Allelism Found between Two Common Bean Genes, Hilum Ring Color (*D*) and Partly Colored Seedcoat Pattern (*Z*), formerly Assumed to Be Independent

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ABSTRACT. Inheritance of two phenotypes, the virgarcus pattern of partly colored seedcoats and the margo *d* seedcoat pattern, were studied in common bean (*Phaseolus vulgaris* L.) materials that segregated jointly for genes controlling the two phenotypes to test the hypothesis of allelism of two genes, *D* and *Z*. The F₂ progeny from the cross *j* margo BC₃ 5-593 × *t z* virgarcus BC₃ 5-593 produced an unexpected phenotypic class, margo *d*, suggesting possible allelism of *D* and *Z*. The F₂ also produced another unexpected phenotypic class, white seedcoat, for which the genetic hypothesis *t j z* was made. The F₂ from the cross *t j* marginata BC₃ 5-593 × *t z* virgarcus BC₃ 5-593 provided supporting evidence for the new genotype, *t j z*, for a white seedcoat. Analysis of the F₂ and F₃ progenies of 80 random F₂ plants from the cross *t z* virgarcus BC₃ 5-593 × *d j* (margo *d*) BC₃ 5-593 provided support for the hypothesis that the *D* and *Z* loci are allelic. Production of two different phenotypes (white vs. white with two tiny pale gray dots, one each at the raphe and micropyle) for *t j z* in two different genetic and cytoplasmic backgrounds is discussed. The F₂ from the crosses *d j* (margo *d*) BC₃ 5-593 × *j v* margo BC₂ 5-593 and *d j* (margo *d*) BC₃ 5-593 × *j* margo BC₃ 5-593 segregated for *d* (vs. *D*) phenotypes, which were found not to be independent of a randomly amplified polymorphic DNA (RAPD) marker (AM10₅₆₀) associated (1.4 cM) with the *Z* locus. Because the *Z* gene symbol has priority, we propose to retain *Z* for the locus.

Prakken (1970) wrote a comprehensive review of all previous research on seedcoat color genetics, excepting the genetics of red seedcoat colors. He also gave a detailed treatment of the inheritance of color in the hilum ring of seedcoats. The hypothesis of Kooiman (1931) and Prakken (1970) is that the presence or absence of hilum ring color is controlled by two genes, *J* and *D*, where *d* has expression only with *j/j*. Thus, with *J/-* or *j/j D/-* hilum ring color is present, and with *j/j d/d* it is absent (white hilum ring). The hue of the hilum ring is influenced by the entire set of genes that control seedcoat color (Prakken, 1970). Lamprecht (1951) had developed a much more complicated hypothesis, in which each of four genes, viz., *G*, *B*, *Can*, and *Ins* can produce color in the hilum ring. Prakken (1970) gave a detailed critique of Lamprecht's (1951) hilum ring color hypothesis, extensively demonstrating its errors; and the hypothesis of Kooiman (1931) and Prakken (1970) was later confirmed by Bassett (1996a).

The basic genetics of partly colored seedcoats was reviewed by Lamprecht (1934). The gene *T*, for totally colored seedcoats, prevents partly colored seedcoat expression, whereas *t/t* permits expression of any partly colored pattern. The types (shape and extent) of the partly colored patterns are controlled by interaction of *t* with at least three other genes, *Z* (for zonal), *L* (for limiter),

and *Bip* (for bipunctata) (Schreiber, 1940). There is evidence that *t* also interacts with the seedcoat color gene called Joker (*j*) to form a pattern similar to marginata (Bassett, 1994a, 1996a). There is close linkage (1/8 approx. 1 map unit) between the locus for plant habit, *Fin*, and the *Z* locus (Bassett, 1997a). The interaction of *t* with *d* has never been investigated although Lamprecht (1934) made crosses that segregated for *t* and *d*. The material of Lamprecht (1934) segregated for too many other genes to permit successful Mendelian analysis.

Because of the complexity of the interactions among the genes for partly colored seedcoats, one cannot perform allelism tests between many combinations of interest without first developing genetic tester stocks with known genotypes. To investigate the possibility of allelism between the genes *D* and *Z*, a prerequisite was the development of genetic tester stocks with three gene combinations: *t j*, *t z*, and *j d*. Additional stocks with only *j* or *t* were also needed to explore all possible interactions of the gene set: *t*, *z*, *j*, and *d*. A more straightforward approach to testing for allelism between *d* and *z* is not possible because of two epistatic interactions: *d* only expresses with *j* and *z* only expresses with *t*.

