# HORN INHERITANCE IN GALLOWAY-HOLSTEIN CATTLE CROSSES.

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(With One Text-figure.)

## Introduction.

A number of reports have been made on crosses between horned and polled breeds of cattle. The data have been fairly complete in some cases even for the $F_2$ generation. The results obtained in the Galloway-Holstein cross-breeding experiment conducted in Alaska by the U.S. Department of Agriculture, and embodied in the present paper, are not materially different from those previously reported by others. However, in all of the experiments apparent exceptions, consisting chiefly of horns and scurs in the males, have occurred. The object of the present paper is not only to present new data, but to offer a genetic explanation for these exceptions. To do this it will be necessary to present some of the essential details of other experiments as well as of our own.

Gowen (1918) reported on crosses between the polled Angus breed and such horned breeds as the Holstein, Guernsey, Jersey, and Ayrshire. With two exceptions all of the $F_1$ females were polled. It should be noted, however, that both of these were obtained when Angus cows were mated to horned bulls. One of the bulls was a Jersey, and his $F_1$ daughter had "slight stubs just through the skin". The other bull, a Holstein mated to another Angus cow, sired a daughter with "very small, loose scurs". The remaining four daughters from the above type of mating were polled, while the three sons either had "loose scurs" or "loose horns".

In the reciprocal mating, Angus bull to horned cows, all of the seven $F_1$ cows were polled, while, of the twelve $F_1$ bulls described, nine had either scurs or horns and three were polled. One of the two $F_1$ bulls with horns was out of an Ayrshire cow and the other out of a Guernsey. In these two the horns were "large and quite solidly attached". The other seven $F_1$ non-polled bulls either had scurs that, according to Gowen, were either loose or tight, or had horns that were movable.

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Gowen does not point out the difference between a scur and a horn. However, in a recent communication to the junior author he states that he applied the term "horn" to those structures on the head that were comparatively large and, in addition, horn-like in shape. Cole (1925), on the other hand, has but two categories: (1) horns, no matter what their length or shape, firmly attached to the skull, and (2) scurs, loosely attached.

Watson (1921) mated four Angus bulls to seven West Highland cows (horned) and obtained six polled $F_1$ females, and one male with horns 4 in. long at 18 months and 10 in. at 6 years. The only other $F_1$ male was polled, but was sold when 3 months old. The horned $F_1$ bull mated to the six $F_1$ cows produced eighteen female offspring, fifteen of which were polled and three horned. There were only seven male offspring; two were polled, one had "hard" scurs (firmly attached to skull), and four were horned. Watson is positive the $F_1$ horned bull was heterozygous for polled, and there is good reason for believing that such is the case, as will be shown later. An interesting observation recorded by Watson is that in crosses made in Dumfriesshire, between Red Polls and Ayrshires, many of the $F_1$ males are horned while the females usually are polled.

Lloyd-Jones and Evvard (1916) did not take sex into consideration in reporting the distribution of polled, scurred, and horned among the $F_1$ and the $F_2$ animals of the Shorthorn-Galloway cross. They obtained in the latter generation twenty polled animals and eight horned, a close approximation to the expected 3 : 1 ratio.

Cole (1924) states that in the Jersey-Angus cross the twelve $F_1$ animals obtained by reciprocal matings were polled except for the presence of scurs which are "usually absent or small on the females, but may reach a length of several inches on the males, particularly on those which are not castrated at an early age". He obtained similar results among the fifteen $F_1$ animals in the Holstein-Angus cross. None of the $F_1$ animals had horns. No report seems to have been made as yet upon the $F_2$ generation.

Smith (1927) gives the results of some matings made in Africa between pure-bred Angus bulls and native cows which showed a slight intermixture of Hereford and Shorthorn blood. The details of only one case are complete. Here, the Angus bull produced twenty-seven females, all entirely polled, and twenty-four males, nine of which were polled and fifteen "mostly with distinct horns or buds". In the photograph of the $F_1$ bulls the horns appear heavy and of good length, though apparently not as long as those of the one native cow pictured. An interesting sidelight in connection with the $F_1$ polled cows is that all of them in Smith's Fig. 4 appear to have flat, rounded, "Roman" polls as contrasted with the high, pointed, "Gothic" poll characteristic of pure-bred Angus cattle. In another cross similar to the above, the complete data are not available, but the results obtained were practically the same. Some of the $F_1$ bulls, however, had scurs instead of horns. Smith makes the statement that castration of the males appears to have very little effect in modifying the horn growth. His paper contains neither $F_2$ nor back-cross data.

