**FRENCH BULLDOG COAT COLOR INHERITANCE**

**By Linda J. Moore**

Several years have passed since I wrote a series of articles on the inheritance of coat color that were published in the French Bullytin, along with illustrations provided by the editor, Kathy Dannel Vitcak. The publication of the articles roughly coincided with the beginning of molecular genetics that eventually resulted in the genetic tests for coat color genes that are available from genetic labs today. Research continues in this relatively new field and is complicated by the large number of coat color genes that are thought to exist. The articles in the French Bullytin were based on the information available at the time, primarily the research of Clarence C. Little, ScD, and his book The Inheritance of Coat Color in Dogs, and Genetics of the Dog by Malcolm B. Willis, PhD, along with my observations of color results in my own litters and those of others.

There are differences in the theory of coat color inheritance between that currently proposed by genetic labs and the classic coat color theory that existed prior to genetic testing. My own observation of French Bulldog coat color inheritance differs from both. This article will discuss the genes relevant to French Bulldogs from all perspectives.

Before moving on I would like to discuss the problems created by the vocabulary used to describe coat colors, patterns, and pigment, employed by dog fanciers across all breeds which serve to obscure the genes involved. Some terms are fanciful and not used in any other breed and some terms are used incorrectly. One fanciful term used by breeders in the U.S. is “honey pied” in place of a more precise term. For the purposes of this article I will limit my use of terms to the relevant gene itself, so that instead of using the term honey pied I will use the term cream piebald and instead of the term liver I will use the term brown brindle.

Before discussing the genes relevant to French Bulldogs I suggest using a trick that helps me keep track of the numerous coat color genes that each dog inherits. If thought of as an equation, all of the gene loci added together results in the actual coat color, pattern, and pigment of the dog:

A + B + C + D + E + I + K + M + S + T = Color/Pattern/Pigment

By learning which genes every Frenchie can inherit at each of these gene loci it becomes possible to predict breeding outcomes, and if a pedigree is known, what the genetic makeup of a particular dog is likely to be. The breeder lore that many people learn is no substitute for learning the actual genes that determine coat color, patterns, and pigment. It is well established science that dogs have 39 pairs of chromosomes and that each parent contributes one of the 39 pairs of chromosomes. Along each chromosome are loci, or gene pairs, at specific points that number in the thousands. Each gene occupies space on the chromosome and is comprised of hundreds to thousands of base pairs. The number of genes that can be inherited at each gene locus can vary, and there is an order of dominance of the genes at each gene locus. Some breeds of dogs have very limited variation in their coat color genes, while breeds such as French Bulldogs have a great deal of variation. An upper case letter will be used to designate a dominant gene and a lower case letter will be used to designate a gene recessive to the dominant gene. Genes that are inherited at a particular gene locus will all carry the same letter designation, such as A, B, C, etc. We now move on to a discussion of relevant genes.

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**Classic Coat Color Inheritance Theory vs. Current Theory**

**The A (Agouti) Locus** in the past was thought to have the following genes:  *As* solid or black, with the following genes in order of descending dominance – *ay*yellow, *aw* wild or agouti, and *at*tan point. Sometime in the 70’s or 80’s it became clear that a recessive black gene also existed and that it had to be located at this gene locus. It is now designated as *a* and is recessive to the other genes on the A Locus.

The *As* gene that had been thought to be the dominant gene in this serieshas been renamed dominant black, designated as *Kb*, and moved to what is now known as the blacK or K Locus, leaving the gene for yellow *Ay* as the dominant gene, and in the same descending order the genes for agouti, tan point, and recessive black. The yellow gene allows for expression of pheomelanin, or red/yellow pigment. The agouti gene is expressed in the coat as different bands of color on a single hair and is responsible for the appearance of breeds such as Norwegian Elkhounds or Keeshond. Tan point expression can vary from the tan points on a Rottweiler to the very large amounts of tan on a Beagle or German Shepherd with a saddle. Finally, the recessive black gene was originally limited to a few herding breeds but may now appear in others due to indiscriminate color breeders. Recessive black is recessive to agouti, sable/fawn and tan point dogs, and is impossible to distinguish from a dominant black by observation alone.

It is possible for a dog to inherit any of the four genes that exist at this gene locus, and is limited only by restriction of the genes that were established at the time the gene pool was closed in the case of purebred dogs. In the past the only gene at this locus that was of concern to French Bulldog breeders was the gene for yellow, but Frenchies with tan points are now being bred. Whether introduced by color breeders or a natural mutation, the gene is now established. French Bulldogs are *AY/AY* at the Agouti Locus unless it is a tan point, in which case it will be *at/at*. Such dogs can be black and tan, brown and tan, dilute and tan, Isabella and tan, and merle with tan points. Tan point dogs can also inherit brindle, which can be detected by the dark markings in their tan points and are called trindles by color breeders. Standard color Frenchies can carry the tan point gene and would be *Ay/at*, but unless bred to a tan point dog or another dog carrying the tan point gene it will not produce any tan point offspring. However, its offspring have a 50% chance of inheriting a tan point gene even if bred to a dog that is *Ay/AY*.

