
The Domestication of Cucurbita (Cucurbitaceae)

Author(s): Michael Nee

Source: *Economic Botany*, Vol. 44, No. 3, Supplement: New Perspectives on the Origin and Evolution of New World Domesticated Plants (Jul. - Sep., 1990), pp. 56-68

Published by: Springer on behalf of New York Botanical Garden Press

Stable URL: <http://www.jstor.org/stable/4255271>

Accessed: 28-12-2016 19:05 UTC

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://about.jstor.org/terms>



Springer, New York Botanical Garden Press are collaborating with JSTOR to digitize, preserve and extend access to *Economic Botany*

The Domestication of *Cucurbita* (Cucurbitaceae)

MICHAEL NEE¹

The genus Cucurbita consists of about thirteen species or species groups. "Squashes" have been domesticated independently from five of these thirteen taxa. The wild ancestor for one domesticated squash was identified in the 1930's, ancestors for two others were determined in the 1980's, but the wild ancestors of the other two domesticates remain unknown.

The genus *Cucurbita* is well known to both botanist and layman who marvel at the bewilderingly varied and often bizarre fruits of the domesticates. Fruit shape ranges from globose (as in most wild species) to pear-shaped, or variously elongated or flattened; and the fruit apex may bear a peculiar protuberance. The surface of the fruit may be smooth or warted; ribs or furrows may be present or not. Fruit colors range through various shades of green, whitish, tan, brown, blue-gray, yellow, orange and orange-red; fruits may be either of a uniform color or striped or speckled. Fruits range from 4–15 cm in diameter (as in the wild species) to some of the "pumpkins" of *Cucurbita maxima* Lam., which are the largest fruits known, measuring up to a meter in diameter and weighing 300 kg.

Botanists have applied about 435 names, at various taxonomic ranks, to this diversity (T. Andres, pers. comm.). However, I believe there are only five domesticated species of *Cucurbita* and that they are separated by sterility barriers as well as a convincing number of morphological features of the trichomes, leaves, calyces, corollas, stamens, pedicels, and seeds. Four of the five cultivated species (*Cucurbita maxima*, *C. pepo* L., *C. moschata* (Lam.) Poir., *C. ficifolia* Bouché) and the sterility barriers between them were delimited by the mid-1800's in France (Naudin 1856). L. H. Bailey accepted these four in his treatments of the cultivated species (1929) and of the wild species (1943, 1948). Currently, an additional cultivated species, *C. argyrosperma* Huber [recently shown by Mabberley (1985) to be the correct name for what has generally been called *C. mixta* Pang.] is generally recognized for certain cultivars treated by Bailey and most preceding authors under *C. moschata* (Cutler and Whitaker 1956). The most complete and certainly the most readable treatment of the cultivated *Cucurbita* species is by Bailey (1929), who stated astutely that

"Pumpkins and squashes, as we now understand them, are unknown in a native wild state. This is one of the enigmas in the plant world. But the earth is yet little explored for such things and our interest in the botany of the group is not sufficient to make the search thus far conclusive. The fact that there is an apparently native undefined *Cucurbita* in southern Florida [*Cucurbita okeechobeensis* (Small) Bailey] suggests how little we know about these kinds of plants. If there has been an unrecognized kind in Florida, may there not be others in Mexico or Central America or elsewhere that have some relation to the origin of the cultivated kinds?" (Bailey 1929:65)

¹ New York Botanical Garden, Bronx, NY 10458.

TAXONOMY

Cucurbita is a well defined New World genus within the tribe Cucurbitae and is characterized by large, yellow-orange (rarely pale yellow) flowers pollinated in early morning by pollen gathering solitary bees of the genera *Peponapis* and *Xenoglossa* (Hurd and Linsley 1964, 1966, 1967) and by hard, spherical, indehiscent fruits. Various unrelated large-fruited cucurbits were included in *Cucurbita* by Linnaeus and other early botanists, but these have now been removed to other genera, i.e., the bottle gourd, *Lagenaria siceraria* (Mol.) Standl.; wax gourd, *Benincasa hispida* (Thunb.) Cogn.; cassabanana, *Sicana odorifera* (Vell.) Naud.; and watermelon, *Citrullus lanatus* (Thunb.) Mats. & Nakai.

Peponopsis, described in 1862 from flowering material, is a little-known monotypic genus of the tribe Cucurbitae. The fruits and seeds of *Peponopsis adhaerens* Naud. were finally discovered in 1985 in northeastern Mexico, and it is now apparent that *Peponopsis* is not closely related to *Cucurbita* (Andres, unpublished). All of the other genera of the tribe Cucurbitae (Jeffrey 1990), i.e., *Sicana*, *Polyclathra*, *Schizocarpum*, *Penelopeia*, *Anacaona*, *Tecunumania*, *Calycophysum*, *Cionosicyos*, *Selysia*, *Abobra*, and *Cayaponia* also present various floral or fruit characters that differ sharply from those of *Cucurbita*. These genera are not believed to be involved in the recent evolution of *Cucurbita* and its cultivated species.

Cucurbita is usually considered to include about 20 to 26 species (Jeffrey 1978; Cutler and Whitaker 1961). Most of the wild species of *Cucurbita* known to Bailey (1943) were based on incomplete descriptions from three or fewer herbarium specimens that often lacked roots, fruits or seeds. His key to species, although detailed, is difficult to use in practice. I believe the genus contains only twelve or thirteen species (Table 1). Since most of the reductions to synonymy or transfers to infraspecific rank have not yet been made, currently available species names will be applied here to taxa that may eventually be treated differently.

Cucurbita has been divided into two groups: (1) the arid zone perennials with storage roots; and (2) the more mesophytic annuals or short-lived perennials without storage roots (Whitaker and Bemis 1975). An arid-zone perennial, *Cucurbita foetidissima* H.B.K., is currently under intense selection by modern plant breeding and may become domesticated in the extraordinarily short period of a few decades (DeVaux and Schultz 1985).

