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The Genes of Pumpkin and Squash

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***Abstract*. Pumpkin and squash (*Cucurbita* L. spp.) are important cucurbit crops and are grown in almost all arable regions of the world. The three economically important species, *Cucurbita pepo* L., *Cucurbita moschata* Duchesne, and *Cucurbita maxima* Duchesne are highly polymorphic in fruit characteristics, inspiring much research into their inheritance. A comprehensive list of genes for *Cucurbita* was last published more than a decade ago. This new gene list for pumpkin and squash includes descriptions of gene interactions and the genetic background of the parents that had been used for crossing to allow easy confirmation of previous work and provide a sound foundation for further investigation. This gene list includes 79 loci for phenotypic/morphological traits and 48 polymorphic allozyme loci. Linkage and mapping are discussed.**

Pumpkin and squash (*Cucurbita* L. spp.), collectively, are a major vegetable crop and are grown in almost all regions, from cool temperate to tropical. The FAO (2005) lists nearly 1.5 × 10^6 ha being devoted to pumpkins, squash, and gourds, with about 60% of the over 19 × 10^6 Mg of production in Asia and most of the remainder in Europe and North America.

The words pumpkin and squash are often used interchangeably, but the origin and root meaning of these two terms are different. Generally, the edible *Cucurbita* fruit that are round or nearly round are referred to as pumpkins and those that are nonround are referred to as squash; inedible *Cucurbita* fruit are referred to as gourds, but gourds can also refer to fruit of other genera of the cucurbit family. Hence the FAO figures may include these other genera, two of which, *Benincasa hispida* (Thunb.) Cogn. (wax gourd, winter melon) and *Luffa acutangula* (L.) Roxb. (angled luffa), are regionally important vegetables in south, east, and southeastern Asia (Robinson and Decker-Walters, 1997). Although *Cucurbita* plants and fruit are grown for various reasons, most often they are grown for human consumption of their entire young fruit or mature fruit flesh. Cultigens with fruit deviating greatly from a 1:1 length-to-width ratio usually are grown for their immature fruit whilst those with fruit deviating little from this ratio usually are grown for their mature fruit (Paris, 1989). Different characteristics needed for the optimal use of the mature versus the immature fruit over the course of domestication and cultivar development may have been the igniter, together with cultivation at different localities, of the explosion of phenotypic variability in the fruit of each of the three major species, and resulted in their extreme polymorphy. This polymorphy has in turn inspired scientific investigation, especially into the genetic basis of fruit characteristics.

All of the dozen or so species of *Cucurbita* are native to the Americas. Most *Cucurbita* species grow wild in widely scattered regions of Mexico (Nee, 1990; Whitaker, 1947). Five species were cultivated by the inhabitants of the Americas for several thousand years before the arrival of Europeans. The domestication of a North American species, *C. pepo* L., is ancient, perhaps having begun 10,000 years ago (Smith, 1997).

The three economically important species, *C. pepo*, *C. maxima* Duchesne, and *C. moschata* Duchesne, differ in their climactic adaptation and therefore are distributed differently among the world's agricultural regions. Some *Cucurbita*, particularly the tropical pumpkins (*C. moschata*) are an important source of nutrition in less-developed countries having a tropical climate. Other *Cucurbita*, most notably zucchini squash (*C. pepo*), are of high monetary value in the economically developed countries having temperate climates. In addition to *C. pepo*, *C. maxima*, and *C. moschata*, two other species, *C. argyrosperma* Huber and *C. ficifolia* Bouché, are grown in some areas. There is evidence that a sixth species, *C. ecuadorensis* Cutler & Whitaker, had been domesticated and later abandoned by inhabitants of Ecuador (Andres and Robinson, 2002).

Pumpkin and squash were dispersed to other continents by transoceanic voyagers at the turn of the 16th century and have become familiar and important in many countries outside of the Americas. The highly populous countries, China and India, lead the world in production, with 5.6 and 3.5 × 10^6 Mg produced last year. Other major producers are, in order, Ukraine, U.S., Egypt, Mexico, Iran, Cuba, Italy, Turkey, South Africa, Spain, and Argentina (FAO, 2005).

Like most other members of the gourd family, Cucurbitaceae, pumpkin and squash are herbaceous and frost-sensitive, with large palmate leaves borne on usually trailing, tendril-bearing vines. The cultivated species are mesophytes having fibrous root systems. They are monoecious, bearing large, intensely orange-yellow, nectar-producing, unisexual flowers that are foraged by bees and that develop into prominent fruit. The greatest degree of polymorphism among genotypes is expressed in the fruit. The fast growth rate of pumpkin and squash, their large size, polymorphism, decorative value, and role as common table vegetables have fostered fascination and wonder in people of widely different cultures (Norrman and Haarberg, 1980).

A complete list of genes for *Cucurbita* species was last published 12 years ago (Hutton and Robinson, 1992). Since then, only updates have been published (Robinson and Hutton, 1996; Robinson and Paris, 2000).

This new gene list for *Cucurbita* contains much more detail concerning the sources of information, being modeled after the one for watermelon, *Citrullus lanatus* (Thunb.) Matsum. & Nakai, presented by Guner and Wehner (2004). To allow more easy 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. Names of cultivars or designations of inbred lines are included wherever possible, but as cultivars and inbreds tend to be replaced over the years, we have indicated their genetic background by cultivar-group (for *C. pepo*) (Paris, 2000d) or market type (for *C. maxima*, *C. moschata*) (Andres, 2004), where known, in the description of the parents. We have also included descriptions of gene interactions, which had been left out from the previous gene list for *Cucurbita*.

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, s-2, spn*, and Wmv^{ecu}. Those that have been published since the last update are: *Cmv, grl, prv, qi, sl, wmv, Zym-2*, and *Zym-3* and additional alleles at the *l-1* and *l-2* loci. Furthermore, 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* Bailey, with the separate designation *Pm-0* for resistance in and derived from *C. okeechobeensis* Bailey), and *Zym* (with separate designations for different sources of resistance, viz. zym^{ecu} from *C. ecuadorensis*, *Zym-0* from *C. moschata* Nigerian Local landrace, and *Zym-1* from *C. moschata* Menina landrace, and zym^{mos} from *C. moschata* 'Soler').

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. Genes affecting phenotypic/morphological traits are listed in Table 1. The data upon which are based identifications and concomitant assignment

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Table 1. The genes of *Cucurbita* affecting phenotypic and morphological characteristics.

