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Numerical Analysis of Seed Morphology in *Cucurbita pepo*

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ABSTRACT. Quantitative data were collected for 24 commercial cultivars of *Cucurbita pepo*, four *C. pepo* collections from Mexico, six populations of *C. texana* from Texas, and three spontaneous populations of *texana*-like plants from Alabama, Arkansas, and Illinois. Canonical variate and principal component analyses revealed variation in the size and shape of *C. pepo* seeds which was similar to recently documented patterns of allozyme variation. Additionally, variation in seed characters appears to reflect effects of human selection. Stepwise selection was used to select four characters useful in discriminating between *C. texana* and *C. pepo* var. *ovifera* seeds. Most significant were characters describing the sinus area near the seed scar. A discriminant function based on these characters was capable of correctly identifying seeds with 86% accuracy, indicating inherent differences between these taxa. On the basis of this discriminant function, the spontaneous populations from Alabama, Arkansas, and Illinois were classified. Although 80% of the seeds from these populations were classified as *C. pepo* var. *ovifera*, the general nature of these populations was one of intermediacy between the two taxa. This intermediacy is an important consideration in interpreting the relationship between *C. texana* and *C. pepo*. Although generally assumed to be feral populations of relatively recent origin, these populations could also represent remnants of the wild species in an area northeast of its current distribution in Texas.

Cucurbita pepo L., represented by cultivated forms of squash, pumpkins, and ornamental gourds, is a morphologically diverse species. This diversity has been the basis for several attempts to classify cultivars (Naudin 1856; Alefeld 1866; Goff 1888; Castetter 1925; Bailey 1929; Erwin and Haber 1929). These classifications, which have been based primarily on qualitative observations of fruit structure and plant habit, suggest the need for more discriminating analyses. Although qualitative seed characters have been employed to discriminate among species of *Cucurbita* (Russell 1924), variation in seeds of *C. pepo* has not been systematically evaluated, even though descriptions indicate that quantitative differences exist (Tapley et al. 1937). There are several other advantages to examining seeds of *C. pepo*: they are durable and easy to obtain in large quantities from field collections as well as from seed companies; on the basis of personal observation, they appear to be less influenced by environmental factors than are vegetative and fruiting characters (Sinnott 1932; Whitaker and Davis 1962); mature versus sterile seeds are easily determined; and they are prominent in the archeological record (Cutler and Whitaker 1961).

The purpose of this research was to generate quantitative data for seed characters and to employ these data in numerical analyses. These analyses address: 1) the extent to which seeds are useful indicators of variation among cultivars; and 2) the degree to which seed morphology variation corresponds to other patterns of variation documented for *C. pepo*.

In addition, the relationship between *C. pepo* and wild *C. texana* (Scheele) Gray was examined within the context of seed morphology. *Cucurbita texana* has an overall morphology very similar to that of the ornamental gourds (*C. pepo* L. var. *ovifera* Alef.). The morphological similarity, as well as the ability of the two species to hybridize without loss of fertility, has led some authors to regard them as conspecific (Bailey 1943; Erwin 1938). Spontaneous populations of *texana*-like plants occurring outside of Texas are problematic. Spontaneous populations within Texas are referred to as *C. texana*, while those occurring beyond Texas are usually classified as *C. pepo* var. *ovifera* (cf. Steyermark 1963), reflecting the general assumption that *C. texana* is endemic to Texas (Correll and Johnston 1979) and spontaneous populations occurring elsewhere are escapes from cultivation. In an attempt to clarify the systematic position of all spontaneous populations, seeds from both Texas and non-Texas populations were examined in addition to the *C. pepo* cultivars.

TABLE 1. Accessions of *C. pepo*, *C. texana*, and three unidentified populations used in the analyses. [a] Groups are defined and described in Decker (1985) and Castetter (1925). [b] Currently, all representative seed, vegetative, and floral material resides in the laboratory of Hugh D. Wilson, Dept. of Biology, Texas A&M University. Each accession is vouchered using the lab ID preceded by the cultivar code (e.g., ATJ 59). * Source information for starred accessions, which are those included in the allozyme study (Decker 1985), is listed in that publication. Collection data on the remaining accessions are as follows: ATJ 93—Ball Seed Co., 1984. CST 212—Henry Field Seed Co., 1984. XV? 225—Mexico. Chihuahua: Rancho Las Vegas near Yepachia. May 83, *Nabhan GN8420.* X?I 124—Increased seed from USDA, P.I. 442305. Original fruit from Mexico, Querëtaro. Front gate of Campo Experimental del Instituto Tecnológico de Monterrey. Unidad Querëtaro. 24 Oct 79, *Knight and Whitaker K792-085.* Accessions OBB 3, OBM 2, and OEN 1 were obtained from Geo. W. Park Seed Co., Inc. in 1982. OSB 46 was purchasesd from same in 1983. The remaining unstarred Ovifera accessions were obtained from Stokes Seeds Inc. in 1984, except for OPB 10 which was purchased in 1982. All TEX accessions were collected in Texas: TEX 1—San Patricio Co. Aransas River bottoms, Big Li Ranch, 10 km NE of St. Paul. 1977, *Hill 5847.* TEX 4—Gonzales Co. Along Guadalupe River, near bridge at Independence Park in Gonzales. 1977, *Wilson 3173.* TEX 5—Fayette Co. Along tributary to the Colorado River, 7 km W of La Grange. 12 Mar 78, *Wilson 3170.* TEX 6—Boundary of Lee and Washington counties. Along Cedar Creek 1.5 km S of Nails Creek State Park. 15 Feb 80, *Wilson 3633.* TEX 10—Lee Co. Along Yegua Creek at origin of Lake Sommerville. 10 Nov 79, *Wilson 3625.* TEX 36—Robertson Co. Along Navasota River at Camp Cooley Ranch. 2 Aug 84, *Wilson and Decker 5299.* ?AL 30—Alabama. Greene Co. In roadside ditch near Zion Creek, 5 km S of Eutaw on Rt. 43. 15 Oct 82, *Roberts 5665.* ?AR 18—Arkansas. Boundary of Miller and Lafayette cos. Along Red River. 3 Feb 81, *Wilson 3653,* collected by L. R. Oliver. ?IL 24—Illinois. Randolph Co. Kaskaskia Island on the Mississippi River. Fall 1981, *Wilson 3651,* collected by T. J. Powell.

