TRICOLOR INHERITANCE. II. THE BASSET HOUND[1]

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Part I of the present series deals with the inheritance of the tricolor condition in guinea-pigs. One of the reasons for undertaking that work was to shed some light on the inheritance of the tricolor coat in Basset hounds, which were studied biometrically by GALTON (1897) as a test of his "law of ancestral inheritance."

In the years intervening between the publication of GALTON's paper and the present it has been thoroughly established in a large number of mammals that color is inherited in Mendelian fashion. It seems perfectly reasonable to suppose, therefore, that the same is true in Basset hounds. The object of the present paper is to discuss the probable genetic factors involved in the production of the coat color in Basset hounds, their relation to each other, and test matings which could be made to determine how closely the factors and relationships proposed fit the actual cases.

CASTLE (1912) has given a rather brief and incomplete explanation on the Mendelian basis. It seems probable from some of his statements that he was not quite certain of the actual appearance of the Basset hound. A clear conception of the distribution of the color markings is necessary before one can hope to work out successfully the factors involved and their relationships. It therefore seems advisable, before proceeding farther, to sketch briefly the history and general appearance of the Basset hound, laying special stress on the distribution of the color markings.

The Basset is probably a very old breed of dog, having been known to exist in France for several centuries (BARTON 1910). It was first brought into prominence in England by Sir EVERETT MILLAIS, who imported from France in 1874 a famous Basset, called "Model."

In "The dog" (1881(?), p. 336), edited by VERO SHAW, appears a

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letter by MILLAIS in which is given a description of the Basset. The letter is undated, but it is clear from the context that it was written in 1880, thus being one of the earliest if not the earliest English description of the breed. To quote from the letter, "Colour of course is a matter of fancy, although I infinitely prefer the 'tricolor,' which has a tan head and black-and-white body." In the same volume is a colored plate showing three prize-winning Bassets imported by GEORGE R. KREHL in 1881. All three have tan-and-white heads, with black patches on the back, but with the black running into tan on the hind quarters.

KREHL wrote a description of the breed for "The dogs of the British islands", edited by "STONEHENGE" (J. H. WALSH 1886). He gave what he called the "Points of the Basset hound." These were subsequently adopted by the Basset hound Club. Point 8 is, "The colour should be black, white and tan. The head, shoulders and quarters a rich tan, and black patches on the back. They are also sometimes hare-pied." Figure 1 represents what BARTON considers a "typical smooth-coated Basset bitch."

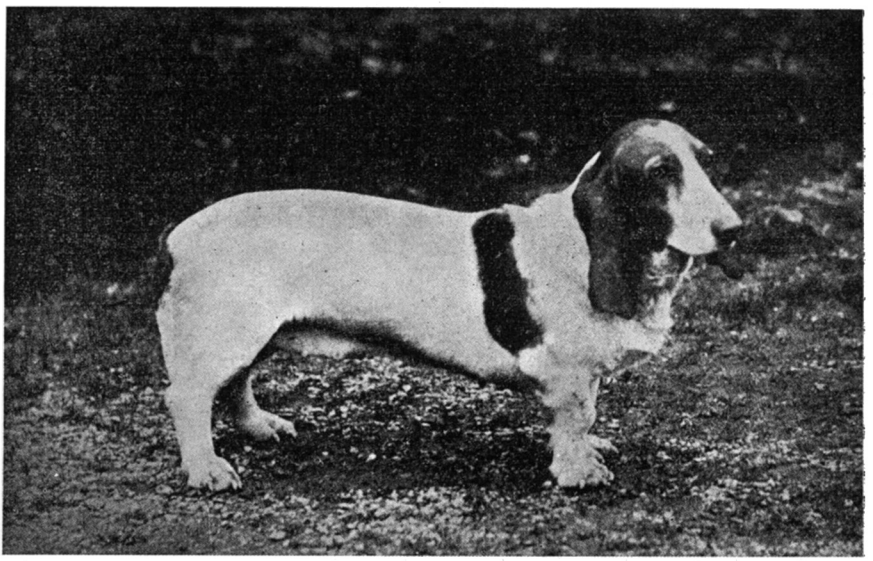

Figure 1. Basset hound. Characterized by BARTON as a "typical smooth-coated Basset bitch." Note the tan on the head and the small black patches on the back and at the base of the tail. (From BARTON 1910.)

