THE ABC OF COLOR INHERITANCE IN HORSES

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THE study of color inheritance in horses was begun in the early days of genetics. Indeed many facts concerning it had already been established earlier, by DARWIN in his book on "Variation of Animals and Plants under Domestication." At irregular intervals since then, new attempts have been made to collect and classify in terms of genetic factors the records contained in stud books concerning the colors of colts in relation to the colors of their sires and dams. A full bibliography is given by CREW and BUCHANAN-SMITH (1930).

By such studies, we have acquired very full information as to what color a colt may be expected to have, when the color of its parents and grandparents is known. This knowledge is empirical rather than experimental in nature. For horses being slow breeding and expensive are rarely available for direct experimental study, such as can be made with the small laboratory mammals, mice, rats, rabbits and guinea pigs.

We have definite information that color inheritance in horses involves the existence of mutant genes similar to those demonstrated by experimental studies to be involved in color inheritance of other mammals. But the horse genes have been given special names, as they were successively discovered, and it is difficult at present to correlate them with the better known names and genetic symbols used by the experimental breeders.

The present paper is an attempt to make such a correlation. Just as in morphological studies *comparative* anatomy was found useful and still is used to establish homologies between systems of organs, so in mammalian genetics, a comparative study of gene action in the production of coat colors and color patterns may also be of value.

BASIC COLOR GENES OF MAMMALS

1. *The color gene C*

Three basic color genes of mammals constitute what I shall call the *A B C* assemblage of genes. The first to be dealt with here is the dominant color gene, *C*, which must be present and active in order that any color whatever may be produced in skin, hair, or eye. Eye pigmentation, as the comparative morphologist will tell you, is only a special localized development of the general integumentary pigmentation of a mammal, and there is a definite relation, amounting in some cases to a positive correlation, between coat color and eye color. To this point we shall return later.

The dominant color gene *C* is subject to mutation to a recessive allele, in a

great majority of mammals. Albinism is the earliest observed and best known of color mutations in most mammals. Mutation to a completely inactive state, of the color gene, expressed by the symbol *c*, constitutes when homozygous, *cc*, a true and complete albino having a wholly unpigmented skin, coat, and eyes. The eyes appear pink because of the red blood corpuscles in the back of the eye, the red color of which "shows through" because not screened by intervening pigment cells as in the eyes of animals of normal full color. Familiar examples of true albinos are found in white mice, white rats, and the commonest variety of white rabbit.

There occur in certain mammals, recessive mutations of the color gene, in which color is produced in reduced amounts as compared with full colored individuals. STURTEVANT (1913) called attention to a now well known case, Himalayan rabbit, which has pink eyes but a coat generally white, yet with colored extremities, ears, tail and feet. The Himalayan allele of the color gene has been designated, c^H. As pointed out by STURTEVANT, this case and similar ones discovered later, gave a body blow to the presence-absence theory of gene mutation previously held by geneticists, for it showed that a gene may change to a reduced (or more rarely to an accelerated) degree of activity without disappearing or becoming wholly inactive. In the rabbit the known alleles of the color gene number at least six, the best known being *C*, c^{ch}, c^H and *c*, found respectively in normal full-colored, chinchilla, Himalayan, and ordinary white rabbits. Dominance occurs in the order named, but heterozygotes are frequently intermediate in degree of pigmentation. No true albino mutation of the color gene is known among horses, though several varieties of white horse are popularly known as albinos. To their discussion we shall return later.

As a result of the activity of the dominant color gene *C*, a mammal begins to produce black pigment in its integumentary system even before birth, the first formed pigment generally being visible in the eye. Later the skin of the extremities and eventually the emerging hairs also become pigmented. The pigment of the eye consists exclusively of black granules located in the cytoplasmic portions of cells of the eye capsule.

In the emerging hairs also the first formed pigment consists of intensely black pigment granules, so the hair tips are regularly black. Later the hair, as it emerges from the hair follicle, may cease for the time being to produce black pigment, replacing it with a less granular and more diffuse yellow pigment. Thus the black hair tip may come to have below it a band of yellow or red, as in the familiar *agouti* pattern of wild rodents, and of many other wild mammals.

