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Introduction to Coat Color Genetics

A system of classification of horse coat colors and markings is important in any program of identification of horses as individual animals. To have accurate and uniform application of the terminology for color classes, the system should stress recognition of basic, definable characteristics and should minimize the importance of subtleties which cannot be clearly defined. A scheme of coat color classification based on recognition of the effects of the alleles of seven genes provides the necessary rigor, and with training can be uniformly applied by anyone to define most of the common colors encountered in horses.

Outline

- Introduction and Basic Genetics
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- Gene G: Exclusion of Pigment from Hair
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Basic Genetics

For every living thing millions of instructions called *genes* are used for its growth, appearance and maintenance. It is not possible to see a gene, even with the most sophisticated microscope available. We recognize the presence of genes because of their effects on the organism in ways that we can see or measure.

In order to understand coat color genetics, one must first learn to pick out the conspicuous characteristics affected by each gene. This can be likened to observation and study of a basket of mixed fruit. At first glance we may see a melange of shapes, colors and textures, but with a second glance the trained eye can see the distinctive presence of apples, oranges and bananas. Similarly, the potpourri of horse colors can be focused into a structured subject by attention to the effects of seven different genes.

Every cell contains a duplicate set of genes. Each set is derived from the single gene sets contributed at conception by both the mother and the father. The gene sets contain similar, but not necessarily identical, information. For example, both sets may contain a gene determining hair structure, but one set may contain the instructions for straight hair and the other for curly hair. The alternative forms of each gene are called alleles. If both alleles are identical, then the animal is said to be homozygous at that gene; if the alleles are dissimilar, then the animal is said to be heterozygous at that gene. Information about the homozygosity or heterozygosity for various genes can be inferred from information about parents and/or progeny and can be used for predicting the outcome of matings. For most of the alleles of horse coat colors one cannot tell by

looking at an animal whether it is homozygous for any coat color gene, so zygosity information will not be critical for purposes of identification. Sometimes, however, information about coat colors of parents may be used as an indication of incorrect parentage or erroneous identification, so some familiarity with genetic relationships may be useful.

Both sets of genes function simultaneously in the cell. Often when the gene pair is heterozygous, one allele may be visibly expressed but the other is not. The expressed allele in a heterozygous pair is known as the *dominant* allele, the unexpressed one as the *recessive* allele. The term dominant is given an allele only to describe its relationship to related alleles, and is not to be taken as an indication of any kind of physical or temperamental strength of the allele or the animal possessing it. Likewise, possession of a recessive allele does not connote weakness.

For simplicity in constructing models, geneticists symbolize genes by letters such as A, B and so on. A dominant allele of a gene can be symbolized by an italicized capital letter, e.g., A, and the recessive by an italicized lower case letter, e.g. a. For each of the seven genes of horse coat color to be considered, only two alternatives will be considered.

In any animal expressing the dominant allele of a gene, it cannot be determined by looking at the animal whether the second allele is a dominant or a recessive one. The presence of a recessive allele may be masked by a dominant allele, which leads to the expression "hidden recessive." Dominant alleles are never hidden by their related recessive alleles.

Gene W: Inability to Form Pigment in Skin and Hair

This gene and the gene G, to be discussed in the next section, will be presented first because they have alleles whose actions can obscure the actions of the other coat color genes. If either allele W of the W gene or allele G of the G gene is present in the hereditary material of a horse, it is difficult or impossible to determine its other coat color genes by superficial examination, so the colors these alleles produce can be simply dealt with at the onset of this discussion.

In the presence of the dominant allele W, a horse from birth will typically lack pigment in skin and hair. The skin is pink, the eyes brown (sometimes blue), and the hair white. Such a horse is termed white (Fig. 1A). Sometimes such a horse is called albino.

The W allele is only rarely encountered. All non-white horses are ww.

Gene G: Exclusion of Pigment from Hair

Everyone is familiar with the process of progressive silvering of human hair color in which the hair color of youth, such as blond, brunette or redhead, turns to gray or white with age. Horses show a similar phenomenon of hair silvering with age in a color called gray (Fig. 1B). In horses, gray is controlled by the dominant allele G.

