TOWARD CONSISTENCY OF TAXONOMIC RANK
IN WILD/DOMESTICATED CUCURBITACEAE

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ABSTRACT

A taxonomic review and formal nomenclatural summaries are provided for certain species and species complexes of Citrullus, Cucumis, and Cucurbita that occur in the FNANM region in an attempt to apply consistent taxonomic ranking to those including both wild and closely related domesticated forms. Taken here as an archetypical starting point are examples in Cucurbita where two paired taxa are morphologically distinct but molecularly identical or near-identical, the domesticate with some certainty derived from the wild form — these are recognized as conspecific subspecies. Citrullus. Molecular studies show that the lineage including the cultivated watermelon (Citrullus lanatus sensu stricto) and the lineage including the citron melon (C. lanatus var. citroides) have a sister relationship but distinct haplotypes, and they apparently diverged from a common ancestor between 0.6–0.9 million years ago. The citron melon is appropriately recognized at specific rank — as Citrullus caffer Schrad. — rather than a variety of C. lanatus. At varietal rank, it is commonly identified as Citrullus lanatus var. citroides (L.H. Bailey) Mansf., but the correct name instead is Citrullus lanatus var. caffrorum (Alef.) Fosberg. A lectotype is designated for Citrullus caffer Schrad. and for Citrullus vulgaris var. citroides L.H. Bailey, and a photograph of each type is provided. The sister and probable progenitor of cultivated watermelons (subsp. lanatus) apparently is similar to west African wild types identified as C. lanatus subsp. mucosospermus. Cucumis. Cultivated forms of Cucumis melo (e.g., canteloupe) have long been known to be similar to morphologically distinct wild and feral races generally identified as C. melo subsp. agrestis and recent studies have confirmed their molecular identity or near-identity. The forms comprising subsp. melo are known strictly as cultivars and almost certainly have arisen from subsp. agrestis, thus their taxonomic treatment as conspecific subspecies is appropriate, although multiple independent domestications from within subsp. agrestis complicate the interpretation. The domesticated Cucumis sativus sensu stricto and the free-living C. hardwickii are closely related and perhaps justifiably interpreted as sister taxa. Cucumis sativus, however, is highly variable in morphology and some feral expressions intergrade with C. hardwickii, but the latter is isozymically distinct and its recognition at varietal rank seems appropriate, as C. sativus var. hardwickii. The relationship apparently is not one of wild progenitor/domesticate. Cucurbita. Closely related pairs of Cucurbita taxa (regarded as wild progenitor/domesticate) with identical haplotypes and hypothesized to have diverged in response to artificial selection are treated as conspecific subspecies — e.g., C. argyrosperma (1866, cultivated) includes C. sororia (1943, wild) as C. argyrosperma subsp. sororia. Cucurbita pepo sensu stricto comprises cultivars and landraces of southern Mexico and Guatemala and its wild ancestor has not been identified. Its haplotype differs from plants of the eastern USA and northeastern Mexico generally treated as C. pepo subsp. ovifera, from which a separate group of domesticates has arisen. Subsp. ovifera (nom. superfl. illeg.; the earlier subsp. texana is correct) is treated here at specific rank, as Cucurbita melopepo L., including var. melopepo (the domesticates), var. ozarkana (Decker-Walters) G.L. Nesom, comb. nov., var. texana (Scheele) G.L. Nesom, comb. nov., and var. fraterna (L.H. Bailey) G.L. Nesom, comb. nov. A lectotype is designated for C. melopepo L. and for C. pepo var. condensa L.H. Bailey. Subsp. texana (Scheele) G.L. Nesom, comb. nov., includes var. texana, var. ozarkana, and var. fraterna; subsp. melopepo includes var. melopepo.

KEY WORDS: Citrullus, Cucumis, Cucurbita, taxonomic rank, typification
In preparation of the taxonomic treatment of Cucurbitaceae for the Flora of North America North of Mexico, inconsistencies became apparent in concepts of species and infraspecific taxa, including cultivars and cultivar groups. Differences in biology and patterns of evolution, as well as degrees of subjectivity in judgement, make it difficult to apply a consistent system of taxonomic ranks across all genera. Nevertheless, whatever consistency can be attained is useful.

Emphasizing examples from the Cucurbitaceae, Jeffrey (1968) proposed a system for cultivated plants that incorporates a hierarchy of names — species, subspecioid, convar, provar, and cultivar. Similarly, Grebenscikov (1953) presented a detailed hierarchical classification for *Cucumis* cultivars, but mostly, even in the Cucurbitaceae, application of horticultural names seems to have remained somewhat idiosyncratic from one genus to the next. The current review deals primarily with names and ranks that are applicable at levels where both wild plants and horticultural taxa are involved in the classification.

Particularly challenging for classification are instances where a wild progenitor/domesticated derivative relationship (e.g., see Crawford 2010) is hypothesized to exist as a result of artificial selection. Taken here as an archetypical starting point, an incipient convention, for consistency are several examples in *Cucurbita* (see details below) where two paired taxa are morphologically distinct but molecularly identical or near-identical, the domesticate with some certainty derived from the wild form. These are recognized as conspecific subspecies.

1. **CITRULLUS**

Molecular studies have shown that the cultivated watermelon, *Citrullus lanatus* (Thunb.) Matsum. & Nakai sensu stricto, and the citron melon, generally identified as *C. lanatus* var. *citroides* (Bailey) Mansf., represent closely related but distinct lineages (Navot & Zamir 1987; Jarret & Newman 2000; Levi et al. 2001; Dane & Lang 2004; Dane et al. 2004; Dane & Liu 2007; Mujaju et al. 2010). The two taxa have distinct haplotypes and appear to have evolved from a common ancestor perhaps closely similar to *C. ecirrhosus* Cogn., with which they share several substitutions and indels at non-coding cpDNA regions (Dane & Lang 2004). This evolutionary divergence is estimated to have occurred at least 0.8–0.9 million years ago (Dane & Lang 2004) or at least 0.6 million years ago Dane & Liu 2007).

In *Citrullus* as a whole, which includes 5 species (as interpreted here), two main clades are evident: (a) *C. colocynthis* (L.) Schrad. (the bitter apple) and (b) a lineage in which *C. rehmii* De Winter is sister to a clade comprising *C. ecirrhosus* and *C. lanatus* sensu lato (Dane & Lang 2004), the latter regarded here as *C. lanatus* sensu stricto plus var. *citroides* (see comments below). An earlier ITS analysis of *Citrullus* phylogeny, however, placed *C. rehmii* as sister to *C. lanatus* sensu lato (Jarret & Newman 2000), and Dane et al. (2004) found that *C. rehmii* showed almost the same haplotype as *C. lanatus* var. *citroides* with the exception of a unique insertion at a cpSSR site. *Citrullus rehmii* (annual) and *C. ecirrhosus* (perennial) are endemic to the Kalahari Desert region of Namibia.

*Citrullus lanatus* sensu stricto — domesticated sweet melons and the egusi-type melons.

*Citrullus lanatus* sensu stricto includes two morphological types — subsp. *lanatus* (the cultivated, dessert watermelons, including red sweet watermelon; Fig. 5) and subsp. *mucospermus* Fursa (the egusi-type melons, including wild, semi-cultivated, and cultivated forms in west Africa, which are grown primarily for their large, soft, oil- and protein-rich seeds). The egusi melons are relatively small and have white, bitter flesh similar to the citron melons, but the egusi/citron similarities apparently are plesiomorphic.
The cultivated watermelon and the egusi-type melon have the same cpDNA haplotype. Both are reported to lack molecular variation at cpDNA regions (Dane & Lang 2004) and also have a narrow genetic base in other kinds of assessments (e.g., Levi et al. 2001; Levi & Thomas 2005). Mujaju et al. (2010), however, reported that cultivated sweet melons in Zimbabwe are as diverse molecularly as the citron melons; Nimmakayala et al. (2010) identified 583 AFLP bands that are polymorphic within var. lanatus; Levi et al. (2004) found high polymorphisms among watermelon heirloom cultivars using inter-simple sequence repeat (ISSR) and amplified fragment-length polymorphism (AFLP) markers.