## NEW DATA.

As previously stated, the new data incorporated in the present paper were obtained from crosses made in Alaska between pure-bred Galloways and pure-bred Holsteins. The Galloway herd was maintained for 26 years, and during that time reached a total of 368 animals, all of which were completely polled. Needless to say, the Holstein herd bred true for horns.

Reciprocal crosses were made in the production of the $F_1$ generation. The Holstein bull, 1 H, mated to Galloway cows, sired six female and seven male offspring. The females were all polled, while four of the males, or approximately one-half, had small, loose scurs. The remaining three males had clean polls. Another Holstein bull, 20 H, produced two polled daughters when mated to Galloway cows. Thus the totals for the above type of mating are eight females, all polled, and seven males, four of which have scurs and three are polled.

Four Galloway bulls were mated to nine Holstein cows in the production of the ten $F_1$ animals from the reciprocal mating. The four female offspring were polled. One of the six males had loose scurs, but the remaining five were polled. With the exception of one $F_3$ male, no animal with scurs was produced after the $F_1$ generation.

Three $F_1$ bulls and nine $F_1$ cows were used in the production of the $F_2$ animals. Table I gives a summary of the results. As already mentioned, none of the twenty $F_2$ polled animals had scurs. Our $F_2$ results combined with those of Watson and Lloyd-Jones and Evvard give a total of fifty-seven polled and twenty-five horned. The deviation from a perfect 3 : 1 ratio in the above data is $4{\cdot}50 \pm 2{\cdot}64$.

Reciprocal back-cross matings were made, although the heterozygous polled individuals used were not always $F_1$ animals, nor were the horned animals all pure-bred Holsteins. Two of the heterozygous polled bulls were $F_1$ animals [Nos. 66 (with scurs) and 33 (clean polled)], while the third, No. 46 (clean polled), was an $F_2$ individual. These three bulls mated to horned cows, none of which were pure-bred Holsteins, produced four polled and five horned females, three polled and six horned males. The horned males used in the reciprocal cross were pure-bred Holsteins and the heterozygous polled cows were all $F_1$ animals. A comparatively small number of offspring was produced: viz. one polled and three horned daughters, two polled and two horned sons. The combined results for both matings, disregarding sex, were ten polled and sixteen horned. The deviation from a perfect 1 : 1 ratio is $3{\cdot}00 \pm 1{\cdot}72$.

TABLE I.

*$F_2$ generation of Galloway-Holstein cross.*

| | | Offspring ($F_2$ generation) | | | |
|---|---|---|---|---|---|
| | | Females | | Males | |
| $F_1$ bulls | $F_1$ cows (all polled) | Polled | Horned | Polled | Horned |
| No. 6 (with scurs) | Nos. 1, 3, 5, 14 | 4 | 1 | 1 | 2 |
| No. 66 (with scurs) | Nos. 16, 52 | 2 | 1 | — | — |
| No. 33 (clean polled) | Nos. 3, 5, 14, 16, 18, 31, 39 | 7 | 1 | 6 | 4 |
| | Total | 13 | 3 | 7 | 6 |

Total (both sexes combined): 20 polled, 9 horned

## Discussion.

It is evident from the foregoing account of our experiments, as well as of those of others, that the polled character is due to a single dominant gene. It is not so evident what constitutes the recessive allelomorph of this gene, nor is there as yet a satisfactory explanation for the scurred and the horned individuals that are produced when homozygous polled animals are mated to horned.

Another unsettled point is the matter of classification. Are we to follow Gowen and assume that scurs may be either loosely or firmly attached to the skull and with a similar situation in regard to horns, or to follow Cole and have but two types, scurs that are always loosely attached and horns that are always firmly attached? A recent paper by Dove (1935) throws light on this problem. He found that in typical horns the bony core fuses with the skull, that in typical scurs a bony core forms at the distal end of the scur while at the same time a bony deposit is formed on the skull at the base of the scur. The bony deposit at the base of the scur may extend upward only a short distance, in which case the scur is loose. It may, however, extend far enough up to give complete rigidity, but without reaching the bony core at the distal end of the scur. Dove believes that these rigid scurs are often mistaken for horns. One gathers from his results that loose horns would be practically an impossibility in nature. However, he found that they can be produced experimentally by the transplantation of horn-forming tissues to places on the skull where connective tissue is allowed to intervene. Thus Dove's findings are not in accord with those of either Cole or Gowen, but should be given preference since they are based on a special study of the subject.

Dove obtained most of his material for the study of scurs from Cole's cross-bred animals at the University of Wisconsin. None of these had "horns" like those reported by either Gowen, Watson or Smith. So far as can be determined, Dove has never had the opportunity to investigate structures of the above type. Until someone makes such an investigation it seems advisable to consider them as true horns, *i.e.* that they have bony cores, continuous with the skull, extending throughout their length. Under such an assumption there would be two distinct types of horns, (1) those found in the ordinary horned breeds, and "recessive" to polled, and (2) those found in polled-horned cross-breds, and "dominant" to polled.

