Euphytica (2025) 221:173
https://doi.org/10.1007/s10681-025-03627-z

REVIEW

Southern Italy: birthplace of the Cocozelle squash, *Cucurbita pepo* subsp. *pepo*, Cocozelle Group

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Received: 26 June 2025 / Accepted: 24 September 2025 / Published online: 4 October 2025
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Abstract Cocozelle squash are the most elongate fruits of *Cucurbita pepo*. Their length-to-broadest width ratio ranges from 3.5 to 8.0, and at maturity they can attain a length of 75 cm. Cocozelle squash bulge toward the stylar end and are obviously narrower at the mid-portion or peduncle end. Cocozelle squash are harvested when very young, usually just 0–3 days past anthesis. The ovaries and the corollas of the pistillate flowers of many Cocozelle cultivars are huge and the pistillate flowers are frequently offered for sale in Italian markets. Our goal is to review the history and evolution under cultivation of the Cocozelle squash. The word *cocozelle* is derived from a southern Italian dialect, being a diminutive of the word *cocozze*, the bottle gourd. The earliest-known images of Cocozelle squash date to the late sixteenth century. The Swiss botanist Johann Bauhin described a Cocozelle squash in the seventeenth century and the French plant scientist Antoine Nicolas Duchesne illustrated and described Cocozelle squash in the late eighteenth century. The Cocozelle 'San Pasquale' was mentioned by the Italian horticultural scientist Filippo Re in 1811. The culinary use of long-fruited summer squash is documented in Italian cookbooks of the seventeenth century. There are very many cultigens of Cocozelle squash, including landraces and old, open-pollinated cultivars mostly from Italy but also from France, Spain, Turkey, and North Macedonia. In recent decades, many hybrid Cocozelles have been developed in Italy and elsewhere. Although the word *cocozelle* is not currently in fashion in the seed industry, in fact the seeds of many Cocozelle hybrids are offered for sale around the world, by local companies as well as multinationals.

Keywords Crop evolution · Crop history · Cucurbitaceae · Evolution under cultivation · Fruit-shape diversity · Summer squash

Introduction

Cocozelle squash are a large group of cultivars and landraces of *Cucurbita pepo* L. (Cucurbitaceae). These cultigens are defined by their extreme extent of fruit elongation, having a length-to-broadest-width ratio of at least 3.5 and often of 5.0 or more (Paris 1986). This is the most extreme fruit elongation in *C. pepo* (Nerson et al. 2000; Paris et al. 2012).

This work is based on a presentation by Harry S. Paris at the Eucarpia Cucurbitaceae 2024 Conference held in Vico Equense, Campania, southern Italy, on November 4, 2024.

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Cucurbita pepo is a highly diverse and economically important crop species. It is native to North America and has been cultivated there for thousands of years (Whitaker 1947). *C. pepo* was domesticated at least twice, first in what is now southern Mexico approximately 10,000 years ago and second in what is now the eastern half of the United States around 5000 years ago (Whitaker and Carter 1946; Whitaker and Cutler 1971; Decker 1988; Cowan 1997; Teppner 2004; Smith 2006). Both domestications are thought to have occurred via the ruderal pathway, in which plants benefit from and adapt to changes in the environment wrought by anthropic disturbance in and around areas of human activity (Fuller et al. 2025). The descendants of the two independent domestications of *C. pepo* form two distinct genetic lineages. The descendants of the southern domestication are generally classified as subspecies *pepo* and those of the eastern domestication as subspecies *ovifera* (L.) D.S. Decker. The Cocozelle is ultimately derived from the Mexican lineage, subsp. *pepo* (Katzir et al. 2000; Gong et al. 2012; Paris et al. 2015).

The first European explorers of North America encountered *Cucurbita pepo* and brought fruits and seeds back to Europe. European artists, beginning in the sixteenth century, illustrated the foliage, flowers, and fruits of *Cucurbita pepo* (Paris 2000a; Teppner 2000). From these images, we can learn of the diversity of *C. pepo* that existed at the time. The images include representations of both subspecies.

We have not found any illustrations of long-fruited *Cucurbita pepo* subsp. *pepo* that antedate the year 1580. A few native North American landraces of *C. pepo* subsp. *pepo* contain individual plants bearing markedly elongated fruits but, in spite of the high genetic diversity for microsatellite and chloroplast loci observed in ancestral Mexican *C. pepo* subsp. *pepo* (Castellanos-Morales et al. 2019; Martínez-González et al. 2021), to our knowledge long fruits have not been described as being characteristic of any Mexican landrace. This suggests that the evolution of longfruitedness as a consistent trait of any cultigen of subsp. *pepo* was post-Columbian.

The present review is based on a presentation that the first author contributed at the Eucarpia Cucurbitaceae 2024 conference held in Vico Equense, southern Italy (Paris 2024). Based on that presentation, our goal here is to review the evolution under cultivation and history of the Cocozelle squash. We will show that the bulk of the evidence indicates that the birthplace of the plurality of Cocozelle cultigens is the southern half of Italy. We will not repeat details given in the comprehensive review of a decade ago of the history of *Cucurbita pepo* in Italian kitchens and gardens (Lust and Paris 2016), but instead give some of the highlights therein that are relevant to the Cocozelle. To these we will add sixteenth-century iconographic evidence uncovered more recently. We will also discuss the present status of the Cocozelle with regard to its modern cultivars.

Crop evolution and divergence in *Cucurbita pepo*

Wild plants of *Cucurbita pepo* bear prettily striped but bitter, small, 3–5 cm diameter, spherical, globular, or pyriform fruits, which likely attracted the attention of early hunter-gatherers (Nee 1990). Probably the first food use of these gourds by people was the eating of their seeds (Whitaker and Cutler 1965). The seeds are calorie-rich and not bitter, containing ≈ 40% oil (Jarret et al. 2013), and are easily washed free of the bitter placental tissue surrounding them (Lira and Montes 1994). During both domestications of *C. pepo*, ancient peoples encountered occasional plants which bore non-bitter fruits. These plants were nurtured (Paris 2018) and eventually underwent what has been coined *vegetabling* (Goldman 2025), transforming from gourds into the pumpkins and squash that are so valued today.

