# NOTES ON THE INHERITANCE OF COLOUR AND MARKINGS IN PEDIGREE HEREFORD CATTLE.

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(With Plates VII—X.)

CONTENTS.



## 1. Introduction.

The following notes and observations on the inheritance of colour and markings in pure-bred Hereford cattle are only published because, as far as the writer is aware, no work has been done on the genetics of this breed, and comparatively little on that of other kinds. These notes are necessarily imperfect and incomplete, for cattle, on account of their slow rate of increase, are bad subjects for the study of heredity, but such facts as have been noted and are here given may serve to draw the attention of other workers to a breed of which the genetics have hitherto been neglected.

The notes have chiefly been made on the pedigree Herefords belonging to Mr W. J. Pitt, of Bridgnorth, Shropshire. Nearly every beast bred for some years past has been photographed as a calf and the picture placed in a herd book under that of its dam; thus the produce of each cow can be seen at a glance. This system keeps a trustworthy record,

the collection of photographs enabling one to draw conclusions and arrive at results which would not otherwise have been apparent. Characters which appear to be fluctuating variations are shown by this book to be inherited as unit characters in a Mendelian manner. It must be mentioned that owing to the value of the material no experimental breeding has been attempted, though had it been possible to do so most interesting results might have been obtained. With cattle worth hundreds apiece[1] experimental breeding for undesirable points is out of the question in a herd run on commercial lines.

## 2. The Typical Hereford.

Before considering the manner in which different characters are inherited it will be necessary to give a description of the typical Hereford. It is a deep red beast, with white face and underparts, white feet, white at the end of the tail, and a white patch along the top of the neck. Sometimes there is a trace of red round the eyes. The stranger to the breed is generally impressed by the constancy of these markings; still, variations from the type do occur. It is hardly necessary to add that the Hereford is a very heavy fleshed beast, fattening rapidly, and is the premier beef breed of the world, having spread to every country where beef raising is a considerable industry.

Minor points that breeders attend to are: coat colour, which should be a rich purple red, not a yellow-brown; a clean, clear nose, without spots and markings; and the horns, which should be free from pigment at the tips.

## 3. Variations Studied.

I. *Reduction of the Pigmented area, or Excess of White:* This variation is the one most frequently met with, certain families being known to "throw white" occasionally. Pl. VII, fig. 2 shows a bad example of this departure from the type, in which the white markings have spread out and much reduced the coloured area. Pl. VII, fig. 3 shows another example, in which the animal has a streak of white down the spine and somewhat more than it should have in other parts. It will hereafter be shown that the variation is caused by a recessive factor that will be designated by the letter "*W*."

[1] In the autumn of 1918 a herd of 84 pedigree Herefords were dispersed at an average of over £500 each, including the stock bull, Ringer, which fetched 9000 guineas.

II. *Extension of Pigmented area, or "Dark Neck":* Is a not uncommon departure from type. The white patch on the crest is lost, the pigmented area shows a general tendency to encroach on the white parts, the tail being often coloured to the end, and the limbs down to the ground. See Pl. VII, figs. 4 and 5, and grade + 3 on Pl. VIII. The character has been found to be produced by a dominant factor for which the letter "*D*" will be used.

III. *Pigment Surrounding the Eyes:* This is a ring of red round each eye, which varies in amount. As long as it is not excessive breeders do not object to it, and red, or "cherry" eyes are characteristic of some families of Herefords. See Pl. VII, figs. 5 and 6. The character is designated "*R*" in this paper.

IV. *Pigmented or "Dirty" Nose:* Spots of brown, and black, and of black and brown mixed, sometimes appear on the noses of Hereford cattle. Occasionally the whole nose is dark. Such "dirty" noses are greatly disliked by breeders, who invariably eliminate the bearers of them from their herds, yet dark noses continue to crop up in even the best-bred strains of cattle, and very often accompany the sought after and fashionable claret-coloured coat. "*P*" will herein be used for this character. See Pl. VII, fig. 7, and Pl. X, for examples of the "dirty" nose character.

V. *Coat Colour:* Two alternative characters are here dealt with, the first and dominant being the pale brown shade sometimes known to breeders as "yellow," and the deep plum tint called "claret" or "purple," which behaves as a recessive to the paler type of pigmentation. The lighter colour was at one time the more general, but having become unfashionable is not so common now. The pale brown factor is herein styled "*B*," and that for the "claret" coat is called "*C*."

I. *Excessive White.*

As already stated there are degrees of excessive white, which possibly indicates the presence of two or more complementary factors, such as give rise to the fluctuating character of "hooding" in rats, but the figures at present available are too small to permit of analysis. All that can be said with certainty is that too much white acts as a recessive to normal colouration. I first obtained evidence of this in the progeny of a bull called Lowland Paradigm (26986). He was an exceptionally fine animal, and his colour and markings were all that could be desired, yet five of his produce were badly marked, and more "white" individuals appeared in subsequent generations. The fact of the white appearing

in the first generation proves the genetic constitution of the parents. Both bull and cows must have carried the factor for too much white. The five normally marked cows with which Lowland Paradigm was mated, and which were proved by their produce to be heterozygous for the character in question, had by him seventeen calves, twelve being well marked and five badly. The ratio expected from the mating of heterozygotes is 3 : 1 when dominance is, as in this case, complete; but the difficulty of getting at the facts when working with such small figures is apparent, for the shifting of an individual from one class to another will make all the difference whether the result agrees with expectation or not. The figures obtained are 12 : 5, a really satisfactory agreement with expectation.

Lowland Paradigm was also the sire of thirteen calves from five cows believed to be homozygous for the typical markings. These calves were all normal in appearance. Half of them should according to theory have carried the factor for excessive white, but unfortunately the majority could not be tested as they were sold young, only three heifers being kept to breed from. These three young cows proved when bred to a bull known to carry the factor for white to be two pure dominants and one heterozygote. The latter, Olive Oil by name, has so far produced three well marked to one badly marked calf. This it will be noted is in exact agreement with the expected 3 : 1 ratio.

Lowland Paradigm's five badly marked calves from the cows that carried the factor for white were, as would be expected, pure for excessive white, i.e. they were extracted recessives. If we indicate those individuals homozygous for the typical markings by the letters *NN*, those bearing both factors by *NW*, then the calves referred to above will be of the genetic constitution $WW^1$. That this assumption was correct was proved by their produce. Four out of the five were heifers and were kept for stock. Up to date these young cows have had 21 calves by heterozygous bulls, the result being 10 typically marked, to 11 with too much white. 11 : 10 is again a very fair approximation to the expected 1 : 1 ratio that results from the mating of a homozygous recessive with a heterozygote.

To take now the produce of another bull, by name Bounds Chance

[1] As the white face of the Hereford is dominant in crosses with distinct breeds, and even with species such as the bison, it seems that the white is due to the *presence* of a factor, and not merely due to the absence of that for normal pigmentation, so I have indicated excessive white by a capital *W*, and not by the small letter which is used to show the absence of a factor.

(29544). This was also a very fine typical animal, well marked, and most fashionably bred, yet evidently heterozygous for too much white. When mated with six cows of normal appearance but believed to carry the factor for white he sired 18 calves, of which 13 were well marked and 5 badly. Taking into consideration the smallness of the numbers, when the transposition of a unit will effect the agreement with expectation, this again is a fair approach to the 3 : 1 ratio. His matings with 13 cows homozygous for normal markings resulted in 39 typically marked calves in accordance with expectation. Theoretically half of these should be heterozygotes, but so far too few have been bred from to afford any evidence as to what proportion of them bear the factor for excessive white. Lastly Bounds Chance has had from four badly marked cows, presumably pure recessives, 16 offspring, 9 being too white, and 7 properly marked—expectation 8 : 8.

