GENETIC AND DEVELOPMENTAL
ANALYSIS OF THE N-TYPE STRAINS OF THE ROMNEY MARSH BREED OF SHEEP.

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CONTENTS.

General introduction.

The N-type strains of the Romney Marsh breed of sheep differ from normal in the occurrence of either the N or the nr genes. These genes are independent genetically, being non-allelic and differing in their dominance relations. The N gene is a partial dominant and the nr gene is an almost complete recessive. Their effects include a number of aspects of the structure of the fleece, the occurrence of brown pigment in the tips of birthcoat fibres and the formation of horns. The two genes are remarkably similar in their effects, differences where they exist being quantitative rather than qualitative.

The main problem raised by these genes is the manifold nature of their effects. This can be due to either a 'true' or 'spurious' pleiotropy of the initial gene action, as has been emphasised by Gruneberg (1943). The obvious approach to the problem is the retrograde analysis of each of the effects, to determine if these can be traced to some initially unitary effect, which due to the complexities of development results in a complex end effect (Gruneberg 1947)

The genetic and developmental analysis of the N and nr genes has been the main subject of research by Dr.F.W.Dry and his students for the last twenty years. During this period considerable data have been collected, which is available mainly in the form of theses for the M.Sc., and M.Agr.Sc. degrees or as undigested laboratory notes. Only a minute fraction of these results have been published and therefore the first problem of the author on joining Dr.Dry was to condense, assimilate, and edit this data.

As this work progressed and a coherent scheme became apparent, it was obvious that further data would be necessary, to provide connecting links, and to examine tenetative hypotheses rigorously. At this stage the author was joined by Mr.G.M.Wright, a mathematician, and Miss J.M.Ross, a histologist. Although the author was fortunate in being allowed by Dr.Dry to integrate the work of this team, the actual results cannot be separated with any precision as the responsibility of one or other of the members of the team, since our attitude was not determined by the necessity to write a thesis, and the work proceeded therefore more or less anonymously. The results in an over-simplified sentence were to show that the effects of the N and nr genes differed between the different types of follicles which occur in sheep skin.

At this point the author left New Zealand and the remainder of the work was completed at the Institute of Animal Genetics, Edinburgh. This consisted of a theoretical study of the shapes of birthcoat fibres, leading to the conclusion that the actual rate at which a follicle forms its fibre is determined by the intensity of the competition of adjacent follicles for fibre substrate, the competition being in terms of the efficiencies of follicles. This hypothesis when applied to the various effects of the *N* and *nr* genes on the structure of fibres, allows these to be explained as due to an initial effect on the efficiencies of follicles. This explanation of one section of the N-type differences was then expanded, and the total phenotype explained in terms of the genes having an initially unitary and tissue specific effect on the keratinisation function of the epidermis.

This work is presented in the form of the several separate papers , written for publication by the author, since the re-writing as a more orthodox thesis would have been a formidable task, and would have resulted in over-statement of the author's position.

2. Segregation genetics. (F.W.Dry and A.S.Fraser)

The term 'N-type' designates a phenotype which is determined by one or other of two apparently monogenic substitutions. These sheep which were discovered in the Romney Marsh breed differ very markedly from normal in a number of characters, being horned instead of polled, and having a 'carpet' rather than a 'longwool' type of fleece. This series of papers is concerned with the description of the origins of the stocks, their perticular characterseitics, the genetics of the differences from normal, and the developmental analysis of the syndrome which is collectively called N-type. The present paper which is primarily intended as an introduction to the rest of the series, details the origins and the segregation analysis of the several N-type stocks.

Origins of the N-type stocks.

One strain originated from a single ram. This ram had large horns and a very coarse fleece, both points which separated him qualitatively from normal Romneys. When crossed to normal Romney ewes this ram gave a progeny which segregated in an approximate 1:1 ratio for the N-type of fleece. Crosses between his N-type offspring gave a 3:1 ratio of N-type:non-N-type, suggesting very strongly that the original ram was heterozygous for a gene (N) which is dominant to its normal allele ($+^N$). A large number of sheep have been bred which carried the N gene, and as will be shown below the accumulated evidence is in very close agreement with the dominant single factor hypothesis. This stock of N-type sheep is called the 'Nielsen' stock, since the original ram was donated by Mr.P.A.Nielsen, a neighbouring Romney Marsh stud breeder.

A second stock of N-type sheep (the Massey stock) originated from the Massey College flock of stud Romneys. This also differes from normal by a dominant gene, which crosses have shown to be allelic with the N gene. In the present analysis the data from the Nielsen and Massey stocks have been pooled in order to simplify the discussion. The senior author intends to present the separate Nielsen and Massey data in a later paper, in which many of the points raised in this paper will be treated in greater detail.

A third stock of N-type sheep (the recessive stock) originated from a ram which although N-type itself, gave no N-type progeny when crossed to normal Romney ewes. When crossed to his daughters, however, he gave a progeny which segregated in a 1:1 ratio. The intercross of his sons and daughters gave a 1:3 ratio. These results indicate and the later results confirm

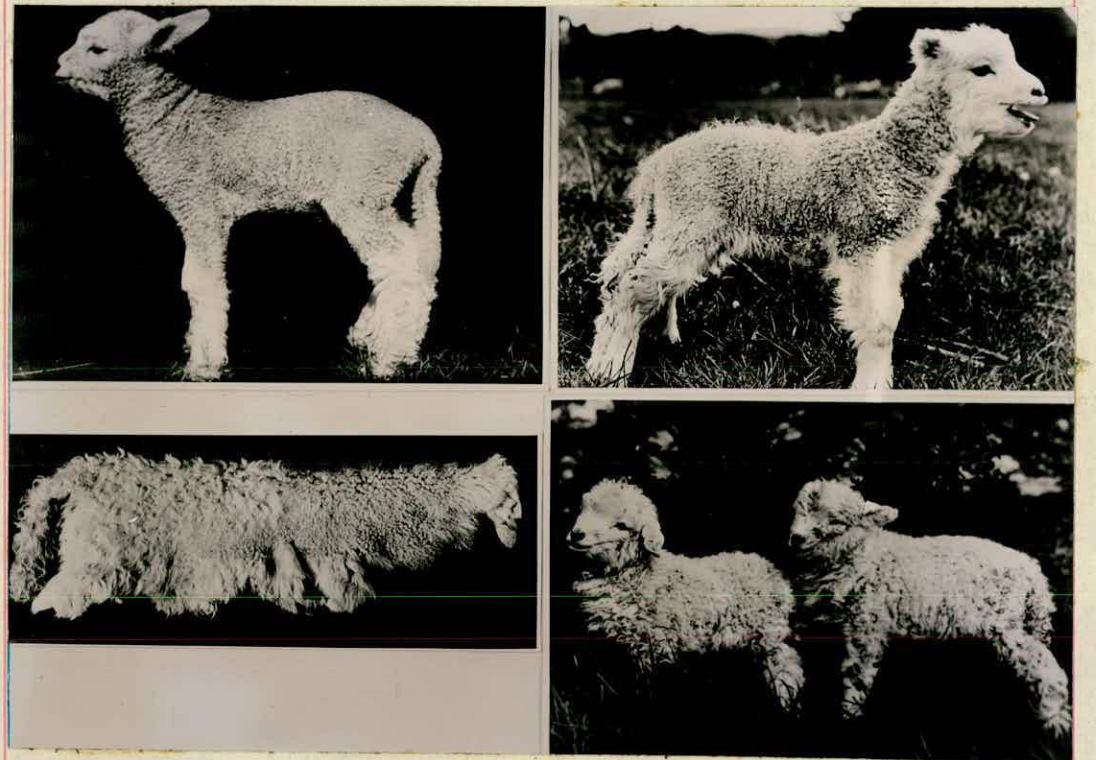
	N-type Romney	Non-N-type Romney
Birthcoat.	Very high frequency of halo-hairs	Very low frequency of halo-hais
Brown tipped fibres.	Large patches scattered over the birthcoat in many lambs.	Light scattering on the back of the neck in a few lambs.
Hairiness.	Very 'hairy' fleece of carpet type.	Hair almost absent in fleece of longwool type.
Crimping.	No obvious crimps or locks.	Well defined crimps in definite staples.
Kemps.	High frequency of fibres shed as kemps.	Kemp fibres very rare.
Horns.	Large horns occur in most males. Medium horns occur in many females.	Very small horns occur in a few males; females are polled.

Table 1. The main characters which comprise the N-type syndrome and their appearance in N-type and Non-N-type Romneys.

that the original ram was homozygous for a gene (nr) which is recessive to its normal allele ($+^{nr}$). The ancestry of this ram cannot be defined rigorously, since at that time the matings were made *en bloc* in the paddocks, and it is possible that a ram from an adjoining paddock may have trespassed. Later matings since that year have all be made in mating pens under strict supervision.

The N-type syndrome.

The *N* and *nr* genes affect a number of characters: the main ones are listed in table 1, with a rough description of the differences which occur between N-type and non-N-type sheep in these characters. This table gives an idea of the complex effect of these genes. The segregation analysis has been made primarily on a single character, the halo-hair frequency; discussion of the complexity of the pleiotropic effect is postponed to the later papers of this series. The halo-hair grade is an estimate of the frequency of halo-hairs which occur in the birthcoat. Halo-hairs are long, coarse fibres which project above the rest of the coat giving it a fuzzy outline (see plates III and IV). The halo-hair frequency is estimated by eye judgement within a few days of birth. Since this grading has been done only by the senior author any error will be a personal one, which due to long experience is likely to be small. The whole range of halo-hair frequencies has been divided into seven grades from grade I in which no halo-hairs occur (see plate I), to grade VII in which the coat is a dense mat of halo-hairs (see plates II and III). The halo-hair grade of normal Romney lambs ranges from grade I to grade VI, and in plate IV is shown a typical Romney lamb which has a grade III halo-hair frequency. No grade VII lambs have been found which did not carry either the *N* or the *nr* genes.



Plates I-IV. I-Romney Marsh lamb of back halo-hair grade I. The extremities of this lamb(poll, britch, brisket, and tail) have no or very few halo-hairs.

II-Twin Romney Marsh lambs, both N/N, with a full grade VII halo-hair frequency all over the body.

III-Skin of lamb which has grade VII frequency of halo-hairs on the back, with a big reduction in frequency on the front of the body and part of the side. This lamb was N/+ .

IV-Typical Romney Marsh lamb with a back halo-hair grade III. The extremities have abundant halo-hairs.

The halo-hair frequency is not usually constant over the main body region. Normally it decreases in a postero-anterior gradient which often has a marked discontinuity (see plate III). The region around the middle of the back always shows the highest frequency, and the primary grading of an animal is therefore made solely on this region. In the following analysis only these primary grades are used.

Inheritance of halo-hair grade in normal Romney Marsh sheep.

The work on N-type sheep originated from some early work of the senior author on the inheritance of halo-hair grade in normal Romneys. The range of halo-hair grades in normal Romneys is shown in table 2 and parents whose halo-hair grade was known were mated together in various combinations as shown in table 3. These matings gave the progenies also shown in the table, which demonstrate that the grade is fairly strongly inherited, but also that no simple Mendelian explanation can be formulated.

These measurements of the heritability of the halo-hair grade led to an attempt to select a stock with high halo-hair grades. As a basis for this stock neighbouring farmers were requested to look out for lambs with a high frequency of halo-hairs. One farmer

PARENTS	PROGENY						
	VII	VI	V	IV	III	II	I
VI x V	-	-	1	-	1	-	-
VI x I	-	-	-	-	-	3	-
V x V	-	1	2	2	1	-	-
V x IV	-	1	2	2	1	-	-
V x III	-	-	1	2	-	3	-
V x I	-	-	1	1	4	14	2
IV x IV	-	-	-	1	1	3	-
IV x III	-	-	2	4	8	2	2
IV x I	-	-	-	-	-	8	5
III x II	-	1	2	-	1	15	3
III x I	-	-	-	-	1	12	7
II x II	-	-	2	-	8	32	7
II x I	-	-	-	-	-	2	1
I x I	-	-	-	-	4	20	45

Table 3. Inheritance of halo-hair abundance in normal Romneys.

Cross	Grades VII VI	V	Grades IV III II I	X^2
N/+ x N/+	87	1	22	1.34
N/+ x +/+	297	13	305	.108

	X^2	P
Deviation	.64	.3 -.5
Heterogeneity	.81	.3- .5
	1.45	

Table 4. Segregation date of the N gene, analysed by the combined estimation method, after grouping of h-h grades.

Mr.Nielsen, donated a ram lamb which had a very high frequency of halo-hairs, higher than had been previously noted in the breed. This ram as stated above was the original animal of the Nielsen 'dominant' N-type stock.

Genetics of the N-type dominant stocks.

The original 'Nielsen' ram was crossed to a number of normal Romney ewes, but it was not realised until the second year that this ram's progeny were showing a 1:1 segregation for high halo-hair frequency. When this was noted crosses were made to test the hypothesis that the segregation in these progeny was due to the ram being heterozygous for a dominant major gene. These crosses gave the expected 1:1 and 3:1 ratios. It seemed reasonable to conclude that the original ram was heterozygous for a dominant major gene (N). The segregations of this gene in outcrosses and intercrosses are shown in table 4. They are independent of sex. Although the initial separation is into seven grades, the examination is facilitated by grouping. Grades VII and VI are grouped as N-type. Grades I,II,III, and IV are grouped as non-N-type. Grade V is rejected as intermediate. The data were analysed by the combined estimation method.

The agreement of expected with actual ratios

RAM		VII	VI	V	IV	III	II	I
305	crossed to low grade unrelated ewes. Progeny:-	8	3	-	1	2	6	2
		11			11			
E882	crossed to low grade unrelated ewes Progeny:-	12	8	-	4	4	8	4
		20			20			
E1204	crossed to low grade unrelated ewes Progeny:-	16	7	2	3	1	20	11
		23			35			
50.5	crossed to low grade unrelated ewes Progeny:-	19	-	-	2	2	15	3
		19			22			

Table 5. Pedigree of four successive N-type rams which were testcrossed to normal Romney ewes, showing the continued segregation of the gene.

cannot be taken as proof of the existence of the N gene, since the phenotypic descriptions are liable to subjective errors, and since an arbitrary division has been made of the range. One reasonable proof is the segregation continuing after repeated back-crossing. Data are available of three linear descendants of the original ram. Each is the progeny of the cross of an N-type ram to normal Romney ewes. This is shown in table 5.

A second question which can be raised is of the effect of selection for halo-hair grade on the segregation. This selection can be made on the grade of the N/+ or the +/+ parent. In table 4 the segregation is given for crosses in which the N/+ parent was grade VII or VI and the +/+ parent was grade I,II,III, or IV. These results can be separated in terms of the grade of the +/+ parent, allowing comparisons of the segregations from +/+ parents of different grades from I-IV. This separation is shown in table 6. There is no evidence of selection for halo-hair grade in the +/+ parent having any effect on the segregation.

The next step was the isolation of N/N rams. Rams from the intercross of grade VII animals were test-crossed to 10-15 normal ewes. Those rams which gave only high grade progeny were taken as N/N. At a later stage it was possible to expand the stocks and, for this purpose, all available rams, both N/N

-----	Grades VII + VI	V	IV + III + II + I	χ^2
N/+ x +/+ (IV)	12	-	11	.043
N/+ x +/+ (III)	9	-	5	1.14
N/+ x +/+ (II)	38	-	31	.71
N/+ x +/+ (I)	69	2	75	.25
Total	128	2	122	.144

	χ^2	df	P
Deviation	.144	1	.5-.7
Heterogeneity	2.002	3	.7-.8
	2.146		

Table 6. Test cross data of the N gene, separated in terms of the h-h grade of the +/+ parent; all N/+ parents were grade VII or VI. Selection of the grade of the +/+ parent has no effect on the segregation.

VII	VI	V	IV	III	II	I
478	76	17	9	13	3	1
90.1%	12.7%	2.8%	1.5%	2.2%	0.6%	6.2%

Table 7. Frequency distribution of halo-hair grades in progeny of tested N/N rams crossed to normal Romney ewes.

Grade of N-type parent	VII VI	V	IV III II I	x^2
VI	13	-	20	1.484
VI	23	2	35	2.482
VI	21	-	15	1.000
V	2	1	4	----
IV	14	1	16	.133
III	6	1	16	4.545
Total	79	5	106	3.984

	x^2	df	P
Deviation	3.984	1	.05-.2
Heterogeneity	6.198	4	.2-.3(Contingency)

Table 8. Segregations of genetically N/+ rams whose h-h grade was less than VII.

and N/+ , were crossed to large numbers of normal ewes. These crosses verified the distinction of homozygote and heterozygote, but they also showed that the dominance of the N gene was not complete; the range of expression in heterozygotes overlaps with that of normal. In table 7 are given the frequencies of halo-hair grades in the progeny of the cross of tested homozygotes to normal ewes i.e. of the expression of heterozygotes.

This wide range of expression of the N gene in heterozygotes was not expected. Therefore as many of the non-N-type progeny were test-crossed as was practical. These animals are N/+ by pedigree, and they should give a 1:1 ratio in the test-crosses. The actual results are given in table 8. Small but significant deviations occur from the expected 1:1 ratio. These results can be taken to show that the initial animals were N/+ genotypically, although the N gene had not expressed itself phenotypically. The deviations in the test-progeny of these rams are probably due to modifiers carried by the rams, which inhibit the expression of the N gene.

A further test of the existence of the N gene can be made by comparing the expression of N/+ animals in the segregations, with that of N/ animals derived from the cross of N/N rams with +/+ ewes. This test is shown in figure 1, in which the percentage frequency distributions are shown of the +/+ type(see table 2), of the N/+ type(see table 7), and of the progeny of the cross N/+ by +/+ . The agreement is very close.

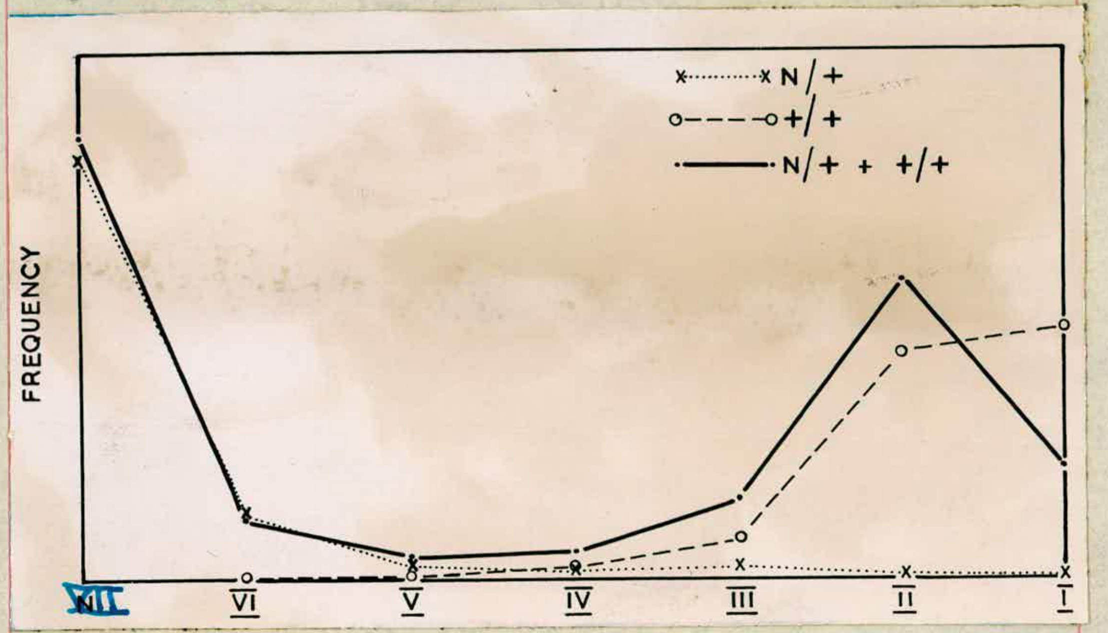


Figure 1. Frequency distributions of halo-hair grades in N/+ , +/+ , and in the segregation from the cross N/+ by +/+ . The latter distributions should equal the sum of the other two.

The above evidence taken as a whole is strong support of the single factor hypothesis. The major criterion, however, is the consistency with which the results have agreed with expectation through many generations of breeding.

Genetics of the N-type recessive stock.

As stated above the 'recessive' stock originated from an N-type ram which gave only non-N-type progeny when crossed to normal ewes. When crossed to his daughters he gave a 1:1 segregation. The cross of

Cross	VII VI	V	IV III II I	x^2
nr/nr x nr/	139	3	137	.014
nr/+ x nr/+	16	1	30	1.265

	x^2	P
Deviation	.57	.3-.5
Heterogeneity	.71	.3-.5
	1.28	

Table 9. Segregation of the nr gene, analysed by combined estimation, after grouping as in table 4.

Cross	Progeny						
	VII	VI	V	IV	III	II	I
nr/nr x nr/nr	48	3	-	-	-	-	-
nr/nr x +/+	5	2	1	2	30	94	41

Table 10. Expression of the nr gene in the nr/nr and +/nr types.

his sons and daughters gave a 1:3 ratio. This indicated that the original ram was homozygous for a gene (nr) which is recessive to its normal allele. Several generations of breeding have given results in agreement with this hypothesis and showed the nr gene to be independent of sex. The total results are given in table 9, grouped as in table 4 for the segregation of the N gene. The data have been tested by the combined estimation method which shows them to be in agreement with the recessive single factor hypothesis.

N-type animals of the recessive stock when bred together give only N-type progeny (see table 10). When N-type animals of this stock are outcrossed to normal ewes they should give only low grade progeny. However in such crosses a few of the normal ewes drop high grade lambs (see table 10). These aberrant high grade animals constitute the most difficult remaining problem of the genetics of the N-type stocks. They cannot be explained by some of the normal Romney ewes being +/nr as is possible, because some of these aberrant high grade animals when crossed to normal Romneys have given segregating progenies, which cannot be explained on this hypothesis.

Allelism of the N and nr genes.

It is necessary to determine whether the N and nr genes are allelic. This has been done by

Cross	VII VI	V	IV III II I	x^2
N/+ .nr/+ x +/+.nr/nr	20	-	7	.049 (p=.8-.9)
N/+ .nr/+ x N/+.nr/+	78	2	7	6.2 (p=.02-.01)

Table 11. Test of allelism of N and nr genes.

intercrossing and backcrossing N/+ . +/nr animals. These animals were bred by crossing N/N and N/+ ewes to nr/nr rams. All the progeny must, therefore, carry the nr gene, and the high grade progeny can be taken as carrying the N gene. The results of the crosses are given in table 11. The results are in reasonable agreement with the two genes being completely independent i.e. located on separate chromosomes.

Discussion.

Several purely genetic problems still remain to be solved. Selection for halo-hair grade has no effect on the N/+ segregation if made in the +/+ parent, but it has an effect if made in the N/+ parent. Either a sub-genotype exists which affects only the expression of the N gene having no effect on that of the $+^{N}$ gene, or a sub-genotype exists which can be selected more easily in N/+ than in +/+ . Distinguishing between these alternatives presents a difficult problem.

The N and nr genes are mimics, both conditioning the same complex phenotypic differences. This is not surprising since in mice several groups of mimic genes are known which condition very similar complex differences. However, there is at least a possibility that the nr gene originated from the N gene, and it is possible that the two genes are related cytologically. The junior author has investigated this possibility, but the small size of sheep chromosomes and the difficulties of mammalian cytology, did not allow any definite answere to be found. Pairing appeared normal but a small translocation would not have been noted. Such a small translocation, if it were viable when homozygous, would explain many of the complexities of N-type genetics: the non-allelism, the dominance relations, the mimic effects, and the aberrant animals which have occured. However, until evidence of such a translocation is found, it is not reasonable to base the work on such sophisticated postulates.

Summary.

N-type sheep arose in the New Zealand Romney Marsh breed. They differ from this breed in having horns and a 'carpet' type of fleece instead of being polled with a 'longwool' type of fleece.

The N-type/non-N-type difference is conditioned by the substitution of the N or nr genes fo r their normal alleles. The N gene is autosomal, partially dominant, and the expression in heterozygotes overlaps with that of the normal breed. The nr gene is autosomal, completely recessive, and non-allelic with the N gene.

Acknowledgements.

We are grateful to Dr.J.H.Sang for assistance in preparation of the manuscript.

3. Development of the follicle population.

(J.M.ROSS).

N-type sheep differ from non-N-type in a number of characters of the fleece which are inherited as a unit, being caused by one or other of two monogenic substitutions (Dry and Fraser, part 2). Gruneberg (1943) has emphasised that complex phenotypic effects of single genes can be explained as secondary to the initially unit action of the gene in development. It is , therefore, necessary to examine the follicles of the skin since the N and nr genes may produce their effects by an action on the follicles which is primary to the effects on the fleece.

Several workers (see Carter 1943) have shown that the adult follicle population is made up of different kinds which are arranged in a definite pattern and formed in a definite sequence, and this has been shown to be constant over a large number of breeds. The present study of follicle development in N-type sheep is based on the description of this sequence of follicle formation, and attention has been concentrated on the times of formation and frequencies of the different follicles, their relative positions within a follicle group, and the occurrence of accessory structures.

Material.

The foetuses used were from the cross of a tested N/N ram to a random sample of New Zealand

Romney Marsh ewes (+/+). These foetuses are therefor N/+ . 37 foetuses were available, covering the period from 40 days gestation to term. Attention was concentrated on the side region since Carter (1943) in his studies on the Merino breed limited his description to this position.

Development of the follicle population.

The sequence of development of a follicle from the differentiation of the anlagen to the production of a fibre follows the same course in N-type as in other breeds (Duerdon and Ritchie 1924, Carter 1943).

The development of the follicle population has been well described by several workers, particularly Carter (1943) in the Merino. This is best reviewed in reference to the completed follicle group. Such a group is shown in figure 2.

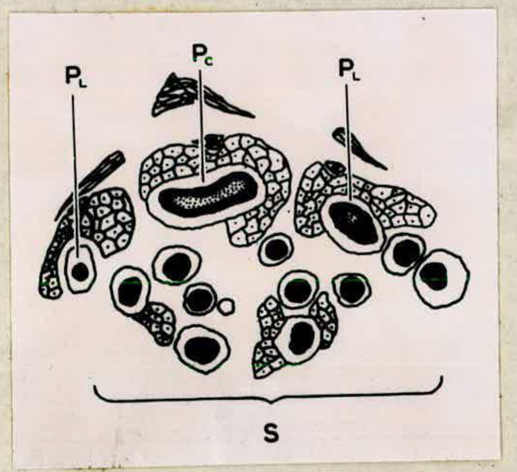


Figure 2. Camera lucida drawing of section across

a typical N-type follicle group. The trio of primary follicles are located across the top of the group. The fibres of the P_c and the right P_1 follicles are medullated.

The first follicles to appear are the primary central follicles (Pc) around which the completed groups are ultimately organised. After a lapse of about a week two further primary follicles, the primary laterals (P_1), are formed close to and on opposite sides of the central follicles. After a further lapse of two to three weeks, the formation of secondary follicles commences . These are formed to one side of the trio of primary follicles, and their formation continues until several weeks after birth.

Comparison of N-type with other breeds.

The first point of comparison between N-type and other breeds is the age at which the first follicles appear. Carter (1943) found the first appearence of follicle anlagen on the poll and face regions as early as 35-40 days, and that follicles were established all over the body by 56-60 days. Galpin (1935) found in the Romney that follicles appeared first on the poll and neck at 49 days, and all over the body at 59 days. N-type does not differ from either the Romney or the Merino since in N-type foetuses follicles were found on the poll and neck at 49 days, and all over the body at 59 days.

	Number of follicles										Mean ratio
Primary central	24	21	26	18	21	21	16	17	14	18	1.000
Primary lateral	43	48	46	39	33	37	32	32	22	30	1.897

Table 12. Ratio of primary central (P_c) / primary lateral (P_l) follicles in skin of N/+ foetuses.

A second point on which N-type could differ from other breeds is in the formation of the trio of primary follicles. Carter(1943) noted that solitary and couplet groups were chracterised by larger fibres than trio groups. This suggests that the N and nr genes might cause their effects on the fleece by an effect on the formation of the trio group i.e. N-type might contain a high frequency of solitary and couplet groups. The ratio of the $P_c:P_l$ follicles found from ten post-trio stages is 1.000:1.897 (table 12) which differs only slightly from the ratio of 1:2 which is expected if all the groups of primary follicles are trios. The trio group is the fundamental group in N-type, as in non-N-type.

The primary and secondary follicles have been noted in all previous studies to differ in the occurrence of accesory structures. The P follicles possess an arrector pili muscle, a sudoriferous gland, and an sebaceous gland. The S follicles possess only sebaceous glands and may lack even these. The same differences have been noted in N-type.

A significant difference between N-type and the Merino occurs in the diameters of the Primary and Secondary fibres. In N-type(figure 2) the diameter of the primary fibres is much greater than that ofthe seconddry fibres, whereas Carter (1943) shows for the

Genotype		Primary	Secondary	P/S
+/+		23	88	1.0/3.83
		15	58	3.87
		42	118	2.81
		32	61	1.91
		42	79	1.88
		47	90	1.91
		49	86	1.76
		34	89	2.62
		38	78	2.05
	Total	322	747	1.0/2.31 ✓
N/+		41	139	1.0/3.39
		54	96	1.78
		51	134	2.63
		40	95	2.38
		75	195	2.60
		59	110	1.86
		47	123	2.62
		46	120	2.61
		48	85	1.77
		88	170	1.93
		35	129	3.69
	Total	584	1396	1.0/2.39 ✓
Overall total		906	2143	1.0/2.37 ✓

Table 13. Frequencies of P and S follicles in the skin of +/+ and N/N lambs at birth.

Merino that primary and secondary fibres have the same small diameter. The same difference occurs between the two types of fleece: the N-type fleece contains very thick and very thin fibres, whereas the Merino fleece contains only thin fibres. This occurrence of a characteristic feature of the N-type fleece at such an early embryonic age shows that the N and nr genes have a detectable effect as soon as the first fibres are formed, and therefore that the action of these genes probably affects the follicle anlagen.

A third point on which N-type could differ from other breeds is in the ratio of P:S follicles. A number of counts of P:S follicles were made from skin snippets taken at the standard back sampling region (Galpin 1935) from non-N-type (+/+) and N-type Romneys within a day or two of birth. The complete counts are given in table 13. The ratio of P:S follicles does not differ between N-type and non-N-type , being 1:2.31 in +/+ , and 1:2.39 in N/+ . This of course does not esclude the occurrence of differences in the formation of follicles after birth. However, the N-type to non-N-type differences can be seen quite clearly at birth and, therefore, the effects of the N and nr genes on the fleece cannot be explained only by a change in the frequency of S follicles formed after birth.

Relationship of type of fibre to type of follicle.

In N-type sheep the fibres formed by the primary follicles differ markedly in size from those formed by the secondary follicles. This suggests that in N-type it might be possible to classify fibres in terms of the follicles which formed them. A classification of birthcoat fibres has been formulated by Dry (1934). This classification may be related to the differences between the types of follicles, i.e. certain types of follicles may form only certain types of fibres. The following discussion examines this possibility.

The classification of birthcoat fibres is based on the shape of the tip curl and the occurrence of medulla. The different types are halo-hairs, super-sickles and sickles which all have a sickle shaped tip curl, and hairy-curly-tips and plain-curly-tips which have a regularly curled tip, and histerotrichs which have an indefinitely shaped tip. The latter type is initiated after birth and, therefore, does not concern us here. Some fibres have medullation occuring in their tips. These are the halo-hairs, super-sickles, sickles, and hairy-curly-tips. Descriptions of fibres are given in great detail by Dry(1934) and Goot(1940) and in section 8 below.

In normal Romney lambs the birthcoat contains only super-sickles, sickles and plain-curly-tips. In N-type lambs the super-sickles and sickles have been replaced by halo-hairs, and some of the plain-curly-tips by hairy-curly-tips. The analysis of these differences would be facilitated by the identification the type of follicle formed by each type of follicle.

Rudall (personal communication) found from dissection of birthcoat skin samples that sebaceous glands, errector pili muscles and sudoriferous glands were associated with follicles which formed halo-hairs super-sickles and sickles, and checked-curly-tips. This latter type differ from ordinary plain-curly-tips in having a larger number of crimps in the part formed before birth. The majority of plain-curly-tips were found to be formed by follicles which lacked accessory structures. It can be concluded from his results that the halo-hairs, super-sickles and sickles are invariably formed by primary follicles whereas the plain-curly-tips are usually formed by secondary follicles. He used only non-N-type material in which hairy-curly-tips are rare. Therefore his results give no indication of the type of follicle which forms these fibres.

These results of Rudall's are supported by comparisons of the tips of fibres from foetal material with those of birthcoat fibres. At about 115 days the primary follicles have formed fibres which have pierced the skin; the secondary follicles have just commenced forming their fibres at this stage. Therefore if the tips of fibres from foetuses of about 115 days are compared with those of birthcoat fibres, it should be possible to determine the types of fibres formed by primary follicles. Samples of skin were available from 113 and 119 day foetuses, and examinations were made in these of fibres formed by the primary follicles i.e. of fibres which had pierced the skin. Most of them were medullated i.e. they were of the halo-hair, super-sickle or hairy-curly-tip types. A few were non-medullated and had very small curled tips like those of plain curly tips. Therefore it seems that primary follicles are capable of forming all of the birthcoat fibre types except histerotrichs. This agrees with the deduction from Rudall's results.

As an approximation it is postulated 1) that primary follicles can form fibres of all types except histerotrichs, 2) that secondary follicles which initiate their fibres before birth form fibres of the plain-curly-tip types, 3) that secondary follicles which initiate their fibres after birth form fibres of the histerotrich type. Further Fraser(unpublished) has suggested that the curly-tips formed by primary follicles are either of the hairy-curly-tip or checked curly-tip types. The next paper of this series will give results which extend this postulated relation of type of follicle to type of fibre, and will demonstrate the use of this relationship in the analysis of the effects of the N and nr genes on the birthcoat.

Discussion.

The sequence of development of the follicle population in N-type sheep has not been found to differ in any obvious aspects from that given for the non-N-type Romney by Galpin(1935) or the Merino(Carter 1943). The N-type fleece is similar to that of 'carpet wool' breeds, such as the Scottish Mountain Blackface breeds, and it differs qualitatively from the demi-lustre 'longwool' type of fleece of the Romney, and the'superfine' fleece of the Merino. Since no developmental differences were found between these representatives of the three main types of fleece, we conclude that the timing of development of the follicle population is not a major cause of variation of fleece type and that an explanation must be sought from other aspects of fibre and follicle development.

Acknowledgements.

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4. Development of the fibre population (A.S.Fraser, J.M.Ross and G.M.Wright)

The N-type syndrome, which includes the formation of horns, consists primarily of differences in the character of the fleece. The number of halo-hairs in the birthcoat is increased; complex changes occur in the frequencies of the different types of fibres which comprise the birthcoat; patches of brown fibres are frequent in the birthcoats; the hairiness (medullation) and length of the mature fleece are very markedly increased as is the shedding of fibres as kemps. The non-N-type fleece is even and separates into well defined staples; that of N-type is very uneven and made up of untidy locks, with no definition into staples. Finally the size of crimps which is very even in non-N-type, is very uneven in N-type.