As the gourds borne by wild *Cucurbita pepo* are usually round or nearly so, the fruits of the first non-bitter cultigens grown for food were also probably round. For consumption of the seeds, fruit roundness is advantageous, as round fruits contain more seeds than elongate fruits (Nerson and Paris 2001; Nerson 2005). The fruit flesh (mesocarp) of mature fruits of these new cultigens was likely toughly fibrous, dry, and thin, like that of their gourd ancestors. Over time, people selected for larger fruits and seeds, and for a moister, less fibrous, and thicker mesocarp (Whitaker and Bemis 1964). Preparation of mature, large fruits involves cutting and separating the seeds from the fruit flesh, as these two components would be treated differently in their preparation and cooking.

After banishment of bitterness, the use of the immature fruits as food would have been straightforward. Young fruits are succulent and not fibrous, thus

not requiring the same extent of improvement in palatability as mature fruits. Still, the young round fruits had a thin mesocarp and much endocarp consisting of soft, stringy placenta and many young, developing seed coats (Loy 2004). To obtain a better cooked product, the fruits would have to be cut and the relatively large volume endocarp scooped out. But people noticed that variant fruits deviating from roundness were firmer, having proportionally more of the firm mesocarp, than the typical round fruits (Sinnott and Durham 1929; Nerson et al. 2000). Successive increments of divergence from roundness further improved eating quality.

Differing usage of the fruits of *Cucurbita pepo* brought with it divergence in plant architecture. Resource allocation is fundamentally different in plants on which fruits are allowed to grow to maturity as opposed to plants that are continually harvested for their young fruits (Loy 2012). The first-developing fruits inhibit further plant growth and fruit production (Zack and Loy 1981; Stephenson et al. 1988). Continual removal of young fruits, though, releases the plant to grow and produce more fruits (El-Keblawy and Lovett-Doust 1996). Plants cultivated for their mature fruits can be allowed to develop freely, growing and branching in all directions until the end of the growing season. However, harvesting of young fruits requires many visits to the field, which inevitably results in trampling and damage to the plants bearing them, and time-consuming searching under the foliage for the small fruits. These difficulties were eventually overcome by selection of rare, mutant plants that were less spreading and less branched.

Fruit-shape groups of edible *Cucurbita pepo*

The very many edible-fruited cultigens of *Cucurbita pepo* can be sorted into eight cultivar-groups or morphotypes based on their differing fruit shapes (Paris 1986). Four of them are classified in subsp. *pepo* and four in subsp. *ovifera*. They are formally referred to as Groups (Brickell et al. 2004) and are listed and schematically illustrated in Table 1. Photographs of young fruits from each Group are presented in Fig. 1.

The Cocozelle is one of the four Groups of edible-fruited of *Cucurbita pepo* subsp. *pepo* (Paris 2000a). Cocozelle cultivars bear long fruits, but although the fruits are generally cylindrical, they are distinctly broader toward the distal, stylar end, wherein most of the ovules and developing seeds are located (Nerson and Paris 2001). It is in this way that the Cocozelle is distinguished from another Group of subsp. *pepo*, the familiar Zucchini. The Zucchini cultivars bear cylindrical fruits that have a uniform diameter along most of the length of the fruit and are usually not as elongated as the Cocozelle. The two other Groups of this subspecies are the Vegetable Marrow, which has tapered, shorter fruits and the Pumpkin, which is characterized by round fruits (Table 1; Fig. 1).

DNA-sequence polymorphisms have been applied in a number of investigations to assess genetic diversity in *Cucurbita pepo* and the results have validated the differentiation into the subspecies and fruit-shape Groups. For example, Gong et al. (2012), using simple sequence repeats (SSRs), observed two main clusters within *C. pepo* corresponding to the two subspecies. Within each subspecies, accessions belonging to the same Group mostly sub-clustered with one another. Although domestication of subsp. *pepo* antedated that of subsp. *ovifera* by 5000 years (Smith 2006), genetic dissimilarities (GD) among the subsp. *ovifera* Groups were greater than those among the subsp. *pepo* Groups. This suggests that subsp. *ovifera* split into Groups earlier than subsp. *pepo*, consistent with findings of rind fragments in pre-Columbian Kentucky (Watson and Yarnell 1966, 1969; Cowan 1997) and various images of Acorn and Scallop squash in sixteenth-century herbals (Paris 2000a; Teppner 2000). Using principal component analysis, Gong et al. (2012) also observed that subsp. *pepo* has a central core comprised mostly of Pumpkin Group accessions but also several from both, the Vegetable Marrow and Cocozelle Groups. The Pumpkin Group had the majority of its cultivars within the core, the Vegetable Marrow cultivars were mostly just outside the core edge, the Cocozelle cultivars were more distant from the core and the Zucchini cultivars were the most distant. Although both, the Cocozelle and the Zucchini are of Italian origin and have quite elongate fruits, they appear to be less closely related to one another than each is to European accessions of the Pumpkin Group (Paris et al. 2015; Xanthopoulou et al. 2019), suggesting that they evolved independently. Recently, Perez-Moro et al. (2025) used SNP calling to assess Cocozelle and Zucchini cultivars. The two Groups formed separate clusters when compared for genetic variants in morphology, gibberellin

Table 1 The eight fruit-shape morphotypes or cultivar-groups of edible-fruited *Cucurbita pepo*

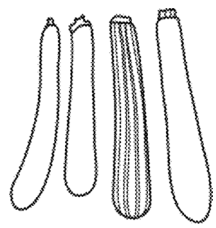
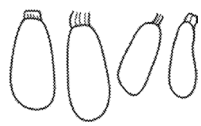
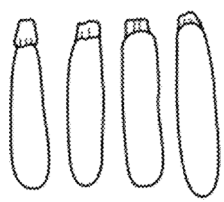
Subspecies	Morphotype	Description	Schematic illustration
ovifera	Acorn	Turbinate, furrowed	
ovifera	Crookneck	Elongate, narrow-necked	
ovifera	Scallop	Flattened, scalloped	
ovifera	Straightneck	Elongate, proximal constriction	
pepo	Cocozelle	Long, bulbous cylindrical	
pepo	Pumpkin	Round	
pepo	Vegetable Marrow	Short, tapered cylindrical	
pepo	Zucchini	Uniformly cylindrical	