One of the perils of simply using genetic stocks reported previously to have certain genotypes is that they may carry cryptically certain other genes that will make problems when making test crosses. The best strategy for minimizing the danger posed by cryptic genes is to develop all the genetic stocks by backcrossing selected recessive genes into a single recurrent parent. The larger the number of genes that are backcrossed into the same pure line recurrent parent, the less the chances that cryptic genes can remain undetected. The recurrent parent chosen for the backcross program was a line designated 5-593, which is described below.

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Fig. 1. A ventral view (left seed) and a side view (right seed) of the virgarcus pattern of partly colored seedcoat.

This paper investigates the interactions of all combinations of four genes-*t*, *z*, *j*, and *d* - as expressed in partly colored and other types of seedcoat patterns. This paper also presents evidence that there is allelism between the hilum ring color gene *D* and the gene *Z* affecting patterns of partly colored seedcoats.

Materials and Methods

In 1985 a program was initiated to develop genetic tester stocks for common bean seedcoat colors and patterns by backcrossing selected recessive alleles, singly and in combination, into a recurrent parent 5-593, a Florida dry bean breeding line with the seedcoat genotype *T Z P [C r] D J G B V Rk* (Bassett, 1994b; Bassett and Blom, 1991). Details of the backcross procedure for developing genetic tester stocks were described previously (Bassett, 1994c). The seedcoats of 5-593 are shiny, unpatterned black.

Six genetic tester stocks (including BC_2 and BC_3 versions of two of them) were used in experiments described herein: *t* self-colored BC_2 5-593, *t z* virgarcus BC_3 5-593, *j* margo BC_3 5-593, *j v* margo BC_3 5-593 (also *j v* margo BC_2 5-593), *t j* marginata BC_3 5-593, and *d j* (margo *d*) BC_3 5-593 (also *d j* (margo *d*) BC_2 5-593). The development of *t* self-colored BC_2 5-593 was described previously (Bassett and Blom, 1991). Although the *t/t* allele genotype produces white flowers and potentiates partly colored seedcoat expression, the seedcoat is self-colored (unpatterned) because this stock has genotype *Z l⁺* and probably an unidentified gene that converts the expansa pattern to self-colored. The development of *t z* virgarcus BC_3 5-593 was described previously (Bassett, 1996b) and is illustrated (Fig. 1). The development of *j* margo BC_3 5-593 and *d j* (margo *d*) BC_3 5-593 was described previously (Bassett, 1996a). The *d j* (margo *d*) BC_3 5-593 stock differs in appearance from *j* margo BC_3 5-593 in two ways: *d* produces a loss of color in the hilum ring (white or often nearly white) and a slightly paler color (with *B V*) over the remainder of the seedcoat.

The *t j* marginata BC_3 5-593 genetic tester stock (Fig. 2) was created synthetically in 1996 from the cross *t* expansa with fibula arcs BC_3 5-593 $\times$ *j* margo BC_3 5-593. The interaction of *t* with *j* produces a seedcoat highly similar to the marginata pattern of Schreiber (1940) and will be called *t j* marginata BC_3 5-593 in this

paper. Color illustrations of the *j* interactions with *t* were published previously (Bassett, 1994a).

The cross *j* margo BC_3 5-593 $\times$ *t z* virgarcus BC_3 5-593 was made in 1994, and the F_2 was planted in the field Spring 1995. Data were recorded on flower color and seedcoat color and pattern for the F_1 and F_2 progeny. The cross *t z* virgarcus BC_3 5-593 $\times$ *d j* (margo *d*) BC_3 5-593 was made in 1995, and the F_2 was planted in the field Spring 1996. Data were recorded on flower color and seedcoat color and pattern for the F_1 and F_2 progeny. During Winter 1996-1997 remnant F_2 seed from the cross *t z* virgarcus BC_3 5-593 $\times$ *d j* (margo *d*) BC_3 5-593 was planted in the greenhouse to produce seed for an F_3 progeny test. In Spring 1997, 80 F_3 progenies were grown in the field from randomly selected F_2 plants of the cross *t z* virgarcus BC_3 5-593 $\times$ *d j* (margo *d*) BC_3 5-593. Each F_3 progeny row had 40-50 plants. Data were recorded on flower color and seedcoat color and pattern in F_2 and F_3 progeny.

In Fall 1996 the cross *t j* marginata BC_3 5-593 $\times$ *t z* virgarcus BC_3 5-593 was made, and the F_2 was planted in the field Spring 1997. Data were recorded on flower color and seedcoat color and pattern in F_1 and F_2 progeny.