The first possible cause of these effects is that the genes affect the development of the follicle population. Since this population develops normally (Ross, section 3 above), the N-type effect must be the result of differences in fibre development. In fact, the effects on fibre development are extensive and complicated and it is therefore necessary to attempt to organise the data under some relatively system of classification. Ross' work(section 3 above) suggests a basis for such a classification, showing that the various types of follicles which comprise the follicle population form different types of fibres. Therefore, an attempt was made to classify fibres interms of the follicles which formed them. Such a classification must bring together 1) Dry's (1934) classification of fibre types, 2) fibre growth rates, 3) incidence of shedding, 4) the occurrence of brown pigment, and should provide a basis for separating the birthcoat into groups of fibres each formed by a different type of follicle, and hence to a comparison of the degree to which fibres formed by different follicles are affected by the N and nr genes.

Classification of follicles into types.

The development of the follicle population up to birth has been described by Ross (section 3) and it is necessary to emphasise only that from birth two types of follicles can be distinguished histologically: primaries(P) and secondaries(S). Two types of primaries, centrals(P_c) and laterals(P_l), can be distinguished up to about five weeks before birth. The follicle population at birth consists, therefore, of three types of follicles (P_c, P_l and S).

The frequencies of P and S follicles have been shown by Ross(section 3 above) to be unaffected by the N gene; she determined their frequencies in several N/+ and +/+ animals and found no differences; the ratio of P:S being 1:2.39 in the former and 1:2.31 in the latter (table 13). Her estimate of the P:S ratio was made from newborn lambs, and this age, birth, has been taken as the standard age for the comparison of fibre and follicle frequencies. The overall ratio 1.0:2.37 is taken as the ratio common to both N-type and non-N-type lambs.

Ross(section3) also found from examinations of several N/+ foetuses that the ratio of $P_c:P_1$ follicles was 1.0:1.897 i.e. there is no marked deficiency of primary lateral follicles in N-type (table 12). This ratio is here taken as the standard for the Romney Marsh breed, and it allows the complete ratio to be given for the follicle population at birth. This is P_c(1.0) : P_1 (1.9) : S (6.87), or in percentages, 10.2% (P_c), 19.4% (P_1), X 70.4% (S).

The use of these data for comparison with fibre type frequencies entails a possible error in that follicles may have been counted which have not yet formed a fibre long enough to be included in a fibre sample. No estimate of the error can be made but the follicle counts were made specifically of follicles which contained a definite fibre, and this will minimise any such error.

Classification of birthcoat fibres.

Dry (1934) has given the basic description and classification of birthcoat fibres, using as criteria the shape of the tip curl, and the occurrence of medulla in the tips. His classification can be reduced to seven types: four which have seickle shaped tips, two which have regularly curled tips and one which has an indefinitely shaped tip.

The type which has an indefinitely shaped tip is called the histerotrich (Hi). These start growing just before or after birth and constitute numerically the main type of fibre. Since only the secondary follicles commence the formation of their fibres just before or after birth, all Hi fibres are formed only by the late secondary follicles. Not very much attention has been given to the Hi group, most of the descriptions having been restricted to the other types of fibres which all appear before birth. It is on these types that the present analysis is based and they may be formed by P_c, P_1, or early S follicles.

The two types of fibres with regularly curled tips are separated on the basis of the occurrence of medulla in the part of the fibre formed before birth. Both types are called curly-tips, the one which lacks medulla is called the plain-curly-tip(PCT) the one with medulla is called the hairy-curly-tip(HCT). It must be emphasised that in Dry's classification only medullation of the region of the fibre formed before birth is considered; later parts are not considered in the primary system at all, although a secondary system has been formulated in which each of the primary types are divided into further classes based on medullation of the parts formed post-natally. This

Type of fibre	Shape of tip	Medullation	Symbol
Halo-hair	Sickle	Complete	H-H
Super-sickle A'	"	Broken at birth point	SSA'
Super-sickle B	"	Broken at neck of tip curl	SSB
Sickle-tip	"	Only in tip curl	Sk
Hairy-curly-tip	Regular curl	Present	HCT
Plain-curly-tip	"	Absent	PCT
Histerotrich	Indefinite	Absent	Hi

Table 14. Classification of fibres into types on the basis of the shape of their tip curls, and the occurrence of medullation in the region formed before birth.

secondary classification is not considered here.

The four types of fibres with sickle shaped tips curls are also separated on the occurrence of medulla, but the seperation is more subtle. Those completely medullated from tip to the part of the fibre formed after birth are called halo-hairs(HH). In the next type a break in the medullation occurs at the part of the fibre formed at the time of birth (the birth point). This type is called the super-sickle A'(SSA'). The next type, called the super-sickle B type (SSB), has a break in the medulla at the neck of the tip curl. Finally, the sickle type(Sk) is medullated only in the tip curl or even not at all.

Summarising, this classification is made first on shape into three groups: sickle, curly and indefinite. No subdivision is made of the indefinite group. The curly-tip group are separated into two types on the presence or absence of medulla and the sickle group are sub-divided into four types essentially on the presence or absence of breaks in the medullation. The classification is given in tabular form in table 14.

Relation of type of fibre to type of follicle.

The subsequent analysis is easier to follow if a summary is given of the results obtained. These show that the various follicles differ in the types of fibres which they can form, but that no differences occur between N-type and non-N-type if these differences are considered solely in terms of the shape of the tip curl. Primary central follicles can form fibres with a sickle shaped tip curl. These fibres may be of the HH, SSA', SSB or Sk types, depending on genotype. Primary lateral follicles can form fibres with a regularly curled tip which may be NCT or PCT again depending on genotype. Early and late secondaries form regularly curled or indefinitely tipped fibres respectively and no obvious differences are apparent between genotypes. This relationship of type of follicle to shape of fibre is illustrated in figure 3 for a typical follicle group.

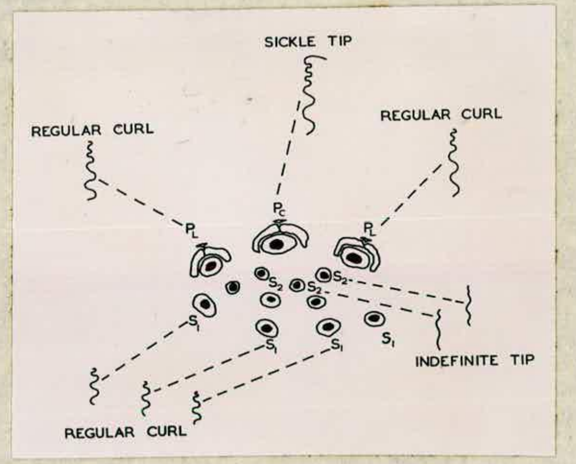

Figure 3. Relationship of the shape of fibres to the different types of follicles which comprise a follicle group.

The relationship of fibre to follicle was found first from a comparison of the frequencies of follicles with those of the different types of fibres. These comparisons are given below.

Genotype	n	HH	SSA'	SSB	Sk	All sickle types	HCT	PCT	Hi	PCT+Hi
N/N	33	8.99	1.10	0.15	0.00	10.2	19.6	53.8	16.4	70.2
N/+	65	7.05	1.40	1.12	0.60	10.2	13.7	59.7	16.4	76.1
nr/nr	17	9.00	0.71	1.61	0.29	11.6	23.8	48.2	16.4	64.6
Total	115	7.89	1.21	0.91	0.36	(10.4)	(16.9)	56.3	16.4	(72.7)
Expected values from follicle frequency counts						(10.2)	(19.4)			(70.4)

Table 16. Fibre type frequency distributions in percentages, corrected to the values which would have occurred at birth.

Type.	Percentage of histerotrichs								X^2
N/N	18.1	14.7	12.6	16.8	12.8	15.7	14.5	15.0	16.4
N/+	24.4	16.2	18.8	15.9	16.9	20.3		18.7	

Table 15. Percentage frequency of histerotrichs in samples taken at birth.

Frequencies of different types of birthcoat fibres.

Ross (1945) during a study of kemp succession in N-type sheep, collected a large amount of data on the frequencies of different types of birthcoat fibres. These data were obtained from N-type animals of the N/N, N/+ , and nr/nr types, whose halo-hair abundance was grade VI or VII. The samples used were taken from the standard back sampling region (Galpin 1935), at various ages during the hogget year. Since the age of sampling varied, the frequency distribution of fibre types must be corrected for variation in age. This variation is only of the histerotrich frequency since all other types of fibres commence their growth before birth. Therefore if the frequency of histerotrichs present at birth is known, all the data can be corrected for variation in histerotrich frequency to the standard age of birth. This data will, after this correction, be comparable with that of follicle type frequencies. The frequencies of histerotrichs present in samples cut from the skins of N/N and N/+ lambs which died at birth, are given in table 15.

The overall average frequency of histerotrichs is 16.4% at birth. Using this as a correction factor, Ross' data have been transformed to the frequencies at birth. The average fibre type frequency distributions for each genotype, and overall genotypes are given in table 16.

The frequencies of the different types of fibres present at birth can be compared with the frequencies of the different types of follicles present at this age. The most obvious point is that the sum frequency of sickle fibres (HH SSA' SSB Sk) is remarkably constant between the different classes of material, and almost identical with the frequency of P_c follicles. Similarly the frequency of HCT fibres is very close to that of P_1 follicles, suggesting that this type of fibre is formed by the P_1 follicles. This relationship of fibre to type of follicle is an extension of Ross' (1950) suggestion that P follicles can form both sickle and curly-tip fibres, whereas S follicles can form curly-tip and histerotrich fibres.

The close agreement between actual frequencies of fibres and those expected from follicle type frequencies, suggests that any errors in the latter are small. A possible source of error has been mentioned above, namely, the counting of S follicles as forming a fibre which are not yet developed enough to do so. This error would appear to be unimportant.

A slight discrepancy occurs in the N/+ type between the actual frequency of HCT fibres, and that expected if all the P_1 follicles form HCT fibres. The expected frequency is 19.4%, in the N/+ type the actual frequency is 13.7%. This can be explained if the P_1 follicles can form both hairy- and plain-curly tips; the effect of the N and nr genes being to cause P_1 follicles to progressively change from forming plain- to forming hairy-curly-tips; this change being proportional to the dosage of these genes, and presumably not complete in the N/ type. P_1 follicles are certainly capable of forming plain-curly-tips because in non-N-type Romneys, hairy-curly-tips are very rare, and therefore the P_1 follicles must be forming plain-curly-tips.

A further check of this frequency equation can be made from some data of Goot (1940) who determined the fibre type frequencies of non-N-type Romneys. In these all of the sickle group fibres are either super-sickles or sickles, the majority being sickles, and they differ in this respect very markedly from N-type in which the sickle group are predominantly halo-hairs. Applying the same correction for variation of histerotrich frequency with age to his data, we find that the frequency of sickle group fibres present at birth is 13.0%, which is in reasonable agreement with the expected value of 10.8%.

An equation of frequencies cannot be taken as proof- so other methods were used to relate types of fibres to types of follicles. These depend on the primary follicles forming their fibres faster than secondary follicles, in N-type.

Fibre length frequencies.

Goot(1940) noted in a sample from an N-type lamb that the frequency distribution of fibre lengths was distinctly bimodal. He found that this bimodality was related to the fibre type distribution since sickle group and HCT fibres occurred only in the longest mode. If, as has been indicated above, sickle group fibres and HCT fibres are formed only by P follicles, then it follows from Goot's observations, that the longest group of fibres are also formed by P follicles, and the shortest group by S follicles. This hypothesis is examined below.

The fibre length distributions of N-type birthcoats are, as found by Goot(1940), bimodal but only during the first few weeks after birth. At a later stage a third mode becomes apparent. This is not of interest in the present analysis since it does not appear until after birth and the fibres of it are therefore formed by late secondary follicles. The three length groups around these modes are called the A,B and C groups respectively, where the A group is the longest and the C group is the shortest. The C group fibres will be discussed in the last section of this thesis. The present problem is whether differences occur between the A and B groups in the follicles which form them.

										Length gr	
0.0/0.5	0.5/1.0	1.0/1.5	1.5/2.0	2.0/2.5	2.5/3.0	3.0/3.5	3.5/4.0	4.0/4.5	4.5/5.0	A	B
279	243	57	203	97	23	5	-	-	-	349	558
26	19	14	14	-	6	20	6	1	2	35	73
70	41	21	10	48	7	5	3	-	-	66	139
59	53	29	41	15	9	-	-	-	-	76	130
36	69	36	18	76	9	10	2	-	-	104	154
67	65	10	27	51	17	11	1	-	-	94	145

Actual ratio 1.00: 1.66

Ratio expected from P/S follicle counts1.00: 2.37

Table 17. Fibre length fistributions of N/N lambs taken from birth samples. Distributions are separated into the A and B length groups as detailed in the text, and the totals in each group are given in the columns on the right. Their ratio is compared with that expected from the ratio of P/S follicles.

If Scot's results were generally correct over all N-type material, it follows that the sum frequency of A group fibres should equal that of the P follicles, and that the A group fibres should only be of the sickle group and HOT types since, as shown above, the fibre type frequencies indicate that these types of fibres are formed only by primary follicles.

A number of measurements were made of the fibre length distributions in samples from newborn lambs of the N/N type. These are given in table 17.

The separation into A and B groups, although qualitatively obvious, introduces an error in the separation of the overlap region. No rigorous statistical method is available for the solution of this problem, therefore this region was divided proportionately between the two groups. The actual A/B ratio and that expected from follicle type ratios (P/S), are shown in table 17. The discrepancy may be due to 1) the loss of very small fibres from the sample, 2) the inclusion of S follicles in the P/S ratio which have not yet formed fibres long enough to be included in a fibre sample, 3) errors in the division of the overlap region between the two length groups. Since the first two sources of error are cumulative, and in the direction of the discrepancy, it can be assumed that A group fibres are formed only by P follicles. The second error has been mentioned previously in the equation of fibre type and follicle type frequencies. The accuracy of that equation suggests that this error is negligible, while the present case indicated that it may be large. No answer is available to this problem.

The relationship of A group fibres to the P follicles can be tested by determining the complete fibre length and fibre type frequency distributions. These should show that all the sickle group and HCT fibres are in the A group length range. Several such analyses were made. They are in complete agreement; all the A group fibres are of the sickle group and HCT types, all the B group fibres are of the PCT and Hi types. One such compound frequency distribution is shown in figure 4.

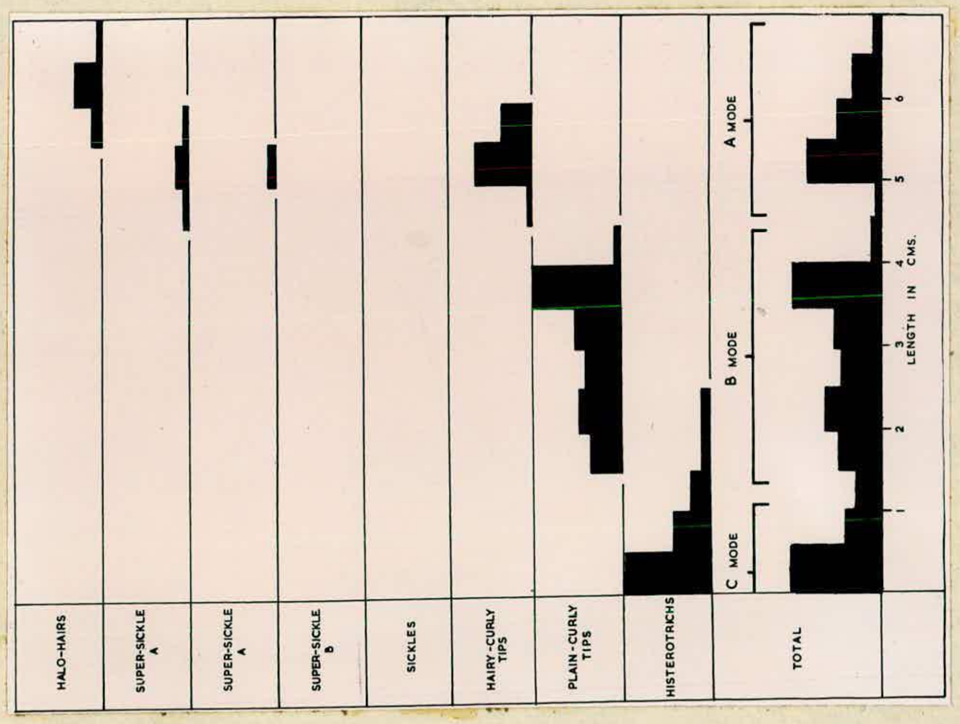

Figure 4. Compound fibre length-fibre type frequency distribution of N/N sample.

Growth rates.

The rate of increase in length of A group fibres can be found from the regression of their mean length on age. This regression when extrapolated to intersect with the base line, will give an estimate of the age at which the formation of the A group fibres commence, which should be of the order of 100-110 days foetal age if these fibres come from the primary follicles.

The fibre length distributions of samples from N/N lambs of varying ages were determined, and then plotted against age, as in figure 5. The average lengths of A and B group fibres were found from consideration of the mid-point of the ranges, and the medians, as shown in figure 5. The complete data are too unwieldy to be given in detail, so only the estimates of the average lengths are given in figure 6.

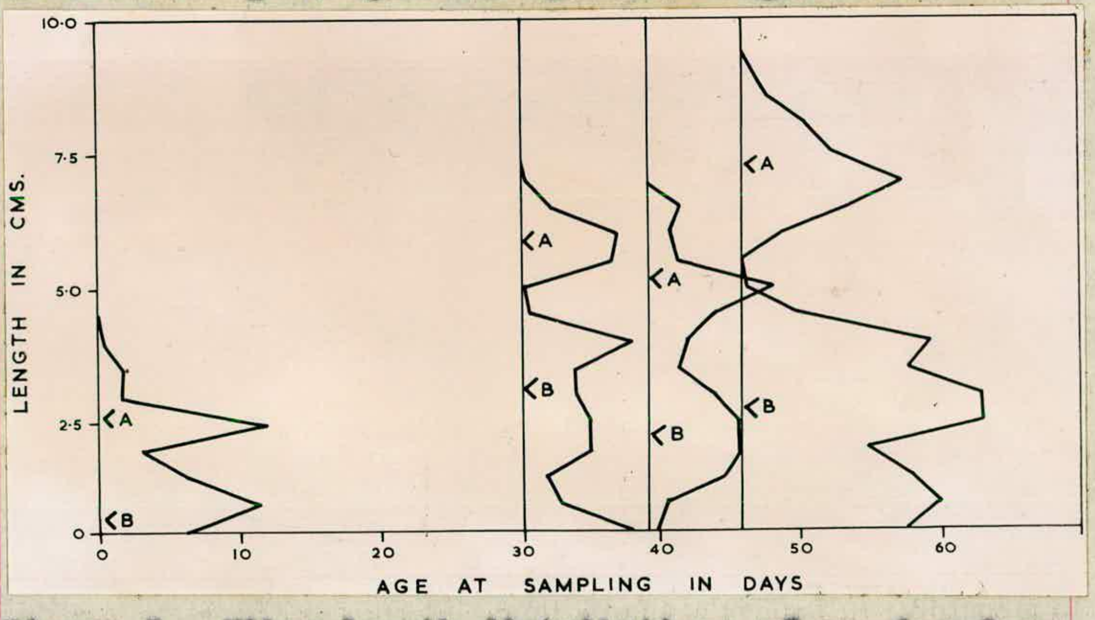

Figure 5. Fibre length distributions of samples from N/N lambs illustrating the bimodality and the average lengths of the A and B length groups.

Regression lines were fitted to the averages of the A and B groups; these are shown in figure 6. The use of linear regressions assumes that the rate of increase in length is constant over the period studied (0-60 days after birth). As a first approximation this is not likely to lead to any serious error. It will be noted that a number of means are given at birth. These are not clearly shown in the figure.

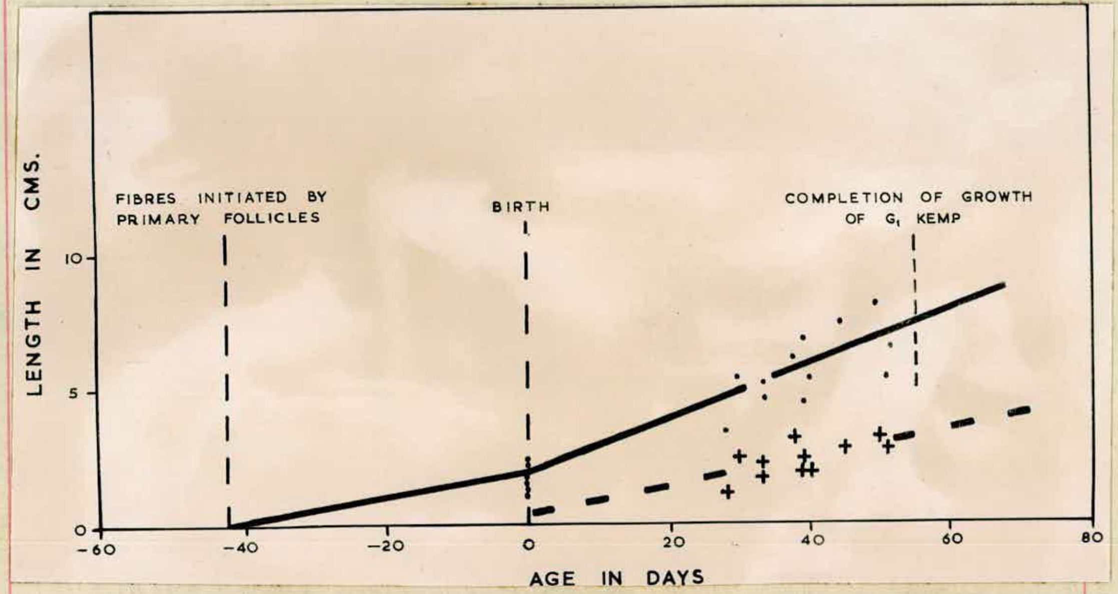

Figure 6. The rate of increase in length of A and B mode fibres; the former shown by the solid regression line, the latter by the broken regression line. The A mode regression has been extrapolated after correction (see text) to intersect with the base line, giving an estimate of the age at which the A mode fibres are initiated. The length of G_1 kemp has been interpolated into the A mode regression line to give an estimate of the age at which G_1 kemp complete their growth.

The extrapolation of the A group regression line to intersect with the base line cannot be made without first correcting for differences in the rate of growth of fibres before and after birth. Such a correction can be found from a comparison of the sizes of crimps in the pre- and post-natal regions of fibres since Barker, Norris et al. (Barker 1932) have shown that crimp sizes can be used as estimates of variations in growth rate along a fibre. The ratio of pre- to post-natal crimp size is 1.0:2.3. In figure 6 the extrapolation of the A group regression line has been made on the basis of this ratio of pre- to post- natal growth rates. The age at which this extrapolation intersects with the base line is -40 days (approximately 100 days foetal age). Ross (1946) states that primary fibres are initiated at about 95-105 days foetal age which agrees well with the age of initiation of A group fibres found from extrapolation. Although this extrapolation cannot by itself be taken to have any general validity, taking these various length analyses together it is reasonable to postulate that primary follicles form the A group fibres, secondary follicles form the B group fibres.

Kemp succession.

Dry (1934.1940) has shown that the shedding of fibres as kemps is related to the type of fibre. In sheep with a birthcoat containing a high frequency of halo-hairs and hairy-curly-tips, many fibres are shed as kemp, commencing about two months after birth with the shedding of birthcoat fibres which are called C_1 kemp. In sheep in which the birthcoat contained few or no halo-hairs, shedding as kemps is rare. Further

Type.	H-H	SSA'	SSB	Sk	HCT	FCT
N/N	98.1	92.7	50.0	-	18.3	0.1
N/+	99.7	89.5	80.8	42.8	13.7	0.4
nr/nr	99.9	98.1	85.4	-	9.5	0.0

Table 18. Percentage frequency with which the different types of fibres are shed as G_1 kemp.

he has shown that G_1 kemps are rarely of the Sk, plain-curly-tips or Hi types, being predominantly of the HH, super-sickle, or HCT types. This is demonstrated by the data shown in table 18.

The relationship of shedding to fibre type shows that this is restricted to the types of fibres formed by primary follicles. This can be checked by interpolating the average length of G_1 kemp in the A group regression line. If shedding occurs mainly or only from primary follicles then this interpolation should give an estimate of the time of shedding which agrees with that found from the examination of lambs. The latter is stated by Dry (unpublished) to occur at about 9-11 weeks. The value found from interpolation is about 8 weeks. The discrepancy can be explained by the latter being an estimate of the time of cessation of growth, whereas the former is an estimate of the time of shedding, which would be expected to occur a week or two later. Interpolation in the B group regression line would give an estimate of 12-14 weeks which is obviously incorrect. The interpolation can be taken to agree with the shedding of fibres as kemps being restricted to the A group fibres and therefore to the primary follicles.

Brown tips to fibres.

In N-type lambs patches of the birthcoat have brown tips. This dissapears a month or two after birth due to the shedding of the brown fibres or to the breakage of their tips. A number of samples have been examined from these brown patches, and the brown pigment has been found to occur only in the medullated parts of the fibres. It also occurs only in the regions of the fibres which were formed before birth. Since brown occurs only in the medullated parts of fibres formed before birth, and since only primary fibres are of the types which are medullated in their prenatally formed regions, it follows that the brown pigment occurs only in the fibres formed by primary follicles.

Discussion.

The different types of follicles differ in four characters of the fibres which they form. These characters are the birthcoat type, the growth rate, the shedding as kemps and the occurrence of brown pigment. The birthcoat type is based on two separate characters: the shape of the tip curl and the occurrence of medulla in the portion of the fibre formed before birth. The simplest procedure is to consider each of these characters separately.

The tip curl may be sickle-shaped, regularly curled or indefinitely shaped. Fibres of all three types occur in the birthcoats of both N-type and non-N-type, and in both are formed by the same type of follicle. Sickle shaped fibres are formed by P_c follicles, regularly curled fibres are formed by P_1 follicles and early S follicles and indefinitely shaped fibres are formed by late S follicles. It can be concluded that the substitution of the N and nr genes affects the size of the tips curls but not thêâr shape.

The size of crimps differs between N-type and non-N-type; this difference being very marked in the tip curls of the birthcoat fibres. The sickle shaped fibres in N-type are predominantly halo-hairs which have a very large tip curl, in non-N-type they are sickle-tips which have a very small tip curl. Similarly, in N-type the P_1 follicles form hairy-curly tips which have a very large tip curl, in non-N-type they form plain-curly-tips which have a very small tip curl. The secondary follicles form fibres with different sizes of crimps in N-type and non-N-type, but these differences are small compared to those which occur in the primary fibres. The substitution of the N and nr genes causes the primary follicles to form fibres with much larger crimps than normal, but it does not cause any correspondingly obvious changes in the sizes of the crimps of secondary fibres. Since Barker, Norris et al (see Barker 1932) have shown that variations in crimp size are due to the variations of fibre growth rates, these differences in sizes of crimps can be taken as secondary to the differences of growth rates which have been shown to be caused by the N and nr genes.

The occurrence of medullation similarly differs between follicles. The substitution of the N and nr genes cause the primary follicles to form more medullated types of fibres, but does not cause any corresponding change in the secondary fibres. This applies similarly for the shedding as kemps and the occurrence of brown tips. These characters occur only in the primary fibres of N-type birthcoats, but not in any of the fibres of non-N-type birthcoats.

In N-type the fibre length frequency distribution is trimodal, and each of the modes is made up of fibres formed by a different type of follicle: The A group by primary follicles, the B group by early secondary follicles and the C group by late secondary follicles. In non-N-type the length distribution is is bimodal(this will be demonstrated in the last section below), and the longest group is made up of fibres formed by both primary and early secondary follicles; it is, therefore, a composite of the A and B groups of the N-type length distribution. In N-type the primary (A group) fibres grow faster than the early secondary (B group) fibres; this results in a separation of the A-B group of the non-N-type length distribution into the A and B groups of the N-type distribtuion. The substitution of the N and nr genes causes the primary fibres to form their fibres faster than the early secondaries; data are not available on the effects of these genes on the rates of growth of early and late secondary fibres; observation suggests that any differences are small. The further analysis of the effects of these genes on the fleece must consider differences between fibres formed by the secondary follicles. This analysis which will be presented in the last section below, is facilitated by the above finding that the tip of a fibre can be used to determine the type of follicle which formed it.

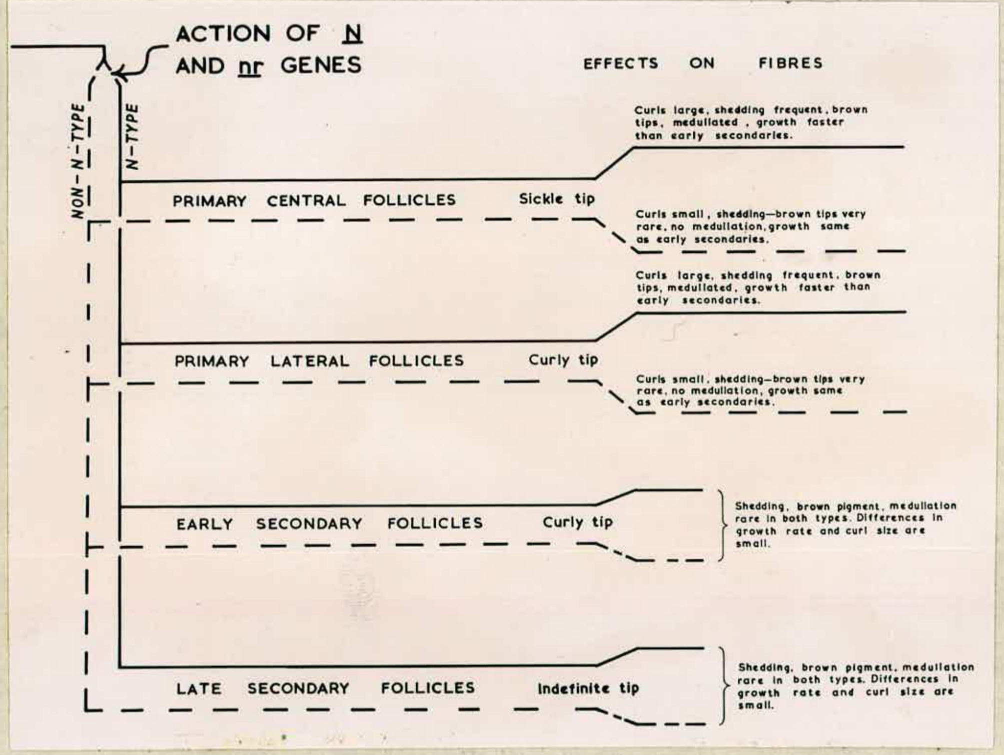

Figure 7. The restriction of the effects of the N and nr genes to fibres formed by the P_c and P_l follicles. The gene action is taken to occur similarly in the developmental tracks of each type of follicle.

The N-type fleece differs from non-N-type in length, medullation, size of crimps, occurrence of shedding, and brown pigment. These effects of the N and nr genes have been shown to be restricted to the fibres formed by primary follicles.

Acknowledgements.

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5. Kemp succession. (A.S.Fraser, J.M.Ross, G.M.Wright)

In normal Romney Marsh sheep almost all of the follicles form their fibres without periodic shedding. A few follicles shed their fibres 2-3 months after birth, but these rarely continue shedding their fibres in the mature fleece. In N-type strains of this breed the situation is radically different. A proportion of the primary follicles shed their fibres periodically throughout the life term, and consequently the fleece contains a high proportion of shed fibres.

The periodic shedding of fibres is rare in the 'fine-wool' breeds, but it is a constant feature of the 'carpet-wool' breeds, which the N-type strains resemble closely. The shed fibres of 'carpet-wool' breeds are called 'kemps'. Miller (1937) has given a very complete description of kemps of the Scottish Mountain breed and since shed fibres which occur in N-type fleeces follow this description closely, they cam also be called 'kemps'.

Kemp succession.

Dry (1934) has shown, by use of protected staples, that it is possible to study the succession of kemps formed through a period. It is necessary to review his work so that his terminology may be introduced. His method of protecting and tying staples retains the kemps in the region of the staple formed at the time of their shedding. This shows that kemps occur together at different heights of the staple i.e. successive generations of kemps are shed synchronously within a region. The restriction of shedding to definite periods allows successive generations of kemps to be distinguished readily and Dry et al. (Dry 1940) have made extensive studies of the frequencies with which successive generations of kemps occur.

The first kemp generation (the G_1 or birthcoat kemp) are shed at about 2-3 months after birth. Subsequent generations are shed at about a 3-4 month interval.

The G_1 kemps are, apart from having been shed, normal birthcoat fibres, and, therefore, can be classified into birthcoat types. Dry (1934) has shown that the occurrence of shedding differs between these, some types being shed almost invariably, others rarely being shed. This relationship of shedding to birthcoat types demonstrates that the potential for shedding is high in primary follicles and low in secondary follicles(previous section).

The separation of a typical sample which has been protected from weathering, and tied to prevent the shifting of kemps, is illustrated in figure 8. This figure also illustrates the relatioship of shedding to type of follicle. The sample is from an N-type sample, hence the large number of shed fibres.

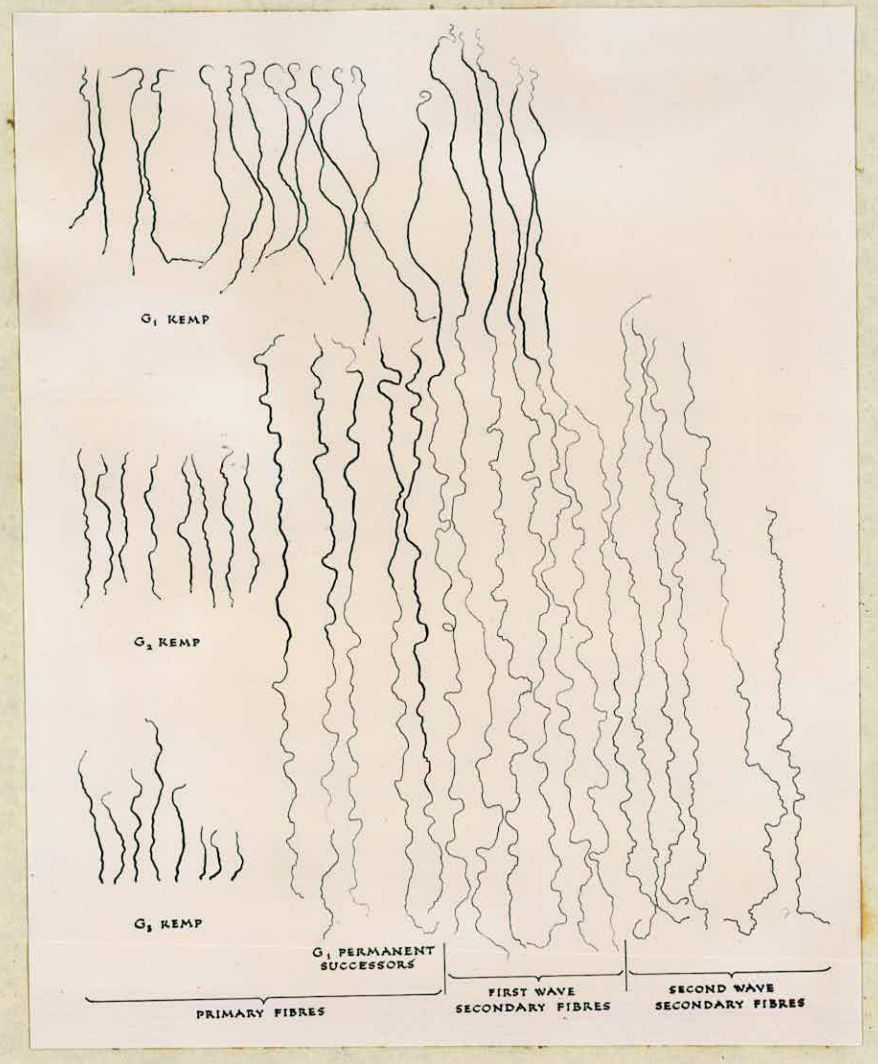

Figure 8. A sample of fibres from a protected staple in which the various generations of kemp have been retained at their region of shedding. The G_3 kemp had not completed their growth at the time of sampling.