**Citrus lanatus var. citroides — citron melons and tsamma melons.**

Fursa (1972) recognized another entity closely similar to var. citroides — C. lanatus var. caffer (see nomenclature below), the wild “tsamma” melon of the Kalahari Desert. cpDNA studies, however, have shown that when the citron/tsamma melons are considered together, three haplotypes exist among them (Dane & Liu 2007). These three entities apparently have not been unambiguously recognized by formal nomenclature, or at least the genetic affinities of names potentially associated with these haplotypes are not known. The ancestral citron/tsamma haplotype is known from Swaziland and South Africa; each of the other two ranges across southern Africa. A number of distinct landraces that are cultivated in Kalahari region (including the tsamma melons) may represent early forms of domestication, as also suggested by Maggs-Kolling et al. (2000).

**Two species rather than one.**

The domesticated watermelon and the primarily wild-type egusi melon, which are identical in cpDNA haplotype and essentially so in other molecular features, are recognized here as conspecific subspecies within *Citrus lanatus*. The citron/tsamma melon, divergent both morphologically and molecularly from *C. lanatus*, is recognized as a separate species.

At specific rank, the citron/tsamma melons are correctly identified as *Citrus caffer* Schrad. ex Eckt. & Zeyh., 1834; if at varietal rank, then as *C. lanatus* var. caffrorum (Alef.) Fosberg. The epithet “caffrorum” at varietal rank was first validly published by Alefeld in 1866 as “*Citrus vulgaris* var. caffrorum,” preceding Bailey’s proposal of “*Citrus vulgaris* var. citroides” in 1930.

In the USA, the two species can be distinguished by the following contrasts.

1. Leaf blades ovate to lanceolate-ovate or ovate-triangular in outline, mostly 8–20 cm; fruits globose to oblong-ellipsoid, 12–35 cm (or more) in diam., rind hard but not durable, flesh juicy, red, yellow, or greenish, sweet; seeds commonly black .......................................................... **Citrus lanatus**

1. Leaf blades ovate in outline, 3–10(–14) cm; fruits globose to globose-ovoid, 14–25 cm in diam., rind hard and durable, flesh dry, whitish, bitter; seeds tan to brown or reddish ........ **Citrus caffer**

Without mature fruits, the distinction may be difficult. Leaf shape seems generally to separate them, but leaves overlap in size and shape. Stems are villous in both species. Habitat is a good clue, since *C. lanatus* is almost always found where seeds were recently discarded by people and the plants rarely if ever form reproductive populations. *Citrus caffer* is free-living and occurs in a wider range of habitats.

Several African accessions morphologically identified as *Citrus caffer* were found to have the cpDNA haplotype of *C. lanatus* (Dane et al. 2004; Mujaju et al. 2010), possibly as a result of introgression, and Levi et al. (2001) found four plants of *C. lanatus* with genes perhaps introgressed from *C. caffer* (three from Africa, one from China). The citron melon also has been observed to form spontaneous hybrids with *C. colocynthis* (bitter apple) — in the USA (Fulks et al. 1979), in India (Singh 1978), and in Australia (Herrington et al. 1986).

### a. **SUBSPECIES LANATUS**

*Cucurbita citrullus* L., Sp. Pl. 2: 1010. 1753. *Anguria citrullus* (L.) Mill., Gard. Dict. (ed. 8). 1768. *Cucumis citrullus* (L.) Ser. in DC., Prodr. 3: 301. 1828. *Citrullus citrullus* (L.) H. Karsten, Deut. Fl. [Pharm. med. Bot.] 889. 1882. *Colocynthis citrullus* (L.) Kuntze, Rev. Gen. Pl. 1: 256. 1891. **TYPE:** [Italy.] “Apulia, Calabria, Sicilia” Not designated (fide Jarvis 2008). As noted by Jarvis, Jeffrey (1967) designated as lectotype: LINN -1151.5 (digital image!), but this was not original material for the name. Recognizing this, Jeffrey later noted (1980, p. 791) that “This is perhaps better to be regarded as a neotype, since although annotated as this species by Linnaeus, it may not have been studied by him prior to the writing of the ‘Species Plantarum.’” Jarvis, however, observed that because original material is in existence, designation of LINN-1151.5 as a neotype would be contrary to ICBN Art. 9.11.


Authorities of names in *Citrullus* proposed in Ecklon & Zeyher's Enumeratio Plantarum Africæ Australis Extratropicae sometimes have been cited as "Schrader ex Ecklon & Zeyher" but the author of the whole Cucurbitaceae treatment (pp. 275–280) is explicitly noted (p. 275) to be H.A. Schrader. Morphological descriptions were provided for *Citrullus* (the genus) and *Citrullus amarus*, thus the authority for those is correctly cited as "Schrad. in Eckl. & Zeyh." or simply as "Schrad." *Citrullus vulgaris* and *Citrullus caffer* were not validly published until 1838 in a posthumous manuscript, with the authority from that publication also as "Schrad." or "Schrad. in Schlecht." (Linnaea vol. 38, see notes below).

### b. **SUBSPECIES MUCOCOSPERMUS**


Schrader first published the name *Citrullus caffer* in a seed catalogue (Ind. Sem. Hort. Goetting., 2. 1834), indicating that the name was based on "*Cucurbita caffra* Eckl." from another 1834 seed catalogue (Coll. Sem. Capensium), with the implication that original
material should be sought among collections by Ecklon or Ecklon & Zeyher. A still later entry by Schrader (in Ecklon & Zeyher's Enum. Pl. Afric. Austral. 2: 279. 1836), however, cited both names from 1834, implying that the concept of original material would be broadened to include specimens seen by Schrader, especially since the name is formally credited only to him.

The entry in Index Seminum Horti Academicici Gottingensis, 1834: "Citrullus caffer Schrad. Synonym. est: Cucurbita caffra Eckl. coll. sem. capensium. Plura de hac aliiisque Cucurbitaeis alio loco." This seed catalogue entry was quoted in Linnaea 10 (Litteratur-Bericht 1835 & 1836): 109. 1836. Provided by the Editor, D.F.L. von Schlechtendal). It seems that Schrader in 1834 was acknowledging that his use of the epithet was based on the slightly earlier seed catalogue publication by Ecklon [& Zeyher] of Cucurbita caffra (see below), thus implying that the name in Citrullus would be correctly cited as C. caffer (Eckl.) Schrad., 1834. This interpretation also is indicated by the 1836 entry in Enum. Pl. Afric. Austral. — "ind. sem. hort. Goetting. 1834" was cited as the place of publication of Citrullus caffer, and immediately following that, the citation continues with “Cucurbita caffra Eckl. et Zeyh. coll. sem. 1834.”

Peter Goldblatt (pers. comm.) notes that he does not know about the "sem. capensium" catalogue but that "Ecklon and Zeyher distributed herbarium collections and seeds under names they often invented or had in mind to publish. Quite a few of their names remain 'in manuscript'.". The Goettingen seed catalogue provided neither a description nor specimen citation for Citrullus caffer, and it is assumed here that the entry in the "Capensium" catalogue was similar.

In any case, neither of the seed catalogue entries for Citrullus caffer in 1834 nor the entry in 1836 provided a description and the name was not validly published until 1838. Shortly after Schrader's death in 1836, a brief biography — with various incomplete taxonomic manuscripts appended, including one on Cucurbitaceae — was published in Linnaea, presumably by the editor Schlechtendal (Reliquiae Schraderianae. Linnaea 38: 353–476. 1838; Cucurbitaceae, pp. 401–423). There, a morphological description of C. caffer was provided. Reliquiae Schraderianae also was published as a separate in 1838 (see Google Books).

