

Gene List for *Cucurbita* species, 2004

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A complete list of genes for *Cucurbita* species was last published 12 years ago (33). Since then, only updates have been published (72, 73).

The genus *Cucurbita* L. contains 12 or 13 species (50). As far as is known, all have a complement of 20 pairs of chromosomes ($2n = 40$).

This new gene list for *Cucurbita* contains much more detail concerning the sources of information, being modeled after the one for cucumber presented by Wehner and Staub (96) and its update by Xie and Wehner (100). In order to more easily allow confirmation of previous work and as a basis for further work, information has been added concerning the genetic background of the parents that had been used for crossing. Thus, in addition to the species involved, the cultivar-group (for *C. pepo*), market type (for *C. maxima*, *C. moschata*), and/or cultivar name are included in the description wherever possible.

Genes affecting phenotypic/morphological traits are listed in **Table 1**. The data upon which are based identifications and concomitant assignment of gene symbols vary considerably in their content. No attempt is made here to assess the certainty of identifications, but gene symbols have been accepted or assigned only for cases in which at least some data are presented. The genes that are protein/isozyme variants are listed in **Table 2**. It can be seen from Tables 1 and 2 that a large number of genes, 65, have been identified for *C. pepo* L. For *C. moschata* Duchesne and *C. maxima* Duchesne, 21 and 19 genes have been identified, respectively, and for the interspecific cross of *C. maxima* × *C. ecuadorensis* Cutler & Whitaker, 29, of which 25 are isozyme variants. One or two genes have also been identified in four of the wild species (*C. okechobeensis* Bailey, *C. lundelliana* Bailey, *C. foetidissima* HBK and *C. ecuadorensis*) and in several other interspecific crosses. Notably, no genes have been identified for the other two cultivated species, *C. argyrosperma* Huber and *C. ficifolia* Bouché.

Some genes are listed as occurring in more than one species. This does not necessarily indicate that these genes reside at identical locations in the genome of different species.

New additions to the list of *Cucurbita* genes include a number of omissions as well as a number of new genes published after the last update. Those that had been omitted are: *Bn*, *pm-1*, *pm-2*, and *s-2*, and *Wmv^{ecu}*. Those that have been published since the last update are: *Cmv*, *grl*, *l-1^{BSI}*, *l-1^{ISI}*, *L-2^w*, *m-zym^{mos}*, *prv*, *qi*, *sl*, *wmv*, *zym^{mos}*, *Zym-2*, and *Zym-3*. In addition, there are many additions to the list of isozyme variants.

Symbols of genes that have been published in previous lists but have been modified for this list are *Pm* (to be used solely for powdery mildew resistance in *C. lundelliana*, with the separate designation *Pm-0* for resistance in and derived from *C. okeechobeensis*), and *Zym* (with separate designations for different sources of resistance, viz. *zym^{ecu}* from *C. ecuadorensis*, *Zym-0* from *C. moschata* ‘Nigerian Local’, and *Zym-1* from *C. moschata* ‘Menina’, and *zym^{mos}* from *C. moschata* ‘Soler’).

Before choosing a gene name and symbol, researchers are urged to consult this Gene List as well as the rules of Gene Nomenclature for the Cucurbitaceae that appears near the end of this Cucurbit Genetics Cooperative Report in order to avoid confusion arising from duplication of gene names and symbols. Please contact us if you find omissions or errors in this Gene List.

Several cases of genetic linkage have been reported: *D – mo-2* (56) and *M – Wt* (*C. pepo*) (66) and *Bi – Lo-2* (*C. ecuadorensis* × *C. maxima*) (30). Some of the isozyme variants observed by Weeden & Robinson (95) were also found to be linked to one another. RAPD markers have been categorized and organized into linkage groups and are not listed here but can be found in Brown and Myers (4) and Zraidi and Lelley (101). These two maps cannot be easily compared, as they were constructed using different mapping populations; RAPD markers are population-specific. Neither map gives complete coverage of the *Cucurbita* genome. Both maps contain morphological traits, either as single genes or as quantitative trait loci (QTLs). These traits are listed in **Table 3** along with the most tightly linked RAPD markers.

In many species, knowledge of the genome has moved beyond mapping markers linked to phenotypic traits to isolating and sequencing the genes that control the traits. Sequenced genes can be valuable to breeders and geneticists, as the differences in the gene sequences that result in the phenotypes of interest can be used as markers in marker-assisted selection. Unlike random markers, these gene-specific, allele-specific markers are completely linked to the genes of interest. Genes can be isolated through widespread sequencing of genomic or cDNA libraries, through map-based cloning, or by functional homology with sequenced genes from other species. In addition, genes which code for a known protein such as an enzyme can be isolated by working backwards from the protein. Many of the genes sequenced in *Cucurbita* at present have been sequenced this way. Map-based cloning is the most effective way to identify the DNA sequence of genes for phenotypic and morphological traits. This requires maps of much higher resolution than those presently available for *Cucurbita*. Most of the genes sequenced in *Cucurbita* have been isolated by researchers doing comparative studies of specific genes across plant families; usually only a single allele is available. Nonetheless, we have included a list of the sequenced genes in **Table 4** as the sequences could be useful as a starting point for breeders interested in isolating the genes from lines of differing phenotype. In addition to the genes listed here, there exists a collection of partial sequences from mRNA for genes differentially expressed during seed development in *C. pepo*. These expressed sequence tags were identified in a study of the naked seed trait. The Gene Accession numbers for these sequences are CD726806 through CD726832.

