The Genes of Pumpkin and Squash

Harry S. Paris¹

Department of Vegetable Crops and Plant Genetics, Agricultural Research Organization, Newe Ya'ar Research Center, P.O. Box 1021, Ramat Yishay 30-095, Israel

Rebecca Nelson Brown

Department of Plant Science, University of Rhode Island, Kingston, RI 02881

Additional index words. Cucurbitaceae, Cucurbita pepo, Cucurbita maxima, Cucurbita moschata, genetics, vegetable breeding

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 \times 10⁶ ha being devoted to pumpkins, squash, and gourds, with about 60% of the over 19 \times 10⁶ 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 cultivargroup (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

Received for publication 2 Mar. 2005. Accepted for publication 15 May 2005. Contribution 107/2005 from the Agricultural Research Organization, Bet Dagan, Israel.

¹Corresponding author, e-mail hsparis@volcani. agri.gov.il.

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

Preferred SynopyingCharacterizationClaracterizationClaracterizationaambraceboxFound in "Creace" (produces configpagesMatchell, 1970BmatchellRecoder Precessions yellow fruit pignerration; pages, modelingpagespagesBRecoder Precessions yellow fruit pignerration; remaining and a bin flagpagesShiftins; 1955, 1981; systemB**B-2Recoder Precessions PI InSSing Transmitting and B in flagParis stageShiftins; 1955, 1984; Paris staged anomanal goard B in flagB**B-2Recoder Precessions yellow fruit pignerration, from subsg. and/enname PI 16555; C. matcher stage, matcal of light yellow, frain-fisch other C. matcher stage, matcal other stage, stage C. matcher stage, matcal other stage, stage C. matcher stage, matcal other stage, stage C. matcher stage, st	Gene s	ymbol		<i>a</i> 1	
a and advectors. Found in Greeker'; produces only pepo Kableki, 1970 B B pelostropic, affecting frait and folinger. modified by Fp-1, Fp-2 and Sec-B Originality from "Vaughts" Pear Shaped' commentaling out, B in the C moticable Peorless of Host Sec-B Originality from "Vaughts" Pear Shaped' commentaling out, B in the C moticable Peorless of Host Sec-B Originality from "Vaughts" Pear Shaped' commentaling out, B in the C moticable Peorless of Host Sec-B Originality from "Vaughts" Pear Shaped' commentaling out, B in the C moticable Peorless of Host Sec-B Originality from "Vaughts" Pear Shaped' commentality to L-2 Brooks. Proceedings View Sec. Sec. B Peorless Commentation, from material and the Sec. Sec. Sec. Sec. Sec. Sec. Sec. Sec	Preferred	Synonym	Characteristic	Cucurbita species	Reference(s)
B Bickey Processing sellew flag meaning: pcpp. morcheta Shifting, 195, 1981; B Bickey Processing sellew flag meaning: pcpp. morcheta Shifting, 195, 1981; B Bickey Processing Configuration, pcpp. morcheta Shifting, 195, 1981; B Bickey Processing Configuration, pcpp. morcheta Shifting, 195, 1981; B Bickey Processing, Configuration, parts, 1988 B Bitter Juni, High coundrising, Configuration, from maximum, B Bitter Juni, High coundrising, Configuration, from maximum, C maximum, contains, including 'Queenshand Blue; eccaudoreans, the form and contains, and contains and contains and contains and contains and the form and chini stage. Contains, 1935 B Bitter Juni, High coundrising the form and contains. maximum, Contains, 1935 B Bitter Juni, High coundrising the form and contains. maximum, Mutchela and Pearsen, 1987 M Bitter Juni, High coundrising the form and contains. maximum, Mutchela and Pearsen, 1987 Bitter Juni, High coundrising the form and	а		androecious. Found in 'Greckie'; produces only	реро	Kubicki, 1970
B Decoder Precodes yellow intel page-tailon; plexitory, affecting from the folding. page 3000000000000000000000000000000000000	P		male flowers, recessive to A.		C1:C: 1055 1001
 peodotopic, affecting Turia and Politage. medifield and Polyce, and Polyce,	В		Bicolor. Precocious yellow fruit pigmentation;	pepo, moschata	Shifriss, 1955, 1981;
$ \begin{array}{c} \label{eq:constraint} \begin{tabular}{l c c c c c c c c c c c c c c c c c c c$			pleiotropic, affecting fruit and foliage,		Schaffer and Boyer, 1984;
$ \begin{array}{c} \operatorname{Viagan} a \ from single or numerical goin J at interval \\ \operatorname{Cons} C \ (Constraints) $			modified by <i>Ep-1</i> , <i>Ep-2</i> and <i>Ses-B</i> . Originally from		Paris et al., 1985a;
$ \begin{array}{c} c. machina reconsider (10000) and constrained and the constraints of the constraint of the con$			Vaugnn's Pear Snaped ornamental gourd. B in the		Paris, 1988
$ \begin{array}{cccc} & Booler Proceedings under the set of the se$			<i>C. moschata</i> Precocious PI 165561 breeding line derived		
p^{am} $B-2$ Interfaces or angle, listed of gar years, from from maximaShiftiss, 1966, 1989 Bi Bi Bi and Bi representing view in the parametric from maxima, C canazina subsp. and/maxima (b from maxima, c canazina subsp. and/maxima, including 'Queensland Blue', eccadorexit, Linked to $D-2$. For C parametric for the parametric for maxima, including 'Queensland Blue', eccadorexit, Bi Contaction, 1995; bi bi bi from zucchini squash. Bi contacted, bi is a parametric of the parametric for maxima, including 'Queensland Blue', eccadorexit, Bi Herrington and Brown, 1988 bi Bi Bi contacted, from 'New Hampshire Butternat', moxchataMutschler and Pearson, 1987 Bi Bi Bi contacted, from 'New Hampshire Butternat', moxchataMutschler and Pearson, 1987 Bi Bi Bi contacted, from 'New Hampshire Butternat', moxchataMutschler and Pearson, 1987 Bi Bi Bi from 'New Fisher Butternat', moxchataMutschler and Pearson, 1987 Bi Bi Bi from 'New Fisher Butternat', moxchataMutschler and Pearson, 1987 $CarwCacurable moxie virws resistance. From Nigerian Local, maxchataBurem et al., 2003crCacurable moxie virws resistance. From Nigerian Local, maxchataBrown et al., 2003crCacurable moxie virws resistance. From Nigerian Local, maxchataBrown et al., 2003crCacurable developments', Cr from C. moxchata' 'Butternat', okacchata'', and orange for C/C).maxchatacrcacurable developments', Cr from C. moxchata'' 'Butternat', okacchata'', and orange for C/C).maxchatadr<$			from C. pepo infough backcrossing. Complementary to L-2		
$ \begin{array}{ccc} accord backgroup with the product matrix of the product $	Dmax	D 1	Disclar Procession valley fruit nigmentation from		Shifting 1066 1080
Bit Bitson, and a 11 bitson Construm, and Construm, and Construmts, in from macture x Construm, and construmts, including 'Queenland Blue' Construmt, and construmt, and construction of period in the construmt of the period in the period i	D	D-2	subsp. andreana DI 165558	maxima	51111188, 1900, 1989
and and convertion using analysis and a form and a conversion of the form and the analysis and the analysis of the an	Ri		<i>Bitter</i> fruit High encurbitacin content in fruit <i>Bi</i> from	marima	Contardi 1030
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $	Di		<i>C</i> maxima subsp. and reana and <i>C</i> ecuadorensis: bi from	maxima ×	Grebenšikov 1955:
Linked to Lo_2 , For C , rego: B if from wild Texan gourd, bi perportHerrington and Brown, 1988bibile fruit color. Incompletely recessive to Bl for green fruit color, maximaHutchins, 1935 Bn^* Butternut Tuit shape. From 'New Hampshire Butternut', monochataMutschler and Pearson, 1987 Bu Bush habit. Short internodes, dominant to vine habit, h_n in $pepo$, young plot stage. For C_{pero} , Bu in 'Canada Crookneck'.Shifriss, 1947; Bu Bush habit. Short internodes, dominant to vine habit, h_n in $pepo$, and $Also a near-segenic line of 'Table Queen', h_n in more habit. Short internodes, dominant to van inbread line, the maxima and also a near-segenic line of 'Table Queen', h_n in mShifriss, 1947;ConvConvention to com for assistance. From Nigerian Local, moschataBrown et al., 2003CrowConvention to com for assistance. From Nigerian Local, moschataBrown et al., 2003crowconvent of conjectory from C. moschata 'B Muternut', okeccholoceusis; C rinon C. moschata 'B Muternut', okeccholoceusis; C rinon, C moschata 'B Muternut', okeccholoceusis; C rino, C moschata 'B Muternut', okeccholoceu$			<i>C</i> maxima subsp. maxima including 'Oueensland Blue'	ecuadorensis	Grebensikov, 1955,
from zacchini squash. P_{FP} P_{FP} bitobservedobserved to the for green fruit color, in hubbard squash.Hutchins, 1935 Bn^* Butternut' fruit shape Fron 'New Hampshire Butternut', and also a near-isogenic line of Table Queer', but in and also a near-isogenic line of Table Queer', but in and also a near-isogenic line of Table Queer', but in and also a near-isogenic line of Table Queer', but in and also a near-isogenic line of Table Queer', but in and also a near-isogenic line of Table Queer', but in dominant to or for susceptibility from a maxima.Brown et al., 2003ConvCucumber moxici vitra resistance. From Nigerian Local, dominant to or for susceptibility from a dominant to or for susceptibility from concent of colyledons of 'Early Queer', but in the peaks of Circ, and orange for CirC, resum orolla. Cleam to nearly while peaks for Circ, and orange for CirC, or cucumbarized and the intermediate-age fruit for for dark stern or the alternut'. Accenture or colyledons of 'Early Golden Bush Scallop'. Cu for high countraince more of 'Black Zucchni'.Brown et al., 2003DDark stern add nei intermediate-age fruit, D' for dark stern with dominance D > D's d' D for 'Infohok Zucchni'. D' for dark stern add rak intermediate-age fruit, D' for dark stern durk intermediate-age fruit for the applito 'Loeminator', d' for light intermediate-age fruit f			Linked to Lo-2 For C pepo: Bi from wild Texan gourd: bi	neno	Herrington and Brown 1988
blblue fuil color, incompletely recessive to Bf for green fruit color, in hubbard squash.Hutchins, 1935Bn*Buternut fuit shape, From 'New Hampshire Buternut', dominant to bn for crocknek, fuit shape is an 'Canad Crocknek'.Mutschler and Pearson, 1987BuhBush habit, Short internodes; dominant to vine habit, bn, in "lable Queen" score, <i>C peop. Bin</i> 'Gin 'Gin Vellow Straighteck' maxima and also a near-isogenic line of 'Table Queen', ison, in "Table Queen' score, <i>Proc. Davi. Dir. Gin Vellow Straighteck' maxima</i> and also a near-isogenic line of 'Table Queen', ison, ison more character of the Queen' score, <i>Prot. C maxima</i> , <i>Bu from an inbred line,</i> b from 'Delicious'.Brown et al., 2003CrowCucurbar mosaic virus resistance. From Nigerian Local, dominant to orm for susceptibility from 'Waltham Butternut'. c. <i>deechobeensis, C from C maxima</i> , <i>Bu from an inbred line,</i> to conscharta 'Butternut'. c. <i>deechobeensis, C from C moscharta</i> 'Butternut'. <i>dominant to orty for susceptibility from 'Waltham Butternut'.</i> c. <i>deechobeensis, C from C moscharta</i> 'Butternut'. <i>dominant to orty for susceptibility from 'Waltham Butternut'.</i> <i>dominant of colytodoms of 'Early Golden Bash Scallop', Cu for</i> hgb curubtaicn content of Colytodoms of 'Back Zucchini'. <i>prot.</i> Dur A stem. Series of three alleter observed in C. <i>pepo.</i> Dur from 'Table King' and dr fai light series delice due and fraid all steaded. Recessive to <i>P or M. J. Bins</i> . Dur 'Indi and afferd due target frait from a variant zgallifor is curued' paris and Nexes, 1985, Paria and Nexes, 1986, Paria and Nexes, 1986, Paria and Nexes, 1986, Paria and Nexes, 1987, Dir form 'Table King' acom, aviant zgallifor breeding stock.Hathell, 1971 Lopez-Anido et al., 2003 <i>CawDerin Tably Folicianation - D. O's d.</i>			from zucchini squash	popo	normigeon and Brown, 1900
in hubbard squaph. L^{1} for the theorem is the form the problem is the form the problem is the problem is provided in the problem in the problem is provided in the problem is provide	bl		<i>blue</i> fruit color. Incompletely recessive to <i>Bl</i> for green fruit color	or. <i>maxima</i>	Hutchins, 1935
Bn^* Butternut fruit shape, From 'New Hampshire Butternut', moschaa Matschler and Pearson, 1987 Buh Bush habit, Short internedes; dominant to vine habit, bn ; in "pepo, and also a near-sogenic line of 'Table Queen', bn in "Table Queen', bn in "Table Queen', bn in "Table Queen' acoustication". Grebenšikov, 1985; Dema and Munger, 1963 $Core Cucumber mosaic virus resistance. From Nigerian Local, moschata × dominant to em for susceptibility from 'Waltham Butternut'. execution of the construction of $			in hubbard squash.	- ,	···· -, · · ·