It is evident from the above that the ideal to be striven for was quite early fixed in the minds of the breeders. In spite of this, however, it was found impossible to get the tricolors (black-white-and-tan) to breed

true. Tan-and-whites occasionally cropped out and these when bred together produced tricolors besides tan-and-whites. In a letter to the author, dated March 22, 1915, J. SIDNEY TURNER, editor of "The kennel encyclopedia," writes that tricolors "still throw a considerable number of tan-and-whites when bred together." It was this phenomenon which GALTON studied and to which he applied his law of ancestral inheritance.

Before going into a more detailed description of the color relations in the breed it is probably best to name and describe those factors pertaining to color which have already been studied in dogs and which may possibly have some application to color inheritance in Basset hounds.

LITTLE (1914) has made a study of coat color inheritance in Pointer dogs. He finds that two factors by their presence or absence determine all the colors produced. The factors are *B* and *E*. *B* is the factor for black, *b* for liver (chocolate or brown), *E* is the extension factor. When *E* is present it extends the black (*B*) or liver (*b*) so that the pigmented part of the coat is either black (*EB*) or liver (*Eb*). When *E* is absent and *B* present, i.e., *eB*, the black is not extended and is found only on the nose, the pigmented part of the coat being tan (red or yellow). When *B* also is absent, i.e., *eb*, the pigmented part of the coat is tan and the nose brown. LANG (1910) had previously determined that black is dominant to liver or brown.

BARROWS and PHILLIPS (1915) worked with Cocker spaniels. They find that the factors *B* and *E*, in addition to others controlling white spotting, dilution, etc., are concerned in the color inheritance of these dogs also. What is of special interest in connection with their work, because of its application to the Basset hound color, is their study of the "bicolor" condition. By "bicolors" they mean black-and-tans, liver-and-tans and "red[tan]-and-lemons." A black-and-tan Cocker spaniel is a "black dog having dark or light red or lemon spots over each eye, and extended red areas distributed on the sides of the muzzle, inside of the ear, posterior surfaces of the legs, and on the ventral sides of the chest, abdomen, and tail" (BARROWS and PHILLIPS 1915, p. 395). A liver-and-tan is liver(chocolate)-colored where a black-and-tan is black. In a red-and-lemon the body color is red, while those portions which are tan in a black-and-tan are here lemon in color. BARROWS and PHILLIPS apply the term "bicolor" only to the colors mentioned above and not to dogs showing a combination of one of these colors with white. The black-and-tan pattern as found in Cocker spaniels is probably the one usually found in dogs. Some black-and-tan breeds, as for instance Airedale terriers, have more than the usual amount of tan. According

to the Airedale "standard" the "head and ears, with the exception of dark markings on each side of the skull, should be tan, the ears being of a darker shade than the rest. The legs up to thighs and elbows being also tan. The body black or dark grizzle."

My own experience with self black, tortoise and self red guinea-pigs (IBSEN 1916) had led me to suppose that black-and-tan in dogs might correspond to tortoise in guinea-pigs. In Part I tortoise in guinea-pigs was interpreted as being due to a modification of the extension factor (E), being the middle term in the allelomorphic series E, e^p and e. Such, however, does not seem to be the case in dogs. BARROWS and PHILLIPS state that the bicolor condition is recessive to the non-bicolor or self-colored. Since both self black (E) and self red (e) dogs are non-bicolors and bicolor is recessive to both, it is evident that the bicolor condition is not due to a modification of the extension factor (E), but to some entirely independent factor.