In this paper will be given data of the frequencies of G_1, G_2 and G_3 kemps in the fleeces of various of the N-type strains. These will be analysed to show 1) the differences between the N-type strains, 2) the differences between the central and lateral types of primary follicles, and 3) the differences between fibre types.

Material and methods.

Fibre type and kemp frequencies have been determined in three of the availanle genotypes (N/N, N/+ , and nr/nr). Only animals with a halo-hair abundance of VI or VII were used, selected without reference to genotype. The sampling of the N/+ type is, therefore, neither representative nor random, since as shown in the introductory paper to this series, approximately 10% of the N/+ type have a halo-hair grade of less than VI. In some of this material the classification of dominants as N/N or N/+ could not be based on pedigree e.g. the progeny of the cross N/N by N/+ . In such cases the classification was based on the descriptions of the birthcoat which, due to the incomplete dominance of the N gene, allows an almost complete phenotypic identification (this is discussed at length in sections 6 and 8 below). The results for pedigree and classified material were analysed separately so that there were five groups: N/N pedigree, N/N classified, N/+ pedigree, N/+ classified, nr/nr.

Bundles of fibres were tied a few weeks after birth, and covered to protect the tips of the fibres from weathering (Dry 1934). By preventing movement of the wool the cover evidently causes the kemps to be held in situ at the level at which they were shed, so that secondary kemps can be classified as G_2, G_3, G_4 with little risk of error.

Samples were taken from hoggets before shearing, all fibre types were counted, shed and non-shed separately, and expressed as percentages of the total number of fibres excluding histerotrichs. This ranged from 200-900 per sample. The G_1 count is the sum of all the shed birthcoat fibres. Some cut hairy fibres at the base of the staple may be mistaken for G_3 kemps and this explains cases where more G_3 than G_2 kemps were recorded.

As most of the percentages were small, the angular transformation was used for all figures except those of PCT and Hi. The angles are distributed more normally than the crude percentages, and the tests of significance are more sensitive. It was not thought necessary to use weighted angles (Beale 1939) in spite of the occurrence of many zeros.

The average percentage of fibre types as calculated via the angular transformation are consistently less than, and close to, the direct mean; the greatest difference occurring where a particular type of fibre is recorded for only a few sheep of a genotype. The mean of the angles corresponds more closely to the mode than to the mean of the original fibre type

		G_1	G_2	G_3	n
N/N	Pedigree	18.72	4.97	3.90	9
	Classified	16.63	9.33	6.78	24
	Overall	16.38	8.02	5.92	33
nr/nr		15.85	4.26	2.94	17
N/+	Pedigree	12.58	4.40	2.59	38
	Classified	14.38	5.73	3.81	20
	Overall	13.16	4.84	2.98	58
Variance ratio		4.88**	5.16**	6.31**	108

Table 19. Kemp frequencies stated as percentages of pre-histerotrich fibres.

		Shed as G_1 kemp						Not shed as G_1 kemp							
		HH	SSA'	SSB	Sk	HCT	PCT	HH	SSA'	SSB	Sk	HCT	PCT	Hi	n
N/N	Pedigree	11.58	0.32	0.01	—	2.95	—	—	0.04	0.02	—	18.79	64.22	57.89	9
	Classified	9.93	0.66	0.01	—	4.44	0.01	0.04	0.11	—	—	17.48	64.21	72.42	24
	Total	10.35	0.55	0.01	—	4.01	0.01	0.02	0.09	0.01	—	17.86	64.21	68.45	33
nr/nr		10.37	0.31	0.76	0.06	2.43	—	0.01	0.01	0.13	0.01	25.27	57.65	71.59	17
N/+	Pedigree	7.36	1.07	0.73	0.14	1.36	0.04	0.02	0.11	0.24	0.22	10.86	73.26	67.18	38
	Classified	8.33	0.71	0.37	0.03	3.03	0.02	0.03	0.11	0.03	0.02	14.03	68.15	61.90	20
	Total	7.69	0.94	0.39	0.09	1.86	0.03	0.02	0.11	0.14	0.12	11.91	71.50	65.36	58
Variance ratio		9.96^{**}	2.24	18.0^{**}	6.52^{**}	4.26^{*}	1.88	—	1.21	3.25^{*}	7.41^{**}	15.1^{**}	20.5^{**}	0.72	108

Table 20. Frequency distributions of birthcoat fibre types stated separately for those shed or not shed as G_1 kemp.

frequency distribution which is heavily skewed. It will be noted that the frequency of G_1 kemps found directly (table 19) is greater than the frequency found from the summation of the individual frequencies with which different types of fibres are shed as G_1 (table 20). This is due to the use of the angular transformation.

Results.

1. Differences between the N-type strains.

Observations on the occurrence of kemps in the mature fleeces of +/+ and +/nr show that in these types the kemp frequency is qualitatively different from that in N-type animals. High kemp frequency thus parallels the dominance relations of high halo-hair abundance, being dominant in the N stock, and recessive in the nr stock. The frequencies og G_1, G_2, and G_3 kemps are given in table 19 for all five classes of material, and in figure 9 for the N/N, N/+ , and nr/nr totals. These cannot be compared quantitatively with the kemp frequencies in the +/+ and +/nr types since no quantitative data are available for these two types.

A further similarity between halo-hair abundance and kemp frequency occurs between N/N and N/+ . Figure 9 shows that the kemp frequency is greater in N/N than in N/+ in all three kemp generations. This parallels the halo-hair abundance which is greater in N/N than in N/+ .

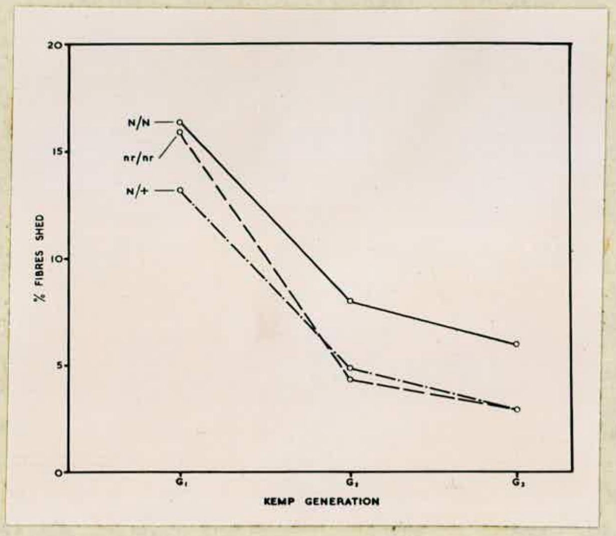

Figure 9. Frequencies of G_1, G_2 and G_3 kemps in N/N N/+ and nr/nr sheep.

The close similarity of the dominance relations of kemp frequency and halo-hair abundance show that these characters are both affected by the N and nr genes conjointly. This method of describing the pleiotropy of the N and nr genes will be used in later papers for other characters of the N-type syndrome. Sheep are too unwieldy as genetic material to allow the more substantial proof of pleiotropy from complete linkage.

2. Differences between the P_0 and P_1 follicles in the frequency with which they shed their fibres.

In the preceding paper the shedding of fibres has been demonstrated to occur only in primary follicles. Although two types of primary follicles occur, central and laterals, no attempt was made to determine whether these differ in their frequency of shedding. Such a comparison can be made for the G_1 kemps if these are classified into birthcoat types, since P_c follicles form only HH, SSA', SSB and Sk types, and P_1 follicles form only HCT and PCT types. Intable 20 are given the fibre type frequencies stated separately for fibres shed or not shed as G_1. These data allow estimates to be found of the proportions of P_c and P_1 follicles which shed their fibres.

The total frequency of shed and non-shed fibres of the HH, SSA', SSB and Sk types can be taken as an estimate of the frequency of P_c follicles. The frequency with which these types occur as G_1 kemps can similarly be taken as an estimate of the frequency of P_c follicles which shed their fibres. In table 21 are given the estimated proportions found in this way.

In the N/N and nr/nr types the frequency of HCT can be takeh as estimates of the frequency of P_1 follicles, since in these types all of the fibres formed by this type of follicle are HCT. In the N/+ type some of the P_1 follicles form HCT, others form PCT. Therefore the HCT frequency in this type does not give an estimate of the P_1 frequency. Approximately 29% of P_1 follicles form PCT fibres, therefore in the N/+ type 29/71 must be added to the HCT frequency in order to estimate the P_1 frequency.

		p_c	p_l
N/N	Pedigree	0.98	0.13
	Classified	0.91	0.20
	Overall	0.91	0.18
nr/nr		0.98	0.08
N/+	Pedigree	0.93	0.07
	Classified	0.97	0.12
	Overall	0.95	0.10

Table 21. Proportions of central and lateral primary fibres shed as kemps.

The frequency of HCT shed as G_1 kemp can be taken in all types as an estimate of the frequency of P_1 follicles which shed their fibres. The estimated proportions are given in table 21 for comparison with those found for the P_c follicles.

It is obvious that the two types of primary follicles differ markedly in the frequency with which they shed their fibres. P_c follicles shed 0.91 to 0.98 of their fibres whereas the P_1 follicles shed only 0.08 to 0.20 of their fibres. This difference between the P_c and P_1 follicles is correlated with the differences between the types of fibres which they form. P_c follicles form sickle group fibres which are more medullated and longer than the HCT and PCT fibres formed by the P_1 follicles. This correlation between the characteristics of fibres and the frequency of shedding will be amplified in the next section.

The ratios given in table 21 do not differ between N/N and N/+ for the P_c follicles, but they are consistently greater for the P_1 follicles in the N/N type. This can be explained by the N gene having reached a limit in its effect on the shedding of P_c fibres but not in its effect on the P_1 follicles. In other words, the gene is completely dominant in its effect on the shedding of P_c fibres, but only partially dominant in its effect on the shedding of P_1 fibres.

		H-H	SSA'	SSB	Sk	HCT	PCT
N/N		1	1	.5	-	.18	.0
nr/nr		1	1	.85	-	.09	.0
N/+	Pedigree	1	.9	.75	.39	.11	.0006
	Classified	1	.9	.93	.5	.18	.0003
	Overall	1	.9	.79	.43	.14	.0006
Overall types		1.00	.95	.76	.44	.14	.0005

Table 22. Proportion of total fibres of each type shed as G_1 komp. No Sk fibres were found in the N/N and nr/nr types.

3. Differences in frequency of shedding between types of fibres.

The proportion of fibres of any type shed or not shed as G_1 kemp can be found from the data given in table 22 for all types of fibres over all five classes of material. It can be concluded from these figures that the proportion of fibres of a specific type which are shed is a characteristic of the type of fibre, since differences between the classes of material are small compared with the differences between the types of fibres. It is unfortunate that no data are available from non-N-type material of the proportionate shedding of fibre types, since such data would allow a more rigorous examination, being based on a wider difference in fleece type than the present comparison.

In the preceding section the comparison of Pc with P_1 follicles showed that these differ in their frequency of shedding, and it was observed that this difference is correlated with differences in the characteristics of the fibres formed by the two types of follicles: P_c fibres are longer and more medullated than P_1 fibres. The same correlation of increase in frequency of shedding with increase in length and medullation can be seen in the HH,SSA', SSB and Sk series of fibres i.e. in the fibres formed by P_c follicles. The proportionate shedding of these types can be seen from table 22 to decrease from HH to Sk. The length and medullation also decrease from HH to Sk i.e. the

the frequency of shedding is correlated with length and medullation within P_c follicles as well as between P_c and P_1 follicles. In the preceding paper the same correlation has been shown to occur between P and S follicles. It can be taken as a general rule that the shedding of fibres is developmentally correlated with the incidence of medullation and the length growth rates.

Discussion.

In the preceding paper a difference has been shown to occur between P and S follicles in the effects of the N and nr genes on the growth rates, medullation, shedding, crimp size and brown pigmentation of their fibres. These effects are very marked in the P follicles, negligible in the S follicles. In the present paper the analysis has been carried a stage further in that a difference has been demonstrated to occur between the two types of primary follicles in the effect of the N and nr genes on the shedding of their fibres. This frequency is 0.94 in P_c follicles, 0.12 in P_1 follicles.

The occurrence of differences between P_c and P_1 in the other characters: growth rate, crimp size and brown pigmentation have not yet been studied quantitatively. However, a very large number of samples have been studied qualitatively, and these observations indicate that in N-type the P_c follicles form fibres which are longer, more medullated and have larger crimps than those fibres formed by P_1 follicles. On the basis of these observations, and the above analysis of kemp frequencies, it is reasonable to postulate that the characters which differ qualitatively between P and S follicles, differ quantitatively between P_c and P_1 follicles.

This and the preceding paper have clarified the analysis of the N-type fleece to the point where it is possible to define the residual problems. These are 1) the basis of the developmental linkage of growth rate, medullation, shedding, crimp size and brown pigment, 2) the basis of the differences between P_c, P_1 and S follicles in the effects which the N and nr genes have on their fibres. These will be considered in the later sections below.

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6. Sex modification of horns. (F.W.Dry and A.S.Fraser)

The N and nr genes, which cause the N-type of fleece, also cause the ocurrence of horns in most males and a proportion of the females. This is illustrated in figure I which shows a number of N-type rams; non-N-type rams have never been noted to have even a small fraction of this expression of horns.

Figure I. A...group of N-type rams showing the very large horns. B and C... skins of N-type lambs showing the occurrence of a shoulder patch in the one but not in the other. D... ram lamb with four horns. E... horns removed from +/nr rams.

The evidence for horns being caused by the N and nr genes will be presented below and considered in reference to the occurrence of horns in other breeds of sheep. The different types of horns which are breed characteristics have often been studied genetically in crosses between the various breeds. This problem has received special attention because of the differences in the horn expression between sexes within a breed. There are three main types of expression of horns: both sexes horned, males having larger horns than females.....Dorset Horn type; male sex horned, females infrequently having small horns or scurs.....Merino type; both sexes hornless(polled), males infrequently having small horns or scurs.....Polled type. The Romney Marsh breed is of the latter type.

Although the numerical data is scanty the genetic differences which cause these differences of expression of horns can be accepted as autosomal and monogenic. Warwick and Dunkle (1939) postulate that three genes condition the three horn types, and that these are an allelic series. Further they state that it is more probable that the differences between sexes within a breed are not specifically due to the 'horn' genes, but rather to the occurrence of physiological differences between sexes which differently modify the effects of the 'horn' genes. Ibsen (1944) on the other hand postulates a triple locus hypothesis involving complicated epistatic relationships and specific actions of the 'horn' genes on the sex-modification of horn expression. As yet the necessary crosses to test whether the triple allele theory is an over-simplification have not been made.

The N-type strains of the Romney Marsh breed, although they throw no light on to the genetics of the differences between breeds, do present an example of the sex-modification of horn expression within a breed. The occurrence within one breed of strains with all three types of horn expression make the N-type strains useful, particularly since the N and nr genes which cause these differences in horn expression, can for the most part be traced genetically from their effects on the fleece.

In the present paper the first section details the identification of the various genotypes, the second section details the horn expression of these different genotypes.

Identification of the genotypes.

The identification of the various genotypes can be made fairly rigorously from the halo-hair abundance at the middle of the back, which is loww in +/+ and +/nr, and high in all the other genotypes (see the introductory section below). However since both N/N and N/+ animals have a high halo-hair grade, this character cannot be used to separate them. It is not possible to progeny test females in sheep and therefore it would not seem possible to identify the N/N type, except in progeny tested females. However in the last ten years we have come to be able to identify N/N ewes phenotypically with a very small chance of error. This identification is based on a) the occurrence of horns being recessive in females of the 'dominant' stock, and b) the occurrence of differences between the N/N and N/+ lambs in the extent to which they are covered with a grade VI or VII halo-hair abundance; the primary halo-hair grade is estimated only from the middle of the back without reference to the rest of the body. The use of these characters will be discussed in general terms below; the senior author will present the numerical proofs in a later paper which covers the genetical analysis of these genes in greater detail than has been given in the present series.

If the occurrence of horns is recessive in N stock females then certain corollaries follow.
a) In crosses where N/N progeny are expected, the proportion of horned ewes should agree with the expected proportion of N/N. This is so.
b) Horns should be absent or occur at a low frequency in N/ ewes. Less than 10% of N/+ ewes have definite horns.
c) In the cross of horned ewes with +/+ or nr/nr rams none or very few of the progeny should be N-type. Less than 10% of the horned ewes which have been tested in

this way have proved themselves to be N/+ .

These results agree with the recessivity of horns in the N stock ewes, except that this is not complete; some N/+ ewes have horns. It is reasonable to assume that 0.90 - 0.95 of horned ewes are N/N.

In order to increase the rigour of identification of N/N an examination was made of the birrthcoats of the progeny of the cross of horned ewes by tested N/N rams. Only a negligible proportion of these progeny are expected to be N/+ and therefore their expression can be taken as an estimate of the expression of the N/N type.

During the routine description of lambs it had been noted that a considerable variation occurred between grade VII lambs in the extent to which the high frequency of halo-hairs extended over the body. This difference in 'coverage' had also been noted to vary between types, but it was not until the above sample of N/N lambs was obtained that it was realised that N/N and N/+ differed markedly: all or the majority of N/N lambs have a complete coverage, whereas all or the majority of N/+ lambs have at least a small region of low halo-hair grade i.e. their coverage is incomplete.

The last stage of incomplete coverage occurs at the side of the neck and the shoulder patch. This latter region is extremely important since approximately 0.95 of N/N lambs have no shoulder patch whereas 0.95-1.00

of N/ lambs have at least a shoulder patch of low halo-hair grade. In figure I above are shown two shoulder patch regions: one of complete coverage, the other of low halo-hair grade.

The difference between N/N and N/+ in coverage can therefore be simplified in terms of the presence or absence of a shoulder patch, where presence of a shoulder patch includes all degrees of incomplete coverage. In a sample of N/+ lambs only 1 in 300 had no shoulder patch at all, and only 18 had a very small shoulder patch. Therefore allowing a certain degree of misclassification, 95% of the N/+ type can be said to have incomplete coverage. The progeny from N/N by horned ewes, N/N by N/ and N/+ by N/+ include a proportion of lambs with complete coverage; this proportion in each case agrees well with the expected proportion of N/N. It is reasonable to conclude that 95% of lambs which have no shoulder patch are N/N.

This analysis reaches its cyclic conclusion in the use of the shoulder patch criteria to identify N/N animals, so that their horn expression can be compared with that of other types.

Expression of horns 1. Measurement.

Measurements of horns have been made as part of the routine of sheep description in the N-type flocks. These are made in terms of lumps-horns which have not broken through the skin; scurs-horns which have broken through the skin but which are less than an inch long; horns-full horns are measured in inches from the base to the tip along the upper side of the horn. The classification of horns into lumps, scurs or full horns is illustrated in figure II for a group of 14 months old ewes.

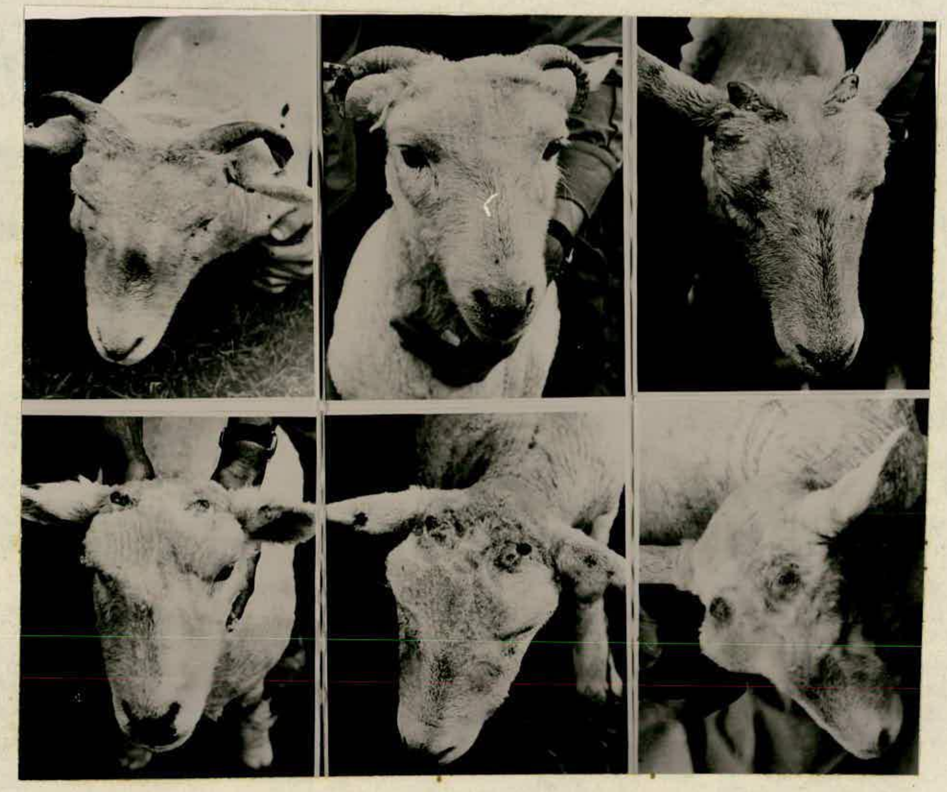

Figure II. Horns of 14 month old ewes. A-B, full horns. C-D, scurs. E, small scurs on top of large lumps. F-lumps.

The frequencies of animals having lumps, scurs or horns and the approximate rates of growth of horns can be found from the flock records. Since in many cases these are fragmentary due to castration etc., the rates of growth of horns have been determined only for the early growth period.

2. Expression of horns in the various types.

The expression of horns in the various genotypes is best detailed separately.

A... +/+ . Several hundred lambs from normal Romney Marsh flocks have been examined when they were several weeks old. 3-5% of the ram lambs had some small trace of horn growth, usually lumps. No traces of horn growth were found in the ewe lambs. Small horns are known to occur occasionally in older rams, but by the standards of the breed type they are undesirable and it would take time and tact to obtain accurate data. Many mature ewes have been examined and no traces of horn growth were noted, but in 90 breeding ewes from non-stud flocks, five had small scurs.

B... +/nr. All ram lambs are polled at birth but scurs have been noted in approximatly 40% of the ram lambs examined at 50-60 days after birth (22 had lumps or scurs out of 56 examined). Occasionally fair sized horns may develop from these scurs. Horns removed from adult rams are shown in figure I. Horns have been noted which are 11 inches long. As in +/+ the ewes are usually polled but in 38 examined 4 had small scurs.

C... nr/nr. A high frequency of rams have small lumps at birth which develop into large horns at maturity. The majority of ram lambs have at least a trace of horn growth by a few weeks after birth. Clean polled adult rams have not been noted but rams do occur which have only small horns and one ram had only scurs at 20 months after birth. The majority of ewes are clean polled but a small proportion develop lumps some months after birth. Of the existing ewes numbering 29, 8 had lumps and 1 had scurs.

D... N/+ As in the last type the majority of ram lambs have lumps at birth and these develop into large horns at maturity. A few rams have nothing larger than scurs. We have no record of a ram reaching the age of 6 months without growing at least scurs.

Horns vary considerably in size and a correlation appears to hold between the age at which horns appear and the mature size of horns. The effect of castration is variable- growth may cease entirely or proceed at a slower rate.

The majority of ewes are clean polled but a fairly high proportion develop lumps or scurs (15-22%) and a number develop definite horns (3-10%).

E...N/N. In general the horn expression is greater than in N/+ . All rams have large lumps or scurs at birth and these develop into horns at a faster rate than in N/+ . Females are all polled at birth but they develop lumps soon after birth and, as in Dorset Horn females, horns are formed from these after a few months. Two ewes which on birthcoat and breeding are thought to be N/N have at the age of one year horn only large lumps from which scurs protrude. It is concluded that 9/10 of N/N ewes have definite horns.

F... N/+ . +/nr. In general the horn expression is intermediate between that of N/+ and N/N. All ewes are polled at birth but many develop horns later. In 23 ewes examined, 6 were polled, 9 had lumps, 4 had scurs, and 4 were horned. In some ewes 4-5 inch horns have been noted but they are usually smaller.

3.Factors modifying horn expression.

There is a hint that horn growth is affected by modifying characters. One N/+ ram which had only scurs at maturity sired three N/+ sons. One of these grew good horns during the first six months (6 inches) but these were then broken. Another son had 2 inch horns at four months when the usual size of horns in the N/+ type is 6 inches or more. The third son never had more than scurs. This last ram had only one N-type son, and at four months this ram which was N/+ had only 2 inch horns. These breeding results are not conclusive but we have here an indication that inherited modifying factors affect the size of horns, even to the extent of determing whether horns or scurs are formed.

4.Animals with four horns.

Two lambs have been noted in the N stock which had four horns. The extra pair of horns were located between and behind the main pair(see figure I).

5. Rate of growth of horns.

The above description of the expression of horns in the various genotypes can be extended by finding estimates of the rates of growth of horns. The following discussion of horn growth rates is restricted to the males of the N/N, N/+ and nr/nr types, and to females of the N/N type, since only in these types is the penetrance of horns complete.

The available data upon horn growth can be examined 1) between individuals, 2) between sexes and genotypes within the Romney breed, and 3) between breeds. In figure 10 are shown the growth rates of horns for several animals in each of the various classes of material. This shows that the rate of increase in length over the period 0-140 days is constant, since no consistent deviations occur from linearity.

Since horn growth rates can be taken as linear within an animal it is probable that no serious error will be introduced from the use of linear regressions for the comparisons between genotypes. In figure 11 are shown the scatter diagrams of measurements of horns made upon 14 animals each of the various types; some of these will have been measured 2-3 times, others 4-5 times, and therefore the overall regressions will be weighted differently for each animal. The overall regressions are also shown in the same figure.

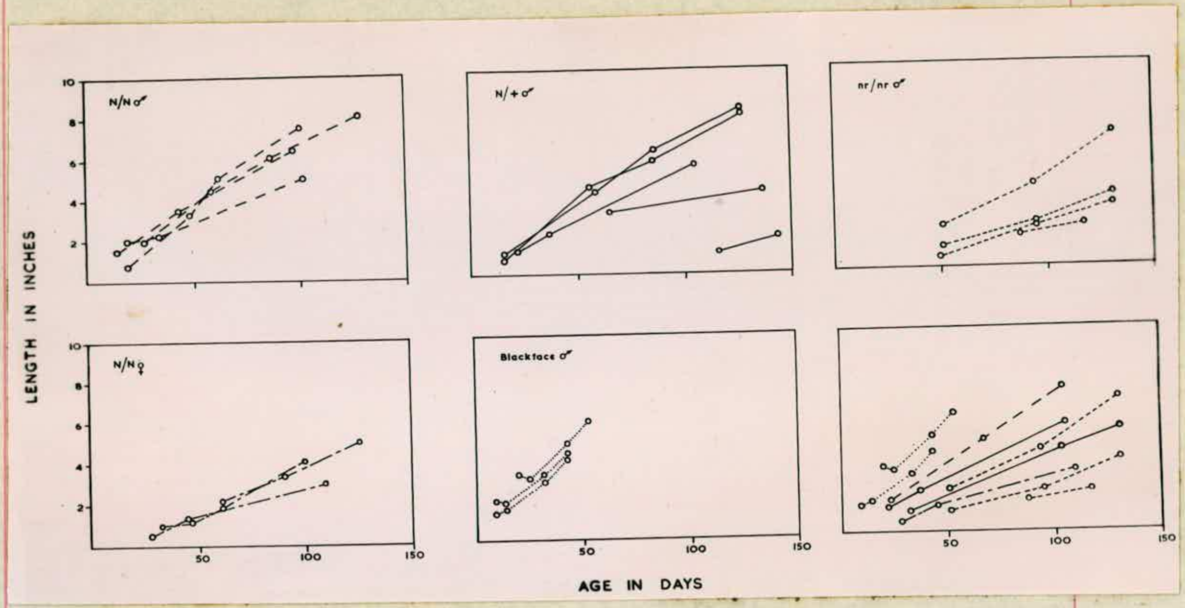

Figure 10. Growth rates of horns plotted for individual animals to show linearity of growth. The bottom right square includes individuals of all types.

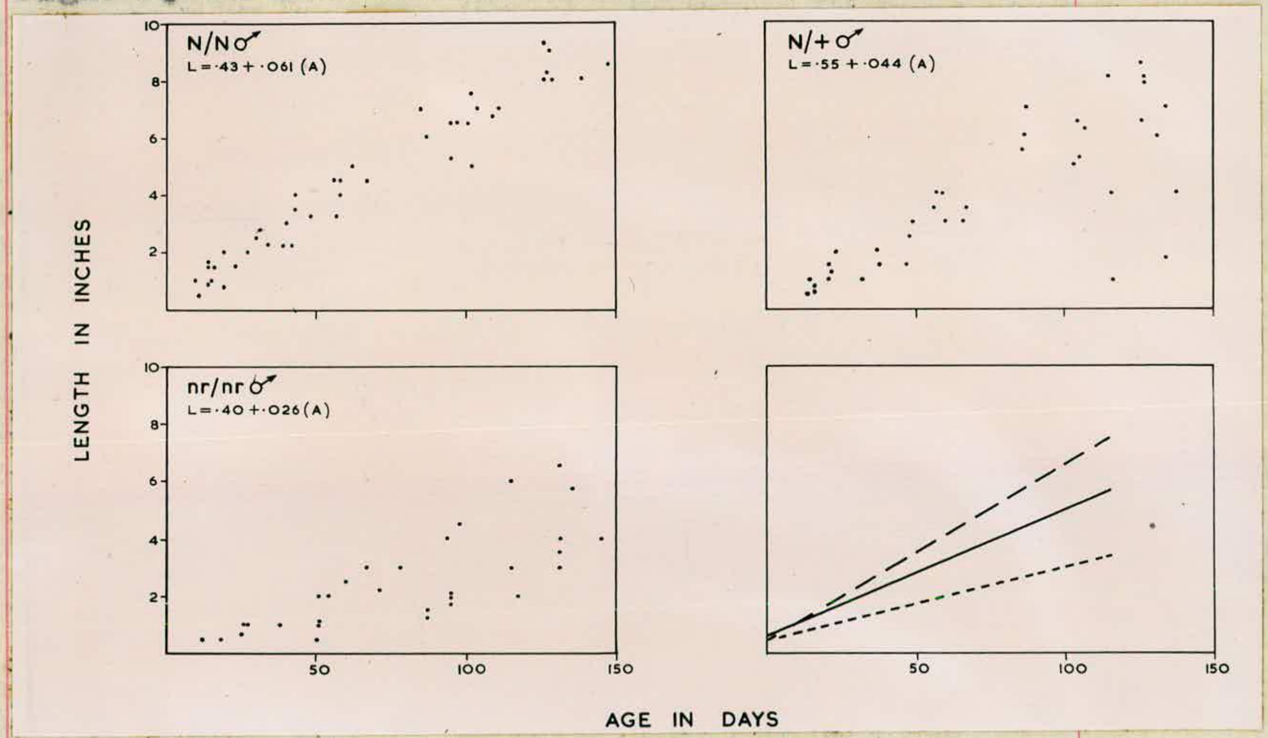

Figure 11. Overall regression diagram and scatter diagrams of horn measurements of 14 animals of each of the types.

The overall regressions shown above differ significantly but the basis of this difference needs closer examination. All the N/N animals have very similar growth rates of horns. The N/+ animals on the other hand have a wide range of growth rates, and a high proportion have the same rate as is characteristic for the N/N type. It would appear that the difference between these two types is that in N/N all animals are forming their horns at the maximum possible rate whereas in N/+ only a proportion of the animals reach this maximum. This does not invalidate the conclusion that the rate of growth of horns is faster in N/N than in N/+ .

It is of interest to compare the horn expression of N-type with that of a normally horned breed. Measurements were therefore made by the junior author and Mr.M.Hamada on the Scottish Mountain breed, which is completely horned in both sexes, and the females grow large horns at maturity. The rates of growth of horns of several B'face rams are shown in figure 10 above. As for N-type there are no consistent deviations from linearity. In figure 12 are shown the scatter diagrams and regression lines of horn measurements for the B'face breed and for the N/N type, since the latter type is the only N-type strain in which the penetrance of horns is complete in both sexes.

In the B8face breed very little difference occurs between male and female in the rate of horn growth, the difference being mainly in the age at which horn growth commences, whereas in N-type the female horn growth not only starts later it also is at a lower rate. Between breeds the B'face definitly

TYPE		MALE		FEMALE	
		Penetrance	Expressivity	Penetrance	Expressivity
Romney	+/+	3-5%	Very small lumps or scurs.	0-5%	Very small lumps or scurs.
	+/nr	39%	Small scurs and horns.	0%	—
	nr/nr	100%	Medium horns $L = .40 + .026(A)$	28%	Small scurs.
	N/+	100%	Large horns $L = .55 + .044(A)$	32%	Small scurs and horns.
	N/+ . +/nr	100%	Large horns.	73%	Medium horns and scurs.
	N/N	100%	Very large horns	90-100%	Medium horns and scurs. $L = .072(A) - .21$
Blackface		100%	Very large horns $L = 1.02 + .074(A)$	100%	Medium horns $L = .072(A) - .53$

Table 23. Summary of the expressions of horns in the various types of sheep studied. The period of measurement is approximately the first 6-12 months after birth.

grows its horns at a faster rate.

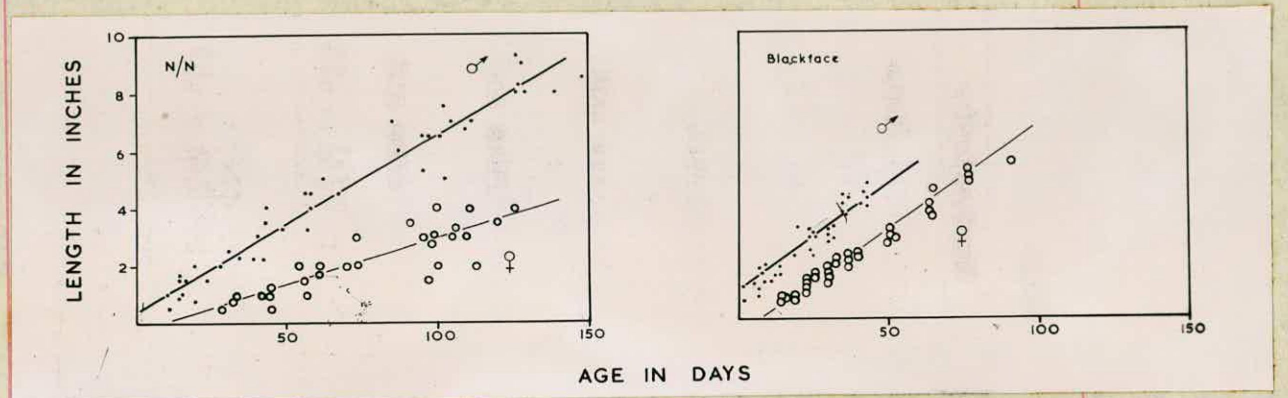

Figure 12. Overall regression diagrams for both sexes of the B8face breed and the N/N type of Romney.