Table 1. Phenotypic/Morphological Characteristics

<u>Gene Symbol</u>				
Preferred	Synonym	Character	Species	Reference(s)
<i>a</i>		<i>androecious</i> . Found in ‘Greckie’; produces only male flowers, recessive to <i>A</i> .	<i>pepo</i>	39
<i>B</i>		<i>Bicolor</i> . Precocious yellow fruit pigmentation; pleiotropic, affecting fruit and foliage, modified by <i>Ep-1</i> , <i>Ep-2</i> and <i>Ses-B</i> . Originally from ‘Vaughn’s Pear Shaped’ ornamental gourd. <i>B</i> in <i>C. moschata</i> ‘Precocious PI 165561’ derived from <i>C. pepo</i> through backcrossing. Complementary to <i>L-2</i> for intense orange, instead of light yellow, fruit-flesh color.	<i>pepo, moschata</i>	52, 68, 78, 85, 87
<i>B^{max}</i>	<i>B-2</i>	<i>Bicolor</i> . Precocious yellow fruit pigmentation, from subsp. <i>andreana</i> PI 165558	<i>maxima</i>	86, 89
<i>Bi</i>		<i>Bitter</i> fruit. High cucurbitacin content in fruit. <i>Bi</i> from <i>C. maxima</i> subsp. <i>andreana</i> and <i>C. ecuadorensis</i> ; <i>bi</i> from <i>C. maxima</i> subsp. <i>maxima</i> , including ‘Queensland Blue’. Linked to <i>Lo-2</i> . In <i>C. pepo</i> , <i>Bi</i> from wild Texan gourd; <i>bi</i> from zucchini squash.	<i>maxima, maxima</i> <i>× ecuadorensis,</i> <i>pepo</i>	11, 28, 30
<i>bl</i>		<i>blue</i> fruit color. Incompletely recessive to <i>Bl</i> for green fruit color, in hubbard squash.	<i>maxima</i>	31
<i>Bn*</i>		<i>Butternut fruit shape</i> , from ‘New Hampshire Butternut’, dominant to <i>bn</i> for crookneck fruit shape, as in ‘Canada Crookneck’.	<i>moschata</i>	48
<i>Bu</i>		<i>Bush</i> habit. Short internodes; dominant to vine habit, <i>bu</i> , in young plant stage. In <i>C. pepo</i> , <i>Bu</i> in ‘Giant Yellow Straightneck’ and near-isogenic line of ‘Table Queen’, <i>bu</i> in ‘Table Queen’ acorn. In <i>C. maxima</i> , <i>Bu</i> from inbred line, <i>bu</i> from ‘Delicious’.	<i>pepo, maxima</i>	17, 29, 84
<i>Cmv</i>		<i>Cucumber mosaic virus resistance</i> , from Nigerian Local. Dominant to <i>cmv</i> for susceptibility, from ‘Waltham Butternut’.	<i>moschata</i>	3
<i>cr</i>		<i>cream</i> corolla. Cream to nearly white petals, <i>cr</i> from <i>C. okeechobeensis</i> ; <i>Cr</i> from <i>C. moschata</i> ‘Butternut’ incompletely dominant (yellow petals for <i>Cr/cr</i> , and orange for <i>Cr/Cr</i>)	<i>moschata ×</i> <i>okeechobeensis</i>	75
<i>cu</i>		<i>cucurbitacin-B</i> reduced; <i>cu</i> for reduced cucurbitacin-B content of cotyledons of ‘Early Golden Bush Scallop’; <i>Cu</i> for high cucurbitacin content of cotyledons of ‘Black Zucchini’.	<i>pepo</i>	83
<i>D</i>		<i>Dark</i> stem. Series of three alleles observed in <i>C. pepo</i> : <i>D</i> for dark stem and dark intermediate-age	<i>pepo, maxima</i>	25, 42, 55, 56, 59, 67, 80

		fruit, <i>D^s</i> for dark stem but fruit not affected, and <i>d</i> for light stem and fruit not affected, with dominance $D > D^s > d$. <i>D</i> from ‘Fordhook Zucchini’, <i>D^s</i> from ‘Early Prolific Straightneck’; <i>d</i> from ‘Vegetable Spaghetti’. Epistatic to genes <i>l-1</i> and <i>l-2</i> when either is homozygous recessive; linked to <i>mo-2</i> . In <i>C. maxima</i> , only the fruit was observed: <i>D</i> for dark intermediate-age fruit from the zapallito ‘La Germinadora’; <i>d</i> for light intermediate-age fruit from a variant zapallito breeding stock.		
<i>de</i>		<i>determinate</i> plant habit; stem lacking tendrils and terminating with female flowers. Recessive to <i>De</i> for indeterminate plant habit. <i>De</i> from ‘Jeju’ and ‘Sokuk’, <i>de</i> from inbred designated “Det”.	<i>moschata</i>	40
<i>Di</i>		<i>Disc</i> fruit shape. From scallop squash, dominant to spherical or pyriform.	<i>pepo</i>	91, 97
<i>Ep-1</i>		<i>Extender of pigmentation-1</i> ; modifier of <i>B</i> . <i>Ep-1</i> incompletely dominant to <i>ep-1</i> and additive with <i>Ep-2</i> . <i>Ep-1</i> from ‘Small Sugar 7 × 7’ pumpkin; <i>ep-1</i> from ‘Table King’ acorn.	<i>pepo</i>	90
<i>Ep-2</i>		<i>Extender of pigmentation-2</i> ; modifier of <i>B</i> . <i>Ep-2</i> incompletely dominant to <i>ep-2</i> and additive with <i>Ep-1</i> . <i>Ep-2</i> from ‘Table King’ acorn; <i>ep-2</i> from ‘Small Sugar 7 × 7’ pumpkin.	<i>pepo</i>	90
<i>Fr</i>		<i>Fruit fly (Dacus cucurbitae)</i> resistance. <i>Fr</i> from ‘Arka Suryamukhi’, dominant to <i>f^r</i> for susceptibility.	<i>maxima</i>	49
<i>fv</i>		<i>fused vein</i> . Fusion of primary leaf veins, subvital male gametophyte; found in hull-less-seeded pumpkin breeding line.	<i>pepo</i>	7, 8
<i>G</i>	<i>a, m</i>	<i>Gynoecious</i> sex expression; dominant to <i>g</i> for monoecious sex expression.	<i>foetidissima</i>	18, 23
<i>Gb</i>		<i>Green band</i> on inner side of base of petal, from a scallop squash; dominant to <i>gb</i> , for no band, from a straightneck squash.	<i>pepo</i>	19
<i>gc</i>		<i>green corolla</i> . Green, leaf-like petals, sterile; in unspecified F2 population.	<i>pepo</i>	92
<i>gl</i>		<i>glabrous</i> , lacking trichomes	<i>maxima</i>	37
<i>Gr</i>	<i>G</i>	<i>Green rind</i> . Dominant to buff skin of mature fruit. <i>Gr</i> from ‘Long Neapolitan’, <i>gr</i> from ‘Butternut’.	<i>moschata</i>	71
<i>grl</i>		<i>gray leaf</i> . Recessive to green leaf. Recessive <i>grl</i> derived from cross of zapallito-type line of <i>C. maxima</i> and a butternut-type line of <i>C. moschata</i> . Dominant <i>Gr1</i> from zapallito-type <i>C. maxima</i> .	<i>maxima</i> × <i>moschata</i>	41
<i>Hi</i>		<i>Hard rind inhibitor</i> . <i>Hi</i> , for hard-rind inhibition, from <i>C. maxima</i> ‘Queensland Blue’; <i>hi</i> , for no hard-rind inhibition, from <i>C. ecuadorensis</i> .	<i>maxima</i> × <i>ecuadorensis</i>	30