A young horse with a G allele will be born any color but gray and will gradually become white or white with red or black flecks as an aged animal. Earliest indications of change to gray can be seen by careful scrutiny of the head of a young foal, since often the first evidence of the gray hairs will be seen around the eyes (Fig. 1C). In intermediate stages of the graying process, the horse will have a mixture of white and dark hairs, a most confusing stage for trying to identify color.



Fig. 1A - Dominant white (Ww). This horse has been white from birth. Note pink skin, clearly seen around mouth, nostrils, eyes. Eyes are brown in this horse and most white horses, but occasionally may be blue.

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Fig. 1B - Gray (G). This gray Arabian stallion was foaled a non-gray color and turned white with age. In comparison with *Ww* horse, note black skin around mouth, nostrils and eyes.





Fig. 1C - Gray (G) pony mare with her red tobiano foal turning gray (*Gg*, *ee*, *TOto*). Note rings around eyes of gray hair interspersed with red color. When mature, it will not be obvious that the foal was red at birth, and the spotting will only be evident as a pink-skinned pattern in the skin.

In contrast to white (W) horses, gray horses are born pigmented, go through lightening stages, but always contain pigment in skin and eyes at all stages of coloration change.

A gray horse will be either GG or Gg. It is not possible to tell by looking at the horse whether it is homozygous for G. For simplicity in notation, a horse expressing a dominant allele can be symbolized as, for example, G. Use of a single allele designation in this paper for color assignment implies that no information about the second allele of the pair is available. All non-gray horses will be gg. For homozygous recessive colors, both alleles are written in the notation for color assignment, since a horse showing a color or pattern produced by recessives is by definition homozygous for the recessive alleles.

Since gray is produced by a dominant gene, at least one parent of a gray horse must be gray. If a gray horse does not have a gray parent, then it should be seriously considered that the purported parentage is incorrect.

Gene E: Black Hair Pigment

The first step for defining the coat color of a horse which is neither gray nor white is to decide if the animal has any black pigmented hairs. These hairs may be found either in a distinctive pattern on the points (such as legs, mane and tail), or black hair may be the only hair color (with the exception of white markings) over the entire body. If a horse has black hair in either of these patterns, then the animal possesses an allele of the E gene which contains the instructions for placing black pigment in hair. Geneticists symbolize this allele of the E gene E. The alternative allele to E is e. Allele e allows black pigment in the skin but not in the hair. The pigment conditioned by the e allele makes the hair appear red.

If an animal has no black pigmented hair, it has the genetic formula ee. Basically, an ee animal will be some shade of red ranging from liver chestnut to dark chestnut (Fig. 1 D) to chestnut (Fig. 1E), or sorrel (Fig. 1F). Manes and tails may be lighter (flaxen), darker (not black), or the same color as the body. These pigment variations of red cannot yet be explained by simple genetic schemes. Furthermore, the shades of red are not consistently defined by breeds or regions of the country, so usage of specific terms for the shades of red can be confusing. For discussion purposes this group of colors is lumped under the term red.

Since the red animal is not gray and not white, its genetic formula in terms of the three genes discussed so far is ww, gg, ee. Notice that when two red horses are bred together $(ww, gg, ee \times ww, gg, ee)$, the offspring should also be red (ww, gg, ee). If the offspring has black pigment (E) or is gray (G) or white (W), then the parentage as given is most likely incorrect.

Gene A: Distribution of Black Pigmented Hair

The gene that controls the distribution pattern of black hair is known as A. The allele A in combination with E will confine the black hair to the points to produce a bay (Fig. 1G). Various shades of bay from dark bay or brown through mahogany bay, blood bay to copper bay and light bay exist. The genetics of these variations has not been defined. Any bay horse will include A and E in its genetic formula as well as ww and gg.



Fig. 1D - Dark chestnut (ee). Arabian mare, Tamasina. For purposes of identification, this color as well as the next two (E, F) are best referred to as red in order to avoid differences in regional and breed specific terminologies for the red series.



Fig. 1E - Chestnut (ee). Thoroughbred gelding, Mr. Maz Jr. For identification puposes this color should be called red.



Fig. IF - Sorrel (ee). Thoroughbred gelding, Flying Comedian. This horse is registered as a chestnut, but Western regional terminology would describe this light color variant as sorrel. In order to avoid confusion, the use of the term red is preferred.



