

make linkage tests of the dilution gene, whether we consider it an incompletely dominant or an incompletely recessive modifier of color.

The black gene, B: Gene *B* acting in conjunction with gene *C* produces black pigment in mammals in general, including horses. It has a recessive allele, *b*, which when homozygous, (*bb*), replaces black pigment with brown. This replacement is very clear in laboratory rodents as well as in dogs, where there are parallel series of black pigmented (*B*) and brown pigmented (*bb*) genotypes; such as black, black-and-tan, and black agouti, *vs.* brown, brown-and-tan, and brown agouti, the latter series being regularly recessive to the former.

In horses, a similar relationship is found between dominant bay and black, *vs.* recessive chestnut, sorrel and liver, and it seems logical to adopt here the same genetic symbols, *B* for the black series, *b* for the brown series.

The coat pattern gene, A: Gene *A*, acting in conjunction with genes *B* and *C*, produces a coat pattern which is found in mammals in general in the wild ancestral stock and in the domestic derivative which most closely resembles the ancestral stock in coat pattern.

In rodents this is the agouti coat pattern, in which black-tipped hairs having a subterminal band of yellow are distributed over the greater part of the body.

In horses the ancestral coat pattern is bay, in which black is the predominant color in the peripheral parts of the coat (head, legs, mane and tail) but in the central body regions a mixture of yellow-red with black hairs or a complete replacement of black with red is found.

ODRIOZOLA (1951) recognizes in horses four alleles of gene *A* and these we shall adopt with slight modifications. They are *A*⁺, *A*, *a*^t, and *a*.

1. *A*⁺ is the allele found in the wild ancestral stock, exemplified in the surviving Prejvalski horse of Mongolia. It has the coat pattern of the domestic bay together with markings commonly lacking in the bay, such as a dark spinal stripe, a dark vertical bar on the shoulders, and transverse zebra bars on the front legs. As a group these may be referred to as zebra markings. One or more of them is of frequent occurrence in certain domestic breeds, as well as in feral horses in Argentina.

2. *A* is the allele which is responsible for the coat pattern of the domestic bay horse (*AB*), and its counterpart, the chestnut (*Abb*). Zebra markings are commonly lacking in such horses.

3. *a*^t is the allele which is responsible for the coat pattern of the seal brown horse (*a^tB*). This genotype has zebra markings much oftener than does the bay.

4. *a* is the allele which, when homozygous (*aa*), involves entire absence of the bay coat pattern and zebra markings.

The genotype *aaB* is that of the recessive uniform black horse; *aabb* is the genotype of uniform chestnut or sorrel, and in the combination *aabbE* is known as liver chestnut.

Gene E, extension of dark pigment: Gene *E*, acting in conjunction with genes *B* and *C*, governs the extension (or restriction) of dark pigment in the coat of mammals. It has three known alleles, *E*, *e*, and *E*^p.

1. *E* governs the full extension of black (or brown) pigment throughout the

coat, as among horses in the ancestral wild type, and in domestic bay, black, and chestnut varieties.

2. e , the recessive allele of E , when homozygous (ee) causes restriction of dark pigment to peripheral parts of the coat leaving the central body region yellow-red in color. In horses this makes the difference between mealy bay (ABE) and red bay ($ABee$).

3. E^D , dominant extension, is a mutation of gene E first clearly demonstrated in the rabbit by PUNNETT, but since found to be of rather wide occurrence among mammals. It results in a marked increase in the production of dark pigment, so great that when homozygous ($E^D E^D$) it may completely hide the presence of an A coat pattern gene. In the heterozygote $AE^D E$, or $AE^D e$ of the rabbit, the agouti pattern shows feebly and this phenotype is designated by PUNNETT, agouti-black.

In horses the E^D allele occurs, either homozygous ($E^D E^D$) or heterozygous ($E^D E$ or $E^D e$), in the *dominant black* genotype which, unlike *recessive black*, is born jet black and nonfading.

