

THE INHERITANCE AND VARIATION OF CERTAIN COLOR  
CHARACTERS IN GUERNSEY CATTLE

by

INGE KALLESØE KJAR

Graduate in Agriculture,  
Royal Veterinary and Agricultural College  
of Copenhagen, Denmark, 1931

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## INTRODUCTION

A considerable amount of study has been made of inheritance in cattle. Thus far color has probably received more attention than other characters. This may be due to the fact that color from earliest history has been the chief distinguishing feature of the breeds, and the fixing of definite color characteristics has been emphasized. The breeders of today lay more stress upon development of conformation and of increase in milk-yield. The inheritance of these latter characters, however, seems to be even more complicated than the inheritance of color.

Ibsen (1933) has reviewed and analyzed the literature on the more important color genes and has offered explanations and suggestions for further investigations. The present study represents suggestions made directly or indirectly in his paper, and his terminology for the different factors is used.

The purpose has been to study the inheritance and variation of certain color characters in Guernsey cattle. These characters are as follows:

1. Distal leg-spot
2. Irregularity in outline of pigmented areas on body.

3. Pigmented nose, Ps
4. Variation in distribution of white.
5. Variation in shade of red.

#### MATERIAL AND METHODS

The Guernsey herd of the Department of Dairy Husbandry of the Kansas State College has been used as the basis for this study. Forty animals were included in the investigation. Photographs were taken of both sides of each animal, and additional ones were taken if an animal showed special characteristics.

In each case an attempt was made to include the four hoofs, and a front view of the head. All the photographs of an animal were placed on a separate sheet, and to this were added the name and pedigree number, date of birth, and the names of the sire and the dam. If distal leg-spots were present, diagrams of the legs showing the exact location of the spots accompanied the photographs.

A list of the characters studied has already been given. It may be advisable at this time to give some of the details concerning these characters.

Most attention has been given to distal leg-spots, which are small pigmented areas located immediately above



one or more of the hoofs. They vary from one-half inch to two inches in diameter, but have no definite shape or outline.

Irregularity in outline of the pigmented areas on the body occurs most commonly in the Ayrshire breed. Only a small proportion of Guernsey cattle show this character, but when present it is as a rule easily recognized. It is, however, more conspicuous the more white the animal shows. Since the individuals in the college Guernsey herd have a comparatively small amount of white it has been found in a few cases that the amount of white is so small that it is difficult to determine whether or not the pigmented areas have an irregular outline.

Pigmented nose (Ps) refers to black pigmented spots in the noses of Guernseys and Shorthorns. The pigment is always black and apparently is not due to any other known factor. The pigment may be extended entirely or only partially over the nose, indicating that the factor expresses itself in different degrees. Pigmented (black) nose differs decidedly in appearance from the yellowish brown color usually found. The latter is the result of the interaction of red (R) with other factors occurring in the Guernsey and Shorthorn breeds.

Investigations in regard to the location and the amount of white resulting from recessive white spotting (s) have been carried on in the Holstein breed by Lauprecht (1926). In spotted breeds like Holsteins and Guernseys it is difficult to determine the border line between animals which are either homozygous or heterozygous for the white spotting modifiers, Lw and lw. Dominance is incomplete. Homozygous dominants (LwLw) should have a small amount of white, heterozygotes (Lwlw) an intermediate amount, and the recessives (lwlw) a large amount. Most of the individuals in the Guernsey breed are probably LwLw, and one of the purposes of this study was to investigate the variation in the amount and the distribution of white in such animals.

To determine the distribution of white, each photograph was looked over carefully and the white areas were located under the following headings: (1) ventral part of body; (2) limbs; (3) head; (4) other parts of body. (Under the last heading each location was given). Each heading was divided into three columns (small, medium and large) which referred to the amount of white present in the different locations. After the material had been classified in this manner, it was hoped that a determin-

ation could be made of the relation between the amount of white and its location, and of the correlation between the amount of white in different parts of the body.

