THE INHERITANCE OF HORSE COAT COLOR WITH SPECIAL HERENON TO 13 RELATION TO HISTOLOGICAL AND PHYSICO-CHEMICAL PROPERTIES OF THE HAIR

by

CHEN-HSIA SIEH

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INTRODUCTION

Any hereditary character existing in the living organism, from the biological point of view, can be explained by means of the genetic factors. The inhoritance of horse coat color, of course, also follows this rule without exception. It has been popularly recognized that the study of color inheritance might be considered as a stepping stone for research in the improvement of livestock. Truly, as one of the pioneer horse eneticists, Anderson (1914), said:

The law governing the heredity of colors promises to be of the greatest value as an indication of the method for further research for the laws controlling the transmission of gait, speed, style, conformation, intelligence, stamina, docility and all the qualities which add to the value of the horse.

The principal difficulty in studying horse inheritance, which should be stressed, is the fact that the observation of the progeny for about ten generations by one person without discontinuance is hardly possible because of the long gestation period and the low feeundity and prolificacy as compared with other domestic and laboratory animals. Therefore, most data regarding horse inheritance have to be obtained from the Stud-Book, in which errors are unavoidable, usually through the misjudging of the coat color before the colt was registered, or through the misusing of color terms. At any rate, the inheritance of color is a problem involving other sciences concerned with animal improvement, thus being worthy of study. Further-

more, color inheritance can be more easily studied than other characters, such as disease resistance, because it is a character that is always visible.

Two different laboratory techniques, histological and physico-chemical, were carried out in the present study in order to obtain a basic knowledge regarding the formation and the character of the horse hair colors.

CLASSIFICATION AND CENETIC FACTORS OF THE HORSE HAID COLORS

Horse hair color varies so widely that early authorities classified 50 or more colors and patterns. As a result of selection and other breeding methods the colors in most of the breeds have been limited to a few, or, in some breeds, a single color. The genes responsible for certain colors have been studied by a number of authors; however, the behavior of some color genes does not have a satisfactory explanation. An attempt has been made here to use the genes for cattle color inheritance, proposed by Ibsen (1933), to explain the genes responsible for certain colors in horses.

Black (B), the darkest color, can be subdivided into two shades, the jet black which is intensive black with brilliant lustre, and rusty black which is black except for the muzzle, flank and abdomen where the hairs are somewhat dark brown.

Chestnut (C) is typically a medium golden color. It is expressed only when the black is not extended (60). Chestnut may

be subdivided into three groups: light chestnut, referred to as a sorrel; red chestnut, a fairly uniform red; and dark chestnut, a cinnamon shade bordering on brown.

A bay varies from yellow to dark brown and has a black mane, tail, and lower legs. Castle (1940) postulates an allelomorphic series, one of which, Ab, is responsible for bay. Bay can be subdivided into five groups: light bay, cherry bay, mahogany bay, dark bay, and brown.

A typical dun has a black or dark mane, tail, and dorsal stripe, and often carries zebra markings on the legs, withers, and shoulders, and occasionally on the abdomen. The dun color seems to be descended from Fquus prejwalski, the wild steppe horse. The shade of dunvaries from white-gray to dark yellow or buckskin. According to Castle (1940), the gene for dun is a wild pattern gene, designated as A, considered by him to be in the same allelomorphic series as the gene for bay.

Cray (C), according to Sturtevant (1912), Grew and Smith (1930), and Castle (1940), is epistatic to the above mentioned genes. In grays, white hair is interspersed with black hair.

Roan (N) is composed of either black, bay, chestnut or dun hair more or less equally intermixed with hair. Accor'ng to Grew and Smith (1930), Munckel (1929), Salisbury (1941), roan is epistatic to all colored hairs. Castle (1940) postulates that the roan gene, which in combination with any genetypes of the foregoing colors, with or without gray gene, produces roan hair.

The Palomino breed of horses is characterized by a yellowish or cream shade with silver mane and tail. According to Salisbury and Britton (1941), it is an unfixable heterozygous condition and is due to the existence of a dominant dilution gene. Castle (1946) suggests <u>Ddbb</u> as the genetic formula of the Palomino. The formula suggested here is <u>DdCCBBee</u>.

There are two types of albinism. According to Salisbury and Britton (1941), the one is due to the homozygous dilute chestnut and sorrel; the other is due to a single dominant dilution gene (DD) is responsible for the first type, and the gene (M) for the second type.