Fig. 1 Young fruits of the eight edible-fruited cultivar-groups of *Cucurbita pepo*. Top row, subsp. *ovifera*, left to right: Acorn (produced at Newe Ya'ar, Israel 2025), Crookneck (produced at Newe Ya'ar, Israel 2025), Scallop (marketed in Brisbane, Queensland, Australia 2014), Straightneck (marketed in Columbia, Maryland, U.S.A. 2024). Bottom row, subsp. *pepo*, left to right: Cocozelle (marketed in Ventimiglia, Liguria, Italy 2009), Pumpkin (marketed in Nahariyya, Israel 2025), Vegetable Marrow (marketed in Ramat Yishay, Israel 2025), Zucchini (marketed in Ramat Yishay, Israel 2025)

regulation, leaf development, and pigment accumulation. Thus, evolution under cultivation for marked deviation from fruit roundness occurred at least four times in *C. pepo*, to Crookneck and Scallop in subsp. *ovifera* and to Cocozelle and Zucchini in subsp. *pepo*. The repeated selection for this trait underscores its culinary importance.

Word evolution and lexicon

The word *cocozelle* is from an old Italian dialect, being the plural feminine diminutive of the much older Italian word *cocuzze* (also rendered *cucuzzi*, *cocozze*, *cucuzza*) which was, and still is, used for bottle gourds, *Lagenaria siceraria* (Mol.) Standl. (Lust and Paris 2016). Bottle gourds have been cultivated in Mediterranean lands at least since the Roman period. The Roman Latin word for the bottle gourd was *cucurbita*. Bottle gourd fruits are moist when young but as they mature their rinds lignify and their interiors desiccate. Mature bottle gourds of various shapes and sizes had various uses, such as jugs for carrying liquids. Young bottle gourds having a very elongate shape were a common culinary item in Italy and elsewhere around the Mediterranean during the Roman period (Janick et al. 2007). Eventually, the Latin *cucurbita* evolved into the southern Italian *cucuzza*. Further north, the word *cucuzza* underwent a deletion and an inversion to become *zucca*. The process of inversion within words is not unique. For example, in English, a *butterfly* is, actually, a *flutterby*.

Cucurbita arrived in Italy by 1518, at the very latest (Janick and Paris 2006). The new arrivals were sensational curiosities well-adapted for growing in much of Italy, and were quickly adopted into Italian gardens and kitchens. The plants grew quickly and bore their flowers and fruits much earlier in the summer than the bottle gourds and yielded prolificly, allowing Italian gardeners to quickly select for compact plant growth and improved culinary adaptation and palatability of the fruits. Foliage, flowers, and especially the young fruits of *C. pepo* were harvested and used in Italian kitchens by the mid-sixteenth century (Lust and Paris 2016). By the mid-seventeenth century, young round and long, narrow fruits of *C. pepo* were addressed as separate culinary items in Italian recipes. By the eighteenth century, the long

C. pepo fruits began replacing long bottle gourds in the kitchen. As various *Cucurbita* became common, the words *cocuzza* and *zucca*, which were originally applied to bottle gourds, became more commonly applied to pumpkins and squash. The new small, young fruits of *C. pepo* were in need of a separate name, though, and an easy option could have been based on their diminutive size.

The Italian language seems to have a love of diminutive suffixes and the *Grande Dizionario della Lingua Italiana* (Battaglia 2002) indicates numerous examples. Among the suffixes adopted in Italian gardening literature and cookbooks for the new, small *cocuzze* or *zucche* were *-elle*, *-ette*, *-ine*, and *-ettine*. Among the possible combinations derived from diminutization of the words for gourds there are *cocozelle*, which would be a diminutive (fem. pl.) of *cucuzzi*, and *zucchini*, which would be a diminutive (masc. pl.) of *zucche*.

Many dialects were spoken in various parts of Italy and there was a very large number of words that were used for small gourds. With unification of the country in 1870, a Standard Italian, based on a Tuscan dialect, gradually came into use throughout the country. The word *zucchino* (masc. sing.) displaced the many older dialect terms that had been in use for various young squash (Lust and Paris 2016). Today, the words *zucchino* and *zucchine* (fem. pl.) are used in Italy much as the term *summer squash* is used in American English. Italian seed packets display pictures of summer squash, regardless of shape, with the descriptor *zucchino*. At markets, summer squash are displayed as *zucchine*.

History of the Cocozelle squash

The earliest-known illustration of a Cocozelle squash is in the painting *La Fruttivendola* (*The Greengrocer* or *The Fruit Seller*) by Vincenzo Campi in 1580, held in the collection of the Pinacoteca di Brera, in Milan (European Research Council 2017). A high-resolution reproduction can be seen here: https://refashioningrenaissance.eu/fruitseller. This painting contains realistic images of various fruits and vegetables. Among the many subjects are a few flower buds of *Cucurbita pepo* (Fig. 2). The two largest buds, one staminate and one pistillate, show some yellowing of the outside of the corolla, indicating that they were picked on the day prior to anthesis. The ovary of the pistillate bud is 3.6 times longer than at its widest portion, which is near the calyx and corolla, that



Fig. 2 Top, magnification of the image of squash flowers and foliage in Vincenzo Campi's painting *Fruttivendola* (1580). Center, photographic re-creation of Campi's image using flowers and foliage from the Cocozelle 'Romanesco' and its likely derivative 'Lunga di Toscana'. Bottom, staminate flowers of 'Romanesco' and 'Lunga di Toscana'. Notice the similarity of the staminate flower receptacle in Campi's image (top) with those of the present day (center and bottom)

is, at its stylar end. It is also strongly ribbed, thereby resembling ovaries of the extant cocozelle 'Romanesco', also known as 'Costata Romanesca'. Presently, both staminate and pistillate squash flowers are used in a variety of culinary preparations in Italy and other Mediterranean countries (Milc et al. 2016). Some doubts had been raised concerning the taxonomic identity of the buds, noting a resemblance to those of okra, *Abelmoschus esculentus* (L.) Moench (Malvaceae) (Paris 2023a), but the bulging receptacle of the large staminate flower is consistent with the flowers of *C. pepo* but not *A. esculentus*.

