The Inheritance of Horns in Sheep

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SUMMARY

 \mathbf{I}^{N} this paper different degrees of hornedness in male and female Merinos are described and two hypotheses concerning the genetic control of horns in the two sexes are put forward.

I. INTRODUCTION

The study of the inheritance of horns in sheep has received considerable attention during the last fifty years. Following the rediscovery of Mendel's Laws, hornedness was apparently considered to be a suitable character in the sheep for genetical investigation, and numerous workers have published interpretations of their observations on Merino and British breeds of sheep and some crosses. Many different hypotheses have been formulated to explain the inheritance of horns in sheep, and, in general, they have increased in complexity over the years.

Since 1951, observations on the inheritance of hornedness have been made at the National Field Station, "Gilruth Plains", Cunnamulla, Queensland. Mostly these have been on a flock of medium-Peppin Merino sheep, while a limited number of observations have been made on sheep of the fine non-Peppin, medium non-Peppin and strong non-Peppin strains, and two further medium-Peppin strains of different origins from the large medium-Peppin flock. Numerous rams of polled Merino origin have been mated singly to ewes of different degrees of hornedness, and a Border Leicester ram and some of its male progeny have been mated to Merino and crossbred ewes.

II. HORNEDNESS PHENOTYPES IN THE MERINO

A scoring system has been devised to record the considerable phenotypic variation found in the degree of hornedness of both sexes of the Australian Merino. Some important categories in this system of classification are as follows:—

Depression:	A concave depression in the bone of the skull on the horn site.
Knob:	A bone knob on the horn site with no keratinised material present which cannot be removed by rubbing.
Scur minus:	A bone knob on the horn site with keratinised material present which cannot be removed by rubbing and which is less than 0.1" high.
Horn growths	All horn growths longer than 0.1" are measured to the
longer than 0.1":	nearest 0.1", measurements being made along the edges of the horn growths which are dorso-medial as they leave the head.

The sexes differ in their patterns of expression of hornedness. In the female the range extends from a depression (which may or may not contain a small knob or short scur), through knobs of various sizes to the classification scur minus and measurable horn growths greater than 0.1" long. The latter fall into two populations. Those which have been designated "female scurs" are loose, without a large horn core, and may be up to 4" in length. Those defined as "female horns" are firm, well grown on cores approximately 1.5" to 3" long, and may themselves be from 5" to 12" long. The curvature of female scurs or female horns may vary considerably; the longer scurs generally coil forwards towards the eye, while horns may sweep forwards towards the eye, point almost straight out from the head, or sweep backwards over the ears.

At the polled end of the range in the male are found depressions, which may not be as even or as clearly defined as those found in the female. Sometimes horn sites are undulating. The measurable horn growths of males have been divided into four types on the basis of measurement and nature of the horn

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growth. "Male short scurs" are scurs up to approximately 3'' in length in adults. "male long scurs" may be approximately 5'' to 10" long, "male aberrant horns" approximately 10" to 15" long, while "male true horns" are much longer and more massive in growth than all other types, being the horn type commonly seen in Australian Merino flocks. Long scurs generally are somewhat oval in cross-section, do not have sharp points, and may curl forwards or grow outwards from the head. Aberrant horns generally are angular in cross-section at the dorso-medial edge, have sharp points, and sweep forwards as do true horns in early stages of growth. The definitions of the male scurs and horns are based on many fewer observations than are those of the female scurs and horns, and, therefore, are subject to confirmation.

III. GENETIC HYPOTHESES

To explain the major phenotypic differences summarised, two hypotheses have been formulated on the inheritance of hornedness. Each explains satisfactorily all matings made to date, although there are several phenotypes which require further explanation.

One hypothesis is that there are two major pairs of alleles, one pair (Pp) being expressed in both sexes and the other (Hf, hf) in the female only. This hypothesis is as follows:-

36.1.

(a) There is a single dominant autosomal gene whose action produces "polledness" in both sexes. The expressions of the gene, here termed P ("polled"), and its recessive allele p in animals of different phenotypes and sex are detailed below.

Genotype

Phenotype

Female

		:/lale	Female			
Pp		An undulating horn site, or a	A depression. Possibly also a			
1		depression with or without a	small knob or short scur set			
	small bone knob or a small in a depression.					
		amount of superficial horny	1			
		growth. Probably has little or				
		no horn core.				
pp		A male short scur, long scur,	A depression, or a small knob			
••		or aberrant horn.	or short scur set in a de-			
			pression.			
PP		A male true horn.	A knob, female scur or female			
			horn.			
			(See (b)).			
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The differences described in the phenotypes of PP and Pp males are based on observations on 4 males proven PP by breeding and 7 males proven Pp. They are thus subject to confirmation on a greater number of animals. There may be, for instance, some PP males with a greater degree of horn growth than indicated, while some males with only superficial scurs or horn sites without definite depressions in the bone may be Pp. To be able to distinguish PP rams from Pp rams is a most important practical point.

(b) There is a single dominant autosomal gene which initiates the growth of horns in ewes. To date, the expression of this gene has not been discerned in males. The expressions of this gene, here termed Hf ("horns in females"), and its recessive allele hf in animals of each sex which do not carry the P gene are detailed below.

Genotype		Male	Phenotype	Female
Hf Hf Hf hf	Ĵ	A male true horn.	}	A female horn.
hf hf	J			A knob or female scur.

