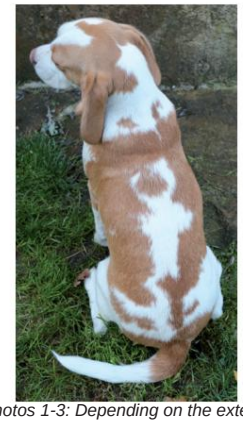
A NEWLY DISCOVERED "OLD" COLOR: DOMINO AKA PIED IN THE BEAGLE

All dog colors are composed of two types of pigments: eumelanin (black) and pheomelanin (yellowish, reddish or cream-colored). Different mutations at different gene loci result in different patterns and color shades.



Photos 1-3: Depending on the extent of white spotting, more or less of the base color can be seen (the left dog has a recessive red base color, the middle and right dogs have a hare-pied base color). Photos: Udo Jarosch (1 and 3), Oliver Niehoff (2)

White spotting occurs when the pigment cells are stopped early on their migration from the inside of the body into the skin during the embryonic period. This means that the white spotted areas in the dog's coat are unpigmented (see photos 1, 2 and 3). In other words, a so-called tricolor dog is genetically black and tan, but in some areas the pigment cells have not reached the hair follicle cells. For our further considerations we ignore the white piebald, because now it is about the basic color (i.e. the distribution of eumelanin and pheomelanin).

The following gene loci are particularly relevant for the basic color: K locus, A locus and the complex of E locus, eA locus, EM locus (and depending on the breed, other gene loci such as EG locus and EH Lo kiss).

Here it is decided whether a dog can only store phaeomelanin in the hair or also eumelanin, and whether the eumelanin is suppressed to a greater or lesser extent.

You can imagine the basic color of a dog like a painting on a canvas: The genotype of the A locus represents the first application of color. There are four different alleles, each of which produces different combinations of eumelanin and phaeomelanin.

These alleles are shown in Table 1.

The base color black and tan can be modified to saddle tan. The tan marks continue to expand over the course of the first year of life, so that in the adult dog the

Eumelanin only extends like a saddle to the upper part of the trunk.
Typical breeds with saddle tan are the Beagle, the Yorkshire Terrier, the Blood dog, the Airedale Terrier and the German Shepherd. Dogs with saddle tan have the genotype at/ on the A locus at.

	genotype	phenotype	example
Descending Dominanz episode	ay/-	Dominant yellow (or red or cream), more or less pronounced dark hair tips.	
	aw/-	wild colors	
	at/-	Saddle tan	
		Black and tan	
	a/a	recessive black	

Table 1 (Photos: Anna Laukner)

The K locus represents the second color application. The genetic variant KB (dominant black) is located here. If a dog has at least one KB allele (i.e. the genotype KB/KB or KB/ky), a uniform layer is formed over the “lower” color layer of the A locus

Eumelanin (black pigment) applied. The genotype ky/ky causes no change (to stay with the picture, you can think of this as a layer of clear varnish over the first application of paint through the A locus).

The flow occupies a special position. The flow factor causes the color to alternate between KB and ky.

So in our painting here, stripes of the eumelanin color would be applied over the first layer of the A locus.
Brindle dogs have the KB/ky genotype at the K locus and are therefore genetically indistinguishable from heterogeneous dominant black dogs. The flow factor is inherited independently of the A locus. Each expression of genotypes at the A locus therefore exists in a brindle and in a non-brindle variety, whereby black stripes can only be seen in body areas where pheomelanin is present (e.g. the tan marks in Black and -tan).

There is no dominant black on the Beagle. Also brindle does not occur in the purebred Beagle. Beagles always have the genotype ky/ky at the K locus.

Finally, the third layer represents the alleles of the E locus complex.

So far, the variants have been identified that can be found in Table 2 (see below).

Depending on the genotypes at the A and K locus, the variant eA, which was only recently identified through molecular genetics, causes the changes in the basic color that can be seen in Table 3 (next page).

Eumelanin is black in the "wild form", but can take on a blue-grey color due to the Dilutions variants (d1, d2, d3). Black eumelanin is modified to brown by the brown alleles le (bc, bd, bs, b4 and be). If both dilution and brown meet, the result is diluted brown, so-called lilac.