$Bu \qquad bu for cooleace fluit shape as in 'Canada Crookneck': bu first, 1947; Grebenšikov, 1958; bu first, 1947; Grebenšikov, 1959; Grefor, 1948; Brebueck, Beessive Cu for feduce decurbination-B pepo Construction of cotyledons of 'Early Golden Bush Scallop'; Cu for high cucurbitacines of 'Early Golden Bush Scallop'; Cu for dark stem and dark intermediate-age fruit, D' for dark stem maxima period, and dro first and for Golden Sub Scallop'; Cu for dark stem and dark intermediate-age fruit from the rapalito 'La Greminadora'; D' for dark stem and fauta of first and for Golden Sub Scallop, Schöninger, 1952; Gi loberson, 1966; Prais, 1996; 1997; 2000; D' for dark stem and taking tendris and terminating moschata defauxed as the raviant zgalitic 'La Greminadora'; D' for dark stem and taking tendris and termination be appaid to be call to mo-2. For C. maxima: and terminating moschata 'La Greminadora'; D' for dark stem and scallop squask, dominant to period in decembratic plant habit. Stem lacking tendris and terminating moschata 'Kwack, 1995 'Linked to mo-2. For Complexity up the first and Served'; D' for dark stem and the stem and thabit. Stem lacking tendris and terminating moschata 'La Grefform$	Bn*		Butternut fruit shape. From 'New Hampshire Butternut',	moschata	Mutschler and Pearson, 1987
Bush habit. Short internedes: dominant to vine habit, bx, in pepo. Shiftiss, 1947; young plant stage, Por C. pepo. Busit (Ciant Vellow Straightneck' maxima and also a near-isogenic line of 'Table Queen', bu in 'Ciant Vellow Straightneck' maxima and Munger, 1963 Shiftiss, 1947; Core Carebox moscie virus resistance. From Nigerian Local, moschata Brown et al., 2003 Brown et al., 2003 cr creater corolla. Create no to nearly white petals, cr from moschata Mitternut'. Roe and Bemis, 1977 cu creater corolla. Creater hose and the curve train the petals. cr from moschata 'S maxima' and thall, 1971 Roe and Bemis, 1977 cu cucurbutane. To educed Recessive cu for reduced cucurbitation-B pepo Sharma and Hall, 1971 content of oxlycloons of 'Early Golden Bush Scallop'; Cu for Schoninger, 1952; D Dark stem, Series of three alleles observed in C. pepo: pepo. Schoninger, 1952; D Dark stem, Series of three alleles observed in C. pepo: pepo. Schoninger, 1952; D Dark stem, and dark internediate-age fruit, Dr for dark stem maxima pepo. Schoninger, 1969; bush thrist, residence, and for light stem and fruit not affected, and dro light heir is honoxypous recessive; Intervelowed stem in the rapalito' is conting stock. peris and Nerson, 1969; de determinate plant habit. Br			dominant to bn for crookneck fruit shape as in 'Canada Crookne	ck'.	,
	Bu		Bush habit. Short internodes; dominant to vine habit, bu, in	pepo,	Shifriss, 1947;
			young plant stage. For C. pepo: Bu in 'Giant Yellow Straightr	neck' maxima	Grebenšikov, 1958;
			and also a near-isogenic line of 'Table Queen', bu in		Denna and Munger, 1963
			'Table Queen' acorn. For C. maxima: Bu from an inbred line,		-
ConvCucumber mosaie virus resistance. From Nigerian Local, dominant to curb for susceptibility from 'Waltham Butternut', cream corolla, Cream to nearly white petals, cr from moschata 'Butternut', okeechobeensis', and orange for CrCh,Brown et al., 2003cucucurbite::orcer, content of cotyledons of 'Early Golden Bush Scallog', Cu for high cucurbitation content of cotyledons of Black Xucchini'. DBarma and Hall, 1971DDark stem. Series of lince alleles observed in C. pepo, but fruit not affected, and dir hitermediate-age fruit, Dr for dark stem but fruit not affected, and dir hitermediate-age fruit, Dr for dark stem. Epo Schöminger, 1952; Globerson, 1969; Dark stem. Series of lince alleles observed: D from 'Early Prolific Straightneck'; d' from 'Vegetable Spaghetti'. Lopez-Anido et al., 2003decucurbitation content of cotyledons observed: D for dark stem and fruit non affected, Paris and Nerson, 1986; Paris and Nerson, 1986; Dift for form 'Early Prolific Straightneck'; d' from 'Vegetable Spaghetti'. Lopez-Anido et al., 2003dedor light intermediate-age fruit from a variant zapallito breeding stock. de determinate plant habit. Ure fruit shape. From scallop squash, dominant to pero Shiftiss and Paris, 1981Ep-1Extender of pigmentation-1. Modifier of B. Ep-1 pepo Shiftiss and Paris, 1981Ep-2Extender of pigmentation-2. Modifier of B. Ep-1 pepo Shiftiss and Paris, 1981Ep-1Extender of pigmentation-2. Modifier of B. Ep-1 pepo Shiftiss and Paris, 1981Ep-2Extender of pigmentation-2. Modifier of B. Ep-1 pepo Shiftiss and Paris, 1981Ep-2Extender of pigmentation-2. Modifier of B. Ep-1 pepoEp-2Ex			bu from 'Delicious'.		
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $	Cmv		Cucumber mosaic virus resistance. From Nigerian Local,	moschata	Brown et al., 2003
crcream corolla. Cream to nearly white petils, or frommoschat ×Ree and Bernis, 1977C. dokechobeensis incompletely dominant (vellow petals for Cr/cr, and orange for Cr/cr).okeechobeensiscucucurbitacin-B reduced. Recessive cu for reduced cucurbitacin-B pepopepoSharma and Hall, 1971DDark stem. Series of three alleles observed in C, pepo D for dark stem and dark intermediate-age fruit, D for dark stem maximapepoSchöninger, 1952; Globerson, 1969; Paris and Nerson, 1986; Paris and Nerson, 1986; Paris and Nerson, 1986; Paris and Nerson, 1987, D' from Early Prolific Straightneck'; d from 'Vegetable Spaghetti'. D' from Early Prolific Straightneck'; d from 'Negetable Spaghetti'. D' from Early Prolific Straightneck'; d from 'Negetable Spaghetti'. D' from Early Prolific Straightneck'; d from 'Negetable Spaghetti'. D' from 'Situit to gene. J and J a' when cither is homoxygous recessive; linked to mo-2. F or C. maxima: only the fruit was observed: D' for dark intermidiate-age fruit from ta variant zapallito breeding stock. de d for light intermediate-age fruit from the xgallots 'Cuc Core.' D' for motod discipated 'Det''.Kwack, 1995DiDisc fruit shape. From scallop squash, dominant to prom 'Simal Sugar 7 × 7' pumpkin, ep-1 mos Table King' acom.pepoShiftiss and Paris, 1981Ep-1Extender of pigmentation-1. Modifier of B. Ep-1 from 'Small Sugar 7 × 7' pumpkin.pepoShiftiss and Paris, 1981 <td< td=""><td></td><td></td><td>dominant to <i>cmv</i> for susceptiblity from 'Waltham Butternut'.</td><td></td><td></td></td<>			dominant to <i>cmv</i> for susceptiblity from 'Waltham Butternut'.		
$ \begin{array}{cccc} C. okeechobeensis; Cr from C. moschata 'Butternut' okeechobeensis in incompletely dominant (vellow petals for Cr/cr, and orange for Cr/cr, and orange for Cr/cr). \\ cu cucurbitation: B reduced. Recessive cn for reduced cucurbitacin-B pepo Sharma and Hall, 1971 content of cotyledons of 'Back Zucchini'. \\ D \\ D \\ Dark stem. Series of three alleles observed in C. pepo: pepo, Schöninger, 1952; \\ D for dark stem and dark intermediate-age fruit, D for dark stem maxima Globerson, 1969; \\ D i for thark stem and dark intermediate-age fruit, D for dark stem maxima Globerson, 1969; \\ D i for thark stem and dark intermediate-age fruit, D for dark stem maxima Globerson, 1969; \\ D' from 'Early Polific StringithueCk'; d forn 'Vegetable Spaghetti'. Lopez-Anido et al., 2003 Epistatic to genes I-I and I-2 when either is homozygous recessive; linked to mo2. For C. maxima: only the fruit was observed: D for dark intermediate-age fruit from the zapallito 'La Germinadora'; d for light itermediate-age fruit from the zapallito 'La Germinadora'; d lor light itermediate-age fruit from the zapallito 'La Germinadora'; d for light itermediate-age fruit from the zapallito 'La Germinadora'; d for light itermediate-age fruit from the zapallito 'La Germinadora'; d for light itermediate-age fruit from a virant zapallito breeding stock. de with frame flowers. Recessive to De for indeterminate plant habit. Di Dic fruit shape. From scallop squash, dominant to pepo Sinnott and Durham, 1922; white fraue 1 gigmentation-1. Modifier of B. Ep-1 pepo Shiftriss and Paris, 1981 incompletely dominant to ep-2 and additive with Ep-2. Ep-1 Extender of pigmentation-2. Modifier of B. Ep-1 pepo Shiftriss and Paris, 1981 Ep-1 incompletely dominant to ep-2 and additive with Ep-1. Ep-2 from 'Small Sugar 7 × 7 pumpkin. From 'Small Sugar 7 × $	cr		cream corolla. Cream to nearly white petals, cr from	moschata ×	Roe and Bemis, 1977
			C. okeechobeensis; Cr from C. moschata 'Butternut'	okeechobeensis	
			incompletely dominant (yellow petals for Cr/cr,		
cucucurbitation-B reduced. Recessive cri for reduced cucurbitation-B pepoSharma and Hall, 19/1cucurbitation content of cotyledons of "Black Zucchini".DDark stem. Series of three alleles observed in C. pepo: pepo, But fruit not affected, and d for light stem and futi not affected, with dominance $D > D > D > D > D > D > D > D > D > D $			and orange for Cr/Cr).	5	
	си		<i>cucurbitacin</i> -B reduced. Recessive <i>cu</i> for reduced cucurbitacin	-В реро	Sharma and Hall, 1971
$ \begin{array}{ccccc} D & Dark stem. Series of three alleles observed in C, Pepc. peop. Schöninger, 1952; Globerson, 1969; Dir dark stem and dark intermediate-age fruit, D' for dark stem maxima Globerson, 1969; Paris and Nerson, 1966; With dominance D > D > d. D from 'Fordhook Zucchini', Paris, 1996, 1997, 2000e; Lopez-Anido et al., 2003 Epistatic to genes l \cdot l and l \cdot 2 when either is homozygous recessive; Inkect to mo-2. For C. maxima: only the fruit was observed: D for dark intermediate-age fruit from the scapallito 'L Germinadora'; d for light intermediate-age fruit from the scapallito 'L Germinadora'; d for light stem and habit. Stem and habit.$			content of cotyledons of 'Early Golden Bush Scallop'; Cu for		
DDark stem. Series of three alleles observed in C. $pepo:$ pepo. D for dark stem and dark intermediate-age fruit, D' for dark stem maxima Globerson, 1969; Paris, 1966, 1997, 2000c; D' from 'Early Prolife Straightneck'; d from 'Vegetable Spaghetti', Lopez-Anido et al., 2003 Epistatic to genes I-1 and I-2 when either is homozygous recessive; Inked to mo-2. For C. maxima: only the fitti was observed: D for dark intermediate-age fruit from the zapalitio 'La Germinadora'; d for light intermediate-age fruit from a variant zapalito breeding stock.Kwack, 1995dedeterminate plant habit. Stem lacking tendrils and terminating with female flowers. Recessive to De for indeterminate plant habit. De from 'Equ' and 'Sokuk', de from inbred designated "Det".Sinnott and Durham, 1922; Whitaker, 1932DiDisc fruit shape. From scallop squash, dominant to spherical or priform.pepo Whitaker, 1932Ep-1Extender of pigmentation-1. Modifier of B. Ep-1 incompletely dominant to p-1 and additive with $Ep-2$. Ep-1 from 'Small Sugar 7 × 7' pumpkin; ep-1 from 'Table King' acorn.pepoFrFrom 'Grigmentation-2. Modifier of B. Ep-1. Ep-2 from 'Table King' acorn. 'Small Sugar 7 × 7' pumpkin; ep-2 from 'Small Sugar 7 × 7' pumpkin; frpepofrFrom 'Grigmentation-2. Modifier of B. Ep-1. Ep-2 from 'Table King' acorn: 'Small Sugar 7 × 7' pumpkin; ep-1 from 'Small Sugar 7 × 7' pumpkin; ep-2 and additive with Ep-1. Ep-2 from 'Table King' acorn; ep-2 from 'Small Sugar 7 × 7' pumpkin; frfor fisteed vein, Fusion of primary leaf veins, Ep-1. Ep-2 from 'Small Sugar 7 × 7' pumpkin; ep-1. Ep-2 from 'Small Sugar 7 × 7' pumpkin; ep-1. Ep-2 from 'Small Sugar 7 × 7' pumpkin; frfor fisteed vein, Fusion of primary leaf veins, <br< td=""><td>D</td><td></td><td>high cucurbitacin content of cotyledons of 'Black Zucchini'.</td><td></td><td>G 1 m 1052</td></br<>	D		high cucurbitacin content of cotyledons of 'Black Zucchini'.		G 1 m 1052
	D		Dark stem. Series of three alleles observed in C. pepo:	pepo,	Schoninger, 1952;
			but fruit not affected and d for light stom and fruit not affected	d maxima	Daris and Marson, 1086:
$E_{p-2} = (C_{p}) = (C_{$			but null not anected, and a for light stem and null not anected with dominance $D > D^s > d$. D from 'Eardbook Zucchini'	a,	Paris 1006 1007 2000c
By Item 2 in the binner binn			D^{s} from 'Early Prolific Straightneck': d from 'Vegetable Space	rhetti'	I ans, 1990, 1997, 2000c, Lonez-Anido et al. 2003