The doubts concerning the taxonomic identity of the flower buds in Campi's painting were assuaged upon retrieval of images that had been published a mere 12 years later, in the *Archetypa studiaque patris* of the Flemish nature illustrator Joris Hoefnagel (Hoefnagel 1592). Hoefnagel had travelled in various parts of Europe, including southern Italy. The Frontispiece of Part 2 of his *Archetypa studiaque patris* shows a large, ≥40 cm long fruit, nearly cylindrical but swollen at its stylar end, the stylar scar being clearly visible (Fig. 3). This fruit is quite elongate and, accounting for its curvature and tilting in the image, has a length-to-width ratio approximating 3.5. This high length-to-width ratio coupled with the obviously swollen stylar end indicates that this fruit is a cocozelle squash and, with its prominent ribs, it strongly resembles the cocozelle 'Romanesco'. The illustrated mature fruit was well beyond its peak of culinary usefulness but would certainly have remained a fit subject for illustration, for a much longer period of time before deteriorating, than would a flower or young fruit. A second illustration of a mature 'Romanesco' cocozelle is found elsewhere in Hoefnagel's *Archetypa studiaque patris* (Paris 2023b).

Johann Bauhin (1651), in his immense *Historia plantarum universalis*, described very many forms of *Cucurbita pepo*, some accompanied by woodcut illustrations including foliage and fruits. Five of the descriptions appear under the heading *Cucurbita aspero folio flore luteo semiarcus in morem intorta* (gourd with rough foliage and yellow flowers, twisted into an arch), the yellow flowers indeed indicating *Cucurbita* (as opposed to *Lagenaria*), and the rough foliage indicating *C. pepo*. Among these five, the fourth was described as having slender, broadly ribbed fruit of length one-and-a-half cubits (≥60 cm), and of a blotched, vibrant green color. The length as well as the slenderness of this *C. pepo* fruit could only indicate a cocozelle, as the Cocozelle Group is the only *C. pepo* that can commonly attain a fruit length of 60 cm or more.



Fig. 3 Magnification of part of the Frontispiece of Part 2 of Joris Hoefnagel's *Archetypa studiaque patris* (1592) showing a large, ≥40 cm long mature Cocozelle fruit

Italian cookbooks from the seventeenth century contain recipes for preparation of the young fruits of *Cucurbita pepo*, indeed even separate recipes for the use of round or elongate young fruits (Lust and Paris 2016). One of these, published in Rome in 1638, gives directions for preparing *cocuzzette longhe tenere* (tender, long *cocuzzette*). Another, published in Naples in 1692, gives directions for preparation of *picciole cocuzze* (tiny *cocuzze*). Given the late sixteenth century illustrations by Campi and by Hoefnagel (1592) and the description by Johann Bauhin

(1651), the long-fruited young squash used in seventeenth-century Italian kitchens were very likely cocozelles.

Antoine-Nicolas Duchesne, the French amateur plant scientist and an early, strident proponent of the biological species concept, described and illustrated fruits of several cocozelles (Duchesne 1786; Paris 2000b, 2007). The most stunning of the gouache images shows a highly realistic and detailed, nearly fully grown fruit, very long and slender, curved, green-striped, with part of the plant attached. Duchesne labelled it *Cucurbita aspero folio flore luteo, semiarcus in morem intorta J.B.* (Fig. 4).

Filippo Re (1811), an Italian horticultural scientist, wrote that the *coconzelli* were the small, freshly formed squash that are sold in markets for kitchen use. The leaves of the summer squash plants were scabrid and the stems prostrate, the flowers were eaten as well as the very small fruits shortly after they were fertilized. There were different kinds differing in shape and external color in shades of whites and greens of which the one in Napoli (Naples) was called *Coccozelli di San Pasquale*. 'San Pasquale', one of the oldest-known named cultivars of summer squash, is offered by many Italian seed companies to this very day. It is quite common in the Campania region of Italy, especially in the vicinity of Sarno, San Marzano, and San Valentino Torio.

Cocozelles were soon thereafter named outside of Italy. 'Courge d'Italie' was listed in the vegetable gardening book of the king of France in 1820 (Jacobsohn 2005) and 'Coucourzelle, courge d'Italie' appeared in other French gardening books, beginning in 1827 (Paris 2000a). 'Cocozelle' was named in American gardening books as early as 1863 and described as having long and narrow, striped fruits that were used when very young, 10–14 cm long, just as the flower drops off. Thereafter, Cocozelle cultivars, under various names, were commonly offered by seed companies in Europe and America.



Fig. 4 Drawing of Cocozelle squash by Antoine-Nicolas Duchesne. No. 93n, labelled *Cucurbita aspero folio flore luteo, semiarcus in morem intorta J.B.* (dated 4 September 1775)

In an interesting contrast, no illustrations or descriptions have been found that are sufficient to identify a zucchini squash prior to 1855. The word *zucchini* (masc. pl.) first appeared in Italian literature in 1809, but it was applied to small, mature, desiccated bottle gourds that were used for storing tobacco (Lust and Paris 2016). Later on, with the impending unification of Italy and standardization of the Italian language, the word *zucchini* appeared in cookbooks and was applied in general to young squash, regardless of shape. The earliest-known description of a zucchini cultivar, the *zucca verde quarantina* (40-day green gourd), is in a book on agriculture published in Milan in 1855; however, it does not contain the word *zucchini*. Use of this word for summer squash of uniformly cylindrical fruit shape arose in American English, in California, U.S.A. around 1919 (Tapley et al. 1937; Goldman 2004).