The produce of the above bulls may be set forth as follows:

| | | *NN* or *NW* | | *WW* |
|---|---|---|---|---|
| Lowland Paradigm | *NW* × 5 cows *NW* = | 12 | : | 5 |
| Bounds Chance | *NW* × 6 cows *NW* = | 13 | : | 5 |
| | Totals ... ... | 25 | : | 10 |
| | *Expectation* ... | *26·25* | : | *8·75* |

| | | *NN* or *NW* | | *WW* |
|---|---|---|---|---|
| Lowland Paradigm | *NW* × 5 cows *NN* = | 13 | : | 0 |
| Bounds Chance | *NW* × 13 cows *NN* = | 39 | : | 0 |
| | Totals ... ... | 52 | : | 0 |
| | *Expectation* ... | *52* | : | *0* |

| | | *NN* | | *NW* | | *WW* |
|---|---|---|---|---|---|---|
| Bounds Chance | *NW* × 4 cows *WW* = | 0 | : | 7 | : | 9 |
| | *Expectation* ... | *0* | : | *8* | : | *8* |

*Recessive Nature of the White Factor Illustrated by a Pedigree:* Diagram 1 is a pedigree, traced through six generations, which illustrates in another manner the way in which excessive white crops up among normally marked cattle. The family shown has produced six individuals marked with too much white. The pedigree enables one to see at a glance, what has already been set out in the previous tables, that excessive white is due to a simple Mendelian factor acting as a recessive to that for normal colouration. The futility of the ordinary methods of elimination is also apparent. It must be added that the genetic constitution of the cattle shown in this pedigree is deduced from their entire produce, which of course are too many to be shown completely in the diagram.

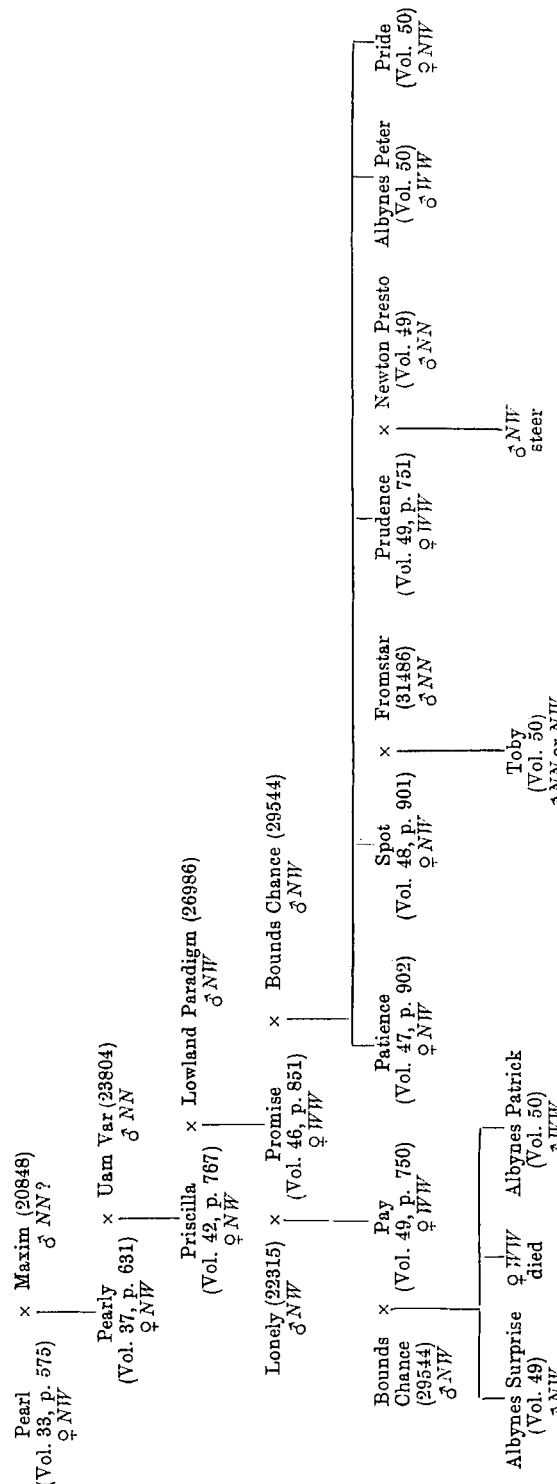


Diagram 1. Pedigree of a family which has produced six individuals marked with too much white and from which it will be seen that the factor for excessive white is a simple Mendelian recessive to that for normal colouration. The pure recessives in the above pedigree are indicated by the letters *WW*, the pure dominants by *NN*, and the heterozygous individuals by the letters *NW*.

*Variability of the Somatic Expression of the Factor for White:* Promise 2nd, the first pure recessive to appear in the above mentioned family, was not of the extremely badly marked type such as her daughter, Pay, shown on Pl. VII, fig. 3, but was a grade $-1\frac{1}{2}$ animal; however, her progeny have proved her pure for the white factor, and her first calf, as already mentioned, was an exceedingly white heifer. Her produce, by heterozygous bulls, have been 3 *WW*, and 4 *NW*, the three recessives being particularly badly marked. I have mentioned this to show that, though the somatic effect of the white factor varies somewhat, any beast having white beyond the shoulders may be confidently assumed to be a homozygote of the constitution *WW*. Of the four cows proved to be pure for white with which Bounds Chance (*NW*) was mated, two, Princess 2nd and Promise 2nd, were rather too white and two, Olivette and Pay, were exceedingly badly marked, yet genetically they behaved in a similar way. The latter had between them eight calves, four being normal, to four with too much white. The other cows had also eight calves, three with typical markings, and five badly marked. This shows, as stated before, that not only is the factor for excessive white variable in its somatic expression, but that individuals in which it does not reach its full expression are identical genetically with those in which it is fully displayed.

*Summary:* The above evidence shows that extra white in Hereford cattle acts as a simple Mendelian recessive to the normal type of markings, normal and badly marked cattle occuring in the ratio of 3 : 1 when heterozygous individuals are mated together. The factor for excessive white has been styled herein the *W* factor, the capital letter being used because the disappearance of pigment from the white areas is probably due to the presence of a special factor, and not merely to the absence of that for the typical markings. This conclusion is arrived at because the white face of the Hereford is dominant in crosses with most other breeds of cattle, and it is logically impossible to comprehend how a thing which does not exist can dominate that which is present. The dominance of the white face *must* be due to some special factor or gene, for the absence of factors for colour could hardly cause the disappearance of those for pigmentation from the gametes of fully pigmented breeds with which the Hereford happens to be crossed. If the white face and extremities are due to the presence of a special factor it becomes apparent that the extension of the white is almost certainly due to another similar factor, that which has been styled *W*. This can only show itself in the absence of the factor for the normal amount of pigmentation. The expression of the factor *W* varies somewhat, and

we have seen that some pure recessives are not so white as others, but so far all individuals bearing too much white that have been studied have given identical results when bred from.

II. *Extension of the Pigment or "Dark Neck."*

Pl. VII, figs. 4 and 5 and Plate VIII, grades + 2 and + 3 show the type of colouring referred to as "dark-necked"; this kind of pigmentation is apparently nearly but not quite completely dominant to the ordinary white-necked description of marking.

In the case of a cow called Shelsley Cypress, that was dark-necked, only two out of six calves, all by normally marked bulls, have shown any white on the neck. Presumably the cow is a pure dominant for the character, the sires being heterozygous, but dominance not being always complete[1] white shows in some of the heterozygous offspring. The following pedigree will make this clear. That one of

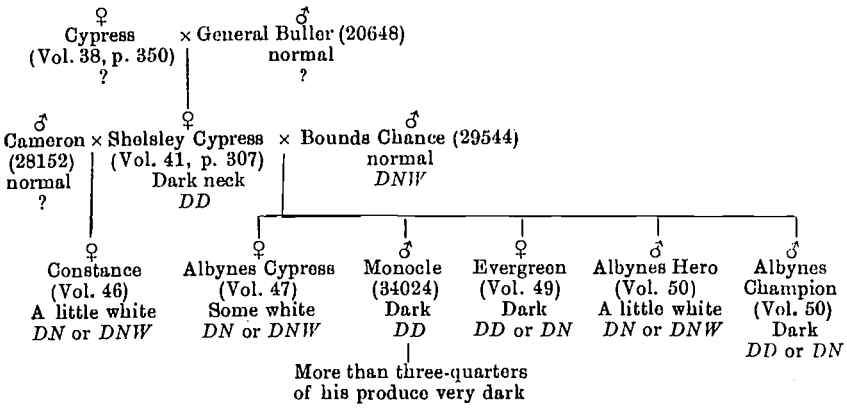


Diagram 2. Pedigree showing the Inheritance of the "Dark Neck" character.

