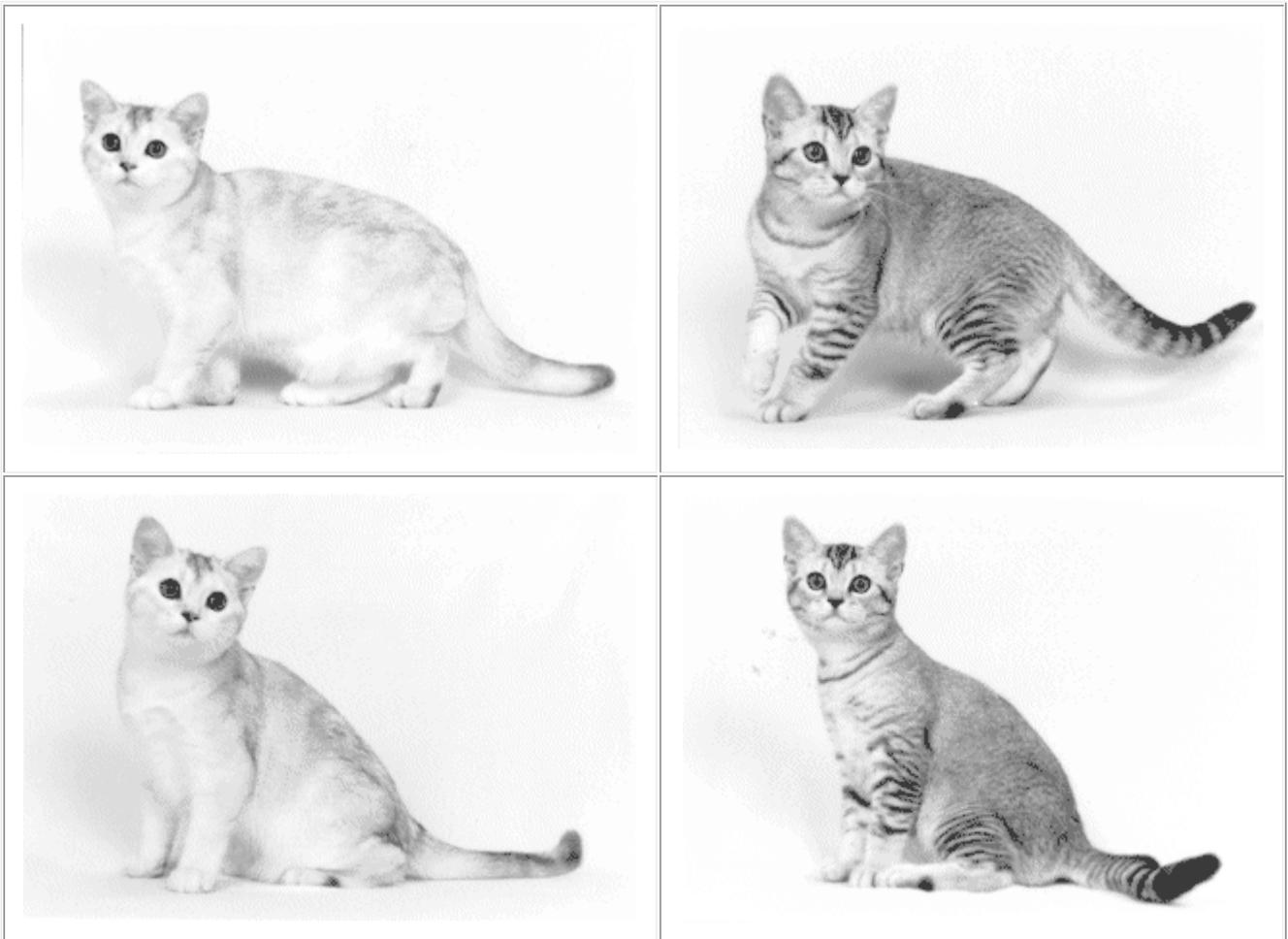


## Genetics of the shaded American Shorthair (and Striped Tabbies too!!!)

By Carol W. Johnson, DVM, PhD

### INTRODUCTION

There has been much controversy concerning the genetics of unpatterned tabbies in the American Shorthair (ASH) breed. In Figures 1a and 1b, are two female kittens about 4 months old. These half-sisters were born 2 weeks apart. Neither is the outcross of another breed. The sire of both kittens is a purebred shaded silver male: GC, GP Melodygarden Stargazer. The dam of the kitten in Figure 1a was a shaded cameo female (CH, PR Melodygarden Tidy Tips) and this is a kitten picture of GC Melodygarden Northern Lights, CFA's first grand champion shaded tortoiseshell ASH. The dam of the kitten in Figure 1b is CH Solmer Ophelia of Stedam, a gold-eyed white masking brown-patched tabby. This kitten was registered as a silver ticked tabby in 1996 before CFA declared that no ASH ticked tabbies were registerable in the breed. Kittens of this coloration naturally arise when a clear shaded cat, regardless of lineage or color is crossed with a classic tabby or a solid masking classic tabby.



1a. Shaded tortie 4 mo kitten	1b. 'Ticked' tabby 4 mo kitten
-------------------------------	--------------------------------

Figure 1 - These kittens share the same sire, a shaded American Shorthair.

The purpose of this article is to describe the genetics that make up the shaded ASH pattern based on actual breedings. It not based on theoretical of "how it is thought to be or ought to be" but rather "how it is." The same genetics have been consistent with 6 lines of shaded cats crossed with classic tabbies from several different lines. Although written from experience with shaded American Shorthairs, the genetics are applicable to other breeds and many of the same genes work in nonshaded patterns, such as the classic tabby pattern. This manuscript is meant to provide the readership with information about to the genetic inheritance of the shaded pattern and to show the relationship of shaded and unpatterned tabbies with stripes. Because the genetics are similar in other breeds and hopefully the readers will find the information useful regardless of breed or color.

### **HISTORY OF THE SHADED AMERICAN SHORTHAIR**

Before diving into the genetics, a short history of the shaded ASH pattern is helpful. The history of the shaded ASH has been more extensively reviewed elsewhere [1, 2]. The shaded silver is one of the oldest ASH colors. In 1913, a shaded chinchilla female was accepted for CFA registration as a "Domestic Shorthair", a breed designation that later gave rise to both American and British Shorthairs [3] The first silver shaded ASH competed for championship in 1951. Cameo and shell cameo shaded ASH were accepted for championship in 1971 and in 1993, other colors including shaded blue, cream, tortoiseshell, dilute tortoiseshell and their chinchilla/shell counterparts were accepted. Non-silver shaded ASH (such as shaded golden) are currently not recognized for championship. "Ticked" tabby ASH were originally accepted as AOV, but later declared a disqualifier in 1993. They continued to be accepted for registration as AOV by CFA until about 1996.

Currently, the shaded silver ASH is the 3rd most popular color registered with CFA, surpassed only by silver and brown tabbies. The color peaked in popularity in the late 1970's then declined markedly in the 1980s. One contributing factor was that shaded ASH breeders tended to breed shaded-to-shaded to produce good color, but the cats became inbred and the type did not keep up with the slow, but constant refinements necessary to be competitive in the show ring. As a result, the shaded ASH became less competitive at the shows and sometimes got a reputation for having poor dispositions, genetic defects, and poor reproductive performance.