The five domesticated species of *Cucurbita* have arisen from the mesophytic group; and a sixth, *C. ecuadorensis* Cutler & Whitaker, may prove to have been partially domesticated. In contrast, among the ca. 335 remaining species of Cucurbitaceae in the New World (Jeffrey 1978) only chayote, *Sechium edule* (Jacq.) Sw.; achojcha, *Cyclanthera pedata* (L.) Schrad.; cassabanana, *Sicana odorifera*; and bottle gourd, *Lagenaria siceraria*, were domesticated. In New World agriculture perhaps only two genera can claim a similarly impressive number of domesticated food plants: *Capsicum*, with three to five species (depending on the author) out of approximately 25 wild species (D'Arcy and Eshbaugh 1974; Eshbaugh 1975); and *Solanum*, with seven cultivated species out of approximately 160 species of *Solanum* section *Petota* (Hawkes and Hjerting 1989).

DOMESTICATION

Cucurbita is present in the archaeological record of the New World from the earliest stages of agriculture (Whitaker 1981) and has formed a part of nearly all

TABLE 1. THE THIRTEEN SPECIES OR SPECIES GROUPS OF *CUCURBITA*.^a

Mesophytic annuals (or short-lived perennials), without storage roots.

1. **C. maxima* Lam., 1786.
C. andreana Naud., 1896. Warm temperate Argentina.
2. **C. pepo* L., 1753.
C. texana (Scheele) Gray, 1850. U.S.A.: Texas, other southeastern states.
C. fraterna Bailey, 1943. Mexico: Tamaulipas, Nuevo León.
3. **C. argyrosperma* Huber, 1867. [= *C. mixta* Pang., 1930]
C. sororia Bailey, 1943. Pacific coast, from Mexico to Nicaragua, Gulf coast of northeastern Mexico.
C. palmeri Bailey, 1943. Pacific coast of northwestern Mexico.
C. kellyana Bailey, 1948. Pacific coast of western Mexico.
4. **C. moschata* (Lam.) Poir., 1818. Cultivated in lowlands of tropical and subtropical America.
5. **C. ficifolia* Bouché, 1837. Cultivated in mountains from Mexico to northern Chile and Argentina.
6. *C. ecuadorensis* Cutler and Whitaker, 1969. Pacific coast of Ecuador.
7. *C. okeechobeensis* (Small) Bailey, 1930. U.S.A.: Florida.
C. martinezii Bailey, 1943. Mexico: Gulf coast and foothills.
8. *C. lundelliana* Bailey, 1943. Yucatan lowlands of Mexico, Guatemala, Belize.

Arid-zone perennials with storage roots.

9. ?*C. galeottii* Cogn., 1881. Mexico: Oaxaca.
 10. *C. radicans* Naud., 1866. Central Mexican plateau.
C. gracilior Bailey, 1943.
 11. *C. pedatifolia* Bailey, 1943. Mexican plateau, Querétaro.
C. moorei Bailey, 1948.
 12. *C. foetidissima* H.B.K., 1817. U.S.A.: Great Plains; northern Mexico.
[*C. scabridifolia* Bailey, 1943, probably a hybrid of 11 and 12.]
 13. *C. digitata* Gray, 1853. Southwestern U.S.A., northwestern Mexico, includes some or all of the following closely related taxa.
C. californica Wats., 1876.
C. palmata Wats., 1876.
C. cordata Wats., 1889.
C. cylindrata Bailey, 1943.
-

^a Names are followed by date of effective publication and are grouped under the oldest name; native range of wild species and approximate pre-Columbian range of cultivated species; the additional names will eventually be treated as subspecies or as synonyms; * = a domesticate; ? = poorly known.

the indigenous cultures of the New World from southernmost Canada to Argentina and Chile. The wild species of *Cucurbita* might be considered tempting to early New World hunters and gatherers because the relatively large fruits are quite conspicuous and easily gathered during the dry and/or winter season. The nutritious and palatable seeds were probably the main attraction for first gathering, and later for domestication. Seeds extracted from fresh or dried fruits can easily be washed free of the nauseatingly bitter cucurbitacins found in the fruit flesh. The young and mature fruits can be eaten if they are repeatedly boiled in changes of water; the rare non-bitter mutants can be consumed with minimal preparation. The ripe fruits and seeds are easily stored for long periods. The widespread use of the fruits for washing, because of their detergent saponins, would probably be only a subsidiary reason for domestication.

The latest summaries on domestication are by Whitaker (1980) and Whitaker

and Bemis (1975). My current assessment of the origin of the five cultivated species differs considerably from these; it is based to a large extent on dissertation research by T. Andres, D. Decker and L. Merrick at Texas A&M University and Cornell University. Each domesticate in *Cucurbita* seems to have arisen from a different wild species (or two closely related wild species), and these progenitors are still extant as wild species, even if interacting with their cultivated descendants. Hybridization in the genus seems to occur almost exclusively between each domesticate and its wild progenitor(s). The center of diversity of the domesticate is within the general range of the wild progenitor, and the archaeological record is longest in the area of domestication and progressively younger elsewhere.

Cucurbita andreana—*C. maxima*

Cucurbita maxima includes the ‘hubbard’, ‘banana’, ‘buttercup’, ‘turban’ and the giant reddish-orange “squashes” often seen at Halloween time in the United States (and confused with the orange jack-o-lantern “pumpkins,” which are *C. pepo*). A diverse range of landraces occurs in South America, including bush types with small fruits consumed in the immature state like “summer squashes.” *Cucurbita maxima* is characterized by nearly entire or very shallowly lobed leaves with soft hairs. The lower portion of the corolla tube is nearly tubular. The mature pedicel is soft, corky, and enlarged. Its seeds are often tumid, without a distinct raised margin, and either chalky white or handsome chestnut brown.

