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CUCURBITA MIXTA, PANG. ITS CLASSIFICATION AND RELATIONSHIPS[1]

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Cucurbita mixta is the least known of the four squash and pumpkin species commonly cultivated in the United States. The Indians cultivated it prior to 1492, and several varieties are widely grown in the warmer parts of the country but the species was until recently considered a variation of *C. moschata.* Pangalo (1930) originally described it from material collected by Russian plant expeditions to the New World. The first useful description of the species in English was published in 1950 (Whitaker and Bohn 1950). It is likely that *C. mixta* will become better known when the virtues of this species are fully appreciated. Like *C. moschata, C. mixta* grows well in warm weather. In a test of flavor of about 85 kinds of pumpkin and squash, grown near Chicago, Cutler and Rhodes (unpublished data) found that well ripened Japanese Pie and some strains of Green Striped Cushaw, both varieties of *C. mixta,* ranked not far behind the five best flavored squashes. The best quality squashes are varieties of *C. maxima.* However, *C. maxima* is not adapted to warm summers, and its soft stem and peduncle are quickly attacked by squash borers (*Melittis satyriniformis* Hbn.). On the contrary, varieties of *C. mixta* do well under high temperatures, and are resistant to squash borers, while the flavor is almost as good and the fruits have a storage life equal to most varieties of *C. maxima.*

Nomenclature and description. CUCURBITA MIXTA Pangalo in Bull. Appl. Bot. Genet. & Plant Breeding 23 (3): 258, 1930.

C. mixta stenosperma Pangalo *ibid.*

C. mixta cyanoperizona Pangalo, *ibid.*

C. argyrosperma Hort., ex L. H. Bailey in Gentes Herb. 7: 457. 1948.

Since Pangalo did not designate a type specimen for his new species, we have selected an herbarium specimen grown from commercial seeds of Green Striped Cushaw, a variety similar, if not identical, to the most common variety grown in late pre-Columbian times by the Pueblo Indians of Arizona and now grown widely through the Southern United States (fig. 1). The fruit pictured in the upper left of figure three in Pangalo's paper is similar to this variety. The specimen, collected by Cutler and Whitaker, is deposited in the herbarium of the Missouri Botanical Garden.

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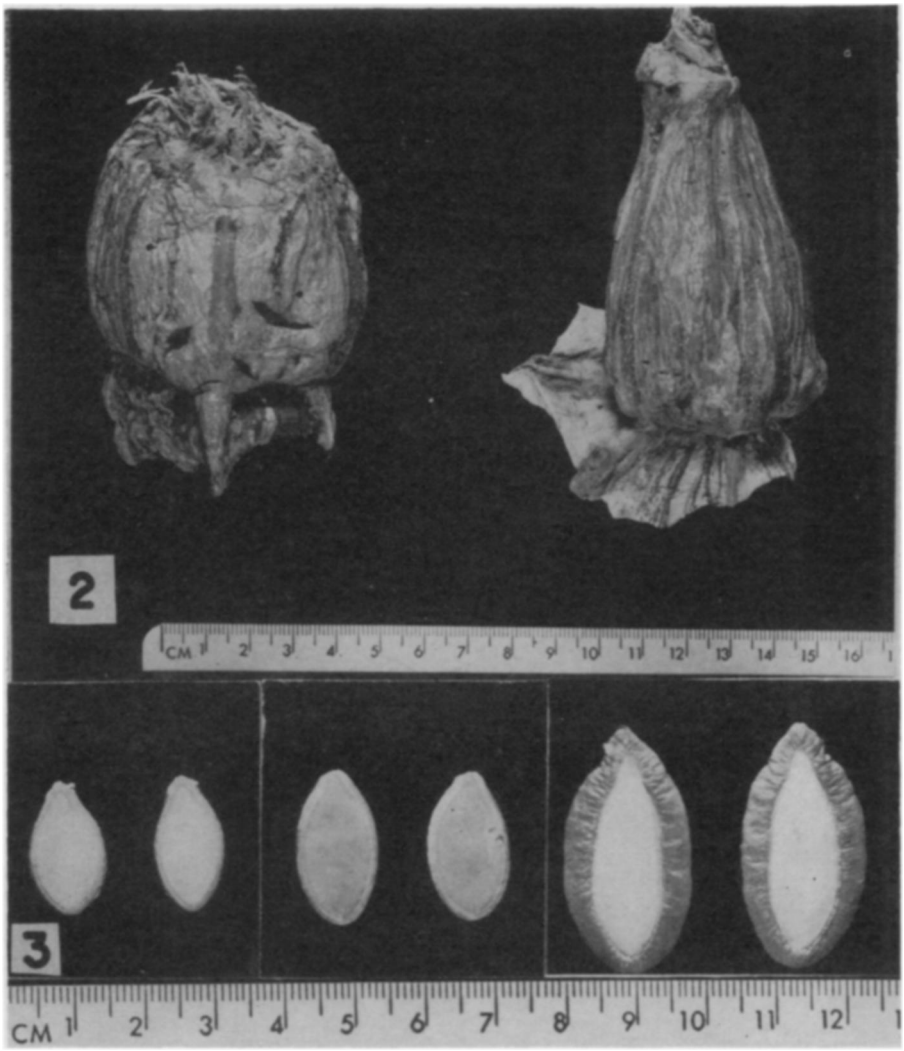
Plant annual, frost sensitive and intolerant of cool temperatures; vine pilose, not harsh, to almost glabrous; stem hard, five-angled; leaf large, broad cordate to cordate-ovate, shallowly to moderately lobed with broad, obtuse sinuses, with (or rarely without) whitish blotches, margins irregularly denticulate, major veins frequently with corky thickening; corollas yellow to yellow orange, often conspicuously striate, broad apiculate lobes, closed the evening before anthesis; androecium usually long and slender, columnar; stigmas large, bright yellow to orange or green, rough; young peduncle pilose, angled and clasping the fruit like that of *C. moschata,* mature peduncle usually moderately hard, corky, basically five-angled, the five angles may be represented only by five smooth lines, although when the stem is greatly expanded the slight enlargement at the fruit is usually concealed by firm, warty cork that slightly to greatly increases the pedun-