The shaded color pattern is experiencing a comeback in the 1990s. Key to this comeback is a need to breed shaded ASH to tabby ASH, because there are insufficient shaded ASH lines to be genetically viable. Also an understanding of the genetics behind the shaded color is essential to being able to utilize tabbies in a shaded ASH program. Beginning with some of the earliest shaded ASH breedings there has been an impression that it is hard to nearly impossible to get the color back after outcrossing with tabbies or other

colors. Knowledge of the genetics behind the shaded and classic tabby patterns helps explain why it takes between 2 and 4 generations to get the color back following a shaded to tabby breeding.

## **THINK OF COLOR PATTERNS IN SMALL UNITS**

To follow the genetics, the reader must have an open mind and be willing to drop some of the preexisting ideas or paradigms regarding "color" inheritance. Cat "colors" are best described in terms of the small independent attributes that are inherited. For example, a silver tabby can be genetically defined as: agouti (tabby), classic pattern, black (eumelanin), silver inhibitor gene, and a moderate undercoat width. A cameo tabby is genetically similar to a silver tabby except the black (eumelanin) pigment is replaced by a red (phaeomelanin) pigment. A black smoke differs from a silver tabby only that it has the non-agouti gene, etc.

The vocabulary for several color attributes have never before been defined so the terms are lacking while other terms may mean different things to different people. For example, the terms "ticked" or "ticking" means something different to different people. For example, in Abyssinians, the term "ticked" conjures up a cat that has multiply banded hairs and no striping anywhere, while in Orientals the same term conjure up a cat that is noted for having stripes on the head, neck, legs, and tail and the banding on the hairs is not defined. American Shorthair breeders may use "ticking" to refer to the intermixing of hairs in the dark and light striped areas on a classic tabby. To provide a common ground, I have either selected a single definition where several have previously existed, or have invented vocabulary where it has previously not existed.

## **DEFINING SHADED AND TICKED TABBY PATTERNS**

A shaded cat regardless of breed is defined by overall appearance, not by genetics. "Shaded" is a pattern and not a color. Color refers to pigment and may be black (eumelanin), red (phaeomelanin), blue (dilute eumelanin), etc. Shaded ASH may be black-silver (silver shaded), red-silver (cameo shaded), blue-silver (dilute shaded), black non-silver (shaded golden), or other colors. Patterns define where color is present and typical patterns may be classic or mackerel tabby, non-agouti, or unpatterned.

The best definition of a shaded pattern is one in which the hairs are tipped with color and the overall appearance is of a cat without striping, slightly darker along the top midline and shading to untipped (white on a silver shaded) on the belly. A silver tabby shorthair has a white undercoat, but is **not** a shaded cat because it has a striped pattern on the torso. The presence of a the silver inhibitor gene (described in more later on) does not define a shaded cat, nor is it necessary for a shaded, as in the example of shaded golden Persians. The perfect shaded silver shorthair has black tipped hairs with a white (silver) undercoat that extends at least 1/2 the way to the tip [4], unbarred legs, neck and tail, a white underbelly and insides of the legs. Shaded and chinchilla patterns are grouped together as shaded cats in this paper, since the difference between the shaded and chinchilla cats varies only in one pattern attribute, the width of the white undercoat. Evidence of a

pattern or barring on the legs, neck, and tail or, worse, on the body is effectively penalized in every breed, even when not specifically prohibited in the certain breed standards, such as the ASH standard.

Closely related to the shaded shorthairs are "ticked tabbies". Both cats lack stripes on the body, but a ticked tabby has stripes on at least 2 of the following: head, neck, legs, or tail. As in shaded, the pattern is defined by overall appearance of the cat, not by the tipping of the hair. The hairs maybe tipped or multiply banded. Generally, a ticked tabby appears darker than a shaded silver for one of three reasons: the hair banding frequency is even, the hair banding frequency is short giving the hairs multiple bands, or the color travels far down the hair shaft. A moderately dark, distinctly-marked 4 month old silver "ticked" tabby kitten is pictured in Figure 1b. I prefer to use the term "unstriped or unpatterned tabby" to describe shaded and "ticked" patterned cats combined.

### **Shaded genetics may differ with coat length**

The genetics governing mackerel and classic patterns are relatively simple and largely involve a single gene,  $Tm\_$  (T- has also been used for mackerel) or  $t^{b,b}$  respectively. Shaded genetics are considerably more complicated. Regardless of breed, the genetics behind the shaded pattern is composed of many genes working in concert. Although the overall appearances of shaded patterned cats are quite similar from breed to breed, the genetics behind the longhair breeds and shorthaired shaded shorthairs can be slightly different.

Shaded shorthair cats do not have the luxury of having a long coat to obscure a pattern. Although some "shaded" shorthairs may have a classic or mackerel tabby pattern at birth, remnants of the pattern generally are apparent throughout life and these cats are generally considered to have a pattern fault that requires most to be shown as tabbies, if shown at all. The clearest ASH and OSH are unstriped or unpatterned tabbies. Unpatterned tabbies are not restricted to the ASH or OSH breeds. They are a fundamental pattern also found in other breeds including Abyssinians, Singapuras, Siamese, Burmese, and more rarely in Persians and Russian Blues. The minimal requirements to produce a shaded ASH are the following attributes: agouti gene, silver inhibitor gene (ASH non-silver inhibitor cats are not recognized), the undercoat width genes (widebanding genes), genes that affect the number of bands of color on each hair, and genes that cause an unstriped body type. Other minor genes are important in producing the pale sparkling appearance and to clear up the residual striping on both the torso and extremities.

The shaded pattern in Persians appears to differ slightly from shaded shorthairs in only two attributes: 1) They occasionally can be non-agouti (a very light version of smoke), although this appears to be relatively rare; and 2) they are more usually born striped (usually classic or mackerel tabby) than unpatterned. Because of the long hair coat, they can afford more variability than can shaded shorthairs. Otherwise, the genetics behind the color patterns of the Persians and shorthaired breeds are very similar.