<i>Hr</i>		<i>Hard rind</i> . <i>Hr</i> for hard (lignified) rind in ornamental gourd, straightneck squash, and zucchini; <i>hr</i> for soft (non-lignified) rind in ‘Small Sugar’ pumpkin and ‘Sweet Potato’ (‘Delicata’). Complementary to <i>Wt</i> for <i>Warty</i> fruit.	<i>pepo</i>	44, 79
<i>i</i>		<i>intensifier</i> of the <i>cr</i> gene for cream flowers. <i>Cr</i> /– <i>I</i> /– for intense orange or yellow flowers, <i>Cr</i> /– <i>i</i> / <i>i</i> for light orange or yellow flowers, <i>cr</i> / <i>cr</i> <i>I</i> /– for cream flowers, <i>cr</i> / <i>cr</i> <i>i</i> / <i>i</i> for white flowers. <i>I</i> from <i>C. moschata</i> ‘Butternut’, <i>i</i> from <i>C. okeechobeensis</i> .	<i>moschata</i> × <i>okeechobeensis</i>	75
<i>I-mc</i>	<i>I_{mc}</i>	<i>Inhibitor</i> of <i>mature</i> fruit color; dominant to <i>i-mc</i> for no inhibition. <i>I-mc</i> in a scallop squash.	<i>pepo</i>	9
<i>I-T</i>		<i>Inhibitor</i> of the <i>T</i> gene for trifluralin resistance. <i>I-T</i> from ‘La Primera’; <i>i-t</i> from ‘Ponca’ and ‘Waltham Butternut’.	<i>moschata</i>	1
<i>l-1</i>	<i>c, St</i>	<i>light fruit coloration-1</i> . Light intensity of fruit coloration. Series of five alleles observed in <i>C. pepo</i> which, in complementary interaction with the dominant <i>L-2</i> allele, give the following results: <i>L-1</i> for uniformly intense/dark fruit coloration, from ‘Fordhook Zucchini’; <i>l-1^{BSt}</i> for broad, contiguous intense/dark stripes, from ‘Cocozelle’; <i>l-1St</i> for narrow, broken intense/dark stripes, from ‘Caserta’; <i>l-1^{ISt}</i> for irregular intense/dark stripes, from ‘Beirut’ vegetable marrow; <i>l-1</i> for light coloration, from ‘Vegetable Spaghetti’, with dominance of <i>L-1</i> > (<i>l-1^{BSt}</i> > <i>l-1St</i>) ≥ <i>l-1^{ISt}</i> > <i>l-1</i> . In <i>C. maxima</i> , <i>L-1</i> from the zapallito ‘La Germinadora’; <i>l-1</i> from a variant zapallito breeding stock.	<i>pepo, maxima</i>	25, 42, 57, 62, 63, 67, 76, 85
<i>l-2</i>	<i>r</i>	<i>light fruit coloration-2</i> . Light intensity of fruit coloration. Series of three alleles observed in <i>C. pepo</i> , which, in complementary interaction with dominant alleles at the <i>l-1</i> locus, give the following results: <i>L-2</i> for intense/dark fruit coloration, with <i>L-1</i> from ‘Fordhook Zucchini’ and intense/dark fruit stripes, with <i>l-1^{BSt}</i> from ‘Cocozelle’; allele <i>L-2^w</i> has delayed and weaker effect than <i>L-2</i> , from <i>C. pepo</i> subsp. <i>fraterna</i> ; <i>l-2</i> for light coloration, from ‘Vegetable Spaghetti’, with dominance of <i>L-2</i> > <i>L-2^w</i> > <i>l-2</i> . Dominant <i>L-2</i> is also complementary with <i>B</i> for intense orange, instead of light yellow, fruit-flesh color and with recessive <i>qi</i> for intense exterior color of young fruit. In <i>C. maxima</i> , <i>L-2</i> from the zapallito ‘La Germinadora’; <i>l-2</i> from a variant zapallito breeding stock.	<i>pepo, maxima</i>	25, 42, 52, 58, 60, 67
<i>lo-1</i>	<i>l</i>	<i>lobed leaves-1</i> ; recessive to <i>Lo-1</i> for non-lobed leaves	<i>maxima</i>	20
<i>Lo-2</i>		<i>Lobed leaves-2</i> . <i>Lo-2</i> for lobed leaves in <i>C. ecuadorensis</i> dominant to <i>lo-2</i> for unlobed leaves in <i>maxima</i>	<i>ecuadorensis</i> × <i>maxima</i>	30