There is solid evidence for a link between *C. maxima* and its wild ancestor, *C. andreana* Naud. (Millán 1945). *Cucurbita maxima* is known from very early in the archaeological record of South America (Whitaker 1981), but not outside that continent before Columbus. *Cucurbita andreana* is a weedy species known from Uruguay and Argentina in warm temperate South America (Fig. 1). The vegetative and reproductive structures of *C. andreana* closely resemble those of *C. maxima*; but *C. maxima* is more robust, and its fruits are larger and more palatable than those of *C. andreana*, features presumably under selection pressure for human use. *Cucurbita andreana* has at times been considered a feral escape from cultivated *C. maxima*, but this would only force one to search elsewhere in South America for a wild ancestral species, all of whose characteristics would be precisely those of *C. andreana*.

Cucurbita fraterna and/or *C. texana*—*C. pepo*

Cucurbita pepo is the best-known squash in the United States, both currently and prehistorically, with a phenomenal range of fruit types including orange jack-o-lantern pumpkins; the ‘acorn’, ‘zucchini’, ‘vegetable marrow’, ‘spaghetti’, and ‘pattypan’ squashes; and the numerous types of ornamental gourds. It is characterized by acutely and prominently lobed leaves with harsh spiculate hairs; strongly angled, hard fruiting pedicels, which sometimes continue as ridges onto the fruit surface; and uniformly pale tan seeds with a raised margin.

It has often been noted (Heiser 1985) that the fruits and vegetative parts of certain cultivars of ornamental gourds are nearly identical to those of the inter-fertile *C. texana* (Scheele) Gray, a geographically restricted, wild-growing species best known from sandy riverine habitats of a few river systems of Texas, but apparently sporadically distributed elsewhere in the south central United States

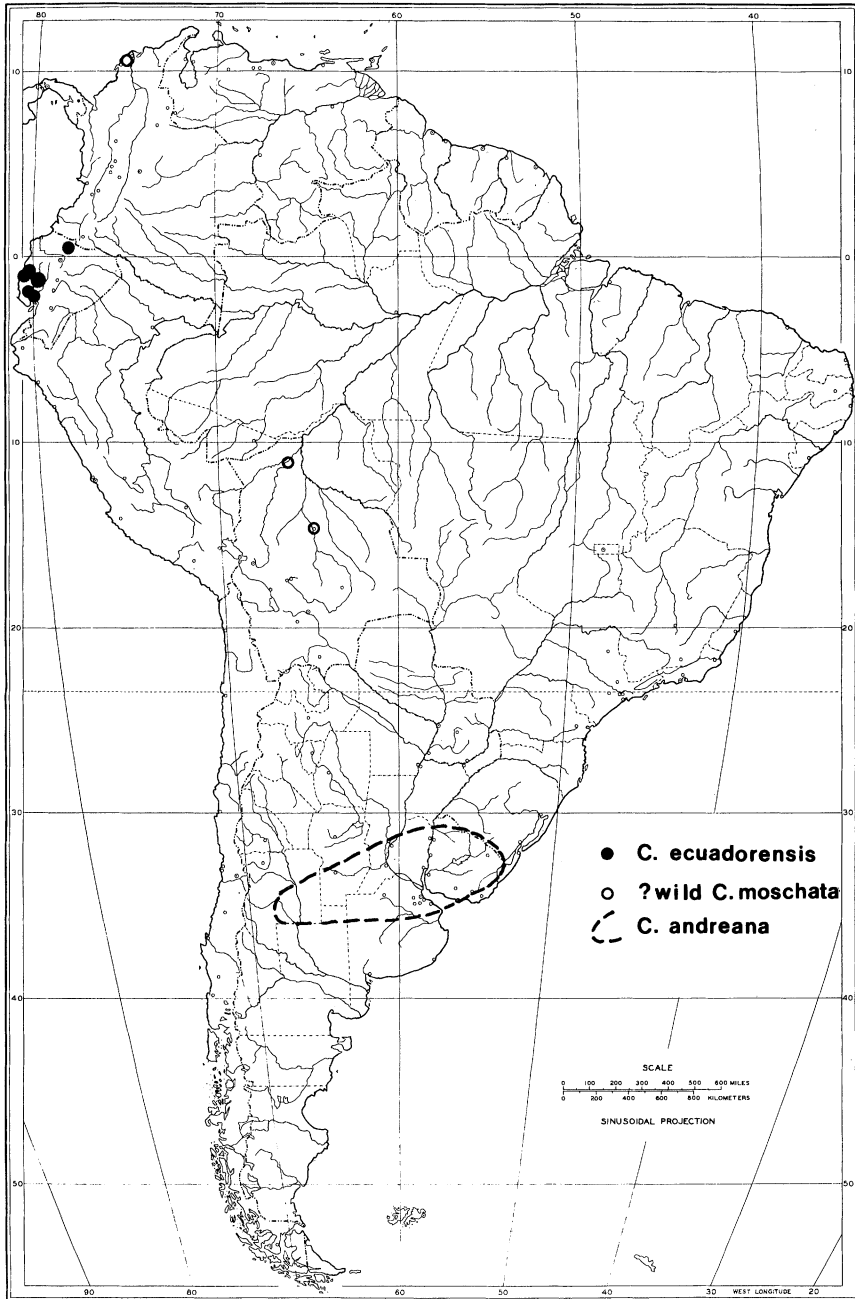


Fig. 1. Map of South America with ranges of *Cucurbita ecuadorensis* and *C. andreana* taken from herbarium specimens at BH, NY, GH, US. The hollow circles indicate reports of possible wild *C. moschata*.