The frequency of the gene Hf in the large medium-Peppin flock is approximately 0.1.

- (c) P is almost completely epistatic to Hf. The effect of P in Hf Hf or Hf hf females has often been discerned as small scurs or knobs set in depressions. As the phenotypes of PP and Pp males are more variable than those of PP and Pp females, the effect of Hf in these males has not been discerned.
- (d) Variation in scur length of pp hfhf ewes is possibly under polygenic control to some extent, although no estimates of heritability have been obtained. A considerable amount of variation in scur length is environmental, being the result of accidental breakages.

- (e) Variation in the lengths of short scurs, long scurs and aberrant horns in Pp males may be under the control of further major pairs of alleles and polygenes.
- (f) Aberrantly horned males carry the gene P. Two such rams have been shown on breeding to be Pp.

The second hypothesis is that there is a series of triple alleles, the dominant allele having the effect of the gene P in the first hypothesis, the intermediate gene having the effect of the gene Hf, and the recessive allele having the effect of p or hf. If this is the case, the dominance of the equivalent of the P gene over the intermediate gene producing horns in females is not quite complete. The remainder of this alternative hypothesis is as detailed in (d), (e) and (f) of the first hypothesis.

For the purpose of this paper the observations are interpreted in the light of the first hypothesis. It has not been disproved in favour of the second because there have not yet been enough matings in which both pairs of genes are segregating. The P gene has been located in mating groups in which two rams with very small or no scurs were the parent sires. Both sires were proven to be PP. The Hf gene is segregating in a larger flock of approximately 1,300 ewes in which horned rams (pp hfhf, pp Hfhf or pp Hfhf) have been used exclusively.

In 1954 the two parent polled sires were mated individually, each to forty horned ewes. These matings are the first in which the genes P and Hf have been thrown together wittingly. By backcrossing Pp Hfhf progeny to enough pp hfhf individuals it will be possible to choose between the two hypotheses.

IV. RELATIONSHIP OF HORNS TO WOOL AND LAMB PRODUCTION

Miss N. Hemingway, of the McMaster Laboratory, has been investigating the correlation between horns and wool and lamb production in ewes. So far staple length is the only character which may possibly be correlated **pheno**typically with female horns. Horned ewes may have slightly greater staple lengths than scurred ewes in some ewes investigated.

Some data are available which may give an indication of any differences between depression and knob ewes in wool or lamb production, but these are not very extensive.

V. RELATIONSHIP BETWEEN BREEDS OF SHEEP

It is dangerous to argue from the observations on Merinos reported here that hornedness is inherited similarly in different breeds of sheep. However, several interesting possibilities suggest themselves. The Dorset Horn breed, for example, could be homozygous for Hf and p. Attempts to produce a polled strain of the Dorset Horn would then involve the production of Dorset Horn type animals homozygous for P. . If the first hypothesis holds, such a strain could have the alleles Hf, hf segregating; if the triple allele hypothesis holds, Hf would tend to be eliminated from the strain as the frequency of P increased.

The Border Leicester breed could be homozygous for P, as the matings of several Border Leicester x Merino animals have suggested. Just how many British breeds polled in both sexes are similar to the Border Leicester as far as polledness is concerned is a matter for conjecture. The Suffolk may be one breed to differ.

The horned and polled strains of the Polwarth could differ essentially only in that the former strain is pp, the latter PP with perhaps a few Pp individuals.

VI. FUTURE WORK

There are several aspects of the work which are receiving attention at the present time. The first is a choice between the two hypotheses. If the hypothesis involving two pairs of alleles is accepted, an estimate of the linkage between them will be attempted.

The second is a more detailed study of the phenotypes and related breeding performances of polled males with different scur and horn lengths.

The third is a study of the relationship between different wool characters and the Hf, hf alleles being continued by Miss Hemingway, while a similar study will be attempted on less extensive data involving the P, p alleles.

DISCUSSION

Mr. KNIGHT: What results does one expect from the mating of a ram with depressions to ewes with depressions?

ANS.: Ewes with depressions would be PP or Pp. Rams with depressions would probably be PP, if one accepts the limited evidence on the phenotypic differences between PP and Pp rams. If the ram were PP and the ewes PP or Pp, all progeny would be polled, **but** some ram and ewe progeny would themselves not breed true, being Pp.

It is easy to determine whether a ram is PP or Pp; the ram can be mated to a number of **knobbed** (pp) ewes, and presence or absence of segregation in the progeny noted. It is much more difficult to determine whether a depression ewe is PP or Pp, and in a polled flock one would not be surprised if a number of Pp ewes were present even after a considerable period of selection against p. They could be identified only by their producing a horned ram or **knobbed** ewe when mated to a polled sire, which was Pp, or to a horned sire, which was pp.

Professor McCLYMONT: Have any observations been made on the effect of testosterone or an oestrogen on horn growth?

ANS.: An experiment has been carried out on the effect of testosterone propionate on horn growth of pp entires and castrates. Testosterone propionate had no effect on the horn growth of entires, but the two levels applied had the effect of increasing the horn growth on the castrates, the increase being greater in the group given the higher level.

By castrating pp males at birth it has been possible to produce wethers which have either small scurs or only bone knobs with removable keratinous material on the knobs.

No observations have been made on the effect of oestrogens on **horn** growth.