**The B (Brown) Locus** was originally thought to only have two genes – the dominant gene *B* that allows the expression of black pigment and the recessive gene *b* that causes brown pigment. Dogs that inherit two brown genes are not able to produce any black pigment in their bodies, and their noses, lips, eye rims and pads will be brown as will be any dark pigment in their coat. There are now three known mutations of the brown gene, designated as *bs*, *bd* and *bc*.The genes for brown are well established in the French Bulldog and appear in several show lines, and there is every reason to think that all three different mutations exist. The FBDCA standard calls this color “liver” which is incorrect, as “liver” is used to denote dogs that would be black if they had not inherited two brown genes. Since there are no purebred black French Bulldogs, only brindles, the term liver should be expunged from standards. Calling for a black nose (which would include the eye rims, lips, and pads) eliminates creams and fawns with brown pigment from competition as well as brindles. Some brown brindles have extremely dark brown eyes and noses and are able to pass for brindles with black pigment. Brown brindle piebalds can be especially difficult to detect but a comparison side by side with a brindle with black pigment will highlight the difference. Brown dogs that also inherit two dilute genes are called Isabella which will be covered in the discussion of the D Locus.

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A standard color Frenchie can carry any one of the brown genes as a recessive. As in the case of the tan point gene, all offspring will have a 50% chance of inheriting the brown gene, and if bred to a dog that is *B/B* no brown offspring will result. Genetic labs do test for brown genes, however not all labs are able to test for all three brown genes, and I understand that some brown Frenchies have genes, that in lab parlance, are “untestable”. In other words, there could be another brown gene that has yet to be identified. Nose leather on cream Frenchies with brown pigment is likely to be a pinkish color.

**The C (Chinchilla) or Cream Locus**

This gene locus is called the Albino locus by some geneticists and is thought to have a dominant gene for full pigmentation, designated as *C,* and various other genes recessive to *C* that cause a reduction or lightening of coat color*.* The most relevant gene to Frenchies is the chinchilla gene *cch*. The others include a gene that causes complete albinism although there seems to be significant agreement that the albino gene is not present in dogs. There are differing opinions regarding the C Locus, from claims that it does not exist in dogs to a claim that a genetic test exists for *C*. In horses it is known that a Cream Locus exists, with the cream gene being the dominant gene. In horses if a cream gene is inherited it will lighten a chestnut to palomino, a bay to buckskin, and black to smoky black. If two cream genes are inherited it lightens the color one step further respectively to cremello, perlino, and smoky cream. The horses that inherit two cream genes are not be able to produce offspring with full pigment, meaning they are unable to produce chestnut, bay, or black offspring even if bred to one.

Dr. Little wrote extensively about the chinchilla gene, attributing to it the ability to lighten red/yellow pigment pheomelanin but not black pigment eumelanin, so in this sense it differs from the cream gene in horses. He felt it was the cause of lighter color variations of dogs that had inherited two recessive restriction of pigment genes at the Extension Locus, or *e/e*., sometimes referred to as recessive red. This explains how Irish Setters and yellow Labs which are both *e/e* can be a different color, with the Irish Setter being dark red due to having full pigmentation *C* and the Labs being yellow due to the chinchilla gene. It follows then that the chinchilla gene is also able to lighten coat color of sable/fawn dogs with full extension of pigment *E*, superextension of pigment *Em*, and also lighten the color of tan points. My observation is that the chinchilla gene not only lightens the coat color of a dog that is *Em*, it also suppresses the extension of pigment so that black hair does not appear on the face. It also has the ability to lift and lighten nose pigment.

A scientific study released earlier this year has identified the location of the Intensity gene locus on the twentieth chromosome in a group of dogs comprised of breeds that include white individuals (that are not piebalds), along with wolves. It is thought that the dominant gene allows for full pigmentation while the recessive gene reduces pheomelanin. What effect this gene could have on French Bulldogs is not clear at this point in time, but it is possible that the intensity gene lightens pheomelanin expression of all three of the genes of the Extension Locus.

Little, Willis, and current theory consider all cream dogs to be *Ay/Ay*  *e/e*, and in general this provides a workable explanation for the inheritance of the color - except for French Bulldogs and a few other breeds.

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I strongly suspect that the chinchilla gene does exist, that it is the dominant gene of the locus, and that it is responsible for a type of dominant cream in a few breeds of dogs and exerts a similar genetic influence in dogs as the cream gene does in horses. I will go into greater detail in the discussion of the Extension Locus and will explain how this type of cream is dominant to black mask fawn, and how some dominant creams are unable to produce black mask fawns even if bred to one, and how the gene can be carried undetected by brindles.

**The D (Dilute) Locus**

Dilute is perhaps the most misused word in our coat color vocabulary. The dilute gene is actually the gene responsible for what most people call “blue”. There are two genes, the dominant *D* gene that allows for expression of black pigment, and the recessive dilute gene *d* that lightens eumelanin or black pigment to a slate gray color and which reduces pheomelanin or red/yellow pigment to a lesser extent but is still discernable. If two dilute genes are inherited (and anytime the same two genes are inherited it is said to be **homozygous**) no black pigment can appear in the coat or on the nose, eye rims, lips, or pads. Dilute pigment in brindle dogs will be most noticeable since their brindle markings will change to a slate gray color. Dogs that are fawns with a mask will be more noticeable than fawns without masks or creams, because the pigment of their mask will be dilute, not black. The coat color of fawns and creams is affected but to a lesser degree. The term “mouse” that appears in our standard is entirely inadequate to describe the change of pigment, but luckily most people are able to detect that dilute dogs do not have black pigment unlike the brown brindles that can be so dark they escape detection, and the red fawns with brown pigment that so confuse the eye that some people are unable to detect the brown pigment.