Gene symbol				
Preferred	Synonym	Characteristic	*Cucurbita* species	Reference**(s)**
a		*androecious*. Found in 'Greckie'; produces only male flowers, recessive to *A*.	*pepo*	Kubicki, 1970
B		*Bicolor*. Precocious yellow fruit pigmentation; pleiotropic, affecting fruit and foliage, modified by *Ep-1*, *Ep-2* and *Ses-B*. Originally from 'Vaughn's Pear Shaped' ornamental gourd. *B* in the *C. moschata* Precocious PI 165561 breeding line derived from *C. pepo* through backcrossing. Complementary to *L-2* for intense orange, instead of light yellow, fruit-flesh color.	*pepo, moschata*	Shifriss, 1955, 1981; Schaffer and Boyer, 1984; Paris et al., 1985a; Paris, 1988
B^{max}	*B-2*	*Bicolor*. Precocious yellow fruit pigmentation, from subsp. *andreana* PI 165558	*maxima*	Shifriss, 1966, 1989
Bi		*Bitter* fruit. High cucurbitacin content in fruit. *Bi* from *C. maxima* subsp. *andreana* and *C. ecuadorensis*; *bi* from *C. maxima* subsp. *maxima*, including 'Queensland Blue'. Linked to *Lo-2*. For *C. pepo*: *Bi* from wild Texan gourd; *bi* from zucchini squash.	*maxima*, *maxima* × *ecuadorensis*, *pepo*	Contardi, 1939; Grebenšikov, 1955; Herrington and Brown, 1988
bl		*blue* fruit color. Incompletely recessive to *Bl* for green fruit color, in hubbard squash.	*maxima*	Hutchins, 1935
*Bn**		*Butternut* fruit shape. From 'New Hampshire Butternut', dominant to *bn* for crookneck fruit shape as in 'Canada Crookneck'.	*moschata*	Mutschler and Pearson, 1987
Bu		*Bush* habit. Short internodes; dominant to vine habit, *bu*, in young plant stage. For *C. pepo*: *Bu* in 'Giant Yellow Straightneck' and also a near-isogenic line of 'Table Queen', *bu* in 'Table Queen' acorn. For *C. maxima*: *Bu* from an inbred line, *bu* from 'Delicious'.	*pepo*, *maxima*	Shifriss, 1947; Grebenšikov, 1958; Denna and Munger, 1963
Cmv		*Cucumber mosaic virus* resistance. From Nigerian Local, dominant to *cmv* for susceptiblity from 'Waltham Butternut'.	*moschata*	Brown et al., 2003
cr		*cream* corolla. Cream to nearly white petals, *cr* from *C. okeechobeensis*; *Cr* from *C. moschata* 'Butternut' incompletely dominant (yellow petals for *Cr/cr*, and orange for *Cr/Cr*).	*moschata* × *okeechobeensis*	Roe and Bemis, 1977
cu		*cucurbitacin*-B reduced. Recessive *cu* for reduced cucurbitacin-B content of cotyledons of 'Early Golden Bush Scallop'; *Cu* for high cucurbitacin content of cotyledons of 'Black Zucchini'.	*pepo*	Sharma and Hall, 1971
D		*Dark* stem. Series of three alleles observed in *C. pepo*: *D* for dark stem and dark intermediate-age fruit, D^s for dark stem but fruit not affected, and *d* for light stem and fruit not affected, with dominance $D > D^s > d$. *D* from 'Fordhook Zucchini', D^s from 'Early Prolific Straightneck'; *d* from 'Vegetable Spaghetti'. Epistatic to genes *l-1* and *l-2* when either is homozygous recessive; linked to *mo-2*. For *C. maxima*: only the fruit was observed: *D* for dark intermediate-age fruit from the zapallito 'La Germinadora'; *d* for light intermediate-age fruit from a variant zapallito breeding stock.	*pepo*, *maxima*	Schöninger, 1952; Globerson, 1969; Paris and Nerson, 1986; Paris, 1996, 1997, 2000c; Lopez-Anido et al., 2003
de		*determinate* plant habit. Stem lacking tendrils and terminating with female flowers. Recessive to *De* for indeterminate plant habit. *De* from 'Jeju' and 'Sokuk', *de* from inbred designated "Det".	*moschata*	Kwack, 1995
Di		*Disc* fruit shape. From scallop squash, dominant to spherical or pyriform.	*pepo*	Sinnott and Durham, 1922; Whitaker, 1932
Ep-1		*Extender* of *pigmentation-1*. Modifier of *B*. *Ep-1* incompletely dominant to *ep-1* and additive with *Ep-2*. *Ep-1* from 'Small Sugar 7 × 7' pumpkin; *ep-1* from 'Table King' acorn.	*pepo*	Shifriss and Paris, 1981
Ep-2		*Extender* of *pigmentation-2*. Modifier of *B*. *Ep-2* incompletely dominant to *ep-2* and additive with *Ep-1*. *Ep-2* from 'Table King' acorn; *ep-2* from 'Small Sugar 7 × 7' pumpkin.	*pepo*	Shifriss and Paris, 1981
Fr		*Fruit fly* (*Dacus cucurbitae*) resistance. *Fr* from 'Arka Suryamukhi', dominant to *fr* for susceptibility.	*maxima*	Nath et al., 1976
fv		*fused vein*. Fusion of primary leaf veins, subvital male gametophyte; found in hull-less-seeded pumpkin breeding line.	*pepo*	Carle and Loy, 1996a, 1996b
G	*a, m*	*Gynoecious* sex expression. Dominant to *g* for monoecious sex expression.	*foetidissima*	Fulks et al., 1979; Dossey et al., 1981
Gb		*Green band* on inner side of base of petal, from a scallop squash. Dominant to *gb*, for no band, from a straightneck squash.	*pepo*	Dutta and Nath, 1972
gc		*green corolla*. Green, leaf-like petals, sterile; in unspecified F2 population.	*pepo*	Superak, 1987
gl		*glabrous*. Lacking trichomes.	*maxima*	Korzeniewska, 1992
Gr	*G*	*Green rind*. Dominant to buff skin of mature fruit. *Gr* from 'Long Neapolitan', *gr* from 'Butternut'.	*moschata*	Robinson, 1987
grl		*gray leaf*. Recessive to green leaf. Recessive *grl* derived from cross of zapallito-type line of *C. maxima* and a butternut-type line of *C. moschata*. Dominant *Grl* from zapallito-type *C. maxima*.	*maxima* × *moschata*	Lopez-Anido et al., 2002

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Table 1 (continued). The genes of *Cucurbita* affecting phenotypic and morphological characteristics.