It is a well known fact that Guernseys vary in shade of red. Up to the present no one has attempted to ascertain the underlying genetic reasons for these variations. In making the study hair samples were taken from each animal at three different times and from two different locations on the body. One of these locations was about three inches to the right of the spinal column and about fifteen inches posterior to the shoulders. The other was on the middle of the right leg about eight inches dorsal to the hock joint. The hairs from the first location represent approximately the average shade, while those from the second represent a typical light shade. The first samples were taken toward the end of the summer, after the animals had been exposed to the hot sun for a number of months. The second samples were taken in December at the beginning of winter; and the third samples were taken in March, at the end of winter. The hair samples were kept in separate paper envelopes and these in turn were kept in a dark drawer to prevent any changes, due to light, in the shade of the hair samples.

Each animal was carefully examined for the different characters being investigated, and a short description of each was given. The sheets containing data on separate individuals were arranged chronologically, based on the age of each animal. The material used for each study was tabulated and analyzed.

For identification purposes the Guernsey Association requires a diagram of every registered animal, showing the location of the pigmented areas. Oftentimes close examination is necessary for the recognition of distal leg-spots, since they may be covered with dirt. Extreme accuracy is not necessary in making the required diagrams and this, at least partially, accounts for the fact that the distal leg-spots are not always indicated. Therefore it was decided to use in this study only animals present in the herd, and in addition, five cows not in the herd, whose diagrams definitely showed the character under discussion. For similar reasons, only animals present in the herd or animals of which photographs could be obtained were used to study the inheritance of the irregularity in outline of pigmented areas on the body.

No herd could be found near Manhattan in which the bull did not show the distal leg-spots, nor could a bull

be found in this locality whose spots were irregular in outline. This proved a serious handicap when the attempt was made to determine the mode of inheritance of the characters in question. The numbers concerned in regard to all the characters studied were small, thereby making it necessary to draw only tentative conclusions in regard to all of them.

#### REVIEW OF LITERATURE

With the exception of a paper by Gowen (1918) and one by Ibsen (1933) there is little in the literature on color inheritance in Guernsey cattle. In Ibsen's paper a comparison is made between pigmented leg (Ibsen and Riddell, 1931) and distal leg-spot. The former is described as pigmentation concentrating around the hoof and extending upward. The gene also causes small pigmented areas to appear on the head. This character is found only in the Ayrshire and Shorthorn breeds in this country. It has probably been eliminated in the Holstein breed through selection, since its presence bars the animal from registration. Small black spots, similar in appearance and location to the red distal leg-spots of Guernseys, also bar animals of the Holstein breed from registration.

Ibsen is the only author who has called attention to the fact that irregularity in outline of pigmented areas on the body is found in the Guernsey breed. He also comments on the frequency with which the character occurs in the Ayrshire breed.

Pigmented nose (Ps) is assumed by Ibsen to be due to the same gene which causes black pigmented skin in animals not carrying black (B) or black spotting (Bs). Miss Pitt (1920) is the first to mention that "smutty" (black-spotted) nose is found in Herefords, and that it is apparently due to a dominant gene. She restricts the effect entirely to the nose, however.

Several papers have been published on variation in distribution of white spotting. Gowen (1918) made a study of the inheritance and location of the individual spots throughout the coat of crosses between dairy and beef breeds of cattle. He came to the conclusion that the individual spots except for the inguinal region are inherited as recessives. He also enumerated the different locations of the spots.

Dunn, Webb and Schneider (1923) made a study of inheritance of the degrees of spotting in Holstein cattle. They attempted to define and describe the variation in



the gross amount of white spotting in this breed, and to determine whether variations in the amount were inherited, and, if so, in what manner. By superimposing a diagram containing very small squares they were able to compute the approximate amount of black and therefore also the approximate amount of white on each diagram. They selected four bulls representing different degrees of pigmentation. From the register book they chose at random about fifty cows to which each bull had been mated, and investigated the offspring of these animals. They did not come to any conclusions, but state that the results of their study indicate that differences in the amount of spotting in Holstein cattle are inherited, that the darker grades are probably dominant over the lighter grades, and that somatic variation may have some influence. From the evidence furnished in their paper Ibsen concluded that they were working with a single pair of modifiers affecting recessive white spotting (g). He proposed Lw for the factor causing a small amount of white. The results obtained by Dunn, Webb and Schneider proved this factor to be incompletely dominant to its recessive allelomorph lw, which causes a larger amount of white.