It is likely that there are two different dilute gene mutations, one which lightens pigment with no health consequences and another dilute gene mutation that can cause color dilution alopecia. In most breeds where the dilute gene is present there are no skin issues as a result of the color and even in the breeds where dilute dogs do have skin issues not all dilute dogs are affected. It is possible that in a few breeds with dilute pigment there is another gene that inherits with it and causes CDA, but is not widespread. This is subject to future research which will hopefully resolve the issue, but as a general rule dilute dogs are just as healthy as those with black pigment.

As a recessive gene dilute inherits in the same manner as tan point or brown. A standard color can carry the dilute gene, and if only bred to *D/D* dogs can never produce a dilute offspring. However, there is a 50% chance that offspring of a dilute dog will inherit the dilute gene.

With the rise of color breeding, it was inevitable that both brown and dilute would be bred together to produce Isabella color Frenchies. This color combines both *b/b* and *d/d* genes;some examples are Weimaraners and Isabella Dobermans which are the same genetically, except the Weimaraner is an otherwise black dog and Dobermans are all tan point dogs. The pigment of Isabella dogs is lightened considerably (the Weimaraner is known as the gray ghost) and in Frenchies is obvious on brindles as well as masked fawns, fawns without masks, and creams. Nose leather on the creams in particular may be lightened to a light pinkish color.

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To lend clarity to discussions of the variations that are due to changes in pigment, I suggest that when speaking of dogs with dilute pigment we use the words dilute brindle, dilute masked fawn, dilute fawn, and dilute cream. When speaking of dogs with brown pigment use the words brown brindle, brown masked fawn, brown fawn, and brown cream. The same for Isabella brindle, Isabella masked fawn, Isabella fawn, and Isabella cream. Brown tan point, dilute tan point, and Isabella tan point can also occur. We have previously discussed that brindle can appear in tan points and we cannot forget that

the merle pattern can be present with or without tan points and is also subject to brown, dilute, and Isabella pigment. There are also fawn/sable merles and cream merles. The point is to state the ***pigment*** of the dog, which is inherited separately from the ***color and pattern***. Doing so provides clarity and removes color breeder nomenclature from the discussion.

**The E (Extension) Locus**

In classic coat color theory four different genes were thought to occur at this gene locus, each determining the extent to which pigment was expressed in the coat.  *Em*, superextension of pigment, is the dominant gene of this series and causes what we call a mask. In combination with the yellow gene from the Agouti Locus *Ay* and two yellow genes from the K Locus *ky/ky*, *Em* causes dark hair to appear on the face of the dog. This combination of genes is called a masked fawn in Mastiff breeds and a masked sable in herding breeds, with black pigment capable of being modified by brown, dilute, or a combination of brown and dilute genes. This gene is also expressed in dogs that are agouti *aw/aw* and results in a wolf gray color with a mask. Masks will not be visible in black, brown, dilute or Isabella dogs, including tan point dogs, but may be visible in brindle dogs. It is common for brindle French Bulldogs to have black masks except in the U.S. Masked dogs may carry either the gene for full extension of pigment (fawn/sable) or restriction of pigment gene (red recessive) and would be *Em/E* or *Em/e.*

The next gene in descending order is *E*, the full extension of pigment gene. In combination with the yellow gene from the Agouti Locus and two yellow genes from the K Locus the gene produces the color fawn in Mastiff breeds and sable in herding breeds. Black hair on the body may be present on dogs with both super and full extension of pigment, but a mask will not appear on the face of a dog with full extension of pigment. Fawn/sable dogs with full extension of pigment have the same variation of color as dogs with superextension of pigment, from very pale fawn to dark red. This gene may carry a recessive red gene and would be *E/e*, and is subject to the same changes in pigment as dogs that are *Em*.

In classic coat color theory the next descending gene is the brindle gene, described by Little as partial extension of pigment. Little considered the dark stripes of the brindle pattern to be an incomplete extension of eumelanin pigment over a light pheomelanin base color, and considered the brindle pattern to be infinitely variable. He commented on “cryptic brindles”, or dogs that are so lightly marked they escape detection as brindles. He also commented on dogs so heavily marked they appear to be black. Current coat color genetics has removed the brindle gene from the Extension Locus and it is now considered to be one of the three genes on the blacK or K Locus, which will be discussed later.