2. *The color pattern gene A*

The second basic color gene of the mammalian system of genes, may accordingly be called a *color pattern gene*, or a wild color gene, exemplified in the agouti gene, *A*, of rodents. Nearly all mammals have such a pattern gene, and many of them have carried it over into domesticated races. Everyone is familiar with the gray (agouti) pattern of the cotton-tail rabbit. The hairs of back and sides are black-tipped, with a sub-apical band of yellow, succeeded by a more diffuse bluish-black base. The hairs of the belly and under side of the tail are

white without black tip. There are other details of the pattern which we need not go into. All owe their existence to a single coat pattern gene, *A*, interacting with the gene for color production, *C*. Thus a rabbit of genetic constitution, *A A C C*, is a true breeding gray, like wild rabbits generally.

If the pattern gene *A* becomes completely inactive by mutation to the recessive allele, *a*, an animal homozygous for the mutant gene, *a a*, will completely lack the wild pattern and will be uniform black, all over. Thus the genetic formula of a black rabbit may, as regards genes *A* and *C*, be written *a a C C*. It will of course be true breeding because homozygous.

A less extreme mutation of the pattern gene, *A*, in rabbits results in an allele a^t, which when homozygous, $a^t a^t$, produces a black-and-tan rabbit. Such an animal has a black (not a gray) back and sides, with whitish belly and tail, and agouti banded guard hairs in the border between belly and sides. As compared with the gray allele, *A*, the black-and-tan allele, a^t, when homozygous, produces a greatly reduced agouti pattern, but not a completely lacking one, as the *a* allele does when homozygous. Thus in rabbits the pattern gene, regularly present in wild rabbits, which are gray, *A A*, may by mutation to $a^t a^t$ become black-and-tan, or as more commonly by mutation to *aa* become uniform black.

In rabbits and certain other mammals, the wild color pattern may be obscured more or less completely, by dominant mutation in a gene *E* (extension of dark pigment) to E^D, as a consequence of which the amount of black pigment is either greatly increased or its distribution extended so that it hides the wild pattern, even though the wild pattern gene is still retained. The genetic formula of this mutation, which has been called *dominant black*, is *A A* (or *A a*) *B B* (or *B b*) $E^D E^D$ (or $E^D E$). It differs from recessive black, *aa B B* (or *B b*) *E E*, in its retention of the wild pattern gene *A*, though this is hidden in the presence of E^D. If a dominant black is outcrossed resulting in a separation of E^D from *A* then the *A* may again become visible. Thus a dominant black rabbit may produce gray offspring, when mated with recessive blacks, a thing which recessive black rabbits mated with each other cannot do.

Among both dogs and cats a similar mutation of *E* to E^D has been observed. resulting in the production of a dominant black variety. Elsewhere I have suggested that a similar mutation may have occurred in the *A* gene in horses, and that this may be the explanation of the puzzling but seemingly authentic records in certain stud books, of the production of bay colts by black parents supposed to be homozygous recessives. To this matter we shall return later.

When we come to the discussion of the coat pattern genotypes of horses, we shall need to have in mind the gene mutation possibilities illustrated in the case of the rabbit and other rodents.

3. The black color gene B

We have noted that the color gene, when fully active, and with no modifying action of a pattern gene, results in a black pigmented integument including eyes, skin and hair.

But a mutational change from black to brown in the *quality* of the pigment produced, indicates that another gene, which we may call the gene for black, *B*, acts with *C* to produce black integumentary pigment. For if this hypothetical black gene, *B*, mutates to a recessive allele, *b*, which then becomes homozygous, *b b*, the resulting pigment produced is chocolate brown instead of black. Examples are found among mice, rats, rabbits, guinea pigs, and dogs.

Of the three basic color genes, *A B C*, which have been discussed, we may by appropriate breeding operations secure the genetic combinations listed in table 1. This has been repeatedly demonstrated in the case of laboratory mammals, mice, rats, rabbits, and guinea pigs.

TABLE 1

Genetic and phenotypic variation resulting from various combinations of the three basic color genes of mammals, A, B, and C.

GENOTYPES	PHENOTYPES
1. *AA* (or *Aa*) *BB* (or *Bb*) *CC* (or *Cc*)	Wild color pattern, black pigmented.
2. *AA* (or *Aa*) *bb CC* (or *Cc*)	Wild color pattern, brown pigmented.
3. *aa BB* (or *Bb*) *CC* (or *Cc*)	No wild pattern, black pigmented.
4. *aa bb CC* (or *Cc*)	No wild pattern, brown pigmented.
5. Combinations 1–4 of *A* and *B*, with *cc*.	Albinos, all alike in appearance, but differing in breeding potentialities as indicated by the combinations of *A* and *B* listed under 1–4.