*D* indicates the factor for the pigmentation of top of the neck, etc.
*N* indicates the factor for normal colouration, and
*W* is for excessive white.

the completely dark-necked calves was a pure dominant is shown by the fact that when subsequently used in a herd of non-pedigree general utility Herefords this young bull sired practically all dark calves. I have unfortunately not been able to obtain the exact figures relating to his produce, but his present owner, a very careful and accurate man,

[1] Further on in this paper it will be shown that the factor for excessive white has an inhibiting or neutralising effect on that for "dark neck," so that these calves may have been heterozygous for too much white.

assures me that, though all the cows were white-necked, in some cases very white, the proportion of white-necked calves has been exceedingly small. Again the evidence seems to point to the almost complete dominance of the factor for the extension of pigment.

Another case is that of a cow named Lady 4th, in which we have an individual apparently heterozygous for the character. She has two or three small spots of white hair on the shoulders. I have records of five of her calves. Judging by their markings these five offspring by normally marked bulls have been two dark-necked dominant homozygotes, one heterozygote with just a little white, and two well-marked homozygous recessives. Of course the heterozygotes are the class that one would have expected to be the most numerous, and possibly they are so in reality, for it will be shown presently that it is conceivable that sometimes the expression of the dark-necked factor is inhibited by the presence of another factor.

A third example is a cow called Playful, almost normally marked, but apparently carrying the factor for the extension of pigment. Three out of her five calves by well-marked bulls have shown no white whatever on the neck, while the two that had a little bore only very small patches.

This case and that of Lady seem to indicate that the sires with which they were mated likewise carried the factor for the dark neck. The bulls in question were known to be heterozygous for excessive white, and the suggestion is therefore made that the presence of the *W* factor inhibits the expression of that, which will be hereafter styled *D*, for dark neck. If this is correct it would explain the production of dark-necked calves by normally marked parents, and the complete and incomplete dominance of the dark neck in other cases. When only the factor for normal colouration is present *D* is a dominant, when that for *W* occurs it cannot fully express itself. How far this conjecture is in accordance with the truth only the collection of much more evidence will show. But the following case supports it—Gaiety, a perfectly marked cow, whose sire and dam were both well marked, had a calf by a bull called Wetmore Laurel, whose markings were typical in all respects, yet their calf was exceedingly dark, without a trace of white on the neck, and was an example of a grade + 3 animal. It was apparently homozygous for the extension of pigment, so each parent must have borne the factor for this character, the expression of which was inhibited by that for excessive white. This supposition is confirmed when we find that Gaiety's grand-dam was dark-necked. Unfortunately I have not been able to obtain any information concerning the appear-

ance of Wetmore Laurel's ancestors further than the first parental generation. The pedigree so far as the characters of the animals is known is set forth in the accompanying diagram.

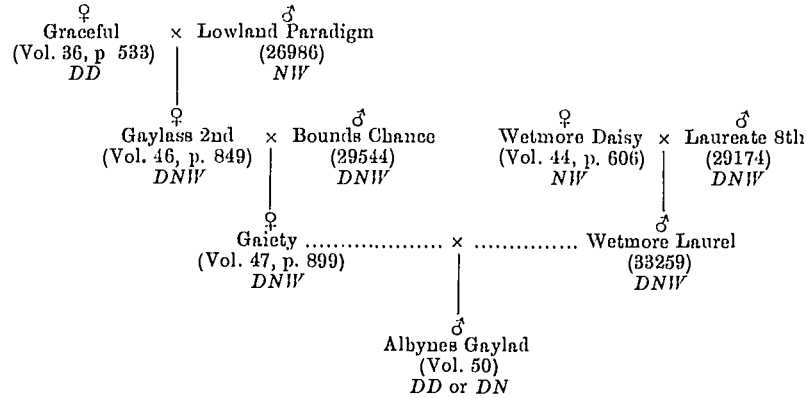


Diagram 3. A pedigree set forth to show how the dark-necked character, which is normally dominant, may be carried for several generations by typically marked cattle its expression being inhibited by the factor for excessive white, until a suitable recombination of the factors occurs in which that for too much white is eliminated, and the dark-necked character shows again in full force.

The matings in which the "dark-necked" character has been concerned may be tabulated as follows:

| | | *DD* or *DN* | *DN* or *DNW* | *NN* or *NW* |
|---|---|---|---|---|
| *DN* × *DNW* | Lady 4th × Newstead (30814) ... ... | 1 | 0 | 1 |
| | ,, × Bounds Chance (29544) ... | 1 | 0 | 2 |
| | Playful × Lowland Paradigm (26986) ... | 1 | 0 | 0 |
| | ,, × Bounds Chance (29544) ... | 2 | 2 | 0 |
| | Totals ... ... | 5 | 2 | 3 |
| *DD* × *DNW* | Shelsley Cypress × Bounds Chance (29544) | 4 | 1 | 0 |
| *DNW* × *DNW* | Gaiety × Wetmore Laurel (33259) ... | 1 | 0 | 0 |

*Summary:* The evidence so far to hand leads one to believe that the "dark-necked" factor is dominant to that for normal colouration from which it segregates in the ordinary Mendelian ratio, but it becomes more or less recessive in the presence of the factor for excessive white which inhibits its full expression, so that a mating between outwardly normal individuals may give rise to a grade + 3 animal, as in the case of Gaiety and Wetmore Laurel just cited.

III. *Pigment Surrounding the Eyes.*

"Red-eyes," as the character is called by breeders, is quite common in English Herefords, about two-thirds of the cattle showing it (out of 110, 73 showed more or less colour about their eyes), though it has

never been the subject of selection, our breeders not regarding it as of any importance. In certain countries, Jamaica for one, cattle with pigment round the eyes are actually preferred on account of their supposed immunity to the attacks of flies and certain eye diseases. As far as English flies are concerned they certainly bite the eyes of red-eyed quite as badly as white-eyed Herefords, and I have been unable to see that the presence or absence of colour makes the least difference. However as some buyers for export choose red-eyed cattle the character has after all a certain interest for the breeder.

The coloured area varies from a comparatively large circle of red round each eye (Pl. VII, figs. 5 and 6) to the merest trace of pigment on one eye (Pl. IX, *F*). It is not uncommon for one eye to be well marked and the other plain (Pl. IX, *C*). When this is so, and in cases where only a little pigment is present round each eye, we have apparently expressions of the heterozygous condition.

The accompanying diagrams (4 and 5) show that the presence of pigment round the eyes is dominant to its absence, segregation following the simple Mendelian ratio. But dominance is not so complete as, for instance, in the classical case of the round and the wrinkled pea, and, as mentioned above, heterozygotes generally betray their constitution by the reduced amount of pigment present.