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The final and third gene of this series is the restriction of pigment gene *e,* also known as recessive red, which can be carried as a recessive gene by masked fawns/sables or fawns/sables. Color can vary from fire engine red to extremely pale cream, with the lighter colors thought to be modified by Chinchilla or Intensity genes. Little was able to confirm that dogs with the combination of *e/e* genes were unable to express black pigment in their coat by breeding experiments at his kennel facility. This distinguishes them from dogs with full extension of pigment *E* which can have black tipping or shading in their coat, however there is an overlap of dogs that are *E* that do not have black in their coat and dogs that are *e/e* which cannot be distinguished from one another visually. Recessive *e/e* dogs are also subject to the same changes in pigment as dogs that are *Em* or *E.*

Historically, classic coat color theory attributed all variations of cream and fawn in French Bulldogs to the restriction of pigment gene. Although prevalent in Europe, the black mask gene was not initially identified in French Bulldogs by geneticists. In my early days in the breed I observed the appearance of French Bulldogs that were fairly brown or light brown which were indistinguishable in color from dogs that were black mask fawns. That observation, in combination with the French Bulldog’s direct descent from the Bulldog, led me to identify the superextension of pigment gene *Em*, the full extension of pigment gene *E*, and the restriction of pigment gene *e* in the French Bulldog.

**Implications of current Extension Locus theory**

Current theory includes all three of the genes from the Extension Locus in French Bulldogs, and considers all cream and some clear red dogs to be *e/e*. With the brindle gene removed from the Extension Locus it logically follows that the inheritance of two *e/e* genes is capable of blocking the expression of brindle eumelanin in the coat, meaning that two *e/e* genes becomes **epistatic** to brindle and is able to “hide” brindle. Two *e/e* genes are also thought to “hide” dominant black. A recent interesting development is a theory that Samoyeds are white as a result of two recessive black genes *a/a* in combination with two restriction of pigment genes *e/e.* I suggest that this conclusion, based no doubt entirely on genetic test results alone, needs to be confirmed by controlled breeding experiments.

If all cream Frenchies and some reds with no black in their coat are *e/e*, they are then able to carry the brindle gene undetected. This gives an explanation for the appearance of brindle puppies from a cross of two non-brindle parents which seems to happen most frequently in crosses between a black mask fawn and a cream.

However, I doubt that the restriction of pigment gene occurs with enough frequency in French Bulldogs for this to be the only explanation for the appearance of brindle puppies to two non-brindle parents.

The most frequent genes from the Extension Locus that should be expected in French Bulldogs are the superextension of pigment *Em* and to a lesser extent the full extension pigment *E* based on its Mastiff inheritance. The crosses in the early days of the breed could have brought in the restriction of pigment gene, but it logically would have never achieved a high frequency due to the preference for brindle dogs in Europe at the time and a population of fawns that were largely masked fawns. To this day the FCI does not permit cream French Bulldogs in the show ring.

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According to the current theory, in order for a French Bulldog to be brindle it must have at least one *Em* or *E* gene. If this is true, then it would follow that since there are many more cream French Bulldogs in the U.S. than masked fawns or fawns, that many creams “hide” the brindle gene, since it is common practice to breed brindles to creams. Logically the number of brindles born to two non-brindle parents should be much higher than it is.

The genes involved in a cross between a homozygous black mask fawn and a recessive cream with “hidden” homozygous brindle markings results in an entire litter of black mask brindle puppies (relevant genes only):

HomozygousBlack mask fawn Cream with Homozygous hidden brindle

*Ay/Ay  Em/Em ky/ky*x*Ay/Ay  e/e Kbr/Kbr*

=

All black mask brindle puppies

*Ay/Ay  Em/e Kbr/ky*

All brindle litters can result in a cross between a homozygous fawn *E/E* and a cream with hidden homozygous brindle markings as well, except the brindle offspring do not have black masks. While theoretically possible these two scenarios occur infrequently, if at all. What does seem to happen from time to time from such crosses is that the litter will have black mask fawns or fawns, as well as creams along with brindle puppies. Cream puppies should only result from a black mask fawn or fawn parent that is heterozygous *Em/e* or *E/e*, **if** all creams are *e/e*.

What is well known and observed is that brindle dogs from the result of a cross of two brindle parents can be homozygous for brindle (sometimes called “pure” for brindle) meaning that if bred to a cream, fawn, or black mask fawn the result will be all brindle puppies. The majority of brindles in the U.S. are heterozygous for brindle and such dogs roughly produce 50% brindle offspring if bred to creams, fawns, or black mask fawns, as expected. Heterozygous brindles are (relevant genes only):

*Ay/Ay Em/Em* (or *Em/E, Em/e, E/E,* or *E/e*) *Kbr/ky*

Current genetic theory also allows for the possibility for brindles to be heterozygous based on inheritance at the E Locus (relevant genes only):

*Ay/Ay Em/e* (or *E/e) Kbr/Kbr*

In this case the gene that allows for the expression of the homozygous brindle genes is inheritance of the *Em* or *E* gene. This would mean that that dogs that are “pure for brindle” must not only be homozygous for brindle, but must also not have inherited a restriction of pigment gene. A “pure for brindle” dog would be restricted to the following genotypes (relevant genes only):

*Ay/Ay Em/Em*  (or *Em/E* or *E/E*) *Kbr/Kbr*

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**Forgotten cryptic brindles**