6. Penetrance and expressivity of horn expression.

The expression of horns varies both in the percentage of animals which are horned and in the size of horns which occur i.e. it varies both in penetrance and expressivity. These terms are not used in the precise meaning defined by Timofeef-Ressorvsky (1934) but in the more general sense as used by Goldschmidt (1938). The present data do not allow precise estimates of penetrance, but scanty as it is, it does allow the conclusion that penetrance and expressivity are closely correlated. This can be seen from the estimates of penetrance and expressivity given in table 23. The penetrances have been found from the data given above, and the expressivities are given as the regressions of length of horns on age where these are available.

Discussion

I. Pleiotropic effects of the N and nr genes on horns and fleece.

The existence of the N and nr genes is recognised from their effects on the fleece; the primary diagnostic character being the marked increase which they cause of the halo-hair abundance of the birthcoat. The two genes differ markedly with each other in their dominance relations to normal for this character. The N gene is dominant but only partially so, since the halo-hair abundance of N/N is greater than that of N/+. The nr gene is recessive and almost completely so since the +/nr type has only a slightly greater abundance than normal. These genes occur in three strains of Romney Marsh sheep: two carry the N gene, one carries the nr gene. Since these strains have different origins, the simultaneous occurrence of horns in all three suggests that the horns are an aspect of the action of the N and nr genes. This suggestion could be checked by continually outcrossing the genes to the normal breed for several generations to see if the two characters become separated, but in sheep one generation takes two years and so the backcrossing method is obviously impracticable. Over the few generations of outcrosses which have been made, horns and high halo-hair abundance remained linked. Since complete linkage cannot be rigorously tested, another method must be used. This involves the demonstration that the dominance relations of horns parallels that of halo-hair abundance i.e. that the occurrence of horns is dominant in the N stock, recessive in the nr stock.

The comparison of N/+ with N/N and of +/nr with nr/nr show that the dominance of horns is the same as that of halo-hair abundance. It is reasonable to state from the above evidence that the occurrence of horns is dominant in the one stock, recessive in the other. This is a very strong argument that the substitution of the N or nr genes causes both the occurrence of horns and the changes in the fleece.

This can be carried a stage further by considering differences between N/N and N/+ . The growth rates of horns given in figure 11 and the general observations made in the N stock, show that the N/N males have the greater growth rate. Similarly more N/N females have horns than in N/+ , and these are larger. This partial dominance of horns in the N stock parallels that found for halo-hair abundance and is a further argument for these two factors having the same genetic causality.

II. Sex modification of horns.

In the N-type strains of the Romney Marsh the occurrence of horns has been shown to be caused by the substitution of the N or nr genes for their respective normal alleles. The effects of these genes on the fleece are not sex-modified showing the action of these genes to be constant between sexes.

In all of the genotypes which have been considered the expression of horns was greater in males than in females, ranging from the N/N type in which the penetrance is complete in both sexes but the size of horns is greater in males, to the +/+ type in which the penetrance of horns is very low, and only in males. It is unreasonable to postulate that the differences between sexes in the effects of these genes on horns are due to the genes having a lesser action in one sex than in the other, and very reasonable to postulate that the differences are due to the sex difference modifying in some way the effect, but not the action of the gene.

The mechanism of this modification can be found in the endocrine difference between sexes. Since ovariectomy has no apparent effect on horn formation (Marshall 1912), the female sex hormones, the estrogens, can be excluded as major determinants of the rate of horn formation. On the other hand the castration of males causes the cessation of horn growth in Merinos and the assumption of the female rate of horn growth in Dorset Horn males. Therefore the male sex hormones, the androgens, are major determinants of the rate of horn formation and it is reasonable to postulate that the difference between sexes in the rate of formation of horns is due to the differences in level of androgen production. The adrenals are known to produce androgens (Wintersteiner 1941) and the differences between the female types and the male castrate type on the one hand and the complete male on the other can be explained as due to the lower level of androgen formation by the adrenals alone in the former case, and the higher rate of androgen formation by the testes and adrenals in the latter. Since the level of androgen formation by any sex almost certainly does not differ markedly between breeds, the role of androgens in horn growth is that of partial determination. It is postulated that the androgens do not determine the rate of horn fomation, but only modify the 'potential' rate of horn formation which is determined by the ' horn ' genes.

Acknowledgements.

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7. Growth of wool fibres in sheep (A.S.Fraser)

Duerden (1927) discovered that the tips of some fibres in the birthcoats of Merino lambs were shaped like sickles. He later (1932) found that such fibres occurred generally in domestic breeds of sheep. These observations were extended by Dry (1933,1934 and 1940) into a full classification of birthcoat fibres into types. He based this classification on the shape of the tip curl, but also included other characters.

Fibres differ in the age at which they were initiated, and these differences in the age of initiation are related to differences in shape. The comparison of the types of fibres present at birth with those in samples taken several weeks after birth shows that fibres formed before birth have a very definitely shaped tip, whereas the fibres initiated after birth have no definite shape to their tip. In addition to this difference in the shape of the tip curl, differences occur in the general pattern of crimps along a fibre. Fibres which are initiated before birth have atip region of small crimps followed by a region of large crimps. Those fibres initiated after birth do not show any such tip region. The change in size of crimps along a fibre occurs at about birth. These differences allow fibres to be divided on the basis of their shape into two groups: one of fibres initiated before birth, the other of fibres initiated after birth.

The division of fibres on the basis of their morphology into groups has been extended by Fraser, Ross and Wright(section 4 above), who have shown that the different types of follicles which occur in sheep each form a restricted range of types of fibres. Since the sequence of development of the follicle population is known, this equation of type of fibre to type of follicle allows the sequence of dvelopment of the different types of fibres to be described.

The basis of the equation of types of fibres to types of follicles is the classification of these into types. The classification of follicles has been detailed above (Ross, appendix I) and therefore will not be considered again here. The classification of fibres has been briefly described above (Fraser, Ross and Wright, section 4) and it is necessary to go over this again since the present analysis of the shapes of fibres is based on the equation of different types of follicles to different types os fibres.

A complete follicle group consists of a trio of primary follicles and several secondary follicles. Occasionally less than two lateral primary follicles are formed beside each central primary follicle, but this is infrequent (see Ross, section 3 above). This is illustrated in figure 13 for a follicle group from a sample of skin from a Scottish Mountain Blackface lamb.

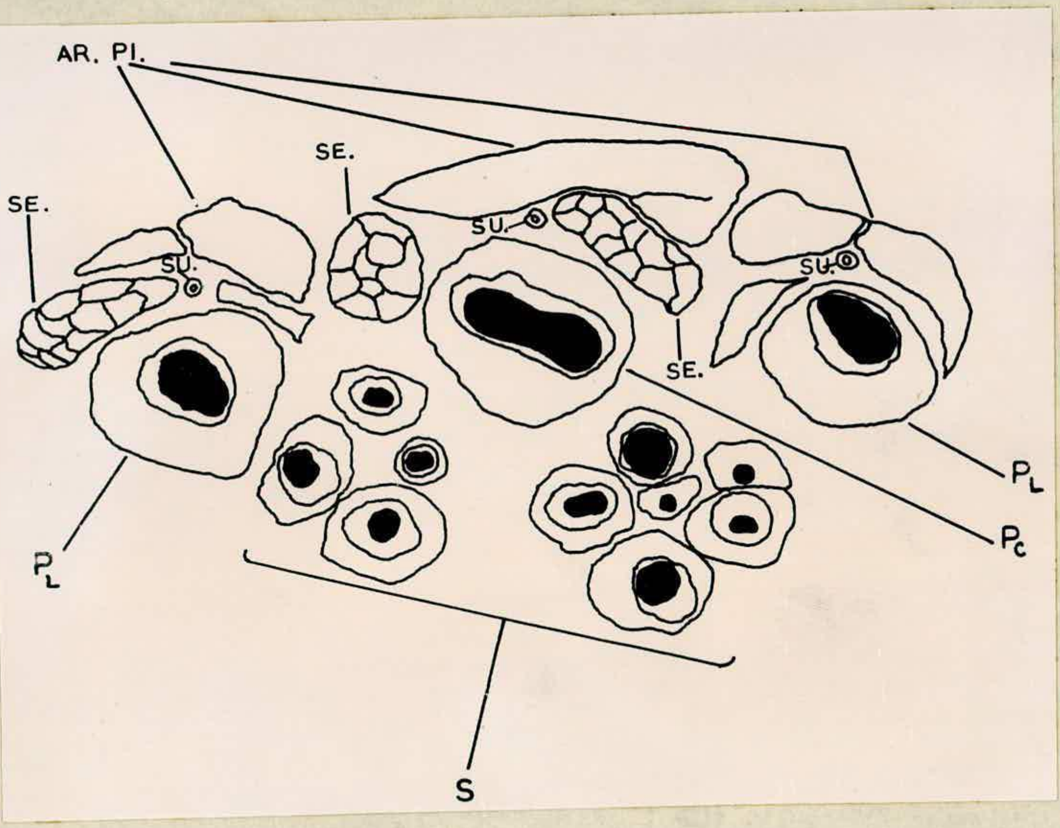

Figure 13. Follicle group of Scottish Mountain B'face from a sample taken a few days after birth, showing the different types of follicles which comprise a group. SE-sebaceous gland, AR.PL- arrector pili muscle, SU- sudoriferous gland.

The relation of the different types of fibres to the different types of follicles will be discussed below in terms of the classification of fibres. The fibres are first separated into two groups on the occurrence of a tip region of definite curls. Those fibres which do not have such a region are termed histerotrichs. These are initiated just before, but more usually after birth. Since the fibres of primary follicles are initiated well before birth, the heterotrichs are formed by secondary (S) follicles.

The remianing group of fibres, those with definite tip curls, can be separated into two further groups on the shape of the tip curls, which may be sickle-shaped or regularly curled. In most samples the distinction is fairly clear and intermediates are rare. In coarse wool breeds the high degree of medullation is correlated with an absence of definition of the crimps. In such sheep the distinction between 'sickle' and 'curly' tipped fibres is based on (i) differences in length, (ii) differences in the degree of medullation, (iii)differences in the shape of the extreme tip of the tip curl, which is straight in 'sickle' fibres. This difficulty of classification occurs only in sheep with a very high degree of medullation.

The fibres with regularly curled tips are formed by both P_1 and S follicles, whereas the formation of sickle tip fibres is restricted to the P_c follicles. Since the P_c follicles are the first to initiatet their fibres, this means that the sickle tipped fibres are initiated before the others.

The formation of regularly curled fibres by both P_1 and S follicles, raises the problem of separating this group into those formed by each type of follicle. Fraser, Ross and Wright (section 4 above) have shown that in very heavily medullated fleeces, the curly-tip fibres can be separated into two groups on the basis of the occurrence of medulla in the portion of the fibre formed before birth. If the fibre is medullated in this portion of the fibre it is formed by a P_1 follicles, whereas if it is not medullated in this portion it is formed by an S follicle. This separation is complete only if the incidence of medulla is high enough to occur in all P_1 follicles.

An investigation is in progress to determine if a separation of the curly tipped group can be effected on the basis of some other character than pre-natal medullation. One which appears to be of use is the number of crimps in the prenatal portion. This is greater (2-3 more crimps) in P_1 fibres, than in the first S fibres. The efficiency of this separation and its range of application have not been determined. It appears to be most efficient in very fine birthcoats. The difference in number of crimps between P_1 and S fibres is expected from the work of Barker, Norris et al. (see Barker 1932). They have demonstrated that crimp number is independent of fibre length, and that the crimp number is an estimate of the time over which the fibre has been growing. Since the time taken to form a single crimp is 5-8 days (Norris and van Rensburg 1930) and since the P_1 follicles commence forming their fibres approximately two weeks before the first

S follicles, it is expected that the P_1 fibres should have 2-3 more crimps than the earliest S fibres.

It seems reasonable to separate the curly tipped fibres into two groups: primary curly tips formed by P_1 follicles, and secondary curly tips formed by S follicles. The criteria of this separation are (i) the occurrence of medulla in the tip region, (ii) the occurrence of 2-3 more crimps in the pre-natal region. Figures 14,15,16, and 17 illustrate the classification of fibres in samples from lambs having different degrees of coarseness.

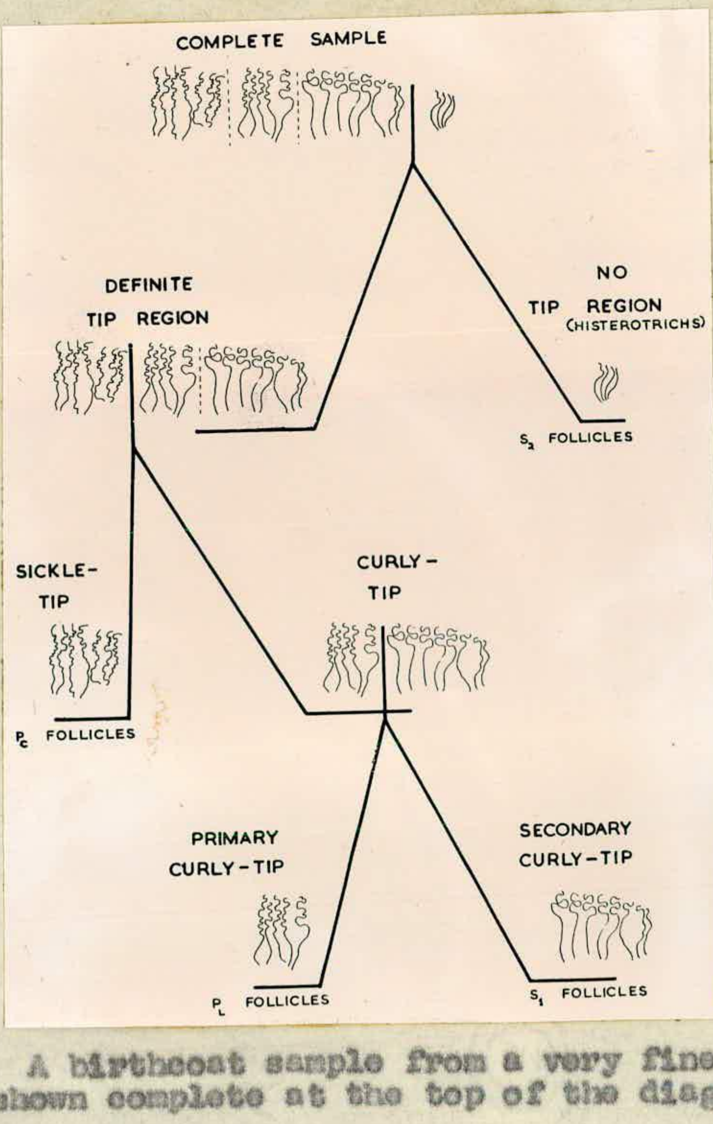

Figure14. A birthcoat sample from a very fine type which is shown complete at the top of the diagram, and

then separated into the different groups formed by each of the types of follicles. An important feture is the qualitative difference between primary and secondary curly tips.

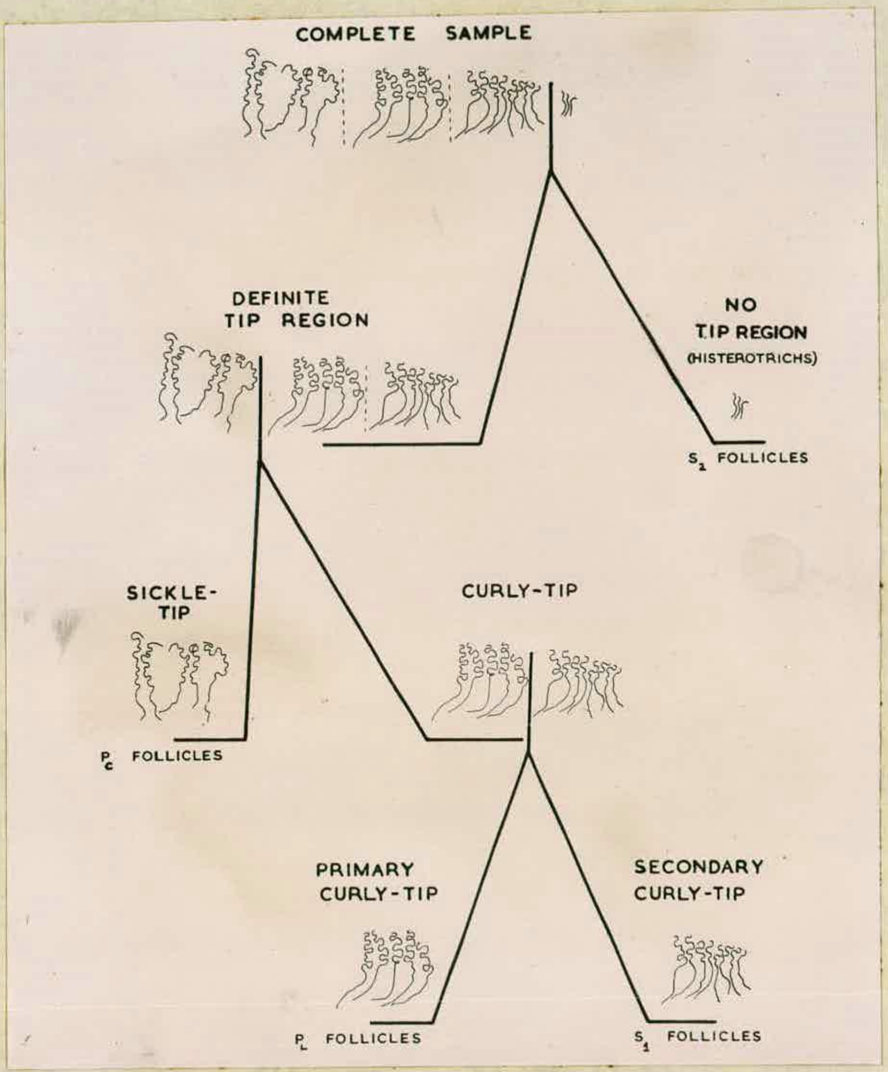

Figure 15. As for figure 14, but for a slightly less fine sample. Although the distinction between primary and secondary is still possible, it is not so clear as in the previous sample.

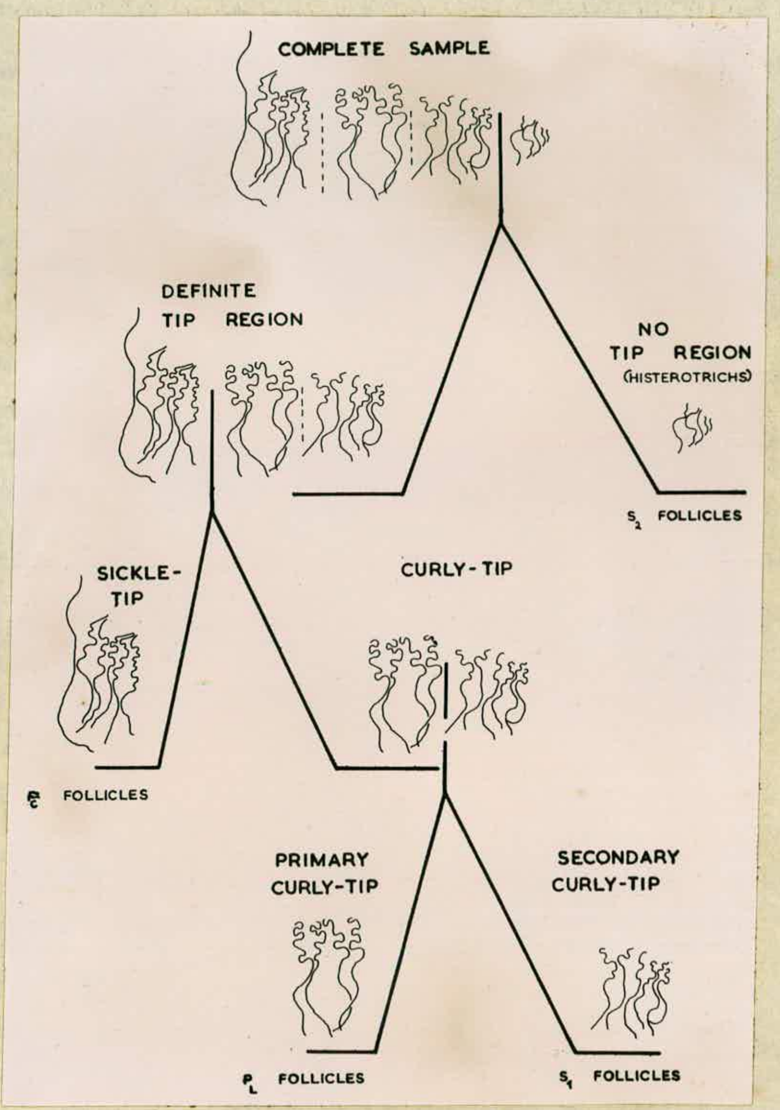

Figure 16. As for figure 14, but for a coarse sample containing an appreciable fraction of halo-hairs. The separation into primary and secondary curly tips although clear is not based on the crimp number but on the occurrence of medulla. the method of drawing does not show medullation.

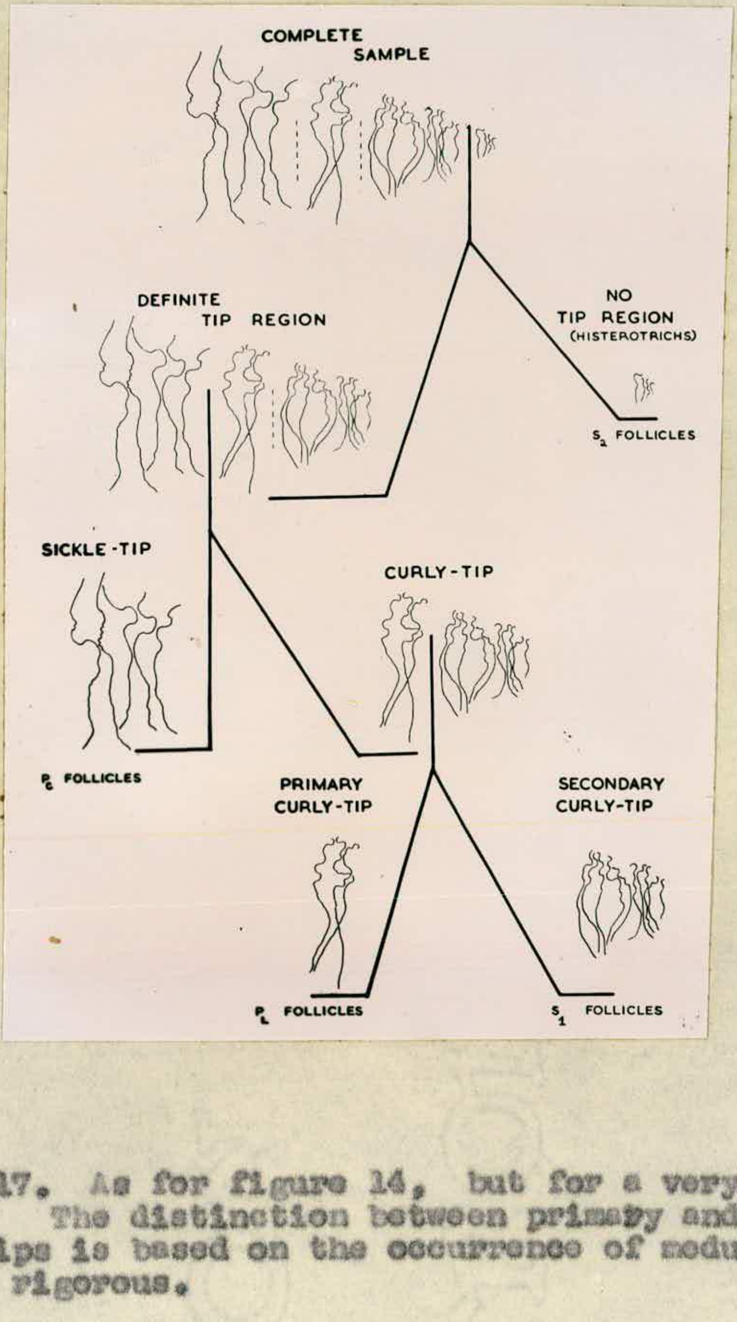

Figure 17. As for figure 14, but for a very coarse sample. The distinction between primary and secondary curly tips is based on the occurrence of medulla and is very rigorous.

The equation of the sickle tip, primary curly tip, secondary curly tip and histerotrich types of fibres to the P_c, P_1, S_1 and S_2 follicles allows a sample of fibres to be studied in terms of their sequence of initiation. Examination of Dry's (1933) analysis of the 'pre-natal check' phenomenon in light of this work shows that he assumed this relation of the shape of fibres to their age of initiation.

Several problems arise from the equation of certain types of fibres to certain types of follicles. (1) What are the causes of the differences in shape between fibres? (2) What are the causes of the differences between follicles in the shapes of the fibres which they form ? (3) How does the development of the follicle group affect the shapes of fibres? The present aim is an examination of these problems.

Material and methods.

The illustrations of fibres given in this paper were taken from birthcoat samples made available by Dr.F.W.Dry and Mr.Wilson of New Zealand and Boghall Experimental farm, Edinburgh. I am indebted to both for this material.

Fibres are initially separated on black velvet into the groups defined above. Representative fibres of each group are placed on lantern slides which are projected through a standard projector at a shortened focus. The projected fibres are then drawn without reference to diameter. In the figures of complete samples, the sequence from left to right is (i) sickle-tip, (ii) primary curly-tip, (iii) secondary curly-tip, and (iv) histerotrichs. This corresponds to the sequence of initiation; those to the left being initiated first, those to the right being initiated last. Each figure is as far as is possible representative of the variation occurrent in the particular sample.

In figure 18 are shown a number of sickle tipped fibres selected from a number of samples cut at about the same age.

The shape of fibres.

(1) Sickle tips. A sequence of sickle tips are shown in figure 18. This demonstrates that they consist of three well defined regions: the sickle shaped tip curl; the tip region of small regular crimps; a region of large regular crimps. The first two regions are formed before birth, the last region is formed after birth.

Figure 18. A selection of sickle tipped fibres from a number of birthcoat samples.

Since the sickle tip and the region of small regular crimps are formed before birth, it is impracticable to determine the rate at which they are formed sincw this would necessitate the slaughter of foetuses. Barker, Norris et al. (see Barker 1932) have shown that it is a reasonable assumption to assume that each crimp of a fibre was formed in the same period of time. This was based on two lines of evidence, (i) no correlation occurs between length and number of crimps in full fleece samples where all fibres have been formed over the same period of time, and (ii) in a series of samples taken at monthly intervals from the same animal, the average number of crimps formed per month was constant. Therefore the number of crimps can be taken as independant of fibre growth rates, and differences in the sizes of crimps can be taken as estimates of differences in the rate at which the fibre was formed. Similarly differences in the shapes of crimps can be taken as due to differences in the rates at which parts of the crimp were formed. This is applicable to the shape of the sickle tip of P_c fibres, which can be explained by the interaction of a constant rate of fibre curvature with a progressively decreasing rate of increase of fibre length. This is illustrated in figure 19.

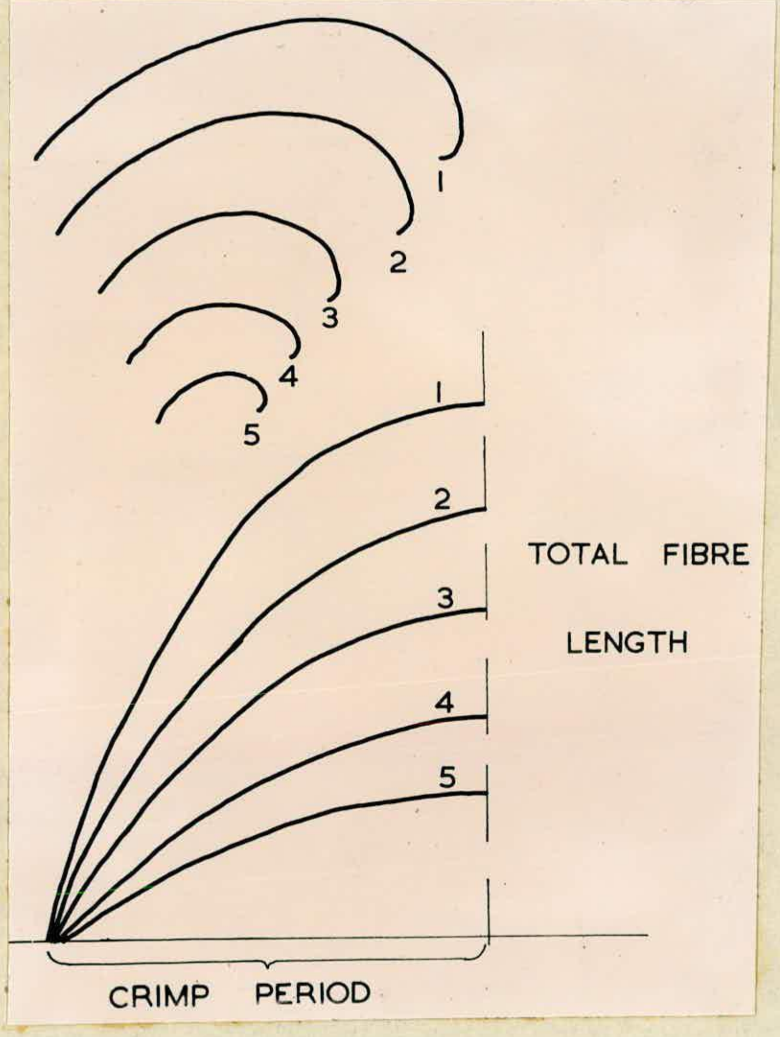

Figure 19. Relationship of the shape of crimps to the rate of increase in length, showing how a decreasing rate of increase in length, interacting with a constant rate of fibre curvature results in a sickle shaped fibre.

This use of the differences between crimps as estimates of differences in the rate of increase of fibre length can be extended to ther regions of the sickle tip fibres. The shape of the crimps, after the first, is regular, and therefore, it can be deduced that the rate of increase of fibre length does not vary during the formation of a crimp after the formation of the first crimp. The length of the sickle crimp is greater than that of a single crimp of the next region. Therefore, the rate of increase of fibre length is decreased after the formation of the first, sickle, crimp. Similarly, the portion of the fibre formed after birth has regular crimps which are larger than those of the preceding portion. The rate of increase of fibre length over this period is theerefore constant and greater than that of the preceding portion.

The changes in the rate of increase of length which have been deduced, from the shape of crimps, to occur during the formation of sickle tipped fibres are illustrated in figure 20 (line 1). These changes are (i) from a fast, progressively decreasing rate to a slow constant rate, and (ii) from a slow constant rate to a fast constant rate. These changes occur after the formation of the sickle tip, and birth, respectively.

(2) Curly-tips. The sequences of fibres shown in figures 21 and 22 include both primary and secondary

curly tips, and it can be seen that both of these consist of two regions: a tip region of small regular crimps and a region of larger regular crimps. The change in size of crimps occurs at birth.

The division of the curly tips into two regions, one of small, the other of large crimps, shows that these two regions are formed at different rates. The regularity of the shape of the crimps shows that each region is formed at a constant rate. This is illustrated in figure 20 (lines 2,3,4, and 5). The changes which occur in the rate of increase of length of curly tip fibres differ significantly from those of sickle tipped fibres in the absence of an initial phase of fast growth at a changing rate.

(3) Histerotrichs. This type of fibre is illustrated to the right of figures 21 and 22. It differs from the other types in the absence of a tip region of well defined crimps i.e. in the absence of any differentiation into regions of different sized crimps.

The shape of these fibres can be attributed to (i) their initiation at a period when growth is vigorous and crimping therefore ill-defined, (ii) to their formation at a constant rate which does not show any qualitative changes. This is illustrated in figure 20 (lines 6,7, and 8).

(4) Relation of fibre growth rates to the follicle group. In figure 20 the patterns of growth rates which have been deduced for the different types of fibres are illustrated in reference to the sequence of initiation of fibres by a follicle group.

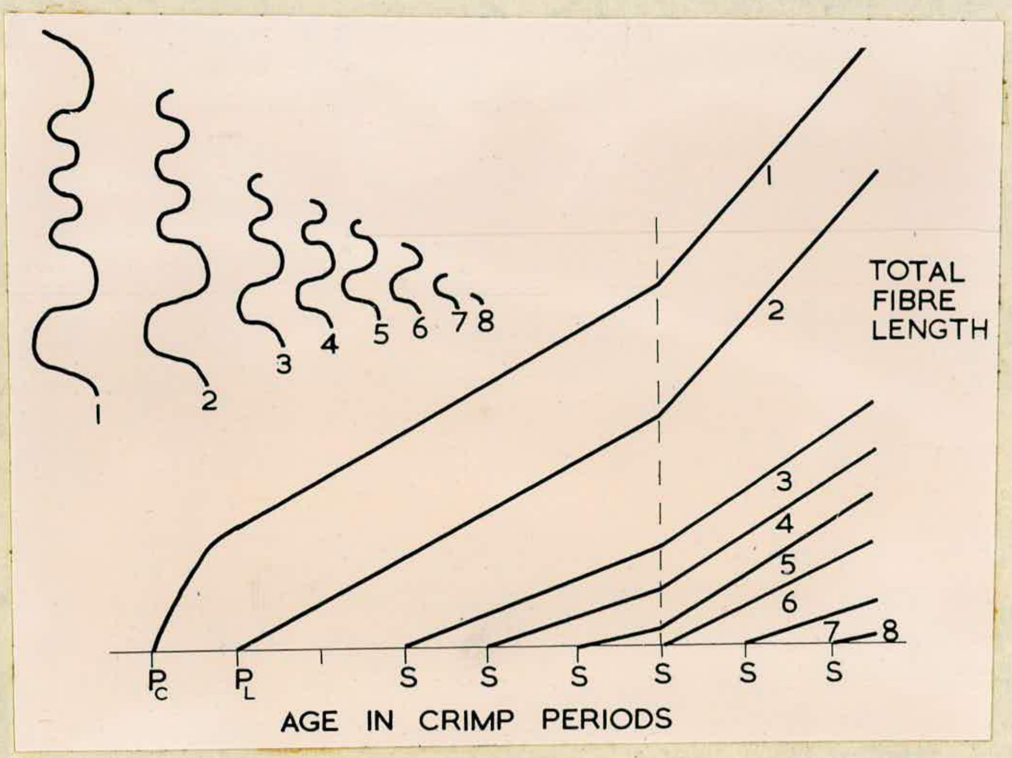

Figure 20. Relationship of the shape of crimps along the different types of fibres to the rates of increase of length, for each of the fibres formed by an average follicle group.

This total pattern of fibre growth rates shows that three main changes occur during the formation of fibres by a follicle group. These are (i) the change from a fast, progressively decreasing rate. This change occurs after the formation of the first crimp of the P_c fibre, and before the initiation of any other fibres. (ii) an increase which occurs at birth, affecting all fibres. (iii) a gradient of decrease of growth rate which is basic to the first two changes (the later a follicle initiates its fibre, the slower it forms it.)

The correlation of the growth rates of fibres to the sequence of development of the follicle group appears to be the basic cause of the differences in shape, both along and between fibres, and will be discussed in the next section in which a hypothesis to explain this correlation is formulated.

