Symposium on the Biochemical Systematics, Genetics and Origin of Cultivated Plants

IX. On the history and origin of citrus

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Scora, Rainer, W. (Dept. Plant Science, Univ. California, Riverside 92502). On the history and origin of citrus. Bull. Torrey Bot. Club 102: 369-375. 1975.—Two areas of origin are respectively proposed for the subgenera Papeda and Citrus, tropical and subtropical. A polyphyletic origin of cultivated Citrus is postulated for citron, pummelo and mandarin. Three complexes were formed: the citron with the limes, lemons and rough lemons; the shaddock, primarily with grapefruit; and the mandarin with the sweet and sour oranges. A brief historical and cultural review is presented. Centers of origin for the base species are advanced on the basis of their morphology, genetics and biochemistry.

Much confusion exists regarding the classification of the genus Citrus, and this confusion is not likely to be resolved soon. As more taxonomic research is conducted, the gaps in our knowledge grow narrower; nevertheless, they still exist.

I will first talk about the history and folklore of citrus and then present some taxonomic data to define and support my theory of *Citrus* origins.

The oldest known reference to Citrus appears in the Sanskrit literature. In the Vajasaneyi Samhita, a collection of devotional texts dated prior to 800 B.C. and which is part of the Brahmin sacred book called the White Yahir-veda, the name applied to citron and lemon is jambhila.

The oldest Chinese reference to Citrus is contained in the book "Tribute of Yu." The Citrus names occur in a list of tribute items sent to the mythical Emporer Yu (founder of the equally mythical Hsia Dynasty) and god of irrigation. Wild tribes from the not-yet very sinicized areas of central and south coastal China sent small mandarins and probably Yuzu² along with other forest items as tribute. The Shu Ching of which the above mentioned book is a part was finalized between 776 and 600 B.C. and restored about 200 B.C. The materials in the Shu Ching were already old and traditional by the time they were written down; thus the tribute lists may

refer to conditions well before 700 B.C., though probably not before 1,000 B.C.

Confucius knew two kinds of citrus in the fifth century, the Yu and Chü, and Lu's Spring and Autumn Annals of the third century B.C. mention the beauty of both. The first really extended description of citrus appears in the poem cycle Chiu Chang, where, in the eighth poem, a youth is praised through comparison with a mandarin tree which is described fully in very flattering terms. This poem cycle is part of the Ch'u Tzu, 'songs of the state of Ch'u,' in the central Yangtze Valley, compiled about 250–300 B.C. by the Ch'u poet Chu'u Yuan and probably some disciples of his.

In 1,179 A.D., Han Yen-Chih named and described some 27 varieties of the sweet-sour orange-mandarin group in his Chü Lu, the oldest known monograph of Citrus. So far, there had been no Citrus positively identified from the ancient culture of Egypt, Sumer and Assyria, as sometimes claimed.

The citron (Citrus medica L.) was sanctified in India, and consecrated to the elephant-headed Ganesh, god of knowledge and wisdom. The Buddhist art of Java features the treasure god Kuvera holding a citron in his hands. Once this fruit was dispersed over the hellenistic Near East, it became an important part of the Jewish feast of Tabernacles, which was originally based upon Canaanite manhood rites. Through the Jewish communities, the fruit was traded over the entire Mediterranean region. Its sanctity, pleasant odor, good appearance and relative imperishability suited for prolonged travel made the citron

¹ I thank Dr. Gene Anderson (Anthropology Department, University of California at Riverside) for his research of citrus in Chinese literature.

² Citrus junos Tanaka, probably a hybrid of Ichang papeda × mandarin.

the forerunner of all Citrus to reach the West and the first citrus fruit to come to the attention of Europeans. From the records of Alexander's scientific staff accompanying his Macedonian army into Persia, Theophrastus at about 310 B.C. described the citron as the apple from the lands of the Medes. The fruit was also described in Latin, by Virgil, Dioscorides and Plinius.

Centuries apart, but probably in order, sour oranges, lemons and sweet oranges reached Europe. The Romans were acquainted with lemons and probably sour oranges as well as citrons. Many citrus groves, however, were abandoned during the disintegration of their empire and simply vanished. The next advance and diffusion of citriculture in the West came through the rise of Islam and the Arab empire. By 1,150 A.D. the Arabs had brought citron, sour orange, lemon and pummelo into North Africa and Spain.