The character appears to segregate independently of other pigmentation factors, for I have seen very white cattle with red eyes, and very dark ones with white eyes; but it is possible that the red-eyed factor can only reach its full somatic expression when in company with that for extension of pigment, and that the factor for normal colouration inhibits its full development. This is suggested because specially heavy pigmentation round the eyes has been chiefly met with in company with absence of white from the neck. Out of 18 dark-necked cattle 14 had red eyes, of which 3 had conspicuous pigmented rings round their eyes, *but* one very red-eyed calf had a fair amount of white on the neck. The examination of the 110 cattle already referred to gave the following figures:

| | |
|---|---|
| | 56 normally marked Herefords with red eyes |
| | 14 dark-necked with red eyes |
| | 3 very white with red eyes |
| Total ... | 73 red-eyed cattle |
| | 28 normally marked white-eyed cattle |
| | 4 dark-necked white-eyed ones |
| | 5 excessively white and with white eyes |
| Total ... | 37 white-eyed Herefords |

Though the records of a number of matings show that the presence of pigment round the eyes is dominant to its absence, the evidence is insufficient to show to what extent, if any, the factors affect each other. It is certain that the heterozygotes tend to exhibit less pigment than the pure dominants, but the accurate division of one from the other by appearance alone is a somewhat difficult matter, so it is probable that some individuals classed as *Rr* are really *RR* (the "red-eyed" character is herein styled *RR*), and as I have already mentioned it is possible that the presence of the factor for normal markings tends to inhibit the full expression of that for "red-eyes"; only breeding will reveal the genetic constitution of these doubtful animals, but as, at the time of writing, the majority are calves or yearlings it will be some years before any certain conclusion can be arrived at.

The results achieved so far may be summarised as follows: 18 cows, believed *Rr*, had by 5 *Rr* bulls, 54 calves, 42 red-eyed to 12 white-eyed recessives. 42 : 12 is a fair approximation to the 3 : 1 ratio which in this case gives an expectation of 40·5 : 13·5.

As already explained too few of the red-eyed class have been tested by breeding for their genetic constitution to be anything but guess work. Some have hardly any pigment round the eyes, others a considerable amount, the colouring being so heavy in the case of seven as to make one convinced that they at any rate are homozygous for the character, which gives a result of 7 *RR* : 35 *Rr* : 12 *rr*. This makes the *RR* class too small, expectation being 13·5 : 27 : 13·5.

Matings of heterozygotes with recessives give the following results: 7 cows of the constitution *Rr* had by 5 *rr* bulls 17 calves, 8 red-eyed to 9 white-eyed. Three *rr* cows when mated with an *Rr* bull had 10 calves, being 4 *Rr* to 6 *rr*. Total 12 *Rr* : 15 *rr*; expectation being 13·5 : 13·5.

Considering the smallness of the figures dealt with the results support the general conclusions.

With regard to *Rr* × *RR* matings the evidence is unfortunately still more scanty, but what there is agrees with theoretical anticipations.

A *RR* cow had four calves by an *Rr* bull, two of the produce being undoubtedly pure dominants, and the other two heterozygous for the character. This cow also had a calf by a white-eyed bull which was clearly of the constitution *Rr*.

*Summary:* It is evident from the foregoing evidence that the presence of pigment round the eyes of Hereford cattle is dependent on a single dominant factor, which is allelomorphic to its absence, and that this

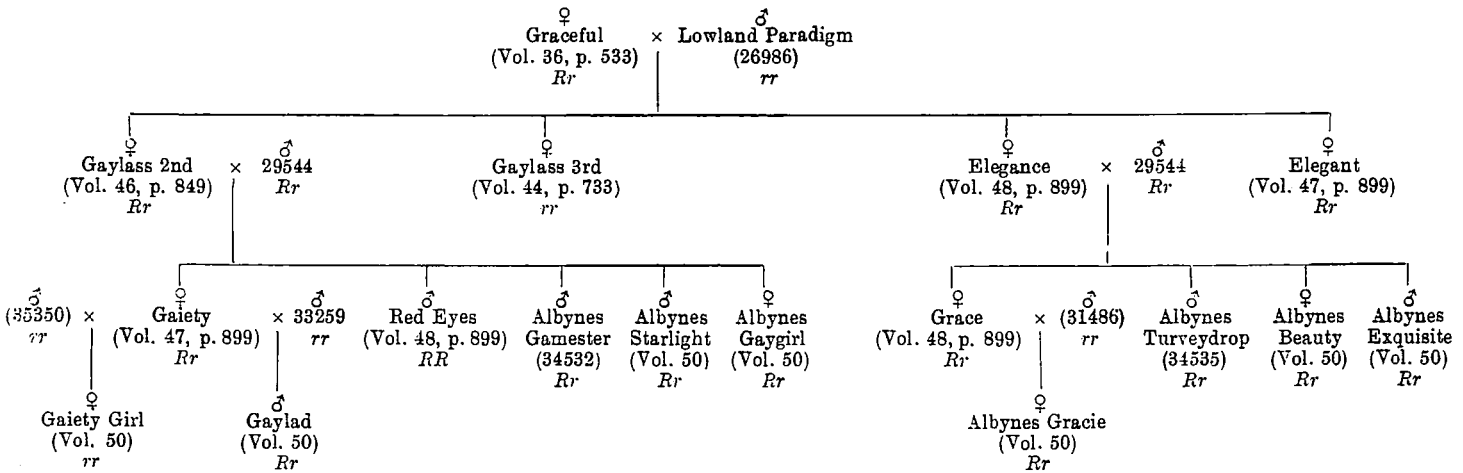


Diagram 5. Pedigree of a family of "Red-eyed" Herefords.

*RR* indicates heavy pigmentation round the eyes.
*Rr* is for less colour, in some cases only one eye being red—presumed to be the heterozygous individuals.
*rr* indicates absence of pigment; i.e. the pure recessives.

The sires used are to save space shown, with one exception, by their numbers. Their names are as follows :

29544—Bounds Chance.
35350—Newton Glance.
33259—Wetmore Laurel.
31486—Fromestar.

factor segregates, independently of other pigmentation factors, in the simple ratio of 3 : 1, or really 1 : 2 : 1. Dominance is not in all cases quite complete, so that the *RR* and *Rr* classes are not always easy to distinguish with certainty. It is possible and even probable that the factor for normal colouration has a modifying, or partially inhibiting effect on the full somatic expression of that for "red eyes," so that a normally marked red-eyed beast would not have such well-marked eyes as a dark-necked red-eyed one, though both would transmit the red-eyed factor in equal purity to their offspring.

IV. *Pigmented Nose.*

Pigment sometimes appears on the nose in Hereford cattle in quantities varying from a mere spot or two up to a completely dark nose. All forms of dirty nose are objected to by breeders, but brown spots alone are not considered so bad as black, or "blue" (dilute black). Very often an examination of a dark nose will show that both pigments are present, this being perhaps a commoner type of dirty nose than either pure black or brown. My observations concerning the inheritance of brown pigment on the nose are insufficient to justify any conclusions being formed. More information has been collected concerning black, and black and brown combined. The first point that appears is that this form of dirty nose is usually found accompanying that deep rich coat colour known as claret. Out of 41 Herefords examined, which were of this tint, 15 had pigment on the nose, and 26 had clean noses. But pigment on the nose *can* occur independently of the "claret" coat, as I have met with two pale brown, or yellow-brown animals that had well spotted noses. These were a cow called Olive Oil (see Pl. VII, fig. 7) and her bull calf Oliphant. As this cow was without a trace of the fashionable plum tint, and the marks on her nose were particularly black, it shows that the pigmented nose is not necessarily correlated with a claret coat, and the factors for the two characters can segregate independently, yet there appears to be some association between them, as out of 11 "yellow" coated animals examined the two mentioned above were the only ones showing any trace of colour or marking, the rest having perfectly clean noses, though in the case of claret-coloured cattle the proportion rises to more than half.

I have mentioned that black and brown pigments are often combined in the dirty nose, and I have notes concerning the inheritance of such a type of nose through a pedigree of three generations. This pedigree is fully set out in the accompanying diagram, and from it, it will be seen

that not only does the presence of pigment on the nose behave as a unit character, but that it acts as a simple Mendelian dominant to the absence of the pigment, expectation being exactly realised in every instance.

