

The Inheritance of Coat Colour in the Cardigan Welsh Corgi

Part II

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Introduction

The inheritance of the main patterns of coat colour in the Cardigan Corgi may be accounted for within the scheme of coat colour inheritance devised by Little. Its application to the Cardigan has been described previously. In brief the main patterns follow from the interaction of genes in the A and E groups, using two genes in each group, as follows.

- a^y which restricts the formation of dark pigment
- a^t which produces the 'tan point' pattern
- E which allows the full extension of dark pigment according to the control of a^y and a^t
- e^{br} which allows dark pigment to appear as brindle markings.

This allows the following gene combinations (genotypes)

- $a^y a^y E e^{br}$ brindle - produces brindle and red
- $a^y a^y e^{br} e^{br}$ brindle - produces brindle only
- $a^y a^t E e^{br}$ brindle - produces brindle, red and tricolour
- $a^y a^t e^{br} e^{br}$ brindle - produces brindle and tricolour

- $a^t a^t E E$ tricolour - red/tan points
- $a^t a^t E e^{br}$ tricolour - brindle points
- $a^t a^t e^{br} e^{br}$ tricolour - brindle points.

This scheme accounts for the main colour groups which we observe, and their inheritance.

The scheme, however, does not account for some important colour variations which we observe in the breed.

- (a) It can easily be shown that animals which, on account of their parentage and/or offspring are genotypically $a^y a^t E E$ fall into two groups or phenotypes

- animals which are essentially red
- animals which are sable, i.e. have extensive black markings in the coat which usually 'shadow' the tan point marking pattern, associated with a^t

Hence there are two phenotypes associated with the same genotype. This indicates that the two-group genotype statement is inadequate.

- (b) The brindle colour in the Cardigan Corgi is found in a wide range from very lightly marked brindle to the almost black. The colour range might be roughly divided into four groups, light brindle, mid brindle, dark brindle and black brindle, these being defined in terms of the intensity of the brindle markings and without reference to the ground colour (which may range from bright red, through paler shades, almost to a grey). However, the brindle range is practically continuous, and while there might be considerable agreement in assigning many dogs to these four groups, in many cases such an assignment would be very subjective. While Little's scheme offers four genotypes producing brindle colouring, they do not correspond to the four phenotype groupings we have discussed. It is possible, on account of their parentage and/or offspring, to classify the genotype of many of the well known dogs according to the scheme, and to show that dogs within a given genotype cover the whole phenotype range. Table 1A discusses dogs which are genotypically $a^y a^t E e^{br}$. Hence the two-group genotype statement based on Little's scheme is adequate to describe and define the inheritance and transmission of brindle colouring, but is unable to adequately define the colour range.
- (c) In the Cardigan Corgi, the tan point pattern always produces what one might term a full tricolour, with black cap, back, sides and upper limbs. The saddle back tricolour is seldom, if ever found. However, within the tricolours, one may distinguish dogs which have a light red/tan undercoat and those which have a black undercoat. Within the tricolours themselves, the distinction is not important. However, it can be of some importance in considering tricolours for blue merle breeding. If a blue merle (which can be considered as a modified tricolour) carries a red/tan undercoat, it gives a red cast to or can show through a blue topcoat. The genotype statements based on Little's scheme do not distinguish the light and dark undercoat phenotypes in the tricolours.

This paper discusses the possibility of extending the two-group genotype statement, by inclusion of a third gene group, its ability to account for the phenotype differences discussed above, and, based on the comparison with breeding experience, the properties which are required for this group to move towards an adequate genotype-phenotype matching. This paper discusses the problem in relation to the Cardigan Corgi, but the introduction of such a third gene grouping into the description of basic coat colour patterns could be important with respect to other breeds. This will be discussed in a later paper.