In the 1836 entry for Citrullus caffer, the provenance was cited as "In cultis provinciarum ‘Uitenhage et Albany’ et in terra ‘Kafferland.’ Jan. Incolis: ‘Kafferwatermelon.’" "Caffraria (Cafferland and variants) was the eastern part of 'Cape Colony' and is now Eastern Cape Province. Uitenhage was the first town there and usually meant in that district. Albany was one of magisterial districts in past time (of Cape of Good Hope), when it was a province of South Africa and no longer has any political meaning" (Peter Goldblatt, pers. comm., February 2011).

In treating this entity as "var. caffrorum" within Citrullus vulgaris, Alefeld (1866) cited Citrullus caffrorum Schrader and Cucurbita caffra Eckl. & Zeyh. immediately following his proposal of the varietal name, which presumably was intended to be homotypic with both of the latter names.

The epithet “caffrorum,” however, appeared in Schrader’s 1838 entry (Linnaea 12: 413. 1838) for Citrullus caffer — as “2. Citrullus (C. caffrorum) caffer.” — and it is not clear why Schrader included the parenthetical element, especially since immediately following in the entry was the citation “Cucurbita caffra Eckl. et Zeyh. Coll. sem. 1833 seq. Verz. 1833.” It might appear that Schrader was attempting to correct his earlier citation of the Eckl. & Zeyh. name from an 1834 seed catalog, with the intention of attributing authorship of the basionym to Ecklon & Zeyher, again indicating the correct name to be “Citrullus caffer (Eckl. & Zeyh.) Schrad.. 1834.” In any case, it appears that “caffrorum” as an epithet at varietal rank was first validly published by Alefeld in 1866 (as also explicitly interpreted by Fosberg, who noted “Var. caffrorum Alefeld here lectotypified by Cucurbita caffra Eckl.
Zeyher seems to be the earliest varietal epithet for the common red-fleshed cultivated watermelon.”). Fosberg’s interpretation of the biological identity this entity was mistaken, as these names refer to the citron melon, but at varietal rank within Citrullus lanatus, the correct name for the citron melon is C. lanatus var. caffrorum (Alef.) Fosberg.

Citrullus vulgaris var. citroides L.H. Bailey, Hortus (ed. 1), 152. 1930. Citrullus lanatus var. citroides (L.H. Bailey) Mansf., Kulturpfl., Beiheft 2 [Verzeichnis], 421. 1959. Citrullus colocynthis var. citroides (L.H. Bailey) Millan, Darwiniana 14: 697. 1969. LECTOTYPE (designated here): [USA, Colorado.] "Trade or Label Name: Citron," Dreer 536, cultivated at Ithaca, N.Y., [collected, presumably, by L.H. Bailey] 20 Sep 1930 (BH digital image!; Fig. 4). This label also is annotated at the top with "photo." Packet attached. The protologue has only this: “Var. citroides. CITRON OR PRESERVING MELON. Fr. small, with white hard flesh, used only for preserving; seeds not marked or marbled (as they usually are in watermelon).”

The original publication of var. citroides has been generally cited as “Gentes Herb. 2: 186. 1930,” but in that publication Bailey provided neither a description nor type citation, noting (p. 186) that “the var. was included in a brief account of Citrullus for Hortus, and [the] type has now been plated and the page released for printing although the present paper will be actually published in advance of that book.”

Several sheets at BH are possibly interpreted as original material of var. citroides. The label heading of the 1889 specimen is "Garden Herbarium of Cornell University Experiment Station;" the others have "Herbarium of L. H. Bailey."

1. Identified as "Citrullus vulgaris Schrad.," Trade or Label Name: Colorado Citron, University Garden: Sept 15, 1889.

2. Trade or Label Name: Citron, Dreer 536, Cultivated at Ithaca, N.Y., Sown May 6, [coll.] Sept 15, 1930.

3. Trade or Label Name: Citron, Dreer 536, Cultivated at Ithaca, N.Y., [coll.] Sept 20, 1930, This label also is annotated at the top with "photo." Packet attached.


5. Trade or Label Name: Colorado Preserving Citron, Dreer 536, [coll.] Sept 22, 1938, Ithaca.

Seeds from which collections 2-5 were grown apparently were made as one gathering either by Henry A. Dreer (1818-1873), who operated a seedhouse and nursery in Philadelphia, or his son, William F. Dreer (1849-1918), who ran a large nursery in Riverton, New Jersey, and left an annual endowment to the Cornell Horticulture Department. At least one other specimen grown from seeds from H.A. Dreer is in the BH herbarium (see Cucurbita notes below). It is possible that collection 1 was grown from the same lot, as both it and collection 5 are noted to be the "Colorado Citron." In any case, collection 4 is the only one identified as "var. citroides," but neither it nor collection 5 was made until after publication of the name. Presumably collections 2 and 3 were those that Bailey would have regarded as type material, and collection 3 is designated here as the lectotype. With his long-standing interest in Cucurbitaceae, Bailey himself probably made the herbarium collections; it apparently is his handwriting on the labels.

Index indicates that specimens of K.I. Pangalo are in the herbarium of the N.I. Vavilov Institute of Plant Industry (WIR).

In a note below the entry for *Citrullus vulgaris* var. *citroides*, Bailey (1930, p. 186), observed the following: “I now find that the watermelon has been newly studied in Russia and the papers are just at hand after my account is ready (Bulletin No. 3 of Applied Botany and New Cultures, Leningrad, 1930). Perhaps the species, *Citrullus colocynthis*, there proposed by K.I. Pangalo, includes the garden preserving citron here named *Citrullus vulgaris* var. *citroides*; that new species includes “citron forage watermelons,” growing of their own accord in the southern part of Soviet Russia something like a weed, nobody cultivating them, recently utilized as forage plants. The illustration of the fruits of these spontaneous melons shows some of them to be externally like the American garden citron melon and others very different from anything I have seen. It will be interesting to determine, if possible, whether the preserving citrons originated from Russian or Asian stocks. The name *colocynthis* is proposed as an independent species of *Citrullus*, not as a var. of *Citrullus vulgaris*, and therefore it and var. *citroides* are not in nomenclatorial conflict, even though we may find (as I suspect) that the American and Russian plants are equivalent for purposes of systematic diagnosis.”

Citron melons have not been commonly documented as naturalized in the USA, but they appear to be scattered as weeds in pinelands, sandy fields, cotton fields, and orange groves, and along roadbanks, railroad banks and tracks, and roadways and other disturbed sites; known from collections and literature from Arizona, California, Florida, New Mexico, Nevada, and Texas (Fulks et al. 1979; Grichar et al. 2001; Stephens 2003; Hall et al. 2004). In addition to citron melon, vernacular names for *Citrullus caffer* in English-speaking countries are red-seeded citron, preserving melon, jam melon, and stock melon.

**Literature Cited (introductory comments and Citrullus)**


2. CUCUMIS

Only two formal infraspecific taxa within Cucumis melo were recognized by Kirkbride (1993), following an earlier informal proposal by Jeffrey (1980a) — subsp. melo and subsp. agrestis. Grebenscikov (1953) recognized C. melo and C. agrestis at specific rank and arranged many other infraspecific taxa in a hierarchical system of horticultural names. Kirkbride also suggested that other variants described within C. melo should be treated with horticultural names, and classification of melons into two major lineages has been generally supported by molecular phylogenies (e.g., Stepansky et al. 1999; Decker-Walters et al. 2002). **Subsp. melo** comprises the large-fruited, sweet
“dessert” melons of commerce (cantaloupe, honeydew, and muskmelon, and the snake melon/cucumber melon) — var. melo (including var. cantalupo), var. inodorus, and var. flexuosus — originating mostly in western Asia and Europe, all known strictly as cultivars. Molecular resolution between var. cantalupo and var. inodorus is slight (Staub et al. 1997; Silberstein et al. 1999; Stepansky et al. 1999), despite significant differences between them in morphology and physiology.

Subsp. agrestis comprises a group of cultivars and landraces, as well as free-living wild forms and feral forms, essentially the generally smaller, mostly non-sweet, and morphologically more variable types, which originated mostly in India and southeast Asia.