Pheomelanin can take on different color intensities (from red to yellow to cream - in the Beagle these three color intensities are called red, tan and lemon)).

Depending on the eumelanin color (black, Blue, brown or lilac) and Phäomela nin intensity are thus a multitude of other variations of the basic color possible.

"Domino" aka "Pied" in the Beagle

The term "Domino" for a specific marking pattern comes from the Afghan Hound breed, since this marking was first described in a male dog named Domino. In Afghans and some other breeds, this pattern is caused by the genetic variant EG at the EG locus in combination with a black-and-tan base colour.

Allele EG has an analogous effect to variant eA, which was identified only recently. The allele eA also causes a displacement of eumelanin and leads, for example, to the Siberian Husky typical "husky markings" (also in combination with a black and tan base colour). eA also occurs in the Chihuahua and, in combination with the basic color black and tan, creates the same markings as in the husky, so that the term "husky colors" has become common for the Chihuahua for dogs marked in this way. Since the tricolor Beagle has almost no black and tan base color any more, only saddle tan, the eumelanin is only suppressed in the saddle area. At the head is already

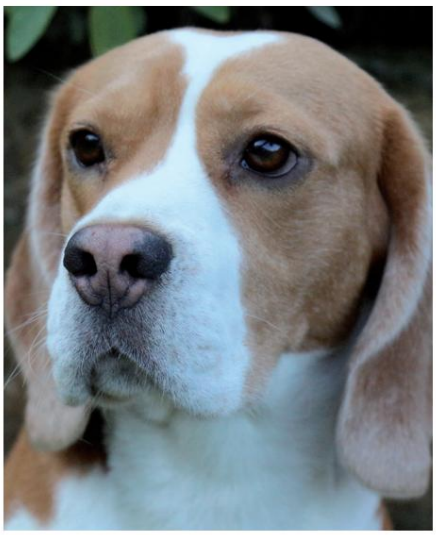


Photo 4. Photo: Jarosch

Due to the saddle tan, there is no longer any eumelain that could be pushed back into a typical "husky mask". Beagles with the genotype at/
at with eA/e or eA/eA does not show a "husky pattern" due to the saddle tan, but a hare-pied pattern.

Another typical feature of the Domino factor is a partial one

genetic variant	Effect	genetic test
EM	Stores eumelanin in the area of fan ge (“black mask factor”)	EM locus
N	Does not cause any change (“wild type”) One	assumes the genotype N/N if all testable genes location of the E complex no variant EM, eA, eg, eh, e, e2 or e3 was detected. However, it is likely that there are other variants that are not currently identified (as of November 2020)
eA (eg, eh)	Causes a suppression of Eu melanin, the resulting color or Drawing depends on the genotype at the A and K locus (see Table 3).	eA locus (EG locus) (EH locus)
e (e2, e3)	No eumelanin can be stored in the hair at all.	E locus (E locus e2, so far only detected in the Australian Cattle Dog; e3 so far only detected in the Husky)

Table 2

Right: genotype at the K locus Bottom: genotype at the A locus	KB/-	ky/ky
ay/-	Eumelanin is suppressed, the hair base is therefore lighter, the overall impression of a dominant black dog is mottled greyish yellow.	Dark ends of hair are pushed back, the dog appears uniformly reddish-yellow, yellow or cream.
aw/-	Eumelanin is suppressed, the hair base is therefore lighter, the overall impression of a dominant black dog is mottled greyish yellow.	The dog has banded single hairs on the rump with a spread light hair base. The areas of tan marks are expanded, forming a typical domino mask. The nose may have a central lightened stripe.
at/- (black and tan)	Eumelanin is suppressed, so the hair base is lighter, the overall impression of a dominant black dog is grey.	The dog has dark single hairs on the body with a light hair base. The areas of tan marks are extended and form a typical domino mask. The nose may have a central lightened stripe.
at/- (saddle tan)	Eumelanin is suppressed, so the base of the hair is lightened, the overall appearance of a dominant black dog is gray (legs, chest and face may be lighter than the saddle area).	In the area of the saddle, the dog shows single dark hairs with a very extensive light-colored hair base. (In the case of the Beagle, this marking is called "hare-pied"). The nose may have a central lightened stripe.
a/a		Eumelanin is pushed back in the area of the tan markings, the base of the hair on the trunk is also pushed back a little. Visually, such dogs resemble black-and-tan or dark fawn-colored dogs.

changing nose. This means a nose in which the pigment is lightened in the middle (see photo 4).