Lauprecht (1926) studied spotting in Holsteins from the standpoint of the location of pigment centers. He stated that the total amount of black is correlated with the amount at each center, but did not state whether the same was the case concerning white. He did observe, though, that animals having a large amount of white are white ventrally and posteriorly and to a less extent anteriorly.

## THE EXPERIMENT

### Distal Leg-spot

It has been shown that pigmented leg (Pl), is inherited as a dominant (Ibsen and Riddell, 1931). Although the factor for distal leg-spot has apparently only one effect, this character resembles pigmented leg more than it does any other known character, and, coincidentally, the mode of inheritance for both appears to be the same.

When studying inheritance in cattle it is usually necessary to obtain data from animals used for other purposes, and thus it often becomes difficult to obtain the right sort of material in large enough numbers. In this study of the inheritance of distal leg-spot (Plate I),



observations were made on forty-four animals. Nineteen cows were chosen, all of which had offspring sired by the two bulls now in the herd. Both bulls show the character. These cows and their offspring were divided into two groups, the line of demarcation being the presence or absence of distal leg-spot in the cow.

Group I contains matings in which both parents show distal leg-spot. Thus it includes the offspring of sixteen of the nineteen cows mentioned above, sired by either of the two bulls. These sixteen cows and their offspring have been divided into two sub-classes:

1. Five cows with ten offspring, four showing distal leg-spot, six not showing it.
2. Eleven cows with fifteen offspring all carrying distal leg-spot.

Only by assuming that distal leg-spot is due to a dominant gene, can we find a plausible explanation for the six offspring without spots in class 1. The five cows and the two bulls would under the circumstances be considered heterozygotes (Ldld), and the offspring not showing the character, recessives (ldld). Each of the two bulls has produced at least one recessive offspring and is therefore correctly listed as a heterozygote.

Some of the eleven cows in class 2 are undoubtedly heterozygotes, but, due to the small number of offspring, did not chance to produce any that were recessives. The fact that both bulls are heterozygotes lends support to the supposition that a large per cent of the cows also are. If the genotypic composition of all the cows were known, and the offspring of all the heterozygotes were combined, the phenotypic ratio would unquestionably have been nearer to 3:1 than that actually obtained (4Ld:6ldld).

Group II contains those matings in which one parent, in this case the bull, carries distal leg-spotting, and is heterozygous, and the other parent does not, and is therefore recessive. Only three recessive cows were present in the herd, and when mated to one of the heterozygous bulls produced three heterozygous calves, the theoretical ratio being 1:1.

The evidence that distal leg-spot is due to a dominant gene is rather meager, but it is at least consistent. One form of evidence entirely lacking, however, is that recessives breed true. In other breeds, on the other hand, such evidence can easily be found. The distal leg-spot seems to be almost entirely lacking in Holsteins, and many examples could be obtained of animals breeding true for the absence of it.

### Irregularity in Outline of Pigmented Areas

Irregularity in outline of pigmented areas on the body is of common occurrence in the Ayrshire breed. The fact that this characteristic seems to breed true without any selection being practiced suggests that it is inherited as a recessive. It is not quite so common in the Guernsey breed, but the evidence indicates that it is inherited in the same manner as in Ayrshires. On examination of eight cows showing the character it was found that in at least seven of them there were "halos" (mentioned by Ibsen, 1933) surrounding the pigmented areas. On the other hand, no halos were found surrounding pigmented areas with a smooth outline. This leads one to suspect that the halos may be due to the same gene (or genes) that cause the irregularity in outline of the pigmented areas (Plate I).