Taxon	Group[a]	Cultivar/population	Cultivar code	Lab IDs[b]
C. pepo	Acorn	'Jersey Golden Acorn'	ATJ	59*, 93, 120*
		'Table Queen'	ATQ	40*, 51*, 65*, 107*
	Crookneck	'Early Prolific Straightneck'	CST	36*, 73*, 117*, 212
		'Early Yellow Summer Crookneck'	CYE	118*, 199*, 214*
	Marrow	'Black Zucchini'	MBZ	206*
		'Grey Zucchini'	MGZ	46*, 48*, 209*, 235*
	Pumpkin	'Jack O'Lantern'	PJO	71*, 83*, 203*
		'Small Sugar'	PSU	72*, 81*
	Scallop	'Benning's Green Tint'	SFB	205*, 207*
		'Early White Bush Scallop'	SWB	61*, 119*
	Unknown	'Vegetable Spaghetti'	UVS	50*, 200*
	Mexican	'Calabaza Criolla'	XCC	163*, 172*
		'Vavuli'	XV?	225
		'Calabaza de India'	X?I	124
C. pepo var. *ovifera*	Ovifera	'Bicolor'	OBB	3
		'Miniature (Ball)'	OBM	2, 54
		'Orange Ball'	OBO	53
		'Yellow Ball'	OBY	19*, 59*
		'Crown of Thorns'	OCT	58
		'Nest Egg'	OEN	1
		'White Egg'	OEW	62
		'Flat Striped'	OFS	55
		'Bicolor Pear'	OPB	10
		'Striped Pear'	OPS	18*, 57*
		'White Pear'	OPW	60
		'Spoon'	OSB	46, 61
		'Orange Warted'	OWO	56
C. texana	—	Texas populations	TEX	1, 4, 5, 6, 10, 36
???	—	Spontaneous Alabama population	?AL	30
		Spontaneous Arkansas population	?AR	18
		Spontaneous Illinois population	?IL	24

TABLE 2. Seed characters used in the analysis of 51 accessions of *Cucurbita pepo*, six populations of *C. texana*, and three unidentified populations. [a] See figure 1 for further clarification.

Character	Definition[a]
AREA	area calculated from the face view of seed
WIDTH	maximum width of seed (face view)
LENGTH	maximum length of seed (face view)
IMAGEPER	image perimeter of seed (face view)
SVWIDTH	maximum width of seed (side view)
RCPWD	diameter CP divided by WIDTH
RCRWD	diameter CR divided by WIDTH
RCTWD	diameter CT divided by WIDTH
REOAR	partial area EO divided by AREA
REPAR	partial area EP divided by AREA
REQAR	partial area EQ divided by AREA
REVAR	partial area EV divided by AREA

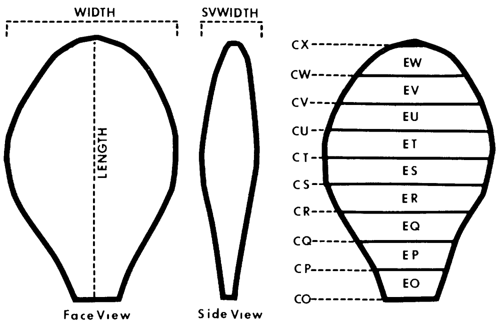

FIG. 1. Examples of seed measurements. The 'C' series represents partial widths. The 'E' series represents partial areas.

MATERIALS AND METHODS

Materials and data collection. Data were collected for 24 commercial cultivars of *C. pepo*, four *C. pepo* collections from Mexico, six populations of Texan *C. texana*, and three spontaneous populations from beyond Texas (table 1). All commercial cultivars, except for 'Vegetable Spaghetti' and the ornamental gourds, were assigned to one of six horticultural groups defined by Castetter (1925). Castetter's classification, which groups cultivars on the basis of fruit characters, has proven useful in a previous systematic study (Decker 1985). 'Vegetable Spaghetti' and the ornamental gourds were not included in his treatment. These have been assigned to the Unknown and Ovifera Groups, respectively, while all Mexican collections have been assigned to the Mexican Group following Decker (1985).

Ten seeds were measured for each of the 60 accessions. Individual seeds from commercial seed packets and the Mexican market collections (XCC 163 and 172) were assumed to represent different plants. An unknown number of fruits and plants were sampled for Mexican collections XV? 225 and X?I 124. Of the spontaneous populations (incl. *C. texana*) only 10 seeds of ?AL 30 were known to come from 10 separate plants. Seeds of TXE 36 were collected from 10 fruits from five plants. Seeds from ?AR 18 came from an unknown number of plants or fruits, while seeds from the remaining spontaneous populations came from 10 different fruits representing an unknown number of plants. As noted in table 1, many of the accessions surveyed here were recently tested for their allozymic frequencies (Decker 1985). Most of the additional accessions used in this study were cultivars of *C. pepo* var. *ovifera* (the ornamental gourds). Emphasis on the ornamental gourds is justified by their diversity in fruit forms as well as their key position with respect to *C. texana*.

Quantitative data were taken utilizing a Tektronics Local Graphics Processing Unit and "Garner," an image analysis program developed for our laboratory by Ranch to Market Incorporated, Austin, Texas (Wilson 1985). Approximately 40 measurements were taken per specimen. Some of these are listed in table 2. All measurements except SVWIDTH were taken from the face view of the seed. In addition to whole image measurements such as AREA, LENGTH, and WIDTH, many measurements were based on division of the seed from bottom (seed scar) to top by 10 equidistant diameters (fig. 1). These partial areas and widths were generated to identify parts of the seed providing the most useful information.

Character selection. Various ratios were substituted for some original characters. Most of the ratios represented an attempt to standardize some measurements by size. Two character subsets were selected from the total character list. One subset was chosen for an analysis of intraspecific variation in *C. pepo*, while the purpose of the other subset was to discriminate between the ornamental gourds and *C. texana*.

TABLE 3. Cultivar and population means and standard deviations for characters used in the analysis of 51 accessions of *Cucurbita pepo*, six populations of *C. texana*, and three unidentified populations. [1] Under each variable, the means are in the first column and the standard deviations are in the second column. All distances are in mm. However, values for the ratio variables should be multiplied by 10^{-2}. [2] This character was used only in the discrimination of ornamental gourd accessions and *C. texana* populations.