BASIC COLOR GENES OF HORSES

1. Gene C

In horses there must be a basic dominant color gene, *C*, as in other mammals, since all horses are colored, if not in their coat, at least as regards their eyes and, if they live long enough, as regards skin spots also. But no true albino mutation of the color gene is known among horses. Certain types of horses popularly known as "albino" are really colored animals in which the amount of pigment production is reduced or localized by the action of one or another mutant gene, presently to be discussed.

2. Gene A

A dominant color pattern gene is present in the wild Prejvalski horse, the sole surviving variety of horse not in domestication. The same pattern is expressed in the bay variety of domestic horse, as defined by SALISBURY (1941). We shall designate the pattern gene *A*, as in other mammals.

3. Gene B

A mutation of the black gene *B*, to the recessive allele, *b*, was one of the

first described color mutations of horses. Its validity is acknowledged by practically all investigators.

In table 2 are listed the theoretically possible combinations among horses of

TABLE 2

Genetic and phenotypic variation of horses resulting from various combinations of the basic color genes A and B.

GENOTYPE	PHENOTYPE
1. *AA* (or *Aa*) *BB* or (*Bb*)	Bay, also "brown" in many stud books.
2. *AA* (or *Aa*) *bb*	Chestnut, sorrel, also "brown" in many stud books.
3. *aa BB* (or *Bb*)	Black.
4. *aa bb*	Liver.
5. (Hypothetical) *A'A'* (or *A'A* or *A'a*) *BB* (or *Bb*)	Dominant black.

the dominant genes, *A* and *B*, and of their recessive mutants, *a* and *b*. Also listed is the hypothetical "dominant black." If it really exists, the reported anomaly of bay colts produced by black parents would be explainable as follows.

The gametes of a dominant black of constitution *A'ABB* would be either *A'B* or *AB*. Mating together two such animals would result as follows:

		Gametes of dam	
		A'B	*AB*
Gametes of sire	*A'B*	*A'B* *A'B* Black	*AB* *A'B* Black
	AB	*A'B* *AB* Black	*AB* *AB* Bay

Mating of such a dominant black with a recessive black would result thus:

		Gametes of dominant black	
		A'B	*AB*
Gametes of recessive black, all	*aB*	*A'B* *aB* Black	*AB* *aB* Bay

If the dominant black parent were homozygous for A', all colts would be dominant black ($A'aBB$) in a mating with a recessive black. So it will be seen that if dominant black horses are a rare occurrence, the production among their progeny of bay colts would be an even rarer event, when the mate was a recessive black, as most black horses are.

In the foregoing account I have not thought it necessary to assume the existence of an independent extension factor E, separate from A, as has been done in the case of mammals with the agouti type of wild coat. Because the wild pattern of horses is itself a sort of *extension* factor, localizing black-brown pigment principally in mane, tail and legs. Whether the assumed change of bay to dominant black has occurred by mutation in the bay factor A or in an independent E factor may well be left an open question. For the purposes of description, I am employing the former assumption, but no direct evidence in its favor is at present known. Indeed the very existence of a dominant black mutation in horses is purely hypothetical, but its existence in rodents and carnivores has been so clearly demonstrated that its occurrence also in horses is not improbable, and is strongly suggested by the stud book records of bay colts from parents both black.

SALISBURY lists the basic phenotypes of horses as recorded in stud books as follows.

"1. *Bay.* A bay horse or pony is one having a black mane and tail, black feet and legs, the black often extending as high as the knees and hocks, and a red-colored body of several different shades, which may vary from a light bay through the various intermediate shades to a dark, cherry red.

2. *Brown, brown-black or seal brown.* The brown color is sometimes confused with bay and, if the individual is especially dark, may be confused with black. It is accompanied by black mane, tail, feet, and legs. The body is brown varying to black, but the muzzle, the region about the eyes, the flanks and the underlines, especially in the groins, are a lighter shade of brown. These "light points," as they have been designated by GREMMEL (1939), are variable in extent and intensity of pigmentation. This fact has led to confusion in the identification of animals for registration purposes and explains the rather high proportion of browns resulting from the black times black mating shown in table 1.

3. *Black.* Black is a uniform color found most commonly in the Percheron breed of horses and Shetland ponies. It is particularly subject to bleaching in sunlight. Bleached-black horses exhibit a marked red tinge to the hair which approaches bay or brown in color.