Fig. IG - Bay (A, Ee). Arabian stallion, Aurtal. (Michael Bowling photograph).

The alternative allele a does not restrict the distribution of black hair and thus in the presence of the allele E of the E gene a uniformly black (Fig. 1H) horse is produced. In most breeds of horses, the a allele is rare, so black horses are infrequently seen. Many black horses will sun-fade, especially around the muzzle and flanks and such animals may be called brown. The term brown can be used for several genetic combinations (various reds, bays and dark bays (Fig. 1I), as well as some blacks).

Neither A nor a affects either the pigment or its distribution in red (ee) horses. Thus it is not possible to determine by examination of coat color which alleles of the A gene a red horse has.



Fig.IH - Black (aa, E).Trakehner stallion.



Fig. 1I - Dark bay (A, E). Arabian mare, Narah Bint Neziah. This color may variously be called dark bay, black bay, mahogany bay or brown. In order to obviate confusion, it is suggested that the basic color be described simply as bay in recognition of the black pigment in an obvious points pattern.

Gene C: Pigment Dilution

An allele of the C gene, known as Ccr, causes pigment dilution. Fully pigmented horses are CC. Heterozygous horses (CCcr) have red pigment diluted to yellow but black pigment is not affected. A bay (E, A) becomes a buckskin (Fig. 2A) by dilution of the red

color body to yellow without affecting the black color of the mane and tail. The genetic formula for a buckskin is ww, gg, A, E, CCcr. A red horse (ee) becomes a palomino (Fig. 2B) by dilution of the red pigment in the body to yellow with mane and tail being further diluted to flaxen. The genetic formula for a palomino is ww, gg, ee, CCcr. A genetically black horse (E, aa) can carry the dilution allele without expressing it, since CCcr only affects red pigment.

In homozygous condition, CcrCcr completely dilutes any coat color to a very pale cream with pink skin and blue eyes. Such horses are often called cremello (Fig. 2C), also perlino or albino. Typically, such horses are the product of the mating of two dilute-colored animals such as palominos or buckskins. Cremello may be difficult to distinguish from white unless critical judgments can be made about hair color. The hair of CcrCcr animals will be cream-colored, whereas the hair of W horses will be white. As with W and G horses, for CcrCcr horses it is not possible to determine which alleles of other genes are present.



Fig. 2A - Buckskin (A, E, CCcr) pony mare. Note that this horse is basically a bay, but the areas of red pigment have been diluted to yellow.



Fig. 2B - Palomino (*ee*, *CCcr*) pony mare. The presence of a dilution gene dilutes red pigment to yellow.



Fig. 2C - Cremello (CcrCcr) pony mare. Compare with figures of Ww and G horses. Note the cream-colored hair, pink skin and blue eyes as the group of special characteristics of cremello.

Gene D: Dun Pattern and Pigment Dilution

The D gene determines a second kind of dilution of coat color and its effects can be confused with those of *Ccr*. However, there are several important differences of the effects of *D* and *Ccr* on color. First, *D* dilutes both black and red pigment on the body, but does not dilute either pigment in the points. Red body color is diluted to a pinky-red, yellowish-red or yellow; black body color is diluted to a mouse-gray. Second, in addition to pigment dilution, a predominant characteristic of the allele *D* is the presence of a particular pattern which includes dark points, dorsal stripe (list), shoulder stripe and leg barring. Third, homozygosity for *D* does not produce extreme dilution to cream as does *Ccr*.

This pigment dilution pattern is called dun. In an otherwise red horse, the D allele produces a pinkish-red horse with darkened points known as a red dun or claybank dun (ww, gg, ee, CC, D). In an otherwise bay animal, the D allele produces a yellow or yellow-red animal with black points known as a buckskin dun (ww, gg, E, A, CC, D) (Fig. 2D). An otherwise black animal with the D dilution allele is a mouse gray color with black points known as a mouse dun or grulla (ww, gg, E, aa, CC, D).

The effect of D and Ccr can be easily confused in A, E horses so care must be taken in identification. It is possible for an animal to have both the Ccr and D dilutions, a situation which may be difficult to distinguish except by breeding tests.

D is found only in a few breeds of horses, and probably in the United States would only be seen in stock horse breeds, as well as in some ponies.