After the Arab influence, the Crusades brought feudal Europeans in contact with the superior civilization and luxuries of the East. Lemon, lime and sour oranges were mentioned by European historians

only after the Crusades.

When the Mediterranean Sea and the land connections were blocked by the Turks, the Portuguese who succeeded in rounding southern Africa soon brought better sweet oranges from India or the Far East to Europe. By the sixteenth century, sweet oranges had become well-established and had assumed commercial importance in Europe. The mandarin, native to China, was brought to Europe only recently, in 1805. It first came to England, and spread from there to Malta, Sicily and Italy.

From Europe Citrus spread to the New World. According to Las Casas, Columbus brought the first seeds to Haiti on his second voyage in 1493. In 1518 the orange reached Mexico; Spanish settlers brought Citrus to Florida probably to St. Augustine, in about 1565. In 1577 Citrus was already established on the offshore islands of South Carolina. In the early years of the eighteenth century Citrus spread to Arizona. The northern California missions administered by the Franciscans received plant and animal supplies from Baja California, and among these were lemons and oranges.

In 1788 orange, lime and lemon trees were picked up in Rio de Janeiro by the settlers of the first English fleet sailing for Australia. These trees were planted at Port Jackson.

The island of Saint Helana, a stopover to India, supplied the first sweet orange trees to the Dutch, who then planted these in their colony at Capetown.

It is easy to see, then, the spread of Citrus species as a consequence of travel, exploration, war, and politics. In order to prevent the introduction of citrus pests or diseases, today we closely regulate the movement of citrus species and thus attempt to prevent their random spread.

Folklore. The long history of Citrus has generated much folklore concerning the various species. According to non-rabbinic Jewish tradition, a citron in the house would keep the Karines or bad spirits away. If, after the Feast of Tabernacles, an expectant woman would eat the style of the etrog (sacramental citron), her child would be a son. Merchants who supplied northern European communities with citrus took names like Esroger (after the Hebrew word for citron) and Pomerantz (from the German word for sour orange). One of the basic body oils the Romans used was citrus oil; and boxes and small furniture made from citrus wood were literally worth their weight in gold and often used as gifts.

During the plague years European doctors were hooded gowns with tremendous breaks in which they had linen soaked with citrus oil, which as we know today has some bactericidal properties. From these days, a custom survived in some areas of the Black Forest in Germany, where Protestant mourners still carry lemons at funerals and then pelt the coffin with them. At popular shooting matches in the early 16th century in Breslau, the capital of Silesia, mounted riders pierced sour oranges resting on the hands of boys.

Sweet oranges were, at first, an expensive food item. Medieval cookbooks tell exactly how many orange slices a visiting dignitary was entitled to. Kings rated 21 slices with their dish of fish. Citrus soon became the fashion of the nobility and rich merchants. In many parts of northern Europe, orangeries were built where citrus was grown and propagated. By withholding water and nutrients, and by using pruning techniques, French gardeners were able to make citrus trees bloom during the entire

year, to the delight of Louis XIV. Citrus motifs formed themes in sculpture, mosaics, embroidery, weaving, paintings, poems, and songs, throughout history. To this day, orange blossoms are prized as floral ornaments at weddings.

Taxonomy. The vast majority of Citrus and its wild relatives are native to southeastern Asia, New Guinea, Australia, the East Indian Archipelago, New Caledonia and Melanesia. No Citrus or citrus relatives have been endemic to Europe or the New World. The fact that another group of citrus relatives (5 genera in all) occurs in tropical Africa has long puzzled taxonomists. Unless we assume either their separate origin in Africa or their migration from Asia into tropical Africa, these 5 genera might be remnants of an ancient flora which was confluent with that of India before the two continents separated. When the Australian plate separated from its position south of Africa and rafted east and north, it interacted with the Asiatic plate. During late Oligocene and Miocene an uplifting began; and submerged New Guinea, which defines the leading edge of the Australian plate, now emerged, providing extensive land areas in the tropics and permitted the crossing and mixing of biota. It must have been in these times that a citrus relative like Microcitrus crossed into Australia, and there in response to an expanding dry climate evolved into Eremocitrus and Microcitrus of today. Eremocitrus is totally Australian and xerophytic. Microcitrus consists of 5 semi-xerophytic species native to Australia and its most primitive species still native to New Guinea. The land connection to Australia was submerged again before any member of the genus Citrus, including the primitive papedas, had reached Australia. Had the genus Citrus already existed at that time, we might assume that its species would have crossed into Australia.