4. *Chestnut.* This color is variable in shade and is generally broken into three classes: the liver chestnut, the chestnut, and the sorrel. This group is characterized by a reddish-brown color varying in shade from a dark chocolate, in the case of the so-called black chestnut and liver chestnut, to the lighter, reddish, golden-brown of the sorrel. There is much confusion in the designation of these colors. Saddle horse breeders usually refer to all of these colors as chestnut, while the draft horse breeder and the western stockman often classify all

but the liver chestnuts as sorrels. The mane and tail of this color group is the same color as the body, or lighter. In some cases the mane and tail may be nearly perfect white. This is an independently inherited characteristic and occurs on each of the shades of chestnut. The pasterns and legs are generally lighter in shade than the body. The color is lightest around the hoof-heads and fetlock joints, becoming progressively more like the body color farther up the leg."

A comparison of SALISBURY's list with table 2 shows these correspondences or discrepancies. The stud book designation "brown" is ambiguous, since it includes horses both of genotype 1 and genotype 2, table 2. SALISBURY's category black corresponds with genotype 3 of table 2, recessive black, but he does not recognize the existence of the hypothetical dominant black.

Under SALISBURY's definition, a wild Prejvalski horse would be classified as light bay, but with traces of black pigment persisting in the body areas which are red or yellow in a typical bay. There can be no doubt accordingly that the Prejvalski horse possesses the primitive wild color pattern of horses, which in our classification of basic mammalian coat color genes has been designated *A*. For this gene the Prejvalski horse is probably homozygous, *AA*, since it is said to breed true for the wild pattern.

Among domestic horses of many different breeds, black as well as bay horses occur, and it is well known that black is in general recessive to bay. Bay horses which are heterozygous for black produce both color classes in an approximate ratio of three bays to one black. From this we may conclude that the wild pattern gene *A*, has undergone at some time, perhaps repeatedly, mutation to the recessive, *a*, no wild pattern. A bay stallion which produces only bay colts when mated to black mares (*aa*) must be homozygous, *AA*. One which produces both bay and black colts by black mares, must be heterozygous, *Aa*.

Several investigators, who have tabulated the colors of colts recorded in stud books, note the occurrence of a few bays among the colts produced by black times black matings in as high a percentage as 3.6 (WENTWORTH 1913). These are contrary to expectation, if black is recessive to bay, and are usually explained as due to inaccuracies of description of newly born foals. It is possible however that dominant mutation in *A* (or in an associated gene *E*) has resulted in the production of a dominant black phenotype, which in matings with recessive black might produce an occasional bay colt, as already explained.

A dominant gene for black pigment, *B*, is undoubtedly present in bay, and black horses. In some it is homozygous, in others heterozygous. Those which are heterozygous carry the recessive allele, *b*, and are in genetic formula *Bb* animals. Mated with each other, they produce three black pigmented to one brown pigmented colt. Brown pigmented colts are homozygous recessive, *bb*, and are true breeding for the *b* gene, What their phenotype is will depend on whether or not they also carry the pattern gene, *A*.

We may accordingly recognize as valid the possible combinations of *A* and *B* listed in table 2. The color gene, *C*, is omitted from the formulae, since it is assumed to be present and active in all of them.

GENES WHICH MODIFY THE BASIC ABC COLOR COMBINATIONS OF HORSES

1. The dominant dilution gene D, known also as the "dun" factor

The descriptive term dun is used in horse literature in two very different senses. By DARWIN and many others it was used as descriptive of the supposed primitive color of wild horses, which was assumed to be lighter in color than the bay of domestic breeds. After the discovery and capture of Prejavlski wild horses, this assumption of DARWIN was found to be quite correct.

Concerning dun colored horses of the supposed ancestral color, DARWIN has this to say (Animals and Plants, vol. 1, p. 59) "Before entering on any details I must premise that the term dun-colored is vague, and includes three groups of colors, viz., that between cream color and reddish brown, which graduates into light bay or light chestnut—this I believe is often called fallow dun; second leaden or slate-color or mouse-dun, which graduates into ash-color; and lastly, dark dun, between brown and black."

The first and last of DARWIN'S categories of dun-colored horses would apparently involve association of wild coat pattern, *A*, with a red or yellow body color. It is doubtful whether either of them includes the dominant dilution gene, *D*, which is basic to the constitution of buckskin horses, Palominos, and albinos of types *A* and *B*. But it is possible that the second category (slate color or mouse-dun) does include *D*, corresponding to genotype 3, table 3.