A total of thirty-three Guernseys were examined in this study. The data were collected under two groupings. Group I includes matings in which both parents were smooth. Seven cows mated to three bulls produced eight offspring, seven with smooth outlines and one with irregular. The results obtained fit in with the assumption that the gene causing a smooth outline to the pigmented areas is dominant

to the one causing an irregular one. It is not known, however, how many of the above parents were heterozygous. Two at least were - one bull and one cow. These produced the calf with the irregularly outlined spots. The cow later gave birth to a smooth calf after having been mated to another smooth bull.

Group II consists of the matings of three smooth sires to eight irregular dams. Of the eleven offspring two were irregular (one being a border-line case), and nine smooth. The undoubtedly irregular offspring was sired by the same bull that sired the irregular animal in Group I, while the other irregular was sired by a different bull. Thus we are certain of only one bull being heterozygous. On the other hand, the numbers are too small to justify one in assuming that either of the other two bulls was a homozygous dominant.

Besides the two groups of matings above mentioned, a record was obtained of the mating of an irregular bull to a smooth cow. The calf was irregular, thus proving that the cow was heterozygous.

The results, so far as they go, fit in with the hypothesis above mentioned that a dominant gene is responsible for the smooth outline to the pigmented spots, and

its recessive allelomorph for the irregular outline. The type of evidence entirely lacking in the Guernsey material herein presented is that recessives breed true. This deficiency, however, can be abundantly supplied from the Ayrshire breed.

#### Pigmented Nose, Ps (Pigmented skin-spots)

Most Guernseys have a yellowish-brown nose color. According to Ibsen (1933) the intensity of this color is correlated to a large extent with the shade of the hair. Pigment due to Ps, however, is always black, although the amount present and its location may vary. In his discussion of the factor Ibsen postulates that it may produce black skin-spots on any part of the body, but that these spots will not show readily under pigmented hair. Guernseys are to a large extent pigmented, and therefore in this study only the presence or absence of black spots on the nose will be taken into consideration.

In the study of the inheritance of pigmented nose in the Guernsey breed, observations were made on twenty-four animals. Neither of the two bulls used showed the character. Eleven cows and their offspring were divided into two groups, determined by the presence or absence of pig-

mented nose in the cows. In Group I, seven cows with pigmented nose mated to the two bulls produced nine offspring, four with pigmented nose (Ps), and five not showing the character (psps).

Pigmented nose has probably not been subject to selection and the possibilities are that most of the seven cows, if not all, are heterozygous (Pps). If that is the case, a 1:1 ratio would be expected when these cows were mated to recessive bulls (psps). The ratio obtained (4:5) fits closely with the assumption that pigmented nose is inherited as a dominant character. It may be of interest to mention that in one of the offspring the pigment was extended all over the nose making it entirely black, which, to say the least, is an unusual expression of this factor.

Group II consisted of four cows, not showing pigmented nose, mated to the two bulls. Four offspring were produced, all like the parents. This indicates that the absence of the character breeds true, and that pigmented nose in the Guernseys may be looked upon as being due to at least one dominant gene. The numbers, however, are too small to justify any final conclusions. It may be of interest to note that results published by Miss Pitt (1920) indicate that pigmented nose in Herefords also is inherited as a dominant.



### Variation in Distribution of White

Several authors have studied variation in distribution of white, and they also have made attempts to determine the relation between the amount of white and its location. The Holstein breed, however, has apparently furnished most of the material for these studies. As yet no observations pertaining to this matter seem to have been made in the Guernsey breed.

The material for the present study has been obtained from thirty-seven Guernseys. When a tabulation was made of the location of the white areas, it was found that all thirty-seven animals showed white on the switch of the tail, on the ventral part of the body and on the distal ends of the limbs. Thirty-two of the thirty-seven animals had varying amounts of white on the head. Two of the remaining five, although not having any white on the head, had white on other parts of the body besides those enumerated above. The remaining three were entirely pigmented except for the switch of tail, ventral part of the body, and the limbs. For these three the amount of the white was small in each of the different locations. Thirty animals, besides having white on the tail, underline and legs, also

had white on other parts of the body such as the shoulder, thighs, tail-head, rump or above the udder. Twenty-eight of these showed white on head. One animal had red hairs intermixed with white in the switch of the tail; all other animals in the herd had white tail-switches.

