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Illustrated coat colour inheritance

about the Varieties of the Belgian Shepherd Dog

This is a work in progress. Genetics is a rapidly evolving field, and updates will be made.

Melanocytes.

How do skin, hair and iris colouring take place? In the skin, the hair and the iris there are cells that secrete pigmented granules in their environment. These cells are called **melanocytes** because they have a pigment named **melanin.** If there is an absence (or lack of activity) of melanocytes, the skin and the hair are white and the eye is red because of the presence of blood vessels. Melanocytes protect the organism against sun radiations and absorb light.

Melanocytes cells secrete:

- either ***eumelanin*** that determine the coat, nose, lips and eyes with **black** colour or **brown/liver/chocolate** colour**.**
- either ***phaeomelanin*** that determine only the coat with **yellow/red** colour that covers everything from deep red (like Irish Setters) to light cream.

In conclusion, all coat colours and patterns in dogs are created by these two pigments. As well as being found in the coat, eumelanin is present in the other parts of the dog that need colour – most notably the eyes (irises) and nose. Phaeomelanin is produced only in the coat. It does not occur in the eyes or the noses.

In July 2009, the FCI approved a standard nomenclature for coat colour. The words “fawn” and “sand” (for diluted fawn colour) are mentioned. The translation into French of “fawn with black overlay” and “sand with black overlay” are “fauve charbonné” and “sable charbonné”. “Sable”, in French, means “sand” and is used to indicate the shade of colours that come from phaeomelanin diminution of intensity.

Colour Alleles

Genes are all tied into a long strand of DNA. Each point on this strand of DNA is called a locus (plural loci). Each locus is occupied by two doses of each gene, one inherited from each parent. The variant forms of the gene are called **alleles**. Alleles are identified by letter names; the letter name may include a superscript, as in A^y. The several alleles present at a given locus are called a series.

It is only in very recent years that research in molecular genetics has begun to identify the genes responsible for colour. Until now, using DNA, alleles are known to exist at 9 genes or loci: http://homepage.usask.ca/~schmutz/alleles.html. 3 other genes are postulated to exist based on breeding data.

To make things easier, we don’t take into account the loci without influence on the colour of our Belgian Shepherd (loci: C (Colored), M (Merle), H (Harlequin), G (Progressive greying) and T (Ticked). Since all Belgian Shepherd only produce black eumelanin and not brown/liver/chocolate eumelanin, we don’t detail the B locus (mapped to chromosome 11). All the alleles at each locus are listed in order of dominance.

Before we start discussing inheritance, it might be helpful to review some of the terminology:

Homozygote characteristic
If **both alleles** on the same locus are **identical**, the character will be homozygote (homo = same, zygote = egg).

Heterozygote characteristic
If **both alleles** on the same locus are **different**, the character will be heterozygote (hetero = other).

Character produced by a dominant allele
The character produced by a dominant gene becomes evident even if that allele is found **only in one copy** and comes only from **one of the parents**.

Character produced by a recessive allele
Contrary to this, the effect from the recessive allele is hidden in the pair by its dominant allele. Its action is only apparent and phenotypically noticed when it is in both copies and so it comes from **both parents**.

When mating dogs with a dominant character and the result is a puppy with a recessive character, for example, a fawn from two blacks, not only the male but also the female is responsible. *« If the black male Groenendael Kisch-Kisch,* says Auguste Caspers*, has often given a fawn puppy Tervueren, he could not have done so without a female that is carrying the fawn recessive character hidden by her black dominant character* ".

Epistasis
Not only can alleles interact with other alleles at the same locus, but in some cases, with alleles at other loci. While the conception of dominance involves an interaction between alleles located on the same locus, epistasis (i.e. action of on gene upon another) involves an interaction between alleles of different loci.

Hypostasis
Hypostasis is the inability of an allele to produce its usual effect when coupled with another allele at another locus that is epistatic toward it. Such a gene is called hypostatic.

