before their earliest recorded presence in Moorish Spain, in the *Cordoban Calendar* of 961 CE (Pellat, 1961).

Athenaeus (late second century) quoted Phaenias as stating that the *pepon* is edible, except for the seeds, when the flesh becomes soft (Olson, 2006) and Quintus Gargilius Martilus (mid-third century) wrote that the *pepone* are good to eat after the rind and seeds have been removed (Maire, 2007). The *Jerusalem Talmud* (*Ma'asrot* 1:2, 2b) instructs that the seeds of the *melafefonot* are tithed and those of the *avattiah* are not, because the former were eaten and the latter were not (Feliks, 2005). Thus, in Roman times around the Mediterranean, the tender, sweet, juicy ripe fruit flesh of the watermelons was consumed and the seeds were not. In Byzantine-era mosaics (350–600 CE) in Israel, watermelons of a variety of sizes and rind colour patterns are depicted. One mosaic has what appears to be a cut fruit with yellow-orange flesh and white seeds (Avital and Paris, 2014).

Watson (1983) cited the medieval Arabic names *battikh hindi* and *battikh sindi* as evidence for the derivation of the sweet dessert watermelon in the Indian subcontinent. The former name was first recorded in the *Cordoban Calendar* of 961 CE (Pellat, 1961) and the latter as the source of the modern Spanish word for watermelon, *sandia*, Sind being a province in Pakistan. Although *Citrullus lanatus* is native to Africa, it is conceivable that a cultivar of sweet watermelon could have emerged elsewhere, isolated from local wild or cultivated plants having inferior horticultural traits. Indeed, contamination of an elite

watermelon cultivar was described by the late 15th-century writer Ibn Shihna (Sarkis, 1909). Seeds of an excellent watermelon, 'Raqqi' (from the environs of Raqqa, adjacent to the Euphrates River in Syria), were imported annually by Gazans because seeds taken from 'Raqqi' fruits grown in Gaza and planted the following year produced inferior fruits. Undoubtedly, growing in or near Gaza were local cultivars or wild populations of insipid or bitter *Citrullus*; some such populations still exist (Shemida' and Danin, 1983). To the present, watermelons in Iraq are called *raqqi* (Chakravarty, 1966; Perry, 2005; Nasrallah, 2007) and therefore it is possible that, similarly, the names *battikh hindi* and *battikh sindi* reflected the introduction of a superior cultivar from the Indian sub-continent or, at least, from a land to the east. Such a watermelon was grown in Khwarizm, near the Aral Sea in Central Asia, and its fruits were carefully packed and shipped to the caliphs Wathiq and Ma'mun of Baghdad during the first half of the ninth century (Bosworth, 1968; Said, 1973). On the other hand, there is also much precedent for the use of exotic names for cucurbits as a marketing ploy. The *Cucurbita moschata* Duchesne 'Tahitian' squash has an exotic name, but it is not proof of its geographic origin (Robinson, 1980). Indeed, the familiar dessert watermelon 'Congo' was bred in the USA (Levi *et al*., 2004). The Indian or Sindian *battikh* would have sounded exotic in medieval Andalusia, as Spain was at the far western end and Pakistan was at the far eastern end of the Islamic Empire. Significantly, *battikh hindi* and *battikh sindi* were given as synonyms of *dulla'* in the medieval lexicon of northern Africa and Andalusia (Meyerhof and Sobhy, 1938; Dozy and Engelmann, 1915; Pellat, 1961; Amar, 2000). *Dulla'* is a Berber word for sweet dessert watermelon which appears to share the same Semitic root, *d-l-'*, as the Hebrew word for bottle gourd, *dela'at*. The existence of the Berber word indicates an established regional familiarity with the sweet watermelon. Indeed, Ysaac Judaeus, a physician of Qayrawan, Tunisia, in his *Book of Particulars in Diet* (∼ 920) (Sabbah, 1992), mentioned the *dulla'* four decades prior to the first recording of the *battikh hindi* and *battikh sindi* in Spain (Pellat, 1961). Also, it is tempting to parallel the juggling of bottle gourd with sweet watermelon between Hebrew and Berber with that of *kolokynte* and *pepon* by various Greek writers, as related by Atheneaus (Olson, 2006). Whitaker and Davis (1962) believed, based on historical records and indigenous names for watermelon of Egyptians and Berbers, that the sweet dessert watermelon has its origins in Africa.

The combination of literary evidence, especially that in Hebrew, with the archaeological and iconographic evidence from Egypt and Sudan, and the modern distribution of wild and primitive watermelons in Sudan and neighbouring countries, is overwhelming. Dessert watermelons are native to northeastern Africa and sweet dessert watermelons were selected in Mediterranean lands by no later than the second century CE.

CONCLUSIONS

The dessert watermelon, *Citrullus lanatus*, is native to northeastern Africa. Wild *C. lanatus* populations in Sudan, reported as bearing small, round, inferior-quality fruits, are living representatives of the wild ancestor of the sweet dessert watermelon. Ancient seeds, fruits and images of watermelons have been found in Sudan and Egypt and one image seems to depict the serving of a large, oblong, striped fruit which likely had non-bitter, tender flesh but was not sweet by modern standards. Hebrew-language literature from the first centuries CE indicates that, by Roman times, sweet dessert watermelons were esteemed in the Land of Israel and thus likely were present in other Mediterranean lands as well. The ripe fruit flesh, which was probably distinctly coloured rather than pale, was eaten raw and had sweetness comparable to that of figs, grapes and pomegranates. The seeds were not consumed. During or prior to the Roman era, the citron watermelon arrived in Mediterranean lands and its fruit flesh was consumed after being cooked.

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