My alternate theory to unexpected brindle puppies from non-brindle parents is that one of the parents is a cryptic brindle - in other words a dog that is a black mask brindle or brindle with markings so light they are not apparent, yet able to pass on a brindle gene to offspring. Since the majority of unexpected brindle puppies appear to occur from a black mask fawn and cream cross, I suspect cryptic black mask brindles are the more likely cause of brindle puppies being born to two non-brindle parents than *e/e* recessive creams carrying a brindle gene. Little’s knowledge of cryptic brindles from his breeding experiments in breeds without restriction of pigment genes being a factor provides a good explanation for unexpected brindle French Bulldog puppies. A personal observation is that black mask fawn imports to the U.S. with black tipping in their coat or black mask fawn or black mask fawn pieds with “watermarking” around white markings produce brindle offspring when bred to creams. Watermarking is a term for the black line that appears between the fawn portion of the coat and white markings and is especially noticeable on black mask fawn pieds.

**Dominant cream**

At this point in the discussion of the Extension Locus, the prevalence of cream French Bulldogs in the U.S. needs to be addressed. The challenge to genetic theory is how does a color that is presumed to be recessive, and as far as I know was never deliberately bred for by the vast majority of breeders in the US, come to exist in much higher numbers than fawn or black mask fawn dogs that are theoretically dominant, and which also hides the brindle gene, a color/pattern also favored by breeders?

The answer is that a dominant cream exists in French Bulldogs, just as dominant cream exists in horses, and the gene responsible for dominant cream is the chinchilla gene from the C or Chinchilla Locus. The genetic makeup of a homozygous dominant cream Frenchie would be as follows (relevant genes only):

*Ay/Ay  Cch/Cch  Em/Em (or Em/E, Em/e, E/E, E/e, e/e) ky/ky*

Such cream dogs, if bred to a brindle, will produce brindle offspring at the expected 50% rate, and would not “hide” brindle genes – unless two *e/e* genes are inherited. The chinchilla gene the brindle puppies inherit will not lighten the black eumelanin pigment of the brindle markings and is essentially undetectable in brindle dogs. It should be noted that a substantial majority of brindle Frenchies in the U.S. do not have black masks unlike the brindles in the rest of the world, and as in the case of dominant creams the superextension of pigment, or mask, is prevented in brindle dogs that have inherited a chinchilla gene along with *Em*. In addition, the majority of brindle dogs in the U.S. have clear colored nails, as do creams. A homozygous dominant cream Frenchie bred to a black mask fawn cannot produce black mask fawn puppies, only creams (with an occasional unexpected brindle), thus deserving the name “dominant cream”.

The brindle Frenchies that are homozygous for cream (chinchilla) will produce only cream and brindle puppies if bred to a black mask fawn. Since the chinchilla gene does not affect brindle markings, the gene can pass down for generations without being detected in brindle to brindle crosses. While it is possible to explain a small percentage of the brindle and cream litters resulting from a brindle and black mask fawn cross by assuming that both parents are heterozygous *Em/e*, given the large percentage of cream dogs in the US it is as much or more likely to be the result of a homozygous dominant cream, given that the genetic inheritance of the breed should be largely composed of *Em* individuals.

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Human population genetics has proven how persistent genes can be, having found that people of non-African descent still carry Neanderthal genes. Given this persistence, the question is why are there so few black mask fawns in the U.S.? The answer is that they are here, but their coat color has been lightened by the dominant chinchilla gene to cream.

**American Fawn**

Dogs described as “American fawns” have obvious lightening of their coat with darker ear rims which is sometimes accompanied by a darker dorsal stripe, and have extremely dark edges on their ears at birth. To set the record straight, no one in the greater dog world would call these dogs “fawn”, as they are clearly cream in color. The matter is further confused by the appearance of cream dogs that lack the darker ear rims and dorsal stripe which many breeders call “true creams”.

Upon careful examination of an “American fawn”, it will be noted that the dog will have extremely dark skin between the front legs and the chest and on the belly and inner thighs where no white markings are present. There will be even darker skin on the face where a black mask would be, if the dog were a black mask fawn. I call this a “shadow mask”. This extremely dark skin can also be noted on cream piebalds, although it may not be complete or present unless markings develop on the face. It is important to note that cream markings on piebalds are not present at birth, as the puppies are born entirely white. They can easily be mistaken for cream puppies, although the edges of their ears are pink and not the dark color cream puppies are born with. Cream spots begin to appear around two weeks of age and may continue to emerge for some time. This is in contrast to piebalds with fawn markings, which are present at birth. The fawn markings may in fact be very dark in color, which lightens as the puppy matures. There is no explanation in either classic or current coat color inheritance theory that explains fawn markings not being present at birth, and the only conclusion is that what is called “American fawn” is actually a dominant cream.