The two taxa are distinguished by these contrasts.

1. Hypanthium or youngest fruits pilose to lanate with spreading hairs; stems glabrous sparsely villous; fruit greater than 10 cm in diam., in cultivated forms commonly fragrant and sweet

.................................................. ................................................. Cucumis melo subsp. melo

1. Hypanthium and youngest fruits retrorsely or antrorsely sericeous with short appressed hairs; stems hispid with retrorse hairs; fruit 2.5–5 cm in diam., mostly not fragrant and not sweet, but with numerous exceptions .............................................. Cucumis melo subsp. agrestis

Statements that wild forms exist in both subspecies (e.g., Jeffrey 1980b; Zohary & Hopf 1983; Stepansky et al. 1999; Pitrat et al. 2000) appear to have been based on taxonomic arrangements that regard the Himalayan entities Cucumis trigonus Boiss. and C. callosus (Roettl.) Cogn. & Harms as synonyms of C. melo subsp. melo. Parthasarathy & Sambandam (1980) found that crosses between C. melo (presumably subsp. melo) and plants identifiable as C. callosus resulted in abundant and fully fertile seeds and F1s with normal meiosis; they concluded that C. callosus (with C. trigonus as a synonym) does not warrant separate species status and is "nothing but a progenitor of C. melo."

Jeffrey (1980b) noted that Cucumis callosus is a synonym (a "tropical wild variant") of Cucumis melo, while Chakravarthy (1982) treated C. callosus as a distinct species. Verma and Pant (1985) treated C. trigonus as a synonym of C. callosus, but Matthew (1983) regarded C. trigonus as a distinct species of peninsular and western India. Earlier, Clarke (1879) treated C. melo var. agrestis as a synonym of C. trigonus and noted that C. melo is "perhaps the cultivated form of C. trigonus." Nazimuddin and Naqvi (1984) regarded C. callosus and C. trigonus both as synonyms of C. melo var. agrestis. Diversity and ambiguity of interpretation are widespread.

Recent study by Sebastian et al. (2010) indicates that both Cucumis trigonus and C. callosus are morphologically distinct species (morphology not discussed in their report) but with DNA sequences “nearly identical to those of C. melo.” They observed (p. 1472) that C. trigonus and C. callosus “likely represent the wild progenitor of cultivated melon.” Their cladogram, however, appears to show samples of subsp. agrestis and subsp. melo in a sister relationship, more closely related to each other than to C. trigonus and C. callosus. Perhaps a more accurate summary of their portrayal would be that the wild progenitor of cultivated melon (C. melo subsp. melo) is equally as likely to be represented by C. trigonus and C. callosus as by free-living forms of subsp. agrestis.

With acceptance of Cucumis trigonus and C. callosus as distinct species, patterns of diversity in landraces of subsp. agrestis need to be reexamined in terms of taxonomic recognition and rank. Landraces of Cucumis melo in south and eastern Asia (including India) show a high level of variation isozymes, DNA, and morphology (Sujatha et al. 1991; Akashi et al. 2002; Dhillon et al. 2007; Tanaka et al. 2007; Dwivedi et al. 2010) and some of them might ultimately be recognized at higher rank. As best I can infer, if C. trigonus and C. callosus are accepted as distinct species, it appears that no wild forms are represented within subsp. melo. Wild forms and apparently primitive expressions exist in several lineages of subsp. agrestis.
Taxonomic rank of subsp. agrestis.

If recognized at specific rank in order to emphasize an evolutionary and taxonomic status coordinate with that of Cucumis trigonus and C. callosus, the correct name of subsp. agrestis would be Cucumis dudaim L. (see below). It seems likely, however, that cultivars of subsp. melo have been derived from one expression or another of subsp. agrestis, and treatment of the two as a conspecific subspecies parallels that of wild progenitor/domesticated derivative pairs in Cucurbita.

On the other hand, the molecular identity (or near-identity) of subsp. agrestis and subsp. melo apparently is matched in various other pairs/groups of accepted wild species within Cucumis (Ghebretinsae et al. 2007; Schuman et al. 2007; Renner et al. 2007), thus the biological rationale for assigning rank is not exactly analogous to Cucurbita. Further, sterility barriers in Cucumis exist only between species groups rather than species — Jeffrey (1980a) formally divided Cucumis into five cross-sterile species groups within two subgenera.

The occurrence of sweet-fruited genotypes at least in vars. agrestis and conomon of subsp. agrestis indicates that multiple domestications have occurred in parallel with domestication in subsp. melo (Jeffrey 1980a; Stepansky et al. 1999; Pitrat et al. 2000; Sebastian et al. 2010). Stepansky et al. (1999) suggested that occasional occurrence of sweet agrestis fruits also may have resulted from hybridization between wild and feral genotypes with sweet or vegetable landraces. Parallel trends among entities in the two subspecies also exist in vestiture, fruit morphology, duration, and sexuality. Cucumis melo var. flexuosus is variable in hypanthium vestiture but molecular data place it within subsp. melo (Silberstein et al. 1999; Stepansky et al. 1999; López-Sesé et al. 2003). Further sampling will be necessary to assess the potential pattern of independent domestications.

Status of Cucumis melo var. texanus.

A landrace of Cucumis melo subsp. agrestis — C. melo var. texanus Naud. — is widespread and relatively abundant in the southeastern USA (Nesom 2011 and references therein). Morphological and molecular data (Decker-Walters et al. 2002) indicate that var. texanus has differentiated there in situ but shows the greatest genetic affinities to var. chito and to cultivars from Eastern Asia, including var. conomon. Stepansky et al. (1999) found var. conomon to be strongly differentiated from other varieties within subsp. agrestis (vars. agrestis, chito, dudaim, and momordica). Relationships among the latter four taxa are less strongly resolved on the basis of morphological and molecular data.

Among possible scenarios for the origin of var. texanus in the Western Hemisphere (see Decker-Walters et al. 2002) is that its progenitor was brought in by humans intentionally (perhaps by Asian immigrants) or unintentionally (as seeds mixed with those of other introduced crops). Given the distinctive genetic differentiation of var. texanus, the time of its introduction likely was pre-Columbian. Decker-Walters et al. also noted (p. 194) that "The relatively uniform morphological and genetic character of wild populations in North America supports a single origin of introduction to that continent." Unlike the situation in Cucurbita melopepo (see below) of the USA, there appears to be little introgression from cultivars of Cucumis melo into the wild populations of var. texanus.

Plants identified as Cucumis melo var. dudaim, a modern and independent introduction to North America, are encountered outside of cultivation in Arizona and California along waterways and irrigation canals, fields, and roadsides.

Decker-Walters et al. (2002) compared wild North American populations (var. texanus) of Cucumis melo with a range of samples of var. dudaim, var. chito, small-fruited Old World populations, and a small set of other varieties and recorded detailed measurements of morphological
features of vars. *texanus*, *dudaim*, and *chito*. The key below draws from their observations; measurements are given as an approximate average ± one standard deviation

1. Plants monoecious; fruit 40 ± 5 mm wide, 49 ± 11 mm long, rind yellow, striped; flesh bitter; seeds 4.6 ± 0.4 mm long; hypanthial hairs 0.8 ± 0.1 mm long .............................. *Cucumis melo* var. *texanus*

1. Plants andromonoecious; fruit 61 ± 9 mm wide, 67 ± 17 mm long, rind yellow or orange to red, striped, streaked, or speckled; flesh commonly sweet; seeds 7.2 ± 0.7 mm long; hypanthial hairs 1.7 ± 0.4 mm long.

2. Rind with red to orange or brown stripes on a yellow to orange background  .. *Cucumis melo* var. *dudaim*

2. Rind usually with stripes, but sometimes streaked or speckled, on a yellow background

(Commonly recognized infraspecific taxa/cultivar groups of *Cucumis melo*.)