A mating of a dominant black of genotype $ABE^D E$ with a recessive black of genotype $aaBE$ may occasionally produce a bay colt from a gametic union $ABE + aBE = AaBBEE$, bay.

Gene D for dilution: Gene D for dilution of color is peculiar to horses. Its existence, though known to previous investigators, was first clearly stated in its relation to Palomino and dun genotypes by SALISBURY and BRITTON (1941) who say, in their summary "Palomino color is produced by an incompletely dominant dilution gene superimposed over the basic chestnut or sorrel color [bb genotypes]. This same gene in combination with the basic colors, bay, brown, or black [B genotypes] produces a dilute which may be a dun, buckskin, or mouse."

SALISBURY and BRITTON did not suggest a genetic symbol for the hypothetical dilution gene, but in a working hypothesis CASTLE (1916) used D and has continued to do so, despite the apparent violation of priority rules in mammalian genetics, since d had long been used for recessive blue dilution in rodents.

There is however an important point of difference between incompletely dominant D for dilution of color in horses and the completely recessive d for blue dilution in rodents.

Further knowledge of Palomino and related genotypes

1. The conclusions of SALISBURY and BRITTON were fully verified in a breeding experiment conducted by FRANK L. KING of Lafayette, California (CASTLE 1946).

2. The further point, that the A allele is an indispensable component of Palomino and dun genotypes, was shown in a further report of KING's breeding experiments (CASTLE and KING 1951).

3. A matter of uncertainty still exists as to why (a) Palominos have mane and tail *lighter* in color than the body, whereas (b) duns and buckskin have mane and tail *darker* than the body.

The only difference in genotype between the two groups is that one is bb and the other B . Mane and tail in one group are diluted brown and in the other diluted black. We must assume therefore that diluted brown is optically less conspicuous than the diluted yellow of the body, whereas diluted black is more conspicuous.

4. In previous discussions of the genotypes of Palomino and buckskin, the alleles of gene A taken into consideration have been only A and a . The allele a^t , now a recognized constituent of the seal brown genotype, was unknown up to 1951, when its existence was predicated by ODRIOZOLA, but was unrecognized elsewhere until 1960.

The a^t allele, in the combination a^tBE , results in the production of an all black horse resembling recessive black ($aaBE$) but differing from it in showing traces of the bay pattern in the form of light areas notably on muzzle and flank. It is called black-brown, seal brown or simply brown in stud book records.

Its effect in an a^tbbD genotype, as shown by data as yet unpublished, is to produce a phenotype known by such popular names as yellow dun, red dun, or *claybank dun*.

Of course none of these is a true dun (genotype BD). They differ from a Palomino only in having an a^t allele instead of an A . Frequently they have zebra markings (spinal stripe or bars on legs or both); mane, tail and legs are usually somewhat darker than the body indicating that diluted brown pigmentation *concentrated peripherally* is darker than in its more diffuse state mixed with yellow in the central body region.

It remains to consider what effect the presence of D will have on a genotype which includes neither the A nor the a^t allele, but instead is aaD . Such a genotype will be either black or chestnut in phenotype, depending on whether it has the B or the bb constituent.

A diluted black ($aaBD$) is known as *mouse*, as stated by SALISBURY and BRITTON and supported by an examination of Shetland Pony stud book records, Volumes 1 and 2, in which more than 20 individuals are registered as mouse (or moose) in color. Several of these were produced in matings in which one parent was dun or buckskin.

Combinations of genes A, B, E, and D, see Table 1: The genotype which includes dominant alleles of the four genes A , B , E , and D is known as dun. Its genotype is identical with that of the domestic bay except for the addition of D , whose diluting action lightens the entire coat. In the dun, mane, tail and legs are black, as in bays, though of less intensity. Body color is pale sooty yellow or straw color.

(1) Replacement in the dun genotype of B with bb results in the production of a Palomino ($AbbED$), which has "white" rather than black mane and tail.