	Characters[1]																							
Cultivar	AREA		WIDTH		LENGTH		IMAGEPER		SVWIDTH		RCPWD		RCRWD		RCTWD		REOAR		REPAR		REQAR[2]		REVAR	
ATJ	64.3	7.7	7.3	0.6	12.1	0.8	30.3	1.8	2.4	0.2	42.9	3.1	84.6	2.9	99.2	0.7	4.5	0.3	8.3	0.4	11.6	0.4	11.5	0.4
ATQ	55.4	8.6	6.9	0.7	11.0	0.9	27.9	2.2	2.6	0.3	43.2	3.6	84.7	3.1	99.3	0.7	4.5	0.4	8.4	0.4	11.7	0.4	11.4	0.4
CST	66.1	7.3	7.6	0.5	12.1	0.7	30.5	1.7	2.4	0.3	43.4	3.4	88.8	2.8	98.7	0.9	4.8	0.4	8.7	0.6	12.4	0.5	10.4	0.5
CYE	60.5	7.6	7.1	0.5	11.6	0.7	29.2	1.8	2.4	0.3	47.5	2.6	87.3	2.5	99.4	0.4	5.2	0.3	8.9	0.4	12.0	0.4	10.9	0.4
MBZ	72.9	5.5	8.0	0.4	12.2	0.5	31.7	1.2	2.9	0.3	51.2	1.4	90.2	1.3	99.0	0.5	5.7	0.2	9.3	0.2	12.3	0.2	10.6	0.1
MGZ	80.8	14.7	8.2	0.8	13.3	1.3	33.7	3.1	2.9	0.5	46.9	3.5	87.9	2.9	99.4	0.4	5.2	0.5	8.8	0.5	12.0	0.4	10.9	0.4
OBB	36.2	3.0	5.2	0.3	9.7	0.6	23.5	1.2	1.8	0.1	47.4	3.0	85.2	1.9	99.2	0.4	5.2	0.5	8.9	0.3	11.8	0.3	10.6	0.5
OBM	38.3	5.6	5.5	0.5	9.5	0.8	23.6	1.8	1.9	0.3	49.2	5.0	83.8	4.5	98.7	0.9	5.4	0.5	8.9	0.6	11.5	0.6	11.3	0.6
OBO	61.8	8.0	7.6	0.5	11.3	0.7	29.3	1.8	2.5	0.4	43.2	2.8	86.5	1.9	98.9	0.8	4.5	0.3	8.6	0.5	12.0	0.4	11.0	0.4
OBY	42.2	6.6	5.9	0.6	9.9	0.9	24.7	2.0	1.9	0.3	44.5	4.5	80.4	3.7	98.6	0.6	4.9	0.6	8.3	0.5	11.1	0.4	11.7	0.5
OCT	52.3	5.0	6.7	0.6	10.9	0.6	27.6	1.2	2.1	0.1	42.9	3.1	81.4	3.0	97.6	1.8	4.9	0.3	8.2	0.4	11.3	0.4	11.6	0.4
OEN	51.2	8.2	6.6	0.6	10.8	0.7	27.2	1.9	1.9	0.2	42.3	1.9	82.1	4.0	99.3	0.3	4.7	0.3	8.0	0.3	11.2	0.5	11.5	0.3
OEW	41.1	5.3	5.9	0.3	9.6	0.8	24.2	1.7	1.9	0.3	46.8	2.9	86.3	1.1	98.9	1.4	5.2	0.5	8.8	0.3	11.9	0.2	10.9	0.4
OFS	42.0	6.1	5.8	0.6	9.8	0.7	24.6	1.7	2.0	0.3	45.5	2.5	83.2	1.9	98.9	0.5	5.1	0.3	8.4	0.3	11.3	0.2	11.4	0.2
OPB	36.1	4.0	5.6	0.3	9.0	0.6	22.7	1.3	2.0	0.2	42.3	3.2	81.2	2.1	99.3	0.3	4.8	0.4	8.1	0.4	11.2	0.3	11.6	0.4
OPS	36.5	5.2	5.6	0.4	9.0	0.7	22.8	1.7	1.9	0.3	44.8	3.1	83.0	2.7	98.9	0.6	5.0	0.3	8.4	0.4	11.4	0.4	11.3	0.4
OPW	37.6	7.2	5.9	0.7	8.8	0.8	22.7	2.2	1.4	0.5	43.1	2.5	84.2	2.7	99.5	0.4	4.6	0.4	8.3	0.4	11.6	0.4	11.3	0.4

TABLE 3. Continued.