$ \begin{array}{ccccc} \begin{tabular}{lllllllllllllllllllllllllllllllllll$			Enistatic to genes <i>l</i> -1 and <i>l</i> -2 when either is homozygous rece	sive.	Lopez-Ando et al., 2005
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $			linked to mo-2 For C maxima: only the fruit was observed:		
d for light intermediate-age fruit from a variant zapallito breeding stock.dedeterminate plant habit. Stem lacking tendrils and terminating moschata with female flowers. Recessive to De for indeterminate plant habit. De from 'leju' and 'Sokuk', de from inbred designated "Det'.Kwack, 1995DiDisc fruit shape. From scallop squash, dominant to spherical or pyriform.pepoSinnott and Durham, 1922; Whitaker, 1932Ep-1Extender 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.pepoShifriss and Paris, 1981Ep-2Extender of pigmentation-2. Modifier of B. Ep-2 from 'Small Sugar 7 × 7' pumpkin. 			D for dark intermediate-age fruit from the zanallito 'La Germ	inadora'.	
dedeterminate plant habit. Stem lacking tendrils and terminatingmoschataKwack, 1995 $Def from 'Igiu' and 'Sokuk', de from inbred designated "Det".Def from 'Igiu' and 'Sokuk', de from inbred designated "Det".Sinnott and Durham, 1922;DiDisc fruit shape. From scallop squash, dominant topepoSinnott and Durham, 1922;Ep-1Extender of pigmentation-1. Modifier of B. Ep-1pepoShifriss and Paris, 1981Ep-1Extender of pigmentation-2. Modifier of B.pepoShifriss and Paris, 1981Ep-2Extender of pigmentation-2. Modifier of B.pepoShifriss and Paris, 1981Ep-2Extender of pigmentation-2. Modifier of B.pepoShifriss and Paris, 1981Ep-2Extender of pigmentation-2. Modifier of B.pepoShifriss and Paris, 1981Ep-2 incompletely dominant to ep-2 and additive withEp-1. Ep-2 from 'Table King' acom.eppoShifriss and Paris, 1981FrFruit fly (Dacus cucurbitae) resistance. Fr fromsuburbation of primary leaf veins,subvital male gametophyte; found in hull-less-seededpumpkin breeding line.pepoCarle and Loy, 1996a, 1996bGa, mGynoecious sex expression. Dominant to g formonoecious sex expression.full set al., 1979;Dossey et al., 1981GbGreen band on inner side of base of petal, from a scallop squash.pepoSuperak, 1981gcgreen corolla. Green, leaf-like petals, sterile;in unspecified F2 population.pepoSuperak, 1987gdglabrows. Lacking trichomes.maximaMaximaKorzeniewska, 1992Robinson, 1987$			d for light intermediate-age fruit from a variant zapallito bree	ding stock.	
with female flowers. Recessive to De for indeterminate plant habit. De from 'Jeju' and 'Sokuk', de from inbred designated "Det". Disc fruit shape. From scallop squash, dominant to pepoSinnott and Durham, 1922; Whitaker, 1932DiDisc fruit shape. From scallop squash, dominant to spherical or pyriform.PepoSinnott 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: $ep-2$ incompletely dominant to $ep-2$ and additive with $Ep-1$. $Ep-2$ incompletely dominant to $ep-2$ and additive with $Ep-1$. $Ep-2$ incompletely dominant to $ep-2$ and additive with $Ep-1$. $Ep-2$ incompletely dominant to $ep-2$ and additive with $Ep-1$. $Ep-2$ incompletely dominant to $ep-2$ and additive with $Ep-1$. $Ep-2$ incompletely dominant to $ep-2$ and additive with $Ep-1$. $Ep-2$ incompletely dominant to $ep-2$ and additive with $Ep-1$. $Ep-2$ incompletely dominant to $ep-2$ and additive with $Ep-1$. $Ep-2$ from 'Table King' acorn; $ep-2$ from 'Small Sugar 7 × 7' pumpkin.FrFruit fly (Dacus cucurbitae) resistance. Fr from 'Arka Suryamukhi', dominant to fr for susceptibility.fvfixed vein. Fusion of primary leaf veins, subvital male gametophyte; found in hull-less-seeded pumpkin breeding line.Ga, mGynoecious sex expression. Dominant to g for to monoecious sex expression.GbGreen band on inner side of base of petal, from a scallop squash. Dominant to gb, for no band, from a straightneck squash.gcgreen corolla. Green, leaf-like petals, sterile; in unspecified F2 population.glglabrous. Lacking trichomes. Gr	de		<i>determinate</i> plant habit. Stem lacking tendrils and terminating	moschata	Kwack, 1995
DeDe from 'leju' and 'Sokuk', de from inbred designated "Det".DiDisc fruit shape. From scallop squash, dominant to spherical or pyriform.pepoSinnott 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' acon.pepoShifriss and Paris, 1981 $Ep-2$ Extender of pigmentation-2. Modifier of B. $Ep-2$ incompletely dominant to $ep-2$ and additive with $Ep-2$ incompletely dominant to $ep-2$ and additive with $Ep-1$ from 'Small Sugar 7 × 7' pumpkin.pepoShifriss and Paris, 1981FrFuttiffy (Dacus cucurbitae) resistance. Fr from 'Small Sugar 7 × 7' pumpkin.maximaNath et al., 1976FrFuttiffy (Dacus cucurbitae) resistance. Fr from 'Small Sugar 7 × 7' pumpkin.maximaNath et al., 1976fvfused vein. Fusion of primary leaf veins, subvital male gametophyte; found in hull-less-seeded pumpkin breeding line.pepoCarle and Loy, 1996a, 1996bGa. mGynoecious sex expression. Dominant to g for monoccious sex expression. Dominant to g for bominant to gb, for no band, from a straightneck squash. genopepoSuperak, 1981gcgreen corolla. Green, leaf-like petals, sterile; in unspecified F2 population.pepoSuperak, 1982glglabrous. Lacking trichomes. for from 'Long Neapolitan', gr from 'Butternut'. gray leaf. Recessive to green leaf. Recessive grid derived from grid ergs leasible. The pepoSuperak, 1982grGrGGreen rind. Dominant to buff skin of mature fruit. Gr			with female flowers. Recessive to <i>De</i> for indeterminate plant	habit.	,
DiDisc fruit shape. From scallop squash, dominant topepoSinnott and Durham, 1922; Whitaker, 1932 $Ep-1$ $Extender of pigmentation-1. Modifier of B. Ep-1pepoShifriss and Paris, 1981Ep-1incompletely dominant to ep-1 and additive with Ep-2.Ep-1 from 'Table King' acorn.pepoShifriss and Paris, 1981Ep-2Extender of pigmentation-2. Modifier of B.Ep-2 incompletely dominant to ep-2 and additive withEp-2 incompletely dominant to ep-2 and additive withEp-2 incompletely dominant to ep-2 and additive withEp-1. Ep-2 from 'Table King' acorn; ep-2 from'Small Sugar 7 × 7' pumpkin.Shifriss and Paris, 1981FrFruit fy (Dacus cucurbitae) resistance. Fr from'Arka Suryamukhi', dominant to fr for susceptibility.maximaNath et al., 1976fvfused vein. Fusion of primary leaf veins,subvital male gametophyte; found in hull-less-seededpumpkin breeding line.pepoCarle and Loy, 1996a, 1996bGa, mGyneecious sex expression. Dominant to g formonoecious sex expression. Dominant to g for no band, from a scallop squash.Dominant to gh for no band, from a scallop squash.pepopepoDutta and Nath, 1972gcgreen corolla. Green, leaf-like petals, sterile;in unspecified F2 population.pepoSuperak, 1987glglabrous. Lacking trichomes.Gr for 0'Long Neapolitan', gr from 'Butternut'.Gr for m'Long Neapolitan', gr from 'Butternut'.maximaKorzeniewska, 1992grelgray leaf. Recessive to green leaf. Recessive grid revired fromcross of zapallito-type line of C. maxima and a butternut'.gras leaf.Lopez-Anido et$			De from 'Jeju' and 'Sokuk', de from inbred designated "Det"		
Ep-1Extender 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.Whitaker, 1932Ep-2Extender of pigmentation-2. Modifier of B. Ep -2 incompletely dominant to ep -2 and additive with Ep -2 incompletely dominant to ep -2 and additive with Ep -2 incompletely dominant to ep -2 and additive with Ep -2 from 'Table King' acorn; ep -2 from 'Small Sugar 7 × 7' pumpkin.pepoShifriss and Paris, 1981FrFruit fly (Dacus cucurbitae) resistance. Fr from 'Arka Suryanukhi', dominant to fr for susceptibility.maximaNath et al., 1976fvfitsed vein. Fusion of primary leaf veins, subvital male gametophyte; found in hull-less-seeded pumpkin breeding line.pepoCarle and Loy, 1996a, 1996bGa, mGynoecious sex expression. Dominant to g for monoecious sex expression. Dominant to g for monoecious sex expression.pepoSuperak, 1981GbGreen band on inner side of base of petal, from a scallop squash. Breen in unspecified F2 population.pepoSuperak, 1987gcglabrous. Lacking trichomes.maxima moschataKorzeniewska, 1992GrGGreen rind. Dominant to buff skin of mature fruit. Gr from 'Long Neapolitan', gr from 'Butternut'.moschata moschataRobinson, 1987grlgray leaf. Recessive to green leaf. Recessive grl derived from cross of zapallito-type line of C. maxima and a butternut'. gray leaf. Recessive to green leaf. Recessive grl derived from cross of zapallito-type line of C. maxima and a butternut'.Lopez-Anido et al., 2002	Di		Disc fruit shape. From scallop squash, dominant to	реро	Sinnott and Durham, 1922;
Ep-1Extender of pigmentation-1. Modifier of B. $Ep-1$ pepoShiftiss and Paris, 1981incompletely dominant to $ep-1$ and additive with $Ep-2$. $Ep-1$ from 'Table King' acorn. $Ep-2$ from 'Small Sugar 7 × 7' pumpkin; $ep-1$ from 'Table King' acorn. $pepo$ Shiftiss and Paris, 1981 $Ep-2$ Extender of pigmentation-2. Modifier of B. $Ep-2$ incompletely dominant to $ep-2$ and additive with $Ep-2$ incompletely dominant to $ep-2$ and additive with $Ep-1$. $Ep-2$ from 'Table King' acorn; $ep-2$ from 'Small Sugar 7 × 7' pumpkin. $pepo$ Shiftiss and Paris, 1981FrFruit ffy (Dacus cucurbitae) resistance. Fr from subvital male gametophyte; found in hull-less-seeded pumpkin breeding line. $pepo$ Carle and Loy, 1996a, 1996bGa, mGynoecious sex expression. Dominant to g for monoecious sex expression. Dominant to g for monoecious sex expression. $pepo$ Dutta and Nath, 1972GbGreen band on inner side of base of petal, from a scallop squash. g green corolla. Green, leaf-like petals, sterile; in unspecified F2 population. $pepo$ Superak, 1987glglabrous. Lacking Irchomes. Gr form 'Long Neapolitan', gr from 'Butternut'. Gr form 'Long Neapolitan', gr from 'Butternut'. gr for 'G' Graven rind. Dominant to buff Skin of mature fruit. Gr for 'Long Neapolitan', gr from 'Butternut'. gr for 'G' and' Lopez-Anido et al., 2002Lopez-Anido et al., 2002			spherical or pyriform.	* *	Whitaker, 1932
incompletely dominant to $ep-1$ and additive with $Ep-2$. $Ep-1$ from 'Small Sugar 7 × 7' pumpkin; $ep-1$ from 'Table King' acorn. $Ep-2$ Extender of pigmentation-2. Modifier of B. $Ep-2$ incompletely dominant to $ep-2$ and additive with $Ep-1$ incompletely dominant to fr for susceptibility.fvFruit fly (Dacus cucurbitae) resistance. Fr from 'Arka Suryanukhi', dominant to fr for susceptibility.fvfused vein. Fusion of primary leaf veins, subvital male gametophyte; found in hull-less-seeded pumpkin breeding line.pepoCarle and Loy, 1996a, 1996bGbGynoecious sex expression. Dominant to g for monoecious sex expression. Dominant to gb , for no band, from a scallop squash. pepopepoDutta and Nath, 1972GbGreen band on inner side of base of petal, from a scallop squash. green corolla. Green, leaf-like petals, sterile; in unspecified F2 population.maximaKorzeniewska, 1987glglabrous. Lacking trich	Ep-1		Extender of pigmentation-1. Modifier of B. Ep-1	реро	Shifriss and Paris, 1981
Ep-1 from 'Small Sugar 7 × 7' pumpkin; $ep-1$ from 'Table King' acorn. $Ep-2$ $Extender$ of $pigmentation-2$. Modifier of B . $Ep-2$ incompletely dominant to $ep-2$ and additive with $Ep-1$. $Ep-2$ incompletely dominant to $ep-2$ and additive with $Ep-1$. $Ep-2$ from 'Small Sugar 7 × 7' pumpkin.pepoShifriss and Paris, 1981FrFruit fly (Dacus cucurbitae) resistance. Fr from 'Arka Suryamukhi', dominant to fr for susceptibility.maximaNath et al., 1976fvfused vein. Fusion of primary leaf veins, subvital male gametophyte; found in hull-less-seeded pumpkin breeding line.pepoCarle and Loy, 1996a, 1996bGa, mGynoecious sex expression. Dominant to g for monoecious sex expression.pepoDutta and Nath, 1972GbGreen band on inner side of base of petal, from a scallop squash. Dominant to gh for no band, from a straightneck squash.pepoSuperak, 1981gcglabrous. Lacking trichomes.maxima maximaKorzeniewska, 1992GrGGreen rind. Dominant to buff skin of mature fruit. Gr from 'Long Neapolitan', gr from 'Butternut'.maxima maximaLopez-Anido et al., 2002grlgray leaf. Recessive to green leaf. Recessive $grid$ derived from cross of zapallito-type line of C. maxima and a butternut-type x moschataLopez-Anido et al., 2002			incompletely dominant to ep-1 and additive with Ep-2.		