(Fig. 2). Perhaps simply because of the epithet *texana*, the populations outside of Texas have seldom been identified as *C. texana* and have usually been dismissed as escaped *C. pepo*. This situation has led to two longstanding and opposed opinions: (1) *C. texana* is the ancestor of *C. pepo*; and (2) *C. texana* merely

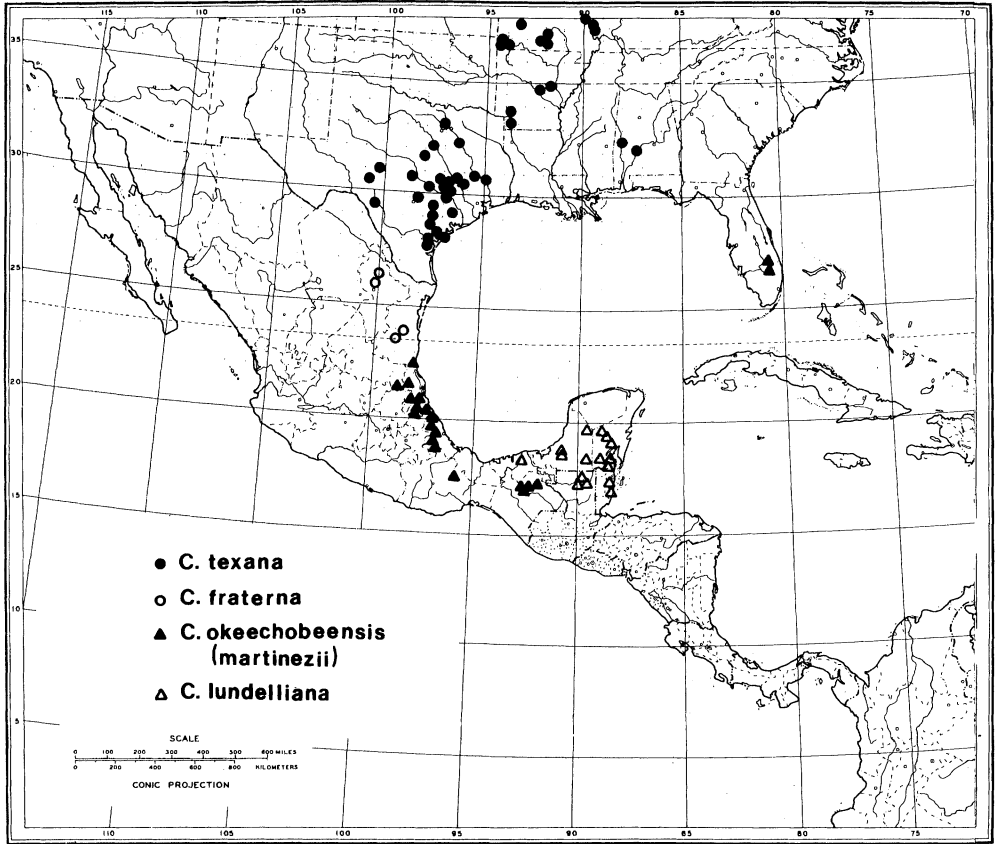


Fig. 2. Map of ranges of *Cucurbita texana* (some dots outside of Texas may represent feral *C. pepo*), *C. fraterna*, *C. okeechobeensis* (and the probably conspecific *C. martinezii* in Mexico), and *C. lundelliana*.

represents feral forms of *C. pepo*, which itself must have originated elsewhere (Heiser 1985).

Recent detailed work on the isozymes of *Cucurbita pepo* has culminated in a very interesting division of this species (Decker 1988): *C. pepo* ssp. *pepo* includes a large group of edible cultivars; *C. pepo* ssp. *ovifera* (L.) Decker var. *ovifera* includes other edible cultivars and some ornamental gourds, whereas the remaining ornamental gourds and the wild-growing populations are treated as *C. pepo* ssp. *ovifera* var. *texana* (Scheele) Decker. The recent rediscovery of *C. fraterna* Bailey in northeastern Mexico, its ability to cross with *C. pepo*, and the isozymatic similarity between the two species have opened up new questions (Andres 1987; Decker 1988; Decker-Walters 1990). In Tamaulipas *C. fraterna* has a short life cycle. It germinates with the early fall rains and blooms in mid-September; the fruits are mature and the vines dry up by mid-December. Apparently some populations of *C. fraterna* have non-bitter fruits (J. Dieterle, on herbarium label). This species, unlike *C. texana*, is not a streamside plant but is found in disturbed upland soils derived from limestone or volcanic bedrock. Derivation of *C. pepo* in part or in whole from a relatively cool season plant

would be consistent with its predominance as a vegetable crop in the northern United States and later in northern Europe. *Cucurbita fraterna* is currently known from only three populations but certainly is more widespread. Much more field-work is needed in northeastern Mexico to establish its range, ecology, local uses, and to assess the possibilities of hybridization *in situ* with the possibly primitive local landraces of *C. pepo*, similar to hybridization of *C. texana* with *C. pepo* in Texas (Kirkpatrick and Wilson 1988). Some of the earliest agricultural remains in the New World, including *Cucurbita* seeds, occur in caves in the Ocampo valley, Tamaulipas (Whitaker 1981), a particularly inviting area for further field investigation. *Cucurbita fraterna* is known from only 80 km to the northeast of the Ocampo valley, and *C. sororia* Bailey has also been found nearby.

A systematic search of the older literature may reveal clues to the general geographic origin of the ornamental gourds, which on morphological grounds would seem to be the most primitive domesticates of *C. pepo*, but which do not seem to be grown in Mexico now or in pre-Columbian times. Clarification of these points is needed, but the rediscovery of *C. fraterna* has probably added a key element to unravelling the full history of *C. pepo*.

Cucurbita sororia—*C. argyrosperma*

Cucurbita argyrosperma includes the 'Japanese pie pumpkin', 'white cushaw' and various Mexican and Central American cultivars, some of which are grown for their large nutritious seeds rather than for the flesh. It is characterized by softly pubescent young vegetative growth and expanded and hard-corky pedicels. The seeds are strongly bordered, and sometimes a prominent gray-green margin contrasts with a white body. The fruits are often white or very pale tan with a green reticulate pattern.

In the original description, *Cucurbita sororia* was named as the "sister" of *C. texana*, but Bailey (1943) had no other comments as to its affinities. An unidentified wild species, now known to be *C. sororia*, was suggested to be the ancestor of *C. argyrosperma* by Whitaker (1980). This species group is currently under detailed study by L. Merrick (Merrick and Bates 1989; Merrick 1990), and its systematics are proving to be somewhat more complicated than the synopsis presented below.