The alleles known to exist, using DNA, are preceded with a red dot.

A. The three loci that determine the coat colour

a) **A locus** (A from **A**gouti)

Locus A receives its name from the Agouti which is a small rodent mammal whose coat is made up of alternating light stripes (yellow) and shade stripes (black).

The Agouti gene has been mapped to chromosome 24. A pigment switch/patterning gene, it does not produce pigment, but controls where and when eumelanin and phaeomelanin based pigment are deposited in the coat, according to the area in the body. This is a pattern locus that allows for the increasing distribution of eumelanin pigment over phaeomelanin in a recessive manner.

The agouti series is composed of the following alleles:

- ***allele*** A^y ***(y from yellow).***
  The allele $\mathbf{A^y}$ restricts eumelanin pigment distribution with variable expression of dark hairs; that determines a pattern of fawn coats with black overlay (fawn hairs with darker tips with some solid black hairs intermingled amongst fawn hairs). This is the dominant allele for the Malinois, the Tervueren and the Laekenois.

Tervueren, long hair with black overlay and black mask

Malinois, short hair with black overlay and black mask

Laekenois, rough hair with traces of black overlay, mainly on the muzzle and the tail

fawn with light overlay

fawn with complete dark overlay

- ***allele a^w (w from wild)***
  a^w is the "wild-type" allele and gives wolf-grey colouring. The colour is characterized by a pattern of banded hairs, typically black at the tip, with a light central band, and a dark base. The amount of light and dark on the hair varies, distributing darker shading on the back. The colour appears grey at a slight distance. The Norwegian Elkhound is one of the breeds of dog with banded hair. **This allele is not associated with the Belgian Shepherd Dog gene pool.**

- ***allèle a^t (t from tan points) (tan = fawn)***
  This allele gives the pattern **black with fawn markings** (« black and tan » in traditional nomenclatures). It produces eumelanin in central areas and phaeomelanin in the extremities. The dog is predominantly black, with tan markings on the muzzle, over the eyes, on the chest, legs, and under the tail. The Dobermann, the Rottweiler or the Beauceron are usual examples of the black with fawn markings. It is only dominant over recessive black. **This allele is not associated with the Belgian Shepherd Dog gene pool.**

black with fawn symmetrical markings (= Black & Tan)

fawn with mantle coat (the genetic formula of this dog is "$\mathbf{A^y}a^t$")

- allèle **a** (recessive black)
  This allele gives uniform (or solid) black coat with no phaeomelanin in the coat at all, except for white markings. This allele causes no modification to the production of eumelanin. The dog needs to be homozygous aa in order to express the black coat. Some Groenendael are born from Tervueren parents. This proves the existence of a recessive black allele.

Black short hair

For Belgian Shepherd dogs, the recessive black exists since the origin of the breed but not more recognized since 1974. Recessive black seems confined to a few herding breeds (like Shetland Sheepdog). The black recessive allele is the one responsible for the black German Shepherd dog. Many Schipperkes are recessive black.

b) **K locus** (K - last letter of Blac**K**)

The locus K series has been mapped to chromosome 16. This locus has been referred to as the “dominant black” locus. For this locus, there are three alleles:

- allele $\mathbf{K^B}$ - it causes a one-colour **black** coat (solid black)

The hair is black from root to end. This is the allele that dominates the group and produces only eumelanin which it distributes to all the parts of the body without any trace of another colour (except a little white). $\mathbf{K^B}$ is epistatic over the A locus. In other words, any genes on the A locus will not be visible. Most of the Groenendael are $\mathbf{K^B K^B}$ or $\mathbf{K^B} k^y$.

Groenendael, black long hair

allele $\mathbf{k^{br}}$ (**br**indle)

Black stripes on a phaeomelanin background. k^{br} is dominant over k, so a dog only needs one k^{br} in order to be brindle. Black stripes are epistatic over the allele $\mathbf{A^y}$. All the brindles dogs are $\mathbf{k^{br}/k^{br}}$ or $\mathbf{k^{br}}/k^y$. Actually has become fairly rare in the Belgian Shepherd Dogs (and not more recognized since 1974), although it sometimes still appears.