### **GETTING THE STRIPES OFF THE BODY**

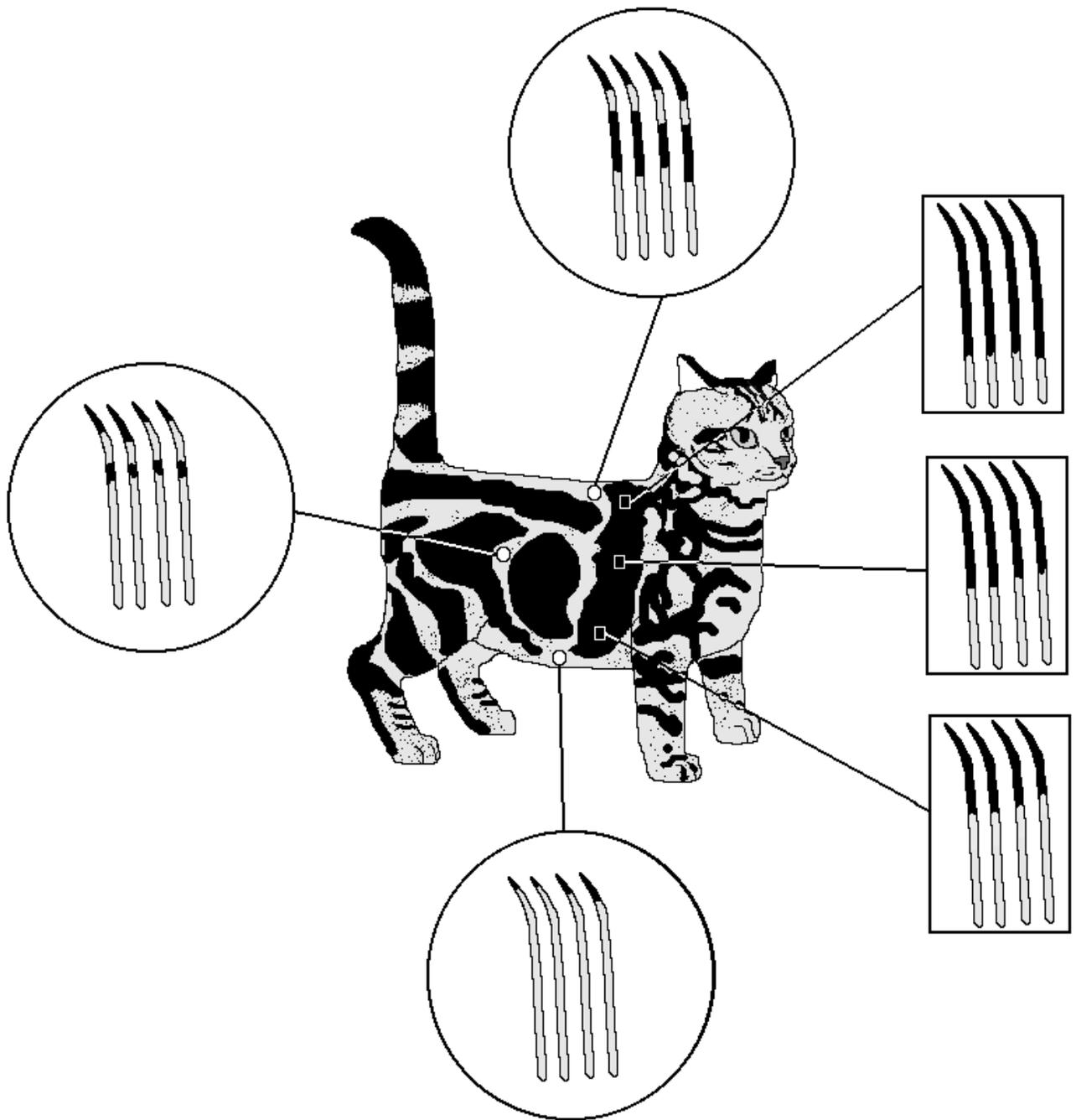
Shaded ASH are agouti (tabby) patterned - the agouti gene, A<sub>+</sub>

All silver shaded ASH cats are genetically agouti or "tabby-patterned cats". Normally shaded shorthair cats are not a variant of the non-agouti (black smoke) pattern as had been suggested by early publications [3]. Although some shaded Persians are probably non-agouti, in shorthaired cats, even non-agouti (black smoke) cats with a very wide silver undercoat tend to have a black mask that betrays the true color. The tabby nature of the shaded can be seen in the following attributes: shaded ASH cats have pigmentation around the eye (eg black "eyeliner" in a shaded silver) surrounded by a white (silver) zone, pigmented lips, a brick red or pink nose, colored paw pads, and frequently colored hair the back of the feet. Genetically, however, the unpatterned cats carry either classic or mackerel or both traits "masked" by the unpatterned tabby pattern.

The agouti gene (A<sub>+</sub>) is a dominant gene that allows the hairs to be banded so the cat appears as a tabby (Figure 2). The converse gene, the non-agouti recessive mutation (aa), causes the banding to disappear as melanin is over produced. An example of an agouti cat is a brown tabby and its non-agouti converse is a solid black.

The term non-agouti is a misnomer - the cats still carry the genes for hair banding and because of this, often a faint tabby pattern can be seen on solid black cats. The agouti gene is still somewhat operative, but melanin synthesis remains hyperactive despite the activity of the gene. The terms "melanistic" or "hypermelanistic" are probably better terms than non-agouti. Agouti and non-agouti hairs are depicted in Figure 2. Most of the molecular knowledge of the agouti gene has been extrapolated from mice. In wild type brown agouti mice, the agouti gene encodes an inhibitory protein, the agouti protein and is responsible for the light banded areas of the hair. When a new hair is growing, the melanocytes start laying down eumelanin (black pigment) producing a black band.

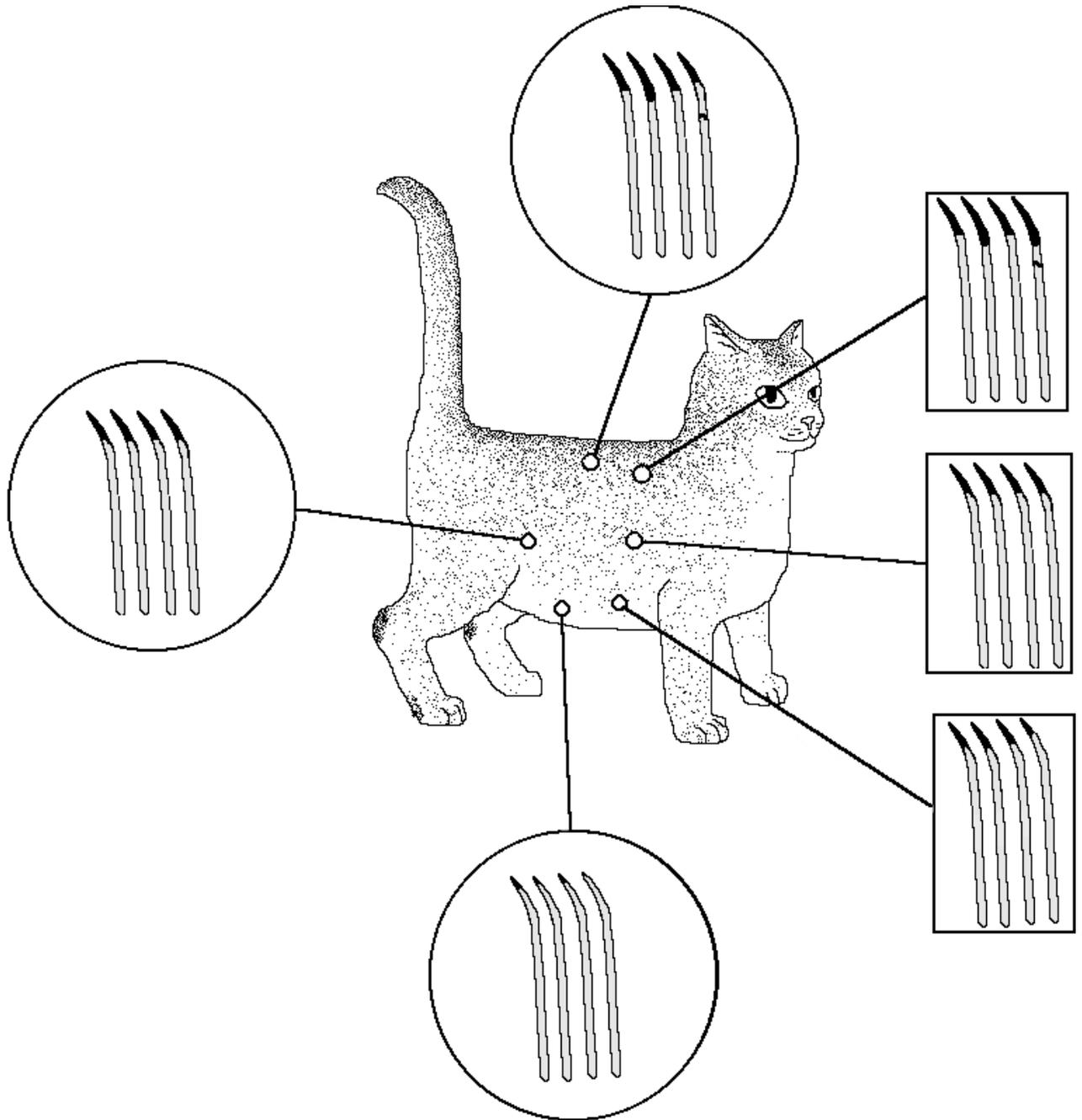
Microscopically, the hairs look coated with dense black pigment. The agouti protein is produced at the same time and when concentrations reach a certain high level, the agouti protein causes eumelanin to be down-regulated (turned down or off) and replaced with pheomelanin, producing a brown pigment band in the case of a brown tabby. Microscopically, the pheomelanin is less dense and has a reddish cast. After a while the agouti protein itself becomes down-regulated and eumelanin synthesis resumes. The result is a new black band. The turning off an on is more or less efficient and although the bands look fairly sharp to the eye, microscopically switch from eumelanin to pheomelanin sputters a bit so the boundaries are somewhat indistinct. The hair in Figure 2 is divided into two areas, the colored tip and an area, I will refer to as the "undercoat width" because in cats, these two areas act as if they are regulated by different genes that are inherited separately. The undercoat width genes are described in more detail later in this paper.