The confusion is understandable. We have previously discussed that fawns with either superextension of pigment or full extension of pigment (*Em* and *E*) can range in color from deep red to pale fawn and that the dark skin is caused by the superextension of pigment gene, *Em*, which can be noted in all black mask fawn dogs. If a chinchilla gene is inherited it lightens the coat color of the dog, and if the dog was going to be a dark red fawn it will retain some of that color along the ear rims and dorsal stripe. The color of a lighter colored fawn dog will also be lightened but it won’t have the dark ear rims and dorsal stripe. Clarence Little observed that the inheritance of one chinchilla gene lightened the coat color by one step, and the inheritance of two chinchilla genes lightened the coat color even further, just as the cream gene does in horses which further explains the variations seen in cream color dogs. One other note is that many people observe, and indeed the FBDCA breed standard allows for, a lighter colored nose in creams - and has now been mistakenly allowed for fawns as well. The authors of the previous standard understood that the **pigment** of cream dogs should be black, but is often lightened, without understanding the genetic cause. The explanation is that the chinchilla gene is also able to lift color from the nose. This caveat for nose color was exploited by some fanciers who exhibited creams with brown pigment, since some judges were not able to detect the brown pigment and even if they did, had no way to disqualify the dog. The mistake of identifying creams as “American fawns” caused an error to be written into the current standard which now allows all shades of fawn dogs to have lighter colored noses, which unethical exhibitors will exploit to the detriment of the breed. Of particular concern are the red fawns with brown pigment that have gone undetected by judges in the past and which are now allowed by the standard, but still have the brown genes to pass on to their offspring.

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At this point I hope that I have presented a coherent argument that the great majority of cream dogs in the US are not recessive creams, but are instead dominant creams that are black mask fawns at the same time, similar to palomino horses which are dominant creams but which are also chestnuts at the same time. If this is indeed true, the logical extension of this argument is that a cross between two heterozygous dominant creams or a cross between a heterozygous dominant cream and a brindle heterozygous for chinchilla has the potential to produce a black mask fawn or a black mask brindle, just as a cross between two palominos can produce a chestnut foal.

Heterozygous Dominant Cream x Heterozygous Chinchilla Brindle

*Cch/c Em/Em ky/ky Cch/c Em/Em Kbr/Kbr*

=

Black Mask Brindle

*c/c Em/Em Kbr/ky*

Or

Heterozygous Dominant Cream x Heterozygous Dominant Cream

*Cch/c Em/Em ky/ky* *Cch/c Em/Em ky/ky*

=

Black Mask Fawn

*c/c Em/Em ky/ky*

Since the expression of the black mask is determined by the genes on the C Locus, the expected ratio of puppies born with a black mask from both proposed crosses will be one in three.

**The I (Intensity) Locus**

As previously stated, this gene locus has recently been located and the recessive intensity gene may be found to affect coat color in French Bulldogs. If so, individuals homozygous for intensity (*i/i*) could exhibit lightening of pheomelanin coat color whether they were a black mask fawn, fawn, or recessive red (*Em*, *E,* or *e*) dog. This is a possible explanation for recessive cream French Bulldogs, which genetically would have to be homozygous for both restriction of pigment (*e/e*) as well as intensity (*i/i*). Geneticists have known for decades that a gene must exist that lightens pheomelanin but not eumelanin, and this exciting advance may provide an explanation. It is possible that the Intensity Locus is simply a restatement of the Chinchilla Locus since the authors of the study indicate that other, unnamed genes are involved, or it may be that both gene loci are present in dogs since the inheritance of Chinchilla that Little describes differs from Intensity.

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**The K (blacK) Locus**

This recently proposed gene locus came about after a scientific paper presented evidence that the brindle gene did not exist on the Extension Locus. My first thought was that if it was proven to be true, the brindle gene was likely to occupy its own gene locus, in the same manner as the merle gene since both are genes for patterns. While I imagined only two genes at the Brindle Locus with brindle being the dominant gene and a recessive gene being non-brindle, or yellow, the gene formerly designated as *As*, considered the most dominant gene in the Agouti Locus was included as well. This provides the basis for the name of the locus, since the gene was thought to be responsible for dominant black. The three genes thought to occupy this locus are the two co-dominant genes, dominant black *Kb* and brindle *Kbr*, along with the recessive gene designated as *ky* which allows for the expression of pheomelanin, or red/yellow pigment.

The brindle gene *Kbr* and the yellow gene *ky* are present in the French Bulldog.

The brindle gene causes a pattern of dark stripes (eumelanin) to appear on a lighter pheomelanin (fawn) background. The pattern has a wide degree of expression, from dogs that are brindles but appear to be black (or brown, dilute, or Isabella) to dogs that are brindles but are marked so lightly they are not recognized as brindles and are referred to as cryptic brindles.

Dogs may inherit both a dominant black gene as well as a brindle gene, however the brindle markings will not be visible, and this would be true for all variations in pigment – brown, dilute, and Isabella.

A brindle gene may also inherit with a merle gene, resulting in a muddled color in which black spots can be observed but with brindle markings in what would normally be the lighter colored areas. Such dogs may also have blue or merle colored eyes that can inherit with the merle pattern, as well an tan points.

There are many terms breeders use in an attempt to describe brindles, such as fawn, red, or black brindle, which are confusing and inaccurate descriptions since the brindle itself is black (or brown, dilute, or Isabella) on a red fawn, fawn, or cream base color. Reverse brindle is a term used in the breed to describe a lightly marked brindle, which has the opposite meaning in other breeds of dogs. We can achieve greater clarity of communication describing the brindle pattern simply by saying the dog is **heavily marked** (very little lighter base color showing) or **lightly marked** (very distinct black stripes with a majority of the lighter base coat showing). As previously mentioned, greater clarity can be achieved by referring to brindles with brown pigment as **brown brindles** instead of liver, brindles with dilute pigment as **dilute brindles** instead of blue, and Isabella as **Isabella brindles** instead of lilac brindles.

