	The normal pigment found in the coat is black and yellow, this pigment is present in the hair as tiny granules, the colour, and shape of these granules determines the colour of the hair. In the black areas of the coat, these granules are oval and intensely brown in colour, in the yellow areas they are round, smaller and yellowish in colour. Normally the pigment granules are disposed regularly in the hair as it grows. This disposition tails off at the base of the hair, and consequently the colour becomes less intense. For example, black hairs will appear intensely black at the tip, but will become gradually paler as you go down the length of the hair until they appear bluish at the root. This is due to there being less pigment granules in the hair near to the skin, this effect can be seen in all colours.
A	The most common colour phenotypes in the border collie are due to the agouti series of alleles (A-) and the Extension series of alleles. (E-) Between them, these two series control the appearance of the black and yellow pigment in the majority of colours. They are listed separately below in order to describe the mutant alleles belonging to each series before discussing how they interact together to produce many well-known colours. The following colours are recessive to the colours above them in their series, and dominant to those below them in their series. **<u>The agouti alleles</u>** Solid black A^{s} (Solid black,) Dominant yellow A^{y} (this can be a clear yellow – golden or clear sable , or combined with a number of black tipped hairs on the head shoulders back and tail shaded sable) Agouti A (wolf grey colour) Saddle pattern a^{sa} (producing a V shaped saddle area of dark pigment on each side of the body to a variable degree) Tan a^{t} (Producing the typical tri colour, with tan areas on

	the eyebrows, cheeks, chest, inside front and back legs, and under the tail to a variable degree.)
E	**<u>Extension Alleles</u>** The extension alleles are, like the A alleles, concerned with the distribution of the black and yellow pigment throughout the coat. They are :- Brindle E^{br} This is responsible for the brindled (striped) effect of black and yellow and is thought to be dominant to E Normal extension E This is the normal extension, and is responsible for normal production of black pigment. Non-extension e This causes the non-extension of black throughout the coat, effectively changing all of the dark brown granules to yellow producing a yellow colour. This only affects the pigment in the hair, the pigment of the eye rims, nose lips and pads are unaffected.
	The expression of the A alleles are dependant on the presence of E, which governs the normal extension of black pigment throughout the coat. Therefore they may be written as:- Solid black A^s – E- A^y yellow A^y-E- Saddle pattern a^{sa}- E- Tan pattern (tri) a^ta^t E- When E has mutated to e all of the pigment in the hair is changed to yellow. The agouti alleles cannot find expression. So all of the above become yellow with the substitution of ee for E:

	E yellow A^s – ee A^y – ee A^{sa} –ee a^ta^t – ee There are two, genetically different types of yellow in the dog, these are described as A^y and e yellow, and each behaves as a recessive to black. The A^y yellow can be distinguished from the ee yellow when shaded sable, saddle pattern or tri colour is produced from a mating of two yellow individuals. A mating between two ee yellow individuals can only produce ee yellow pups, this can cause some confusion however as occasionally two A^y yellow individuals can also produce pups with no visible black hairs. The mating of ee yellow to A^y yellow would be expected to produce a litter of black pups. Brindle E^{br} can induce its characteristic brindling of black and yellow stripes, only in the yellow areas produced by the agouti alleles. This can be visualised as inducing black pigmentation, in the form of stripes or brindling upon a yellow background.
bb	In brown coloured individuals, the brown pigment is a lighter brown than that found in the black hairs, while the yellow granules are unchanged. The mutant brown gene only acts upon the brown pigment granules lightening their colour, the effect upon the eye is to change black hairs to brown.
dd	In normal hair the pigment granules are disposed regularly as it grows, in 'blue' individuals there is a reduction in the number of these granules., and they are deposited in the hair in an irregular manner, in 'fits and starts' , some areas may have a normal quota, while some may have clumps or none at all. To the eye, a black coat composed of such hairs will appear blue, and a yellow or red coat will appear fawn or cream. The difference of this pigment distribution is due to D for normal disposition and d for abnormal disposition. (D for dense d for dilute) In combination with the A^s and E genes, these can produce the following combinations. Black A^s –B –D –E