The closest relatives of the genus Citrus are 5 genera in the subtribe Citrinae, which belong to the True Citrus Fruit Trees, Clymenia Swing., Fortunella Swing. (kumquat), Poncirus Raf. (trifoliate orange), and the above mentioned Eremocitrus Swing. (Australian desert lime) and Microcitrus, Swing. (Australian wild lime).

Swingle divided the genus Citrus into the subgenera Papeda and Citrus. The primitive Papeda is characterized by extralarge petiole wings, small inflorescences, and granular pulp vesicles possessing acrid oil droplets which make the fruit unpalatable. The Papeda group includes C. hystrix, DC., C. macroptera, Montr., C. micrantha, Wester and others, species evolved in tropical areas, all frost-tender and polyembryonic. Two other species, C. latipes (Swing.) Tan. and C. ichangensis Swing., are intermediate, having flower characters much like those of Citrus and leaf characters much like those of Papeda. These intermediate species are frost-hardy and monoembryonic. They originated in the sub-Himalayan area, and are distributed in southwestern China, northeastern India, and northern Burma, far north of the range of the other Papedas.

Of the edible Citrus species, two, the lime and the pummelo, originated under tropical conditions. The lime is always associated with the Papeda group throughout Malaysia and into the Philippines. The pummelo is most probably indigenous to the Malayan archipelago. All other edible Citrus species developed in the cooler sub-Himalayan region, where members of all representative groups still exist. Citrus nana Tanaka, the primitive citron, occurs in eastern Bhutan and C. aurantium L. and C. sinensis Osbeck, the sour and sweet oranges, in the Naga hills of Assam, where C. indica Tanaka, a primitive mandarin, is abundant. From eastern India, Assam, and upper Burma, the citron, lemon and oranges spread west as did the pummelo, once it reached India from the south. The mandarin, along with the related genera Fortunella and Poncirus developed separately in China. J. D. Hooker at first thought the citron to be indigenous to India. but Bonavia doubted it since it had no Sanskrit name. The presence of many varieties suggested an Indian origin. More recent suggestions of an origin in southern Arabia or Palestine have not been substantiated.

The Assam-Burma area was the most important resource area. From there, Citrus migrated not only to the west, but also eastward into China. Because of the cold winter temperatures in the Yangtze Valley, frost-tender lime and most citrons did enter China through the warmer Pacific route. This is evidenced by Citrus nana, the most

primitive citron found in Assam and the Philippines. This Pacific route, in turn, played an important role in transmitting the Chinese elements of later developed mandarins and the kumquats south into Malaysia, from where they spread throughout the world (Tanaka 1969a).

Much confusion exists regarding the classification of the genus Citrus L. in the Rutaceae, subfamily Aurantioideae. A partisanship has developed around two major systems of classification; Swingle's (1946) recognizes 16 species and Tanaka's (1969b) recognizes 159. To a lesser extent, about a half dozen other classification systems also have their adherents. Much of the difficulty in delimiting Citrus taxa is due primarily to repeated cross pollination and to adventitious nucellar embryony, a form of apomixis which stablises and perpetuates these hybrid taxa.

Tanaka (1969a) proposed that the limes were derived from the Papeda group and that the citron-lemon complex and the pummelo were derived from the lime. He proposed that the orange group was derived from the pummelo.

Rather than accepting this theory of a monophyletic origin of cultivated Citrus through the lime, I assume a polyphyletic origin encompassing citron as the oldest species, pummelo and mandarin. There just is no satisfactory evidence at this time for the derivation of citron and pummelo from the lime, nor sour or sweet oranges from the pummelo alone by simple reduction in size and increase in carotenoid pigmentation.

In Citrus I recognize 3 basic species: C. grandis (L.) Osbeck, the pummelo, C. medica L., the citron, and C. reticulata Blanco, the mandarin. The pummelo is self-incompatible and monoembryonic, i.e., sexually reproducing, and thus a free gene flow seems to be assured. It seemingly has introgressed with the mandarin to form the sweet and sour oranges.