Under the listing quoted from SALISBURY, a Prejvalski horse would be rated light (yellowish) bay. This is probably what DARWIN rightly conjectured that the primitive color of wild horses was. He called it dun. There is no reason to think that a "dun" horse of this sort possessed the dominant dilution factor, *D*. Horses which *do* possess the dominant dilution gene *D* in heterozygous combination, *Dd*, in association with *B*, will in this discussion be called dun, or by a more sharply defined descriptive term current in the southwestern United States, *buckskin*.

Where or when the dominant dilution (dun) mutation of horses originated is uncertain. It is believed among horsemen to have been brought from Spain to Mexico by the Spaniards and to have spread thence into Texas and California. Certain it is that buckskin and particularly Palomino mounts have long been popular in cowboy circles in the southwest. Movie patrons have seen beautiful Palomino mounts ridden in thrilling Westerns. The genetics of the Palomino horse has been discussed in detail by CASTLE 1946.

For the known and hypothetical combinations of the basic genes *A* and *B* with the dominant dilution gene *D*, see table 3.

The ideal Palomino is described by its fanciers as a horse with body color of golden yellow "like new-minted gold," but with a white mane and tail. How can a yellow horse acquire a white mane? For a tentative explanation, see the following section.

2. The special gene f for light mane in sorrel and Palomino horses

According to WENTWORTH (1913) some sorrel horses have mane-and-tail of the same general reddish color as the body, while other sorrels have mane-and-tail lighter in color than the body, being known popularly as "sorrels with flaxen mane-and-tail." WENTWORTH found light mane to be a recessive character, a conclusion which SALISBURY and BRITTON (1941) accept with qualification.

We should expect sorrels of uniform color all over to be of genotype 4, table 2, lacking the dominant *A* gene which would segregate chocolate brown pigment in the mane-and-tail from red pigment prevailing in the body. But sorrels which show a contrast between body and mane probably owe this to the action of the pattern gene *A*. If so, they should have predominantly chocolate-brown pigment in the mane, and predominantly red pigment on the body.

How then can the mane be *lighter* in color than the body, since chocolate-brown pigment is certainly darker than red?

For an answer to this question, we may with profit look again to the genetics of rodents. In mice, rats, and guinea-pigs, mutations are known which act differentially on black-brown pigmentation and yellow-red pigmentation respectively. The mutant gene for pink-eye, *p*, a recessive, is best known in mice and rats in the phenotype called "pink-eyed yellow." Here the black or brown pigment is so reduced in amount that the eye is practically unpigmented, whereas the coat shows yellow-red pigment in wholly unreduced amount.

In rats a mutation known as "red-eyed yellow" has similar but less extreme effects than those of the pink-eye mutation. In this mutant, enough black-brown pigment is produced to obscure partially the color of the red blood reflected toward the observer from the back of the rat's eye. So the eye appears reddish-black, the coat yellow. This mutant gene is designated *r*.

In the genotype *aa rr* (non-agouti red-eye) the body pigmentation, it would seem, *should be uniform black*. As a matter of fact, it appears to be a *muddy yellow*. Rat fanciers call it "cream" to distinguish it from the bright "yellow" of the genotype *AA* (or *Aa*) *rr*. In the "cream" phenotype, the coat-pigment is really *black* (as modified by the action of gene *r*). Optically, it looks more like a yellow, than a black.

This case is described to show that mutations can and do occur among mammals which affect differentially production of black-brown pigments and yellow-red pigments respectively.

The suggestion is offered that the special gene for light mane in sorrel horses, reported by WENTWORTH and by SALISBURY, belongs in the category of genes reducing the intensity of black-brown pigmentation without affecting appreciably the intensity of yellow-red pigmentation. We may for convenience refer to it as gene *f* (flaxen mane-and-tail).

Evidently its action in reducing the intensity of black-brown pigments is much less than that of the pink-eye or even of the red-eye gene of rats, but it may be sufficient in amount to make the *brown* pigment of a sorrel horse's

mane-and-tail *lighter* in color than the *yellow-red* pigmentation of its body.

SALISBURY states, in the passage quoted on page 28, that in sorrel horses having a light mane, pasterns and legs as well as mane and tail are lighter in shade than the body. These regions are precisely those in which brown pigment predominates.

It is doubtful whether the dilution gene *D* in horses, itself has a differential action like that of gene *f*. For when it is heterozygous (*Dd*) as well as when it is homozygous (*DD*), it produces reduction in intensity both of black-brown and of yellow-red pigments. Thus a buckskin colt (genotype 1, table 3) has

TABLE 3

Genetic and phenotypic variation of horses resulting from various combinations of the basic color genes, A and B, with the dominant dilution gene D.