Cultivar	Characters[1]																							
	AREA		WIDTH		LENGTH		IMAGEPER		SVWIDTH		RCPWD		RCRWD		RCTWD		REOAR		REPAR		REQAR[2]		REVAR	
OSB	31.1	4.7	5.3	0.4	8.2	0.6	20.9	1.6	1.7	0.2	44.8	2.0	82.8	3.0	98.7	1.0	4.9	0.4	8.4	0.3	11.4	0.4	11.3	0.4
OWO	61.4	9.5	7.0	0.7	12.1	0.8	29.9	2.0	2.6	0.3	45.3	3.1	83.7	3.1	98.9	1.1	4.8	0.5	8.5	0.4	11.5	0.4	11.2	0.4
PJO	112.7	19.6	9.4	0.9	16.6	1.6	40.8	3.6	2.6	0.3	42.7	3.4	85.7	2.5	99.4	0.5	4.7	0.4	8.3	0.5	11.8	0.4	11.1	0.4
PSU	101.8	20.6	9.0	1.0	15.4	1.6	38.3	3.8	2.4	0.6	44.6	3.6	86.8	2.5	99.2	1.0	4.9	0.6	8.6	0.5	12.0	0.3	11.0	0.3
SFB	64.6	9.4	7.5	0.6	11.7	1.1	29.9	2.3	2.3	0.2	44.7	4.3	86.4	3.0	99.3	0.5	4.6	0.4	8.6	0.6	11.9	0.4	11.3	0.4
SWB	66.4	12.0	7.6	0.7	11.9	1.3	30.5	2.9	2.5	0.3	43.5	4.3	85.0	3.0	98.9	0.6	4.8	0.6	8.4	0.6	11.7	0.4	11.3	0.5
UVS	93.8	9.7	9.1	0.5	14.2	1.0	36.2	2.1	3.0	0.3	44.9	3.2	85.5	2.0	99.5	0.3	4.9	0.5	8.5	0.4	11.7	0.3	11.1	0.3
XCC	127.5	20.2	8.8	0.6	19.9	2.1	46.3	4.1	2.6	0.3	45.3	5.1	84.0	3.5	99.2	0.6	5.1	0.6	8.4	0.5	11.5	0.4	11.2	0.4
XV?	131.6	12.1	9.0	0.6	20.0	1.3	46.6	2.5	2.4	0.4	47.0	4.3	87.6	3.1	99.0	0.6	5.2	0.7	8.7	0.5	11.9	0.4	11.0	0.4
X?I	112.7	9.8	8.7	0.6	17.8	0.8	42.4	1.7	2.5	0.6	43.7	2.0	84.8	2.3	99.4	0.4	4.7	0.3	8.2	0.3	11.5	0.4	11.4	0.3
TEX 1	39.2	4.6	5.9	0.4	9.4	0.5	23.7	1.3	1.8	0.2	39.2	2.5	81.2	2.6	99.2	0.5	4.4	0.5	7.6	0.4	11.1	0.4	11.7	0.3
TEX 4	43.6	3.7	6.5	0.3	9.7	0.6	25.1	1.2	1.6	0.2	35.2	1.3	77.5	3.1	99.2	0.5	4.1	0.4	6.9	0.4	10.4	0.4	12.3	0.4
TEX 5	40.5	5.9	6.1	0.5	9.4	0.8	24.1	1.9	1.8	0.1	37.2	2.1	80.8	3.0	99.3	0.4	4.3	0.5	7.5	0.4	11.2	0.4	11.7	0.3
TEX 6	41.4	2.9	6.2	0.2	9.5	0.4	24.3	0.9	1.8	0.2	37.5	3.3	80.5	3.3	99.2	0.5	4.1	0.3	7.6	0.5	11.1	0.4	11.9	0.4
TEX 10	44.2	6.1	6.3	0.6	9.9	0.6	25.1	1.6	1.6	0.1	36.5	2.8	81.1	2.8	99.0	0.6	4.1	0.5	7.4	0.4	11.1	0.4	11.9	0.3
TEX 36	44.9	3.8	6.5	0.3	9.8	0.6	25.3	1.1	1.7	0.2	36.8	3.6	80.9	3.4	99.5	0.7	4.2	0.7	7.3	0.6	11.1	0.4	11.6	0.4
?AL	40.8	5.8	6.0	0.5	9.5	0.7	24.2	1.6	1.8	0.1	40.1	2.4	80.5	4.0	99.2	0.7	4.6	0.3	7.9	0.4	11.0	0.5	11.7	0.3
?AR	39.2	3.3	5.8	0.2	9.5	0.5	23.8	1.0	1.6	0.3	42.4	2.3	80.8	2.6	98.8	0.7	4.6	0.5	8.1	0.3	11.1	0.3	11.8	0.4
?IL	47.6	3.8	6.4	0.3	10.5	0.6	26.4	1.1	1.8	0.4	39.2	3.9	77.9	4.6	98.5	0.6	4.2	0.4	7.5	0.5	10.7	0.6	12.2	0.5

TABLE 4. Plotting scores for the canonical variate (fig. 2), principal component (fig. 3), and discriminant analyses (fig. 4) performed on 51 accessions of *C. pepo*, six *C. texana* collections, and three unclassified populations. [a] PCA scores have been standardized to unit variance.

Analysis variable	CVA 1	CVA 2	PCA[a] 1	PCA[a] 2		CVA 1	CVA 2	PCA 1	PCA 2	DA 1
Accession					Accession					
ATJ 59	0.00	1.67	0.01	0.72	OBB 3	−3.36	−3.08	−0.16	−1.77	1.1
ATJ 93	0.21	1.17	−0.36	1.02	OBM 2	−3.61	−2.68	−0.26	−2.27	2.3
ATJ 120	−1.08	0.89	0.13	−0.39	OBM 54	−2.90	−1.66	−0.37	−1.40	1.5
ATQ 40	−0.61	1.75	−0.19	0.79	OBO 53	−0.84	1.90	0.15	−0.10	0.6
ATQ 51	−2.19	0.55	0.10	−0.78	OBY 19	−2.88	−1.61	−1.04	−0.54	1.0
ATQ 65	−0.97	1.94	−0.10	0.51	OBY 59	−2.79	−1.35	−0.85	−0.51	0.9
ATQ 107	−2.00	0.39	−0.43	0.13	OCT 58	−1.67	0.15	−0.73	−0.49	0.7
CST 36	−0.43	1.29	0.43	−0.40	OEN 1	−1.55	−0.09	−0.68	0.29	−0.1
CST 73	−0.12	1.85	0.59	−0.54	OEW 62	−3.14	−1.15	−0.15	−1.57	0.9
CST 117	−0.06	1.79	0.94	−0.86	OFS 55	−2.77	−1.26	−0.55	−0.84	0.5
CST 212	−0.65	1.46	0.47	−0.48	OPB 10	−4.20	−1.73	−1.05	−0.22	0.3
CYE 118	−0.55	0.89	0.50	−0.61	OPS 18	−4.08	−1.89	−0.69	−1.22	0.7
CYE 199	−0.42	0.93	0.79	−1.11	OPS 57	−3.86	−1.66	−0.77	−0.73	0.5
CYE 214	−0.69	0.98	0.67	−1.09	OPW 60	−4.05	−1.74	−0.92	−0.45	−0.2
MBZ 206	0.81	2.43	1.56	−1.65	OSB 46	−5.14	−2.94	−0.94	−1.32	0.4
MGZ 46	2.48	1.50	1.47	−0.42	OSB 61	−5.01	−2.72	−1.02	−1.16	0.5
MGZ 48	0.85	1.83	0.97	−0.35	OWO 56	−0.09	0.63	0.15	−0.21	1.2
MGZ 209	0.49	1.90	0.98	−0.59	TEX 1	—	—	−1.42	0.55	−1.6
MGZ 235	2.85	1.76	1.24	0.25	TEX 4	—	—	−2.09	1.86	−2.4
PJO 71	4.14	0.01	1.14	1.16	TEX 5	—	—	−1.47	0.92	−2.3
PJO 83	4.74	−0.49	0.96	1.73	TEX 6	—	—	−1.55	0.98	−1.4
PJO 203	5.07	−0.87	1.23	1.41	TEX 10	—	—	−1.62	1.18	−2.3
PSU 72	2.24	0.89	0.93	0.18	TEX 36	—	—	−1.44	1.27	−2.8
PSU 81	4.48	−0.75	1.23	1.04	?AL 30	—	—	−1.25	0.36	−0.3
SFB 205	0.05	1.85	0.04	0.80	?AR 18	—	—	−1.29	−0.13	0.4
SFB 207	−1.14	1.04	0.31	−0.78	?IL 24	—	—	−1.65	1.01	−0.4
SWB 61	0.44	1.70	−0.02	0.59						
SWB 119	−0.92	1.66	0.25	−0.43						
UVS 50	2.33	2.31	1.33	0.19	Percent variance	59	19	54	27	100
UVS 200	3.09	1.55	0.79	1.29						
XCC 163	8.42	−4.73	1.95	0.86						
XCC 172	7.39	−2.64	0.95	2.00						
XV? 225	7.77	−3.98	1.83	0.79						
X?I 124	5.93	−1.64	0.97	1.55						