		<i>C. maxima</i> . Linked to <i>Bi</i> .		
<i>lt</i>		<i>leafy tendril</i> . Tendrils with laminae; <i>lt</i> found in ornamental gourd.	<i>pepo</i>	77
<i>ly</i>		<i>light yellow corolla</i> . Recessive to orange yellow; <i>ly</i> found in ornamental gourd.	<i>pepo</i>	77
<i>M</i>		<i>Mottled</i> leaves. <i>M</i> for silver-gray areas in axils of leaf veins, dominant to <i>m</i> for absence of silver-gray. For <i>C. maxima</i> , <i>M</i> in ‘Zuni’ and <i>m</i> in ‘Buttercup’ and ‘Golden Hubbard’. For <i>C. pepo</i> , <i>M</i> in ‘Caserta’ and inbred of ‘Striato d’Italia’ cocozelle; <i>m</i> in ‘Early Prolific Straightneck’ and ‘Early Yellow Crookneck’. For <i>C. moschata</i> , <i>M</i> in ‘Hercules’ and ‘Golden Cushaw’, <i>m</i> in butternut type. Weakly linked to <i>Wt</i> .	<i>pepo, maxima, moschata</i>	13, 66, 76, 81
<i>Mldg</i>		<i>Mottled light and dark green</i> immature fruit color; germplasm unspecified. Dominant to <i>mldg</i> for non-mottled.	<i>moschata</i>	5
<i>mo-1</i>		<i>mature orange-1</i> ; complementary recessive gene for loss of green fruit color prior to maturity. <i>Mo-1</i> from ‘Table Queen’ acorn; <i>mo-1</i> from ‘Vegetable Spaghetti’.	<i>pepo</i>	56
<i>mo-2</i>		<i>mature orange-2</i> ; complementary recessive gene for loss of green fruit color prior to maturity. <i>Mo-2</i> from ‘Table Queen’ acorn; <i>mo-2</i> from ‘Vegetable Spaghetti’. Linked to <i>D</i> .	<i>pepo</i>	56
<i>ms-1</i>	<i>ms₁</i>	<i>male sterile-1</i> . Male flowers abort before anthesis, derived from a cross involving ‘Golden Hubbard’, recessive to <i>Ms-1</i> for male fertile.	<i>maxima</i>	82
<i>ms-2</i>	<i>ms₂</i>	<i>male sterile-2</i> . Male flowers abort, sterility expressed as androecium shrivelling and turning brown; <i>ms-2</i> from ‘Eskandarany’ (PI 228241).	<i>pepo</i>	22
<i>ms-3</i>	<i>ms-2</i>	<i>male sterile-3</i> .	<i>maxima</i>	37
<i>m-zym^{mos*}</i>		<i>modifier</i> of dominance of <i>zucchini yellow mosaic</i> virus resistance; confers resistance to otherwise susceptible <i>Zym^{mos}/zym^{mos}</i> heterozygotes. <i>M-zym^{mos}</i> in ‘Soler’, <i>m-zym^{mos}</i> in ‘Waltham Butternut’ and ‘Nigerian Local’.	<i>moschata</i>	51
<i>n</i>	<i>h</i>	<i>naked</i> seeds. Lacking a lignified seed coat, <i>n</i> from oil-seed pumpkin.	<i>pepo, moschata</i>	27, 80, 87, 99, 102
<i>pl</i>		<i>plain light</i> fruit color, <i>pl</i> from ‘Beirut’ vegetable marrow and ‘Fordhook Zucchini’; <i>Pl</i> in ‘Vegetable Spaghetti’.	<i>pepo</i>	53
<i>Pm, Pm-0*</i>		<i>Powdery mildew</i> resistance. Resistance to <i>Podosphaera xanthii</i> ; <i>Pm</i> from <i>C. lundelliana</i> ; <i>Pm-0</i> from <i>C. okeechobeensis</i> and in <i>C. pepo</i>	<i>lundelliana, okeechobeensis, pepo</i>	10, 12, 35, 70

<i>pm-1</i>		<i>powdery mildew</i> resistance in <i>C. moschata</i> . Series of three alleles: <i>pm-1^P</i> for susceptibility from ‘Ponca’ dominant to <i>pm-1^L</i> for resistance from ‘La Primera’, which is dominant to <i>pm-1^W</i> for susceptibility in ‘Waltham Butternut’.	<i>moschata</i>	2
<i>pm-2</i>		<i>powdery mildew</i> resistance in <i>C. moschata</i> ‘Seminole’, recessive to <i>Pm-2</i> for susceptibility	<i>moschata</i>	2
<i>prv</i>		<i>papaya ringspot virus resistance</i> , in Nigerian Local, recessive to <i>Prv</i> for susceptibility, in ‘Waltham Butternut’.	<i>moschata</i>	3
<i>qi</i>		<i>quiescent intense</i> . Recessive to <i>Qi</i> for not intense and complementary to <i>L-2</i> for intense young fruit color; little or no effect on mature fruit. <i>Qi</i> from ‘Vegetable Spaghetti’; <i>qi</i> from ‘Jack O’Lantern’ pumpkin and ‘Verte non-coureuse d’Italie’ cocozelle.	<i>pepo</i>	58, 61
<i>Rd</i>		<i>Red</i> skin. Red external fruit color; dominant to green, white, yellow and gray. <i>Rd</i> from ‘Turk’s Cap’; <i>rd</i> from ‘Warted Hubbard’.	<i>maxima</i>	43
<i>ro</i>		<i>rosette</i> leaf. Lower lobes of leaves slightly spiraled, <i>ro</i> derived from an ornamental gourd.	<i>pepo</i>	44
<i>s-1</i>	<i>s</i>	<i>sterile</i> . Male flowers small, without pollen; female flower sterile. Derived from crossing ‘Greengold’ with ‘Banana’.	<i>maxima</i>	32
<i>s-2</i>		<i>sterile</i> . Male flowers small, without pollen and female flower sterile; mutant in powdery mildew resistant, straightneck squash breeding line.	<i>pepo</i>	6
<i>Ses-B</i>		<i>Selective suppression</i> of gene <i>B</i> . Suppression in foliage of precocious yellowing conferred by <i>B</i> . <i>Ses-B</i> in straightneck breeding line dominant to <i>ses-B</i> in ‘Jersey Golden Acorn’.	<i>pepo</i>	88
<i>sl</i>		<i>silverleaf</i> resistance. Recessive to <i>Sl</i> for susceptibility. <i>Sl</i> from ‘Soler’; <i>sl</i> from PI 162889 and butternut types.	<i>moschata</i>	26
<i>Slc</i>		<i>Squash leaf curl</i> virus resistance; derived from <i>C. moschata</i> .	<i>pepo</i>	46
<i>sp</i>		<i>spaghetti</i> flesh, breaking into strands after cooking	<i>pepo</i>	45
<i>T</i>		<i>Trifluralin</i> resistance. Dominant to susceptibility to the herbicide; modified by <i>I-T</i> . <i>T</i> in ‘La Primera’; <i>t</i> in ‘Ponca’ and ‘Waltham Butternut’.	<i>moschata</i>	1
<i>uml</i>		<i>umbrella-like</i> ; leaves shaped like partially opened umbrella. Recessive <i>uml</i> derived from a cross of <i>C. maxima</i> ‘Warzywna’ and a <i>C. pepo</i> inbred; dominant <i>Uml</i> from ‘Warzywna’.	<i>maxima</i> × <i>pepo</i>	69
<i>v</i>		<i>virescent</i> . Yellow-green young leaves, <i>v</i> found in ‘Golden Delicious’.	<i>maxima</i>	21