Having a common origin with our Belgian Shepherd, we find brindle in the Dutch Shepherd in the three varieties (= coat texture by the Dutch Shepherd Dog): long hair, short hair and rough hair. The two colours are the fawn brindle (background fawn $\mathbf{A^y}$) and the sable brindle (background sand - see locus I).

Dutch Shepherd - short hair - fawn brindle

- allele k^y
  A k^yk^y dog will express whichever alleles are on its A locus. All the fawn dogs are k^yk^y.

c) E locus (E from **E**xtension)

The locus E series has been mapped to chromosome 5. For this locus, there are three known alleles:

- allele $\mathbf{E^m}$ (m from **m**ask)

  Allele $\mathbf{E^m}$, causes the black mask. The mask can vary greatly, covering anything from just the end of the muzzle to the whole of he muzzle, eyebrows and ears. Black mask may also cause black hairs on the chest and/or back and tail. $\mathbf{E^m}$ is the dominant allele of the E series, so a dog needs only one $\mathbf{E^m}$ allele to have a mask, regardless of which other E locus allele it carries.

- For the Belgian Shepherd, the possible combinations are: $\mathbf{E^mE^m}$ or $\mathbf{E^mE}$.

black mask

without mask

A black mask is not visible on a black dog. This is why Tervueren from Groenendael without mask (a priori, impossible to know) inherit a light face or lack of mask. Tervueren from Groenendael parents often do not carry the full masking. For the Malinois and the Tervueren, the mask has become obligatory (standard of 1978).

- allele **EG** (G from Grizzle)
  EG causes the phenotype « grizzle » by the Saluki and « domino » by the Afghan Hound. The allele E^G will express only in presence of alleles $a^t a^t$.

- allele **E**
  E allows for he normal production of eumelanin or phaeomelanin pigment. Usually written with a capital letter, is recessive to $\mathbf{E^m}$. This allele does not modify the colours controlled by the series of locus A.

- allele **e**
  Only “phaeomelanin” produced in hair, except for

white markings. If a dog has an **ee** pair present, then it will stop the production of eumelanin and produce only the phaeomelanin pigment. This recessive allele is epistatic over almost everything else. It is therefore impossible to have any black in its coat. However, the colour of the eyes, nose and lips are unaffected.

B. The two loci that could affect the colour intensity

a) **locus D** (D from **D**ilution)
The locus D series has been mapped to chromosome 25. For this locus, there are two alleles:

- allele **D**
  Normal pigmentation. No dilution. All the varieties of the Belgian Shepherds are **DD**.

- allele d: d is recessive. If a dog has an pair dd present, then it produces dilution as follow: black becomes bleu (1); brown becomes beige; fawn becomes sable (2). **This allele is not associated with the Belgian Shepherd Dog gene pool.**


« bleu-grey »


« black »

(1) The term ‘blue’ means colour ‘slate blue’ or ‘grey-blue’. The nose and the palate are blue-black. It dilutes the colour of the eyes (smoky eyes). The coats diluted by dd, are predisposed to a certain form of alopecia (loss of hair).

(2) ‘**dd**’ dilutes phaeomelanin subtly. The action of ‘**dd**’ on phaeomelanin flattens the colour or makes it less brilliant (flattening or dulling).

b) **I locus** (I from **I**ntense)

Recent studies have found that the **C** (for Chincilla) series is not responsible for the dilution of canine coat colour. It is replaced by the “**I** locus” that only affects the intensity of the phaeomelanin pigment.

This allele is not actually known – but a hypothesis.

For this locus, there are two alleles:

- allele **I**
  Fawn, not diminution of intensity.

- allele **i**
  This recessive allele decreases the phaeomelanin pigment intensity. Co-dominant, so i/i dogs are paler than I/i dogs.