GENOTYPE	PHENOTYPE
1. *AA* (or *Aa*) *BB* (or *Bb*) *Dd*	Buckskin ("dun"). Body color yellow, eyes dark, mane and tail black.
2. *AA* (or *Aa*) *bb Dd*	Palomino. Body color golden yellow, eyes dark, mane and tail usually "white" (lighter than body color).
3. *aa BB* (or *Bd*) *Dd*	Mouse. Body color, as well as mane and tail, yellowish black; no light points.
4. *aa bb Dd* (hypothetical)	Body and mane of same color, cream; eyes dark.
5. *AA* (or *Aa*) *BB* (or *Bb*) *DD*	Albino, type B. Body color cream; mane darker than body, cinnamon-buff of RIDGEWAY, eyes blue.
6. *AA* (or *Aa*) *bb DD*	Albino, type A. Body ivory white, mane white (lighter than body,)* eyes blue, skin pink.
7. *aa BB* (or *Bb*) *DD* (hypothetical)	Albino, type D. Body and mane same color, sooty cream; eyes blue, skin pink.
8. *aa bb DD* (hypothetical)	Albino, type C. Body and mane of same color, very pale cream, eyes blue, skin pink.

* "Practically colorless, closest to RIDGEWAY'S pale olive buff, but paler," Authority Dr. S. Benson.

a cream colored body and a black mane, but a type *B* albino (genotype 5, table 3) has a much paler yellow body color and a rust colored rather than a black mane. Both body and mane pigmentation are simultaneously reduced in intensity in the homozygote, as compared with the heterozygote.

It becomes clear accordingly that if the Palomino breeder wants to realize his color ideal, of "a coat like newly minted gold, but with white mane and tail," he needs only to synthesize the genotype *AA* (or *Aa*) *bbDdff*, a genotype homozygous for two recessive genes, *b* and *f*, preferably also for *A*, but *heterozygous for D.*

3. *The dominant white gene, W, contrasted with other types of "albino" mutations*

True albino horses are unknown, but the name albino has been applied to certain combinations of the basic color genes *A* and *B* with the gene for dominant dilution *D*, as indicated in table 3. The name albino has also been applied to white horses which possess a gene for dominant white, epistatic in crosses with all colored types of horses.

The AMERICAN ALBINO HORSE CLUB INC. of Butte, Nebraska has registered as "albinos" several hundred white horses most of which would seem to be dominant white. Their color is a clear white, not ivory white as in type A albinos (table 3). The eye color is brown (rarely blue), skin pink. Most of the horses bred on the White Horse Ranch at Butte are descendants of a white stallion known as Old King bred to colored (mostly Morgan) mares. At least 50 percent of his colts were white, so that his genetic formula was beyond question *Ww*. The same heterozygous constitution seems to have been found in the white stallions, descendants of Old King, which replaced him at the head of the White Horse stud. For none of them has produced 100 percent white colts when bred to colored mares, though a majority of the colts are white when both parents are white. This fact suggests to a geneticist that the *WW* genetic combination is possibly lethal as it is known to be in dominant white mice. Such lethality need not involve abortions or production of abnormal embryos, but merely an increased proportion of "misses," when white is bred to white, as compared with that observed when a white horse is bred to a colored mate.

All the offspring of a dominant white horse which inherit the *W* gene will likewise be dominant white animals. The color of colts which do *not* inherit the *W* gene, will be determined by the genetic constitution of sire and dam, irrespective of the occurrence in one of them of the *W* gene.

An albino of type A, genotype 6, table 3, which owes its white color to a double dose of dilution acting on brown pigment in the presence of the *A* gene, as a rule differs slightly in appearance from a dominant white horse. Instead of being clear white, its coat is ivory white having a tinge of very light cream. Its eyes also are blue, and its skin pink. The preferred type of dominant white horse has brown eyes, but if its genotype has become *bb Ww*, as the result of chestnut or Palomino ancestry, it is conceivable that the eye color might become blue as in type A albinos, rather than brown. Such an animal would be difficult to distinguish in appearance from a type A albino.

It is probable that the ALBINO HORSE CLUB would admit to registry without hesitation white horses of either genotype, although one would be a heterozygous dominant white, *bb Ww*, and the other a homozygous dominant dilute, *bb DD*. They propose to distinguish the two as type W and type A respectively.