One of the changes which occur during the formation of a fibre group is defined by the general relation between the age of initiation of a fibre and its rate of formation. This was taken in figure 20 to decrease with age i.e. the later a follicle forms its fibre, the slower it forms that fibre. This corresponds to a coarse type of fleece, but it does not hold for fine types of fleeces where this basic relation of growth rate to age of initiation is more complex. Dry (1933) has studied this problem, and has expressed it in terms of the 'pre-natal check' hypothesis.

(5) The pre-natal check. Dry (1933 et seq.) studied the variation of fibres within samples on the basis of an assumed relation of the shape of fibres to their age of initiation i.e. he first arranged fibres into

a sequence which he assumed was analogous to the age of initiation sequence since the shape of the tip curls varied according to a continuous sequence, placing the sickle tipped fibres first, the regularly curled fibres next and the histerotrichs last. Having formed such a sequence he then studied the relative length and coarseness alâng the sequence. Granting the validity of his initial assumption, this method allows the lengths and coarseness of fibres to be compared relative to their age of initiation. Since Fraser, Ross and Wright (section 4 above) have shown that specific types of fibres are formed by specific types of follicles, it follows that Dry's initial assumption is correct, namely that the shape of a fibre is an index of its age of initiation.

Dry (1933) compared the sequences of fibres (which he calls fibre type arrays) from sheep with different types of fleece, and found that the relation of length to age of initiation varied according to fleece type. In coarse birthcoats a fairly simple relation holds, in which the first fibres are the longest fibres and there is a gradual decrease as the age of initiation increases. This is the general rule for mammalian coats. In figure 21 are shown a number of fibres all from the same sample froma coarse birthcoat. The fibres on the left were initiated first, those on the right were initiated last. It is obvious from this sequence that the first fibres are the longest, the last fibres the shortest. In figure 22 is shown a sequence from a sample from a fine birthcoat in which Dry found a more complex relation between length and age of initiation. The first fibres to be initiated are not the longest but they are longer than the last fibres. In a sequence of fibres from a fine fleece, moving from the first to the last to be initiated, thelength growth rate is first low, then increases to a maximum, then decreases to a minimum in the last fibres.

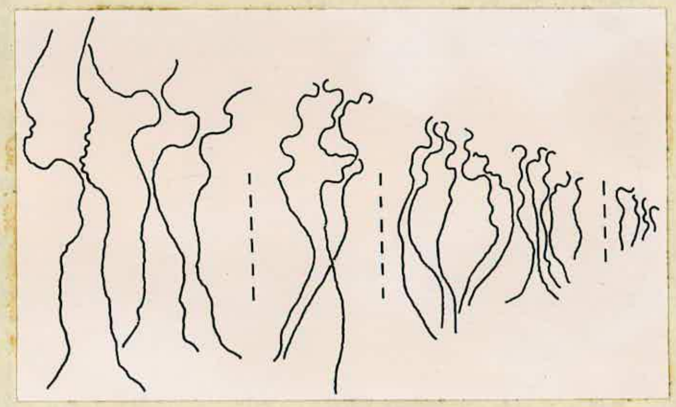

Figure 21. Sequence of fibres from a coarse birthcoat showing that the first fibres to be initiated, those on the left, are the longest.

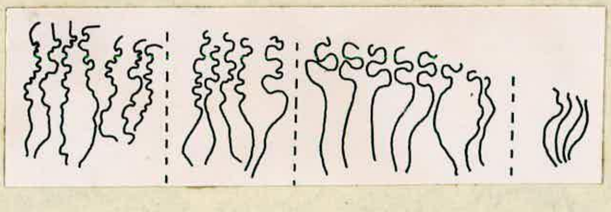

Figure 22. As for figure 21 but for a sample from a fine birthcoat, showing how the first fibres to be initiated, those on the left, are not the longest.

It must be emphasised that in both sequences the arrangement was made without reference to length;

being made on the shape of the tip curl primarily, and on the number of crimps secondarily.

One can find a complete sequence between these two extremes in which the variable is the length of the first initiated fibres relative to that of the later initiated fibres. With increase in the fineness of the coat, there is a decrease in the length of the first initiated fibres relative to those of later fibres. This decrease Dry interprets in terms of the 'pre-natal check', which he postulated to affect the relation of fibre growth rate to age of initiation. In a sequence of fibre type arrays from that shown in figure 21 to that shown in figure 22, hepostulates that the effect of an undefined character, the pre-natal check, increases resulting in a decrease in the rate at which the first follicles form their fibres. This concept is illustrated diagramatically in figure 23. Each curve represents a sequence of fibres which have been arranged in relation to their age of initiation. The whole family of curves represents the transition from a coarse to a fine type of fleece.

The concept of the 'pre-natal check' will be considered in a more explicit terminology in the section below.

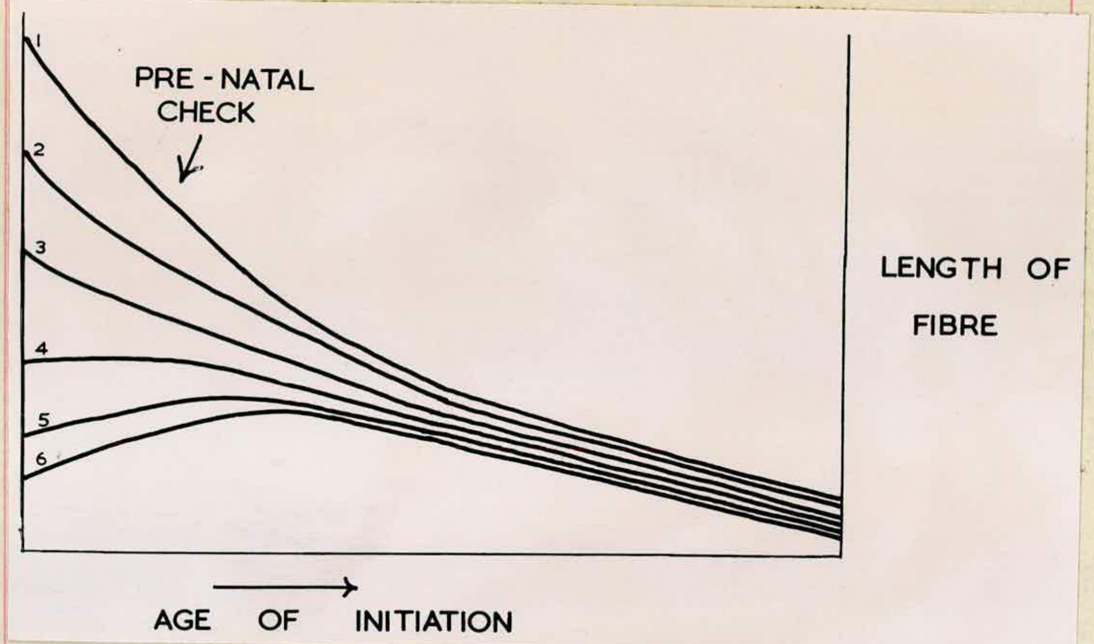

Figure 23. A hypothetical arrangement of several sequences of fibres in terms of their ages of initiation: each line representing a different sequence, ranging from a very coarse type (line 1) to a very fine type (line 6).

Conclusions. Follicles differ in the shapes of the fibres which they form and these shapes are due to differences in the rates at which the fibres were formed. Follicles therefore differ in the variations of the rate at which they form their fibres, and these variations interacting with a constant crimping mechanism, cause the differences in the shape of fibres.

These variations in fibre growth rates are related to the sequence of development of the follicle group, a therefore a primary problem is the explanation of this relation. An attempt will be made below to formulate such an explanation by considering the follicle group in terms of the competition of follicles for a limited amount of fibre substrate.

Competition between follicles for fibre substrate.

Galpin (1947) has established that a specified region of skin is capable of forming only a limited amount of fibre. This limitation is defined by the area (A) of the region and the feed level (F). The relation of area to weight of fibre (W) can be stated as,

$$W = kA,$$

where k is a coefficient defined from the feed level as,

$$k = f(F),$$

where f(F) tends to a limit (K) when the feed level is sufficiently high. K is a constant between sheep in Galpin's material.

This can be stated in terms of a hypothetical fibre substrate. The amount of fibre substrate available to a unit of skin is independent of the follicle density, and is a constant independent of feed level when that is sufficiently high. Consequently, the amount of fibre substrate available to a follicle is determined (i) by the feed level, and (ii) by the follicle density.

As a simplification it will be assumed that the feed level is sufficiently high for k to have reached its limit value, K. Variations of fibre growth rates by individual follicles will therefore be entirely due to variation in the neighbouring follicle density. This raises two questions, (i) is there any limit to the rate at which sheep follicles can form their fibres, i.e. to the amount of fibre substrate that they can use, and

(ii) do adjacent follicles obtain equal or different proportions of the available fibre substrate.

There does not seem to be any physiological limit to the rate at which follicles can form their fibres, since some breeds form fibres which are up to five times longer than that found in other breeds.

In answer to the second question, follicles obviously obtain different fractions of the available fibre substrate since adjacent follicles often form their fibres at markedly different rates. This means that follicles differ in some factor which defines the proportion of fibre substrate which they obtain. This factor will be given the name ' efficiency' and represented by the symbol (e). The efficiency of a follicle is considered as a basic property which determines the relative rate of growth of its fibre. The actual rate of growth is decided by the food level, follicle density, and efficiencies all interacting.

The rate at which a follicle forms its fibre is related to the age of initiation of that follicle. The e of a follicle is therefore also related to the age of initiation of the follicle.

The relative growth rates of fibres give some idea of the properties of follicle efficiencies. These appear from qualitative experience to (i) be invariant with age , and (ii) to be independent of food level. These points will have to be examined qualitatively.

The concept of efficiencies can be so stated that an expression can be derived which relates the weight of fibre formed by an individual follicle to the weight of fibre formed by the region. The expression given below defines this partition of the available fibre substance.

$$w_1 = \frac{e_1}{\Sigma E}.W = \frac{e_1}{\Sigma E}.kA.$$

where w_1 is the weight of fibre formed by an individual follicle whose efficiency is e_1 and W is the total weight of fibre formed by the region. e is the sum of the efficiencies of all the follicles in the region.

This expression gives the rate at which a specific follicle forms its fibre if both Σe and A are constant. Since both of these vary during the development of the follicle population it should be possible by definition of Σe and A as a function of time, to calculate w_1 as a function of time. Since the present approach is primarily qualitative the rather clumsy method of graphic analysis has been used. In figure 25 values of $\Sigma e = f(t)$ and $A = f(t)$ are shown, and from these the rate at which a specific follicle forms its fibre, i.e. $w_1 = \frac{e_1}{\Sigma E}.A$ This has been done for several follicles and their patterns of fibre growth rates are shown in figure 26.

For this construction it is necessary to define $\Sigma e = f(t)$ and $A = f(t)$. The latter cannot be obtained from direct data since none are available for both the pre- and post-natal periods. Since only a qualitative determination is required, use can be made of the data of increase of body weight: body weight being related to body area by simple regressions. In figure 24 the data of Winter and Feuffel (1937) and Foster (1926) on the Shropshire breed are added to give the relation of body size to age. Body area is closely related to body weight and can be stated within reasonable limits as the 2/3 power of weight. The data shown in figure 24 therefore define a function relating body sise to age which can be used as an approximation of the relation of body area to age. The estimate of $A = f(t)$ given in figure 25 is taken from these wight data; the main point being that area increases at a much faster rate after birth.

The expression $\Sigma e = f(t)$ is the result of the interaction of two separate expressions, $(e) = f(T)$ and $(n) = f(t)$, where n is the follicle number. The time at which a follicle is initiated is given the symbol (T) to differentiate it from age which is given the symbol (t). It is therefore necessary for the definition of the rate of increase of the sum of efficiencies, to define both the rate of increase of the follicle number and the relation between the age of initiation of a follicle and its efficiency, since

$$\Sigma e = n_1 e_1 + n_2 e_2 + n_3 e_3 \ldots\ldots\ldots$$

where n_1 is the number of follicles initiated at an age T_1 when the efficiency is determined as e_1, and etc for n_2, n_3,....

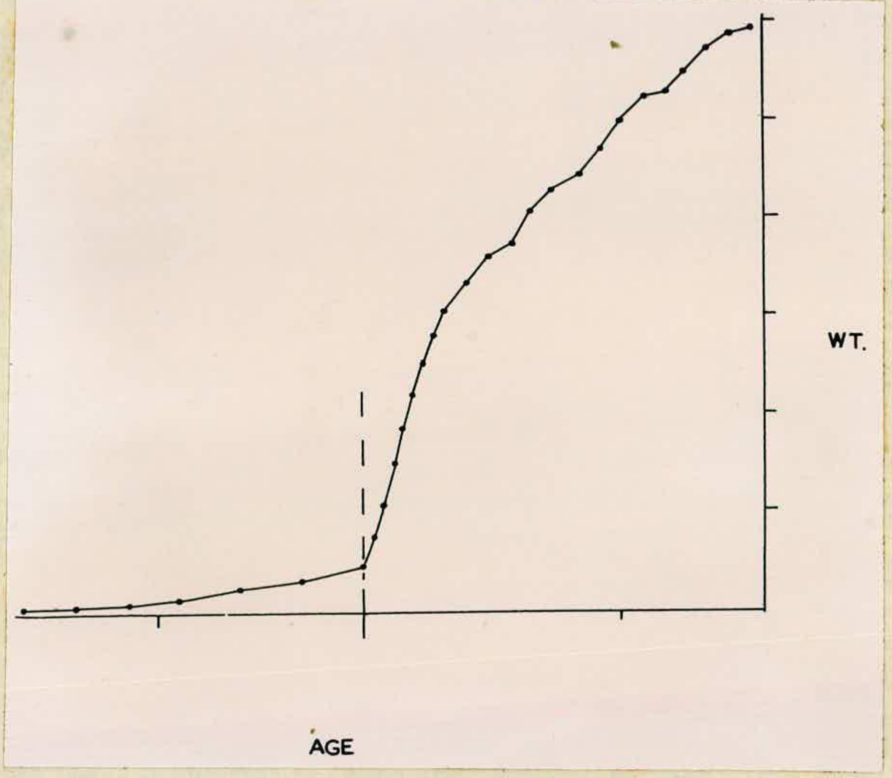

Figure 24. Body weight plotted against age for the Shropshire breed, to show how the rate of increase becomes greater after birth.

As a simplification, the following discussion is restricted to a single follicle group. The rate of increase of follicle number can be defined with sufficient precision for the present analysis from the data of Wildman (1932), Galpin (1935), Carter (1943), Carter and Hardy (1949) and Ross(section3 above).

The relation $\sum e = f(T)$ varies with fleece type, and as will be shown below, provides a precise statement of Dry's 'pre-natal check'. In the present construction, a linear negative relation is used which approximates to that which would hold for a coarse type of fleece.

Given $(n) = f(t)$ and $(e) = f(T)$ then $\sum e = f(t)$ can be found from the sequential addition illustrated below.

$$(\sum e)_{t_1} = n_1 e_1$$

$$(\sum e)_{t_2} = n_1 e_1 + n_2 e_2$$

$$(\sum e)_{t_3} = n_1 e_1 + n_2 e_2 + n_3 e_3$$

etc.,

This completes the information necessary for the calculation of $w = f(t)$, which is done by solving the expression,

$$w = \frac{e_1}{\sum e}.A$$

for a series of times, and then sequentially adding these values, giving the rate of increase of the total weight of fibre formed by a specific follicle. This has been done from the values of $\sum e = f(t)$ and $A = f(t)$ shown in figure 25. The calculated fibre growth rates are shown in figure 26.

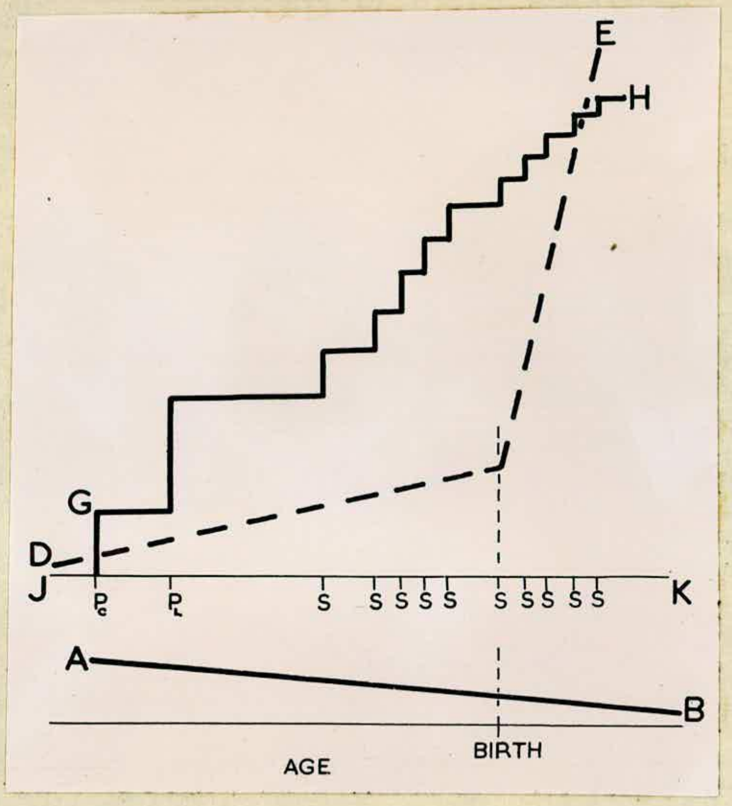

Figure 25. The values of (e) = f(T), A = f(t), n = f(t) discussed in the text are shown, with the value for Σe = f(t) found from the interaction of the functions of (e) and (n). A-B is the relation of efficiency to age of initiation (e = f(T)). D-E is the value taken for A = f(t). J-K is the base line of the main figure and along it are shown the rate of increase of follicle number (n). The zig-zag line, G-H, is the value of Σe = f(t), i.e. the rate of increase of the total efficiency of the whole follicle group.

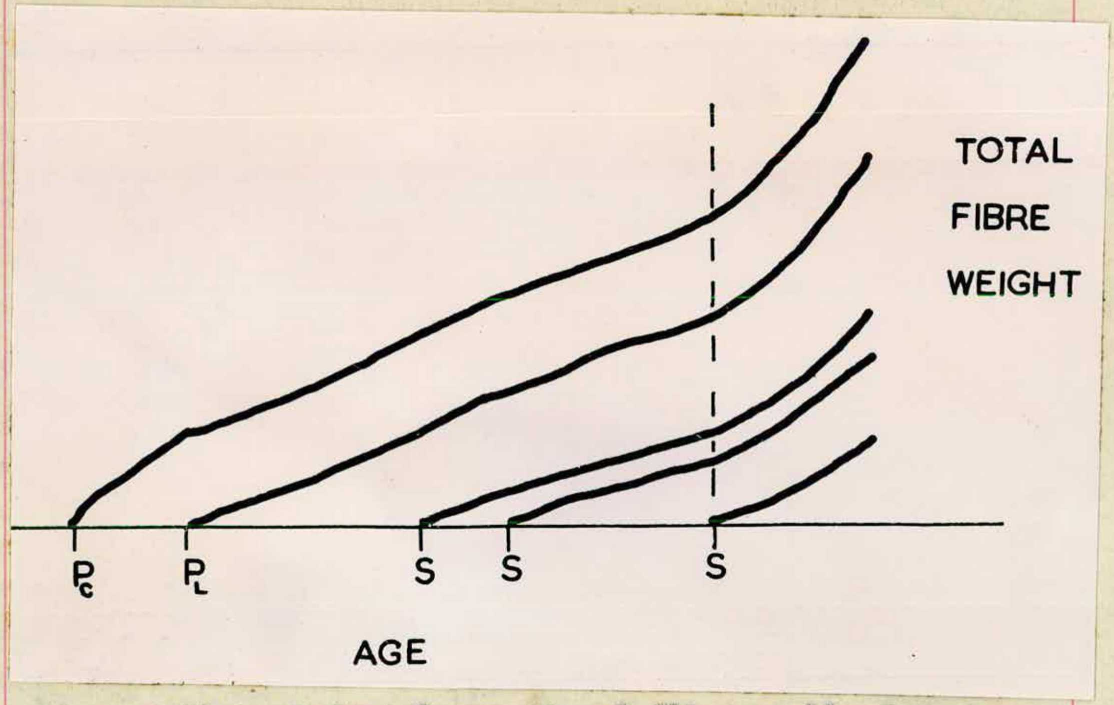

Figure 26. Rate of growth of fibres calculated as stated in the text from the data expressed in figure 25. The main points are the decrease of the rate of growth of the Pc fibre when the Pl follicles commence their fibres, and

the increase in the rate of formation of all fibres which occurs just after birth.

Since Galpin (personal communication) has shown that the measurement of fibre growth rate as length, weight or diameter can by simple transformations give equal estimates i.e. they all measure the same basic factor, it follows thats the rates shown in figure 26 although stated as fibre weight, can be directly compared with the rates of fibre growth given as length in figure 20. The comparison of these two patterns of fibre growth rates show them to be almost completely identical. Since these were derived from independent premises, their identity gives very strong support to the validity of their derivation.

One difference remains which can be removed by a simple modification of the efficiency concept. This difference is the progressively decreasing rate of increase of length of the first crimp of the P_c fibre. A more logical statement of efficiencies is that the follicle commences its formation of fibre at a low efficiency which then increases until it reaches the limit for the follicle. It is this limit efficiency which has been used above, defined by the function $(e) \approx f(T)$. This change in the concept of efficiencies is illustrated in figures 27 and 28 which are otherwise identical to figures 25 and 26 but stated for the P_c fibre only. The rate of growth of fibre by the P_c follicle which has been calculated from this new definition of efficiencies, shows a definite curvilinear decrease at the time when the P_1 follicles are commencing the formation of their fibres. A very slight re-definition thus removes the discrepancy between the pattern of fibre growth rates derived from the shape of fibres, and that calculated from the efficiency concept.

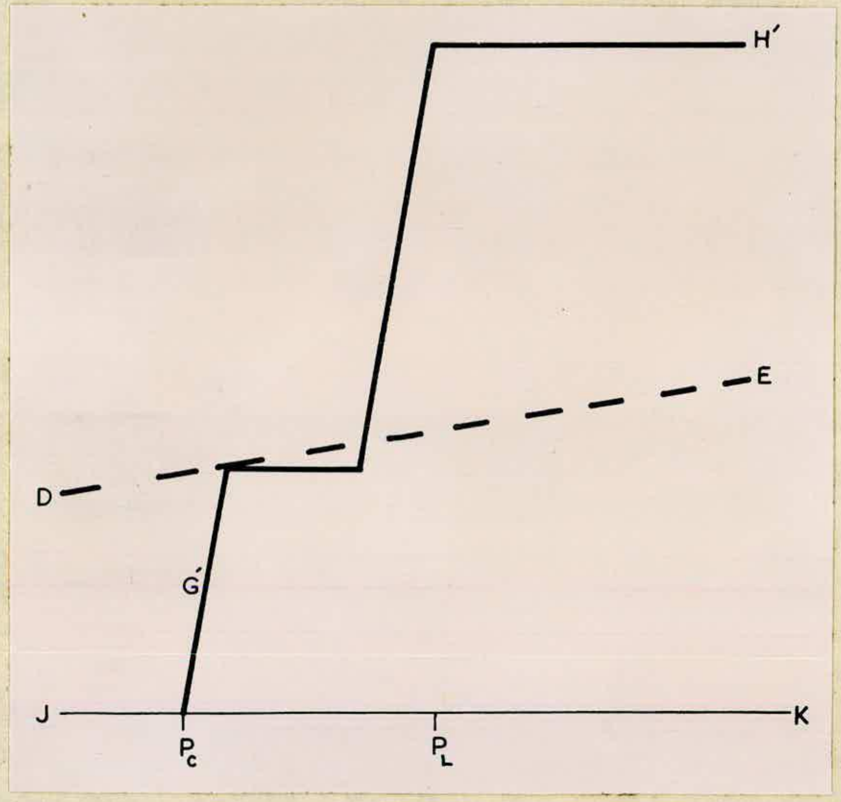

Figure 27. Extension of the model shown in figure 25 based on the follicles reaching their limit efficiency gradually over a short time period. This appears on the diagram as a slope of the steps of increase of Σe which are vertical in the previous construction.

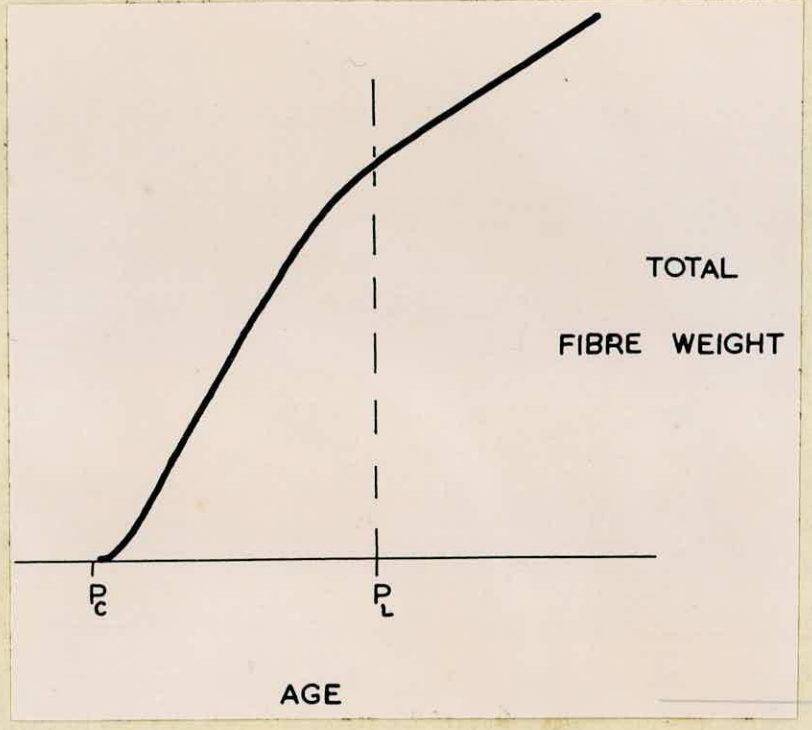

Figure 28. Growth rate of the P_c fibre calculated from the model shown in figure 27, illustrating the gradual decrease of growth rate, similar to that deduced from the shape of the sickle tip in figure 19.

It is not suggested that this constitutes a proof of the concept of efficiencies, but thhe agreement fully demonstrates the applicability of this approach to the problems of wool biology.

It is stated above that the relation $(e) \simeq f(T)$, gives an exact statement of the 'pre-natal check'. In figure 29 are shown a number of values of this function which essentially differ in the efficiencies of the first formed follicles. They form a related sequence in which the second curve is the same as that used in the construction shown in figure 26.

If the other curves are substituted for this curve in analogous constructions, then the resultant growth rate patterns are found to form a series which corresponds to the series from which Dry deduced the occurrence of the ' pre-natal check '. The ' pre-natal check ' on this hypothesis appears as a factor which determines the value of the function relating (e) to (T). In the next paper the effects of the N and nr genes on the fleece will be analysed in terms of their primary action being to cause the substitution of different values of the (e) = f(T) function.

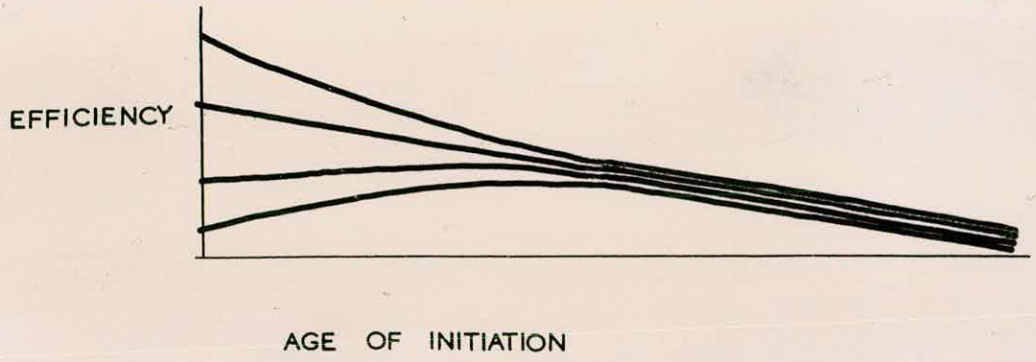

Figure 29. Curves of various efficiency functions which will result in typical patterns of fibre growth rates, from that normal to a fine fleece (bottom line) to that normal for a coarse fleece (top line).

Conclusions.

The initial basis for the present analysis was the occurrence of differences in shape between fibres. This led to the derivation, on the basis of researches by many workers in several fields of wool biology, of an expression which integrates the main determinants of fibre growth rates. These are,

(1) the feed level (F).
(2) the relation (k) = f(F).
(3) the rates of increase of skin area $A = f(t)$.
(4) the rate of increase of follicle number $n = f(t)$.
(5) the relation of the efficiency of a follicle to its age of initiation (e) = f(T).

The expression derived in the preceding section contains a partition term $e_1/\Sigma e$. This is based on a new concept of fibre development, that of the efficiencies of follicles. The primary questions which arise from this work are (i) what methods are available to measure follicle efficiencies, and (ii) what are the physical bases of these efficiencies.

The measurement of efficiencies presents a very complicated problem which could be possibly solved by the use of dye-banding methods. Essentially a dye band is applied to a staple at or very near skin level. After a period the staple is either cut off at skin level or a second dye band is applied. The parts of the fibres between dye bands, or between the cut base of the staple and the dye band will all have been formed over the same period and therefore the rates of formation of fibres can be stated weight
w_1/W, where w_1
relative quantities;

of fibre formed by a single follicle, and W is the total weight of fibre formed by the region. Since w_1/W is related to $e_1/\Sigma e$, this method gives an estimate of the partition coefficient , but it does not allow an estimate of the absolute value of the efficiency of a follicle. This can only be determined from measurement of the physical basis of efficiency, which may be indicated from some work of Galpin (personal communication). She has shown that the rate at which a follicle forms its fibre is related to the depth to which it extends into the skin. The depth of a follicle will be closely related to its area(α) It is possible to consider the efficiency of a follicle as its area, since if the total available amount of fibre substrate is determined in some way by the inter-follicular tissue, then the amount obtained by a follicle will be correlated with the area of that follicle, and defined by the total ratio of its area to the total area of all the follicles in the competition region i.e. it will be defined from $\frac{\alpha_1}{\Sigma\alpha}$

Acknowledgements.

I am indebted to Dr. F.W.Dry and my fellow students, Miss J.M.Ross and Mr.G.M.Wright, for both practical assistance and vigorous discussion during the first phase of my introduction to wool biology. The assistance of Dr. Palmer and her associates enables me to proceed with this analysis, since it is based to a great extent on their work which was discussed very freely with me. I am grateful to Mr. G.Knight and Mr.J.Armstrong for technical assistance. The second section of the work was completed at the Institute of Animal Genetics, whilst the author held a maintenance grant from the Agricultural Research Council.

8. Manifold effects of the N and nr genes (A.S.Fraser)

The first paper of this series detailed the evidence showing that the N and nr genes are the main genetic determinants of the differences between the N-type and non-N-type strains of the Romney Marsh breed of sheep. Three strains of N-type sheep exist of which two carry the N gene,the other carries the nr gene. As far as they can be traced the two 'dominant' stocks are independent. They are called the 'Nielsen' and 'Massey' stocks respectively. The parentage of the initial 'recessive' ram cannot be traced rigourously, and he may be descended from the 'Massey' stock. In the following analysis several comparisons will be made of the effects of the N and nr genes. These are based on the 'Nielsen' and 'recessive' stocks, since these have completely independent origins whereas the 'Massey' and 'recessive' stocks may be related. If both the N and the nr genes similarly differ from the normal breed in some character, it is unlikely that this character is determined independently of the N and nr genes i.e. it is unlikely that the two independently originated stocks should differ from normal by genes other than the N and nr genes. If this character should be dominant in the N stock, and recessive in the nr stock, then it is almost certain that the character is an effect of the N and nr genes i.e. the actions of these genes are similarly pleiotropic. This method of describing the effects of these genes is unorthodox and obviously not rigorous. In sheep the orthodox methods of genetics often cannot be applied, since relatively simple experiments would extend over the life term of a worker.

Although the N-type flocks differ from the normal breed in a number of characters, the original identification and genetic analysis was based solely on the single character, of the abundance of halo-hairs in the birthcoat, which is very high in N-type lambs, very low in non-N-type lambs. As the work progressed and the size of the flocks increased, it became apparent that these genes had effects other than that on the halo-hair abundance. The relationship of these secondary characters to the halo-hair abundance was very close between stocks, and genetically in outcrosses the characters remained linked, and it became obvious that at some time a study would be necessary to determine the mechanism of these manifold effects. Therefore Dry (unpublished) extended the flock recording system to include all characters in which N-type differed from non-N-type. These records have provided the core of data for the present analysis.

The various characters which are affected by the N and nr genes are (1) halo-hair abundance, (2) fibre type constitution of the birthcoat, (3) the medullation, size of crimps, and length of the fleece, (4) the frequency of shedding of fibres as kemps, (5) the occurence of brown pigment in the tips of birthcoat fibres, (6) the occurrence of horns. In preceding papers of this series the halo-hair abundance, the frequency of shedding as kemps, and the occurrence of horns have been shown (1) to occur in the N-type but not in the non-N-type flocks, (2) to be 'dominant' in the N stocks, 'recessive' in the nr stock, and (3) to remain 'linked' with the high halo-hair abundance in several consecutive outcrosses. This can be taken as reasonable proof that these characters are aspects of the action of the N and nr genes. It remains to consider the characters of the full fleece; medullation, size of crimps, and length, and of the brown fibres of the birthcoat. It is also necessary to expand the analysis of the fibre type constitution of the birthcoat.

As Gruneberg (1938) has emphasised, the manifold effects of genes are almost certainly due to the developmental complication of initially unitary actions i.e. each gene has a unitary primary action which may react with the normal sequence of development to cause a number of apparently separate effects. The complex effects of the N and nr genes are considered below in terms of their having an initial effect which is primary to all the effects listed above.

I. <u>Birthcoat and fleece</u>.

(a) Fibre types of the birthcoat.

The increase of halo-hair abundance caused by the ^{N} and nr genes is only the most visible effect of these genes on the birthcoat, and can be taken as an aspect of the more complex changes of the constitution of the birthcoat. This has been shown by Dry (1934) who found that the increase of halo-hair frequency is an aspect of complex changes of all the fibres of the birthcoat. He did not consider the follicle population in his analysis of the fibre types of the birthcoat, and it will therefore be necessary toextend his work, since Fraser, Ross and Wright (section 4 above) have shown that the different types of follicles which comprise the follicle population, differ in the types of fibres which they can form.

Dry and his co-workers have over the last twenty years built up a very detailed description of the differentiation and growth of the fleece. This is based on the classification of birthcoat fibres into types, formulated by Dry (1934). This classification is made primarily from the characters of those parts of fibres which are formed before birth. All of the fibres do not start growing before birth, and those which are initiated after birth are grouped as a single type, the histerotrichs, which show little variation, all of them being fine without a definite shape to their tip.

The fibres which commence growing before birth all have definite shapes to their tip curls, and the shape of the tip curl is one of the major criteria of Dry's classification. Some fibres have a sickle shaped tip curl, others have a regularly curled tip. On the basis of the shape of the tip curl it is therefore possible to separate the birthcoat sample into three groups of fibres: the sickle group, the curly-tip group, and the histerotrich group. The first two groups are further separated into types on the basis of medullation.