(2) Replacement of E with ee results in the production of a buckskin, which differs from true dun only in having a clear yellow body color, rather than a dingy yellow.

(3) Replacement of A with a^t results in the production of a seal brown.

TABLE 1

Color classes resulting from different combinations of genes A, B, and E, with or without gene D

Combinations of A, B, and E Genotype	Phenotype	Combinations of A, B, E, and D Genotype	Phenotype
A^+BE	Ancestral type, bay with zebra markings		
ABE	Dark or mealy bay	$ABED$	Dun, body light sooty yellow, mane and tail black, dorsal stripe
$ABee$	Red bay	$ABeeD$	Buckskin, body clear light yellow; otherwise like dun
a^tBE	Seal brown, light areas inconspicuous	a^tBED	Light seal brown
a^tBee	Seal brown, light areas inconspicuous	a^tBeeD	Light seal brown
$aaBE$	Recessive black, uniform	$aaBED$	Mouse, uniform dilute black
$aaBee$	Recessive black, mane and tail darker than body	$aaBeeD$	Mouse, "Grullo," mane and tail darker than body
$AbbE$	Chestnut	$AbbED$	Palomino, mane and tail white, body sooty yellow-red
$Abbee$	Sorrel, light mane and tail	$AbbeeD$	Palomino, body clear cream to golden yellow, mane and tail white
a^tbbE	Chestnut "brown"	a^tbbED	Claybank
a^tbbee	Sorrel "brown"	a^tbbeeD	
$aabbE$	Chestnut uniform, "liver"	$aabbED$	Light chestnut uniform
$aabbee$	Sorrel uniform	$aabbeeD$	Light sorrel uniform
ABE^D	Dominant black, intense and uniform, "jet" black	ABE^D	Dominant black
		$ABEDD$	Perlino=
		$ABeeDD$	Albino type B, CASTLE (1948)
		$AbbEDD$	Cremello=
		$AbbeeDD$	Albino type A, CASTLE (1948)

(4) Replacement of A with aa results in uniform recessive black, mouse.

(5) Doubling of the D constituent in a dun or buckskin converts it into a perlino, a name unknown to CASTLE when in 1948 he designated it albino type B.

(6) Similar doubling of the D constituent in the genotype of a Palomino converts it into a cremello, equivalent of type A albino of CASTLE (1948).

What change, if any, would be made in the phenotype of perlino or cremello by substitution of a^t for A in its genotype, is at present uncertain.

Gene S in Shetland ponies: In Shetland ponies a new diluting gene, S for silver, made its appearance by mutation about 1886 in the mare Trot., 31 described as fawn color with white mane and tail.

This gene is stronger in its diluting action than gene D . Instead of being incompletely dominant, as gene D is, it is almost completely dominant, the homozygote, SS , being only slightly more dilute than the heterozygote Ss .

In single dose S dilutes black (BE) into a color resembling true chestnut (bbE).

Thus the genotype *ABES* is a silver dappled chestnut with white mane and tail; and in double dose, in the homozygote, *ABESS*, the color is still the same, only of a lighter shade.

But *ABeeS* is sorrel with white mane and tail, lacking dapples; and adding a second *S* to the genotype making it *ABeeSS* changes it only slightly to a lighter shade of the same color.

An example of a homozygous (*SS*) genotype is found in the light silver dappled stallion Magic B, 20,568. In matings with black mares he sired 12 colts, all silver dapples; and in matings with dappled mares, he sired 20 colts, all dappled. This is strong evidence that he was *SS* and so transmitted *S* to each of his colts.

Gene *D* occurred in the foundation stock of Shetland ponies imported into the U.S. and Canada and still occurs among their present day descendants resulting in true Palominos and an occasional Cremello. The new mutant gene *S* has created a phenotype, sorrel with white mane and tail, which closely resembles a true Palomino, and it is possible that many ponies of this genotype are now registered as Palominos (Table 2).