**Figure 3 - Hairbanding in Classic Tabby**

The agouti gene probably works similarly in cats and brown tabbies appear to produce both eumelanin and phaeomelanin similar to the wild type agouti mouse. However, agouti mice are stripeless and mouse genetics are unable to explain how stripes occur in cats. Stripes are remarkable because they represent variable expression of the agouti gene. Both the light and the dark striped areas have multiply banded hair, but the banding frequency (discussed later) varies in these sites. In a classic tabby, in the black stripes areas the hair follicles are coordinated to produce hairs with a black (eumelanin) tip

followed by a brown (phaeomelanin) band in the undercoat in the case of a brown tabby or no melanin in the case of a silver tabby (Figure 3). In the light areas, the hair follicles collaborate to form a different banding pattern with shorter pigmented tips and higher banding frequency. Here, the hairs are multiply banded, usually black, light, black followed by a light undercoat. As one moves from the back to the belly, the frequency and length of the colored bands decreases.



**Figure 4 - Hairbanding in Silver Shaded**

The drawing in Figure 4 shows a similar change in a shaded silver cat, though as will be discussed in a later section, the hairs often are not evenly banded. Exactly how stripes are molecularly regulated so the dark and light stripe areas are distinct is not clear. In shaded shorthairs, stripes are suppressed so a shaded shorthair appears similar to an agouti mouse.

### **Silvery appearance - the Silver Inhibitor Gene, I<sub>s</sub>**

In the ASH breed, all shaded cats are required to have a silver inhibitor genes (I<sub>s</sub>) and currently shaded cats lacking the silver inhibitor gene (such as shaded goldens) are not recognized for championship in the breed. The silver inhibitor gene is dominant and the genetics have been recently reviewed by Heather Lorimer [5]. The term "silver" refers to the white banded areas of the hair, not to the pigmented areas, such as the black tip on a silver shaded or classic tabby. Silver classic tabbies are more accurately described as black-silver tabbies, as they are in some non-CFA registries. A cameo tabby is more accurately described as a red-silver tabby, a pewter tabby a blue-silver tabby, etc.

In the purest form, silver differs from white predominantly by mechanism. In white cats, either the melanocytes (the cells that make the pigment), are lacking because they failed to migrate to the white areas of the coat (for example, in the case of the dominant white gene or the white spotting gene) or the melanin biochemistry is abnormal and can't be made (as in the case of some of rarer recessive whites). The lack of melanin is called amelanotic and a cartoon of a white hair is seen in Figure 5.

In silver tabbies, the melanocytes can produce melanin normal for that color, but expression is down-regulated to severely decrease or stop melanin production in the areas of the hair that would normally be colored phaeomelanin in a brown tabby. In a silver tabby, these areas appear white as seen in Figure 5. Microscopically, the melanin does not just turn off, but may sputter a bit and low levels of melanin may be present even in areas that appear white to the eye. Because of the residual melanin, the undercoat should be technically described as silvered, not white. However, because of common use in breed standards, a silvered undercoat will be referred to as "white". If an inhibitor gene is unable to completely block phaeomelanin, the resulting cat appears bronzed or "tarnished".

The silver inhibitor gene has a slightly different effect in a non-agouti cat. As seen in the last drawing in Figure 5, the silver inhibitor gene does not affect the tip of the hair, but rather only

lightens the undercoat area. If the inhibitor gene is unable to completely block residual eumelanin production, the undercoat appears gray, a common problem in some black smoke cats.

Heather Lorimer has suggested that the silver inhibitor gene may and may be a mutation of the gene responsible for turning the phaeomelanin (brown pigment) off and on. As she has noted, the silver inhibitor gene can have a more profound effect on red (sex-linked

orange gene) than it does on black pigment in all breeds. Because of this complexity, this paper deals predominantly with black pigmented (shaded silver) cats. The effect of the silver gene in combination with the red can be exaggerated.

### **To Stripe or Not to Stripe - the major unpatterned tabby gene, U\_**

Although much has been made about distinguishing between shaded cats that are born without a tabby pattern from those born with a tabby pattern, the two types are genetically similar and differ only in gene or gene cluster that defines stripes or no-stripes on the body. Traditionally, tabby cats are thought of as cats with stripes. There are two genetically distinct patterned tabbies: classic and mackerel tabbies. Spotted tabbies are variants of mackerel or classic tabbies and have other genes (spotting genes) that influence the mackerel or classic patterns to break into spots. Unpatterned shorthair tabbies without stripes on the body have traditionally been divided into shaded cats and "ticked" tabbies.

Older textbooks [4, 6] report there are 3 tabby patterns: the unstriped Abyssinian-type ( $T^a$ \_), mackerel ( $Tm$ \_), and classic ( $t^b t^b$ ) that are present at the same genetic site (allele). Because a cat has paired chromosomes, a cat can carry only 2 genes at that site. The classic pattern is recessive to other patterns. The Abyssinian type pattern is reported to be dominant to both mackerel and classic patterns while the mackerel pattern is dominant to the classic pattern. Most texts indicate all three patterns are alleles of the same gene [4, 6]. Contrary to popular belief,  $T^a$  probably does not determine the banding frequency of hairs on the hairs on the body (eg, determine whether the hairs are "ticked" versus "tipped"), but rather determines whether there is striping on the main part of the body, the torso.

The unstriped tabby pattern of ASH (U\_ denoting unpatterned or unstriped tabby) appears to be genetically similar to or the same as the Abyssinian-type tabby ( $T^a$ ), although whether they are identical has been a matter of debate. U\_ of the ASH appears dominant (or at least partially dominant) over both the mackerel and classic patterns for the first generation of crossing shaded to the recessive classic pattern. Crossing clear shaded ASH to classic tabbies produces first generation (F1) kittens that have tabby markings on the neck, legs, and tail, and generally no or weak tabby markings on the body. This is illustrated in Figure 6 and an actual First generation breeding is found in Table 1.