It was not known until recently what an albino colt would look like if one of its parents was a Palomino and the other a buckskin which transmitted gene *B* to the colt. SALISBURY and BRITTON made this guarded statement in 1941. "It is our opinion based on insufficient data for acceptance as absolute

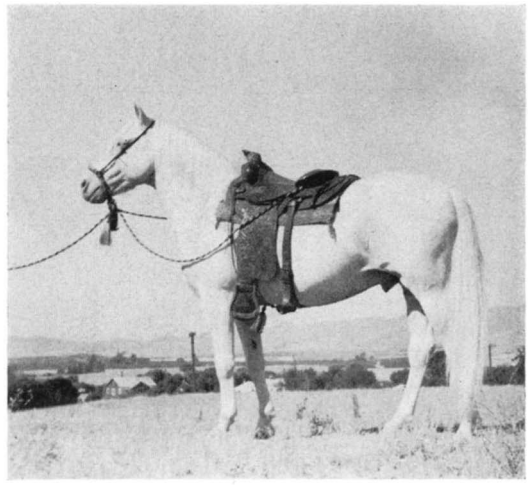

FIGURE 1. A. Type A albino, the stallion Algiers owned by MR. FRANK L. KING of Lafayette, California.

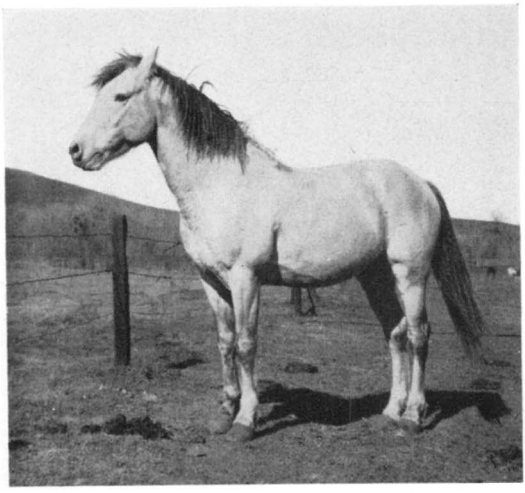

FIGURE 1. B. Type B albino, photo. by courtesy of MRS. HARRIET HALLONQUIST of Alameda. California.

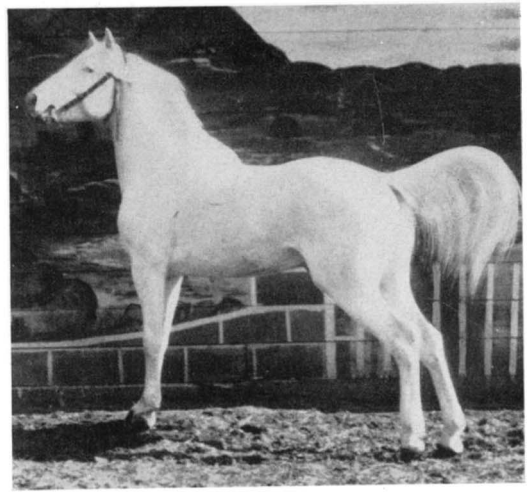

FIGURE 1. W. Type W albino, the stallion White Wings known to be heterozygous, Ww, since he sired a black colt by a white mare. Courtesy of THE AMERICAN ALBINO HORSE CLUB OF Butte, Nebraska.

proof, that, in the presence of the gene for black, the homozygous dominant dilution gene would produce a washed-out light dun." How right they were is shown by the description of the phenotype corresponding to genotype 5 of table 3, based on a carefully verified case.

This case was brought to light by an "incident" reported in the Sept.-Oct. 1947 number of the Western Horseman by MRS. HARRIET HALLONQUIST.

The owner of a blue-eyed albino mare desiring to produce a Palomino colt (by the procedure outlined by CASTLE 1946) bred the mare to an Arabian stallion of a light chestnut color, both of whose parents and all of whose four grandparents were chestnut in color. But the colt instead of being Palomino as expected, was buckskin in color, with black mane and tail. How, the author inquired, was this exceptional result to be explained. The author did not state what the parents of the albino were as regards color. From the color of the colt it is clear that the dam was a type B albino (table 3). Mr. F. L. KING and the writer, after the case was called to their attention, were able to interview MRS. HALLONQUIST who kindly made it possible for us to see the mare and her buckskin colt. A glance at the mare sufficed to show that she was very different in phenotype as well as genotype from the type A albino stallion Algiers, who on MR. KING's ranch had been bred to 24 chestnut or sorrel mares, with the production of 24 colts all Palominos.

The same stallion, when bred to bay mares (*Bb* in constitution) had produced 2 buckskin and 3 Palomino colts, expected 1:1.