FIG. 1. Fruits of *Cucurbita mixta* var. Green Striped Cushaw showing peduncle and corky ridges at stem end of the fruit (courtesy Lawrence Robinson & Sons).

cle diameter; (fig. 2) fruit variable, hard or soft-shelled, usually dull in color, often with warty edges or bumps especially near the peduncle, and extending as ridges over the stem end of the fruit; fruit flesh usually moderately dry, white to pale tan or yellow (orange unknown), coarse grained with coarse but not gelatinous fibers; placenta collapsing at maturity; seeds separating readily and clearly from the plup; plump, usually ovate ellipsoidal, with symmetrical or slightly asymmertical, obtuse funicular attachment (fig. 3); seed body white, soft, usually split in various patterns, or tan, smooth and hard; margin barely scalloped, separating into threads, or threads adhering together, sometimes thin and of a different color from the body of the seed, or the margin greatly enlarged, silvery-green or silvery-blue.

Like maize and several other cultivated plants, the species of *Cucurbita* have many variations which can be combined in numerous ways. Certain

combinations may be most common in definite areas, yet, because there are many combinations of characters and because the varieties are frequently found far from the centers in which they are most abundant, it



FIGS. 2–3. Peduncles and seeds of *Cucurbita mixta*. FIG. 2. Peduncles of *C. mixta;* left—Japanese Pie, right—Green Striped Cushaw. FIG. 3. Seeds of *C. mixta;* left—Green Striped Cushaw, center—Taos, right—Silverseed Gourd.

is usually futile to describe definitely a kind of squash and give it a scientific subspecific designation. All three of the synonyms cited above are based on seed characters. These characters are inherited independently

and appear to be almost valueless for delimiting botanical varieties as are colors or endosperm characters in maize. Yet in the past, before extensive movement and mixing of *Cucurbita* species and varieties occurred, seed characters probably were associated with certain kinds of squash. We can distinguish three types of seeds in *C. mixta* ("green striped cushaw," "taos," and "silverseed"). Most common and most widespread is the "green striped cushaw" type with quite large (1.0×1.1 mm. to 1.6×0.9 mm.), soft, white-bodied seeds found in the Green Striped Cushaw and Japanese Pie squashes of today, in many Mexican varieties and in most of the *C. mixta* in the Southwest grown by present-day Indians and found in late pre-historic ruins. "Taos" type seeds (2.2×1.2 mm. to 2.0×1.1 mm.), closely resemble those of the Banana varieties of *C. maxima* and are known from Mexico, from a few fruits collected at Taos and several other Rio Grande Pueblos and from late pre-historic sites in the same general region. The "silverseed" type (3.5×1.8 mm. to 3.3×1.8 mm.), is found in Mexico.