Current status of the Cocozelle

The Cocozelle Group contains a very large number of cultigens. Most of them are old, open-pollinated (OP) cultivars and landraces (Fig. 5). Seeds of many are maintained in gene banks in Europe and the United States. Those from European gene banks that we have seen in the field include numbers IG 200104, 200209, and 202035 (Instituto de Germoplasma, Bari, Italy) and IPK 285 and 288 (Institut für Pflanzengenetik und Kulturpflanzenforschung, Gatersleben, Germany), all of which were collected in Italy. Of those from the United States Plant Introduction Service, we have seen in the field quite a few, including nine collected in Turkey, six from North Macedonia, and one from Spain. Altogether, we have observed in the field 47 OP accessions of the Cocozelle Group. For comparison, we have seen a similar number of OP accessions of cultivars of the Pumpkin Group (51) and Vegetable Marrow Group (40), but we have been able to acquire only 13 OP cultivars of the Zucchini Group



Fig. 5 One representative young fruit, with peduncle, from 12 accessions of Cocozelle squash (seed sources indicated in parentheses). Left-to-right: 'Cocozelle' (unknown), 'Genovese' (Tezier, France), IPK 285 (Corleto, Basilicata, Italy), 'Long Cocozelle' (Ledden, U.S.A.), 'Lungo Bianco di Sicilia' (S.A.I.S., Italy), 'Lungo di Toscana' (S.A.I.S., Italy), PI 177370 (Merzifon, Amasya, Turkey), PI 261610 (Valladolid, Castilla León, Spain), 'Romanesco' (Semitalia, Italy), 'San Pasquale' (Esasem, Italy), 'Striato d'Italia' (S.A.I.S., Italy), 'Striato Pugliese' with corolla (Ingegnoli, Italy). Length-to-broadest-width ratio as measured along the fruit axis ranged from 4.0 for 'Striato Pugliese' to 8.1 for 'Striato d'Italia', with a mean of 5.4 for the 12 accessions. Length of PI 261610 fruit = 36 cm

for observation. In the collection at the A.R.O. Newe Ya'ar Research Center (Paris 2001), the Zucchini Group has the most accessions (90) but 77 of them are hybrids and, of those, many no longer appear to be in commerce and their seeds may not have been deposited in the various gene banks.

Many of the traditional, OP Italian cocozelles have names suggestive of where they have been grown and read like a travelogue of the country: 'Alberello di Sarzana', 'Cocozella di Napoli', 'Genovese', 'Lungo Bianco di Sicilia', 'Lungo Fiorentino', 'Lunga di Toscana', 'Ortolano di Faenza', 'Romanesco', 'Striato d'Italia', and 'Striato Pugliese'. Other OP cultivars are available from seed vendors in France and other countries but there are many cases in which the same or similar names are used for different cultivars or different cultivars have the same name, mostly depending on the seed vendor (Paris 2001). A number of new hybrid cocozelles have been bred not only for markets in Italy but also for Brazil (for example, 'Ortano', 'Bossa Nova'), South Korea ('Bulam House'), Turkey ('Ma'yan'), Israel ('Arlika'), and the U.S.A. ('Italiano Largo', 'Sunstripe').

As a Group, the Cocozelle contains a wealth of variation, covering the entire gamut of foliage traits and plant growth habit, specifically degree of prickliness of the foliage, presence or absence of silver mottling of the leaf laminae, degree of serration of the leaf laminae, stem color, petiole thickness at the stem base, petiole length, internode length, viney or bushy growth ranging from prostrate to erect, overall open or closed plant structure derived from petiole angle tending toward horizontal or vertical and presence or absence of branching. Much variation also occurs in this Group with regards to flowering traits, including plant sexuality, earliness to flower, staminate and pistillate flower sizes and firmness, and ovary and corolla sizes at anthesis. The Cocozelle Group also varies widely in fruit traits (Paris 2000a), including length-to-width ratio (minimum 3.5 to as much as 8.0), fruit ribs (rounded prominences over the 10 many carpellary tracts of the ovary/fruit, strongly expressed to almost absent), shaping along length of the fruit (whether narrowest at peduncle end or in middle of the fruit), peduncle length and width, young fruit color intensity, absence or presence of striping and boldness of striping (Fig. 5), amount of fruit stippling, and mature fruit size and color (Paris et al. 2012). Cocozelle accessions also differ widely in parthenocarpic tendency (Martinez et al. 2014).

Cocozelles are most commonly grown for the use of their young fruits, at up to five days past anthesis, as is typical of all summer squash. Among Cocozelle cultigens, though, the young fruits can differ widely in flavor. For example, the fruits of the ribbed 'Romanesco' and similar cultivars are richly flavored. Those similar to 'Cocozelle' and 'San Pasquale' have a green-vegetable flavor. Others are rather bland.

The Cocozelle differs from all other summer squash by often being harvested early in the morning on the day of anthesis and sold that same day at the market (Fig. 6). Cocozelles grown for such use have large, even enormous, pistillate flowers, in regards to both, the corolla and the ovary (Fig. 7). The Cocozelle Group, as a whole, has the longest fruits and highest length-to-width ratio within the species *Cucurbita pepo*. This would result in the highest surface area to volume ratio, even moreso if the additional surface area rendered by prominent ribs, as in 'Romanesco', is taken into account. From this extreme elongation, it is not surprising, then, that the cocozelle squash are often used younger than any other squash, on the day of flowering.



Fig. 6 Marketing of pistillate flowers of Cocozelle squash. Top left: Ventimiglia, Italy (2009). Bottom left: Pagani-Nocera wholesale market, Campania, Italy (2009). Right: Rome, Italy (2024)

SSR-sequence polymorphisms in *Cucurbita pepo* as viewed with principal coordinate analysis have suggested the existence of several subgroups within the Cocozelle Group (Gong et al. 2012). Within the central core of subsp. *pepo*, which includes the bulk of the Pumpkin Group, were also included two strongly ribbed cocozelles, 'Romanesco' and 'Lunga di Toscana', the latter cultivar probably being a descendant of the former. The cocozelles from Turkey and North Macedonia were found outside of the central core in one direction while the smooth-rinded cocozelles from Italy and France were further outside of the core but in another direction. PI 261610, a semi-bush landrace from Valladolid, Castilla León, Spain, was also found in the central core, and may represent yet another subgroup of cocozelles (Formisano et al. 2012). Given the early dates of evidence for the existence of 'Romanesco', these core-based, primitive cocozelles might have been derived directly from Mexican germplasm by selection in Europe for long fruits and bushier plants (Paris 2023a). Overall, the results using DNA-sequence polymorphisms show that the Cocozelle Group is genetically diverse and may be derived from four separate ancestral pathways. In stark contrast, the highly popular and cosmopolitan Zucchini Group has a narrow, unique genetic basis (Gong et al. 2012; Paris et al. 2015).