*Theory of inheritance.*

The theory, as formulated by the junior author, postulates two genes, occupying different loci, for horns, and a third gene, whose location cannot as yet be definitely stated, for scurs. It has usually been assumed that the genes for polled and horned are allelomorphic, but since two distinct, non-allelomorphic, determiners for horns are now postulated, some restatement of the matter is necessary. Under the circumstances it seems advisable to retain the symbol **P** to denote the completely dominant gene for polled and to let **p** signify merely the absence of **P**. The dominant polled gene (**P**), as will be explained in the following paragraphs, differs in its epistatic relations to the two horned factors as well as to the factor for scurs.

The method we shall follow is to give a brief statement in regard to each of the above genes, at the same time showing their interactions with each other, and to point out later how, by means of them, a satisfactory explanation can be found for the various cases already reported in this paper. New results, obtained by the junior author from cattle breeders in Kansas, will also come in for consideration.

The allelomorphs **P** and **p** have already been mentioned. The first gene for horns to be considered is **H**. This gene is assumed to be always present and to be always, therefore, in the homozygous condition. The polled gene, **P**, is completely epistatic to it in both sexes. It is evident that **H** corresponds very closely in its properties to those usually ascribed to **p**.

The other horn factor is the one whose presence in the native cattle of Africa becomes apparent when they are crossed with polled breeds, such as the Angus. Smith's paper (1927) on these crosses has already been reviewed. The gene is also present in other breeds, but not to the same extent as in the African cattle. For this reason it is designated **Ha**, the **a** referring to Africa. The allelomorph, **ha**, is merely the absence of **Ha**.

The interaction of **Ha** with other genes will be considered next. So far as can be determined at present, **Ha** has no modifying effect in an otherwise horned animal. For example, **PP HH haha** and **pp HH HaHa** animals are similar in appearance. It seems quite possible, however, that careful investigation may reveal certain differences. If all cattle were horned there would be no evidence for the existence of **Ha**. It is in the crosses with polled that its presence becomes known. Here, animals of the composition **Pp HH Haha** are horned if males and polled if females. This is as far as our knowledge in regard to the character goes. If it is inherited in the same sex-limited manner as baldness is purported to be inherited in man, one would expect that either **Pp HH HaHa** or **PP HH HaHa** animals would be horned whether males or females.

More is known concerning the remaining character to be considered, viz. scurs. Even here, however, our knowledge is not by any means complete. The greatest void is in regard to the locus of the gene. There are at least two possibilities. One is that the gene for scurs and the **Ha** determiner are allelomorphic, and the other that the scur factor has its own individual locus. The latter alternative will be adopted in the present discussion. Critical tests that could be made in regard to locus determination will be taken into consideration later.

It is suggested that the symbol **Sc** be used for the scur gene, and that **sc**, the allelomorph, represent merely the absence of **Sc**. The horned gene, **H**, is epistatic to **Sc**. Thus a **pp HH haha ScSc** animal would be horned, and the same would be true if **Ha** were also present. Males of the composition **Pp HH haha Scsc** have scurs, while females of the same composition are polled. Thus **Sc** is inherited in the same sex-limited fashion as **Ha** and is therefore always epistatic to polled in males. In addition, there is fairly good evidence that homozygotes (for **Sc**), **Pp HH haha ScSc**, have scurs whether they are males or females, indicating that in females **Sc** in the homozygous condition is epistatic to polled. If the above animals also carried **Ha**, and were therefore of the composition **Pp HH Haha ScSc**, they would probably be horned if males and scurred if females, but both sexes would probably be horned if they were homozygous for **Ha**.

It does not seem possible at present to offer a satisfactory genetic explanation for tight scurs. Of course one possibility is that the **Ha** gene is responsible, producing tight scurs instead of horns, but, until further evidence is available, it seems advisable to look upon the "tightness" as being due to a modifier acting upon **Sc**.

According to the interpretation outlined in the preceding pages, a clean-polled male is always **HH haha scsc**, since the genes **Ha** or **Sc** if present will express themselves. On the other hand, a clean-polled female may be heterozygous for either **Ha** or **Sc**, or both. Similarly, animals lacking **P** are horned whether or not they carry **Ha** or **Sc**, and whether they are males or females. Also, two clean-polled (**PP**) animals may produce 50 per cent. scurred male offspring and no scurred females, provided the female parent is **Scsc**. If the male parent is polled and the female scurred, all the sons will be scurred and none of the daughters. In crosses between horned and polled animals, scurred females (**ScSc**) will be produced only when horned males (carrying **Sc**) are mated to polled females that are **Scsc**.