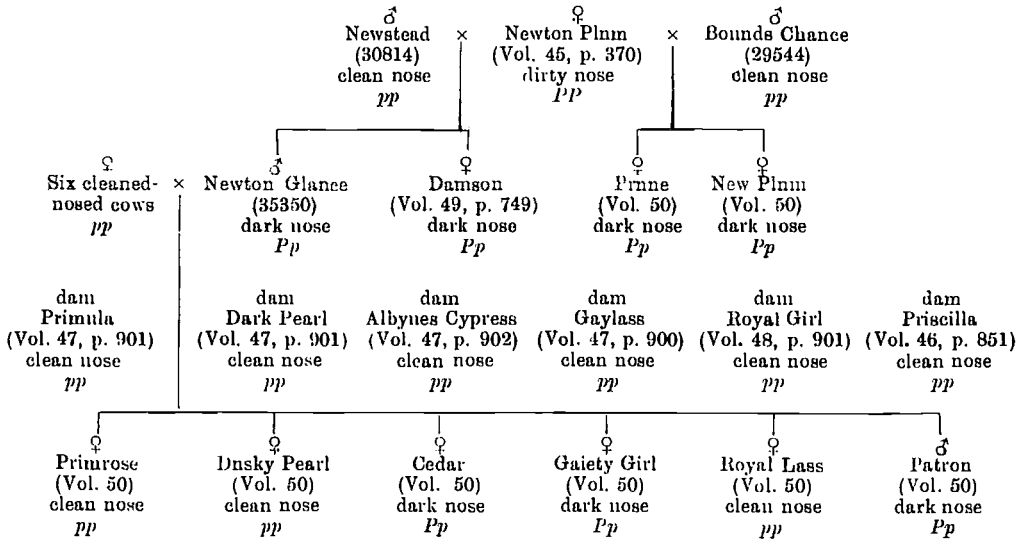


Diagram 6. Pedigree showing the inheritance of the dark or "dirty" nose through three generations. The factor for pigment on the nose is indicated by *P*, and its absence by *p*.

Except for the "purple" coat the dirty nose character is inherited independently of other factors. I have seen a very white cow (grade − 3) with a heavily spotted nose, and dark cattle (grade + 3) with perfectly clean noses. The figures collected in relation to this are as follows:

| | Clean nose | Spotted | Heavily pigmented |
|---|---|---|---|
| Dark-necked +3 and +2 ... ... | 7 | 1 | 0 |
| Very white −2 to −4 ... ... ... | 7 | 0 | 1 |
| Claret coloured ... ... ... | 26 | 0 | 15 |
| Pale brown ... ... ... ... | 9 | 0 | 2 |

The matings of clean-nosed with dirty-nosed cattle that I have records of may be summarised as below:

| | | *PP* | *Pp* | *pp* |
|---|---|---|---|---|
| *PP* × *pp* | Newton Plum × Newstead (30814) ... ... | 0 | 2 | 0 |
| | do × Bounds Chance (29544) ... | 0 | 2 | 0 |
| | Total ... ... | 0 | 4 | 0 |
| | *Expectation* ... | *0* | *4* | *0* |
| *Pp* × *pp* | Six clean-nosed cows × Newton Glance (35350) | 0 | 3 | 3 |
| | *Expectation* ... | *0* | *3* | *3* |

*Summary:* The dirty nose is clearly a unit character, dominant to the clean nose, and segregating independently of the other characters with the possible exception of the factor for the "purple" coat. As 15 out of 41 claret-coated cattle showed a spot or two of pigment on the nose some connection seems certain, but as the dark nose appears occasionally in company with the pale brown or "yellow" coat it is evident that the association is not complete.

V. *Coat Colour, with reference to the Claret and Pale Brown shades.*

The rich "claret" or "purple" colour is a dark plum tint which of late years has found much favour with breeders, though at one time a pale brown or "yellow" coat was preferred. In hot climates the dark coat is particularly sought after as it does not become so faded and bleached as the paler red-browns. "Claret" is the deepest shade found in Hereford cattle, "yellow" (actually a pale red-brown) being the lightest, but intermediate shades are often met with. Not only are there shades between the two extremes but the cattle vary much according to the time of year and the state of their coats, so that it is often most difficult, if not impossible, to be sure how a beast should be classed. For this reason many animals have had to be excluded from the following tables and calculations, in which only those that clearly belong to one class or the other have been included.

The claret factor proves to be recessive to that for pale brown, as the matings of seven "yellow" Hereford cows with two purple-coated bulls resulted in 14 pale brown calves to one dark one. This is somewhat surprising, as, judging by analogy with chestnut and bay horses, one would have expected the paler colour to prove the recessive. That the purples are really pure recessives is proved by the produce of purple × purple matings, which with one exception were all dark. The exception was the calf of a doubtful cow, which was probably a heterozygote and should not have been included among the pure purples.

The results may be set forth as follows, the pale brown factor being shown by the letter *B*, and that for claret by *C*:

| | |
|---|---|
| 7 matings $BB \times CC = 14\ BC : 1\ CC$? | *Expectation 15 BC.* |
| 10 matings $CC \times CC = 33\ CC : 1\ BC$? | *Expectation 34 CC.* |

I have no records of the results of $BC \times BC$ and $BC \times CC$, and it can be only by keeping most careful notes over a number of years that the heterozygous matings will be worked out.

The pale brown coat factor is clearly inherited independently of all other pigment characters, but that for claret is rather frequently accom-

panied by those for red eyes and "dirty" nose. 52 beasts gave the following figures:

Excessive White.

| Pale Brown | Claret |
|---|---|
| 11 | 41 |
| 1 *WW* : 10 *NN* or *NW* | 2 *WW* : 39 *NN* or *NW* |

Dark Neck.

| Pale Brown | Claret |
|---|---|
| 11 | 41 |
| 3 *DD* or *DN* : 8 *NN* | 8 *DD* or *DN* : 33 *NN* |

"Dirty" Nose.

| Pale Brown | Claret |
|---|---|
| 11 | 41 |
| 2 *PP* or *Pp* : 9 *pp* | 15 *PP* or *Pp* : 26 *pp* |

Red Eyes.

| Pale Brown | Claret |
|---|---|
| 11 | 41 |
| 7 *RR* or *Rr* : 4 *rr* | 37 *RR* or *Rr* : 4 *rr* |

*Summary:* Coat colour in Hereford cattle is controlled by two pigment factors, "*B*" for the pale brown coat, which is dominant over "*C*," the darkest shade, which is a deep rich purple or claret. Intermediate tints are probably attributable to the heterozygous condition, but further evidence is wanted on this point. The factors for coat colour segregate independently of those controlling the distribution of pigment on the body, but there appears to be some association between the *C* factor and those for red eyes and the "dirty" nose. It is undoubtedly significant that more than a third of the dark-coated beasts should have pigmented noses, while the proportion in the pale brown cattle is 1 : 4·50.

## 4. NOTES ON THE HISTORY OF HEREFORD CATTLE WITH REFERENCE TO THEIR MARKINGS AND VARIATIONS.

Writing in 1627 Speed said that no "place in England yieldeth more or better conditioned cattle than Herefordshire" (1). In 1788 we find the colour of the animals was "a middle red with a bald face" (2) showing that the type as now established was even then common. By 1804 "the prevailing colour" was "a reddish brown with white face" (3). Other types prevalent at that time were "whites"—really pale

roans,—"greys" or deep roans, entirely red cattle, and many with blue mottled and ticked faces (10). Many of the "red with white face" variety were much whiter than we should like in these days, the white extending right along their backs, and being splashed upon sides and flanks. Some of these cattle had large patches of red round the eyes and across the face. The four principal types are illustrated by pictures of four celebrated bulls in the first volume of Eyton's Herd Book (pub. 1846). The statement that the majority of the Herefordshire cattle belonged to the "red with white" face variety is borne out by an examination of the first two vols. of the herd book, which contain the pedigrees of 551 bulls, whose markings are also recorded in 326 cases. They were 191 "red with white face," 98 "mottle-face," 30 "grey," and 7 "light grey." The red with white face class had a majority of 56 over all other types combined. Twelve years later, out of 235 bulls (registered in Part 1, vol. II of the Herd Book, 1853) only two were recorded as "greys," the rest being "red with white face." By 1877 the breed was so uniform in appearance that the cattle were no longer described when registered in the herd book.