Ep-2Extender of pigmentation-2. Modifier of B.pepoShifriss and Paris, 1981Ep-2incompletely dominant to ep -2 and additive with Ep -1. Ep -2 from 'Table King' acorn; ep -2 from 'Small Suga 7 × 7' pumpkin.maximaNath et al., 1976FrFruit fly (Dacus cucurbitae) resistance. Fr from 'Arka Suryamukhi', dominant to fr for susceptibility.maximaNath et al., 1976fvfused vein. Fusion of primary leaf veins, subvital male gametophyte; found in hull-less-seeded pumpkin breeding line.pepoCarle and Loy, 1996a, 1996bGa, mGynoecious sex expression. Dominant to g for monoecious sex expression.foetidissimaFulks et al., 1979; Dossey et al., 1981GbGreen band on inner side of base of petal, from a scallop squash. Dominant to gb, for no band, from a straightneck squash.pepoSuperak, 1987gcglabrous. Lacking trichomes. G reen vind. Supolition.maximaKorzeniewska, 1992glglabrous. Lacking trichomes. G reen vind. Dominant to buff skin of mature fruit. Gr from 'Long Neapolitan', gr from 'Butternut'.maximaKoinson, 1987grlgray leaf. Recessive to green leaf. Recessive grl derived from cross of zapallito-type line of C. maxima and a butternut-type x moschataLopez-Anido et al., 2002			<i>Ep-1</i> from 'Small Sugar 7×7 ' pumpkin; <i>ep-1</i> from		
Ep-2Extender of pigmentation-2. Modifier of B. $pepo$ Shifriss and Paris, 1981 $Ep-2$ incompletely dominant to $ep-2$ and additive with $Ep-1$. $Ep-2$ from 'Table King' acom; $ep-2$ from 'Small Sugar 7 × 7' pumpkin.maximaNath et al., 1976 $FrFruit fly (Dacus cucurbitae) resistance. Fr from'Arka Suryamukhi', dominant to fr for susceptibility.maximaNath et al., 1976fvfused vein. Fusion of primary leaf veins,subvital male gametophyte; found in hull-less-seededpumpkin breeding line.pepoCarle and Loy, 1996a, 1996bGa, mGynoecious sex expression. Dominant to g formonoecious sex expression.foetidissimaDossey et al., 1979;Dossey et al., 1981GbGreen band on inner side of base of petal, from a scallop squash.Dominant to gb, for no band, from a straightneck squash.pepoSuperak, 1987gcglabrous. Lacking trichomes.maximaMaximaKorzeniewska, 1992Gr = GGreen rind. Dominant to buff skin of mature fruit.Gr in unspecified F2 population.maximamaximaKorzeniewska, 1992grlgray leaf. Recessive to green leaf. Recessive grl derived fromray teaf. Recessive to green leaf. Recessive grl derived fromray teaf. Recessive to green leaf. Recessive grl derived fromray teaf.Lopez-Anido et al., 2002$			'Table King' acorn.		
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.FrFruit fly (Dacus cucurbitae) resistance. Fr from 'Arka Suryamukhi', dominant to fr for susceptibility.maximaNath et al., 1976fvfused vein. Fusion of primary leaf veins, subvital male gametophyte; found in hull-less-seeded pumpkin breeding line.pepoCarle and Loy, 1996a, 1996bGa, mGynoecious sex expression. Dominant to g for monoecious sex expression. Dominant to g for a, mfor a straightneck squash. Dominant to gb, for no band, from a straightneck squash.pepoDutta and Nath, 1972gcgreen corolla. Green, leaf-like petals, sterile; in unspecified F2 population.maxima from 'Long Neapolitan', gr from 'Butternut'.maxima monoecious exercessive gr! derived from moschatamaxima maxima korzeniewska, 1992grlgray leaf. Recessive to green leaf. Recessive gr! derived from cross of zapallito-type line of C. maxima and a butternut-type x moschataLopez-Anido et al., 2002	Ep-2		<i>Extender</i> of <i>pigmentation-2</i> . Modifier of <i>B</i> .	реро	Shifriss and Paris, 1981
$Ep-1. Ep-2$ from 'Table King' acorn; $ep-2$ from 'Small Sugar 7 × 7' pumpkin.Fr $Fruit fly (Dacus cucurbitae)$ resistance. Fr from 'Arka Suryamukhi', dominant to fr for susceptibility.fvfused vein. Fusion of primary leaf veins, subvital male gametophyte; found in hull-less-seeded pumpkin breeding line.pepoCarle and Loy, 1996a, 1996bGa, mGynoecious sex expression. Dominant to g for monoecious sex expression. Dominant to g for Dominant to gb, for no band, from a straightneck squash. gcpepoDutta and Nath, 1972gcgreen corolla. Green, leaf-like petals, sterile; in unspecified F2 population.pepoSuperak, 1987glglabrous. Lacking trichomes. Gr for 'Long Neapolitan', gr from 'Butternut'. gray leaf. Recessive to green leaf. Recessive grl derived from gray leaf. Recessive to green leaf. Recessive grl derived from ross of zapallito-type line of C. maxima and a butternut-type \times moschataLopez-Anido et al., 2002			<i>Ep-2</i> incompletely dominant to <i>ep-2</i> and additive with		
FrFruit fly (Dacus cucurbitae) resistance. Fr from 'Arka Suryamukhi', dominant to fr for susceptibility.maximaNath et al., 1976fvfused vein. Fusion of primary leaf veins, subvital male gametophyte; found in hull-less-seeded pumpkin breeding line.pepoCarle and Loy, 1996a, 1996bGa, mGynoecious sex expression. Dominant to g for monoecious sex expression.foetidissima Dossey et al., 1979; Dossey et al., 1981GbGreen band on inner side of base of petal, from a scallop squash. Dominant to gb, for no band, from a straightneck squash. gcpepoSuperak, 1987glglabrous. Lacking trichomes. Gr for 'Log Neapolitan', gr from 'Butternut'.maximaKorzeniewska, 1992gray leaf. Recessive to green leaf. Recessive grl derived from cross of zapallito-type line of C. maxima and a butternut-type \times moschataLopez-Anido et al., 2002			<i>Ep-1</i> . <i>Ep-2</i> from 'Table King' acorn; <i>ep-2</i> from		
FrFruit fly (Dacus cucurbitae) resistance. Fr frommaximaNath et al., 1976'Arka Suryamukhi', dominant to fr for susceptibility.'Arka Suryamukhi', dominant to fr for susceptibility.pepoCarle and Loy, 1996a, 1996bfvfused vein. Fusion of primary leaf veins,pepoCarle and Loy, 1996a, 1996bglgynoecious sex expression. Dominant to g forfoetidissimaFulks et al., 1979;GbGreen band on inner side of base of petal, from a scallop squash.pepoDutta and Nath, 1972Gcgreen corolla. Green, leaf-like petals, sterile;pepoSuperak, 1987glglabrous. Lacking trichomes.maximaKorzeniewska, 1992GrGGreen rind. Dominant to buff skin of mature fruit.moschataRobinson, 1987gray leaf. Recessive to green leaf. Recessive grl derived frommaximaLopez-Anido et al., 2002			'Small Sugar 7×7 ' pumpkin.		
'Arka Suryamukh', dominant to fr for susceptibility.fvfused vein. Fusion of primary leaf veins, subvital male gametophyte; found in hull-less-seeded pumpkin breeding line.pepoCarle and Loy, 1996a, 1996bGa, mGynoecious sex expression. Dominant to g for monoecious sex expression.foetidissimaFulks et al., 1979; Dossey et al., 1981GbGreen band on inner side of base of petal, from a scallop squash. Dominant to gb, for no band, from a straightneck squash.pepoDutta and Nath, 1972gcgreen corolla. Green, leaf-like petals, sterile; in unspecified F2 population.pepoSuperak, 1987glglabrous. Lacking trichomes. Gr from 'Long Neapolitan', gr from 'Butternut'.maximaKorzeniewska, 1992grlgray leaf. Recessive to green leaf. Recessive grl derived from cross of zapallito-type line of C. maxima and a butternut-type × moschataLopez-Anido et al., 2002	Fr		Fruit fly (Dacus cucurbitae) resistance. Fr from	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 Gr G Green rind. Dominant to buff skin of mature fruit. Gr from 'Long Neapolitan', gr from 'Butternut'. maxima Korzeniewska, 1992 gray leaf. Recessive to green leaf. Recessive grl derived from cross of zapallito-type line of C. maxima and a butternut-type x moschata Lopez-Anido et al., 2002	<i>c</i>		'Arka Suryamukhi', dominant to fr for susceptibility.		G I II 1007 1007
subvital male gametophyte; found in hull-less-seeded pumpkin breeding line.Ga, mGynoecious sex expression. Dominant to g for monoecious sex expression.foetidissimaFulks et al., 1979; Dossey et al., 1981GbGreen band on inner side of base of petal, from a scallop squash. Dominant to gb, for no band, from a straightneck squash.pepoDutta and Nath, 1972gcgreen corolla. Green, leaf-like petals, sterile; in unspecified F2 population.pepoSuperak, 1987glglabrous. Lacking trichomes. Gr form 'Long Neapolitan', gr from 'Butternut'.maximaKorzeniewska, 1992grlgray leaf. Recessive to green leaf. Recessive grl derived from cross of zapallito-type line of C. maxima and a butternut-type maximaLopez-Anido et al., 2002	fv		fused vein. Fusion of primary leaf veins,	pepo	Carle and Loy, 1996a, 1996b
Ga, mGynoecious sex expression. Dominant to g for monoecious sex expression.foetidissima foetidissimaFulks et al., 1979; Dossey et al., 1981GbGreen band on inner side of base of petal, from a scallop squash. Dominant to gb, for no band, from a straightneck squash.pepoDutta and Nath, 1972gcgreen corolla. Green, leaf-like petals, sterile; in unspecified F2 population.pepoSuperak, 1987glglabrous. Lacking trichomes. Gr from 'Long Neapolitan', gr from 'Butternut'.maximaKorzeniewska, 1992grlgray leaf. Recessive to green leaf. Recessive grl derived from cross of zapallito-type line of C. maxima and a butternut-type × moschataLopez-Anido et al., 2002			subvital male gametophyte; found in hull-less-seeded		
G a, m Gynoecious sex expression. Dominant to g for foetialssima Fulks et al., 1979; monoecious sex expression. 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 x moschata Lopez-Anido et al., 2002	C		pumpkin breeding line.	6	E II. (1 1070
GbGreen band on inner side of base of petal, from a scallop squash. Dominant to gb, for no band, from a straightneck squash.Dotta and Nath, 1972gcgreen corolla. Green, leaf-like petals, sterile; in unspecified F2 population.pepoSuperak, 1987glglabrous. Lacking trichomes. Gr from 'Long Neapolitan', gr from 'Butternut'.maximaKorzeniewska, 1992grlgray leaf. Recessive to green leaf. Recessive grl derived from cross of zapallito-type line of C. maxima and a butternut-type × moschataLopez-Anido et al., 2002	G	<i>a, m</i>	Gynoecious sex expression. Dominant to g for	Joetiaissima	Fulks et al., $19/9$;
gc green corolla. Green, leaf-like petals, sterile; pepo Superak, 1987 gl glabrous. Lacking trichomes. maxima Korzeniewska, 1992 Gr G Green rind. Dominant to buff skin of mature fruit. 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 × moschata Lopez-Anido et al., 2002	Gh		monoccious sex expression.	h nana	Dutta and Nath 1072
gc green corolla. Green, leaf-like petals, sterile; pepo Superak, 1987 gl glabrous. Lacking trichomes. maxima Korzeniewska, 1992 Gr G Green rind. Dominant to buff skin of mature fruit. 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 x moschata Lopez-Anido et al., 2002	00		Dominant to <i>ab</i> for no band, from a straightness group -	п. реро	Dutta anu math, 1972
gl glabrous. Lacking trichomes. maxima Korzeniewska, 1992 Gr G Green rind. Dominant to buff skin of mature fruit. 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 x moschata Lopez-Anido et al., 2002	<i>ac</i>		green corolla Green leaf like potale storile:	nana	Superal 1097
gl glabrous. Lacking trichomes. maxima Korzeniewska, 1992 Gr G Green rind. Dominant to buff skin of mature fruit. 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 maxima Lopez-Anido et al., 2002	80		in unspecified F2 population	pepo	Superak, 1907
Gr G Green rind. Dominant to buff skin of mature fruit. moschata Robinson, 1992 grl gray leaf. Recessive to green leaf. Recessive grl derived from cross of zapallito-type line of C. maxima and a butternut-type x moschata Lopez-Anido et al., 2002	al		alahrous Lacking trichomes	maxima	Korzeniewska 1992
grl Gr from 'Long Neapolitan', gr from 'Butternut'. moschata Roomson, 1987 grl gray leaf. Recessive to green leaf. Recessive grl derived from cross of zapallito-type line of C. maxima and a butternut-type × moschata Lopez-Anido et al., 2002	5' Gr	G	Green rind Dominant to huff skin of mature fruit	maximu moschata	Robinson 1987
<i>grl gray leaf.</i> Recessive to green leaf. Recessive <i>grl</i> derived from <i>maxima</i> Lopez-Anido et al., 2002 cross of zapallito-type line of <i>C. maxima</i> and a butternut-type × <i>moschata</i>	01	U	Gr from 'Long Negpolitan' or from 'Rutternut'	moschulu	
cross of zapallito-type line of <i>C. maxima</i> and a butternut-type × moschata	orl		grav leaf Recessive to green leaf Recessive arl derived from	maxima	Lopez-Anido et al 2002
	0. •		cross of zapallito-type line of <i>C. maxima</i> and a butternut-type	× moschata	2002
line of C. moschata. Dominant Grl from zapallito-type C. maxima.			line of C. moschata. Dominant Grl from zapallito-type C. ma	xima.	