Cream color Frenchies have been born in the US with small black markings on them. While it is tempting to consider this a somatic mutation or a chimera, it is more likely that the dog is a very lightly marked cryptic brindle with a single black marking. According to classic and current theory, this should not be able to happen since all creams are *e/e* which “hides” all black pigment. However, if the cream is a dominant cream it follows that it is just a natural variation in brindle marking. At present since no genetic test for brindle exists, test matings would be required to confirm the presence of a brindle gene in a dog that appears to cream with a small black marking.

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**The M (Merle) Locus**

The Merle locus is relevant to this discussion because color breeders have introduced the merle gene via cross breeding into many breeds of dogs, including the French Bulldog. It is not clear whether the AKC has registered any merle Frenchies at this point in time, but given the history of other breeds of dogs it will happen.

There are two genes at this gene locus – the dominant gene for merle *M* and the recessive gene for non-merle *m.*  The merle gene lightens the base color in a pattern that is extremely variable, but generally appears as a lighter background with dark spots. In appearance merle dogs, like brindle dogs, may be heavily or lightly marked, so that there may only be a very small spot of lighter color on some dogs to dogs that have minimal darker spotting. The variation of the expression of the gene was well known to Little who described cryptic merles. As a dominant gene, the inheritance of a single merle gene means the dog will be merle and it will have a good chance of inheriting a blue or mottled brown eye. The excuses given for merle dogs suddenly appearing in breeds where the pattern previously did not exist lack any credibility. There absolutely must be a cross to a breed in which the pattern is established.

The merle gene is the only coat color gene that has predictable adverse health consequences, which only occur when two merle genes are inherited. Such dogs are known as double merles, or defective whites since they are predominantly if not totally white. They will almost certainly be deaf and will likely suffer from loss of vision if not outright blindness. Such preventable catastrophic birth defects should never happen, but this does not deter color breeders who have no regard for the harm the practice of crossing merles with merles causes these poor dogs. A great cause for concern is that sable/fawn dogs, and dogs that are recessive or dominant creams mask the appearance of an inherited merle gene, and if they have brown eyes may unwittingly be bred to a merle which would result in unintended double merles. An example of the concern breeders have with this possible scenario is the ban of sable merle Collies from the show ring in the U.S., while allowing blue merles. With the introduction of merle genes in Frenchies, it is possible that an undetected brown eyed cream or fawn merle Frenchie could be bred by accident with a normal blue merle, or a dilute, brown (red), or Isabella merle to produce double merle offspring.

The allure of breeding merles in such an array of colors and pigments is irresistible to color breeders, with additional options of producing them with or without tan points as well as with brindle markings. The controversy over dilute and brown Frenchies will be remembered as quaint and tame compared to the firestorm that will erupt if merle Frenchies are allowed to be registered, since it can be assured that color breeders will produce defective whites as a by-product of their breeding practices.

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**The S (Spotting) Locus**

There are four genes that are known to exist at this gene locus, with *S* as the dominant gene,which produces a self colored dog with minimal white spotting. There are three genes for white spotting which are all recessive to *S*. The gene for Irish Spotting *si* is a fairly predictable pattern of white spotting that is recognizable on Collies, Shelties, and other breeds, with a white chest, white forelegs, white rear feet, a white tail tip, and possible white collar and white blaze on the head. In order for a dog to show this white spotting pattern two Irish spotting genes *si/si* must be inherited. While recessive to *S* the Irish Spotting gene is dominant to the two piebald genes. The next gene in descending order is the gene for normal piebald spotting, *sp*. A normal pied (contraction of the word piebald) Frenchie will generally have one or two “hoods” on the head with good sized color markings appearing on the body. Normal pieds are *sp/sp*. The most recessive gene in the series is the extreme piebald gene, designated as *sw*. Inheritance of two extreme piebald genes may result in a totally white dog, or a nearly white dog with minimal spots of color on its head and possibly one or two small spots on the body.

The *S* gene is an incomplete dominant gene, which means that if one of the white spotting genes is inherited it may affect the appearance of the dog and cause or increase white spotting. In some breeds a white stripe up the front of the rear leg can indicate that a piebald or extreme piebald gene has been inherited. Irregular white spotting on a Frenchie can indicate that a piebald or extreme piebald gene has been inherited. I have also observed that white haws may indicate presence of a piebald gene. The possible combinations of genes for a solid colored dog can be *S/S, S/si,S/sp* , and *S/sw*. The Irish Spotting gene will most likely not cause irregular white spotting, but that possibility increases with the normal piebald gene and is most likely to happen with an extreme piebald gene. On the other hand, a solid colored dog may inherit an extreme piebald gene and have no irregular white spotting at all.

The possible combination of genes for a dog with an Irish Spotting pattern can be *si/si, si/sp,* and *si/sw*.

If inherited, the normal piebald and extreme piebald genes can cause increased white markings and/or additional white markings to appear as white spots on the body.