The material has been classified as shown in Tables I and II. Table I includes nineteen animals which apparently show correlation between the amount of white at the different locations. These animals have been divided into three groups, based on the relative amount of white present. From this table it will be noted that, of the nine animals which show a small amount of white (Group I), three, in class 1, have the white restricted to the ventral part of the body and limbs (the white on the switch is left out of consideration). Three animals show white also on the head and are therefore placed in class 2; and, finally, three animals which also have white on other parts of the body are found in class 3 (Plate I). The same classifications are used for the three groups. Thus, in the medium (II), and large (III) groups, all of the animals except one are in class 3 (Plate I).

Eighteen of the animals examined apparently did not show perfect correlation between the amounts of white on



the different parts of the body. Table II represents these animals arranged in accordance with the total amount of white they carry. The seven animals first considered have all a small amount of white on the ventral part of the body. One of these has white on the head and legs but does not have any on other parts of the body, another does not have any white on the head. One of the bulls, No. 2, has a large amount of white on the head, but only a medium amount on other parts of the body, an unusual distribution. It will be found, however, that even in Table II, which contains the exceptions, there is a fairly close correlation between the amounts of white on different parts of the body.

The evidence obtained in this study indicates that in Guerneseys having a small amount of white the white will usually be located at the switch of the tail, the ventral part of the body, and the limbs. As the amount increases it is usually found first on the head, then on the shoulders, thighs and above the udder. Other locations are the tail-head and the rump. It was also noted that an increase in the amount of white often consists in an expansion of some one area, rather than in increase in the number of white areas.

Table I.- Nineteen animals showing correlation between amount of white at different locations.

		Class 2			Class 3
		Class 1			
		White on ventral part of body	White on limbs	White on head	White on other parts of the body
I	: Animal : No.				
Small amount of white	: 17	: x	: x		
	: 21	: x	: x		
	: 33	: x	: x		
	: 18	: x	: x	: x	
	: 28	: x	: x	: x	
	: 25	: x	: x	: x	
	: 5	: x	: x	: x	: x
	: 23	: x	: x	: x	: x
	: 15	: x	: x	: x	: x
II "Medium" amount of white	: 9	: x	: x	: x	
	: 29	: x	: x	: x	: x
	: 31	: x	: x	: x	: x
	: 22	: x	: x	: x	: x
	: 1	: x	: x	: x	: x
	: 27	: x	: x	: x	: x
III "Large" amount of white	: 41	: x	: x	: x	: x
	: 10	: x	: x	: x	: x
	: 20	: x	: x	: x	: x
	: 37	: x	: x	: x	: x

Table II.- Variation in distribution of white spotting in Guernseys. In these eighteen animals there is imperfect correlation for the amounts of white on the different parts of the body. The first animal in the table has the smallest total amount of white, and the last has the largest amount.

Animal number	White on ventral part of body	White on legs	White on head	White on other parts of body
38	small	small	medium	none
24	small	small	none	small
34	small	medium	medium	small
36	small	medium	medium	small
32	small	medium	small	small
35	small	medium	medium	small
16	small	small	medium	medium
4	medium	medium	small	small
7	medium	small	none	small
2	small	medium	large	medium
8	small	small	small	medium
3	medium	small	medium	medium
19	large	medium	small	medium
6	medium	medium	medium	large
13	medium	medium	medium	large
11	medium	medium	large	large
12	large	large	small	large
14	large	medium	medium	large

### Variation in Shade of Red

The fading effect of the sun is more conspicuous in black breeds, such as the Angus, than in breeds of other colors. The fact, however, that animals exposed to the same environment vary greatly in shade suggests that genetic factors also are involved. Most Guernseys are of a rather light shade of red, but there is considerable individual variation. The purpose of the present investigation is to determine, if possible, the causes for this variation.