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

Gene	symbol			
Preferred	Synonym	Characteristic	Cucurbita species	Reference(s)
Hi		<i>Hard</i> rind <i>inhibitor</i> . <i>Hi</i> , for hard-rind inhibition, from <i>C. maxima</i> 'Queensland Blue'; <i>hi</i> , for no hard-rind	maxima × ecuadorensis	Herrington and Brown, 1988
**		inhibition, from C. ecuadorensis.		
Hr		<i>Hard rind. Hr</i> for hard (lignified) rind in ornamental gourd, straightneck squash, and zucchini; <i>hr</i> for soft (nonlignified) rind in 'Small Sugar' pumpkin and 'Sweet Potato' ('Delicata').	реро	Mains, 1950; Schaffer et al., 1986
i		<i>intensifier</i> of the <i>cr</i> gene for cream flowers. <i>Cr/- I/-</i> for intense orange or yellow flowers, <i>Cr/- i/i</i> for light orange or yellow flowers, <i>cr/cr I/-</i> for cream flowers, <i>cr/cr i/i</i> for white flowers. <i>I</i> from <i>C. moschata</i> 'Butternut',	moschata × okeechobeensis	Roe and Bemis, 1977
I-mc	I_{mc}	<i>i</i> from <i>C. okeechobeensis.</i> <i>Inhibitor</i> of <i>mature</i> fruit <i>color</i> ; dominant to <i>i-mc</i> for no inhibition	n. pepo	Clayberg, 1992
I-T		<i>I-mc</i> in a scallop squash. <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 Butternu	moschata t'	Adeniji and Coyne, 1981
<i>l-1</i>	c, St	<i>light</i> fruit coloration-1. Light intensity of fruit coloration.	pepo, maxima	Scarchuk, 1954;
		Series of five alleles observed in <i>C. pepo</i> which, in complementary interaction with the dominant <i>L</i> -2 allele, give the following results: <i>L</i> -1 for uniformly intense/dark fruit coloration, from 'Fordhook Zucchini'; <i>l</i> -1 ⁸⁵ for broad, contigue intense/dark stripes, from 'Cocozelle'; <i>l</i> -1 ^{5t} for narrow, broken intense/dark stripes, from 'Caserta'; <i>l</i> -1 ^{5t} for irregular intense/dark stripes, from 'Beirut' vegetable marrow; <i>l</i> -1 for light coloration, from 'Vegetable Spaghetti', with domin of <i>L</i> -1 > (<i>l</i> -1 ^{85t} > <i>l</i> -1 ^{5t}) ≥ <i>l</i> -1 ^{5t} > <i>l</i> -1. For <i>C. maxima</i> : <i>L</i> -1 from th	ance e	Shifriss, 1955; Globerson, 1969; Paris and Nerson, 1986; Paris and Burger, 1989; Paris, 2000a, 2003; Lopez-Anido et al., 2003
1-2	r	Zapallito 'La Germinadora'; <i>l-1</i> from a variant zapallito bredir light fruit coloration-2. Light intensity of fruit coloration. Series of three alleles observed in <i>C. pepo</i> that affect exterior color intensity of the fruit in complementary interaction with alleles at the <i>l-1</i> locus. Interactions of the dominant <i>L-2</i> allele, derived form 'Fordhook Zucchini', 'Cocozelle', and 'Caserta', with the various <i>l-1</i> alleles are as described above. Interactions <i>L-2^w</i> allele, derived from <i>C. pepo</i> subsp. <i>fraterna</i> , are delayed a weaker in comparison. The <i>l-2</i> allele, derived from 'Vegetable Spaghetti', confers light coloration and may be sub- Dominance is <i>L-2 > L-2^w > l-2</i> . The top dominant <i>L-2</i> allele is a complementary with dominant <i>B</i> for intense orange, instead of yellow, fruit-flesh color and with recessive <i>qi</i> for intense exterior color of young fruit. For <i>C. maxima</i> : <i>L-2</i> from the zapallito 'La Germinadora'; <i>l-2</i> from a variant zapallito breeding stock.	ig stock. <i>pepo,</i> <i>maxima</i> of the nd vital. ulso light or	Globerson, 1969; Paris and Nerson, 1986; Paris, 1988, 2000b, 2002a, 2002b; Lopez-Anido et al., 2003
lo-1 Lo-2	l	<i>lobed</i> leaves-1; recessive to <i>Lo-1</i> for nonlobed leaves. Lobed leaves-2. <i>Lo-2</i> for lobed leaves in <i>C. ecuadorensis</i> dominant to <i>lo-2</i> for unlobed leaves in <i>C. maxima</i> .	maxima ecuadorensis × maxima	Dyutin, 1980 Herrington and Brown, 1988
lt		Linked to Di.	neno	Scarchuk 1974
ly		<i>light yellow</i> corolla. Recessive to orange yellow; <i>ly</i> found in ornamental gourd.	реро	Scarchuk, 1974
M		Mottled leaves. M for silver-gray areas in axils of leaf veins,	pepo,	Scott and Riner, 1946a;
		dominant to <i>m</i> for absence of silver-gray. For <i>C. maxima: M</i> in 'Zuni' and <i>m</i> in 'Buttercup' and 'Golden Hubbard'. For <i>C. pepe 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: M</i> in 'Hercules' and 'Golden Cushaw', <i>m</i> in butternut type. Weakly linked to <i>Wt.</i>	maxima, p: moschata	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		<i>mature orange-1</i> . Complementary recessive gene for loss of green fruit color before maturity. <i>Mo-1</i> from 'Table Queen' acorn; <i>mo-1</i> from 'Vegetable Spaghetti'.	реро	Paris, 1997
<i>mo-2</i>		<i>mature orange-2</i> . Complementary recessive gene for loss of green fruit color before maturity. <i>Mo-2</i> from 'Table Queen' acorn; <i>mo-2</i> from 'Vegetable Spaghetti'. Linked to <i>D</i> .	реро	Paris, 1997
ms-1	ms ₁	<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.	maxima	Scott and Riner, 1946b
ms-2	ms ₂	<i>male sterile</i> -2. Male flowers abort, sterility expressed as androecium shrivelling and turning brown; <i>ms</i> -2 from (Eskandarany) (PI 228201)	реро	Eisa and Munger, 1968
ms-3	<i>ms</i> -2	male sterile-3.	maxima	Korzeniewska, 1992