HISTOLOGICAL STUDY OF HORSE HAIR

The variation in the color, arrangement, and quantity of pigment granules was studied histologically in order to know how the action of the genes affects the pigment granules in the production of the various colors and shades.

MAT RIALS AND METHODS

The hair samples for this study were obtained from two sources: (1) Chinese indigenous horses, especially the dun hairs from Mongolian horses; (2) American horses, which were present at the 1947 American Royal Horse Show. The hair samples, except for a few from American horses, were taken

before November. The remainder were taken during the winter.

The cross sections were made by the use of the Hardy Thin Cross-section Device. By the use of this method sections 8-12 microns thick were obtained.

Whole mounts of hairs were also made. The hairs were treated with carbon tetrachloride and mounted in gum damar. Hairs defatted by Soxhlet's apparatus for chemical study were also used in order to observe whether this method had any effect on the structure of the hair.

Results of Histological Study

The structure of horse hair is basically similar to that of other mammalian species. The surface of the hair is covered by a transparent single layer of over-lapping scales of an irregular and somewhat flat shape. The tip of every over-lapping scale projects a little outward, and points distally. It is too thin to affect the coloration within the hair which is chiefly due to the pigment granules in the cortex.

The medulla contains a dark brown, twisted, somewhat thread-like mass. Smith (1940) stated that the medulla contains finely dispersed pigment and small granules which resemble the eleiden droplets of the stratum lucidum of the epidermis. According to Sission (1947), the medulla of the horse hair is the central core of softer, cubical or polyhedral cells, it contains some pigment and air spaces. In the extreme tip of the

hair no medulla exists. The medulla sometimes breaks transversely as shown in Plate I, Fig. 2.

The cortex occupies a large portion of the hair shaft, but its size varies greatly with the size of the medulla. The more or less eval pigment granules which range from 0.2 to 0.6 micron, are distributed through the cortex or occur in aggregations. In whole mounts the granules always appear in beadshaped strands. As a rule, the darker hairs have more pigment granules in the cortex. The colored hairs, except the true blacks, usually have more granules at the tip of the hair and the proximal portion of light hairs contains few granules or none, which is illustrated in Figs. 1 and 2.

A more detailed histological description of each hair color follows:

Black Hair. In whole mounts of jet black hair pigment granules are distributed evenly throughout the cortex and prevent light passing through the shaft. There is but one kind of black pigment granule in both Chinese and American horse hairs. Diffuse pigment was found in black and other colored hairs in the immediate vicinity of the granule cluster. It is dark yellow in color. Plate II, Figs. 3 and 4 show cross sections of jet black hair.

In rusty black hair, both black and amber colored granules can be distinguished in cross sections; however, no one hair contains granules of both kinds. The percentage of hairs with amber granules probably determines the degree of rusting. Figure 5 shows a typical rusty black.

Black hairs were bleached to determine whether black granules could be changed to red by exidation. Thirty percent hydrogen peroxide was used. After 2 hours of bleaching the hair became mahogany color, after 4 to 5 hours, brownish, after 12 hours, red chestnut, 24 hours and thereafter, the hair was a light chestnut and made no further change. Thus it might seem that all colored hairs are chemically alike.

Eay. The quantitative difference of pigment granules results in variation of coat hair color. This is obvious in bays and chestnuts. In brown animal, Fig. 6, hairs with amber pigment granules are much more numerous than those with black granules. The red bay, Fig. 7, shows the amber granules much crowded. The yellow bay, Fig. 8, has a smaller number of granules. It is noticeable that the amber granules occupy the distal portion while the proximal portion is either colorless or contains a countable number of pigment granules.

Chestnut. Chestnut, regardless of shade, differs from the bay coat hair chiefly in having comparatively fewer pigment granules. The amber granules are distributed evenly in the body shaft, especially at the tip of red and dark chestnut, Figs. 9 and 10. Dilute black granules sometimes occur in the latter. The light chestnut, Fig. 11, is characterized by a concentration of the granules at the distal portion, thus being similar to the Palomino hair, Plate III, Fig. 13. The sorrel, Plate III, Fig. 12, has about the same distribution of pigment gran-

ules as the common chestnut; however, in some of the lighter sorrels the granules are clustered on one side of the cortex but not so distinctly as in dun hair.