The sickle group includes five main types. These are (1) the halo-hairs (H-H) which are completely medullated, (2) the super-sickle A' type (SSA') which are completely medullated apart from a break usually only a millimetre or two long which occurs at the birth point, (3) the super sickle B type (SSB) which have a break at the neck of the tip curl as well as at the birth point, (4) coarse sickle tips (Sk_c) which are medullated only in the sickle tip, (5) fine sickle tips (Sk_f) which are completely fine. The last two types are usually grouped together as sickle tips, which may or may not be medullated in the tip curl, but are otherwise fine in the pre-natal portions of the fibre. The classification is based only on those parts of the fibre formed before birth and all of these types may be medullated in the parts formed after birth.

(Sutherland,1940, has considerably extended the fibre type classification on the basis of the occurrence of medulla in the post-natal portions of fibres).This extension is not used in the present analysis. The separation of the sickle group into types is illustrated in figure 38.

These five types of sickle fibres are by definition discrete morphological units, but Galpin (1936) has emphasised that they are actually ranges of a continuous sequence from the completely medullated halo-hairs to the completely fine sickle-tips. A similar sequence is found in the curly-tip group ranging from the completely medullated types to the completely fine types. This range is divided into two types: the hairy curly-tips (HCT) and the plain curly-tips (PCT). The former are medullated, the latter are not.

The plain curly-tips can be divided into a further pair of types. Dry (1934) noted that in fine birthcoats where all the curly-tips were of the plain type, an obvious separation could be made on the basis of the size and number of crimps in the pre-natal portion. Some curly-tips were fine and had a large number of very small crimps. He termed these the checked curly-tips. The remainder of the curly-tips differed qualitatively from these in that they were coarser and had a smaller number of much larger crimps.

He termed these the peak curly-tips. The separation of the curly-tip group into hairy-curly-tips, peak curly-tips and checked curly-tips is illustrated in figure 30.

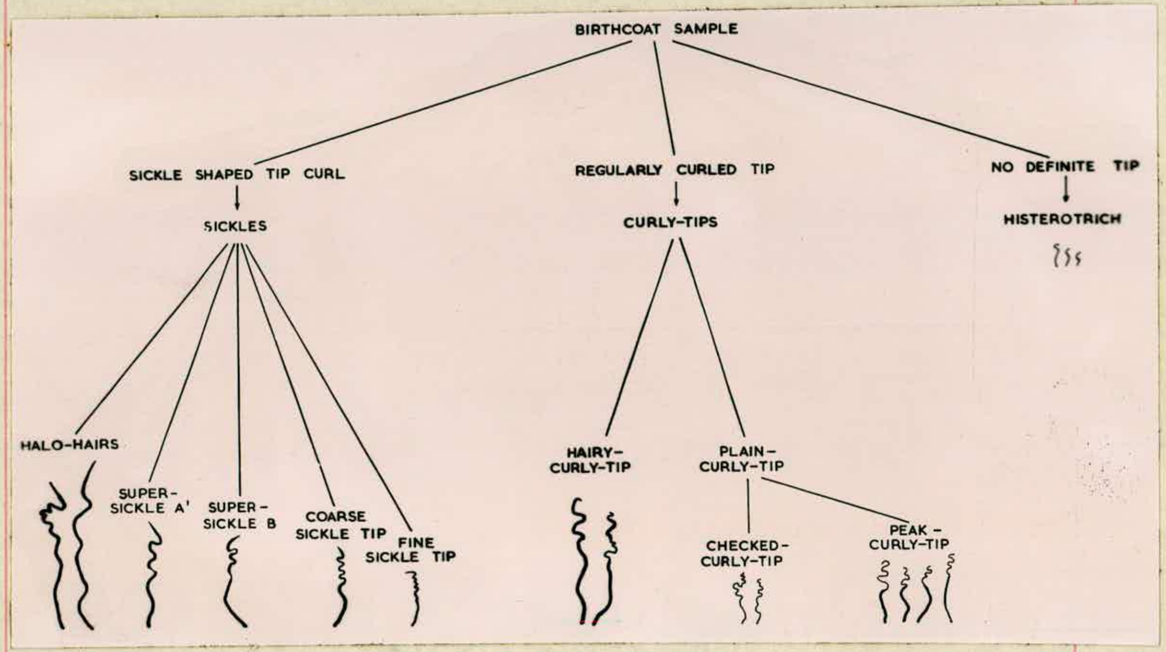

Figure 30. Classification of fibres on the basis of the shape of the tip, and the occurrence of medulla. The relative thicknesses of medullated and fine regions have been exaggerated. Compare this diagramatic representation with the drawings of actual fibres given in figures 14-17, 21-22 and 31.

This classification defines nine distinct types of fibres. Having shown how Dry separated a sample into different types of fibres, the next step is to show the relationship he found between halo-hair abundance, coarseness and fibre type constitution in the birthcoats of Romney Marsh lambs.

Halo-hair abundance	Type of fibre							
	Sickle group				Primary curly group		Secondary group	
	H-H	SSA'	SSB	Sk	HCT	checked-CT	FCT	Hi
HIGH	8.99 7.05	1.10 1.40	0.15 1.12	0.00 0.80	19.6 13.7	None "	55.8 59.7	39 39
MEDIUM	0.85	1.07	3.45	7.95	-	(Not seperable)		40
LOW	0.09	0.16	1.69	11.06	None	Approx. 20%	Approx. 30%	38
	P_c				P_1		S_1 and S_2	

Table 25. % frequencies off fibre types in N-type samples(high halohair abundance) and in non-N-type samples(medium and low halo-hair abundance).Analysed by Fraser and Wright from the data of Fraser, Ross and Wright(section 4) and Goot(1940).

(b) Halo-hair abundance and fibre types.

The halo-hair abundance is an eye judgement of the frequency of halo-hairs. It is closely related to the coarseness of the birthcoat. This is expected since the greater part of the medullation (coarseness) occurs in the halo-hairs. Similarly the halo-hair abundance is related to the fibre type constitution. In birthcoats with a high abundance, the sickle group fibres are predominantly of the halo-hair type, and the curly-tip group are predominantly of the hairy- and peak-curly-tip types. In birthcoats with a low abundance the sickle group fibres are predominantly sickle-tips, coarse or fine and the curly tips are of the checked- and peak-curly-tip types. The relation of fibre type constitution to Halo-hair abundance will be considered in fair detail since their understanding is necessary for the appreciation of the N-type analysis.

If a number of birthcoat samples are selected to represent the range from high to low halo-hair abundance, and these samples are seperated into the different fibre type groups, it can be seen that some types of fibres occur frequently only in samples from one part of the range of abundance. This has been studied in detail by Goot (1940) and he gives the essence of his results in a table relating fibre type constitution to coarseness (Goot, 1941). Table 24 below is a modification of this to emphasise the replacement of one type of fibre by another with change of halo-hair abundance.

These changes of fibre type constitution will be readily understood, if considered in terms of the follicle population. The constitution of the follicle population is not affected by the N gene, and presumably, it is also not affected by the nr gene (Ross, section 3 above). The separation of the follicle population into different types of follicles underlies the separation of the birthcoat into different groups of fibres, since Fraser, Ross and Wright (section 4 above) have shown that each type of follicle forms only a few of the possible types of fibres. Therefore the variation in occurrence of certain types of fibres can be explained by a certain type of follicle forming one type of fibre in a coarse birthcoat and another type in a fine birthcoat,i.e. one type is replaced by the other. Consider the changes shown in table 24 from this aspect. The sickle group of fibres consists almost entirely of halo-hairs in the coarse birthcoats. As the coarseness of the birthcoats decrease the frequency of halo-hairs also decreases, these being replaced by less medullated types i.e. super-sickles and sickles, until in fine birthcoats the sickle group consists entirely of sickle-tips. Correlated with these changes in the make-up of the sickle group are analogous changes in the structure of the curly-tip group. In coarse birthcoats the frequency of hairy curly-tips is high, and these are very heavily medullated. As the coarseness decreases these are replaced, first by less heavily medullated hairy-curly-tips and then by fine curly-tips, which are replaced by checked curly-tips. The two substitutions which have been studied in detail, of sickle-tips for halo-hairs and of checked curly-tips for hairy-curly-tips, are fully explicable if the formation of each pair is restricted to a specific type of follicle i.e. if halo-hairs and sickles are formed by one type of follicle, and hairy-curly-tips and checked curly-tips are formed by another type of follicle. This has been shown to be true by Fraser, Ross and Wright (section 4 above). The classification of follicles has been considered in detail by Ross(section 3 above) and will not, therefore, be considered here.

Three main types of follicles characterise the follicle population. Nine main types of fibres comprise the fibre population. Fraser, Ross and Wright(section4) following Rudall (unpublished) and Ross (section 3) have shown the relationship between these two types of populations. The primary central follicles form only sickle group fibres, and are the only follicles which form these types. The secondary follicles form only plain curly-tips and histerotrichs, depending on whether their fibre is initiated before or after birth. The primary lateral follicles form only hairy curly-tips or checked curly-tips and in the N-type to non-N-type range are the only follicles to form these types.

The changes of fibre type constitution shown in table 24 can now be readily understood. The relation of fibre type to follicle type is shown at the bottom of the table. As the halo-hair abundance decrease, the primary central follicles form fibres of the sickle-tip instead of the halo-hair type, and the primary lateral follicles change from the formation of hairy-curly-tips to the formation of checked curly-tips. The secondary follicles form the same types of fibres regardless of the halo-hair abundance, namely, peak-curly-tips and histerotrichs. Changes do occur in the fibres formed by secondary follicles, but these are not measurable by the fibre type method. Various approximate observations suggest that the size of crimps of peak-curly-tip fibres is greater in samples from low abundance animals. Also the diameter of histerotrichs appears to be larger in animals of low abundance.

Before proceeding to the analysis of these changes, their illustration is necessary. In figure 31 are shown a number of fibre type sequences taken from the standard back samples of lambs whose birthcoats ranged from a very high to a very low halo-hair abundance, all of the Romney Marsh breed, either N-type or non-N-type. The samples were taken about four weeks after birth. The genotype is shown beside each sample. It should be emphasised that sampling occurred over a fairly wide age range, and therefore some of the differences in length between samples may be due to differences in the age of sampling; the relative differences of length between types of fibres are the most important in this comparison.

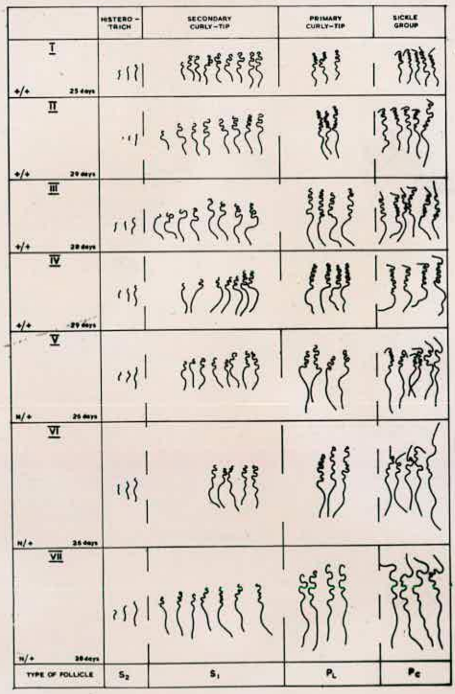

Figure 31. Number of fibre sequences separated into sickle, primary and secondary curly-tips and histerotrichs. Each sample is from a lamb of different halo-hair abundance.

The relationship of fibre type constitution to halo-hair abundance illustrated in figure 31 is a constant feature both in N-type and non-N-type. Therefore the following discussion of the mechanism underlying this relationship holds equally for both.

The changes of fibre type constitution are best considered separately between fibres formed by the same type of follicle. In P_c fibres there is no change in the shape of the tip curl which is sickle shaped in all types, followed by a region of smaller crimps, followed by a region, that formed after birth, of large regular crimps. The changes which do occur in P_c fibres with increase of halo-hair abundance are (1) increase in length, (2) increase in size of all crimps, (3) increase in the occurrence of medulla. Similarly no change occurs in the overall shape of the P_1 fibres: they all have a tip region of small regular crimps, and a region, that formed after birth, of large regular crimps. The changes which occur in these fibres with increase of halo-hair abundance are the same as in the P_c fibres. The differences between the fibres formed by these two types of follicles is due to the difference in shape i.e. P_c fibres have a sickle shaped tip curl, whereas the P_1 fibres have a regularly curled tip. This is on a qualitative basis since the increase in length etc. caused by the N and nr genes, is , although common to both types of follicles, greater in the P_c fibres. This point will be discussed below.

The secondary follicles as stated above form fibres which are all of the same type regardless of the halo-hair abundance of the sample from which they were taken. However they do show differences in the crimp size and length, which are unexpectedly in the opposite direction to those which occur in P_c and P_1 fibres. As the halo-hair abundance increases the length and crimp size of S fibres decreases, instead of increasing, as in the P fibres. This is a very important point as will be seen from the discussion of the 'pre-natal check' and 'competition' hypotheses of fibre growth determination. This point is not very well indicated in the samples shown in figure 31 since the samples were deliberately taken at random. Passing from the grade I sample to the grade VII sample it can be seen that the crimp size of the secondary curly tips is at first larger than that of the primary curly tips, and later the same as the primary curly-tips and finally, in the coarse samples, smaller than the crimps of the primary curly-tips.

The changes of crimp size can be taken as corollaries of the changes in the length growth rates since Barker et al. (see Barker 1932) have shown thhat the crimp number is independent of the length growth rate, and therefore the crimp size is directly correlated with the length growth rate. This correlation is not complete (Lang 1947) but it is sufficient to allow explanation of the changes in crimp size as due to the changes in length growth rates. It can be argued that medullation is similarly a direct corollary of fast growth rates, and therefore that the fibre type system measures primarily changes of fibre growth rates. This point will be considered further below.

The analysis of the fibre type sequences shown in figure 31 should therefore be made in terms of the fibre growth rates, and it would be desirable to compare the lengths of P_c,P_1,S_1 and S_2 fibres in birthcoats of verying halo-hair abundances. This however would involve a very large amount of measuring of fibres all taken at the same age, from lambs of the same wt. etc. Since such samples are not available, the following diagram must be taken as hypothetical, even though it is based on many analyses of birthcoats of Romney lambs. It shows the average length of Pc, P_1,S_1 and S_2 fibres from samples at four different levels of halo-hair abundance. In this diagram four lines, 1-1,2-2,3-3,4-4, are shown joining the estimated average lengths of fibres from the four types of follicles. Each line represents a different level of halo-hair abundance, with 1-1 the highest, 4-4 the lowest.

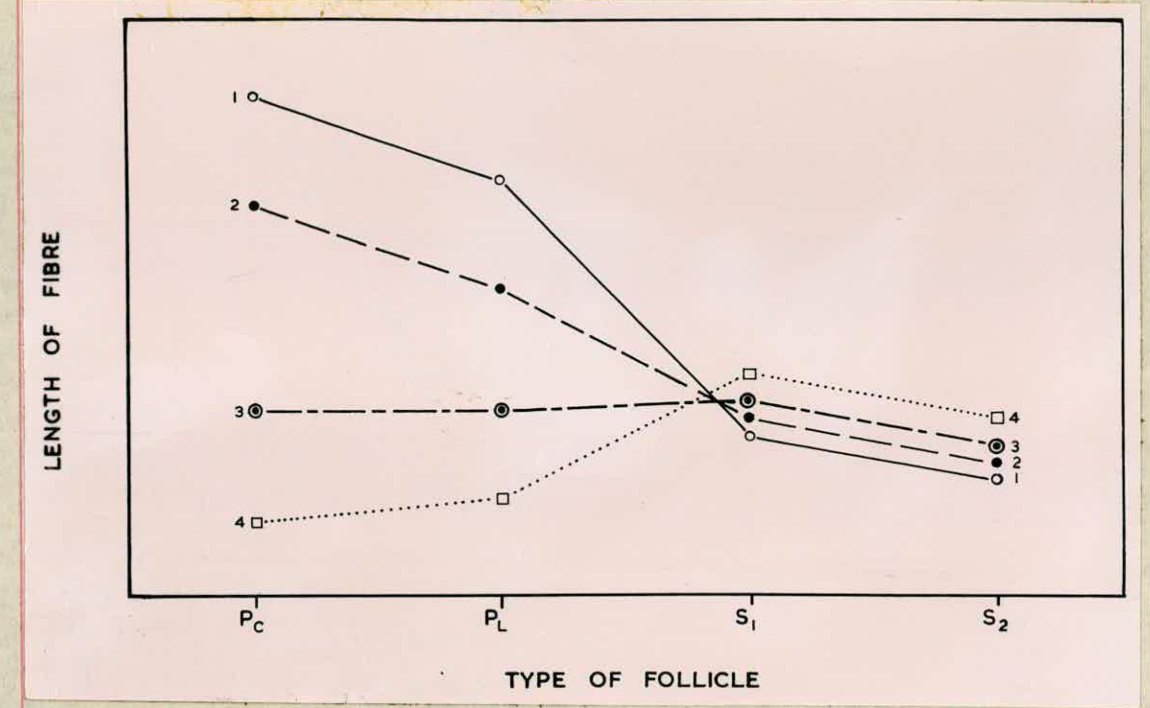

Figure 32. Relationship of the length of fibres to their age of initiation for a series of types of birthcoat, fromm 1-1, very fine, to 4-4, very coarse, showing the decrease in length of the first fibres, and the compensatory increase in length of the last fibres.

This diagram shows that between the samples, the lengths of the P fibres decrease from high to low abundance samples, and that there is an increase of the lengths of the S fibres; the latter is much smaller than the former. Dry (1934) has concentrated on the former aspect, namely, the changes in length of the P fibres, without giving detailed attention to the changes which occur in the S fibres. He describes the decrease in length of the P fibres as due to a factor, the 'pre-natal check' which is postulated to act at an early enough stage to affect only the P fibres. The finer a birthcoat, the greater is the intensity and extent of the pre-natal check, where intensity measures the drop in growth rates and extent measures the proportion of fibres affected. This concept has been useful but it suffers from the absence of ideas on the physical basis of the check, and more forcibly it does not include an explanation of the changes which occur in the S fibres. Since these changes are in the opposite direction to those which occur in the P fibres, it is obvious that the 'check' hypothesis requires drastic revision. Such a revision has been formulated by Fraser(section 7 above) and this will be considered in the next part below.

(c) Efficiency and competition concept of fibre growth rates.

The efficiency concept of fibre growth (Fraser, section 7 above) is based on the occurrence of competition between adjacent follicles for any fibre substrate which is available. This competition is postulated to be in terms of the 'efficiencies' of follicles where efficiency is a quality which determines the proportion of the fibre substrate which the follicle shall receive. The efficiency concept was derived from the analysis of the shape of fibres, in which the aim was to explain why some follicles form fibres with sickle shaped tips, whereas other follicles form fibres with regularly curled tips. This study showed that if follicles have fixed efficiencies then the difference between follicles which form fibres with sickle shaped tips from those which form fibres with regularly curled tips, can be explained as due to differences in the intensity of competation which occur during the formation of the follicle group. In the course of this study it was found that the 'efficiency' concept provides a very adequate statement of the 'pre-natal check'. This point was not treated in detail since it was obvious that such treatment would be more usefully placed in the present paper.

The efficiency (e) of a follicle is a quantity which is determined during the formation of the follicle. Once a follicle is fully determined it is considered to have a fixed efficiency. This means that some developmental sequence determines the efficiencies of follicles, and as will be seen later, the 'pre-natal check' is an aspect of this sequence.

The symbols used below have been defined previously (Fraser, section 7 above) and therefore will not be discussed further here.

Although the efficiency of a follicle is a fixed quantity, differences of efficiency occur between follicles, and these differences aret the basis of the differences in the rates at which fibres are formed. Efficiencies are correlated with the age of differentiation of the follicles. The function which relates efficiency to age of differentiation varies between sheep but the possible values of such variation are limited since only certain values will describe the variations of growth rate patterns which do occur. These all belong to the simple family of curves which are shown in figure 33. Each curve represents the value for one type of fleece.

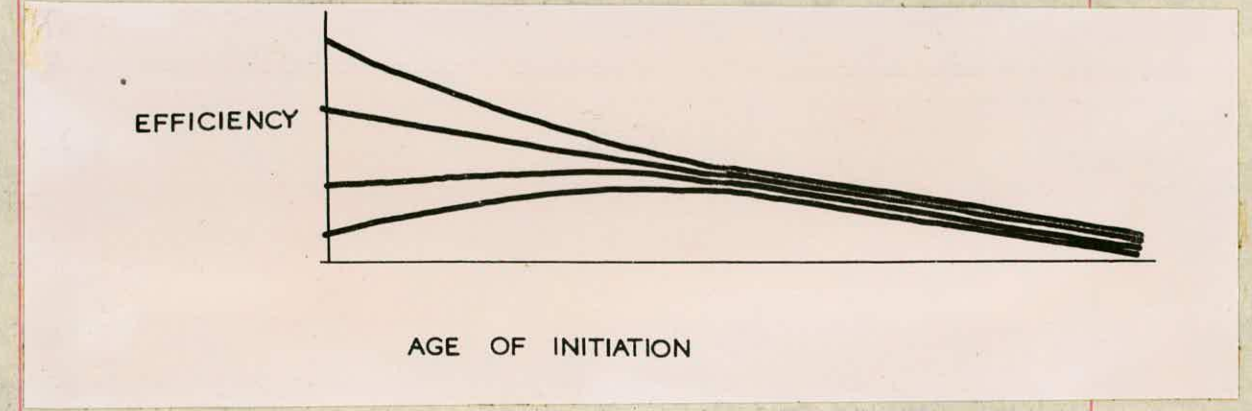

Figure 33. Curves relating the efficiency of follicles to their ages of initiation. Each curve represents one type of fleece

A similarity exists, as expected, between these curves of efficiency to age of differentiation, and those of length to age of differentiation given in figure 32. Certain differences are however obvious. In figure 32 the curves cross over each other, whereas in figure 33 the efficiency/age of dâfferentiation curves do not cross over each other. A simple arithmetric examination shows how the competition concept gives an explanation of how the simple curves of efficiency to age of differentiation cause the more complex curves of length to age of differentiation. For simplicity consider that follicles are initiated at only four periods, and that one type of follicle is initiated at each period. Different numbers of each type of follicle are formed in the ratio of 1:2:6:6 for the Romney breed (Ross, part 3 above). Consider the final efficiency equations when two different efficiency to age curves are examined; the first when the efficiencies are 10,8,5,3 respectively for the P_c, P_1, S_1 and S_2 follicles; the second when the efficiencies are 2;3;4;2. respectively. If the weight of available fibre substrate is invariant, then the proportion which a follicle obtains will be e/Se where Se is 74 for the first curve, and 44 for the second curve. The values of e/Se for each type of follicle are 0.135, 0.108, 0.067, 0.040 for the first curve and 0.045, 0.068, 0.090, 0.045 for the second curve. This comparison of the effects of the two curves on the rates at which the follicles form their fibres shows that even though the efficiencies of S_1 and S_2 follicles are lower (5...4 and 3...2 respectively) they form their fibres at a faster rate (0.067...0.090 and 0.040...0.045 respectively). In other words the growth rate to age of differentiation curves cross over. This is illustrated in figure 34.

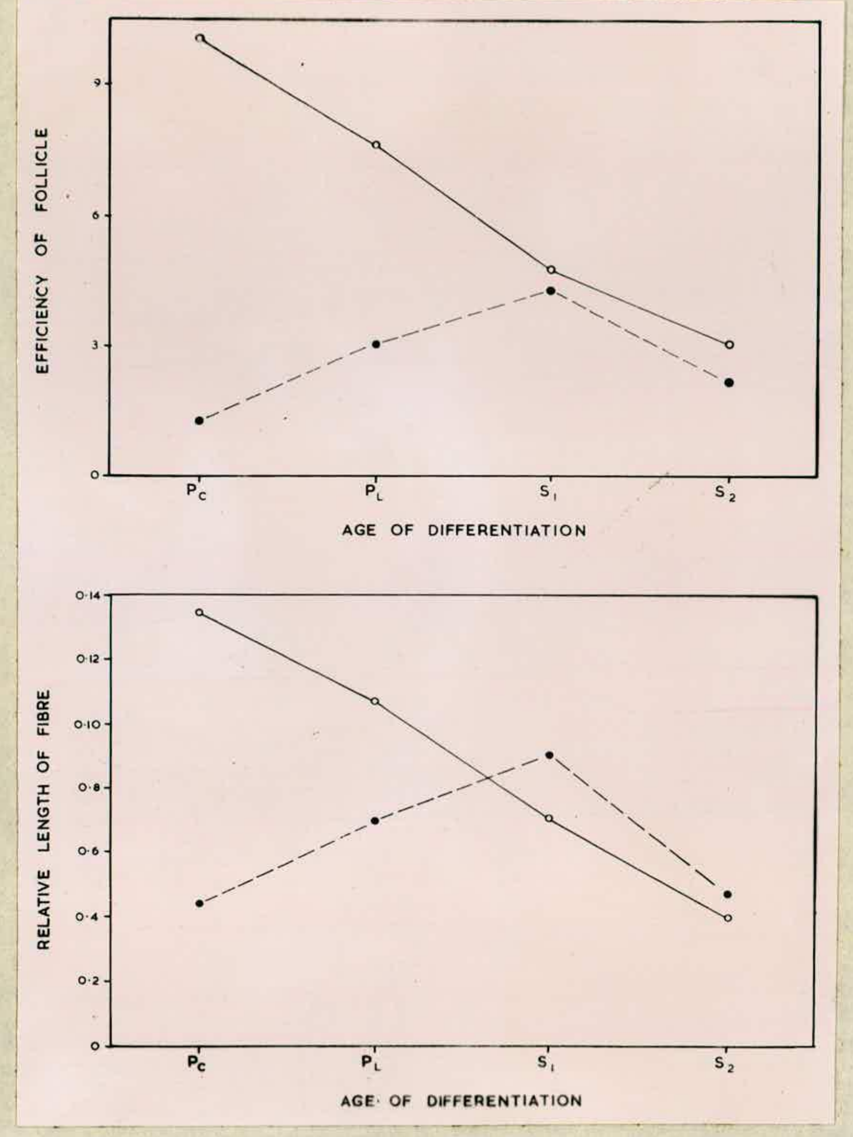

Figure 34. In top square are shown two lines relating efficiency to age of differentiation, one for a coarse growth pattern, the other for a fine growth pattern, as enumerated in the text. In bottom square are the growth rates calculated from these two efficiency relations, showing how competition results in a crossing over of the two lines i.e. a compensatory increase occurs of the growth rates of the S_1 and S_2 fibres.

This application of the efficiency concept explains how the 'pre-natal check' decreases the growth rates of the first fibres and increases the growth rates of the last fibres. Some mechanism determines which one of the family of curves shown in figure 33 should occur, and it follows as a fixed corollary that these simple curves of efficiency result in the more complex curves of length. The efficiency concept does not invalidate the 'pre-natal check' concept, it simply phrases it in more exact terminology, and removes some of the ambiguities. The total scheme of development is illustrated in figure 35.

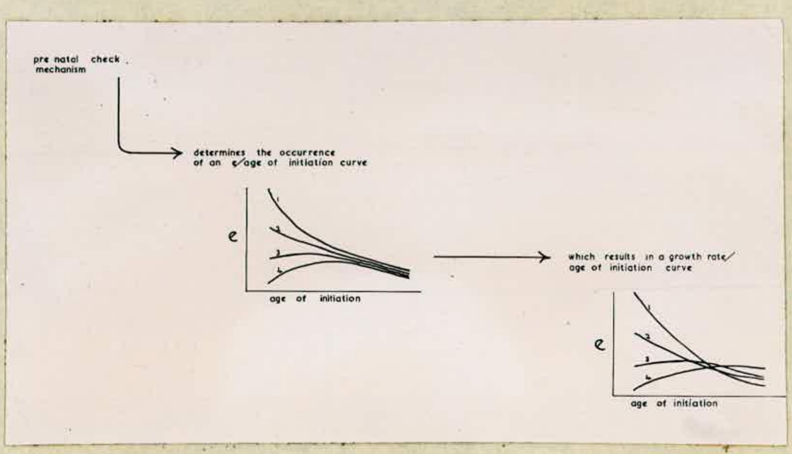

Figure 35. Diagram showing how the pre-natal check by determining which efficiency curve occurs, decides the growth rate pattern and thence determines the fibre type constitution, and thence the halo-hair abundance.

The above long and complicated analysis of fibre development in sheep has shown how the halo-hair abundance is a feature of the fibre type constitution; how the latter is due to changes in the medullation, crimp size and length growth rates of fibres, and how the growth rates of fibres can be analysed in terms of the efficiencies of follicles. It is now possible to consider the effects of the N and nr genes on the halo-hair abundance, since the above analysis has provided a possible explanation.

(d) Effects of the N and nr genes on halo-hair abundance and fibre type constitution.

The N and nr genes are detected by the increase of halo-hair abundance which occurs when they are substituted for their respective normal alleles. This increase varies from a very small increase in the +/nr type to a very large increase in the N/N type. Most of the animals carrying the N gene have a very high halo-hair abundance, as also do the nr/nr type. It has been shown above that this increase of the halo-hair frequency is only the most obvious aspect of a large number of changes in the constitution of the birthcoat, and it can be taken as a dependent corollary of these changes.

The changes of fibre type constitution are completely correlated with the halo-hair abundance. The N gene is for the fibre type constitution, as it is for the halo-hair abundance, a partial dominant, which is incompletely penetrant in the heterozygote. The nr gene is correspondingly a complete recessive. It would be over scrupulous to demonstrate this point which has been shown by Dry et al. from hundreds of analyses of birthcoat samples from the N-type flocks. Comparisons of the fibre type frequency distributions for N/N, N/+ and nr/nr (Fraser,Ross and Wright, section4 above) with those for +/+ (Goot 1940) illustrates the type of data which was found (see table 24).

The changes which these genes cause in the fibre type constitution can, as has been shown above, be taken as dependent corollaries of changes in (1) length growth rates, (2) the size of crimps, (3) the occurrence of medullation. Barker et al (see Barker 1932) have shown that variations in crimp size can be taken as secondary to changes in the length growth rate, and it follows that the effects on the crimp sizes of fibres by the N and nr genes can be explained as due to an initial effect on the length growth rates. It will be argued below that the occurrence of medulla is also directly dependent on changes of fibre growth rates. Therefore it will be taken that fibre growth rates are unitary determinants of (a) crimp size, (b) medullation, (c) fibre type constitution, (d) halo-hair abundance.

The effects of the N and nr genes on fibre growth rates are most obvious in the P follicles, since they cause these follicles to form their fibres at a markedly faster rate. It has been shown above that these changes in the first fibres will, if the efficiency concept is correct, result in compensatory changes in the later fibres. This depends (a) on the genes having no effect on the constitution of the follicle population, and (b) on their having no effect on the level of fibre production. The former has been investigated by Ross (section 3 above) who showed that

Age at shearing	Genotype				
	N-type			non-N-type	
	N/N	N/+	nr/nr	+/nr	+/+
1	7.9(22)	8.6(65)	6.4(3)	8.6(17)	-
2	9.0(9)	9.7(51)	7.5(11)	8.2(11)	-
3	8.9(21)	8.7(52)	8.1(7)	7.8(19)	9.9(20)
4	8.7(2)	9.1(6)	7.4(2)	8.3(15)	8.6(58)
5	9.3(2)	8.3(10)	6.3(5)	7.4(6)	7.6(18)
6	7.2(8)	7.2(4)	6.1(2)	6.6(1)	6.9(14)
7	9.0(1)	7.8(4)	4.8(1)	7.5(7)	7.4(9)
8	7.7(1)	6.4(2)	4.5(1)	-	-

Table 25. Average weights in pounds of the unscoured fleeces of ewes from 1-8 years old. Numbers of sheep are given in brackets.

Age at shearing	Halo-hair grade	
	VII	VI-III
4	9.0(10)	6.8(1)
3	8.1(21)	8.5(9)
2	9.8(45)	9.1(5)
Hogget	8.3(84)	10.2(9)

Table 26. Average unscoured fleece weights of N/+ ewes. These are separated into two groups, one having a high halo-hair grade birthcoat, the other having low halo-hair grade birthcoats. Both groups are of the N/+ type.

the genes do not affect the timing of the development of the follicle population, or the ratios of the different types of follicles. The absence of an effect on the level of total fibre production is evident from the examination of the fleece weights (unscoured) of ewes of the N-type flocks. These are given in table 25. No consistent differences occur between the various genotypes.

The independence of fleece weight and birthcoat type can be seen from the comparison of the fleece weights given in table 26. These are all of N/+ animals, and the two groups differ in the penetrance of the effect of the N gene on the birthcoat. One group consists of ewes whose birthcoats were of grade VII, the other of ewes whose birthcoats were of grades ranging from VI-III.

It follows from this evidence that, if the efficiency theory is correct, the N and nr genes should cause a decrease of the growth rates of later fibres. This can be tested by comparing the lengths of P, S_1 and S_2 fibres, either in samples of the same age, or as regressions of length on age, in N-type and non-N-type. This comparison will be detailed in the next section.

(e) Patterns of fibre growth rates.

Goot (1960) found that the fibre length distribution of a birthcoat sample from an N-type lamb was distinctly bimodal. Fraser, Ross and Wright (section 4 above) extended this observation in their study of fibre length distributions in N/N lambs, finding that the length distribution was distinctly trimodal: the third mode was not observed by Goot, since his sample was taken too soon after birth. The trimodality was found to be associated with the division of the follicle population into primaries, first wave secondaries, and second wave secondaries. Each type of follicle forms its fibres at a different rate, and therefore as the fleece grows, the three groups of fibres separate into a trimodal length distribution. The primaries which start first do so at the fastest rate, and the primary fibres are therefore the longest group. These are called the A group fibres. The first and second waves of secondary follicles form their fibres at progressively slower rates, and these form the shorter length groups called the B abd C_1 groups respectively. The separation of the length distribution into three distinct modal groups is an obvious feature of N-type birthcoats. The A group fibres, since they grow at a much faster rate than the B and C_1 groups, form the very definite outer coat. The B and C_1 groups do not differ so markedly, and they form the inner coat. The trimodality of a typical

N-type fibre length distribution is shown in figure 36.

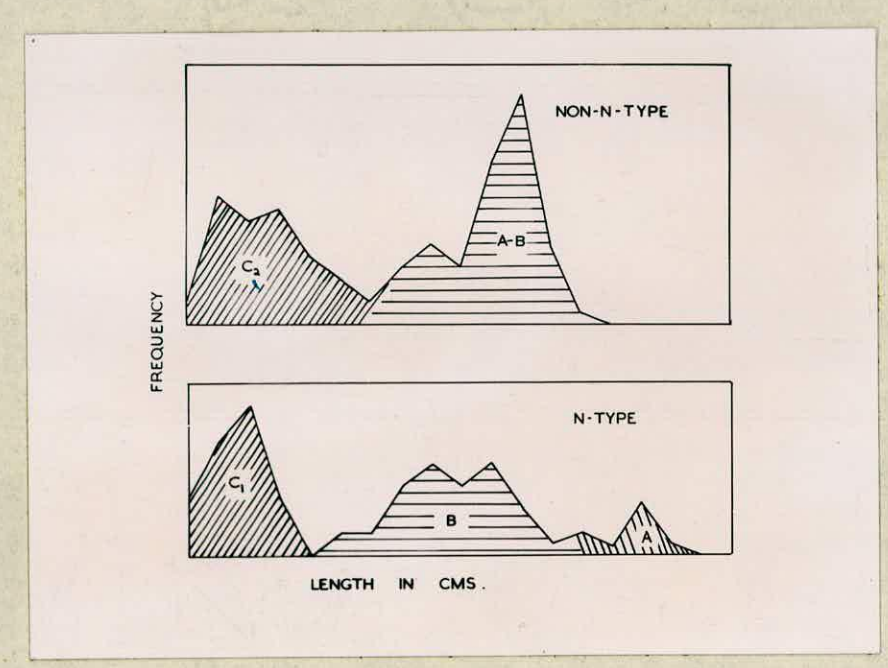

Figure 36. Typical fibre length frequency distributions from three month samples of N-type and non-N-type lambs, showing the trimodality of the former and the bimodality of the latter.