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

Gene s	symbol			
Preferred	Synonym	Characteristic	Cucurbita species	Reference(s)
m-zym ^{mos} *		<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	moschata	Pachner and Lelley, 2004
	I.	Soler, <i>m-zym^{mos}</i> in Waltnam Butternut and "Nigerian Local"		Sahäningar 1052:
n	n	<i>n from oil-seed pumpkin.</i>	pepo, moschata	Schoninger, 1952; Grebenšikov, 1954; Xianglin, 1987;
				Zraidi et al., 2003
pl		plain light fruit color. Recessive pl from 'Beirut'	pepo	,
*		vegetable marrow and 'Fordhook Zucchini'; <i>Pl</i> in 'Vegetable Spaghetti'.		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	okeechobeensis,	Contin, 1978;
		Podosphaera xanthii. Pm-0 from C. okeechobeensis and introgressed to C. pepo. Not known if this is the	реро	Jahn et al., 2002; Cohen et al., 2003
		same or a different locus from Pm .		
pm-1		powdery mildew resistance-1. Resistance to	moschata	Adeniji and Coyne, 1983
		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'.		
pm-2		<i>powdery mildew</i> resistance-2. Resistance to <i>Golovinomyces cichoracearum</i> in <i>C. moschata</i> . Allele <i>pm</i> -2 ^s for resistance in 'Seminole' is recessive to	moschata	Adeniji and Coyne, 1983
		<i>Pm-2</i> for susceptibility in 'Ponca'.		
prv		papaya ringspot virus resistance. In 'Nigerian Local', recessive to Prv for susceptibility in 'Waltham Butternut'.	moschata	Brown et al., 2003
qi		<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 noncoureuse	pepo i';	Paris, 2000b, 2002b
Rd		<i>Red</i> skin. Red external fruit color; dominant to green, white, yellow and gray. <i>Rd</i> from 'Turk's Cap';	maxima	Lotsy, 1920
ro		rd from 'Warted Hubbard'. rosette leaf. Lower lobes of leaves slightly spiraled,	реро	Mains, 1950
s-1	S	sterile-1. Male flowers small, without pollen; female flower steri	le. maxima	Hutchins, 1944
s-2		<i>sterile-2.</i> Male flowers small, without pollen and female flower sterile; mutant in a powdery mildew-resistant straightneck squash breeding line	реро	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 see-B in 'Lersey Golden Acorr'	реро	Shifriss, 1982
sl		<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	moschata	Gonzalez-Roman and Wessel-Beaver, 2002
Slc		Sauash leaf curl virus resistance. Derived from C. moschata.	neno	Montes-Garcia et al., 1998
SD		spaghetti flesh. Flesh breaking into strands after cooking.	реро	Mazurek and Niemirowicz-Szczvtt, 1992
spn*		spineless foliage. Petioles and abaxial surfaces of leaf laminae glabrous, lacking spiculate trichomes. Derived from male pare of 'Multipik' hybrid straightneck. Spininess, Spn, from various straightneck inbreds is incompletely dominant	pepo nt	Superak, 1999
Т		<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'	; <i>moschata</i> Butternut'.	Adeniji and Coyne, 1981
uml		<i>umbrella-like</i> . Leaves shaped like partially opened umbrella. Recessive <i>uml</i> derived from a cross of <i>C. maxima</i> 'Warzywna'	maxima	Rakoczy-Trojanowska and Malepszy, 1999
		and a <i>C. pepo</i> inbred; dominant <i>Uml</i> from 'Warzywna'.	× pepo	Duritin and Afanas'ava 1081
V W		Weak fruit coloration [formerly White fruit]. Dominant to w for	pepo	Sinnott and Durham, 1922;
		Complementary to Wf for white external fruit color.		Paris et al., 1952; Paris, 1995
wc		<i>white corolla</i> . Derived from 'Ispanskaya' × 'Emerald'. Recessive to <i>Wc</i> for normal orange-yellow corolla	maxima	Korzeniewska, 1996
Wf		White flesh. Dominant to wf for colored flesh.	реро	Sinnott and Durham, 1922;
5		<i>Wf</i> in a scallop squash, <i>wf</i> in a straightneck squash.	1	Dutta and Nath, 1972;
Wmv		Complementary to <i>W</i> for pale orange or white external fruit co <i>Watermelon mosaic virus</i> resistance. 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> .	lor. moschata	Paris, 1995 Gilbert-Albertini et al., 1993; Brown et al., 2003

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

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

*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* \times *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 populationspecific. 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*

(Covne, 1970; Paris et al., 2004; Scarchuk, 1954; Scott and Riner, 1946a). Some of the progeny in a cross of C. maxima \times 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 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;

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 \times 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).

spinelessness has been found in this species,

Afanas'eva, 1981).

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 \times 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-1^{BSt}* (Paris, 2000a; Paris et al., 2004), narrow, broken intense/dark stripes from *l-1st* (Paris, 2002b; Paris and Burger, 1989; Scarchuk, 1954; Shifriss, 1955), and irregular intense/dark stripes from $l-1^{iSt}$ (Paris, 2003). The effects of dominant alleles at *l-1* are delayed and weakened in the presence of $L-2^{w}/L-2^{w}$ 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 vellow-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 Wis 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/dL-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.

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, zymecu (Robinson et al., 1988). Five genes for resistance residing at separate loci have been identified in C. moschata. A recessive gene for resistance, zvm^{mos}, is possessed by 'Soler' and was identified in a cross with the susceptible 'Waltham Butternut'. It is modified by *m-zym^{mos}*, which confers resistance to Zym^{mos}/zym^{mos} heterozygotes which would otherwise be susceptible (Pachner and Lelley, 2004). Zvm-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 $pm-l^L$ for resistance from 'La Primera' being dominant to $pm-1^{W}$ for susceptibility from 'Waltham Butternut' but recessive to the allele for high susceptibility, *pm-1^P*, from 'Ponca'. Another gene for resistance, pm-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, 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 vellow 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 F₂ 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 vs. 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

Table 2. The isozyme variants of Cucurbita.

Gene s	ymbol	Alleles		Cucurbita	
Preferred	Synonym	observed (no)	Character	species	Reference(s)
Aat 1	Aat	0	Aspautate aminetuansferase 1	species	Ignort and Weeden 1094:
Adl-1	Adl	0	Aspariale aminoiransjerase-1.	реро	Ignart and weeden, 1984,
			variant among accessions.		Decker-walters et al., 1993
Aat-3		2	Aspartate aminotransferase-3.	реро	Decker-Walters et al., 1993
			Variant among wild populations.		
Aat-4		3	Aspartate aminotransferase-4.	реро	Decker-Walters et al., 1993
			Variant among wild populations.	* *	
Aat-mh		2	Aspartate aminotransferase-microbody	maxima × ecuadorensis	Weeden and Robinson 1986
Aat ml		2	Aspartate aminotransferase mitochondria 1	maxima × acuadoransis	Weeden and Pobinson, 1986
Aut-m1		2	Aspuriule uninoir unsferuse milochondriu-1.		Weeden and Dahimann 1096
Aat-m2		2	Aspartate aminotransferase mitochonaria-2.	maxima × ecuadorensis	weeden and Robinson, 1986
Aat-p2		2	Aspartate aminotransferase plastid-2.	maxima \times 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 \times ecuadorensis	Wall and Whitaker, 1971:
		-			Weeden and Robinson 1986
Gal 1		2	B calactoridano 1	maxima × aquadononsis	Weeden and Pobinson, 1966
Gal-1		2	p-galaciosiaase-1.	maxima × ecuadorensis	Weeden and Kobinson, 1980
Gal-2		2	β-galactosidase-2.	$maxima \times ecuadorensis$	Weeden and Robinson, 1986
G2d-1		3	Glycerate dehydrogenase-1.	реро	Decker-Walters et al., 1993
			Variant among wild populations.		
G2d-2		2	Glycerate dehydrogenase-2.	реро	Decker-Walters et al., 1993
			Variant among wild populations	F T	
Got 1		5	Chitamina oralogastata 1	nano	Deaker 1095
001-1		5	Variant and a consider wild a coulation	pepo	Winley stricts at al. 1005.
			variant among accessions, wild populations,		Kirkpatrick et al., 1985;
			and among Cucurbita species.		Decker and Wilson, 1987;
					Wilson, 1989
Got-2		3	Glutamine oxaloacetate-2.	maxima × ecuadorensis	Wilson, 1989
			Variant among species		,
Gni		2	Glucosenhosnhate isomerase	nano	Ignart and Weeden, 1984
Opi		2	Viciosephosphule isomeruse.	pepo	Ignart and weeden, 1984
<i>a</i>			variant among accessions.		
Gpi-3		2	Glucosephosphate isomerase-3.	pepo	Decker-Walters et al., 1993
			Variant among wild populations.		
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 dehvdrogenase-1	neno	Decker 1985
10// 1			Variant among accessions, wild nonulations	pepo	Kirkpatrick et al. 1085:
			variant among accessions, who populations,		Declear and Wilson 1007.
			and Cucurolla species.		Decker and wilson, 1987;
					Wilson, 1989;
					Decker-Walters et al., 1993
Idh-2		2	Isocitrate dehydrogenase-2.	реро	Decker, 1985;
			Variant among accessions, wild populations.		Kirkpatrick et al., 1985:
			and <i>Cucurbita</i> species		Decker and Wilson 1987
			and chemistra species.		Wilson 1989:
					Dealerr Walters et al. 1002
111.2		2			Deckel-wallers et al., 1995
Tan-3		2	Isocitrate aenyarogenase-3.	pepo	Decker, 1985;
			Variant among accessions and populations.		Kirkpatrick et al., 1985;
					Decker and Wilson, 1987;
					Decker-Walters et al., 1993
Lan-1	Lan	4	Leucine aminopentidase	maxima × ecuadorensis: neno	Wall and Whitaker 1971
Lup 1	Lup	•	Variant among C nano accessions	contactor ensits, pepo	Ignart and Weeden 1984:
			variant among C. pepo accessions.		Waadan and Dahingan 1086
					weeden and Kobinson, 1980,
		_			Decker-Walters et al., 1993
Mdh-1	Mdh	7	Malate dehydrogenase.	реро	Ignart and Weeden, 1984
			Variant among accessions.		
Mdh-2		3	Malate dehydrogenase-2.	реро	Decker, 1985;
			Variant among accessions, wild populations.	1 1	Kirkpatrick et al., 1985:
			and Cucurbita species		Decker and Wilson 1987
			and Cucurbita species.		Wilson 1000:
					WIISOII, 1969,
					Decker-wallers et al., 1993;
Mdh-3		3	Malate dehydrogenase-3.	pepo	Decker, 1985;
			Variant among accessions, wild populations,		Kirkpatrick et al., 1985;
			and Cucurbita species.		Decker and Wilson, 1987;
			*		Wilson, 1989:
					Decker-Walters et al 1993
Mdh_m1		2	Malate debudrogenase mitochondria 1	marima × pougdorousis	Weeden and Robinson 1096
Male 2		2	Malate dehuduo zen age mite de multin 2	maxima ~ ecuadorensis	Weeden and Debinery 1000
$Mun-m^2$		2	Malue denyarogenase mitocnonaria-2.	maxima ~ ecuaaorensis	weeden and Kobinson, 1986
Mdh-c2		2	Malate dehydrogenase cytosolic-2.	$maxima \times ecuadorensis$	weeden and Robinson, 1986
Per-1		2	Peroxidase-1.	maxima × ecuadorensis	Weeden and Robinson, 1986
Per-2		3	Peroxidase-2.	реро	Decker, 1985;
			Variant among accessions and wild population	15.	Kirkpatrick et al., 1985:
					Decker and Wilson 1987
Par. 2		2	Paroridasa_3	marima × acuadoronsis	Weeden and Pohinson 1004
Dai 1		2	Dhoghhoghuggo isomouso 1		Docker 1095
rgi-1		2	r nospnogiucase isomerase-1.	реро	Deckel, 1985
Pgi-2		2	Phosphoglucase isomerase-2.	pepo	Decker, 1985;
			Variant among Cucurbita species.		Kirkpatrick et al., 1985;
					Wilson, 1989

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

			Recombination	
Trait	Symbol	Linked marker(s) ^z	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	В	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

^zThese 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 cultivargroups 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.