Gene symbol				
Preferred	Synonym	Characteristic	*Cucurbita* species	Reference**(s)**
Hi		*Hard* rind *inhibitor*. *Hi*, for hard-rind inhibition, from *C. maxima* 'Queensland Blue'; *hi*, for no hard-rind inhibition, from *C. ecuadorensis*.	*maxima* × *ecuadorensis*	Herrington and Brown, 1988
Hr		*Hard rind*. *Hr* for hard (lignified) rind in ornamental gourd, straightneck squash, and zucchini; *hr* for soft (nonlignified) rind in 'Small Sugar' pumpkin and 'Sweet Potato' ('Delicata'). Complementary to *Wt* for *Warty* fruit.	*pepo*	Mains, 1950; Schaffer et al., 1986
i		*intensifier* of the *cr* gene for cream flowers. *Cr/– I/–* for intense orange or yellow flowers, *Cr/– i/i* for light orange or yellow flowers, *cr/cr I/–* for cream flowers, *cr/cr i/i* for white flowers. *I* from *C. moschata* 'Butternut', *i* from *C. okeechobeensis*.	*moschata* × *okeechobeensis*	Roe and Bemis, 1977
I-mc	I_{mc}	*Inhibitor* of *mature* fruit *color*; dominant to *i-mc* for no inhibition. *I-mc* in a scallop squash.	*pepo*	Clayberg, 1992
I-T		*Inhibitor* of the *T* gene for trifluralin resistance. *I-T* from 'La Primera'; *i-t* from 'Ponca' and 'Waltham Butternut'.	*moschata*	Adeniji and Coyne, 1981
l-1	*c, St*	*light* fruit coloration-*1*. Light intensity of fruit coloration. Series of five alleles observed in *C. pepo* which, in complementary interaction with the dominant *L-2* allele, give the following results: *L-1* for uniformly intense/dark fruit coloration, from 'Fordhook Zucchini'; *l-1*^{BSt} for broad, contiguous intense/dark stripes, from 'Cocozelle'; *l-1*St for narrow, broken intense/dark stripes, from 'Caserta'; *l-1*^{iSt} for irregular intense/dark stripes, from 'Beirut' vegetable marrow; *l-1* for light coloration, from 'Vegetable Spaghetti', with dominance of *L-1* > (*l-1*^{BSt} > *l-1*St) ≥ *l-1*^{iSt} > *l-1*. For *C. maxima*: *L-1* from the zapallito 'La Germinadora'; *l-1* from a variant zapallito breeding stock.	*pepo, maxima*	Scarchuk, 1954; Shifriss, 1955; Globerson, 1969; Paris and Nerson, 1986; Paris and Burger, 1989; Paris, 2000a, 2003; Lopez-Anido et al., 2003
l-2	*r*	*light* fruit coloration-*2*. Light intensity of fruit coloration. Series of three alleles observed in *C. pepo* that affect exterior color intensity of the fruit in complementary interaction with alleles at the *l-1* locus. Interactions of the dominant *L-2* allele, derived form 'Fordhook Zucchini', 'Cocozelle', and 'Caserta', with the various *l-1* alleles are as described above. Interactions of the *L-2*^{w} allele, derived from *C. pepo* subsp. *fraterna*, are delayed and weaker in comparison. The *l-2* allele, derived from 'Vegetable Spaghetti', confers light coloration and may be sub-vital. Dominance is *L-2* > *L-2*^{w} > *l-2*. The top dominant *L-2* allele is also complementary with dominant *B* for intense orange, instead of light yellow, fruit-flesh color and with recessive *qi* for intense exterior color of young fruit. For *C. maxima*: *L-2* from the zapallito 'La Germinadora'; *l-2* from a variant zapallito breeding stock.	*pepo, maxima*	Globerson, 1969; Paris and Nerson, 1986; Paris, 1988, 2000b, 2002a, 2002b; Lopez-Anido et al., 2003
lo-1	*l*	*lobed* leaves-*1*; recessive to *Lo-1* for nonlobed leaves.	*maxima*	Dyutin, 1980
Lo-2		Lobed leaves-*2*. *Lo-2* for lobed leaves in *C. ecuadorensis* dominant to *lo-2* for unlobed leaves in *C. maxima*. Linked to *Bi*.	*ecuadorensis* × *maxima*	Herrington and Brown, 1988
lt		*leafy tendril*. Tendrils with laminae; *lt* found in ornamental gourd.	*pepo*	Scarchuk, 1974
ly		*light yellow* corolla. Recessive to orange yellow; *ly* found in ornamental gourd.	*pepo*	Scarchuk, 1974
M		Mottled leaves. *M* for silver-gray areas in axils of leaf veins, dominant to *m* for absence of silver-gray. For *C. maxima*: *M* in 'Zuni' and *m* in 'Buttercup' and 'Golden Hubbard'. For *C. pepo*: *M* in 'Caserta' and inbred of 'Striato d'Italia' cocozelle; *m* in 'Early Prolific Straightneck' and 'Early Yellow Crookneck'. For *C. moschata*: *M* in 'Hercules' and 'Golden Cushaw', *m* in butternut type. Weakly linked to *Wt*.	*pepo, maxima, moschata*	Scott and Riner, 1946a; Scarchuk, 1954; Coyne, 1970; Paris et al., 2004
Mldg		*Mottled light* and *dark green* immature fruit color; germplasm unspecified. Dominant to nonmottled.	*moschata*	Cardosa et al., 1993
mo-1		*mature orange-1*. Complementary recessive gene for loss of green fruit color before maturity. *Mo-1* from 'Table Queen' acorn; *mo-1* from 'Vegetable Spaghetti'.	*pepo*	Paris, 1997
mo-2		*mature orange-2*. Complementary recessive gene for loss of green fruit color before maturity. *Mo-2* from 'Table Queen' acorn; *mo-2* from 'Vegetable Spaghetti'. Linked to *D*.	*pepo*	Paris, 1997
ms-1	ms_1	*male sterile-1*. Male flowers abort before anthesis, derived from a cross involving 'Golden Hubbard', recessive to *Ms-1* for male fertile.	*maxima*	Scott and Riner, 1946b
ms-2	ms_2	*male sterile-2*. Male flowers abort, sterility expressed as androecium shrivelling and turning brown; *ms-2* from 'Eskandarany' (PI 228241).	*pepo*	Eisa and Munger, 1968
ms-3	*ms-2*	*male sterile-3*.	*maxima*	Korzeniewska, 1992

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Table 1 (continued). The genes of *Cucurbita* affecting phenotypic and morphological characteristics.

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Preferred	Synonym	Characteristic	*Cucurbita* species	Reference**(s)**
m-zym^{mos}*		*modifier* of dominance of *zucchini yellow mosaic* virus resistance. Confers resistance to otherwise susceptible *Zym*^{mos}/*zym*^{mos} heterozygotes. *M-zym*^{mos} in 'Soler', *m-zym*^{mos} in 'Waltham Butternut' and "Nigerian Local".	*moschata*	Pachner and Lelley, 2004
n	*h*	*naked* seeds. Lacking a lignified seed coat, *n* from oil-seed pumpkin.	*pepo,* *moschata*	Schöninger, 1952; Grebenšikov, 1954; Xianglin, 1987; Zraidi et al., 2003
pl		*plain light* fruit color. Recessive *pl* from 'Beirut' vegetable marrow and 'Fordhook Zucchini'; *Pl* in 'Vegetable Spaghetti'.	*pepo*	Paris, 1992
Pm		*Powdery mildew* resistance. Resistance to *Golovinomyces cichoracearum; Pm* in *C. lundelliana*.	*lundelliana*	Rhodes, 1964
*Pm-0**		*Powdery mildew* resistance-*0*. Resistance to *Podosphaera xanthii*. *Pm-0* from *C. okeechobeensis* and introgressed to *C. pepo*. Not known if this is the same or a different locus from *Pm*.	*okeechobeensis,* *pepo*	Contin, 1978; Jahn et al., 2002; Cohen et al., 2003
pm-1		*powdery mildew* resistance-*1*. Resistance to *Golovinomyces cichoracearum* in *C. moschata*. Series of three alleles: *pm-1*^{P} for high susceptibility from 'Ponca' dominant to *pm-1*^{L} for resistance from 'La Primera', which is dominant to *pm-1*^{W} for susceptibility in 'Waltham Butternut'.	*moschata*	Adeniji and Coyne, 1983
pm-2		*powdery mildew* resistance-*2*. Resistance to *Golovinomyces cichoracearum* in *C. moschata*. Allele *pm-2*^{S} for resistance in 'Seminole' is recessive to *Pm-2* for susceptibility in 'Ponca'.	*moschata*	Adeniji and Coyne, 1983
prv		*papaya ringspot virus* resistance. In 'Nigerian Local', recessive to *Prv* for susceptibility in 'Waltham Butternut'.	*moschata*	Brown et al., 2003
qi		*quiescent intense*. Recessive to *Qi* for not intense and complementary to *L-2* for intense young fruit color; little or no effect on mature fruit. *Qi* from 'Vegetable Spaghetti'; *qi* from 'Jack O'Lantern' pumpkin and 'Verte noncoureuse d'Italie' cocozelle.	*pepo*	Paris, 2000b, 2002b
Rd		*Red* skin. Red external fruit color; dominant to green, white, yellow and gray. *Rd* from 'Turk's Cap'; *rd* from 'Warted Hubbard'.	*maxima*	Lotsy, 1920
ro		*rosette* leaf. Lower lobes of leaves slightly spiraled, *ro* derived from an ornamental gourd.	*pepo*	Mains, 1950
s-1	*s*	*sterile-1*. Male flowers small, without pollen; female flower sterile. Derived from crossing 'Greengold' with 'Banana'.	*maxima*	Hutchins, 1944
s-2		*sterile-2*. Male flowers small, without pollen and female flower sterile; mutant in a powdery mildew-resistant straightneck squash breeding line.	*pepo*	Carle, 1997
Ses-B		*Selective suppression* of gene *B*. Suppression in foliage of precocious yellowing conferred by *B*. *Ses-B* in straightneck breeding line dominant to *ses-B* in 'Jersey Golden Acorn'.	*pepo*	Shifriss, 1982
sl		*silverleaf* resistance. Recessive to *Sl* for susceptibility. *Sl* from 'Soler'; *sl* from PI 162889 and butternut types.	*moschata*	Gonzalez-Roman and Wessel-Beaver, 2002
Slc		*Squash leaf curl* virus resistance. Derived from *C. moschata*.	*pepo*	Montes-Garcia et al., 1998
sp		*spaghetti* flesh. Flesh breaking into strands after cooking.	*pepo*	Mazurek and Niemirowicz-Szczytt, 1992
*spn**		*spineless* foliage. Petioles and abaxial surfaces of leaf laminae glabrous, lacking spiculate trichomes. Derived from male parent of 'Multipik' hybrid straightneck. Spininess, *Spn*, from various straightneck inbreds is incompletely dominant.	*pepo*	Superak, 1999
T		*Trifluralin* resistance. Dominant to susceptibility to the herbicide; modified by *I-T*. *T* in 'La Primera'; *t* in 'Ponca' and 'Waltham Butternut'.	*moschata*	Adeniji and Coyne, 1981
uml		*umbrella-like*. Leaves shaped like partially opened umbrella. Recessive *uml* derived from a cross of *C. maxima* 'Warzywna' and a *C. pepo* inbred; dominant *Uml* from 'Warzywna'.	*maxima* × *pepo*	Rakoczy-Trojanowska and Malepszy, 1999
v		*virescent*. Yellow-green young leaves, *v* found in 'Golden Delicious'.	*maxima*	Dyutin and Afanas'eva, 1981
W		*Weak* fruit coloration [formerly *White* fruit]. Dominant to *w* for intense-pigmented mature fruit; *W* from scallop squash. Complementary to *Wf* for white external fruit color.	*pepo*	Sinnott and Durham, 1922; Whitaker, 1932; Paris et al., 1985b; Paris, 1995
wc		*white corolla*. Derived from 'Ispanskaya' × 'Emerald'. Recessive to *Wc* for normal orange-yellow corolla	*maxima*	Korzeniewska, 1996
Wf		*White flesh*. Dominant to *wf* for colored flesh. *Wf* in a scallop squash, *wf* in a straightneck squash. Complementary to *W* for pale orange or white external fruit color.	*pepo*	Sinnott and Durham, 1922; Dutta and Nath, 1972; Paris, 1995
Wmv		*Watermelon mosaic virus* resistance. From 'Menina' and 'Nigerian Local', dominant to *wmv* for susceptibility in 'Musquée de Provence' and 'Waltham Butternut'. May be linked with or identical to *Zym-1*.	*moschata*	Gilbert-Albertini et al., 1993; Brown et al., 2003