Genomic research in *Cucurbita* lags behind that of other cucurbit crops (Montero-Pau et al. 2016). Even though well over 100 consensus quantitative trait loci affecting fruit size and shape have been inferred in cucumber, melon, and watermelon, only a handful of investigations have had focus on the genetic and genomic basis of fruit shape in pumpkins and squash (Pan et al. 2020). Likewise, pangenomic research has not yet been reported for pumpkins and squash, even though it has been undertaken for other cultivated cucurbits (Shigita et al. 2025). Efforts at elucidating the genetics and genomics of fruit elongation in *Cucurbita pepo* could result in a much improved insight as to the evolution under cultivation of long-fruitedness in *C. pepo* subsp. *pepo* and the ancestry of the Cocozelle and the Zucchini. The diversity present in the Cocozelle Group has been and represents an important potential source for breeding enhancement of Zucchini.

Conclusions

As a Group of edible-fruited *Cucurbita pepo* cultivars, the Cocozelle dates back to late sixteenth-century Italy. The word *cocozelle* comes from a southern Italian dialect, being a diminutive derived from the dialect word *cucuzzi*, which is still in use for bottle gourds. In *C. pepo*, selection for long fruits has reached its greatest extent in the Cocozelle Group. Depending on the cultivar, the fruits usually have a

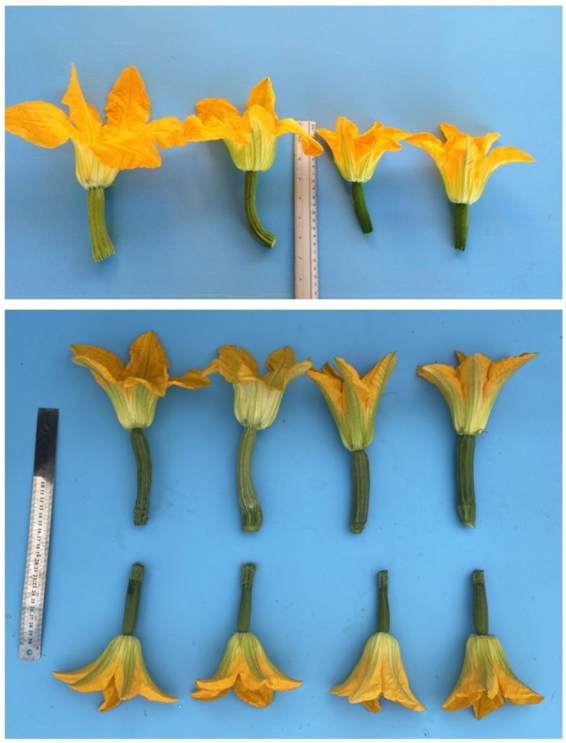


Fig. 7 Pistillate flowers of *Cucurbita pepo* subsp. *pepo*. Top photograph, left to right: Cocozelle 'Lungo Fiorentino', Cocozelle 'San Pasquale', Zucchini 'Black Zucchini', Zucchini 'Nero di Milano'. Bottom photograph, upper row: Cocozelle flowers, left to right, of 'Cocozelle', 'Romanesco', 'San Pasquale', and 'Striato Pugliese' and lower row: Zucchini flowers, left to right, of 'Black Zucchini', 'Fordhook Zucchini', 'Nero di Milano', and 'True French'. Notice the huge size of the Cocozelle flowers with regards to both, the corollas and the ovaries, as compared with the Zucchini flowers

length-to-width ratio between 4:1 and 6:1. Selection for very long fruits may have occurred four times independently, the two of greatest impact in southern Italy. The first one, for strongly ribbed fruits such as 'Romanesco', occurred no later than 1580, and a second occurred before 1770, resulting in especially long but not strongly ribbed fruits such as 'San Pasquale', 'Striato d'Italia', and 'Lungo Bianco di Sicilia'. A third appears to have occurred in Turkey and the Balkans and a fourth in Spain. The pistillate flowers of many Italian Cocozelle cultivars are quite large and, often, they are harvested and sold on the day of anthesis. Today, Cocozelle squash are widely popular in Italy and other Mediterranean countries, and well beyond. The Cocozelle Group is represented by dozens of open-pollinated cultivars of wide phenotypic and genetic diversity. Landraces and old cultivars from Italy, Spain, Turkey, and North Macedonia are preserved in genebanks in Europe and North America. Among the numerous commercially available Cocozelle hybrids are 'Ortano', 'Albatros', 'Aquilone', and 'Cavilli'.

Acknowledgements The first author expresses his gratitude, as a retiree of the Agricultural Research Organization, for his being granted volunteer status.

Author contributions The first author initiated the manuscript. Both authors researched and wrote the manuscript.

Funding Open access funding provided by The Agricultural Research Organization of Israel. This study was not funded by an outside source.

Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

Ethics approval The authors declare that no funds, grants, or other financial support were received during and for the preparation of this manuscript.

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References

Battaglia S (2002) Grande Dizionario della Lingua Italiana, vol 21. Turin, pp 1100, 1103–1104

Bauhin J (1651) Historia Plantarum Universalis, vol 2. Yverdon, pp 212–232

Brickell CD, Baum BR, Hetterscheid WLA, Leslie AC, McNeill J, Trehane P, Vrugtman F, Wiersema JH (2004) International code of nomenclature for cultivated plants.