So far as is known, no attempt has been made previously to ascertain the degree to which the shade of hair varies during the lifetime of an individual. Seven growing animals were examined with this purpose in mind (Table III). The first hair samples in each case were taken before the calf was six months of age, and the remaining two during the succeeding months of December and March.

The seven animals have been arranged in Table III in accordance with the shade of the first sample. Thus the sample of No. 488, the first animal, is the lightest, and that of No. 493, the last, is the darkest. It will be noted that for the first three animals the hair becomes

darker by December, while for the remaining four it becomes lighter. Consequently there is much less variation in the second samples than in the first. It is impossible, with the meager information available at present, to determine whether or not the early variation is of an hereditary nature. The fact that the third sample resembles the second fairly closely indicates that the permanent shade of hair is probably attained before the animal is a year old. This assumption is supported by the fact that hair samples taken from five animals, one to two years of age, showed practically no change over a period of eight months. The samples were taken in July-September and March. The animals spend the intervening time outside.

Table IV shows the variation in hair shade of twelve older animals. The first samples were taken during the period July to September (1933); the second during December (1933), and the third during March (1934). No consistent differences were obtained between any two of the three sets of samples, thus demonstrating that such environmental factors as sunlight were not having a uniform effect. It seems probable that the differences between the samples of the same animal were of a fluctuating nature, due to shedding, etc.

During the course of the present study 134 hair samples were taken. Although this may seem like a large number, it is comparatively small when one considers the magnitude of the problem. Enough information has been obtained, however, to justify the statement that considerable change in hair shade may take place during the early life of a Guernsey and that slight fluctuations continue to occur during the lifetime of the adult animal. In studying the hereditary factors underlying the variation in intensity of pigmentation it should be necessary to have a record of the hair shade of both the young and the mature animal.

Table III.- Variation in shade of red in Guernseys. Based on hair samples taken from seven growing animals. The first samples were taken when the animals were under six months of age; the second and third samples were taken December, 1933 and March, 1934 respectively. The arrangement of the animals in the table is based on the shade of the first sample. The one with lightest shade is placed first and that with darkest placed last.

Animal number	Second sample compared with first			Third sample compared with second			Third sample compared with first	
	back	legs		back	legs		back	legs
488	darker	darker	:	lighter	no change	:	darker	darker
490	darker	darker	:	lighter	darker	:	no change	darker
494	darker	darker	:	lighter	darker	:	darker	darker
491	lighter	lighter	:	no change	no change	:	lighter	lighter
489	lighter	no change	:	no change	darker	:	lighter	darker
492	lighter	darker	:	no change	no change	:	lighter	darker
493	lighter	darker	:	no change	no change	:	lighter	darker



Table IV.- Variation in shade of red in twelve Guernsey cows thirty months of age, or older.  
Based on hair samples taken (1) July-September, 1933; (2) December, 1933 and (3) March, 1934.

Name of animal	Second sample compared with first		Third sample compared with second		Third sample compared with first	
	back	legs	back	legs	back	legs
Pallas King's Darling	darker	darker	no change	darker	darker	darker
Pallas King's Cowslip	darker	darker	no change	darker	darker	darker
Uncas Dobbie	darker	darker	darker	darker	darker	darker
Pallas King's Elsie	darker	no change	darker	darker	darker	darker
Elk Meadows V. L.	lighter	lighter	no change	no change	lighter	lighter
Uncas Alyssium	lighter	no change	lighter	no change	lighter	no change
Uncas Goldenrod	darker	darker	lighter	lighter	lighter	no change
Venturers Clematis	darker	lighter	no change	darker	darker	darker
Venturers Halesia	lighter	darker	darker	no change	no change	darker
Venturers Ghelaine	no change	lighter	no change	darker	no change	no change
Venturers Dahlia	no change	lighter	darker	lighter	darker	lighter
Venturers Mina	lighter	no change	lighter	no change	lighter	no change



## SUMMARY

1. Several color characters in the Guernsey herd of the Kansas State College have been studied from the standpoint of heredity, and several others for the purpose of determining the degree and the method of variation.