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Table 1 (continued). The genes of *Cucurbita* affecting phenotypic and morphological characteristics.

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Wmv^{ecu}*		*Watermelon mosaic virus* resistance. From *C. ecuadorensis*, in a cross with an unspecified *C. maxima*.	*maxima* × *ecuadorensis*	Weeden et al., 1984
Wt		*Warty* fruit. Dominant to nonwarted, *wt*, and complementary to *Hr*, with fruit wartiness being expressed only in the presence of the dominant *Hr* allele. *Wt* in straightneck, crookneck, and 'Delicata'; *wt* in zucchini, cocozelle, and 'Small Sugar' pumpkin. Weakly linked to *M*.	*pepo*	Sinnott and Durham, 1922; Schaffer et al., 1986; Paris et al., 2004
wyc		*white-yellow corolla*. Isolated in 'Riesen-Melonen'. Recessive to *Wyc* for normal orange-yellow corolla.	*maxima*	Korzeniewska, 1996
Y		*Yellow* fruit color. *Y* for yellow fruit color of intermediate-age fruit, from straightneck and crookneck squash, dominant to *y* for green intermediate-age fruit color, from vegetable marrow, ornamental gourd, and cocozelle.	*pepo*	Sinnott and Durham, 1922; Scarchuk, 1954; Shifriss, 1947, 1955; Paris et al., 2004
yg		*yellow-green* leaves and stems.	*maxima*	Korzeniewska, 1992
Ygp		*Yellow-green placenta*. Dominant to yellow placental color. *Ygp* in a scallop squash, *ygp* in a straightneck squash.	*pepo*	Dutta and Nath, 1972
ys		*yellow seedling*. Lacking chlorophyll; lethal.	*pepo*	Mains, 1950
zym^{ecu}		*zucchini yellow mosaic* virus resistance. Recessive to susceptibility; zym^{ecu} from *C. ecuadorensis*, Zym^{ecu} from *C. maxima* 'Buttercup'.	*ecuadorensis*	Robinson et al., 1988
zym^{mos}*		*zucchini yellow mosaic* virus resistance. Recessive to susceptibility; zym^{mos} from 'Soler', Zym^{mos} from 'Waltham Butternut'.	*moschata*	Pachner and Lelley, 2004
*Zym-0**		*Zucchini yellow mosaic* virus resistance. *Zym-0* from *C. moschata* 'Nigerian Local' dominant to *zym-0* for susceptibility from 'Waltham Butternut'. Perhaps one of two separate genes for resistance in 'Nigerian Local'.	*moschata*	Munger and Provvidenti, 1987; Brown et al., 2003; Pachner and Lelley, 2004
Zym-1		*Zucchini yellow mosaic* virus resistance. *Zym-1* from *C. moschata* 'Menina' dominant to *zym-1* for susceptibility from *C. moschata* 'Waltham Butternut'. *Zym-1* transferred via backcrossing to *C. pepo* 'True French' zucchini, in which it confers resistance through complementary interaction with *Zym-2* and *Zym-3*. *Zym-1* is either linked with *Wmv* or also confers resistance to watermelon mosaic virus.	*moschata*, *pepo*	Paris et al., 1988; Gilbert-Albertini et al., 1993; Paris and Cohen, 2000; Pachner and Lelley, 2004
Zym-2		*Zucchini yellow mosaic* virus resistance-*2*. Dominant to susceptibility and complementary to *Zym-1*. *Zym-2* from *C. moschata* 'Menina'. *Zym-2* in *C. pepo* derived from *C. moschata*, in near-isogenic resistant line of 'True French' zucchini; *zym-2* from *C. pepo* 'True French'.	*moschata*, *pepo*	Paris and Cohen, 2000
Zym-3		*Zucchini yellow mosaic* virus resistance-*3*. Dominant to susceptibility and complementary to *Zym-1*. *Zym-3* from *C. moschata* 'Menina'. *Zym-3* in *C. pepo* derived from *C. moschata*, in near-isogenic resistant line of 'True French' zucchini; *zym-3* from *C. pepo* 'True French'.	*moschata*, *pepo*	Paris and Cohen, 2000

*Proposed new gene symbol.

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 F_2 and/or backcross 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, 66, have been identified for *C. pepo*. For *C. moschata* and *C. maxima*, 21 and 19 genes have been identified, respectively, and for the interspecific cross of *C. maxima* × *C. ecuadorensis*, 29 genes have been identified, of which 25 are isozyme variants. One or two genes have also been identified in four of the wild species (*C. okeechobeensis*, *C. lundelliana*, *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* and *C. ficifolia*.

As far as is known, all *Cucurbita* have 20 pairs of chromosomes (2n = 2x = 40). Given this high basic chromosome number, relatively few cases of linkage of genes affecting the phenotype have been found. Some of the isozyme variants have also been found to be linked to one another.

RAPD markers have been categorized and organized into linkage groups. They are not listed here but can be found in Brown and Myers (2002) and Zraidi and Lelley (2004). 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.

Gene Loci Affecting Vegetative Characteristics

Characteristics of seedlings. A recessive lethal, *ys*, has been found in *C. pepo* that causes seedlings to lack chlorophyll (Mains, 1950). The cucurbitacin-B content of cotyledons is controlled by locus *cu* in *C. pepo*, with higher content being associated with the dominant allele (Sharma and Hall, 1971).