<i>W</i>	<i>Weak</i> fruit coloration. Dominant to <i>w</i> for intense-pigmented mature fruit; <i>W</i> from scallop squash. Complementary to <i>Wf</i> for white external fruit color.	<i>pepo</i>	54, 91, 97
<i>wc</i>	<i>white corolla</i> . Derived from ‘Ispanskaya’ × ‘Emerald’. Recessive to <i>Wc</i> for normal orange-yellow corolla	<i>maxima</i>	38
<i>Wf</i>	<i>White flesh</i> . Dominant to <i>wf</i> for colored flesh. <i>Wf</i> in a scallop squash, <i>wf</i> in a straightneck squash. Complementary to <i>W</i> for white external fruit color.	<i>pepo</i>	19, 54, 91
<i>Wmv</i>	<i>Watermelon mosaic virus resistance</i> . From “Menina” and “Nigerian Local”, dominant to <i>wmv</i> for susceptibility in ‘Musquée de Provence’ and ‘Waltham Butternut’. May be linked with or identical to <i>Zym-1</i> .	<i>moschata</i>	3, 24
<i>Wmv^{ecu}*</i>	<i>Watermelon mosaic virus</i> resistance. From <i>C. ecuadorensis</i> , in a cross with an unspecified <i>C. maxima</i> .	<i>maxima</i> × <i>ecuadorensis</i>	95
<i>Wt</i>	<i>Warty</i> fruit. Dominant to non-warted, <i>wt</i> , and complementary to <i>Hr</i> , with fruit wartiness being expressed only in the presence of the dominant <i>Hr</i> allele. <i>Wt</i> in straightneck, crookneck, and ‘Delicata’; <i>wt</i> in zucchini, cocozelle, and ‘Small Sugar’ pumpkin. Weakly linked to <i>M</i> .	<i>pepo</i>	66, 79, 91
<i>wyc</i>	<i>white-yellow corolla</i> ; isolated in ‘Riesen-Melonen’. Recessive to <i>Wyc</i> for normal orange-yellow corolla.	<i>maxima</i>	38
<i>Y</i>	<i>Yellow</i> fruit color. <i>Y</i> for yellow fruit color of intermediate-age fruits, from straightneck and crookneck squash, dominant to <i>y</i> for green intermediate-age fruit color, from vegetable marrow, ornamental gourd, and cocozelle.	<i>pepo</i>	66, 76, 84, 85, 91
<i>yg</i>	<i>yellow-green</i> leaves and stems	<i>maxima</i>	37
<i>Ygp</i>	<i>Yellow-green placenta</i> . Dominant to yellow placental color. <i>Ygp</i> in a scallop squash, <i>ygp</i> in a straightneck squash.	<i>pepo</i>	19
<i>ys</i>	<i>yellow seedling</i> . Lacking chlorophyll; lethal	<i>pepo</i>	44
<i>zym^{ecu}</i>	<i>zucchini yellow mosaic</i> virus resistance, recessive to susceptibility; <i>zym^{ecu}</i> from <i>C. ecuadorensis</i> , <i>Zym^{ecu}</i> from <i>C. maxima</i> ‘Buttercup’.	<i>ecuadorensis</i>	74
<i>zym^{mos}*</i>	<i>zucchini yellow mosaic</i> virus resistance, recessive to susceptibility; <i>zym^{mos}</i> from ‘Soler’, <i>Zym^{mos}</i> from ‘Waltham Butternut’.	<i>moschata</i>	51
<i>Zym-0*</i>	<i>Zucchini yellow mosaic</i> virus resistance. <i>Zym-0</i> from <i>C. moschata</i> ‘Nigerian Local’ dominant to <i>zym-0</i> for susceptibility from ‘Waltham Butternut’. Perhaps one of two separate genes for resistance in ‘Nigerian Local’.	<i>moschata</i>	3, 47, 51

<i>Zym-1</i>	<i>Zucchini yellow mosaic virus</i> resistance. <i>Zym-1</i> from <i>C. moschata</i> ‘Menina’ dominant to <i>zym-1</i> for susceptibility from <i>C. moschata</i> ‘Waltham Butternut’. <i>Zym-1</i> transferred via backcrossing to <i>C. pepo</i> ‘True French’ zucchini, in which it confers resistance through complementary interaction with <i>Zym-2</i> and <i>Zym-3</i> . <i>Zym-1</i> is either linked with <i>Wmv</i> or also confers resistance to watermelon mosaic virus.	<i>moschata, pepo</i>	24, 51, 64, 65
<i>Zym-2</i>	<i>Zucchini yellow mosaic virus</i> resistance-2. Dominant to susceptibility and complementary to <i>Zym-1</i> . <i>Zym-2</i> from <i>C. moschata</i> ‘Menina’. <i>Zym-2</i> in <i>C. pepo</i> derived from <i>C. moschata</i> , in near-isogenic resistant line of ‘True French’ zucchini; <i>zym-2</i> from <i>C. pepo</i> ‘True French’.	<i>moschata, pepo</i>	64
<i>Zym-3</i>	<i>Zucchini yellow mosaic virus</i> resistance-3. Dominant to susceptibility and complementary to <i>Zym-1</i> . <i>Zym-3</i> from <i>C. moschata</i> ‘Menina’. <i>Zym-3</i> in <i>C. pepo</i> derived from <i>C. moschata</i> , in near-isogenic resistant line of ‘True French’ zucchini; <i>zym-3</i> from <i>C. pepo</i> ‘True French’.	<i>moschata, pepo</i>	64

*Proposed new gene symbol.