*Application of theory of inheritance.*

It will be our purpose in the following paragraphs to show how the results summarised earlier in this paper can be explained by the theory just outlined. Each paper will be discussed in the same order that was followed in the summarisation.

Gowen obtained both scurred and horned animals in the $F_1$ generation of the Angus crosses with various horned breeds. It is interesting to note that the only scurred females, two of them, were produced when horned males were mated to polled females. The explanation, as previously indicated, is that both parents carried **Sc**, the scur factor:

| Horned | | Polled | | | Males | Females |
|---|---|---|---|---|---|---|
| pp HH haha Scsc | × | PP HH haha Scsc | = | 1 Pp HH haha ScSc | Scurred | Scurred |
| | | | | 2 Pp HH haha Scsc | Scurred | Polled |
| | | | | 1 Pp HH haha scsc | Polled | Polled |

Gowen's data, as shown above, indicate that at least two of his pure-bred Angus cows carried the scur gene (**Sc**). Such females when mated to pure-bred Angus bulls should have sons half of which are scurred. That scurs do occur in the pure breed is shown by the fact that the *American Aberdeen-Angus Herd Book* application blank contains the following statement among the rules of entry:

"Males and females red in colour or with a noticeable amount of pure white above the underline, or on leg or legs, or feet, or with scurs, shall not be eligible to entry for breeding purposes."

It seems to be a fairly well-established fact (1) that practically every individual in the Angus breed is homozygous for polled (**P**) and (2) that no horned offspring are ever produced. These two statements taken together mean that the genetic composition of the breed is **PP HH haha**. If any of the pure-bred polled cows were **Haha** they would have had some horned sons, even when mated to pure-bred polled males. Therefore, the production of horned $F_1$ males in Gowen's crosses can be explained only on the assumption that the **Ha** gene was carried by the horned parent. The two horned $P_1$ animals carrying this gene were a pure-bred Ayrshire and a pure-bred Guernsey cow.

None of Gowen's Holstein or Jersey animals showed evidence of carrying the **Ha** gene unless we except a Jersey bull which sired a male with "loose horns" when mated to an Angus cow. We will anticipate by stating that Cole found the same thing to be true for these breeds in his crosses, and in the Alaskan experiment similar results were obtained for the Holsteins. Thus, it seems to be a fact that relatively few individuals in our pure-bred horned dairy breeds (Holsteins, Ayrshires, Guernseys, and Jerseys) carry the **Ha** gene, while a relatively much larger number carry **Sc**.

In Watson's experiment, since one of the two $F_1$ males was horned, evidence is furnished that **Ha** was present in at least one of the West Highland $P_1$ cows. There is no tangible evidence, however, that any of the $F_1$ polled cows carried **Ha**. If any of them had, and if **HaHa** females carrying **P** were horned, one would have expected more than 25 per cent. of the $F_2$ females to be horned:

| Horned $F_1$ male | | Polled $F_1$ female | | | Males | Females |
|---|---|---|---|---|---|---|
| | | | | 3 **P HaHa** | Horned | Horned |
| | | | | 6 **P Haha** | Horned | Polled |
| **Pp HH Haha** | × | **Pp HH Haha** | = | 3 **P haha** | Polled | Polled |
| | | | | 1 **pp HaHa** | Horned | Horned |
| | | | | 2 **pp Haha** | Horned | Horned |
| | | | | 1 **pp haha** | Horned | Horned |
| | | | | | 13 Horned | 7 Horned |
| | | | | | 3 Polled | 9 Polled |

The actual numbers in the $F_2$ females were fifteen polled and three horned. Thus we are forced to conclude that there is no evidence that any of the $F_1$ cows carried **Ha**. If, on the other hand, we take for granted that several of the $F_1$ cows did carry this gene, it would lend support to the hypothesis that **HaHa** females carrying **P** are not horned, but polled. No data of a critical nature relating to this question are available at the present time.

So far as Watson's $F_2$ males are concerned, it is relatively immaterial whether or not their $F_1$ polled mothers carried **Ha**. Even if none of them did, there should still be more horned than polled males in the $F_2$ generation:

| Horned $F_1$ male | | Polled $F_1$ female | | | Males | Females |
|---|---|---|---|---|---|---|
| | | | | 3 **P Haha** | Horned | Polled |
| **Pp HH Haha** | × | **Pp HH haha** | = | 3 **P haha** | Polled | Polled |
| | | | | 1 **pp Haha** | Horned | Horned |
| | | | | 1 **pp haha** | Horned | Horned |
| | | | | | 5 Horned | 2 Horned |
| | | | | | 3 Polled | 6 Polled |

It will be recalled that the actual numbers obtained by Watson in the $F_2$ males were five horned and two polled, a very close approximation to the theoretical expectation shown above.