The Postulated Third Gene Group

The phenotype differences in the red sable, brindle and tricolour coat patterns discussed above might be expected to be accounted for by separate modifiers, but this paper examines the possibility of linking the effects to the operation of a single modifier group. It is postulated to act interactively with the well established A and E groups. In the Cardigan Corgi, it is necessary to postulate two genes in the group, designated as η and η^+ . η^+ promotes the extension of dark pigments in the coat, relative to the effect of η , within the basic patterns governed by the A and E group genes. It is further postulated that η is dominant to η^+ . Consideration of breeding data however shows that the dominance may not be complete, and that the penetration may vary according to the A and E group genes present: there appears to be more penetration of the effects in the brindles than in the red sables.

At present the postulated scheme has been established with reference to only a limited amount of breed data. It must therefore be clearly recognised as an hypothesis, providing a basis and framework for further testing.

Red Sables

It is postulated that, of dogs having the genotype $a^y a^t EE$, those carrying the genes $\eta\eta$ have few if any black hairs in the coat, while those carrying $\eta^+\eta^+$ have extensive sable markings. Trying and testing this postulate against case history, it would appear that in this case η is dominant to η^+ , and dogs carrying $\eta\eta^+$ show little black in the coat.

The Dilwel line was founded on the red pointed tricolour bitch Blinkbonny Morva, and

progressed through the brindle Dilwel Gweno ($a^y a^t E e^{br}$) and the red Dilwel Glesni ($a^y a^t EE$). Yet it produced very few tricolours. This is believed to be due to extensive use of red dogs having the genotype $a^y a^y EE$, notably Teilo Bryn and his son Ch. Southpark Gerwyn and records support this view. The line did however produce some heavily marked sables, Ch. Dilwel Gwynfil, Dilwel Magpie, SA.Ch. Dilwel Rosina and Am.Ch. Dilwel Rowena, the two latter daughters of the red bitch Dilwel Gwarwen by Teilo Bryn x Dilwel Gweno. Using the η scheme, we would postulate as follows:

$$\begin{array}{c}
 \text{Teilo Bryn } (a^y a^y EE) \times \text{Dilwel Gweno } (a^y a^t E e^{br}) \\
 \downarrow \\
 \text{Ch. Southpark Gerwyn } (a^y a^y EE \eta \eta^+) \times \text{Dilwel Gwarwen } (a^y a^t EE \eta \eta^+) \\
 \downarrow \\
 \text{Dilwel Rowena } (a^y a^t EE \eta^+ \eta^+)
 \end{array}$$

The important pair here are Gwarwen and Rowena. Since Rowena was a heavily marked sable, postulated to be $\eta^+ \eta^+$, Gwarwen must carry η^+ , yet being a red with no black coat hair, must herself have been $\eta \eta^+$. Hence η must be dominant to η^+ . Also, Gwarwen must carry a^t to be able to transmit it to Rowena.

A similar case may be made with respect to Dilwel Magpie

$$\begin{array}{c}
 \text{Teilo Bryn } (a^y a^y EE) \times \text{Dilwel Glensi } (a^y a^t E e) \\
 \downarrow \\
 \text{Ch. Southpark Gerwyn } (a^y a^y EE \eta \eta^+) \times \text{Int.Ch. Dilwel Maggie } (a^y a^t EE \eta \eta^+) \\
 \downarrow \\
 \text{Dilwel Magpie } (a^y a^t EE \eta^+ \eta^+)
 \end{array}$$

Dilwel Maggie was a red bitch, with little if any black in the coat. The a^t gene is certain since, mated to Am.Ch. Springdale Droednoeth in USA, she produced the tricolour Am.Ch. Hillsborough Lets Pretend.

Note that in using the η group, genes must be assigned to the $a^y a^y EE$ red dogs. The η genes would not then be expected to produce black hair in the coat, since the A and E group genes present work against that, but they are important in determining the colour of the offspring, and must be correctly assigned. This requirement may make it more difficult to establish the AE η group scheme than the AE scheme. Clearly considerably more work is required using detailed data on other breeding lines: preliminary work done to date is encouraging.