Literature Cited

- Adeniji, A.A. and D.P. Coyne. 1981. Inheritance of resistance to trifluralin toxicity in *Cucurbita moschata* Poir. HortScience 16:774–775.
- Adeniji, A.A. and D.P. Coyne. 1983. Genetics and nature of resistance to powdery mildew in crosses of butternut with calabaza squash and 'Seminole Pumpkin'. J. Amer. Soc. Hort. Sci. 108:360–368.
- Andres, T.C. 2004. Diversity in tropical pumpkin (*Cucurbita moschata*): a review of infraspecific classifications, p. 107–112. In: A. Lebeda and H.S. Paris (eds.). Proceedings of Cucurbitaceae 2004. Palacký Univ., Olomouc, Czech Republic.
- Andres, T.C. and R.W. Robinson. 2002. Cucurbita ecuadorensis, an ancient semi-domesticate with multiple disease resistance and tolerance to some adverse growing conditions, p. 95–99. In: D.N.

Maynard (ed.). Cucurbitaceae 2002. ASHS Press, Alexandria, Va.

- Brown, R.N. and J.R. Myers. 2002. A genetic map of squash (*Cucurbita* sp.) with randomly amplified polymorphic DNA markers and morphological markers. J. Amer. Soc. Hort. Sci. 127:568–575.
- Brown, R.N., A. Bolanos-Herrera, J.R. Myers, and M.M. Jahn. 2003. Inheritance of resistance to four cucurbit viruses in *Cucurbita moschata*. Euphytica 129:253–258.
- Cardosa, A.I.I., P.T. Della Vecchia, and N. Silva. 1993. Inheritance of immature fruit color in *C. moschata*. Cucurbit Genet. Coop. Rpt. 16:68–69.
- Carle, R.B. 1997. Bisex sterility governed by a single recessive gene in *Cucurbita pepo*. Cucurbit Genet. Coop. Rpt. 20:46–47.
- Carle, R.B. and J.B. Loy. 1996a. Genetic analysis of the fused vein trait in *Cucurbita pepo* L. J. Amer. Soc. Hort. Sci. 121:13–17.
- Carle, R.B. and J.B. Loy. 1996b. Fused vein trait in *Cucurbita pepo* L. associated with subvitality of the male gametophyte. J. Amer. Soc. Hort. Sci. 121:18–22.
- Clayberg, C.D. 1992. Reinterpretation of fruit color inheritance in *Cucurbita pepo* L. Cucurbit Genet. Coop. Rpt. 15:90–92.
- Cohen, R., A. Hanan, and H.S. Paris. 2003. Single-gene resistance to powdery mildew in zucchini squash (*Cucurbita pepo*). Euphytica 130:433–441.

- Contardi, H.G. 1939. Estudios geneticos en *Cucurbita* y consideraciones agronomicas. Physis 18:331–347.
- Contin, M. 1978. Interspecific transfer of powdery mildew resistance in the genus *Cucurbita*. PhD thesis. Cornell Univ., Ithaca, N.Y.
- Coyne, D.P. 1970. Inheritance of mottle-leaf in *Cucurbita moschata* Poir. HortScience 5:226–227.
- Decker, D.S. 1985. Numerical analysis of allozyme variation in *Cucurbita pepo*. Econ. Bot. 39:300–309.
- Decker, D.S. and H.D. Wilson. 1987. Allozyme variation in the *Cucurbita pepo* complex: *C. pepo* var. *ovifera* vs. *C. texana*. Syst. Bot. 12:263–273.
- Decker-Walters, D.S., T.W. Walters, C.W. Cowan, and B.D. Smith. 1993. Isozymic characterization of wild populations of *Cucurbita pepo*. J. Ethnobiol. 13:55–72.
- Denna, D.W. and H.M. Munger. 1963. Morphology of the bush and vine habits and the allelism of the bush genes in *Cucurbita maxima* and *C. pepo* squash. Proc. Amer. Soc. Hort. Sci. 82:370–377.
- Dossey, B.F., W.P. Bemis, and J.C. Scheerens. 1981. Genetic control of gynoecy in the buffalo gourd. J. Hered. 72:355–356.
- Dutta, L.P. and P. Nath. 1972. Inheritance of flower and fruit characters in squash, *Cucurbita pepo* L., p. 69–74. 3rd Intl. Symp. Sub-Trop. Trop. Hort.
- Dyutin, K.E. 1980. Spontaneous mutant of *Cucurbita maxima* Duch. squash with lobed leaves (in Russian). Genetika 16:176–178.
- Dyutin, K.E. and E.A. Afanas'eva. 1981. Inheritance of the yellow-green color of young leaves of the squash *Cucurbita maxima* Duch. (in Russian). Tsitologiya i Genetika 15(5):81–82.
- Eisa, H.M. and H.M. Munger. 1968. Male sterility in *Cucurbita pepo*. Proc. Amer. Soc. Hort. Sci. 92:473–479.
- FAO 2005. http://faostat.fao.org/faostat/collections ?subset=agriculture.
- Fulks, B.K., J.C. Scheerens, and W.P. Bemis. 1979. Sex expression in *Cucurbita foetidissima* HBK. Cucurbit Genet. Coop. Rpt. 2:36.
- Gilbert-Albertini, F., H. Lecoq, M. Pitrat, and J.L. Nicolet. 1993. Resistance of *Cucurbita moschata* to watermelon mosaic virus type 2 and its genetic relation to resistance to zucchini yellow mosaic virus. Euphytica 69:231–237.
- Globerson, D. 1969. The inheritance of white fruit and stem color in summer squash, *Cucurbita pepo* L. Euphytica 18:249–255.
- Gonzalez-Roman, M. and L. Wessel-Beaver. 2002. Resistance to silverleaf disorder is controlled by a single recessive gene in *Cucurbita moschata* Duchesne. Cucurbit Genet. Coop. Rpt. 25:49–50.
- Grebenšcikov, I. 1954. Zur Vererbung der Dünnschaligkeit bei Cucurbita pepo L. Züchter 24:162–166.
- Grebenšcikov, I. 1955. Notulae cucurbitologicae II. Über Cucurbita texana A. Gr. und ihre Kreuzung mit einer hochgezüchteten C. pepo-Form. Kulturpflanze 3:50–59.
- Grebenšcikov, I. 1958. Notulae cucurbitologicae III. Kulturpflanze 6:38–60.
- Guner, N. and T.C. Wehner. 2004. The genes of watermelon. HortScience 39:1175–1182.
- Herrington, M.E. and J.P. Brown. 1988. Inheritance of leaf and fruit characteristics in *Cucurbita maxima* Duch. cv. Queensland Blue × *C. ecuadorensis* Cutler and Whitaker. Queensland J. Agr. Animal Sci. 45:45–48.
- Hutchins, A.E. 1935. The interaction of blue and green color factors in hubbard squash. Proc. Amer. Soc. Hort. Sci. 33:514.

- Hutchins, A.E. 1944. A male and female sterile variant in squash, *Cucurbita maxima* Duch. Proc. Amer. Soc. Hort. Sci. 44:494–496.
- Hutton, M.G. and R.W. Robinson. 1992. Gene list for *Cucurbita* spp. Cucurbit Genet. Coop. Rpt. 15:102–109.
- Ignart, F. and N.F. Weeden. 1984. Allozyme variation in cultivars of *Cucurbita pepo* L. Euphytica 33:779–785.
- Jahn, M., H.M. Munger, and J.D. McCreight. 2002. Breeding cucurbit crops for powdery mildew resistance, p. 239–248. In: R.R. Bélanger, W.R. Bushnell, A.J. Dik, and T.L.W. Carver (eds.). The powdery mildews, a comprehensive treatise. Amer. Phytopathol. Soc., St. Paul, Minn.
- Kirkpatrick, K.J., D.S. Decker, and H.D. Wilson. 1985. Allozyme differentiation in the *Cucurbita pepo* complex: *C. pepo* var. *medullosa* vs. *C. texana*. Econ. Bot. 39:289–299.
- Korzeniewska, A. 1992. New genes in *Cucurbita maxima* Duch., p. 75–78. In: R.W. Doruchowski, E. Kozik, and K. Niemirowicz-Szczytt (eds.). Proc. Cucurbitaceae '92: The 5th Eucarpia Meeting on Cucurbit Genetics and Breeding.
- Korzeniewska, A. 1996. Two independent loci for white and white-yellow corolla in *Cucurbita* maxima Duch., p. 78–81. In: M.L. Gomez-Guillamon, C. Soria, J. Cuartero, J. Tores, and R. Fernandez-Munoz (eds.). Proc. Cucurbitaceae Towards 2000: The 6th Eucarpia Meeting on Cucurbit Genetics and Breeding. Graficas Axarquia, Velez-Malaga, Spain.
- Kubicki, B. 1970. Androecious strains of *Cucurbita* pepo L. Genet. Polon. 11:45–51.
- Kwack, S.N. 1995. Inheritance of determinate growth habit in *Cucurbita moschata* Poir. J. Kor. Soc. Hort. Sci. 36:780–784.
- Levi, A., C.E. Thomas, T.C. Wehner, and X. Zhang. 2001. Low genetic diversity indicates the need to broaden the genetic base of cultivated watermelon. HortScience 36:1096–1101.
- Lopez-Anido, F., E. Cointry, I. Firpo, S.M. Garcia, and S. Gattuso. 2002. Inheritance of gray leaf color in a material derived from a *Cucurbita maxima* Duch. × *C. moschata* Duch. hybrid. Cucurbit Genet. Coop. Rpt. 25:46–48.
- Lopez-Anido, F., V. Cravero, P. Asprelli, E. Cointry, I. Firpo, and S.M. Garcia. 2003. Inheritance of immature fruit color in *Cucurbita maxima* var. Zapallito (Carrière) Millan. Cucurbit Genet. Coop. Rpt. 26:48–50. http://www.umresearch. umd.edu/CGC/cgc26/cgc26 15.pdf.
- Lotsy, J.P. 1920. *Cucurbita* Strijdvragen. II. Eigen Onderzoekingen. Genetica 2:1–21.
- Mains, E.B. 1950. Inheritance in *Cucurbita pepo*. Papers Mich. Acad. Sci. Arts Lett. 36:27–30.
- Mazurek, Z. and K. Niemirowicz-Szczytt. 1992. Inheritance of spaghetti traits in *Cucurbita pepo*, p. 70–74. In: R.W. Doruchowski, E. Kozik, and K. Niemirowicz-Szczytt (eds.). Proc. Cucurbitaceae '92: The 5th Eucarpia Meeting on Cucurbit Genetics and Breeding.
- Montes-Garcia, C.E., S. Garza-Ortega, and J.K. Brown. 1998. Inheritance of the resistance to squash leaf curl virus in *Cucurbita pepo* L., p. 328–330. In: J.D. McCreight (ed.). Cucurbitaceae '98: Evaluation and Enhancement of Cucurbit Germplasm. ASHS, Alexandria, Va.
- Munger, H.M. and R. Provvidenti. 1987. Inheritance of resistance to zucchini yellow mosaic virus in *Cucurbita moschata*. Cucurbit Genet. Coop. Rpt. 10:80–81.
- Mutschler, M.A. and O.H. Pearson. 1987. The origin, inheritance, and instability of butternut squash (*Cucurbita moschata* Duchesne). HortScience 22:535–539.
- Nath, P., O.P. Dutta, S. Velayudhan, and K.R.M. Swamy. 1976. Inheritance of resistance to fruit

fly in pumpkin. Sabrao J. 8:117-119.