The first character subset was chosen by evaluating variation among and within populations and cultivars of *C. pepo*. Initial screening involved removal of linearly-related characters and those which were substantially more variable within populations (>80% of total variation) than between populations. The resulting 22-character list was further subjected to a stepwise selection technique based on Wilks' lambda (procedure STEPDISC in SAS [Ray 1982]). Characters meeting 0.005 significant levels to enter and stay in the model to discriminate among cultivars formed the first subset of characters. Included were AREA, WIDTH, LENGTH, IMAGEPER, SVWIDTH, and the following ratios: RCPWD, RCRWD, RCTWD, REOAR, REPAR, and REVAR (table 2). Cultivar and population means for these variables are listed in table 3.

Characters useful for discriminating between the ornamental gourds and *C. texana* were chosen in a similar manner, using 0.01 significance levels for the stepwise selection procedure. The result was a subset of four characters:

TABLE 5. Eigenvectors associated with the CVA (fig. 2), PCA (fig. 3), and DA (fig. 4). [a] CVA and DA coefficients have been normalized to give canonical variates with unit within-class variance when applied to the standardized variables.

	CVA[a]		PCA		DA
Characters	1	2	1	2	1
AREA	−1.938	−9.471	0.388	0.304	0.258
WIDTH	−0.366	6.332	0.336	0.301	—
LENGTH	−2.036	6.171	0.324	0.309	—
IMAGEPER	7.701	−2.895	0.335	0.309	—
SVWIDTH	−0.006	0.639	0.337	0.085	—
RCPWD	0.983	−0.155	0.262	−0.402	−0.777
RCRWD	−0.077	1.052	0.345	−0.191	—
RCTWD	0.041	0.016	0.118	0.214	—
REOAR	−0.229	0.275	0.245	−0.387	—
REPAR	−0.796	−0.005	0.291	−0.394	2.867
REQAR	—	—	—	—	−1.647
REVAR	−0.291	0.841	−0.309	0.263	—

AREA, RCPWD, REPAR, and REQAR (table 2). To test the discriminating power of these variables, a classification function (subprogram DISCRIMINANT in SPSS [Klecka 1975]) was calculated using nine of 10 seeds randomly chosen from each ornamental gourd and *C. texana* accession. The remaining seeds (one from each accession) were then used as a test group. Prior probabilities were set proportional to the ornamental gourd and *C. texana* sample sizes. Because Box's M (Cooley and Lohnes 1971) indicated unequal group covariance matrices, classification was based on individual group covariance matrices of the canonical discriminant function. All observations were classified on the basis of posterior probabilities. Among the observations used initially to define the discriminant function, the classification was 95% correct. Classification of the test group was 86% correct. This congruence indicated that the variables chosen to produce the discriminant function would be adequate for classifying non-Texan spontaneous populations.

Data analysis. Once character subsets were chosen, populations were analyzed within the context of canonical variate (SAS procedure CANDISC), principal component (SAS procedure PRINCOMP), and discriminant analyses. To minimize the effect of variation within accessions, accessions were the groups for comparison in the canonical variate analyses, and accession means were used for the principal component analysis. In both procedures, linear combinations of variables were chosen to maximize distances among accessions, without regard to cultivar, Group, or species membership. Canonical variate analysis of only *C. pepo* accessions was followed by canonical variate and principal component analyses which included *C. texana* and the other spontaneous populations. These analyses were performed to test the alignment of all spontaneous populations within the context of characters chosen to define relationships within *C. pepo*. A more detailed analysis of the ornamental gourds, *C. texana*, and the unclassified spontaneous populations was based on the four-character subset. Using all ornamental gourd and *C. texana* seeds to redefine the discriminant function, the other spontaneous populations were classified. Prior probabilities were set at 50% because information concerning true population sizes or the cost of misclassification was unavailable.

RESULTS

Variation in C. pepo. Results of the canonical variate analysis performed on *C. pepo* accessions are presented in tables 4 and 5 and in figure 2. Canonical correlation values measure the degree of relatedness between the canonical discriminant functions and the accessions. The values for the first two canonical variates were 0.96 and 0.89 respectively, indicating their usefulness in explaining variation among the accessions. Together, they accounted for 78% of the total variation. The information in these canonical variates is graphically displayed in a