We concluded that the mare of the "incident" shown to us by MRS. HALLONQUIST, was a type B albino (table 3). Further, that the buckskin colt resulted from the fertilization of a *B D* egg by *b d* (chestnut) sperm, thus: *B D* egg + *b d* sperm = *Bb Dd* (buckskin) colt, genotype 1, table 3. One parent (or both) contributed the dominant *A* gene, which causes segregation of black in mane, tail and legs, leaving the body color yellow (dun).

The color of the albino mare of this "incident" is as stated for genotype 5, table 3. The body color is cream, sharply delimited on the hind feet from her clear white ankles. Her much darker mane, as carefully rated by DR. SETH BENSON, in RIDGEWAY's color standards, "comes closest to cinnamon-buff." The effect of double dilution (*DD*) is seen in the mare's eyes, which are blue notwithstanding the presence of *B* in her genotype.

4. Other genes which modify the basic colors or the basic color pattern of horses

1. Gray is a simple dominant gene, epistatic to all the genotypes listed in table 2. A colt which inherits the gray gene from one or both of its parents is born black, but as the juvenile coat is shed the new coat comes in black with interspersed white hairs which become increasingly abundant with each subsequent moult. In old age, a gray horse may become almost white, so numerous are the white hairs in the coat. In this it resembles a gray haired human being.

A horse homozygous for the gray gene produces only black colts which later become gray, by dams of all the four genotypes listed in table 2.

A horse heterozygous for the gray gene produces 50 percent of black colts destined to become gray, and 50 percent of colts of some other color. Horses which are not themselves gray do not transmit the gray gene.

2. Roan is due to a dominant gene epistatic to all the genotypes listed in table 2. Like gray it consists of a mixture in the coat of colored and uncolored hairs. The colored hairs may be black, brown, red or yellow in color.

Unlike gray, a roan horse has white hairs present in its juvenile coat. Roans, like grays, may be either homozygous or heterozygous for the mutant gene.

3. Several different gene mutations are responsible for the production of white markings and white color patterns in horses.

White feet, white stockings, a white star in the forehead and a white blaze are examples of white spotting supposed to be either recessive or weakly dominant in crosses with self-colored mates.

Extensive white markings such as are seen in Pinto ponies have usually been described as simple dominants, either homozygous or more often heterozygous in constitution, and so producing either 100 percent or more often 50 percent of Pinto colts. But one author has described a form of extensive white marking which is recessive and only comes to full expression when homozygous. All forms of white spotting are fully developed at birth and do not change their outlines subsequently.

SUMMARY

The basic color genes of mammals are three in number. The first to be considered is a wild pattern gene, *A*, which acting in cooperation with two other genes *B* and *C*, produces the coat pattern of the species prior to its domestication. The basic pigment is black, produced by the activity of a gene *B*, in an animal which possesses the dominant gene for color, *C*. By recessive mutation of *A* to *a*, the animal loses its wild coat pattern; by mutation of *B* to *b*, the pigment formed becomes brown instead of black; by recessive mutation of *C* to *c*, the coat becomes unpigmented, the true albino condition. Less extreme recessive mutations of *C* may result in albino alleles only partially pigmented.

Horses possess a basic color gene for primitive wild type of coat pattern *A*, which in the presence of *B* and *C* results in the bay type of coat. If *A* persists but *B* mutates to recessive *b*, a chestnut or sorrel type of coat results.

Mutation of *A* to *a*, involving loss of wild type coat pattern, results in uniform (recessive) black. Similar mutation of *A* to *a*, simultaneously with mutation of *B* to *b*, results in uniform brown, liver chestnut. The color gene has not undergone an albino mutation in horses. A possible dominant mutation of *A* to *A'* may have produced in some strains of horses, a dominant black, such as has occurred in rabbits, cats and dogs.

Genes which modify the basic *ABC* color combinations of horses are:

(1) Dominant dilution, *D*, which when heterozygous in the presence of *B* produces buckskin; in the presence of *bb*, produces Palomino. Homozygous combinations of *D* in the presence of *B* produce type B albinos; in the presence of *bb*, type A albinos.

(2) Dominant white, *W*, is epistatic to all color types, and is probably lethal when homozygous.

(3 and 4) Gray and Roan are epistatic forms of silvering of the coat, resulting in interspersing of white with colored hairs.

(5) Some types of white spotting are dominant and epistatic to uniformly colored coat, others recessive or weakly dominant.

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