Although BARROWS and PHILLIPS determined the general relation of bicolor to the self-colored condition, they made no attempt to treat the relation factorially. This I am doing by introducing the factor T. When T is present the animal is self-colored; in its absence it is bicolored. In the presence of E the bicolored condition manifests itself as black-and-tan; in the absence of E as red-and-lemon. In order that complete extension of black or chocolate pigment be realized it is therefore necessary that T be present as well as E. The relation of T to the other factors may be shown in the following manner:[2]

BET = self black,
BEt = black-and-tan,
BeT = self tan (red) with black nose,
Bet = red-and-lemon with black nose.

On this interpretation a self tan of the formula $BBeeTT$ mated to a black-and-tan ($BBEEtt$) should have only self black offspring ($BBEeTt$). There is no record of such a mating in BARROWS and PHILLIPS'S paper.

The black-and-tan factor in dogs differs decidedly from the factor for a pattern with the same name in rabbits. In the latter it is a modification of the agouti factor and forms an allelomorphic series with agouti (A) and non-agouti (a) (CASTLE and FISH 1915). There are also black-and-tan mice but the inheritance of the pattern in these animals has not as yet been reported on.

[2] I am assuming for the sake of simplicity that the animals are entirely pigmented, i.e., there is no white.

There is one more color factor in dogs which should be mentioned. BARTON (1910), in the section on Dachshunds, writes,

"As a rule, the crossing of a black-and-tan Dachs with a red one, produces puppies true to type, i.e., some are black-and-tan, others red, and not a mixture of these two colours. *A red dog and bitch, will, however, sometimes throw a black-and-tan puppy*,[3] or a black-and-tan sire and dam produce a whole-red puppy. This is precisely what happens with certain other varieties."

It seems, therefore, that in dogs we have a red which is dominant to black-and-tan. HAGEDOORN (1912) also makes mention of this factor. The probabilities are that it is a restriction factor which inhibits the production of black pigment in the coat. I am calling this factor *R* (restriction or dominant red). If we can believe the statements of fanciers the *R* factor is found in rabbits also, since Rufus Reds bred together may have self black offspring.

We are now in a position to take up somewhat in detail the inheritance of color in the Basset hound. It is evident that the tricolor coat is due to black-and-tan plus white spotting. The tan covers more of the body than it does in most black-and-tans, but there are breeds, such as the Airedale terriers, previously mentioned, which have as much tan and as comparatively little black as have the Bassets. The white spotting may be disregarded factorially because it is always present. Besides, its exact relation to the entirely pigmented coat has not as yet been satisfactorily settled, and it would only unnecessarily complicate matters to bring in the discussion of this relation.

Tricolor Bassets never have liver-colored (chocolate or brown) spots instead of black, and they must therefore be homozygous for black (*B*). They may, however, have progeny without any black spotting whatever, which makes it fairly certain that they can be heterozygous as well as homozygous for *E*. This will be discussed later. They must always be homozygous for the absence of *T*, because if *T* were present none of the tan would show and we would have black-and-whites instead of tricolors. There is no record of any black-and-whites ever occurring among Basset hounds. The *R* factor must also be absent, otherwise the dog would be a tan-and-white instead of a tricolor. The zygotic composition of a tricolor Basset hound may therefore be put down (disregarding white spotting) as either *BBEEttrr* or *BBEettrr* depending on whether it is homozygous or heterozygous for *E*.

At this point it will be necessary to consider the distribution of white

[3] Original not italicized.

spotting in dogs in order to show how it may affect the appearance of the black-and-white pattern. ALLEN (1914) has given diagrams (figure 2) showing the usual location of the white areas in a series of dogs