All this goes to show that a heavy fleshed breed of cattle (of which the oxen fattened readily when their days at the yoke were finished) was found in Herefordshire early in the 17th century, and that by the middle of the 18th century the conspicuous "red with white face" type was well-established, though the varieties, grey, mottle-face, etc., were equally accepted as good Herefords, but, fashion setting in favour of the red, these varieties were ultimately weeded out, so that the word Hereford came to signify a red beast with a white face. But the interesting question is how did the well-known white face arise, for it is not only such a marked character but is nearly always dominant even in crosses with distinct species like the bison (12, p. 533). Early writers refer to whole red cattle like the Devons (5 and 8), and the appearance of the white face is variously attributed to the introduction from Flanders of white-faced cattle towards the latter part of the 17th century (10, p. 11), to crosses with the old white Welsh cattle (10, p. 19), to the use of white-marked bulls from the north (10, p. 27), and to the sudden appearance of a white-faced calf in a herd of dark cattle. This case rests upon the authority of the Mr Tully who was a famous breeder in the early part of the 19th century. He says "About the middle of the last century, the cowman came to the house announcing as a remarkable fact that the favourite cow had produced a white-faced bull-calf. This had never been known to have occurred before; and as a curiosity it

was agreed that the animal should be kept and reared as a future sire" and "the progeny of this very bull became celebrated for white faces" (8).

This calf, born about 1750, appears to have been a true sport or mutation, and as he had considerable influence on the breed it is possible that we here have the origin of the strongly dominant white face as it at present exists, but it must not be forgotten that we find it recorded that by 1788 the white-faced variety was so widely spread as to be considered typical of the cattle of the county, so probably there were many white-faced beasts in existence prior to 1750, for we can hardly credit that the progeny of one bull would have over-run the district in the space of 38 years.

We see from these few notes that the Hereford has arisen by selection from the nondescript cattle bred in the county of Herefordshire during the 17th and early part of the 18th centuries, that all sorts of colours and markings prevailed, among which the red with white face was most common, and that it is probable a mutation occurring in a herd of dark cattle helped to fix this characteristic, which, when the beef qualities and other points of the breed began to receive attention, became the most popular type of marking among breeders, other colours being eventually eliminated, so that it is only in a few small variations and departures from type that we see in the modern Hereford any survival of the variously marked and coloured cattle of the early days of the breed.

## 5. GENERAL SUMMARY AND CONCLUSION.

The evidence that has been gone into in these pages establishes the fact that Mendelian inheritance is the rule with regard to the colours and markings of Hereford cattle, each character being controlled by a separately heritable factor, so that it would be possible, were experiments with such slow breeding and valuable animals a financial possibility, to combine the factors for all the characters mentioned in a single beast.

We have seen that excessive white is a simple recessive to the typical form of pigmentation, that extension of pigment is due to a dominant factor, which is neutralised in its action when it chances to be combined with the *W* factor, so that a normally marked beast might carry both characters, and transmit them separately, or combined, to its progeny. If this animal had a pale brown coat, and was heterozygous for the recessive purple-coat factor, and had in addition a dirty nose and red eyes we should have such a beast as that referred to above, combining

in one individual all the characters that have been dealt with in this paper.

Lest it should be thought that normal markings are always produced by the combination of the *W* and *D* factors I may say there is undoubtedly a special factor for the typical form of pigmentation, as many strains of Herefords breed pure to it and never throw either dark or white variations. Were it otherwise, any and every line would be liable to produce individuals both too white and too dark, which is not the case.

Though the characters are inherited as clear and separate entities there is some indication of association between purple (or claret) coat colour and the dark nose, but this is certainly not complete, as badly spotted noses have been met with on pale brown cattle.

There are undoubtedly many other characters than those which have been more or less dealt with which would repay study, some of considerable economic importance, as, for instance, the ability to put on the maximum amount of flesh on the minimum amount of food. There is some slight evidence that dark-coated cattle do not feed so quickly as pale brown but put on their flesh more evenly, and that the "yellow" feed faster, getting excessively fat[1], but tend to become patchy and uneven, the fat accumulating in lumps. As the evidence on these points is not sufficient to be conclusive they are only mentioned here to show that the study of heredity in this breed may have considerable importance for the practical as well as the scientific man.

The notes on the history of the Hereford breed show that the pigmentary characters are survivals from earlier times when no selection was practised of colour or markings, and that the faults which appear and reappear in the present day Herefords are not, as some breeders believe, spontaneous variations, but due to Mendelian factors, carried by apparently normal animals, which cause the characters concerned to appear when a suitable combination of gametes gives them the opportunity.

There can be no doubt that the modern Hereford has been evolved from the old cattle found in the County of Hereford by a purifying process, by selecting and selecting from what was originally most heterogeneous material, until the more or less homogeneous breed as we know it to-day has resulted.

That many if not most of our domestic breeds have been produced in a similar manner can hardly be doubted. It is by selecting and re-

[1] It is stated (11, p. 120) that yellow mice are prone to get exceptionally fat.

arranging their characters that the breeder has produced his great results, *but* has this artificial process any likeness or parallel to the natural evolution of a species—can we visualize the production by any such process of a geographical race of a mammal, bird, or insect?

## EXPLANATION OF PLATES VII—X.

### PLATE VII.

Fig. 1. *A Perfectly Marked Hereford*, Grade 0. A prize winning show heifer, Albynes Beauty, at fifteen months old. Note the patch of white on the neck, the white face, under-parts, brisket, and end of the tail, that the feet are white, and that her nose is clear and unspotted, also that her horns are free from pigment at the tips. In colour she is a rich red.

Fig. 2. *Excessive White*. Olivette, a grade −3 cow.

Fig. 3. *Excessive White*. Pay, a grade −4 animal.

Fig. 4. "*Dark Neck*," or *Extension of Pigment*. Shelsley Cypress, a very dark grade +3 cow.

Fig. 5. *Extension of Pigment*, also "*Red Eyes*." Graceful, a dark grade +3 cow with red eyes.

Fig. 6. "*Red Eyes*." Belladonna, a red-eyed cow, and a good example of this character.

Fig. 7. "*Dirty*" *Nose*. Olive Oil, a cow with a black spotted nose, but a pale brown coat.

### PLATE VIII.

Grades of pigmentation in Hereford Cattle, 0 being the normal.

### PLATE IX.

Variations of the "Red-Eyed" Character in Hereford Cattle.

### PLATE X.

Pigmentation of the nose in Hereford Cattle, "*a*" being a completely dark nose, and "*d*" a clean unspotted one. The extreme "*a*" is rare, but "*b*" and "*c*" are not uncommon.

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(*Note:* the numbers after the bulls' names, and the volume and page numbers after the cows' names, given in the pedigrees, etc., refer to the Herd Book of Hereford Cattle, and will enable any one to trace the full ancestry of the animals in question.)