Table 2. Isozyme Variants

<u>Gene Symbol</u>		No. alleles observed	Character	Species	Reference(s)
Preferred	Synonym				
<i>Aat-1</i>	<i>Aat</i>	8	<i>Aspartate aminotransferase-1</i> . Variant among accessions.	<i>pepo</i>	16, 34
<i>Aat-3</i>		2	<i>Aspartate aminotransferase-3</i> . Variant among wild populations.	<i>pepo</i>	16
<i>Aat-4</i>		3	<i>Aspartate aminotransferase-4</i> . Variant among wild populations.	<i>pepo</i>	16
<i>Aat-mb</i>		2	<i>Aspartate aminotransferase – microbody</i>	<i>maxima</i> × <i>ecuadorensis</i>	95
<i>Aat-m1</i>		2	<i>Aspartate aminotransferase mitochondria-1</i>	<i>maxima</i> × <i>ecuadorensis</i>	95
<i>Aat-m2</i>		2	<i>Aspartate aminotransferase mitochondria-2</i>	<i>maxima</i> × <i>ecuadorensis</i>	95
<i>Aat-p2</i>		2	<i>Aspartate aminotransferase plastid-2</i>	<i>maxima</i> × <i>ecuadorensis</i>	95
<i>Acp-1</i>		2	<i>Acid phosphatase-1</i>	<i>maxima</i> ×	95

				<i>ecuadorensis</i>	
<i>Acp-2</i>		2	<i>Acid phosphatase-2</i>	<i>maxima</i> × <i>ecuadorensis</i>	95
<i>Aldo-p</i>		2	<i>Aldolase – plastid</i>	<i>maxima</i> × <i>ecuadorensis</i>	94
<i>Est-1</i>	<i>Est</i>	2	<i>Esterase</i>	<i>maxima</i> × <i>ecuadorensis</i>	93, 95
<i>Gal-1</i>		2	β -galactosidase-1	<i>maxima</i> × <i>ecuadorensis</i>	95
<i>Gal-2</i>		2	β -galactosidase-2	<i>maxima</i> × <i>ecuadorensis</i>	95
<i>G2d-1</i>		3	<i>Glycerate dehydrogenase-1</i> . Variant among wild populations.	<i>pepo</i>	16
<i>G2d-2</i>		2	<i>Glycerate dehydrogenase-2</i> . Variant among wild populations.	<i>pepo</i>	16
<i>Got-1</i>		5	<i>Glutamine oxaloacetate-1</i> . Variant among accessions, wild populations, and among <i>Cucurbita</i> species.	<i>pepo</i>	14, 15, 36, 98
<i>Got-2</i>		3	<i>Glutamine oxaloacetate-2</i> . Variant among species.	<i>maxima</i> × <i>ecuadorensis</i>	98
<i>Gpi</i>		2	<i>Glucosephosphate isomerase</i> . Variant among accessions.	<i>pepo</i>	34
<i>Gpi-3</i>		2	<i>Glucosephosphate isomerase-3</i> . Variant among wild populations.	<i>pepo</i>	16
<i>Gpi-c1</i>		2	<i>Glucosephosphate isomerase cytosolic-1</i>	<i>maxima</i> × <i>ecuadorensis</i>	95
<i>Gpi-c2</i>		2	<i>Glucosephosphate isomerase cytosolic-2</i>	<i>maxima</i> × <i>ecuadorensis</i>	95
<i>Idh-1</i>		4	<i>Isocitrate dehydrogenase-1</i> . Variant among accessions, wild populations, and <i>Cucurbita</i> species.	<i>pepo</i>	14, 15, 16, 36, 98
<i>Idh-2</i>		2	<i>Isocitrate dehydrogenase-2</i> . Variant among accessions, wild populations, and <i>Cucurbita</i> species.	<i>pepo</i>	14, 15, 16, 36, 98
<i>Idh-3</i>		2	<i>Isocitrate dehydrogenase-3</i> . Variant among accessions and populations.	<i>pepo</i>	14, 15, 16, 36
<i>Lap-1</i>	<i>Lap</i>	4	<i>Leucine aminopeptidase</i> . Variant among <i>C. pepo</i> accessions.	<i>maxima</i> × <i>ecuadorensis</i> ; <i>pepo</i>	16, 34, 93, 95