Watson also reports on some crosses in Scotland between Red Polled and Ayrshires in which the $F_1$ males were mostly horned and the females polled. The **Ha** gene is quite prevalent, therefore, in this particular strain of Ayrshires, making them similar in that respect to the native cattle of Africa discussed by Smith.

Cole's results have been discussed to some extent already. For example, attention has been called to the fact that none of the $P_1$ Jerseys or Holsteins showed evidence, by means of their offspring, of carrying **Ha**. They also are interesting in another respect. He states that reciprocal matings were made between the two horned breeds and the polled Angus breed and that some $F_1$ females with scurs were produced, but he does not state which sort of mating gave rise to the scurred cows. If the theory herein presented is adequate the parents of all these cows were horned males (**Scsc**) and polled females (**Scsc**).

The theory has already been applied to enough cases so that the results reported by Smith on crosses between pure-bred Angus bulls and native African cattle offer no special difficulties. He states that the native cattle had been intercrossed to some extent with Herefords and Shorthorns, and that not quite all of the $F_1$ bulls were horned, while all of the females were polled. One gets the impression that the "uncontaminated" native cattle are all **HaHa** but that previous intercrossing has caused some of the animals used as parents of the cross-breds to be heterozygous for this gene. If all the native cattle had been homozygous for **Ha**, all of the male offspring would have been horned and all of the females polled:

| Polled male | | Horned females | | | Males | Females |
|---|---|---|---|---|---|---|
| **PP HH haha** | × | **pp HH HaHa** | = | **Pp HH Haha** | Horned | Polled |

Smith had no records on the $F_2$ generation; such records would be interesting, however, if they could be obtained. The theoretical expectation for the $F_2$ generation has already been given in the discussion of Watson's results. If horned $F_1$ bulls are used, if all the $F_1$ polled cows are **Haha**, and if cows carrying **P** are horned when homozygous for **Ha**, the expected ratio in the $F_2$ generation should be thirteen horned males to three polled, and seven horned females to nine polled. If the **HaHa** females carrying **P** are polled, the ratio amongst the females should be three polled to one horned.

Smith quotes a number of authorities to show that the earliest ancestors of present-day cattle were polled and that these were succeeded by species in which the males were horned and the females polled. If **HaHa** females carrying **P** are polled, it should be possible at the present time to develop a true-breeding strain of cattle corresponding to the last-mentioned species. All that is necessary is to obtain animals homozygous for both **P** and **Ha**:

| Male, horned | | Female, polled | | | Males | Females |
|---|---|---|---|---|---|---|
| **PP HH HaHa** | × | **PP HH HaHa** | = | **PP HH HaHa** | Horned | Polled |

On the other hand, if the **PP HaHa** females were horned, the above mating would demonstrate that it is possible for cattle to be homozygous for **P** and still produce no polled offspring, nor be polled themselves.

The data obtained by the senior author in Alaska present a few angles not evident in the results published by others. In the first place, careful records were kept for a number of generations on the ancestors of the polled $P_1$ animals, the Galloways. Since no scurs occurred among 368 individuals, there would be good reasons for assuming that the stock was **scsc**. The results obtained fit in with that assumption.

When pure-bred Holstein bulls were mated to Galloway cows, the eight $F_1$ females were all polled. It is in such a mating that scurred $F_1$ females would be expected if any of the polled $P_1$ cows were **Scsc**. On the other hand, four of the seven $F_1$ males, all sons of the Holstein bull 1 H, were scurred and the remainder polled, thus demonstrating that the horned bull was **Scsc**:

| Horned male | | Polled females | | | Males | Females |
|---|---|---|---|---|---|---|
| **pp HH Scsc** | × | **PP HH scsc** | = | **Pp HH Scsc** | Scurred | Polled |
| | | | | **Pp HH scsc** | Polled | Polled |

In the reciprocal cross, nine Holstein cows mated to four Galloway bulls produced six sons, one of which was scurred and the remaining five polled. The results, though meagre, point to the fact that the **Sc** gene was present in only a relatively small number of the Holstein $P_1$ animals. The four female offspring from the above cross were all polled, as would be expected.