The U\_ gene is not a true complete dominant, since the heterozygote allows the striping on the head and extremities to be expressed. Partial, incomplete, or co-dominance is probably closer to the truth.

Second generation breedings indicate the three patterns (mackerel, classic and unpatterned) can not be at the same allele. In the second generation (Table 1) three tabby patterns emerged: unstriped, classic, and mackerel (Figure 7).

This example clearly illustrates that all three tabby patterns can not be on the same gene group. Because the male was a recessive classic, he could not carry either mackerel or unstriped tabby. The female had to carry all 3 patterns.

**Table 1**  
**FIRST GENERATION (F1)**  
**Classic red tabby male x silver unpatterned agouti (shaded silver) female**

---

<b>Unpatterned agouti</b>	<b>Classic tabby</b>	<b>Mackerel tabby</b>
1M black smoke (non agouti masking unpatterned tabby)		
2F "shaded" tortoiseshell		
1M "shaded" silver		

**SECOND GENERATION (F2)**  
**Classic red tabby male x shaded tortoiseshell female F1 [3 breedings]**

---

<b>Unpatterned agouti</b>	<b>Classic tabby</b>	<b>Mackerel tabby</b>
1F shaded cameo	1F brown patch	1M cameo
2F shaded tortoiseshell	1F cameo	1M silver
1M shaded silver	1M brown	1F brown patched
	1F silver patch	2F, 1M red
	1M red	

M=male  
F=female

## "F1 shaded" x Classic - 2nd Generation

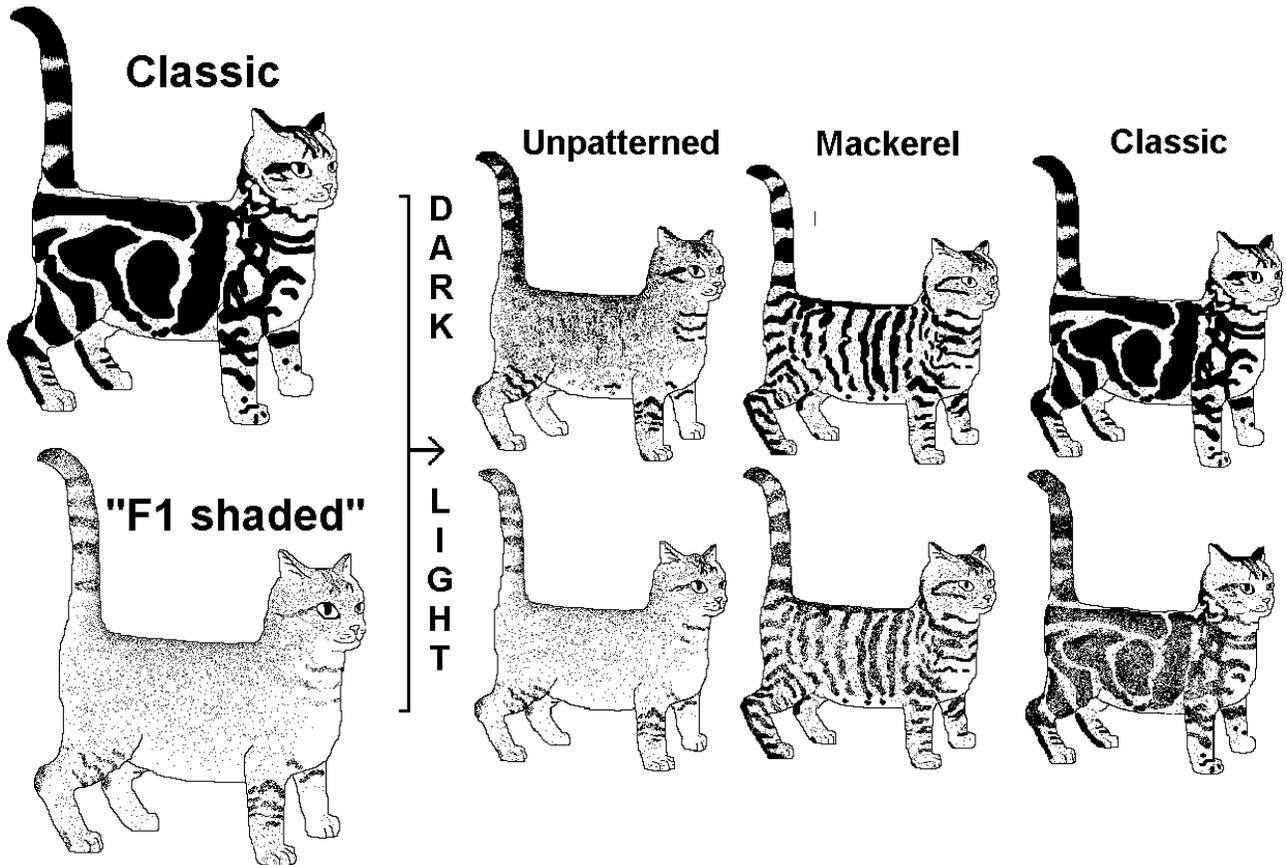


Figure 7 - F1 shaded bred to Classic Tabby

If the gene behind shaded ASH's is a single dominant gene  $U_{\_}$ , it is on a separate allele that "masks" the underlying tabby pattern. Table 2 illustrates the expected inheritance if a single dominant gene,  $U_{\_}$  produced unstriped tabbies. For the sake of illustration, a shaded "homozygous" shaded female is bred to a classic male without a shaded background.

**Table 2**

**Expected inheritance with a single unpatterned gene  $U_{\_}$   
Homozygous classic tabby ( $uut^{b_t^b}$ ) x  
homozygous shaded carrying mackerel tabby ( $UUTmTm$ )**

**First generation (F1) Table 2a**

	<b>Parent 2</b> <b><math>U Tm</math></b>
--	---

<b>Parent 1</b> <b>u t<sup>b</sup></b>	UuTmt <sup>b</sup> = Unpatterned tabby carrying mackerel and classic patterns
---	---

**Homozygous classic tabby (uut<sup>b</sup>t<sup>b</sup>) x heterozygous shaded female (UuTmt<sup>b</sup>)**

**Second Generation (F2) Table 2b**

	<b>Parent 2</b>			
<b>Parent 1</b>	<b>U Tm</b>	<b>U t<sup>b</sup></b>	<b>u Tm</b>	<b>u t<sup>b</sup></b>
<b>u t<sup>b</sup></b>	<b>UuTmt<sup>b</sup></b>  Unpatterned tabby carrying mackerel and classic patterns	<b>Uut<sup>b</sup>t<sup>b</sup></b>  Unpatterned tabby carrying classic pattern	<b>uuTmt<sup>b</sup></b>  Mackerel tabby	<b>uut<sup>b</sup>t<sup>b</sup></b>  Classic tabby

U\_ = Unpatterned tabby

uu = Patterned tabby

uuTm\_ = Mackerel tabby

uut<sup>b</sup>t<sup>b</sup> = Classic tabby

The shaded masks homozygous mackerel tabby as is true with most homozygous shaded ASH, in my experience. The recessive inversion of U\_ will be called u and uu allows the cats to express a stripped mackerel (Tm\_) or classic tabby pattern . Because both parents are homozygous (shaded - UUTmTm, classic uut<sup>b</sup>t<sup>b</sup>) all F1 kittens are unstriped tabbies carrying both mackerel and classic tabby patterns (UuTt<sup>b</sup>). This fits the data of the example. Table 2 shows what happens when the F1 kittens are bred to a classic tabby. Again, this fits the example seen in Table 1.