Wide extremes of variation and horticultural selections exist within *Cucumis melo*, especially as based on fruit characters (e.g., size, shape, surface features, color, texture, taste, composition). The species includes feral, wild, and cultivated forms, including “dessert” melons, as well as non-sweet forms that are consumed raw, pickled, or cooked. This has led to a proliferation of names for the variants, and various systems of infraspecific classification have been proposed.

A widely used system proposed by Naudin (1859), dividing *Cucumis melo* into a single wild variety — *C. melo* var. *agrestis*, and six cultivated ones, *cantalupensis*, *inodorus*, *conomon*, *dudaim*, *flexuosus* and *momordica* — has been variously modified and simplified (e.g., Munger and Robinson 1991) as well as extended into a detailed hierarchical system (Grebenscikov 1953; see comments by Hammer et al. 1986). An excellent overview of infraspecific nomenclature in *C. melo* was provided by Pitrat et al. (2000; largely repeated by Burger et al. 2010 but “adapted to the International Code of Nomenclature for Cultivated Plants”), who proposed a similar alternative, with 5 cultivar groups in subsp. *agrestis*, 11 cultivar groups in subsp. *melo*, but molecular data have not supported their apportionment of the groups among the two subspecies. Many of these names may be encountered for plants potentially found outside of cultivation, and a simplified system more similar to the earlier ones is summarized here, followed below by formal nomenclatural summaries.

**SUBSPECIES MELO.**

a. *Cucumis melo* var. *melo*. Formally includes the more commonly recognized var. *cantalupo*.

a. *Cucumis melo* var. *cantalupo*. Asia, Africa; fruits aromatic, large to medium-large, round slightly ovoid or depressed-globose, moderately to strongly ribbed, rind smooth or warty, whitish to yellow, orange, greenish, or nearly black, flesh orange or green, sweet, dessert melons; usually andromonoecious. Examples: Charentais, Prescott Fond Blanc.

b. *Cucumis melo* var. *reticulatus*. Europe, western Asia, North America, South America, Japan; fruits aromatic, large to medium-large, round to slightly ovoid, ribbed or unribbed, rind reticulate to finely netted, variable in colour, flesh orange or green, sweet, dessert melons; andromonoecious. Pitrat et al.
(2000) equated var. reticulatus with cultivars "mainly developed this century in the U.S.A." (as in the brief description above and as cited in cultivar names following) but the neotype or lectotype presumably would be chosen from among heirloom races in cultivation in Europe before 1828 (see comments below). In the original description by Seringe, "Melon des Carmes" was noted as an example and the currently available Noir des Carmes apparently is similar. Examples of USA cultivars: Rocky Ford, Top Mark, Netted Gem, Bender, Hearts of Gold, Hales Best.

c. Cucumis melo var. inodorus. Asia, Spain; fruits non-aromatic, large, round to ellipsoid, non-climacteric and long-storing, rind thick, smooth, wrinkled, or warty, white to yellow or green, flesh white, dessert melons; usually andromonoecious. Examples: honeydew, winter melon, muskmelon, casaba.

d. Cucumis melo var. flexuosus. Middle East, Asia, northern Africa; fruits very elongated, rind light green to green-striped, ribbed or wrinkled, flesh white, non-sweet, eaten immature as cucumbers or pickled; usually monoecious. Examples: snake cucumber, snake melon, cucumber melon, Armenian cucumber.

**SUBSPECIES AGRESTIS.**

e. Cucumis melo var. agrestis. Africa and Asia as free-living forms; fruits very small (less than 5 cm), inedible with very thin mesocarp and small seeds; monoecious.

f. Cucumis melo var. chito. Asia, or reportedly of American feral origin; fruits aromatic, small, plum-size, rind yellow, flesh white, used as pickles; monoecious. Combined with var. dudaim by some (e.g., Munger & Robinson 1991; Robinson & Decker-Walters 1997) but found to be distinct by Pitrat et al. (2000), Decker-Walters (2002), and others. "This type seems to occur mainly in Central America as a feral and is not really cultivated. It was probably introduced by African slaves to that region" (Pitrat et al. 2000, p. 35). Examples: mango melon, vine peach, glass melon.

g. Cucumis melo var. conomon. Eastern Asia cultivars; fruits smooth, white-fleshed, with thin rinds and often eaten as pickles; andromonoecious. Sometimes said to include var. acidulus Naud., which has orange rind. Examples: oriental pickling melon, Freeman's cucumber, Shiro-Uri.

h. Cucumis melo var. texanus. North America as free-living populations; fruits usually not aromatic, small, rind smooth, yellow, flesh white, bitter; monoecious.

i. Cucumis melo var. dudaim. Persia, grown as ornamental (for the aroma), sometimes for edible fruits; fruits aromatic, small, red to orange or brown striped; andromonoecious. Examples: dudaim melon, Queen Anne's pocket melon, smellmelon, pomegranate melon, plum granny.

j. Cucumis melo var. chate. Northern Africa, western and central Asia; fruits medium-size, round to elongate, ribbed, light to dark green, flesh white to light orange, eaten raw or pickled; monoecious or sometimes andromonoecious. Example: Carosello.

k. Cucumis melo var. momordica. India; fruits not aromatic, large, non-sweet, with thin rind splitting at maturity, flesh mealy-white, bland; monoecious. Examples: Indian snapmelon, phoot.

**Formal nomenclature for commonly recognized infraspecific taxa of Cucumis melo.**

Nomenclatural summaries are provided here for a selection of the most generally used names relating to the Cucumis melo complex. Details of nomenclature for other names, which number more than 500, can be found in Kirkbride's monograph (1993).

The lectotype has no fruit but the expression of Cucumis melo that Linnaeus had in mind can be inferred. Bauhin and Cherler's Historia Plantarum Universalis (vol. 2, 1651), cited by Linnaeus in the protologue, illustrates a plant (p. 242; shown here in Fig. 6) with similar fruits. The accompanying description refers to fruits that are 'torose' (apparently the "torulose" = warty condition described by Linnaeus), channeled, reticulate, and green-colored. Entries in Hortus Cliffortianus (1737) and van Royen's Florae Leydensis (1740) both refer to Robert Morison's Plantarum Historiae Universalis (1680, Vol. 2), which includes a drawing (tab. 6, fig. 4; shown here in Fig. 7). The illustrated fruits are channeled and show what appears to be a shallowly warty rind. They are very similar to fruits of plants later described by Seringe as Cucumis melo var. cantalupo (see notes above and below), especially modern domesticates such as Charentais and Noir des Carmes.

a. SUBSPECIES MELO


None of the nomenclatural proposals listed above cited a specimen, but all probably referred to the same entity and it seems likely that all of them past 1828 had Seringe's description in mind. Cucumis cantalupo Haberle ex Reichenb. of 1831 (without an attribution to Seringe) preceded C. cantalupensis Haberle ex M. Roem. of 1846, which was superfluous. At varietal rank within C. melo, Naudin's proposal of 1859 was superfluous.

Cucumis melo var. reticulatus Ser. in DC., Prodr. 3: 300. 1828. TYPE: Apparently not designated. No specimen was cited in the Prodromus entry by Seringe. "Fructu rotundato vel oblongo, cortice reticulato griseo." Fruits were described as large to medium in size, and "M.[elon] des Carmes" was included among examples.

Var. reticulatus is probably correctly considered a formal synonym of Cucumis melo sensu stricto (var. melo).

An earlier proposal by Jacquin (**Cucumis melo inodorus** Jacq., Monogr. melon, 173. 1832) provided an infraspecific name for a "group" of melons composed of several "varieties," thus the epithet was proposed without a rank and the valid varietal name was only later established by Naudin. Protologue of Jacquin: “Nous avons cru devoir donner à ce groupe le nom de melons inodores, parce que toutes les variétés qui le composent sont absolument dépourvues d’arome; excepté quelques-unes qui, plus anciennement cultivées sous de climats de l’Europe, exhalent une légère odeur, mais qui est, ainsi que nous l’avons dit, une modification résultant de notre nature et des procédés que nous employons pour les cultiver.” A later listing of **Cucumis melo var. inodorus** by C.O. Harz (Landw. Samenk. 2: 783. 1885) was superfluous if it indeed was intended as a new nomenclatural proposal.