Acta Horticulturae 647. International Society for Horticultural Science, Leuven
Castellanos-Morales G, Ruiz-Mondragón KY, Hernández-Rosales HS, Sánchez-de la Vega G, Gámez N, Aguirre-Planter E, Montes-Hernández S, Lira-Saade R, Eguiarte LE (2019) Tracing back the origin of pumpkins (*Cucurbita pepo* subsp. *pepo* L.) in Mexico. Proc R Soc B 286:20191440
Cowan CW (1997) Evolutionary changes associated with the domestication of *Cucurbita pepo*. In: Gremillion KJ (ed) People, plants, and landscapes: studies in paleoethnobotany. University of Alabama Press, Tuscaloosa, pp 63–85
Decker DS (1988) Origin(s), evolution, and systematics of *Cucurbita pepo* (*Cucurbitaceae*). Econ Bot 42:4–15
Duchesne AN (1786) Essai sur l'Histoire Naturelle des Courges. Panckoucke, Paris
El-Keblawy A, Lovett-Doust J (1996) Resource re-allocation following fruit removal in cucurbits: patterns in two varieties of squash. New Phytol 133:583–593
European Research Council (2017) Blog: the fruit seller, by Vincenzo Campi (1580). https://refashioningrenaissance.eu/fruitseller. Last seen 10 Feb 2025
Formisano G, Roig C, Esteras C, Ercolano MR, Nuez F, Monforte AJ, Pico MB (2012) Genetic diversity of Spanish *Cucurbita pepo* landraces: an unexploited resource for summer squash breeding. Genet Resour Crop Evol 59:1169–1184
Fuller DQ, Denham T, McClatchie M, Wu X (2025) Commensal domestication pathways amongst plants: exploring segetal and ruderal crop origins. Philos Trans R Soc Lond B Biol Sci 380:20240190
Goldman AP (2004) The compleat squash. Artisan, New York
Goldman IL (2025) To vegetable: seasons that require us. Crop Sci 65:e70025
Gong L, Paris HS, Nee MH, Stift G, Pachner M, Vollmann J, Lelley T (2012) Genetic relationships and evolution in *Cucurbita pepo* (pumpkin, squash gourd) as revealed by simple sequence repeat polymorphisms. Theor Appl Genet 124:875–891
Hoefnagel J (1592) Archetypa Studiaque patris Georgii Hoefnagelii. Part 2, Frontispiece. Viewed at https://archive.org/details/archetypastvdiaq00hoef/page/n29/mode/2up, 02 Jan 2023. Also viewed at https://www.nga.gov/collection/artist-info.2569.html, 02 Jan 2023
Jacobsohn A (2005) Summer squash, winter squash. In: Jacobsohn A (ed) L'Épopée des Courges. École Nationale Supérieure du Paysage, Versailles, pp 84–101
Janick J, Paris HS (2006) The cucurbit images (1515–1518) of the Villa Farnesina, Rome. Ann Bot 97:165–176
Janick J, Paris HS, Parrish DC (2007) The cucurbits of Mediterranean antiquity: identification of taxa from ancient images and descriptions. Ann Bot 100:1441–1457
Jarret RL, Levy IJ, Potter TL, Cermak SC, Merrick LC (2013) Seed oil content and fatty acid composition in a genebank collection of *Cucurbita moschata* Duchesne and *C. argyrosperma* C. Huber Plant Genet Resour 11:149–157
Katzir N, Tadmor Y, Tzuri G, Leshzeshen, E, Mozes-Daube N, Danin-Poleg Y, Paris HS (2000) Further ISSR and preliminary SSR analysis of relationships among accessions of *Cucurbita pepo.* In: Katzir N, Paris HS (eds) Proceedings of Cucurbitaceae 2000, the 7th Eucarpia meeting on cucurbit genetics and breeding. Acta Horticulturae, vol 510, pp 433–439
Lira R, Montes S (1994) Cucurbits (*Cucurbita* spp.). In: Hernandez JE, Leon J (eds) Neglected crops: 1492 from a different perspective. FAO, Rome, pp 63–77
Loy JB (2004) Morpho-physiological aspects of productivity and quality in squash and pumpkins (*Cucurbita* spp.). Crit Rev Plant Sci 23:337–363
Loy JB (2012) Breeding squash and pumpkins. In: Wang Y-H, Behera TK, Kole C (eds) Genetics, genomics and breeding of cucurbits. CRC Press, Boca Raton, pp 93–139
Lust TA, Paris HS (2016) Italian horticultural and culinary records of summer squash (*Cucurbita pepo*, Cucurbitaceae) and emergence of the zucchini in 19th-century Milan. Ann Bot 118:53–69
Martinez C, Manzano S, Megias Z, Garrido D, Pico B, Jamilena M (2014) Sources of parthenocarpy for zucchini breeding: relationship with ethylene production and sensitivity. Euphytica 200:349–362
Martínez-González C, Castellanos-Morales G, Barrera-Redondo J, Sánchez-de la Vega G, Hernández-Rosales HS, Gasca-Pineda J, Aguirre-Planter E, Moreno-Letelier A, Escalante AE, Montes-Hernández S, Lira-Saade R, Eguiarte LE (2021) Recent and historical gene flow in cultivars, landraces, and a wild taxon of *Cucurbita pepo* in Mexico. Front Ecol Evol 9:656051. https://doi.org/10.3389/fevo.2021.656051
Milc J, Caffagni A, Ronga D, Francia E, Pasquariello M, Laviano L, Mazzamurro V, Pecchioni N (2016) Evaluation of *Cucurbita pepo* germplasm for staminate flower production and adaptation to the frozen food industry. Sci Hortic 213:321–330
Montero-Pau J, Esteras C, Blanca J, Ziarsolo P, Cañizares J, Pico B (2016) Genetics and genomics of *Cucurbita* spp. In: Grumet R, Katzir N, Garcia-Mas J (eds) Genetics and genomics of Cucurbitaceae. Springer International, Cham, pp 211–227
Nee M (1990) The domestication of *Cucurbita* (Cucurbitaceae). Econ Bot 44(Supplement):56–68
Nerson H (2005) Effects of fruit shape and plant density on seed yield and quality of squash. Sci Hortic 105:293–304
Nerson H, Paris HS (2001) Relationship between fruit shape and seed yield in *Cucurbita pepo*. Cucurbit Genet Coop Rep 24:82–86
Nerson H, Paris HS, Paris EP (2000) Fruit shape, size and seed yield in *Cucurbita pepo*. In: Katzir N, Paris HS (eds) Proceedings of Cucurbitaceae 2000: the 7th Eucarpia meeting on cucurbit genetics and breeding. Acta Horticulturae, vol 510, pp 227–230
Pan Y, Wang Y, McGregor C, Liu S, Luan F, Gao M, Weng Y (2020) Genetic architecture of fruit size and shape variation in cucurbits: a comparative perspective. Theor Appl Genet 133:1–21
Paris HS (1986) A proposed subspecific classification for *Cucurbita pepo*. Phytologia 61:133–138
Paris HS (2000a) History of the cultivar-groups of *Cucurbita pepo*. Hortic Rev 25:71–170
Paris HS (2000b) Paintings by A. N. Duchesne and the history of *Cucurbita pepo*. Ann Bot 85:815–830