  By the Belgian Shepherd, this is the case for the Tervueren sand incorrectly called “*grey*” in the standard (black overlay on a pale base coat gives the illusion of “*grey*” - the dominant allele G of the Progressive Graying is not present in the BSD). Frequent by the long hair, he is rare by the short hair.

Long hair sand with black overlay

C. White markings

Any of the above colours and patterns can be accompanied by white markings that are present from birth. White is not a colour in itself, but an absence of pigment. It is a lack of both eumelanin and phaeomelanine. The presence of white markings is very frequent amongst all the Belgian Shepherd varieties, and it sometimes shows some hairs on the chest and on the toes. Many breeds tolerate a white marking on the chest or on the toes.
For the Belgian Shepherd, the standard stipulate that white marking on the chest forming tie and white on the feet going beyond the toes are faults. Too widespread white markings on the chest especially if they reach as far as neck and white on feet going more than halfway up the front or he back pasterns and forming socks are disqualifying faults.

About white chest spots, the website of Dr. Sheila Schmutz (http://homepage.usask.ca/~schmutz/dogspots.html) gives us the following information:

Because melanocytes migrate down from the spinal column during embryogenesis, not all animals complete this process by birth or thereafter. In dogs, it is therefore not uncommon to see white toes on an otherwise black or red dog. This is probably more a random event than the result of a specific allele. Another common "white spot" on dogs occurs on the chest. This must again be a site where melanocyte migration occurs very late in fetal development and a cold or other developmental delay prevents the completion of melanocyte migration.


White markings on forechest

It may be that the rate of melanocyte migration is itself inherited. Some standards mention this as a fault. This is likely simply incomplete pigment migration in the particular individual, and not an inherited trait.

S locus (Spotting) = (MITF)

Note that this gene is certainly involved in piebald spotting, but may or may not be involved in Irish spotting.

- allele S = Solid, or more correctly, minimal to no white markings
- allele s = piebald or random spotting, also called particolor.

Instructional chart - Belgian Shepherd Dog - coat colours (1)

Phenotype

Genotype

K locus

$K^B K^B$; $K^B k^{br}$, $K^B k^y$

(dominant) black

Dutch Shepherd Dog

$k^{br}k^{br}$, $k^{br}k^y$

brindle

$k^y k^y$

neutral

Does not belong to the patrimony of the breed

B locus

BB

black eumelanin

nose > black

bb

brown eumelanin

nose > brown

A locus

$A^y A^y$, $A^y a$

black

$a^w a^w$

black

$a^t a^t$

black

aa

black

3 coat patterns

black > Groenendael

fawn with black overlay & black mask > Tervueren

sand with black overlay & black mask > Tervueren sand

A locus

$A^y A^y$, $A^y a$

fawn with black overlay

$a^w a^w$

fawn with agouti mantle (banded hairs)

$a^t a^t$

black with fawn markings & fawn with mantle coat

aa

(recessive) black

E locus

$E^m E^m$, $E^m E$

black mask

EE

neutral

ee

only fawn produced in hair

D locus

DD

no dilution of black

dd

black diluted > grey-blue

nose > grey-blue; iris > blue

I locus (2)

II

no reduction of intensity

Ii is co-dominant

ii

fawn > sand

(1) In accordance with the FCI standardized nomenclature of coat colours in dogs.

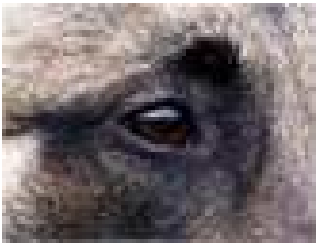
(2) Affects only the fawn (phaeomelanin) pigment in the coat. Gene not yet identified in dogs, using DNA.

JMV, September 2014.

D. Eye and Extremities Colour.

Colour influence can act on different parts of the eye, on the iris (it is the coloured part) and on what we commonly call the white part of the eye. The dog's pupil aperture is round.