The genetic stocks *d j* (margo *d*) BC_2 5-593 and *j v* margo BC_2 5-593 were developed previously (Bassett, 1994a, 1996a). The cross *d j* (margo *d*) BC_2 5-593 $\times$ *j v* margo BC_2 5-593 was made in the greenhouse Fall 1993, and the F_2 was planted in the field Spring 1994. Data were recorded on segregation for flower color and seedcoat color and pattern. Remnant F_2 seed from the crosses *d j* (margo *d*) BC_2 5-593 $\times$ *j v* margo BC_2 5-593 and *d j* (margo *d*) BC_2 5-593 $\times$ *j* margo BC_2 5-593 was sent to the laboratory of P.E. McClean, Dept. of Plant Sciences, North Dakota State University, Fargo, to perform a test (plants grown in the greenhouse) with a previously developed (Brady et al., 1998) randomly amplified polymorphic DNA (RAPD) marker (AM10₅₆₀) for the *Z* locus. The phenotypic segregation at the *D* locus was tested for independence of the segregation of the AM10₅₆₀ RAPD marker, which is associated with (1.4 cM) the *Z* locus (Brady et al., 1998). The procedures of Brady et al. (1998) were followed for DNA isolation and RAPD analysis. Thus, the linkage of *D* and *Z* was tested using the marker AM10₅₆₀. Genetic linkage was calculated by the maximum likelihood method of Allard (1956), and orthogonal contrasts to detect and quantify segregation disturbances were calculated by the method of Mather (1957).

Fig. 2. A ventral view (left seed) and a side view (right seed) of the marginata pattern of partly colored seedcoat.

Table 1. Segregation for seedcoat colors and patterns in the F₂ from the cross *j* margo BC₃ 5-593 × *t z* virgarcus BC₃ 5-593.

Genotype ^z	Seedcoat phenotype ^y	Expected		No. observed	χ ² components 36:9:3:9:3:3:1	<i>P</i>
		Ratio	No.			
<i>T/- J/-</i>	Black	36	92.81	97	0.189	
<i>T/- j/j Z/-</i>	Margo	9	23.20	30	1.991	
<i>T/- j/j z/z</i>	Margo <i>d</i>	3	7.73	8	0.009	
<i>t/t J/- Z/Z</i>	Expansa	3	9	19	0.761	
<i>t/t J/- Z/z</i>	Ambigua	6				
<i>t/t j/j Z/-</i>	Marginata	3				
<i>t/t J/j z/z</i>	White ^x	3	7.73	3	5.864	
<i>t/t j/j z/z</i>						
<i>t/t J/J z/z</i>	Virgarcus	1	2.58	1	0.069	
Total		64		165	8.953	0.18

^zThe hypothesis is that *z* and *d* are allelic. Thus, *z/z* (XapproxX) *d/d* and the *z* interaction with *j* produces the same phenotype as reported previously for *d j*.

^yThe margo seedcoats have immature color over the entire seed except for the margo zone, a broad swath around the hilum. The margo *d* seedcoats are similar to margo except for a white hilum ring and corona due to the *d* allele effect. The expansa partly colored seedcoat pattern is totally colored except for a small white area at the micropyle end of the seed (toward the dorsal side). The ambigua partly colored pattern is highly variable, most of the micropyle end (especially the dorsal side) of the seed being white. Illustrations are provided for the virgarcus (Fig. 1) and marginata (Fig. 2) seedcoat patterns.

^xThe white class includes a near white phenotypic class with genotype *t/t J/j z/z*, which produces color only at the raphe and micropyle, whereas *t/t j/j z/z* produces a truly white seedcoat.

Results and Discussion

The F₁ plants from the cross *j* margo BC₃ 5-593 × *t z* virgarcus BC₃ 5-593 had purple flowers (due to *T/t*) and shiny, unpatterned black seedcoats (data not shown). The F₂ segregated for seven phenotypic classes that could be distinguished from each other without ambiguity (Table 1). Two phenotypic classes, white and near white, were combined (under white) because originally the near-white phenotype was suspected of being artifactual. One of the classes is actually a combination of the expansa and ambigua classes, which cannot be distinguished unambiguously in F₂ (Table 1). The F₂ segregants with *t/t* could always be identified by their white flowers (data not shown). The observed segregation fit a genetic model based on segregation at three loci, *T*, *J*, and *Z*. One of the seven phenotypic classes is a surprising anomaly, viz., margo *d* (with *T/-*), the succinct label for a partly colored pattern that we give to the phenotype of the *d j* (margo *d*) BC₃ 5-593 genetic tester stock (Bassett, 1996a). Thus, the F₂ appeared to be segregating at the *D* locus, but neither of the two parents was expected to carry *d*. Obviously, the *j* margo BC₃ 5-593 parental stock cannot be the source of the *d* allele, or the phenotype would be margo *d*. The anomaly can be explained by the hypothesis that the *z* allele in the *t z* virgarcus BC₃ 5-593 stock interacts with *j* to produce the observed margo *d* phenotype. Thus, the *d* in the margo *d* label is a synonym for *z* because the *D* and *Z* genes are allelic.