While this is a simplest view of unpatterned inheritance, the genetics of shaded cats is more complex. A shaded shorthair is more than a homozygous unpatterned cat. A shaded ASH must have a silver inhibitor gene, a wide undercoat width, and proper banding of the hair so it appears tipped with color. While the homozygous unpatterned gene (UU) may be the most important attribute for removing striping, other minor unpatterned genes are important in removing the residual striping and giving the final appearance of shaded. The minor genes also probably are important in shaded Persians.

**GETTING RID OF THE RESIDUAL STRIPING - Chaos, Confusion, and Erase polygenes**

Although the unpatterned gene in the homozygous state, UU, removes most of the pattern on the torso and extremities, other genes are necessary to complete stripelessness and remove the remnants of bars and enhance the appearance of being shaded. These minor genes are inherited separately from U\_ and appear to be inheritable from each other. The concept of minor genes has been long accepted and one text refers to these minor genes as polygenes [6]. Most, if not all, probably are coded by multiple genes.

Because these genes are inherited separately from the unpatterned gene U\_, patterned (striped) tabby cats can inherit them and show attributes normally associated with unstriped cats and vice-versa. As illustrated in Figure 7, tabbies that inherit some of the minor polygenes tend to have ticked or faded patterns. There are at least 2 attributes that are associated with the shading on the torso and main body of shaded ASH. These genes have not been previously described, so for lack of better terms. I will name them Chaos and Confusion. A third gene was proposed by Cathy Galfo from her work with shaded OSH. It has been called 'Erase' and appears to remove some of the residual barring on the extremities.

### **Confusion**

A good shaded silver ASH the tipping on the ends of the hair may appear even on quick inspection, but close inspection reveals that, like snowflakes, nearly every hair is different from each other (Figure 8). One has a short black banded tip, the next may have 2 dark bands, the next may have a medium black tip, etc. Thorough inspection reveals some hairs are even solid black or all white. And some hairs are utterly preposterous - my all-time favorites are the hairs that are multiply banded from the tip to the base of the hair with the record being 7 dark bands in one hair. This loss of coordination from hair to hair, I term "Confusion". This is in sharp contrast to Abyssinian-type banding that tends to be very even.

The major differences in the darkness of the two kittens in Figure 1 is not the width of the white undercoat or the tipping (both discussed in the next section), but rather the evenness of the hair banding. The shaded kitten in Figure 1a, has a very high level of Confusion and has hairs characterized by very uneven band width as seen in the photograph (Figure 8a) and cartooned in Figure 9. Confusion serves to give the shaded cat the "sparkling" appearance and appears to influence the gradual blending and fading of the color from top to bottom. In Figure 8b, the ticked tabby kitten has an even tipping with all hairs having bands about the same width inherited from its tabby parent. For this kitten, 10 hairs removed from the upper torso and are similar to the Abyssinian type banding cartooned in Figure 8. Confusion present in the shaded kitten has the effect of making the torso darker on the top and gradually shading to white below. The ticked tabby kitten has even color which stops abruptly at the pale abdomen.



8a. Shaded tortie 4 mo kitten

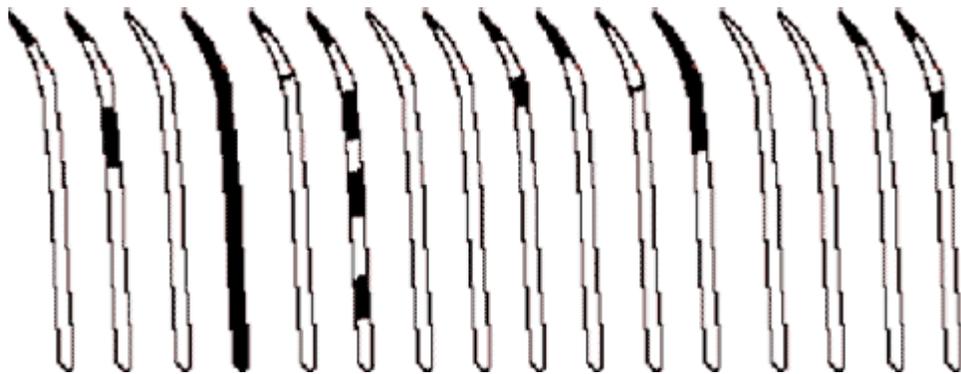


8b. 'Ticked' ta

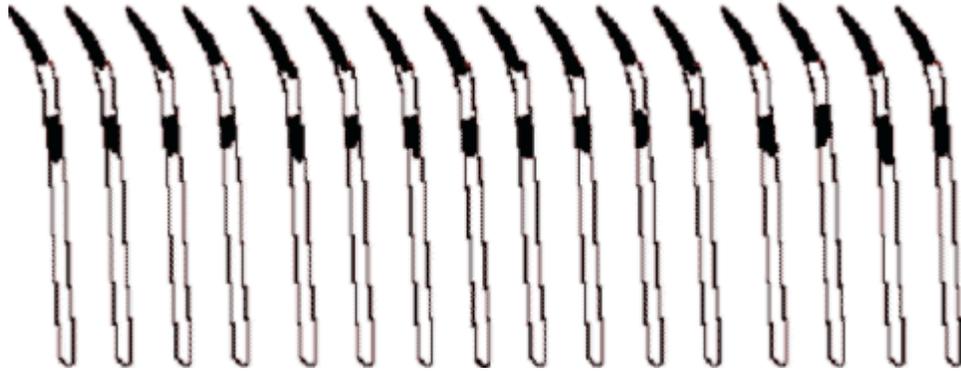
Confusion appears to be a loss coordination of the hair follicles to make hairs with the same banding frequency as its neighbors. A good classic tabby has a very even color and a low level

of 'confusion'. Within a stripe, the hairs in any location have nearly the identical banding frequency as their neighbors (Figure 10).

Uneven "confused" banding  
**Shaded type banding - Shaded Tortie**



Even banding  
**Abyssinian type banding - "ticked" tabby**

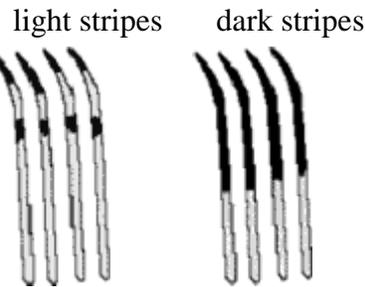


**Figure 9 - Shaded tortie and ticked tabby**

**Uneven shaded type  
banding**



**Even tabby banding**



**Figure 10 - Shaded and classic tabby banding.**

The hair follicles are coordinated to produce the same amount of melanin for the same distance on the hair. The width of the dark band may be longer on the top of the cat compared to the bottom, but the progression is smooth and the dark tipping appears very even. Similarly, in the light striped areas, the hairs are multiply banded but the banding is very even. The hair follicles in the stripe areas are well coordinated with each other and relate to what the other is doing.