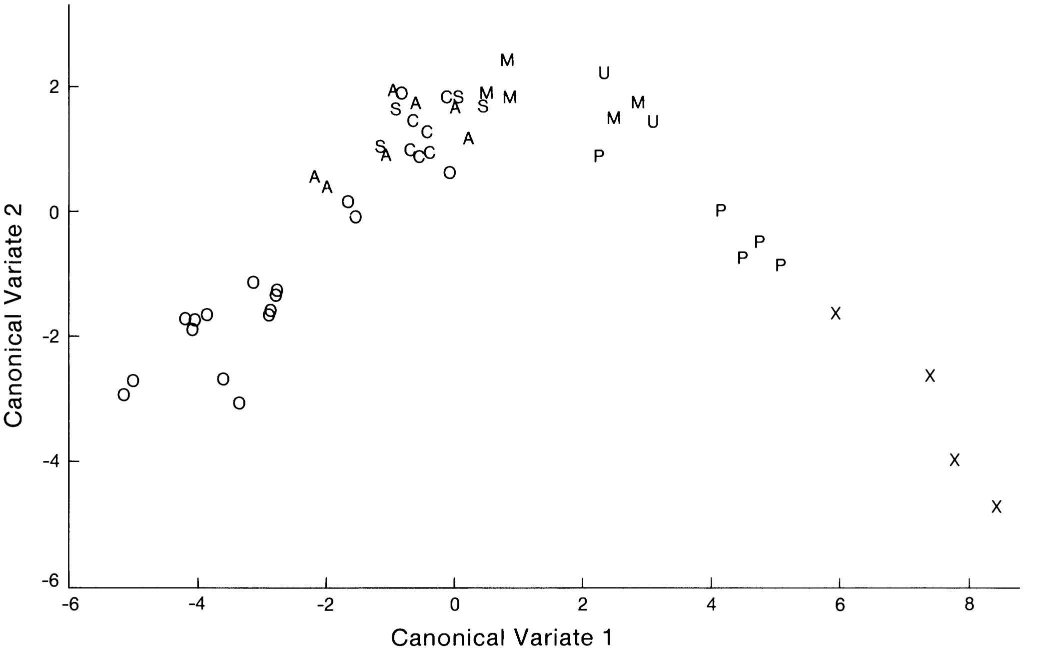

FIG. 2. Plot of *C. pepo* accession centroids for the first two canonical variates. Analysis based on 11 seed characters. The plotting character is the first letter of the cultivar code and indicates Group membership (table 1). Plotting scores are given in table 4. Accession CST 117 is hidden behind accessions CST 73, SFB 205, and ATJ 59.

plot of the accession centroids (fig. 2). Plotting scores are listed in table 4 to facilitate identification of specific accessions. The plotting character is the first letter of the cultivar code and indicates Group membership (table 1). The standardized canonical coefficients (table 5) suggest that CV1 is dominated by IMAGEPER. Correlations between CV1 and AREA (0.98), WIDTH (0.88), LENGTH (0.99), and IMAGEPER (0.99) were all very high, indicating that size, as revealed by these variables, accounts for the distribution of accessions along this axis (fig. 2). The canonical coefficients for CV2 suggest the importance of an inverse relationship of AREA with WIDTH and LENGTH. In plots (not shown here) of AREA juxtaposed against WIDTH, LENGTH, and IMAGEPER, only the four Mexican collections strayed as a group from essentially linear relationships among these variables. Thus, the relationship among these variables that is indicated by CV2 coefficients was useful only in removing the Mexican collections from the others. In looking elsewhere to explain the dispersion of other accessions along the second canonical variate axis, it is notable that of the original variables SVWIDTH had the highest correlation with CV2 (0.53). A plot of AREA by SVWIDTH (not shown here) showed separation of the ornamental gourds from other accessions along the SVWIDTH axis. This may explain the position of the ornamental gourds (O) along the CV2 axis.

With respect to Groups of cultivars, this analysis best defined the Mexican accessions (X), the pumpkins (P), and the ornamental gourds (O). It should be noted, however, that centroids rather than individual seeds have been plotted; more overlap actually occurs among cultivars than is pictured in the CVA plot. Wedged between the pumpkins and a mixed cluster of acorn squashes (A), crooknecks (C), and scallops (S) are the 'Vegetable Spaghetti' accessions (U) and the marrows (M) (fig. 2). The grouping of 'Vegetable Spaghetti' with the marrows may be a natural one inasmuch as their fruit shapes and allozyme frequencies (Decker 1985) are very similar. Plotting scores for ornamental gourd cultivars (table 4) reveal that OBO 53 and OWO 56 lie within the sphere of acorn squashes, crooknecks, and scallops. OCT 58 and

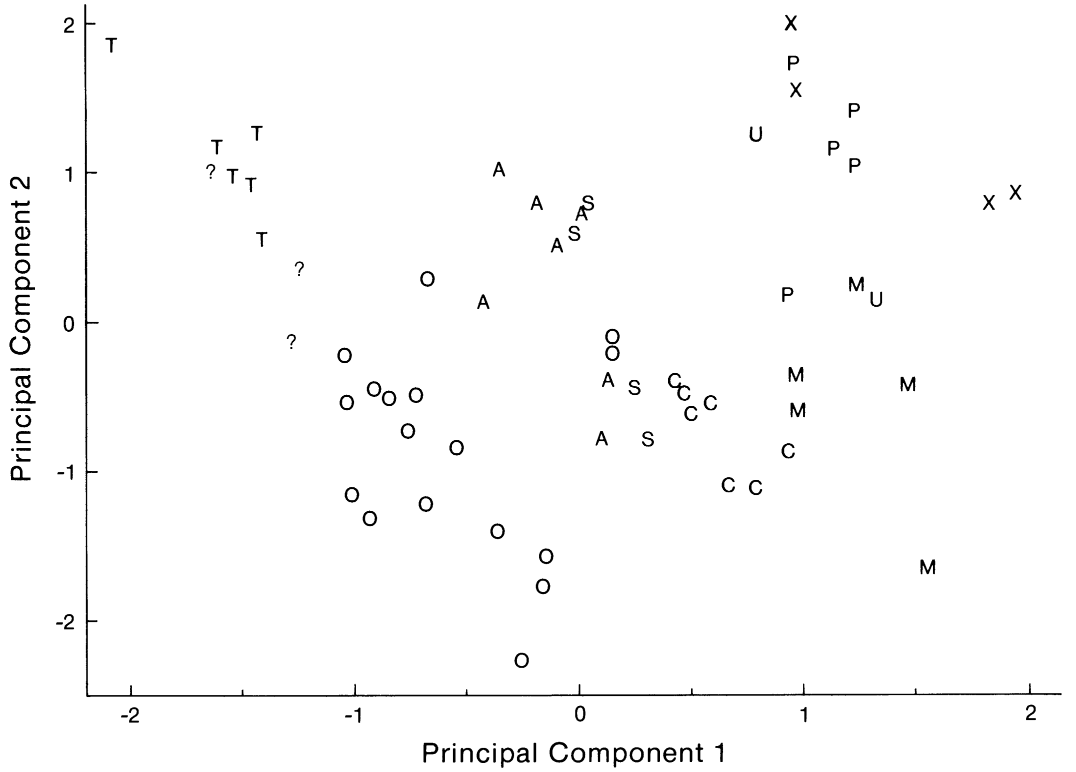

FIG. 3. Plot of the first two principal components. Analysis was based on 11 character means for 51 accessions of *C. pepo*, six *C. texana* collections, and three unclassified populations. The plotting character is the first letter of the cultivar code and indicates Group membership (table 1). Plotting scores are given in table 4.