Brindles

It is postulated the brindle carrying the $\eta\eta$ genes will be light brindles and dogs carrying the $\eta^+\eta^+$ genes will be dark brindles. We have seen that, in the sables, the a^t gene with the $\eta^+\eta^+$ doublet would be expected to and apparently does lead to black hair in the coat. Hence we might expect that brindles carrying $a^t\eta^+\eta^+$ would be dark. On the other hand, $a^t\eta\eta$ does not produce dark hair in the red/sable. Hence we might expect little difference in colour between $a^y a^y \eta\eta$ and $a^y a^t \eta\eta$ brindles. Table 1B lists several dogs which can be classified in the AE group scheme: these can be compared also with the dogs in Table 1A. Examination of these data suggests that the darkness of the brindle markings is not sensitive to whether Ee^{br} or $e^{br}e^{br}$ genes are carried. It is thought that the important factor is the η and η^+ genes, reacting with a^t . Hence we would expect a 'colour scale' rather as given below; with at present some uncertainty in the middle range of the scale.

$a^y a^y Ee^{br} \eta\eta$	}	$a^y a^t Ee^{br} \eta\eta$	}	light brindle
$a^y a^y e^{br} e^{br} \eta\eta$	}	$a^y a^t Ee^{br} \eta\eta$	}	light brindle
$a^y a^y Ee^{br} \eta\eta^+$	}	$a^y a^t Ee^{br} \eta\eta^+$	}	mid brindle
$a^y a^y e^{br} e^{br} \eta\eta^+$	}	$a^y a^t Ee^{br} \eta\eta^+$	}	mid brindle
$a^y a^y Ee^{br} \eta^+ \eta^+$	}	$a^y a^t Ee^{br} \eta^+ \eta^+$	}	dark brindle
$a^y a^y e^{br} e^{br} \eta^+ \eta^+$	}	$a^y a^t Ee^{br} \eta^+ \eta^+$	}	dark brindle
		$a^y a^t Ee^{br} \eta^+ \eta^+$	}	black brindle
		$a^y a^t e^{br} e^{br} \eta^+ \eta^+$	}	black brindle

Consideration of some breeding data suggests that this scheme can be successfully used. It suggests however, that in the brindle range penetration is not complete, and that while $\eta\eta$ dogs are light brindle and $\eta^+\eta^+$ dogs dark, $\eta\eta^+$ animals are not light brindles, as they would be if η was dominant to η^+ in the brindles, but are mid brindle shades. Thus η and η^+ genes are interacting with the e^{br} gene. Thus we find that in some cases matings of mid brindles can produce light brindles, and in other cases, such matings can produce dark brindles, suggesting that the mid brindles in these cases carry $\eta\eta^+$. For examples we may cite

Ch. Joseter Mudwin and Apollinaris Columbine producing the light brindle Ch.
Beckonpenn Gwyneth

Ch. Baileswood Gwythyr and Ch. Baileswood Bloddeuwedd producing the black brindle Ch. Baileswood Essyllt.

We might further note, in support of this explanation of the light-dark brindle range, that there are some brindle strains which tend to produce light brindles, and others which tend to produce dark brindles.

Again, while work done to date is encouraging and supports the proposed scheme, much further testing is required against a substantial body of evidence. Again, it will be necessary to correctly identify the η and η^+ genes carried by the red dogs involved.

Tricolours

It is postulated that in tricolours, dogs carrying the $\eta\eta$ gene combination may be expected to have light coloured undercoat, while dogs carrying $\eta^+\eta^+$ would have black undercoats.

At present it is not possible to offer any evidence to support or to test this hypothesis.

Tricolours are rather few in number and there are no recorded reliable data on the undercoat colours.

Reds

It has been pointed out that in using the proposed three group AE η scheme, it is necessary to correctly assign η and η^+ genes to the $a^y a^y EE$ red dogs involved in the breeding lines. While it is postulated that η and η^+ affect the black colour in the coat, it should be remembered that there is dark pigment in the coat of the red dogs, but the melanine granules are distributed and not aggregated. It is possible that this distribution, or granule size and shape might be influenced by the η and η^+ genes, and that this might influence the red colour. If it proves possible from an examination of an extensive body of breeding data to assign η and η^+ genes to a large number of red dogs, it will be desirable to see if there is any correlation between the red shade and the η and η^+ genes carried.