The mandarin is a native Chinese element. It has an extremely broad genetic base, and produces zygotic and nucellar embryos, which means it reproduces both sexually and adventitiously. By hybridization with the pummelo it seems to have produced the sour orange (C. aurantium L.) and the sweet orange [C. sinensis (L.) Osbeck], the latter being morphologically closer to the mandarin. The differences between the sweet and sour orange probably

depend upon that part of the broad mandarin gene base with which the introgression from the pummelo took place.

The monoembryonic citron is the third base species. By hybridization with the lime it gave rise to the lemon [C. limon (L.) Burm. f.]; by hybridization with the mandarin it gave rise to the rough lemons (C. jambhiri Lush.). Its characteristics occur in many other biotypes including the lime [C. aurantifolia (Christm.) Swing.], which in my opinion is a hybrid type between the citron and a biotype of the primitive subgenus Papeda.

We have looked at a number of chemical components to see if they might help in discerning taxonomic relationships. Enzymatic browning of shoot homogenates is due to the presence of a polyphenol substrate and its corresponding enzyme. The closely related genera of the True Citrus Fruit Trees lack both the substrate and the enzyme. The same is true of citrons, limes and lemons, while sour oranges, sweet oranges and mandarins possess both the substrate and enzyme. Pummelo also lacks both, but grapefruit possesses the substrate (Esen and Scora 1975).

Distribution of browning fits my concept of citrus quite well (Fig. 1), since the basic species C, medica and C, grandis lack both substrate and enzyme, and C. reticulata possesses both. Browning is dominant over nonbrowning and a single-locus control for the presence of the substrate was indicated by Esen and Soost (1974). The Papeda-lime-citron-lemon complex lacks both substrate and enzyme. The rough lemons possess both and could have received them from the mandarin, which possesses both. Similarly the sour and sweet oranges might have inherited substrate and enzyme from the mandarin parent. The grapefruit, which is heterozygous for the substrate, might have inherited this from the sweet orange. The presence or absence of polyphenol and its corresponding oxidase enzyme fits a proposed pattern of inheritance and also fits my proposed taxonomic relationships.

Essential rind oils are similar for the citron, lime and lemon (Malik et al. 1974). There is little similarity to the Papeda group. Good affinity exists among C. halimii, the sweet and sour orange and the mandarin, primarily in their high (80–90+%) content of d-limonene. There is less

similarity between these latter species and the kumquats or even the pummelo. Leaf oils are much more varied than the rind oils. The citron, lime and lemon have very similar patterns. The outstanding components linking these taxa are neral, citronellol and geranial. Mandarin and sweet orange are much alike, while the sour orange and the pummelo are vastly different (Scora and Malik 1970). Alkane profiles of Citrus thus far have neither confirmed nor denied any established taxonomic grouping.

Isoenzymes of amylase from shoot tips (Fig. 2) showed some affinity between limes and lemons with the citron standing rather apart. The mandarin is practically identical with the sweet orange (except for the last 2 electrophoretic bands 88 and 90.5) and with the sour orange. The grape-

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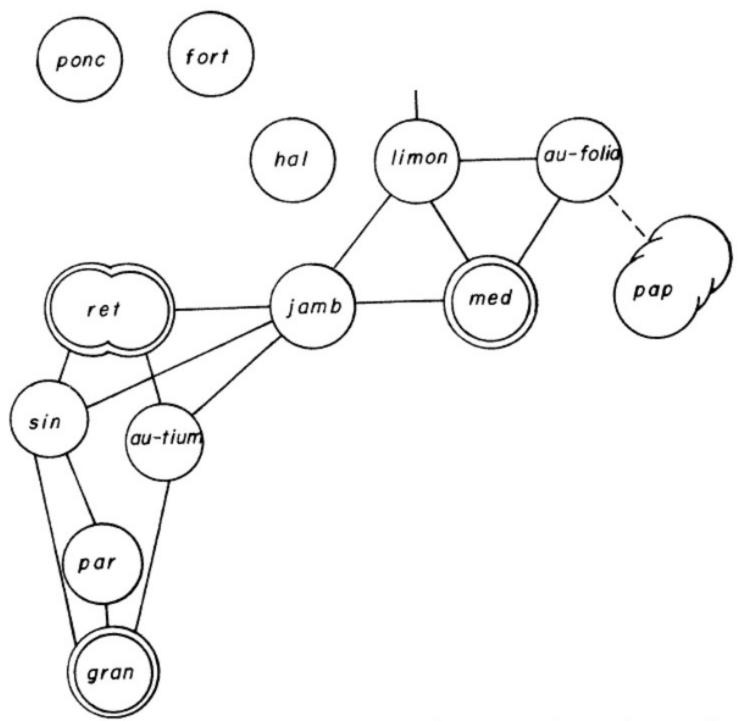