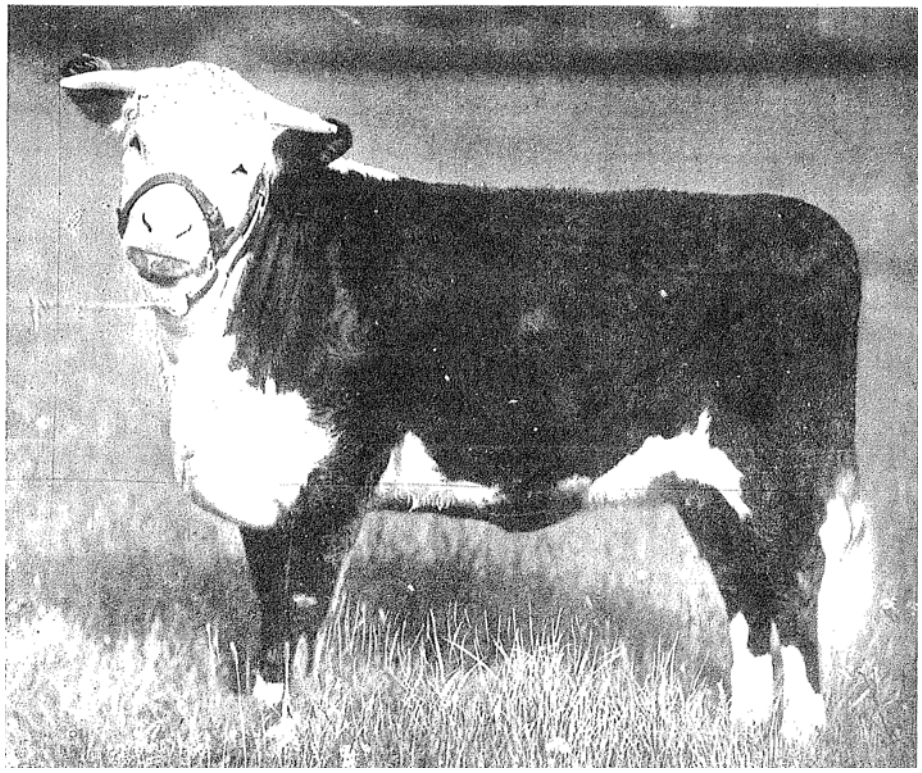
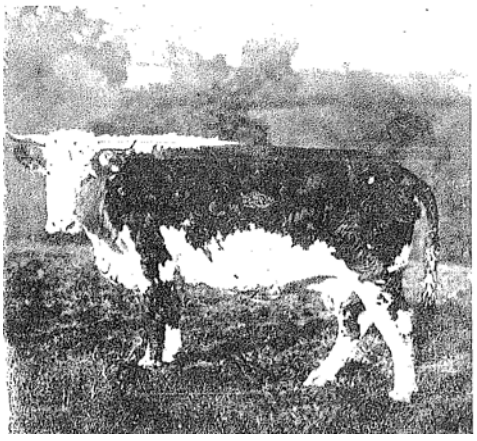


Fig. 1.



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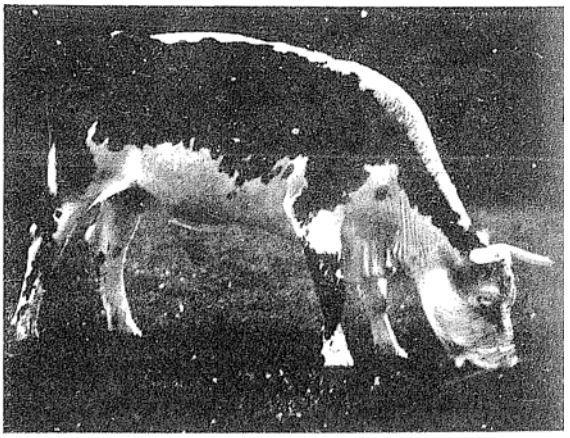

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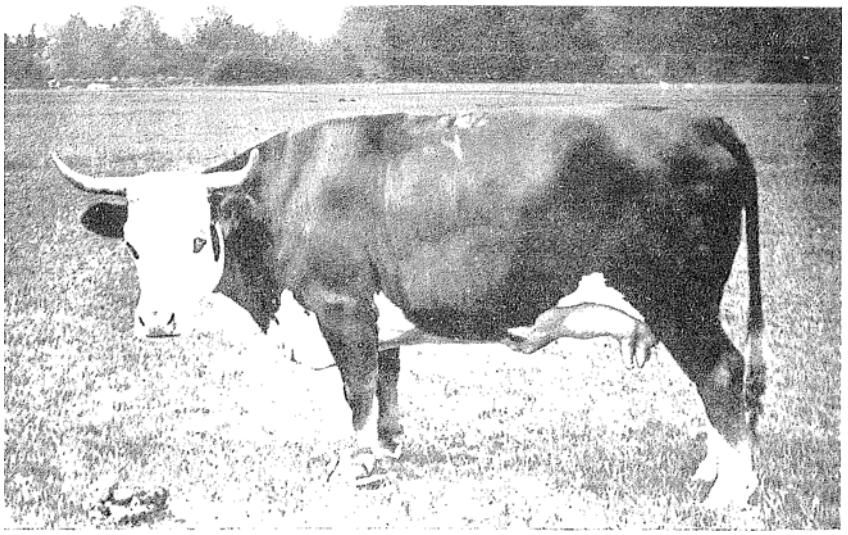

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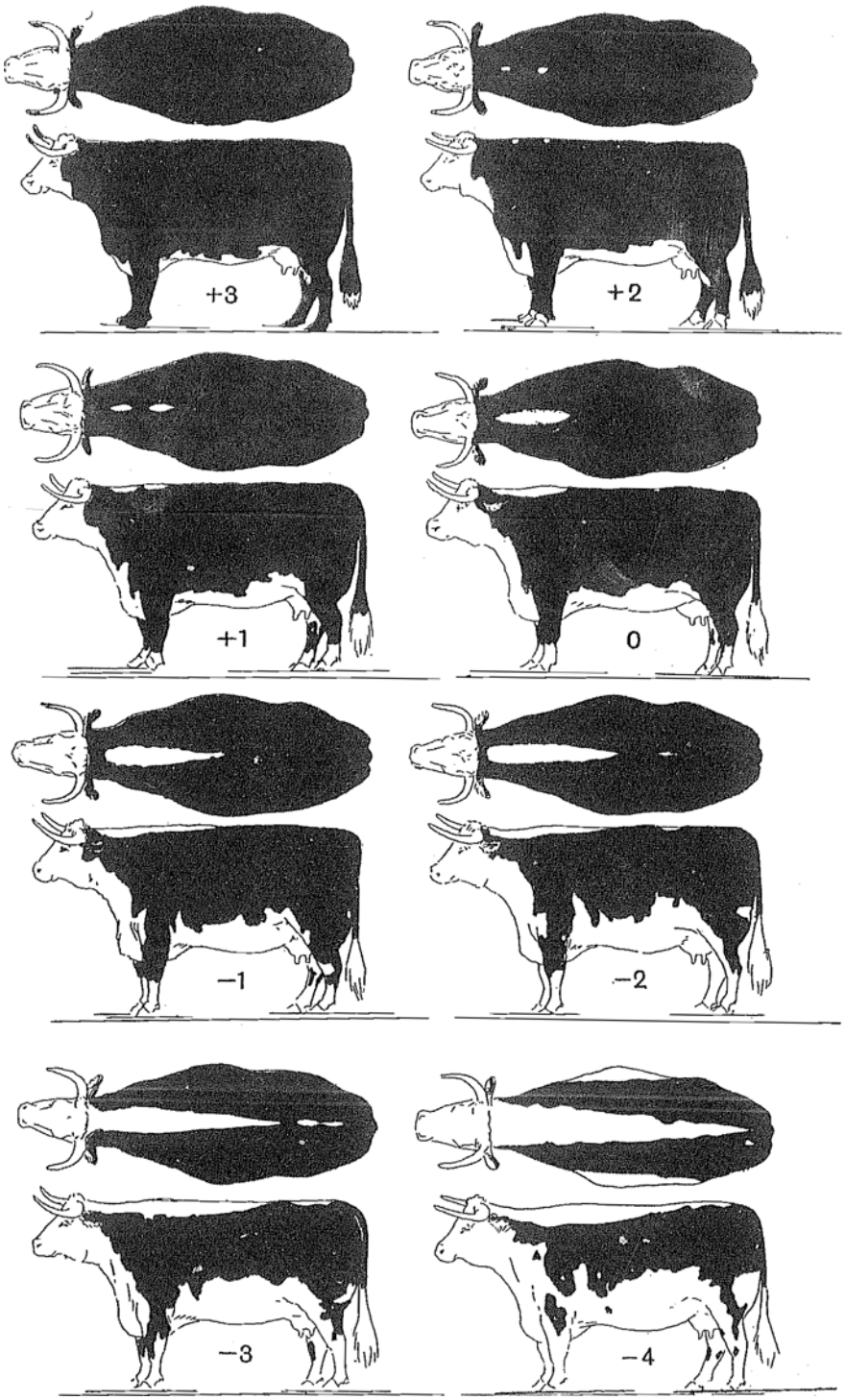
Fig. 6.