OEN 1 are on the periphery of this group while the remaining ornamental gourds appear to be well-removed.

Canonical variate and principal component analyses were performed to examine the relationship of *C. texana* and the unclassified spontaneous populations to cultivars of *C. pepo*. Since the results of these analyses were similar with respect to the spontaneous populations, only the PCA, which presents a slightly different view of variation within *C. pepo*, is presented here. The first two principal components (fig. 3) accounted for 54 and 27% of the total variation, respectively. As in the CVA of *C. pepo* accessions, the Mexican material and the ornamental gourds occupy opposite ends in a continuum of cultivars. Among the ornamental gourds, OBO 53 and OWO 56 again fall amongst the acorn squashes and scallops, with OEN 1 nearby. In contrast to the CVA, the crooknecks are somewhat removed from the scallops and acorn squashes in the PCA plot. Also, it appears that differences between the Mexican material and pumpkins were not weighted so heavily.

Cucurbita texana populations formed a distinct group in this analysis (fig. 3). Along the PC1 axis, they lie closest to the ornamental gourds. Considering the small size of *C. texana* seeds this alignment is not surprising. Eigenvector values (table 5) suggest that size plays a role in PC2 as well. More importantly, differences in the sinus area near the seed scar, as revealed by REOAR, REPAR, RCPWD and RCRWD, are probably responsible for the separation of *C. texana* and ornamental gourds along that axis. In the PCA plot (fig. 3), the spontaneous population from Illinois falls among *C. texana* populations, while populations from Arkansas and Alabama occupy a more intermediate position with respect to the two species.

C. texana *and* C. pepo *var.* ovifera. AREA,

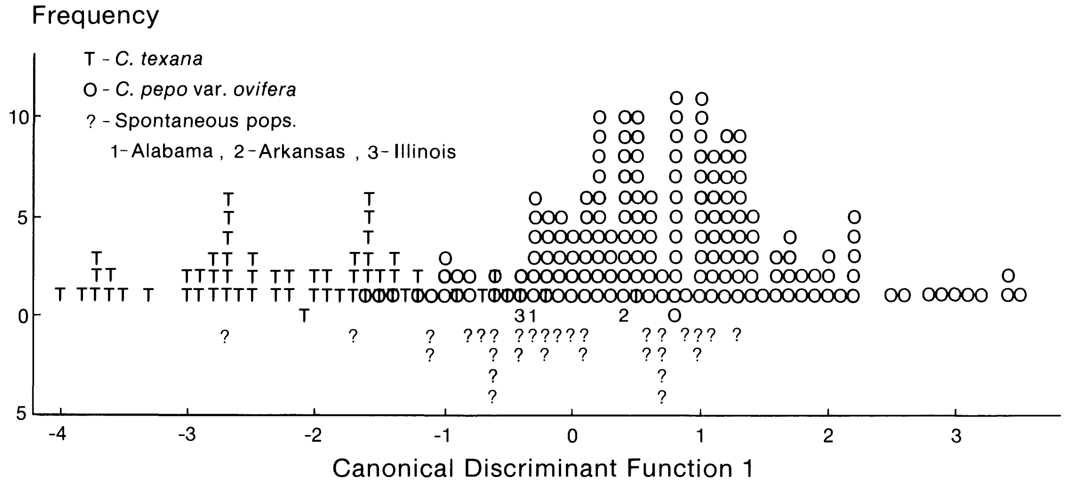

FIG. 4. Histograms of discriminant scores for seeds. Analysis based on four characters. Data from six *C. texana* populations, 17 accessions of *C. pepo* var. *ovifera* (plotted above the y-axis origin), and three unclassified spontaneous populations (plotted below the y-axis origin). Group centroids are plotted along the y-axis origin. All scores have been rounded to the nearest tenth. Population and accession scores are given in table 4.

RCPWD, REPAR, and REQAR were selected to define a single canonical discriminant function for *C. texana* and *C. pepo* var. *ovifera* seeds. This discriminant function had an eigenvalue of 1.62 and a canonical correlation of 0.79. With an overall high success rate (92%), 93%, and 90% of the ornamental gourd and *C. texana* seeds respectively, were correctly classified. The distribution of individual seeds along the canonical axis is illustrated in figure 4. Examination of accession centroids (table 4) reveals the proximity of specific ornamental gourd cultivars to the *C. texana* populations. As in the PCA, 'White Pear', 'Bicolor Pear', and 'Nest Egg' lie closest to *C. texana*. According to the standardized canonical coefficients (table 5), seeds whose partial areas EQ and EP were about the same size received higher positive values than seeds where EQ was much larger than EP. This agrees with observations that the sinus area near the seed scar is more pronounced and does not extend as far up on *C. texana* seeds as it does on ornamental gourd seeds (fig. 5).

In this analysis, the spontaneous populations from beyond Texas occupied an intermediate position with respect to the two taxa, although closer to the ornamental gourd centroid in all cases. Twenty-four (80%) of the 30 seeds were classified as *C. pepo* var. *ovifera*. Of those classified as *C. texana*, one came from the Arkansas population, two from Illinois, and three from Alabama.

DISCUSSION

Seeds of *C. pepo* display variation in size and shape to the extent that some Groups of cultivars can be distinguished. In general, this variation exists as a continuum with Mexican and pumpkin seeds representing one extreme and the ornamental gourds the other (figs. 2 and 3). This pattern suggests that there has been much divergence within the species, especially with respect to the Mexican and Ovifera Groups. Such a divergence is in keeping with observations on allozyme frequencies, which indicated that 'Vegetable Spaghetti', the Mexican material, pumpkins, and marrows are well-removed from the other Groups of cultivars (Decker 1985).