A low frequency (1/64) of the F₂ progeny from the cross *j* margo BC₃ 5-593 × *t z* virgarcus BC₃ 5-593 had white seedcoats attributed to the genotype *t j z* (Table 1). Further testing of that hypothesis was achieved with the cross *t j* marginata BC₃ 5-593 × *t z* virgarcus BC₃ 5-593, for which the F₁ plants produced seed with the ambigua pattern of partly colored seedcoats due to *t/t Z/z J/j* (data not shown). The F₂ segregated into four phenotypic classes, which fit a ratio of 9:3:3:1 for a combined class, the two parental classes, and the white seed class, respectively (Table 2). The first three classes have a genetic basis that is well established in the literature (Bassett, 1997b). The observed data support the hypothesis that *t j z* produces white seedcoats, which is a new genotype for white seedcoats in common bean.

To test further the allelism hypothesis for the *Z* and *D* genes, another test cross with the virgarcus tester was performed and

analyzed. For the cross *t z* virgarcus BC₃ 5-593 × *d j* (margo *d*) BC₃ 5-593 the F₁ plants had purple flowers (due to *T/t*) and shiny, unpatterned black seedcoats (data not shown).

The F₂ segregated for only four phenotypic classes (Table 3). The F₂ segregants with the *t/t* genotype could always be identified by their white flowers (data not shown). The observed data (Table 3) fit a genetic model that segregates at only two loci (*T* and *J*) (Table 3).

There were two single recessive gene phenotypes expected in F₂ that did not appear, viz., *t* alone, giving the expansa pattern of partly colored seeds, and *j* alone, giving the margo phenotype (Table 3). Those apparent anomalies are explained if *d* is a synonym for *z* and all F₂ plants carry *z/z*. Thus, every *t/t* segregant must always carry *z/z* too, giving virgarcus as the most extensively colored pattern permitted by that genotype. Similarly, every *j/j* segregant must always carry *z/z* (same as *d/d*) too, giving the margo *d* phenotype each time.

These data (Table 3) provide another line of support for allelism. One of the two-gene recombinants expected (assuming segregation for four independent genes) was the *t j* marginata pattern (see Table 2), which did not appear. If, on the other hand, every F₂ plant carries *z/z* (assuming allelism of *D* and *Z*), then each *t j* segregant will in reality be a *t j z* segregant with a white seedcoat. Thus, a *t j* marginata segregant would be unexpected. If *D* and *Z* are not allelic, the *t j Z* marginata class would be expected in the F₂ due to complemen-

Table 2. Segregation for number of plants with various seedcoat colors and partly colored patterns in the F₂ from the cross *t j* marginata BC₃ 5-593 × *t z* virgarcus BC₃ 5-593.

Self-c, exp, amb ^z <i>Z/- J/-</i>	Plants observed (no.)			χ ² components 9:3:3:1	<i>P</i>
	Virgarcus ^y <i>z/z J/-</i>	Marginata ^x <i>Z/- j/j</i>	White <i>z/z j/j</i>		
220	78	72	23	0.396	0.94

^zSelf-c = self-colored, exp = expansa, amb = ambigua.

^yThe virgarcus class also includes a more restricted pattern produced by the fibula arcs factor interacting with *t z* (Bassett, unpublished data).

^xThe *t j* marginata pattern has seedcoat color only in the hilum ring and a small raphe stripe.