**b. SUBSPECIES AGRESTIS** (Naud.) Pangalo


**Cucumis melo var. chate** (Hasselq.) Sageret, Mém. Agric. Soc. Roy. Centr. Agric. 58: 488. 1825. **Cucumis chate** Hasselq., Iter Palaest., 491. 1757. **Cucumis melo** subsp. chate (Hasselq.) Hassib, Cucurbit. Egypt 133. 1938. **NEOTYPE:** (Jeffrey 1980c, fide Kirkbride 1993): Plant cultivated at Uppsala, Sweden, presumably from Egypt. Herb. LINN 1152.11, digital image!). Kirkbride (1993) noted that Jeffrey cited the Species Plantarum number (1152/5) rather than the LINN number (1152.11). The protologue: “Terra praegnans post inundationem Nili circa Cairo, nec in ullo alio loco universi Ägypti colitur, neque alius sert solum.”


Nesom: Nomenclature in domesticated/wild Cucurbitaceae


_Cucumis melo_ var. _momordica_ (Roxb.) Duthie & Fuller, Field & Garden Crops 2: 50, t. 49. 1883. _Cucumis momordica_ Roxb., Fl. Ind. 3: 720. 1832. **NEOTYPE** (Kirkbride 1993, p. 114): Roxburgh, Icones Roxburghianae, t. 456. 1964. India; described from cultivation from Tanjore country and southern parts of Karmatik.


**The wild progenitor of _Cucumis sativus_?**

Features and properties of the free-living _Cucumis hardwickii_ Royle have been reported in numerous studies (e.g., Horst & Lower 1978; Puchalski et al. 1978; Kupper & Staub 1988; Bisht et al. 2004; Choudhary & Singh 2010). It is obviously closely related to _C. sativus_ L., the two — alone in the genus — sharing the derived chromosome number of 2n = 14, and _C. hardwickii_ sometimes has been posited as the ancestor of _C. sativus_ (see Sebastian et al. 2010). The geographic range of _C. hardwickii_ is the northwestern Himalayas southward into the Eastern and Western Ghats and the central Plateau region of India.

In a series of reciprocal crosses among cucumber, muskmelon, and 19 wild species of _Cucumis_, Robinson and Kowalewski (1978) found that the only species that successfully crossed with _C. sativus_ was _C. hardwickii_ — producing fully fertile _F_1s — and they regarded the two as conspecific entities (they suggested the rank of subspecies but did not make a formal nomenclatural proposal). Puchalski and Robinson (1990) and others also have treated the two taxa as conspecific varieties.

Among plants identified as _Cucumis hardwickii_, Bisht et al. (2004) found a high diversity for morphological as well as RAPD markers, and gene flow between _C. hardwickii_ and _C. sativus_ was indicated by the presence of segregating populations of apparent natural hybrids in several regions. Morphological variants have been recognized within var. _hardwickii_ (Schuman et al. 1985; Staub & Kupper 1986).

Kirkbride (1993) and Jeffrey (1980b, 2001) observed that _Cucumis hardwickii_ can be identified and recognized in its typical form but that morphological intergradation argues against its recognition as a distinct evolutionary entity with formal taxonomic recognition. Whitaker and Davis (1962) seconded earlier suggestions that _C. hardwickii_ is an expression of some feral form of _C. sativus_, rather than an ancestor. A study by de Wilde and Duyfjes (2010) agreed that _C. hardwickii_ is not sharply demarcated from feral forms of _C. sativus_ and reduced its formal rank within _C. sativus_ to forma.
On the other hand, *Cucumis hardwickii* is reported to be isozymically distinct from *C. sativus*. Knerr & Staub (1991) found that *C. hardwickii* possesses alleles for *Per-4* and *Idh* which were not present in the remainder of their samples of *C. sativus*. Meglic et al. (1996) also found that *C. hardwickii* is isozymically distinct from a large number of *C. sativus* samples.

Without consistent morphological differentiation between *Cucumis hardwickii* and the highly variable domesticated and feral forms of *C. sativus* sensu stricto, but with an apparent molecular distinction, their recognition at varietal rank seems appropriate. Rank of forma (as interpreted here) would imply that "hardwickii" is a populational variant. At least the relationship is not clearly one of progenitor-derivative.


**a. Cucumis sativus** var. *sativus*


Another distinctive, formally named expression of *Cucumis sativus* has recently been recognized in the Bhutan flora (Grierson 1991): *C. sativus* var. *sikkimensis* Hook. f. Grierson distinguished it from the common cucumber by the following contrasts.

1. Leaves 3–5-lobed; ovary with 3 placentae; fruit greenish ............................................ var. *sativus*
1. Leaves 7–9-lobed; ovary with 5 placentae; fruit mottled yellow and brown .......... var. *sikkimensis*

Kirkbride (1993) placed var. *sikkimensis* in the synonymy of *Cucumis sativus*, but I have not encountered the name among samples evaluated in taxonomic studies of *C. sativus*. Presumably var. *sikkimensis* is derived from within the *C. sativus* lineage but this appears to be unconfirmed.

Comments by Hooker in the protologue are at least vaguely suggestive that he thought var. *sikkimensis* might be derived from *Cucumis hardwickii*. "The origin of the common Cucumber, which is supposed to be unknown, is in all probability the *C. Hardwickii*, Royle, of the Himalaya Mountains, which inhabits the sub-tropical region of the range from Kumaon to Sikkim. This opinion, founded on specimens gathered by myself in the latter country, is also adopted by M. Naudin, upon the same materials (Ann. Sc. Nat., l.c., p. 30). The flowers and leaves of the two plants are almost identical, but the fruit of *C. Hardwickii* is small, smooth, and very bitter; it is, however, striped with white and green, a very usual character with the Sikkim cultivated Cucumbers. ... [The Sikkim cucumber] is grown in all parts of the Sikkim and in the Nepal Himalaya, up to 5000 feet elevation, in prodigious quantities."

Literature Cited (*Cucumis*)


3. CUCURBITA

In two instances in *Cucurbita*, progenitor-domesticate pairs have been treated as conspecific subspecies (Whitaker & Bemis 1975; Nee 1990; Merrick 1995; Sanjur et al. 2002). *Cucurbita andreana* Naudin, a wild species native to Argentina and Bolivia is identical in haplotype (no base pair differences) to the domesticated *C. maxima* and is recognized as *C. maxima* Duchesne subsp. *andreana* (Naudin) Filov. Similarly, the wild gourd *C. sororia* Bailey of Mexico and Central America is identical in haplotype to the domesticated *C. argyrosperma* Huber and is treated as *C. argyrosperma* subsp. *sororia* (Bailey) Merrick & Bates. Ecological, morphological, and isozymic evidence and crossing studies also support the close relationships of these paired taxa.

The domesticated species *Cucurbita ficifolia* Bouché and *C. moschata* Duchesne have unique haplotypes and no wild progenitor has been proposed for either. Mitochondrial DNA data combined with other information suggest that the wild ancestor of *C. moschata* will be found in lowland northern South America (Sanjur et al. 2002); Nee (1990) noted that the ancestor, from reports from Bolivia and Colombia, may be extant but undescribed. *Cucurbita ficifolia* has a preference for cool, high-elevation habitats and probably originated in South America (Nee 1990; Sanjur et al. 2002), from where the only reliable archaeological records of the species have come.