The chief characteristic of dun hair is the tenden-Dun. cy for the pigment granules to ag regate on one side of the cortex. Chestnut dun, Fig. 14, contains amber granules with a few dilute black granules. The yellow dun, Fig. 15, has fewer granules than the former, and the clustering of the granules on one side of the cortex is not so distinct. Gray dun, Fig. 16, shows amber and black granules in separate colored hairs, and a few dilute amber granules in white hairs, the proportion of the hairs with amber granules to those with black granules varies with the grade of graying. In white dun, only dilute amber granules are visible. Diffuse pigment, which occurs in intimate association with the pigment granules, is of special interest in dun hair. On the side of the cortex where the pigment granules aggregate, yellowish diffuse pigment can be observed. On the opposite side, where no granule cluster exists. no diffuse pigment is present.

The hair of the dorsal stripe was also observed. The clustering of the pigment granules is more distinct on one side of the cortex than in typical dun hairs. Figure 16 shows the granule clusters of the yellow-dun dorsal stripe in which the hairs with black pigment granules were also found. Figure 18 shows the amber granule clusters of white-dun dorsal stripe hairs.

Gray. The distribution of pigment granules in gray hair

varies with the age of the animal. In old horses the hairs contain scattered dilute amber granules or are devoid of granules. In iron gray, Fig. 18, the black granules are predominant over amber granules, the latter appearing in the distal portion of the hair, the black granules only occur in black hair. However, the interspersed white hairs of an aged gray are hardly distinguishable from the white hairs of an albino.

Roan. In the roan the color of the granules and distribution of the granules are dependent on the color of the pigmented hairs. The white hairs cannot be distinguished histoligically from those of the albino. For instance, bay-roan, Fig. 19, shows the pigment granules in red hairs to be similar to those seen in red bay hairs.

Albino. There is no true albino in horses. In horses of slightly cream body color, which Castle (1948) designated as albino type B, or A-B-DD, the hair contains a few dilute amber granules at the tip of the hairs. Figure 20 does not show the granules because they are too few to be shown.

It seems worth mentioning here that the medulla plays no part in the coloration of the hair in spite of its dark brown color and the fact that it occupies seven-tenths of the hair shaft, and is surrounded only by the very thin translucent cortex in the case of albino hair, Fig. 1.

White hairs secured from areas where wounds had healed on black horses were also examined. These hairs were the same as those of albinos, with the exception that a few dilute amber granules were present. The medulla of these hairs was also smaller than the medulla found in albinos.

Discussion

Based on the present study, pigment granules can be classified into two main kinds: black and amber (red). The distribution of these granules is chiefly governed by the black gene and the extension gene. Some dilute black and dilute amber granules also can be distinguished in the lighter colors. These dilute granules may be interpreted as the result of the oxidation of the two main types of pigment granules. The process of oxidation supposedly is regulated by dilution factors, possibly due also to certain modifiers, such as the gray gene and the dun gene.

The results of the present study agree with those of Gremmel (1939) in a number of respects: (1) the fact that the pigment granules form in clusters, (2) the distribution of the granule clusters determines the color and shade of the hair, (3) pigmentation of the cortex, particularly in its outer portion, plays a major role in the variation of color and shade, (4) the cuticle is too thin to have any effect on the color.

However, the results herein presented do not agree with his statements: "There is but one pigment that produces color in horse hairs and this pigment is amber color." and "No diffuse pigment is formed." Diffuse red pigment has been found in human hair by Trotter (1932), in cattle hair by Bogard and Ibsen (1937) and in guinea pig hair by Harman and Case (1941). In the present study, it has been found in close proximity to the granule clusters. Although the red and black pigment granules are alike chemically, all workers, with the exception of Gremmel (1939), are agreed that they look different.

The observations made here differ in a number of other respects from those of Gremmel. He states that the tendency for the granule clusters to form on one side of the hair is characteristic only of dum hair. A similar tendency has been found in a relatively large number of sorrel hairs. Gremmel also is of the opinion that if the medula is relatively large, it may affect the appearance of the hair. The present study shows that white hairs are not modified even though they have a very large medulla.

PHYSICO-CHEMICAL STUDY OF HORSE HAIR

In the preceding histological study, it was stated that the pigment granules, though different in color, were similar in chemical character. This, however, could not be determined by histological observation. Thus it became necessary to resort to the present study through the aid of the spectrophotometer. The physical study of the horse hair pigment has been carried out in recent years by some research workers who used the colorimeter and the spectrometer. It has been known for

some time that the spectrophotometric method is better for such determinations. It analyzes color by measuring the actual radiant energy emitted or absorbed, and has been used successfully for the study of hair pigment of other animals.