In contrast to the allozyme data (Decker 1985), analysis of seed characters has not produced any distinct groupings. Most likely, this is due to selection pressures which affect the seeds but not the allozymes. While the allozymes have diverged, human selection practices have produced parallel trends among seeds in different Groups in some cases, and in other cases, rapid divergence within a Group. For example, according to several Mexican informants, the lo-

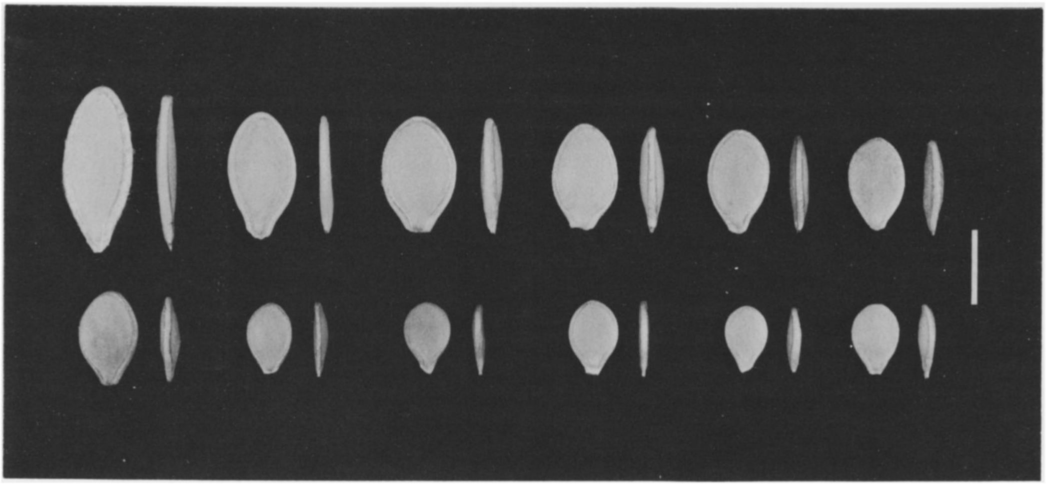

FIG. 5. Face and side views of seeds representing eight Groups of C. *pepo*, one population of C. *texana*, and three spontaneous populations from beyond Texas. Seeds along top row from left to right represent the Mexican, Pumpkin, Unknown, Marrow, Scallop, and Acorn Groups. Along bottom row from left to right are seeds from the Crookneck and Ovifera Groups, C. *texana*, and the populations from Alabama, Arkansas, and Illinois. Scale = 1 cm.

cal C. *pepo* pumpkins are grown primarily for their edible seeds and only secondarily for the flesh. Selection for larger seeds is a logical explanation for the Mexican material. The practice apparently dates from prehistoric times (Whitaker and Cutler 1971). Such selective practices also explains the relatively large size of pumpkin seeds versus the much smaller ornamental gourd seeds. Whereas pumpkin flesh and seeds have a long history of human consumption, most ornamental gourd cultivars produce small, inedible, bitter fruits with very hard rinds. These fruits have served primarily as decorative oddities and possibly as containers (Gilmore 1931). Acorn squashes, crooknecks, scallops, and marrows produce seeds more intermediate in size. Interestingly, viney marrows such as 'Long Green Trailing' have larger seeds than bushy marrows like 'Black Zucchini', although fruit sizes are comparable (Tapley et al. 1937). Assuming that the bushy types are of more recent origin, the trend towards smaller seeds in the marrows appears to be a concomitant result of historic selection practices. Inasmuch as marrow seeds are used only for propagation and immature fruits with few, small seeds are desirable, evolution in this direction is not surprising. Among pumpkins, where seeds are easily removed from the hollow cavity of the mature fruit, selection for smaller seeds would not be necessary. On the contrary, individuals derived from large seeds with robust embryos might be more successful in the next generation. This type of selection is indicated in the CVA (fig. 2) where SVWIDTH contributed heavily to the second canonical variate axis (table 4). Of the seed characters analyzed here, SVWIDTH is the most obvious reflection of embryo development. This character distinguishes ornamental gourds from other Groups (fig. 2 and table 3), suggesting a differential interest in the propagation of edible versus inedible cultivars. Cultivars with the largest means for SVWIDTH (table 2) were 'Vegetable Spaghetti' and the zucchinis. This is consistent with the fact that the marrows are the most intensely cultivated of modern commercial cultivars.

While seed size may reflect both ancient and modern selective regimes, these analyses also indicate inherent differences in shape which are not as easily explained. In particular, Mexican seeds are distinctively long and narrow (table 3 and fig. 5). The presence of long and narrow C. *pepo* and C. *mixta* Pang. seeds among the archeological remains from the Tehuacan Caves, Mexico, prompted Cutler and Whitaker (1967) to suggest hybridization between these species. Among other Groups, PCA indicated differences in size and shape of the sinus area near the seed scar. Though the causes of these differences are not clear, it is possible that they indicate natural relationships within the species rather than conscious selection by man.

Both CVA and PCA revealed a wide range of variation among ornamental gourd seeds. Of particular interest are 'Orange Ball' (OBO) and 'Orange Warted' (OWO) which clustered among the acorn squashes and scallops. Size, including SVWIDTH, appears to be responsible for this clustering (table 3). The reason for larger seeds in these cultivars is not apparent. Interestingly, 'Orange Ball' and 'Orange Warted' apparently belonged to taxa which once were considered distinct from *C. pepo* var. *ovifera*: *C. aurantia* Willd. and *C. verrucosa* L., respectively.

PCA and discriminant analysis of *C. texana* and *C. pepo* var. *ovifera* revealed that, although the distance between these taxa is less than some distances among cultivars of *C. pepo*, *C. texana* seeds from Texas populations are distinctive. In particular, the sinus area near the seed scar appears to be the spot of greatest differentiation. The discovery of differences in seed characters between these species could be important with respect to identifying archeological seeds. These analyses also indicate that the spontaneous populations from beyond Texas are intermediate, albeit in the direction of the ornamental gourds, in their expression of morphological seed characters. While the general opinion that these populations are *C. pepo* escapes cannot be refuted on the basis of the seed data, affinity of these populations to similar populations from Texas supports an alternate view: that *C. texana* may once have been more widely distributed than it is today. Affinity of these populations to the domesticate could be explained as the result of genetic interaction between wild and cultivated populations. Comparative analysis, using more characters from a larger sample, should improve our understanding of *C. texana* and its role in the origin and evolution of *C. pepo*.

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