Patterned classic ASH tabbies are selected for even hair tipping (little Confusion), otherwise the pattern looks very uneven and mottled. In many cases, when a shaded cat is crossed with a classic tabby, the evenness of tipping appears to be dominant and the F1 generation are ticked tabbies similar to the one shown. Confusion is common in silver Persians - most silver and Chinchilla Persians have some banded hairs, if observed closely. Some Chinchilla Persian breeders have reported that some judges will put a Chinchilla Persian in a Silver category if they see solid black hairs. Based on the ubiquitous nature of this gene, it probably is not appropriate to classify a Persian based solely on this single attribute and the color probably should be assigned based on the overall appearance of the cat regardless of a few solid black hairs.

Abyssinians are selected for evenness of banding and they tend to less Confusion expression, as a general rule than do shaded ASH. It is a subtle difference, but Abyssinians tend to have a sharper demarcation between where the body ticking ends and

the unticked underbelly or insides of the legs begins. In shaded ASH, this contrast is softened so the tipping of the body subtly blends into white on the belly. Patterned tabby ASH, on the other hand, are selected very even coat patterns and either lack Confusion genes or perhaps have a different set of genes that resist Confusion expression (hypothesized Unconfused genes).

A special category of Confusion attribute is called Roaning. Roaning is a rare trait in which solid white hairs are intermixed with normal hairs. A black roan has white hairs intermixed with black, giving it a flea-bitten look. Roaning can be inherited separately from the more common uneven Confusion banding width and is relatively rare. In shaded ASH, Roaning is one genetic strategy by which a shaded may become a chinchilla.

### **Chaos**

Chaos also disrupts the striped pattern, but appears to be inherited independently of Confusion. In a classic tabby, Chaos causes an intermixing of the light striped areas into the black and vice-versa and is probably responsible for many cases of what ASH breeders call "ticking" of a classic tabby pattern. In these cats, the coat banding is even for the type of hair expressed, it is just that the hairs occur at an abnormal site.

In shaded ASH, Chaos serves to eradicate residual striping that "breaks through" on the torso. Unstriped cats that lose these Chaos attributes tend to show "ghost" striping as can be seen on the back of the ticked tabby in Figure 8b. "Ghost stripes" on an unpatterned tabby are different than those of a true mackerel tabby. In a true mackerel tabby, the dark striped areas have different banding than the light striped area as for classic tabbies cartooned in Figure 10. "Ghost dark stripes" generally have the same number of bands as the "light stripe" areas, it's just that the tipping has changed a little to line up evenly suggesting some coordination of banding. "Ghost striped" unpatterned tabbies are also genetically different from true mackerel tabbies. Breeding two "ghost striped" unpatterned tabbies together can produce a clear unpatterned shaded, while breeding two true mackerel tabbies together never produce a clear unpatterned shaded.

### **Erase and other genes that affect the stripes on the extremities**

Residual striping on the extremities (neck, legs and tail) may persist even in the presence of homozygous UU, Chaos, and Confusion. Other clean-up genes are necessary to remove the residual stripes. Cathy Galfro has proposed an "Erase" gene as it appears to be inherited discretely to "erase" the residual markings on shaded OSH.

The defined leg markings on Singapuras indicate that minor tabby patterns on the extremities can be genetically fixed with appropriate selection while all other tabby striping are suppressed. Stripes in these same places can be present on homozygous shaded cats as residual markings. In shaded ASH, Erase or several Erase-like genes appear to be needed to remove striping on the legs, neck, and tail.

### **TIPPING IS AN ILLUSION - Undercoat width and banding frequency polygenes**

The natural banding of an unpatterned cat hair is similar to the light striped areas on classic tabbies and usually starts with a dark band, followed by a light band, followed by a dark band. Getting this multiple banding down to just a colored tip has been accomplished in shaded ASH by using several genetic strategies. All shaded cats have a wide undercoat width, so this section will start with a description of the "Widebanding genes".

### **Undercoat Width Genes (Widebanding genes)**

The first description of genes that determine the width of the undercoat has been credited to Joan Wasselhuber who coined the term "Widebanding" genes. Undercoat width genes determine the width of the undercoat whether or not the cat has a silver inhibitor gene. The term "undercoat" used in this paper refers to part of the hair shaft closest to the body and includes both guard hairs and the shorter hairs often referred to as "undercoat" hairs. As previously illustrated in Figure 2, both silver and non-silver cats can have hairs characterized by a pigmented banded tip and an unpigmented (eg. Silver tabby) or phaeomelanin pigmented (brown tabby) "undercoat".

The width of the undercoat varies depending on where it is on the cat. An example of distribution of the undercoat width was seen in a silver tabby in Figure 3. The undercoat width is narrowest closest to the spine line and longest close to the belly. In the ASH breed, all colors with a silver inhibitor gene are required to have a "white" undercoat present on all parts of the cats, including along the spine line. When the pigment goes to the roots, it is considered a pattern-fault in silver tabbies.

The undercoat width for nonsilver colors is not defined in the ASH breed. Some brown tabbies have a wide undercoat as evidenced by a warm brown color underlying the black stripe area, while in others the black striped areas are black to the roots. Even in these dark cats, microscopically the eumelanin is less dense at the base of the hair. In the ASH brown tabby, either of these patterns is considered correct.

In mice, the silver inhibitor gene may strongly influence the width of the undercoat. This is different than in cats, where the silver inhibitor gene probably has little influence on the width of the undercoat when the melanin type is eumelanin (black pigment) but may have an effect with sex-linked orange phaeomelanin. If the width of the undercoat was linked to the expression of the silver inhibitor gene, logically all the silver kittens arising from a silver shaded to brown tabby breeding should all have the broad white undercoat of the shaded parent responsible for donating the silver inhibitor gene. Instead as noted by others [5], the kittens express a variety of undercoat widths ranging from very narrow (dark) to very broad (light). Shaded cats crossed with very dark tabbies often have very dark silver offspring.

The widebanding genes (Wb) are probably polygenetic which would allow for the great variability seen in the undercoat widths in cats. Precisely how the agouti, silver inhibitor, and widebanding genes interact on a molecular level is not clear. One possibility is the widebanding genes influence the agouti protein production to remain high so that

eumelanin pigment remains inhibited or down-regulated. Another possibility is that the widebanding gene encodes for a second inhibitory protein that also down-regulates eumelanin.

In the case of the black smoke, a cat that has both non-agouti and silver inhibitor, the two genes appear at odds with each other. As mentioned previously, the non-agouti gene is able to suppress the influence of the silver inhibitor gene at the tip of the hair, but not at the base (in the widebanding zone) so a silver undercoat is present (Figure 5). However, in many cases the effect is not perfect. Black smokes may have color faults, especially if one of these genes are expressed at a higher level than the other. In some cases, a poorly expressed non-agouti gene or an over-expression of the silver inhibitor gene will lead to a pale "washed out" black smoke. Over-expression of the non-agouti gene or under-expression of the silver inhibitor gene will cause the undercoat to appear gray instead of white.

All shaded cats (both long- and shorthaired breeds) need a broad undercoat width to give the shaded its pale silvery appearance. If a short undercoat width is present, the cat appears as a tabby (mackerel, classic or unstriped "ticked" tabby depending on the underlying genetics).

### **Banding Frequency genes**

Banding frequency can be defined as the number and width of the pigmented bands present on the hair of an agouti cat. The agouti gene permits the hairs to have banded colors, but other genes (banding frequency genes) influence the number of bands that actually occur on the hairs. An ideal shaded silver hair is characterized by a single broad eumelanin band at the tip while Abyssinian-type banding is characterized by multiple (at least 2) small eumelanin bands interspersed with light bands (phaeomelanin). At a molecular level, banding frequency probably translates to the time interval in which an agouti protein that turns on and off. Even though the banding looks precise to the eye, under the microscope, black pigment (eumelanin) may appear in the light band (phaeomelanin) areas.