Paris HS (2001) Characterization of the *Cucurbita pepo* collection at the Newe Ya'ar Research Center, Israel. Plant Genet Resour Newsl 126:41–45

Paris HS (2007) The drawings of Antoine Nicolas Duchesne for his natural history of the gourds. In: Érard C (ed) Les Planches et les Mots. Muséum National d'Histoire Naturelle, Paris

Paris HS (2018) Consumer-oriented exploitation and conservation of genetic resources of pumpkins and squash, *Cucurbita*. Isr J Plant Sci 65:202–221

Paris HS (2023a) A late 16th-century look-alike of the 'Romanesco' cocozelle squash. Cucurbit Genet Coop Rep 46:23–27

Paris HS (2023b) Cucurbits illustrated in the late 16th-century by Joris Hoefnagel (1542–1601). Cucurbit Genet Coop Rep 46:38–42

Paris HS (2024) Southern Italy: nativity of the cocozelle squash (*Cucurbita pepo* subsp. *pepo*, Cocozelle Group). Abstract Book, 13th Eucarpia Meeting on Cucurbit Genetics and Breeding 17. https://www.eucarpia.eu/images/publications/2024_Eucarpia_Cucurbit_Abstract_Book.pdf

Paris HS, Lebeda A, Křistkova E, Andres TC, Nee MH (2012) Parallel evolution under domestication and phenotypic differentiation of the cultivated subspecies of *Cucurbita pepo* (Cucurbitaceae). Econ Bot 66:71–90

Paris HS, Doron-Faigenboim A, Reddy UK, Donahoo R, Levi A (2015) Genetic relationships in *Cucurbita pepo* (pumpkin, squash, gourd) as viewed with high frequency oligonucleotide-targeting active gene (HFO–TAG) markers. Genet Resour Crop Evol 62:1095–1111

Perez-Moro C, D'Esposito D, Capuozzo C, Guadegno A, Perez-de-Castro A, Ercolano MR (2025) Discovery of variation in genes related to agronomic traits by sequencing the genome of *Cucurbita pepo* varieties. BMC Genomics 26:335. https://doi.org/10.1186/s12864-025-11370-x

Re F (1811) L'Ortolano Dirozzato. Milan 1:66, 2:391–396

Shigita G, Tanaka K, Kato K (2025) Current and future pangenomic research in cucurbit crops. Breed Sci 75:34–50

Sinnott EW, Durham GB (1929) Development history of the fruit in lines of *Cucurbita pepo* differing in fruit shape. Bot Gaz 87:411–421

Smith BD (2006) Eastern North America as an independent center of plant domestication. Proc Natl Acad Sci USA 103:12223–12228. https://doi.org/10.1073/pnas.0604335103

Stephenson AG, Devlin B, Horton JB (1988) The effects of seed number and prior fruit dominance on the pattern of fruit production in *Cucurbita pepo* (zucchini squash). Ann Bot 62:653–661

Tapley WT, Enzie WD, van Eseltine GP (1937) The vegetables of New York, vol 1, Part 4. J. B. Lyon, Albany

Teppner H (2000) *Cucurbita pepo* (*Cucurbitaceae*)—history, seed coat types, thin coated seeds and their genetics. Phyton (Horn) 40:1–42

Teppner H (2004) Notes on *Lagenaria* and *Cucurbita* (*Cucurbitaceae*) – review and new contributions. Phyton (Horn) 44:245–308

Watson PJ, Yarnell RA (1966) Archaeological and paleoethnobotanical investigations in Salts Cave, Mammoth Cave National Park, Kentucky. Am Antiq 31:842–849

Watson PJ, Yarnell RA (1969) The prehistory of Salts Cave, Kentucky. Reports of investigations 16, Springfield

Whitaker TW (1947) American origin of the cultivated cucurbits. Ann Mo Bot Gard 34:101–111

Whitaker TW, Bemis WP (1964) Evolution in the genus *Cucurbita*. Evolution 18:553–559

Whitaker TW, Carter GF (1946) Critical notes on the origin and domestication of the cultivated species of *Cucurbita*. Am J Bot 33:10–15

Whitaker TW, Cutler HC (1965) Cucurbits and cultures in the Americas. Econ Bot 19:344–349

Whitaker TW, Cutler HC (1971) Prehistoric cucurbits from the valley of Oaxaca. Econ Bot 25:123–127

Xanthopoulou A, Montero-Pau J, Mellidou I, Kissoudis C, Blanca J, Pico B, Tsaballa A, Tsaliki E, Dalakouras A, Paris HS, Ganopoulou M, Moysiadis T, Osathanunkul M, Tsaftaris A, Madesis P, Kalivas A, Ganopoulos I (2019) Whole-genome resequencing of *Cucurbita pepo* morphotypes to discover genomic variants associated with morphology and horticulturally valuable traits. Hortic Res 6:94

Zack CD, Loy JB (1981) Effect of fruit development on vegetative growth of squash. Can J Plant Sci 61:673–676

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