Since none of the $P_1$ Galloways and very few of the $\mathbf{P_1}$ Holsteins carried the **Sc** gene, one would assume it to be carried by very few of

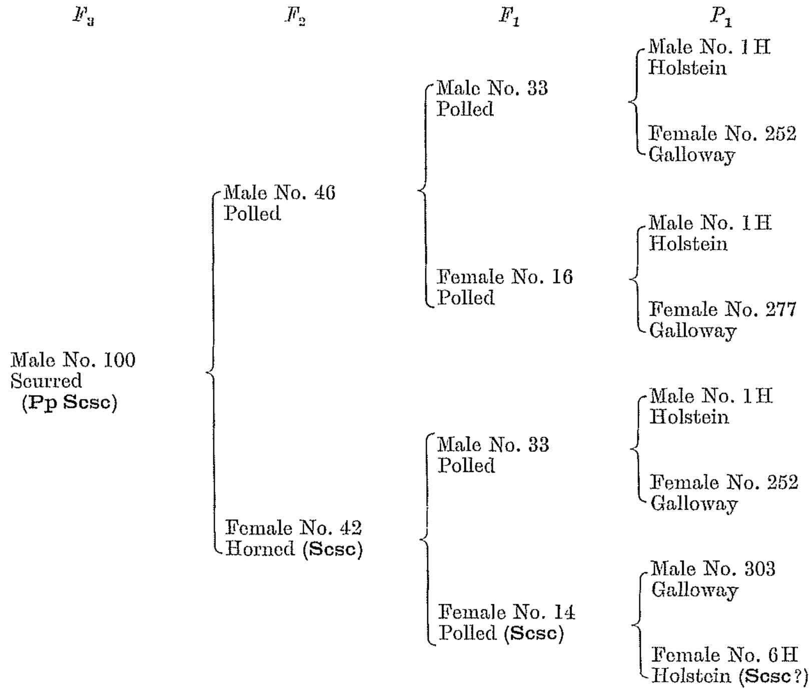


Fig. 1. Pedigree of the $F_3$ scurred male.

the $F_1$ polled females. The results obtained are in agreement with that supposition. None of the twenty $F_2$ polled animals (Table I) had scurs.

As previously mentioned, only one scurred animal occurred subsequent to the $F_1$ generation. This was the $F_3$ male No. 100. His pedigree (Fig. 1) is of interest, because one can trace it back to the $P_1$ female from which the character was inherited. The scur gene was transmitted entirely through females. The $F_1$ and $F_2$ males were all clean polled and consequently could not have carried **Sc**.

### *Frequency of* **Ha** *and* **Sc** *in Herefords.*

The animals that have been discussed in this paper in regard to scurs and the **Ha** gene have come either from horned dairy or from polled beef breeds. Nothing has been said concerning horned beef breeds because nothing that could be used in the above connection has been published. However, the junior author has received some reliable information pertaining to the Hereford breed. Part of this information comes from Prof. C. W. McCampbell of the Kansas State College, Manhattan.

He states that approximately twenty years ago Mr Robert H. Hazlett of Eldorado, Kansas, a famous breeder of pure-bred horned Herefords, sold a horned bull to Mr Alexander Philip of Hays, Kansas, another well-known Hereford breeder. The bull when mated to Mr Philip's cows, all of which were horned, sired a fairly large proportion of polled offspring of both sexes. Further details are not available, since Mr Philip unfortunately is dead. It is obvious that the horned bull having polled offspring actually carried **Ha** and was of the composition **Pp**. Our theory is that the **Ha** gene is fairly common in Herefords, at least in the Hazlett herd, and that a dominant mutation (**P**) took place in the production of gametes by one of the parents of the **Pp Haha** bull.

In a recent communication from Mr Hazlett we have been informed that two polled animals, both heifers, have been produced in his herd during its existence of approximately forty years. One of these came a considerable number of years ago and the other was born in 1933. A third animal, a scurred female, also was born some years ago. Up to the present no polled or scurred males have appeared. Mr Hazlett's herd in recent years has consisted of from three to four hundred breeding females and a proportionate number of males. Practically no outside blood has been introduced into the herd for many years.

Prof. McCampbell also informs us that a clean-polled heifer cropped out in the Kansas State College pure-bred Hereford herd about fifteen years ago and was sold to a breeder of polled Herefords. No other polled animal from horned parents has been produced in the herd since that time. This also looks to us like a case of mutation occurring in the immediately preceding generation.

Polled mutations in horned breeds have been utilised in the production of polled strains in these breeds. For example, there are many herds of polled Jerseys, Holsteins, Shorthorns, and Herefords in the

United States, but, so far as can be learned, there are not as yet any polled Guernseys or Ayrshires.