Table 3. Segregation for seedcoat colors and partly colored patterns in the F₂ from the cross *t z virgarcus* BC₃ 5-593 (*t J z*) × *d j* (margo *d*) BC₃ 5-593 (*T j z*).^z

Genotype	Seedcoat phenotype ^y	Expected ratio	No. observed	$\chi^2_{(n-1)}$	
				components	<i>P</i>
<i>T/- J/-</i>	Black	9	84	0.350	
<i>T/- j/j</i>	Margo <i>d</i>	3	27	0.021	
<i>t/t J/j</i>	White ^x	3	22	0.688	
<i>t/t j/j</i>	White				
<i>t/t J/J</i>	Virgarcus	1	7	0.350	
	Totals	16	140	1.4095	0.70

^zThe hypothesis is that *z* and *d* are synonyms for the same allele. Hence, all F₂ progeny are homozygous *z/z* (or *d/d*), and the *z* gene symbol has priority.

^yThe margo *d* phenotype has dull, dark purple seed with colorless (white) hilum ring and corona.

^xThe genotype *t/t J/j* really produces a nearly white seed (with two tiny, pale gray dots; one each at the raphe and micropyle), but this phenotype was combined with white (*t/t j/j*) in this experiment.

tation of these loci. The F₂ data lack any supporting evidence for independence of *D* and *Z*.

There is one anomaly in the F₂ data from the cross *t z virgarcus* BC₃ 5- 593 × *d j* (margo *d*) BC₃ 5-593 that will be discussed further. The white seedcoat class (Table 3) was really a combination of two classes: a near-white class (genotype *t/t J/j*) with two pale gray dots, one at the raphe and the other at the micropyle, and a

second class that has pure white seeds (*t/t j/j*). Those two classes were combined in the original classification of the F₂ material and called white. When the classification was originally made, there was a concern whether the near-white types were a stable and heritable expression or an artifact of weathering on the seedcoats. When additional F₂ plants were later grown in the greenhouse (using remnant F₂ seed), we observed that the near- white class was stable and not dependent on environmental conditions for its expression.

The hypothesis of allelism between *D* and *Z* was tested further in the F₃ generation produced from remnant F₂ seed of the cross *t z virgarcus* BC₃ 5-593 × *d j* (margo *d*) BC₃ 5-593. The F₃ genetic model and the observed F₃ data are combined and presented in one table (Table 4).

When the seed from the 80 F₂ plants grown from remnant seed were classified, a new phenotypic class (near white) was added to those given above. This class has a tiny, pale gray dot at the raphe and another at the micropyle and is otherwise a white seed. In previous work given in Tables 1 and 3 the near-white class was lumped into the white seed class for reasons discussed above. Thus, there were five phenotypic classes of F₃ seed planted in the field (Table 4).

The F₂ plants with self-colored (*T/- J/-*) F₃ seed segregated for the expected four different types of progenies (Table 4). The F₂ plants with margo *d* phenotype (*T/- j/j*) in F₃ seed segregated for the expected two different types of progenies (Table 4).

For the *T/t J/J* genotype, there was a surprising lack of fit to a 3:1 segregation for self-colored to virgarcus for the combined data. This was due to the significant deviation of two plots from the expected 3:1 segregation (Table 4, footnote u). There may be

Table 4. Segregation for seedcoat colors or partly colored patterns in F₃ progenies of 80 randomly selected F₂ progeny from the cross *t z virgarcus* BC₃ 5-593 × *d j* (margo *d*) BC₃ 5-593.^z

				<i>t/t</i> White flower						
F ₂ plant		F ₃ progenies		<i>T/-</i> Purple flower		Near			$\chi^2_{(n-1)}$ ²	<i>P</i>
Phenotype ^y	Genetic hypothesis ^x	No. observed	Total plants	Black seed ^y <i>J/-</i>	Margo <i>d</i> seed ^y <i>j/j</i>	Virgarcus seed ^w <i>J/J</i>	white seed ^v <i>J/j</i>	White seed <i>j/j</i>		
Self-c	<i>T/T J/J</i>	10	448	448					(3:1)	
Self-c	<i>T/T J/j</i>	8	359	267	92				2.571	0.11
Margo <i>d</i>	<i>T/T j/j</i>	5	208		208					
Self-c	<i>T/t J/J</i>	9	392	315		77			(3:1) 6.000 ^u	0.01
Self-c	<i>T/t J/j</i>	25	1361	797	260	73	147	84	(9:3:1:2:1) 7.721	0.10
Margo <i>d</i>	<i>T/t j/j</i>	7	362		267			95	(3:1) 0.298	0.59
Virgarcus	<i>t/t J/J</i>	1	47			47				
Near white	<i>t/t J/j</i>	9	553			129	267	157	(1:2:1) 3.488	0.18
White	<i>t/t j/j</i>	5	223					223		

^zThe hypothesis is that *z* and *d* are allelic. Thus, *z* not only produces virgarcus pattern with *t*, but also produces colorless hilum ring and corona with *j*.