Characteristics of vine and stem. Most *Cucurbita* are large, indeterminant, viney plants having long internodes. In *C. pepo* and *C. maxima*, short internodes are conferred by allele *Bu*, which is dominant early in plant development and recessive later on (Denna and Munger, 1963; Grebenšcikov, 1958; Paris, 2002b; Shifriss, 1947). A recessive gene, *de*, confers determinant plant growth in *C. moschata* (Kwack, 1995). Dark, almost black stems are controlled by *D* and D^s in *C. pepo*; D^s affects stems only, while *D* also darkens intermediate-age fruit (Globerson, 1969; Paris, 1996, 2000c, 2002a; Paris and Nerson, 1986; Schöniger, 1952). *D* is dominant to D^s and both *D* and D^s are dominant to the allele for light stems, *d*. Yellow-green leaves and stems are caused by recessive *yg* in *C. maxima* (Korzeniewska, 1992).

Characteristics of leaves. Silver patches in the axils of leaf veins, referred to as silver mottling, is conferred by the dominant allele *M* in *C. pepo*, *C. maxima*, and *C. moschata*

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(Coyne, 1970; Paris et al., 2004; Scarchuk, 1954; Scott and Riner, 1946a). Some of the progeny in a cross of *C. maxima* × *C. moschata* were observed to have entirely silver-gray, rather than green, leaf laminae; this mutant characteristic is caused by a recessive allele, *grl*, from *C. moschata* (Lopez-Anido et al., 2002). In some *C. maxima*, the young leaves are yellow-green rather than green; this is caused by a recessive allele, *v* (Dyutin and Afanas'eva, 1981).

Cucurbita leaves have trichomes. The absence of trichomes in some *C. maxima* is caused by a recessive allele, *gl* (Korzeniewska, 1992). The foliage of *C. pepo* is ordinarily harshly spiculate, due to stiff, spiny trichomes; spinelessness has been found in this species, however, and observed to be conferred by a single recessive gene, *spn* (Superak, 1999).

Fusion of the primary leaf veins is caused by *fv* in *C. pepo* (Carle and Loy, 1996a, 1996b). Rosette leaves, in which the lower lobes are slightly spiraled, are controlled by *ro* (Mains, 1950). Umbrella-like leaves, conferred by recessive allele *uml*, were found in a *C. maxima* × *C. pepo* cross (Rakoczy-Trojanowska and Malepszy, 1999), the recessive allele apparently derived from *C. pepo*. Lobed leaves are recessive in *C. maxima*, conferred by *lo-1* (Dyutin, 1980). However, lobed leaves are conferred by allele *Lo-2* in *C. ecuadorensis* which is dominant to *lo-2* for unlobed leaves in *C. maxima* (Herrington and Brown, 1988). Leafy tendrils with laminae are conferred by *lt* in *C. pepo* (Scarchuk, 1974).

Gene Loci Affecting Flowering Characteristics

Flower function and sexuality. A number of genes control flower function and sexuality. Three genes have been found to cause male sterility: *ms-1* and *ms-3* in *C. maxima* (Korzeniewska, 1992; Scott and Riner, 1946b) and *ms-2* in *C. pepo* (Eisa and Munger, 1968). Two recessive mutants for complete plant sterility have been identified, *s-1* in *C. maxima* (Hutchins, 1944) and *s-2* in *C. pepo* (Carle, 1997). Most *Cucurbita* species are monoecious but dominant *G* in *C. foetidissima* confers gynoecy (Dossey et al., 1981; Fulks et al., 1979). A recessive mutant in *C. pepo*, *a*, results in androecious plants (Kubicki, 1970).

Corolla color. Most *Cucurbita* species have yellow to orange corollas, but in *C. okeechobeensis* the corollas are white. In the cross of *C. okeechobeensis* × *C. moschata*, light-colored corollas were found to be conferred by a recessive allele, *cr*, the effect of which is enhanced by another recessive allele, *i* (Roe and Bemis, 1977). In *C. pepo*, the recessive gene *ly* confers light yellow corolla (Scarchuk, 1974), recessive *gc* confers green leaf-like petals (Superak, 1987), and dominant *Gb* confers a green band on the inner side of the base of the corolla (Dutta and Nath, 1972). Two recessive genes have been observed to affect corolla color in *C. maxima*, *wc* for white and *wyc* for white-yellow (Korzeniewska, 1996).

Gene Loci Affecting Fruit Characteristics

Fruit size and shape. Fruit size and fruit shape are highly polygenic characteristics that almost completely defy simple Mendelian analysis. Notwithstanding, two genes have been identified that affect fruit shape. In *C. pepo*, *Di* controls disc versus pyriform or spherical shape (Sinnott and Durham, 1922; Whitaker, 1932). In *C. moschata*, *Bn* controls butternut (bell) shape, as opposed to the elongated crookneck shape of the homozygous recessive (Mutschler and Pearson, 1987).

Fruit color. Fruit color is highly variable, especially in *C. pepo*, for which over a dozen genes have been identified, several of which are multiple-allelic and among which occur a number of nonadditive interactions. Two of the most important loci are the multiple-allelic *l-1* and *l-2*. Dark, intense coloration of the fruit throughout its development results from the complementary interaction of the top dominant *L-1* and *L-2* alleles (Paris and Nerson, 1986); when either or both *l* genes are homozygous recessive, the fruit are lightly colored. When the dominant *L-2* allele is present, the other three alleles at *l-1* give the following results: broad, contiguous intense/dark stripes from $l\text{-}1^{BSt}$ (Paris, 2000a; Paris et al., 2004), narrow, broken intense/dark stripes from $l\text{-}1^{St}$ (Paris, 2002b; Paris and Burger, 1989; Scarchuk, 1954; Shifriss, 1955), and irregular intense/dark stripes from $l\text{-}1^{iSt}$ (Paris, 2003). The effects of dominant alleles at *l-1* are delayed and weakened in the presence of $L\text{-}2^{w}/L\text{-}2^{w}$ and are slight or unexpressed in the presence of *l-2/l-2* (Paris, 2002a). Intense color in young fruit is also conferred by the recessive *qi* allele in complementary interaction with the dominant *L-2* allele (Paris, 2000b, 2002b). Dark intermediate-age fruit can also be caused by the top-dominant *D* allele, which is epistatic at that age of fruit development to *l-1* and *l-2* when either is homozygous recessive (Paris, 1996, 1997; Paris and Nerson, 1986).

There are several other important loci affecting fruit color in *C. pepo*. Gene *Y* is incompletely dominant over *y*; when homozygous, it confers a yellow color to the young fruit, which remains yellow or turns yellow-orange or orange as it matures; when heterozygous, the yellow-orange color is conferred beginning at intermediate age of the fruit (Paris et al., 2004; Scarchuk, 1954; Shifriss, 1947, 1955; Sinnott and Durham, 1922). Gene *W* is dominant over *w*, conferring a weak coloration to the fruit exterior by preventing the accumulation of green and orange pigments (Paris, 1995; Paris et al., 1985b; Sinnott and Durham, 1922). *Wf* confers white fruit flesh color and is dominant to *wf* for colored fruit flesh; by preventing the accumulation of yellow pigments, it is complementary to *W* for conferring pale orange or white mature fruit (Paris, 1995; Sinnott and Durham, 1922; Whitaker, 1932).

The most intriguing locus of all that affects fruit color is *B*, a mutant gene that confers yellow color or patches of yellow color on the ovary from the time it is differentiated (Schaffer and Boyer, 1984; Shifriss, 1955, 1981). These precociously yellow-affected ovaries or parts thereof remain yellow or turn orange as the fruit sets, develops and matures. *B* is incompletely dominant to *b* for normal entirely green coloration of the ovary. When the ovary is completely yellow, the adjacent peduncle, calyx, and corolla may also be yellow; the extent of the yellow is determined by whether *B* is homozygous or heterozygous and by the dosage of the incompletely dominant and additive modifiers, *Ep-1* and *Ep-2*, that enlarge the yellow-affected area (Shifriss and Paris, 1981). *B/b* with 0 to 1 dominant *Ep* alleles gives bicolor green and yellow fruit; 2 to 4 dominant alleles extend the yellow coloration throughout the fruit. *B/B* with 0 to 1 dominant *Ep* alleles gives completely yellow fruit; 2 to 4 dominant alleles extend the yellow coloration into the peduncle and the corolla. Dominant *B* interacts with dominant *L-2* to confer intensely orange fruit flesh (Paris, 1988). *B* can be expressed also in leaf laminae, as numerous round intense-yellow spots, in the presence of recessive *ses-B* (Shifriss, 1982).