Some data obtained recently from John Lewis and Sons of Larned, Kansas, through the courtesy of one of the sons, Walter, have a bearing on the prevalence of the **Ha** gene among pure-bred Herefords. Lewis and Sons are breeders of the polled variety, and have succeeded in combining desirable beef qualities with the polled character. In order to attain this end, they still use horned bulls occasionally in their matings. Scurred bulls are also employed. The females used for breeding purposes, with very few exceptions, are either polled or scurred. Table II is a summary of the 1934 calf crop; the offspring of four different males are given. More detailed accounts of coming calf crops will be obtained in the future.

TABLE II.

*Data from pure-bred "polled" Herefords—1934 calf crop.*

| Parents | | Offspring | | | | | |
|---|---|---|---|---|---|---|---|
| | | Males | | | Females | | |
| Male | Females | Polled (clean) | Scurred | Horned | Polled (clean) | Scurred | Horned |
| Horned (from pure-bred horned stock) | Nearly all are clean polled. A few are either scurred or horned | 8 | 3 | 4 | 11 | 2 | 0 |
| Scurred. Scurs only about ½ in. long at 8 months: at 5 years only 2 in. | Do. | 15 | 7 | 4 | 23 | 3 | 2 |
| Scurred. At 3 years only a "button" | Do. | 5 | 1 | 3 | 10 | 1 | 0 |
| Clean polled | Do. | 7 | 2 | 0 | 7 | 0 | 0 |
| | Total | 35 | 13 | 11 | 51 | 6 | 2 |
| | Grand total | | 59 | | | 59 | |

One thing evident from a perusal of the table is that all of the scurred daughters were sired by either the horned or the scurred bulls. This would be expected if the theory presented in this paper is correct. It is also evident that there are more horned sons than daughters. The differences are not great enough, with the present small numbers, to be significant statistically; but nevertheless there seems justification for assuming that several of the horned male offspring are **P** animals carrying **Ha**. In fact, we have been informed by Walter Lewis that many of their horned bulls have been sold to ranchmen having horned herds, and in a number of cases these horned bulls sired polled individuals.

In two of the matings recorded in Table II all of the horned offspring, seven in number, are males. The deviation from a 1 : 1 ratio, 3·5, is 3·93 times its probable error. If these horned males actually are **P** animals carrying **Ha**, it means that the latter gene was present, but not expressing itself, in the dams of some of these males. It also means that when a polled male is mated to a number of females, whether polled or horned, and has some horned sons but no horned daughters, he may still be homozygous for **P**. If one or more of his daughters are horned, however, he must be **Pp**. Thus the data, so far as they go, point to the conclusion that the **Ha** gene is fairly common in pure-bred Herefords.

In spite of the fact that the **Ha** gene is carried by a number of animals in the Lewis herd, at least two polled bulls have been produced which when bred to many females have never sired a horned animal. No satisfactory explanation can be offered for these cases unless one assumes that no horned male offspring carrying both **P** and **Ha** were obtained. It seems advisable, however, to defer further discussion of these cases until the facts in regard to them are more thoroughly investigated.

*Time and frequency of occurrence of the* **P** *mutation.*

Dove (1935) does not favour the idea that the polled character in horned breeds is due to a mutation in the immediately preceding generation. He assumes instead that the **P** gene has been present in the breed from the beginning, but has been kept from expressing itself because of the epistatic effects of the (tight) scur gene. He has not considered the possibility of the existence of the gene **Ha**, postulated by us. It would be this gene, if any, which kept the polled character from cropping out.

If the polled gene (**P**) were in the horned breed from the beginning of the breed's history, it necessarily would have been carried from generation to generation almost entirely by means of the males. Females might have carried it provided they were homozygous for **Ha**, but there is no evidence at hand in regard to whether or not such animals would be horned. Even if these females were horned, they would be comparatively quite rare in the pure breeds of North America, since the **Ha** gene itself is uncommon in these breeds.

On the other hand, although there would be the possibility of the existence in a horned breed of horned males with the composition **Pp Haha**, such males would be discarded as soon as they sired a number of polled offspring. It even seems reasonable to assume that the horned offspring of these males would be viewed with suspicion by the breeder and therefore be eliminated from the herd. At any rate, it does not seem possible to us that the **P** gene could have remained very many generations in a horned breed even though the **Ha** gene were present to help mask it.

Since we are taking for granted that every polled, scurred, and **Pp Haha** horned individual in a horned breed is due to the mutation of **p** to **P** in the immediate ancestors of these individuals, it may be of interest to speculate on the frequency with which these mutations occur. Based on the rate of occurrence in Hazlett's herd and on the apparent ease with which polled varieties of horned breeds have been established, one would probably be justified in hazarding the guess that the mutation rate is at least 1 in 20,000.