Fig. 7.


+3
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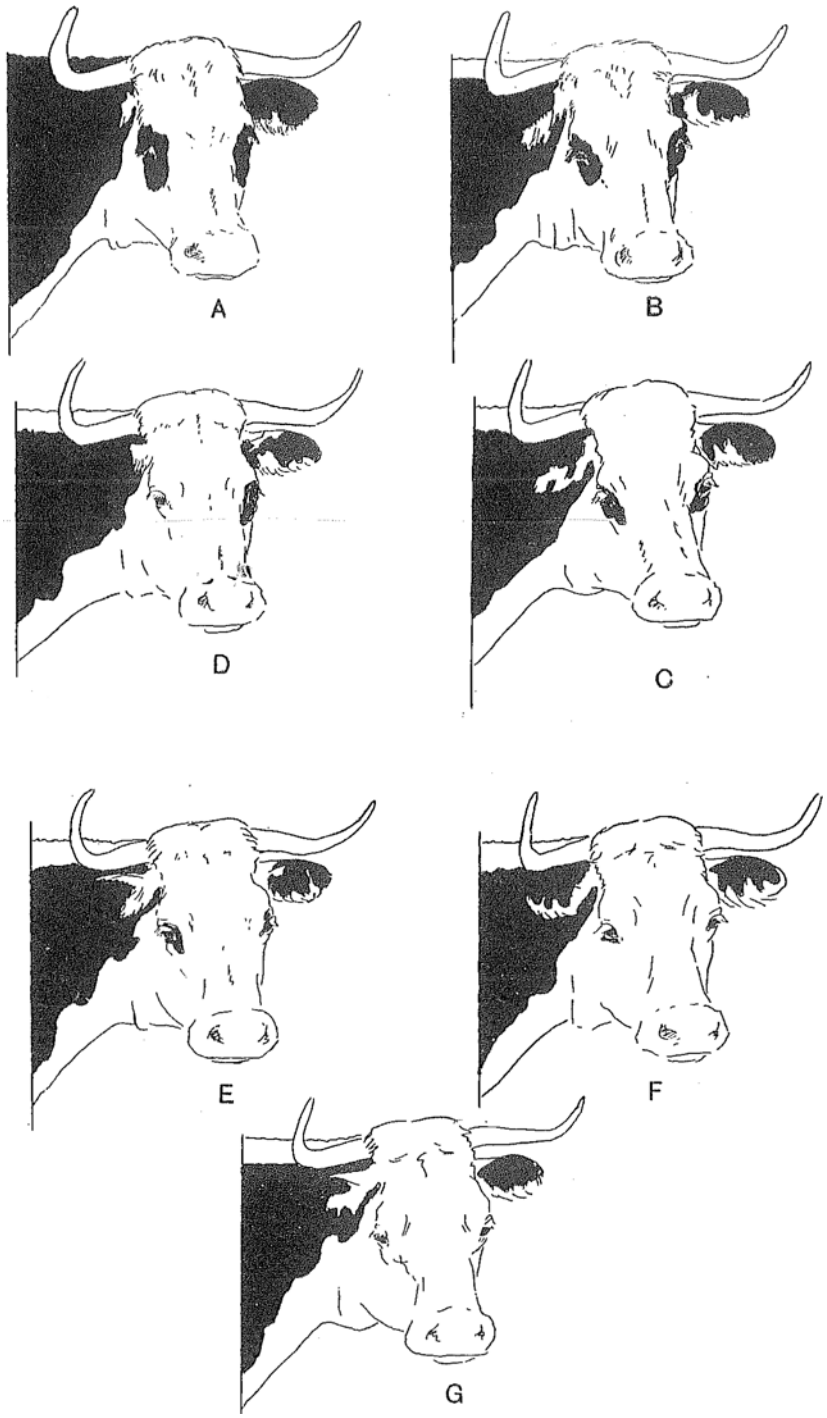
A
B
D
C
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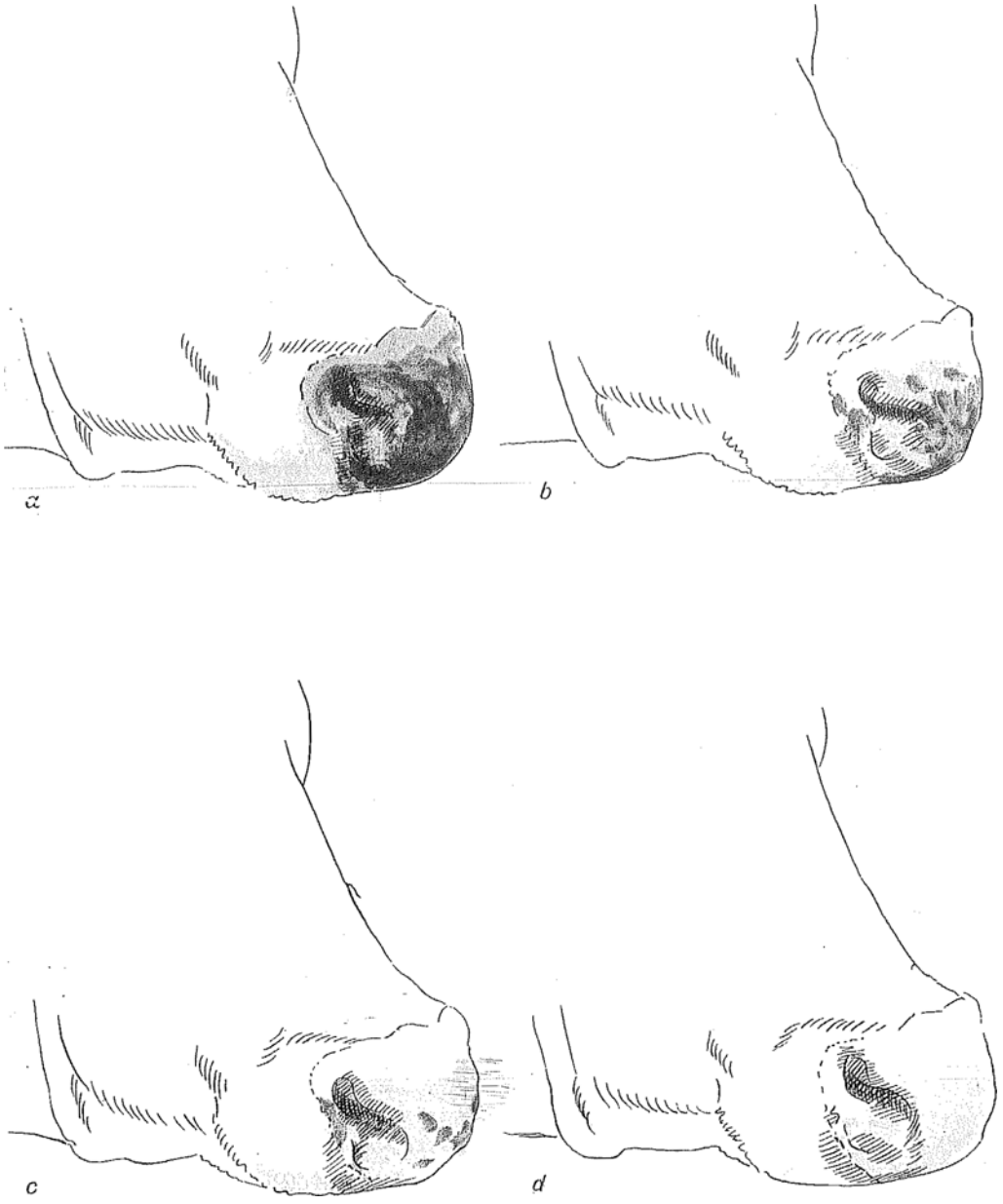


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