In addition to the genes mentioned above, there are several others that have relatively minor effects on fruit color or that are generally hypostatic to the genes described above. Plain light-colored intermediate-age fruit is conferred by the recessive allele *pl* in the presence of genotype *d/d L-1/–l-2/l-2* (Paris, 1992). The loci *mo-1* and *mo-2* are complementary recessive genes which cause loss of green color of the fruit before its maturity (Paris, 1997). The dominant allele *I-mc* inhibits mature fruit coloration, including striping (Clayberg, 1992). Yellow-green placenta is caused by *Ygp* in *C. pepo*; the recessive phenotype is yellow placenta (Dutta and Nath, 1972).

Precocious yellow fruit color in *C. maxima* is controlled by B^{max}, which is not allelic to *B* from *C. pepo* (Shifriss, 1966, 1989). Other fruit color genes are *bl* for blue fruit (Hutchins, 1935), and *Rd* for red fruit (Lotsy, 1920). As in *C. pepo*, a three-gene interaction has been shown to control color intensity in immature fruit of *C. maxima* (Lopez-Anido et al., 2003). The genes are assumed to be the same as *L-1*, *L-2*, and *D* but no allelism tests have been conducted. Basic fruit colors in *C. moschata* are buff or green, determined by alleles at *Gr* (Robinson, 1987). The dominant allele at *Mldg* causes mottled light and dark green immature fruit color, with the recessive *mldg* conferring nonmottled immature fruit color (Cardosa et al., 1993). The precocious yellow trait is controlled by *B*, transferred in from *C. pepo* (Paris et al., 1985a).

Other fruit characteristics. Three genes affecting rind texture have been identified. The dominant *Hr* allele confers lignification of the rind of *C. pepo* (Mains, 1950). The dominant *Wt* allele confers warty fruit (Paris et al., 2004; Sinnott and Durham, 1922). *Hr* and *Wt* are complementary, warts appearing only in the presence of the dominant alleles at both loci (Schaffer et al., 1986). Dominant *Hi* was reported to inhibit hard rind in *C. maxima* (Herrington and Brown, 1988).

Wild *Cucurbita* fruit are extremely bitter. Bitterness is conferred by the dominant allele at the *Bi* locus in *C. pepo*, *C. maxima*, and *C.*

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ecuadorensis (Contardi, 1939; Grebenšcikov, 1955; Herrington and Brown, 1988).

The spaghetti squash cultivars of *C. pepo* have flesh that separates into strands after cooking. This characteristic is reportedly conferred by the recessive allele, *sp* (Mazurek and Niemirowicz-Szczytt, 1992).

Formation of a lignified seed coat is controlled by locus *n*, with the recessive phenotype having naked, that is hull-less, seeds in *C. pepo* (Grebenšcikov, 1954; Schöniger, 1952; Zraidi et al., 2003). A recessive gene of similar effect has been reported in *C. moschata* (Xianglin, 1987).

Gene Loci Affecting Resistance to Maladies and Pests

Resistance to viruses. The genetic control of resistance in *Cucurbita* to a number of diseases has been determined. In *C. moschata*, resistance to cucumber mosaic virus is conferred by a single dominant gene, *Cmv* (Brown et al., 2003). Resistance to watermelon mosaic virus is also conferred by a single dominant gene, *Wmv* (Brown et al., 2003; Gilbert-Albertini et al., 1993). Papaya ringspot virus resistance is conferred by a single recessive gene, *prv* (Brown et al., 2003).

Resistance to squash leaf curl virus is conferred by *Slc* and is dominant in *C. pepo*; *Slc* is derived from *C. moschata* (Montes-Garcia et al., 1998). Watermelon mosaic virus resistance has also been reported to be conferred by a single dominant gene in *C. ecuadorensis* (Weeden et al., 1984), to which the symbol Wmv^{ecu} is assigned.

Zucchini yellow mosaic virus is a major disease in *Cucurbita* and resistance has been extensively studied. The two sources of resistance utilized in breeding are from *C. ecuadorensis*, used with *C. maxima*, and from *C. moschata*, used with *C. moschata* and *C. pepo*. The resistance from *C. ecuadorensis* is expressed in the cross with *C. maxima* as a single recessive gene, zym^{ecu} (Robinson et al., 1988). Five genes for resistance residing at separate loci have been identified in *C. moschata*. A recessive gene for resistance, zym^{mos}, is possessed by 'Soler' and was identified in a cross with the susceptible 'Waltham Butternut'. It is modified by $m\text{-}zym^{mos}$, which confers resistance to Zym^{mos}/zym^{mos} heterozygotes which would otherwise be susceptible (Pachner and Lelley, 2004). *Zym-0* is a dominant gene for resistance derived from the Nigerian Local landrace (Brown et al., 2003; Munger and Provvidenti, 1987; Pachner and Lelley, 2004). *Zym-1* was identified in the 'Menina' landrace from Portugal and is dominant to the susceptible allele from 'Waltham Butternut' (Pachner and Lelley, 2004; Paris et al., 1988). *Zym-1* also confers resistance to watermelon mosaic virus or is tightly linked to a gene conferring watermelon mosaic virus resistance, possibly *Wmv* (Gilbert-Albertini et al., 1993). Resistance from Menina behaves as if controlled by a single gene in crosses with other *C. moschata*. However, when the resistance trait was introgressed into a zucchini cultivar of *C. pepo*, it became clear that there were additional, complementary genes involved. These complementary dominant genes, derived from *C. moschata*, are known as *Zym-2* and *Zym-3* (Paris and Cohen, 2000).

Other resistances. Powdery mildew caused by two fungi, *Podosphaera xanthii* (formerly *Sphaerotheca fulginea*) and *Golovinomyces cichoracearum* (formerly *Erysiphe cichoracearum*), is a significant disease problem on *Cucurbita*. Two dominant genes have been identified that confer resistance to powdery mildew. The dominant *Pm* allele, derived from *C. lundelliana*, was reported to confer resistance to *G. cichoracearum* (Rhodes, 1964). The dominant *Pm-0* allele, derived from *C. okeechobeensis* (Contin, 1978), has been introgressed into *C. pepo* (Jahn et al., 2002) and confers resistance to *P. xanthii* (Cohen et al., 2003). Resistance to *G. cichoracearum* has also been reported in *C. moschata* (Adeniji and Coyne, 1983). The *pm-1* locus was described as a 3-allele series, with $pm\text{-}1^{L}$ for resistance from 'La Primera' being dominant to $pm\text{-}1^{W}$ for susceptibility from 'Waltham Butternut' but recessive to the allele for high susceptibility, $pm\text{-}1^{P}$, from 'Ponca'. Another gene for resistance, $pm\text{-}2^{S}$, is from 'Seminole' and is recessive to the allele for susceptibility, *Pm-2*, from 'Ponca'. Allelism tests showed that *pm-1* and *pm-2* are indeed separate loci.

Leaf silvering is a severe disorder of *Cucurbita* related to whitefly feeding and drought stress. Resistance to silverleaf has been found in *C. moschata* that is conferred by a single recessive gene, *sl* (Gonzalez-Roman and Wessel-Beaver, 2002).

A dominant gene, *Fr*, confers resistance to fruit fly (*Daucus cucurbitae*) feeding in *C. maxima* (Nath et al., 1976). In *C. moschata*, resistance to the herbicide trifluralin is conferred by a dominant gene, *T*, except when another dominant gene, *I-T*, is also present (Adeniji and Coyne, 1981).