Cucurbita argyrosperma certainly seems to be derived from *C. sororia*, a widespread wild species in the lowland thorn-scrub vegetation of the Pacific (more rarely the Gulf) coast of Central America from Mexico south to Nicaragua. *Cucurbita argyrosperma* is known from the archaeological record in Mesoamerica and even today is scarcely known outside Central America, Mexico and the southern United States. Evidence of inadvertent crossing with *C. sororia* is known from various places in Mexico and experimental crosses give fertile hybrids (Merrick 1990; T. Andres, pers. comm.). The process of domestication seems still to be occurring in western Mexico where bitter fruits from wild plants of *C. sororia* are sometimes eaten after boiling the flesh in several changes of water to rid them of the cucurbitacins. Sometimes the wild *C. sororia* or hybrids with *C. argyrosperma* are deliberately fertilized to increase production (T. Andres, pers. comm.).

Cucurbita ?—*C. moschata*

Cucurbita moschata includes the 'butternut squash', 'golden cushaw', and most of the common *Cucurbita* cultivars of the West Indies, lowland Central America and much of lowland tropical South America. It is characterized by soft pubescence on the leaves and young parts, calyx lobes that are often expanded and foliose, and a hard, smoothly angled pedicel which flares at the fruit attachment and then abruptly contracts. The seeds are variable but always have a prominent border differentiated in color from the body.

Cucurbita moschata is often difficult to distinguish from *C. argyrosperma* and the latter was usually included in *C. moschata* until this century. Although the vegetative parts, flowers and even seeds are often very similar, the pedicels are usually distinctive enough to separate the two. *Cucurbita moschata* shares isozyme bands with *C. argyrosperma*, although the electrophoretic patterns are distinctive (Puchalski and Robinson 1990). Even though these two cultigens are partly interfertile, they do not generally appear to hybridize where grown together (Merrick 1990; T. Andres, pers. comm.). All this would seem to indicate that *C. moschata* and *C. argyrosperma* have different origins, probably from different wild ancestors.

No obvious candidate for a wild ancestor of *Cucurbita moschata* is known at this time. None of the wild species now known match the vegetative or floral characters of *C. moschata* very closely. The gray-green seeded *C. lundelliana* Bailey, confined to the limestone lowlands of the Yucatan peninsula, and previously proposed as the ancestor of *C. moschata* by Whitaker (1980), does not seem to be closely related (Merrick 1990). I have heard reports of wild *Cucurbita* in the lowlands of Bolivia (Fig. 1). Near Riberalta, Depto. Beni, a wild cucurbit is reported to produce hard, bitter fruits and to hybridize with the local cultivated *C. moschata*. Wild *Cucurbita* plants at Trinidad, Depto. Beni, identified by Cárdenas (1969) as *C. andreana*, almost certainly cannot be that species whose natural range is so much farther to the south in a very different ecological zone.

The most promising area for discovering the wild ancestor of *C. moschata* seems to be northern Colombia where cultivars with the greatest diversity of fruit types are found, including types with very small and presumably primitive fruits and unique seed colors (Zhiteneva 1929–1930). Between Cartagena and Barranquilla, Colombia, I have heard reports of locally grown squashes occasionally being bitter, suggesting hybridization of cultivars with a local wild *Cucurbita*. However, the nearest known wild species are *C. sororia* which ranges from Mexico through Nicaragua, and *C. ecuadorensis* from coastal Ecuador.

Cucurbita ?—*C. ficifolia*

Cucurbita ficifolia is the most distinctive of the five cultivated species, with peculiar fruits resembling large oblong watermelons and broad black seeds. Its leaves have prominent rounded lobes, and the stamen filaments are pubescent. It is generally grown at much higher altitudes than the other domesticated species of *Cucurbita*. In the Americas it is common in the mountains from northern Mexico to northern Argentina and Chile (Fig. 3, 4); and in the Old World it is rarely grown in Europe, but has been popular for many centuries in Asia. In nearly all taxonomic keys and descriptions it is said to be a perennial, but it does not