Fig. 2D - Buckskin dun (A, E, D). Compare with buckskin (A, E, CCcr). Note the dun pattern (dorsal stripe, shoulder patch, leg barring on front legs) associated with the D dilution factor.



Fig. 2E - Red tobiano (ee, TOto) Paint stallion, Dandy Diamond.

Gene TO: Tobiano Spotting Pattern

Several different white spotting patterns exist in horses, but so far only that of tobiano (Fig. 2E) has been clearly shown to be conditioned by a single gene. Tobiano spotting, symbolized by *TO*, is a variable restricted pattern of white hair with underlying pink skin which can occur with any coat color. The pattern is present at birth and stable throughout life. In general, white extends from the neck crest, withers on top of the croup in an apparent top-to-bottom distribution on the body. The white areas may merge to form an extensive white pattern of generally smooth outline. The legs are white, but the head is usually dark except for a facial marking pattern.

Editor's note: Tobianos can now be screened for their potential to be true breeding for the tobiano pattern.

Other Coat Color Patterns and Markings

In addition to the coat colors and patterns already discussed, the presence of other distinctive features should be noted for any horse identified, even though their genetics has not been adequately defined. Some distinguishing features to be noted include the following:

- White face and leg markings are commonly found on most horses and should be precisely described.
- One or both blue or partial blue eyes (Fig. 2F) can be found on any color horse, not just cremellos and horses with spotting patterns, and should be noted.
- A horse with a mixture of white and dark hairs of any color is known as roan (Fig. 2G). The extent of the pattern can vary from a few hairs in the flank to extensive involvement of the body. In the most extensively roaned horses, a typical pattern seen is that in which the body is silver due to a high percentage of white hair, but the legs and head are dark due to the preponderance of non-white hair. The roaning pattern may be present at birth or may not be conspicuous until the first foal coat is shed. Generally, roaning is not a progressive silvering phenomenon as is gray, although often the summer coat may appear lighter than that of winter. Young gray horses can mistakenly be classified as roan, but information about the color of the parents may help clarify the situation, since a gray will have at least one gray parent. Roan is inherited as a dominant trait. The inheritance of scattered white hairs, sometimes called roaning, is not defined.
- Several variable spotting patterns collectively known as Appaloosa (Fig. 2H) spotting can be found in any coat color. The spotting patterns include leopard, blanket, snowflake and roan. Permanent identification of Appaloosas can be difficult, since the white patterns may not be stable from birth. In general, besides white spotting, Appaloosas can be recognized by striped hooves, mottled skin (especially evident around muzzle and eyes) and prominent white sclera.
- A stable pattern of variable white spotting known as overo (Fig. 2I) is characterized by white on the belly or sides of the midsections which appears to extend upward to, but not including, the center line of the back. White may also occur on the side of the neck and flank as separate areas or merged with

midsection white. Large white areas characteristically have a jagged outline. At least one, and usually all four legs are colored, but they may have white markings. It is possible for a horse to have both the overo and tobiano spotting patterns (as well as appaloosa) and a precise definition of such a coat color may be difficult. The overo pattern is generally transmitted as a dominant trait with occasional exceptions.

Editor's note: For more information on the genetics of overo please look at the article The New Genetics of Overo.



Fig. 2F - Blue eye on a bay pony mare.



Fig. 2G - Red (ee) roan Quarter horse mare, Miss Bar Depth and her red roan foal, Pepermint Pati Kid.



Fig. 2H - Black (aa, E) Appaloosa stallion, Twice as Bright.



Fig. 2I - Bay (A, E) Paint overo stallion, Forecast Too.

Assignment of Coat Color by Genetic Formula

In order to define the color of a horse in a systematic way, one must learn to assign genetic symbols to the horse to be identified. With study and practice this becomes easy. Careful application of genetics to coat color definition can gloss over any inconsistencies due to regional or breed definition, age or season.

Defining the coat color of a horse is a stepwise process. The first step is to determine if either G or W is present. If yes, then the animal is gray or white and this is the end of the identification task.

If the horse is neither gray nor white, then assignment of alleles of the other genes can be made to define the color. First, one must decide if the horse has E. When E is present, then it must be decided whether the horse has E. If the animal does not have E, then a decision about E cannot be made. If none of the colors is diluted and if no spotting pattern is present, these decisions about E and E will define the colors bay, black and red.

