

Inheritance of the harlequin color in Great Dane dogs

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ABSTRACT: The harlequin color pattern of Great Dane dogs differs from merle in that the background is white instead of blue. Harlequin by harlequin matings produced 60 black, 77 harlequin, 42 merle, and 35 homozygous merle pups. Harlequin by black matings produced 44 black, 26 harlequin, 25 merle, and one white (homozygous merle?) pups. All harlequins produced some merles. These data best fit the hypothesis that harlequin is a modification of merle (*Mm*) caused by an autosomal dominant mutation that is lethal to homozygotes, and to about half of heterozygotes when combined with the *MM* genotype. The symbol *H* is proposed for this mutation.

THE HARLEQUIN pattern in Great Dane dogs consists of a white background on which are scattered ragged black patches². Occasional patches are blue, but these are not desired by breeders. The pattern has been described as being related to the merle pattern, from which it differs by having the white background instead of the usual blue background on merles³⁻⁵. The merle pattern occurs on heterozygotes (*M/m*) while the homozygote (*M/M*) is very pale (or white) all over, and has ear, eyes, and brain abnormalities⁶.

The breeding records of two kennels were available for study. Both kennels are breeding specifically for the harlequin pattern, and results of matings are presented in Table I. Many of the dogs classified as black also had white spotting (white on distal legs, tail, and chest or neck). These marks are fairly common in harlequin breeding since it is desirable for the neck on harlequins to be white, and white spotting in this area assures the correct marking. The black dogs with white trim are classified as black in Table I. Breeders refer to this as the "Boston" pattern, and have no difficulty in distinguishing it from the true harlequin since the black areas have smooth edges instead of ragged ones, and the white is restricted to certain areas rather than the more random distribution of white on the harlequins. Harlequin by harlequin matings produced 60 black, 77 harlequin, 42 merle, and 35 white (homozygous merle) pups. Harlequin by black matings produced 44 black, 26 harlequin, 25 merle, and 1 white pups. These results were produced by 25 harlequin and 7 black dogs. No merle dogs were used for breeding, as

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merle is not a desired color phenotype in Great Danes.

The records indicate that merles are consistently produced, even though no merles are used for breeding. This contradicts an earlier hypothesis that merle and harlequin are alleles at the same locus⁵. Merle is most likely due to a transposable genetic element, and if the merle and harlequin were allelic the presence of merles could occur from mutation, movement of the element, or crossover at the appropriate place in the allele^{7,8}. Merles are much too common for any of these mechanisms to account for their occurrence. All breeding animals produced merles; none produced only harlequins.

If the harlequins and merles are grouped together as a single group and compared to the accepted inheritance of merle as an incomplete dominant then the expected progeny classes from harlequin × harlequin breedings are 1 white: 2 harlequin/merle: 1 black. The data yield a chi-square value of 8.126 ($P < 0.01$), indicating that some additional mechanism is present. The crosses of black × harlequin should result in a ratio of 1 black: 1 harlequin/merle. The presence of the one white pup refutes this, unless this pup is a misclassified heterozygote. This is probably possible in a low percentage of harlequins, as the number and size of intense black patches varies markedly. If the one white pup is lumped with the harlequin/merle class the resulting chi-square is 0.667 ($P > 0.05$). Alternatively, this pup could have resulted from reentry of the transposable element into the merle locus. This action has never been documented, but would indicate that the element remains in the genome of non-merle animals. A third possibility is that this pup is a

harlequin or merle with a dilute blue (*dd*) background color. Such pups in the Australian shepherd breed are nearly white at birth (Betty Nelson, pers. comm.). Since blue dilute does occur in the Great Dane breed, this is the most likely explanation. Whatever the explanation of this one pup, the data from the harlequin × harlequin breedings clearly indicate that some progeny classes are deficient.

Table II presents several hypotheses by which merle (*M*) could be modified by an allele at a separate locus (*H*) to produce the harlequin phenotype. Under the first hypothesis of no lethality the results differ significantly from those expected from crossing harlequin and harlequin.

The fact that all harlequins produced merles in addition to harlequins is evidence for some lethal action. These harlequin dogs are the result of several generations of breeding specifically for the harlequin color and if no lethality were present the harlequin genotype should have been homozygous in at least some individuals. The results under various hypotheses that postulate lethality to certain genotypes all deviate significantly from the results expected. The closest fit occurs if only a portion of the genotype *MMHh* is lethal. The *MM* genotype alone is abnormal and subvital, and may well interact with *Hh* to produce lethality a portion of the time. This is the hypothesis that best fits the data. Reduced litter size in harlequin breedings would strengthen this hypothesis. The average size of the 33 litters in this study was 9.4 pups. This is in agreement with a published range of 8-10 pups in the Great Dane breed¹, but this estimate was not qualified by the method used to obtain it, or by the color of parents. If *MmHh* were only partially lethal it seems likely that it would act late in gestation and increase the number of still births. This, however, has not been the experience of these breeders, and so *MmHh* pups that die in utero must die early enough so as to be unnoticed as a part of the litters.