Materials and Method

The hair samples were selected from those used in the previous histological study. It seemed unnecessary to examine all the hairs, as the following colors were deemed sufficient to represent the variation of the horse hair colore. Those hairs were: (1) black, (2) red hay, (3) red chestnut, (4) yellow dun, (5) gray with few dispersed black hairs, and (6) albino.

The hairs were defatted for two hours in a Soxhlet's apparatus with carbon tetrachlorate (CCl₄). A sample made up of 0.25 g of the defatted hairs was boiled in 100 cc of 1% NaOH solution for one hour. As horse hair is fairly sensitive to caustic, it took only 20 to 30 minutes for the hairs to be completely dissolved. The solution containing the pigment was cooled to 40-50° C. and filtered. The filtrate was kept at approximately the same aqueous volume it had before boiling and stored in corked flasks at room temperature, 70-75° F.

Bausch & Lomb's spectrophotometer was used for this study. Readings were made at eight wave lengths in the visible range of the absorption bands between 475-650 mu (equal to 4750-6500 A). The logarithm of the optical density was plotted against

the wave length, giving linear curves.

Statistical methods for comparing the curves were used in order to make more accurate comparisons. This method had been adopted previously only by Baker and Andrews (1944). The method of least squares modified the curves to comparable straight lines, thus affording a statistical value, the regression coefficient, which was calculated as the change in log optical density per change of 10 mu in wave length.

For contrast, dopa melanin solution and horse hoof extract were also examined. The former was made about six years ago, and had been examined by Baker and Andrews. The horse hoof was yellowish in color, and corresponded chemically to the keratin of hair. It was donated by the Anatomy Department of the Kansas State College Veterinary School. It was dissolved in the same percentage of NaOH solution, and with the same procedure as that for preparing the hair solution.

Results of Optico-Chemical Study

Each sample of hair solution, made in accordance with the above mentioned procedure, was tested for its optical density ($\log \frac{I_0}{I}$). The log optical density and regression coefficient are given in Table 1.

Table 1. Spectrophotometric results of horse hair solutions.

Sam-	:	:Log optic	1	0
ple				:Color of solution
no.	Samples	at 550 mu	: 0001.	after filtration
1	Jet black	-0.0000	-0.0135	Blackish
24	Jet black	-0.0132	-0.0136	Blackish
3	Jet black	-0.1871	-0.0166	Blackish
40	Ordinary black	-0.2218	-0.0160	Blackish
5#	Ordinary black	-0.3665	-0.0220	Dark brown
6#	Rusty black(winter)	-0.3979	-0.0176	Dark brown
7	Rusty black(winter)	-0.3979	-0.0152	Park brown
8	Rusty black(winter)	-0.4089	-0.0219	Dark brown
94	Darker red bay	-0.4815	-0.0382	Red wine or dark amber
104	Darker red bay	-0.4881	-0.0445	Concentrated red wine
11	Medium red bay	-0.4980	-0.0448	Concentrated red wine
12	Darker red chestnut		-0.0312	Brownish
13#	Darker red chestnut	-0.4318		Brownish
144	Darker red chestnut	-0.4559	-0.0346	Amber
15	Medium red chestnut	-0.5229	-0.0390	
16	Medium red chestnut	-0.5768	-0.0304	
17	Light dun	-0.8861		Yellowish
18	Light dun	-1.3010		Yellowish
19#	White (old gray)	-1.5229	-0.0125	Ivory, slightly yellowish
20	White (old gray)	-1.6990		Ivory, slightly yellowish
21#	Albino hair 1	-1.2218		Slightly golden yellowish
22	Albino hair 1	-1.3979	-0.0173	Slightly golden yellowish
23#	Albino hair 2	-1.0000	-0.0062	Slightly golden yellowish
24	Albino hair 2	-1.0000	-0.0041	Slightly golden yellowish
25	Horse hoof	-1.3468	-0.0150	Ivory, slightly yellowish
26	Dopa melanin	0.1914	0.0124	Tan black

[#] Hair from American horses.