The above frequency seems to be much greater than is the case for the reverse mutation, **P** mutating to **p**. So far as can be learned, the two polled breeds, Angus and Galloways, never produce horned offspring. Even if the possibility of the recessive mutation occurring is completely excluded, it seems remarkable that homozygosity for the dominant polled gene was fixed in both breeds at such a comparatively early date. It leads one to suspect that **P** and **Sc** are linked and that in the early history of the breeds **Sc** was brought in by the horned ancestors, thus making scurs at that time a "marker" for many of the heterozygous (**Pp**) males. It is also conceivable that **Ha**, instead of **Sc**, might have served this purpose.

*Linkage relations of* **P**.

No experiment has as yet been conducted in the conventional manner to test the linkage relations of polled with other genes. But some results obtained by Watson (1921) and by us show rather conclusively that polled is not linked with either black (**B**) or self (**S**).

In Watson's experiment the $P_1$ animals were black polled, and red horned. The $F_2$ generation consisted of eight black, polled; five black, horned; two red, polled; and one red, horned. For the total of sixteen the ratio is very close to that expected in independent inheritance.

Similarly, our $P_1$ animals consisted of polled self, and horned white-spotted. In the $F_2$ generation the actual numbers were ten self, polled; five self, horned; four white-spotted, polled; and two white-spotted, horned. For the total of twenty-one and assuming independent inheritance, the theoretical ratio should have been 12 : 4 : 4 : 1.

*Testing for genetic relations of* **Sc** *to* **Ha**.

In an earlier section it was stated that with our present knowledge it was impossible to determine whether **Sc** and **Ha** were allelomorphic, linked, or on separate chromosomes, but that until further information was available it would be taken for granted that they were inherited independently, each having its absence as an allelomorph.

In the meantime it may be of interest to determine which type of mating is most likely to give the desired information. Since according to our theory a clean polled male is a double recessive (**scsc**, **haha**), one homozygous for polled (**P**) should prove the best kind for testing purposes. The best females would be those horned animals which produced at least one horned male when mated to the above type of bull. If one of these females produced not only horned but also scurred and clean polled male offspring it would be clear-cut evidence that **Sc** and **Ha** are not allelomorphic. The difficulty would be in getting females producing enough males for the test.

If **Ha** and **Sc** were not allelomorphic, but were either linked or independent, all three types of males should be produced by the doubly heterozygous females, but the numbers would be too small in any one mating to be statistically significant for either of the two kinds of inheritance. Here it would be of advantage to use a horned (**pp**) male carrying both **Ha** and **Sc**, in the heterozygous condition if one can be found, and mating him to homozygous polled females of the composition **scsc haha**. The other difficulty would be to get such females, since even in pure-bred Angus and Galloways the scur gene is still carried but not expressed by some individuals of this sex.

What seems to be the nearest approach to a test in regard to the genetic relations of **Ha** and **Sc** was obtained by Gowen (1918). The pure-bred Ayrshire cow, Dot Alaska, when mated to the pure-bred Angus bull, Kayan, had two sons. One was horned and the other scurred. The only other offspring from this mating was a clean polled female.

## Summary.

1. In crosses between homozygous polled and horned cattle many of the $F_1$ animals are polled, but the remainder, mostly males, are either scurred or horned.

2. The theory formulated to explain the above results is as follows. All cattle are assumed to be homozygous for the horned gene, **H**. Polled animals carry a dominant gene, **P**, which is completely dominant to **p** (absence of polled) and also completely epistatic in both sexes to **H**. Two other factors are postulated, **Ha** ("African" horns), and **Sc** (scurred). The latter is sex-limited to the extent that in both the heterozygous

and the homozygous condition it is epistatic to **P** in males, while it is epistatic only in those females that are homozygous for the gene. A similar relationship applies to **Ha**, except that it has not yet been determined whether or not homozygous **Ha** females carrying **P** are horned. In non-polled (**pp**) animals **H** is epistatic to **Sc** in both sexes and apparently is epistatic to **Ha**, although it is quite conceivable that **H** and **Ha** each has a modifying effect on the other, making the epistacy incomplete.

3. The theory has been applied to explain the results of various workers and also those obtained in Alaska in crosses between Galloways and Holsteins.

4. Data have been obtained from several breeders in Kansas showing that the **Ha** and the **Sc** genes are fairly common in the Hereford breed.

5. There is evidence for assuming that the mutation of **p** to **P** occurs more frequently in cattle than the reverse mutation.

6. It is shown that **P** is linked with neither black (**B**) nor self (**S**).

7. Methods for determining whether **Ha** and **Sc** are allelomorphic, linked, or on separate chromosomes are discussed. The last-named condition is assumed temporarily in the present paper.

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