



1 - Black



2 -Gold (Light)



3 - Gold



4 - Gold (Rich Red)



5 - Black and Tan (Light gold)



6 - Black and Tan



7 - Black and Tan (Rich Red)



8 - Blue/Grey



9 - Blue/Grey and Tan



10 - Chocolate/Brown



11 - Chocolate/Brown and Tan



12 - Gold Dilute

Coat Color Genetics in Tibetan Mastiffs

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*"Mere color, unspoiled by meaning, and unallied with definite form,
can speak to the soul in a thousand different ways."*

Author: Oscar Wilde



Have you ever been to a show that sports Tibetan Mastiffs appearing in a variety of colors and asked yourself where these colors come from, or how a breeder can predict what colors will appear in a given litter? Well, hopefully, this article and some color photos will begin to shed some light on this colorful subject. Before we get to the fun stuff, however, we will have to review a little genetics.

Most vertebrates, including dogs, have two copies of every chromosome (except sex chromosomes). Since genes make up the chromosomes, this means that there are two copies of every gene present in every cell of every dog. However, the two copies do not have to be identical. They can be different versions (alleles) of the same gene. For example one could be an allele for Black coat and one for Gold coat. Hmm, this must be a Black and Gold spotted dog! No, because some alleles are dominant to others. Since Black is dominant to Gold, this dog will appear as solid Black.

Although the above example shows a simple relationship between two alleles located at one gene locus, coat color in dogs is ultimately quite complicated and not fully understood. Many genes, some of which have more than two allele choices, control the variety of colors and patterns seen in canine coat color. The many different genes interact by intricate rules, to create the final coat.

For the sake of discussion, each gene locus and all the alleles related to coat color are given alphabetical designations. Dominant alleles are shown in capital letters and recessive alleles are given in lower case letters. For the purposes of this article, only those loci and alleles seen in the Tibetan Mastiff will be discussed. Given that this breed is so colorful, that happens to be most of them.

Okay, back to our example. The gene locus involved in the example is the Agouti, or **A** locus. Three alleles of this gene are found in the Tibetan Mastiff: the allele for Black, designated **A**; the allele for Gold **Ay**; and the allele for Black and Tan, designated **at**. These alleles are given here in order of dominance, where Black is the most dominant and Black and Tan is the most recessive. Although there are three different alleles that are found in the Tibetan Mastiff breed, any given dog can only carry one or two of the three; two copies of the same allele, or two different alleles. (There is some new evidence that the dominant black gene may be at another locus, thus not an allele in this series. If so this would change some of the expectations from any breeding with a dog carrying dominant black. The relationships between **Ay** and **at** would be unaffected. However, the presence of the dominant black gene, now given another name at a new locus would mask any differences at the **Ay/at** locus and just make the dogs look black.)

Why two? Well, every dog has two sets of chromosomes (they get one set from each parent) and each set of chromosomes contains one copy of each gene. Hence every dog has two copies of each gene, one from each parent. In our example, the dog is **A/Ay**. This is written so that we see both alleles, Black and Gold, with the most dominant allele, Black, written first. Remember, this dog appears Black, but so would a dog that is **A/A** or **A/at**. Thus, if a dog appears Black (image 1), we may have no idea what the second allele is until we breed that dog and find out what is passed to the offspring. Likewise, dogs that are **Ay/Ay** or **Ay/at** will appear Gold (image 3), as Gold is dominant to Black and Tan. Only when a dog is **at/at** does it appear Black and Tan (image 6).

What we call "Gold" actually ranges in color from Light Gold (image 2) to rich Reddish Gold (image 4), with the precise shade being determined by modifying genes. We do not know the identity or the mode of action of these modifying genes, but we can describe a model of how they are inherited based upon what we see when we breed the dogs. They act like, well, a collection of checkers (lets say red and white checkers). For example, if a dog has mostly red checkers in its collection, it will appear Reddish Gold. If a dog has mostly white checkers, it will appear Light Gold, and if a dog has a balance of red and white checkers, it will appear Gold. Each puppy receives a handful of checkers from each parent, so Red Gold puppies are unlikely to come from two Light Gold parents and vice versa. These same genes work to determine the shade of tan on Black and Tan dogs. The dogs shown in images 5, 6, and 7, are all Black and Tan (determined by the **A** locus), but the tan varies considerably. So, as in the example above, Black and Red-Tan puppies are unlikely to come from parents that are Light Gold and/or Black and -Tan (Light Gold Tan).

So far, the discussion has focused solely on dogs that have what is called full pigmentation. That is, their genetic makeup allows them to develop all colors to their fullest extent: pitch blacks and bright red-golds, golds, and light golds, all with black noses. There are some genes whose effect is to dilute the pigmentation. In other words, whatever **A** locus alleles the dog has will be expressed as expected, but the pigmentation will be diluted, even in the eyes and on the nose leather. In the Tibetan Mastiff, two different genes cause dilution effects. Each of these genes has only a dominant and one recessive allele.