General Observations

The introduction of an additional group of genes, reacting interactively with the A and E groups, appears to offer a considerably more accurate description of the colours found in the Cardigan Corgi, than is possible using the A and E groups alone. The properties required for this additional gene group can be adequately defined and are reasonable and simple. The preliminary work done to date supports the hypothesis.

Using the two group A and E group scheme, 9 genotypes could be identified, giving rise to an extensive range of litter or breeding patterns, as has been discussed previously. Using the three group AE η group scheme, there are 27 possible genotypes, $\eta\eta$, $\eta\eta^+$ and $\eta^+\eta^+$ variants being possible with each of the previous 9. Hence the possible pattern of offspring of matings is very extensive, and since the numbers of whelps in a litter is so small a fraction of the possible range of variants, there is little point in trying to use the scheme predictively. Indeed it might cynically be argued that with so wide a range of possible genotypes it should be possible to offer an explanation for anything!

Another consequence of this range of variety is that there is little point in seeking support for the proposed scheme or model in the ratios of identifiable phenotypes. There can indeed be no very hard test. All that appears to be possible is to test the consistency of the model through several litters from the more well known dogs, and through several generations. Insofar as that can be done through individual dogs, results to date are encouraging but whole litter data are required to increase both the input data and the severity of the test.

Some Further Extensions and Applications of the Three Group Scheme

There are two possible further extensions and applications to which it is worth drawing some attention at this time.

There are very few data available in the UK on off-coloured merles. The ginger merle so called is the product of blue merle and brindle matings, and is essentially a brindle modified by carrying the M gene which produces merling. However, there is evidence in the breed history, though limited, that brindle dogs have been known which carried and transmitted the M gene. Such dogs as adults were apparently normal brindles: it is not known if they showed

any marks of merling in the very young puppy coat. Why the difference? This effect may be related to the η and η^+ genes carried. However, at present this can be no more than a suggestion, and considerably more input data are required to test it.

A possible extension of the scheme proposed may explain the one or two cases recorded which suggest that brindle offspring have been produced from matings of two reds. This appears to be very rare in the breed, but is not unknown in other breeds: Little instances data in Great Danes which he explains by suggesting that in one of the dogs the brindle markings may have been so slight that they were not noticed! The extension would be to include in the series a η^- gene, which reduced the amount of dark pigment relative to the η gene. Logically it would be expected to be at the head of the η group, and be dominant to η . Thus $\eta^-\eta$ dogs carrying the e^{br} gene might be phenotypically reds, but mated to red dogs carrying η and/or η^+ genes, might be expected to produce brindle offspring. If the gene η^- was ever prevalent in the breed, it would appear from general experience to be very rare now, if present at all. In the recorded case of brindles from reds which is important, the red offspring in the litter were very little bred from. It is of course quite possible to easily eliminate effects associated with a dominant gene from a breed, simply by not breeding from the stock involved. It is generally acknowledged that in the prewar years, there was a much higher proportion of reds than brindles: that may or may not be associated with the presence at that time of η^- in the breeding stock.

Table 1A

Cardigan Welsh Corgis of genotype

Ch. Robgwen Fordwell Deborah	light brindle
Ch. Dilwel Gweno-yr-Ail	light brindle
Dilwel Gweno	brindle
Ch. Robgwen Gregson	brindle
Ch. Baileswood Dyddanwy	brindle
Ch. Withybrook Brock	dark brindle
Dilwel Gwilym	dark brindle
Black Mawddach	dark brindle
Ch. Kentwood Curigwen	dark brindle
Ch. Pharaoh of Joseter	dark brindle
Ch. Kentwood Cymro	black brindle

Table 1B

Other Genotypes

 $a^y a^y E e^{br}$

Ch. Joseter Mudwin	dark brindle
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 $a^y a^y e^{br} e^{br}$

Ch. Parmel Pilot	brindle
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 $a^y a^t e^{br} e^{br}$

Ch. Apollinaris Cenydd	dark brindle
Ch. Robgwen Welsh Minstrel	dark brindle
Ch. Wendac Robgwen Midnight Special	black brindle

Written in the early 1980's

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