It is the great number of melanocytes in the conjunctive stroma of the iris, and in particular on the anterior surface, which is responsible for the genetic differences of the eye colour. If there are many melanocytes the iris appears brownish black. If there is absence of melanocytes, the iris is blue.



dark iris

yellow iris

The yellow eye is a defect in most breeds. It is classified as light eye or bird of prey eye. In the Saarloos, we prefer yellow eyes (but this is a wolf-dog).

The dominance order of the three alleles in the locus **Ir** (=Iris) (This is not actually known – but a hypothesis) is as follows:

- **Ir** = dark iris (dark brown)
- **ir^{m}** = hazel iris (shade called intermediate)
- **ir^{y}** = yellow iris.

Among these three alleles, the dominance is not complete and, as a consequence, the various possible combinations belong to the different shades.

The colour of the iris is transmitted as a whole, independently of the coat colour. Genes dd and bb can dilute the iris. A non-pigmented iris gives a blue shade. In general, it is believed that it is transmitted in a recessive way.


blue eyes

Nose colour (blue, brown, beige or reddish) is often associated with coat colours. For the Belgian Shepherd, the question of extremities is relatively simple. Whatever colour the coat is, the nose, the lips, the eyelids, the upper eyelashes, the ears' rim, the ano-vulvar mucosa, the scrotum and the nails are normally black.

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Coat texture inheritance

A. Hair textures

The Belgian Shepherd dog presents three coat textures:

Short hair
Long hair
Rough hair

The first two ones, short hair and long hair, are smooth hair. The third one, the rough is of a different texture. The length and the texture are important features that determine final visual effect. In fact, all hair types do not « receive » the colour in the same way. This variation with regards to pigmentation explains the different coat tones observed in the body.
Different environmental factors such as the sun, the cold, or licking can influence colour expression as does moulting. The age is also an important factor that modifies the expression.

In order to explain all these variations, genetically speaking, it is necessary to refer to the principal alleles whose symbols are:

1. The gene that determine the length of the hair

For this gene FGF5 located on chromosome 32 or locus **L**, in order of dominance, the two alleles that determine the length of the hair are:

L = short hair

l = long hair

Therefore, the three possibilities are:

homozygote **LL** = short hair
hétérozygote **L**l = short hair carrier of the long hair allel
homozygote ll = long hair

2. The gene that determines the rough hair and presence of facial furnishings (e.g. beard, moustache, eyebrows)

For this gene RSPO2 located on chromosome 13 or locus **Wh** (from ***wire hair***), in order of dominance, the two alleles are:

Wh^{w} = rough hair
wh = non-wire hair

Therefore, the possibilities are:
homozygote **Wh^{w}Wh^{w}** = rough hair with facial furnishings
hétérozygote **Wh^{w}**wh = rough hair with facial furnishings carrier of the wh allel
homozygote whwh = non-wire hair

The dominant allel **Wh^{w} is** epistatic (very rare case of incomplete dominance exists) over the **L** locus. The recessive allel wh express the alleles of the **L** locus.

For the Belgian Shepherd Dog, the genetic formulas are the following:

- for long hair: ll, $w^{h}w^{h}$
- for short hair: **LL** or **L**l, $w^{h}w^{h}$
- for rough hair: **LL** or **L**l, **W^{h}W^{h}** or **W^{h}**w^{h}

B. Dominance rules.

1. **Long hair**

As in other dog breeds, short hair can produce long hair but long hair can never produce short hair. It means that long hair is recessive. Two long-haired dogs will always produce only long-haired dogs. In the same way, long hair never produces rough hair. As a consequence, long hair is completely homozygote with regards to hair length.

2. **Short hair**

For short hair, it is less simple. In fact, as short hair **L** is dominant over long hair l, three cases can be observed:

a) Mating of two short hair homozygotes (**LL** + **LL**).
In this case, we can only expect short-haired dogs.

b) Mating of a short hair homozygote with a short hair heterozygote (**LL** + **L**l).