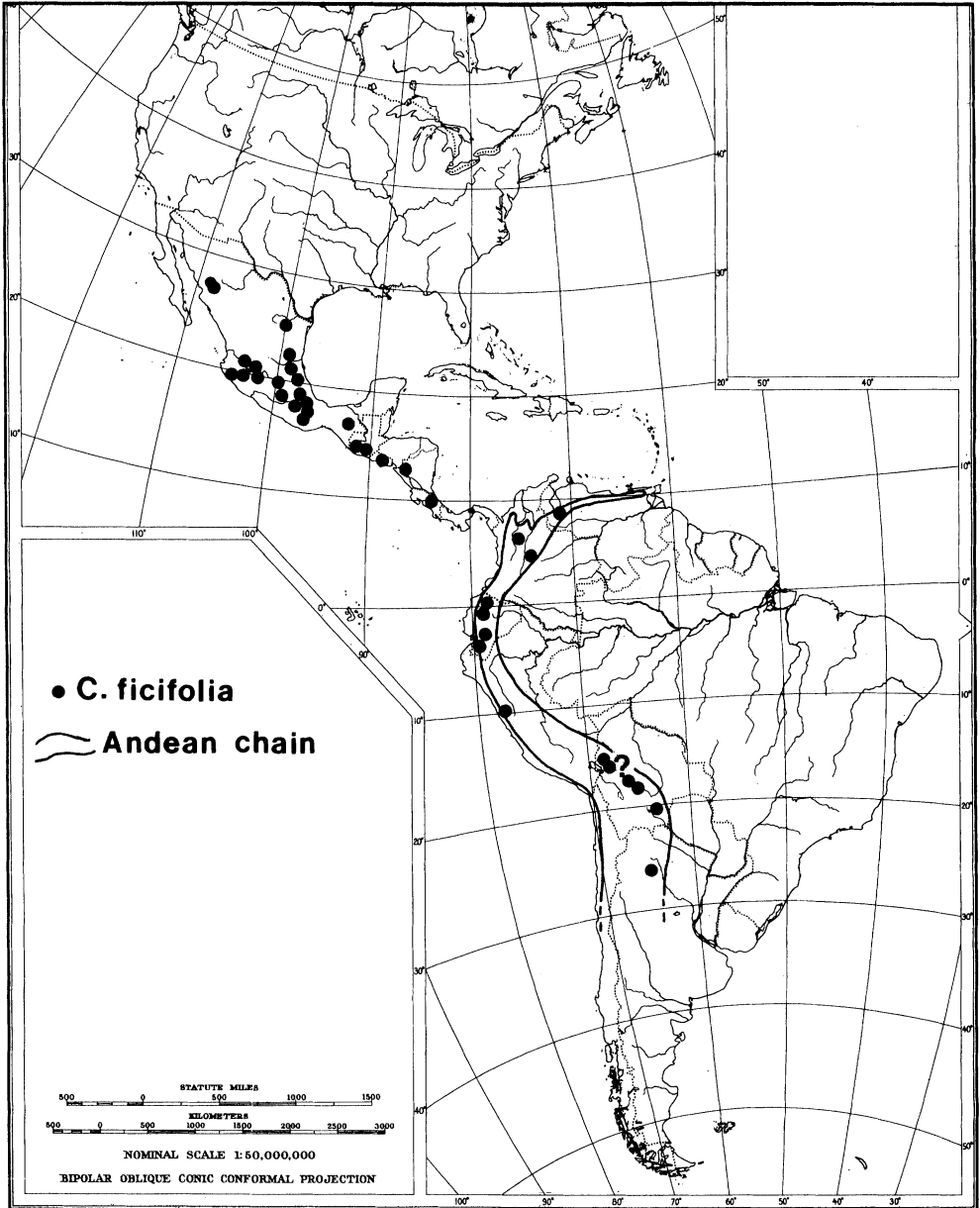


Fig. 3. Map of the New World distribution of *Cucurbita ficifolia* as a cultivated plant, taken from herbarium specimens at BH, GH, NY, US, and U.S.D.A. Plant Introduction records. The question mark indicates a report of a possible wild form.

have enlarged storage roots like the species in the xerophytic group of *Cucurbita*. Under favorable conditions without excessive drought or frost all the cultivated species, but especially *C. ficifolia*, may live longer than a year (Andres, pers. comm.). In puzzling contrast to the other species of *Cucurbita* its fruit shape, size, and color are uniform. A single field anywhere in its range may contain essentially all the variation in fruit morphology known for the species.

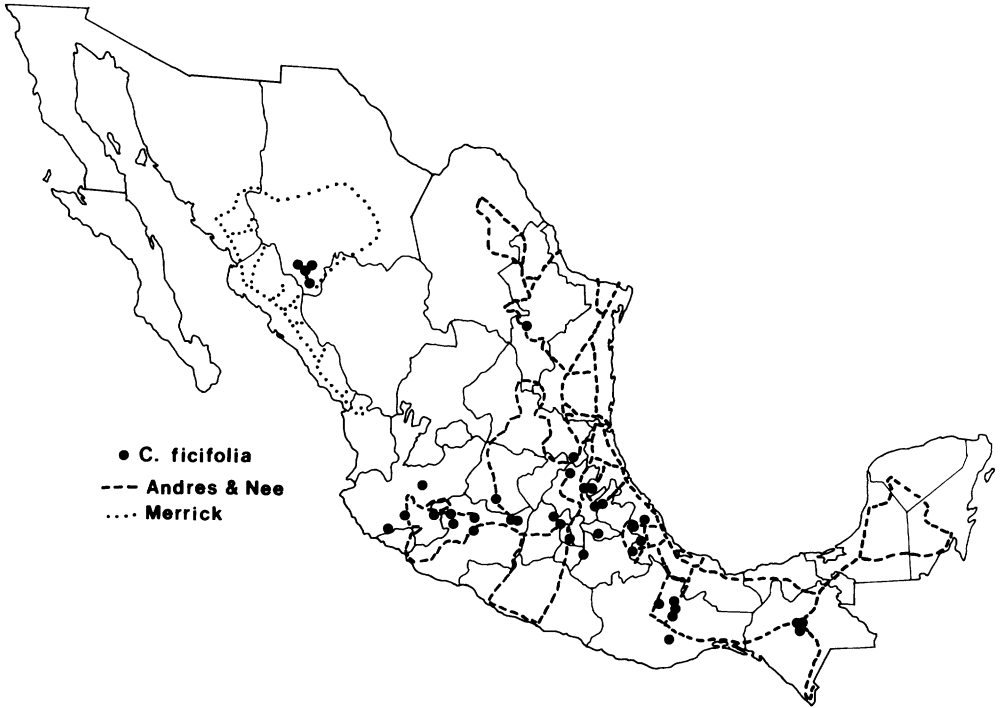


Fig. 4. Map of Mexico with itinerary for germplasm collecting by M. Nee, T. Andres and L. Merrick in 1985–1986. Dots indicate records from herbarium specimens at BH, GH, NY and US and from germplasm collections.

Although a single seed of *Cucurbita ficifolia* is reported from very early in the archaeological record in Mexico, this report must be verified. There are more numerous and reliable reports of *C. ficifolia* from pre-Columbian sites in coastal Peru (Whitaker 1981). There is little indication from crosses that *C. ficifolia* is readily interfertile beyond the F_1 with any known wild species. It does cross with the very different *C. foetidissima* and *C. radicans* to form a sterile F_1 (Andres 1990). Its seed morphology and color, its pubescent filaments, and the peculiar dimpling of the fruit surface are absent from any known wild species. Its leaf lobing resembles that of *C. ecuadorensis* but this is a lowland species which differs greatly from *C. ficifolia* in other respects. *Cucurbita martinezii* Bailey of the Gulf Coast of Mexico has been proposed as the possible ancestor (Whitaker 1980), but this seems highly improbable for the reasons discussed below under that species.