This genetic mechanism has importance to the breeding for this color, since the harlequins are desired at the expense of all other color classes. Merles are usually culled, as are homozygous merles and some blacks with extensive white trim. Matings of harlequin × black should result in 50 percent black, 33 percent harlequin, and 17 percent merle if the black

Table I. Results of various color crosses involving Great Dane dogs

Parental color	Pup colors				Total
	black	harlequin	merle	white	
Harlequin × harlequin	60	77	42	35	214
Black × harlequin	44	26	25	1	96

Table II. Goodness-of-fit of the results of the harlequin × harlequin mating using several hypotheses with different lethal interactions[†]

Lethal genotype	Expected ratio				χ^2
	black	harlequin	merle	white	
None	4	6	2	4	15.226**
- <i>HH</i>	3	4	2	3	9.117**
- <i>HH</i> plus <i>MMHh</i>	3	4	2	1	10.548**
<i>M-HH</i>	4	4	2	1	17.718**
- <i>HH</i> plus half <i>MMHh</i>	3	4	2	2	0.723

[†] *MmHh* × *MmHh* where *MmHh* is harlequin, *MM--* is white, *Mmhh* is merle, and *Mm--* is black
** $P < 0.01$

carries the harlequin modifier, and 50 percent black, 25 percent harlequin, and 25 percent merle if the black does not carry the modifier. Since the results of the kennel records closely approximate the 50:25:25 results from black X harlequin breedings it is unlikely that any blacks carried the *H* allele. This in turn is unusual, since the black dogs resulted from harlequin parents. Only 11 breedings took place in black dogs, and four of these were to a single animal. It is possible that this animal is *mmhh*, and that the large contribution of this animal to the data accounts for the apparent lack of the harlequin modifier in black animals. The mating of harlequin X harlequin results in 18.2 percent homozygous merles, 18.2 percent merles, 36.3 percent harlequins, and 27.3 per-

cent blacks. The most reliable way to produce harlequins, then, is to breed harlequin to harlequin, but even then the production of undesirable colors occurs.

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Inheritance of purple and purple-stripe testa colors in the peanut

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ABSTRACT: In the peanut, *Arachis hypogaea* L., the purple and purple-striped testa colors were found to be monogenically and digenically inherited, respectively. Incomplete dominance was observed for the solid purple color. An interaction of incomplete and complete dominance also was observed for the purple-stripe appearance. However, when either loci are homozygous recessive, stripes are not expressed. Linkage was not detected between these two testa character-

istics. Gene symbols, *Vsp₁* and *Vsp₂*, are suggested for the variegated purple-striped alleles.

IN RECENT peanut (*Arachis hypogaea* L.) genetic reviews, Hammons⁴ and Wynne and Cof-felt¹⁰ have amply discussed the gene interactions regarding testa color expression. Currently, seven loci are known to be involved in the solid phenotypes: white, tan, red, and purple.

Several earlier reports indicated monogenic dominance for purple over the tan (brown, flesh, pink, rose, or russet) colors^{1,2,6-9,11}. In general, distinct classification of the purple heterozygous genotype, *Pp*, was demonstrated.

However, no reference was found pertaining to tan with purple-stripe variegated testa. Yet, two rust (*Puccinia arachidis* Speg.) resistant germplasm lines possess this unusual characteristic⁵. Thus, the ensuing objective of this study was to determine the mode of inheritance for the purple-striped trait and its relationship with the solid purple testa color.

Materials and Methods

Three diverse pure lines were purposely chosen for this study. As previously reported, Krinkle (T-900) has a tan testa genotype (*rr F₁F₁F₂F₂D₁D₁D₂D₂*)³. PI 262129 (466 GKP) was selected because of its variegated testa, tan with purple-stripes, and PI 331334 (169 HL) was selected because of its solid purple colored seed.

Cross combinations were made in the greenhouse between Krinkle X PI 331334 and reciprocal, PI 262129 X Krinkle, and PI 331334 X PI 262129. The F₁, F₂, and F₃ generations were field grown at the agronomy farm near Tifton, Georgia during 1981, 1982, and 1983, respectively. Visual classification was made on individual plant samples after harvesting, drying, and shelling. Segregating populations were analyzed for goodness-of-fit to expected ratios by chi-square tests.

Results and Discussion

The F₁ testa phenotype from Krinkle X PI 331334 and reciprocal cross was classified as light purple. This observation suggests incomplete dominance for solid purple coloration. The PI 262129 X Krinkle cross resulted in a few purple stripes on approximately half of the F₁ seed per plant. Thus, this variegated testa also would appear to be incomplete in dominance, expressivity, and penetrance. F₁ testa color of PI 331334 X PI 262129 exhibited a combination of few purple stripes with a light purple background color.

The F₂ populations segregated into a 1:2:1 ratio without reciprocal differences for the crosses between Krinkle and PI 331334 (Table I). However, F₂ segregation from PI 262129 X Krinkle fit a digenic ratio of 3:6:7. This genetic ratio is a modification of the 9:7 ratio with incomplete dominance of the second gene. The

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Table I. F₂ segregation and chi-square results from solid and variegated testa color cross combinations in the peanut

Cross Population	No. families	F ₂ testa color class*							Expected ratio	χ ²	P
		prp	s/lt. prp	s ^f /lt. prp	lt. prp	s/tan	s ^f /tan	tan			
Krinkle X PI 331334 and reciprocal	4	659	—	—	1276	—	—	597	(1:2:1)	3.194	0.10-0.25
PI 262129 X Krinkle	3	—	—	—	—	70	174	202	(3:6:7)	2.735	0.25-0.50
PI 331334 X PI 262129	4	61	23	12	14	22	28	25	(16:6:12:14:3:6:7)	9.674	0.10-0.25

* prp = solid purple; lt. prp = lighter purple; s/ = many purple-stripes; and s^f = fewer purple-stripes