<i>Mdh-1</i>	<i>Mdh</i>	7	<i>Malate dehydrogenase</i> . Variant among accessions.	<i>pepo</i>	34
<i>Mdh-2</i>		3	<i>Malate dehydrogenase-2</i> . Variant among accessions, wild populations, and <i>Cucurbita</i> species.	<i>pepo</i>	14, 15, 16, 36, 98
<i>Mdh-3</i>		3	<i>Malate dehydrogenase-3</i> . Variant among accessions, wild populations, and <i>Cucurbita</i> species.	<i>pepo</i>	14, 15, 16, 36, 98
<i>Mdh-m1</i>		2	<i>Malate dehydrogenase mitochondria-1</i>	<i>maxima</i> × <i>ecuadorensis</i>	95
<i>Mdh-m2</i>		2	<i>Malate dehydrogenase mitochondria-2</i>	<i>maxima</i> × <i>ecuadorensis</i>	95
<i>Mdh-c2</i>		2	<i>Malate dehydrogenase cytosolic-2</i>	<i>maxima</i> × <i>ecuadorensis</i>	95
<i>Per-1</i>		2	<i>Peroxidase-1</i>	<i>maxima</i> × <i>ecuadorensis</i>	95
<i>Per-2</i>		3	<i>Peroxidase-2</i> . Variant among accessions and wild populations.	<i>pepo</i>	14, 15, 36
<i>Per-3</i>		2	<i>Peroxidase-3</i>	<i>maxima</i> × <i>ecuadorensis</i>	95
<i>Pgi-1</i>		2	<i>Phosphoglucose isomerase-1</i>	<i>pepo</i>	14
<i>Pgi-2</i>		2	<i>Phosphoglucose isomerase-2</i> . Variant among <i>Cucurbita</i> species.	<i>pepo</i>	14, 36, 98
<i>Pgi-3</i>		4	<i>Phosphoglucose isomerase-3</i> . Variant among accessions, wild populations, and <i>Cucurbita</i> species.	<i>pepo</i>	14, 15, 36, 98
<i>Pgm-1</i>	<i>Pgm</i>	2	<i>Phosphoglucomutase</i> . Variant among accessions.	<i>pepo</i>	34
<i>Pgm-2</i>		4	<i>Phosphoglucomutase-2</i> . Variant among accessions, wild populations, and <i>Cucurbita</i> species.	<i>pepo</i>	14, 15, 36, 98
<i>Pgm-5</i>		2	<i>Phosphoglucomutase-5</i> . Variant among wild populations.	<i>pepo</i>	16
<i>Pgm-6</i>		2	<i>Phosphoglucomutase-6</i> . Variant among wild populations.	<i>pepo</i>	16
<i>Pgm-c2</i>		2	<i>Phosphoglucomutase cytosolic-2</i>	<i>maxima</i> × <i>ecuadorensis</i>	95
<i>Pgm-p</i>		2	<i>Phosphoglucomutase plastid</i>	<i>maxima</i> × <i>ecuadorensis</i>	95
<i>Skd-1</i>		6	<i>Shikimate dehydrogenase</i> . Variant	<i>pepo</i>	16

		among wild populations.		
<i>Skdh</i>	5	<i>Shikimate dehydrogenase</i> . Variant among <i>C. pepo</i> accessions.	<i>maxima</i> × <i>ecuadorensis</i> ; <i>pepo</i>	34, 95
<i>Sod-1</i>	2	<i>Superoxide dismutase-1</i>	<i>maxima</i> × <i>ecuadorensis</i>	95
<i>Tpi-c2</i>	2	<i>Triosephosphatase isomerase cytosolic-2</i>	<i>maxima</i> × <i>ecuadorensis</i>	95
<i>Tpi-p2</i>	2	<i>Triosephosphatase isomerase plastid-2</i>	<i>maxima</i> × <i>ecuadorensis</i>	95

Table 3. Mapped Phenotypic/Morphological Characteristics

Trait	Symbol	Linked Marker(s)	Recombination Distance (cM)	Reference(s)
Seed Coat	<i>n</i>	AK11_340	4.4	101
Fruit Length	(QTL)	AE07_165, AC10_490, AJ20_420, P13_750, J01_600, AO20_1200, T08_460, AB08_540, AE09_1600		101
Fruit Width	(QTL)	AE07_165, AJ20_420, AM10_950, AG08_440		101
Fruit Length/width Ratio	(QTL)	AE07_165, AC10_490, AJ20_420, P13_750, J01_600		101
No. of Fruit Chambers	(QTL)	P13_950, AE08_470		101
Precocious yellow fruit	<i>B</i>	I10_1700	27.1	4
Leaf Indentation	(QTL)	F10_400, K11_950, G2_400		4
Leaf Mottle	<i>M</i>	H14_600 U489_1200	13.0 16.3	4
Mature Fruit Color	[none given]	G17_700	9.7	4
Fruit Shape	(QTL)	F8_1050, B8_900, H19_500		4

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Table 4. Genes with known DNA sequence

Gene Symbol*	Gene Accession	(Putative) Function	Source	Ref.
AIG-2	AY666083	aspartic protease inhibitor	<i>C. maxima</i>	**
PRB1	AY326308	phloem RNA-binding protein	<i>C. maxima</i> ‘Big Max’	**
GAIP	AY32630, AY326307	gibberellic acid insensitive phloem protein (two very similar genes)	<i>C. maxima</i> ‘Big Max’	**
FAD2	AY525163	omega-6 fatty acid desaturase	<i>C. pepo</i> zucchini	**
NIP1	AJ544830	Nod26-like protein	<i>C. pepo</i> zucchini	23
PP2	AY312402	phloem protein 2 lectin (includes promoter region)	<i>C. moschata</i> crookneck	**
PP2	AF150627	phloem protein 2 lectin	<i>C. moschata</i> crookneck	**
PP2	Z22647	phloem protein 2 lectin	<i>C. pepo</i> ‘Autumn Gold’	42
PP2	Z17331	phloem protein 2 lectin	<i>C. maxima</i> ‘Big Max’	2
PP2	L31550, L31551, L31552	phloem protein 2 (three alleles)	<i>C. maxima</i>	**
GA2OX, GA20OX, GA3OX	AJ315663, AJ302041, AJ308480, AJ302040	gibberellin oxidases (two sequences for GA2OX)	<i>C. maxima</i> ‘Riesenmelone’	**