Below we have classified according to seed type all the varieties known to us: "green striped cushaw"—Green Striped Cushaw, Tennessee Sweet Potato, Puritan, White Cushaw, Chirimin, Japanese Pie, Kikuza, Saikyo, Yokohama, and most Mexican mixtas; "taos"—Taos; "silverseed"—Silverseed Gourd.

When young, the peduncles of *C. mixta* resemble those of *C. moschata* and *C. ficifolia*. As the peduncle matures, a corky secondary thickening develops so that it is somewhat similar to the corky cylindrical peduncle of *C. maxima*.

In his analysis of the differences which separate *C. mixta* from the other annual cultivated species, Pangalo (1930) found that 13 were like *C. moschata*, 9 like *C. pepo*, and only 4 were similar to *C. maxima*.

Genetic relationships. The genetic affinity of *C. mixta* to the other cultivated species of *Cucurbita* is confused, primarily because it has only recently been recognized as an independent species (Pangalo 1930). Breeders formerly lumped this species with *C. moschata*. As a result, unless varietal names are given, it is difficult to obtain a clear picture of the interspecific breeding behavior of this entity. Nevertheless, some significant data have been accumulated which suggest tentative relationships.

C. mixta x C. pepo. L. H. Bailey (1902) produced the first successful interspecific cross to be reported in *Cucurbita*. Baily obtained two fruits with fertile seed by pollinating Connecticut Field Pumpkin (*C. pepo*) with Japanese Crookneck (*C. mixta*). Eighty-eight F_1 plants were grown from the seed of these two fruits. Evidently the F_1 was fertile, or at least sparingly fertile, since Bailey reports that a number of F_2 plants were grown. However, the F_2 plants must have been very nearly sterile as only

one fruit was produced; no mention was made of it having seed. Castetter (1930) secured one fruit with numerous fertile seed in a cross using Connecticut Field Pumpkin (*C. pepo*) as the pistillate parent and Striped Cushaw (*C. mixta*) as a pollen parent. The F_1 plants were vigorous and healthy, but it is unlikely that they were fertile as no record was made of this feature. Van Eseltine (1937) reports that he obtained fruits from Delicata and Giant Crookneck (*C. pepo*) when pollen from Japanese Pie (*C. mixta*) was used. Whether or not the fruit contained viable seed was not stated. He also obtained fruit from the reciprocal cross using Japanese Pie (*C. mixta*) as the pistillate parent with pollen from Delicata, Giant Crookneck, and Golden Custard (all *C. pepo*).

From the above data, we can draw the conclusion that if the proper combinations are used, along with a great deal of persistence, it is possible to obtain hybrids between *C. pepo* and *C. mixta;* but fertility in the F_1 is variable, and the F_2 is mostly sterile. Evidently the cross is more likely to succeed if a variety of *C. pepo* is used as the pistillate parent.

C. mixta x C. maxima. Halsted (1908) has reported that he obtained a fertile hybrid by crossing Striped Cushaw (*C. mixta*) with Delicious (*C. maxima*), using Striped Cushaw as the pistillate parent. F_1 plants were grown but the experiment was apparently terminated at this point. Castetter (1930) obtained 25 fruits and two fertile seed in matings between Striped Cushaw (*C. mixta*) and Marblehead (*C. maxima*). The F_1 plants were exceptionally vigorous, but completely pollen sterile. Some fruits were obtained by backcrossing to *C. maxima* var. Hubbard, but in no case were any viable seeds found in these fruits. Whitaker and Bohn (1950) indicate that *C. mixta* and *C. maxima* can be crossed in reciprocal matings, but with difficulty. An occasional fruit will set which may be seedless, have flat seeds with poorly developed embryos, or a few plump seeds may be found. The F_1 plants produce flowers that degenerate at various stages up to anthesis. An occasional flower will continue to anthesis, but only abortive pollen grains are produced. The female flowers are apparently normal, but are cross-sterile with pollen from either parent.

It is clear from the above work that interspecific hybrids can be obtained from reciprocal matings between *C. mixta* and *C. maxima.* However, the F_1 is male sterile, and cross-sterile, or nearly so, with each parent.