The situation involving *Cucurbita pepo* L. sensu lato is more complex. Archaeological, morphological, and molecular-genetic research indicate that more than a single lineage exists in the *C. pepo* complex. Subsp. *pepo* is distinct from the rest, which usually has been identified either as subsp. *ovifera* (e.g., Decker and Wilson 1986, 1987; Decker 1988; Decker-Walters et al. 1993) or as subsp. *ovifera* plus subsp. *fraterna* (e.g., Andres 1987; Lira-Saade et al. 1995). Isozyme data indicate that within the range of *C. pepo* sensu lato, "genetic divergence took place long before domestication and over an extensive period of time in at least four disjunct and ecologically distinct regions" (Decker-Walters et al. 1993).

1. Subsp. *pepo*, a Mexican lineage of domesticates, includes jack-o-lantern pumpkins, zucchini, marrow, cocozelle, and Mexican landraces. It differs from subsp. *ovifera* sensu lato by a derived molecular feature (a difference in three adjacent base pairs) that also occurs in *Cucurbita moschata* and the *C. sororia/C. argyrosperma* group (Sanjur et al. 2002). The wild ancestor of subsp. *pepo*,
which presumably shared this derived feature, has not been identified and may be extinct. Forms of subsp. *pepo* presumably were selected from ancestral populations in southern Mexico.

Data from mtDNA and RAPD studies (Sanjur et al. 2002; Decker-Walters et al. 2002) and earlier isozymic and cpDNA studies (e.g., Decker-Walters et al. 1993) also indicate that *Cucurbita pepo* subsp. *pepo* is distinct from the entities of subsp. *ovifera* sensu lato. The clade comprising subsp. *pepo* is basal to that of subsp. *ovifera* (Sanjur et al. 2002).

A landrace of *Cucurbita pepo* recently recognized by Teppner (2000, 2004) as *C. pepo* subsp. *gumala* Teppner, comprises a series of domesticates apparently authochthonous in Guatemala and adjacent southern Mexico, and they may be similar to the ancestral wild form. These have relatively small fruits (13–20 cm in diameter, depressed-globose) and extremely thick rind, ripening orange-yellow, and orange flesh. Teppner observed that the fruits of subsp. *gumala* are similar to ancient ones of *C. pepo* from Guilá Naquitz cave in Oaxaca (Smith 1997).

2. **Subsp. *ovifera*** sensu lato includes three, geographically separate wild forms, all of which have identical mitochondrial DNA sequences (Sanjur et al. 2002) as well as similarities in isozymes and other kinds of DNA (see comments following): var. *fraterna* of northeastern Mexico, var. *texana*, apparently confined to Texas, and the more recently described var. *ozarkana* of the east-central USA. No domesticates derived from var. *texana* have been identified, but various domesticates, mostly identified as var. *ovifera*, have been derived from within var. *ozarkana* — the scallop (pattypan), acorn, crookneck, and straightneck squashes, and a number of ornamental gourds (e.g., Crown of Thorns, Flat-Striped, Striped Pear, Bicolor Spoon, White Egg, Nest Egg, Miniature Ball, and most of those with deep orange color, Mandan, Orange Warted, Warty Hardhead). The ancestor of most of the domesticates is hypothesized to be var. *ozarkana*, because var. *texana* has a isozyme pattern not found in the other varieties (Decker-Walters et al. 1993; Decker-Walters et al. 2002).

The cultivars Orange Ball, Miniature Ball, and Orange Warted showed a close allozymic relationship with *Cucurbita pepo* sensu stricto in several earlier studies (e.g., Decker & Wilson 1987; Decker 1988), but the RAPD study of Decker-Walters et al. (2002) clusters only Orange Ball within *C. pepo* sensu stricto. Miniature Ball showed a high affinity for var. *fraterna* in morphological and allozymic analyses of Andres (1987) but the origin of Miniature Ball in the 2002 RAPD study is indicated to be from var. *ozarkana*. Similarly, White Egg clustered with var. *fraterna* in allozyme studies (Decker-Walters et al. 1993) but later with var. *ozarkana* (Decker-Walters et al. 2002).

Var. *fraterna* is endemic to Tamaulipas and Nuevo León, Mexico, where it grows in seasonably dry, upland thornscrub habitat. It also is reported to be common as a weed in agricultural fields (Lira et al. 2009). It was first described at specific rank (Bailey 1943) and subsequently included within *C. pepo* at either varietal or subspecific rank (see below). Var. *fraterna* appears to be discrete both morphologically and geographically and it has a coordinate (sister) position relative to the two USA entities of subsp. *ovifera* in the cluster diagrams of Decker-Walters et al. (1993) and Decker-Walters et al. (2002).

Isozyme and RAPD data indicate that var. *texana* sensu stricto is limited to south-central Texas (Decker-Walters et al. 1993, 2002), mostly in drainage systems of the Brazos, Colorado, Guadalupe, Nueces, San Antonio, and Trinity rivers (Cowan & Smith 1993). Its habitats — creek and river banks, lake shores, marsh banks, low woods, dunes, and disturbed sandy sites — are distinct from the drier ones of var. *fraterna*. Habitats recorded for var. *ozarkana* are generally similar to those of var. *texana*, except perhaps tending to be more ruderal — creek and river banks, gravel bars, bottomland forests, soybean, corn, and cotton fields, old fields, fencerows, railroad ROWs, roadides, and disturbed sites. Var. *ozarkana* occurs in the central Mississippi Valley and the Ozark Plateau.
Populations in Alabama were included in var. *ozarkana* by Cowan and Smith (1993) but their evolutionary status was considered “uncertain” by Decker-Walters et al. (1993); the Alabama plants do not share the specialized isozyme pattern of var. *texana* but otherwise do not closely cluster with samples of var. *ozarkana*.

Wild populations of subsp. *ovifera* (not further identified to variety) were distributed in the early Pleistocene as far southeast as Florida (Newsom et al. 1993). Some weedy-habitat populations of var. *ovifera* extant in Illinois and Kentucky may have evolved as cultivar escapes (e.g., Wilson 1990), and some of these may also have experienced subsequent introgression with other nearby cultivated, weedy, or wild populations of var. *ozarkana* (Kirkpatrick & Wilson 1988; Decker-Walters et al. 2002 and included references).

Molecular differentiation between var. *texana* and var. *ozarkana* suggests that they have been reproductively isolated for a long period, but Teppner (2004) considered morphological variability as too overlapping to allow their unarbitrary separation. Molecular data reliably separate them and clearly delimit var. *fraterna* as well, but morphology needs to be restudied in detail. Fruits of var. *ozarkana* usually are ivory-white at maturity vs. green-and-white striped in var. *texana*, but this is not completely consistent (Andres 1995; pers. observ.). Fruits of var. *fraterna* are green-and-white striped, turning yellow-orange at maturity.

**Taxonomic rank.**

Entities generally treated as *Cucurbita pepo* sensu lato are here apportioned between two species: *C. pepo* L. (known only from domesticated forms) and *C. melopepo* L. (known from wild forms and domesticates), emphasizing their geographic and molecular differences. *Cucurbita melopepo* (1753) predates *C. ovifera* L. (1766) when that entity is treated at specific rank and is regarded here to include var. *fraterna*, var. *texana*, var. *ozarkana* (the wild forms) and var. *melopepo* (the domesticated forms). The wild forms of *C. melopepo* are geographically and molecularly distinct, but they cluster closely among themselves and form an evolutionary lineage separate from *C. pepo*. It seems likely that the three wild taxa of *C. melopepo* represent geographic segregates (vicariants) of a widespread ancestor, and perhaps *C. pepo* sensu stricto evidences an even earlier vicariant divergence from an ancestor of the entire complex.

For consistency within *Cucurbita* and other genera where wild progenitor/domesticate pairs are identified at subspecific rank, the var. *melopepo* domesticates are recognized as subsp. *melopepo*, coordinate with the three wild varieties, which are treated as *C. melopepo* subsp. *texana*. As currently understood, the domesticates are derived only from var. *ozarkana*, but it is not known whether they had a single common ancestor (populationally) or whether some of them have been independently derived. The possibility also remains that several of the domesticates are derived from var. *fraterna*.

The wild ancestor of *Cucurbita pepo* has not been identified but perhaps will prove to be subsp. *gumala* or some other uninvestigated landrace of southern Mexico.