A suggestive linguistic clue to the origin of *C. ficifolia* is provided by the common name *chilacayote* used in Mexico and a word of known Nahuatl derivation in use for this distinctive plant since at least the time of the Conquest. The terms *lacayote*, *lacahuite* and *cayote* in Peru, Bolivia and Argentina would seem to be derivatives of *chilacayote*. In Bolivia there are neither indigenous Quechua nor Aymara names for this commonly cultivated plant. However, much of central and southern Mexico was searched by Andres and Nee in 1986 for any indication of a wild relative associated with *C. ficifolia* (Fig. 4). The results were uniformly negative. Merrick (pers. comm.) theorizes that *C. ficifolia* is a relatively recent introduction into the Sierra Madre Occidental of northwestern Mexico where *chilacayote* is

the term exclusively used for *C. ficifolia* among non-Nahuatl linguistic groups who have local names for the other squashes.

I believe the chances of finding an undiscovered wild species ancestral to *C. ficifolia* in Mexico are minimal. Since this is a species of medium to higher altitudes (1800–2500 m) throughout most of its range, the other likely place for a wild progenitor species would thus be Andean South America. I have recently received apparently reliable reports from local agronomists of a *pampa lacoya* (Aymara for “wild lacayote”) from the Inquisivi area of Depto. La Paz, Bolivia, at ca. 3000 m elevation, where *C. ficifolia* is commonly grown (Fig. 3). This extremely dissected area on the east slope of the Andes ranges in elevation from 500 m to 6000 m in a horizontal distance of only 20 km, and contains deciduous thorn scrub in the gorges, cloud forest on the slopes, and all intermediate habitats in which a wild *C. ficifolia* might be expected. It is predicted that the wild progenitor of *C. ficifolia* exists somewhere in the Andes; it may never have been collected, or may actually lie unrecognized as such in herbaria.

OTHER SPECIES

The remaining three mesophytic species or species groups can be eliminated from the ancestry of any of the cultivated species:

The poorly known *Cucurbita ecuadorensis* grows in a critical area (Fig. 1), and if reports in the archaeological literature of a “wild” *Cucurbita* from the Peruvian coast are correct (Bonavia 1982), it may once have ranged further south. Although it seems to be wild (T. Plowman, pers. comm.), it could very easily have been semi-domesticated in the past with some modified traits persisting. For example, the fruits are larger than in the other wild species and in some accessions may not be bitter. Nevertheless, morphologically and ecologically it is not a candidate for wild ancestor of other domesticated cucurbits.

Cucurbita okeechobeensis (Small) Bailey, an extremely rare plant restricted to the vicinity of Lake Okeechobee in Florida, is apparently conspecific with *C. martinezii* of Mexico (Fig. 2). The remarkable geographic disjunction and the taxonomic disposition of the two populations are discussed by Andres and Nabhan (1988). When *C. martinezii* was described by Bailey (1943), it was known to him by a single specimen from Atoyac, Edo. Veracruz, Mexico, that lacked roots and flowers. It is now known from the northern coastal plain of Veracruz, the foothills of the Sierra Madre Oriental from Veracruz to Chiapas, and may grow in Guatemala, although it has not yet been collected there. This range is probably mostly natural but the local use in Chiapas of the halved fruit shells as “shot glasses” for alcoholic drinks would indicate that dispersal by humans is entirely possible. *Cucurbita martinezii* grows at forest edges, usually along streams where it can be a high-climbing vine. The forests may be either temperate deciduous, with *Platanus mexicana* Moric., *Liquidambar macrophylla* Oerst., and *Ulmus mexicana* (Liebm.) Planch. at the upper altitudinal limit of about 1500 m, or the subtropical type at lower elevations. It may even be a weed in coffee plantations. It has two characters absent from any of the cultivated species—a pale yellow corolla and gray-green seeds. It has been proposed as the ancestor of *C. ficifolia* (Whitaker 1980), a species with orange-yellow corolla and black or pale tan seeds. In eastern Mexico *C. ficifolia* is cultivated from about 1800–3000 m in altitude in the pine-

oak forest zone. At present these species are never found growing together (Nee, in press), and all their other vegetative characters differ strongly, as has been detailed above.

Of the wild mesophytic species from outside the United States, *C. lundelliana* was the best-known to Bailey (1943), who examined seven specimens from Guatemala, Belize and Campeche, Mexico. *Cucurbita lundelliana* is still known only from the limestone plains of the Yucatan peninsula at elevations near sea level (Fig. 2). Like *C. martinezii*, it has gray-green seeds but its yellow-orange corolla color, leaf shape, and ecology sharply differentiate it from the former species. *Cucurbita lundelliana* has played an important role in speculation on the ancestry of the cultivated species because it seems to have the greatest ability to cross with them. The deeply cut leaves with rounded lobes of *C. lundelliana* superficially resemble those of *C. ficifolia*. The latter species, however, is grown only from about 1800–3000 m in adjacent parts of Mexico and Guatemala. The seed color and shape of *C. lundelliana* and *C. ficifolia* have nothing in common. If *C. lundelliana* were ancestral to a cultivated species, it certainly would have to share a common habitat with that domesticate. Only *C. moschata* and *C. argyrosperma* are cultivated within the range of *C. lundelliana*, but their vegetative and reproductive characters are not at all similar, nor do they cross freely.

Cucurbita galeottii Cogn. of Edo. Oaxaca, Mexico, is known only from the type specimens which lack roots, female flowers, fruits and seeds. Bailey, who saw only photographs of the specimens, placed the species among the xerophytic group, where it probably belongs. Little more can be said until the species is rediscovered in the wild.