	U61385	gibberellin 20-oxidase	<i>C. maxima</i> 'Riesenmelone'	25
	U63650	gibberellin 2 beta,3 beta hydroxylase	<i>C. maxima</i> 'Riesenmelone'	26
	AJ006453	gibberellin 3 beta hydroxylase	<i>C. maxima</i> 'Riesenmelone'	**
	U61386	gibberellin dioxygenase	<i>C. maxima</i> 'Riesenmelone'	24
Moschatin 1 through 5	AF462349, AF504011, AY25646, AY27921, AY279217	ribosome-inactivating protein	<i>C. moschata</i> crookneck	**
CPS1	AB109763	copalyl diphosphate synthase; gibberellin biosynthesis	<i>C. maxima</i>	**
CPS	AF049905, AF049906	copalyl diphosphate synthase; gibberellin biosynthesis (2 genes)	<i>C. maxima</i>	37
Hsc70	AF527794, AF527795, AF527796	cell-autonomous heat shock protein; chaperonin 70 (multiple sequences)	<i>C. maxima</i>	1
	AB061204	thioredoxin h	<i>C. maxima</i>	**
Puga, Pugb, Pucg	AB055116, AB055117, AB055118	glutathione S-transferase	<i>C. maxima</i>	**
CYP88A	AF212990, AF212991	cytochrome P450; ent-kaurenoic acid oxidase (multiple alleles)	<i>C. maxima</i> 'Queensland Blue'	13
PP2	AF520583	phloem protein 2	<i>C. digitata</i> PI 240879	**
PP2	AF520582	phloem lectin	<i>C. argyrosperma</i> subsp. <i>sororia</i>	**
	L32700, L32701	phloem lectin	<i>C. argyrosperma</i>	2
	X56948	malate synthase	<i>Cucurbita</i> sp.*** 'Kurokawa Amakuri Nankin'	29
pMCPN60	X70867, X70868	chaperonin 60	'Kurokawa Amakuri Nankin'	40
PCPK	AY07280, AY072802	phloem calmodulin-like protein kinases	<i>C. maxima</i> 'Big Max'	47
	X55779	ascorbate oxidase	<i>C. maxima</i> 'Ebisu Nankin'	7
AAO	D55677	ascorbate oxidase	<i>C. maxima</i>	21
chitP1	AB015655	chitinase	<i>C. maxima</i> 'Ebisu Nankin'	**
PLC	AF082284	chitinase	<i>C. moschata</i> crookneck	20

PV72	AB006809	vacuolar sorting receptor	'Kurokawa Amakuri Nankin'	36
	D88420	stromal ascorbate peroxidase	'Kurokawa Amakuri Nankin'	28
	D78256	isocitrate lyase	'Kurokawa Amakuri Nankin'	27
	D70895	3-ketoacyl-CoA thiolase	'Kurokawa Amakuri Nankin'	19
	D83656	thylakoid ascorbate peroxidase	'Kurokawa Amakuri Nankin'	45
	D49433	hydroxypyruvate reductase	'Kurokawa Amakuri Nankin'	12
MP28	D45078	membrane protein	'Kurokawa Amakuri Nankin'	16
	D38132	glyoxysomal citrate synthase	'Kurokawa Amakuri Nankin'	18
	D29629	aconitase	'Kurokawa Amakuri Nankin'	10
	D16560	prepro2S albumin	'Kurokawa Amakuri Nankin'	8
	D14044	glycolate oxidase	'Kurokawa Amakuri Nankin'	39
	AF002016	acyl CoA oxidase	'Kurokawa Amakuri Nankin'	9
PP36	AF274589	cytochrome b5 reductase	<i>C. maxima</i> 'Big Max'	**
pAPX	AB070626	peroxisomal ascorbate peroxidase	'Kurokawa Amakuri Nankin'	33
CM-ACS3	AB038559	ACC synthase	<i>C. maxima</i>	43
CmATS	AB049135	acyl-(acyl-carrier protein); acyltransferase	<i>C. moschata</i> 'Shirogikuza'	**
	Y00771	glycerol-3-phosphate acyltransferase transit peptide	<i>C. moschata</i> 'Shirakikuza'	17
	AB002695	aspartic endopeptidase	<i>C. pepo</i>	14
PS-1	AF284038	phloem serpin	<i>C. maxima</i>	46
SLW	AF170086, AF170087	silverleaf whitefly-induced protein (multiple genes)	<i>C. pepo</i> zucchini 'Chefini'	41
aprX	Y17192	anionic peroxidase	<i>C. pepo</i> zucchini 'Black Beauty'	3
cpCPK1	U90262	calcium-dependent calmodulin-independent protein kinase	<i>C. pepo</i> zucchini	6
PP16	AF079170, AF079171	mRNA movement protein; phloem transport (multiple alleles)	<i>C. maxima</i> 'Big Max'	44
AOBP	D45066	transcription factor binding to ascorbate oxidase	<i>C. maxima</i>	22
accW	D01032	auxin-induced 1-aminocyclopropane-1-carboxylate synthase	<i>C. maxima</i> 'Ebisu'	32
	U37774	auxin-induced 1-aminocyclopropane-1-carboxylic acid synthase	<i>C. maxima</i>	31
ACC1	M58323	1-aminocyclopropane-1-carboxylate synthase	<i>C. pepo</i>	34

ACC1A, ACC1B	M61195	1-aminocyclopropane-1-carboxylate synthase (2 genes, tightly linked)	<i>C. pepo</i> zucchini	15
PHP-1	D86306	proton-translocating inorganic pyrophosphatase	<i>C. moschata</i> crookneck	**
PP1	U66277	phloem filament protein	<i>C. maxima</i> 'Big Max'	4
pfiAF4	X81647	trypsin inhibitor	<i>C. maxima</i> 'Supermarket Hybrid'	30
pfiBM7	X81447	chymotrypsin inhibitor	<i>C. maxima</i> 'Supermarket Hybrid'	30
	M15265	phytochrome	<i>C. pepo</i> zucchini 'Black Beauty'	35
NADH	M33154	nitrate reductase	<i>C. maxima</i>	5
	M36407	11S globulin beta-subunit	'Kurokawa Amakuri Nankin'	11
	AF206895	18S ribosomal RNA	<i>C. pepo</i>	**
	AF479108	26S ribosomal RNA	<i>C. pepo</i>	38

* Gene symbols were assigned by the researchers isolating the gene; they have no correspondence to the official *Cucurbita* gene symbols.

**Unpublished: Genes can be submitted directly to Genbank, without being published in a journal.

*** 'Kurokawa Amakuri Nankin' was identified only as "*Cucurbita* sp."

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