All the results will be short hair, but only half of them will be homozygote as show by the following Punnet's square.

x	**L**	**L**
L	**LL**	**LL**
l	**L**l	**L**l

c) Mating of two short-haired heterozygotes (**L**l + **L**l).

x	**L**	l
L	**LL**	**L**l
l	**L**l	ll

From four products, one will be short-haired homozygote **LL** and another one long-haired homozygote ll, and they will reproduce accurately. The other two will be short-haired heterozygote **L**l.

This is why a Malinois sometimes produces a Tervueren. He carries the allele l for long hair, which he sometimes received from distant predecessors and when by chance he is crossbred with a partner who has the same genetic make-over, the long hair allele finds its equal and produces one Tervueren out of four in a litter, rarely two.

At this point, we have to mention that if short hair dominance on long hair is totally accepted for the Belgian shepherd, it usually happens that short hair dominates long hair only imperfectly, that is, the hair is as short as in the true Malinois or as long as in the true Tervueren. Semi-long hair is obtained through intermediate dominance which requires a selection carried along several generations (in general three) before finding again the pure variety in any sense.

As hair length depends not only on one pair of alleles but on several pairs of little alleles, we can only confirm the « synthesis effect », the general result, but we are not capable of separating the individual responsibilities of a pair of alleles in particular. The same happens with regards to height of the withers, weight, growth speed, tail length, etc. This action that involves numerous modifying genes is called “quantitative inheritance”.

In other words, quantitative genetics studies measurable characters. These are determined by a great number of genes, the polygenes which are neither dominant nor recessive.

Essentially, that selection is based on morphological beauty and on capabilities, the breeder or the producer has to deal with quantitative characters. Qualitative or Mendelian genetics take an interest on non measurable characters of a number of reduced genes. Qualitative characters are defined by a quality (coat colour, upright or fallen ears, length of hair, texture of hair, etc.)

3. **Rough hair**

Rough hair is epistatic over short and long hair. Epistasis involves an overlap between alleles of different loci. But this action is not always complete. Short-haired may appear in a litter with rough-haired and the opposite also. It can still be observed, as proven in a recent case of the fawn rough hair Laekenois Yankee du Hameau Saint-Blaise (L.O.S.H. 847363) born on 5 February 1999 in a short hair Malinois litter. Undoubtedly, it has rough hair, shorter and less bushy eyebrows and furnishings on the muzzle.
We can read from the following educational texts (published in *L'Aboi* on 1 September 1946):

A good breeding animal mated with different rough-haired bitches gives birth to five litters always of good rough-haired puppies. In a sixth litter there are mostly short-haired dogs.
Such facts can not be considered as atavism, it is only a very common consequence of Mendel's law. Let us suppose that in one of the mentioned litters of good rough hair, there is still a newly born short-haired puppy. The breeder will be determined to eliminate this puppy. But it is just this short haired puppy who will be surely able to transmit rough hair through inheritance. Only a breeding experience will confirm it, but to assess the importance of the breeding parents, similar cases are really valuable. Therefore, when registering in a studbook, it is advisable to register not only the "good"

products, because it is important to know the breeding result, and therefore the registration of total carriers has to be taken into account.

C. The undercoat

In the Belgian Shepherd, working dog, we can observe the presence of an undercoat which serves as protection against the cold and hair which protects against rain. In all the varieties the hair must always be dense, close-fitting and of good texture, with the woolly undercoat forming an excellent protective covering.

Even though the rule for our Belgian Shepherd states that all of them must have an undercoat as protection from bad weathers, it is a fact that in general our Groenendael and Tervueren are really hairy, the Malinois has less hair and rough-haired dogs often have almost nothing. The absence of undercoat is dominant on normal undercoat. This can sometimes explain less undercoat density in the Tervueren coming from Malinois.