The first of these genes is the Dilute, or **D** locus. The dominant allele **D** is necessary for full pigmentation. The effect of the recessive allele **d** when homozygous (two identical alleles in the same dog), is to dilute Black coat and nose and eye pigment toward Blue/Grey. Although this gene is completely separate from the **A** locus, there is an interaction that produces the final color of the dog. So, if a dog is **A/-, d/d** (where the dash represents any allele choice) it will appear Blue/Grey (image 8). If a dog is **at/at, d/d** then it will appear Blue/Gray and Tan (image 9).

The second gene that serves to dilute coat and pigment is the Brown, or **B** locus. This gene works the same way as the **D** locus. That is, when both copies of the **B** gene are recessive (**b**), in this case the Black coloration fades to Chocolate/Brown. Again, this gene is completely separate from the **A** locus, but the interaction of the two loci determines the final color of the dog. Thus, if a dog is **A/-, b/b** it will appear Chocolate/Brown (image 10). If a dog is **at/at, b/b** it will appear Chocolate/Brown and Tan (image 11). Again, one dominant allele **B** is necessary in any dog

to get the normal black pigment. Any dog with black nose leather is not homozygous for any dilute gene. At least one dominant allele of both of these genes is required for the full black nose coloration.

Finally, a dog can receive a pair of recessive alleles at both the *D* and *B* loci. Although, for the moment, and to our best knowledge, the Western world has not produced a Tibetan Mastiff with this genetic makeup, it is thought that one would appear somewhat like a Weimaraner in color. We are currently referring to this color as Double Dilute. Of course, this would dilute the black coat and pigment in Black and Tan dogs as well, so there could be dogs that can appear as Double Dilute and Tan (*at/at, b/b, d/d*).

Gold dogs with dilution are a little more complicated. They still appear gold, but appear more washed-out than normal, and their nose leather may appear Blue/Grey, Chocolate/Brown, or some muddy combination of the two. These dogs are *Ay/-, d/d* (where the dash represents either *Ay* or *at*), *Ay/-, b/b*, or *Ay/-, b/b, d/d*. The authors are referring to ALL of these colors as Gold Dilute (image 12), as determining exactly which dilutions are at work may be difficult. All of the dogs that are homozygous for either or both of the dilute genes will have nose leather that is obviously lighter than the normal black color. It may be tan or light grey or some other combination of the two.

So far, so good, and the above mechanisms are well established in the dog world, but what follows is not. There is one type of Black Tibetan Mastiff that is turning up more frequently in American litters. Breedings of two Black and Tan dogs (*at/at* mated with *at/at*) are yielding puppies that are all Black. This is completely unexpected! Since the allele for Black, *A*, is dominant to Black and Tan, *at*, neither of the parents could be carrying Black *A*, or that dog would appear Black itself. So, some other explanation must exist for these dogs to appear solid Black. Breeders have found that when bred, some of these dogs produce as if they were Black and Tan, not as Black. So, genetically, they are just what one would expect, *at/at*. One explanation for the conundrum would be that there is a recessive modifying gene present that completely masks the tan, yielding a Black dog. In some cases, a few tan hairs develop between the toes or under the tail, and over time may become more traditional in patterning. However, at birth, these Black pups are indistinguishable from the true Black colored puppies (*A/-*). We are now referring to these as recessive blacks. A recessive Black female is seen in image 13. It is also clear that this recessive masking gene can mask all the gold on genetically gold TM as well. The only way to tell whether a recessive black TM is really a masked black and tan or a masked gold is to breed it and see what you get. These recessive black dogs can also appear in matings of Gold dogs and the explanation is exactly the same. Although we do not know of any cases, we assume this masking gene would also affect dogs carrying the two dilute genes for blue and chocolate, thus converting genetically blue and tan and chocolate and tan dogs into blues and chocolates respectively. Breeding tests have conclusively demonstrated that this recessive black gene is not an allele in the *Ay,at* series.

For clarity, and to move us to the fun part, a couple of genetic word definitions will help; the first is phenotype. This refers to what is seen. A Tibetan Mastiff's color phenotype may be Black, for example, or Black and Tan. The second word is genotype, which describes the genetic recipe (our alphabet soup) carried by that dog. For example, a Tibetan Mastiff genotype may be *A/at* (which may appear as a Black phenotype), or *at/at* (which may appear as a Black and Tan phenotype).

Oh yeah, here is the fun part. Ready?

Let's look at an illustration using dogs that are phenotypically Black (not including the recessive blacks), that is, these are Black dogs with no tan points, although they may have markings like white on the chest (to be discussed in a future article). Keep in mind that Black dogs must have at least one copy of the dominant allele *A*. Now for this dog to be full-pigmented Black, it must also have at least one dominant allele *D* and at least one dominant allele *B*. If we do not know any more than how the dog appears, the genotype of this dog can then be written, *A/-, B/-, D/-* (as alleles represented by the dashes cannot change the phenotype -- how the dog appears). So, we cannot tell by looking at the dog whether it is carrying any or all of the recessive alleles. Only breeding will reveal whether this dog is carrying the

Gold allele (*Ay*), the Black and Tan allele (*at*), the recessive Blue/Grey allele (*d*), or the recessive Chocolate/Brown allele (*b*).