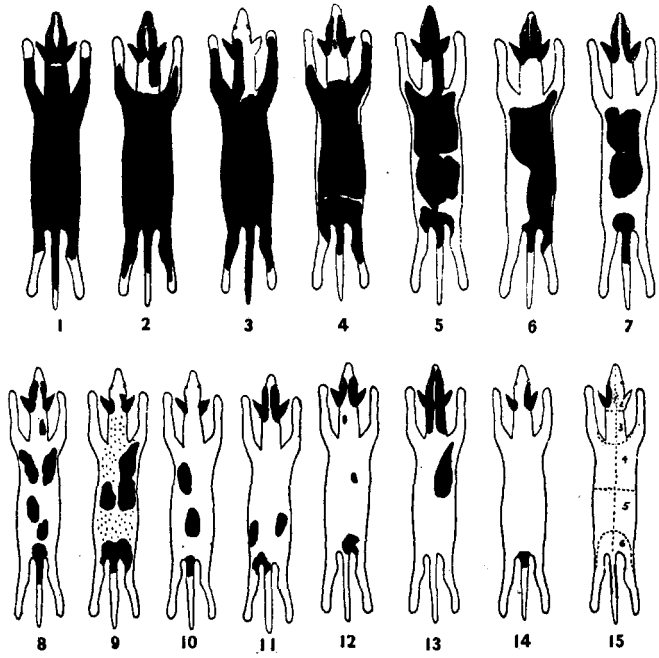

Figure 2. Diagram showing the location of white pigment in a series of dogs (ALLEN 1914).

from those which are largely pigmented to those which have only a small amount of pigmentation. ALLEN used these diagrams to illustrate the fact that as the pigment decreases in amount it draws towards definite centers from which it disappears last. He did not point out what also appears to be a fact in dogs, namely, that the last centers from which the pigment disappears are the ones designated by him the aural patches. It will be noted that every dog in his diagrams has pigment on the head even though the rest of the body is entirely white. It is significant for our purposes that if a dog has the pigment reduced to a single area this is always located on the head, so far as observation goes. This condition is not unusual in some breeds, such as fox-terriers, and may be seen occasionally in a number of others.

We may now take up in some detail the possible kinds of offspring resulting from the mating together of tricolors. The first type of mating to be considered will be that in which at least one parent is homozygous

for the extension factor (E), thus insuring that all the offspring shall carry the E factor. This means in Basset hounds that the head, shoulders and quarters are tan with black patches on the back, providing there is a fairly small amount of white spotting. TURNER, in the previously quoted letter, states, "I remember that MILLAIS told me that it was necessary to return to heavily marked blacks to keep up the tricolours." This means that the offspring of tricolor Bassets oftentimes have a larger amount of white than the parents. If figure 1 is, as BARTON states, a typical Basset, it can easily be seen how a comparatively slight reduction in the amount of pigmentation would leave only the head pigmented. Animals pigmented in this manner would be tan-and-whites. If tricolor Bassets had the more usual black-and-tan pattern (see p. 369), which means the presence of black areas on the head also, the number of E tan-and-whites would be greatly decreased, since it would require more white to blot out all the black. In order for a black-and-white Basset to be obtained from tricolor parents it would be necessary that the entire head, shoulders and quarters be white and that there be a pigmented patch (black) on the back. This, as we have seen, never occurs in dogs. Black-and-whites may be obtained from tricolor guinea-pigs because of the fact that there is no regularity in the distribution of the black and red, and also because there is no regularity in the distribution of the white areas.

Tan-and-white Bassets of tricolor parentage carrying E are necessarily, therefore, pigmented only on the head, and when bred together should get tricolor offspring as well as tan-and-white. I have never seen any photographs of tan-and-white Bassets, but in answer to a query, TURNER, in a letter of March 22, 1915, replies, "Tan is often found on the back of tan-and-white (no black) Bassets and foxhounds." This implies that those with tan only on the head are to be found, and the probabilities are that many of them carry E. In the next paragraph tan-and-whites with tan spots on the back as well as on the head will be discussed.