The fibre length distribution of the non-N-type birthcoat differs radically from that of the N-type birthcoat. It is distinctly bimodal. The cause of this difference between N-type and non-N-type can be found in the differences of the rate of growth of the primary fibres with that of the secondary fibres. These are sufficiently different in N-type to cause a separation of the P and S_1 fibres into two grooups, the A and B groups. In non-N-type they are nearly the same and this results in the P and S_1 fibres merging forming a composite group, called the A-B group. In both N-type and non-N-type the shortest length group is called the C group, since in both it is formed by the second wave secondary follicles. To avoid confusion in the following discussion, the C group is called C_1 in N-type, and C_2 in non-N-type. A typical fibre length distribution of a non-N-type birthcoat is shown in figure 36.

Two problems occur in the comparison of the growth rate patterns of N-type and non-N-type birthcoats. Firstly to demonstrate that primary follicles form their fibres faster in N-type than in non-N-type, and secondaly, to investigate the expectation from the competition theory that the growth rates of the S_2 fibres is greater in non-N-type than in N-type. The following analysis of fibre growth rates is intended to cover these aspects.

The analysis of fibre length growth rates is very laborious, since it involves the measurement of about a hundred fibres per sample to even approximately define the mean lengths of each of the length groups. The methods of measuring fibres have been discussed previously (Fraser, Ross and Wright, section 4 above) and it suffices to state that errors of measurement although low are not negligible, and that the loss of short fibres is inevitable since the samples

Table 28. Frequency distributions of fibre length in N/+ lambs, standard back region (0.5 cm. grouping interval).

Age	.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	16.5	17.0	17.5	18.0	18.5
28	12	14	11	12	7	4	12	1	3	8	6	2	3	2	-																						
32	2	-	8	12	20	19	22	3	2	10	8	6	4	1	-																						
32	8	3	3	6	9	6	9	10	8	2	-	1	20	4	2	-																					
34	16	12	20	14	13	22	27	5	-	6	10	24	28	7	2	-																					
34	20	19	11	16	9	15	31	13	2	9	15	26	14	13	3	-																					
34	6	10	5	8	14	11	10	3	3	7	8	10	8	-																							
37	8	1	13	11	11	21	11	6	19	10	4	4	11	2	5	1	1	-																			
41	2	8	14	7	4	4	17	4	12	11	13	14	13	6	3	3	7	7	-																		
45	8	2	6	11	36	26	29	29	12	13	26	10	1	1	6	4	-																				
48	5	15	10	8	16	11	5	13	12	8	12	3	3	9	6	5	-																				
54	12	12	11	4	9	10	8	23	11	14	19	14	12	5	4	14	10	7	-																		
58	3	3	2	1	4	9	9	5	6	6	6	1	3	5	5	-																					
59	4	15	13	18	9	11	9	18	22	12	20	20	13	11	9	11	8	1	-																		
110	1	4	6	10	-	8	5	10	9	6	9	9	7	5	5	8	9	6	8	2	1	7	2	4	-												
114	6	9	7	2	2	5	4	5	10	3	5	3	3	5	3	4	6	1	-	2	1	1	5	6	3	-											
123	5	7	18	11	14	13	6	17	13	5	4	18	9	8	13	23	26	9	2	3	5	9	7	11	11	7	5	2	1	-							
124	5	4	4	9	4	14	11	8	3	5	5	2	7	8	8	10	9	6	6	4	4	-	2	2	6	2	-										
130	1	3	6	5	8	7	4	5	5	7	-	1	6	6	9	19	8	9	10	10	6	4	9	3	-												
133	6	2	1	-	1	2	5	7	8	12	2	2	-	3	2	1	5	6	4	6	5	8	5	-	3	4	2	5	-	2	-						
133	5	6	6	3	1	5	10	12	13	11	7	6	8	14	5	15	9	11	10	12	14	2	7	4	1	4	4	2	4	1	-						

Age	.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0
56	9	2	11	7	3	6	17	15	18	18	20	47	39	10	1					
57	2	7	48	19	-	6	17	18	22	13	25	21	23	16	5					
58	12	10	22	11	6	2	6	5	10	16	18	18	19	5						
60	6	12	15	25	14	11	17	14	13	14	23	33	9	1						
61	9	2	4	7	7	1	3	4	4	7	11	10	16	14	11	1				
	3	4	7	8	11	3	1	7	8	3	8	17	11	13	10	1				
64	4	11	15	22	24	5	10	17	9	16	13	26	18	18	5					
64	21	12	24	26	13	4	-	3	21	24	33	35	32	45	60	55	20	3		
69	11	10	7	12	16	7	8	5	11	9	16	22	28	24	12					
72	4	7	20	30	22	19	4	3	14	23	41	34	38	38	22	13	5			
73	4	16	14	29	18	11	2	1	1	4	12	12	24	28	27	43	15	1		
75	4	4	3	10	17	18	4	4	5	11	12	14	17	28	18	18	10	5	2	
76	2	9	7	11	30	24	13	5	4	12	21	28	33	37	20	34	12	2		
78	19	10	15	29	19	38	16	11	10	20	22	27	34	34	31	25	26	21	12	6
81	2	6	15	17	15	17	10	2	5	14	30	45	55	57	42	45	25	3		
85	3	8	7	12	10	9	18	14	56	44	9	15	24	28	33	27	26	28	24	2
86	4	13	19	15	2	6	2	6	5	5	1	9	11	8	6	6	10	34	14	2

Table 29. Frequency distributions of fibre lengths in +/+ Romney Marsh lambs from Mr.Ruthven Buchanan's stud flock, standard back position. (0.5 cm grouping interval.

	Pedigree	11.58	0.32	0.01	-	2.95	-	-	0.04	0.02	-	18.79	64.22	57.89	9
N/N	Classified	9.93	0.66	0.01	-	4.44	0.01	0.04	0.11	-	-	17.88	64.21	72.42	24
	Total	10.35	0.55	0.01	-	4.01	0.01	0.02	0.09	0.01	-	17.86	64.21	68.45	33
nr/nr		10.37	0.31	0.76	0.06	2.43	-	0.01	0.01	0.13	0.01	25.27	57.65	71.59	17
	Pedigree	7.36	1.07	0.73	0.14	1.36	0.04	0.02	0.11	0.24	0.22	10.86	73.26	67.18	38
N/	Classified	8.33	0.71	0.37	0.03	3.03	0.02	0.03	0.11	0.03	0.02	14.03	68.15	61.90	20
	Total	7.69	0.94	0.39	0.09	1.86	0.03	0.02	0.11	0.14	0.12	11.91	71.50	65.36	58

Variance ratio 9.96··

Age	2/	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	48	50
64	7	6	8	-	12	6	3	9	9	8	5	-	2	4	7	6	3	-							
67	8	6	5	8	-	3	4	5	7	1	3	3	1	1	2										
67	3	9	10	6	2	2	4	4	5	11	5	-	-	-	1	1	1								
71	1	1	11	10	4	2	4	3	9	10	12	4	4	8	-	2	5	4	3						
74	4	9	10	14	6	22	5	3	7	7	8	11	11	11	10	1	-	1	2	8	2				
74	8	16	14	7	2	14	8	15	7	10	11	5	6	5	5	3	-	1	-	1	2	2	4	3	
77	4	1	11	15	5	7	6	17	16	13	8	10	8	10	8	11	12	2	3	-	-	1	2	7	

Table 30. Frequency distributions of fibre lengths in N/N lambs, standard back region (2/10 inch grouping interval).

63	2	11	9	10	6	4	2	5	7	18	20	7	1							
67	4	3	6	8	11	3	1	4	12	15	6	5	8	1						
72	4	1	4	10	7	5	1	6	1	7	8	16	12	11	8	4	1			
78	-	-	5	4	9	6	6	-	3	5	8	9	10	4	7	9				
89	-	2	4	-	6	6	4	3	1	1	1	4	7	8	8	4	4	3	4	1

Table 30.1 Frequency distributions of fibre lengths in +/+ lambs, standard back region (2/10 inch grouping interval)

Tag no.	Mean lengths			Age at sampling	n
	A	B	C_1		
316	2.0	-	-	0	867
None	3.25	-	-	0	128
None	2.25	-	-	0	205
382	2.25	-	-	0	206
None	1.75	-	-	0	261
158	2.25	-	-	0	239
210	3.75	1.25	-	28	554
145	5.0	2.0	-	28	87
111	5.25	2.75	-	30	346
310	5.25	2.75	-	32	117
311	6.25	3.25	-	32	91
142	6.0	2.75	-	34	206
74	5.25	2.25	-	35	593
141	5.75	3.25	-	34	216
378	6.75	3.25	-	34	217
73	5.75	2.75	-	34	152
144	5.5	2.5	-	34	103
366	6.25	2.75	-	37	130
365	7.25	2.75	.25	39	1156
352	4.75	2.25	-	39	181
351	5.75	2.25	-	40	329
225	8.25	5.0	1.25	41	225
43	7.25	3.25	.75	43	139
84	5.25	2.75	-	45	220
31	7.75	-	-	45	444
160	6.75	3.75	.75	48	144
14	8.25	3.75	1.25	49	664
32	5.75	-	-	51	147
36	6.75	2.75	.75	52	460
170	7.75	4.25	.75	54	199
159	6.75	3.75	-	58	68
163	-	-	1.25	59	343
215	8.1	4.6	1.0	63	78
201	8.0	4.1	.8	64	68
181	7.6	4.6	1.0	67	64
183	-	-	1.0	67	60
140	8.6	5.1	1.5	71	67
130	10.9	4.2	1.0	74	159
121	9.7	6.1	1.8	74	152
126	10.7	4.8	1.7	77	156
None	11.25	-	-	113	93
74	11.0	-	-	128	205
111	15.75	9.75	3.25	128	532
170	-	-	2.75	130	143
163	13.25	9.5	4.25	133	109
43	15.0	9.0	3.75	137	345
31	15.75	8.25	3.75	142	102
36	13.75	-	-	145	450
32	10.25	7.25	4.25	146	117
14	14.25	9.25	4.25	148	162

Table 31. Mean lengths of the A,B, and C_1 groups of fibres in N-type lambs. The tag number, and the number of fibres measured are given.

	Mean lengths			
Tag no.	A-B	C_2	Age at sampling	n
H466	5.75	.75	56	223
Z74	5.25	1.25	57	234
H461	5.25	.75	58	160
L160	5.25	1.75	60	207
H462	6.25	1.75	61	216
189	5.6	1.5	63	103
L167	5.75	1.75	64	207
H459	6.25	1.25	64	413
162	5.3	1.8	67	68
R593	6.0	2.0	69	198
A225	5.75	1.75	72	337
138	6.1	1.9	72	106
U493	7.25	1.75	73	262
H457	7.0	2.5	75	211
S643	6.75	2.25	76	304
R574	6.1	2.3	78	82
A223	6.75	2.25	78	414
S636	5.71	2.2	80	38
A206	6.75	2.25	81	405
Z10	7.25	2.25	85	285
L129	7.6	2.54	89	71

Table 32. Mean lengths of the A-B and C_2 length groups of fibres in non-N-type lambs. Tag numbers and the number of fibres measured are given.

Trends of future work and general conclusions.

The above series of papers have detailed

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genetics

Regression equations for the increase in length of of the mean length of the A,B,A-B; C_1 and C_2 length groups with age.

$A = .0792(X) + 2.946$

$B = .0578(X) + .725$

$C_1 = .0334(X) - .896$

$A-B = .0575(X) + 2.127$

$C_2 = .0460(X) - 1.404$

Comparison of the C_1 and C_2 regressions.

	S.Squares	df	Mean square
Total	6.1455	42	
Within sets	4.5781	41	0.1117
	1.5674	1	1.5674

Test of differences between adjusted means,

F = 14.03(P .001)

Sum of regressions	4.3063	40	0.1077
	0.2718	1	0.2718

Test of differences between regression coefficients,

F = 2.82 (P between .1 and.2)

Table 33. Regression equations, and their comparison, for the averages of the length groups. For details see text.

were taken initially for routine fibre type analyses in which the short fibres are not important. It follows that too rigorous an analysis of the following data is not justified.

In tables 27-30 are given the complete fibre length distributions from which the mean lengths of the A+B, A-B, C_1 and C_2 length groups were found. The mean lengths are given in tables 31 and 32. Due to the laboriousness of measuring several thousands of fibres, the regressions, particularly those ofthe C_1 and C_2 groups are based on only a few points. The work was continued until the author was convinced of the validity of the differences which were found between the regressions, since the number of comparisons necessary to demonstrate the significance of these differences statistically was well above the number which the author could make. In figures 37, 38, and 39 are given the scatter diagrams and regressions of mean group length on age for non-N-type (figure 37), for N-type (figure 38) and conjointly (figure 39).

The comparison of the rates of growth of the C_1 and C_2 groups has been tested statistically and the analysis is given in table 33. The regression equations for all groups are given in the same table.

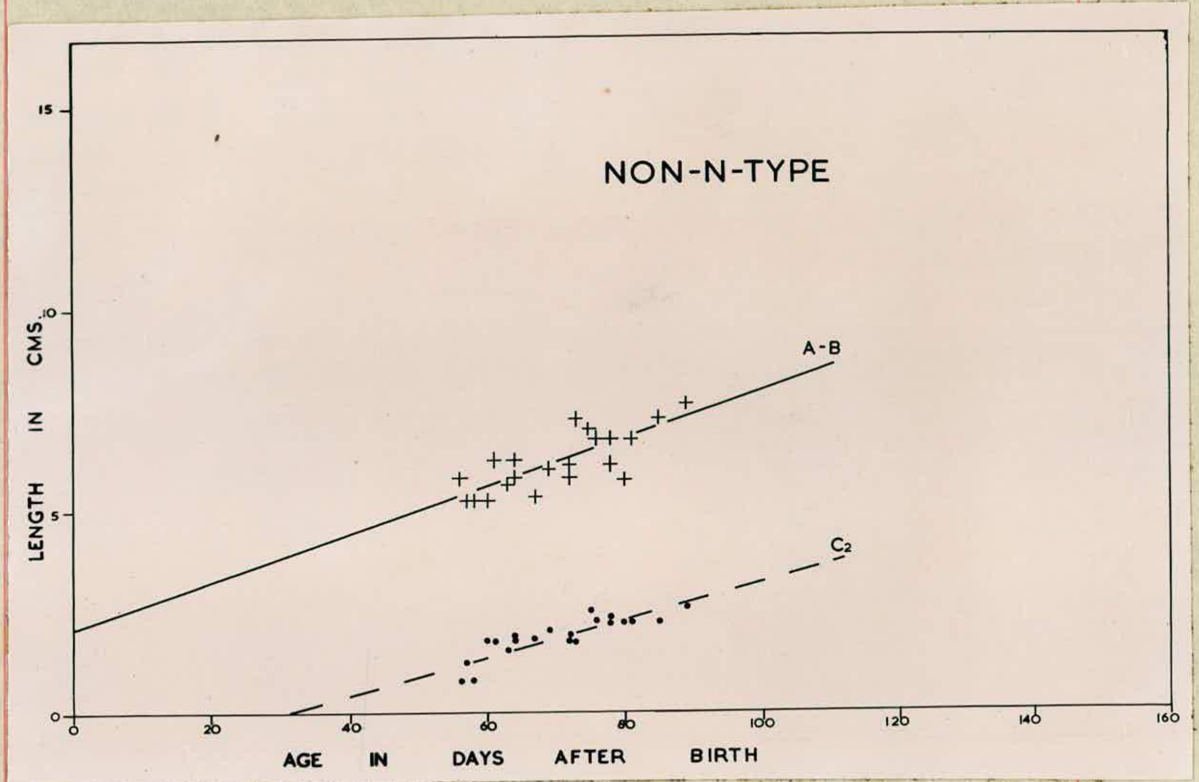

Figure 37. Growth rate pattern of non-N-type showing the similarity of the rates of growth of the A-B and C_2 groups, which results in a very even fleece.

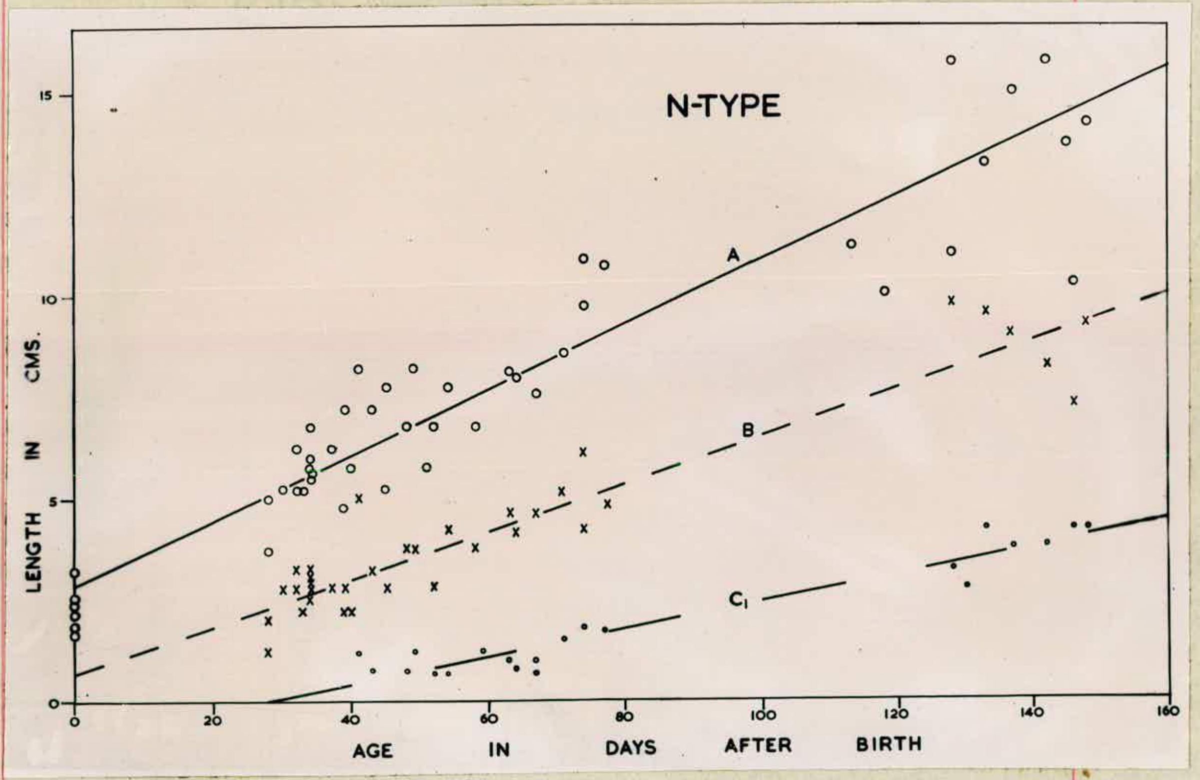

Figure 38. As for figure 37, but for an N-type, showing the differences in growth rate between the A,B and C_1 groups, which results in a very uneven fleece, divided into inner and outer coats.

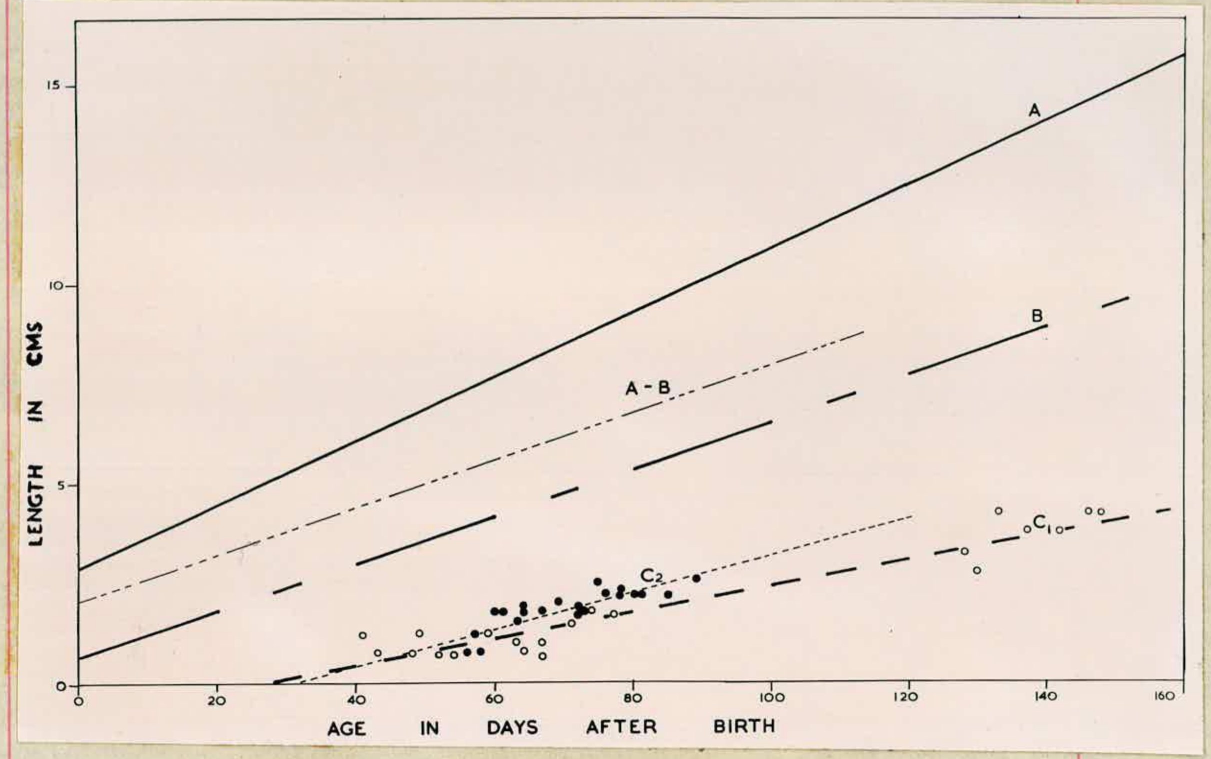

Figure 39. Growth rates, regressions only, of the mean lengths of the A,B,A-B,C_1 and C_2 groups, showing the differences between N-type(thick lines) and non-N-type (thin lines). The major differences are the increase of the rate of growth of A fibres above that of A-B fibres, and the decrease in the rate of growth of C_1 fibres below that of C_2 fibres. The means are shown for the latter comparison; N-type with open circles, non-N-type with closed circles.

The estimation of the mean length of a length group has a questionable accuracy, and the main non-N-type data are from lambs of Mr.Ruthven Buchanans stud flock which is located a few miles from the N-type flock. Therefore in figure 40 are shown the fibre length distributions of N/N and +/+ lambs, both from the N-type flocks, and therefore of reasonably similar breeding, and maintained under similar feeding conditions. These demonstrate a difference between the C_1 and C_2 length groups.

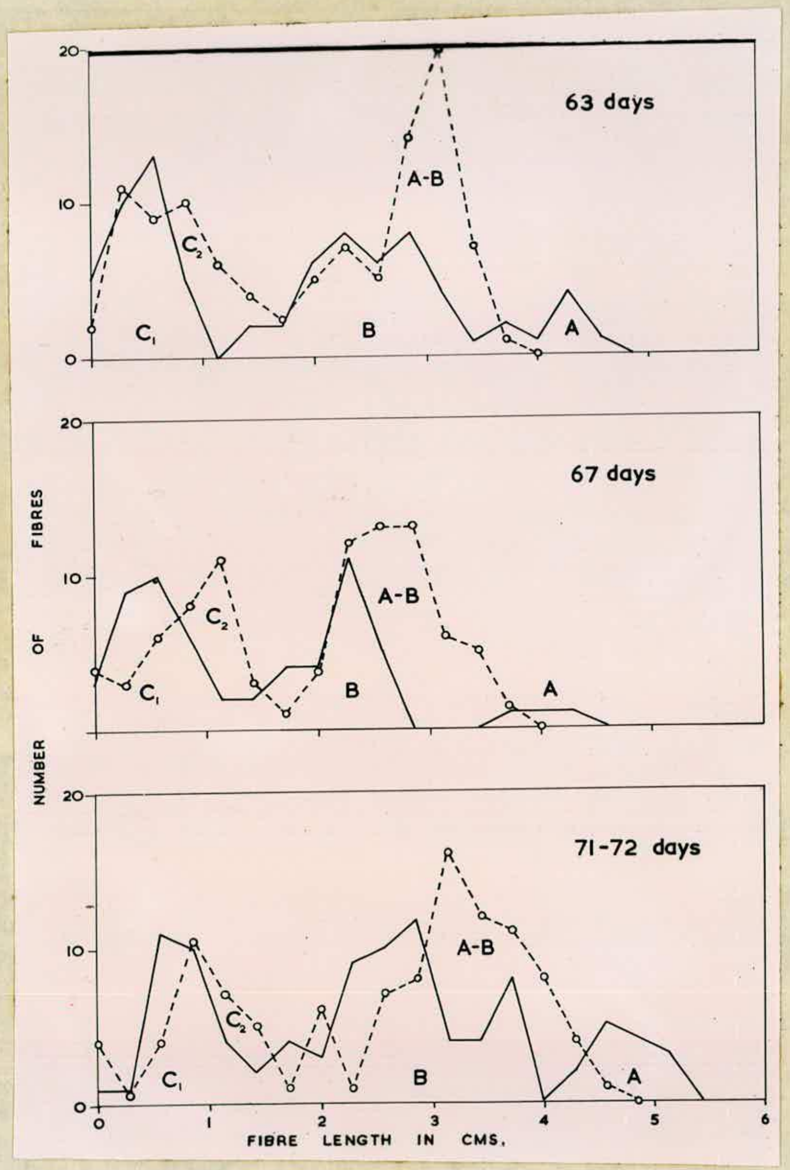

Figure 40. Paired frequency distributions of fibre length from samples taken from N-type and non-N-type lambs at the same age, illustrating the difference in modal structure, and the slight difference between the C_1 and C_2 fibres: the C_2 fibres, as expected, are slightly longer in each comparison.

It is obvious that further comparisons will have to be made, but the best material for such comparisons is not available, namely, segregating progenies from N/+ rams, and further, if samples are taken at later ages than the samples used in this study, then the detection of differences between the C_1 and C_2 groups would be much easier.

The above patterns of fibre growth rates in N-type and non-N-type demonstrate conclusively that the primary fibres are growing faster in N-type, and not so conclusively that the growth of the later secondary fibres (the S_2 fibres) is at a slower rate in N-type than in non-N-type. This agreement with the expectation from the efficiency concept suggests that the N and nr genes have a primary effect on the mechanism which determines which efficiency curve should occur. The whole complex of the effects of these genes on the birthcoat can be ascribed to this initial effect on efficiencies causing a variation in the growth rate pattern which is seen as an increase in the rate of growth of the primary fibres and a decrease in the rate of growth of the secondary fibres, this causing changes in the types of fibres formed by the different types of follicles, since it causes changes of crimp size and medullation. The changes of the fibre types include an increase in the frequency of halo-hairs, which is seen as a change in the halo-hair abundance.

This sequence of changes is illustrated in figure 41 which shows a section of the pedigree of causes of the manifold effects of the N and nr genes. This will be integrated with similar pedigrees below for other effects of these genes.

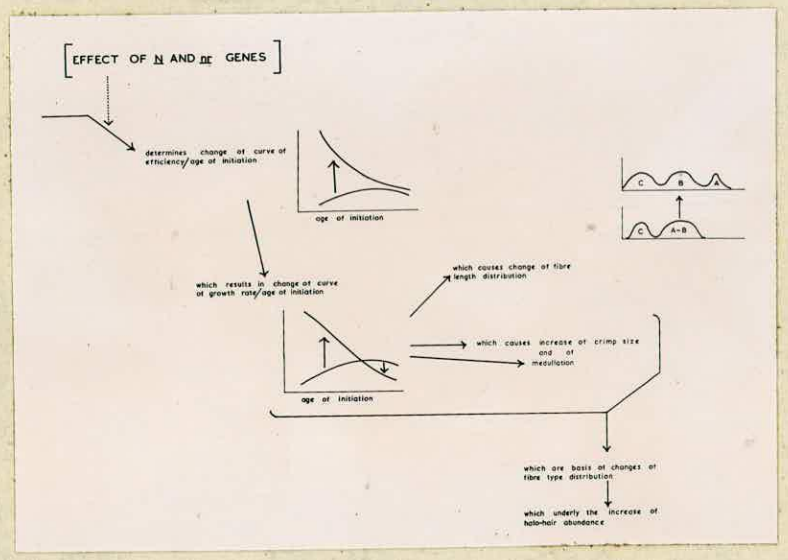

Figure 41. Pedigree of causes of the effects of the N and nr genes on the birthcoat, showing how these can be resolved to being due to initial effects on the fibre growth rates, which can be explained as caused by changes of the efficiency function.

One point of this pedigree of causes has not been discussed in detail i.e. the mechanism of the relation of medullation to fibre growth rates. A wool fibre consists of densely packed spindle shaped cells and has no axis of air spaced cells. A hair fibre on the other hand consists of an outer cylinder of the same dense spindle cells, which is called the cortex and surrounds a central tube of distorted air spaced cells, which is called the medulla. A fairly close correlation holds between the diameter of a fibre and the occurrence of medulla. Very fine fibres always lack medulla, whereas very thick fibres are always medullated. The diameter of a fibres is closely correlated with the length growth rate (Galpin, personal communication) and it follows that the occurrence of medulla is correlated with the length growth rates; the faster a fibre grows, the more likely is the occurrence of medulla. This correlation can be seen (1) developmentally, between fibres of the same sample (Fraser, Ross and Wright ,section 4 above), (2) environmentally, between parts of the same fibre grown at different levels of feeding (Waters, 1935) since fibres grow faster and are more medullated with increase of feed level, and (3) genetically, the increase of medullation caused by the N and nr genes is closely correlated with the increases of fibre growth rates.

The wide range of conditions under which medullation and growth rate are correlated suggest that one is a developmental corollary of the other, or that both are related aspects of some factor so far undescribed. The effects of the N and nr genes suggest that the occurrence of medulla is dependent on the fibre growing faster than a certain threshold rate, since these genes cause detectable changes of the growth rates of unmedullated fibres. It is difficult to perceive any method for showing that the follicle changes from the formation of medulla to the formation of cortex simply because its rate of growth is decreased. However this is a reasonable hypothesis and will be accepted for the purpose of this analysis.

The pedigree of causes shown in figure 41 relates the effects of the N and nr genes on the birthcoat to an initial effect on follicle efficiencies. The changes in the birthcoat are accompanied by changes in the full fleece, and it is necessary to examine these in terms of their similarly being caused by changes in the follicle efficiencies.

(f) Changes in the mature fleece.

The effects of the N and nr genes are not restricted to the characters of the birthcoat; several changes occuring in the full fleece. These are sufficient to cause the N-type fleece to resemble that of 'carpet' breeds such as the Scottish Mountain Blackface rather than that of the parent Romney breed which is of the 'longwool' type.

A 'carpet' type of fleece differs from the 'longwool' type in (a) its separation into an outer coat of long hairy fibres and an inner coat of short fine fibres, (b) its very marked hairiness, (c) its lack of crimp, (d) its lack of definite staples, (e) the occurrence of short, very hairy fibres, called kemps, which have been shed from their follicles. Some of the differences in the full fleece are obviously extensions of changes in the birthcoat, which have been measured by the fibre type technique. The genes cause the primary fibres to grow at a very much increased rate, and the secondary fibres to grow at a slower rate. This heterogeneity of growth rates results in some fibres being very long(the outer coat) and others being very short (the inner coat). Similarly the genes cause the primary fibres to be heavily medullated, and the secondary fibres to be finer. This results in the outer coat being very hairy, and the inner coat being fine. Further the crimping of the primary fibres is increased in size, and distorted by the occurrence of medulla, whereas that of the secondary fibres is decreased. This heterogeneity of crimp size results in a lack of staple crimp, and therefore in a lack of staples, since the staples are to a large extent the interlocking of similarly crimped fibres. This leaves only one character of the full fleece which cannot be accepted as a simple extension of characters already discussed for the birthcoat, namely, the shedding of fibres as kemps.

In longwool fleeces most of the fibres grow continuously. Only a few fibres are shed as a normal sequence of development. This shedding of fibres as kemps is highest for the birthcoat fibres and decreases in frequency with age (Dry 1934,1940). In studies of the shedding of fibres, the main methods have been (a) to count kemps in adult fleeces forming no estimate of their time of shedding, and (b) to collect special samples which allow the kemps to be counted separately according to their time of shedding. This is done by tying bundles of fibres together, and then covering the region with canvas to protect the fibres from weathering. This retains the kemps in the portion of the staple formed at the time of their shedding. Dry et al. have used this method extensively to describe kemp succession in both N-type and non-N-type Romneys (see Ross,Wright, and Fraser, section 5 above). They found that as a first approximation the shedding of fibres occurs synchronously within a region, and at apparently constant biological ages. The first fibres to be shed do so at about 2-3 months after birth. These are called the G_1 kemps. After about 3-4 months the fibres which were formed by follicles which shed their fibres as G_1 kemps may themselves be shed. These are called the G_2 kemps. This alternation of shedding occurs throughout the life term of the animal, and is called the kemp succession.

The initial studies of kemp succession made by Dry used non-N-type lambs, ranging from I-VI in halo-hair grade. His studies were made primarily from the fibre type approach. The G_1 kemps were described in terms of their tips as fibre types and the frequency of G_1 kemps was compared between animals of different fibre type constitutions. It was found that certain types of fibres were shed frequently as G_1 kemps, whereas other types of fibres were shed rarely or not at all. The types of fibres which were shed frequently were of the medullated and fast growing types:halo-hairs, super-sickles and hairy curly-tips. These occur most frequently in animals with a high halo-hair abundance and it follows that animals with high halo-hair grades showed a high frequency of shedding. The results have been interpreted by Fraser, Ross and Wright (section 4) and Ross, Wright and Fraser (section 5) in terms of the relationship of fibre types to follicle types as showing that shedding where it occurs is frequent in primary follicles, very rare in secondary follicles.