Fig. 1. Relationships within the genus Citrus. Double circles represent base species. ponc = Poncirus; fort = Fortunella; hal = C. halimii; limon = C. limon, lemon; au-folia = C. aurantifolia, lime; pap = subgenus Papeda; med = C. medica, citron; jamb = C. jambhiri, rough lemon; ret = C. reticulata, mandarin; $\sin = C$. sinensis, sweet orange; au-tium = C. aurantium, sour orange; par = C. paradisii, grape-fruit; gran = C. grandis, pummelo.

fruit pattern complements both the pummelo and sweet orange in the first two and last two bands, except for the quantity of material.

A herbarsheet, of a montane tropical

Citrus biotype, had been annotated by Tanaka as Fortunella (Pseudo-citrus) punctata n.sp. (Kerr 7417 KEW). This biotype, now known from several localities, and which has been given species standing

AMYLASE PATTERN IN CITRUS

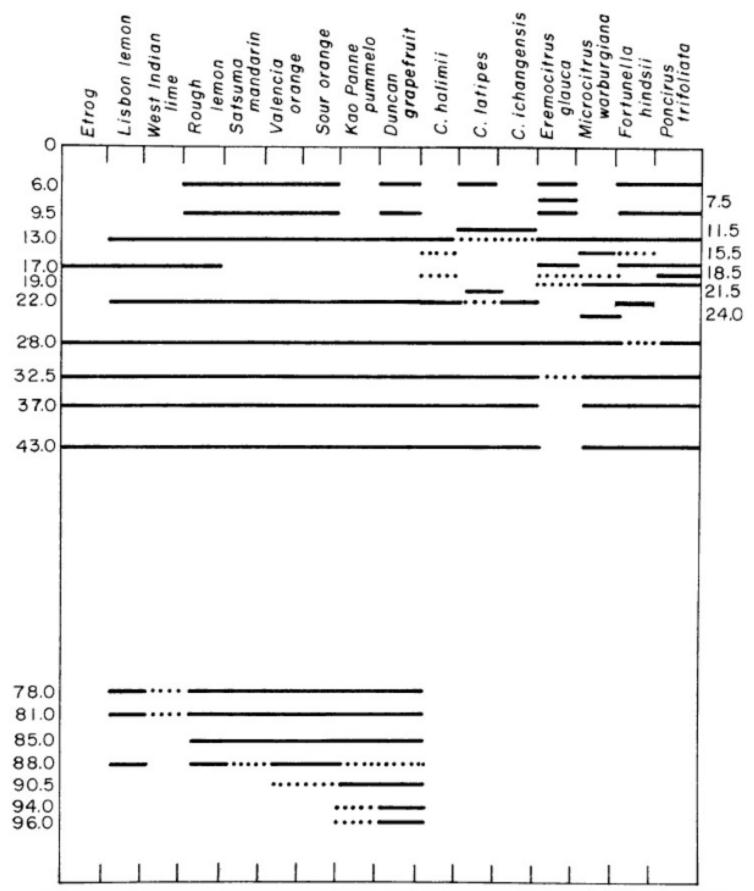


Fig. 2. Unpublished data from Esen and Scora: Amylase polymorphism in Citrus and some related genera.

by Stone et al. (1973), has fruits resembling a lemon-rough lemon assemblage in outward color and morphology, and rind oils similar to those of sweet oranges. Its amylase pattern, however, does not confirm such a relationship. The same holds true for its isoelectric leaf protein pattern. The pattern of *C. halimii* is quite distinct from all taxa which could be thought to be related to it, namely the kumquats, lemons, rough lemons and the sweet and sour oranges.

In summary, I propose that there are two areas of origin, tropical and subtropical for the subgenera Papeda and Citrus, respectively. I further propose three basic species in the subgenus Citrus, C. grandis (pummelo), C. medica (citron) and C. reticulata (mandarin). Morphological, genetic and phytochemical evidence suggests that all other species, no matter how well established in our minds as well as in citriculture, seem to be stabilized combinations primarily among these three basic biotypes.

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