In the case of the Beagle, the following genetic variants of the eA and E locus relevant:

N	Eumelanin can be expressed at the A locus according to the genotype (corresponds to at/at tricolor).
eA	The eumelanin is pushed back a little (corresponds to Hare Pied). A typical feature of hare pied may be partial central hypopigmentation of the nose.
e	Eumelanin cannot be expressed (corresponds to bicolor)

So if a beagle has the genotype e/e, its base color is red, tan or lemon. It is genetically what is known as the recessive red, yellow or cream. One such dog is **Bicolor.**

If, on the other hand, he has one or two alleles N, his alleles of the A locus will be off shaped. On the A locus, Beagles are most likely homozygous for the allele at (black-and-tan or saddle-tan), this corresponds to **tricolor.**

The alleles of the E complex and the A locus are inherited independently. Since the Beagle is most likely homozygous for the allele at on the A locus, the A locus is not considered further here.

A distinction is made between hare-pied, badger-pied and lemon-pied beagles. About 95% of all pied colored Beagles show Hare Pied. Badger pi ed is characterized by lightened hair tips in the saddle area. To what extent Badger Pied differs genetically from Hare Pied is not yet known. Lemon pieds are extremely rare; there are hardly any dark hairs left in the area of the saddle. It is not known how their genetic basis differs from that of Hare Pieds.

Photo 5: Tricolor (Laukner)

Photo 6: Hare-Pied (Jarosch)

Photo 7: Bicolor (Maier-Fidalek)

So the following are possible Genotypes:

Table 4:

genotype	phenotype
N/N	Pure tricolor
N/A	Tricolor (carries pied)
n/n	Tricolor (carries bicolor)
eA/eA	Homozygous Pied
eA/e	Pied (wearing bicolor)
e/e	Pure Bicolor

Crossing tables of the parents can be created using these genotypes. If the genotypes of the parents are known, one can see which colors can fall into this litter and which cannot.

It can be seen from the table above that a bicolor cannot carry the necessary alleles of the E locus complex for hare-pied (eA) and tricolor (N).

The following crossing options are available it:

Table 5: Tricolor x tricolor gives 100% tricolor.

N/N x N/NN		N
N	N/N	N/N
N	N/N	N/N

Table 6: Tricolor (pied carrier) x tricolor gives 100% tricolor (each puppy has a 50% chance of being a pied carrier).

I/eO x N/NN		N
N	N/N	N/N
eA	N/A	N/A

Table 7: Tricolor (pied carrier) x tricolor (pied carrier) gives each pup a 25% chance of being a homozygous tricolor, a 50% chance of being tricolor (pied carrier) and a 25% chance of being pied be.

N/eA x E/ eA	N	eA
N	N/N	N/A
eA	N/eA eA/eA	

Table 8: Tricolor x bicolor equals 100% tricolor (all are bicolor wearers).

N/N xe/ee		e
N	n/n	n/n
N	n/n	n/n

Table 9: Tricolor (pied carrier) x bicolor gives each pup a 50% chance of being tricolor (bicolor carrier) and a 50% chance of being pied (bicolor carrier).

N/eA xe/ee		e
N	n/n	n/n
eA	eA/e	eA/e

Table 10: Pied x Bicolor equals 100% Pied (all are bicolor wearers).

eA/eA x eA/eA e		e
eA	eA/e	eA/e
eA	eA/e	eA/e

Table 11: Pied (bicolor carrier) x bicolor gives each pup a 50% chance of being pied (bicolor carrier) and a 50% chance of being bicolor.

eA/exe/ee		e
eA	eA/e	eA/e
e	e/e	e/e

Table 12: Bicolor x Bicolor equals 100% Bicolor.

e/exe/e	e	e
e	e/e	e/e
e	e/e	e/e

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