LITERATURE CITED

- Andres, T. 1987. *Cucurbita fraterna*, the closest wild relative and progenitor of *C. pepo*. Cucurbit Genetics Cooperative Report 10:69–71.
- . 1990. Biosystematics, theories on the origin, and breeding potential of *Cucurbita ficifolia*. Pages 102–119 in D. M. Bates, R. W. Robinson, and C. Jeffrey, eds., *Biology and utilization of the Cucurbitaceae*. Cornell University Press, Ithaca, NY.
- , and G. P. Nabhan. 1988. Taxonomic rank and rarity of *Cucurbita okeechobeensis*. Cucurbit Genetics Cooperative Report 11:83–85.
- Bailey, L. H. 1929. The domesticated Cucurbits. I. *Gentes Herb.* 2:62–115.
- . 1943. Species of *Cucurbita*. *Gentes Herb.* 6:267–322.
- . 1948. Jottings in the Cucurbits. *Gentes Herb.* 7:449–477.
- Bonavia, D. 1982. *Los gavilanes*. Editorial Ausonia, Lima.
- Cárdenas, M. 1969. *Manual de las plantas económicas de Bolivia*. Imprenta Icthus, Cochabamba, Bolivia.
- Cutler, H. C., and T. W. Whitaker. 1956. *Cucurbita mixta* Pang., its classification and relationships. *Bull. Torrey Bot. Club* 83:253–260.
- , and ———. 1961. History and distribution of the cultivated cucurbits in the Americas. *Amer. Antiquity* 26:469–485.
- D'Arcy, W. G., and W. H. Eshbaugh. 1974. New World peppers (*Capsicum*—Solanaceae) north of Colombia: a résumé. *Baileya* 19:93–105.
- Decker, D. 1988. Origin(s), evolution, and systematics of *Cucurbita pepo* (Cucurbitaceae). *Econ. Bot.* 42:4–15.
- Decker-Walters, D. 1990. Evidence of multiple domestications of *Cucurbita pepo*. Pages 96–101 in D. M. Bates, R. W. Robinson, and C. Jeffrey, eds., *Biology and utilization of the Cucurbitaceae*. Cornell University Press, Ithaca, NY.

- DeVaux, J. S., and E. B. Schultz. 1985. Development of the buffalo gourd (*Cucurbita foetidissima*) as a semiaridland starch and oil crop. *Econ. Bot.* 39:454–472.
- Eshbaugh, W. H. 1975. Genetic and biochemical systematic studies of chili peppers (*Capsicum*—*Solanaceae*). *Bull. Torrey Bot. Club* 102:396–403.
- Hawkes, J. G., and J. P. Hjerting. 1989. The potatoes of Bolivia: their breeding value and evolutionary relationships. Oxford University Press, Oxford.
- Heiser, C. B., Jr. 1985. Some botanical considerations of the early domesticated plants north of Mexico. Pages 57–72 in R. I. Ford, ed., *Prehistoric food production in North America*. Anthropol. Paper 75, Museum of Anthropology, Univ. of Michigan, Ann Arbor.
- Hurd, P. D., Jr., and E. G. Linsley. 1964. The squash and gourd bees—genera *Peponapis* Robertson and *Xenoglossa* Smith—inhabiting America north of Mexico (Hymenoptera: Apoidea). *Hilgardia* 35:375–477.
- , and ———. 1966. The Mexican squash and gourd bees of the genus *Peponapis* (Hymenoptera: Apoidea). *Ann. Entom. Soc. Amer.* 59:835–851.
- , and ———. 1967. South American squash and gourd bees of the genus *Peponapis* (Hymenoptera: Apoidea). *Ann. Entom. Soc. Amer.* 60:647–661.
- Jeffrey, C. 1978. Further notes on Cucurbitaceae: IV. Some New World taxa. *Kew Bull.* 33:347–380.
- . 1990. Appendix: an outline classification of the Cucurbitaceae. Pages 449–463 in D. M. Bates, R. W. Robinson, and C. Jeffrey, eds., *Biology and utilization of the Cucurbitaceae*. Cornell University Press, Ithaca, NY.
- Kirkpatrick, K. J., and H. D. Wilson. 1988. Interspecific gene flow in *Cucurbita*: *C. texana* vs. *C. pepo*. *Amer. J. Bot.* 75:519–527.
- Mabberley, D. J. 1985. “Die neuen Pflanzen von Ch. Huber Freres & Co. in Hyeres.” *Taxon* 34: 448–456.
- Merrick, L. C. 1990. Systematics and evolution of a domesticated squash, *Cucurbita argyrosperma*, and its wild and weedy relatives. Pages 77–95 in D. M. Bates, R. W. Robinson, and C. Jeffrey, eds., *Biology and utilization of the Cucurbitaceae*. Cornell University Press, Ithaca, NY.
- , and D. M. Bates. 1989. Classification and nomenclature of *Cucurbita argyrosperma* Huber. *Baileya* 23:94–102.
- Millán, R. 1945. Variaciones del zapallito amargo *Cucurbita andreana* y el origen de *Cucurbita maxima*. *Revista Argent. Agron.* 12:86–93.
- Naudin, C. 1856. Nouvelles recherches sur les caractères spécifiques et les variétés des plantes du genre *Cucurbita*. *Ann. Sci. Nat. Bot., Ser. 4*, 6:5–72.
- Nee, M. In press. Cucurbitaceae. In *Flora de Veracruz*. INIREB, Xalapa, Mexico.
- Puchalski, J. T., and R. W. Robinson. 1990. Electrophoretic analysis of isozymes in *Cucurbita* and *Cucumis* and its application for phylogenetic studies. Pages 60–76 in D. M. Bates, R. W. Robinson, and C. Jeffrey, eds., *Biology and utilization of the Cucurbitaceae*. Cornell University Press, Ithaca, NY.
- Whitaker, T. W. 1980. Cucurbitáceas americanas útiles al hombre. CIC: Provinica de Buenos Aires, Comisión de Investigaciones Científicas, Buenos Aires.
- . 1981. Archeological cucurbits. *Econ. Bot.* 35:460–466.
- , and W. P. Bemis. 1975. Origin and evolution of the cultivated *Cucurbita*. *Bull. Torrey Bot. Club* 102:362–368.
- Zhiteneva, N. E. 1929–1930. The world’s assortment of pumpkins. *Trudy Prikl. Bot.* 23:157–207.