Ross, Wright and Fraser (section 5) in a study of kemp succession in N-type animals of grade VI and VII halo-hair abundance, found that the frequency of shedding was far greater than that which had been noted in non-N-type, but that the relationship of fibre type to frequency of shedding was the same. The frequency of shedding was also found to parallel the dominance relations of halo-hair abundance, being partially dominant in the N stock, completely recessive in the nr stock. The demonstration of the restriction of shedding to the primary follicles by Fraser,Ross and Wright (section 4 above) was extended by showing that the primary central follicles differ from the primary lateral follicles in the frequency with which they shed their fibres: P_c fibres are shed approximately 6 times as frequently as P_l fibres. The lateral fibres are always slightly less medullated and have smaller crimps than the central fibres, and it can be concluded therefore, that the central fibres grow faster than the lateral fibres, in N-type. Since the frequency of shedding is greater in the central follicles,it follows that shedding is correlated with fibre growth rates, being greater in the faster growing fibres. The same comparison can be made between the primary and the secondary fibres. In N-type, the P fibres are formed at the greatest rate and they are frequently shed, whereas the S fibres are formed at a slow rate, and they are only rarely shed, if at all. Finally, comparing different types of fibres formed by the same type of follicle; the sickle group of fibre types varies from the fast growing halo-hairs to the slow growing sickle-tips, and both are formed by the P_c follicles. The halo-hairs are almost always shed, whereas the sickle-tips are very rarely shed.

This correlation of shedding and fibre growth rates was noted by Dry (1934) who expressed it in terms of the hypothesis that follicles shed their fibres because their growth has been too vigorous. This can be re-stated as follicles having a potential for forming their fibres which is continually being used and renewed. If a fibre is formed too fast, then this potential is used faster than it can be renewed, and the fibre is shed when the follicle's potential becomes too low for it to maintain the growth of its fibre.

This hypothesis cannot be accepted without reservation, since evidence has been found, showing that a mechanism, called the 'crisis' by Dry(1940), causes a marked decrease in the vigour of all fibres, even those which are not shed. This crisis occurs over a short period at the time of the G_1 shedding. It is seen as a thinning of the primary fibres which are not shed. In coarse N-type animals, these fibres are usually medullated before and after the crisis level, which is about a centimetre long. This thinning can often be seen as a band running across the staple. It is most marked in the thickest non-shed fibres (Dry, Ross and Fraser, unpublished).

It therefore appears that two distinct systems determine whether shedding is to occur: the vigour of fibre growth, and the depression of growth caused by the crisis mechanism. It can be postulated that the crisis operates by reducing the rate at which a follicle receives growth potential; this reduction operating for a short period. If follicles have not been forming their fibre vigorously, they will have a high residual potential, and the decrease caused by the crisis mechanism will not affect them, whereas if they have been forming their fibre at a fast rate, they will have only a small residual potential, and any decrease of this, such as is postulated to be caused by the crisis mechanism, will result in the follicle temporarily ceasing formation of its fibre until it has acquired sufficient potential. This postulate also explains how those fibres which are not shed, but which are formed at a fast rate, show a thinning at the time of shedding.

In better terms, the crisis mechanism can be interpreted as affecting the papilla of the follicle, and thus causing changes in the rate of growth, or continuance of growth of the fibre. However it is obvious that the problem of the shedding of fibres will not be explained by the present methods. These have shown however that any future work on shedding will need to include studies of the vigour of follicles, and the basis of the crisis mechanism, probably involving quantitative histological studies of the structure of the papilla. In the present context it seems reasonable to conclude that the increase in frequency of shedding caused by the N and nr genes is due to the increase which the genes cause in the rate of formation of the primary fibres, and not due to any effect on the crisis mechanism, which would then appear to be a constant feature of both N-type and non-N-type, which is expressed only in the presence of fast growing fibres. This is speculative but reasonable.

It can be seen from the above discussion of the effects of the N and nr genes on the adult fleece, that these can be regarded as extensions of effects already described and analysed in the birthcoat, or in the case of the shedding of fibres, taken as due to the increased rates of fibre growth, which the preceding analysis has shown to be a corollary of effects on the efficiencies of follicles. Two further effects of the N and nr genes must be considered before discussing the possible bases of the efficiencies of follicles. These are the occurrence of brown pigment in the tips of birthcoat fibres, and the variation over the body of all the characters so far discussed.

(g) Brown pigmentation of birthcoat characters.

The majority of non-N-type lambs have a birthcoat containing only a scattering of halo-hairs, and these if they do occur, are restricted to the middle of the back and the rump, rarely occurring on the front of the body and the neck. In the few Romney lambs which have halohairs on the back of the neck, a few of these halo-hairs may have reddish brown tips. Such brown fibres are rare, and are all of the halo-hair type.

N-type Romney lambs are thickly coated with halo-hairs, and a large number have patches of brown fibres, which in some give a piebald appearance. The brown occurs very noticeably in the parts of the fibres formed before birth, and is absent from the parts of the fibres formed after birth. It is located in the medullated parts of the fibres.

The occurrence of the patches of brown fibres follows a discontinuous gradient of expression. The majority of lambs which show any brown, do so only on the back of the neck, and the expression varies from a few fibres to a thick brown collar half around the neck. Some in addition to the neck patch have patches of brown at the root of the tail. A few have a large patch on the neck, patches at the root of the tail, and patches scattered around the body. In addition to the brown patches on the trunk the tips of the ears are very often brown. Since this is common in non-N-type as well as N-type Romneys no attention, unfortunately, has been given to it.

The Welsh Mountain breed of sheep shows a very similar type of brown pigment which appears to be identical with that found in the N-type strains. The analogy is very close since in both the pigment is restricted to the medullated tips of the birthcoat fibres, and is similarly located over the body, although the latter differs slightly in the Welsh breed where brown tails are common, whereas brown at the root of the tail is rare. In both N-type and the Welsh breed the predominant location is at the back of the neck. It can be taken that the brown of N-type is analogous with that of the Welsh breed apart from slight differences of pattern. The observations on the Welsh breed were made on two flocks, one in Merioneth, the other at Bangor, and over 600 lambs were examined.

The occurrence of brown has been described in the N-type flock records as small, medium or large patch, etc., and in order to conveniently compare the expression in the different N and nr genotypes, it is necessary to transform these descriptions onto a quantitative scale. A four unit scale is used, where 0-nobrown, 1-small patch, 2-medium patch, 3-large patch. Two grades are given each lamb, one for the neck, the other for the rest of the main trunk region.

	Neck				Main trunk			
	3	2	1	0	3	2	1	0
N/N	5 (15.6)	10 (31.2)	4 (12.5)	13 (40.7)	2 (6.2)	2 (6.2)	-	28 (87.6)
nr/nr	3 (2.7)	25 (24.2)	10 (9.6)	66 (63.5)	-	5 (4.8)	2 (1.9)	97 (93.3)
N/+	11 (3.3)	56 (18.8)	46 (18.3)	128 (62.6)	1 (0.3)	2 (0.6)	12 (3.6)	225 (95.5)
+/nr	-	1 (0.8)	3 (2.4)	119 (96.8)	-	-	1 (0.8)	122 (99.2)

Table 34. Frequency of brown fibres on the back of the neck and the rest of the trunk. Degree of brown is graded on a four unit system, separately for the neck and the rest of the trunk. Percentages are given in brackets.

In table 34 are given the frequency distributions of these grades separately for the neck and the rest of the main trunk.

It can be seen from this table that the expression of brown is high in the N/N, N/+ and nr/nr types, and low in the +/nr type, and that the expression is greater in the N/N than in the N/+ type. In other words the expression of brown parallels the dominance relations of the N and nr genes. This when considered in terms of the rarity of brown in normal Romneys, confirms the postulate that the occurrence of brown is an aspect of the effects of the N and nr genes.

Having shown that the brown patches are an effect of the genes it is necessary to determine (a) the developmental relationship of the formation of brown pigment to the increase of fibre growth rates, (b) the reason for the restriction of brown to the tips of the first formed fibres, and (c) the relationship of the formation of brown patches in the Welsh breed to the formation of the patches in the Romney breed. The latter questions are beyond the scope of the present analysis since they obviously require further study along different lines to the present approach.

Since many of the N-type animals lack brown altogether, it follows that the formation of brown pigment is not a fixed corollary of increased fibre growth rates. Further in both the Welsh and the N-type strains there are strong indications that the degree of expression of brown is affected by genes extra to the ones which determine the coarseness of the birthcoat. The restriction of the brown pigment to the medullated parts of the fibres suggests a possible mechanism relating the occurrence of brown to the structure of the coat. It is postulated that a sub-genotype exists both in N-type and in non-N-type which conditions the occurrence of brown pigment, but that thispigment cannot be formed in the absence of medullation and therefore the 'brown' sub-genotype produces an effect only in the animals which have medullated fibres i.e. it has a maximal effect in the very heavily medullated fibres of the N-type lambs, and a very low effect in the un-medullated fibres of the non-N-type lambs. On this basis the brown patches can be considered as a dependent corollary of the effect of the N and nr genes on medullation.

(h) Regional variation of the fleece.

Most of the detailed studies of fibre development have, both in N-type and in non-N-type, been restricted to one sampling region, usually that termed the standard back region (see Galpin 1938). This restriction is necessary since most characters vary from region to region. This variation is most obvious for the halo-hair abundance: lambs frequently occur which have a very high abundance around the rump and back, and a very low abundance on the shoulders. The variation is related to the dosage of the N and nr genes. Increase of gene dosage causes both an increase of the proportion of animals which have a high grade on the back (see Dry and Fraser, section 2 above) and an increase in the extent to which these lambs are covered with high frequencies of halo-hairs. This latter effect is for convenience called the 'coverage'. It has been discussed and illustrated by Dry and Fraser (section 6 above).

The halo-hair abundance varies from a complete lack of halo-hairs to a density at which no further differences are detectable from eye grading. This limit density is termed the grade VII abundance. Complete absence of halo-hairs is termed the grade I abundance. The range of densities between these extremes has been divided into five sections which, with practise, can be determined with a high repeatability. Animals whose abundance is of these intermediate grades (II-VI) almost always have this only around the standard back position extending to the rump. The animals whose abundance is grade VII at the back vary in their coverage from restriction to the back position, to complete coverage of the body. The range from complete coverage to restricted coverage can be divided into six sections. These are illustrated in figure 42. On this basis the halo-hair abundance of an animal can be described by one of twelve grades, ranging from grade 1 which have no halo-hairs, to grade 12 which have a complete coverage all over the body of high halo-hair density.

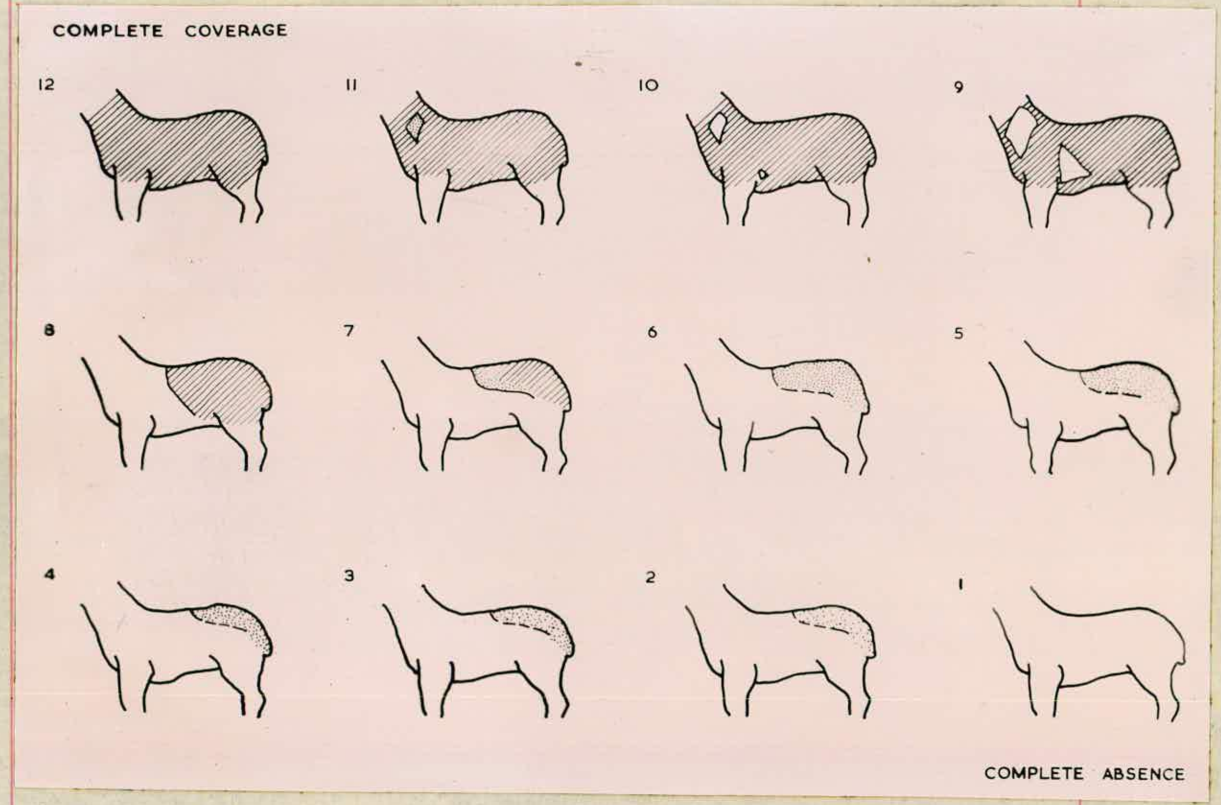

Figure 42. Grading system of halo-hair abundance, integrating Dry's seven grade system based on the back region, with White's five grade scheme based on coverage. Grade 1-absence of halo-hairs, grades2-7-increase in density of halo-hairs, usually restricted to around the back, grades 8-12-increase of coverage of the body with high densities of halo-hairs. In the diagram the white regions lack halo-hairs, the dotted regions have below limit densities of halo-hairs, and the lined regions have limit densities of halo-hairs.

Coverage grade	N/N	N/+.nr/+	nr/nr	N/+
0-6	-	-	-	7(4.1)
7	-	7(11.8)	1(1.8)	34(19.7)
8	-	15(26.8)	15(26.7)	73(44.3)
9	3(7.5)	10(17.7)	5(8.9)	20(11.6)
10	2(5.0)	9(16.3)	16(28.5)	20(11.6)
11	9(23.5)	10(17.7)	14(25.2)	13(7.5)
12	23(65.0)	5(8.9)	5(8.9)	2(1.2)

Table 36. Frequencies of grades of coverage of the body with high halo-hair abundance. % are given in brackets.

Coverage grade												
1	2	3	4	5	6	7	8	9	10	11	12	
90	50	40	26	8	1	-	3	1	1	1	1	Welsh sheep
-	-	-	-	-	-	2	6	34	120	701	769	Romney marsh

Table 35. Frequencies of lambs with different grades of "coverage" in flocks of Welsh mountain sheep, and in flocks of New Zealand Romney Marsh sheep. Since both these distributions show no marked discontinuities, it can be taken that the grading scheme introduces no major errors of scaling.

This scheme of grading halo-hair abundence is a modification of the scheme formulated by Dr.F.W. Dry, to make it analogous with the scheme formulated by Professor R.G.White. The original New Zealand scheme involved dividing the range from restricted to complete coverage into ten grades. The N-type data have been transformed by summation of certain classes to conform with the six grade scheme proposed above. The necessity for a common grading scheme is obvious. The possibility of such grading schemes introducing scaling errors is obvious, but this system has been used for non-N-type sheep whose grades ranged from 1-6 (Dry and Fraser, section 2 above), and for Welsh Mountain sheep whose grades ranged from 4-12. In both cases a smooth curve was found (table 35) showing that the grading scheme does not introduce any major discrepancies.

The frequency distributions of coverage are compared (table 36) for the various genotypes of the N and nr genes. The 1-6 grades have been summed since they have been given as separate grades previously (Dry and Fraser, section 2 above). These data demonstrate clearly the partial dominance of the N gene, since the coverage is greater in the N/N than in the N/+ type. Similarly the comparison of the N/+ . +/+ and N/+ . +/nr types, shows that the two genes interact, since the latter type has the greater coverage.

The variation of coverage over the body follows an antero-posterior gradient which is slightly modified by deviations around the shoulder. This gradient is certainly an aspect of the effects of the N and nr genes, but it would be unreasonable to conclude that the variation is specifically due to the action of these genes, and more likely that it is due to constant differences between regions in the level of gene action necessary to produce a visible reaction i.e. there is a mechanism following a similar gradient over the body which interacts with the action of the genes to determine the level of their reaction. It is interesting to note that the effects of the N gene on halo-hair abundance are almost completely dominant when scored on the back region, and almost completely recessive when scored on the neck region.

Many studies have been made of the regional variation of various fleece characters in normal Romneys : fibre type constitution (Galpin 1936, Goot 1940), degwee of total medullation of the adult fleece (see Goot 1945), fibre fineness and follicle density (see Wildman 1937), fibre diameter and crimp size (Reimers and Swart 1929), staple length (Duerden and Palmer 1932), follicle development and density (Carter and Hardy 1948). These all follow much the same antero-posterior and dorso-ventral gradients. This correlation of gradients of expression of fibre diameter, length, crimp size, and medullation is a further demonstration that these characters are all developmentally related. An explanation can be found in the variation of follicle density which follows exactly opposite gradients, being highest in the frontal regions and lowest in the back regions. Wildman (1957) has suggested that the lower expression of all these fibre characters is due to the greater follicle density in the anterior parts causing a reduction in the growth per follicle. This in terms of the efficiency terminology means that the efficiencies of follicles may be the same all over the body, but that the greater follicle density in the frontal parts reduces the amount of fibre substrate available per follicle. Very little data is available on the regional variation of follicle density in N-type, but Wildman (1957) found that in the Welsh Mountain breed, density followed the same gradients as in breeds with other types of fleece. Further studies are obviously necessary on gradients of expression of follicle and fibre characters, but for the present purpose it is reasonable to assume that the variation in expression of the effects of the genes over the body is not due to any specific action of these genes, but to some factor,probably the follicle density, which exhibits a constant regional variation both in N-type and in non-N-type. The occurrence of brown tipped fibres follows a discontinuous gradient which is very different to that shown in other characters, but the same argument holds, that this is due to some independent gradient mechanism, rather than to a specific action of the genes. A support for this can be found in the slight differences in regional expression of brown between the N-type and the Welsh breeds.

(i) Integration of the effects of the N and nr genes on the birthcoat and fleece.

In figure 41 a pedigree of causes has been given showing how the effects of the genes on halo-hair abundance and fibre type constitution can be taken as secondary to effects on crimp size, medullation and fibre length growth rates. The latter has been shown to be the cause of the differences of crimp size, and probably to be the cause of the effects on medullation. The effects on fibre length, which are in opposite directions in early and late follicles, have been shown to be due to the genes affecting the function relating the efficiencies of follicles to their age of initiation. The sections following this analysis of the the birthcoat have shown that the effects of the genes on the mature fleece, except that on shedding, can be taken as simple extensions of the effects on the birthcoat. The effect on the shedding of fibres, although probably caused by the effect on fibre growth rates, is not a simple extension, since shedding can be concluded to be due to the interaction of fast growth with the 'crisis' mechanism. However it is probable that the increase in shedding is a direct corollary of the increase of fibre growth rates i.e. the genes have no effect on the crisis mechanism. In the sections on brown pigment and regional variation, mechanisms have been suggested which relate these to the fast growth of fibres. Brown pigment occurs only in medullated fibres, and it is suggested that although the formation of medulla does not cause the formation of brown pigment, it does allow the expression of genes which themselves cause brown pigment. The regional variation is suggested to be due to the regional variation of follicle density causing variation of the amount of fibre substrate available to each follicle. This integration of the effects of the N and nr genes is illustrated in figure 43. Due to the many difficulties of sheep as experimental material, a number of the steps of this pedigree of causes are hypothetical. In sheep, one must be satified with finding a reasonable hypothesis, rather than with eliminating all possible hypotheses.

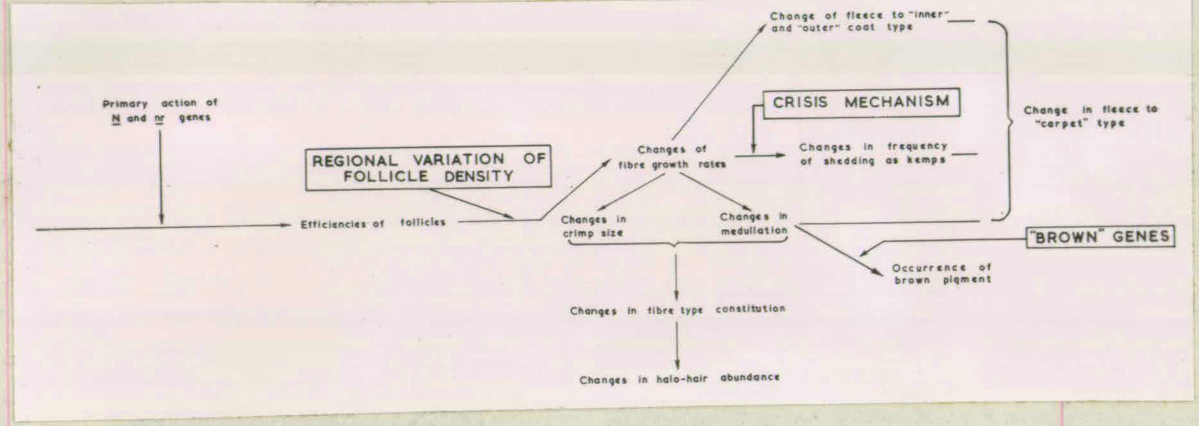

Figure 43. Pedigree of causes, as in figure 41, but expanded to include the effects of the genes on the adult fleece, and on the occurrence of brown pigment.

II. Effects of the genes on horns.

The normal Romney sheep is polled, lacking any signs of horn growth. A few rams may have horns, but these never exceed more than a few inches in length, and are usually much shorter. This contrasts very markedly with the N-type flocks in which all the males have horns, usually very large, and many of the females have horns several inches long. Dry and Fraser (section 6 above) have shown that horns in the N-type flocks can reasonably be taken as due to the action of the N and nr genes. Having shown that the effects on fleece characters of these genes are probably due to an initial effect on follicle efficiencies, two problems remain to be solved: the developmental bases of the efficiencies of follicles, and the relationship of these to the effects on horns.

The comparison of the expression of horns in the various genotypes has shown that the substitution of the N and nr genes causes an increase both in the penetrance and the expressivity of horns, where penetrance is the percentage of animals which have horns, and expressivity is the size of the horns which they have. The correlation of the penetrance and the expressivity of horns suggests that the action of these genes is not to cause an initiation of the differentiation of horns, but rather to cause an increase in the rate of development of an already occurrent sequence of horn differentiation. This point cannot be verified without data of the early phases of horn differentiation and their compprison between N-type and non-N-type.

Although many workers have examined the development of horns, the sequence and inter-dependence of the various parts of horns cannot be authoritatively defined. Numerous workers have reported that the bone core of horns originates from a separate ossification centre, which later fuses with the frontal bones to form the bone base and core of the full horns (Dove 1935, Durst 1905, Marchi 1907, Komura 1926) The latter authors, from the use of transplantation methods come to the conclusion that the keratogenous tissue determines the formation of the os cornu which develops into the horn spike. Dove (1935) found " an inherent potentiality for ossification existing in the tissues located between the epidermis and the periosteum, which when transplanted free in their embryonic condition to a foreign region, differentiate into bone. This differentiation of connective tissue and dermal tissue into bone (os cornu) does not require a stimulus from the keratin epidermis".

Dove found that the horn core anlage lies in the connective and dermal tissue, and he demonstrated by transplantation that this anlage could induce the frontal bones of the skull located under it to be modified into horn base. The horn core anlage later fuses with the horn base to form the horn bone. He also found from transplants that the os cornu and the keratin sheath tissues are both fully determined at birth, and that it was impossible by operative methods to redirect the differentiation of either tissues. The os cornu when transplanted does not induce the formation of a horn sheath by the epidermis lying above the grafted os cornu, and vice versa. After birth the ossifying tissues do not interact determinatively with the keratinising tissues. He states however " there may be a pre-natal interaction" but that " until there is genetic evidence to require a different interpretation the development of horns in all its diverse manifestations can be attributed to the presence of a single genetic factor controlling the production of one leading character - the os cornu-by which all the remaining parts are produced as the interaction of tissues".

Dove has given evidence of a directive action of the os cornu on the frontal bones of the skull. He has not shown that the os cornu directs the formation of the horn sheath or vice versa, since such direction occurs, if at all, before birth. Therefore three possibilities exist. (1) the os cornu is an induction centre which before birth irreversibly determines the formation of the horn sheath, and which after birth, reversibly determines the formation of the horn base. (2) the keratin sheath is an induction centre which irreversibly determines the formation of the os cornu before birth, which in its turn determines the formation of the horn base. (3) Both the keratin sheath and the os cornu are irreversibly determined before birth by some undefined tissue. The first alternative places the induction site of horns in the dermis. The second alternative places theinduction site in the epidermis. The present data does not allow decision between these alternatives. However the last alternative is not scientifically useful in that it does not indicate any methods of analysis, and therefore attention is concentrated on the first two alternatives. It will be shown below that the tissue specificity concept of gene action (Gruneberg 1943) indicates from the effect of the N and nr genes on follicle development that the epidermal induction of the differentiation of horns is the most likely.

IV. Integration of the effects of the genes on horns and follicles.

The analysis of the effects on fibres showed that these can be reasonably argued to be corollaries of an initial effect of the genes on the efficiencies of follicles. The efficiency of a follicle is the value which that follicle has in competition with other follicles for fibre substrate. Galpin (personal communication) in studies of the relations between the dimensions of a follicle, and the rate at which it forms its fibre, has shown that the fibre growth rate is closely correlated with the depth to which the follicle extends into the skin. This suggests that the efficiency of a follicle is a function of its size, either because of the area available for absorbing fibre substrate, or because of greater capillary connection. If this is so then the action of the N and nr genes on fibre growth rates can be resolved as due to an initial action on the mechanism determining the depth to which follicles grow into the skin. This mechanism can have one of three possible effects. (1) a generalised effect on the follicle as a whole, determining the 'field' of both the dermal and the epidermal constituents, (2) a specialised effect on the dermal part, which then causes directive changes in the epidermal part, (3) a specialised effect on the epidermal part which then causes directive changes in the dermal parts. The first does not appear to be likely in view of the heterogeneity of component tissues of follicles, but it cannot be discarded as a possibility. However attention is more usefully concentrated on the latter alternatives, since one of these appears to be more probable. Before considering these a short resume of the development of follicles will clarify the issues.

The follicle commences developments as a downward directed growth of a few cells of the malphigian layer of the epidermis. This growth continues until it forms a rod of cells projecting into the dermis. The first sign of a dermal interaction occurs when a few dermal cells near the base of the epidermal follicle plug, become organised into a compact ball of dermal tissue, which is the pre-papilla of the follicle. The follicle plug grows around the papilla until it nearly encloses it, and then both grow downward further into the dermis. The completed follicle consists of a long tube of epidermal cells with a swollen base which partially encloses the dermal papilla. The surface of the papilla facing into the follicle is covered with a sheet of epidermal cells, and the fibre is formed by division of these epidermal cells. The fibre is therefore totally derived from epidermal cells.

The work of Wang (1944) has clearly indicated the function of the papilla in feather follicles. Feathers in different regions of the fowl grow at different rates, and he transplanted both follicle papilla which had been denuded of the epidermal covering, and pieces of neutral tissue (feather pulp etc.) into follicles of a different region. The results of the transplants were deduced from the characters of the feathers grown by the operated follicles. The results of these transplants showed that they are soon covered with a sheet of epidermal cells,which form a feather only where a papilla has been transplanted. The rate of growth of the feathers corresponded to that of the host not the donor region. This shows that the papilla has no directive function on the rate at which the epidermis grows a feather, but that it is necessary as an activator of undefined feather growth.

Extrapolating these results of experiments on feather growth, it is suggested that in the growth of fibres the epidermis determines the rate of growth of the fibre, and the papilla determines the initiation and maintenance of this growth. Since the N and nr genes affect primarily the rates at which fibres are formed, it follows from this analogy, that the primary effect of these genes is on the epidermal rather than the dermal constituent of the follicle.

It has been concluded above that the primary effect of the genes leading to the formation of horns may be epidermally, or dermally located. Since it is probable that the primary effect on fibres is epidermally located, it follows from the concept of the tissue specificity of gene action (Gruneberg 1943) that the epidermal induction of horns is the more likely. One cannot exclude the possibility that the effects on fibres and horns are dermal in location. This aspect of the N-type problem will require intensive study if a solution is to be found.

The complete pedigree of causes of the N-type effects is shown in figure 44 in terms of the genes having an initial action on the rates of growth of the parts of the epidermis concerned in the keratinised outgrowths of the horns and fibres.

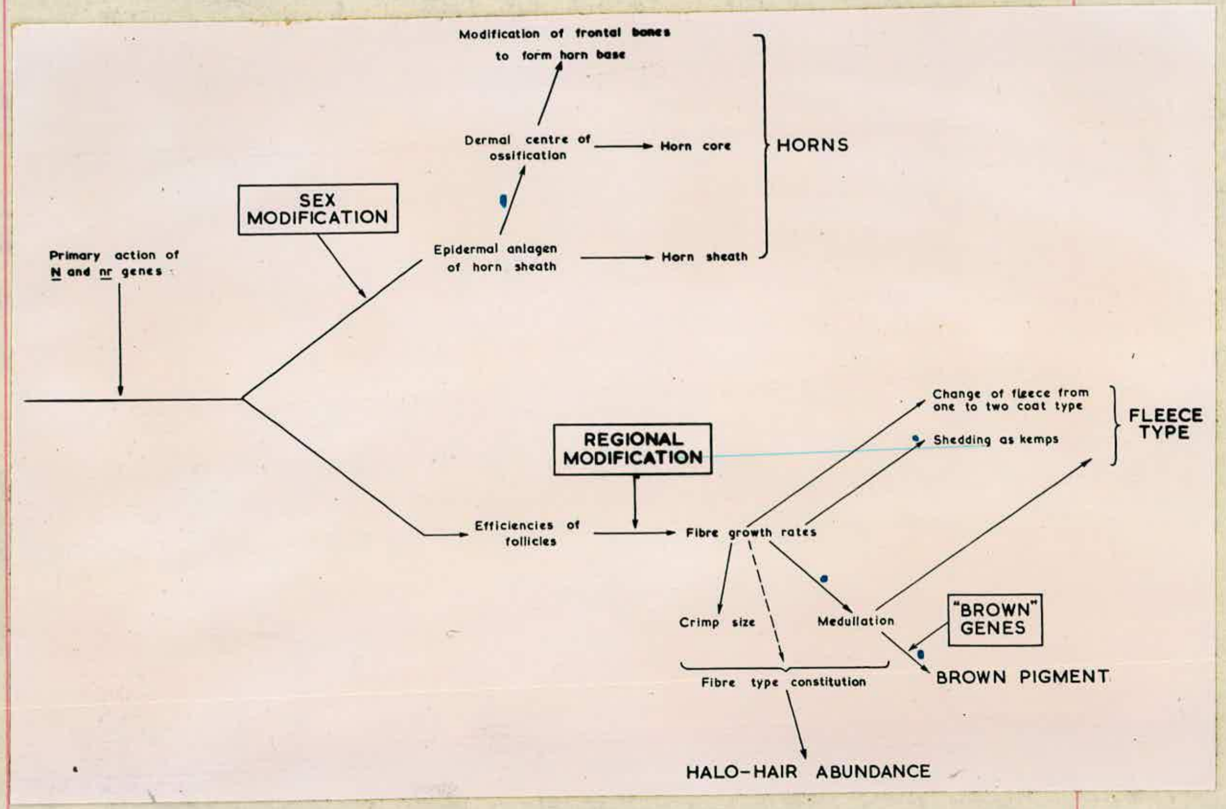

Figure 44. Complete pedigree of causes of the N and nr gene's effects on horns and fleece, on the postulate that they have a primary action on the keratinisation sequence of the epidermis, which in the horn position epidermis results in the formation of horns, and in other epidermis results in the formation of fibres.

Future trends of research on fleece type, and general conclusions.

The above series of papers have detailed genetic and developmental data on the differences between the N-type and non-N-type strains of sheep. From this information several hypotheses have been formulated with the intention of providing a coherent scheme of explanation, which could be used as a basis for rigorous disproof analyses and experiments.

The segregation data, collected over a very long period by Dr.F.W.Dry, show conclusively that the main genetic determinants of the N-type/non-N-type difference, are the N and nr genes. However some abnormal segregations indicate that two other genes, D and Dr, affect the dominance relations of the N and nr genes; the D gene affecting the dominance of the effects of the N gene on the birthcoat, and the Dr gene affecting the recessiveness of the nr gene on both the birthcoat and the horns. It would be of interest to have a complete description of the genes affecting the N-type syndrome.

Crosses of N-type Romney sheep onto the Lincoln breed have shown an intensification of the syndrome, whereas crosses onto the Southdown breed have shown a diminuition of the syndrome. This aspect of the genetics of the N gene is of marked interest since its investigation may lead to an explanation of the factors, genetic and developmental, which determine the differences between the longwool fleece of the Lincoln and Romney breeds, and the Down short wool fleece of the Southdown breeds.

Some aspects of the integration of the N-type syndrome rquire further study: the crisis mechanism of shedding, the correlation of the occurrence of modullation with increased fibre growth rates, the formation of brown pigment, but the developmental analysis of the N-type syndrome has shown that a reasonable argument can be made for all the effects on the fleece being consequences of an initial effect on the growth rates of fibres. This initial effect on fibre growth rates is itself complicated by the genes causing an increase in the growth rates of the first fibres, and a decrease of the growth rates of the last fibres. The complexity of the effects on fibre growth rates can be resolved by considering that the initial action of the genes is on the efficiencies of follicles, and that the genes cause a marked increase of the efficiencies of the first follicles, and only a small increase of the efficiencies of the last follicles. The result of these disproportionate increases is that the last follicles, although they have slightly increased efficiencies, actually obtain less fibre substrate i.e. although the genes have the same type of primary action on all follicles, the marked difference in the degree of this action between early and late follicles results in the last follicles showing a small change in the opposite direction to the large change which occurs in the first follicles.

The efficiency concept has been derived from the formulation of a number of postulates, each of which is derived from scanty evidence. It is necessary to examine these rigorously: the correlation of crimp size with fibre growth rates, the variation of fibre growth rates with follicle density, the relationship of fibre growth rates when measured as weight, length or diameter. The variation of fibre growth rates with changes of follicle density can be compared experimentally, by means of single follicle transplants between regions of the same animal which differ in follicle density.

The N-type/non-N-type difference within a breed, parallels very similar differences between breeds, and it is interesting to speculate that, for differences of fleece type, breeds differ only in as simple genetic and developmental systems as do the N-type/non-N-type strains. The investigation of this possibility requires crosses to be made between 'carpet' breeds such as the Welsh Mountain breed, and 'longwool' breeds such as the Lincoln, Romney, and Wensleydale; these crosses to be carried to an

F_2 with first generation backcrosses. In these progeny examinations can be made for segregations using the scoring system of halo-hair abundance suggested above. If such segregations are found, then it is necessary to test them for several generations by backcrosses to the 'recessive' type. This should test the occurrence of a simple genetic determination of fleece type differences between breeds. The same material from these crosses can be used to determine the extent of developmental correlations of other fleece characters with halo-hair abundance, and then a developmental analysis can be made on the lines of the N-type work, to determine the basic mechanism of differences of fleece type.

In conclusion, the N-type work has shown how analyses of fibre development in sheep cannot be made on the basis of a few animals, using one or two techniques, but must involve sufficiently large numbers, examined in a comprehensive way using the techniques of Dry (1934) for fibre types, Galpin(1948) for total fibre growth, Carter et al.(see Carter and Hardy(1949) for the follicle population, and Fraser et al (see sections 4 and 8 above) for relative fibre growth rates.

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