Isozyme Variants

Forty-eight polymorphic isozyme loci have been found in *Cucurbita*. Of these, 25 were observed as a pair of alleles in the interspecific cross of *C. maxima* × *C. ecuadorensis* (Wall and Whitaker, 1971; Weeden and Robinson, 1986). Some of these loci, as well as the remaining 23, were observed to be polymorphic among accessions and wild populations of *C. pepo*, with as many as eight alleles observed (Decker, 1985; Decker-Walters et al., 1993; Decker and Wilson, 1987; Kirkpatrick et al., 1985; Ignart and Weeden, 1984; Wilson, 1989).

Gene Linkage and Mapping

Most of the genes in this list have not been mapped, as classical linkage maps composed of segregating traits and isozyme variants or on molecular-marker maps. However, some cases of linkage have been reported. These are *Bi – Lo-2* (bitter fruit and one of the genes for lobed leaves) in the progeny of a *C. maxima* × *C. ecuadorensis* cross (Herrington and Brown, 1988), *D–mo-2* (dark stem and one of the genes for mature orange fruit color) in *C. pepo* (Paris, 1996), and *M–Wt* (silver leaf mottling and warts on the fruit) in *C. pepo* (Paris et al., 2004). In *C. moschata* Menina landrace, a gene for resistance to watermelon mosaic virus is either tightly linked to or identical with the gene for zucchini yellow mosaic virus resistance (*Zym-1*) (Gilbert-Albertini et al., 1993).

Weeden and Robinson (1986) examined 22 isozymes in a segregating *C. maxima* × *C. ecuadorensis* population. They observed the following linkages: *Aat-mb–Mdh-m2*, *Gal-1–Gal-2*, *Aat-p2–Gpi-c2*, *Est-1–Tpi-c2*, *Pgm-c2–Acp-1*, and *Pgm-c2–Pgm-p*. Also, *Aldo-p* was observed to be linked to a gene for watermelon mosaic virus resistance, Wmv^{ecu}.

Two linkage maps of *Cucurbita* have been constructed using molecular markers. Brown and Myers (2002) used 148 RAPD markers to map the BC_1 progeny of a cross between a *C. pepo* straightneck squash and *C. moschata* 'Nigerian Local'. The map has 28 linkage groups covering 1,954 cM, which is estimated to be 75% of the genome. Traits mapped as either single gene markers or QTLs included precocious yellow fruit color (*B*), leaf mottle (*M*), mature fruit color, fruit shape, and the depth of indentation between primary leaf veins. Zraidi and Lelley (2004) used 254 RAPD markers and 3 simple sequence repeats (SSRs) to map the F_2 progeny of a cross between an oil-seed pumpkin and a zucchini (both *C. pepo*). The map has 36 linkage groups and covers 1,425 cM. Traits mapped as either single gene markers or QTLs included nonlignified seed coat (*n*), fruit length, fruit width, fruit length-to-width ratio, and the number of fruit chambers. The two maps cannot be directly compared, as RAPD markers are population-specific.

Conclusions

Table 1 lists and describes 79 genes identified in *Cucurbita* from over 80 years of research in classical genetics. Many of these genes are readily available in cultivars that can be associated with particular market types and/or cultivar-groups. Other genes, however, are unique and/or deleterious and are no longer available. Those that have been lost or at least were of unknown availability to Hutton and Robinson (1992) include *a*, *ro*, *s*, and *ys*. Increasingly restrictive laws concerning transport of seeds across international boundaries have made preservation of existing rare mutants, by one or several experts willing to act as gene curators, increasingly difficult and impractical. This has further increased the precariousness of the existence of these unique mutants.

Given the high basic chromosome number of *Cucurbita*, it is not surprising that little is known about possible linkages of these genes and none have been mapped to specific chromosomes or sequenced. In Genbank, over 90 genes are listed as having been sequenced from *Cucurbita*; however, none have been associated with a phenotype. Although isozymes and DNA markers are valuable for taxonomic studies, they are also of potential value for their linkage to genes affecting phenotypic and morphological characteristics. Unfortunately, few of the isozyme variants listed in Table 2

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Table 2. The isozyme variants of *Cucurbita*.

Gene symbol		Alleles		*Cucurbita*	
Preferred	Synonym	observed (no.)	Character	species	Reference(s)
Aat-1	*Aat*	8	*Aspartate aminotransferase-1*. Variant among accessions.	*pepo*	Ignart and Weeden, 1984; Decker-Walters et al., 1993
Aat-3		2	*Aspartate aminotransferase-3*. Variant among wild populations.	*pepo*	Decker-Walters et al., 1993
Aat-4		3	*Aspartate aminotransferase-4*. Variant among wild populations.	*pepo*	Decker-Walters et al., 1993
Aat-mb		2	*Aspartate aminotransferase–microbody.*	*maxima* × *ecuadorensis*	Weeden and Robinson, 1986
Aat-m1		2	*Aspartate aminotransferase mitochondria-1.*	*maxima* × *ecuadorensis*	Weeden and Robinson, 1986
Aat-m2		2	*Aspartate aminotransferase mitochondria-2.*	*maxima* × *ecuadorensis*	Weeden and Robinson, 1986
Aat-p2		2	*Aspartate aminotransferase plastid-2.*	*maxima* × *ecuadorensis*	Weeden and Robinson, 1986
Acp-1		2	*Acid phosphatase-1.*	*maxima* × *ecuadorensis*	Weeden and Robinson, 1986
Acp-2		2	*Acid phosphatase-2.*	*maxima* × *ecuadorensis*	Weeden and Robinson, 1986
Aldo-p		2	*Aldolase – plastid.*	*maxima* × *ecuadorensis*	Weeden et al., 1984
Est-1	*Est*	2	*Esterase.*	*maxima* × *ecuadorensis*	Wall and Whitaker, 1971; Weeden and Robinson, 1986
Gal-1		2	β-*galactosidase-1*.	*maxima* × *ecuadorensis*	Weeden and Robinson, 1986
Gal-2		2	β-*galactosidase-2*.	*maxima* × *ecuadorensis*	Weeden and Robinson, 1986
G2d-1		3	*Glycerate dehydrogenase-1*. Variant among wild populations.	*pepo*	Decker-Walters et al., 1993
G2d-2		2	*Glycerate dehydrogenase-2*. Variant among wild populations.	*pepo*	Decker-Walters et al., 1993
Got-1		5	*Glutamine oxaloacetate-1*. Variant among accessions, wild populations, and among *Cucurbita* species.	*pepo*	Decker, 1985; Kirkpatrick et al., 1985; Decker and Wilson, 1987; Wilson, 1989
Got-2		3	*Glutamine oxaloacetate-2*. Variant among species.	*maxima* × *ecuadorensis*	Wilson, 1989
Gpi		2	*Glucosephosphate isomerase*. Variant among accessions.	*pepo*	Ignart and Weeden, 1984
Gpi-3		2	*Glucosephosphate isomerase-3*. Variant among wild populations.	*pepo*	Decker-Walters et al., 1993
Gpi-c1		2	*Glucosephosphate isomerase cytosolic-1.*	*maxima* × *ecuadorensis*	Weeden and Robinson, 1986
Gpi-c2		2	*Glucosephosphate isomerase cytosolic-2.*	*maxima* × *ecuadorensis*	Weeden and Robinson, 1986
Idh-1		4	*Isocitrate dehydrogenase-1*. Variant among accessions, wild populations, and *Cucurbita* species.	*pepo*	Decker, 1985; Kirkpatrick et al., 1985; Decker and Wilson, 1987; Wilson, 1989; Decker-Walters et al., 1993
Idh-2		2	*Isocitrate dehydrogenase-2*. Variant among accessions, wild populations, and *Cucurbita* species.	*pepo*	Decker, 1985; Kirkpatrick et al., 1985; Decker and Wilson, 1987; Wilson, 1989; Decker-Walters et al., 1993
Idh-3		2	*Isocitrate dehydrogenase-3*. Variant among accessions and populations.	*pepo*	Decker, 1985; Kirkpatrick et al., 1985; Decker and Wilson, 1987; Decker-Walters et al., 1993
Lap-1	*Lap*	4	*Leucine aminopeptidase*. Variant among *C. pepo* accessions.	*maxima* × *ecuadorensis*; *pepo*	Wall and Whitaker, 1971; Ignart and Weeden, 1984; Weeden and Robinson, 1986; Decker-Walters et al., 1993
Mdh-1	*Mdh*	7	*Malate dehydrogenase*. Variant among accessions.	*pepo*	Ignart and Weeden, 1984
Mdh-2		3	*Malate dehydrogenase-2*. Variant among accessions, wild populations, and *Cucurbita* species.	*pepo*	Decker, 1985; Kirkpatrick et al., 1985; Decker and Wilson, 1987; Wilson, 1989; Decker-Walters et al., 1993;
Mdh-3		3	*Malate dehydrogenase-3*. Variant among accessions, wild populations, and *Cucurbita* species.	*pepo*	Decker, 1985; Kirkpatrick et al., 1985; Decker and Wilson, 1987; Wilson, 1989; Decker-Walters et al., 1993
Mdh-m1		2	*Malate dehydrogenase mitochondria-1.*	*maxima* × *ecuadorensis*	Weeden and Robinson, 1986
Mdh-m2		2	*Malate dehydrogenase mitochondria-2.*	*maxima* × *ecuadorensis*	Weeden and Robinson, 1986
Mdh-c2		2	*Malate dehydrogenase cytosolic-2.*	*maxima* × *ecuadorensis*	Weeden and Robinson, 1986
Per-1		2	*Peroxidase-1.*	*maxima* × *ecuadorensis*	Weeden and Robinson, 1986
Per-2		3	*Peroxidase-2.* Variant among accessions and wild populations.	*pepo*	Decker, 1985; Kirkpatrick et al., 1985; Decker and Wilson, 1987
Per-3		2	*Peroxidase-3.*	*maxima* × *ecuadorensis*	Weeden and Robinson, 1986
Pgi-1		2	*Phosphoglucase isomerase-1.*	*pepo*	Decker, 1985
Pgi-2		2	*Phosphoglucase isomerase-2.* Variant among *Cucurbita* species.	*pepo*	Decker, 1985; Kirkpatrick et al., 1985; Wilson, 1989