C. mixta x C. moschata. Because of the confusion in nomenclature, there is little precise evidence from the early breeders regarding this cross. Pangalo (1930) has reported *C. mixta* to be cross-sterile with *C. moschata.* Bohn (unpublished) reports that dissimilar results are obtained in reciprocal matings of the two species. When *C. mixta* is used as the male parent, the flowers that set have flat, abortive seeds with small embryos, or perhaps a few plump seeds. In the reciprocal mating the flowers

usually slough. If fruit set occurs, the fruit have only small flat seed with no, or poorly developed, embryos. During the summer of 1952 numerous pollinations were made using the variety Long Genoa Queen (*C. moschata*) as the pistillate parent and pollen from plants of a *C. mixta* seed collection from Mexico. Most of the flowers sloughed or the young ovary failed to develop properly and decayed. However, four fruits were obtained; one was parthenocarpic; one was poorly developed, with a few plump seeds; two were fairly well developed with a few plump seeds, some of them germinating within the fruit. In the reciprocal cross two fruits were obtained. The seeds were flat, numerous with small, poorly developed embryos. These data indicate that hybrids can be obtained between *C. mixta* and *C. moschata* but only if *C. moschata* is used as the pistillate parent.

When the plump seeds from the above successful matings were planted only two seedlings emerged and developed into mature plants. They were about intermediate between the two parental varieties with respect to the morphological characteristics of the vines and flowers. The fruits were oblong, oval (23 cm. long × 11 cm. wide), with orange skin color, mottled with dark green. The peduncle was somewhat similar to *C. moschata,* and not at all enlarged or corky like *C. mixta.* Male and female flowers were sparingly produced. Pollen fertility averaged 31 percent (scored as stainable pollen, from aceto-carmine counts). Comparable counts from *C. moschata* (L.G.Q.) the female parent, and *C. mixta,* the male parent were, 83% and 90% fertile pollen, respectively. Of 20 cells examined at 1M, the number of bivalents ranged from 11 to 18. Seventeen was the number most frequently found; the remainder were unpaired. Quadrivalents very rarely occurred. These cytological irregularities more than likely account for two-thirds of the pollen grains being sterile.

Four fruits were obtained from the F_1 plants; two by selfing and two by backcrossing to *C. moschata.* Of the selfed fruits, one contained a single seed, while the other had about two dozen seed, but they were slightly flat, the embryos not being fully developed. The fruit from backcrosses to the female parent (*C. moschata*) were devoid of seed, and were evidently parthenocarpic.

In a series of crosses, Rhodes (unpublished) obtained fruits from crosses between *C. mixta* and *C. moschata.* Using the mixta variety Green Striped Cushaw as the pistillate parent, and the moschata varieties, Kentucky Field and Butternut as staminate parents, he obtained several fruits from each mating with a few fertile seeds. Except for the Green Striped Cushaw markings on the fruit, the F_1 plants and fruit were remarkably similar to the moschata parent. The fertility of the F_1 plants was not determined.

Discussion. The evidence from morphology and the breeding tests suggests that *Cucurbita mixta* is separated from the annual cultivated species of the genus by clear-cut differences. Among the most obvious morphological differences are the hard, enlarged peduncle, and certain fruit characters, specifically the color of the flesh, and the collapsed placenta from which the seeds separate readily.

The data from interspecific matings of *Cucurbita mixta* with the other annual cultivated species indicate that sterility barriers have developed that for the most part prevent gene exchange between them.

Although there is good archeological material of cultivated cucurbitas from many sites in the New World, *C. mixta* does not appear until relatively late. The earliest material known is that from the Ocampo Caves, (Whitaker, Cutler and MacNeish, *in press*) tentatively dated as about 650 to 1050 A.D. *C. mixta* must have originated at a late date, perhaps as the result of hybridization of *C. maxima* and *C. moschata.* Its present area of distribution within the region in which *C. moschata* is common and north of the area of most *C. maxima* would account for its greater similarity to *C. moschata.*

There is no experimental work to indicate the relationship of *C. mixta* to the cultivated perennial, *C. ficifolia,* or to the wild perennial species of the genus.

SUMMARY

1. The nomenclature of *Cucurbita mixta* is reviewed, and a botanical description of the species based on the study of a number of varieties is given.

2. The varieties of the species are separated into three classes on the basis of seed type.

3. There is available sufficient evidence from hybridization experiments, to indicate that *C. mixta* is separated from the other annual species of *Cucurbita* by sterility barriers so effectively that its status as a good species cannot be questioned. The evidence from morphology leads to the same conclusion. Likewise, the results of interspecific hybridization suggest that *C. mixta* may be more closely related to *C. moschata* than to *C. pepo* or *C. maxima.* This is not surprising, since the geographical distribution of these two species points to the same conclusion.

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