If Ee tricolors are bred together we may expect somewhat different results. There is always the possibility of getting E tan-and-whites, pigmented only on the head, but in addition we would expect one-fourth of the offspring to be tan-and-whites due to the absence of E. These may or may not have tan spots on the back, depending on the amount of white. We see from the foregoing that tan-and-whites pigmented only on the head, from tricolor parents, may or may not carry the E factor; but tan-and-whites pigmented also on the back, from tricolor

parents, are always *ee* and should therefore breed true. We should expect these animals to have a somewhat lighter shade to the tan spots on the head than to the tan spots on the back since they are of the formula *BBeettrr* and hence white-spotted red-and-lemons. It is impossible to determine from GALTON's data whether or not tan-and-whites ever breed true or whether they ever show the red-and-lemon pattern. In the studbooks the distribution of the tan spots is never denoted and it seems that the only method whereby these questions can be settled is by actual breeding tests.

So far we have avoided the *R* factor by starting out with parents both of which were tricolors and hence *rr*. There is no way at present of determining whether or not this factor is found in the Basset hound. If it were, all the animals carrying it would necessarily be tan-and-whites. It is possible that they might differ in some respects from the previously described tan-and-whites, but nothing seems to be known on this subject. One could be certain that the factor existed in the breed if two tan-and-whites with tan patches on the back should get tricolor offspring. This would indicate that both parents were *Rr*.

GALTON (1897) states that among the 818 animals whose colors were known to him there was one which was described as a black-and-tan.[4] CASTLE (1912) thinks this corresponds to the black-and-whites found in the tricolor series in guinea-pigs. HAGEDOORN (1912) on the other hand is of the opinion that the animal in question was a tricolor showing very little white and therefore bringing the black-and-tan pattern more into evidence. This explanation seems reasonable.

HAGEDOORN makes other statements which seem less incontrovertible. He states,

"In those cases in which two tricolor parents gave lemon-and-white offspring, I feel sure, such young were of that color only because they happened not to be pigmented in a spot where sable [similar to black-and-tan] dogs show black color."

In other words tan-and-whites are genetically tricolors in which the areas that would normally be black are white, but in which some tan spots remain. This would assume that tricolors are always *EE* and therefore may get *E* tan-and-white but never *ee* tan-and-white offspring. He thinks, since tricolors are always black on the back, that all tan-and-whites with tan spots on the back must carry a dominant red factor (*R*). He fails to recognize that tan-and-whites of this description may result from the loss of the extension factor.

[4] This individual was disregarded by GALTON in his inheritance studies.

The question as to the presence of the factor *R* in Basset hounds, as well as some of the other unsettled points, can only be determined by more detailed records or by actual breeding tests.

SUMMARY

1. Basset hounds were imported into England from France by Sir EVERETT MILLAIS in 1874.

2. There are two kinds, (1) tricolors and (2) tan-and-whites. Black-and-whites do not occur in the breed. Tricolors are described as "black, white and tan. The head, shoulders and quarters, a rich tan, and black patches on the back." Tan-and-whites have tan heads and "tan is often found on the back."

3. The factors involved in color inheritance in Basset hounds are: (1) *B*, the factor for black, always present in Bassets. (2) *E*, the extension factor, which extends the black (or chocolate) and may be present or absent. (3) *T*, the factor for uniform pigmentation; animals without *T* are either black-and-tan, liver-and-tan or red(tan)-and-lemon. *T* is always absent in Bassets. (4) *R*, the factor which inhibits the formation of black (or chocolate) pigment in the coat. It is questionable whether this factor is ever present in Bassets.

4. By means of ALLEN's (1914) diagrams of distribution of pigmentation in dogs and by reference to various breeds, etc., it is demonstrated that pigmented dogs always have some pigmentation on the head; when pigmentation is very slight the head is often the only place where it is to be found. Bassets pigmented only on the head are tan-and-whites. Black-and-whites never occur because the head is never entirely devoid of pigment in this breed.

5. Tricolors may be of the formula *BBEEttrr* or *BBEettrr*. *Ee* tricolors mated together get some *ee* offspring which are tan-and-whites and which should breed true. These may have tan spots on the back. In this case, when *T* is absent, the tan on the head should be of a lighter shade than the tan on the back.

6. If *R* is present in Bassets then *BBEE*(or *Ee*)*ttRr* tan-and-whites (with tan on the back) bred together should get some tricolor offspring. This cannot be determined from available data.

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