If dilution of the basic colors to yellow, light red, mouse gray or cream is present, then further definition can be made with addition of the alleles of C and D to the basic formula containing W, G, E and A. In the absence of white spotting these decisions will define the colors palomino, buckskin, cremello, red dun, buckskin dun and mouse dun.

If a white spotting pattern is present which meets the definition of tobiano, *TO* can be assigned to the genetic formula.

The outcome of decisions about the genes W, G, E, A, C, D and TO results in the assignment of alleles for each gene. Each assignment should be carefully reviewed to consider if the chosen alleles are likely to be found in the breed of horse being identified.

Some of the genetic formulas and their color definitions which can be assigned by this process are shown in Table 1.

Table 1

Genetic Formulas and Color Definitions			
Genetic Formula	Color		
W	White		
G	Gray		
E, A, CC, dd, gg, ww, toto	Вау		
E, aa, CC, dd, gg, ww, toto	Black		
ee, aa, CC, dd, gg, ww, toto	Red		
E, A, CCcr, dd, gg, ww, toto	Buckskin		
ee, CCcr, dd, gg, ww, toto	Palomino		
CcrCcr	Cremello		
E, A, CC, D, gg, ww, toto	Buckskin dun		
E, aa, CC, D, gg, ww, toto	Mouse dun		
ee, CC, D, gg, ww, toto	Red dun		
E, A, CC, dd, gg, ww, TO	Bay tobiano		
ee, CC, D, gg, ww, TO	Red dun tobiano		

The final step in the coat color identification process is to add any other pertinent markings and patterns to the description such as face and leg markings, roaning, appaloosa and other spotting. Using the genetic system for coat color identification, most of the colors found in horses can be identified. Horses whose color cannot be defined may rarely be encountered, but a systematic appraisal of the genes likely to be found will provide a better identification than descriptive adjectives lacking a defined basis.

Conclusion

With colors from bright to dull and patterns from delicate to gaudy, domestic horses provide a fascinating variety of choices for both aesthetic and scientific appreciation, as well as a task for horse identifiers. An understanding of the effects of each of a series of coat color genes, as well as their combined results, is important for competent identification of horse coat colors. It is not necessary to be an expert at applying rules of genetics so that outcomes of matings can be predicted, but the major distinguishing features of each of the various coat color genes should be clearly understood. Familiarity by horse identifiers with horse coat color genetics should ultimately result in clearly defined and consistent identification of horse coat colors (Table 2).

Table2

Alleles and Actions of Horse Coat Color Genes		
Gene	Alleles	Observed Effect of Alleles in Homozygous and Heterozygous Condition

W		WW : Lethal
	W W	Ww : Horse typically lacks pigment in skin, hair and eyes and appears to be white.
		ww: Horse is fully pigmented.
G	G g	 GG: Horse shows progressive slivering with age to white or fleabitten, but is born any non-gray color. Pigment is always present in skin and eyes at all stages of silvering. Gg: Same as GG. gg: Horse does not show progressive silvering with age.
		gg. Horse does not snow progressive snvering with age.
	E	EE : Horse has ability to form black pigment in skin and hair. Black pigment in hair may be either in a points pattern or distributed overall.
E	е	Ee : Same as <i>EE</i> .
		ee: Horse has black pigment in skin, but hair pigment appears red.
А	A a	 AA: If horse has black hair (E), then that black hair is in points pattern. A has no effect on red (ee) pigment. Aa: Same as AA. aa: If horse has black hair (E), then that black hair is uniformly distributed over body and points. A has no effect on red (ee) pigment.
С	C Ccr	 CC: Horse is fully pigmented. CCcr: Red pigment is diluted to yellow; black pigment is unaffected. CcrCcr: Both red and black pigments are diluted to pale cream. Skin and eye color are also diluted.
D	D d	 DD: Horse shows a diluted body color to pinkish-red, yellow-red, yellow or mouse gray and has dark points including dorsal stripe, shoulder stripe and leg barring. Dd: Same as DD. dd: Horse has undiluted coat color.
то	TO to	 TOTO: Horse is characterized by white spotting pattern known as tobiano. Legs are usually white TOto: Same as TOTO toto: No tobiano pattern present.

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