2. Forty-four animals were available for the study of the inheritance of distal leg-spot, a small pigmented area occurring on one or more of the pasterns, directly above the hoof. The results, so far as they go, indicate that distal leg-spot is due to a dominant gene, and is a modifier of recessive white spotting (s).

3. The inheritance of irregularity in outline of pigmented areas was studied in thirty-three animals. The evidence here justifies one in assuming that a recessive gene is responsible for the irregular outline of the pigmented areas. This gene may also be looked upon as a modifier of recessive white spotting (s).

4. In the study of pigmented nose, observations were made on twenty-four animals. The conclusion reached is that pigmented nose in Guernseys is due to at least one dominant gene.

5. Variation in distribution of white-spotting was studied in thirty-seven animals. All animals showed white on the switch of the tail, on the ventral part of the body and on the limbs. Increasing amounts were found to appear first on the head, then on the shoulders, the thighs and above the udder. There is evidence that Guernseys show correlation between amounts of white on the different parts of the body.

6. Hair samples totalling 134, taken from twenty-four animals, showed that considerable change in hair shade may take place during the early life of Guernseys, and that slight fluctuations continue to occur during the lifetime of the adult animal.

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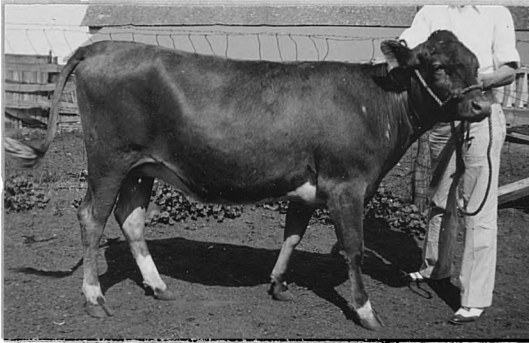
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## Plate I

## Explanation of Figures

- Fig. 1, No. 21 - showing distal leg-spots.
- Fig. 2, No. 19 - showing absence of distal leg-spots and also showing smooth outline of pigmented areas.
- Fig. 3, No. 20 - showing irregularity in outline of pigmented areas.
- Fig. 4, No. 23 - an example of consistently small amounts of white at different locations on the body.
- Fig. 5, No. 31 - an example of consistently "medium" amounts of white at different locations on the body.
- Fig. 6, No. 37 - an example of consistently "large" amounts of white at different locations on the body.

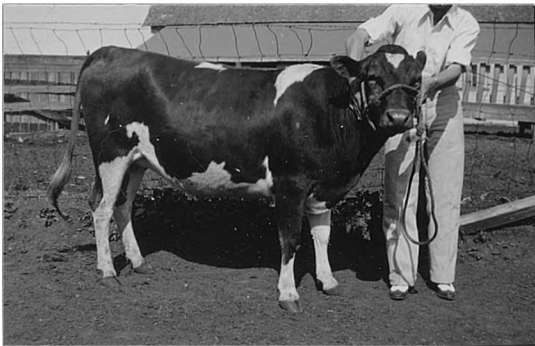
**Plate I**



**Fig. 1**



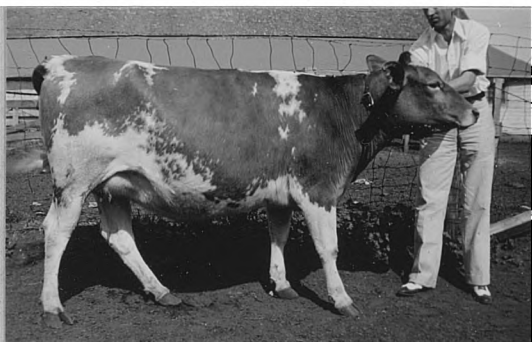
**Fig. 4**



**Fig. 2**



**Fig. 5**



**Fig. 3**



**Fig. 6**