^yBlack seed [_{XapproxX}] self-colored [_{XapproxX}] self-c; and the margo *d* seed have dull, dark purple seedcoats with colorless (white) hilum ring and corona.

Table 5. Segregation for seedcoat pattern gene *D* and RAPD marker AM10 linked (in coupling) to partly colored seedcoat pattern gene *Z* in the F_2 from two crosses: 1) *dj* (margo *d*) BC_2 5-593 (*d/d*) $\times$ *jv* margo BC_2 5-593 (*D/D*) and 2) *dj* (margo *d*) BC_3 5-593 (*d/d*) $\times$ *j* margo BC_3 5-593 (*D/D*)^z.

Cross no.	Margo <i>jD</i> AM10 +	Margo <i>jD</i> AM10 -	Margo <i>jd</i> AM10 +	Margo <i>jd</i> AM10 -	Linkage $\chi^2_{(3:1)}$	<i>P</i>
1 ^y	63	0	2	13	43.128	< 0.001
2 ^x	52	2	1	21	78.69	< 0.001

^zRecombination value for the combined data is 3.364 ± 1.48 , homogeneity $\chi^2_{(3:1)} = 0.09$.

^yThe $\chi^2_{(3:1)}_{AM10}$ (3:1) = 1.385, *P* = 0.28 and $\chi^2_{(3:1)}_{AM10}$ (3:1) = 2.889, *P* = 0.09.

^xThe $\chi^2_{(3:1)}_{AM10}$ (3:1) = 0.63, *P* = 0.43 and $\chi^2_{(3:1)}_{AM10}$ (3:1) = 1.123, *P* = 0.29.

another gene not presented in the model that with *t/tJ/J* can disturb the segregation of virgarcus phenotypes, but the data are not sufficient to determine the identity of the hypothetical gene.

The most stringent test of the model was provided by the 25 plots that fit (singly and collectively) the expected segregation ratio 9:3:1:2:1 for self-colored (black), margo *d*, virgarcus, near white, and white, respectively. Those plots were hypothesized to carry the F_2 dihybrid genotype *T/tJ/j*, where the F_3 progeny genotype *t/tJ/j* produced the near-white phenotype. The hypothesis that the three phenotypes - virgarcus, near white, and white - are controlled by genotypes *t/tJ/J*, *t/tJ/j*, and *t/tj/j*, respectively, was confirmed by the observed segregation for the self progenies of F_2 parental plants with near-white seedcoats (Table 4). The one F_2 plant with virgarcus pattern (*t/tJ/J*) was true breeding in F_3 (Table 4). The five F_2 plants with white seedcoats were true breeding in F_3 progenies (Table 4). Thus, the hypothesis that *tj* (*z* or *d*) produces white seedcoats was supported by all the data (Table 4), a discovery which has not been reported previously. Among the 80 F_3 progenies classified, all the nine expected genotypes produced by selfing the dihybrid genotype *T/tJ/j* were observed, and the frequencies of the nine genotypes fit the expected ratio of 1:2:1:2:4:2:1:2:1 for the phenotypes given (Table 4). If the *D* and *Z* loci were closely linked, but not allelic, evidence of complementation should have been observed in the above experiments. Absent that evidence, one must conclude that the hypothesis of allelism is supported.

The hypothesis that the *D* and *Z* genes are not independent was supported by a molecular marker test involving a RAPD marker (AM10₅₆₀) for the *Z* locus. For the crosses *dj* (margo *d*) BC_2 5-593 $\times$ *jv* margo BC_2 5-593 (*D/D*) and *dj* (margo *d*) BC_3 5-593 $\times$ *j* margo BC_3 5-593 (*D/D*), the segregation in the F_2 showed very close association of AM10 with *D* (Table 5).

The close linkage of AM10 with both *Z* and *D* supports the hypothesis that the two genes are not independent loci as formerly assumed.

The hypothesis that the *Z* and *D* genes are allelic is supported by the data presented. Furthermore, all the evidence supports the more specific hypothesis that *z* and *d* are synonymous for the same recessive gene. We propose that the gene symbol *Z* be used for the locus based on prior appearance in the literature. Lamprecht (1934) renamed the *Z*₁ of von Tschermak (1912) as *T* because they were identical, and he renamed the *Z*₂ of von Tschermak (1912) as the *Z* locus. The *D* locus symbol was created by Kooiman (1920) for the hilum ring factor at a later date.

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