Curves plotted in Fig. 21 represent the hairs of each color as described above. For comparison the extinction curves of alkali solution of long hairs (mane and tail) given by Zwicky and Almasy (1937) were reproduced in the same figure. However, these investigators did not use the statistical method to determine the regression coefficient and another method was used in the preparation of the solution. The regression equation for some representative curves shown in Fig. 21 were:

No. 5 black hair E = 0.8427-0.0220X

10 red bay E = 1.9580-0.0390X

15 red chestnut E = 1.6030-0.0390X

18 light dun E = 0.4865-0.0146X

21 albino E ==0.5453-0.0150X

25 horse hoof E ==0.5453-0.0150X

Thus the regression coefficient of black hair was fairly low as compared with that for intense black guinea pig hairs, determined by Baker and Andrews (1944). The latter stated that the regression coefficient was in the range -0.017 to -0.24, and from animals that were raised in the same colony. The intensity of pigmentation in black horse hairs varies to some extent because these samples were taken from different sources. Red bay hair solutions gave the highest regression coefficients, and obviously corresponded with that of the cherry red guinea pig hairs of Baker and Andrews. As discussed in the histological study, it was shown that both bay and chestnut coat hairs of the

same shade were similar in respect to the distribution of the red pigment granules and supposedly were due to the same genes except for the long black hairs found in the mane and tail of bays. This interpretation was also confirmed by the spectrophotometrical observations. For instance, the sample No. 14 has the regression coefficient close to its correlated shade, red bay. No. 9, but the average chestnut regression coefficient was relatively lower if compared with that for bay. As shown in above list. the regression coefficient for bay was in the range -0.0448 to -0.0382, but that for chestnut was -0.0346 to -0.0283. The light dun solutions gave regression coefficients approaching those for white and albino hairs. Another sample of yellow dun, macroscopically very similar to yellow chestnut, gave an optical density of -1.0458 at the same wave length and a regression coefficient of -0.0220. White was not put into the above list because one value was not considered sufficient. The white hairs of an aged gray animal, which appeared somewhat whiter than the hairs of an albino gave a regression coefficient very similar to that for the first two albino hairs. Two solutions which were made of albino hairs from another animal were saved to examine as late as 60 hours after the solutions were made in order to observe any possible change. Obviously, the straight line of these albino solutions, if plotted in the same table, would be close to horizontal because they gave the lowest regression coefficient.

The optical behavior of horse hoof extract furnished evidence regarding its similarity to white and albino hairs. Because the horse hoof corresponds chemically to the keratin of hair and contains no pigment granules, one would expect its optical density and regression coefficient to be quite similar to that for albinos. The dopa melanin solution (1 g dopa in 1000 cc water) obviously seemed darker than the same material when it was examined four years ago. Light could scarcely be transmitted through the solution unless the plungers were set at a depth of 0.5 cm.

Some observations were made regarding the effect of oxidation on place pigment in NaOH solutions for varying periods extending up to one month. The results furnish evidence that the black melanin has been converted into red melanin through oxidation, Table 2.

Recently Baker and Andrews (1944) analyzed the heir pigments of the guinea pig spectrophotometrically. They concluded that the red and black melanins were distinguishable; qualitative differences might exist between different black hairs; chocolate and black were chemically alike, and the red melanin was an exidation product of black melanin.

Optical change of black hair melanin solutions. Table 2.

Comma D		. Days	Days of examination after the solutions were made	on after	the soluti	erew suc	made
000		I.	6	14	16	21	30
н	Log optical density Regres. coef.* Color changed to	-0.000 -0.0135 blackish		-0.5528 -0.0197 brown	400	-0.6198	-0.5607
27	Log optical density Regres. coef.*** Color changed to	blackish	-0.5428 -0.0147 deep brown	-0.8539 -0.0213 brown	-0.9031 -0.0249 amber	8080°0-	mov

Solution No. 1 was the same as Optical density was read at 550 mm wave length. 44 Solution No. 27 was made from 0.125 in the previous list.

that the solution No. 5 was treated with 1% NaOH soaking for 28 days without Its filtrate was dilute brownish, with log optical density -0.5507, g hair dissolved in 100 ce MaOH solution. 16th day and thereafter was indistinguishable Indicates that the solution at the regression coefficient -0.0128. from the red bay solution. Indicates that the solution bolling. 春中中立 中心の

CONCLUSIONS

Two kinds of pigment granules, black and amber, exist in horse hairs. The dilute pigment granules from these are also distinguishable. All the granules have the same pigment, melanin, and possess the same chemical characteristics. The dilution of the pigment and the variation of shade are due to the exidation of melanin.