It is generally accepted that dogs fifty percent white or more with areas of color are piebalds. Piebalds with fairly regular areas of color are *sp/sp* . A normal piebald can also inherit an extreme piebald gene *sp/sw* which can result in a dog somewhere between a normal piebald and an extreme piebald, which is *sw/sw.* Homozygous extreme piebald dogs can be completely white although these dogs will typically have some color on their head and possibly one or two spots of color on their body, frequently above the tail.

In addition to the influence that the recessive white spotting genes can have on the appearance of a dog with any heterozygous combination of spotting genes, Little described “plus” and “minus” modifiers that can also influence the extent of the white spotting pattern, so that two dogs with an identical genetic makeup might still differ in appearance. He also noted that the white spotting genes were more efficient at removing color from dogs with red/yellow pigment than dogs with black pigment in their coat. This means that brindle and fawn piebalds typically have larger spots of color than cream piebalds, which as previously discussed are born completely white.

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Any of the three white spotting genes have the potential to cause pink spots on the nose if the nose is surrounded or touched by a white marking. While it may take an extended period of time, in my experience the pink spots caused by white markings will ultimately fill in and the nose will be completely black, although dogs with a lot of white on their heads or large white blazes may have pink pigment on their muzzles. Genetically this is of no consequence and does not alter the pigment of the dog.

There is a greater frequency of deafness in piebald dogs than dogs that are a solid color, with no difference in frequency noted between normal piebald and extreme piebald dogs. It is thought that a lack of pigment in the inner ear caused by the piebald gene contributes to the death of the follicles of tiny hairs that transmit sound waves as nerve impulses to the brain, leading to deafness. This deafness can be bilateral or unilateral, and in the case of unilateral dogs may go undetected. There is certainly more to be discovered about this cause of deafness, and hopefully at some point in the future we will be able to avoid breeding dogs that are deaf as a result of inheriting two piebald genes.

A final note on white spotting is that white spots can appear on self colored dogs that do not have a genetic cause. Frenchies vary widely in the amount of white markings on chests; those in the U.S. tend to have white spots on their chests but this is less prevalent in other countries.

**The T (Ticking) Locus**

It is thought that that two genes occur at this locus - a dominant gene *T* for ticking and a recessive gene *t* for a non-ticked or clear coat. Ticking only occurs in white areas and begins to appear around two weeks of age. Genes for ticking go undetected in self-colored dogs and will only become known when piebald or self-colored offspring with large white markings develop the markings in the white areas of their bodies. Ticking is generally considered undesirable in French Bulldogs.

**Urajiro Markings**

Urajiro markings are cream to white markings that are required on all colors of Shiba Inu dogs. While the placement of the markings are reminiscent of tan point markings, there are differences. Urajiro markings occur in both sable/fawn dogs as well as tan point dogs, and appear in other breeds as well, which have probably always been thought of as unusual tan point markings. Something of a mystery, there is speculation that Urajiro has its own gene locus. It is not clear whether Urajiro is a dominant or recessive gene, or what its heirarchy might be among multiple alleles on a gene locus, so its inheritance is uncertain. I have personally observed these markings on Bulldogs and French Bulldogs but they are extremely rare. These markings can also appear on brindles, however they would be extremely difficult to detect since the brindle markings would appear within the Urajiro markings, just as they do in tan points. Urajiro markings are not mentioned in any French Bulldog standard but breeders need to be aware of them, since when inherited it disrupts the appearance of black mask fawns and fawns to make it appear as if the dog is prematurely gray.

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**CONCLUSION**

There has been undeniable advancement in understanding canine genetics thanks to the research by molecular geneticists. Dog fanciers now have numerous genetic tests that can reveal recessive genes that might or might not be desired in a breeding program. However, I feel a word of caution needs to be made about claims by for-profit genetic labs. The test results you pay for will most likely not tell you anything you don’t already know or suspect if you have extensive knowledge of the pedigree behind a particular dog. And, if the dog in question is bred recessive genes may become apparent in offspring, such as a self- colored dog producing a piebald puppy. The greatest use of coat color genetic testing is to determine in advance of a breeding whether or not recessive dilute, brown, or piebald genes are present. Test results are also available for the Agouti, Extension, and blacK gene loci. It is notable that no test is available for brindle, and I have significant doubt that the results for Extension and blacK locus genes are reliable. The dominant black gene simply does not exist in purebred French Bulldogs, yet it is being reported on genetic tests with no explanation given. We have no way to know how many inaccurate test results are being reported to owners. What is certain is that labs are in competition with each other, that they are an unregulated industry, and that the data they collect from submission of genetic material will be kept confidential. What is also certain is that unless confirmed by controlled experimental breedings a large segment of current coat color inheritance theory remains unproven, and claims of absolute certainty in absence of that proof should be viewed with healthy skepticism.

Especially so if money is involved.

In the meantime, advancements in knowledge of canine genetics will continue to occur and the conversations we will have ten years from now will not be the ones we are having today. Mastery of canine coat color genetics places a breeder on a path to success as it provides a foundation for a greater understanding of the genetic influences that affects every breeding decision we undertake, all of which hopefully ends with the goal of breeding better French Bulldogs.

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