*Cucurbita pepo*, with Herb. Burser XVII: 103 (UPS) as type, was proposed as conserved type of the genus by Jarvis (in Taxon 41: 562. 1992). However, the proposal was eventually ruled unnecessary by the General Committee (see Barrie, l.c. 55: 795-796. 2006 for a review of the history of this and related proposals). [quotation continues]

Bailey (in Gentes Herb. 2: 79. 1929) reproduced the protologue and various of the original elements (including a Dalechamp figure and a LINN sheet) and provided an
extensive discussion. Keraudren-Aymonin's (1975) type choice of 1151.4 (LINN) has priority over that of the Burser material designated by Jeffrey (in Jarvis, *l.c.* 41: 562. 1992) and becomes the type with the failure of the conservation proposal" (two paragraphs above quoted from the online database of The Linnaean Plant Name Typification Project — accessed January 2011).

**A. SUBSPECIES PEO**


*Cucurbita pepo* var. *medullosa* Alef., *Landw. Fl.*, 218. 1866. **TYPE**: Not designated. Protologue: "Frucht kleiner und etwas weicher als bei der Vorigen, oboi d-oblong, regelmässig, dadurch der folgenden Gruppe ähnlich. — In England un Nordamerika sehr beliebt, wie Gurken zubereitet, also vor der Reife." Generally cited at varietal rank, but Alefeld described it without rank within his "Var.-Gr. 1" and it is perhaps better interpreted at "subvar." rank. Explicitly identified by Alefeld as "Vegetable marrow."

**B. SUBSPECIES GUMALA**


Comments of Bailey (1929, p. 84): "This plant according to Linnaeus, is erect, not climbing or procumbent although he states that it bears tendrils; the leaves are lobed, the fruit depressed or flattened endwise and knotty. It is the 'Melopepo clypeiformis' of Caspar Bauhin's *Pinax* and 'Cucurbita clypeiformis' of Johann Bauhin's *Historia*; the latter has a picture, which is reproduced in Fig. 40; clypeiformis means shield-shaped or buckler-shaped; the plant is undoubtedly what we know as Bush Scallop squash. ... In the herbarium of Linnaeus there is no specimen of *C. melopepo* named by him." In the entry for *Cucurbita melopepo* in "Order Out of Chaos," Jarvis (2007) noted "Type not designated."

**A. SUBSPECIES MELOPEPO**

a. *Cucurbita melopepo* L. var. *melopepo*

Nesom: Nomenclature in domesticated/wild Cucurbitaceae


"The first validly named ornamental gourd was C. ovifera in 1767. The closest extant cultivar to Linnaeus's description and type specimen appears to be either the 'Striped Pear' or 'Egg' gourd. ... The full scientific name for the ornamental gourds today is practically always written C. pepo var. ovifera (L.) Alef. Yet Alefeld transferred the epithet to the rank of 'Var.-Gr.,' not to 'var.' The first traceable authority to validly publish the name C. pepo var. ovifera was Harz in 1885. Other varietal names for the ornamental gourds precede this, such as C. pepo var. oviformis Vilm. described in 1863, but the name ovifera has priority over all of these" (Andres 1995, pp. 67–68).

Subsp. ovifera is used in various places in the present discussion, reflecting the prevalent use of that name in recent literature, but within Cucurbita pepo, subsp. texana (Scheele) Filov (1982) has priority over subsp. ovifera (1988). Few publications have used the correct name (e.g., Paris et al. 2002).

Cucurbita lignosa Mill., Gard. Dict. (ed. 8), Cucurbita sp. no. 5. 1768. Type: Not designated. Locality not indicated in the protologue. "The fruit of the fifth sort hath a hard shell when ripe like the first, which may be dried and preserved many years: these are of very different forms and size; some are shaped like a Pear, and are no bigger than a large Catherine Pear; some are as large as quart bottles, and almost of the same form; others are round and shaped like an Orange, and are of the same size and colour, but these are very variable." Synonym of C. pepo, fide Andres (1995). If acquired by Miller from along the coast of east-central Mexico, it suggests that it might be derivative from C. fraterna or C. pepo sensu stricto.


As noted in pencil on the sheets, 8 collections of Cucurbita pepo — most with a photo or drawing of the mature fruit — were in a BH folder labeled C. pepo var. condensa: 2 of "Green-Striped Bush, 2 of Scallop, 2 that approach Crown of Thorns, 1 of "Egg Plant Bush," and 1 of Pineapple (a variant of 'turban' morphology). All of these have labels with a printed heading of "Garden Herbarium of the Cornell University Experiment Station" and all were collected on September 17 and 18, 1890. Bailey did not cite a specimen and none of these is annotated as "var. condensa," but it seems clear enough that these can be considered original material. Bailey (1929) listed var. condensa as a synonym of C. pepo var. melopepo.

a. **Cucurbita melopepo** var. **ozarkana** (Decker) G.L. Nesom, comb. nov. *Cucurbita pepo var. ozarkana* Decker-Walters, J. Ethnobiol. 13: 69. 1993. **TYPE:** **USA.** **Arkansas.** Independence Co.: 200 m downstream from Batesville, 100 m from edge of White River on first terrace, 6 Nov 1990, B. Smith & C.W. Cowan 115 (holotype: US digital image!).

b. **Cucurbita melopepo** var. **texana** (Scheele) G.L. Nesom, comb. nov. *Cucurbita texana* Scheele, Linnaea 21: 586. 1848. **TYPE:** **USA.** **Texas.** Comal Co.: Upper Guadeloupe [River], [margins of thickets,] in moist woods, Sep [1845], F.J. Lindheimer Fasc. III. 4000 (holotype: B, presumably; possible isotypes: GH, MO-2 sheets digital images!). The protologue in Linnaea cites as collection data only this: "Niederliegend oder über niedrigem Gebüschen rankend an der Guadalupe: Lindheimer. Juni." One of the MO sheets has a handwritten label noting the number "472" with a date of "Sept 1845," but the printed label has 1846. The other MO sheet (3265652) has a handwritten label noting the number "360" with a date of "Juni Juli 1846." It is not clear that any of the collections at GH and MO are duplicates of the type; those dated September presumably are not.


**Literature Cited (Cucurbita)**


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Figure 1. Lectotype of *Citrullus caffra* Schrad. (GOET). See text.
Figure 2. Isolectotype of *Citrullus caffra* Schrad. (GOET). See text.
Figure 3. Isolectotype of *Citrullus caffra* Schrad. (GOET). See text.
Figure 4. Lectotype of *Citrullus vulgaris* var. *citroides* L.H. Bailey (BH). See text.
Figure 5. "Mini seedless" triploid watermelon, *Citrullus lanatus*, at the end of its remarkable odyssey beginning from a small, fertile-diploid, bitter-flesh African ancestor. This one was grown in Mexico, according to its label.
Figure 6. "Melones" in Bauhin and Cherler's Historia Planta Universalis (1651, vol. 2, p. 242). The page with the illustration was cited by Linnaeus in the 1753 protologue of *Cucumis melo*. Along with the protologue and lectotype, this illustration and the one from Morison's Plantarum Historiae Universalis (in Fig. 5) provide a fuller morphological formulation of Linnaeus's concept of the species and of *C. melo* var. *melo* in the strict sense.
Figure 7. "Melo" in Robert Morison's Plantarum Historiae Universalis (1680, vol. 2, series 1, tab. 6, fig. 4). This illustration is referred to in Hortus Cliffortianus (Linnaeus 1737) and Florae Leydensis (van Royen 1740), both cited by Linnaeus in the 1753 protologue of *Cucumis melo.*
Figure 8. *Cucurbita clypeiformis* from Bauhin and Cherler, Historia plantarum universalis 2: 224. 1651. The page with this illustration was cited by Linnaeus in the protologue of *Cucurbita melopepo* L. (1753) and the illustration is designated above as the lectotype of the species.