The extent and intensity of granule pigment determines the color and shade of hair. The size and pigmentation of the medulla play no part in the coloration of the hair.

Diffuse pigment is present in horse hair in the vicinity of the granule clusters and may possibly be a chemical derivative of the granules.

Spectrophotometrical examination indicated that there may possibly be no distinction between black, and red (bay and chestnut) a mically, although some physical and qualitative differences do exist.

EXPLANATION OF PLATE I

- Whole mounts of horse hairs (x 200) from left Fig. 1. to right:
 - (1) A proximal portion of brown hair. Proximal portion of dorsal stripe hair of dun contains few granules, thus appears nearly white. Its distal portion shown in Fig. 2 (4).

Red bay, the granule clusters appear in a bead-shaped streak. The same is true of brown and red chestnut.

- (4) Albino, note the medulla, which apparently occupies seven-tenths of hair shaft. It is evidence that the medulla does not affect the color of the hair.
- Fig. 2. Whole mounts of horse hairs (x 60) from left to right:

Red chestnut.

(1) Distal portion of the same albino hair as shown in Fig. 1 (4).

(3) The same hair as shown in Fig. 1 (3). Distal portion of the dorsal stripe hair of

dun, where pigment granules concentrate. Its proximal portion was shown in Fig. 1 (2).

(5) Body shaft of black hair, light could not penetrate it.

(6) Body shaft of yellowish dun appears lighter. Note the broken medulla.

PLATE I

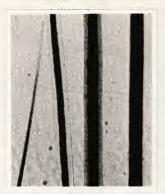


Fig. 1.



Fig. 2.

EXPLANATION OF PLATE II

- Cross sections (r 200) were made of Chinese horse hairs (except the Palomino). It seemed valuable for comparison with cross sections of American horse made by Gremmel. Some differences in the clustering of pigment granules are distinguishable.
 - Fig. 3. Jet black hairs (12 microns) which are hardly distinguishable from the ordinary black microscopically.
 - Fig. 4. Black hairs, same as Fig. 3 (8 microns).
 - Fig. 5. Rusty black (12 microns).
 - Fig. 6. Brown (12 microns), black bay is about the same. Black granules appear in the darker cross section.
 - Fig. 7. Red bay (12 microns). No black granules occur.
 This section shows amber granules much crowded,
 but some darker shades of bay have a few black
 granules.
 - Fig. 8. Yellow bay (12 microns). Small amount of amber granules and lighter diffuse pigment are seen in the same section.
 - Fig. 9. Dark chestnut (12 microns). Both amber granules and dilute black granules are present.
 - Fig. 10. Red chestnut (12 microns). No black granules present. It is the same shade of red as a red bay, but the medulla in this case is smaller than that shown in Fig. 7. Hairs of this section and Fig. 9, are finer than the others.
 - Fig. 11. Yellow chestnut (12 microns). It is hardly distinguishable from the yellow bay. The Palomino hair gives the same pigmentation. Only amber granules and lighter diffuse red pigment are present.

PLATE II



Fig. 3.



Fig. 4.



Fig. 5.



Fig. 6.



Fig. 7.



Fig. 8.



Fig. 9.



Fig. 10.

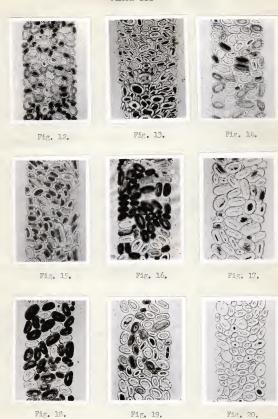


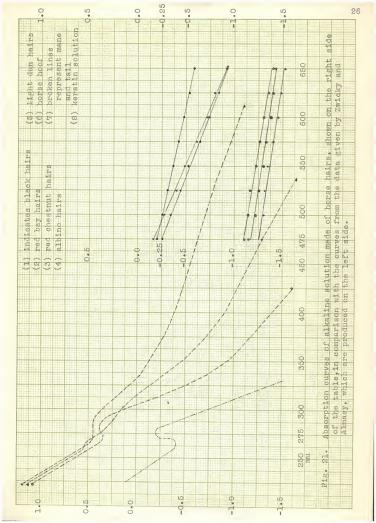
Fig. 11.