Feral horses in South America: The domesticated horse was introduced on the western hemisphere by the Spaniards in the early part of the 16th century. Mounted horsemen were a source of terror to the natives of Mexico and Peru and so were helpful to the invaders.

In the course of time some horses escaped from their masters and running loose on the pampas of Argentina produced numerous feral offspring of a variety of colors, some of them already well known, others being novel recombinations of color genes.

The keen-eyed cowboys of Argentina designated these by names which have passed into other languages than Spanish, including our own. The genetic constitution of the color varieties which were discriminated by the gauchos was of course unknown to them and is only becoming clear to us through comparative study of coat color in other mammals.

It was our privilege recently to inspect color photos, kindly loaned to us by PROFESSOR DEWEY G. STEELE of the University of Kentucky, of a criollo band of horses in Venezuela, produced by selective breeding from a strain of feral horses.

The band consisted mostly of dun horses of varying shades, with an occasional

TABLE 2

Parallel series of genotypes involving genes D and S in Shetland ponies

Genotype	Phenotype	Genotype	Phenotype
<i>ABED</i>	dun, yellow body color, mane and tail black	<i>ABES</i>	Silver dapple chestnut body color, mane and tail, white
<i>ABEDD</i>	Perlino	<i>ABESS</i>	Light silver dapple
<i>AbbeeD</i>	Palomino	<i>ABeeS</i>	Sorrel, white mane and tail
<i>AbbeeDD</i>	Cremello	<i>ABeeSS</i>	Light sorrel, white mane and tail

bay, and at least one dun of so light a color that we should unhesitatingly classify it as a Perlino.

If the band was produced by mating dun to dun, we should expect it to consist of three genotypes, bay, dun, and perlino, in an approximate ratio of 1:2:1, and that seems to be the reality. Such a population is the counterpart of that produced by mating Palomino to Palomino, resulting in genotypes, chestnut, Palomino and Cremello in a 1:2:1 ratio.

Rules for producing Palomino colts: Rules for the production of Palomino colts, based on theory and verified in the experience of breeders are as follows.

1. Matings of Palomino with Palomino may be expected to produce colts in the ratio, 1 chestnut or sorrel:2 Palomino:1 cremello.

2. Matings of cremello with Palomino may be expected to produce colts in the ratio, 1 cremello:1 Palomino.

3. Matings of cremello with chestnut or sorrel may be expected to produce only Palomino colts.

SUMMARY

1. In the production of the coat color of the Palomino horse, five major color genes are concerned. The dominant alleles of these genes may be labelled with the capital letters *A*, *B*, *C*, *D*, and *E*.

2. All of these, except *D*, are found in mammals in general. *D* is peculiar to horses.

3. Albinism, complete or incomplete, arising through a recessive mutation of the color gene *C*, though common in many other mammals, is unknown in horses.

4. Combinations of the three genes *A*, *B*, and *E* result in color varieties bay, brown, black, chestnut, and sorrel. The same genes, when combined with *D* in single dose result in color varieties of dun and Palomino; and when combined with *D* in a double dose (*DD*) result in pseudoalbino varieties designated perlino and cremello respectively.

5. The recent demonstration of the existence of a fourth allele of gene *A* (namely *a'*), has for the first time made clear the genotypes of seal brown and claybank horses.

6. In Shetland ponies a second diluting gene, *S* for silver, arose by mutation about 1886. Its diluting action is similar to that of *D* but stronger, converting black into a color resembling true chestnut. Unlike *D* which is incompletely dominant, it is almost completely dominant. Genotypes *Ss* and *SS* differ little in their diluting action, the latter being only a trifle more powerful than the former.

7. The genotype *ABeeS* in Shetland ponies, the phenotype of which is sorrel with white mane and tail, resembles rather closely the true Palomino, and may at times be registered under the name of Palomino.

8. It remains an open question for further study, whether *D* and *S* are alleles of a common genetic locus or are independent diluting genes.

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