- Nee, M. 1990. The domestication of *Cucurbita* (Cucurbitaceae). Econ. Bot. 44(3, Suppl.):56–68.
- Norrman, R. and J. Haarberg. 1980. Nature and language: A semiotic study of cucurbits in literature. Routledge & Kegan Paul, London.
- Pachner, M. and T. Lelley. 2004. Different genes for resistance to zucchini yellow mosaic virus (ZYMV) in *Cucurbita moschata*, p. 237–243. In: A. Lebeda and H.S. Paris (eds.). Proceedings of Cucurbitaceae 2004. Palacký Univ., Olomouc, Czech Republic.
- Paris, H.S. 1988. Complementary genes for orange fruit flesh color in *Cucurbita pepo*. HortScience 23:601–603.
- Paris, H.S. 1989. Historical records, origin, and development of the edible cultivar groups of *Cucurbita pepo* (Cucurbitaceae). Econ. Bot. 43:423–443.
- Paris, H.S. 1992. A recessive, hypostatic gene for plain light fruit coloration in *Cucurbita pepo*. Euphytica 60:15–20.
- Paris, H.S. 1995. The dominant *Wf(whiteflesh)* allele is necessary for expression of "white" mature fruit color in *Cucurbita pepo*, p. 219–220. In: G. Lester and J. Dunlap (eds.). Cucurbitaceae '94 Gateway, Edinburg, Texas.
- Paris, H.S. 1996. Multiple allelism at the *D* locus in squash. J. Hered. 87:391–395.
- Paris, H.S. 1997. Genes for developmental fruit coloration of acorn squash. J. Hered. 88:52–56.
- Paris, H.S. 2000a. Gene for broad, contiguous dark stripes in cocozelle squash. Euphytica 115:191–196.
- Paris, H.S. 2000b. *Quiescent intense (qi)*: A gene that affects young but not mature fruit color intensity in *Cucurbita pepo*. J. Hered. 91:333–339.
- Paris, H.S. 2000c. Segregation distortion in *Cucurbita pepo*. In: N. Katzir and H.S. Paris (eds.). Proceedings of Cucurbitaceae 2000. Acta Hort. 510:199–202.
- Paris, H.S. 2000d. History of the cultivar-groups of *Cucurbita pepo*, p. 71–170. In: J. Janick (ed.). Horticultural reviews. vol. 25.
- Paris, H.S. 2002a. Multiple allelism at a major locus affecting fruit coloration in *Cucurbita pepo*. Euphytica 125:149–153.
- Paris, H.S. 2002b. No segregation distortion in intersubspecific crosses in *Cucurbita pepo*. Cucurbit Genet. Coop. Rpt. 25:43–45.
- Paris, H.S. 2003. Genetic control of irregular striping, a new phenotype in *Cucurbita pepo*. Euphytica 129:119–126.
- Paris, H.S. and Y. Burger. 1989. Complementary genes for fruit striping in summer squash. J. Hered. 80:490–493.
- Paris, H.S. and S. Cohen. 2000. Oligogenic inheritance for resistance to zucchini yellow mosaic virus in *Cucurbita pepo*. Ann. Appl. Biol. 136:209–214.
- Paris, H.S., S. Cohen, Y. Burger, and R. Yoseph. 1988. Single gene resistance to zucchini yellow mosaic virus in *Cucurbita moschata*. Euphytica 37:27–29.
- Paris, H.S., A. Hanan, and F. Baumkoler. 2004. Assortment of five gene loci in *Cucurbita pepo*, p. 389–392. In: A. Lebeda and H.S. Paris (eds.). Proceedings of Cucurbitaceae 2004. Palacký Univ., Olomouc, Czech Republic.
- Paris, H.S. and H. Nerson. 1986. Genes for intense pigmentation of squash. J. Hered. 77:403–409.
- Paris, H.S., H. Nerson, and Y. Burger. 1985a. Precocious PI 165561 and Precocious PI 165561R pumpkin breeding lines. HortScience 20:778–779.
- Paris, H.S., H. Nerson, Z. Karchi, and Y. Burger. 1985b. Inheritance of light pigmentation in squash. J. Hered. 76:305–306.

- Pitrat, M. 2002. 2002 gene list for melon. Cucurbit Genet. Coop. Rpt. 25:76–93.
- Rakoczy-Trojanowska, M. and S. Malepszy. 1999. Inheritance of umbrella-like leaf shape in materials derived form *Cucurbita maxima* × *C. pepo* hybrids. Cucurbit Genet. Coop. Rpt. 22:50–52.
- Rhodes, A.M. 1964. Inheritance of powdery mildew resistance in the genus *Cucurbita*. Plant Dis. Rptr. 48:54–55.
- Robinson, R.W. 1987. Inheritance of fruit skin color in *Cucurbita moschata*. Cucurbit Genet. Coop. Rpt. 10:84.
- Robinson, R.W. and D.S. Decker-Walters. 1997. Cucurbits. CAB Intl., Wallingford, Oxon, U.K.
- Robinson, R.W. and M.G. Hutton. 1996. Update of gene list for *Cucurbita* spp. Cucurbit Genet. Coop. Rpt. 19:91–92.
- Robinson, R.W. and H.S. Paris. 2000. Cucurbita gene list update—2000. Cucurbit Genet. Coop. Rpt. 23:137–138.
- Robinson, R.W., N.F. Weeden, and R. Provvidenti. 1988. Inheritance of resistance to zucchini yellow mosaic virus in the interspecific cross *Cucurbita* maxima × C. ecuadorensis. Cucurbit Genet. Coop. Rpt. 11:74–75.
- Roe, N.E. and W.P. Bemis. 1977. Corolla color in *Cucurbita*. J. Hered. 68:193–194.
- Scarchuk, J. 1954. Fruit and leaf characters in summer squash. J. Hered. 45:295–297.
- Scarchuk, J. 1974. Inheritance of light yellow corolla and leafy tendrils in gourd (*Cucurbita pepo* var. *ovifera* Alef.). HortScience 9:464.
- Schaffer, A.A. and C.D. Boyer. 1984. The influence of gene *B* on fruit development in *Cucurbita pepo*. J. Amer. Soc. Hort. Sci. 106:432–437.
- Schaffer, A.A., C.D. Boyer, and H.S. Paris. 1986. Inheritance of rind lignification and warts in *Cucurbita pepo* L. and a role for phenylalanine ammonia lyase in their control. Z. Pflanzenzüchtg. 96:147–153.
- Schöniger, G. 1952. Vorläufige Mitteilung über das Verhalten der Testa- und Farbgene bei ver-

schiedenen Kreuzungen innerhalb der Kürbisart *Cucurbita pepo* L. Züchter 22:316–337.

- Scott, D.H. and M.E. Riner. 1946a. A mottled leaf character in winter squash. J. Hered. 37:27–28.
- Scott, D.H. and M.E. Riner. 1946b. Inheritance of male sterility in winter squash. Proc. Amer. Soc. Hort. Sci. 47:375–377.
- Sharma, G.C. and C.V. Hall. 1971. Cucurbitacin B and total sugar inheritance in *Cucurbita pepo* related to spotted cucumber beetle feeding. J. Amer. Soc. Hort. Sci. 96:750–754.
- Shifriss, O. 1947. Developmental reversal of dominance in *Cucurbita pepo*. Proc. Amer. Soc. Hort. Sci. 50: 330–346.
- Shifriss, O. 1955. Genetics and origin of the bicolor gourds. J. Hered. 46:213–222.
- Shifriss, O. 1966. Behavior of gene B in Cucurbita. Veg. Improv. Nwslt. 8:7–8.
- Shifriss, O. 1981. Origin, expression, and significance of gene *B* in *Cucurbita pepo* L. J. Amer. Soc. Hort. Sci. 106:220–232.
- Shifriss, O. 1982. Identification of a selective suppressor gene in *Cucurbita pepo* L. HortScience 17:637–638.
- Shifriss, O. 1989. Relationship between the *B* genes of two *Cucurbita* species, II. Cucurbit Genet. Coop. Rpt. 12:75–78.
- Shifriss, O. and H.S. Paris. 1981. Identification of modifier genes affecting the extent of precocious fruit pigmentation in *Cucurbita pepo* L. J. Amer. Soc. Hort. Sci. 106:653–660.
- Sinnott, E.W. and G.B. Durham. 1922. Inheritance in the summer squash. J. Hered. 13:177–186.
- Smith, B.D. 1997. The initial domestication of *Cucurbita pepo* in the Americas 10,000 years ago. Science 276:932–934.
- Superak, T.H. 1987. A green corolla mutant in *Cucurbita pepo*. Cucurbit Genet. Coop. Rep. 10:103.
- Superak, T.H. 1999. Plants and seeds of *Cucurbita* pepo having a genetic factor for spinelessness.

United States Patent 5,959,184. www.uspto. gov/patft/index.html.

- Wall, J.R. and T.W. Whitaker. 1971. Genetic control of leucine aminopeptidase and esterase isozymes in the interspecific cross *Cucurbita ecuadorensis* × *C. maxima*. Biochem. Genet. 5:223–229.
- Weeden, N.F. and R.W. Robinson. 1986. Allozyme segregation ratios in the interspecific cross *Cucurbita maxima* × *C. ecuadorensis* suggest that hybrid breakdown is not caused by minor alterations in chromosome structure. Genetics 114:593–609.
- Weeden, N.F., R.W. Robinson, and F. Ignart. 1984. Linkage between an isozyme locus and one of the genes controlling resistance to watermelon mosaic virus 2 in *Cucurbita ecuadorensis*. Cucurbit Genet. Coop. Rpt. 7:86–87.
- Whitaker, T.W. 1932. Fertile gourd-pumpkin hybrids. J. Hered. 23:427–430.
- Whitaker, T.W. 1947. American origin of the cultivated cucurbits. Ann. Mo. Bot. Gard. 34:101–111.
- Wilson, H.D. 1989. Discordant patterns of allozyme and morphological variation in Mexican *Cucurbita*. Syst. Bot. 14:612–623.
- Xianglin, Z. 1987. A study on the breeding of naked kernel pumpkin and its genetic behavior (in Chinese, with English summary). Acta Hort. Sin. 14:115–118.
- Xie, J. and T.C. Wehner. 2001. Gene list 2001 for cucumber. Cucurbit Genet. Coop. Rpt. 24:110–136.
- Zraidi, A. and T. Lelley. 2004. Genetic map for pumpkin *Cucurbita pepo* using random amplified polymorphic DNA markers, p. 507–514. In: A. Lebeda and H.S. Paris (eds.). Proceedings of Cucurbitaceae 2004. Palacký Univ., Olomouc, Czech Republic.
- Zraidi, A., M. Pachner, T. Lelley, and R. Obermayer. 2003. On the genetics and histology of the hullless character of Styrian oil-pumpkin (*Cucurbita pepo* L.). Cucurbit Genet. Coop. Rpt. 26:57–61.