EXPLANATION OF PLATE III

- Fig. 12. Sorrel (12 microns). Note the distribution of granules in the cortex. They are not evenly distributed and tend to collect on one side to some extent. Thus it appears like a yellow dun shown in Fig. 14. No black granules were present.
- Fig. 13. Light Falomino hair (12 microns). Many of the cross sections do not contain granules. A deeper Palomino is similar to the yellow chestnut. There are only amber and dilute amber granules.
- Fig. 14. Yellow dun (12 microns). The granules are not evenly distributed, being collected at one side. There are amber granules with a few dilute black granules.
- Fig. 15. Gray dun (12 microns). Granule clusters occupy one side of the cortex. Both dilute black and dilute amber granules are present.
- Fig. 16. Dorsal stripe hairs of yellow dun (12 microns).
 Granule cluster is also formed on one side. A
 few dilute black granules are present.
- Fig. 17. Dorsal stripe hairs of white (old gray) dun (12 microns). The hairs are dark tan in appearance. Granule cluster is strikingly formed on one side. Both dilute amber and dilute black granules were present.
- Fig. 18. Iron gray (12 microns). The black hairs are completely similar to those shown in Fig. 3. The white hairs are undistinguishable from the albino hair shown in Fig. 20. The black roan is quite similar to iron gray in cross section.
- Fig. 19. Bay-roan (12 microns). The darker hairs are red, which are entirely like those in Fig. 7 or 8, the rest are the white hairs or the proximal portions of red hairs.
- Fig. 20. Albino hair (8 microns). The cortex appears translucent, some of these sectioned hairs contain a few dilute amber granules.

PLATE III





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LITERATURE CITED

- Anderson, W. S.
 The inheritance of coat color in horses. Ky. Agr. Expt.
 Sta. Bul. 180. 121-145. 1914.
- Baker, M. R. and A. C. Andrews.
 The melanins. I. Studies of the hair pigments of the guinea pig. Genetics. 29: 104-112. 1944.
- Bodansky, M. Introduction to physiological chemistry. New York. Wiley and Sons. 686 p. 1944.
- Bogart, R. and H. L. Ibsen.
 The relation of hair and skin pigmentation to color inheritance in cattle, with some notes on guinea pig pigmentation. Jour. Conet. 35: 31-59. 1937.
- Castle, W. E.
 The genetics of coat color in horses. Jour. Hered. 31: 127-129. 1940.
- Castle, W. E. Cenetics of the palemino horse. Jour. Hered. 37: 35-38. 1946.
- Castle, W. E. The ABC of color inheritance in horses. Genetics. 33: 22-25. 1048.
- Cook, A. H. '
 The chemistry of natural coloring matters. New York.
 Reinhold Publishing Corp. 354 p. 1945.
- Crew, F. A. E. and A. D. B. Smith.
 The genetics of the horse. Bibliographia genetica.
 124-147. 1930.
- Gremmel, F. Coat color in horses. Jour. Hered. 30: 437-445. 1939.
- Harman, M. and A. A. Case. Cenetic aspects of pigment production in the guinea pig. Genetics. 26: 474-436. 1941.
- Ibsen, H. L. Cattle inheritance, 1 color. Genetics. 18: 441-480. 1933.

Munckel, H.

Undersuchungen ueber Farben und Abzeichen des Pferdes und ihre Vererbung. Zeitehr. Tiezucht und Zuchtungsbiol. 16: 1-200. 1929.

Salisbury, G. W.

The inheritance of equine coat color 1. The basic color and patterns. Jour. Hered. 32: 235-240. 1941.

Salisbury, G. W. and J. W. Britton.

The inheritance of equine coat color 2, the dilutes with special reference to the Palomino. Jour. Hered. 32: 255-261. 1941.

Sturterant, A. H.

A critical examination of recent studies on color inheritance in horses. Jour. Hered. 2: 41-51. 1912.

Sission, S.

The anatomy of the domestic animals, revised 3rd ed. Philadelphia. W. B. Saunders Co. 972 p. 1947.

Smith, E. Philip, editor.

Bailey's textbook of histology, 10th ed. Baltimore. William Wood and Company. 762 p. 1940.

Trotter, M.

Cowdry's special cytology, 2nd ed. New York. Paul B. Hoeber, Inc. Vol. I. 552 p. 1932.

Zwicky, H. and F. Almasy.

Optische Untersuchungen ueber das Haarpigment. Biochem. 2tschr. 281: 164-165. 1937.