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Table 2 (continued). The isozyme variants of *Cucurbita.*

Gene symbol		Alleles		*Cucurbita*	
Preferred	**Synonym**	observed (no.)	Character	species	Reference(s)
Pgi-3		4	*Phosphoglucase isomerase-3.* Variant among accessions, wild populations, and *Cucurbita* species.	*pepo*	Decker, 1985; Kirkpatrick et al., 1985; Decker and Wilson, 1987; Wilson, 1989
Pgm-1	*Pgm*	2	*Phosphoglucomutase.* Variant among accessions.	*pepo*	Ignart and Weeden, 1984
Pgm-2		4	*Phosphoglucomutase-2.* Variant among accessions, wild populations, and *Cucurbita* species.	*pepo*	Decker, 1985; Kirkpatrick et al., 1985; Decker and Wilson, 1987; Wilson, 1989
Pgm-5		2	*Phosphoglucomutase-5.* Variant among wild populations.	*pepo*	Decker-Walters et al., 1993
Pgm-6		2	*Phosphoglucomutase-6.* Variant among wild populations.	*pepo*	Decker-Walters et al., 1993
Pgm-c2		2	*Phosphoglucomutase cytosolic-2.*	*maxima* × *ecuadorensis*	Weeden and Robinson, 1986
Pgm-p		2	*Phosphoglucomutase plastid.*	*maxima* × *ecuadorensis*	Weeden and Robinson, 1986
Skd-1		6	*Shikimate dehydrogenase.* Variant among wild populations.	*pepo*	Decker-Walters et al., 1993
Skdh		5	*Shikimate dehydrogenase.* Variant among *C. pepo* accessions.	*maxima* × *ecuadorensis*; *pepo*	Ignart and Weeden, 1984; Weeden and Robinson, 1986
Sod-1		2	*Superoxide dismutase-1.*	*maxima* × *ecuadorensis*	Weeden and Robinson, 1986
Tpi-c2		2	*Triosephosphatase isomerase cytosolic-2.*	*maxima* × *ecuadorensis*	Weeden and Robinson, 1986
Tpi-p2		2	*Triosephosphatase isomerase plastid-2.*	*maxima* × *ecuadorensis*	Weeden and Robinson, 1986

Table 3. Mapped phenotypical and morphological loci in *Cucurbita.*

Trait	Symbol	Linked marker(s)^z	Recombination distance (cM)	Reference(s)
Seedcoat	*n*	AK11_340	4.4	Zraidi and Lelley, 2004
Fruit length	(QTL)	AE07_165, AC10_490, AJ20_420, P13_750, J01_600, AO20_1200, T08_460, AB08_540, AE09_1600		Zraidi and Lelley, 2004
Fruit width	(QTL)	AE07_165, AJ20_420, AM10_950, AG08_440		Zraidi and Lelley, 2004
Fruit length to width ratio	(QTL)	AE07_165, AC10_490, AJ20_420, P13_750, J01_600		Zraidi and Lelley, 2004
Number of fruit chambers	(QTL)	P13_950, AE08_470		Zraidi and Lelley, 2004
Precocious yellow fruit	*B*	I10_1700	27.1	Brown and Myers, 2002
Leaf indentation	(QTL)	F10_400, K11_950, G2_400		Brown and Myers, 2002
Leaf mottle	*M*	H14_600	13.0	Brown and Myers, 2002
		U489_1200	16.3	Brown and Myers, 2002
Mature fruit color	(none given)	G17_700	9.7	Brown and Myers, 2002
Fruit shape	(QTL)	F8_1050, B8_900, H19_500		Brown and Myers, 2002

^{z}These RAPD markers (for example, AK11_340) are identified by the primer used (AK11) and by the size in base pairs (340) of the band produced. RAPD markers are population specific because they are identified primarily by size.

have been linked to the genes in Table 1. The linkage maps by Brown and Myers (2002) and Zraidi and Lelley (2004) included both Mendelian traits from Table 1 and QTLs for more complex quantitative traits (Table 3). However, these maps were constructed using population-specific markers which are not immediately useful in breeding. Also, neither map covers the entire *Cucurbita* genome.

Cucurbita genetics is clearly lagging behind that of other important vegetable crops. Within the Cucurbitaceae, well over 100 genes affecting phenotypic/morphological traits have been identified in melon (*Cucumis melo* L.) (Pitrat, 2002) and cucumber (*Cucumis sativus* L.) (Xie and Wehner, 2001). Less than 50 phenotypic/morphological loci have been listed for watermelon (*Citrullus lanatus*) (Guner and Wehner, 2004), which is not a highly polymorphic species (Levi et al., 2001). Several genetic maps have been constructed for both, melon and cucumber. Not only are these maps more complete than either of the *Cucurbita* maps, SSR markers have been used to align the maps across both populations and species.

Much genetic variation within the genus *Cucurbita* has not yet been subjected to classical genetic analysis. There is also a need for reference maps and populations of recombinant inbred lines, at least for *C. pepo*, *C. moschata* and *C. maxima*. Reference populations based on relatively long-lived, open-pollinated cultivars and/or germplasm maintained in gene banks that are associated with particular cultivar-groups or market types would have long-term value for classical genetic analysis and breeding in addition to providing a solid foundation for extensive QTL mapping and genetic comparisons within and among the species.

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