	Blue A^s–B–dd E- Brown A^s–bbD-E- Lilac A^s-bbddE- Black & tan $a^t a^t$B-D-E- Blue & tan $a^t a^t$B-ddE- Brown & tan $a^t a^t$bbD-E- Lilac & tan $a^t a^t$bbddE- Black brindle A^y-B-D-E^{br} Blue brindle A^y-B-ddE^{br} Brown brindle A^ybbD-E^{br} Lilac brindle A^y-bbddE^{br}- As the d gene effects both black/brown and yellow pigment it should be noted that the tan in the blue and lilac will be diluted to a cream colour.
M	The merle gene produces a mixture of dark and lighter, pigment deficient, areas in the coat. The darker areas being the 'normal' colour, and the lighter areas being those that are pigment deficient. The M gene is dominant to normal colouring, therefore mm would be a normal 'solid' coat, Mm would show the merle coat pattern and MM would be the dominant form, these dominant 'double' merles are often predominantly or solid white, with smaller or non existent eye balls and often also deaf and sterile. Obviously, for this reason it is extremely unwise to mate two Mm individuals together. The merle gene does not appear to have such a diluting effect on the yellow pigment as on the black pigment, so in ee yellow individuals the effect is not apparent, however in A^y shaded sables the merle pattern can been seen, the extent depending on the amount of dark shading present in the normal areas of coat.
C	**Albino alleles** The albino series fundamentally control pigment production throughout the coat. They are Full colour C Chinchilla C^{ch}

Blue eyed albino c^b
Albino c

All dogs with normal expression of coat colour have the C gene, this permits the full expression of colour. Each gene below C permits less expression of coat colour, until you get to c – the full albino. Though this would be very rare to see in a border collie.
The most common mutation in the border collie would be C^{ch} This gene affects the yellow pigment changing it to cream, so a cream from an ee red would be $C^{ch}C^{ch}ee$, the affect on the sable A^y would be to produce a paler cream coat with dark grey tips to the hairs, similar in appearance in both cases to the affect of the d diluting gene.

There are a number of polygene's that also have an affect on the coat colour. These are inherited independently and affect the depth of colour amongst other things.

Umbrous

The umbrous polygene is responsible for the variation in the density of the dark hairs seen in sables. This can range from just a few dark hairs, to an almost black, and could be responsible for the variation sometimes referred to as seal. Clarence C Little was of the opinion that the shaded sable is produced by a combination of A^y (yellow) and A^t (tri) while Roy Robinson felt it is due to the A^y (yellow) and the effect of the umbrous gene. Either or both could be correct.

Rufism

The Rufus polygene can have an effect on the intensity of the yellow genes. the action of this gene seems to be in plus direction, in that they deepen the colour, producing a richer colour , this can be seen in the variation of colour in both ee and A^y individuals and in the variations seen in the tan of tri coloured and saddle pastern animals.

WHITE PATERN

The white pattern, typically seen in border collies, as a blaze, collar, belly, legs and tip of tail is due to a white pattern gene, this is normally referred to as white spotting, and can range from a white area on the nose chest feet and tip of tail, to a predominantly white dog, that is pretty much just one big spot! The white areas form a fairly regular pattern, and is due to an absence of pigment producing cells in the skin at the root of the hairs. These genes can be described as

Self (non white) S-

Irish spotting s^i (typical classic collie markings)

Piebald spotting s^p (white extending up over the stifle and loin, extending up from the belly onto the sides and some white areas on the body

Extreme white spotting s^w a white dog with a few small coloured patches.

The expression of white is partially controlled by modifying polygenes

Ticking (Mottled)

Ticking, or freckles in the white areas are due to a ticking gene, this is believed to be a dominant gene, and the ticking can vary from a few small freckles to extensive ticking, giving an almost roan appearance.
Ticking does not have an effect on colour, so the colour of the ticking will be the same as the colour that would normally be expected at that location.
Ticking is not the same as merle, and merles can have ticking as a separate gene, confusion can occur when a predominately white dog, has some coloured areas and profuse ticking, but with such heavy ticking it would not be expected to see the normal white collar and legs, as all white areas could be expected to display heavy ticking.