So, how does a breeder find out the exact genotypes of his/her breeding stock?

The first thing to remember is that each parent contributes to their offspring exactly one of the two alleles it is carrying for every gene in its chromosomes. This means that when the sperm containing one allele of each gene fertilizes the egg containing one allele of each gene, then the offspring will once again have two alleles for each gene. As an example, let's say a breeder crosses a Black dog (image 1) with a Gold bitch (image 3). For simplicity sake, it is assumed that no recessive dilution alleles are carried by either parent. So, the Black sire has to be *A/-* because he is Black, and the Gold dam has to be *Ay/-* because she is Gold. The result yielded 8 puppies: 4 Blacks, 2 Golds, and 2 Black and Tans.

Why are there more Blacks than anything else? Where did those Black and Tans come from? To answer these questions, the breeder reasons backwards. If the breeding yields any Black and Tan puppies at all, then considering that these puppies' genotype MUST be *at/at*, we then know that each parent must also carry *at*. So now the breeder knows exactly what the genotypes of the parents must have been. The Black parent was *A/at* and the Gold parent was *Ay/at*. To find the ratios of what the breeder should expect in the litter, a list of all combinations should be made.

The Black male can produce sperm containing the *A* allele, but he will produce an equal number with the *at* allele. The Gold female can produce eggs with the *Ay* allele and an equal number with the *at* allele. What follows is a list of all possible outcomes.

A from father, *Ay* from mother offspring will be *A/Ay* and appear Black

A from father, *at* from mother offspring will be *A/at* and appear Black

at from father, *Ay* from mother offspring will be *Ay/at* and appear Gold

at from father, *at* from mother offspring will be *at/at* and appear Black and Tan

Notice that the ratio is 2 Blacks to 1 Gold to 1 Black and Tan, which is the same as the 4:2:2 that was yielded in the litter. It is important to say that the 2:1:1 ratio is EXPECTED in the offspring, but not guaranteed. Statistical variation will determine what actually appears. Although many combinations are possible, most litters from these parents will yield colors near that ratio. A breeding between different Black and Gold parents could produce either all Black puppies, or half Black puppies and half Gold puppies. It is left to the reader to work out the genotypes necessary to produce these results.

As another example, our breeder crosses a Black and Tan male having medium toned tan points, with a Gold female like the one pictured in image 3. Remember that the tan points on this male appear as a medium tan because of the rufous polygenes (in this case, a balanced checker collection). Assuming the Gold female (also with a balanced checker collection) is *Ay/Ay*, and knowing that the male is *at/at*; what will the breeder get? The male can only produce sperm with *at* and the female can only produce eggs with *Ay*, so all of the offspring will be *Ay/at*, and appear gold, right? Well, yes and no. All the offspring will be *Ay/at* alright, but because the male had a pattern of rufous polygenes that determined his tan points should be medium toned (about equal numbers of red and white checkers, to return to our analogy) and the female the same medium toned Gold; the offspring could be anything from rich Red (having randomly received lots of red checkers from both parents) to Light Gold (having randomly received lots of white checkers from both parents).

There was some prejudice against Light Gold in some Tibetan Mastiff circles, mainly in Europe where this color was not seen in or produced from the original few dogs that were imported there. (These cases where an original small group of founders do not include an accurate sample of the genes in the whole population are well known sampling errors and are referred to as founder effects in genetics.) This example above shows (and many breedings have confirmed it) that you will often get Light Gold puppies from parents of "acceptable" colors, carrying "acceptable" genes. All of these offspring in the above cross are genetically identical *Ay/at* with respect to the main color determinants, but they can exhibit the full range of gold colors. Only variation in the modifying genes determining richness of the tan accounts for the differences in color. Because this is a polygenic trait, as evidenced by the continuous nature of the phenotypes (no clear cut breaks in the colors of light gold to dark red gold) the lighter color golds can be produced in any litter. This supports the inadvisability of having color prejudice against any color found in Tibetan Mastiffs in Tibet (now China) or the rest of the range. It simply further limits an already limited gene pool while discriminating against otherwise sound dogs.

One last interesting point, it is theoretically possible (but unlikely in the extreme, you would probably need to produce over 100 puppies to see all of the statistically unlikely combinations) to breed a Black dog with a Gold dog and get all the possible colors discussed in this article. For this to happen, however, the genotypes of the parents would have to be *A/at, D/d, B/b* for the Black parent and *Ay/at, D/d, B/b* for the Gold parent. This cross will give Blacks, Golds, Black and Tans, Chocolate/Browns, Chocolate/Brown and Tans, Blue/Greys, Blue/Greys and Tans, Gold dilutes, Double Dilutes, and Double Dilutes and Tans (and recessive blacks if those recessive genes are also present). If the reader wants to work out the ratios, it is suggested he/she finds Punnet squares in an old genetics text and makes up one with 8 squares on a side. Good luck.