Several genetic strategies appear to play a part in producing the illusion of tipping in the shaded phenotype. In the ideal shaded cats, the tip of the hairs are pigmented, but the shaft is non-pigmented or otherwise silver. In Figure 11, three possible genetic strategies are depicted. In the first genetic strategy, shown in drawings Ia-c, the banding frequency decreases, but the undercoat width (square brackets) remains the same. In the first drawing (Ia)

a hair has 3 rather small black bands suggesting the agouti protein turns on and off fairly rapidly. In drawing Ib, the banding frequency changes so agouti protein is influenced to produce 2 medium black bands before it turns off. Finally, with more selection, the banding frequency is selected to produce only one band (Ic). In this model, the hair is truly tipped with color; changing the width of the undercoat does not influence the tipping.

In the second genetic strategy, drawings IIa-c, the banding frequency remains the same but the undercoat width is selected to be progressively wider, until it cuts off the second dark band. This gives the illusion that only a single band is present, while genetically the cat is coded for multiple bands, but the bands closest to the base are "masked" by the undercoat width. Decrease the undercoat width and the multiple bands become apparent again.

In the third genetic strategy (IIIa-c), the turning off and on of the agouti protein is progressively slowed. As slowing occurs, all the bands become broader. Finally, the second black band is pushed into the white undercoat, which in this model remains stable. Again, there is only an illusion of tipping in this model. If the undercoat width decreases to a very small width, the second dark band becomes apparent.

The most common genetic strategies in shaded ASHs appear to be a combination of II and III. The dark bands become broader and a wide undercoat is necessary to produce the illusion of tipping. The evidence for this is present microscopically. On many hairs a band of increased melanin is often microscopically apparent in the region where the second dark band would normally be present. In other words, tipped hairs are genetically banded hairs, but the melanin synthesis in the inner band is down-regulated, probably by the influence of the widebanding genes, so visually it appears only one band is present. The single band frequency (strategy 1) either is very rare or does not occur in shaded ASH. In contrast, Abyssinians are selected for a banding frequency that turns off and on rapidly so multiple bands are apparent before the undercoat cuts off the remaining bands or selection of a relatively narrow undercoat.

Classic tabbies have multiply banded hairs present in the light striped areas. As previously illustrated (Figure 3), the banding varies according to location on the body. Tabbies also show variation in banding frequency with most tabbies having 2 colored bands along the spine, some having 3 colored bands, and a few having only 1 colored band. This multiple banding in the classic tabby parent influences the banding frequency of the F1 generation of a shaded x tabby outcross and multiple bands usually dominate.

### **Taking apart the shaded color**

So what actually happens when shaded ASH are bred to classic tabbies? First generation outcrosses of a clear shaded silver (no leg bars) with a classic tabby result in all the kittens having no striping on the torso but bars on the extremities and head. Similar genetics occur regardless of the tabby or shaded lines. I and other ASH breeders have found this to be the pattern in a variety of other shaded lines including Allstar, Banchory, Darksun, Erosgata, Fanthai, Gatico, Marya, Norpark, and Sanabel. Barring on the first generation kittens occurred even though a variety of classic tabby lines were used: Amex, Solmer, Murjani, Obiwan, or Stedam lines.

Whether these kittens are light or dark depended on the classic partner. Some classic tabbies appear to be permissive to the shaded traits and the kittens are light enough to be registerable as shaded. Other classic tabby lines are clearly not shaded-permissive and

all the kittens are dark (and registered as ticked tabbies in my cattery until this was prohibited by CFA). Generally the darkness of the F1 has been linked to a narrow widebanding gene and excessively even color, both attributes that contribute to a clear classic tabby pattern. As mentioned above, multiple banding is more frequent than single banding tipping. Rather than being evidence of hybridization, these are predictable recombinations of traits inherited from both parents.

The shaded ASH phenotype is a collection of attributes, not a single gene or gene product. The shaded ASH genotype is probably nearly identical to that in Oriental Shorthairs and differs from most Persians, probably only in the presence of the unpatterned gene. Recently a Chinchilla breeder sent me pictures of her kittens which do not have patterns at birth, laying to rest the myth that Persians do not have unpatterned cats.

### **Putting it back together**

It will come as no surprise to a shaded breeder of any breed that outcrossing to tabbies or any other non-shaded cats can make it hard to regain the shaded pattern. It is hoped that this article will lend better understanding as to why it is so difficult to regain a shaded pattern following outcrossing to a tabby pattern. The complexity of the shaded pattern is unequalled by any other pattern/color combination. At least 6 independently inherited traits need to be recovered to form the shaded pattern following breeding of a shaded to a classic.

Breeding back to a homozygous shaded stock often results in loss of type, while breeding two superior type outcross heterozygotes together results in better type, but regaining the shaded pattern is hit-and-miss (and with the law of averages, mostly miss). Rarely are the progeny of two outcrosses homozygous at all genes. With patience, close observation, and a sound understanding of the genetics behind the pattern, progress is possible in 2 to 4 generations, even in the shaded ASH pattern.

### **SUMMARY**

The shaded shorthair genotype is one of the oldest American Shorthair color patterns and genetically most complex color patterns ever reported. Many attributes that make up the shaded shorthair phenotype: agouti, unpatterned tabby (U<sub>-</sub>), at least 3 sets of polygenes that clean up the residual striping, and at least 2 sets of polygenes that influence the number of bands on the hairs. The outcrossing of shaded ASH with classic tabbies show these attributes are independently inherited. First generation kittens show distinct stripes on the head, neck, legs, and tail and may appear very light (shaded) or very dark (ticked tabby) depending on the recombination of genes inherited from each parent. A sound understanding of the genetics behind the shaded color is essential to being able to utilize tabbies in a shaded ASH program. Knowledge of the genetics behind the shaded and classic tabby patterns helps explain why it takes between 2 and 4 generations to get the color back following a shaded to tabby breeding.

## **ACKNOWLEDGEMENTS**

Special thanks to Dawn Skupin for her review and encouragement. The writer would like to thank the following persons for their input: Margo Melles for scientific review; Heather Lorimer and Lorraine Sheldon for scientific discussion; Dawn Skupin, Leo Halblieb, Gail Johnson, Kathy Needham, Janee Waterman, Wayne Park, David DeOre, and Dee White for sharing their breeding stock and for Nobuko Kuruso, Mary Robinson, Gayle Johnson, Charlene Rankin, Howard Webster, and Jeanette McCormick for sharing their experiences with shaded American Shorthairs.

## **REFERENCES**

1. Johnson CW. The shaded American Shorthair. In 1999 Cat Fanciers' Association Yearbook, Cat Fancier's Association Inc, New Jersey, in press
2. Johnson CW The shaded American Shorthair. Cat Fanciers' Almanac 15(7):14, 1998
3. Edwards VA A rainbow of colors. American Connection, Fall 1994
4. Stephen G. Legacy of the Cat. Yama-Kei Publishers Co. Ltd 1989 Japan
5. Lorimer. The silver inhibitor gene. Cat Fancier's Journal
6. Wright M, Walters S. eds. The Book of the Cat. Summit Books, 1980, New York